THE BIONOMICS OF ENTOMOPHAGOUS COLEOPTERA

by

WALTER VALENTINE BALDUF, Ph. D.
Assistant Professor of Entomology
University of Illinois

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INTRODUCTION

The almost endless variety of ways in which insects live cannot fail to fascinate any person who will give them the proper attention. The interest which nature has in insects is illustrated quite as much by the diverse and ingenious habits of these creatures as by the need to devise means of control for pests or the desire to employ the beneficial forms to man's advantage. However, economic necessity has long caused the human spirit to give major consideration to the destructive hexapods that not infrequently flourish in his midst and contest with him his right to food, material, clothing, and dwelling. One the other hand, it is not generally appreciated that man derives from insects benefits that are far in excess of the losses sustained through them. To be sure, the contributions of the silkworm, the bee and the lam scale are not unfamiliar, but the most effective services of friendly insects are performed, and without blare of trumpets, by a host of parasites and predators that assures the bodies of other members of their class. While this entomophagous host does not discriminate strictly between destroyer and benefactor in the selection of its food, it is nevertheless true that it is frequently instrumental in bringing major pests into check and in preventing numerous potential plagues from developing to serious menace.

This army of insect allies includes a large division composed of several thousand species of entomophagous beetles. These constitute the subject of the present study. The ensuing discussion of their biologies was prompted by a long-standing interest in the habits and development of beneficial insects and by the need for a conveniently available statement of the essential facts of their life for the information of biologists, students, and interested laymen. Only casual insight is needed to demonstrate that our knowledge of entomophagous beetles and their beneficial relatives is still largely fragmentary. Moreover, it is plain that the utilization of our useful insects is contingent to a considerable degree on a fuller appreciation of their modes of life. Therefore, if this essay serves to make the available facts about entomophagous beetles more accessible and stimulates additional investigators to devote themselves to the biologies of this group, the writer's objectives will have been fulfilled.

The text was written on the assumption that the student has already acquired a general knowledge of the recognition, structure and habits of insects as a class. The figures were selected to illustrate the less familiar features of beetle biologies. But this has been done only in so far as published drawings and the availability of specimens made it possible, and the writer believes that the principal emphasis in a discussion of the biologies of entomophagous beetles is placed on food and feeding, other features including reproduction, postembryonic development, habitats, special features of purpose and protection and economic significance are treated as fully as the available facts permit. While it is both undesirable and impossible to include every published detail regarding the beetles, it has seemed important to provide not only the conclusions reached but also a body of reference articles cited contain bibliographies which may be consulted when more particulars are desired.

In view of the fact that the text treats species native to lands around the earth it has seemed best for the interests of all to use the scientific names adopted by Coleopterorum Catalogus, Junk and Schenkling, Berlin, parts 1-14, 1930 - date. However, also Catalogus Coleopterorum Europae by Heyden, Berlin, 1899-1927, and Catalogue of the Coleoptera of America North of Mexico, by Lang, 1920-1925, were frequently used as guides in determining the names to be employed. The name of the authority is cited only in the index and at the place in the text where the bioticial is first used.

ACKNOWLEDGMENTS

When concerned with a study based largely on published data, writers must feel themselves obliged first of all to the investigators of the past and presents, whose thirst to understand what they see in nature is responsible for such satisfying knowledge as we possess. Permission has been requested of all writers or publishers, or both, to reproduce all the borrowed illustrations employed in the text, and it is the writer's sincere wish to give full credit to all for these favors. Acknowledgment for their use is made to writers and sources beneath the figures where these appear in the following pages. Consent was given by Wilhelm Engelmann, Leipzig, publisher, to reproduce figures from Professor Korschelt's Bearbeitung Einheimischer Tiere, and by the Macmillan Company, New York, to use two figures from Professor Engel's work, Insects of Western North America. These favors and also the fine spirit of cooperation shown by contributors and editors of the several serial publications in permitting the use of illustrations are appreciated. Special thanks are due also to Mr. W. V. Salditiz who has given much valuable aid in redrawing many of the illustrations, making the original figures of Cymatodera undulata and Epilocus vitellata, and in doing much of the typing and other tasks involved.

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W. V. Salditiz
All the major food habits are represented in the order Coleoptera. A survey of the taxonomic divisions employed by Leng (Cat. Col. Amer. N. of Mex., 1920) discloses a considerable degree of correlation between the food habit of the predatory groups and their phylogenetic position within the order. The more generalized suborder Adephaga contains a higher ratio of carnivorous species than occurs in any division of similar size among the beetles. Together, the Cicindelidae, Carabidae, Dytiscidae and Gyrinidae of the world total approximately 65,000 species, the majority predominantly predatory upon other insects, land molluscs and similarly small animals. The Halipidae, once thought to be predatory, have been shown by Hickman (Am. Ent. Soc. Amer. 24, 1931) and earlier investigators to eat filamentous algae, both as larvae and as adults.

The predatory food relation is well exemplified also in the lower groups of the suborder Polyphaga. In the series Palearctica, at least the larvae are entomophagous; among the Brachyphyta, some Staphylinidae and many Staphylinidae and Histeridae are known to have this habit; while in the Polyphaga occur such proved predators as the Lampyridae, Cantharidae and most Cleridae. In the Rhaphidophora and Melolonthidae, the larval food habit has become specialized in the direction of parasitism, and that of the adult blister beetles is entirely beyond the flesh-eating level. Among the many families of Coleoptera only the Cucujidae, Colydiidae and Coccinellidae include a number of entomophagous forms, and even these families embrace a number of phytophagous groups. Furthermore, only a few scattered predatory beetles have been reported from the overwhelmingly plant-eating series, the Phytophaga and Rhynchophora. In the latter groups, the habit perhaps signifies a secondary development not derived from the predatism prevailing in the lower strata of the order.

1. CICINDELIDAE. TIGER BEETLES

GENERAL FEATURES

The tiger beetles win our interest by their striking patterns of metallic colors that frequently blend with the surroundings, their ability to escape the collector by their speed on foot and in flight, and their adaptations for obtaining their prey. The larvae uniformly inhabit burrows prepared by their own efforts in the soil and in the branches of trees. In these they lie, ever ready to seize other small animals that pass by their lairs. For the major contributions to the knowledge of their mode of life we are indebted to Enock, Cridde, V. E. Shelford, van Leeuwen, Rie, von Lengerken and Hamilton.

ACTIVITIES OF THE ADULT

Habits. Cicindelidae live in two distinct kinds of situations, arboreal and terrestrial. The majority of the species, including those of the largest tribe Cicindelini, the African Mantichorini and the Meiacanthinae, are principally terrestrial. Manticha and Mantichora inhabit deserts and steppes, whereas Cicindela brunetii Gory of Africa and the South American C. cyanitaris Kol. and Chitonycha auripennis Luc. prefer the large tropical termite nests. Wasmann ('96) suggests that these latter species may be termitophilous. Certain tropical forms habitually occupy the shaded woods, which is also the established habitat of the North American Cicindela sexguatta Fabr. But the majority of the species of the north temperate zone live in relatively exposed and fairly dry situations with little or no vegetation to obstruct their activities. Paths, roads, bare fields and sandy levels, such as are frequented by ants and other small creatures, are the preferred haunts of these insectan tigers.

A number of terrestrial forms have adopted the margins of bodies of water, and can properly be described as semiaquatic. Fletcher ('07) reported Cicindela birmanosa Fabr. abundant on deep sand along the water's edge in Ceylon; on Madagascar, he saw C. triplinoda Klug settle on the water, rise and fly a few yards, settle again, then fly out of sight. C. 12-
The arboreal species belong to the tropical and subtropical tribes Ctenostomini and Colymbatini. Most of the species live upon the trunks, branches and leaves of trees and bushes, and are active both in running and in flight. The immature stages also live above ground on trees, indicating that the arboreal habit is not casual but deep-seated in these tribes.

Locomotion. Although the Cicindellidae are generally regarded as extremely agile to elude their enemies and to catch their prey, not a few are clumsy in their movements. Most of the species of Cicindela are cremacean and fly awkwardly at times. The three related genera, Amblychila and Pycnochila, lack wings and have the elytra fused. This condition is not casual but deep-seated in these tribes.

Burrows and Burrowing. The tiger beetles commonly dig burrows in the soil for shelter during the tight, inclement weather and the winter. Those used for the first two purposes are shallow and are therefore quickly prepared, but the excavation of holes occupied during the long cold Canadian winters require labor extended over many days. The first steps in the process of preparing the burrows are essentially the same in all cases. Cridde ('07) describes the construction of the hibernating burrows of several Canadian species, and von Longerken ('16) observed it in Cicindela maritima Ltr. and G. hybrida L. in Germany. The mandibles are employed to loosen the particles of sand or soil and to pry out larger pieces. By scraping energetically with one front leg they pile up a small heap of material under themselves, which is then pushed further backward by a middle leg and finally thrown clear of the body by a hind leg. According to von Longerken, this transfer of the soil is accomplished quickly, and only one leg is in action at any given moment, the other five serving to prop the body. Cicindela repanda Dej. was observed (Moore, '06) to use its legs alternately, first working with those of one side, then those of the other.

In preparing the much deeper hibernating burrow, the hole is dug at an angle for the first three to eight inches, after which it usually goes down in an almost vertical direction. But it often happens that when starting again after an interval of rest, the beetles take a slightly different direction so that the hole turns first one way and then another. For the first six to thirteen inches the earth is thrown out from the mouth of the burrow, after which the hole is gradually filled in moderately tightly, from four to ten inches being left unfilled at the bottom to enable the beetle to work its way out in the following year. The hole is nearly always wide enough at all points to allow the beetle to turn around, and is always so at the bottom. When the burrow is completed, the beetle turns around and faces the top, ready for digging its way out the next spring.

The depth of the hibernation burrows varies considerably both among and within the species studied by Cridde. The records of the shallowest and deepest burrows found by this author are given in inches: G. furmosa manitoba Long., 25 to 48; C. venusta Loc., 12 to 32; C. limbata Say, 7 to 17; C. purpurea limballii Ehr., 16 to 19 in sand, 3 to 6 in clay; G. duodecimguttata Dej., 2 to 20 in sandy soil, 2 to 10 in clay or gravel; C. repanda, 16 to 22 in sand, 8 or 9 in clay; C. tranquillaria Host., 11 to 24 in sandy land, 6 to 18 in clay; E. scutellaris laconeti Hald., 10 to 22 in sandy soil; G. punctulata Oliv., 16 to 26.

Tropisms. Particularly the species living in exposed places make prompt responses to changes in light, moisture and temperature. Their locomotion, feeding and mating are strikingly and intimately affected by the brightness and warmth of the sun. Thus, Cicindela maritima hide in the beach vegetation on cloudy or rainy days, their long legs spread far apart and

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the apex of the abdomen resting on the ground. But scarcely has the sun begun to shine when they are almost instantly agile again. On the other hand, when a cloud even temporarily obscura, the sun on a hot day, all activity ceases as promptly as it began. Sometimes refuge from inclement weather or cover for the night is sought under sticks, stones and other surface objects, but burrows especially constructed for the purpose more often constitute the hiding places. Moore ('06) observed that C. repanda Dej. remained hidden in its dug-out constantly during a rainy period of three days, and C. carnea Dej. and C. angulata (Say) was left alone in the soil on dull days, according to Rufe ('15). After excavating its hole, C. transqueariensis turned about and backed into it, leaving the mouth of the tunnel open, and rested with head and mandibles visible at the entrance. C. campestris, C. repanda, C. maritima and C. hybrida have similar bedtime habits. The beetle prepares its burrow in the afternoon, between four and seven o'clock, the time depending on temperature and light. C. repanda usually remained inactive in its night quarters until eight or nine in the morning, but emerged somewhat earlier on very warm days. However, C. maritima and C. hybrida seemed not to hole themselves in daily, nor expressly to spend the night, but chiefly after very hot dry days and energetic copulatory activities, selecting moist places for the occasion. Thus heat and drought produce the same burrowing responses as cold, rains and darkness.

Protective Form and Coloration. In addition to many common species of Cicindela, whose colors are well known to blend with their surroundings, some tropical forms are of unusual interest. Robinson ('03) maintains that the deep jungle species of the Malay Peninsula act as models imitated by large numbers of other insects but more especially by beetles of other families and by Orthoptera. He considered that the mode of flight and the predatory appearance was greatly intensified, giving the impression that a combat to the death would presently ensue. Usually, however, the affair stops with this threatening posture. Only when two individuals encounter each other in a hasty run from opposite directions, do they bite one another for an instant and roll over a few times in the sand like a couple of battling street urchins, but soon cease and proceed each on its own affairs.

Food and Feeding Habits. Adult tiger beetles are generally regarded as carnivorous, but Mitchell ('02) states that the apex of the abdomen resting on the ground. But scarcely has the sun begun to shine when they are almost instantly agile again. On the other hand, when a cloud even temporarily obscura, the sun on a hot day, all activity ceases as promptly as it began. Sometimes refuge from inclement weather or cover for the night is sought under sticks, stones and other surface objects, but burrows especially constructed for the purpose more often constitute the hiding places. Moore ('06) observed that C. repanda Dej. remained hidden in its dug-out constantly during a rainy period of three days, and C. carnea Dej. and C. angulata (Say) was left alone in the soil on dull days, according to Rufe ('15). After excavating its hole, C. transqueariensis turned about and backed into it, leaving the mouth of the tunnel open, and rested with head and mandibles visible at the entrance. C. campestris, C. repanda, C. maritima and C. hybrida have similar bedtime habits. The beetle prepares its burrow in the afternoon, between four and seven o'clock, the time depending on temperature and light. C. repanda usually remained inactive in its night quarters until eight or nine in the morning, but emerged somewhat earlier on very warm days. However, C. maritima and C. hybrida seemed not to hole themselves in daily, nor expressly to spend the night, but chiefly after very hot dry days and energetic copulatory activities, selecting moist places for the occasion. Thus heat and drought produce the same burrowing responses as cold, rains and darkness.

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Cicindela flavopunctata rectilatera Chd. also ate algae and the fine green moss around springs in southern Texas. It is possible, however, that they were only absorbing water from this vegetation. The food taken by Cicindelidae usually is supposed to consist mainly of ants, but observations in nature show that almost any available living animal, which they can overcome, is utilized. Mitchell saw Tetrao carolina (L.) capture insects many times, and C. rectilatera ate any small insects they could catch, including ants, and also very young fiddler crabs and marine fleas. C. brimosa often captured a Muscid fly (Fleischer, '07), and C. truncuheraria Bbst. fed upon ants, small beetles, flies and worms, including some caterpillars, but gnat and medium sized spiders were also taken (Goldsmith, '16). C. repanda feeds on Inachus nadeida in reducing the Hemipterous rice pest, Leptocorisa varicornis (Vuillet, '12). C. punctulata was observed devouring nymphal chinch bugs, Rilassus leucoterus, in Illinois (Baldur, '25). C. formosa matsura ate the flea beetle, Disonycha quinquevittata, and other Chrysomelidae as well as ants, and C. tranquebarica Bbst. fed upon ants, small beetles, Aphids, cut-worms and other insects. Snow ('77) concluded that no living insect comes near to the nocturnal Amblychila cylindriformis, and it seemed especially fond of all sorts of caterpillars and nymphs of Orthoptera. In another instance they ate other adults of their own kind. The South African Mantis horaria latipennis Waterh. preyed on the Cicada, Callipsaltria longula (Fouton, '06) and the Orthopteran, Hololopha asina (Born, '06).

In captivity the beetles accept an even greater range of food than in nature. Observers commonly kept their subjects alive on a diet of lean meat such as beef, but quite as often provided freshly killed insects, particularly blowflies, house flies, maggots, small caterpillars and ants. C. rectilatera accepted the flesh of fish, rabbit and moosain, and A. cyllindriformis thrived on the mature caterpillars of Anisota rubicunda alba, Catena minata and almost every other insect pest regards garden and orchard. Colymbus bonalli Guer., C. suberculata Mac. L. and Tricondyla cyanum Df., regularly ate Aphids in captivity, sucking out the body liquids and casting the empty skins away. Ants were seized by them only when no other food was at hand. Various species displayed their voracious nature by consuming their own larvae and pupae that were left within reach.

Cicindela repanda and C. purpurea took no notice of insects that passed them more than four inches away (Moore), but when discovered, the intended prey was rushed and seized in the powerful toothed mandibles. In attacking ants, C. purpurea bit its victim and gave it a toss, then rushed and bit it again, and again, until the ant appeared lifeless. Goldsmith reports a group of C. repanda devouring colony after colony of small red ants. In one instance, two beetles waited at the ants' doorway and alternated in catching the ants as they appeared until no more remained. But this species seems not as tigerlike in attacking larger and more active prey, such as large black ants. The beetles usually made one dauntless charge, retreated suddenly if met by a counter attack, and gave up in fear when repulsed. Nevertheless, the persistence of tiger beetles in successfully pursuing smaller victims nets a large total of prey.

In feeding, C. maritima sinks its mandibles completely into the prey, and first drinks up the liberated body juices, and then eats the more solid parts of the fly. The mandibles (Fig. 1) serve to pass the food to the maxillae which comminute it by quick grinding movements. These stop momentarily at brief intervals to permit the mandibles to open slowly and take a new hold on the food (von Lengerken). After catching a chinch bug in its jaws, C. punctulata invariably struck the victim briskly against the ground several times in rapid succession (Baldur). It took C. repanda four or five minutes to devour a house fly, and eight or ten flies were not too much for one meal for C. purpurea.
single C. maritima and hybrid often ate several house flies in one meal on hot days, and C. punctulata was seen to catch and consume nine mature nymphs and one adult of the chinch bug in twenty-six minutes of consecutive feeding in the field. C. repanda, eating continuously for twelve minutes, required an average of ninety-five seconds to finish each small red ant. In all careful observations it was seen that the tiger beetles ate only the liquid and soft parts of the prey, discarding the head, legs, wings and exoskeleton.

The Drinking of Tiger Beetles. These beetles appear to take water as regularly as food. C. campestris were seen lying with their mandibles thrust into drops of free water (Hule), and T. carolina, upon being active at evening, hungrily drank at the water's edge, thrust their mandibles deep in, and took a long drink (Mitchell). C. repanda refused to drink from a glass receptacle in the cage (Moore), but like Amblychila cylindriformis, C. maritima and C. hybridis imbibe their water from wet sand. In drinking, C. repanda seize a morsel of moist sand with its mandibles, and with the head thrown back holds the sand free from the ground and sucks the water from it. If the sand was quite wet they sunk their jaws into it almost as deep as the eyes, and drank with the mandibles spread far apart. They were very thirsty beings, drinking after every feeding, after emerging from their burrows in the morning and at various other times of the day. Especially in hot weather they eagerly sucked up the water.

Mating. The mating process in Tetraphax carolina and several species of Cicindela has been described by Mitchell ('02), Moore ('06), Shelford ('09), Hule ('16) and von Lengerken ('16). The males as a whole exhibit a strong desire to mate, and spend much time in pursuing the females to this end. In all cases, the male pounces bodily upon his mate, fastening his mandibles on her body at the constriction between the pronotum and the elytra. The front and middle pairs of legs embrace the abdomen, while the hind legs support the male on the ground. This position may be maintained for a long time before copulation is effected in C. purpurea, according to Shelford. In general, the act of copulation may require only a few seconds, or continue for ten minutes or more. But the female does not always welcome these advances, sometimes succeeding in escaping the male entirely, resisting the union by struggling, or turning the tip of her abdomen toward the substratum to make cotton temporarily impossible. Mitchell observed the male of C. flavopunctata rectilateralis run quickly away after copulation to escape the counter attack of the female. It is possible that some nocturnal species of Megacephala mate in the daytime. (Horn '08).

Oviposition. The ovipositor of the Cicindellidae consists of the eversible, attenuated terminal segments of the abdomen and their chitinous gonapophyses. By means of this organ the female excavates holes in the soil or hollow cavities in branches of trees for the reception of her eggs. It has been observed that C. campestris and C. purpurea first seek the ground with the everted ovipositors to find soil of a texture suitable for digging. Usually one or two shallow test pits were made and abandoned before the right situation was found. As the hole deepened, the beetle raised herself on her front legs till her body assumed an almost perpendicular position. The female of C. repanda likewise raised up her cephalic end until she almost stood on the end of her abdomen while ovipositing. The finished hole varies in depth from one-quarter to one-half inch, and the available records indicate that tiger beetles never place more than one egg in a hole. About fifty ovate translucent eggs 2 mm. long are laid, singly, in such holes by one female C. purpurea. C. campestris always carefully filled the hole up again after the egg was laid. Lastly, she raised the surface over with the curved chitinous picks of her ovipositor till only a few grains of loose sand marked the spot. One female was seen to oviposit five times between 9 A.M. and 2 P.M. of a sunny day in June. The whole operation of preparing a hole, laying the egg and filling it with sand, was done deliberately, and occupied from 15 to 25 minutes.

The arboreal Collyris bonelli, C. bicolorata and Tricondyla cyanae, observed by W. Docters van Leeuwen ('15) in Java, place their eggs chiefly in the slender bud-bearing twigs of Coffea arabica and C. libérica. The hooks of the ovipositor are adapted for splintering and tearing out the fibers of the branch (R. Shelford '07). In this manner a short vertical tunnel is bored into the bark and hardwood. The ovipositor is then turned upward into the pithy center of the twig, the completed cavity having a depth of about 6 mm. Splinters partly block the entrance, which is closed by the beetle with a plug of wood bark. After the egg is laid, pruning out injured branches and blocking the galleries with tar are measures advocated
to control these beetles on coffee trees.

ACTIVITIES OF THE LARVA

Adaptations. The life of the larvae of Cicindelidae is spent in burrows. To this end their bodies have undergone several remarkable morphological adaptations, fitting them to guard themselves against adverse conditions, to construct their tunnels, to climb up and down in them and to capture their prey (Fig. 2). First, the head and pronotum, normally bent ventrad at an angle of forty-five degrees, are strongly chitinized above and form a sub-circular plate that closes the mouth of the burrow. In nature, this plate bears sand or dirt that effectively blends with the surroundings and thus obscures the larval site. Second, the prominent and powerful jaws bend upward and constitute a tool for prying, scooping up, transporting and flipping out the soil in the course of digging the hole, and later rest at the entrance of the burrow where they serve to seize passing prey. Third, the venter of the head is hard and greatly bulged for tamping or compacting the soil or sand that form the walls of the burrow. Fourth, several structural features combine to enable the larva to scuttle quickly up or down the shaft, or to anchor itself when occasion requires. Specifically, locomotion within the tunnel is facilitated by the long, sharp tarsal claws, the forward-curved hooks on the dorsal hump of the fifth abdominal segment, and the flexible S-shaped body. This shape and the dorsal hooks safeguard the larva against a sudden removal from its burrow should it chance to seize a disproportionately large prey animal.

Burrows and Burrowing. The newly hatched larvae of Collyris and Tripionycha observed by van Lennep ('10) at once begin to remove the stopper of borings that closes the tunnel in the branches where the egg was laid, requiring a whole day to accomplish their freedom. As the larva grows, the bast fibers that partly block the entrance become dry, and are gradually removed by the occupant. According to Sheldrup ('09), the small larvae of Cicindela purpurea soon makes its way out of the oviposition hole to the ground surface, thereby packing the soil and forming a cylindrical burrow. Soon thereafter, the hole made by the ovipositor of the parent beetle, is extended downward to a depth of four to six inches. Enock ('03) observed some burrowing larvae of O. campestris through the glass sides of a jar. In beginning its digging, the larva loads its head by sinking it into the surface sand, whereupon it throws the material over its back and out of its way. By repeating this operation, the larva soon disappears beyond sight in the ground.

In deepening the burrows, the mandibles were used as picks and their heads as shovels and elevators. Excavating, head downward, they drove their long pointed tarsal claws into the sides of the burrow above. By making a larger excavation on one side of the burrow, they provided space for passing the sand upward. This they did by simply turning their heads up and ramming the sand past and above the ends of their abdomen. Having accumulated a sufficient amount in this manner, the larva reversed its position, put its head and pronotum underneath the load, then simply pushed and pushed until the sand was elevated to the ground level. Here a large heap was formed, which the larva scatters from time to time, using its head to shovel up and flip the sand away backward a distance of several inches. Many hours are occupied in preparing the burrow which sometimes reaches a depth of ten inches. As soon as the hole is cleared out, the larva takes mouthfuls of sand from the edge of the entrance and horns them clear. This is continued until a rough excavation is made around the entrance. With its chin, the larva then hammers the mouth of the burrow into a smooth, saucer-shaped depression. It now retreats into the entrance, drawing its head up level with the top, and is then ready to procure food.

At the approach of winter, the larvae commence deepening their burrows (Criddle, '07), loosening the earth with the mandibles, and shoveling it up with the head and prothorax. The larva then turns round
and works its way up, holding the load in a horizontal position until it gets level with the top of the hole, when the soil is suddenly thrown two or three inches away. Certain larvae required from 70 to 113 seconds between loads when the holes were about 14 inches deep. Early in the prehibernation season most of the work is done in the evening or at night, but later the digging goes on also in the daytime, especially if the weather is cold. When finished, the hole is usually closed near the top, and the larva retires to the bottom for the winter.

The holes prepared in any season vary somewhat in depth, form, grouping and habitat, not only among, but also within, the species. Their location and grouping (Fig. 3) is obviously predetermined by the choice by the female parent of a spot for oviposition. Their depth is apparently influenced by the texture of the substratum, the age of the larva, the distance to ground water and perhaps other factors.

The shaft of the mature larva of Cicindela sylvatica Latr. varies in depth from 6 to 10 inches (Reineck, '23). Griddle, who dug the larvae of several species out in September at Awese, Manitoba, found the first year individuals of C. lepida Dej., a sand-inhabiting species, at 30 to 32 inches, whereas the larger ones descended to depths ranging from 58 to 75.6 inches. The older larvae of C. formosa manitoba and C. venusta were situated at average depths of 76 and 46 inches, respectively. On the other hand, the burrows of C. scutellaris lecontei were found chiefly in the sheltered borders of old fields and averaged only 28 inches in depth. The larvae of C. purpurea limbalis live not more than six feet from water and seem to have burrows only about eight inches deep, their comparative shallowness probably influenced by the level of the ground water. The larger holes of Amblychia cylindrigaformis were about one-half inch in diameter and approximately 30 inches deep in western Kansas (Williams and Hungerford, '14).

The burrows of most Cicindelid larvae are straight and extend perpendicularly inward from the surface, which may be horizontal, vertical or at an indeterminate angle (Fig. 4). In tunneling, the larva of C. sylvatica was found sometimes to circumvent stones or roots which it could not penetrate or remove. The burrows of A. cylindrigaformis seem habitually to be almost vertical above but turn to a subhorizontal plane in their lower part. That of C. formosa manitoba represents a rather distinct type, consisting of a cuplike pit at the surface (Fig. 4, G). From one side of the pit the main shaft descends at once sharply downward and continues vertically to the bottom.

The burrows of tiger beetle larvae may occur in colonies, occupying a small patch of ground of uniform texture (Fig. 3). It may perhaps be presumed that all the larvae inhabiting such groups of burrows are the progeny of a single female beetle. The holes of A. cylindrigaformis were usually found in groups of two to eleven, many of the separate burrows being not more than one and a half inches apart, and usually a colony was limited to a ten inch radius, and often situated near some larger hole, as that of the field mouse or bad-
ger. Sometimes 30 to 35 burrows of Caryocercis sylvicola lay grouped in a square meter of space, and Macnamara (1922) found instances of five or six shafts of Caryocercis an inch or two distant from one another. These examples do not, however, necessarily indicate a fixed colonial habit in these species.

Food and Feeding. The larvae of the arboreal species, Collyris bonelli, C. humberti and Tricondyla cyanescens (Fig. 5) lie in their burrows with the head in the entrance, waiting for hours at a time with mandibles widely opened to seize little animals that pass by. Only when danger threatens do they speedily retreat into the tunnels. If a small caterpillar, an ant or other insect crawls by, the predator suddenly throws its head forward, simultaneously emerging a short distance out of the entrance and snapping the mandibles shut upon the prey, then backing into the burrow again. Not infrequently the attempt fails.

In addition to serving as a place to lurk for prey, the burrow provides also a retreat for the larva during molts, for hibernation, for rest when not engaged in awaiting prey, and for shelter against adverse and inclement weather. Caryocercis and C. campestris are known to be very sensitive to approaching objects, and even a shadow causes the larvae to drop quickly to the bottom of their burrows. Criddle observed that the larvae of Caryocercis venusta, limbata, lecontei and probably others, often passed long intervals of inactivity during the summer months. During such times the insects closed their burrows at the top and apparently remained without food, and did not grow appreciably. A few individuals opened the burrow at night, threw out much earth, and retired again. Dry soil and extreme solar heat are suggested as possible factors causing this particular reaction.

What is the resting position of a terrestrial larva when it awaits prey? Enock, observing C. campestris through glass, saw that the feet were driven into the sides of the burrow below the mentum, and the fifth abdominal segment drawn up until the hump was wedged in close to the thorax. The spurs of the hump were driven at right angles into the sides of the burrow. The remaining abdominal segments curved around with the anal spines entering the wall at the other side. In this manner the larva was held securely in place, especially against possible forced removal should large prey be seized. Yet, by releasing the anal spines and straightening the abdomen it could drop down to
the bottom of the burrow instantly.

Enock succeeded in analyzing the flash-like preying movements of these larvae by attaching a thread to the leg of a fly which he offered to a larva sitting in the mouth of its burrow. When the fly was brought within five-eighths of an inch of the head, the larva struck out. In doing this, it turned a back somersault, throwing all its legs out clear of the burrow, and the abdomen formed a semicircular arch between the hole and the seized fly. The vertical spines of the dorsal hump formed a fulcrum, while the longer and curved anterior spines were driven deeply into the sides of the burrow and securely anchored the larva during the seizure. Considering that they have in general a common structure, it is probable that the larval Molybitae and Micromelidae capture their prey in this manner.

The arboreal species drew very small victims into the burrows, while larger prey was left in front of the opening. In most cases observed, the chitinous inedible remains of the food animal were flipped away from the entrance by means of the head and propeltal shield. But the bottom of the shafts of Amblychila cylindriformis were invariably tightly packed with the remains of former repasts, indicating that the larvae may take their prey below to consume it. Williams and Hungerford observed also that the remnants of prey provided experimentally were later found both outside and inside the tunnel.

The food of the larvae consists of land Crustacea, centipedes, spiders, dragonflies, butterflies, flies, beetles, and larvae of all sorts, and in fact any small animals that come within reach (V. E. Sheldrake, 1926). Big blue-bottle flies seemed to be the favorite food of C. campestris in nature (Hufnagel), and were often seen caught by the head and sticking out of the larval burrow. In feeding experiments both in captivity and out, a considerable variety of creatures and materials were accepted. The larvae of Tetraechus carolinus readily took ants, sowbugs and the like dropped into their holes (Mitchell), while the insects received by Amblychila cylindriformis included a mantid (Litaneutria), a Phyllophaga beetle, an adult Myrmelooncid, wasps of the species that of Cheylidion and Palomenus, as well as a Mutilid, a Pentatomid bug and a ground beetle (Passalidae). The Carabid was later found head downward and not actually injured an inch and a half down in the burrow. A Cicindela beetle, caught as it ran over the lips of a larval Amblychila, succeeded in escaping its attacker. Collyris and Cicindelyla accepted flies, small beetles, large ants and long-haired caterpillars without distinction in captivity. Small ants common on the coffee tree may be eaten in a larval chamber; but even the larger larvae required two to three hours to consume a caterpillar three cm. long. In feeding larvae in cages, the food turned a back somersault, throwing all its legs out clear of the burrow, and the abdomen formed a semicircular arch between the hole and the seized fly. The vertical spines of the dorsal hump formed a fulcrum, while the longer and curved anterior spines were driven deeply into the sides of the burrow and securely anchored the larva during the seizure. Considering that they have in general a common structure, it is probable that the larval Molybitae and Micromelidae capture their prey in this manner.

On the contrary, C. campestris promptly ejected maggots dropped bodily into the burrow, and Criddle found that his Chelydron species seldom accepted Hemiptera and when they did so rejected them at once.

A. cylindriformis dragged a Trox beetle partly out of sight but soon cast it clear of the hole by a flip of the head. Thus, Cicindelyla larvae are apparently not omnivorous predators even though not highly selective.

Larval Molts. LARVA has been recorded concerning the number of instars during the growth of Cicindelyla larvae. In Cicindelyla purpurea, this stage comprises three stadia. When about to molt, the larva probably always closes the mouth of the burrow. The larven when forced to move around in a burrow or when they did so rejected them at once.

The stems inhabited by the larvae of Collyris bonellii expand noticeably where the burrows occur, which enlargements seem also to provide adequate space for pupation. Just before entering the prepupal state, the larvae exhibit an extraordinary voraciousness, after which they lie for a considerable time, without much change, at the outer end of their burrows. This species then closes the entrance with an oral secretion which turns brown and hard in the air. The liquid is applied with the mouth parts to the edge of the entrance. By consecutive deposits, the entrance becomes walled off with a convex covering, thick at the margin but gradually thinner toward the middle, only...
a minute air hole being left at the center (Fig. 6). Pupation occurs in the inner cavity of the burrow (van Leeuwen).

![Image](image-url)

**Fig. 6**


The soil inhabiting Cicindelid larvae have the habit of closing the burrow above and constructing a special cell of various forms at different depths just before pupation (Fig. 4, p.c.). The larvae of *C. campestris* were found by Enoch to ram the burrow full of sand to within an inch of the pupal chamber at the bottom of the shaft. *C. purpurea* likewise first fills the upper part of its tunnel (Shelford), and Criddle reports similar preparations made by Canadian species. The larvae of *C. forrscae* and *C. punctulata* also fill the burrow full of sand to within an inch of the pupal chamber at the bottom of the larval pit; and *C. purpurea* transforms in a vertical and divergent side cavity about four inches from the bottom (Shelford). *C. punctulata* oviposits in latter July, and most of the larvae develop to the last instar by September, and hibernate. Feeding is continued from the next April to June, and the new imagines issue from the pupal cells in July. Especially among the species having a two-year cycle is there a marked variation in the seasonal occurrence of the stages. Shelford recognized two types of life histories among them. In the first, exemplified by *C. purpurea*, *p*. *pugetana* and *p*. *formosa* genera, eggs are deposited in late spring or early summer, the larvae pass the first winter usually in the third instar, pupate in the second summer, and the second winter is spent by the adults which reproduce in the following May and June.

Accordingly, the life cycles are heterogeneous not only in regard to duration of the development, but this quality extends also to the seasonal distribution of the stages in any one class of species. The larvae of *C. campestris* are oval and slanting, or ovoid enlargement near the lower end. The position and form of other pupal cells are shown at A, B and F of Figure 4. Having carefully packed and smoothed the walls of the cell with its mandibles and ram-like mentum, the larva of *punctulata* rests its body against one side of the pupal chamber with head uppermost. Gradually it becomes less active, the cuticle splits in the middorsal line of the head and thorax, slips backward, and frees the head. Prominent bristle-bearing dorsal tubercles on the first five abdominal segments assist in stripping the exuviae from the body and serve to hold the pupa clear of the substratum during its transformation (Shelford, '09). It is obvious that the newly formed emerging adult must dig its way upward through a considerable column of soil or sand to become free.

**THE LIFE CYCLE**

The species of tiger beetles whose habits have been studied, require from one to four years for a generation. This extreme range in duration of the cycles can apparently be attributed in part to the differences in regional temperatures, and partly to normal differences in rate of growth of the species. The Japanese *Cylindrus bennelli* and *Cicindela punctulata*, in the Chicago area, are reported as having one generation per year; *C. purpurea*, *C. forrscae* and *C. campestris*, formosa *pugetana*, *lepida* and *cuprascens* Lec., studied by Shelford in northern Illinois, require two years for a single cycle; *C. purpurea* pugetana, formosa *manitoba* and other species of *Cicindela* were believed by Criddle to make their metamorphoses in three years in Manitoba, and larvae feed through the second winter by September, and hibernate. Feeding is continued from the next April to June, and the new imagines issue from the pupal cells in July. Especially among the species having a two-year cycle is there a marked variation in the seasonal occurrence of the stages. Shelford recognized two types of life histories among them. In the first, exemplified by *C. purpurea*, *p*. *pugetana* and *p*. *formosa* genera, eggs are deposited in late spring or early summer, the larvae pass the first winter usually in the third instar, pupate in the second summer, and the second winter is spent by the adults which reproduce in the following May and June.

The development of *C. purpurea* may be cited in greater detail. Shelford ('09) captured specimens on April 22, which copulated within a half week. The larvae hatched after an incubation period of about two weeks in laboratory cages in May. After feeding three to four weeks, the small larva closes the mouth of its burrow with soil and goes to the bottom to molt, returning again to the surface at the end of five to seven days. With adequate food and optimum weather conditions, the second instar is completed in about five weeks, then molting again occurs in the manner already described. Upon reappearing at the surface, the third instar larva feed through the second winter and during September when they close the burrow and descend below to hibernate. The holes were found opened again in the early part of April. After feeding three to four weeks, the new imagines issue from the pupal cells in July.
and fill the burrow in preparation for pupation. Transformation is accomplished in about two weeks, and the new imagoes appear in latter August. They feed during the early autumn, and in October dig special burrows in which they pass the second winter. They come forth again the following April to feed and reproduce.

The second type of history differs essentially from the first in that the species start their development later, in midsummer. The second larval instar hibernates the first year and the third stadium brings the species through the second winter. They pupate in May of the second year, and the adults are at hand to multiply by midsummer. C. lepida and C. eugracensa were found to have this type of seasonal distribution of the stages.

In the life cycle of C. campestris, as determined by Hulse, the egg stage occupied the month from mid-June to mid-July, 1918; the larval period nearly three years, from mid-July, 1915 to June, 1918; pupation, six or seven weeks, from early June to early August, 1918; the adult reached its maturity early in August, 1918, and remained in the pupal chamber through the following winter and issued in latter April, 1919. Oviposition began in six weeks, or in mid-June and continued into September. No year is without adults or larvae, owing to the unequal start in life given to the young larvae of the same year. However, every fourth year a "beetle year" occurs, and each of the intervening years has a predominance of larvae of a size characteristic of that year.

In all types of cycles, the larval stage occupies a longer time than any other. That of C. punctulata requires ten months, the species of the first two-year type spend twelve to thirteen months as larvae, and those of the second two-year type live twenty-one months in this stage. C. furcata manitoula, venusta, limbata, and limbalis, spend twenty-four to twenty-six months in the larval period (Cridde, '10). The larvae of C. campestris occupy nearly three years of the four-year cycle.

Owing to the length of the larval stage, all species having a generation in two or more years hibernate mostly as larvae. In C. campestris, the first three winters are passed in the various larval instars, and the Manitoba species go through the first two years as larvae. In the Canadian forms studied, the third winter is passed as adults in specially prepared burrows, whereas C. campestris remains as a newly developed imago in its pupal cell to go through the fourth winter.
2. CARABIDAE. GROUND BEETLES

GENERAL FEATURES

The ground beetles have depressed bodies, legs fitted for running, and powerful prognathous jaws. The family is believed to be largely beneficial owing to the entomophagous habits of both active stages, but some forms take plant tissue with their flesh food. A few are myrmecophilous and representatives of several taxonomically diverse genera parasitize other insects. Complete biologic studies have been made only of Calosoma sycophanta L., and less exhaustive accounts are at hand for several Carabus species and others of the Calosoma group. Valuable investigations of stomach contents were made by Forbes, and King reported on the unusual oviposition of Chlaenius, Brachinus and forms having similar egg-laying habits.

Habitat. The majority of Carabidae live under cover on the ground and become active chiefly at night, but they may not all be regarded as terrestrial and nocturnal. Some species of Lebia climb about on low plants in full daylight, Brachinus and Morton monilicornis Latr. live under bark of trees (Schwarz, '84), and the Hawaiian Pteronotus and Pterosternus are described as arboreal (Sharp, '03). Calosoma frigidum Xny., scrotator Fabr., willcoxi Lec. and exterius Say readily climb trees to feed as do also both larvae and adults of C. sycophanta (Burgess and Collins). Although terrestrial, several species of Dyschirius inhabit burrows in sand in association with Bledius (Krogreus), the Japanese Crespronotus libitans Schum digs tubular shafts 10 to 18 inches deep in the ground, Anopthalmus and perhaps other blind forms are cavernicolous, and a few species are believed to share the nests of ants and termites. None may be regarded as aquatic although the Elaphrini, Lophoglossus and others inhabit the very wet margins of bodies of water.

Locomotion and Distribution. Few apterous Carabidae exist but many are flightless, having vestigial wings. Of 294 Hawaiian species, 184 can not fly and only 30 are fully winged. This proportion of flightless to flying species is believed to be reversed in most continental regions (Sharp). However, owing to their secretive habits, Carabidae are rarely seen in flight. C. scrutator is frequently attracted to lights, and other species of the genus have been so found. C. sycophanta flies rather freely, particularly in the spring, and Aconoderus palpebrum (Fabr.) is on wing in immense numbers at night in midwestern United States in years of abundance. Experiments indicate that the adults of C. sycophanta tolerate submergence in cold water up to fifteen days, which greatly favors their spread by the agency of running water in spring floods. A newly hatched larva of this species crawled a total distance of 9,058 feet, or 1.71 miles in about 70 hours without receiving food from without (Burgess, 11a).

Natural Enemies. Although fierce in their attacks on other small animals, the Carabidae are not without enemies of their own. In New England, Calosoma sycophanta was eaten by raccoons, boxes and skunks (Burgess and Collins, '94), and shrews devoured Carabids in pits prepared to trap forest caterpillars in Germany (Kern, '25). Toads are recorded catching C. caliginosus Fabr. and a Carabus (Burgess '96) believed that insectivorous birds are undoubtedly the chief agency in checking the increase of Carabidae and from the literature names the crow, the blue jay, kingbird, black-tailed cuckoo, yellow-billed cuckoo, hairy woodpecker, downy woodpecker, purple grackle, robin, catbird, and several thrushes as proven enemies of these beetles. Thirteen percent of the food of the purple grackle consisted of Carabids, according to studies by Beal. In Germany, the stomachs of a number of storks contained an average of 48 Carabus each, and in Massachusetts, crows fed the adults of Calosoma sycophanta to their nestlings.

Gregarine intestinal parasites are reported by Forbes ('83a) from Harpalus pennsylvanicus DeG. and Cratacanthus dubius (DeGeer) as forming considerable masses which fill the intestines. Its relative, Magazystis longa, effects parasitic castration of Carabus nemoralis Will., which therefore make no attempt to copulate or oviposit (Delkeskamp, '30). Chlaenius tomentosus (Say) contained a nematoid parasite (Forbes), and young beetles of C. sycophanta were killed by the nematodes, Rhadites calosoma and R. diplonoeptidus, which were taken also from a larva of Carabus monilis Fabr. (Burgess, '11). Kern reports a Gordiid threadworm from a Carabus. An Ichneumonid parasite was obtained from the larvae of Carabus silvestris Fanz. by
Letzner in 1854, and Holste ('15) reared about fifty Phaenoserphus (Proctotrupes) violator from one larva of Calosoma inquisitor L. in Germany. The parasitic larvae live internally, and pupate externally in cocoons. The eggs of Brachynus cyanipennis Say yielded a Scelionid Serphoid, Hoplyron, and those of Chlaenius spp. were heavily parasitized by the related Proscarantha caraborum (King, '19).

An European Tachinid fly, Viviana cinerea has long been known according to Baer ('21), to parasitize adults of large Carabids, including Carabus coriaceus L., Zabrus tenellus Goeze, Carabus violaceus L., hortensis L., glebatus F., gemmatus L., clathratus L. and cancellatus Illig. The maggots pupate in the dead host. Burgess ('16) found nine eggs of the Tachinid, Biomyia georgiae on the thorax of Calosoma calidum in Massachusetts, and reared seven flies from puparia within the host. Quillet had this species also from regrinator Guer. in California.

Protection. Their nocturnal activity, obscure habitats and rapid locomotion probably afford the Carabidae noteworthy protection. But a few species possess a special protective device in the form of a volatile, irritating acid secretion produced from anal glands. The liquid is discharged with an audible pop, and upon exposure to air, changes into a visible cloud of vapor. On the human skin, this substance causes a burning sensation the effect of which persists for a considerable time. The fleeing beetles shoot the charge of gas into the faces of their pursuers, and can repeat the shots a number of times in rapid succession. Doubtless this device serves to ward off such enemies effectively. The species of Brachinus, or bombardier beetles, are the best known bombers, but Galerita janus Fabr. sometimes employs this method of defense, while Frost ('10) reports its occurrence in C. auratus L., C. violaceus and C. glebatus, and Harpalus caliginosus (Fabr.) gave off a rather large amount of dense smoke when it was attacked by Psalidolycus capreolus in a cyanide jar. (Fattig, '33). The latter writer also describes discharges of a smoky gas, that seemed, however, to emanate from the sides of the thorax and abdomen. The beetles concerned were Dicaelus, including elongatus (Bon.) and squillipes (Say).

Kirchner ('27) and Delkenkamp ('30) state that the secretions which some Carabidae produce orally for extraintestinal digestion of the prey, are also used for defense. The liquid thus secreted has an disagreeably sharp odor, gives an acid reaction and burns the skin of man. Carabus cancellatus can squirt its secretion as far as ten inches, and a female Carabus coriaceus sprayed it a distance of a meter. C. nemoralis and violaceus are regarded as employing this same method of defense. Considering its irritating effect on the human skin, it is within reason that this liquid is not without effect upon small enemies of the beetles. Verhoeff ('27) found that the pupae of Carabus ulrichii Germ. and C. granulatus L. also give off a sharp, penetrating aromatic vapor which he regards as defensive. Blue litmus paper placed under a pupa became a positive red.

ACTIVITIES OF THE ADULT

Food and Feeding. The sharp mandibles (Fig. 7) tear a wound in the victim to make access to the soft internal organs, the fatty tissue and the body fluids. Some species of Carabus inject a brown mid-intestinal secretion which is believed to poison or deaden the prey as well as hasten the digestive process. However, prey is not always overpowered at once or so easily. Carabus ulrichii, in captivity, made strenuous but vain efforts to penetrate the round smooth abdomens of the Scarabaeids, P了吗trophorus so1stitialis (Verhoeff), but other Carabus species appear able to break the exoskeletons of Coleopterous prey with little difficulty. (Bluhweiss, '09). When living earthworms were thrown into the cages of C. granulatus, C. auratus and C. nemoralis, a vigorous struggle followed. Upon being seized in the mandibles of the beetles, the worm writhes and twists, and drags or tosses the tormentor about, yet the beetle holds fast. Other beetles in the cage are attracted by the commotion, and there begins a bugging and tearing in all directions. The beetles sometimes fight among themselves to obtain their share of the food. A large worm is able to shake the attacker off.
especially when slime has been secreted and makes the slippery body surface difficult to grip. Not infrequently the mandibles become gummed by the slime and then the beetle must retreat to remove the obstruction. Eventually the worm tires, and the secretion of slime slows and for each beetle sooner or later tears off a suitable piece and sneaks away to eat it in seclusion (von Lengerken, Gertel, Delkeskamp). In the period of most intensive life, they often ate for two hours or more at a time. Distended and sluggish they go into hiding to rest while the meal is being digested. The mode of attack on caterpillars and other forms of prey is similar. Calosoma scrutator usually seized its caterpillars in the middle of the back. But with such a prey, a struggle rarely ensues because predator and victim are more nearly of the same size.

The act of feeding is not one of simply biting or tearing off bits of the prey and gulping them down in their entirety. The mandibles and maxillae alternate when engaged in taking food, and each pair of mouth parts has a characteristic action. The mandibles are capable only of opening and closing in a horizontal plane. The maxillae, because of their jointed structure, can move over a semi-circular path in opening outward and forward, and in closing fold back in the direction of the mouth. When the mandibles close, the maxillae open and take a new hold on the morsel of food chewed off. The mandibles press upward from the prey and the maxillae press downward. The palpi press upward from below against the morsels of food chewed off, acting as a buttress for the jaw. These observations were made on Carabus nemoralis and C. cancellatus.

However, the fleshy food is not always prepared for ingestion by this physical action of the mouth parts alone. Certain species of Carabus are said to produce from the mouth a fluid that acts chemically to reduce the flesh to a brothy liquid. Only in this form can it be ingested for the reason that the mouth is surrounded by a dense brush of bristles that screen out all solid substance. When flesh of prey is thus broken down before it is swallowed, the process is described variously as extraintestinal, extrasmal, extrascutal or preoral digestion. The occurrence of this phenomenon in the animal kingdom was reviewed by Jordan ('10) who also investigated the process in Carabus auratus. This special method of digesting food obtains when the prey is difficult to overcome by the ordinary physical mode of swallowing the food animal in toto, or tearing and biting off single pieces to be ingested as such. Moreover, such digestion may be made necessary by conditions either within the prey or in the predator itself. The prey may be much too bulky or too strong to be overpowered, may have an armor penetrable only with difficulty, or possesses flesh too tough to be readily masticated by the physical action of the mandibles alone. On the other hand, extraintestinal digestion may possibly arise owing to inadequate mouthparts of the predator or an esophagus too narrow to permit swallowing of large morsels of flesh, but as a rule we may expect it to appear in predatory insects in which food is upon smalls and Arthropods. The Arthropods, because they possess a definite exoskeleton, are believed to furnish especially favorable conditions for the preoral dissolution of flesh. By means of its strong sharp mandibles the predator punctures its catch, then squirts the digestive secretion into its body, whose tissues are thereby dissolved in situ. The liquified substance may then be sucked out through a small hole in the body wall, and all the contents of the victim, including even the muscles of the legs, may be utilized as food.

Extraintestinal digestion was found by other German investigators to occur also in Carabus cancellatus, nemoralis, violaceus and infractus L., and is believed to be the characteristic mode of feeding in some other species of this genus. Thus food is prepared for ingestion by a combination of both a physical and a chemical action, the mandibles breaking the exoskeleton to provide an entrance for the digestive juices.

But when a morsel of exposed beef is provided, the mode of procedure differs somewhat from the above. At first the jaws are put into play upon a portion of it, kneading and drawing the feeding point out into a nipple-like process. Simultaneously with the pressing and pinching of the flesh by the mandibles, the feeder pours out a heavy brown fluid from the mouth upon the food. At the point of feeding the flesh then turns brown, and shortly dissolves into a thick brothy fluid. The secreted liquid is regarded especially as a solvent for proteins and an emulsifier of fats. It has been rather conclusively shown to originate in the epithelium of the mid-intestine rather than in the salivary glands as formerly supposed. Verhoeff (G1) denies the occurrence of preoral digestion, but stands alone in this view among the several
students of feeding in Carabus. However, it may be safely stated that some Carabidae tear off and swallow flesh in small bites; this is demonstrated by the stomach analyses made by Forbes ('83a), who found recognizable fragments, including hairs, of various insect prey in Calathus elegans, adults of the Elaterid, Limonius californicus; C. chineus Euplocamia curculionis, and Dendrolimus gibbrous and Barathra memnoniae (Matsunura, '20); C. frigida, larvae of Portheria dispar and Heterocampa guttivitta; C. minutus, larvae of Phyllophaga (Davis), and the cutworm, Peltroloma margaritosa (Burgess and Collins); C. lugubrc L., attacking May beetles beneath street lights (Davis, '22); C. pyrana, larvae of Portheria dispar; Carabus auratus, fed variously on Julius, Staphylinus, adults of Epilachna corrupta (Schilder), larvae of Porthetria dispar, and adults of Epilachna corrupta and dispar; Ophonus calceatus auratus, consumed both shelled and naked earthworms beneath street lights (Davis, '22), and the galls of the small nest cardinals and sucked their blood to the extent that two of them were killed.

However, the bulk of the prey taken consists of insects. Of these, the larvae of Leptodoptera are most often recorded, but the grubs and adults of beetles also are frequently consumed, and also representatives of the order Diptera have been included in the diet of Carabidae. A lack of specificity in food selection is indicated in Calosoma frigidum which accepted the larvae of one or more species belonging to eighteen diverse genera of Leptoptera. The food records cited below further exemplify the variety of insects consumed by members of this family: Amara fercida (Lec.), probably eats the larvae of Phorbia brassicae (Gibson and Trenner), and is known to destroy the strawberry root weevil, Brachioryzus ovatus L.; Semidium trechiforme Lec., and H. mutatum G. and H., probably eat the larvae of P. brassicae; Hemedion spp., both feeding stages probably preying on the fossil larva of Phyllttnia viridula, Bledius (Krogcrus); Bothriopterus oblongopunctata P., consumed most of a Molell, Cantaris rusticta eaten by an excavating (Pledder); Sigeous cephalotes L., adults of the Elaterid, Limonius pilosus and Agriotes lineatus (Thomas); Calosoma calidum, adult may beetles (Phyllophaga) (Davis, '22), cutworms, and larvae of Portheria dispar; C. cancellatum Esch., adults of the Elaterid, Limonius californicus; C. chineus Euplocamia curculionis, and Dendrolimus gibbrous and Barathra memnoniae (Matsunura, '20); C. frigida, larvae of Portheria dispar and Heterocampa guttivitta; C. minutus, larvae of Phyllophaga (Davis), and the cutworm, Peltroloma margaritosa (Burgess and Collins); C. lugubcr L., attacking May beetles beneath street lights (Davis, '22); C. pyrana, larvae of Portheria dispar; Carabus auratus, fed variously on Julius, Staphylinus, adults of Epilachna corrupta (Schilder), larvae of Porthetria dispar, and adults of Epilachna corrupta and dispar; Ophonus calceatus auratus, consumed both shelled and naked earthworms beneath street lights (Davis, '22), and the galls of the small nest cardinals and sucked their blood to the extent that two of them were killed.

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In some species little distinction is made between fresh and decaying animal or plant tissue. *Carabus auratus* killed and ate various Arthropoda in nature but fed also upon crushed snails, dead nesting birds and decomposing mice, and in captivity accepted rotted fruits (von Lengerken, 1911). *O. granatini* show a particular preference for soft fruit, pears, decaying plums and similar things (Bartel, '64). The mycrococoled, *Tachyura insurge* (Say), found abundant in the nests of *Formica ulkei* Emery by Park ('29), feeds upon the store of food carried in by the workers and attacks both the ants and other co-inhabitants of the nest when these are dead or disabled.

But a still larger number is known to take more or less living plant substance along with the fleshy ingredients of their diet. Forbes ('83) analyzed the stomach contents of 178 *Carabidae* collected in the field. The species dissected belonged to the genera *Harpalus*, *Anisodactylus*, *Amara*, *Anisopterus*, *Acanthus*, *Dinodes*, *Elaterus*, *Euryops*, *Galerita*, *Carcinus*, *Staphylinus*, *Allothrix*, *Lebia*, *Platynus*, *Mecaelus*, *Bryodcurus* and *Patrobus*. The first ten genera were represented by enough specimens to give an indication of their average food. On the whole fifty-seven per cent of their food consisted of animal substance. According to miscellaneous published records, the vegetation more frequently eaten by *Carabidae* was spores of fungi, pollen, tender leaves of grass and immature seeds. Forbes ('96) and Phillips ('09) treat *Clivina impressifrons* Lec. and *Acanthodes pallipes* (Fabr.) as pests of planted corn seed, and some *Harpalus* species are reputed to be enemies of the fruit of strawberry, but were also found on a number of occasions eating the soft seeds of ragweed (*Ambrosia*). In addition to the above, representatives of *Articus*, *Beelamillus*, *Broscaus* and *Omphorion* have been reported eating parts of living plants at times in nature. However, despite the widespread inclusion of living plant matter in the diet of *Carabidae*, no species has yet been positively shown to be entirely phytophagous. The flexibility of tastes which admits several types of food is doubtless to be regarded as advantageous to these allies of man in that it enables them more certainly to maintain themselves in numbers adequate to meet outbreaks of insect pests as these may arise.

Studies have been made on the quantity of food consumed by *Carabus cancellatus*, *C. auratus* and several species of *Calosoma*. The average length of time during which *C. auratus* and several species of *Calosoma* and *C. cancellatus* plus *C. nemoralis* occupied the period of active reproduction. After a fast of fifty hours, two males and two females of *C. auratus* weighed 630, 788, 420 and 360 mg. Given a full meal, the individual weights of the males increased to the extent of 68 and 47 percent but decidedly less in the females. The beetles were then allowed to feed normally for a week, and during a meal of four hours duration they took on an average of 195 mg., the increase of the males again greatly exceeding that of the females. Similarly, two females and two males of *C. cancellatus* weighed 680, 690, 600 and 550 mg. at the inception of a feeding experiment. A meal of chopped meat and banana added an average of 100 mg. to their weight and upon being deprived of food for 23 hours they again lost an average of 65 mg. One female of *C. nemoralis*, weighing 560 mg., when captured, almost doubled her weight in two and a half hours of feeding. From the above tests with *C. auratus* and *C. cancellatus*, it is apparent that the females are much heavier than the males. But despite their smaller size, the males consumed an actual larger quantity of food than the females of their species in the same period of time. In view of the normal discrepancy in the bodily bulk of the sexes, the more rapid rate of increase in

16
weight of the males must be followed by an equally faster rate of decrease in order to maintain their lower average body weight. Such a faster decrease in weight of the males was observed in C. cancellatus. On the other hand, the females of the two species experienced a steadier and less extreme rise and fall from their average weight as a result of their feeding and subsequent fasting. However, Delkeskamp's data for C. nemoralis show that the increase of weight from feeding in the females is greater than in the males, and that during a period of fasting the amount of weight lost by the female exceeds the loss of the male.

Two other females and two other males of C. cancellatus were weighed daily in a five-day period of normal feeding during September when the reproductive activity for the year had ended. The weights before and after meals wavered only slightly above and below the average as compared with the extreme fluctuations observed when the beetles were at the height of the mating and oviposition season. In Calosoma species also, the largest quantity of food per day was, in general, consumed during the period of greatest reproduc­tivity. It may be deduced that these insects are especially sensitive to a scarcity of food in the season of intense reproduction.

Burgess found further that the age of the beetles affects the rate of reproduction and the amount of food required. Adults of C. sycophanta two or three years old consumed more food during their reproductive periods than did the one-year-old beetles, a fact believed to be correlated with the higher rate of reproduction of the more mature individuals.

The Carabidae tolerate starvation for considerable periods and appear to be affected only slightly, if at all, by diseases, poison or other possibly harmful ingredients of their food. Carabus auratus freely ate Meloidae in feeding tests, and Bothriopterus oblongopunctatus voluntarily devoured the abdomen of a living Cantharis rustica in nature, suggesting that the stringent properties of cantharidin are not deterrent to them. Carabus auratus prized several fungi, including Psalliota arvensis Schaeff., said to be the most poisonous fungus in Germany. This beetle, however, did not eat hairy caterpillars or gypsy moth larvae affected by tetrahebral disease, but Burgess and Collins ('15) fed a pair of C. sycophanta on gypsy moth larvae having this disease and while they ate slightly less than a pair fed healthy caterpillars, they entered hibernation and exhibited no ill effects.

Further, each year large numbers of gypsy moth larvae given caged beetles to eat died from the disease, but no harmful effect on the predators was noted. Nor was any wholesale injury caused the beetles by their feeding on caterpillars poisoned with insecticides.

Starvation experiments with two pairs of first year beetles and two pairs of old beetles were carried out on C. sycophanta. The two young males lived 30 days and 33 days, respectively, whereas the females of the same age tolerated hunger for 29 days and 43 days. The males of the older pairs survived 34 and 61 days and one female lived 51 days, the other being still alive at the time of the report. Old beetles appear to withstand starvation better than young beetles, and males die sooner than females. Carabus nemoralis is able to endure hunger for a week without harm, provided that it have access to water (Delkeskamp).

Drink. The water requirements of Carabus are not entirely satisfied by liquids obtained incidentally along with their food. They appear to drink free water especially after feeding, and otherwise were seen to drink with some regularity daily. C. auratus and nemoralis imbibed droplets of water hanging on grasses and small stones, and C. cancellatus eagerly drank from a small cup. More frequently these species inserted their mandibles into wet sand to press and suck out the moisture from it, as is commonly done by the Cicindelidae.

Swallowing Air. According to von Lengerken ('21), the older beetles of Carabus auratus fill their alimentary tracts with air taken in through the mouth. Its physiological significance is not clear. Excepting the air, the tract contained nothing. Air-swallowing has been demonstrated in the newly hatched larvae of several species of Carabus.

Hibernation. A good number of records indicates that the large majority of the species of Carabidae are in the adult stage during the winter season. The adults of seventy-seven of the 217 species of Carabidae known to Blatchley ('96) from Vigo County, Indiana were taken during the winter months. The larger number of these are members of Seliini, Tachys, Pterostichus, Platynus, Lebia, Chlaenius, Harpalus and Anisodactylus; but twenty other genera are represented. In his winter trips into the district infested with the gypsy moth, Burgess ('96) collected Carabidae of the genera Amara, Platynus, Pterostichus, Lebia,
Zurius and some species of Platynus may remain beneath leaves or mold in wood in rather damp situations. The rep­
winters in numbers beneath the close .fit­
winter unless the soil is so hard that
was found beneath the bark of logs. Vari­
bus auronitens in moss oovered soil.
and Pterostiohus under logs and chunks of
ground were selected by the remaining spe­
Brachinus. All the species of Carabus and
representatives of Anisodactylus. Labia, Har­
place, and all so placed tbat at most their
cancellatus and C. intricatus also ooourred
in the drier uplands. Tachyta
ous surface litter or logs lying on the
Platynus seem to favor superficial oover
this is impossible. Occasional specimens
ed areas, but this is not believed to be
the usual habit. The winter burrows
ranged mostly from 2 to 15 inches in depth,
but some were 20 inches deep. Blatchley
(1'96) found the species of Bembidium, Tach­
ye, Chlaenius and some species of Piatynus
and Pterostichus under logs and chunks of
wood in rather damp situations. The rep­
resentatives of Antecdactylus, Lebia, Har­
palus and some members of Pterostichus and
Piatynus seem to favor superficial cover
in the drier uplands. Tachytta nana (Gyll.)
was found beneath the bark of logs. Vari­
ous surface litter or logs lying on the
ground were selected by the remaining spe­
cies of Carabidae listed by Blatchley.

A few species give evidence of pre­
gartlessness in hibernation. Tachytta nana
winters in numbers beneath the close fit­
ting bark of various kinds of trees recent­
ly failed, including oak, hickory and tu­
lip. Delsky (Eern, '21) found eleven Cara­
bus aurontiens in moss covered soil. C.
cancellatus and C. intricatus also occurred
in companies, the latter species so in a
place, and all so placed that at most their
tarsi were in contact (von Lengerken).

In the careful studies of German in­
vestigators on Carabus and Burgess on Cal­
ossa it was learned that the overwinter­
ing beetles are mostly young individuals
that reached the imaginal state in the
summer or autumn preceding. But a second
onial adult of Calosoma sycophanta win­
tered the second year. These were almost
exclusively females that did not oviposit
in their first year, and may be recognized
by their faded colors and the usually tat­
ted body. In a few instances, adults of
Calosoma sycoophanta remained dormant in
the ground continuously for nearly two
years. One pair entered hibernation on
July 26, 1910, and did not emerge from the
ground until June, 1912. In every case
where this has occurred the beetles were
more than a year old. Also in some species
of Carabus the adults may live two years,
and possibly spend two winters in this
stage.

In their hibernation studies on Cal­
ossa sycophants, Burgess and Collins found
a mortality that varied with the sex and
the age of the beetles, the higher rates
death occurring among the second and third
year males. During the winter of 1908-09,
35 percent of the old male and 28 percent
of the old female beetles died, and in the
following autumn these percentages were
31 and 27, respectively. Of the young beetles,
22 percent of the males and none of the fe­
male succumbed to the rigors of the winter
of 1908-1909. The experiments were con­
ducted under favorable cage conditions.

Aestivation. In captivity, and ap­
parently also in nature, the adult Carabus
memoralis seems to have a period of summer
sleep. Delkeskamp (1930) saw that one af­
ter the other of his sixty beetles disap­
ppeared suddenly in the latter half of May, and reappeared, one now and then, in mid­
July without having fed in the meantime,
and always again promptly burrowed into
hiding. Attempts to trap the species out
of doors at the same time failed where many
were so obtained during the winter, which
suggests an aestivation response also in
nature. After their summer sleep the cap­
tive beetles gave evidences of much increased
age, they left their burrows only when dis­
turbed, fed only a brief time and the males
no longer attempted to copulate. Their
life's function had been accomplished dur­
ing the spring months, and their summer dor­
manoy seems merely to signify a natural in­
activity accompanying old age. But it is
not stated whether this phenomenon exists
also among the younger individuals which, it
may be presumed, are present in the same
season.

Mating. This act has been described
for Carabus auratus, C. nemoralis and C. cancellatus. With antennae directed obliquely forward, the male dashes upon the female from the side or behind, taps her a moment with his antennae, then pushes himself forward until his palpi touch those of his mate who simultaneously bends her head upward. This contact of the palpi is temporary and obviously serves only as a stimulus to copulation. In the final copulatory position, the first two pairs of legs embrace the female, and the hind reaches the ground. Hungry females crawl about and feed in the normal way during copulation. Coitus lasted from several minutes to a half hour in auratus, one-half to three-fourths of an hour in cancellatus, and most of a day in nemoralis, in one instance. These species and Calosoma sycophanta mate repeatedly during the reproductive season. A pair of C. sycophanta copulated thirteen times between June 27 and July 26 (Burgess, '11). Carabus auratus, C. cancellatus and others continued mating into the latter part of summer but did not oviposit after the last coitus. Females of sycophanta, impregnated in the autumn, do not lay fertile eggs in the following year without mating again in the spring. Species of both these genera that live two or more years in the adult state mate repeatedly in each of these years.

Oviposition. So far as known, the ground beetles deposit their eggs (Fig. 8) either upon objects above ground, or in cavities made in the soil (Fig. 9). By scraping soil upon it with her hind legs. Eggs are laid in similar holes also by C. granulatus, C. ulrichi and C. nemoralis, and by the species of Calosoma, Agonoderus pallipes, and Poesilius coeruleomaculatus Dej. (Bolodori), and probably the majority of the other Carabidae. Their depth in known instances varies from one-eighth of an inch to two inches. Craspedonothus tilbialis lays the eggs in small cells or chambers one-half inch deep, which angle off in a downward direction from the sides of its burrow. After oviposition, the entrances to the egg cells are filled with sand. After the female of Pterostichus multipunctatus places her eggs in the cell, she stands over them and also the larvae during their first instar. When the nest is disturbed, she crouches over it and exhibits a determination to protect it (Bolodori).

Fig. 9

The female of Carabus cancellatus extends the terminal segments of the abdomen teleo- optically, and by moving backward pushes it into the earth. The anterior part of the body is elevated by straightening the front and middle legs and the tips of the elytra come to rest upon the soil at the edge of the hole. When an egg has been deposited, the female rapidly conceals it by scraping soil upon it with her hind legs. Eggs are laid in similar holes also by C. granulatus, C. ulrichi and C. nemoralis, and by the species of Calosoma, Agonoderus pallipes, and Poesilius coeruleomaculatus Dej. (Bolodori), and probably the majority of the other Carabidae. Their depth in known instances varies from one-eighth of an inch to two inches. Craspedonothus tilbialis lays the eggs in small cells or chambers one-half inch deep, which angle off in a downward direction from the sides of its burrow. After oviposition, the entrances to the egg cells are filled with sand. After the female of Pterostichus multipunctatus places her eggs in the cell, she stands over them and also the larvae during their first instar. When the nest is disturbed, she crouches over it and exhibits a determination to protect it (Bolodori).

Riley ('84) reported the rather remarkable habit of Chlaenius impunctifrons Say which places its eggs on foliage encased in a mud cell. Subsequently King ('19), determined by the rearing method that not only C. impunctifrons, which was also studied by Claassen ('19), but C. amnicola Forster, C. tricolor Dej., Brachinus cyanipennis and Galerita bicolor Drury, too, deposit their eggs in such cells (Fig. 10). The beetle collects a pellet of mud at and around the tip of the abdomen, the cell then formed being in reality a mold of the caudal abdominal segments. The lid of the cell is formed from a thin layer of mud which covers the dorsal
portion of these segments. When the egg has been laid the abdomen is withdrawn and used to bend down the dorsal flap or lid and close the cell. Owing to the soft texture of the mud at the time of construction, the lid of the cell is self-sealing. The cases of each species seem to be distinct in their form, size, structure and immediate location. Those of C. impunctiferons are almost always smoothly convex and dull, and measure about 3.6 mm. in length and 2.28 mm. in width. About ninety percent of the cells of this species occur on living plants, the under surface of smooth leaves being most often selected. Their actual distance from the ground varied between a few inches to seven or more feet.

On the other hand, C. aestivus Say built her egg cells on dead twigs and tree trunks, and Chlaenius cyanipennis on twigs, stems and stones (King).

In most recorded instances, the female Carabid deposits only one egg at one time and in a cell, whether it be in the soil or in mud cases off the ground. Boldor reports finding from 6 to 19 eggs in each cell of the maternalistic Pterostichus multipunctatus. The number of eggs laid by individual females and the rate of oviposition has been determined in part for several species. Craspedonotus tibialis formed 9 to 11 egg cells off her subterranean burrows and Chlaenius impunctiferons may construct seven to twenty cells during one night, and eighty-two cells in a season. One female of Carabus granulatus oviposited four times from May 25 to July 21, producing 0 to 11 eggs in each of the four days and a total of 41 for the period (Oertel). One C. cancellatus laid eggs on twelve different days between the 10th and July 29, producing one to ten eggs on each such day, and a total of 43 (Kirchner); and Verhoeff observed thirteen ovipositions between June 2 and July 29, at intervals of one to nine days, in one individual of the latter species. But we have a more complete picture of the reproductive habits and capacity in Hallocerodes alytus. In 1906, twenty ovipositing females of this species laid a total of 1,662 eggs, or an average of 83 per individual; in 1909, fifty-two produced 810 eggs, or 158 for each female and in 1910 seventy-two laid 8,780, or 121 eggs per individual. The 144 females deposited a grand total of 10,481 eggs, or an average individual yield of 72.8 eggs (Burgess, '11). One female C. frigidus deposited 180 eggs from June 4 to August 19. The maximum number by a single C. alytus in one year was 658.

Nearly one-third of the C. alytus beetles observed in any year did not oviposit, and these proved to be mostly young or first year individuals. It further appears that a certain proportion of the beetles does not oviposit at all in the first season, and when eggs are laid the number is smaller than in the second year. A definite relation seems to exist between active oviposition and food consumption. An abundance of food naturally stimulates the activities and reproductive capacity of the beetle, and the insect accordingly exhausts itself more rapidly and consequently curtails its life to some extent. Such evidence as Burgess had at hand shows that, for any reason, the food supply is scanty, the majority of the beetles are able to survive to the next year, although their activities and rate of reproduction are materially decreased. Age as a factor affecting oviposition seems to operate indirectly through food consumption as the following facts from Burgess show. Four
young beetles ate an average of 214 caterpillars in a summer, two producing 92 larvae, the other two none, whereas four old beetles simultaneously consumed an average of 303 caterpillars and produced an average of 162 larvae. Rearing experiments and data secured from field colonies indicate that a considerable number of eggs may be laid during the first year if conditions are very favorable, while if they are unfavorable, oviposition is postponed to the second or third summer. Thus, it sometimes happens that eggs are laid in the first and third summers, but not during the second. But at any rate, all females eventually lay about the same number of eggs in their lifetime. In the species that live two or more years as adults, oviposition may accordingly be expected in any or all of these years. Such repeated annual egg laying has been observed in *C. sycophanta*, *C. frigidum* and several species of European *Carabus*. It has been noted further that more eggs are normally produced by large females than by small ones and that the size of the males has no important influence on the number of eggs that the females lay.

**Incubation.** The duration of the incubation period varied from 3 to 10 days in *C. sycophanta* and depended largely on the temperature. In May the eggs hatched after an average incubation period of seven days, in June they required 5.2 days, in July 4.4 days, and only 4.0 in August. In 1908, 4.4 percent of the eggs hatched in 3 days, 26.4 percent in 4 days, 53 percent in 5 days, 11.3 percent in 6 days, 5.6 percent in 7 days, 0.8 percent in 8 days, 0.0 percent in 9 days and 0.2 percent in 10 days. In the hot weather of May and June, the eggs of *Carabus granulatus* hatched in 6 to 8 days, and in cooler temperatures incubation required 8 to 12 days. In *C. cancellatus* their development varied between 6 and 16 days in June and July, with the maximum day temperature at 30°C and the night's minimum at 8°C.

**Hatching.** The matured embryos of *Carabus cancellatus* and *C. ulrichi* inflate parts of the body with blood, the thorax and the abdomen alternating in pressing like a bellows upon the tender egg shell. The emergence of the embryos begins with the tearing of the cephalic portion of the shell, the outward pressure of the body being greatly assisted in this work by two strong spines or egg bursters (Fig. 11) that extend cephalad from the frontal suture on the head. The movements of the embryo operate to apply the bursters to the inner surface of the shell and thus finally tear it open. The embryo comes free however only by the blood pressure exerted upon the rent shell which enables the insect to wriggle its way to the outside.

**ACTIVITIES OF THE LARVA**

**Swallowing Air.** The newly hatched and yet uncolored larvae of various *Carabus* species have been observed to swallow small bubbles of air that have the appearance of a string of pearls when lodged in the digestive tract. By contraction movements of the tract, the bubbles are pushed back and forth in the canal and exert an outward pressure that effects a stretching of the body wall while it is still soft. The residue of yolk in the alimentary tract becomes churned vigorously during the inflation process. Similar distentions of the tract by swallowing air were seen also in *Carabus* larvae following immediately upon each larval molt. Air-swallowing has been reported for the larvae of *C. ulrichi*, *C. cancellatus*, *C. auratus* and *Poecilus celeriacens* by Verbheef, Kirchner and von Lengerken.

**Fig. 11**

_Body of first instar larva of Carabus auratus, dorsal view, E, egg-burster; Fa, frontal suture; Oo, ocellus; On, ocellus; Pm, maxillary palp; Ml, mandible; P1, labial palp; C1, clypeus, After von Lengerken (1925) Zool. Anzeiger._
Larval Growth. The larvae of all the Carabidae that have been carefully reared pass through three instars. This number is known to occur in Carabus ulrichi, C. granulatus, auratus, nemoralis, cancellatus, lampros rufipes, C. callidum, sycophanta and Clasenius impunctifrons (Fig. 12). Just before molting, the larvae of C. sycophanta cease feeding and become sluggish, and the body shortens and thickens. Then by bending the ends of the body downward and toward each other at regular intervals the integument is ruptured lengthwise and transversely in the dorsal region of the thorax, whereupon a pure white larva gradually withdraws from the exuviae. The entire process of molting requires a few hours. In the terrestrial species, the molts occur under stones and surface litter on the ground, but when feeding up in trees C. sycophanta larvae molt in holes or cavities, among masses of gypsy moth pupae or even in crevices of the bark.

The larval stage of a Carabus ulrichi was passed between May 3 and July 12, a period of 70 days, and the larvae of the smaller C. granulatus developed in about 40 days in July and August (Verhoeff). Certel found that the latter species completed its first instar in 6 to 10 days. The second and third instars required approximately as long as the first, and the mature larvae descended into the ground to pupate in about 10 days after the second ecdysis. The duration of the first instar in C. cancellatus varied between 6 and 19 days, but most individuals required 12 days to molt from 5 to 16 days, but 6 as a rule, and the third ended with the disappearance of the larva into the ground in 10 days to 14 days (Kirchner). Delheeskamp reared the first instars of C. nemoralis in 10 to 16 days, with an average of 14, and reared one individual through the second stadium in 21 days. One Clasenius impunctifrons made its larval growth in 27 days, the first and second periods lasting 3 days each and the third 21 days (Claassen).

The influence of temperature on the rate of development is demonstrated in the studies of C. sycophanta (Burgess, '11). Larvae that hatched in May from eggs laid by beetles taken from hibernation in March and April required an average of 5.5 days for the first instar, 6.6 days for the second and 14.5 for the third instar. Larvae from beetles that emerged normally from hibernation and oviposited in June, passed the three instars in 2, 3, and 9 days, respectively.

Fig. 12

Larval Food and Feeding. The first instar larvae of several Carabus species take no food from without during the first two to three and a half days after hatching. Investigations revealed that the alimentary canal of such larvae contains yellow yolk derived from the egg in the embryonic state, on which the larva is nourished during the first few days of its active life. This mode of feeding early in the first instar has been reported for the larvae of C. ulrichi, auratus, granulatus, cancellatus, and Pterostichus. Whether or not the newly hatched larvae of all Carabidae have a similar supply of reserve yolk, they are strictly carnivorous during the rest of their larval life, so far as known. Cannibalism has been commonly observed among the larvae of Carabus, Galogomna and Poecilus canescentis under cage conditions.

In the larvae as in the adults of the Carabidae there occur two modes of obtaining food. It is believed that the larvae of some species chew or bite off tiny morsels of solid flesh from their prey and swallow it entire to be digested in the alimentary canal. On the other hand, Davis ('22) cites an instance in which a Carabid larva pierced the skin of a white grub and...
drew out most of the body fluids in about three hours. Moreover, several species of Carabus ingest their food only in a liquid state after having digested it extraintestinally by means of a solvent for protein and fat injected into the prey by the predator. These larvae are said to possess practically no mouth. The mandibles are tong-like (Fig. 13) and provided with longitudinal grooves almost closed to a canal-like condition. The grooves connect with the oral cavity at their base whereas their apices reach into the prey during feeding.

Thus the canals serve first to convey the digestive and deadening ferment from the predator into the newly captured prey, and second to conduct the liquified tissues of the victim to the intestine of the larva.

Von Lengerken ('12) demonstrated this mode of feeding also for C. nemoralis and a species of Calosoma, and ventures the statement that all species of Carabus which live like auratus most likely possess this type of digestion. He established that the brown solvent fluid is poured into the prey at once after the mandibles make the wound. A short time after the injection of the secretion by Calosoma into a caterpillar the entire surroundings of the wound turn brown and the discoloration proceeds to a depth of several millimeters. The dissolving work of the secretion continues even after the predator leaves the remains of its victim. It is claimed also that the secretion has a distinct poisoning power in addition to its property of dissolving flesh. The mature larva of C. auratus is able to paralyze a large earthworm in a few minutes. It was observed that parts nearest the point of seizure are the first to become motionless. If a worm is bitten at the middle, the ends move lively at first, but the lancing effect of the secretion spreads rather quickly forward and backward.

The larvae of certain species of Calosoma are very ferocious, and do not hesitate to attack caterpillars much larger than themselves. They commonly grasp the victims by the under side of the body and cling with great tenacity until it succumbs. If perchance the little larva is shaken off, it persistently renew its attack with greater zeal than before. After succeeding in cutting a hole through the integument with the sharp mandibles, it sucks out the contents of its prey and often becomes gorged almost to the point of bursting. It then repairs as rapidly as its condition allows to a place of shelter under surface cover. Here it remains dormant for a short time and is then ready to start out again in search of more prey (Burgess, '96). The larvae of some Carabus are said to possess a pair of ever-dilatable anal vesicles used to anchor the body during a struggle with its prey and also serve as a means of attachment in locomotion (Ern.).

The rather limited food records at hand for Carabid larvae indicate that they lack the promiscuity of diet found in the adults. The larvae of Ptychius impunctipennis and D. obscurus, like the adults, seem to feed exclusively on the stages of the burrowing Staphylinidae, Eledus ammonius and E. pallipes Gray. (Cuciceps Rye) with which they live in association. The larvae of the soil-inhabiting Craspedonotus tibialis take a number of insect species, including some Scarabaeids. In cages, the larvae of Carabus fed readily upon earthworms, morsels of mammalian flesh and caterpillars, and in general displayed a breadth of taste for animal food equal to that of the adults. Burgess ('96) states that the larvae of Calosoma species do a great amount of good in killing many kinds of cutworms and other injurious caterpillars, and have been reported also feeding on the larvae of Leptinotarsa decemlineata, Hesperis vertans, Phyllophaga fusca and the eggs of Melanoplus susatus. The larvae of C. frigidum first fed on the caterpillars and later also on the pupae of Phyllophaga putativta. Cutworms and other larvae commonly found among the roots of various plants are preyed upon by C. cali-
dum. The young of C. syrphodera, which are most active during the time the gypsy moth is in the pupal stage, destroy many of these pupae, and are frequently found feeding also upon the larvae and crysalises of native Lepidoptera. According to Davis ('22), the larvae of Harpalus pennsylvanicus Dej. (Fig. 14) and to a smaller extent also those of H. caliginosus Fabr., preyed upon the grubs of Phyllophaga both in fields and in underground breeding cages.

The young of Calosoma frigidium is indicated by the studies of Burgess ('96, '10). In an abundance of the pupae of Heterocampa guttivitta on the ground under trees, these larvae had destroyed from 60 to 100% of the crysalises in five sample square yards, and in 24 other such areas an average of 54% of the pupae had been killed. Estimated conservatively, the larval development of this species required two full grown gypsy moth larvae in the first instar, five in the second and seven for the third instar. In one instance, the first instar larva consumed one small cutworm, one third instar larva of the gypsy moth, and three second instar larvae of this moth; in the second instar it ate two fall webworms (Hyphantria cunea), one larva of Petasius minitiae, one armyworm (Leucania unipuncta) and one-half of a gypsy moth egg cluster; in the third instar it required two larvae of D. ministra, two or three integerrima, one Sama acropia and six armyworms. The single larva thus consumed a total of 20 caterpillars and half of an egg cluster while making its entire growth.

Parasitism. In several species of Carabidae, the larval form derives its sustenance from one, or at most a few, individuals of other insects. Lamborn (Blair, '27) reports an instance in which the larvae of a small Carabid, Arilamé grandis, in the tribe Paring, of Nyasaland, Africa, clinging to and feeding upon the larva of the Tenebrionid beetle, Catamerus revoluli Palm. At first the Arilamé sucks out the body juices of the host and in its later instars also devours the solid portion of its prey. Having destroyed the first victim, the predator attaches itself to another and in this way kills a few Catamerus larvae before it is full-grown. This relationship seems on the one hand to be a refined form of predation, the predator devouring only a few food animals on account of the similar size of the predator and the prey. On the other hand, the aggressor species attaches itself to the victim and gains both food and transportation from it, which are characteristic of a parasitic relation. The dangerousness of the host is apparently an important factor in encouraging this relationship of the two forms.

But in the following instances, each larva derives from one host all the food it requires for its development. These belong to Brachinus and Lebia, and to Pelcium, an aberrant group of the Carabidae. A total of six larvae of P. sulcatum Guer. were found by Salts ('29) in Colombia feeding upon soft millipedes, a beetle pupa and a leaf beetle larva as their hosts. At the time of the observations, all the larvae possessed legs as short in comparison with the unwieldy bulk of the spindle-shaped body that they were incapable of extensive movements. The development of the larvae requires only a few days. One larva feeding on a soft millipede grew from 4 to 9 mm. in length and doubled its bulk several times in about 48 hours. Nothing was learned of the egg and early larval period. The pupal stage is passed in cavities 4 to 8 cm. deep in the soil, and in one instance required five days for transformation.

Brachinus anthenipennis (Dej.) was reared by Wicksam ('84) and by Dimock and Knaub ('04) from the pupal cells of the whirligig beetle, Dineutes, in Iowa and Massachusetts. The subsequent discovery by King that Brachinus cynipennis Say places its eggs in mud cells formed on stones, twigs and stems supports the theory that B. anthenipennis may habitually oviposit on stones along streams and thus establish its progeny close to its hosts. The Brachinus larvae, when first found in the Dineutes cells, were already somewhat developed, being rather robust and maggot-like with legs capable of only slight locomotion (Fig. 15). In the more advanced state, the larva is completely adapted to a parasitic life by its soft, juicy body unprotected by cuticular plates, its weak legs quite useless for ambulatory purposes, and the absence of strong locomotor bristles.
tles. As a whole it has the appearance of a Hymenopterous larva rather than that of a raptorial adephagous Carabid.

The larval life of Lebia scapularis Fourcroy was traced by Silvestri ('04). The young larva is elongate, campodeiform, has well-developed mandibles and legs, and seeks out the pupae of Galerucella luteola Mül., upon which it feeds. After a short time of voracious feeding the larva increases considerably in size, becomes fusiform and bulky and its legs comparatively short and is then capable only of slow movements. It is stated by Rosenberg that the larvae of L. crux-minor L. feed upon those of the gallerucine beetle, Antomia tanaceti L., whose food plant is Achillea millefolia.

From the campodeiform structure of scapularis in its first instar, it may be conjectured that Brachinus and Pelecium have a similar form when newly hatched. Support for this suggestion is found in the occurrence of a like primary larva in such other Coleopterous parasites as the Meloidae, the Aleocharine Staphylinidae and the Rhipiphoridae. In no instance is the parent beetle known to place her eggs directly upon the food of her progeny, accordingly necessitating a period of free life in the first instar during which the parasite seeks out its host. The legs of the larva degenerate and the body becomes correspondingly bulky as the subsequent and truly parasitic relationship is assumed. Pupation in these instances takes place very near, or within, the remains of the host (Fig. 16).

All other records at hand agree that Carabidae pupate in the ground just below stones or leaves and similar cover lying on the surface. The larvae of Calosoma syrphante descended to various depths to make their pupal chamber, the variations being governed by the character of the soil and the amount of moisture which it contains. A number of larvae went to the bottom of a cage containing eight inches of soil, but they probably do not burrow down farther than four to five inches before making the cell under natural conditions. Carabus granulatus pupated five to ten cm. below the ground level, according to Oertel. The pupal cell is formed by burrowing and by turning the body about to compact the soil and smooth the walls. While lying in the pupal cell, groups of spiny hairs on the tergites of the first to the fifth abdominal segments serve to hold the pupa up off the wet floor of the chamber in some Carabus species (Kern) (Fig. 17).
Right larvae of Calosoma sycophanta had a prepupal period of 7 to 15 days, with an average of 10.8 days, whereas that of Carabus cancellatus was 2 to 5 days and G. granulatus 4 to 7 days. Calosoma sycophanta when young, in a preupal condition, in 12 to 15 days, C. cancellatus in 13 days and granulatus in 5 to 10 days after prepupation. Without reference to prepupation periods, it reports a pupation period of 5 days for Peileuctum sulcatum in Colombia, while Dicerca purpuratus Bon. required 10 days in September and Chiasindex impunctifrons only 7 days in June - July. Pupation takes place during the summer and early fall in species that mature as adults, the way developed images usually issuing from the pupal cells in the autumn to hibernate elsewhere.

The Life Cycle. As far as known, the Carabidae mostly require one year to develop from the egg to the adult. In some species of Carabus and Calosoma, the adults live two, three and even four, and in rare instances, five years. Burgess and Collins learned from careful study of the habits of Calosoma sycophanta over a long period that the adults live two or three and sometimes four years. Nickeral (1929) kept an adult female of Carabus auricollis alive in a cage from July 28, 1884 to June 22, 1888, or almost five years. It has generally been agreed that this unusual longevity was favored by the prevention of reproduction, an abundance of food, and shelter against enemies and the elements. Born (1922), who collected Carabids for a half century, concluded that Carabus beetles several years of age are more plentiful in nature than was believed theretofore, but Delkeskamp (1930) of the opinion that Carabus nemoralis, probably like most of the Carabidae, reach the end of their life after one year of adulthood, which mostly terminates with the beginning of the second winter. Most of his one-year-old individuals of Carabus coriaceus, G. violaceus, glabratus, and nemoralis died thus when exposed one week to heavy frost. But there may occasionally occur exceptional individuals, particularly females which, for one reason or another, not having deposited all of their eggs in one season, can under some conditions pass a second winter. Burgess (1911) likewise found that the females of Calosoma sycophanta live two summers, and if the full number of eggs has not been deposited at the end of that time they continue to live until this result is accomplished, provided a sufficient food supply is available.

Thus, longevity, like oviposition, in this species is related with quantity of food.

Because the majority of Carabidae, as far as known, winter as adults and require one year in which to complete their metamorphosis, reproduction must begin in the spring. Kern states that oviposition in Carabids occurs in May and sometimes in April, whereas G. auratus, granulatus, cancellatus, convexus, and arsenalis start egg laying in May, and glabratus, montlis and violaceus commence at the beginning of summer. In 1909, Calosoma sycophanta laid eggs from about June 10 to August 10. The number of eggs laid in a year was varying sharply with the fluctuations in temperature. During each period of high temperature there was an increase in the number of eggs laid. Generally, oviposition appears to continue for several weeks and when adults live two or more years, eggs may be produced also in these additional years.

The larvae of G. sycophanta lived in nature from latter June to early August, and those of the above Carabus species obviously are abroad between May and early autumn. The larval stage of different species requires varying amounts of time for its development. The records show that Carabus urichiitli made its larval growth in 70 days, G. granulatus in 40 days, C. cancellatus in 21 to 49 days, Chiasindex impunctifrons in 27 and Calosoma aurotus reached maturity on an average of 26.6 days in March - April, and 14 days in June - July. The full grown larvae enter the soil to pupate in time to permit the new adults, in most cases, to form and emerge from the soil before winter. The adults generally seem to cease feeding a week or two before becoming dormant. Nickeral observed the appetite of Carabus auricollis dwindle yearly during the second half of September as the time for hibernation approached. The males and females of Calosoma sycophanta cease their activities and become dormant at practically the same date, the time ranging from July 14 and August 15 in 1908 to 1910. There is thus considerable variation in different years, and the average for this species was about August 1. The date when the newly developed adults go into hibernation depends almost entirely on the time when the eggs are laid and whether the larva had an abundance of food.

Upon coming from hibernation the beetles again spend some days without feed-
ing. Carabus auronitens reappeared in April of each year. The date of emergence of Calosoma sycophanta depends on the weather and the location of the insect during hibernation. The very cool weather of May and June, 1909, retarded the average greatest emergence to June 8 - 15, while in 1910 this appearance extended from the first to the seventh of June. Records of 734 individuals reveal very little difference in the date of emergence of males and females. The earliest beetles, regardless of sex, appeared on May 8 and the latest on June 29. In general, most of the emergence takes place in the field during the first week in June, according to records obtained in 1908, 1909 and 1910.

Carabus auratus exhibited aging toward the end of the summer by dimming of its metallic color, and from mid-August they became languid, ate less and less, ceased copulating and burrowing, and rested for hours squatting on the ground, and only water and air were taken into the digestive tract. Parts of the antennae and tarsi were lost, and the beetles finally died. Similar evidences of increasing age have been described for other species of Carabus.
3. DYTISCIDAE. PREDACIOUS DIVING BEETLES

GENERAL FEATURES

The Dytiscidae constitute a large family of common and widely distributed beetles. Our chief interest lies in the adaptations of the larvae and the adults for their life in water. Their adoption of the aquatic habitat has not been complete, considering that the pupal stage is passed out of water and the adults still distribute their kind chiefly by aerial flight. Both of the active stages are almost completely carnivorous, and some of the larger species are known to destroy small fish. Members of the family were among the earliest insects recorded in ancient literature (Blunck, 123). Mordelot of Lyon published a figure of a larval Dytiscus in 1555, and Woufet produced another of this stage and the oldest known sketch of an adult in 1634.

The major investigations in the biology of the family have been made by C. Wesenberg-Lund of Sweden, Brocher of France, Blunck of Germany and Wilson in the United States, and shorter studies have been published by van der Heyde, Ege, Alt, and Balfour-Browne. Wesenberg-Lund, whose papers quickly appeal to the reader for their flowing style and their original and scientific pictures of Dytiscid life, contributed a large body of data on the intimate habits of the Swedish fauna as a result of persistent studies in aquatic and in nature. The process of respiration was extensively studied by Brocher, and our best knowledge of the economic importance of the larger North American species in their relation to pond fishes was developed by Wilson. Blunck furnished an exhaustive life history of the common European diving beetle, Dytiscus marginalis L., in a series of articles from 1909 to 1924 covering every phase of its external life. Because of its size, availability and the ease with which it may be reared in aquaria, this species is regarded as a desirable type of the class Insecta in the study of biology. Accordingly Blunck (18a) gives directions for rearing it, and Korshelt has prepared a two-volume treatise on its complete biology.

Habitats. The Dytiscidae find their most favorable living conditions in relatively small bodies of water having at most slow currents and shallow depth, a rich vegetation and an abundance of small aquatic life. In lakes, like Mendota in Wisconsin, and other larger bodies of water, Dytiscidae are almost entirely lacking, but they constitute one of the most abundant insect groups in ordinary fish ponds (Wilson). They thrive where the water is shared by the nympha or larvae of other aquatic insects, and similarly small Arthropods, which they consume. Dense submerged vegetation affords an abundance of food for their coinhabitants and thus assures an adequate supply of prey for the Dytiscidae themselves. At the same time the plants provide shelter in which the beetles hide, rest, and lurk for their prey. Most species deposit their eggs upon the surfaces or into the tissues of plants, and the active stages commonly utilize the parts of plants as supports while air is taken from the atmosphere. Thus, aquatic vegetation has come to be essential in many of the vital activities of these beetles.

Natural Enemies. At first thought it may seem that an aquatic habitat safeguards its inhabitants to an unusual degree against enemies. However, the Dytiscidae are subject to a set of natural enemies which are likewise adapted to life in water. These include microscopic plants and animals, parasitic worms, entomophasous insects, fish, amphibians and water birds, and certain inorganic influences, which have a similarly deleterious effect. The papers of Blunck (23a) and Wilson provide most of the known facts concerning these destructive agencies.

All stages are somewhat affected by inorganic influences. While few larvae of the Denias Dytiscidae remain in the pools from midsummer to fall, they may sometimes die from the frequent complete evaporation of the water in that season. On the other hand, any stages present in the pupal chambers along the shore are subject to the danger of drowning when the level of the water is raised. Wilson found that the mature larvae, pupae and newly formed adults of Thermomonas ornaticollis (Auber) were quickly killed in this way, and suggested flooding as a means of checking all the injurious water beetles. Subnormally cold weather in the spring may kill many of the larvae. In the studies of Dytiscus marginalis it was learned that many die from inability to hatch, and larvae may succumb on account of unsuccessful molt ing. While migrating, the adults of the larger species in particular are often attracted by electric lights and may perish in the dust on the ground, and when the water, in which the beetles hibernate, freezes to the bottom they are unable to survive.
The bodies of old beetles become wettable from failure of the skin glands to secrete oil, permitting water to penetrate into the tracheae under the wingcases. Certain physiological inconveniences have been noted to prevent normal reproduction and feeding. For example, in gravid females, certain eggs may lodge crosswise and thus also prevent the passage of others from adjacent ovarian tubes. The urinary crystals in the rectal ampulla have sometimes reached such dimensions that they can not be voided and consequently block the rectum.

Among the microorganisms regarded as hostile are numerous and many kinds of Protozoa and small Amebas that are free-living on the bodies of the larvae and adults. Weisenberg-Lund reports that larvae, whose molting was delayed by starvation became so encrusted with minute life that they were unable to shed their skin and died as a result. Adults, but particularly the senile individuals, whose unicellular skin glands cease to function, become greatly inconvenienced by similar burdens. In addition to these, the intestines of the larvae, pupae and adults are sometimes infested by Bractobasidium, an agamic stage of the gregarine, Legoria agilis becomes partly grown shortly after the first molt of D. marginalis, then wanders into the hind intestine and is voided with the larval faeces to mature in a free state in the water. Bothriopodidae and Protophyta and Protozoa that grow upon the larvae and adults, too, become prey to these predatory aquatic vertebrates, and also to the larger marsh and water birds.

The vertebrates add materially to the destruction, attacking in particular the larval and adult forms. The soft and defenseless newly hatched or freshly molted larvae frequently become the booty of fish, frogs and salamanders, as well as such of their own kind that are not also molting at the same time. But fully matured and active larvae and the adults, too, become prey to these predatory aquatic vertebrates, and also to the larger marsh and water birds. When the young of nearly all our food and game fishes reach a length of 25 to 40 mm., or become a year old, they freely eat the larvae as well as the adults of Dytiscus, Cybister and smaller forms of the family, and may continue to eat beetle food as long as they live. Prods and toads probably eat water beetles whenever they have the chance to do so. The excreta of a medium sized snapping turtle contained five beetles, including two Cybister fimbriolatus (Say) and one Dytiscus hybridus (Aubé). The adults of D. marginalis are occasionally eaten by ducks, and Wilson cites data showing that the adult Dytiscidae, among other predacious water beetles, constitute a considerable part of the food of shoal-water ducks, wood ducks, the pintail, and both the green-winged and the blue-winged teal. The mallard takes both larvae and
adults of the family. The stomach of one stock contained 28 larval and 2 adult male Dytiscidae. Storks are known to eat such large beetles as \textit{D. marginalis}, and a little green heron (\textit{Butorides virescens L.}) had eaten one adult of \textit{Laccophilus marginalis} (Germ.), and other aquatic beetles.

Protection. The adults gain a measure of immunity or relief from hostile agencies by means of a trio of defensive devices. The body surface is normally covered with a thick film of unicellular hypodermal glands that makes the surface unwettable and not only facilitates their movement through the water but prevents the attachment of commensal algae and Protozoa that sometimes encumber the body. The secretion has been observed to tend almost entirely to adherence of such organisms on young beetles but is less effective on the rough elytra of certain females and entirely inoperative on old beetles.

The other two defensive measures operate to frighten or discourage enemies bent on attacking the beetles. \textit{Dytiscus marginalis} and \textit{B. latipes} L. are known to contain in their rectal ampulla a strong, rotten-smelling fluid that stinks like uric acid. Blunck (1923) frequently observed the beetles squirt this liquid out with great vehemence from the anus upon pursuing animals. Its loathsome odor infects the water and is displeasing to the pursuers, but seems to have no poisonous effect upon them. But the chief means of defense is the milky secretion from a pair of prothoracic glands that lie in a transverse position under the front edge of the pronotum and embedded in the fat body. Such glands were found in \textit{Dytiscus}, and the milky secretion is produced also from the prothorax of \textit{Cybister}, \textit{Agabus} and \textit{Actius}, and other Dytiscidae. The excretory pore of each gland opens when the beetle bends its head sharply ventrad, but the fluid is voided out with great vehemence from the anus upon pursuing animals. Its loathsome odor infects the water and is displeasing to the pursuers, but seems to have no poisonous effect upon them. But the chief means of defense is the milky secretion from a pair of prothoracic glands that lie in a transverse position under the front edge of the pronotum and embedded in the fat body. Such glands were found in \textit{Dytiscus}, and the milky secretion is produced also from the prothorax of \textit{Cybister}, \textit{Agabus} and \textit{Actius}, and other Dytiscidae. The excretory pore of each gland opens when the beetle bends its head sharply ventrad, but the fluid is voided out by the contraction of muscles pressing lightly upon the storage sacs of the glands. The fresh secretion in \textit{D. marginalis} has a strong aromatic and not unpleasant odor, but in \textit{Cybister} it possesses a more irritant agreeably mild and sweet smell. The secretion had a toxic effect on fish and various aquatic insects placed in water containing it, and also when injected into the veins or skin, or when introduced into the digestive tract of vertebrates. If applied to the ocular or oral membranes of Amphibia and salamanders, the parts turned red, and the gills of fish became covered with a thick mucus. In the final stages of its effect on frogs, fish and salamanders, the heart beats became slower and less intense, and in extreme cases the subject died from the toxic action. Considering that the secretion is produced when the beetle is stimulated by an enemy and that it rarely results in prolonged or permanent injury, it appears to serve mainly as a repellent or a means of frightening its pursuer.

\textbf{ACTIVITIES OF THE ADULT}

Adaptations for Locomotion. Excepting Wesenberg-Lund's suggestion that they developed from a Chrysomelid-like form, it is generally supposed that the Dytiscidae were derived from a terrestrial ancestor of the Carabid type. Various gradations between the swimming and running forms seem still to be retained in the family as it is known today. For example, when removed from water, \textit{Rheasus} is said to rise up on its feet and run like a ground beetle, but swims poorly, whereas \textit{Dytiscus} is an efficient swimmer but correspondingly awkward in locomotion on land. From such differences in locomotor efficiency it has been deduced by Needham and Williamson that increasing fitness for swimming in water is paralleled by increasing unfitness for travel on the ground. However, all the predacious diving beetles have departed to a remarkable extent from the type of body structure of the ground beetles. The loose, angular neck and waist constrictions, characteristic of many terrestrial beetles, have been displaced by rigid compactness and a stream-line form of body with its parts intimately joined, constituting a form that offers a minimum of resistance to the water, and makes twisting in the longitudinal axis of the body almost impossible. Propulsion is facilitated also by certain modifications in the structure of the legs. The first two pairs take little or no part in swimming, and lie withdrawn into concavities in the venter of the thorax. The middle legs serve only to anchor and to guide the beetle in its vertical motion, and have accordingly retained essentially the form of terrestrial legs. The coxae of the hind pair are expanded and fused firmly to the metasternum, and their more distal segments have been shortened and strengthened, and flattened in the horizontal plane. Swimming fringes on the inner edge of the tarsal boot extended during the backward or propelling stroke, thus greatly increasing the surface area, and on the forward stroke collapse against the tarsal segments, thereby reducing resistance to the water. The hind
legs articulate somewhat behind the middle of the body, and by virtue of their position and structure constitute the chief propelling mechanism. In swimming, the two legs operate in unison, and one-sided strokes are made by them only to steer the beetle laterally (Blunck, 16a).

The specific gravity of adult Dytiscidae is approximately that of water. When the bodily weight is considerably increased during meal-times, the specific gravity is kept nearly uniform by emptying the rectal ampulla. In Dytiscus latissimus and D. marginalis, this organ is therefore believed to play the role of ballest reservoir and the fluid to serve as a weight-compensating material. Also, should the beetle inspire an excessive volume of air, a portion of it escapes discharged before descent into the water by swimming is possible. By the same process of unloading air, the specific gravity of the beetle's body may be maintained for a time at 1, or equal to that of water, thus enabling the insects to hover midway under the surface without and/or sink themselves or engaging in swimming movements.

Flight. The terrestrial ancestry of the Dytiscidae is suggested by their ready interchange between life in water and in the air. The flights are necessitated by the drying up of bodies of water, by the absence or dwindling of their food supply, or the lack of suitable water plants or other cover that are essential to their activities. The presence of certain species in bodies of water in one year and their absence there in another year indicates a general movement of the beetle population, induced chiefly by the drying up of the habitat. Mass flights have been reported in Sweden and Germany (Wesenberg-Lund). The migration, whether in large or small numbers, occur mostly by day in spring and autumn, and at night in summer. On hot summer days, Wesenberg-Lund found numerous individuals of Acilius, Dytiscus, Hydius and Agabus resting on the grasses and peracaeans of the drying pools, waiting the night to seek new waters. When preparing to fly, they always first crawl out upon objects that rise above the water level, and appear incapable of going directly and promptly from water into an aerial flight. Unwettable owing to its oily surface, the body dries at once upon coming from the water, but ability to fly hinges upon a shift of the respiratory function from the aquatic to the terrestrial breathing mechanism, the process of change requiring several minutes. The beetle seems well-adapted that the Dytiscidae do not use the same part of the tracheal system, or use it in the same way, in aerial and in aquatic life. Wesenberg-Lund reports seeing the beetles at rest on plants above water spread their elytra and discharge the gas from the dorso-sternal chamber, and presumably also from the internal portion of the respiratory system. Dytiscus marginalis, observed by Blunck (16a), lightens its weight by emptying the fluid contents from the rectal ampulla through the anus. The tracheal system utilized during flight and consisting of large thoracic air sacs connected with the first pair of spiracles, remains collapsed and empty while the insect is in the water. The process of inspiration and inflation is prepared for flight coincident with a lively vibration of the whole body and accompanied by a rushing sound that gradually increases in volume and pitch. When thereby lightened and stocked with air, the beetle moves forward a few steps and lifts itself high on the mesothoracic legs so that the front pair hangs down. The wings are then unfolded suddenly and the beetle at once rises into the air. Only the hind wings propel the beetle during flight, the elytra serving only as supporting planes or gliders.

The tracheal system presumably undergoes a reversed process of preparation when the beetle suddenly returns from the aerial life to resume its aquatic existence. Wesenberg-Lund observed Dytiscidae in nature splashing directly into the water, the impact of their bodies carrying them through the surface film, but they rose again in a few seconds and then always lay for a few minutes breathing on the surface. The extreme modification of the legs for swimming probably disables them for use in alighting upon and quickly clinging to plants. The specific gravity of D. marginalis was increased by taking water into the body, and the legs became stiff. The beetle then rises over midway under the surface water, and discharge the gas from the dorso-sternal chamber, also ventrally called the air space, air reservoir and dorso-sternal chamber. The first two pairs of spiracles belong to the mesothorax and the metathorax, respectively (Korachell), and of the abdominal pairs the first and last are much the larger. The last pair opens at the apex of the abdomen, whereas the
remaining abdominal stigmata connect the dorsal chamber and the tracheae. The subelytral chamber is formed by the dorsal wall of the abdomen and the elytra lined on their inner surface by the wings. The size of the chamber varies considerably among the genera. In Hydroporus, Colymbetes and Hyphyes it is small, and largest in the Dytiscinae. The small size, where it occurs, is produced by the arching upward of the abdomen along the meson, leaving a small air space only in the region of the caudal segments, or in some species it consists only of two lateral canals in which lie the spiracles. The outer borders of the elytra fit like a watch lid into grooves at the edge of the abdominal arch and the elytra are joined at the suture by a device consisting of a fold and groove. The tips of the elytra and the heavily chitinized terga of the terminal abdominal segments fit closely upon each other, but may be separated to provide an aperture for use during respiration. The pygidial hairs, like the inner and outer surfaces of the elytra, are oiled by unicellular hypodermal glands, making them hydrophobic and preventing the entrance of water into the large caudal spiracles and the dorsal air chamber. The hind legs are likewise greasy and used to kick or rake air bubbles and water from the caudal parts (Wesenberg-Lund).

When in need of a fresh load of air, the beetle rises to the surface of the water. Owing largely, if not wholly, to the gases in the dorsal chamber, the beetle is lighter than water, and accordingly floats to the surface. In so doing it assumes the posture taken during the act of respiration at the surface, this being predetermined by reason of the fact that the center of gravity is located near the ventral or the anterior portion of the body. However, when the body is heavier than water, owing to a gravid state in the female or a large meal recently consumed, their weight may be reduced by emptying the rectal ampulla, or they may be compelled to exert their swimming legs. In such instances the beetle arrives at the surface head first, and must therefore turn and about to bring its cauda to the water level. In the final respiratory position (Fig. 18) the beetle comes to rest with the cephalic and ventral aspects facing downward, always hanging at an obtuse angle with the water level and the apex of the abdomen penetrating the surface film to the atmosphere. The tip of the abdomen and the claws of the two hind legs are the points of suspension and form an equilateral triangle.

Earlier writers state that the dorsal chamber contains fresh air inspired through the apical aperture at the water level, thereupon to be drawn into the tracheae through the abdominal spiracles during subaquatic respiration. Later workers, and particularly Ege, Brocher (1923) and van der Heyde, however, maintain that the beetle carries expired gases in its dorsal air chamber and, while hanging at the water’s surface, fills instead the whole tracheal system and particularly the large thoracic air sacs with fresh atmospheric air taken in through the hind pair of spiracles. Accordingly, the air for respiration under water is now said to be carried in the tracheae and not in the subelytral chamber as formerly claimed. Van der Heyde analyzed bubbles of air forced from the dorsal chamber immediately following the intake of air at the surface and again after the beetle was prevented for some time from coming up. The first specimen contained 14.01% O₂ and 85.34% N₂, whereas in the second the oxygen content had decreased to 3.05% and the nitrogen correspondingly increased to 96.31%. From this and similar experiments by Ege, it was deduced that the air in the dorsal chamber nevertheless possesses some respirational value, enabling the submerged beetle to inspire and expire from and into the dorsal space. When the beetle is submerged, the partly deoxygenated gas accumulated in the dorsal chamber renews, to some extent, its oxygen content from the surrounding water by virtue of the fact that the tension of the gas stored in the chamber is then lower than that of the oxygen in the water (Ege). Wesenberg-Lund and others observed submerged beetles extrude and again retract bubbles of gas through the apical aperture of the air chamber. While this performance has commonly been interpreted as having a hydrostatic function, this writer,
like van der Heyde, and Ego after him, suggested that the beetle thereby also in part renews its oxygen supply in the manner described. However, on account of being repeatedly inspired, and despite the partial renewals from the water, the subelytral air yields ever smaller returns of oxygen, and the insect must eventually ascend to the atmosphere. Van der Heyde and Brocher seem to have shown that the first act of the renewal process at the surface is therefore to expire the gases accumulated in the air chamber during the subsurface activity of the beetle. But that a portion of the used air may also be expelled in bubbles while the beetle is submerged has been observed repeatedly. When the stale gas is discharged at the surface, the beetle pumps fresh atmospheric air into its tracheae and tracheal air sacs by way of the pygidal spiracles. Not uncommonly, the beetle then takes in so much air that it becomes much lighter than water and is consequently unable to swim down until a part of it is again expelled.

Many of the Dytiscidae spend the winter as active adults in water under ice. How do they obtain their air, seeing that they can not reach the atmosphere? Wesenberg-Lund kept Dytiscus alive for six days under ice or entirely surrounded by it in aquaria of 150 to 500 ccm. capacity. Air may have come from two sources. At irregular and sometimes long intervals the beetles forced bubbles of air from the subelytral chamber. Its oxygen content may have been renewed by this contact with the water. Again, air bubbles forming in the water as its temperature rose on mornings, gathered on the body of the beetle and could have constituted an important supplementary source of air. But in aquaria planted with Ceratophyllids, numerous small air bubbles came from the vegetation in clear weather and gathered on the under side of the ice. Into these air masses the Dytiscus inserted the tips of their abdomens and visibly reduced the size of the silver bubbles during their stay. Considering that in nature the habitats of Dytiscidae are characterized by rich vegetative growth, it is probable that most of the oxygen used by them in the winter is derived from plants in this manner.

The frequency of a beetle's visits to the surface to renew its oxygen supply is said by Blunck (18a) and Benick to be in proportion to the temperature and the activity of the beetle. Benick also recognizes that the frequency of the returns to the surface may depend on the amount of the activities and food of the beetle. In consequence of vigorous swimming incident to the mating act or other strenuous exercise, the oxygen taken in is quickly used up, and the insect reappears sooner at the surface to breathe. But beetles that descend only to rest by clinging to plants at the bottom are able to remain down a correspondingly longer interval. When at rest the beetles seem disposed to bring bubbles of their air in play with the water, renewing the oxygen content by osmosis. Thus, during work periods, the intervals between surface respirations are noticeably shorter than are those during rest periods. The duration of the intervals of rest between appearances at the surface increased also in ratio to the extent to which the beetle is deprived of food. Individuals subsisting on their reserves of fatty tissue spent longer periods at rest than when they had been allowed to feed after a period of hungering.

Sharp made observations on eight species of Dytiscidae in aquaria to determine the frequency and duration of their returns to exchange gases at the water's surface. The range of the duration of their stay at the surface is indicated herewith in seconds: Oxyiniptilus clypealis Sp., 1-15; Hyphodrurus ovatus L., 1-28; Hydropsus pictus P., 3 seconds; Noterus Clavicornis Dej., 1-20; Laccophilus obscurus Pena., 1-610; Agabus bipustulatus L., an average of 41.6 seconds; Actius salinus L., an average of 12.25, and both sexes of Dytiscus marginalis required approximately 55 seconds to perform the exchange. The maximum and rather exceptional duration was 210 seconds or 3.5 minutes, whereas the stay at the surface generally lasted less than one minute. The average period of time in minutes which the first seven species above spent in submergence was 53, 14.17, 30.66, 10.6, 6.66, 13.23, and 2.75. The males of B. marginalis averaged 8.3 minutes under water whereas the females appeared at the surface every 12.12 minutes, on the whole. These records serve to suggest that Dytiscidae devote a comparatively small part of their time to the exchange of gases at the surface.

Food and Feeding. Dytiscus marginalis can see its prospective prey only when the latter is very near. The senses of small and taste, which are virtually identical in water, determine the edibility of animals seized. B. marginalis and B. octectes sticticus L. of India (Nowrojee, 12)
grasp their food with the first and second pairs of legs and press it against the mouthparts (Fig. 19). At times, D. marginalis overreaches to the extent that it cannot float normally to the surface to respire but must crawl up on vegetation, or may reduce its weight by emptying the rectal ampulla or, that failing to give the necessary reduction, vomits a part of the meal, sometimes doing so 4 or 5 times at short intervals. For example, a female D. lattissimus, having a specific gravity of 1.00 to 1.03 and weighing 4.6 g., before feeding, ate for 48 minutes at a frog and then weighed only 4.2 g. The weight of the food ingested was offset by frequently eliminating the contents of the rectal ampulla (Blunck, 1923). Some species display a preference for the water's surface while feeding, assuming the same posture taken during respiration. The adult Dytiscidae do not digest their food properly but chew or tear off solid bits to be swallowed as such. In D. marginalis a dark brown to olive green midintestinal secretion flows forward into the crop where preliminary digestion is said to take place, and several hours after feeding emit orally a dark fluid containing chitin, bone and other indigestible remnants of its meal.

Dytiscus marginalis, D. semisulcatus Mull. and D. dimidiat us Bergstr., sometimes consumed decaying flesh, including that of their own species, but the adults of the family generally show a preference for living animal tissue. The list of food animals includes most of the creatures that share the beetle's habitat and are small enough to be overcome. The species of Dytiscus commonly devour tadpoles, but also earthworms, small frogs and fish and the nymphs of Odonata, Ephemeroptera, and aquatic Hemiptera. Wilson provides the following food records for five American species: Coptotomus Interrogatus (Parker) and Cybister Flamboyalus ate the nymphs of dragonflies, the latter also consuming the nymphs of mayflies, Corixa, Notonecta and Benacus; Asellus Semisulcatus Aubé fed on the nymphs of Anisoptera and Zygoptera, Ephemerida, Notonecta and Belostoma and the larvae of Hydrophilid beetles; whereas the small Hydrophilus piger Say was seen eating only the pupae of Chironomus, and D. verticillatus Say took tadpoles. In one instance quoted by this writer, the latter killed and devoured seven large eggs of Dytiscus marginalis in one afternoon. The Dytiscid beetles are of little economic importance in fish culture. D. marginalis may destroy much fry or attack very slow and weakened fish, but swift swimmers escape them. Wilson found large Dytiscus and Cybister in the fishponds at Fairport, Iowa, but they were never seen attacking fish fry although they had repeated opportunities to do so.

Mating. The procedure in the mating of the Dytiscidae has been described especially for Dytiscus marginalis (Blunck, 1913) and more briefly for several others of the larger and better known species. In some groups the males have the tarsi remarkably modified for adhering to the bodies of their mates while engaged in copulation and to other surfaces during locomotion or rest. These special adaptations are present on the members of the tribes Colymbetini, Dytiscini and Cybisterini, to which most of the more common species belong. In many of the Dytiscini the middle tarsi are also dilated (Blatchley, '10). The exact composition of the acetabulum varies among the species (Figs. 20 - 22) but its structure is probably basically similar to that described by Törne (112) for Dytiscus lattissimus and D. marginalis (Fig. 20). In these the first three segments of the front and middle tarsi are strongly dilated forming a broad sole and an arched upper surface. The whole organ of each tarsus is margined with a circle of strong, pointed and somewhat curved cuticular bristles. The sole, or ventral surface, is covered with stalked chitinous cupules and sucker disks which together function as a unit to hold the beetle to slippery surfaces. The first segment of the fore legs bears several dozen small cupules and in addition a very large one located laterally and a second, about half as large as the first, situated at the middle. The second and third segments are provided with small suckers only, which, however, are present in large numbers. According to Blunck (12a), the front and middle tarsi of the male of D. marginalis are equipped with a total of...
Writers disagree regarding the exact manner in which the acetabulum functions in adhering to the substratum. Blunck ([16a]) believes that a vaseline-like secretion, presumably arising from the well-known unicellular hypodermal glands of these beetles, aids the sucker disks in adhering to smooth bodies. Wilson ([23]) likewise speaks of a peculiar viscid fluid secreted by glands inside the tarsus and carried by the hollow stalk or pedicel to the disk of the sucker whenever the latter is pressed against any surface. The fluid spreading over the surface of the disk is said to afford secure attachment for the beetle. Trump, however, after careful anatomical studies, maintains that such a secretion has no necessary part in relation to adhesion. None of the hypodermal glands are said to open out upon the disks themselves but in a circle around the base of the stalks, these being structurally similar to the glands that occur widely distributed elsewhere in the body wall. Furthermore, he found that dismembered front legs kept for six months in alcohol and therefore presumably freed of whatever adhesive secretions might have been present, lifted objects weighing 10 to 11 grams or as much as can be held by a tarsus newly removed from a living beetle. He concludes therefrom that no glandular secretion is needed to enable the disks to hold fast and that they function entirely by the elasticity of the chitin. As soon as the edge of the disk comes in contact with the support, the arched middle is pressed down by the beetle, thereby forcing a large part of the water out from under the disk. When the pressure is removed the disk again tends to resume its original cuplike shape owing to its elasticity. Then, for the reason that the water can not readily flow back under the disks from the outside, a lower pressure exists under the disks than outside, and consequently the cuplet adheres to the surface. The hairy fringes bordering the acetabulum and the two larger cuplets are believed to aid in preventing the return of water under the several units after these have been applied to the support. The disk-bearing tarsi are released from the substratum by pulling the disks off one row after the other, beginning at the base of the tarsus and progressing distad.

Dytiscus marginalis in aquaria was unable to perceive its mate at a distance of more than one-half a meter, and can see scarcely 15 to 20 centimeters. Blunck ([12]) found that as long as the beetles are 20 to 30 cm. apart they may be kept in the same aquarium for days during the mating season without discovering each other. Sounds which these beetles are known to make play no role in the attraction of the sexes for mating. From all his observations this writer came to believe in the existence of a sex odor which directs the male to his mate. But actual mating may be long postponed even after the female is discovered. The indisposed female seeks for hours at a time to escape the pursuing male, both beetles dashing and tumbling wildly and aimlessly through the water. Throughout, the male tries by shaking motions of his body, by drumming noises and
by striking her head with his antennae and mouthparts to reconcile the female to his advances. Having seized her with his legs she may still continue her struggles to free herself, and not always unsuccessfully, necessitating a repetition of the long arduous pursuit. Eventually, perhaps after hours or a day of such delays, interspersed with pauses for change of position and respiration at the water's surface, the pair assumes the copulatory posture. Now the male holds the female with both his front and middle tarsi, anchoring himself to her by means of the tarsal suckers. The front pair becomes pressed against the sides of the pronotum and the mid-tarsi attach to the posterior third of the elytra, with the claws of both pairs embracing the edges of her body. The hind legs always remain free and may be directed far forward and arched upward but for the most part are carried almost horizontally over the back of the female. The female holds her legs drawn up close to the body with the hind pair often bowed forward and upward. Similar postures are assumed also by Dytiscus semisulcatus, D. dimidiatus, Coleoptera fusca L. and Agabus undulatus Soln.

During copulation, D. marginalis is seized by a characteristic rigidity of body and remains motionless for minutes at a time. The pair now hangs almost perpendicularly from the water's surface. Soon after the sexes have united, the male very slowly again withdraws the aedeagus from the vagina and simultaneously produces a bright white fluid cement that hardens upon exposure to the air and eventually flows also over the outside of the end of the abdomen of the female where it dries and may adhere for months after copulation. Concurrently the male slowly delivers the mass of sperms contained in a pouch or spermatophore, that is more or less enveloped by the cement, and forces it partly into the vagina. The spermatophore delivered, the male employs the copulatory organ and the parameres for one-half to one hour to press the cement upon the eighth sternite of the female from behind and below to close the vagina. Wesenberg-Lund (15) commonly found the vagina in the females of the species of Dytiscus corked shut with the cement from fall to winter. Accordingly, pairing cannot be repeated until this stopper is removed, but defecation and respiration are said not to be hindered by it. Thus held by the plug of cement, the spermatophore breaks at the anterior end soon after copulation is completed. Contractions of the abdomen of the female upon the sperm sac force its contents anteriorly into the vagina, and by further pumping movements of the latter the sperms are pushed forward into the bursa copulatrix. The more or less emptied sperm sac is then ejected from the vagina by dilatations of the abdomen aided by the swimming legs of the female, according to Blunck. However, the presence of the stopper of cement during the winter season, as seen by Wesenberg-Lund, indicates that the depleted spermatophore may sometimes not be discharged from the vagina promptly after copulation.

While engaged in the preliminary struggles and the copulatory phase of the mating process, the female may be unable to acquire air as frequently as necessary. After at most 20 hours of such deprivation she is no longer capable of swimming or reaching the surface. In such instances the male, still adhering to his mate in the copulatory posture, ascending to the surface to breathe, lifts his weakened mate up with him and thereby enables her to reach the revivifying air. By a few jerking movements to the right and left, the male pulls the tarsal suckers from the female, and the act of mating is finally finished. The process varies in time from a few hours to two or three days. The pairs mating in the fall remain together longer than those that mate in the spring. In D. marginalis one pairing is said to be adequate to insure the fertilization of all the eggs of a female. Polygamy is believed to be somewhat normal in nature, the female accepting a male again should the sperms derived from the first copulation be insufficient, owing to the long life of the adults of this species. The instance of one male that copulated fourteen times with two females in five and one-half months suggests with what vigor the males are possessed. They retain
their sexual potency into the second year of their adult life despite several copulations, and individuals deliberately kept from mating in the first or second year are said to be capable of inseminating the females in the third or even the fourth year. On the other hand, polyandry, or the mating of several males with one female in close succession, seems unlikely, considering that the large store of sperms received in the first copulation probably fills the spermatheca and perhaps indisposes the female to further matings immediately. The cork of cement that is known sometimes to persist for months in the vagina appears to constitute a further factor in preventing the practice of polyandry.

Oviposition. The Dytiscidae observed by Wesenberg-Lund (13) laid their eggs (1) in heaps outside of water, (2) on vegetation floating at the water's surface and (3) in living plant tissue (Fig. 23). These distinct habits appear to be correlated with structural modifications in the ovipositors (Boving, '13).

Acllius sulcatus, which has a long flexible finger-shaped ovipositor, always placed its eggs loosely, usually 30 to 50 in a mass above water among grass roots, in moist soil, under loose bark of fallen branches or trunks of trees in water, under the edges of protruding stones and among semi-wet mats of moss lying along the shore of pools or rising above the water's surface (Wesenberg-Lund; Blunck, '13). In general, the genera which place their eggs on plant surfaces or at most insert them halfway into such tissues are provided with a short vulvar apparatus, and the genital valves are sensory. Polybates fusus arranged its eggs contiguously in rows of 30 or less, like pearls on a string, on the surfaces of the leaves of Ranunculus Phragmites and Hymenia. Some species of Agabus and Bnetus stick their eggs to plant surfaces and others insert them among the new unfolding leaves of Hymenia or sink them deep into the plant. A. undulatus preferred the axils of the leaves of Elodea canadensis for its eggs (Blunck, '13). The eggs of Hydroporus (Dorovites) depressus Fabr. and A. latericeps Falk. are fastened singly to the surfaces of plants, on green algae in the instance of latericeps, by a sticky jelly mass which swells in water and dissolves gradually during the period of incubation (Falkenström, '33). However, the majority of Dytiscidae, so far as their oviposition habits are known, are endophytic, inserting their eggs into parts of living plants by means of cutting ovipositors. Judging by the structure of the ovipositors and also in part from observations, the endophytic species belong to Dyticus, Hydaticus, Graphoderes, Hybila, Agabus, Coptotomus, Cyplanter, Thermonectus, and probably also Leccophilus and Noterus. The formation of the ovipositor suggests that Acllius semisulcatus is endophytic (Wilson), whereas A. sulcatus was found to lay its eggs free in masses. The yellowish-white curved eggs of Dyticus semi sulcatus, D. dimidiatus and D. marginalis are laid singly in such very different parts and kinds of plants as the sheaths of Glyceria spectabilis, the stems of Iris and Typha and the air-filled leaf petioles of Alisma plattagum (Wesenberg-Lund). These species of Dyticus usually make egg pockets in a row composed of 8 to 12 scars one over the other (Fig. 23.C). Ten to twelve eggs were frequently found in one Iris leaf, each bulging the leaf where it lay, but 30 to 40 commonly occur in a single leaf petiole of Alisma. Blunck (16a) adds Sagittarius, Acorus, Potamogeton and Scirpus lacustris to the list of oviposition plants used by D. marginalis. D. leptopous Gyll. chose the leaf sheaths of water grass (Glyceria) planted in the tubs used by Balfour-Browne (15) for observing this species. The parts of plants selected were invariably submerged, living, vertical and strong to afford these heavy beetles a firm support. The eggs may, however, be raised above the water level by the rapid growth of the host plants after oviposition, and such do not complete their development or were almost always

parasitized by Hymenoptera in Denmark. The oviposition holes of *Hydaticus iniger* Deg. and *H. transversalis* Pontopp. were made in rows in Alisma, each puncture receiving not one but apparently many eggs. The eggs of *Graphoderes bilineatus* Deg., laid in the hollow flower stems of *Hottonia palustris*, were arranged in pockets around the holes that were not slit-like as in *Pytiscus*, but appeared to be chewed out with the mandibles. Strangely, this species also placed its eggs in heaps of 40 to 50 in the periphery of the egg cocoons of *Hydropsyche*. The larvae of *H. iniger* invariably hatched first, and as is their habit remained in the cocoons as long as a day thereafter, but never harmed the eggs of the inquilinous *Graphoderes* (Weisenberg-Lund). Larvae of *Agabus* were reared from the leaves of *Hypnum* and the stems of *Ranunculus*, the latter carrying numerous oviposition scars, and some of the eggs extended into the lumen of the stem. Fifty eggs were often found in the walls of a single branch. *Ilybius fennestratus* F. placed her eggs in the stems of *Potamogeton natans*, and *Coptotomus interrogatus*, *Cybister fimbriolatus* and *Tenthmonectes basilaris* (Harr.) deposit eggs singly in the submerged parts of plants. *C. interrogatus* exhibits no preference for host plants, *C. fimbriolatus* makes slits in the stems of rushes, cat-tails, arrowhead and others and *T. basilaris* used the stems of crex grass, rushes and other vegetation. Extensive injury is sometimes done to water plants in Denmark through endophytic oviposition directly, causing shore vegetation to wilt during May, and the scars often become entrance points for the spores of *Phycomycetes* and *Mucoraceae*.

The process of oviposition among endophytic beetles has been described especially for *Agabus undulatus* (Blunck, '13) and *Pytiscus marginalis* (Blunck, 13a; Korshelt, '23). The procedure in the two species differs only in minor respects. Several days before they proceed to oviposit, the gravid females of *D. marginalis* display a noticeable unrest, engaging in constant motion and lurching slowly through the water. From time to time they let themselves down upon the petioles and leaves of plants and while creeping about on them, sense their surfaces vigorously with antennae and palpi. Having located a suitable place, the female comes to rest with her body parallel upon the stem, embracing the latter with the front and middle legs and extending the hind pair backward and parallel with the sides of the body (Fig. 24). The mandibles are often thrust into the plant tissue during these activities, and sometimes the beetle changes her position several times before eggs are actually deposited. As a rule the ovipositor is sunk entirely into the inside of the plant after a few sliding-cutting movements of the valves. The beetle then remains still for about 10 minutes while the egg passes into the incision accompanied by a clear sticky fluid from the vagina.

The ovipositor is then withdrawn, the slit closes, and the beetle may rise or descend a few steps on the stem to deposit another egg in the same manner. The ovaries are composed on the average of 100 ovarioles in a *Pytiscus* studied by Needham and Betten ('01), and Blunck ('13a) recorded a total of production of 11 to 13 eggs, making a total capacity of 1100 to 1300 eggs in the average beetle. Blunck ('13a) observed no sharply defined periodicity in the egg laying of *D. marginalis*, owing to the irregular maturing of eggs in the several ovarioles. One female deposited as diverse a number as 2 to 30 eggs per day, although on most days the variation moved between 7 and 16. The largest number actually laid by one beetle was 203 in 14 days, or an average of 14.5 eggs per day. It is estimated that this species has the potential ability of producing as many as 1000 eggs, with an average of 1000, in the lifetime of a normal individual female.

Incubation and Hatching. The incubation period was about 6 days in *Hydropsyche depressus* and 6 to 7 in the instances of *H. lateralis*. Eggs hatched in 9 days at 28°C, in 11 days at 20°C, in 14 days at 6°C, at 13°C, in 40 days at 8°C, and development is probably at a standstill at 4 to 6°C (Blunck, 16b). This investigator ('14) further observed that in a period of rise of temperature from 7°C to 13°C, the duration of development corresponding decreased from 6 weeks to 10 days. Eggs laid in February and March required 4 to 6 weeks or more to hatch, and in the instance of those laid in
April to June the developmental period decreased to 14 days. Next to temperature, the time required for embryonic growth depends on the length of the plant containing the eggs. It appears that the development of the embryo is favored by their assimilation of the oxygen set free by the plant. It is believed to be only an indirect factor in embryonic development in so far as it may slow up or increase the release of the plant oxygen that is utilized by the eggs of the beetle. This influence may be especially significant for eggs deposited in plant tissue that carries much oxygen, notably Alnus.

Just before hatching, the movements of the embryo of D. marginalis become more lively and energetic than before. The abdomen alternately contracts and dilates, and the head is thrust forward toward the cephalic pole of the egg. Situated on either side of the meson of the vertex is a pair of egg-teeth or egg-bursters. Wesenberg-Lund ('13) reports these hatching spines also for Colymbetes fuscescens, D. semisulcatus and D. dimidiatus. Balfour-Browne found them on the heads of D. punctispinosus and D. cognatus present also in Cybister lateralis, and the bursters are small, pointed and strongly chitinized, and are said by Wesenberg-Lund to fall off later. During the movements of the embryo, they are pressed against the vitelline membrane to tear it, and by the same process the chorion is also soon rent. By pushing and swaying, the larva wriggles upward out of the shell and the oviposition puncture is closed. After standing almost parallel with the plant stem for a moment, the legs are freed. The whole hatching process in D. marginalis, the maintenance of this position up to the time of the splitting of the old cuticle seems to be a necessary preliminary to successful molting. Molting occurs mostly during daylight, a fact probably to be explained by the higher temperatures prevailing by day and resulting accelerated development. A complete defecation seems to precede molting in Dytiscus, and the rectal ampulla also is empty during this act. The larva which otherwise has the form of an interrogation point now becomes straightened. The prothorax bulges abnormally, and the contractions and expansions of the body cause the old cuticle to break along the dorsal meson and the soft-bodied larva works its way to the surface. Just before hatching, the movements vary between several weeks and some months, depending mainly on the season in which the larvae live and the amount of food they obtain. In the first instar the acceleration in the rate of growth is

ACTIVITIES OF THE LARVA

Growth. As in the Cicindelidae and the Carabidae, the larval stage of the Dytiscidae consists of three instars. This has been observed in several species of Dytiscus, Cybister lateralis, Colymbetes fuscescens and Hydroporus. The molts take place while the larva hangs head downward at the surface where they are suspended by a pair of hairy caudal appendages or cerci that lie on the water without breaking the surface tension. In D. marginalis, the maintenance of this position up to the time of the splitting of the old cuticle seems to be a necessary preliminary to successful molting. Molting occurs mostly during daylight, a fact probably to be explained by the higher temperatures prevailing by day and resulting accelerated development. A complete defecation seems to precede molting in Dytiscus, and the rectal ampulla also is empty during this act. The larva which otherwise has the form of an interrogation point now becomes straightened. The prothorax bulges abnormally, and the contractions and expansions of the body cause the old cuticle to break along the dorsal meson and the soft-bodied larva works its way to the surface. Just before hatching, the movements vary between several weeks and some months, depending mainly on the season in which the larvae live and the amount of food they obtain. In the first instar the acceleration in the rate of growth is
very distinct between 11 and 15°C, its duration shortening from about 6 weeks to 9 days. However, when the temperature was raised to 19°C, the acceleration was not correspondingly increased, and duration of the instar being shortened only to 6 days. The optimum heat zone lies somewhere about 27°C, and a persistent temperature of 35°C proved fatal to the small larvae. The second instar developed most quickly in 4 days at 20°C, and most slowly in 14 to 18 days at 13.6°C. The critical low temperature begins at 0.6°C, and larvae held for a long time at +0°C can not be brought to the next molt despite plenty of food. Of 13 species, third instar larvae reared to the pupal stage, one developed in the minimum period of 3.5 to 14 days in an optimum temperature of 18°C, and the longest larval growth was made in 35 days at 14°C. The critical low temperature zone for the third instar begins at 9.6°C, but the larvae are still able to swim at +0°C and to crawl at +0.6°C. In all the instars, 0° is the border between the critical and the fatal cold zones. The larval stage as a whole lasted 6 weeks at 14°C, 4 weeks at 17°C and 3 weeks at 20°C. The reduction of its duration to 2 weeks can be affected only with difficulty, and it is thought that if maintained at 10°C, the larvae would probably require 10 to 14 weeks for their growth. The larval period of Dytiscus circumcinctus Ahr. is passed in about the same period required by D. marginalis, but D. semimaculatus, whose larvae alternate, appears somewhat better fitted to growth in lower temperatures. The total duration of its larval life was 18 weeks at 6°C, 10 weeks at 8°C, 8 weeks at 10°C, 26 days at 12°C, 18 days at 14°C and 16 days at 22°C. In Gylbyaster lateralemarginalis the total larval stage was passed in 48 to 47 days in the summer at Naumburg. The first instar required 2 weeks, the second 12 to 22 days, and the third 16 days to 3 weeks (Blunck, '22). In the instance of Hydroporus depressus, the duration of the three instars was approximately 6, 7 and 9 days respectively, and in H. latensens they averaged 6, 8, 7.3 and 10 days. This stage was regarded as ended when the mature larvae left the water (Falkenstrom).

Regeneration. Blunck ('09) experimented in cutting off the legs, antennae, maxillae and cerci of the larvae of Dytiscus marginalis to determine their capacity to regenerate. The wound thus made persisted until the molt following the operation, when it healed, but the several kinds of appendages varied some-

what in the degree to which they were regrown. The greatest ability to regenerate seems to be inherent in the cerci which reproduce the lost tips and grow new bristles on the larval body and itself. The legs and antennae showed approximately equal capacity to grow out again, and neither can be fully regenerated during the larval stage, but were found to be fully formed when the pupal stage is reached. When the front legs of the first instar larvae were amputated in individuals that developed to males, the acetabula of the adult attained their normal size, form and complexity of structure. But when the operation was made on a second instar larva, the cupules of the adhesive organ were not only smaller in size but their number was reduced from 150, the number normally present on the average beetle, to 60. It seems certain, however, that a lost maxilla can never be completely regenerated, perhaps on account of its highly complicated structure. In general, it is deduced that the lost parts are regenerated more fully in size and form in the first instar larvae than in larvae of the second stadium.

Locomotion. Despite their general similarity in structure, the larvae of this family are not all adapted to the same type of swimming. Of 13 species, those overcompensated or heavier than water and the forms that are undercompensated or lighter than water. It is to be recognized, however, that the place of any one species in the classification may vary from time to time owing to circumstances attending its growth and the volume of food and air taken. From the viewpoint of specific gravity, the larvae of Dytiscidae form an evolutionary series from burrowing and creeping through swimming to suspending forms. Those of the first, or overcompensated, class remain in burrows in the bottom as is believed to be the habit of Noterus larvae, or are able to reach the surface only by creeping or swimming. The known creepers are species of Agabus, Colymbetes, Hydroporus, and Hyphydrus. Wilson specifically names Hydroporus niger as a crawler, while the Danish Colymbetes fuscus sinks and can come up only by climbing. The larvae of Hyphydrus paranid Ser., of India, were observed by Nowrojee (112) to run up the sides of drums as a way of reaching the surface. Thus, the creepers are sluggish, living chiefly on floating vegetation, are poorly equipped for swimming, reach the atmosphere mainly by crawling and for most part can not hang from the surface except by resting their
feet on a support. Among those that come to the surface chiefly by swimming are certain species of Agabus, Ilybius, Rhan­tus, Laccophilus, Loptotomus, Thermonec­
and Gybister. Jumping and snapping the body as a means of locomotion supple­ments swimming in a few known species. Jumping and snapping. Wilson notes how A. semi sulcatus may sud­denly flex its body at the first abdomi­nal segment, and by rapidly straightening it out again, throws itself several in­ches. The larvae of Thermonectes, and notably, may, likewise, snap their bodies a distance of 8 or 10 inches when disturbed at the surface of the water.

The second class of Dytiscid larvae, characterized as undercompensated, or lighter than water, can, under some con­ditions, or regularly, reach the surface without engaging in swimming motions and must often hold to plants with their tar­sal claws to remain submerged. Here be­long, so far as known, the larvae of cer­tain Dytiscus, Hydaticus, Graphoderes and Acilius. A. semisulcatus, for example, can come to the surface simply by letting go its hold on submerged plants. However, the presence of well developed swimming fringes on D. hybridus and Acilius sp. (Needham and Williamson) indicates that the flotation method is not the only way in which this class of larvae move to higher levels. Again, Brocher (13) points out that Dytiscus may travel to the surface to breathe by crawling, swimming or floating, depending on vari­ations in its specific gravity.

Respiration. The mechanism and the process of respiration in the larva are much more simple but not less effi­cient than in the adult, the chief dif­ferences being in the absence of wings and large air sacs within the larva. The system of respiratory organs present in the majority of these larvae is prob­ably merely a modification from the type obtaining in related terrestrial forms such as the Carabidae in particular. Ac­cording to the works of Alt (12) on the third instar of Dytiscus marginalis and Mukerji (30) on Cybister confusus Sharp and C. limbatus Fabr. of India, the tra­cheal system of the Dytiscid larva con­sists of ten pairs of spiracles and one main pair of breathing tubes with simple branches leading to the lateral spiracles. The first pair of stigmata is situated on the mesothorax and the second on the metathorax, while the other pairs are arranged on the eight segments of the ab­domen. Mukerji found all the spiracles to be similar in structure excepting those of the mesothorax and the last ab­dominal segment, but the statements of other writers on this point make an excep­tion only of the latter pair, whose mem­bers are differentiated by their larger size, terminal position and their function­al connection with the breathing tubes (Fig. 25). In Cybister, both the meso­thoracic and terminal pairs lack the strainer hairs that project into the lumina of the other spiracles. In the first instar of D. marginalis all the spiracles are said by Blunck (16b) to remain closed, but Korschelt and others state that the caudal spiracles are open and used also in the first instar. In the second instar of this species, all except the large caudal stigmata remain shut, and not until the larva approaches maturity in the third sta­dium and is about to return to a short spell of terrestrial larval life preceding puation, do all the pairs open and become functional. For this reason, Alt selected the third instar for his study of the anatomy of the respiratory system. It has been noted, moreover, that the whole se­ries of spiracles reopen for a short while during each larval molt, after which they again close promptly. The places where the spiracles of the third instar will ap­pear are marked in the earlier instars by very thin chitinous threads that connect the cuticula at these points with the lon­gitudinal tracheal branches (Korschelt).

Fig. 25

The internal phase of the respira­tory system consists primarily of a pair of large longitudinal tracheae that extend forward into the head and open function­ally to the outside only at the caudal spi­racles with which they are continuous. Their truly tracheal character in D. mar­ginalis is indicated by the presence of a

41
lining of spiral chitinous threads throughout. The longitudinal tracheae are not connected by air sacs as in the adult but by a series of small dorsal commissures that probably have little importance for the storage of air.

So far as known, most species rise to the surface at intervals to renew their air supply. Considering that the air is admitted into the tracheae only through the pair of large terminal spiracles, the larva obviously must bring the apex of the abdomen to the surface and with it penetrate the water film to reach the atmosphere (Fig. 26). When the larva of Cybister lateralimarginalis approaches the surface, the telescopically extensible terminal spiracles are alternately everted and retracted until the anal pole reaches the surface, when the larva comes to rest. The undercompensated forms naturally float with the abdomen lifted higher than the rest of the body. But some of their heavier relatives, such as Eunectes sticticus and Cybister fimbriolatus and Acilius sulcatus ascend with the head first and when they reach the atmosphere, if not while still below, change their position to bring the body parallel with, or to hang at an oblique angle to, the surface. While the lighter species need only to turn their cerci down upon the water's surface in order to be suspended, the heavier forms supplement this means of support by resting their anterior legs on submerged plants. However, the larvae also commonly take a position in which the base of the head, the prothorax and the last abdominal segment rest against the surface film, with the center of the body arched down.

However, some species are not obliged to come to the atmosphere to change their air supply. Larvae travel in some apparently of vital significance, according to Blunck (23b), not only in the first instar larva of Dyticus marginalis, all of whose spiracles are said by him to be closed, but also in the larvae of the smaller and to some extent the medium-sized Dytiscidae. Wesenberg-Lund ('13) learned that the larvae of Lythrus and Gyrinus can live in aquaria at least 3 weeks without access to the atmosphere and, seeing that the venters of these larvae are extraordinarily transparent and leave a network of tracheae visible through the cuticle, believed that they may breathe through the ventral skin. Wilson, likewise, found that the larvae of Hydroporus Niger never come to the surface, neither do they possess gills as do the larvae of Coptotomus Interrogatus. The latter remain continually beneath the surface and take air from the water by means of the lateral gills (Fig. 27) that trail inertly along the sides of the body when the larva swims.

Precisely what takes place first when the larva now comes to rest at the surface has not been ascertained. Deoxygenated air must obviously be given off before new air may be inspired if it may be assumed that such gases accumulate in the tracheae while the larva respire under water. Mukerji kept his Cybister larvae from breathing at the surface 'by placing closely woven wire netting just below the water level. Under these conditions, chains of air bubbles streamed out at intervals from the mesothoracic as well as the caudal spiracles. The gases were generally liberated in this manner after the larva had engaged in vigorous muscular exertion. The fact that the mesothoracic spiracles never are brought above the water level even in normal respiration at the surface, strongly suggests that gases are normally expired directly.
into the water through them, and that the caudal pair may, therefore, also serve in part for expiration while the larva remains submerged. The absence of large storage chambers, such as the adult has under its elytra and within the tracheae, seems to preclude the accumulation of large quantities of gases to be liberated exclusively into the atmosphere. If this be the case, a large percent of the gas is perhaps given out piecemeal at intervals under water. Little has been recorded concerning the frequency of the visits made by the larvae to the surface.

From his experiment, Mukerji observed further that the maximum limit of time the larvae can live without acquiring more air at the surface is four hours. Blunck ('23b) similarly confined the larvae of Dytiscus marginalis under water to learn the effect of different temperatures on its endurance without surface breathing. When the intensity of respiration was reduced by a previous starvation period of several days, the larvae died within 16 hours with the water temperature maintained at 21 to 22°C. Individuals treated the same way but kept at 20°C can with certainty not survive longer than one week. The intensity of respiration was therefore at least 6 times greater at the higher temperatures. Laccophilus maculatus (Fig. 26) was able to remain submerged an hour or longer after a new load of air was taken (Wilson). No evidence has been presented that indicates an ability in the larvae to renew their air supply in part or in whole directly from the water.

Food and Feeding Habits. In the larva of Dytiscus marginalis, the mandibles (Fig. 29) are the main feeding organs and have become distinctly modified for penetrating the prey and removing its liquified contents. Each mandible is falcate, curves sharply mesad and tapers to a strong pointed tip. Along the inner margin of each runs a canal that arises sub-apically and continues to the base where it connects with the oral cavity. The canal is not entirely closed to the outside, its outer borders being produced into ridges that approach but do not meet each other. Each ridge, however, bears numerous fine bristles which serve to close the mandibular canal against the exterior and confine the liquids that pass through it. The mouth is closed except temporarily during the molts, and the mandibles have accordingly assumed the entire func-
The larvae of the Dytiscidae are as a whole shortsighted. Blunck (122) points out that those of Cybister lateralis marginalis do not notice resting prey when it is only 2 to 3 cm. away, and slow-moving aquatic insects attracted attention only as far as 6 cm. away. While some species, even despite their agility, generally lie in wait to snap up or pounce upon their food animals that chance to pass nearby, others actively go in pursuit of their prey. However, the precise mode of procedure doubtlessly varies even within a species, depending on the existing circumstances. For example, the larvae of Acilius sulcatus have been observed to hurtle themselves suddenly upon their prey but may also lurk near the surface and simply snap their head and thorax up to seize by the venter the insects that pass by above. But others, so far as observed, seem regularly to enter upon a hunt to chase and thus capture their food. Such is the method employed by the larvae of Colymbetes tuscus and Eusimicus, which lurk above and dash down suddenly into the midst of their prey, or run over the bottom to find and chase it. But the larvae of Dytiscus marginalis and Cybister lateralimarginalis seem regularly to capture their food only when it comes very near to them or actually within their grasp. Its prey detected, Cybister opens its jaws and creeps cautiously forward until the antennae and palpi touch the intended victim. After palping it a while, the larva surround the prey with its mandibles. The larva then elevates its abdomen, brings it down again in a moment, and at the same time vigorously drives the mandibles into the captive. The larva similarly awaits the approach of its prey, then, lashing the abdomen, eats its jaws into the surprised victim. Not until then does the larva pass upon the edibility of its captive, but grasps at any moving thing not too large. Even when larger than the predator, the prey quickly weakens in most cases, yet sometimes first drags its persistent foe through the water.

Fig. 29
Larval mandible of Dytiscus marginalis showing canal along inner margin. After Korshelt (23), Bearbeitung Einheimischer Tiere, Wilhelm Engelmann, Leipzig. Redrawn by Mrs. W. V. Balduin.

Fig. 30

The study of a variety of Pristidae led Blunck (16b) to assert that proral di-
gestion occurs in all larvae of this family, but Wesenberg-Lund (13) states that the mandibles of Noterus grassicorrona M"ull. and N. clavicorrona Dep. are robust and grooved, and appear to lack canals, while they chew their prey and swallow it in small pieces, and moreover believed that Asillus sulcatus may feed in the same way. Nevertheless, most of the Dytiscid larvae that have been observed probably predigest their food externally in essentially the way already described for some of the Carabidae. Evidences of preoral digestion in the Dytiscid larvae are the tong-like canaliculate mandibles, the closed mouth, the ease and promptness with which relatively large and powerful prey is overcome and killed, and their ability to remove all but chitinous parts through small punctures made by their mandibles in the cuticles of their prey. When the prey is seized in the jaws, the larva at once squirts a brown fluid from its digestive tract through the mandibular canals into the captive. The first effect of the fluid is to stupefy and kill the prey, and secondly, it soon reduces the soluble internal parts of the prey to a liquid state. The tissues of vertebrate victims is said, however, to be incompletely soluble by this secretion (Blunck, 23b). During the process of imbuing the liquified food, the larva occasionally pauses to readjust its mandibles and injects more of the solvent fluid. All the cuticles and other chitinous parts of the invertebrate prey may be consumed. Direct and structural evidences indicate that preintestinal digestion probably occurs in Dyticus dimidiatus, B. semisulcatus, D. marginalis, D. legophorus, D. latissimus, D. verticallis, Eunectes sticticus, Cybister laterallimarginalis, C. tripunctatus Oliv., C. fimbriolatus, Copitomus interruptus, Laccophilus maculosus, L. proximus Say, Theremnetes basiliscus, L. ornaticollis and Hyphodus remani. In the last species the tips of the mandibles rest against the sides of the end of a stout median cephalic process.

In the selection of food the larvae are generally governed more by their ability to catch and overcome than by any special tastes for definite types of prey. The variety of food accepted and the amount required to rear the young of a given species is well illustrated in the studies of Blunck (22), on Cybister laterallimarginalis. A single larva of the first instar ate one small caddis worm, 6 nymphs of Leptes and several pill bugs; in its second stadium it required 24 Lestes nymphs and in the third it can be reared on a dozen large nymphs of Aeschna. In general, the first instar larvae accepted the nymphs of Lestes, Apteron, Notonecta and Cordia and the younger larvae of Hydaticus and Rhanthus. In the second instar, they ate the smaller Aeschna nymphs, adults of Notonecta and other aquatic bugs, larger caddisworms and the larvae of smaller water beetles. The food of the last instar comprised especially the more advanced nymphs of Aeschna, but also the larger young and adults of Notonecta and Naucoris and the mature larvae of Stratiomya, Zebania, Stilbia and Trichoptera.

So far as known, a great variety of food is taken also by the larvae of the family as a whole. The first food of the newly hatched larvae of Dyticus marginalis Blunck is the remnant of yolk stored in its mid-intestine. Later they were observed to eat earthworms, leeches, larvae and adults of the great majority of water insects, water spiders, snails, fish, frogs, salamanders and their own kind. But no kind of food is reported taken so consistently by the common species of Dyticus as pollen wags or tadpoles, particularly of Bufo and Rana. While their smaller instars fare best on smaller and less active prey, the larger individuals display an increased aggressiveness as well as greater strength. The larvae of D. b. sullucatus (Blunck, 16), and particularly of D. semisulcatus (Blunck, 18), appear exceptional in that they seem to confine themselves to caddis worms, but are known to have taken also snails in captivity. A sizable body of food records for a number of other genera includes almost all the small aquatic animals. In the statements given herewith, the name of the Dytiscid larva is followed by that of its food animal: Cybister tripunctatus larvae, shrimp; C. fimbriolatus, tadpoles, fish; nymphs of Ephemerida and Odonata, larvae of water beetles including those of Dytiscus and Hydrous triangularis (Wilson); Asillus sulcatus, Daphnia, Ostracoda and especially Cypris viridis; A. semisulcatus, small snails; Colembetes tarsalis, Ostracoda, Culex larvae; Rhanthus, Dipterous larvae; lybius fenestratus, probably Ephemerid nymphs; Hydaticus, Daphnia, nymphs of Ephemerida and Zygoptera; Agabus, Dipterous larvae and small plankton Crustacea; Copitomus interruptus, Chironomid and beetle larvae, but prefer small Ephemerid and Zygopterous nymphs; Hydroporus nigricornis, larvae of Chironomus, Bosipharma, Synthorax, Corethra, Proxystria and Palpomyia; B. lateremara, Cledocera and Copoidea in the first instar, but later eat Chironomid and other
Dipterous larvae (Falkenstrom); Laccophillus maculosus and L. proximus ate larvae of Dixa, Corethra, Ceratopogon, Haigius, Peltodytes and Hydrocorus; Thermoriectes basilaris, nymphs of Notonecta and ~ stoma, and strongly preferred the larvae of Tropisternus; ~ ornaticollis, Copepoda, Entomostraca, Ephemerid nymphs and larvae of Tropisternus. Neither do most Dytiscid larvae spare their relatives or others of their own kind, but these are attacked usually only after the supply of other food has been exhausted. Strict cannibalism has been reported in several species of Dytiscus, Hydaticus, Eunectes, in all instars of Cybister lateralmarginalis, and in S. limbriciatus, Soplotomus, and Laccophillus.

The most noteworthy studies dealing with food in its relation to the factors affecting the growth and duration of the larval stage were made by Blunck ('23b) on Dytiscus marginalis and D. semi sulcatus. In a series of 26 newly hatched larvae of D. marginalis, one took food when 15 hours old, 19 first fed at the age of 24 hours, 5 in 2 days after hatching and one fasted 3 days. A third instar larva ate a polliwog 6 hours after molting and two larvae of D. semisulcatus ate polliwogs 18 and 27 hours, respectively, after shedding their skins. Full grown marginalis larvae ceased feeding one to several days before leaving water to pupate. To determine the amount of food required to complete the larval stage, Blunck fed the larvae of D. semi sulcatus exclusively on caddis worms. The results given represent the average amounts used. The first instar ate 0.38 gr. and its weight increased from 0.03 gr. at the time of hatching to 0.09 gr. at maturity. The total consumed by larvae of the second instar ranged from 0.45 to 1.68 gr. per individual, the majority ranging between 1.0 and 1.6 grams of food. The minimum food requirements of third instar larvae was 2.4 gr., the maximum 9, and the average 7 to 10 gr., and their weights increased from 0.42 gr. immediately after the molts to 1.2 to 1.3 gr. when full grown. The quantities of food eaten by the three instars were in the ratio of 1: 3:10, as compared with 1:13:185 in the related D. marginalis, and the total food needed per individual for the whole larval stage was 8.5 to 10.00 grms. Similar studies show that 25 larvae of D. marginalis required for their complete development an average of 300 to 400 tadpoles 16 to 20 mm. long. The minimum number of tadpoles needed was 150 and the maximum 800 to 900 per larva of different sizes.

The effect of temperature on the amount of food required to bring the larval stage and its instars to maturity was determined for the same species. The larvae of D. marginalis could not be brought to feed at temperatures below +6° C. In an environment of 14°, the first instar larvae daily ate at most 3 tadpoles 16 mm. long, and the instar lasted about 18 days. At 14°, the consumption rose to 4 tadpoles per day; at 18° they required 5 to 6 daily, and at 20° they used 6 to 7. In the last instance, development was completed in 3 days. Between 24° and 27° C, they ate a maximum of 8 to 10 tadpoles per day, and it is thought that the duration of this instar can not be reduced substantially below 3 days. Above 27°, the appetite of the larvae falls off quickly, and they do not feed at 32° C, but the temperature does not become dangerous until it goes above 35°.

TABLE I

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</table>
On the other hand, the first instar larva of D. semisulcatus, and the second as well, still take food just above the freezing point of water, but only when the temperature rises over 23 to 27°C. At higher degrees, above 32°C, marginalis was no longer seen to feed, and semisulcatus took no food when the water became warmer than 30°C.

Economic Importance and Control. It is well known that the larvae of several large Dytiscidae are destructive to fish fry and other small fish in ponds and hatcheries. Their long-like mandibles and the supposedly poisonous intestines of the new larvae, cast to the pond, enable them to overcome fish considerably larger than themselves. The larvae are, for these reasons, more harmful than the adult beetles. Many instances of such losses are recorded, and Blunck ('16a) and Wilson report special studies of the larvae in their relation to fish culture. Blunck calculates that no less than 100 of the progeny of an average female of Dytiscus marginalis develop into mature larvae. He states that a single third instar larva easily kills 10 fish, 3 cm. long, per day in warm seasons, and accordingly has the potential ability to destroy 140 such fish in the 14 days required for that instar. On this basis and on the assumption that no other kind of food is taken, the third instar progeny of an average female marginalis can therefore destroy as many as 14,000 fish. Contrast this with the theoretical considerations of Wilson. This investigator learned that the larvae of Dytiscus and Cobister, and those of the Hydrophilid beetle, Hydrophilus triangularis, destroy small fish under normal conditions in fish ponds. Ordinarily they are kept in check by their enemies, but under especially favorable conditions breed in sufficient numbers to kill the newly hatched fish fry about as fast as it appears. It is only young fish of the year that are seriously menaced by them. Fish a year old are able to escape them and in turn have begun to eat freely both larvae and adults of these beetles.

Because only three species of beetles are really dangerous, while fifty are eminently desirable as food for fish, chemical means of control are out of the question in fish ponds. Blunck makes the interesting proposal that oviposition may be prevented by leaving the pool dry to the end of May, or if this is impossible, keep the host plants of the beetle out of the pool in the spring months. These include especially Iris, Sagittaria and Potamogeton. Considering that the destructive species are most frequent at bright lights, trap lanterns will capture many adults if used by the middle or the last of May before the beetles begin to breed. But the fish culturist wants a remedy that may be applied with sufficient celerity to save the remainder of the batch when once the beetles have begun their ravages, since ordinarily there is no necessity for preventive measures. The only method of removing the beetles quickly is to drain the pond, while the fry is kept in a tank or put in an adjacent pond. This method is preferred to the destruction of the pupae of both harmful and beneficial species by raising the water level of the pond 8 to 12 inches. The original pond can then be stocked with larger fish that will use the beetles for food (Wilson).

Hibernation and Aestivation. So far as known, the Dytiscidae spend the winter either in the adult or the larval stage, but rarely in both. The studies of Wesenberg-Lund ('13) provided most of the present data on this subject. The larger number of the observed species winter as newly developed adults in Sweden. Such are Dytiscus semisulcatus, D. dimidiat us, D. marginalis, Euphractus crassipes, Colymbetesfuscus, Hydaticus seminiger, Graphoderes bilineatus, Agilius sulcatus, Noterus crassicornis and A. clavicornis. Balfour-Browne ('13) found that D. lapponicus winters as an imago in England, and D. marginalis in Germany (Blunck, '16a) hibernates in this stage as it does in Sweden.

The most definite information at hand indicates that they occupy the same general situations in winter that they inhabit in the fall. While skating early in winter, Wesenberg-Lund saw the above Dytiscus species through thin ice and was convinced that they are able to hibernate in an active state under the ice in nature. Similarly, Euphractus, Colymbetes and Agilius are reported definitely to pass the winter
season in water under ice in northern Europe. D. lapponicus disappeared in October and November by burrowing deep into the soft oozy mud at the bottom of the pools or ponds. The species that remain in water are somewhat active in subzero weather, and occasionally rise to the under surface of the ice to get oxygen that accumulates there from pond plants. The small larvae, species on the other hand, appear to undergo a true dormancy during this season.

When small shallow pools dry up during the summer, some beetles migrate to new waters while others appear to enter the desiccating bottom mud of their habitats there to undergo a period of aestivation. The beetles return to active life in the fall when heavy rains again fill the pools. The species of Agabus are believed to pass the summer in this way in Sweden, and while D. marginalis migrates to new waters when the original habitats dry, other species, (Blunck, '16a).

The occurrence of the larvae of D. lapponicus in April suggests that they may hibernate in this stage also. Records indicate that the species of Illyius winter chiefly as larvae, and those of I. fenestratus are found full grown under ice in pools. Apparently most Rhantus and Agabus, and particularly A. rugosipennis Payk., A. guttatus Payk., and A. calcaratus Fons. winter as larvae. Wesenberg-Lund believed that some larvae of the latter two genera which may winter in small pools that freeze to the bottom, doubtlessly become frozen in solid ice and yet survive. The only species of Dytiscus known to hibernate in this stage in Germany is semisulcatus. Blunck ('23b) has determined that the temperature at which its larval development stops is about 4°C for the first instar, 5.50°C for the second and approximately 6.80°C for the last instar. Death, which follows when the temperature goes below 0.00°C, is caused by the freezing of water in the alimentary canal and the resultant tearing of its tissues.

PUPATION

It is probable that the larvae of all the Dytiscidae remain in the water from a few hours to one or more days after they are full-fed. At this time, the larva of D. marginalis still occasionally snags at prey but lets it go soon, looks around for another, swims back and forth much, has difficulty in reaching the respiratory position at the surface, where they remain but briefly, and display other evidences of uneasiness. So far as known, without exception in the family, the mature larvae then leave their aquatic habitat to prepare a pupal cell on land. The place selected for pupation is usually very near the water’s margin, but the larvae of D. marginalis, D. fenestratus and D. septentrionalis may travel the surprisingly long distance of 40 meters from the water (Wesenberg-Lund). They were in transit mainly in the morning when the grass was wet with dew, or on rainy days. These species dig their pupal cells especially in mole hills, under boards, fallen tree trunks, stones or directly in the mud or turf of the shore. Matheson ('14) found the pupae of Hydroporus septentrionalis Gyll. under stones on a dried river bottom. The larvae of Rhantus atlanticus, Rhynchosoma redandi and Hydroporus semicinctus Ker., burrow into the mud by the water (Nowrojee), while those of Cybister lateralis may run into the mud. Wesenberg-Lund believed that some larvae then leave their aquatio habitat to prepare a pupal cell on land. The place selected for pupation is usually very near the water’s margin. As soon as the larvae of Coptotomus interrogatus leaves the water its spiracles begin to function and the gills dry up and are usually broken off by the time pupation begins. In the majority, where no gills occur, the transition from water to land involves the opening of the lateral thoracic and abdominal spiracles to the functional condition.

The mode of constructing the pupal chambers has been described more or less completely by Matheson, Blunck ('16b, '22), Balfour-Browne, Wilson and others. In most instances, the procedure is essentially like that in Dytiscus marginalis (Blunck). Beginning on the exposed surface or under cover the larva lifts itself up on the end of its legs, bends the head sharply ventrad, and with its mandibles under the thorax digs out a pellet of soil the size of a pea. The larva of Cybister interausitus fashions the particle of mud into a sphere between the mandibles and the labium (Wilson). The pellet is laid aside as the first unit of the cell wall, and others are promptly formed in the same way and arranged in a continuous circular row around the larva. On this as a foundation the larva gradually builds a wall, arching it overhead into a
dome and eventually closing itself completely in. By excavating soil from the bottom of the enclosure, the larva forms a hemispherical pit, which, with the arched dome above, constitutes a spherical pupal chamber. Then the larva polishes and compacts firmly the inner wall by rubbing and striking its body against the surface, as is done also by Hydroporus (Falkenström). A rather distinct mode of construction seems to occur in Agabus bidipustulatus (Blunck, '21) (Fig. 31).

![Fig. 31](image)

Four steps in the formation of the cell of Agabus dipustulatus. Modified from Blunck ('21), Entomolog. Blätter, Berlin.

When its wall is well begun, construction on one side is discontinued while the other is produced into a canopy overhanging the interior cavity of the cell. The soil so used is removed not only from within the chamber but also from under the wall externally, the latter excavation eventually cutting the cell entirely free from its original support. But to enclose itself in the cell, the larva works exclusively on the inside toward the completion or the structure.

The larva of D. marginalis builds the pupal case in at most a few hours, but some finish them in less time and others require as much as a day. That of marginalis lies at a depth of 11 to 15 cm. in the ground, and other species burrow 0.75 inch to 3 or 4 inches deep in the course of cell construction. The chambers of different species are said to vary in size from that of a pea to the dimensions of an apple (Blunck, '23b). The mature larva of Cylindera limniaticus is 76 mm. long and the outside of its cell measures 35 by 30 by 25 mm., while that of Thermonectes ornaticollis has dimensions of only 14 by 16 mm. The cases of D. marginalis, A. bidipustulatus, Hydroporus depressus and H. latens are spherical, but those of C. limniaticus and T. ornaticollis have an oval shape, and H. septentrionalis (Gyll.) makes a somewhat pyriform cell (Fig. 32).

![Fig. 32](image)

Fig. 32

Nest pupal cell of Hydroporus septentrionalis. After Matheson (179), Canadian Entomologist. Redrawn by Mrs. W. V. Maltour.

The larvae of Hydroporus depressus and H. latens completed their pupal cells in 1 to 2 days and preparation required 5 to 6 days. In Dytiscus marginalis, the prephase or prepupal state of transformation mostly lasted 9 to 10 days, and the anaphase of actual process of change of the newly issued pupa to the mature adult condition usually required 10 to 15 days, although a few spent 20 days to more than a half year in this phase. The intermediate step, or mesophase, embracing the period immediately preceding and during the shedding of the larval skin, is obviously relatively brief. After the transformation, the new beetle remained in the cell on the average of one week, but only 3 days at 21°C, and considerably longer at lower temperatures. From the time of burrowing in to make the pupal cell, to the emergence of the young adult, required on the average of five weeks in July and August, but several months were needed earlier in the year. The minimum duration of the three phases is 2 weeks, probably commonly reached during a temperature of about 27°C. At 20°C, it required about 3 weeks; at 15°C, 5 weeks; at 10°C, 8 weeks; at 5°C, it lasted one-half year, and development almost stops at 4°C. But in Laecophilus maculosus, Eunectes sticticus, Hyphydrus renardi and Hypophorus apertus the process of transformation from the date of entrance into the soil to the fully formed adult required only 6 to 8 days in a number of instances. While in the pupal phase proper, the insect may be found lying on its back, venter or side. When the larva of Thermonectes basilaris is changing to the pupa it is on its back on the bottom of
the chamber, and then rests there for 24 hours. It next reverses its position and rests upon the long styli on the pronotum and the cerci at the apex of the abdomen with its dorsum uppermost and the body strongly arched (Wilson). The pupae of Hydronurus depressus are held up off the floor of the cell by bristles on the dorsum of the thorax and abdomen (Falkenström). Different species have been observed in the several postures, and it appears that no particular posture is maintained and that no regular sequence of changes in pose may characterize the pupae. When the adult stage has been reached, the insect lies at rest from one day to about one week to permit the cuticula to harden. The cell wall is then broken, probably by biting, scratching and bodily force, and the beetle emerges to enter the water promptly.

THE LIFE CYCLE

According to data for the most-studied species of Dytiscidae of the north temperate zone, one generation develops in a year. The cycles, however, are of two distinct types with reference to the distribution of the stages in the seasons. In the first class, the larvae hibernate and in the second the winter is passed by the adults. For most of the information concerning seasonal development we are indebted to Wesenberg-Lund. The first group embraces Agabus, Rhabitus, Ilybius and Dytiscus semisulcatus. These complete their larval growth during March, April and May, pupate on the whole in or about May and the new adults are at hand during May to August. In the latter period, mating and oviposition occur, and small larvae become plentiful in August and September, and make more or less of their growth before the hibernating season comes upon them. Hypophorus aper and Hyphydrus renardi, of India, appear to undergo their metamorphoses in the winter season, the larvae and pupae of H. aper being common during December to February, and the larvae of H. renardi entered the mud to pupate early in the latter month. Representatives of the second class, in which the winter is spent by the adults, include the larger number of species. All of the species of Dyticus that have been studied, excepting D. semisulcatus above, and Cylbister laterimalmarginellus, Hyphydrus ovatus, Cylbistes fuscus, Acilius sulcatus and Graphodera bilineata, mostly oviposit in April, but D. marginalis begins at the end of February, as soon as or even before the ice is melted, reaches the peak of oviposition a month later, then declines and becomes rare in July. This species, and perhaps others, continues in the autumn, but also in the spring, and probably for this reason is enabled to begin its reproduction so early in the new year. But Hydaticus and Acilius deposit their eggs in the spring and mainly in May. The larvae of the several species then appear in maximum numbers within the period of latter April to the last of July. The larval stage is mostly passed in a relatively short time, and their rapid development appears advantageous considering that the pools not infrequently dry up in late summer. By this time, most of the larvae have left the pools to pupate, and for most part reach the adult state sometime between July and October or November. The new adults of C. fuscus were already plentiful about July 1, but because the pools dried up in late May nothing was seen of them again until November when the fall rains refilled their habitats. They are thought to survive the winter season by boring into the damp mud in the bottoms from which the rains may bring them in autumn. The new adults of Dyticus that find water in the summer engage in feeding, but delay even their mating activities from June or July, when they become adults, to October or November.

But although an annual cycle may be the rule, the individual adults of some of the larger species are known not infrequently to live and reproduce for two successive years or more. Of three adult Cylbister laterimalmarginellus caught in the fall at Berlin, the male lived 1.5 years, and the two females died after 3.25 and 3.5 years, respectively. Other writers report a duration of life of 2, 4, and 5.5 years for this beetle (Blunck, ’22). Insofar as they are not overcome by diseases, accidents or serious enemies, both sexes of D. marginalis reach an age of 1 to 2 years, and an occasional individual may live 2.6 years, and such as are kept under unusually favorable conditions can complete the third year. Sexual vigor in general declines after the second mating season, but a few remain potent a third year. The females live somewhat longer than the males.
ACTIVITIES OF THE ADULT

Habitat and Gregariousness. The adult Gyrinidae are familiar to almost everyone for their gyrating mode of locomotion and their way of gathering in schools on the surfaces of quiet or slowly flowing water. They are generally found not far removed from vegetation, and usually resort to the shaded banks on bright hot days. Hatch ('25) infers from materials studied by him that the adults form two ecological groups. Enhydrus, Dineutes, Androgyrus, Macrogus, Aulonogyrus and Gyrinus, which constitute the first group, are thought to inhabit standing water, whereas Porrhorhynchus, Orectochilus and certain Dineutes appear to be stream-inhabitants. According to Ochs ('26) the running water forms are characterized by their larger size, extremely attenuated body, anteriorly produced upper lip and the possession of a rudder. The congregations of whirligig beetles are mostly seen in the latter part of the summer and in the fall, and so far as known, are composed of newly developed beetles. The same beetles occur singly or at most in small groups when they emerge from hibernation in the spring. The schools sometimes may embrace representatives of two species or even two genera. Hatch describes cases in which scattered individuals of Gyrinus mixed with a swarm of Dineutes, and also a mixture of P. nigritor Rbts. and P. horni Rbts.

Protection and Locomotion. Persons who have handled whirligig beetles know the somewhat displeasing odor that emanates from them. It is presumably derived from the milky fluid given off from the coriæ, especially those in the region of the prothorax. This odor, while commonly interpreted as protective, does not shield its possessors entirely against fish and probably other predatory aquatic animals.

While swimming on the surface is their chief mode of locomotion, the Gyrinidae also easily dive down into the water and readily take flight. According to Wilson and Bott, neither Gyrinus nor Dineutes is able to fly directly from the surface but take off from the edge of the aquarium or some plant or other object that rises above the water. The gyrating motion of the whole body, with extended eyes and legs, and the schools of whirligigs is not their normal means of progression, but a reaction to a visual stimulus, as the movement of a person on the bank, or actual, as the agitation of the water or contact with an unfamiliar object. The stragglers around the edge of a swarm are the first to become alarmed, dash off and collide with others in the school, which in turn collide with still others, and in a few seconds the whole mass is in a condition of panic. When alarmed, the individuals swim only a few feet, then dive and cling for a few moments to some submerged object, whereabouts on the surface the swarm then reassemble again (Hatch). Only the thoracic legs remain of use in crawling but they function also for anchoring the beetle while submerged, for seizing and holding other objects, for grasping the female during copulation and for steering in swimming, and are carried in grooves on the venter of the thorax when not in use. The external anatomy of these beetles is chiefly a remarkable set of adaptations for surface locomotion. These are fully described by Hatch and Bott. The modifications have resulted in (1) increased bodily rigidity achieved by the compression lengthwise of the body and the rigid union of the several regions, (2) short flat powerful swimming legs (Fig. 33) on the mesothorax and the metathorax, (3) eyes divided along the water line, the ventral or water portions having a considerably greater area than the dorsal aerial parts, (4) a complex sensory Johnston's organ in the pedicel of the antenna, and (5) a streamline form of body.

In thinking of their streamline body, due consideration must be given to the fact that their dorsal half moves in air whereas the ventral portion occupies a medium of much greater density and that accordingly offers more resistance to the body during locomotion. Therefore, if the body form of the Gyrinidae is in fact nicely adapted for movement in its two-fold environment, the upper and the lower portions should possess adaptive structures as different from each other as are the two media through which they pass. The adaptive differences of the Gyrinidae appear to be depicted in the two principles stated by Bott. First, the form of the body which offers least resistance to the air is strongly rounded off in front, reaches its greatest diameter in the anterior third, and from that point tapers off the hind extremity. On the other hand, the resistance of the water to
a submerged body decreases in proportion to the acuteness of the part that noses into it. Furthermore, being bilaterally symmetrical, whether viewed from above or from below, the bodies of whirligig beetles do not affect the direction of the air and water currents. The currents therefore follow the contour of the body surfaces and flow together again at the posterior end of the insect without setting up retarding whirlpools, but may perhaps even exert a noteworthy forward push on the body. The streamlined Gyrinid body in general is characterized by a continuous outline uninterrupted by acute retarding indentations at the junctures of its parts, and lacks prominent vestiture and sculpture. These features, combined with their unwettable surface and the swimming legs capable of turning the narrow edge to the water in the forward stroke, keep the friction between the beetle and the air and water at a minimum.

Two factors appear to account for the ability of whirligig beetles to float on the water. Owing to their dorsal air chamber they are lighter than water, and seeing that they make a depression on the surface, they are obviously carried in part by the surface tension. However, their swimming legs penetrate the surface film as does also the deepest portion of the venter, as shown by the absence of a film at that point (Hatch). Being thus constantly and normally in part submerged, facilitates the act of penetrating bodily through the surface film when these beetles dive. They not only swim under water commonly and of their own volition, but are able to do so dexterously, and can remain submerged for a considerable period of time as is required by their habit of ovipositing on submerged plant materials.

When descending, they carry a supply of air with them in a definite air space under the elytra (Bott, Hatch, Wilson). The structural modifications for air storage and respiration consist of three major features. First, the lateral margins of the mesothorax, the metathorax and the anterior abdominal segments are fused, and raised into a longitudinal ridge. The latter fits into a groove along the edge of the elytra, which, in turn, are interlocked along the median suture by a tongue and groove device. Second, opposite the junction of the mesothorax and metathorax is a rounded peg just inside the edge of each elytron, which fits into a socket in the thorax and holds the elytron securely in place. Third, the air enters the dorsal reservoir through a groove just inside the posterior end of the lateral margin of each elytron (Wilson). From this supply the submerged beetles are said to derive their oxygen through the spiracles that lie on the upper side of the abdomen and within the reservoir. Owing to the load of air taken down with them, the beetles are lighter than water and are therefore obliged to cling with their front legs to solid objects to remain under. While submerged, a part of the air constantly appears in view in the form of a small silvery bubble above the apex of the abdomen at the entrance of the air chamber. Held in place by the vestiture of the last abdominal segment, the bubble buoys the beetle which therefore always swims with the posterior end elevated above the level of the head. When ready to return to the surface, the beetle lets go of the anchoring support and rises up passively without swimming (Bott).

The Johnston's Organ. It has been

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Fig. 33
observed that Gyrinidae do not collide against the sides of the aquarium when swimming on the surface in an undisturbed manner whether in light or in darkness, but bump forcibly into the same when moving below the water's surface. Eggers ('26, '27) experimented with Gyrinus marinus Gyll. to determine what organ is the seat of this ability to avoid obstruction in normal surface swimming. He fastened a very thin glass plate crosswise in various positions near the middle of the aquarium. When the plate was so placed that its lower edge stood at the water surface but not in contact with it, and there was a good number of air cushion set up against the glass. However, with the glass lowered into the water far enough to form a meniscus, the beetle swimming toward the glass turned around before bumping it and frequently did so while still several centimeters away. From these and similar experiments, Eggers concluded first that the ability to deviate from an obstruction is not centered in the sense of sight or the detection of an air cushion set up against the glass wall by the approach of the beetle. The study suggests, rather, that waves reflected by the walls or very thin layers of dust on the surface, but especially the concave meniscus border, aid in avoiding the obstacles. The perception of waves on the sides of a rapid stream is about ascribed to the Johnston's organ borne in the greatly enlarged boot-shaped pedicel of the antennae. Considering that its lower surface is flat and lies on the top of the water, this organ was logically supposed to detect the elevation of the surface at the meniscus and as a result stimulates the beetle to change its course to deviate from the obstruction lying ahead.

Food and Feeding. Although commonly looked upon as predacious, the adult whirligig beetles must rather be described as scavengers. No species has been reported to be cannibalistic in the adult stage. The mandibles are large and strong, but blunt, and approach the herbivorous type more closely than the carnivorous (Wilson). While Miall reports Gyrinus to have eaten some vegetation, all the D. natator substriatus Stal. observed by Bott died in the absence of animal food, with which he was able to keep them alive longer than a year. Almost all the available rearing records indicate that small freshly killed or disabled animals were offered and accepted as food. Bott pursued pieces of earthworms on a darning needle whose ends were then stuck into cork to float the food at the water level. Batch induced Dineutes to eat bits of raw beef, and Wilson reports that they never injure or attack young fish. According to Smith ('26), there are few things that D. americanus Say would not attempt to eat, the only requirement seeming to be that it float, and accepted such a varied diet as live meally bugs, bits of salmon and sardines, meat, apple parings, bread and cracker crumbs, chocolate and many others. The prepared fish food known as "ant eggs" composed mainly of ant pupae made a good food, and fish food was most probably mayflies or similar insects which spend their life over water and fall in accidentally or after their death. They have not been observed to catch and eat living insects occurring in water, and feeding is said to take place only at the surface. D. americanus always used its front legs to hold and turn the food about. What seems to be a typical instance of conduct among the common species at mealtime is aptly described by Wilson in the case of D. americanus in one of the fishponds. "As many would seize the insect as could crowd around it, grasping it with their mandibles. Then they swam off, sometimes going fairly straight away, sometimes whirling around in wild curves and sometimes diving beneath the surface, but always holding on to their prey and tearing out mouthfuls of the insect tissues. When one bit off more than he could swallow at once, he would hurry away with it, pursued by a hungry crowd, each intent on snatching it from him, and he was lucky if he could keep it long enough to finish devouring it."

Copulation, Oviposition, Incubation. Without previous evidence of a tendency to mate, the male of Dineutes americanus makes a dash for the female, and if successful holds her back with his fore tarsi at the juncture of the thorax and eIytra (Smith). The male of Gyrinus natator substriatus possesses an adhesive organ on the anterior tarsi used in clinging to the eIytra of the female (Bott). The middle and hind legs of D.
hormi and D. nigrior are not employed in copulation. Hatch inclined to the belief that the sperms are passed to the female in a spermatophore. Copulation in G. natator lasted at most one minute, and in D. americanus up to nine minutes, but other statements from the literature indicate that the pairs of these genera may sometimes remain united for an entire day. While sexual unions usually take place on the water's surface, Creoctenchilus villosus Mull. is said by Regimbart (Hatch) to come to shore for this act, and G. natator substriatus is sometimes in copulo while under water (Wesenberg-Lund, '13).

So far as known, Gyrinidae habitually deposit their eggs superficially on the surfaces of submerged parts of dead or living plants. When observed by Bott, G. natator substriatus preferred pine needles lying under water for oviposition, but was formerly reported to place them also on living plants or root fibers. Dinutes hormi and D. nigrior selected living plants, sometimes depositing them a few inches below the surface of the water on emergent vegetation. The eggs are laid in rows or in clusters. Wilson found the elongate ellipsoidal eggs of D. americanus in masses of 7 to 40 in number on the under side of the leaves of Potamogeton folioliensis in a fishpond, and arranged diagonally at an angle of 45° with the midrib of the leaf. Each egg of this mass was glued separately to the leaf by a transparent colorless cement, which extends along the whole length of the egg. Those of D. nigrior and D. hormi were arranged end to end, and from 20 to 50 were usually laid by one individual. During oviposition, the female of Gyrinus natator substriatus moves forward slowly on the plant according to the rate at which eggs are extruded, and thus there results a chain of eggs. Often she turns around after a while and lays a second series beside the first. The maximum number at a place was 15, the small numbers being probably traceable to interruptions owing to the need of returning to the atmosphere for air before all the ripe eggs could be deposited, and upon resuming oviposition she starts at a different place.

The known time required for incubation among various species ranges between 5 to 17 days. The eggs of G. natator substriatus hatched in about 14-17 days, and those of Dinutes hormi incubated in 9-15 days, D. nigrior in 11-15 days, and the eggs of D. Discolor Aube reached the hatching stage in 16-17 days (Hatch). The larvae of D. americanus all hatch at about the same time, five or six days after the eggs are laid, and crawl around on the surface of the leaf amongst the empty egg shells for several hours before swimming away (Wilson).

### ACTIVITIES OF THE LARVA

**Habitat; Respiration; Locomotion.**

The larvae (Fig. 34) lead a hidden life on or among dead or living plants, or at the bottom in the water not far from shore.

![Fig. 34](image)

Larva of Dinutes americanus, dorsal view. After Wilson (28), U. S. Bur. Fishes. Redrawn by Mrs. W. V. Halvorsen. Having tracheal gills, they derive all their air directly from the water and are independent of the surface. The thorax bears no gills, but ten abdominal pairs are reported for Gyrinus and Dinutes by Bott, Hatch and Wilson. They are bristle-like and feathery in structure, a trachea extending into and fading out in each toward the apex of the gill (Bott). The first two pairs of the first instar of D. americanus are plumose like the rest, but...
bare on the older larvae. The abdomen of this species maintains a constant trembling motion up and down, which is evidently its mode of breathing. The larvae of Gyrinus are said to breathe and swim in the same manner as Dineutes. The latter swims with a sinuous motion up and down after the manner of a flatworm. The legs have no swimming fringes, but the eight posterior pairs of lateral gills are heavily fringed and serve for locomotion as well as for breathing. By lashing them up and down the larva can move either forward or backward with great rapidity. It can also jump quite a distance by snapping its body by a sudden contraction of the longitudinal muscles of the abdominal segments (Wilson).

Food and Feeding. According to Bott, Hatch and Wilson, the larval mandibles of Dineutes and Gyrinus are slender, curved and acute at the apex (Fig. 35). A tube that opens through a slit near the tip perforates each mandible lengthwise and fits the larvae to suck out their prey in the manner of Dytiscidae, although a pre-oral mode of digestion has not been claimed for the Gyrinidae. These larvae, being provided with typically carnivorous mouth parts, appear therefore to be strictly predacious on living animals despite the statement by Miall that Gyrinus will eat the tender parts of submerged plants when animal food fails.

Fig. 35

The larvae of Gyrinus have been reported by Needham to feed upon the body fluids of bloodworms and other small prey (Wilson), and those of G. natator substratitus use as food the other small animals that share its habitat. Under somewhat abnormal conditions, Dineutes have been known to kill and eat small fish. While D. americanus larvae preferred the nymphs of damselflies and mayflies and the larvae of Chironomus and Corethra, they catch anything that is unfortunate enough to crawl against them. R. Horn and J. Vanin reported by Hatch with small Tubificid worms, and removed all the internal parts, leaving only the transparent cuticula. The newly hatched larvae of these species are said to run about like caterpillars over the leaves, holding their mandibles wide open to snap hold of anything that comes their way. Cannibalism exists especially among the larvae of the larger members of the family and was present to a marked degree in the species observed by Hatch.

THE PUPAL CASE. PUPATION

The larvae of Gyrinus, Dineutes and Orectochilus are known to leave the water when ready to pupate. When D. americanus comes to land, its lateral gills shrivel up and fall off, except the last double pair and a single pair just in front of them, which are used for locomotion. The distance traveled and the place finally selected as a case-building site appear to depend on the moisture of the earth which must be soft enough to be easily worked but not moist enough to be muddy. The materials used so far as known in constructing the pupal cases are always gathered outside of the water. The larva of Gyrinus (Butcher) gathered the dark brown flocculent material that collects on the surface of reeds near the water line; G. natator substratitus used grains of sand, small snail shells and even small seeds; and D. americanus built its cases of pellets of mud mixed with sand grains, small fragments of rock, bits of wood and pieces of leaves. In the instance of the Gyrinus observed by Butcher, the cells are gener- ally attached lengthwise to the stems of Scirpus and Typha at points 2 inches to 4 feet above the water's surface, whereas G. natator substratitus built on the ground, and D. americanus usually chose the under surface of a dead grass or rush stem, these being near enough to the ground for the larva to reach after building material. The cases of all these species are elongate-oval and range in outside dimensions from about 2.5 x 5.0 mm. in Gyrinus to an average of about 9 x 14 mm. in D. americanus. The cells of some species may be secured to either a horizontal or a vertical surface.

The described procedure in constructing the cells differs distinctly between D. americanus and Gyrinus. The larvae of Gyrinus having selected the under surface of a plant stem, clings to the latter with its posterior hooks and reaches to the ground to take a mouthful of material with
its mandibles. Wetting the material with saliva, the larva presses it into place on the stem, and by a repetition of this operation builds up a wall around its body. When the case is finished, excepting a small orifice at one end, the larva transfers enough material to the inside to complete the case. On the contrary, the larvae of Gyrinus sp. (Butcher, '31) and G. natator substriatus crawl over the surfaces of plants and soil, respectively, and with their building stuffs with their mandibles, pile them up on the anterior dorsal portions of their abdomens. In the instance of G. natator substriatus, the load eventually becomes top-heavy and tips over, whereupon the larva, with obvious strain, pulls its abdomen out from under the heap. At once it proceeds to bore its body head foremost and spirally into the center of the heap to form the incipient wall of the case around itself. More particles are then added to the walls with the mandibles, and after building up first one half of the cell wall, and then the other, to the zenith, the remaining cleft in the roof is closed. But the species of Gyrinus described by Butcher, after shifting its load to the posterior part of the abdomen by an almost imperceptible series of body tremors, keeps the end of its body beneath the mass while it bores a hole into the top of the heap by a corkscrew-like movement of the body, as in G. natator substriatus to shape the material into a cell. After the last abdominal segment is withdrawn from beneath the mass and disappears through the dorsal opening, the larva reaches up and closes the entrance, but the emptying of the walls indicates that the work continues for some time thereafter. This larva apparently adds some mucilaginous substance that gives the mass a distinct plasticity and a semiviscous nature.

THE LIFE CYCLE

So far as known, the Gyrinidae of the north temperate zone pass the winter in the adult stage. The available records indicate that Dineutes americanus, and others, winter in the mud, and Gyrinus natator substriatus remains on the water or, when ice covers the stream, holds to plants below the surface. D. americanus made their spring appearance in April at Boston, and were soon active in copulation. The above Gyrinus mated in the middle of May, and D. nigrior and D. horni oviposited in June and July. The overwintered beetles of D. americanus reached their numerical peak in the first week of June, then died off rapidly so few could be found by the last of that month. The larvae of these genera are therefore at hand during the months of the summer. Butcher found the mature individuals of Gyrinus sp. making their pupal cells between June 26 and August 17 in northern Michigan, and Wickham found full-grown larvae and the pupae of D. americanus during the last week of August and the beginning of September in Iowa. The new adults of this species first appeared about August 1 at Boston, and increased to thousands by August 10. These gathered in large schools, which, however, later split up into smaller groups and disappeared to their winter shelter by October 18. Copulation was never observed during the fall among the beetles of the new generation. All the evidence at hand regarding our better known species indicates therefore, that these beetles have one generation in a year in the north temperate region.
5. HYDRORHILIDAE. WATER SCAVENGER BEETLES

GENERAL FEATURES

The common name applied to this family is inappropriate for three reasons. First, some genera of the Sphaeridinae are terrestrial in all of their stages. Second, the adults of the aquatic majority are far more a consumer of living plant tissue than decayed organic matter, and third, the larvae of the whole family, so far as known, prey upon other living animals. The principal bionomic features of the hydrophilous groups are the use of the antennae by the adults during their respiration on the water's surface, their structural adaptations for aquatic locomotion, and the construction, by many, of a special silken egg "cocoon" or case. The aquatic larvae rise to the surface to thrust the apex of the abdomen into the atmosphere to secure air as do those of the Dytiscidae, and pupation, also as in that family, takes place mostly out of water. While many observations have been recorded relative to oviposition and respiration, there remains a great dearth of knowledge concerning the development of this group through the successive seasons of the year.

ACTIVITIES OF THE ADULTS

Habitat and Locomotion. While the family is overwhelmingly aquatic, members of the subfamily Sphaeridinae are said to be terrestrial, living in moist situations such as earth, decaying plants, manure heaps and dung (Wintersteiner; Wesenberg-Lund, '13). Mohr (unpublished thesis) regularly found Cercyon pugnaceus (Ill.), C. haemorrhoidalis (Fabr.), C. quisquillosum (L.), Sphaeridium scarabeoideum (L.) and S. bipustulatum (Fabr.) in cowdung at Urbana, Illinois. The adult beetles come to the dung during the day in which it is dropped. The most common habitat of the aquatic groups is within the confines of small pools, which become filled with grass, algae and other aquatic vegetation as the season progresses. Nevertheless, all the species may be taken in rapidly flowing streams but usually near the banks in the shelter of debris, moss and the like, or in protected bays where the water flows most slowly (Richmond). As a rule, the smaller beetles inhabit the more shallow depths, and some species are said commonly to go out of water onto land.

Of the aquatic Hydrophilidae, Hydrophilus and probably others, are swimmers whereas Holochares pugnaceus P. and Spercheus semipunctatus Scholl, are awkward or sluggish in water, and Lac Nobius, although capable of rapid activity, has the habit of remaining concealed in burrows in mud or on the bottom of the pond. That the aquatic Hydrophilidae on the whole are perhaps less habituated to water, despite their elegant stream line bodies, than are the Dytiscidae seems evidenced in several ways. First, even leaving out of consideration the terrestrial Sphaeridinae, this family has the smaller percentage of swimming species. Second, some leave the water to creep about on the shore, and the readiness with which the transition is accomplished suggests that no elaborate preparation for the change of habitat is required, as in the predacious diving beetles. Third, when swimming, the Hydrophilidae alternate the right and left legs after the more primitive manner of walking terrestrial insects, whereas the Dytiscidae operate the two members of each pair in unison in the way that oars of a row boat are manipulated.

Respiration. The aquatic adult Hydrophilidae, so far as known, rise to the surface of the water to get fresh air. The primary features of the respiratory mechanism are the spiracles, the large tracheal sacs, the hairy areas or tracts on the under side of the body and the antennae. A dorsal subelytral reservoir occurs in Hydrophilus and probably others. Hydrophilus triangularis (Say) possesses nine pairs of spiracles, - one on the mesothorax, the second on the metathorax and seven abdominal pairs. The thoracic and the anterior abdominal pairs are larger than the rest and it is through them that respiration chiefly takes place. The four terminal segments of the short pubescent anten- nae are enlarged and fringed with long bristles in H. triangularis. The belief that the antennae serve in respiration was originated by Nitzsch in 1811 (Blunck and Speyer, '25), and this function has since been confirmed also in Hydrophilus, Hydrobius, Berosus and Limnephilus. Tracts of fine pubescence cover the ventral of the thorax and the first abdominal segment, and extend caudal on the sides of the other abdominal segments along the lower edges of the elytra. The dorsal air chamber is filled with a large flattened air bubble (Wilson, '23).
When at the surface to breathe, Hydrobius triangularis assumes a position about parallel with the level of the water. It then tilts the body side-wise to raise one lateral edge, and particularly the left between the head and prothorax, above the water. The antenna is introduced into the cleft, whose hairy well and the antennal club together form a capillary tube or funnel. The apex of the antenna is pushed up through the surface film and makes contact with the atmosphere. When the vitiated air from the air film on the venter of the beetle has been expelled by way of the funnel and the tip of the antenna, fresh air passes in the opposite direction from the atmosphere to the hairy tracts of the thorax. Situated in the midst of these pubescent areas are the mesothoracic spiracles which alone admit the air to the internal respiratory system. The deoxygenated air becomes expelled from the tracheae by the more posterior spiracles that open into the longitudinal hairy tracts situated along the lower edges of the elytra. This air helps to form the well known silvery film on the venter of these beetles. The longitudinal tract connects along its upper edge with the dorsal or subelytral chamber. Wilson ('23) calls especial attention to the fact that the air enters and leaves the chamber only by way of this ventral film. While engaged in spinning the egg cases the female leaves and enters the chamber at intervals by lifting the ends of her elytra. Other species are reported to take air in the same manner.

Food and Feeding. The adult Hydrophilidae are principally scavengers and plant eaters, and not uncommonly a given species eats both carrion and either living or decaying plant materials. In general, however, the major part of their fare consists of plants and chiefly various kinds of algae. Rengel concluded from the dissection of 100 digestive tracts that the natural food of Hydrobius fusipes L. in most cases is composed exclusively of plant matter. Beracus pere­cimus (Bust.), R. striatus (Say) and R. pantherinus Lec. fed on green algae (Wilson) and decaying leaves of moneywort (Richmond). The adults of Hydrophilus oblongus Say appear to direct especially upon algae, Enchytraeus apparently takes only Splachnyra and Megasminia, Tropisternus feed largely on Anabaena and Clathrocyti­um, and Leobocetus also are vegetable eaters. While Hydrobius fusipes L. seemed to prefer filamentous and other algae, they readily devoured some parts of plants, dead snails and insect larvae (Balfour-Browne, '11). According to Meguasr, Hydrobius sternatus Bäch. and H. fusipes for the most part eat plants but showed a secondary taste for the flesh of fish and frogs. On the other hand, Hydro­philus caraboides L., Helochares griseus, Hydrobius fusipes and Limoxenus oblongus Bust. ate chiefly carrion, but the latter three displayed a liking for filamentous algae. Hydrobius triangularis evidently craved protein foods in addition to plant substance and was therefore regarded by Wilson as a constant potential menace to the breeding of fish.

Mating and Oviposition. A strident sound is voluntarily produced by Hydrobius fusipes, Splachnyra emarginatus, and probably other species. Although produced also when the beetle is disturbed, it is heard especially incident to mating. Buhk (loc. cit.) found a finger-like peg on the side of the first two abdominal segments that rubs across a warty area on the edge of the elytron to produce the sound. In Sper­cheus, the fore tarsal of the male of Hy­drobius triangularis bear tiny suckers like those of Eristalis, that may have a function in the copulatory posture. When in the copulatory posture, the male of H. fusipes holds to his mate with all his legs, and with his head bent down over hers, drums upon her labium with his palpi. A female is very annoyed by the attentions of the male she signifies it by swaying rapidly from side to side. During the courtship he keeps up a faint but distinct stridulation, the ventral side of the abdomen collapsing and bending downward at the apex at the moment the noise is produced. As a rule, copulation is repeated within two minutes after H. fusipes completes an egg case. According to Meguasr, the male of Hydrophilus caraboides transmits the sperms in a spermatophore. The empty cases were found several days after copulation had been completed.

Much of the research in this family has been concerned with the structure of the silken egg cases or "cocoons" and the spinning process. Their construction has been described by Balfour-Browne, Buhk, Bowrooje, Portier, Richmond, Wesenberg-Lund ('12), Wilson ('23, '23a) and others. Evolution in the mode of oviposition appears to be quite closely correlated with the taxonomic system of subfamilies of Lang's catalogue of the Coleoptera. Most genera of the lower or more primitive groups, - the Hydraeninae, Hydroscaphinae,
Limnephilinae and Hydrochilinae, lay their eggs singly, so far as known. Schthebius of the first group provides no cover or only a slight one of loosely applied silk, whereas Hydrochus makes a blanket of closely spun silk; Hydrochaera leaves her eggs uncovered and Limnephilus discolor Casey clothes them only meagerly. On the other hand, the single eggs of Hydrochus aquamifer Lec. are enveloped completely in a definite but simple flat egg case. But the cases reach their most complex structure in the Hydrophilinae, although they are only lightly covered with silk in Paracyrus. The more elaborate type of case which contains two or more eggs enclosed in silk, is found in Hydrophilus, Hydrochus, Tropisternus, Hydrobius, Sphaeridius, Enochrus, Laccobius, Ancus, and Caraboides. The more elaborate type of case which contains two or more eggs enclosed in silk, is found in Hydrophilus, Hydrochus, Tropisternus, Hydrobius, Sphaeridius, Enochrus, Laccobius, Ancus, and Caraboides. Wesenberg-Lund cites an exception in the instance of S. spinosus Stew. that deposits only one egg at a place. In Sphaeridius, Enochrus, Ancus, and possibly Caraboides, the cases are carried by the hind legs and held on the under side of the abdomen (Fig. 36). In several instances noted, the case is fastened to the beetle only by fibers of silk attached to her hind legs. The egg case of Sphaeridius emarginatus projects beyond the abdomen when the beetle is at rest, and must be drawn back up against the venter to make locomotion possible. When the beetle contracts its abdomen, the pygidium snaps into a groove on the under side of the elytra and the case is thus held secure (Buhk, '10). In the other genera that build cases these are constructed free from the body and take various but somewhat characteristic positions in the water. Usually wrapped in a leaf, the cases of Hydrochus and Hydrophilus float free at the water’s surface (Fig. 37), while Tropisternus, Enochrus, Hydrochus, Laccobius and Ancus attaching theirs to plants or debris lying on the water (Richmond). Berosus spinosus sticks its cases in long rows on leaves completely submerged in water. Codinaea orbicularis F. and Helophorus lacustris Lec. formed their cases in carpets or mats of moss or algae in shallow water near the bank. The terrestrial Sphaeridius, Sphaeridium and Ceryon build their egg cases in dung, damp earth or dead leaves.

![Fig. 36](image)

Female of Helochares, ventral view, showing the egg-case attached to the abdomen. Modified from Howroji (1933), Mem. Dept. Agr., India. Redrawn by Mrs. W. V. Balduf.

The silk that composes the egg case is the product of glands which lie in the posterior part of the abdomen and open to the outside by a pair of spinnerets situated on its apex. The spinnerets are a pair of minute slender tapering sharp-pointed appendages (Fig. 38) that are thrust out beyond the apex of the abdomen of the female during the spinning process. The two spinnerets are adjacent and alternately backward and forward, each producing at its apex a fine thread of silk that becomes attached to the support at the end of each outward stroke. The fresh liquid silk extruded by Hydrobius fuscipes will not form threads in water and the spinnerets work the whole time in the air (Balfour-Browne, '11). Just preceding the work of spinning Hydrophilus caraboides employs her mandibles and legs to fold the edges of a leaf toward its midrib to form a bag. She then inserts...
the spinnerets to tie the edges together and line the inner surface with silk. Thereupon the beetle proceeds to construct the egg case and deposit eggs within the bag (Wesenberg-Lund, '13).

In the instance described herewith, the female of Hydrous triangularis held herself in position, back downward near the water's surface and almost parallel with it, by clinging to floating vegetation (Fig. 39). While spinning she moved the spinnerets rapidly to and fro side-wise and at the same time pushed the silk backward with her hind legs. After spinning the roof of the case in this manner for a few minutes she turned over without removing her spinnerets. With her head now some distance below the surface and the apex of her abdomen at the water level, the floor of the case was laid down in the same manner as the roof. The ends of the threads forming the floor were apparently fastened directly at either end to the roof, forming a seam where the two joined.

When the case was thus far completed, she began laying eggs. First the ceiling was
covered with a thick layer of loosely woven silk leaving large open spaces among the threads. From this layer the eggs were suspended with their long diameters vertical, each egg held in place by a thin meshwork of silken threads. The latter were attached to the ceiling and to one another and also formed a continuous enclosure for the lower side of the egg mass. Having deposited the eggs and removed her spinnerets, she swam about for a time, evidently resting. On returning to the case, she replaced her spinnerets in the open end and began to weave a characteristic triangular plate across the upper part of the open end, leaving below it a lunate aperture. The plate was considerably thinner than the rest of the case and fastened on the inside. The large terminal plate was composed of loosely woven silk that covered the roof. Last of all she built a vertical mast-like process on the upper edge of the triangular plate. At intervals of less than a minute during the spinning procedure, the beetle raised the elytra slightly to admit fresh air into the dorsal chamber.

The egg cases of Hydrophilidae further differ in size, shape, number of eggs contained, and in the form assumed by the mast when such is present. The case of Berosus peregrinus, for instance, is scarcely larger than 1.5 mm. in its greatest diameter, contains 0.5 to 1.0 eggs, and entirely lacks a mast or its equivalent in the form of a thread or filament, whereas the case of Hydrophilus triangularis measures 24 by 22 by 15 mm., envelopes as many as 130 eggs and is surmounted by a vertical mast 7 to 8 mm. high. The case of Spercheus emarginatus, for example, has a triangular form and is carried by the female, that of Helophorus lacustris is flask-shaped, in Coelostoma orbiculare the case of Berosus peregrinus, for instance, is Rand. lays 2 to 11; Helophorus lacustris Lec., flat and ribbon-like in width, Corynonea of India.

The records for most part show that the largest number habitually deposited in each case does not vary extremely for a given species; also that the several species of a genus lay a somewhat similar number of eggs. The appendages borne by the cases of some species may be filamentous as in Helophorus lacustris Lec., flat and ribbon-like in width, Corynonea of India, or possess the stout vertical tapering sort variously designated the tube, spike, horn, fig or mast. The mast characterizes the cases of Hydrophilus, Hydrous and some species of Tropisternus.

Writers have engaged in speculations regarding the significance, if any, of the mast for the egg cases, particularly of Hydrophilus and Helophorus. Usually it has been supposed, and not infrequently taken for granted, that it is necessary to the development of the eggs. Further claims to have found a furrow on the surface of the case, through which the eggs hatch, have been made. The eggs of the largest species of Hydrophilus are raised several inches above water's surface or is filamentous or ribbon-like and would therefore hardly contain an air duct. At least the hatching of the eggs deposited in cases without a mast is not contingent on the reception of air, and casts doubt on the necessity for it in instances where masts, filaments or ribbons are characteristic. Wilson adopts the entirely plausible explanation offered by Lyonet that the mast is simply the result of the impulse of the beetle to empty her silk glands entirely of their contents at each oviposition, and has no relation whatever to the development of the eggs. Accordingly, the absence of a mast in some species is to be accounted for by an insufficiency of silk to make it, and where the mast varies in size within a species it may be explained in terms of the quantity of silk remaining in the glands after the case proper has been constructed.
Hatohing

Early Larval Life. So far as known, the Hydrophilidae oviposit principally from April to midsummer, and the eggs hatch for most part in 5 to 10 days. The recorded extreme periods required for incubation are 3 days in Tropisternus lateralis and 14 days in Hydrobius fusipes. The duration of incubation has been determined also for species of Hydraena, Sphercheus, Ancaena, Paracyclus, Enochrus, Laccobius, Cymbodius, Hydrophilus and Hydrous. The larvae of Hydrobius fusipes and Hydrobius triangularis issue from the lower ends of the eggs and escape into the chamber beneath the egg mass. Here they crawl about for approximately 12 hours before venturing out into the open water (Wilson, '23).

Similar delays of one to two days in the egg case by the newly hatched larvae are reported for Hydrobius fusipes, Hydrophilus obtusatus, H. caraboides, Hydrous piceus and Tropisternus. As a result of the retarded emergence, all the larvae of a case hatch before any leave the chamber. An extraordinary gregariousness seems to characterize the newly hatched larvae of Tropisternus mixtus. Wilson found that the larvae originating in two-thirds of a series of 30 cases had left their own shelters and joined with the larvae of the other third, so that each of the latter cases contained 25 to 35 individuals instead of the usual 10 or 12. Moreover, they seemed to be living in perfect harmony in marked contrast with the mutual destruction wreaked by the larvae of T. glaber (Hbst.) and T. lateralis before they left their egg cases. According to Rengel, the young larvae of Hydrobius piceus have the midintestine tightly filled with yolk, food provisions adequate for the first 2 or 3 days, the first of which is spent in the case. The larvae of H. triangularis leave the egg case through the lunate opening left by the female at the lower edge of the triangular plate. The young of certain other species are said to gnaw or break out at various places through the walls of the case. Those of Hydrobius fusipes newly emerged from the case are heavier than water. They crawl about until they succeed in getting their heads above the surface. While in this position for a half minute or more the body swells greatly owing to air taken into the digestive tract, whereupon the larva floats. The intestines of the more advanced larvae likewise contain air bubbles (Balfour-Browne, '11, '13).

Habits and Locomotion. The larvae of most aquatic Hydrophilidae are not swimmers but crawl slowly over the bottom or on the submerged surfaces of aquatic vegetation. Most pseudopneustic and meta-

pneustic larvae of the family occur on plants or stones just where the water laps the shore, lying half in water and half out of it. The crawlers include Laccobius agilis, Enochrus spp., Eneorchus unicolor Cast., Hydrobius fusipes, H. globosus (Say), Sphercheus emarginatus and Hydrophilus app. Having gills, the larvae of Enochrus peregrinus and H. striatus live farther from shore than those of other groups. The larvae of Enochrus nebulosus (Say) may burrow in the mud, and like those of Hydrobius fusipes and Hydrous piceus, spend a considerable part of their time out of water on the shore where they crawl around or live under surface cover. H. nebulosus bears large ventral tubercles on the abdomen which it uses in locomotion as a caterpillar employs its prolegs. On the other hand, Tropisternus lateralis, T. glaber and Hydrous triangularis have swimming larvae. Those of T. lateralis use the setae and the tufts of hairs along the sides of the abdomen to produce a vertical undulatory motion (Fig. 40). The larvae of H. triangularis are provided with fringes of heavy
estae on the femora, tibiae and tarsi, and both the latter parts are strongly flattened. In swimming the body moves rhythmically up and down in a manner very similar to that of a leech (Wilson, '23). The larvae of the terrestrial Sphaeridiae inhabit the situations chosen by the adults.

Larval Growth and Respiration. The larval stage of Hydrobius fusipes and Hydrous triangularis consists of three instars. In H. fusipes the first instar period lasted 6 to 10 days in warm weather, and 15 days in April. The second instar was as long as the first, and the third occupied 5 to 7, or even 8 weeks. In H. triangularis the instars lasted 4, 4 and 7 days, respectively (Riley). The larvae of Berosus emarginatus matured in 30 to 35 days. Hydrophilus obtusatus became full grown in about 30 days, and Anochrus spp. had a larval period of about 2 months. The molts of Hydrous triangularis take place in all sorts of situations in the water, and sometimes when the larva floats on the surface. Nowrojee states that when Hydrophilus is about to shed its cuticula the larva lies at or near the surface of the water.

Berosus peregrinus and B. striatus breathe with gills (Richmond), but the larvae of all other aquatic Hydrophilidae are alike in bringing the tip of the abdomen to the air above the water to breathe. An essentially typical example in the form of Hydrous triangularis is described by Wilson ('23). Although possessing a mesothoracic, a metathoracic and eight abdominal pairs of spiracles, the pair situated on the last segment of the abdomen is the only one that functions. These caudal spiracles open from the bottom of a deep transverse groove, whose front and hind margins form a pair of lips which can be opened or closed at will and thus control the breathing. When the larva seeks air, it swims almost vertically upward until close to the surface, then turns head downward and thrusts the apex of the abdomen and the cerci above the surface file. The cerci then drop upon the surface film at right angles to the long axis of the body. They not only hold the larva to the surface but open the lips of the transverse groove and keep them open as long as the larva remains here. When it has finished taking air the tip of the abdomen is drawn beneath the surface film, thereby straightening out the cerci parallel with the body axis and closing the mouths of the pair of longitudinal air trunks that compose the principal part of the tracheal system. The larva then turns head downward and thrusts the apex of the abdomen and the cerci above the surface file. The cerci then drop upon the surface film at right angles to the long axis of the body. They not only hold the larva to the surface but open the lips of the transverse groove and keep them open as long as the larva remains here. 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simultaneously engage in breathing from the atmosphere and consume their prey in the water. Whether the prey be consumed in air or in water, the strong mandibles (Fig. 41) are first employed to crush the food, but the procedure is somewhat more complex when shell bearing snails are the prey. The larva throws its head backward so that the snail touches the dorsal surface of the thorax or abdomen.

holding it as in a vise. This is the method of Hydrophilus sp. (Nowrojee), Hydrous triangularis (Wilson) and also of H. piceus and H. aterrimus observed by Megusar. The latter writer claims that the asymmetrical mouth parts of piceus and aterrimus are fitted especially for tearing snails to pieces. Having broken into the shell until the snail is reached, the long right mandible bites into the body while the short left jaw further breaks up the shell. Nowrojee states that Hydrophilus sp. neatly cuts a narrow slit along the circumference of the shell by chipping off bit by bit. When the captive of Hydrobicus fusipes and Hydrous triangularis is crushed, the larvae hold it with the antennae, maxillae and labium and therewith turn it round and round, and close the mandibles upon it every second or two to mash, cut and rend it asunder.

There appears to be no uniformity in the extent to which the larvae of the several species of the family consume their prey in its entirety. After reducing it to a pulp, Hydrophilus sp., Hydrous triangularis and Tropisternus lateralis not only swallow the juices squeezed out incidentally to crushing but the solid parts as well. Wilson's dissections of 50 larval stomachs of H. triangularis showed that even pieces of small shells are ingested incidentally with the snail's body. However, Hydrobicus fusipes and Hydrous piceus are reported to leave the crumpled solid parts lying aside after the body juices have been extracted (Rengel; Balfour-Browne). The mode of feeding in Hydrophilus caraboides seems to have become specialized to an unusual degree for the family. While sucking the food juices in by the mouth, the larvae at intervals spit out saliva which froths over the food and digests it. The dissolved and liquified tissues and organs of the prey are then ingested. The preoral digestion was so complete that only the transparent cuticula of a piece of worm was ultimately rejected. Although differing from Dytiscus in possessing an open mouth but no longitudinal sucking canal in the mandibles, the present species exhibits all the other essential characteristics of preoral digestion. In view of its lack of perforated mandibles, it appears absolutely essential to this mode of digestion that the larva keep its head out of water while feeding, which, in fact, is reported to be the habit of this species (Balfour-Browne, '11).

The food animals most often reported to be eaten by Hydrophilid larvae are Enotostraca of the genera Cypris, Cypridopsis, Cyclops and Daphnia. These have formed part of the food of Tropisternus glaber, Helochares masculiceps, Enochrus nudulatus, Hydrobicus fusipes, Limnozonus, H. caraboides and the smaller larvae of H. obtusatus, Hydrobicus aterrimus and H. planus. The latter species was fed on Physa, Planorbis and Lymnaea by Rengel, and snails were also accepted by H. aterrimus, Tropisternus glaber and various species of Hydrobiulus. The Annulid Tubifex is recorded as constituting part of the fare of Enochrus nudulatus, Helochares masculiceps, Hydrobicus fusipes, Limnozonus oblanceus and Hydrophilus caraboides, and Chironomid larvae were taken by the same species. The larvae of Enochrus were consumed by Crenobia flaccida (Cicurita) in an aquarium. Hydrobicus fusipes ate insect larvae, and Mohr (unpublished thesis) found the larvae of Sphaeridium scabricorne feeding on the maggots of Botrymeria flavicosta and Decacorus cuprarius in cow dung. The nymphs of Insects form a large part of the food of Tropisternus lateralis which preferred those of mayflies and damselflies, but also ate Notonecida, Corixida and Pelocoris femorata of that stage. It is probable that the smaller tadpoles quite commonly become the victims of Hydrophilid larvae. Such were reported eaten by Tropisternus glaber and other species. Wilson ascertained that the larvae of Hydrobicus
triaangularis eat fish in considerable quantity. Fifty-two larvae ranging from 20 to 63 mm. in length were taken from a pond containing only small fish. Ten of them had eaten such fish to the extent of 30 to 75 percent of their total food.

The analysis of the stomach contents of the above Hydrous larvae provides the most scientific and complete available example of what may be expected in the way of the natural food range in a given species. The chief food consisted of snails and Chironomus larvae. Half of them, including four mature individuals, had lived entirely on species of snails and Chironomus. The minority food found in them consisted of: the nymphs of Prothemsis and other Libellulidae, Anax, damselflies and belostomastidae; the larvae of caddisflies, Hydrous, Hydropilus, Berothus, Gyrinidae, Dytiscus; the adults of Enochrus, Heiligus and Leachophilus; and species of crayfish, Gyraulus, Arctura, tadpoles and fish. They have also been reported to feed upon snails. The data for the family as a whole indicate that the food animals consumed range in size as the predator grows larger, and the larvae of the bigger species overcome more bulky and powerful prey than do their smaller relatives. There is no conclusive evidence that special tastes have developed in any of the species, but each appears to seize and devour whatever it can catch and overcome. The food records for all species excepting Hydrous triangularis are only fragmentary, and no final deductions can now be safely made.

The nature of the predatism among the larvae is well confirmed by the prevalence of cannibalism. When confined in aquaria, the newly hatched larvae of H. trianogularis go at one another until they are full grown unless other food is available in adequate quantity. Also Hydrous parvulus and H. globoeus were observed to be always quite ready to devour others of their species. This inclination appears to be less pronounced in Combolo dysia fimbriata than in the larger species. A striking contrast obtains in the genus Tropisternus. Whereas T. lateralis freely partakes of its own kind, its congener T. mixtus exhibits no evidence whatever of cannibalism. On the other hand, Leachailus agile, Enochrus nebulosus and, of course, the phytophagous Berothus, may be safely kept together without fear of loss to their own kind.

The mature larvae of almost all Hydrolphilidae whose habits have been studied come out of the water and construct a special cell in which to pupate. The known exceptions to this habit are in the genus Enochrus. Waseberg-Lund (113a) reports that the small E. mixtor F., which lives in the surface mats of Sphagnum, the pupa spins a spherical floating air-filled pupal case of algal threads. The pupae of E. nebulosus were found by Richmond in a similar situation in masses of Oocladophora at the surface of water. On the contrary, Wilson (123a) states that this species burrowed into rather dry mud to pupate. The cells of Paracymus subrugosus (Say) were found 2 feet from the water's edge, those of Hydrous piceus seldom were more than 1 or 2 meters from the shore, and H. triangularis travels from 2 to 8 or 10 feet from the water to prepare the pupal cell and preferred black clayey loam to sandy soil. Tropisternus, Paracymus, Helochares, Sternoholopus, Hydrous, Hepocymbus and Enochrus perplexus (Lecl.) have been reported to make their chambers in mud but do not appear to be obligated to one type of situation. Not uncommonly pupation takes place also under stones and sticks, and in tufts of grass or in piles of dead vegetation on the shore. Not only the food animals chosen increase in size as the predator grows larger, but Spercheus emarginatus is said to construct its cell on plants or objects above the ground. The larvae mostly descend an inch into the ground to hollow out a pupal cell, but some go a distance of 2 to 2.5 inches. Bongel states that the larva of Hydrous places, which pupated in tufts of grass, first dug a shaft half its own length, then a cell 5 to 6 cm. in diameter. The chamber of Tropisternus glaber measures only 10 by 15 mm. on the inside. Regardless of size and depth, the cells so far as described, are almost spherical to sub-spherical in shape.

The cells of Spercheus emarginatus seem to be constructed in a way quite unique for the family. The process is very similar to that of certain Gyrinidae. According to Buhk (110), the larva left the water and selected a place among the plants where the soil was loose. It then picked up particles of soil with its mandibles and laid one after the other upon its own sticky back, beginning at the posterior end and gradually covering the whole abdomen. This work did not require an hour. The larvae then crawled up the stem of the nearest plant, fastened itself securely to the support, then curled up under the cover of soil to pupate. The procedure described by Wilson (123) for Hydrous triangularis is obviously more typical of the family. The
larva uses its mandibles to some extent for digging, biting off chunks of earth and thrusting them to one side and backward; but the burrowing is mainly accomplished by thrusting its flattened head forward and then enlarging the hole by lateral and dorso-ventral movements. After reaching a depth of 2 or 3 inches in this manner the larva elevates its head and tail until the body assumes the shape of a crescent or semicircle. While in this posture the larva rotates its entire body, swinging both ends horizontally around the longitudinal center as an axis. As a result the completed pupal chamber is subspherical in shape, the upper portion flatter than the lower. The cell is usually about 40 mm. in diameter and the walls are more or less smooth, depending largely on the texture of the soil. It required 36 to 48 hours to complete this chamber, but after it is apparently finished externally, the larva still keeps up its rotary action at intervals until it is ready to pupate.

The larva of triangularis remained in the prepupal state from 5 to 6 days, pupated in 7 to 12 days, and the newly formed adult required 4 to 5 days in the cell to become fully colored and hardened. Hydrobius fusipes similarly spent 9 to 10 days in the prepupa, but the smaller Trophisternus lateralis and a Hydrophilus of India shed their larval skins 2 or 3 days after the pupal cell is finished and spent an equal period in the metapupa. The larva of T. lateralis continued to breathe through the caudal atrium since its spiracles do not begin to function until after it becomes a pupa. So far as observed, the entire period of time spent in their pupal chambers is much longer in the larger species than in the smaller ones. It averages 2.5 to 3 weeks in Hydrous triangularis, required 19 to 21 days in Hydrobius fusipes, 12 days in Hydrophilus obtusatus, and about 10 days in H. caraboides. On the other hand, Enochrus spp. changed from larva to adult in about 3 to 4 days, and Tropisternus mixtus made this transformation in 4 or 5 days. Of ten larvae of T. glaber reared by Wilson in 1919, 6 became adults in 4 days, 2 in 5 days and 2 in 6 days. Of the same number reared in 1920, 2 reached the adult state in 3 days, 6 in 4 days and 2 in 5 days.

Whether the pupa lies in its chamber with its venter or the dorsum downward is here, as in other families, a point of uncertain status. Matheson and Wilson agree that the pupa of Hydrous triangularis normally rests on its ventral side, and Hydrophilus sp., according to Nowrojee, and Hydrous piceus observed by Rengel, assume the same posture. On the other hand, Wilson ('23) cites the statements of Lyonet, Miger and Lanoret who reported H. piceus lying back downward in its cell. Moreover, Belfour-Browne ('11) reports that his Hydrobius fusipes turned from one position to another in the cell, and Wilson noticed that if a pupa is inverted in its chamber it can right itself by convulsive movements of the cerci. Accordingly, it may not be assumed that the pupae of this family persistently maintain any one posture during this stage, and no one position can properly be regarded as normal. But whether back downward or venter downward, the body does not rest in direct contact with the floor of the cell. The European Hydrous piceus is said to be supported on three sets of dorsal hooks as on a tripod, and H. triangularis bears curved prothoracic spines which, with the cerci, hold the body aloft (Fig. 42).

Pupae of this species in chambers partly flooded during a heavy rainstorm were resting upon their spines with their backs strongly arched and thereby kept their spiracles well above the water and so prevented drowning (Wilson, '23).

Flooding drowns the stages present in pupal cases, storms wash the adults be- ase ashore and sun-baked soil imprisons the newly developed imago in the pupal cell, but the majority of the known enemies of the Hydrophilidae are vertebrates and insects, according to Wilson. The larvae of the Dipterous Stratiomyia enter the egg cases, roll up in the cavity and devour the beetle's eggs (Wesenberg-Lund, '13).
Wilson ('23) obtained a half dozen Hymenopterous larvae from a larva of Hydrous triangularis just as the latter was about to pupate. It is believed that the adult parasite infested the larva while the latter was hunting a place for its pupal chamber. The parasite remains undetermined. The larvae of Hydrous triangularis are their own worst enemies but fall prey also to the nymphs of Aeschna, Ascalapha and the larger Libellulidae, to the common bulblfrog, the green sunfish, blue gill, large mouthed black bass, the snapping turtle and the horned grebe. The larvae and adults of Laccobius, Enochrus and Troglisternus constitute frequent items in the diet of pond fish, and diverse species of the family are eaten by shoal water ducks, the pintail, both the blue-winged and the green-winged teal and wood ducks. The stomachs of the last not infrequently contained also Hydrophilid egg cases. The immature larvae of Hydrobius fuscipes, known to spend much time on shore, are perhaps largely devoured by small birds (Selfour-Browne). The adults of the present family commonly make a sharp squeaking stridulatory noise or feign death when disturbed. When annoyed, the larvae of Hydrobius squirt a quantity of dirty colored sticky fluid from the caudal end, it may be from the rectal ampulla. However, these protective devices can obviously be of but small value to the beetles against the above bird and fish enemies.

LIFE CYCLE

The seasonal development of even the most studied species of Hydrophilidae is still imperfectly known. All available reports point to the probability that these insects winter only as adults. Hydrobius fuscipes, observed in tubes, spent the colder months in the bottom mud and reappeared in the spring. Spercheus emarginatus descended into the bottom slime of aquaria where they remained from November to March, holding fast to the roots of plants, and Richmond dug Cymbiotus from mud banks on April 11. The occurrence of adults engaged in mating and oviposition early in April and May suggests that Laccobius apilia, Helochares leucosticta, Hydrochus pennsylvanica Kies., Hydrochus squamifer, Tropisternus glaber, Hydrobius plebeus, Hydrophilus caraboides, E. obtusatus, Berosus peregrinus, H. striatus and Enochrus spp. probably also hibernate as adults.

The data at hand indicate that some species develop one cycle while others probably have two generations in a year. The egg cases of Hydrobius fuscipes were found between June 1 and July 27, and mature larvae, pupae and newly developed adults occurred within the period of July 16 and August 9. It is therefore improbable that they have a second cycle. Considering that oviposition in Hydrobius caraboides seems limited to the period of mid-May to mid-July, it is likely that here also only one cycle is passed in a year. On the other hand, two distinct egg-laying seasons seem to characterize Hydrobius fuscipes, Helochares maculicollos and Enochrus. The egg cases of the latter were seen from April to August, those of E. fuscipes occurred in latter April and May and again, in larger numbers, in mid-August, and H. maculicollos oviposited from early June to early July and again in September. Furthermore, the brief four-day pupal periods of such groups as Enochrus signify a rapid development of the whole cycle and the likelihood of two or more generations in a year, as compared with a life of 2.5 to 3 weeks in the pupal cell in the instance of Hydrobius triangularis.
6. SILPHIDAE. CARRION BEETLES

GENERAL FEATURES

The current impression that the Silphidae are principally saprozoic is open to considerable question in the light of several studies. Of the ten species of Silphinae investigated by Heymons, von Lengerken and Bayer ("26-"33), Blitophaga opaca L. and P. undata Müll. are in the main vegetarians, S. ephemera L. developed and reproduced when fed exclusively on either plant food or flesh but grew more slowly on the vegetable fare. S. truncata Ill. flourished on either animal or vegetable substance, and S. tyroldensis Leith ate both plants and carrion. Oeceoptoma thoracica L. preferred flesh and carrion but S. crinita L. accepted only fresh flesh and may prove to be predacious. On the other hand, Xylodrepa quadripunctata L., Phosphuga atrata L. and Ablattaria laevigata Fabr. appear to have well established predatory food habits. Contributions from other observers on S. ephemera and Necrophorus indicate a marked inclination toward predatism, if not a fixed predatory habit, among some of the species. The larger members of the family can usually be found wherever decaying animal matter occurs, while the smaller species live more commonly in decaying fungi and a few occur only in the nests of ants.

FOOD AND FEEDING HABITS

The Adults. The adults of Silphidae known to include living animals in their diet take principally snails, caterpillars and Dipterous larvae. Thanatophilus dispar Hbst., Phosphuga subrotundata Leach, P. atrata and Ablattaria laevigata are reported feeding on snails. Johnson ("13) found P. subrotundata thrusting its head into the opening of a snail's shell and devouring the occupant, and atrata and laevigata show a preference for the species of Helix, according to Heymons and his collaborators, but they get along also on other foods. Fahringer discovered adults of atrata devouring fly larvae pulled out from mines in the leaves of beet. In subrotundata, atrata and laevigata, the head is described as strongly elongated and the mandibles prominently produced forward, enabling the beetles to pursue the small into the more remote parts of its shell. Both atrata and laevigata were repeatedly watched through the process of overpowering and devouring a snail.

P. atrata climbs upon the shell and bites the neck of the snail (Fig. 43), but not without danger of being shaken off by vigorous defensive movements of the victim, whereas laevigata remains on the ground and strikes at the small's foot. Several bites are necessary to cause the withdrawal of the small into its house, - a result that works to the advantage of the assailant which is powerless to overcome the prospective victim while it crawls. When the beetle follows the small into its shell, the latter makes several attempts to reappear but is prevented by more biting. A. laevigata squirted a charge of fluid from rectal glands upon the body of the small as a means of halting the emergence of the latter from its shell. Such glands were also found in atrata. The smalls next respond by secreting a copious amount of viscus slime that completely fills the mouth of the small. P. atrata is said to eat its way through the slime to reach the small, but both species are believed to pour out a midintestinal fluid which first dilutes the viscus barrier and facilitates the entrance of the predator, and when introduced into the small's body, incidental
to biting it, quiets the victim and dissolves its tissues. The dissolving action of the secretion is clearly visible at the points where feeding goes on, and remnants of the small continued to become liquefied long after the beetle had finished its meal. During the period of 47 days between March 1 and April 16, each pair of adults held for observation devoured on the average of 10.4 mature _Helix_, or one snail every 3.9 days. During the active adult life, it alternates the periods of voracious feeding with rest pauses and fasting, during which it lies under cover as if dead.

The adult _Xylodrepa quadrupunctata_ has been recognized as an enemy of arboREAL insects since 1842. It is principally a caterpillar hunter, and prefers the smaller, smooth, hairless leaf rollers and spanworms such as _Tortrix viridana_ and _Geometra_. The beetles dexterously force their way into the leaf rolls of _viridana_ to eat the larvae inside and have no difficulty in penetrating webs where such cover the desired prey. Other scantily haired caterpillars known to have been eaten by this beetle are _Bomurnea_, _Cnethocampa orocessionea_, _Liparis salicis_, _L. dispar_, _similis_ and _chrysorrhoea_. Heavily clothed caterpillars like _Arctia caja_ were eaten only when weakened by injury, disease or parasitism. They also readily consumed the sawfly, _Macrophya albicincta_, plant lice of various species and the adults of the _Chrysomelid_, _Phytodecta viminalis_.

The species of _Silpha_ and _Necrophorus_ are found associated with carcasses, a food utilized in the common practice of setting out flesh or dead animals to attract them. Here they climb over and beneath the decaying matter. In several instances, species of _Silpha_ (Fig. 44) were seen to seize Dipterous larvae present in the decomposing flesh, carry them in their jaws from the carcasses and therupon devour them. The following species of _Silpha_ have been seen to be so engaged: _S. americana_ L., at carcasses of _fish_ (Jacques) and woodchuck (Steele); _S. luridana_ Fabr., at a dead woodchuck (Clarke); _S. novobororeregia_ Forst., at _woodchuck_ (Steele); _S. pygmaea_ L. and _S. vicinata_ Fabr., at the bodies of small animals used as bait (Belrose). When confined experimentally in cages, hungry adults of _S. americana_ and _S. novobororeregia_ refused to feed on carrion but eagerly consumed fly larvae when these were provided (Steele).

Fig. 44
_Silpha ramosa_ Say, adult. After Basig (1837), _Insects of Western North America_, D. Appleton, & Co., Inc. Redrawn by Mrs. W. V. Balduf.

In 1830, Bell ('73) observed what seems to be the first recorded instance of adult _Necrophorus_ (Fig. 45) feeding upon maggots removed by them, in this case, from the decaying carcass of a dog.

Fig. 45
_Necrophorus americanus_. After Blackley (1910), _Coleoptera of Indiana_. Indianapolis. Redrawn by Mrs. W. V. Balduf.

About 40 individuals of _M. humator_ Goeze, _N. spicile L._ and _Necrodus littoralis_ L. were gathered in a sheltered spot about thirty inches from the carcass. The beetles continually raided the latter and captured maggots of a blowfly which bore off writhing in their mandibles to their retreat. Each beetle observed consumed one maggot and set out in search of another about once in five minutes. This significant observation appears to have been overlooked for more than a century and was only recently brought to light by Pukowski ('38). Professor Bell's findings
in England were independently confirmed by Steele ('27) who found Necrophorus orbicollis Say and N. tomentosus Web. eating maggots which they carried out of a well-rotted carcass of a woodchuck. When caged, the individual beetles devoured an average of approximately seven maggots each during a night.

Pukowski ('33) studied the bionomics of Necrophorus humator, N. vespillo, N. vespilloides Bust., N. fonsor Br., N. investigator Zett. and N. germanicus L. and found that these species, during the earlier part of their life, show a distinct preference for Dipterous larvae. N. vespilloides, which lives in rotting fungi, is an exception to this rule. A hungry male of the latter devoured 17 maggots in 35 minutes. In confinement, N. germanicus searched through a quantity of horse dung without ingesting any of it but promptly came from their hiding places to attack adult Geotrupes silvaticus when these were introduced into the cage. The predator seized the victims with legs and mandibles and threw itself upon its back or side, which are also the positions assumed by Necrophorus while eating Dipterous larvae. For most part germanicus slit the Geotrupes open between the prosternum and the mesosternum, whereupon the viscera were eaten out. In a half hour, one female seized and consumed five Geotrupes in this manner. When given a choice between the dung beetle and maggots, this species preferred the larvae. But the species of Necrophorus in general also eat flesh of vertebrates, dead snails, earth worms and larger insects, preferring the less decayed to the highly decomposed material. The Necrophorus studied by Steele likewise ate flesh but only when it was in an early stage of decomposition and therefore very similar in condition to that of living animals. When given a choice between carrion and maggots the former was invariably avoided in favor of the latter. However, after the carcass of a small vertebrate, such as a mole, squirrel or sparrow, has been buried by Necrophorus, the food taken consists entirely of the decomposed carrion, excepting that maggots which may reach the buried flesh were eventually devoured by the beetle (Pukowski).

Food of the Larvae. In the species investigated by Heymons and his associates, the kind and variety of food taken by the larvae parallels that of the adult. The larvae of Phasphuge atrata wandered about until they crossed the slimy trail of a Helix then followed it directly to the snail. Both strata and Ablattaria lasvigata bite the snail and follow it as it withdraws into the shell, providing that the slime does not entangle and incapacitate the smaller larvae. When naked snails were attacked by strata it could be seen that the bites produced a paralyzing effect on them, for the bitten but otherwise unharmed snails were stiff and motionless the next day. The paralytic substance is thought to be a midintestinal product which, as in the adults, also accomplishes the precaval digestion of the prey. The larvae of Xylocrepa quadrupunctata, which is arboreal in the adult stage, feed upon the ground (Fig. 46). In captivity they ate caterpillars, dead insects and fresh beef and pork, but refused carrion. Cannibalism is rather pronounced in some species, and has been reported for Geocentoma, Blitophaga spp. and Silpha obscura. Pukowski has shown that the larvae of Necrophorus spp. are, to some extent, fed orally by the female parent upon liquified decomposed carrion previously ingested by the beetle.

Fig. 46

LIFE HISTORY
The adult Silphini are said to produce a defensive anal fluid that is entirely lacking in their larvae. The brown, ill-smelling droplets are a secretion of countless anal glands and are produced when the muscles become rigid during thanatosis, a persistent death-like akinetic state readily induced by disturbance (Hey-
mons et al.). In view of the remarkable and distinct developmental procedure of Necrophorus, it is desirable to describe these in a separate section which follows the ensuing general account.

Copulation, Oviposition, Incubation. Copulation in Phosphuga atrata and Xylo-
draga quadripunctata occurs frequently in the course of the reproductive period, but separation of the sexes of atrata after the first mating did not reduce the number of eggs laid or affect their fer-
tility. The females of atrata, quadrupunctata, Ablattaria inaequalis and Silpha
inaequalis Fabr. uniformly deposited their eggs in the soil. Considering that the latter species is associated with car-
riage, it is of interest that the eggs are not laid in that material. P. atrata and
X. quadripunctata placed their own singly in holes about one cm. deep, but A. inae-
qualis always laid them in lots. From 6 to 12 hours before oviposition the female
dug to a depth of 2 to 4 cm. into the soil and prepared an elongate oval cavity in which she laid 3 to 11 eggs side by side in the course of a few hours. Having completed a deposition, she frequently remained in the cavity up to 12 hours, sitting sprawled out over the eggs. In a period of 48 days, three females of P. atrata laid an average of 159.3 eggs each, the individual yields being 83, 193 and 302, respectively. One female of A.
laevigata laid 101 eggs in 13 depositions during a period of 41 days. Incubation
in P. atrata required 8 days in a tempera-
ture of 21.6°C and 9.6 days at 19.7°C; in A. laevigata an average of 7.5 days in an average temperature of 19.0°C, and in A. laevigata an average of 8.6 days at 22.6°C, the extreme periods required in the latter species being 4.8 and 7.5 days. The embryonic phase of Necrophorus was passed in five days (Pukowski).

Shortly before hatching, a pair of point-
ed egg bursters situated on the labium
are visible on the embryo of P. atrata and A. laevigata. While they presumably
break the vitelline membrane they do not rupture the chorion, which is said to be broken by pressure exerted by the embryo.

Larval Life. The first act of the newly hatched larva of atrata, quadrupunctata and Silpha obscura is to swallow air. Before the atrata larva has freed itself from the egg shell the top of the head pulsates rhythmically and the fore intestine engages in swallowing movements. The translucent integument makes it poss-
able to see that the whole body becomes filled gradually with air bubbles and stretches from 7.5 mm. to a length of 9 to 10 mm. The larvae of quadripunctata, when disturbed, easily enter a death tint accompanied by the excretion of a semi-
fluid, reddish, milky, anal excrement.

In all the species studied by Hey-
mons, von Lengerken and Bayer, in Silpha
inaequalis (Boe., '19), and the species of Necrophorus observed by Pukowski, the larva-
lar stage consists of three instars. The average duration of each of the three in-
stars was found to be as follows, in days: P. atrata, 7.1, 6.6, 8.3; Silpha carinata, 4.0, 3.5, 4.8; X. quadripunctata, 5.3, 6.5, 8.6, and A. laevigata, 5.0, 3.9, 11.1, while the average duration of the entire larval stage in these species was 22, 11.8, 17.6 and 20.1 days, respectively. The re-
cords for X. quadripunctata were obtained in an average temperature of 20°C, and in the instance of A. laevigata the tempera-
ture fluctuated between 21 and 23°C. B. inaequalis made its larval growth in 16
days, in July and August, and the larval life of the Necrophorus observed by Pukow-
ski lasted only 7 days; the instars requir-
ing 12 hours, 24 hours and 6 days, respec-
tively.

The mature larvae of B. inaequalis and of the ten Silphini reared by Heymons
and his co-workers, burrow from 1 to 5 cm. into the ground to prepare a pupal cell. By twisting the body and by beating move-
ments of the abdomen they prepare an oval cavity. The average prepupal periods of P. atrata, S. carinata, A. laevigata and X. quadripunctata were 6.1, 4.6, 4.0 and 15.7 days, respectively, whereas the pupal stage lasted 10.6, 4.8, 4.2 and 11.8 days in these species. The average total de-
velopment from egg to adult in P. atrata required 38.7 days in May to June; in S. carinata, 30.1 days at 23.0°C in June to July; in A. laevigata, 34.1 at an average temperature of 21.8°C, and in the case of X. quadripunctata the cycle was passed in 38.7 days in May to June; in B. inaequalis (Goe, '19), and the species of
Necrophorus observed by Pukowski were made known by Fabre (Souv.
Ent. 6, 1899), the first complete investi-
gation was carried out by Pukowski ('33). H. vespillo, vespilloides, humator and germanicus reach sexual maturity in May, while investigator and reproduce in August. When the two sexes meet at the carcass of a vertebrate animal mating takes place, but a single male stops his burying activities after a while and climbs to an elevated place such as a stone or plant. Here he comes to rest with the mandibles often touching the substratum and the abdomen elevated obliquely and so strongly extenuated that the cuticle becomes visible. He may remain in this place and position up to several hours during which he is presumed to pour forth an odor to attract a mate.

Usually only a pair of beetles is associated with a given carcass. The occurrence of a larger number is prevented by fighting over the possession of the carrion, only beetles of the same sex being usually involved in the combats, excepting that the female usually battles with her mate to drive him out of the burrow shortly after oviposition. However, in some instances, the male and female together in their subterranean cavity throughout the duration of the larval period. When the carcass was removed experimentally after burial, the beetles left the place and took notice of each other thereafter. During the burying process, the pair seems to be held in association by the easily audible chirping sounds which male and female produce, alternately. Since copulation regularly follows in the course of burying, it is probable that the chirps express the sexual impulse. Mating takes place above ground and as soon as the work of burying has progressed beyond the first steps. The fore tarsi of the male grasp the elytral angles of his mate while the middle tarsi clasp the edges of her elytra. The act is completed in only 3 to 4 seconds and may be repeated before the burial is finished.

Size determines the choice of a carcass. If too large it can not be buried, while if too small it is inadequate as a source of food for the beetles and the brood. The bodies of small vertebrates are therefore the principal selections made. Having found a suitable carcass the sexually mature beetle crawls over it in various directions, biting into it lightly here and there the while. It then creeps under the animal and begins to excavate a hole for the reception of the booty (Fig. 47). Most often the carcasses are found lying on sod, in which case the beetles employ their mandibles to cut grass and roots and press them aside. Beginning at the space thus cleared beneath the carcass the beetle at first dig a shallow conical cavity, working with the fore legs and throwing the particles free from beneath themselves with the other two pairs. Since the cone-shaped hole is always smaller than the carcass, the latter must be doubled upon itself by the beetle which pulls it down from beneath (Fig. 48).

Fig. 47

Fig. 48

Thereafter the burrow is narrowed and extends with a uniform diameter obliquely into the soil. At the lower end of the shaft the beetle finally prepares a spherical cell or crypt of a diameter somewhat larger than that of the shaft. The booty is then drawn the rest of the way down the shaft and into the crypt, where the beetle rounds it off into a sub-spherical form by much work of pressing with the feet while the back braces against the wall of the crypt (Fig. 49). Such vestiture as still remains on the carcass is now removed with the mandibles, the hair or feathers forming a carpet on the floor of the crypt.
Necrophorus vespilloides, an inhabitant of dry forests, buries its find rather superficially under leaves or in beds of moss. The shafts of germanicus always reached the bottom of its cage, a depth of 20 cm., while humator burrows an average depth of 7.4 cm., the other species going to more shallow levels. A female vespillo buried a mouse in loose soil in three hours, but when roots and stones obstruct, the work requires 8 to 10 hours in nature.

The female Necrophorus now prepares to deposit her eggs. For this purpose she excavates a passage which leads out in a general horizontal direction from the crypt but descends weakly toward the end (Fig. 50). The walls are smooth and the lumen just large enough to enable the female to pass along without hindrance.

Its length varies with the number of eggs, which average 14 to 15 in vespillo, and are placed in small pockets formed by the exerted ovipositor along both sides of the passage. After oviposition, the female returns to the crypt and digs a circular crater-like hole in the top of the carrion ball and feeds on the decomposing flesh. This is the first food taken by her since the work of burying was begun. Now she never leaves the ball without closing the hole and smoothing the surface with the venter of her head. Soft excrement, voided after the feeding, is applied over the upper half of the carrion sphere into which it is soon absorbed. In such activities, alternated with hours of rest, the female Necrophorus passes the five-day period during which the eggs incubate.

The larvae have three instars (Fig. 51) during their growth which is accomplished in the extraordinarily short period of seven days. The first and second molts take place 12 and 24 hours, respectively, after hatching, and the third instar constitutes the rest of the larval period.

The weight of the larvae increases from 0.0033 gr. to 0.3037 gr., or approximately a 100-fold addition of weight from the time of hatching to maturity. Upon hatching in the egg gallery, most of the larvae at once and eagerly crawl along the passage to the crypt, to which they are probably attracted by the odor of carrion, but others take the shorter route, burrowing through 4 or 5 cm. of soil, a task requiring 2 to 3 hours. Upon reaching the crypt the larvae climb to the top of the carrion sphere and join their kind in the crater. The larvae progressively become less active.
and more bulky as they approach maturity, those of the last instar spending their time in a knotty mass in the then greatly enlarged crater.

Although the larvae, upon entering the crater, touch the carrion with their mouthparts they eat none of it. But as soon as the parent beetle nears the crater the larvae raise the head and thorax from the substratum and crowd around her head, competing eagerly with one another in begging to be fed. Now the parent opens its mandibles widely, and very quickly a larva inserts its head between the open jaws to receive a small drop of brown fluid which passes from the parent's mouth to that of the larva. In a few seconds the larva turns away, and another larva raises itself up to reach the source of food in the same manner. Thus the entire brood of larvae is fed by the beetle. In most cases it is the female that cares for the young but the males of N. vespilloides and germanicus were seen to assist in feeding the larvae on several occasions. Preceding each meal time the beetle stands on the top of the sphere and marks time with the front and middle legs. This treading activity may serve as a seismotactic stimulus to call the larvae up out of the crater to be fed. However, the larvae usually need not be persuaded to appear for feeding. In their eagerness, the younger individuals not only follow the parent beetle around over the carrion sphere but creep under her and even climb up to the femora of her front legs where they attach themselves by means of the adhesive disk of the caudal segment in order to reach her mouth. As a result of spilling the fluid incident to receiving it from the parent, the bodies of the larvae soon become brown. The fluid administered to them is a mixture of predigested carrion and an intestinal secretion. But the labor of providing food is soon greatly lightened. At the age of 5 to 6 hours the first instar larvae begin to take food of their own accord, then follow their parent around less and less and spend more time in the crater. However, for two to three hours after the first molt, and again for a shorter period following at once upon the second, the larvae are again greatly dependent on the adult for food. Experiments show that the majority of the larvae develop to maturity when driven, by the removal of the parent beetles, to feed exclusively and directly on carrion, but an abnormally high mortality ensued among the resulting pupae.

Although protected by the subterranean position, Necrophorus must guard her carrion against other scavenger insects including Geotrupes, Oeseoptoma, Silpha and Lucilia sericata. The maggots of Lucilia were eventually devoured by the adult Necrophorus indicating that the beetle possesses a predatory tendency even during the underground phase of its life. Ground moles frequently consumed both the carrion and the Necrophorus larvae in the crypt, while the young were destroyed also by the adult of Staphylinus glens and the larvae of Philonthus, the latter devouring an entire brood of N. vespillo in 24 hours.

The mature grub-like larvae (Fig. 52)

Fig. 52

bore out horizontally through the walls of the crypt as far as a distance of 30 cm. from the larval abode, where they make a pupal cell by rotating the bodies around the long axis for several hours. The pupa lies with the venter downward, the body supported by the pseudocerci and strong bristles on the eyes. The newly formed adult remains in the pupal cell for four days while it hardens and develops its mature color.

SEASONAL DEVELOPMENT

The available data indicate that most Silphidae spend the winter in the adult stage. The following records support this generalization: Phosphuga atrata, Xylocrepa quadrupunctata, Abiattaria levigata and Silpha carnatica winter as newly developed adults (Heymons et al); S. inaequalis, Portland, Oregon; inaequalis and S. surinamensis, January in Indiana (Blatley);
Necrophorus spp. of Indiana, April to July, suggesting that they hibernate as imagoes; N. germanicus, humator, vespillo and vespilloides reach the adult state before winter and hibernate in that stage; however, N. fossor and investigator winter in the prepupal condition in the pupal cell (Pukowski). The above species studied by Heymons and his collaborators construct hibernation cavities which resemble their egg cells and occur at a depth of 3 to 5 cm. in the soil, excepting that the adults of X. quadripunctata are said to winter in their pupal cases if not disturbed. In northern Germany, atrata becomes inactive as early as latter July and its egg-laying season is April to August, whereas quadripunctata, iaeavigata and carinata, that became dormant by the middle of September, oviposited from May to August. The larval and pupal stages therefore occurred in early and mid-summer, and the spent adults died during July and August at which time the new adults made their appearance. The senile individuals of quadripunctata buried themselves in the soil where they remained for many days and died during August. The adults of Necrophorus vespillo, vespilloides, humator and germanicus become sexually mature in May but this state is not reached by investigator and fossor until August. Blatchley mostly collected the Indiana species of Necrophorus and Silpha from April to July. As a whole, the data at hand therefore indicate that the common species of Silphidae in America and Europe go through their cycles once in a year, reproducing in late spring and early summer, pass through the larval and pupal stages during the summer and early fall and mostly reach the adult state in time to hibernate in this form.
7. STAPHYLINIDAE. ROVE BEETLES

GENERAL FEATURES

The rove beetles are familiar for their slender bodies, the extremely short elytra and their habit of elevating the abdomen in a threatening way when disturbed. The casual observer sees the species that occur in fungi, beneath bark, in the dung of animals, decaying plant matter and in carrion. Many others share the nests of ants and termites, a number of tropical forms live as external parasites on vertebrates (Arrow, Kolbe, Notman), and certain Aleocharinae are well known to parasitize Dipterous pupae. It has often been assumed heretofore that most of the 13,000 species of the family are scavengers, but the observations of recent years point to a large degree of entomophagous predatism in the group.

NATURAL ENEMIES AND PROTECTION

Two species of Proctotrupidae are known to parasitize the larvae of Staphylinidae. Verhoeff reared Serphus vitatus from Staphylinus alpestris Er., and Proctotrupes ater has been obtained from Creophilus major L. The anal fluid of adult Staphylinidae is directed chiefly against ants, so far as the records indicate. Beebe writes that the secretion utterly confused the army ants that went to the aid of their crippled fellows which several undetermined rove beetles were devouring. The odor acquired by the ants that came near the defending beetles aroused the suspicion of others for a few minutes until the scent wore off. Defense by this method has been observed repeatedly also among the myrmecophilous species. Megastilicus formicarius Casey emits a whitish fluid which causes its host, Formica exsectoides, to start back "as if a flask of ammonia had been suddenly uncorked in its face, thus giving the beetle time to run away" (Wheeler). When Atemeles antennatus Payk. met an ant in the observation nest, it thrust the tail, which it carried bent over the back, into the ant's face and twiddled the antennae very rapidly. The ant fell back and the beetle was not attacked. Donisthorpe states that this mode of defense is also employed by Lomexenus strumosus Gray, Myrmedonia fusca Donisthorpe, and Microphiala. Glance preserving the repugnant secretion have been found in the abdomen of Lome-

WYMRECOPLIISM

General Statement. Imms estimates that more than 2000 species of Arthropoda are now known to share the nests of ants, including at least 1200 beetles of which the Staphylinidae form a larger percentage than does any other family. The myrmecophiles are grouped into four categories by Wasmann ('94), according to the kind of relation they sustain with the ant host: 1. true guests, or symphiles; 2. indifferently tolerated lodgers, or synoeketes; 3. hostile persecuted lodgers, or synechthrans, and 4. parasites. No parasitic myrmecophilous rove beetles are known. The symphiles, Myrmedonia and Dinarda are chiefly scavengers feeding on the refuse of the nests, the excreta of the ants, and the like, although Lomexenus antennatus Gray, which chiefly inhabits the nests of Agathomyops liger and A. Tulipinus in Britain, devours the larvae of ants, according to Silvestri (Donisthorpe). On the other hand, the symphiles and synechthrans generally prey on the ants or their brood.

Synechthrans. These hostile persecuted lodgers appear to maintain their continuous residence in the nests largely by virtue of a volatile anal discharge which repels the attacks of the ants. Moreover, this means of defense seems to have been the device that originally led to the establishment of the present fixed myrmecophilous relationship. That such was its origin is suggested by the fact that a similar secretion produced by free-living rove beetles is commonly and effectively used against ants at large and that the persecuted Staphylinidae even now constitute the numerically predominant group of myrmecophiles.

All the known synechthrans are Staphylinidae, belonging principally to Myrmedonia, Megastilicus, Brusilla, Lampronius, Quedius, Xantholinus and Staphylinus. These agile beetles force themselves upon their host and generally devour both the adult and the immature stages. While hiding in the corners and at the entrances of the nest, they seize and kill single ants but also consume the helpless eggs and larvae. Their comparatively large size attracts the attention of their...
hosts, whose behavior is always hostile and necessitates escape or the utilization of the defensive discharge.

Symphiles. The best known Staphylinid symphiles are members of the Aleocharine genera Atemeles, Lomechusa and Xenodusa. The true guests are treated by their hosts as these treat their own kind. The ants communicate with them by means of the antennae, clean and lick their bodies, and generally also carry them around as they do their own young. While they are commonly fed with regurgitated food from the mouths of their hosts, they also take food of their own accord, usually devouring the ants' brood. Whereas the persecuted guests gain immunity from attack through their repellent secretions, the symphiles accomplish this end by the possession of special secretory organs whose products are keenly relished by their hosts. The adult beetles bear tufts of red or golden yellow hairs or trichomes on various parts of the body (Fig. 53). In Lomechusa strumosa, these occur on lateral processes of the second, third and fourth abdominal segments, and through a pore in the cuticular layer of the body wall. The trichomes are very sensitive, and when licked by the ants a secretion is at once produced.

But not only the beetles but their larvae also are guests. In addition to rearing them, the ants lick and feed them with regurgitated food just as they treat their own young. However, the larvae may stroke the cheeks of the ants with the front legs, as the adults do also, to beg them for food. When the nest is disturbed, the guest larvae are carried to safety before the ants remove their own. The ants place the larvae of Lomechusa strumosa on their own brood, of which they devour large numbers. And when ready to pupate, the workers cover the guest larvae with soil as they do their own, and in like manner, subsequently dig them, and the pupae, up again. Being too delicate to endure such treatment, the symphiles are thereby inadvertently kept in check, to the great advantage of the ants. Only those guest larvae which the workers overlook are able to reach the adult state. The preference for the adopted guest larvae is all the more remarkable on the trochanters and inner surfaces of the femora. According to Jordan ('13), each trichome articulates in a socket in the cuticle, and a nerve fiber extends inward from the articulation to join with the nerves of neighboring trichomes (Fig. 54). Between the several nerves and directly below the cuticle are many minute glands, each opening to the outside

![Fig. 53](image-url)

Adult of Xenodusa sayi Leo., dorsal view, showing tufts of yellow hairs or trichomes on the abdominal segments. After Elatobia ('10), Coleoptera of Indiana. Redrawn by Mrs. W. V. Balfour.

![Fig. 54](image-url)

Secretory organ of a myrmephilous Staphylinid beetle. 1, cuticle; 2, trichome articulating in cuticle; 3, nerve connecting with base of trichome; 4, unicellular gland; 5, opening of canal from a gland. Modified from Jordan ('13), Zeits. Miss. Zool. Redrawn by Mrs. W. V. Balfour.
Considering that these consume quantities of the eggs and larvae of their hosts.

This predation on the ant brood was believed by Wasmann ('97) to be responsible for the rise of a deformed type of ant having a structure intermediate between the queen thorax with the stature, gaster and head of the worker. They are usually paler in color than the normal worker and very lazy, cowardly and incompetent. In explanation of this queer mongrel form, Wasmann suggests that the pseudogynes are the result of neglect and underfeeding, which grow out of the preference shown by the workers for their guest beetles and their larvae. According to this theory, the larvae intended to become queens are fed with the usual special fare until they reach a condition so advanced that they are no longer able to develop into workers. At this point in their growth they are neglected by their nurses in favor of their guests, with the result that the intermediate pseudogynie type of adult is produced. Wasmann observed that the extent to which Formica sanguinea neglected its own brood was in proportion to the number of Lomechusa larvae in the colony. A reproducing Lomechusa female is like a secondary queen since her progeny is adopted by the worker ants which, in fact, care for those with far greater zeal than they display in nurturing their own kind. The predilection for the guests and its consequent evil social effects has, according to this view, been the fruit of indulgence in the tasty secretions of the guests, the workers yielding their instinctive devotion to the welfare of their own kind for a palatable luxury.

Host relations. The dependence of the symphiles upon their hosts appears to be comparatively less fixed and limited and no definite seasonal alternations are reported. The species of Myrmecodia are chiefly found with ants, but also with termites, throughout the world. Donisthorpe reports A. humeralis Gr., M. cognata Mark., M. lugens Gr. and M. latilabalis Mark. from the nests of Acantholyops fuliginosus. So far as known, the hosts of Myrmecodia are species of Tepinoma, whereas Drusilia canaliculata F. was taken in company with 17 species of British ants. Leprominus insignitus Gr. appears to live generally with Myrmica, but also with Acantholyops fuliginosus, Formica rufo-pilosa and others. Chedius brevis Er., and Xantholinus atratus Beer inhabit the nests of P. rufa and A. fuliginosus. Stephylinus tercarissus Oi. is regarded by Donisthorpe as an incipient myrmecophile experimenting in host selection. It has been collected in nests of Myrmica chiefly, but also in those of Formica, Tetramorium and Polyrhachis in England and France.

RELATIVE FEW OBSERVATIONS ON THE BIOLOGYES OF TERMITOPHILIC ARTHROPODA

Relatively few observations on the bionomics of termitophilous Arthropoda have been made, and little has been written concerning their food relations with the termites. They are said to come with the first three of Wasmann's categories, - symphiles, synoeketes and synechthrans. Mann ('23) described twenty-three new species of termitophilous rove beetles from British Guiana and Trinidad. All belong to the subfamily Aleocharinae and to the genera Spirachtha, Corotea, Thyreoxenus, Bumnicola, Perinhia, Termiotogaster, Cormbogaster, Termitophya, Trachogus, Xenopelta, Xenogaster, Oratoxenus and Blapticoxenus and were taken principally from the nests of Nasutitermes. McIndoo ('23) studied the detailed structure of the three pairs of glandular appendages on Spirachtha mirabilis Mann. The termites carry this beetle from place to place and lick not only the abdominal appendages but the entire bodies.
Members of several genera of Aleocharinae have been found to live ectoparasitically as larvae on the pupae of cyclorrhaphous Diptera. Wadsworth, Scott, and Kemner have contributed the major biometric studies. Coprochara bilineata Gyll., C. (Baryodma) antarctica Casey (Fig. 55), C. vernus Say and Baryodma nitida Gr. are recorded from the puparia of the cabbage root maggot, Phorbia brassicae (Bouché). Some of these names will probably prove to be synonyms.

Fig. 55


Polystoma algarum Fauv. was reared by Scott from the Phycodromid flies, Orygma luctuosum Meig., Coelopa pilipes Hal. and Fucomyia gravis Hal. breeding in decaying seaweed. Kemner had most of his Aleochara curtula Goeze from the puparia of Lucilia Caesar but also from other large Muscid species, and experimentally induced it to parasitize Pegomyia hyoscyami but these did not afford enough food to enable the larvae to mature. A puparium of this fly collected in nature yielded Polychara lavegata Gyll., and Coquillett (Kemner, '26) obtained Maseochara valida (Lee.) from puparia of unknown identity.

The relations between the parasitic rove beetles and their hosts during their metamorphoses are quite uniform, so far as known. The eggs are laid in the ground in the manner of non-parasitic Staphylinidae, and probably in the vicinity of the prospective hosts. The adults of species that parasitize scavenger flies have been found about carrion and decaying vegetable matter, whereas the adult Coprochara bilineata, whose larvae infest the puparia of the cabbage root maggot, have been taken from small crevices in the soil at the bases of cabbage and rape plant. The newly hatched larvae are active, thysanuriform and avoid light by crawling under cover or into the soil where their hosts also occur (Fig. 56).

Fig. 56

First instar larva of Aleochara curtula before it enters the host. Modified from Kemner ('26), Entomologisk Tidskrift. Redrawn by Mrs. W. V. Balfour.

This agile larva seeks a suitable puparium into which it gnaws its way to feed upon the enclosed pupa. The larvae of Aleochara curtula were unable to enter older puparia, obviously because these were too hard to penetrate. It is believed that they select the softer, very newly formed puparia as hosts (Kemner). The point where the larvae enter becomes closed thereafter and remains distinctly marked by a small scar. Two larvae are known to have entered the same host, but one or both die in such instances before maturity is reached. The larvae of the first instar puncture the host pupa with their pointed mandibles and suck up the fluids issuing from the wound. Kemner describes what he regards as an attachment organ on the venter between the middle legs of Aleochara curtula. It consists of an ovate area of thin membranous skin bordered by a slightly more chitinous edge, and is present only in the first instar. After feeding begins, the larva grows rapidly, becoming very much swollen and cylindrical. (Fig. 57).

In the second instar the appendages become greatly reduced, the mandibles are shorter and the body soft, fleshy and el-
most without chitinous sclerites. In this stadium the larva reaches its most extreme adaptive degeneration for its parasitic life. Whereas this larva now feeds on the fluid contents of the host, those of the third instar are said to devour completely the rest of the pupa.

The feeding larva of Coprochara bilineata occasionally excreted a droplet of anal fluid that hardened on the inner wall of the puparium and made the latter opaque so that activities of the parasite were no longer observable (Wadsworth). The first instar larvae of Coprochara bilineata appear to confine themselves to the anterior dorsal region of their hosts, and those of the third always lie lengthwise and parallel with the same, with the head near the junction of the host's head and thorax.

Kemner recognizes two different forms of third instar larvae among the parasitic rove beetles. The first, represented in Aleochara, Baryodma, Polychaetidae, and Maseochara, returns somewhat from its sluggish form to its earlier and more active state, and emerges from the host to pupate externally. The second group contains species of Coprochara and Polychara, whose larvae retain the reduced parasitic form of body and accordingly remain within the puparium of the host to pupate. But whether the parasite emerges from the host as a mature larva or as an adult, it chews an irregular exit hole in the hard pupal case that houses it. The full grown larvae of Aleochara curtula and Polychara laevigata make small cells in the soil, and are said by Kemner to spin fine threads from the anus to form thin cases in which the pupal stage occurs. The puparia of the cabbage root maggot were parasitized to the extent of 8 to 16 percent in the summer in Britain. The beneficial importance of the species is considerably increased by the adult's habit of devouring maggots.

**Fig. 57**

The swollen first instar larva of Aleochara curtula on its host, the pupa of Luepila oestrus. Modified from Kemner (1935), Entomologisk Tidsskrift. Redrawn by Mrs. W. V. Baldwin.

The records indicate that predation occurs rather commonly in the several habit groups of the family. In addition to being fed by its ant hosts, Attemelas ant larvae, dead ants and flies in the observation nests. The hostile persecuted myrmecophiles, all of which are rove beetles, are generally predatory, devouring the host ants or their offspring. Donisthorpe reports both the adults and larvae of Myrmecodia humberella lurking near a nest of Formica rufo and pouncing on the ants. Thousands of the ants must have been killed in this way. Myrmodon, Drosilla canaliculata, Lamprinus saginatus Gr., Xantholinus atratus and Staphylinus stercorarius also feed upon the ants and their pupae as well. The adults of the parasitic Coprochara bilineata and Aleochara curtula, and probably others, retain the essential habits of predators. They are active runners and possess well-developed chewing mouth parts. C. bilineata readily devoured living cabbage root maggots, and A. curtula ate small living fly larvae at carcasses and fed on the older puparia of Britaleta varax in nature. In by far the larger number of records for free living species, the food consisted of the larvae of Muscoid flies, mostly taken by the beetles from the carcasses of small quadrupeds. The predominance of maggots in the fare of these beetles may be significant by way of explaining the origin of parasitism in this family. The species recorded one or more times as preying on fly larvae include Staphylinus fuscator Gr., S. mysticus Gr., Philonthus sp., Dromaphilus villipus (Gr.), E. maxillatus, Ontholestes claviger (Gr.), S. carinatus, A. laevigata Gr., O. punctatus Casey, Xantholinus hamatus Say, Hesperobium californicum Lec., and Mirraea angustata Gyll. The latter four species were observed devouring cabbage root maggots in the field and readily attacked fresh live larvae in captivity (Gibson and Treherne). Xambeau (1907) records nine species of Staphylinus which are said to prey upon the larvae and adults of insects, on worms, myriapods and Mollusca, and Hawkins (Thomas) reported S.
Badipes Lec. eating adults of the Elaterid, 
Agriotes mancus. B. elephas Müll. was found by Pukowski to enter the crypts of 
Necrophorus where it preyed on the larvae of this beetle. All the species of Nudo-
bius, so far as known, are predators and 
are usually found under the bark of trees 
killed by bark beetles. N. pugetanus 
Casey preyed on the larvae of small Dip-
tera and the larvae and adults of Coleop-
tera under the bark of western yellow 
pine infested with Dendroctonus brevi-
comis Lec. (Fig. 58) (Struble). Xambeau 
(T07) states that all species of Philon-
thus are predacious, attacking especially 
Dipterous larvae in disintegrating organ-
ic matter. Nineteen species said to have 
this food habit are listed by this writer. 
Philonthus aeneus L. and P. fimetarius Gr. 
were seen eating the puparia of Eristalis 
tenax (Fahringer). Beebe mentions an un-
named species of rove beetle which ap-
peared in the line of march of army ants 
and attacked the injured workers. Camer-
on found Oligota pallidicornis Cam. on 
manioc where it preyed on a red spider 
mite, and Quayle records O. oviformis 
Casey eating red spiders on citrus trees 
in southern California. The latter con-
sumed an average of 10 red spiders per 
day, and, having a maximum adult life of 
30 days, one beetle is capable of de-
stroying over 300 spiders.

Also the larvae of Oligota oviformis 
prey on red spiders, and destroy about 20 
mostly mature individuals per day. The 
potential rate of consumption during the 
growth of a single larva was estimated at 
200 to 300 spiders. The larvae of Philon-
thus brunneus Gr., P. longicornis Steph., 
P. cyanipennis Pahr. and Belonuchus formo-
anus Gr. were reared in part on mites but 
chiefly on Muscoid and other Dipterous lar-
vae, which they accepted readily (Mank). 
The larvae of a Philonthus sp. entered the 
crypts of Necrophorus on whose grubs they 
feed voraciously (Pukowski). The full 
grown larvae of Philonthus nitidus F. oc-
curred in cattle dung with the grubs of 
Aphodius on which they later fed in captiv-
ity. Yerhoof also met with the larvae of 
Staphylinus ophthalmicus Scop. devouring 
a Diplopod, Pachytylus undicolor Koch, which 
readily overcame living individuals of the 
lette and Tachypodoiulus albipes in cap-
tivity. The predator broke its food ani-
imals into segments and ate these one at 
a time, leaving only a heap of empty rings. 
The larvae of Rudobius pugetanus prey with 
great ease on many of the small Coleopter-
ous and Dipterous larvae associated with 
Dendroctonus brevicomis (Fig. 59). Their 
food included the larvae of Orthia pora-
bris and Platygyna punctigeramos.

Fig. 58
Nudobius pugetanus, A. adult, dorsal 
view; B. mandible of same. After 
Redrawn by Mrs. W. V. Balduf.

Fig. 59
Nudobius pugetanus, A. larva, dorsal 
view; B. mandible of same. After 
Redrawn by Mrs. W. V. Balduf.
Since it preys wholly on the secondary insects, it is of no importance as a check on Dendroctonus. Chapin obtained the larvae of Xantholinus sepheles Say under the bark of dead trees and reared them on small maggots that occur in such situations. Both the adults and the larvae of Yellensius dilatatus F. appear to have a fixed habit of sharing the nests of wasps, and Vespa crabro in particular, but their precise food relations with the hosts remain uncertain. Bischoff fed a larva of this species for a period on the brood of the hornet whose nest it inhabited. It penetrated the wasp's cells to kill and devour the larvae within. A similar habit may characterize Belonochus mordens Er., Triacrus superbus Er., Xeno- pygus analis Er. and Xanthopus tentamen Say, which Luderwaldt took from the nests of Beltonia, Polybia and Tri- gona in Brazil. The larvae of captive predacious rove beetles commonly destroyed their own kind when inadequately fed.

The strong curved mandibles of the larvae seem not to be used for chewing but rather for grasping and penetrating their prey. Mank found no evidence that the larvae of Philonthus, Belonochus, Tachinus and Listotrophus attack their victims but seize them and then suck out the body fluids. In the instance of Oligota oviformis, whose feeding process is described by Mayie, the larva uses its sharp pointed mandibles to puncture the red spider about the center of the body, and by a pump-like action the body contents are sucked out. Since these are red, they may be distinctly observed passing out of the spider and into the alimentary canal of the somewhat transparent body of Oligota. Thereupon, the liquid substance of the spider is spewed along behind the female, both with the abdomen bent sharply upward. The stimulus to pursue is obviously the musk-like odor that emanates from certain glands along the abdominal tergites in both sexes. Soon or later, with the abdomen bent forward over his head, the male's exerted para-

meres seize the dorsum of the female's abdomen and sliding along it, come to hold fast to the apex. With the tips of the abdomens united, the two continue to run along, the anterior end of the male under the abdomen of the female. In the instance of the myrmecophile, Lomechusa strumosa, the male and female, when about to mate, touched their antennae and mouths together and tapped each other quickly, after which the male slowly slid around to the caudal end of the female, touching her constantly with his antennae. Then pushing his head under her body, raising himself on the tips of his front legs and nearly standing on his head, his abdomen was bent forward over his thorax to clasp the elevated abdomen of his mate. During coition, the male dangles from the end of the female's body or walks along on the tips of his anterior legs. Donisthorpe states that the mating process is like this also in Ate- males, Myrmedona and Dinarda. In Vel1eius dilatatus, the abdomens of the beetles similarly join at the apex, but the body, when united, rests parallel with the substratum and in linear fashion (von Rabe). The new adults of Coprochera bilineata always copulated within two or three days after they issued from the host.

Oviposition and Incubation. In most known cases, the rove beetles lay their eggs in the soil. This is true of the parasitic Aleocharinae as well as the free-living species. Three gravid females of Aleochara curtula dissected by Kemner contained 38, 45 and 47 eggs, respectively. Oligota oviformis lays the eggs singly on the under surface of the citrus leaves. Nudobius pugetanus deposits them one at a time at the sides of the egg galleries of Dendroctonus, and the species of Atemeles put theirs on the egg masses of their host ants. Wasmann ('15a) has maintained that Lomechusa strumosa is normally ovoviviparous, and believed that certain Atemeles reproduce in the same manner. Where eggs are known in the latter genus they are not positively distinguishable externally from those of the ants among which they are laid. Also the larvae of these genera bear a very close resemblance to those of their host ants. Incubation required 7 to 9 days in Oligota oviformis, 10 to 12 days in Coprochera bilineata, and 10 days to 2 weeks in the instance of Nudobius pugetanus.

Larval Growth and Pupation. All the parasitic Aleocharinae, so far as known, have three larval instars. This number is reported by Kemner for Aleochara curtula, Baryodma intricata Mannh., Polychara laevigata and Coprochera bilineata. The first is campodeiform and the third cuculiform, 82
only the second having the typically reduced parasitic structure. On the other hand, the larvae of Lomechusa and Atemeles have four stadia, according to Wasmann ('15a). The duration of the larval period was approximately 12 to 15 days in Oligota oviformis, 11 days in Philonomus brunneus, 10 to 14 in Lomechusa strumosa and required 6 to 8 weeks in Nudobius pugetanus in the summer. The larvae observed by Mank neither moved nor ate for a day or two previous to pupation. Technum flavipennis Dej. formed a firm pupal case from a larval exudation. Kemner observed that fine threads were spun from the anus by Aleochara curtula and Polychara laevigata to make their pupal cases. The adults of Philonthus brunneus, P. longicornis, P. cyaneipennis and Belonuchus formosus rested on their backs with the head curved downward (Mank). The duration, in days, of the combined prepupal and pupal states has been reported for the following species: P. brunneus, 7 to 15; P. longicornis, 6 to 10; P. cyaneipennis, 9; P. decorus Gr., 15 to 18; P. splendatus Gr., 22; B. formosus, 9 to 12; Staphylinus similis F., 23; S. opthalmicus, 30; S. fulvipennis Er., 2 weeks, and Coprochara bilineata, 24 to 36 days. The full grown larvae of Lomechusa strumosa are imbedded by the workers of their host ants. Those of Atemeles may be similarly cared for but retain the ability to prepare themselves for pupation. L. strumosa transforms in 13 to 19 days, and A. paradoxus Gr. only 13 to 21 days (Wasmann, '15a).

**Seasonal Development.** The Staphylinidae live in such diverse conditions and ways that uniformity in the number and development of the generations may not be expected. The larvae of L. strumosa are at hand from May to July, when the larvae of their host, Formica antarctica also occur, and the new adults appear from the middle of July to the end of August. This species developed through its stages in 33 to 46 days, and Atemeles emarginatus and A. paradoxus completed the cycle in 52 to 70 days and 40 to 56 days, respectively. Wasmann concluded ('15a) that these species have one generation in a year. The parasitic forms, Aleochara curtula, Barochara intricata, and Polychara laevigata, appear to be similar in their seasonal development and Kemner states that the cycle is completed once each year. The adults of A. curtula and B. intricata were mating and ovipositing in June and July, the larvae and pupae occurred in midsummer, and the newly issued adult is believed to carry the species through the winter in Sweden. Wads worth found evidences that indicate the occurrence of two generations of Coprochara bilineata in Britain, corresponding with the two generations of the host. The first instar larvae enter the host puparia in the fall to winter as such. Adults develop from these larvae in May and June of the next year, and their progeny reaches the adult state during August and September. These reproduce promptly, and their first instar young enter the host for the next winter. It seems probable that Polychara algarum winters in an immature state in the host and emerges therefrom as an adult in the spring. Von Rebe found adult Velleius dilatatus in July and August, and observed copulation in August and September. The old adults probably die in the fall and the winter is spent in one of the immature stages. In the case of Nudobius pugetanus, Stuble found one generation in a year. However, the species winters in both the larval and the adult stages and the seasonal development consequently proceeds in two distinct ways. First, the overwintered adults oviposit during the first part of June, and the resulting early larvae mature and pupate by mid-August. The new adults begin to appear about the first of September. These spend the winter where they were reared, or enter trees which have been killed during the summer. In the second type of cycle in this species, the overwintered larvae become full-grown and pupate by the latter part of June. The adults developing from these in early in July enter trees then inhabited by the mature larvae and the pupae of Dendroctonus brevicornis. Here they oviposit, and a new generation of larvae is started in the second half of August. These larvae become half-grown during the fall, and hibernate in this state of growth. Ten to twelve weeks are required for the development of one cycle.
8. HISTERIDAE

GENERAL FEATURES

The Histeridae are most commonly seen in decomposing plants, rotting wood, dung and carrion, but many species live in the burrows of bark-beetles. Some visit the exuding sap of trees and others may be found in the nests of ants, termites, hornets, moles and particularly in those of rapacious birds. The myrmecophilous species are thought to have the characteristics of symechnurae and synecokeites. Tytlois tritfunatus Mars., Chlamydopsis, Bastaerius tristriatus Horn and H. brunneipennis Rand., which live in the nests of Ants, are typical of true guests, and Wheeler places Triballus in the same class of myrmecophiles. The differently tolerated guests are exemplified by Bastaerius ferrugineus O1., Dendrophiulus pygmeus L. and Myrmetes piceus Plk. Reichensperger reports that some species of Mesnodytes from the nests of Eciton in Brazil and Argentina.

FOOD AND FEEDING

The common occurrence of the Hister beetles about decaying substances is obviously responsible for the old assumption that they are principally scavengers. While the facts are still far from complete, there is growing evidence that they feed upon other living insects. Although fed with regurgitated food by Lasius, Heterius brunneipennis also feeds upon disabled and dead insects in the nest, as do also the synoekeites enumerated above. Reichensperger believes that the larvae of the myrmecophilous Menomysites feed mostly, if not exclusively, upon the larvae of Lasius alienus, bearing the tufts of yellow trichomes typical of true guests, and Wheeler places Triballus in the nest of Lasius alienus. The adults of the following four species of Hister have sometimes eaten Lepidopterous larvae. H. interruptus Gaeauv. was found in the nest of Pteronemus Machaeratoeus, another in the nest of a larva of Psyche, and another in the nest of a larva of a species of Timandra. Reichensperger has observed Heterius brunneipennis feeding on the pupae of a species of Lasius in the nest of a pupal of a species of Lasius, and H. interruptus has been found in the nest of a pupal of a species of Lasius. The adults of four species of Hister have sometimes eaten Coleopterous larvae. H. interruptus Gaeauv. was found in the nest of Pteronemus Machaeratoeus, another in the nest of a larva of Psyche, and another in the nest of a larva of a species of Timandra. Reichensperger has observed Heterius brunneipennis feeding on the pupae of a species of Lasius in the nest of a pupal of a species of Lasius, and H. interruptus has been found in the nest of a pupal of a species of Lasius.
Fig. 60

to eat the larvae of the Staphylinid, Nudobius pugatorius and of Othnius lugubris and Biptera as well as other individuals of their own species. The grubs of Dendroctonus bore into the bark and thus go beyond the reach of this enemy. Also both active stages of Plegaderus nitidus are predacious on the very small Coleopterous and Dipterous larvae under the bark; and the adults, having been found in the egg galleries of Dendroctonus brevicornis, may be of some value as destroyers of the eggs. Furthermore, the writings of Schwarz, Hopkins, Stebbing and Bickhardt indicate that entomophagous predatism prevails among species of Histeridae living under the bark of trees. The prey consists largely of Scolytidae, but Bostrichoïdes, Curculionidae and other xylophagous beetles also form a part of their fare. In the following records the name of the predator precedes the names of its prey: Cylistis, common in galleries of bark beetles; C. cylindrica Payk., preyed on Ips ecophagus and I. calligraphus; Cylistosoma oblongum F. and C. elongatum Oliv., I. spp.; C. dufalli Mars., on Tomius; Hololepta spp., subcortical insects; larvae of Dipontus andrewsi Lewis, on Scolytus; larvae of Ips, as well as other insects; larvae of Polygraphus, Elytas and the Curculionid, Rhynchosus; Euchrorycerus spp., probably prey on other insects (Lewis); Paromalus bistriatus Er., ate pupae of Polygraphus rufipennis; P. difficilis Horn, associated with Polygraphus rufipennis and Dryococetes grandis.
LIFE HISTORY

Very little specific information concerning the seasonal development and habits of this family is at hand. Platysoma punctigerum goes through its cycle twice in a year, whereas Plegaderus nitidus appears to have only one generation annually (Struble). The adult Platysoma hibernates in the egg galleries of Dendroctonus brevicomis, entering by way of the ventilation holes bored by the bark beetles. Oviposition ordinarily begins in May, and continues over a period of 3 to 5 weeks. Eggs were seen in the field from June 14 to July 1. They are deposited along the sides of the egg galleries of Dendroctonus in small groups of usually not more than three. The larvae hatched in 10 to 14 days, and developed in 4 to 6 weeks during June and July. The first mature larvae were seen on July 6, and pupae were first noticed on July 12. The latter stage occurred in subcortical chambers, completing their transformation in 10 to 14 days, and new adults began to appear on July 25. The new beetles either remain in the original host tree or fly to trees which have been recently killed. The second generation completes its development by late September and early October, the resulting adults entering the egg galleries of Dendroctonus to spend the winter. Platysoma begins its cycle 3 to 4 weeks after Dendroctonus has made its attack and for that reason is regarded as having but little value in preventing injury to the pine.

Both the larvae and the adults of Plegaderus nitidus hibernate. The adults probably oviposit during May and June, the larvae mature in 8 to 10 weeks, and pupation occurs in September. The new adults enter the ventilation holes of Dendroctonus to overwinter under the bark. On the other hand, the hibernated larvae matured, pupated and reached the imaginal state by mid-July. The adults enter trees recently attacked by Dendroctonus and their larvae become half-grown before winter stops their growth.
9. CANTHAROIDEA

GENERAL FEATURES

The five families of Cantharoidea have several biological features more or less in common that combine them into a natural group. Photogenic organs are present in most of the Lampyridae and are known also in the Phengodidae. The larviform females of certain sexually dimorphic species, and the larvae of the luminous species, in general, are the glowworms. Sexual dimorphism is well exemplified among the Lycidae, Phengodidae, Lampyridae and the Drilidae. Predation prevails in the latter three families, their principal food animals being snails, but this food habit seems to have reached its highest development in the Cantharidae. While some of the adults of the predacious families feed in part or whole on animal substance, the majority seem to be principally phytophagous or take no food at all.

A. LYCIDAIR

The Lycidae are diurnal, chiefly tropical, and, so far as known, not predacious. The recent studies of Mjoberg on the Bornean Duliticola paradoxa Mjoberg and Withycombe on Calopteron fasciatum Lap., in Trinidad, show that the larvae of both have a kind of suctorial mouth parts used to ingest the juice of decaying wood. The larva of D. paradoxa bears a close resemblance to the extinct trilobites, and no marked pupal stage exists in the female. The sexes are extremely dimorphic, the winged male being only 7 mm. long compared with the 75 to 80 mm. of the wingless larviform female. When the larvae of C. fasciatum became mature they congregated in masses on the underside of a fallen tree trunk for pupation. Around a nucleus of the first coming individuals gathered to pupate, a mass of several hundred may assemble in a radiating pattern.

B. PHENGODIDAE

The belief that the Phengodidae are predacious is based in part on the presence of formidable pincher-like mandibles in the larvae of Phengodes (Fig. 62) (Dahlgren, '17). Moreover, Williams ('17) states that the American species of this genus are known to feed upon Myriapoda. The larvae and the larviform females of the American Zarhipis plioventris Lec., Z. riveroi Horn and P. plumosa (Holl.), are luminous, but the winged flying males lack light organs. Both the luminous stages of P. plumosa are said to give off a bright greenish-light from the sides of eleven body segments, and hide under stones and other cover. The females emerge on June nights and display their lights to attract the males, which have large keen eyes (Dahlgren). Barber found a female of P. laticollis Lec. near Washington D. C. on June 17 that retained her luminosity until about August 10. When exposed in a glass jar, a male was attracted, and the pair copulated a few minutes later. On July 1, the female lay collid around 90 eggs in the soil. Fifty-three or more eggs had been deposited by July 6, when the female was weak and much shrunked.

C. LAMPRYIDAE. LIGHTNING BEETLES

Sexual Dimorphism

Extreme structural gradations appear between the sexes of the Lampyridae. These have developed principally in the eyes, the photogenic organs and the wings and elytra. Frequently the eyes of the male are much larger than in the female, and in some species the antennae also are correspondingly longer. There is a tendency also toward a differentiation in size, particularly the wingless females being greatly larger than the males. All of these modifications from the usual secondary uniformity between the sexes seem to be associated with the nocturnal habit and the luminescence that prevail in the family. Adopting uniformity of structure in the sexes as a criterion, the primitive condition is most nearly retained in Lucidota and Lamprohiza. These forms are diurnal, both sexes have wings and elytra of normal functional size, and
they either lack light organs or have them but slightly developed. The next higher condition is represented by Photinus pennsylvanicus (Med.), in which the photogenic organs are present and alike in both sexes, and both are active flyers and runners. Both sexes of Photinus marginellus Lc. are said to fly actively, but a considerable divergence has developed in the size of their luminescent patches. This difference, moreover, has appeared in all the other species of Photinus, in Pyractomena and in Luciola luminata Charp.. The light organs being always more spacious and brilliant in the males. Both sexes of Photinus marginellus Lc., P. scintillans Say, P. pyralis (L.) and P. consanguineus Lc. have retained fully developed elytra. The state of the wings is not described, but the females of these species fly only occasionally, for example, P. castus, move entirely by crawling. In another series of species, the luminous organs have become larger in the females. Paralleling this condition is an associated loss of the power of flight through a more or less extreme reduction of the wings and elytra. Moreover, their bodies are correspondingly large and bulky, whereas the agile flying males have remained relatively small. This set of conditions is exemplified in its various stages of evolution by well known American and European species. In Pelasia mauritianica L., the female wings have been lost and the elytra reduced to stumps, whereas they may be either entire or abbreviated in the males. Vestiges of the flight organs remain in the females of Microphotus angustatus Lc. of California and in those of Phausia delarouzeei Duv. and P. splendida L. of Europe. Both pairs are completely lost in the females of the European Phausia histericus Goze and Lampyris noctiluca L., and Lamprophorus tenebrosus (Wlk.) of India. In Phausinae and Lampophorus the males also have suffered an abbreviation of their elytra, but have not lost their power of flight. The most extreme divergence in size of sexes seems to exist in Lamprophorus tenebrosus. The male ranges between 20 and 30 mm. in length, whereas his mate attains to 60 or 65 mm. In this species the sexual dimorphism in size also reaches into the larval stage. There is no apparent difference in the general appearance and size in the first two larval instars, but the sexes diverge strongly in the rest of their development, the male having three or four instars and reaches a maximum length of about 40 mm, as compared with the five or six instars and length of 80 mm. in the female. To summarize, there has arisen from the generalized state, in which both sexes were equally luminous and capable of flight, various degrees of specialization in the family. In the female this change has involved essentially a loss of the ability to fly, the evolution of a brilliant light, and a reduction in the power of vision. Obviously the loss of wings and the consequent inability to contribute by flight to the mutual discovery of the sexes has been induced by the substitution of light flashes for the usual means of attraction. On the side of the male, the specialization toward sexual dimorphism is expressed in the retention of his ability to fly and run, in the development of larger and more sensitive antennae and especially of large keen eyes to detect the mating signals of his mate, and a trend toward the decline of his power to flash in return. It is a well established fact that the male of insects as a class takes the initiative in mating. This aggressiveness seems to underlie the persistence of the locomotor ability and the loss of the photogenic powers in the males of luminous Lampyridae and conversely may explain also the tendency of the females to become sedentary, small-eyed and increasingly luminous.

Photogenesis

General Features. The energy of the chemical reaction that is responsible for the familiar luminescence of fireflies and glowworms is transformed almost entirely into light, without appreciable heat (Allard, '20). The light may be emitted by all the stages of luminous Lampyridae. That observed on the eggs radiates from a substance imported to their surfaces before they are laid and usually fades during the first two or three days following oviposition. The larval light organs begin to function one or two days before hatching, and they appear to be present on all species, which are luminous in the adult stage. Moreover, they occur in the larvae of Lucidota festinella (Melsch.), the adults of which are diurnal and lack lights. The larval organs seem to occur rather uniformly as a pair of rounded patches on the sides of the eighth abdominal segment (Fig. 63). This is their position in Photinus consanguineus, P. scintillans, P. pyralis, Photuris pennsylvanica, Lucidota normalis (L.), L. atrna (Fabr.), Pyractomena sp., Luciola cruciata Nots., L. lateralis Nots., L. luminata, L. gorbani Rits. (Nenta), and Lampyris...
Phausis delarouzeri is said to have a pair of luminescent patches at the base of the abdomen and a second near the sixth segment (Bugnion). The larvae of Lamprophorus tenebrosus and Pelania mauretanica also are luminous. The larval lights persist for a part of the pupal period and may function during the first day or two of adulthood. Those of Photuris pennsylvanica, Photinus consanguineus and P. sciintillans continued to be luminous during the pupal period, and in Photuris still glowed until the end of the second day of adult life (Fig. 64).

On the other hand, the lights of the adult became functional when this stage emerged from the pupal case. As a result there is a brief period in Photuris during which the organs of both the larva and the adult produce light simultaneously (Fig. 66). In addition, the pupae of this species glows diffusely over its entire body and especially on the head and the thorax (Hess). The most beautiful luminescence of Luciola cruciata and L. lateralis is emitted by the pupae, the light coming from the abdomen, the thorax and even the head. Also the pupae of both sexes of Lamprophorus tenebrosus glow faintly, but only when disturbed. Aside from this general glow, the pupal stage may be said to have no light peculiar to itself, but is illuminated principally by the organs of the larval and the adult stages.

Location of the Light Organs. The luminescent organs of the adult Lampyridae first appear during the pupal stage as patches of light-colored integument, and later as white areas capable of glowing. Just before the adult issues, these patches become luminous, slowly illuminating and then slowly darkening much as the larval organs do, but later assume a flashing manner of lighting (Dahlgren, '17). The light organs of the adult have mostly departed from the paired condition characteristic of those in the larvae, being confined to the venters of the fifth to the eighth abdominal segments, but occur principally on the sixth and seventh. A number of examples will serve to indicate their shape, position and the various degrees to which they are developed. In the non-luminous Lucidota atra and L. punctata Leo., they are represented only by two small brownish scales on the last segment, whereas in the instance of Photuris pennsylvanica, they occupy the entire ventral surfaces of the sixth and seventh segments in the male but only a portion of these areas in the female (Fig. 66). These sestites bear them also in Phausis splendidula, but in the male those of the sixth consist merely of two small
patches. In the male of *Photinus pyralis* half of the fifth and all of the next two segments are luminous below, whereas the female has a luminescent patch only on the middle third of the sixth. Both sexes of this species have in addition a pair of small spots on the last ventral segment. They are similar in the males of *P. marginellus* and *P. castus*, and in the female consist simply of a small triangular spot on the middle of the sixth segment. The males of *Lusilola cruciata* Kieffer, of Japan, have the last two segments luminous but only the next to the last is so in the female (Kanda). The opposite extreme, in which the luminescent area is much the larger in the female, is exemplified by *Lampyris noctiluca*. These possess large lighting surfaces on the sixth and seventh segments supplemented by inconstant small patches on the eighth. The male produces no light at all or is only very feebly luminous through a pair of small lateral organs on the eighth segment which are carried over from the larval stage. Dahlgreen considers that the median lights of adult Lampyridae were derived by fusion of bilateral pairs and therefore represent a more specialized condition than exists in the larvae.

**Fig. 66**

*Photuris pennsylvanica*, ventral view of abdomen. A, light organs of adult male (AD) represented by shaded portions of sixth and seventh segments; B, same of female adult. After Hess ('20), Biol. Bul.

**Color of the Light.** Little is written specifically concerning the color of Lampyrid light. That of *Lampyris noctiluca* is yellowish, but changes to a yellowish green with the advancing age of the insect. *Photinus pyralis*, the common species in central Illinois, produces a greenish luminescence, while *Lusilola cruciata* and *L. lateralis* of Japan have a blue glow. The light of the American *Photuris pennsylvanica* has a greenish blue or pale blue color that distinguishes it readily from *pyralis*.

**Flash Patterns.** The flashing of fireflies is one of the most familiar natural phenomena and has received consideration in both music and poetry. The flash patterns are to some extent distinctive, but those of several *Photinus* species seem to be very similar, the number of flashes given at one time being identical, the identity extending to both sexes. Thus one flash appears to be characteristic of *P. castus, pyralis, angulata* Say and *scintillans*, whereas both sexes of *consanguineus* produce two short bright flashes in each period. On the other hand, the male of *P. marginellus* emits a single short sharp flash, while the first short bright flash of the female is followed at once by a longer one. The duration of the flashes also differs somewhat among the different species. That of both the male and the female *pyralis* is relatively long and less sharp than in the other *Photinus* named above, which has a single flash. However, Mast concluded that there is a slight difference in the length of the flashes of the two sexes in this species. The male is believed to discern this difference and thereby responds only to the signals of the female. The length of the intervals between flashes, presumably in *pyralis*, is definitely influenced by temperature. At 19.4°C, the male flashed 8.1 times per minute, and the rate increased to 15.4 at a temperature of 28.6°C (Snyder and Snyder). *Photuris pennsylvanica* may be recognized both by its greenish blue light and its pattern of flashes which is dissimilar between the sexes. These are produced in series separated in the females by intervals of 8 to 10 seconds in duration, and in the male they are repeated slightly more frequently (Fig. 67). The male flashes three, four or five times in rapid succession in each series, while the female flashes only one, two or three times (Hess). However, this species is said also to emit a single prolonged flash while flitting around bushes and branches of trees (McDermott, '10). The larviform female of *Lamprophorus tenebrosus* is said not to flash, but glows in response to certain stimuli, and the larvae of luminous fireflies generally react in the same manner.

**Flight and Flashing.** The Lampyridae mostly frequent low and relatively moist areas in the general vicinity of streams where the stages occur in the soil or under
The male of Photuris pennsylvanica, After Hess ('25), Hol. Del.

The male of Photuris pennsylvanica, After Hess ('25), Hol. Del.

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The male of Photuris pennsylvanica, After Hess ('25), Hol. Del.

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The male of Photuris pennsylvanica, After Hess ('25), Hol. Del.

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The male of Photuris pennsylvanica, After Hess ('25), Hol. Del.

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to time dazzling flashes of lightning illuminated the landscape. The air was very warm and humid, and fireflies became unusually abundant and active, especially in a low field adjoining some woods. Here thousands of these insects were wailing low over the ground, flashing incessantly as far as the eye could see. After a while a most remarkable synchronism in the flashing seemed to take place. From time to time, as if moved by a common impulse, great numbers would flash so closely in unison over the entire field that an extensive sheet of tiny light-points would gaze upon the vision for a moment and the visual fields. This synchronism in the flashing sometimes continued several times in succession, giving one the impression of alternate waves of simultaneous excitement and darkness in the expanse. At times the rhythmic impulse ceased for a considerable period over the entire field. At other times it appeared to take place only in large groups occupying particular areas of the field."

But few instances of this sort have been reported, and observers indicate that such flashing is not a common occurrence. Its infrequency suggests that the situation and conditions under which it takes place have several requisite component elements in common that rarely exist simultaneously. What these elements may be deduced in part from the instances of concerted flashing recorded in the literature, but explanations of the phenomenon must still be founded largely on speculation. The common species of the central and eastern United States, from which areas the reported American instances of synchronous flashing are known, are Photuris pennsylvanica and the several kinds of Photinus. Photuris has a distinctive flash pattern in both sexes that can not possibly be executed in concert with that of any species of Photinus. In view of the observations of Mast on the selective vision of the male pyralis, it is unlikely that one species responds regularly, if at all, to the flashes of related species having a similar mode of flashing. It appears probable, therefore, that synchronous flashing may be expected only within the limits of a single species. Moreover, the females of the several species of Photuris rarely, or never, fly, so that only the males can be concerned in this phenomenon. In addition to these biotic features, it appears that a set of certain environmental factors are essential to such an astonishing display of light. Snyder and Snyder suggest that uniformity of moisture, of light, air currents and temperature are probably necessary conditions. In the instances cited by these writers and by Rau and Allard, the night air was warm, humid and still, an atmospheric condition typically existing after an evening shower and not infrequent during June and July when these fireflies are abroad in maximum numbers. However, although this phenomenon may not be possible aside from this set of weather factors, its infrequency is also essentially dependent on the simultaneous and concentrated occurrence of the beetles in abnormally large numbers. In view of the well known numerically fruitful condition of insects in periods of years, the quantitative requirement for concerted flashing may not be expected to exist with annual regularity. Were it dependent on the short span of time the males in close proximity within the range of vision, we should expect such remarkable displays to be very common, even when only ordinary numbers of beetles are present. It has been observed, too, that concerted flashing is always of short duration. In the instance reported by Rau, it lasted perhaps 4 or 5 minutes, then the rhythm was lost in chaos, as usual, and was not resumed. But given adequate numbers under favorable environmental conditions, how may this brief flashing in unison be initiated? Rau suggests that the entire population was ready to rise for its regular evening flight but was held back by show of rain. When this suddenly ceased, they were all in equal readiness and took to wing and flashed together. Since their flashes are at fairly uniform intervals, they continued in unison quite by accident. The beetles observed by Allard were likewise said to flash in unison while they still floated low over the field, and it may perhaps be inferred that they had just taken to the air and that all had begun their flight and flashing simultaneously. Where tremendous numbers occur in concentration, waves of unison flashing could easily recur entirely as a result of chance. But Ruckmick questions the reports of prolonged and absolutely unified flashing when it is implied that it lies outside of the mental activities of the observer.

Biological Significance of Flashing. While the flashing of adult fireflies is definitely known to function in attracting the sexes, its significance, if any, in the larval stage is open to conjecture. It may serve to warn their enemies not to eat them, or illuminate their path during their nocturnal wanderings in search of food, or to assemble their kind around
prey captured by one of them. On several occasions Hess observed numbers of the larvae of Lucidota fenestralis congregated around a captured small or earthworm on which they were feeding. It is possible that passing larvae are attracted by flashes of light from those already at the prey. The adults, however, have become entirely dependent on their light signals in the phase of mating that precedes copulation. The degenerated larval females of Lamprophorus and Lampyris remain on the ground, whereas the more agile but flightless females of Photinus ascend to the top of a plant or the tip of a grass blade. Mast describes the entire process as he observed it repeatedly in Photinus pyralis. The female waits quietly on the vegetation, and the male flies about glowing fairly regularly at intervals of about five seconds. The females do not glow unless light from the males or some other source is flashed on them. But her response is apparently independent of the character of the light. Mast induced her to respond by means of flashes from an electric pocket lamp, matches, tallow candles, kerosene lamps, etc., but in all cases the response was dependent on the duration of the illumination. She failed to respond when the light stimulus was not removed after the proper exposure. Her answer was not due to the light in itself but to changes in its intensity, according to this observer. The males very rarely respond to the flashes or artificial light or to the glow of other males of their own or other species, probably by reason of a slight difference in duration between the flashes of the two sexes. If a male glows within a radius of five or six meters of a female, she usually responds almost immediately by flashing, but just before doing so she raises and twists the abdomen until the luminous area on the ventral surface is directed toward him, no matter where he is located. The male then turns directly toward her in his course and soon glows again. The female again responds and the male takes his bearings once more, the two repeating the exchange of signals until he comes close to her. Now he runs about excitedly until his antennae touch her, after which copulation takes place at once and all illumination ceases. This procedure was seen in very many different cases, and there can be no slightest doubt that the flashes of pyralis serve to bring the sexes together for copulation (Mast, '12). This has been found to be the significance of flashing also in Photuris consanguineus, P. acintillans, Lampyris noctiluca and Luciola italica L. Newport observed that the unfertilized females of L. noctiluca continued to glow vividly each succeeding night and their life is accordingly greatly prolonged, whereas the light of the fertilized females wanes in a few days after mating. The Development and Structure of the Light Organs. The structure and growth of the photogenic organs have been described for the adult of Photuris pennsylvania by Williams ('16) and Hess ('22) and for the larvae of Lampyris noctiluca by Vogel ('13). Hess traces the periodic development of the organ in considerable detail through the embryonic and later stages of the beetle. These investigators agree that the photogenic organs in the Lampyridae develop from the fat body and are accordingly mesodermal in origin rather than hypodermal, as formerly believed. The adult organ is first seen in the larvae when they are near pupation (Fig. 68). It is derived directly from the fat-body by the expulsion of its cells, which migrate to the ventral hypodermis. The cells thus liberated from the fat spheres to form the photogenic organ accumulate as an indefinite mass on the hypodermis and there proliferate. Two layers are gradually formed. The reflector layer, which is dorsal in
position, forms a sort of pavement epithelium of smaller, more clearly defined cells, while the photogenic layer is made up of larger, more rounded cells with more obscure limits. Tracheae and nerves enter both layers. The light-making organs of the larva develop as evident structures in the late embryo. They are derived from neighboring fat cells, by migration and proliferation. As in the adult, they consist of a luminous layer and a reflective layer (Williams). Lund ('11) found that no fundamental structural difference exists in these organs in a series of twelve species from Minnesota and Jamaica. The elementary photogenic mechanism of which the organs are made, - the tracheae, tracheoles, tracheal end - and photogenic - cells with their relation to the nervous system, taken collectively, are the same in all these forms. Their gross structure and arrangement are represented diagrammatically in the drawing by Williams (Fig. 69).

The Photogenic Process. At least water, oxygen and a photogenic substance are believed to be necessary for the production of light in animals. It has been rather conclusively established that the light of the Lampyridae is the result of an oxidation (Kanda) of waste substances formed in the physiological processes of the insect and stored in the cells of the dorsal or reflector layer of the photogenic organ. The precise nature of the chemical involved has not been determined. Lund suggested that nucleic acids are broken down to form the deposits oxidized to produce light, but McDermott ('15) was unable to obtain an active luminescent extract by the use of alkaline solvents. It has also been proposed that the substance may be a fat, an albumin, a lipoid, a nucleoalbumin or a lecithoprotein. Harvey ('14), however, concluded that it is not a true fat or any fat-like body such as lecithin but most likely a protein. This investigator has shown that the luminescent substance has a granular form, is insoluble in water and will not be used up by oxidation in the absence of water. Numerous tracheal branches end in the store of photogenic material and oxidation is thought to take place to produce light at the tracheal ends. The primary control of the organ is by nerves in direct connection with the photogenic tissue and not by an external muscular mechanism regulating the tracheae (Lund). But the photogenic tissue is irritable and also responds locally to mechanical stimuli. Small ('31) analyzed flash curves recorded by use of a photelectric cell and amplifier in connection with the string galvanometer. From these studies it is inferred that two independent mechanisms govern the amount of light in any flash of Photuris pennsylvanica. One affects only the height of the intensity-time curve, the other primarily the duration of the Flash. The mechanism effects the control by regulating the admission of oxygen to the cells containing the photogenic substances. The tracheal end cell is thought certainly to be the responsive mechanism in the control of luminescence.

Food and Feeding

Food of the Adult. The adults of Pelania mauritanica take no food, and Phausis delarouzeei and Lamprophorus tenbro zuer at most lick up dewdrops or may take sweet liquids from flowers. Williams ('17) states that Photinus, Lucidota and Pyractomena may be herbivorous as adults. The males of Photuris pennsylvanica refused all foods in captivity, but Williams and Hess ('20) report, however, that the female of the latter species is a voracious and, sometimes cannibalistic, predator. In cages they readily devoured the males of their own kind. During the evening they are either in flight, or about the base of grasses in search of food. One evening Williams disturbed six separate females engaged in consuming males, but never the females, of Photinus spp. Hess commonly observed the females of this species eating also the males of P. ACU-
tillans, P. marshalli and P. consan-
guineum. It is thought that the frequent
flashings of the female pennsylvaniae at-
ttract the males of the Photinus, thus lur-
ing them to their death.

Food and Feeding of the Larva. So
far as known, the larvae of the Lampyridae
are exclusively predacious and their food
appears to consist largely of snails, both
naked and shell-inhabiting forms being
devoured, but Lucidota fenestralis and
Photuris pennsylvaniae also ate earthworms
in nature, and somewhat of a variety of
food animals was accepted by pennsylvaniae
in laboratory feeding tests. The food of
Luciola gormani consists mainly of worms and
naked molluscs, while a tendency toward gregariousness while feeding has
been observed in the above two species.
Snails are the only food reported for the
larvae of L. tenebrosus, Phausis delarou-
zezi, Lampyris noctiluca and Luciola lu-
sitanica. Pyrophorus similis K. Oliv. of
South Celebes is aquatic and probably eats
water snails (Blair), and Luciola cruciata
and L. lateralis are very fond of Melania
and Oncomelania which are the intermediate
hosts of such Helminths as Schistosomiasis,
Paragonimus and Metagonimus, responsible
for epidemics in certain districts of
Japan. The larvae of Lamprophorus tene-
brosus prey on the African snail, Achatina
fulica, a pest in vegetable and flower
gardens in Ceylon. The male larvae ate
from 20 to 40 snails while the larger fe-
males destroyed 40 to 60 snails, during
their period of development. The male
larvae sometimes go three to four months
without food, but the females rarely fast
more than a month. The regular absence
of snails during the aestivating season
has probably induced this ability of the
larvae to survive for long periods with­
out food. In feeding experiments conduction
by Vogel ('15), the larvae of Lampyris
roctiluca devoured "Limax agrestis .
Helix hortensis, g. arbustorum, g. erice-
and Succinea sp. A larva weighing
55 mg. overcame a hortensis snail that
weighed 1250 gr. or 227 times more than
the predator. It is believed that the
larvae of Pelania maurusitania live on the
small molluscs, Running devoluta, and snails of
various sorts in the nests of the ant,
Mesegar barbarus (Croes, '24). Snails proba-
bly also form the principal food of Pho-
thuris pennsylvaniae. They ate the slugs,
Agriolimax campestri, A. agrestisi and a
small, Buccinum avarei in feeding experi-
ments (Hales, '20), but they killed a small
individuals of Limax terrestris, lar-
va of Leptinotarsa decemlineata, the cut-
worms, Paraagrotis mosaica, P. tesselata,
Peridroma margaritosa and promptly ate
second and third instar nymphs of Anasa
tristia. But they did not kill or eat
Oniscus asellus or the Carabids, Nebria
pallipes and Chlaenius pennsylvaniae,
which indicates that the larvae require a
soft-bodied animal which they can pierce
with their mandibles. Snails and cut-
worms, taken very readily by the pennsylvaniae
larvae, were plentiful at night in
natural situations inhabited by these in-
sects. Williams considers it probable
that the larvae of Photinus and Pyracto-
mana also are predatory.

So far as described, the mouthparts
of Lampyrid larvae are symmetrical, tubu-
lar, tapering and curved inward. The man-
dibular canal opens apically just behind
the tip, and at the base communicates with
the inside of the mouth (Fig. 70). Ac-
cording to most statements concerning the
mode of feeding, the larvae are like those
of the Carabidae and Dytiscidae in digest-
ing their food preorally. The structure
of the jaws indicates that Lamprophorus tenebrosus, Luciola cruciata, L. latera-
lis, L. gormani, Phausis splendidula, Pho-
turis pennsylvaniae, Lucidota fenestralis
and Lampyris noctiluca feed in this man-
ner. The mandibles of larval Lampyridae
are generally described as having a sub-
apical tooth (Fig. 70, 3) on the inner
margin in addition to the longitudinal
canal.

Most Lampyrid larvae are nocturnal
and naturally are abroad when their prin-
Diptal food animals, the worms and snails, also are active. They crawl about with their heads fully exerted and the maxillary palpi and antennae in constant motion, appearing to feel their way by means of these appendages (Fig. 71).

**Fig. 71**

It seems very probable that they find their food by chance. When the antennae touch the food animal, the larva plunges its mandibles into it. Whether a shelled snail or a free-living creature, the victim is bitten repeatedly, and at each bite a small quantity of brown fluid poison injected. The snail is thereby paralyzed and finally killed. The snail attacked by Lamprophorus tenebrarum immediately withdraws into its shell when bitten, and at the same time gives off a quantity of frothy liquid and mucus. The larva gradually sucks up the liquid, and usually follows the snail into its shell. The snail sometimes makes persistent efforts to come out again, but the larva continues to irritate it, and it eventually retires as far as possible into the shell followed by the larva. When a number of *Lucidota fenestrata* larvae attacked an earthworm three inches long, one part of the worm remained sensitive several minutes after other regions of it had become paralyzed. Ten minutes from the time the first larva bit the worm it was dead so far as could be determined (Hess). The number of bites required to paralyze snails attacked by *Lamprophorus noctiluca* depends on the relative size of the predator and prey. In some cases the snail was bitten ten times or more, but one bite of a large larva was sufficient to kill a *Helix* the size of a large pea in two hours. Vogel traced the paralyzing fluid to the mid-intestine, and found that it dissolves protein and gives a weak alkaline reaction. The poison seems to work first on the nerves and muscles controlling locomotion (Vogel). At room temperature the pulse beats of *Helix pomatia* rose from the normal number of 36 to 86 immediately after a bite. The pulse rate then drops with the further working of the poison. However, this midintestinal secretion also serves to liquefy the tissues of the food animal. The fluid was found not only to be injected through the mandibular canals but also poured upon the flesh from the oral opening. The chemical dissolution of the tissues is aided by the constant mechanical action of the mandibles, their two inner teeth, where present, tearing the flesh to pieces. As far as could be observed, the mandibular canals do not serve for the intake of food. The victim's flesh, which is mostly liquefied in situ, extraordinarily, is sucked in through the aperture of the mouth. But Hess noticed that very small pieces are also taken into the mouth where they are played back and forth by the mandibular teeth and dissolved there by the intestinal fluid. A large number of hairs surround the mouth of *Lamprophorus noctiluca*, all pointing inward so that solid particles can not enter the mouth even though it is open. Such particles are strained off and later removed by the caudal brush of the larva (Haddon).

**Life History**

Enemies and Defense. Many adult fireflies, when captured, emit a pale yellow fluid from the pygidium and the joints of the hind coxae, which may be unpalatable to many of their enemies (Hess, '20). However, spiders are known to eat luminescent beetles, and the females of certain Lampyridae devour especially the males of their own or related species, showing that the fluid is not effective against all foes.

Copulation. As already stated, the flashing of adult Lampyridae serves to attract the sexes and leads to copulation. The wingless females of *Lamprophorus tenebrarum* and *Lamprophorus noctiluca* seem to flash from the ground where they also copulate, but *Photinus* spp. and *Lucidota fenestrata* mate at the tips of grass blades, and the like, where the female rests while flashing in response to the males. On the other hand, *Photuris pennsylvanica* was never observed copulating on, or near, the ground, but while clinging to the leaves of trees, often at considerable heights (Hess, '20). The lights become dim during the act of copulation.
but the female glows again at once if separated from her mate. When Photinus pyralis enters in copula the second tip of her abdomen toward the male, the latter being mounted upon her back so that the end of his abdomen extended slightly forward, then he enters the oviposition process in P. marginellus, P. cautus, and P. scintillans is the same as in pyralia. The sexes of Photinus, Lampyris noctiluca and other Lampyridae commonly remain united from one to three hours, and union was repeated frequently in Lucidota fenestralis. Considering that the male Lampyridae generally take little or no food, it is probable that they die shortly after the insemination has been accomplished. Observations to this effect are reported for noctiluca, Lamprophorus tenbroeius and other species.

Oviposition. The eggs of the Lampyridae are generally described as almost spherical, smooth, colorless, adhesive and temporarily luminous. The interval between the emergence of the adult from the pupal cell and the beginning of oviposition is short, or four to five days in Lucidota fenestralis, about seven days in Photuris and Photinus, less in noctiluca and only a day or two in the case of Phausia delarouzzei. The eggs are always deposited one by one. The mating surface cover such as moss and rootlets of grass and other vegetation. Considering that most females of Lampyridae in the reproductive zone flash from the tips of grass blades, it is probable that they lay their eggs at the bases of these plants. In fact, those of Photinus consanguineus and Photuris pennsylvaniae have been found in such situations (Hesse). Lampyris noctiluca does not oviposit until her abdomen becomes greatly distended with eggs, then, within one or two days after copulation, deposits about 100 eggs. The captive female of Lamprophorus tenbroeius sometimes places her eggs in a low heap on the top of the soil, or re-treated to the bottom of a cavity excavated in the soil to oviposit. Throughout the incubation period, which lasts about seven weeks, she curls her body around her eggs and thus keeps guard over them. If removed from her eggs she soon finds her way back and curls up over them again, or if they are scattered, usually collects them one by one into a heap, carrying each egg with the first pair of legs or rolls it over the soil. This maternalistic care recalls similar practices in the earwigs. During the oviposition period of one to three weeks, the females laid from 2 to 30 eggs per day. Twelve individuals deposited a total of 792, or from 30 to 100, or an average of 66 eggs, per female. Pelania mauritianus are deposited in agglutinated masses of 4 to 12. About 60 to 80 eggs are laid by one female, and are doubtlessly placed in the nest by the ants (Cros). The average gravid female of Photuris pennsylvaniae contained 50 mature eggs and 76 to 100 immature ones. While the sluggish females of Lamprophorus tenbroeius lay their eggs in a mass and in a brief period of time, the more agile females of Photinus, Photuris and Lucidota, observed by Hesse, place them singly and more or less separated, and oviposition continues over periods of two to three weeks.

Incubation. On the whole, Lampyrid eggs require a relatively long period for incubation. In the following instances, the duration of this period is expressed in days: Pelania mauritianus, 30 to 60; Lamprophorus tenbroeius, India, 49; Phausia delarouzzei, southern Europe, 36; Luciola luminata, Java, 26 to 36; Lampyris noctiluca, Europe, 27 to 30 in hot weather and 40 or more when cooler; Photinus consanguineus, 20 to 22; P. scintillans, 10 to 21; Photuris pennsylvanica, 22 to 27, and Lucidota fenestralis, 19 to 21 days. The latter four species were observed in the eastern United States.

Larval Life. The larvae are elongate and flat with short legs and a prognathous head, - in short, onisciform (Fig. 71). They share for most part the low moist situations also inhabited by their chief food animals, the snails. Photinus and Lucidota are very largely subterranean while in hibernation. Photuris pennsylvaniae occupies under stones or concealed in depressions in the ground, and many of them were found clinging to moist stones, weeds and the like at the water's edge (Cros). It is said that Pyrostomona is probably in part arborescent. Blair and Ogura have reported four species that habitually live in water. Blair describes two species provisionally determined as Pyrophanes similis and Luciola vespertina Fabr., and Ogura found Luciola cruciata and L. laterale inhabiting water in rice fields in Japan (Fig. 72). L. vespertina occurred among the roots of Pistia stratiotes and possesses a star-shaped caudal funnel, capable of extension and withdrawal, and connected with two longitudinal lateral tracheal trunks. When used during respiration, this organ was thrust into the air masses collected by the ants (Cros).
neath the floating leaves of *Pistia*. *Pyrophanes* and the two species of *Lucidota* bear a pair of sac-like gills on the first eight abdominal segments, each gill containing branched tracheae. When irritated, the larvae of *L. bruchiata* and *L. lateralis* protrude a forked organ from a slit-like crevice on the pleura of the mesothorax, metathorax and abdominal segments. At the time they are protruded, a peculiar odor, believed to be defensive, was perceived. No Hymenopterous or Dipterous parasites, or other specific enemies, seem to be known for Lampyrid larvae.

Fig. 72

Caudal Appendages. The larvae of some species bear a number of finger-like processes on the end of the abdomen. In *Phausis delarouzzei*, according to Bugnion, they take the form of eversible tubules that are projected by blood pressure. They are likewise protrusable in *Photuris pennsylvanica* and *Lamprophorus tenebrosus*, and constitute a cluster of soft, milky white thread-like organs in the latter species. Two bundles of such processes occur on *Pyrophanes similis*, according to Blair, and in *Phausis splendidula* they are armed with terminal hooks (Verhoeft). Similar appendages are known on the larvae of *Luciola lusitanica*, *L. bruchiata*, *L. lateralis*, *Lamprophorus noctiluca*, *Photinus pyralis* and *Pyretrumena* (Fig. 73). A like cluster of retractile organs persists on the larval form female adult of *Lamprophorus tenebrosus*. This is significant in view of the fact that such do not appear in the male. Blair regards them as an adaptation for holding to the surface of stones and other supports in the case of *Pyrophanes*, and McDermott ('10) noticed that *Photinus pyralis* larvae push themselves along with the end of the abdomen. But they are more frequently regarded as cleaning organs. When attacking and eating snails, the larvae commonly become smeared with the mucus secreted by their prey, and during, or at the completion of, the meal curl their abdomens around to apply the brush-like caudal organs to various parts of the body surface.

Fig. 73

Larval Growth. Knowledge concerning the growth and molts of Lampyrid larvae is fragmentary. The larvae of *Lamprophorus noctiluca* have five molts (Voegel, '27), but only four are said to occur in *Phausis delarouzzei*. The larval life of *Luciola lusitanica* is eleven months, but perhaps much longer when food is scarce. After living about one and a half to two months in an experimental nest of *Messor barbarus*, the larvae of *Polaneta mauritanica* left the nest and dwelt under nearby stones. The extreme sexual dimorphism of *Lamprophorus tenebrosus* lies at the bottom of the wide divergence in the mode of development of the larvae. During the first two instars there is no apparent difference between the potential male and the potential female larva. Some potential males molt three times, while others do so four times be-
fore pupating, whereas the female larvae molt either five or six times. Thus, the number of molts is apparently adapted in part to size. The first instar of this Indian species normally occupies from 15 to 24 days. 20.5 days being the average duration of 50 larvae. The second instar was passed in 19 to 28 days, the average period for 44 larvae being 24 days. The third instar of the potential male saw no further great increase in size. Upon entering this stadium it is 35 to 40 mm. long, and after 30 to 50 days goes into the fourth and final period, which may last from 100 to 150 days. During the last growth interval, it makes but little increase in size, and may become 45 mm. long. Pupation follows the fourth instar. However, some of the potential males may persist for 150 to 200 days in the third instar and pupate at the end of that time, and may actually decrease in size owing to long periods without feeding. On the other hand, the potential female larva continued to make a marked increase in size after, as well as before, the second instar. The mature larva may become as much as 70 mm. long. The average duration of the third instar female was about 31 days, and growth was rapid. The fourth is passed in 30 to 70 days, and when six instars occur, the fifth requires 30 and the sixth 70 to 100 days. But female larvae that pupate after five stadia remain in the fifth from 100 to 150 days. It is probable that most of the larvae of both sexes are full grown within 8 or 9 months.

Construction of the Pupal Cell. So far as known, most Lampyrid larvae excavate little pupal cells just below the surface of the ground or under stones. Williams reports this to be the habit of Photinus consanguineus, P. scintillans, Photuris pennsylvanica, Lucidota corruga, and L. lateralis. The larva of Pyractomena sp. suspended itself in the manner of a Cocinellid on a vertical glass wall of a cage by means of an anal secretion. After hanging for a week it pupated there. The larva was found in nature ascending an oak tree. The larvae of Lucidota cruciata and L. lateralis come out of the water to pupate. The manner of constructing the pupal chamber is described by Hess (120) for Photuris pennsylvanica. "A suitable spot on the surface of the ground, usually at the base of moss or grass is chosen, and at once the larva begins building a lattice work of soft earth over itself, in the shape of a small dome, by which it conceals itself in about a day. In the construction of this cell the larva removes earth from underneath itself and mixes it in its mouth for a period of about half a minute. It then extends its head to the lattice work of the dome and regurgitates the moist earth in the form of a short ribbon-like mass, which it applies to the walls of the chamber. By the frequent repetition of this process, the lattice-like frame-work finally entirely covers the larva (Fig. 74).

Even after it has completed the dome, the larva can be seen between the meshes for several hours before it is entirely concealed. By repeatedly removing the earth from the bottom of the chamber and adding it to the inside of the dome-like wall, the chamber is deepened, and its covering is strengthened. After about 100 days. It is probable that most of the larvae of both sexes are full grown within 8 or 9 months.

The larva (Fig. 75) lies on its back throughout the period of transformation and is largely supported by long setae projecting from the sides of the thoracic and abdominal tergites.

Duration of Pupation. So far as determined, the pupal stage of Lampyridae is rather short. Photuris pennsylvanica requires 16 to 18 days out of doors in May and June; Photinus consanguineus transformed in 12 to 15 days and P. scintillans in 9 to 14 days, and in Lucidota cruciata this stage lasted only 7 to 8 days (Hess, '20). Bugnion reports a pupal period of 18 to 20 days for both Phausia delecarteii and Luciola luminosa, in the
Lampyris noctiluca and Lamprophorus ten­ebrosus, which have extremely developed sexual dimorphism, the larval form females transform in 8 days and 7 to 10 days, re­spectively, whereas the males similarly require 11 and 16 to 23 days. According to Vogel ('27), the longer duration of pupation in the case of the relatively small males is explained by the develop­ment of their wings and the large eyes.

According to Vogel ('27), the longer duration of pupation in the case of the relatively small males is explained by the develop­ment of their wings and the large eyes.

Life Cycle. Some species pass through their cycles in a year, whereas others require two years for a genera­tion. So far as known, all of them hibernate as larvae, in the shelter of the ground and under logs and stones. In the two-year species, the first winter is passed by the small larvae, and these have become more or less nearly mature when the second winter overtakes them. The one-year species hibernate in a partly grown larval state. In general, ac­tivities are resumed by the larvae during April. Pupation begins as early as latter April and continues for several weeks. It is a well known fact that the adults or fireflies are chiefly abroad and flashing in the nights of June and July. Blatchley cites the following rec­ords for the more common species of In­diana: Lucidota atra, June 4 to July 7; L. sorruoza, April 1 to October 21; L. fenestrata, June 19 to August 17; Pyra­tomena angulata (Say), May 10 to July 8; Photinus pyramidis, June 8 to July 29; Photuris pennsylvania, May 23 to August 6. The adults of Photinus consanguineus issued from the pupal cases on June 1 to about August 1, and P. scintillans from June 1 to July 20 (Hess). Lampyris noctiluca, Phausis splendidula and Phos­phaenus hemipterus, - the common species}

of Germany, normally become adults in the latter half of June and disappear again during the first half of July (Vogel, '27). Croes states that Photuris angulata is abroad from late May to early July. It is therefore during June and July that the fireflies are principally engaged in copu­lation and the larval stage. However, adults persist beyond the period of the majority and continue their reproductive activities into August or even September. The larvae of Lampyris noctiluca that hatch from eggs deposited late in the sea­son are so small that they are unable to reach maturity during the ensuing summer, and, accordingly, undergo two wintering exper­iences (Vogel). The larval life of Photinus consanguineus, P. scintillans, Lucidota atra, Photuris pennsylvania, and Pyra­tomena extends in most cases over the greater part of two years, both small and large sized larvae appearing together in midsummer (Hess, Williams). The larvae of Phosphaenus hemipterus, Phausis splen­didula and for most part Lampyris nocti­luc שנים make most of their growth during the season of their advent. These species re­quire only one year to complete their en­tire metamorphosis. Bugnion reports a larval life of 11 months, and 8 to 75 days for the other stages, of Luciola lusitanica. Approximately the same amount of time is required for the development of the several stages of Enarsus delarou­zeel. It seems, therefore, that these species also complete a generation in a year. The females of Lamprophorus tene­brosum are usually found in India from October to about January, and the young larvae appear to be most numerous from February to April. It is probable that most of the larvae reach their full growth within 8 or 9 months. The complete cycle is calculated to be about 11 months for both sexes of this species (Hutson and Austin, '24).

**D. DRILIDAE**

**General Features.** That Drillus flavescens Rossi undergoes its metamorphos­is in the shells of snails was recog­nized by Mielzinsky as early as 1864 (Cros, '26). Owing to its extreme sexual dimorphism, the older entomologists re­garded the sexes as representing two distinct genera. The females are large, entirely aperous and larviform, whereas the small males are winged. The males observed by Hirschauer measured from 4.5 to 8.5 mm. in length, and the dried specimens of the female were 18 to 20 mm. long and a living one measured 34 mm.
A similar dimorphism seems to exist also in *Prilus concolor* Abr., *D. mauritanicus* Lucas and *Macrogaster passer* Bassi. The best account of the life history concerns *D. flavescens* which was studied by Crawshay and others.

Food and Feeding. Although kept alive in some instances as long as two to three weeks, the females of these species have not been observed to eat. The larvae seem to feed exclusively on snails, excepting a general inclination among them toward cannibalism. *Cyathostoma volzannum* and *Rumina decollata* appear to be the snails preferred by *D. mauritanicus* in northern Africa (Cros, '26). The larvae of *D. flavescens* fed principally on *Helicella itala*, *H. virgata* and *H. serotina* in England but devoured also *H. cantiana*, *Byr horns rufescens*, *Vitrea celleria*, *Helix nemoralis*, *H. hortensis* and even the largest individuals of *H. aspersa*. It passed indifferently from one to another in the course of its growth (Crawshay).

The first instar larva of *flavescens* is similar in form to the primary larvae of *Melolitae*. The mandibles are strong, sharp and up-curved from following the winding clevity of the snail's shell, and a sucker-like anal foot enables the larva to cling firmly to the surface of the shell. The spiracles lie between two rows of fleshy bristly processes that shield them against the grimy slime of their victim. The larvae are capable of rapid and prolonged running in search of snails. Having found one to its liking, the small larva displays a tendency to work underneath the shell, while the larger ones crawl upon it and examine the surroundings by reaching out to their full length on all sides as they hold on by means of their anal clasping organ. If the place proves to be too exposed, as on a roadway, the larva endeavors to remove the snail to a more concealed situation. In so doing, it grips the shell with its anal claspers, bends itself over to one side of the shell, and taking hold of the ground with its mandibles, hauls the small backward. The larva clammers to the top of the shell from time to time to further examine the surroundings, then resumes the work of moving the snail, which may be continued from one to three hours before a satisfactorily sheltered place is found and the snail attacked. But larger larvae, measuring 14 or more mm. in length, generally attacked the snail very soon without removing it, however exposed the position was. As they crawl along, the larger snails make violent but mostly unsuccessful attempts to dislodge the larva. The latter quickly takes up a position near the orifice and fiercely assails the snail with the mandibles. By the same method, the snail is kept from coming out of its shell. Sometimes, when the victim threw a film of mucus across the orifice, the larva was obliged to work for an hour or a half to penetrate this barrier (Crawshay). Cros observed that the larva of *D. mauritanicus* must overcome the resistant plate of mucus secreted over the orifice by *Rumina decollata*. In so doing, the larva attaches itself to the shell and wedges its mandibles between the shell and the edge of the plate. The snail responds with a copious secretion of slime which free the plate and permits the enemy to enter. The larva of *D. flavescens* forces itself in between the shell and the snail, or, holding to the latter with the mandibles, it may be drawn into the shell by the receding snail. Finally the larva consumes the whole or the greater part of the victim. Because the prey greatly exceeds the predator in size, the latter, which is capable of extreme dilation in the abdominal region, swells to an unrecognizable form and dimensions (Fig. 76).

When about to defecate, the larva creeps backward to the orifice of the shell and squirts the excrement far away. Schmitz (Rüschkamp) found that the vacuoles of the snail still pulsed on the fourth day after the predator entered the shell, which fact suggests that the larvae of *flavescens* differ from those of their Lampyrid relatives in that they produce no paralytic or solvent secretion to inject into their prey during the feeding process. Considering that the meal may continue ten to fourteen
days, it is obvious that a part of the tissues of the snail may become a decaying mass long before they can be consumed.

Copulation. The mating activities of _D. flavescens_ were observed by Russchkamp in the margin of a woody marsh. The female spends the nights hidden in the surf, but stays on the leaves of low plants by day where she scatters a substance having a sharp corrupt odor. A similar material is produced also by the females of _D. mauritanicus_. The male is clasped as soon as he perceives the odor, flies quickly to its source and drops down in the proximity of the female. But the winged female flies hastily as soon as she is discovered and is never voluntarily quiet during the entire act which may last three hours. Often several males go in pursuit on foot. Having caught her, he mounts upon her back and soon moves caudad to enter into copulation. In one instance a female carried two males, one in copula, the other, which had obviously expended himself shortly before, hanging limp from her body. Russchkamp cites three instances in which one female mated with three or four different males within five to ten days. On the other hand, he observed that females that had already mated, waiting day after day in an exposed place as if not adequately impregnated. A satisfied female ceases emitting the attracting odor and the males die within an hour or so after the last copulation. Russchkamp concludes that the sexes of _flavescens_ are represented in about equal numbers, reports to the contrary probably being based on collections that consisted almost entirely of larger snail shells occupied by the female beetles. It has been noticed that the size of the adults is influenced by the volume of the snail upon which the larva fed.

Oviposition. After copulation, the female of _flavescens_ goes down into the grass and turf where she lays her eggs and dies. Crawshay found two dead individuals two inches deep, each lying within a half inch of a compact heap of eggs, composed of about 30 to 35 each. This observer calculated that one female may lay 300 or more eggs, basing his estimate on an instance in which a gravid female contained 267 eggs. Russchkamp saw a female trying the ground with the end of her abdomen to find a suitable place for her eggs. There she remained from 7:30 P.M. to 8:30 A.M., or 13 hours, during which time she laid a loosely joined mass containing 450 or 500 eggs. At the beginning, the eggs were laid at intervals of 6 to 10 seconds, but after several hours the interval increased to 30 seconds, and later were still longer. The abdomen was then empty and crumpled. The individual females of _D. mauritanicus_ are said to deposit 70 to 100 eggs, although the larger lived as long as 14 and 19 days, a second deposition in this species was not seen. The females of _concolor_ lived three weeks without food and laid clumps of fertile eggs two to three days after mating.

Incubation. Incubation in the instance of _concolor_ required 40 days during latter May and June (Deubel). The eggs of _D. flavescens_ hatched in 6 or 7 weeks, and those of _D. mauritanicus_ did so after almost three months, from September 17 to December 14, in northern Africa (Cros).

Larval and Pupal Life. The newly hatched larvae of _flavescens_ remain inactive by their egg shells for two to three days, then engage in a brief period of free life during which they run about actively in search of smalls, transport these to cover and gain entrance into the shell. The snail, after the larval life is terminated, spent within the shells where they feed on the smalls, make their molts and remain for shelter after the prey has been consumed. If touched, they coil the small and the larger larvae respond at once by rolling up and feigning death. The number of instars constituting this stage has not been precisely determined.

In the course of its development, the larva of this species may assume a dormant form that departs strikingly in both physical and physiological respects from the usual active type. Now it is not capable of feeding or of engaging in more than a heavy grub-like motion when disturbed. The segments lack chitinous sclerites, leaving the body almost entirely soft with a dingy white color and almost no hairs excepting on the last three or four segments. The head is small, the mouth parts rudimentary, the antennae minute and the legs short, soft and without claws. An offensive acrid fluid is produced from both ends of the body when disturbed. The assumption of this form seems to be caused by an inadequate food supply, periods of unfavorable weather, or other untoward influences. Crawshay found that larvae entered this state as early as June 2, owing to a period of low temperature preceding the time of molting. Russchkamp was able to prolong or shorten the duration of this state by regulating the amount of moisture and food given the larvae. In one instance he succeeded in bringing the larva...
back to the active state in 13 days. Con­
sidering that it results from various
stringent conditions, including food
shortage, this larva can not properly be
referred to as a winter or a summer type,
as is sometimes done in the literature.
Rischkamp more appropriately calls it the
resting form. It appears to be equivalent,
functionally, and essentially also in re­
gard to structure, to the coarctate larva
of the blister beetles and the hypopus of
certain mites.

The larvae hatch in July and feed
until September, attaining only a small
size in the first year. They then hiber­
nate in the shells last occupied, but
leave them the next spring. In the sec­
ond year, they may feed at regular inter­
vals until September, or are equally
likely to enter the inactive state and
pass nearly the entire warm season in the
shell in this form. Many of the larvae
doubtless become full grown during this
second year, but more of them probably
feed for a third summer, at the end of
which they reach maturity. The several
winters of this species are spent as lar­
vae of the dormant form in the shells of
the snails last consumed. In the spring
prior to pupation, the larva directs its
head toward the orifice of the shell.
Transformation to the adult stage requires
from July to September of the first year,
and they may feed at regular inter­
vals until September, or are equally
likely to enter the inactive state and
pass nearly the entire winter season in the
shell in this form. Many of the larvae
doubtless become full grown during this
second year, but more of them probably
feed for a third summer, at the end of
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winters of this species are spent as lar­
vae of the dormant form in the shells of
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head toward the orifice of the shell.
Transformation to the adult stage requires
from July to September of the first year.

The adults of the family as a whole
are in part predatory and also feed to some
extent on plants. The species of Cantharis,
Chauliognathus and Rhagonycha sometimes oc­
cur in large numbers on flowers and some of
them are believed to eat pollen and nectar.
In southern Ohio, Chauliognathus penna­
vaniaensis Say, fed principally in the blossoms
of Crataegus, Rubus, Achilles, cucumber and
Helianthus strumosus, and eagerly consumed
the pulp of broken watermelons in the field
(Houser and Baldur). However, several
species of Cantharis and Podabrus have been
observed to eat small soft-bodied insects,
and Aphids in particular (Fig. 77). Can­
tharis divius Lec. feeds upon many kinds
of Aphids on cultivated plants, but has
been especially predatory on Rhopalosiphum
prunifolii, Macrosiphum granarium, M. Po­
saes, Aphis gossypii and Myzus persicae, ac­
cording to Essig. G. consors Lec. has been
found destroying Plautia stali and the eggs of Heliothis virescens. Among the
natural enemies of Macrosiphum pisi in Wis­
cconsin (Fluke) are Cantharis lindoe Fab.,
G. carolinus Fab., Podabrus rugulosus Lec.,
and G. tomentosus (Say). C. carolinus was
also seen greedily devouring Macrosiphum
rubeculaeidae on Solidago in Ontario (Motli­
sembert). In Oregon, Podabrus tomentosus
is regarded as one of the most important
agencies in the control of all kinds of plant lice and particularly Myzus cerasi and Aphis rosea, crushing them with the mandibles and extracting the juices (Wilson). Webster cites records showing that it also feeds on Pemphigus popullaceae and F. populicola. Sometimes as many as four individuals waited together at the opening of the galls to catch the mature emerging Aphids, or reached into the cavity to pull out and devour large and small alike.

Fig. 77
Adult of Podabrus tomentosus (Say).
After Essig ('26), Ins. of West. N. Amer., Macmillan Co., Inc. Redrawn by Mrs. W. V. Balduf.

A small number of records indicates that the larvae are principally predacious, preying chiefly on small Arthropods which they find on the ground. The pro-larvae of Rhagonycha fulva Scop. and Cantharis rustica Fall. have yolk in the intestines at the time of hatching, and take no other food for two or three days (Verhoevef). The eggs of Melanoplus spectabilis were destroyed by the larvae of Cantharis bimaculata Say in Minnesota (Webster), and the larvae of undetermined species are known to have killed the caterpillar of Carposopas pomonella and the grubs of Conotrachelus nenuphar. After a series of feeding experiments, Payne concluded that the larvae of Cantharis litturata Fall. should be considered omnivorous. They refused to attack slugs and probably could not catch Carabid larvae, centipedes and millipedes that were offered. But small specimens of Lumbricidae were eaten freely, and they readily devoured the maggots of the Syrphid fly, Plectrophenax albinus, which occurred in numbers in the natural haunts of the Cantharidae, and also consumed with zest the larvae of a Borborid fly and a Lema species. However, they are said to have preferred wheat grains, and also gnawed at pieces of potato, celery and other vegetables. The larvae of Cantharis fusca L. and C. rufa L. were formerly reported attacking wheat in fields (Payne). Many adults of Diabrotica vittata were killed in a field of cucumbers by the almost mature larvae of Chauliognathus pennsylvanicus (Fig. 78). The larvae were common under the vines and caught the beetles made sluggish by the cool fall weather. In seizing the prey from the side, one mandible penetrated the venter and the other an elytron. During the feeding, the beetle's body was broken into pieces and only the soft internal parts were eaten (Houser and Balduf).

Fig. 78
Larva of Chauliognathus curtellaris

Life History
Hibernation and Spring Development.
All the data at hand indicate that the Cantharidae of Europe and North America hibernate as partly grown to mature larvae. This has been established by direct observation on Cantharis litturata, C. rustica, Chauliognathus pennsylvanicus and Melithea flavida Say. The latter wintered in numbers under bark and moss on old
branches of aspen. Moreover, pupation in a number of species is known to occur in April to June, and the adults of most species make their appearance during May and June, from which it may be assumed that hibernation in the larval state is the prevailing condition. Beiling found the mature larvae of Podabrus alpinus Payk., Cantharis abdominalis Fab., C. Rustica C. Rustica, C. livida L., C. rufe, C. discidae Abr., Rhagonycha fulva and Melanodes fulve Wals. in moite hills and the deserted nests of ants in the woods. Here they made their transformations from April to June. The first pupa of Cantharis nitura was seen on May 12, C. labu­cida Fab., pupated in 12 days in April - May, and C. discidae required 10 days. The species observed by Beiling spent about two weeks in this stage, and the larvae descended rather deeply into the ground. Podabrus cornutus pupated 3 to 6 inches deep in earthen cells in moist soil, but the cells of Chauliognathus pennsylvanicus were only an inch or so in the ground. Before pupation the larvae of Cantharis nitura formed circular burrows at a depth of 2 to 3 inches in the field.

Occurrence of the Adults. The adult stage of the family as a whole is abroad during the summer months. Podabrus tene­nus is present in Oregon for about two months beginning May 1, in California from May throughout the summer, and Blatchley reports finding it from May 21 to Oct. 16 in Indiana. P. modestus Bay. which is al­so frequent, was abroad in the latter state from June 3 to 27 and P. rugulosus from May 31 to July 4. Chauliognathus pennsylvanicus was taken from June 30 to September 30 and occurred at Marietta, Ohio from April 22 to at least September 22. C. marginatus Fab. is common in the southern counties of Indiana during June and July. Blatchley gives seasonal re­cords for the more common species of Can­tharis, as follows: C. serratus Lec., May 11 - June 24; C. Carolina, Apr. 25 - July 9; C. limina, May 24 - July 4; C. Stachus Melm., May 24 - June 18; C. rufus Lec., May 12 - July 15; C. terrificus Lec., May 24 - June 1 and C. limbatus. April 22 - June 11. C. carolinus swarmed on Solidago in the first half of June in Ontario. C. divisa is very common during the spring in California, C. livida disappeared by latter July in England, and Rhagonycha fulva is often the most common beetle during July in Germany. In the majority of these species, the adult stage therefore exists in late spring or before mid-July, and reproduction is largely confined to this period of the year.

Oviposition and Incubation. So far as known, they deposit them masses. Podabrus places them either on the soil or shallowly in it. Rhagonycha fulva ovipos­ited under stones or pieces of bark and Chauliognathus pennsylvanicus deposited its eggs in cavities about an inch deep and a half inch wide under the edge of an object lying on the ground of the cage. Two egg masses of pennsylvanicus contained 180 and 197 eggs, respectively; a cluster laid by Cantharis rustica consisted of 70 eggs, and those of P. fulva contained from 149 to more than 200, the latter number prevailing. Incubation required 7 days in fulva, 8 in rustica, and the eggs of pennsylvanicus hatched in 13 days in September.

Larval Growth. Hatching in C. rustica and C. fulva brings forth an embryonic form of larva that recalls the pro-nymph of certain Locustidae and Odonata, and may accordingly be designated the pro-larva. This larva is soft-bodied, and having im­perfectly developed legs, moves slowly. The intestine contains its fill of yolk, and these larvae stay congregated for about two days when they hatched. They then shed the pro-larval skins and become full­fledged larvae, which, in the instance of fulva, continued to remain assembled for three days more (Verhoeff). The number of molts comprising the larval stage of Can­tharidae seems not to have been determined. The larval period of C. rustica extends over at least 10 months, including the hibernation period. Doubtlessly it also oc­cupies the greater part of the year in the other species.

Generations. The above data point to the occurrence of either one or two gen­erations annually in the Cantharidae of the North Temperate region. In the series of species whose adult stage is abroad prin­cipally during May and June, and no adults are reported for August and September, it is probable that one generation de­velops in a year. To this group may belong Podabrus cornutus, P. rugulosus, Chauliognathus marginatus, Rhagonycha fulva and all the species of Cantharis named above. However, Chauliognathus pennsylvanicus and Podabrus tene­nus, that appear in the adult state both early and late in the sum­mer, probably have two cycles annually. This was found to be the case with pennsylvanicus in southern Ohio, where the beetles appeared in two distinct waves, the first generation adults being abroad from April 22 to June 24 with maximum numbers on about May 31, and those of the second from August 22 to September 22 or later, reaching their
numerical peak shortly after the first beetles issued. Mating was observed from April 22 to June 21, and again from August 24 to September 15. There was thus a distinct interval of practically two months in midsummer during which no beetles were present, which no doubt signifies two cycles per annum.

Defense and Enemies. When annoyed, the larvae of Cantharis liturata usually produce a blackish liquid from the mouth. Their bodies were always found to be dry even when coiled up in mud, their coat of short dense hairs excluding the water. Both adults and larvae of Chaulognathus are subject to attack by a fungus. Numerous adults of C. pennsylvanicus bore the mycelial growth, probably of Empusa lampyridarum Thaxter, which formed rings on the abdominal conjunctivae and distended this region abnormally. A similar epidemic was observed among C. marginatus. In both instances, the bodies of the affected beetles stood upward at an angle of 45 degrees, the wings were raised as in flight, and the mandibles firmly gripped the plants on which the insects died (Popenoe and Smyth).

In late September of 1880, thousands of the larvae of C. pennsylvanicus were killed on a fence at Selma, Alabama by what was regarded by the observer (Schwarz, '80) as a fungoid disease. The living individuals bore on all the stigmate a small drop of a whitish, odorless fluid, which had turned pink on those that had recently died. In the larvae which were dead for some time, the fluid had dried up and the bodies had become rigid.
10. CLERIDAE. CHECKERED BEETLES

GENERAL FEATURES

Both the adults and the larvae of most Cleridae are vividly colored, the adults bearing a checkered pattern of sharply contrasting hues and mostly prefer bright sunny days when they may be observed running over infested trees or on flowers. When disturbed they take flight readily or drop and crawl into the debris on the ground. While the majority are diurnal, Brachocerus quadristigmatus Say and Orthopleura damicornis Fabr. are active at night, the former hiding during the day beneath bark, in cracks, or in the debris at the base of trees. The larvae mostly inhabit the galleries and burrows of beetles infesting forest trees. However, those of Necrobia are found among bones, carrion, skin and the like, while the larvae of Trichodes occur in the cells of bees and wasps in logs, stumps and the stems of plants, or in the hives of domestic bees (Böving and Champlain). Jazzykov reports two undetermined species of the latter genus from egg pods of locusts in Turkestan. The fifth abdominal segment of Clerid larvae bears a pair of horny curved processes which perhaps aid in locomotion in burrows. With few exceptions, the species of this family are predacious in both the larval and the adult stages, being among the principal predators attacking wood- and bark-boring beetles. The adults attack the adults of the destructive species, while the larvae feed upon the eggs and brood in the bark and wood.

FOOD AND FEEDING HABITS

Adults. Three types of food are taken by the adult Cleridae (Fig. 79). Three widely distributed species of Necrobia, - ruficollis F., violacea L. and rufipes Dej., are associated with carrion. The precise relation sustained by them to the decaying flesh remains a question. Scott observed ruficollis eat the dead maggots and the soft parts of dead adults of Musca domestica, and found no evidence that they preyed on the living fly larvae. Secondly, Trichodes ornatus Say, T. apivorus Germ., T. nuttalli Kirby, and some species of Enoclerus do not seem to eat prey but feed at least to some extent upon the pollen of the flowers which they frequent. But so far as known, the principal food taken by adult Cleridae consists of living insects and particularly beetles associated with forest trees. Their feeding process is described by Böving and Champlain. "In the usual method of attack the Clerid remains motionless until a wandering Scolytoid or some other insect approaches close enough. Then running with a rapidity that resembles a leap, it seizes the prey. Grabbing it with the front and middle pairs of legs and holding on to the bark by the hind pair, sometimes balanced by the tip of the abdomen against the bark, it proceeds to feed. With its strong jaws it breaks the chitin or separates the segments and feeds upon the soft tissue and viscera within." Thenacrus dubius Fabr., called the American bark beetle destroyer, attacks and feeds upon all kinds of bark beetles which infest spruce, pine and also deciduous trees. T. nigripennis (Lec.) feeds on such small Scolytids as Ips, Pityophthorus and Dendroctonus.
were reared, but preferred portions of vegetable substances on which the maggots feed (Scott). Japyx rufipes is said some time to return to their primitive ways. This view is subscribed to by Taschenberg, Oholodowitch, and Feekes, while Tillus notatus Kug enters the tunnels of the Bostrychid beetles Dinoderus minutus and feeds on their larvae (Stebbing). Tetrodonectes fascioculatus Schreib. of New Zealand feeds on the eggs of the Buprestis carrion and feeds on their larvae (Stebbing). Trogoxodendron fascioculatum Schreib. of New Zealand feeds on the eggs of the Buprestis carrion and feeds on their larvae (Stebbing). Only with considerable difficulty were some of these induced to kill the fly maggots among which they are found in excavating burrows and thus unable to escape. One adult of Cymatodera undulata Say, reared from a larva in a gall of Phyllocaespis mamea, consumed more or less of nineteen adult insects from July 24 to September 27 (Fig. 79). The prey provided was disabled and consisted of two Diabrotica vittata, six D. 13-punctata, one D. longicornis, one Lema trilineata, one Ceratostegia cuelitaria, six Musca domestica and two Adelphocoris punctatissimus (Saldufa, '96). The Corynetine, Phyllobaeus dispar, has been observed feeding on Phyllocaespis thoracicus on red oak. Corbett and Miller ('33) report the following food records for Cleridae but the stage concerned is not indicated: Callidum auratus Chm., feeding on the Zygaenid, Anthotoma catanatha and the Tachinid fly, Phytomyza remotula Ald.; Cylindrus wallacei Thomas, on the Bostrychid beetle, Xylophaga flavipes.

Larvae. As far as known, the larvae of all Cleridae excepting Neocoryda, are predacious, feeding largely on the immature stages of other beetles. The larvae of Neocoryda seem gradually to have substituted the saprophagous food habits for the predatory mode of life, but sometimes return to their primitive ways. This view is substantiated by Taschenberg, Cholecovsky and Scott in the insects of E. puncticollis. Only with considerable difficulty were some of these induced to kill and eat the fly maggots among which they were reared, but preferred particles of vegetable substances on which the maggots fed (Scott). A. rufipes is said sometime to consume pollen in the nest of the solitary bee that stored pollen in the hollows of straws on a thatched roof. The larvae, when young, are said to consume a part of the pollen store but later eat either dead or living bee larvae, or other stages, found in passing from one cell to another in the same straw, and may also migrate to adjacent straws to continue feeding. Cross reports umbellarum from the nests of the bees, C. maura, Anthophora talanta and A. albigena. In feeding experiments the larvae also ate the eggs of Andrena and of the Meloid, Bombylius major, as well as other larvae of its own kind. Lichtenstein and Quelle recorded the larvae of T. amnicus Pabr. as parasitic in the egg cases of grasshoppers in Spain as early as 1866 (Broying and Champlain), and Jazykov recently reported the larvae of two undescribed species of this genus from the egg pods of the locusts, Anabrus cristatus, Duclosius braeusi and D. marocanus in Turkestan.

While most of the Clerid larvae have been reported feeding on beetles infesting dry and living wood, other types of habitats are frequented also to secure food. The larvae of Cymatodera undulata sometimes burrow through the corky stem galls of the Cynipid, Disholcaspis mamea, inhabited by the immature stages of various Schleidiolidae and Cynipidae. In the last 26 days of its feeding life, one such larva ate at least 69 Hymenopterous grubs dissected from these galls (Saldufa). The larvae of the fly, Conopidae, Chora, and the caterpillars of Carpocapsa pomonella in New Mexico (Emserg), and those of Calletcheria aurata Chm., are said to prey on the eggs of the Grasshopper, Anthotoma catanatha, a pest of coconut in New Mexico.
Malaya. Hydnocera palligenus Say and H. pubescens LeC. are reported from the cells of Anthonomus grandis in cotton where they feed on various stages of this weevil. The larvae of subgenus were taken frequently from the cocoons of Microbracon in these cells (Pierce, et al). The pupae of Ischnoschema keidae (LeC.) were found in the mass of annual plants inhabited by Wondereit larvae.

The majority of the food records for Clerid larvae concerns the species that prey on wood-inesting beetles. Usually while still very small, the predacious larvae enter into the galleries or burrows of their prey where they feed. In their search for prey, the larvae of Thanassius bimaculatus move from one gallery to another between the bark and the cambium layer (Stebbing). The larvae of other species are presumably obliged to make similar migrations to secure food adequate for their complete growth. In the records enumerated here, the name of the prey follows that of the predator; Cryptotarsus spp., larvae of secondary wood borers, mostly Cerambycidae and Buprestidae; Thanassius doublis, eggs and young of all kinds of wood beetles in tunnels, pine needle-deciduous trees; T. nigritentris, brood of Ips, Pityophthus and Dendroctonus; T. bimaculatus, larvae of several genera of the Scoyltidae and Platypodidae; T. formicarius L., larvae, pupae and new imagoes of Mycelophilus piniperda and others (Kleine); Enocerus suppressi Van Dyke, the cypress bark beetle, Phloeodes suppressi K., existus Mann., chiefly Phyllophaga in alder, willow et al; H. niger, from cones of Douglas fir infested with bark beetles; H. sphegeus, chiefly grubs and pupae of Dendroctonus spp.; Hydnocera unifasciata Say, from galleries of Hyperplatys sp.; H. verticallus Say, from Calocerus harboring Cerambycidae; Parascolia curus Newman, numerous in tunnels of Lyctus (Prooggat); Tullius birmanicus Och., an enemy of Stromatium, Lyctus and Sinoxylon; T. notatus R., Lyctus, Sinoxylon and Dindorus; Anthicodorus rugicollis Corp., appears to prey on the Scoyltidae, Sphaerotryptes sivalikenses; Dasycerodes torrentius #astw., mainly small Scoyltidae; Tarsopterus unistatus Ross., principally Lyctus africanaus; Tenebrio sigasticollis Cast., probably preys on small Cerambycidae (Sesar); Placopterus thoracicus Oliv., bark beetle brood (Sowing and Champlain).

The larvae of the following Corynet-
in the nest of the host, but in its vicinity, as do the Meliidae that parasitize solitary bees (Cros). However, Goureau states that apiarius and alvearius steal into the hive of the honey bee and deposit their eggs in the cells. The Cleridae that prey on wood-infesting beetles usually place the eggs in or near the gallery of their prey. The females of Thanassius dubius, T. nigriventris, Enoclerus sphageus, E. quadrirugatus and Helocera laticornis are known to have this habit. Tarsostenus univittatus commences laying eggs one or two days after the adult emerges from the pupal cell. Before inserting the egg, the female spends considerable time moving from place to place with the ovipositor extended to find a suitable opening. The end of the body is then placed close to the spot and the ovipositor is inserted into the cavity. After a short time, during which a pumping movement was noted in the ovipositor, the egg was deposited. In one instance, seven minutes were required to deposit seven eggs at one place in this manner. The larvae hatched after an incubation period of ten days. When ready to emerge, the larva begins to push against the posterior end of the egg by alternately contracting and expanding its body. The ninth abdominal segment is armed with stiff setae which are used for piercing the shell (St. George).

Larval Life and Pupation. The larvae of Cleridae in general feed voraciously and grow rapidly (Fig. 80). When mature, they pass a considerable time, often without taking much food, in the prepupal state, during which they construct the pupal cell. This may be made in the earth, the bark, or in the cell of the beetle on which they prey. The larvae of Cymatodera bicolor Say mostly use the pupal cells of their food animals, but some construct special cells in galleries in the wood. Those of Thanassius dubius leave the inner bark when mature and excavate cavities in the outer corky bark to pupate. Enoclerus sphageus makes its cells in the dirt and debris, in the crevices of bark, or any suitable place. The Trionodes which live on Hymenopterous larvae probably pupate within the cells and galleries of the bees and wasps. According to Goureau, the mature larvae of T. apiarius and T. alvearius prepare to transform in the last bee cell occupied by them. Many species, including Necrobia, line their cells with an oral exudation of a white silvery color. Others use this substance to seal the ends of the borer cells which they reconstruct to suit their purpose. Others make a complete case or "cocoon", utilizing the exudation or cement to hold particles of earth together and to form a smoother interior on which to lie as pupae (Boving and Champlain). But Netchesia laticornis and Charicessa pilosa have not been observed to make such a case. The pupal stage, excepting when it occurs during the winter, appears to last only a few weeks. The prepupal and pupal phases, combined, required 23 days in the instance of one Cymatodera undulata.

Hibernation. The Cleridae sometimes hibernate in one stage only, but also in two or even three stages. The variety of their wintering forms and positions, and the types of cover used, are exemplified by a number of North American species. The mature larvae of Enoclerus sphageus alight by night to the ground close to the base of trees where they hibernate in cells located several inches below the surface and lined with a foam-like exudation. The prepupal larvae of Placopterus thoracicus overwinter in the abandoned pupal cells and galleries of the prey. In Charicessa pilosa, the half-grown larvae winter in the first year of the cycle, and are still immature when the second cold season comes upon them. Most of the Cymatodera bicolor spend this time as pupae, but some also hibernate as larvae. Thanassius dubius winters in the larval, pupal and adult stages, but Enoclerus quadrirugatus is reported to do so only in the imaginal state.

Occurrence of the Adults. So far as known, the adult stage is reached, or begins its active life, mostly during the spring or the early part of the summer, and the beetles are generally abroad for sev-
eral consecutive weeks or months. The time and duration of their occurrence is reported as follows: Cymatodera undulata, one individual lived from July 23 to September 23; Enoclerus sphageus appears in May and June, and sometimes continues abroad for four or five months; E. quadrisignatus, June to August; Trichodes ornatipes, June to September; T. nuttalli, June to August; Phyllophagus dialocatus, April to August; Orthopleura damicornis, April to July; Tarsostenus univittatus, India, May to July and September to November; Thanasimus himalayensis, India, May and again in August and September.

Generations. According to Boving and Champlain, some species of North American Cleridae have one cycle in a year, others have more than one and some appear to pass several years in the larval state. In general, this stage lasts far longer than any other in the metamorphosis of this group. Moreover, the cycles seem to be rather closely correlated, both in number and the season of their occurrence, with those of the prey species. Accordingly, the Cleridae constitute a more specialized group of predators than are most Carabidae or Cicindelidae. While the latter capture any available or manageable prey where and when it is needed, the predacious Cleridae have limited their prey to beetles of somewhat uniform habitats and developmental patterns and there is evidence of a tendency towards the circumscribed obligatory host relation that is characteristic of parasitism. Parallelism in the development of predator and prey is indicated by the general fact that the adult checkered beetles prey principally on the imagines of their food species, whereas the larvae feed chiefly upon the immature stages. The nature of this correlation is shown in the following instances. The new adults of E. sphageus appear in May and June, and, for the purpose of ovipositing, search out trees infested with the hibernating generation of Dendroctonus. The eggs must hatch promptly as the larvae must make their appearance and growth before the larvae and pupae of Dendroctonus transform to the adult condition. Moreover, whereas the life cycle of Tarsostenus univittatus is normally annual, the adults appearing in August and September, development may be delayed for 16 to 24 months, giving rise to a second flight in May. This procedure synchronizes with that of its chief prey species, Lyctus africanus, which exhibits a similar delay in development, with two well-marked flight periods. Similarly, the observations of Champlain led to the conjecture that Nolchina laticornis will probably be found to undergo its life cycle twice annually where it feeds on prey species that complete two generations in the same time. In these instances exist indications of a specialized adaptation of the cycle of the predator to that of its principal prey, a tendency that seems to be general in the family, so far as known.
11. RHIPHIPHORIDAE

GENERAL FEATURES

The Rhipiphoridae constitute a small family of wedge-shaped beetles whose antennae are pectinate in the males and frequently serrate in the females (Fig. 81). The adults are not often seen but occur on flowers, and the larvae so far as known, live parasitically, the hosts being principally the larvae of wasps and bees. The bionomic literature chiefly concerns species belonging to Rhipiphorus, Macrosiagon and Rhipidius.

HOSTS

Abelé de Perrin reports that the larva of Rhispidius boisiy Abellé lives as a parasite in the nymph of the cockroach, Estheta livida, and refers to a questionable case in which this or a closely related species is parasitic in a grasshopper. The known hosts of Macrosiagon and Rhipiphorus are mostly the larvae of solitary bees and wasps which construct their cells or nests in such shielded habitats as the soil or stems of plants, and provision them in advance with sufficient food to sustain their larvae to maturity. M. pectinatum (Fabr.) is a secondary parasite, attacking the larvae of Tiphia and perhaps Campsomeris, which live at the expense of white grubs of the genera Phytophaga and Lipygus. M. ferrugineus Fabr. has been reared from the larvae of Odynerus transversus by Chobaut (1911), while M. tricuspides Lep. is believed to parasitize Odynerus, Rimenes or perhaps Meganthes. Pierce found that Rhipiphorus solidagninus (Pierce) develops on Epinomia triangulifera, a large black solitary bee, whose nests are built in burrows in the ground. Fabre took the larvae of R. subdipeterus Roes., while attached to and devouring those of Halictus sexcinctus in their nests (Betts). R. paradoxus L. is the only species known to parasitize a host with social habits. Hamoir, in 1813, expressed the opinion that it develops in the nests of wasps. Since then it has often been associated with Vespa vulgaris, on whose larvae it feeds parasitically. Hoffer reared approximately 600 adult paradoxus from the nests of this species but obtained none from those of V. germanica, sylvestris, media, saxonica or orabro. Vespa vulgaris and V. germanica construct their domiciles under ground whereas those of the other species are built above ground. The rearing of Orawshay, Ormerod, Chapman and others supplement the findings of Hoffer showing that paradoxus is probably limited to the nests of Vespa vulgaris in Europe.

HABIT

The adults are mostly reported from the flowers of herbaceous plants where they are presumed to feed on pollen. Pierce saw several pairs of Rhipiphorus solidagninus in copulation and observed three females engaged in laying their eggs, the beetles being in the flower heads of Solidago in both instances. A Macrosiagon tricuspidae had deposited about 800 eggs in a mass in a flower of Eryngium campestre when interrupted. Several French observers estimated that 500 to 600 eggs may be laid by one individual of this species (Cros). The eggs of M. ferrugineus are said to be placed shallowly in soil. So far as known, the newly hatched larvae of this family have campodiforma bodies, well developed jaws and strong running legs provided with large membranous pulvilli (Fig. 82). One or two caudal appendages terminating in a disk-like cups are described for the larvae of Rhipiphorus paradoxus and R. subdipeterus. By means of the suckers the larvae cling to
the upper parts of plants, and the flowers in particular, and raise themselves into the air to engage in exploring movements. Dependence on carriers subjects the larvae to the hazard of attaching to insects which can not be utilized as hosts. The larvae of Rhipiphorus solidaginis are reported from representatives of nine genera of insects visiting flowers, but only Epinomia is known to serve as a host. It is evident that many larvae are miscarried and fail to develop, probably on account of certain peculiar conditions existent in the nests or habits of such carrier species. A considerable mortality obviously results also from competition among the larvae themselves for the food supply. Since only one parasite develops in a single cell of the host, a large number is lost in instances where a dozen larvae, and probably often many more, are carried by one solitary bee or wasp. However, transportation on a large scale becomes advantageous to the parasite when the host is a social species as in the instance of V. paradoxus in the nests of Vespa vulgaris. This may explain why paradoxus is the most numerous and best known species of the family.

Upon reaching the host's nest, the larva live at the expense of the larva of the bee or wasp. They probably do not feed to any extent upon the animal or plant food stored by the parents of their hosts. So far as known, the host larva has made a considerable part of its growth before the feeding of the parasite seriously affects it. This is indicated by reports that the larva of V. vulgaris lives to form the silken cap that closes the cell as is done by the mature unparasitized larva of wasps. But eventually the larva becomes largely consumed. In so doing the primary larva of V. paradoxus and Macrophagon ferruginea are said to feed for a period externally. When the Vespa host is about one-half grown the paradoxus penetrates into the body cavity, generally lying in the third or fourth segments and bathed in the fluids of the host. Although greatly distended during this period, the parasite is said still to be in its first instar as is shown by the presence of the chitinous plates on the body segments. When the wasp larva forms its cocoon, the paradoxus larva reappears to live externally, encircling the neck of the host. Now it molts the first time, thereby changing to a scarabaeoid or relatively degenerate parasitic form. For a while this larva ingests only the body fluids but later devours also the solid parts of its host. The larva molts again, going into the third and last instar, which retains somewhat of its grub-like stature (Fig. 83). The development of the stage through distinct larval forms recalls the hypermetamorphosis
of the Meloidae and the parasitic Staphylinidae. The mature larva remains within the host's cell to pupate (Chapman). It is thought that the adult paradoxus is incapable of escaping from the cell by its own efforts and must be liberated by the workers of the host colony. In general, the adult issues from the Vespa cells about two days after the wasps that develop in the same comb.

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**THE LIFE CYCLE**

A somewhat speculative account of the life cycles of the better known species may be constructed on the fragmentary results of observation and inferences from the habits of the hosts. When wasps and bees are abroad in flight they are generally in search of food for their larvae. Whether they provide the food in a mass in advance of the presence of their larval progeny or feed their charges progressively, it may be assumed that the larvae are, or soon will be present. The probability that the newly hatched larvae of the parasite depend on the adult wasp or bee for transportation to the host's nest is also of value in interpreting the life cycle. It may be deduced from these generalizations that the primary larvae appear during the flight period of the adult of the host. Obviously, copulation and oviposition of the parasite take place about the time that the primary larvae are at hand. Moreover, the bee or wasp, whether solitary, colonial or highly social, reproduces more or less continuously through the season without marked intervals between broods, thus assuring a constant supply of host larvae of the size preferred by the parasites. It is likely, therefore, that the life of the reproducing adult beetles is more or less coextensive with that of the reproductive stage of the host.

How do these general facts apply to certain species of Rhipiphoridae? Vespa vulgaris, the principal if not only host of Rhipiphorus paradoxus, is engaged in rearing brood from about June to September. Hoffer never found the beetles in the small immature nests during June and early July, these containing at most the larvae and pupae of paradoxus. The absence here of adults in early summer signifies also that they oviposit, not in the nests but in flowers where the young larvae probably mount the visiting wasps of the worker caste. But in latter July and through August and September, and occasionally up to the fourth of October, the nests are inhabited also with adults of both sexes. These have been found in largest numbers during September, which indicates that the rate of increase in numbers of the parasite follows in the wake of the seasonal growth of the host colony. The occurrence of parasitic larvae and pupae of various ages in the Vespa cells during September, and probably also in August, shows that the adults then present in the nests were newly developed. The lateness of the season in which they appear and the absence of mating among the beetles from the nine series of nests examined by various observers, are evidences that the adults carry this species through the winter. Reproduction cannot begin in the spring before the fertilized over-wintered Vespa queen has begun her colony. The Vespa nest is well known to deteriorate more or less during the winter, and the paradoxus probably forsakes it in the fall to hibernate elsewhere. It is probable, too, that paradoxus, like the Vespa host, completes only one cycle in a year. That R. subdipterus may undergo a similar seasonal development is indicated by the occurrence of adults from June to September, and by the discovery of small parasitic larvae on their larval hosts on August 24. The first of these larvae to mature pupated at the end of August, and the tardiness of the season probably permits transformation to the adult state as the hibernating form.

The adults of Rhipiphorus solidaginis appeared late in July and continued to mid-September in Nebraska. During this time, females were seen on three occasions engaged in ovipositing, and a pair was ob-
served in copulation on August 27. Newly hatched larvae were found clinging to the flowers of *Solidago* and on various adult Hymenoptera taken on these plants, and were obtained also from the larvae of the host, *Epinomia*, dug out of their cells in the soil during August and September. The reproductive activities of both host and parasite seemed thus to be in full progress late in the summer, indicating that both perhaps hibernate as larvae and complete their metamorphosis in the following spring. Time would readily permit the parasitic larvae to pupate in June and bring the adults forth by later July, assuming the occurrence of one generation annually. A similar seasonal distribution of the stages has been demonstrated in *Macrostagon ferruginea*. The first adults appear early in July, and eggs found in mid-July hatched after incubating about 16 days. The larvae winter, and pupation has been observed to take place in June.

Judged by the host relations of the above species, it is probable that *Macrostagon pectinatum* is a primary parasite of *Tiphia* from whose cocoons it has been reared. The beetles were so obtained by Davis almost exclusively in the month of July. This is obviously their reproductive season in the latitude of central Indiana. The four species of *Tiphia*, *punctata*, *transversa*, *incornata* and *vulgaris*, which occur in this area, issue from their cocoons in the soil most often during June and July, feed on the flowers of herbaceous plants or the honeydew of *Aphids*, then mate and re-enter the ground to parasitize their hosts, the white grubs. Present knowledge concerning the Rhipiphoridae indicates that the primary larvae of *pectinatum* may be carried by the adult *Tiphia* to their host, the wasp's larva. Or being associated with wasps of somewhat primitive habits, the parasitic larvae may hatch from eggs laid in the ground and search crevices in the soil for the *Tiphia* larvae on the white grubs. Such is the habit of the newly hatched larvae of *Epicauta vittata*, the blister beetle parasitic in the egg pods of grasshoppers. The *Tiphia* host survives the attack long enough to spin its cocoon. Most of the *Tiphia* species winter as larvae in their cocoons and pupate in the following spring, and it is probable that the parasite also hibernates as a larva in the same cocoons. These species of *Tiphia* have one generation in a year, and the development of *pectinatum* appears to parallel closely that of its hosts.
GENERAL FEATURES

The Meloidae form one of the larger families of beetles and are widely distributed over the earth. The species of Meloe, Hornia, Tritianis, Phodoga and others have lost the hind wings and have suffered a reduction in the elytra (Fig. 84), while in the species of Nemognatha and some of its relatives the maxillae are developed into long sucking tubes resembling those of Lepidoptera. The species of Keloe, known as the oil beetles, and also others, secrete a yellowish fluid from the joints of the body and legs which is said to be the product of unicellular hypodermal glands and is regarded as a means of defense (Beauregard). The dried bodies, and especially the elytra, of Lytta vesicatoria Linn. and Mylabrill are the source of cantharidin, formerly employed in making blister plasters, and still used as an aphrodisiac and in the treatment of urino-genital diseases.

ACTIVITIES OF THE ADULT

Copulation. The species that fly and crawl actively may be seen in pairs on the leaves or flowers of their food plants whereas the clumsy and wingless Meloe, Hornia, Tritianis and their like, mate on the ground if indeed not, as Rau ("30) suspects in the instance of Hornia minutipennis Riley, within the pupal cell. This observer found small holes in the sides of the cell through which the pairs may mate, if they copulate at all. The unopened cells commonly contained dead beetles along with hundreds of newly hatched larvae. Fabre found Apalus muralis Forst. (Sitaris humeralis F.) in copulo at the entrances to the galleries of the Anthophora on which it is parasitic. Copulation generally begins with preliminary caresses, the male stroking the female with his antennae and palpi, after which he mounts and may remain so engaged from a few minutes to eighteen hours in the various species. The two sexes of Zontisa are said to mate in a linear position with the caudal ends joined, the smaller male being dragged along while the female continues to feed.

Oviposition and Hatching. As a rule, oviposition begins within a few hours or days after mating. The majority of the Meloidae deposit their eggs more or less remote from the food of the young, the responsibility of finding the same being placed on the newly hatched larvae. Several rather distinct situations are selected by the females for oviposition. The species parasitic in the egg masses of locusts belong principally to Epicauta, Macrobasia and Mylabris, and, in all cases reported, oviposit in hard dry soil as do also their hosts. Moreover, many of the species that develop in the cells of bees still follow this same primitive habit. Newport, Cros and others have shown that this mode of oviposition is retained by Meloe violaceus Marsh, M. procarabaeus L.,

Cros has made a large number of more or less complete observations on the forms native to Mascara in Algeria. The principal papers on American species are by Riley, Parker and Boving, and Million, while Roepke and Verbeek studied certain forms native to Java. Beauregard reviews the earliest publications that deal with the bionomics of the family.
Deg. consisted of 363, and the loose masses of E. pennsylvaniaa fitted an egg.

A single deposition of E. pennsylvaniaa contained several hundred eggs. The eggs are deposited in masses, and are generally said to be rolled with a sticky substance that holds them together. The cavity may extend vertically one and one-half inches deep being composed of several days or weeks. The cavity may extend upward, and reaches depths varying with the size of the cavity excavations one-half to one and one-half inches deep being common.

The cavities of Macrobasis immaculata Say and Euplecta maculata Say are bell-shaped and large enough to enable the beetle to turn around underground, with a smaller cavity in the center of the floor (Milliken). In general, when the burrow is complete, the beetle turns about and inserts the caudal end into it, sometimes backing so far into the hole that only the head remains visible outside. After the eggs are laid, the beetle covers them with the excavated particles, using the legs to scrape the ground into the hole and the abdomen to compact it.

So far as recorded, the eggs of Meloloinae are deposited in masses, and are generally said to be coated with a sticky substance that holds them together. The total number of eggs laid in the lifetime of one individual is fairly large and is deposited at intervals of fourteen days.

The small cavity in the floor of the main burrow of Epicauta maculata and Macrobasis immaculata contained several hundred eggs. The cavity was excavated by the female, and the eggs were laid and cemented together. The cavity was then filled with excavated particles.

A single female of Epicauta vitattata contained an average of 300 eggs. The species of Mylabris observed by Portchinsky placed 24 to 60 eggs in each cavity, while Roepeke found that the masses of Mylabris auripes contained several hundred eggs, whereas Verbeek obtained 30 to 164 eggs per deposition from this species and E. rufipes. The deposition period of one individual is generally 363, and the loose masses of E. pennsylvaniaa are deposited in a number of parts. The small cavity of Epicauta vitattata is generally said to be oviposited with a sticky substance that holds them together. The cavity may extend vertically one and one-half inches deep being common.

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in several species has been found to be
as follows, in days: Macrobasis immaculata, 12-14; Epicauta maculata, 16-21; M. vittata, about 10; M. rufocephala and Mylabris pustulata, 3 - 67, in Java; Mylabris spp. observed by Portchinsky, averaged 20-22 days; M. schreiberi Reiche and M. quadripunctata L., 12 days; M. magneri, 12-13; Aplopus muralis, 23-30; Melolontha melolontha and M. proscarabaeus, ranged between 21 and 47 days but averaged four to five weeks in April, May and June; M. melalis, mostly 20-25 days; M. satanae and Zonabris octodecimmaculata, 35-37; K. circumflexa, mostly 25-37; Zonitis pustulata and Z. preusta annalis, 12-22; Z. immaculata, 4-6; Leptopalpus rostratus, one month; and Nesognatha chrysomelina, about 12 days. At temperatures varying slightly from 70°F., the incubation period in Tricrania sanguinipennis was 12-14 days, whereas the larvae hatched in approximately one month out-doors in March and April when frosts were still frequent at night (Parker and Boving).

THE LARVA AND ITS ACTIVITIES

Hypermetamorphosis. The development through the larval ins tars of the Melolidae is characterized by a marked hypermetamorphosis (Fig. 85). This condition reaches its peak in the species attacking the egg pods of locusts, and is somewhat less pronounced in those from the cells of bees. The more or less differentiated forms assumed in the several stadia are obviously to be interpreted as adaptive modifications resulting from their parasitic mode of life. The newly hatched larva retains a high degree of motility and performs the task of finding the host. To this extent the blister beetles may be said to have clung to their earlier predatory manner of living. The host or food supply is conveniently centered in one place and is adequate for all the subsequent growth of the larvae. These are thus not obliged to travel thereafter in search of food, and there has consequently resulted a progressive degeneration of the locomotor appendages and an equivalent and corresponding increase in bodily bulk in the subsequent instars. Considering that the several steps in the degenerative evolution are still present during the growth of the larva, the material of the locusts' eggs, in particular, constitute a remarkable object lesson to illustrate the

certain deterioration that results from bodily inactivity.

First Instar. The Primary Larva.

Many writers have employed the name "triungulin" for this instar, referring thereby to the supposed three-clawed condition in the tarsal of these larvae (Fig. 86).
The term is derived from the name *Triungulina* proposed by Leon Dufon in 1828 for an insect which he considered to be a sort of louse on *Andrena* (Cros, '17). Boving ('24) points out that "triungulina" is not a suitable name, "partly because only a small minority of the Meloid larvae have the characteristic armature of three claws at the end of the tibia, partly because this armature really is to be interpreted as a single median claw-shaped or spatulate tarsus with two strong setae laterally at the base, and partly because the triunguline armature is not restricted to the larvae of the family Meloidae." Newport, Fabre, Cros and others more happily employ the name primary larva for this instar.

The primary larvae possess a more or less thysanuriform body, whose outstanding features are the inconspicuous antennae, subquadrate head, body tapering toward the back, three pairs of running legs, a rather prominent pair of cerci, and, in at least some species, an anal appendage for adhering to the substratum (Fig. 87).

Fig. 87

The mandibles are said to be smooth or inconspicuously toothed in species parasitic on Hymenoptera but more or less strongly dentate in forms living in the egg pods of locusts (Cros, '27a). Parker and Boving found that the larva of *Triorania sanguinipes* lets itself down head first by spinning a thread when it loses its hold while moving about. These writers also describe a unique abdominal structure which possibly holds a supply of air that prevents water or honey from penetrating into the tracheal system. It was found to be next to impossible to drown them in water. Cros ('20) sets forth the distinctive structures of the primary larvae in the several tribes of the family.

Second Instar. The Caraboid Larva. While similar in general form, the second instar larva differs from its former self in having relatively reduced legs, a more bulky body, and a correspondingly lessened ability in locomotion. Its whole body has taken on a form well described as caraboid because of its resemblance to the larvae of the Carabidae. But while the caraboid larvae of this family possess a general form in common they tend to diverge into two types that correlate with the groups of hosts attacked by them (Fig. 88). In the species from the eggs of locusts, it retains a moderately active and aggressive form, whereas their relatives from the cells of bees digests much more sharply from their primary state. In *Triorania sanguinipes*, and doubtless other species parasitic on bees, the principal features are the fleshy supple mouth parts, weak legs and the prominent venter which is strongly convex both longitudinally and transversely, whereas the dorsum is almost flat. This larva floats on the surface of the nectar in the cell of the bee and has aptly been likened to a duck resting on water. The spiracles are confined to the dorsal segments and remain above the surface of the viscous liquid. These two types of caraboid larvae are probably the outgrowths of the differences in the physical state of the locusts' rather firm egg pods versus the bee's pot of viscous nectar or nectar and pollen mixture, the first type requiring stronger legs and jaws to penetrate and disrupt the egg, the latter finding motion easier or unnecessary and a liquid food that requires no maxillation.

Fig. 88
Second instar larvae of Meloidae. 1, *Epiacuta vittata*; 2, *Triorania sanguinipes*, dorsal view; 3, same, lateral view. Sources as given for figure 87.
Third and Fourth Instars. The First and Second Scarabaeoid Larvae. The divergences of the scaraboid larvae into two types, as noted above, is continued to an even more marked degree in the third and fourth instars. The larvae from the egg packets of locusts assume a form resembling that of Scarabaeid grubs, in which the disproportion between the size and strength of the legs and the volume of the body is increased (Fig. 89). Riley ('77) recognized two instars of the scarabaeoid form, and Verbeek ('32) concurs in this interpretation. They are believed to be present in Epicauta, Macrobasis and probably some species of Mylabris. On the other hand, the third instar of Tricrania sangüinipennis and probably other species from bees, retains the general boat-shaped form of the second instar, and floats on the surface of the honey paste, which gradually becomes harder and more solid as it becomes consumed. The fourth is pale, soft and fusiform-ovate, with both the dorsal and ventral surfaces convex.

A similarly boat-shaped larva that swims in the pool of honey stored by Anthophora, is described for Apalus muralis (Fabre, '77). Although Parker and Böving do not recognize such a form in Tricrania, the descriptions furnished by these authors indicate that the fifth instar is probably equivalent to the pseudopupa of Apalus muralis and Meloe cicatriocuus Leach. However, Fabre's pseudopupa appears actually to be equivalent to the last three instars of Tricrania. In the coarctate larva of Epicauta vittata, the mouth parts and legs are quite rudimentary and tuberculous, and the soft skin becomes rigid and a deeper yellow. According to Milliken, this larva in Macrobasis immaculata is "elongate hemispherical, resembling the half of a peanut kernel if the ends of the latter were bent toward its flat side and its edges thickened; entirely inactive, the skin rigid; location of appendages shown by tubercular projections."

In the fifth instar the larva of Tricrania is entirely enclosed by the exuviae of the fourth, the skin remaining unbroken although detached from the insect. The body bears a thin pellicle but rather rigid skin, is almost regularly ovoid, dorsally and ventrally convex, with the mouth parts greatly reduced and tuberciform, and the segments plainly indicated. Meloe cicatriocuus and Apalus muralis seem to be simi-
ilarly encased in one of their later larval instars whose identity in terms of the Tricrania stadia has, however, not been definitely ascertained.

The Sixth Instar. The Scolytoid Larva. In this instar, the larva of Epi-cautia vittata, and other locust parasites, represents somewhat of a return to the former scarabaeoid form, differing from it only in being smaller and whiter (Fig. 68, 9). Because of its resemblance to the grubs of bark beetles, Riley gave it the descriptive name of scolytoid larva. As in the preceding instars, the sixth larva of Tricrania sanguinipennis does not change so distinctly from the preceding instar form as do the species from locusts' eggs (Fig. 90, 3). In this instar it retains intact the detached but unbroken exuviae of both the fifth and the fourth stadia. The body is now pale cream, ovate and ventrally slightly less convex than above. The final larva of Meloe is said to be half enclosed in the split integument of the pseudolarva (Fabre, '19).

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Thus, in the two most thoroughly studied species of Meloidae, Epicauta vittata and Tricrania sanguinipennis, the larval stage comprises six instars. Cros ('32), however, recognizes only four larval instars, namely the primary larva, the second larva, the psuedonymph and the third larva, which is followed by the pupal stage. It is not likely that such a discrepancy in the number of instars actually exists within a family that is otherwise so homogeneous.

History of the Primary Larva. The true habits of this larva (Fig. 91) remained a mystery that was solved only by repeated efforts extending over at least two centuries. This larva was known to Linnaeus and Reaumur, who, however, regarded it as an apterous external parasite of adult bees, the latter naming it Pediculus apis. Dufour assigned them to a separate genus Tripungculus in 1828. However, their true mode of life had already been determined by Godart in 1857, who first observed the eggs and hatching of the larvae (Parker and Boving). Newport ('61), who had been observing three species of Meloe since 1850, reared the primary larvae and also repeatedly obtained the advanced larvae and pupae in the cells of bees, demonstrating that the larval stage lives at the expense of the progeny and food store of bees. Considering what he learned of their general anatomy and his observation that the primary larvae instantly attach themselves to whatever living insect is placed among them, Newport believed that they are carried into the nests by the parent bees. Here, he argued, they devour either the bee larvae or the food stored for them. But complete proof that the primary larvae are actually transported thus and parasitize the bees was furnished by Fabre in his study of Apalus muralis in 1856. Riley ('77) carried to his study of American Meloidae the then prevailing old world conception that all species are borne in this way by bees. But the primary larvae reared by him from the eggs of Epicauta and Macrophasia refused to climb onto plants or to fasten themselves to bees or other hairy insects as he expected, and showed instead a strong tendency to burrow into the ground. In digging up the eggs of Melanoplus apterus at Manhattan in the fall of 1876, the coarctate larvae were not infrequently met with. This discovery suggested that locust eggs, and not the progeny and stores of bees, might be the food of the primary and later instars of these beetles. The larval habits and development of Epicauta vittata and E. simplex marginata were then easily traced in the area of St. Louis, and their parasitism within locusts' egg pods and their remarkable hypermetamorphosis established. The studies of the past 50 years have revealed no additional basic host relations in the family.

Activities of the Primary Larvae. In a few hours after hatching the larvae become brown or black and capable of moving about actively. Usually they begin at once their search for food. But in some instances there has been observed a strong tendency for the new larvae from one egg mass to huddle or even eiling together in a ball over the egg shell or near them, with little or no motion for many consecutive hours. Such conduct has been reported for Epicauta vittata, E. labrais punctulata in
Eucera for three days and died without re­hazards. In certain species, success de­moved from the prospective host. The con­moist atmosphere and 37 in dry laboratory­ity is adequately demonstrated in the fol­least 11 days in captivity; and those of­Leptopalpus rostratus clung fast to a­twering plant whioh the larvae must­tor the egg pods of locusts, to find which­tor the host but possess remarkable en­bers of the offspring increase the chances­ of success. The larvae are not only well­known for their abil1 ty to run rapidly and­ of Epicauta vittata, 14 days; ]_.

The primary lar­ready charged with the special task of finding the host in­ which the larval stage is to be passed.­hile they are especially fitted by struc­ture and habit to perform this function.­ the ratio of success to failure is prob­ably nevertheless low. Favoring the­s is the fact that the parent beetles­ are prolific so that the very num­bers of the offspring increase the chances­ of success. The larvae are not only well­known for their ability to run rapidly and­ therefore cover much territory in hunting­ for the host but possess remarkable en­durance and tenesity of life. This qual­ity is adequately demonstrated in the fol­lowing examples in which the larvae en­dured without food for periods as indi­cated; Epicauta vittata, 14 days; H. Ru­fipes and Mylebras pusulata, 14 days in­sects that visit the flowers of Antho­phora. In some instances the lar­vae alternate their periods of inactivity in­ huddles with intervals of eager running­ about as if in search of food. The larvae of­Epicauta vittata and Lymus viridatus (Cos­mally) respond to certain disturb­ances by curling up and simulating death.

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As already indicated above, the pri­mary larvae reach their food either by run­ning actively over the ground or by attaching­ to the adult bee host. The first method­ is employed, so far as known, by all species­ that live at the expense of locusts' eggs­ and in addition by some forms parasitic in­ the cells of bees. Apalus has been observed­ specifically in Epicauta vittata by Milkey,­ in H. maculata and Macrobasia immaculata by­ Mulliken and in H. rufipes and Mylebras­ pusulata by Roepke and Verbeek. The lar­vae run eagerly and rapidly over the ground,­ pry their long heads and strong jaws into­ every crease and crevice in the soil and­ search under every piece of vegetable mat­ter and other loose cover on the surface in­ the expectation of finding a packet of loc­ust eggs. Among the species parasitic on­ bees, some are reported to be distributed­ only by running or by carriers, but the com­plete facts have rarely, if at all, been­ made known. In cases where the eggs are de­posited in the nests or galleries of the­ host, the larvae may enter directly into­ the cells constructed and provisioned by­ the new generation of bees, but are also­ possibly carried abroad on bees that leave­ the parental abode to establish themselves­ in new sites or go out to forage. Belief­ in the latter alternative is encouraged by­ the discovery of the larvae of Horia debayi,­ Borna gigantea (Waller), Apalus muralis­ and Apalus analis on adult bees. Moreover,­ it is probable that species which overwinter­ in soil more or less distant from the bees'­ nests are spread both by carriers and by­ their own locomotion, the mostly fragmen­tary and somewhat contradictory available­ observations notwithstanding. For instance,­ the larvae of Melos prossecrabeus, M. vio­lactus and M. cyanis have been taken ti­fixed to bees but those of H. melalis, Le­pta vestinatoria and Cerocoma vahli P., al­l parasites of bees, are said not to be car­ried but to enter the nests of the host di­rectly.

But whatever the whole truth may­ prove to be the above facts, it may be stated that the­ larvae of Apalus muralis were found by Fabre
at Carpentras attached to three-quarters of the Anthophora examined. When the new bees emerge from their cells and come and go in the galleries in the spring, the larvae, which hibernate in the hosts' burrows, fasten themselves to the bee. In doing so they cling to the hairs by the mandibles, the thoracic legs and the anal clasping organ. With the head directed toward the body of the carrier and the caudal end outward, the larva persistently holds on while the bee makes numerous journeys, dives into the narrow galleries, forces its way down the tight throat of a corolla and preens itself frequently with the legs. The story of the larvae of Tricrania sanguinipennis is similar. Hatchin g from eggs laid under loose objects on the ground, the larvae scatter at once in all directions. They not only readily climbed upon and seized the hairs of bees in captivity but were found in numbers of one to four on 60% of the adult bee host, Colletes rufithorax, in nature (Fig. 92). The mandibles are notched on the inner margin, being thus admirably fitted for seizing and holding to the hairs of the bees. As long as the brush, used in experiments to simulate bees, was kept in motion the larvae held on, but let go and scrambled off as soon as movement stopped. This persistent clinging indicates that the larva may be carried for many hours and probably days on active bees while awaiting the development of the proper state of the host's cells to dismount.

Some primary larvae, after hatching in the soil, or gallery of the bee, climb to the top or flower of a plant where they make contact with the carrier. After Parker andoving ('24), Proc. U. S. Nat. Mus.

Assuming now that the larva has mounted on the proper carrier bee, how does it
gain entrance into the host's cell? Pabre found the primary larvae of Apalus muralis and Meloe elata lying on the eggs of Anthophora, as in a raft, in the sealed cell filled with provisions. The absence of entrance holes in the cell left only the possibility that the larva enters when the bee is depositing her egg or at once thereafter while the cell is being sealed. In his experiments the larva either refused to crawl upon the honey in the cells lacking the host's eggs or became fatally entangled in it. The observer therefore concluded that they crawl upon the egg as it is being laid, using it as a means of avoiding contact with the viscous honey. Thus, a number of newly stored cells may become parasitized in succession by the larvae riding among the hairs of a single bee. It appears, however, that the male bee is quite as important in enabling the parasite to reach the egg as is the female. This belief was advanced by Pabre in the instance of Anthophora and confirmed by Parker and Boving in their study of Tricrania sanguinipennis. The males of Anthophora make their appearance a month earlier than the females, in other words during the period when the primary larvae of Apalus were present in largest numbers, and the dispersal of the larvae of Tricrania normally takes place when the male Colletes are most active in searching out their mates. In their searches, the male bees range hither and thither over the nesting site, spending much of their time crawling about over the ground and dodging in and out of the burrows. The larvae of both Apalus and Tricrania are thus given far greater opportunities to attack to the males than to the females of their hosts. It is argued, therefore, that the larvae on the males transfer to the female bees during copulation and only then are in a position to reach the brood chamber of the host. The discovery that the majority of the Tricrania found on the males were attached to the venters whereas they occurred on the dorsum of the females, corroborated the belief in the importance of the male in the process of parasitism. However, the presence of parasites in cells constructed long after the males had disappeared may mean that the larvae are not wholly dependent on the male to reach the female Colletes, but it may also signify that the larvae, after transferring to the female bee, are capable of surviving during most, if not all, her reproductive period.

What is the behavior of the larvae that succeed in finding the egg pods of lonists or the cells of solitary bees? Doubtlessly, more than one larva sometimes enters the same egg mass or cell, but only one ever matures in a single place. This condition gives rise to the belief in cannibalism among the primary larvae, which possibility is confirmed by their well-known pugnacity. Parker and Boving found as many as three Tricrania larvae in one cell in nature, and it was quite evident that the first larva to molt was killed by the second, and this was overcome by the third. In the instances of cells that yield neither bees nor parasites, all the contestants may be killed or starve. Cannibalism is thought to occur also in Epicasuta and Macrobasis as well as in Mylabris, Zonabris and Meloe, according to Riley, Milliken and Goss.

The primary larvae of Epicasuta first consume the mucous deposited on the top of the egg mass of Melanoplus. It next gnaws at an egg, devouring a portion of the shell, then in the course of two or three days sucks up its contents. A second egg is attacked and its contents more or less completely consumed, when a rest ensues and the larva melts into the parasitic form or second instar (Riley). The primary larvae of E. mucicarpa and Mylabris gutulata ate six eggs of Valanga nigripennis in five days, and in doing so work further and further down into the egg mass. The observations of Pabre on Apalus muralis and Meloe elata confirmed by Parker and Boving on Tricrania show that the first larvae eat the single egg of the bee which suffices for the entire instar. Feeding experiments conducted by Goss with the primary larvae of Lyca virginica, L. alpina, L. alpina, Zonabris praestans, Garoonema vahli, Meloe maculalis and M. carentis indicate that they may not be obligatory to an egg diet since they accepted honey and the larvae of bees as well. Parker and Boving reared one Tricrania from egg to adult on pollen and honey stored by Colletes. However, if the larvae generally gain entrance to the cells in the manner described above for Apalus and Tricrania, it seems logical that the egg of the host is the preferred and the only available animal food of these active larvae in nature. Moreover, in devouring the egg, the larva first obtains a nutritious food and second performs an act of self-preservation by eliminating the larva of the bee from competition for the stored food.

So far as observed, growth of the primary larvae is rapid after they have begun to feed. During this instar they commonly become double their original size so
that the white intersegmental areas of the body show conspicuously and become comparable to the gravid queens of termites in general appearance. Duration of the first instar is usually short, and has been shown to be as follows in the series named: Epicauta vittata, 8 days; E. ruficeps and Mylabris pustulata, 4 or 6 days; Lydus algaricus, 3 to 4; Apalus amalisc, one week; Meloe malalis, melted 24 hours after the inception of feeding; Apalus muralis, one week; and in Tricrania sanguinipennis one larva was in this instar more than 23 days.

Activities of the Later Instars.

All the subsequent instars of Meloid larvae are spent within or near by the egg pods of their Locustid hosts or in the cells of bees (Fig. 93). The early suggestion that the larvae of some species bore from one bee cell to another to secure sufficient food has usually not been supported subsequently. However, Twata observed that the "scarabaeoid" larvae of Zonitis pallida first consumed all the pollen and nectar in the sixth cell or Kedachile sculpturalis then perforated the resinous partition into the fifth cell where it half devoured the mature and already dormant Kedachile larva. Later the Keloid returned to the original or sixth cell, mending the broken partition with a yellow oil-like fluid which was presumably produced orally. This fluid softened the hard resin which, however, recovered its original hardness upon drying. Moreover, the fluid soaked down through four other cells present in this situation, killing all the larval bee inhabitants.

Fig. 93

Cell of Colletes rufithorax with fourth instar larva of Tricrania sanguinipennis inside. Note the refuse at the bottom of the cell. After Parker and Hoving (124), Proc. U. S. Nat. Mus.

When the egg of the bee has been devoured by the primary larva, the parasitism changes from the entomophagous to the phytophagous type. The locust eggs or pollen and honey available appear not to be uniformly adequate for optimum development in all instances, as is indicated by the rather pronounced variation in size of some adult blister beetles (Milliken). It is indeed strange that the act of feeding and the growth of the larva appears generally to be confined to the first four instars, the remaining two taking no food at all and actually shrinking in size. This has been shown to be true in Epicauta vittata, E. ruficeps, Macrobasit immaculata and Mylabris pustulata, which develop in the egg masses of Locusts, and in Tricrania sanguinipennis and other species from the cells of bees. During the first four instars, most or all of the food supply is consumed. In the instances of E. ruficeps and M. pustulata, each larva ate an entire packet of about 50 eggs, the caraboid form eating about nine and the two scarabaeoid larvae the remainder. The egg pods of Volucra nigricornis consist of 40 to 70 eggs each, all of which are said to be devoured by one larva of ruficeps or pustulata during its growth period. The rest of the larval instars are devoted to bringing the species through periods of cold and perhaps dry weather, and by gradual steps that involve but little morphological change, lead up to the prepupal stage. Elley, Milliken and Verbeek point out that the mature scarabaeoid larvae of Epicauta, Macrobasit and Mylabris pustulata forsake the depleted egg pods and burrow a short distance into the soil, the direction being principally downward, where they prepare a smooth-walled cavity. The cavities of ruficeps and pustulata, of Java, are oval and formed at a maximum depth of 20 cm. Milliken found that the Scarabaeoid larva of Macrobasit immaculata usually go much deeper than the egg capsules they have emptied, the depth varying between 3 and 6 inches, then turn head upward. There they form an elliptical chamber at a slight angle with the perpendicular. The cells of Epicauta cinerea Forst. are nearly upright and occur from 2 to 5 inches below the surface while those of M. immaculata were found but little deeper than the lower ends of the grasshopper egg capsules, and many of the larvae did not leave the empty capsules at all. The full grown scarabaeoid larva of Epicauta vittata and Macrobasit immaculata stiffens out in its chamber, with its head uppermost, and sheds its skin which, however, persists around the posterior end of the abdomen. Thus the larva enters the cocoonate form, which stands almost vertically on end in the exuviae and is supported.
near the anterior end by resting against the wall of the cell.

The coarctate larva is of unusual biological interest. Such a form is known to occur in Epicauta ruficeps and Mylabris pustulata, M. schreiberi of Algeria, in a number of North American kinds of Epicauta and in Macrobasis immaquillata. What may have been the origin of such a special larval form, and what is its function in the life of the Meloidae? While a similar instar occurs in some related beetles, notably in Drilus, it is obviously most prevalent and specialized here. Moreover, it is doubtlessly a result of certain environmental conditions operating over a long time on the organism. A consideration of its principal physiological characteristics and the factors known to induce the insect to enter, maintain, revert to, or pass from this form, may suggest the fundamental occasions for its rise. This larva is generally said to possess a relatively heavy and tough body wall. Moreover, it always exists within the shelter of a special cavity formed in the soil. Since it neither travels nor eats while it is thus cloathed and housed, it may be regarded as a dormant form. So far as observed, the coarctate larva of Epicauta and Macrobasis in temperate North America and Corditis pallida in Japan carries the species through the cold winter season, while in the Japanese forms, Epicauta ruficeps and Mylabris pustulata it seems especially adapted to tolerate dry soil conditions. Unlike the other instars and the pupae, these larvae were found by Milliken to be resistant to handling, to exposure, to dry- ing or to any soil disturbance that does not crush them, and lost no vitality when overgrown by saprophytic soil fungus. In instances of retarded development among species of Meloidae, the additional time resisted to the species through dependent on these particular hosts. After establishing this obligatory food relation and after the larvae had already suffered their bodily degeneration as a result of sessile living, the hosts may again to this dormant state, should the former conditions that originally induced it be reestablished (Cros, '12b; Milliken). The character of this larva is revealed also by the nature of the influences that cause it to resume development. Transformation to the next, or final, scolytoid larval instar is stimulated by a condition of warm moist soil after hibernation; or when the larvae are very dry during the spring or early summer, their rigid skin often splits immediately if water is thrown directly on it, the final larval form emerging within a few minutes (Milliken). These facts indicate that the coarctate larva is fitted to perform the special function of bringing the species through environmental conditions that are unfavorable to development. In view of this service, this larva is most appropriately described as a resistant form, and is functionally equivalent to the hypopus of some Azarina and to the cyst stage occurring in certain lower animal phyla.

However, these factors seem to be only the causes of the seasonal appearance and disappearance of this larval form. Were they likewise the primitive stimuli to its inception, a similar larva might be reasonably expected to occur in many other insect groups that must have evolved under somewhat similar climatic conditions. It seems very significant, by way of accounting for its origin, that this resistant type of larva appears at the very point in the life cycle where the last of the food supply has been consumed. In all the holometabolous orders of insects, the particular role of the entire larval stage is to feed and grow. But the larvae of the Meloidae as a family now constitute an exception to this elemental principal of insect biology. Here, instead, the function of the entire larval stage is to possess a relatively heavy and tough body wall. Moreover, it always exists within the shelter of a special cavity formed in the soil. Since it neither travels nor eats while it is thus cloathed and housed, it may be regarded as a dormant form. So far as observed, the coarctate larva of Epicauta and Macrobasis in temperate North America and Corditis pallida in Japan carries the species through the cold winter season, while in the Japanese forms, Epicauta ruficeps and Mylabris pustulata it seems especially adapted to tolerate dry soil conditions. Unlike the other instars and the pupae, these larvae were found by Milliken to be resistant to handling, to exposure, to drying or to any soil disturbance that does not crush them, and lost no vitality when overgrown by saprophytic soil fungus. In instances of retarded development among species of Meloidae, the additional time resisted to the species through dependent on these particular hosts. After establishing this obligatory food relation and after the larvae had already suffered their bodily degeneration as a result of sessile living, the hosts may
have become smaller, and consequently produced smaller masses of eggs or stored smaller quantities of pollen and nectar. The reduction in the available food could then have obliged the parasites to make adjustments in their own food requirements, gradually developing a tolerance of somewhat less than the optimum or average amount of sustenance. The necessity for an ability to starve along fell upon the fifth and last instars, which no longer feed at all, since the first four obviously continued to feed in the normal manner and ate all the available stores. The larvae of the last two instars are thus obliged, for the sake of their survival, to consume certain of the reserve materials otherwise intended for the pupal and early adult stages. As a consequence, the larvae shrink in size after the fourth instar, the effect of their inadequate rations being finally expressed in a smaller adult body. Thus, while the current causes of the resistant larvae appear to be adverse climatic conditions, this form appears to have been initiated historically to accommodate the species to a shortage of food.

The activities of the larvae after the coarctate or pseudopupal form are known but fragmentarily. In Epicauta vittata and other North American species from the egg packets of locusts, the final or scolytoid larva is rather active and burrows about in the ground but does not feed, and in a few days transforms to the pupal stage (Fig. 94). That of Macrobasis immaculata, upon wriggling from the coarctate skin, burrowes upward to within one or two inches of the surface as a result of a few days of activity. Epicauta rufipes and Mylabris pustulata retained this form for ten days to about two months. The last instar, commonly designated the "third larva" in old world literature, of species from the nests of bees, is passed within the host's cell. Parker and Böving showed that the fifth instar of Tritonaria sanguinipes is inclosed in the cast but unbroken and retained exuviae of the fourth, and the sixth is spent enveloped similarly but in the skins of both the two preceding instars.

The duration of the several instars following the primary larva is mostly short excepting in species that hibernate as coarctate larvae or spend a large portion of the summer as pseudopupae. In Apalus annalis and Meloe autumnalis cribripennis, the pseudopupa occupies about two and a half months between April and July, while in Apalus muralis it exists continuously through a whole year beginning in June. Macrobasis immaculata, Epicauta vittata and other North American species of the latter genus, spend the months of October to April in the coarctate state. In K. vittata the caraboid and the scarabaeoid instars lasted one week each, and the scolytoid only a few days. Development from the inception of feeding by the primary larva to the coarctate form in vittata required on the average of about a month but as little as 24 days outdoors in September. Mylabris pustulata, in Java, passed the caraboid instar in five days, each of the scarabaeoid stadia in ten, and the scolytoid instar lasted ten days to two months. The larvae of Meloe guttulatus cribripennis developed from the second instar to maturity in April to August. Six Tritonaria sanguinipes completed their larval growth between June 9 and August 22, or in 74 days. The first four instars, or the feeding period, lasted from 26 to 41 days under laboratory conditions.
<table>
<thead>
<tr>
<th>Meloidae</th>
<th>Known Hosts</th>
<th>Distribution</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Mylabris schreiberi</em> Reiche</td>
<td><em>Dotiscatus maroccanus</em>; <em>Schistocerca peregrina</em></td>
<td>North Africa; Southern Europe</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris floralis</em> Pall.</td>
<td><em>D. maroccanus</em>; <em>Ancyptera flavicosta</em>; <em>Xiphidium fuseum</em></td>
<td>Europe and Asia</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris quadripunctata</em> L.</td>
<td><em>D. maroccanus</em>; <em>Podisma pedestris</em>; <em>Caliptamus italicus</em>; <em>Locusta migratoria</em></td>
<td>Europe and Asia</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris sibirica</em> Pisch.</td>
<td><em>Stauronotus brevicollis</em>; <em>Stenobothrus lineatus</em>; <em>Stauroderus marlo</em></td>
<td>Siberia; Turkestan; Russia.</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris ocellata</em> Pall.</td>
<td><em>C. italicus</em></td>
<td>Siberia; Turkestan; Russia.</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris floreli</em> Germ. C. italicus</td>
<td><em>C. italicus</em>; <em>C. turanicus</em>; <em>D. maroccanus</em>; <em>D. kraussi</em>; <em>L. migratoria</em></td>
<td>Siberia; Turkestan; Russia.</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris cineta</em> Ol.</td>
<td><em>D. maroccanus</em></td>
<td>Southern Europe and Asia</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris magnoguttata</em> Heyd.</td>
<td><em>D. maroccanus</em></td>
<td>Russia; Turkestan</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris geminata</em> P.</td>
<td><em>D. maroccanus</em>; <em>A. flavicosta</em></td>
<td>Europe and Asia</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris tekkensis</em> Heyd.</td>
<td><em>D. maroccanus</em>; <em>D. albicornis turcmenis</em></td>
<td>Russia; Turkestan</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris fusca</em> Ol.</td>
<td><em>D. maroccanus</em></td>
<td>Persia; Syria; Asia Minor</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris calida</em> Pall.</td>
<td><em>D. maroccanus</em>; <em>C. italicus</em>; <em>L. migratoria</em>; <em>L. danica</em></td>
<td>Southern Eurasia; Northern Africa</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris crocata</em> Pall.</td>
<td><em>D. maroccanus</em>; <em>A. flavicosta</em></td>
<td>Siberia; Southern Russia</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td><em>Mylabris decespunctata</em> P.</td>
<td><em>Stauronotus brevicollis</em>; <em>C. italicus</em></td>
<td>Southern Eurasia</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td>Meloidae</td>
<td>Known Hosts</td>
<td>Distribution</td>
<td>Source</td>
</tr>
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</tr>
<tr>
<td>Meloidae impar Thumb.</td>
<td>C. italicus, et al.</td>
<td>Siberia; Southern Russia; Asia Minor; Turkestan</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td>Meloidae quadripunctata L.</td>
<td>Podisma pedestris; D. maroccanus; C. italicus; M. migratoria.</td>
<td>Central Russia; Turkestan.</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td>Meloidae pustulata Thumb.</td>
<td>Colemanella ephemeroides; Valanga nigricornis.</td>
<td>China; India; Java.</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td>Meloidae scabiosa Ol.</td>
<td>D. maroccanus; D. kraussi; D. albicornis turcomana; B. crucigerus tartarus.</td>
<td>Syria; Persia; Turkestan; Asia Minor.</td>
<td>Jazykov, '31.</td>
</tr>
</tbody>
</table>
### Meloidae

- **Macrobasis cinerea** F. (unicolor Key)
- **Macrobasis immaculata** (Say)
- **Tetraonyx cyanipennis** Haag.
- **Hemonus confusus** (Say).

### Known Hosts

<table>
<thead>
<tr>
<th>Species</th>
<th>Distribution</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. femur-rubrum</em>; <em>M. affinis</em></td>
<td>Columbia.</td>
<td>Roepke, '17.</td>
</tr>
<tr>
<td>&quot;Doubtless feed on locust eggs.&quot;</td>
<td>Missouri; Texas.</td>
<td>Riley, '77.</td>
</tr>
</tbody>
</table>

### Distribution of Known Hosts

- **Tachytes manticida**
- **Osmia**
- **Solitary Bees**
- **Solitary Bees**
- **Solitary Bees**
- **Osmia Saundersi**
- **Colletes**
- **Anthophora nigroinseta**
- **Anthophora pannata; A. nigroinseta**
- **Andrena malcella**
- **Anthophora plipes; A. retusa; A. personata; A. persicina.**
- **Osmia Saundersi**
- **Panurgus dentipes.**
- **Anthophora occidentalis.**
- **Anthophora abrupta.**
- **Osmia gallicornis.**

### Source

- Fabre, '19.
- Cros, '19.
- Cros, '19.
- Cros, '27a.
- Cros, '27a.
- Cros, '27.
- Cross, '98.
- Sauregard, '90.
- Cros, '13.
- Southern Europe; Asia Minor.
- Algeria.
- Northern Africa.
- Northern Africa.
- North Africa.
- Europe; Siberia.
- Southern Europe; Northern Africa.
- Southern Europe.
- Southern Europe; Northern Africa.
- Europe.
- Southern Europe; Northern Africa.
- Northern Africa.
- Europe; N. Asia.
- Kansas.
- Missouri.
- Balkan Peninsula.
- Andres, '09.
- Fabre, '19.
- Cros, '14a.
- Cros, '14a.
- Fabre, '19.
- Cros, '51.
- Cros, '51.
- Hungerford and Williams, '12.
- Riley, '77a.
- Riley, '77.
Host Relations. The above tables contain the names of the more familiar species of Meloidae and their known hosts. The latter, so far as reported to date, belong to the Hexapod orders Orthoptera and Hymenoptera. In the first group, all are Locustidae with the exception of Mylabris fuscum, a Tettigoniid reported by Portchinsky as a host of Mylabris floralis Pall. and Epicauta sibirica Pall. The Hymenopterous hosts are almost exclusively solitary bees, members principally of the families Megachilidae and Andrenidae. Fabre found the larvae of Cerocoma schaeferi feeding upon the Mantids stored in the cells of the solitary Epeolida wasp, Tachytes mentlicola. Attack upon members of both orders by species belonging to a single taxonomic subdivision of Meloidae is limited, so far as now known, to the genus Mylabris, in which at least four species are reported to parasitize bees and a large number have been reared from the egg pods of locusts. Portchinsky had Mylabris pallida Pall. from egg pods in nature, and Cros induced its primary larvae to develop on Hymenopterous larvae on two occasions in captivity. The selection of hosts appears to be correlated to some degree with the taxonomic arrangement of the subfamilies and tribes of the Meloidae.

Following the system of Borchmann in Coleopterorum Catalogus, 1917, as reproduced in part below, it will be seen that the species from the egg pods of locusts belong exclusively to the subfamily Lyttinae and particularly its tribes Mylabrini and Lyttini. Only a few of the species of these tribes have been obtained from the cells of Hymenoptera. Riley's belief that Henous confertus (Say) has a Locustid host seems to be based on indirect evidence. All the species of Meloe investigated develop in the cells of bees, as, so far as known, do all members of the subfamily Nemognathinae.

1. Subfamily Lyttinae
   a. Cerocoma - bees and Tachytes
   b. Mylabris - bees and locusts
   2. Tribe Lyttini
      a. Epicauta - locusts
      b. Macrobasls - locusts
      c. Lyttina - bees
d. Tetraphyinae - locusts
3. Tribus Melolonthini
a. Henus - locusts
b. Melona - bees

II. Subfamily Nemognathinae
1. Tribus Sitarinini
a. Hornia - bees
b. Sitarobrachys - bees
c. Allendesalazarla - bees
d. Apalus - bees

2. Tribus Nemognathini
a. Zutikia - bees
b. Nemognatha - bees
c. Leptopilina - bees

3. Tribus Hortinini
a. Trierania - bees
b. Hortia - bees

That a given species may attack a number of related hosts may be seen from the above lists of hosts and parasites. However, it has been shown that parasitism can not be extended to all bees of close relationship or similar habits. The factor limiting the choice in the instance of Trierania sanguinipennis, whose host is Colletes rufiglithorax, is discussed by Parker and Wool. Among the nests of rufiglithorax and Andreae perplexa are intermingled promiscuously over the same sunny slope, and the nesting operations of both go on concurrently for a considerable period. Trierania does not parasitize Andreae. There can be no doubt that many primary larvae enter into the nests of both bees. The immunity of Andreae from attack is traceable to its nesting habits. Andreae places a mass of pollen in the cell and on it she deposits an egg, which is placed on end and never in contact with the wall of the cell. She then places on the pollen mass a quantity of thin watery honey that completely surrounds and almost submerges the egg. Thus, the primary larva, seeking to enter the cell, can not reach the egg without first falling into the watery honey. In experiments, the larvae invariably became entangled in the honey and perished. On the other hand, Colletes, which fills her cell with a sticky mass of pollen and honey, attaches her eggs by one end to the side of the cell wall above the food mass. The primary larva can therefore readily reach the egg without coming in contact with the sticky food at all, spends this instar on the egg, and is thereafter structurally fitted to float in the semiliquid mass. This explanation of the failure of Trierania to parasitize Andreae is in contrast with the statement of Fabre that the primary larvae of Apalus muralis are capable of living on the eggs of Anthophora laid on the honey in the cell.

The Origin of Parasitism in the Melolonthidae. While it can not be answered conclusively, the question of origin of parasitism in this group may be partly deduced from a consideration of certain basic facts on criteria in the biology of this family and the order Coleoptera as a whole. We may proceed on the general belief that the order is monophyletic and that the systematists are right in regarding the Adephaga as the more primitive members of the order. Accordingly, the predatory habit, which prevails in that suborder, and constitutes the food relation of both the adults and larvae, may be looked upon as that of the earliest beetles. The stages in the Carabidae in particular are active, aggressive forms that pursue prey which seeks to escape attack. Moreover, predatism occurs in a scattered way and in decreasing degree with the approach to the higher levels of the order. The development of the plant eating habit in the Phytophaga and many other more advanced beetles is thus to be looked upon as a specialisation. In the family Melolonthidae, therefore, the larvae have more nearly retained the ancestral type of food than the adults. However, only the primary larvae still possess their earlier predatory structures and facilities in their running legs and their seizing jaws. Precisely how they have gone over from their undoubted early practice of preying on any manageable available animals promiscuously to the parasitic mode of life, in which they feed on the eggs and stored food of insects belonging to restricted systematic groups, can not be shown with finality. However, assuming with the systematists that the Lyttae are the more primitive subfamily, and considering that they are predominantly parasitic on the eggs of locusts, whereas the Nemognathinae come exclusively from the cells of bees, the Locustidae seem to have been the first or original hosts of the Melolonthidae. The locusts have existed a very long time and appear to have occurred rather regularly in abundance. Their habit of ovipositing in the soil where their eggs were readily available to predators that range over the ground made them an easy and regular source of food for the very small, persistent and negatively phototropic primary larvae of the early blister beetles. The larvae consequently gradually forsok the promiscuous roaming and pursuing manner of securing their food to that of the easier and safer mode of life within masses of nutri-
tious eggs that supplied all the food re­
quired during the entire larval life. The 
physical result of this new limited food relation was bodily degeneration and 
especially the loss of locomotor append­
guments. This regressive change at the same 
time obliged the species to eliminate 
variety from their diet, and thereby a 
specific parasitism slowly developed from 
the early and more promiscuous predation. 

The adoption of the cells of bees 
as a habitation and source of food seems 
at first thought to be a long step from 
the attack upon the egg masses of the 
heterometabolous locusts. However, al­
though widely separated phylogenetically, 
the two distinct orders, in which the 
Meloidae have adopted hosts, have in com­
mon at least one biological feature that 
makes them equally desirable and avail­
able to these parasites. The cells of 
the bees serve as hosts occur al­
most exclusively in the soil, as do all 
the eggs of the Locustidae, and, like the 
latter, contain enough food to mature a 
single larva. The fact that solitary 
soil-inhabiting wasps are not known to be 
parasitized commonly is therefore of in­
terest. The cells of bees are readily 
reached by way of the open burrows and 
parapet. This regression at the same 
time obliterated the species to eliminate 
variety from their diet, and thereby a 
specific parasitism slowly developed from 
the early and more promiscuous predation.

The Economic Importance of Meloid 
Larvae. In as much as solitary bees are 
largely beneficial, principally on account 
of their services in pollinating cultivated 
plants, their Meloid parasites are obvi­
ously destructive also from man's point of 
view. Writing concerning Harris gigantea 
(Wellman), parasitic on Anthophora ociden­talis, Hungerford and Williams ('13) state 
that what was once a prosperous colony of 
four or five hundred bees had been reduced 
to a dilapidated condition by this Meloid. 
Such instances are probably not exception­
al. The limited locomotor ability of cer­
tain adult Meloidae that develop in the egg 
masses of locusts tends to insure a progressive 
destruction of the colony. While the lar­
vae of blister beetles are not known to de­
velop at the expense of the honey bee, Apis 
mellifica, the primary larvae are sometimes 
instrumental in killing the adults. Such 
an instance, which involved Helos variegat­
tus Donov., is described by Beljavsky ('15) 
from southern Russia. The larvae occurred 
in large numbers on flowers and fixed them­
selves with jaws and claws in the inter­
stices of the thoracic and abdominal seg­
ments of the bees, very often entering so 
far that they were hardly visible. There­
by the carrier bees are irritated to the 
extent that hundreds of them die in vio­
 lent convulsions, not being able to free 
themselves of their tenacious riders. Thus 
carried into the hives the larvae may even 
chance to attack the queen, but having at­
tached to the wrong host bee all the larvae 
sooner or later die of starvation.

On the other hand, the species that 
consume the egg masses of Locustidae are a 
noteworthy group in controlling the pest popula­
tion. Each larva consumes all or most of the eggs 
of a mass, which commonly numbers 20 to 50 
or more individuals, each larva thereby 
forestalling the potential development of 
as many voracious nymphs and reproductive 
adults. Portchinsky ('14) estimates that 
each female Meloidae, of which he reared 
sixteen species in Russia, produces suffi­
cient larvae to prevent the hatching of 325 
to 820 locusts, and more than 1750 in the 
instance of Epicauta erythrocephala Pall. 
Each larva of Meloidae appears to destroy 
from 40 to 70 eggs of Valanga nigricornis 
(Verbeek, '30), Riley noticed that a few 
egg pod of Melanoplus differentialis when 
parasitized by Epicauta vititata, but these 
usually consume the entire mass laid by M. 
spretus and other such smaller locusts. 
While the increase of destructive adults 
parallels that of the beneficial larvae, 
the benefit arising from the larval attack 
upon the locusts in their initial stage 
probably overbalances the loss occasioned 
by the phytophagous beetles. Obviously the 
beetle that develops in its immature stage 
at the expense of a mass of 20 to 50 eggs 
consumes less vegetation than would the 
locusts that would hatch were the eggs not 
destroyed.

133
PUPATION, AND EMERGENCE OF THE ADULT

When the coarctate instar is finished, the scolytoid larva burrows one or two inches further through the ground to make a pupal chamber. This is located near to the now depleted egg pod of the host locust. *Macrobasis immaculata* constructs an elongate cell at an angle of 30 to 60 degrees and one or two inches below the ground surface. There it turns on its back and requires several days to become a pupa. The mature larvae of the bee parasites, on the other hand, remain within the cells of the host to pupate. Although these are usually in the ground, Green found the pupae as well as all other stages of *Horia debeyi* in the tunnels of *Zylocoeca tenuecpa* in a dead tree. When becoming a pupa, the larva of *Meloe cloudicapilla* does not entirely throw off its exuviae but simply breaks it along the dorsum and loosens it from the body. It assumes the adult state by throwing off a very thin pellicle, the pupal skin (Newport). Fabre noted that the pupa of *Apalus humerelia* is enclosed in a double vesicular envelope. During its development, the larva of *Triorania sanguinipennis* casts off the first three exuviae, but the fourth and fifth are retained, the larva simply shrinking away from its skin and remaining within it. The skin of the last instar, however, is broken and the pupa pushed to the posterior end of the pupa within the fifth larval skin. The fourth and fifth exuviae thus serve as a protecting case for the pupa, and the adult hibernates within the capsule thus formed (Fig. 96).

Several days before adults of *Macrobasis immaculata* emerge from the pupal cells, twitching movements begin in the tarsi. These become more vigorous toward the end of the pupal period, and finally involve the legs and oral appendages. During its struggle the beetle rights itself and the thin pupal membrane, which loosens on the surface of the body, is torn beyond recognition by the sharp tar- sal claws.

So far as known, none of the Meloidae hibernate as pupae. This stage is, accordingly, relatively short. Four individuals of *Meloe melalis* pupated in 9 to 11 days while a fifth required 28 days in the fall. In *M. eumelas* an instar 13 to 22 days; *Apalus muralis* transformed in 3 to 4 weeks; *Melobrias wagneri* pupated and issued as an adult in 31 days; and *Epilaccus vittata* required only 5 to 6 days to pass through this stage (Fig. 96).
cles is said to require about three years for one generation (Cros, '24), and most individuals of Apalus muralis complete their metamorphoses in two years, while a few do so in one (Valery-Mayet; Fabre). The two procedures in the development of muralis are shown in the accompanying diagram of cycles. The first winter is passed by the primary larvas, which enter the pseudopupal state in the following June. A few of these transform to adults during July and August, and the cycle begins anew, the primary larvas again hibernating. However, most of the pseudopupa persist through the second winter of the cycle, and reach adulthood in August of the ensuing year. In the instance of Domia nymphoides the pseudopupa overwinter, the adults of the first generation appearing in June and those of the second ovipposit in September and October, the resulting larvas again reaching the pseudopupal state in November.

The species having annual life cycles are separable into three groups according to the hibernating stage. The members of Epicauta and Macrobasis observed by Riley and Milliken winter as coarctate larvas, with the possible exception of M. pennsylvanien. They then complete their larval growth, pupate and become adults in the months of April, May and June. Nesting, oviposition and incubation take place chiefly during July, August and September, and the primary larvas enter the new egg pods largely within the same months. They reach the coarctate form principally during August, September, and October. Such is the seasonal distribution of the stages of M. vitatta, M. cernea, M. maculata, M. sertica, M. lapidaria, and M. unicolor, and probably most others dependent on locusts in the United States. Moreover, Zonitis cinerea, E. maculata, E. sericans J. Lec., and most of their hosts, the reproductive seasons of other Meloidae either initiate or make their completion by feeding upon the eggs of their hosts, the reproductive seasons and activities of the host and the parasite must be nearly simultaneous. In the United States, the species of Melanoplus are found to date as the hosts of Epicauta and Macrobasis. These grasshoppers deposit most of their eggs during August and September, and the beetles oviposit between latter July and mid-October. A similar concurrence has been demonstrated in the relations of other Meloidae and their hosts. The seasonal development of sanguinipennis and siccificus is similar. The new adults come from their pupal chambers in the cells of bees to spend a brief period of reproduction in April and May. The larvae feed and grow in May to August, pupate in August and September, and transform to adults in September and October, and the new imagoes remain inactive in their pupal cells until early the next spring. Meloe muralis appears to have an essentially parallel life cycle in Algeria (Cros, '12, '13b). In the latter country, Meloe pennsylvania and M. autumnalis cribripennis depart from the type of cycle possessed by cribripennis because their activities are not interrupted by a cold winter. The adults accordingly engage in mating and ovipositing during November, December and January, thereby gaining time on cribripennis which lies inactive during this season in Europe. But cribripennis again loses its advantage by spending a correspondingly longer time in the pupal state than does cribripennis. In this way, the cycles of the two species retain the same seasonal parallelism year after year. These cycles show also that adverse conditions in a warm season may delay development in the same manner as does the cold of winter.

Considering that the larvae of the Meloidae either initiate or make their complete development by feeding upon the eggs of their hosts, the reproductive seasons and activities of the host and the parasite must be nearly simultaneous. In the United States, the species of Melanoplus are found to date as the hosts of Epicauta and Macrobasis. These grasshoppers deposit most of their eggs during August and September, and the beetles oviposit between latter July and mid-October. A similar concurrence has been demonstrated in the relations of other Meloidae and their hosts.
The species of Anthophora parasitized by Apalus muralis and Meloe cicatricosus winter as pupae, and the new bees mate, build and store their new cells, and also oviposit, in May. The over-wintered primary larvae of Apalus muralis were being carried by the new bees and occurred on the newly deposited eggs during the same month. M. cicatricosus, which hibernates as an adult in the host’s cell, issues to oviposit in April and May, and some of the primary larvae were found attached to the hairs of Anthophora on May 23. Triceratia sanguinipennis, likewise, oviposits in April and May, and the larvae were plentiful on the adult bees in latter May, when these were engaged in storing their new cells and laying eggs.
### A. Parasites of Locusts

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</tr>
</thead>
<tbody>
<tr>
<td><em>E. vitellata</em></td>
<td>Riley '77</td>
<td></td>
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<tr>
<td><em>E. maculata</em></td>
<td>Milliken</td>
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### B. Parasites of Bees

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<tbody>
<tr>
<td><em>T. sanguinipes</em></td>
<td>Parker and Boving</td>
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<tr>
<td><em>M. cicatrici- pennis</em></td>
<td>Fabre and Newport</td>
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<tr>
<td><em>M. autumnalis orbripennis</em></td>
<td>Cros '13</td>
<td></td>
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<tr>
<td><em>A. analis</em> (Sitaris colletta)</td>
<td>Beauregard</td>
<td></td>
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<tr>
<td><em>A. muralis</em> (Sitaris humeralis)</td>
<td>Fabre Valery and Mayet</td>
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13. COCCINELLIDAE. LADYBEETLES

GENERAL FEATURES

The popular names ladybird, Marienkäfer, les betes du bon Dieu and others (Stehr; Strouhal; '26), suggest the gentle nature and beneficent habits of the Coccinellidae, and express the affection and reverence in which these beetles are held by various peoples. For these reasons and the fact that all the stages live mostly rather exposed where they may be easily observed, their bionomics is known with comparative completeness. The food habits of the larvae and the adults are alike. So far as known, the Epilachninae are largely phytophagous, while the food of the Lithophilinae may only be inferred from the predatory dentate mandibles. Most of the ladybeetles fall into the subfamily Coccinellinae, the majority of which prey on other insects but principally Aphids and Coccids. However, some of the Psylloborini have been shown to be fungivorous (Strouhal), and many common forms that are generally rated as carnivorous, ingest varying amounts of plant matter with their fleshy fare. Their beneficial predatism has occasioned the transportation of a number of species to places distant from their native lands to aid in the control of noxious insects. Studies of interest to the geneticist and taxonomist have been made in the Coccinellidae by Johnson ('10), Palmer ('11), Hawkes ('20) and Zarapkin ('30). Much of the literature dealing with the family is cited by Boving ('17).

LIFE OF THE ADULT

Habitats and Dissemination. Choice of habitats is determined by the location of the prey. Fluke has shown by the use of tanglefoot screens that Hippodamia convergens amalgua L., and others fly as high as 29 feet above the ground. The adults of the larger species crawl about largely on exposed parts of plants infested with small insects but also enter rolled leaves curled as a consequence of the feeding of Aphids. Small forms like Chilocorus, Hypaspis and Scymnus sometimes live in hiding under large Cocidae of the type of Pulvinaria upon whose stages they feed. Some species of Braconyxanths, Scymnus and Hypaspis have become associated with ants, but the adults do not seem to have become so much obligated to this mode of life as have the larvae. According to Donisthorpe ('19; '27), Coccinella diversicostata O. (Distincta Ws.) habitually occurs in the neighborhood of the nests of Formica rufa, but does not enter these excepting in the winter when a few adults may hibernate in them. In all these instances the relationship with the ants is indirect and apparently affected by the mutual interest of both ants and ladybeetles in the Homoptera that dwell within or near the nests.

Mating. During mating the male fixes himself on the back of the female, as is done by most other Coleoptera. In the instance of Coccinella septemcinctata L. the duration of copulation varied from five minutes to four and three-fourths hours, in Adalia bipunctata L. from 30 minutes to five hours (Johnssen), and in Coleophora spinicauda Gr. from four to six hours at a time. Mating usually begins rather soon after the adults issue from the pupal cases, as is shown by the following instances: Callinella testudinaria Muls., in seven to twenty days; in Adalia bipunctata, Ol. abdominalis Say, Hippodamia convergens amalgua L., Cyclos, sanguinis L. and Coccinella transversoguttata californica Mann. this interval averaged from 1.6 to 2.7 days (Clau
den) Scymnus nubes Casey, 2-3 days, and Rodolia cardinalis Muls. mated immediately upon emergence from the pupal cases in Palestine (Rodenheimer). Adalia bipunctata was found by Hawkes to be both polyandrous and polygamous.

Although apparently common, frequent mating is not essential to fertilization of the eggs. Only one union was found to be necessary during the life of the eight common Californian species investigated by Clausen. In one instance, fertile eggs were still being laid fifty-five days after copulation. All the eggs laid by a Callinella testudinaria hatched during the first 45 days of the 56-day period after the male was removed (Swezey), and the females of Hippodamia tradecimpunctata produced fertile eggs for about three weeks after mating (Outright). Unmated females of the latter species laid only about one-fourth the usual number of eggs. Inferti
tile eggs generally collapse soon after they are deposited. Palmer observed that all females of J. convergens Guer. and other Coloradoan species which had oviposited before going into hibernation died either during the winter or in the spring.
without laying more eggs.

The preoviposition period has been determined to be as follows, in days: \textit{Coccinella transversoguttata} quinquenotata Kirby, 4-10; \textit{C. novemnotata} Herbst., 1-7; \textit{C. repanda} Thunb., 7; \textit{Hippodamia tricolor} Actinopterata, 3-8; \textit{H. convergens}, usually 5, and \textit{Rodolia cardinalis}, 3.4 in summer and one to three weeks in winter. In the following species, the period elapsing between mating and oviposition was: \textit{Adalia bipunctata}, 13 (Johnsson) and 9.6 (Clausen) days; \textit{Callipara testudinaria}, 0-1; \textit{Coccinella transversoguttata} california, 11.9; \textit{C. septempunctata}, 13; \textit{Coleophora spiniciole}, one week; \textit{Cryptolaemus montrouzieri} Muls., never sooner than 16 hours after mating (Wille); \textit{Cyclonedia sanguinea}, 10.1; \textit{Hippodamia convergens}, 10.6; \textit{H. convergens} ambigua, 9.6; \textit{Hyperaspis lateralis} Muls., 10-12; \textit{Oleis obscuranales}, 8.6; \textit{O. cardinalis} P., 10-12; \textit{O. abdominalis}, 8.6; \textit{O. ocellata} F., 10-12; \textit{Scymnus nubes}, 14.4; and \textit{Verania lineola} F., 0-1 days.

Oviposition. The majority of the better known species deposit their eggs in regular clusters in which the eggs are set on end with the sides contiguous (Fig. 97, B). The number of eggs composing the clusters is indicated in the following instances: \textit{Adalia bipunctata}, 3-50; \textit{A. frigida humeralis} Say, mostly 10-30; \textit{Atolocerus stribellus} Muls., 1-57; \textit{Anasa} quinquedecimpunctata Deg., 10-12 (Britton); \textit{Callipara testudinaria}, 9-64, average 30; \textit{Ceratomia maculata} fucata Muls., 8-34; \textit{Coccinella divaricata}, 7-20; \textit{C. novemnotata}, average 30-50; \textit{C. trisescala} L., 2-28 in 28 masses; \textit{C. repanda}, usually 10-12; \textit{Cryptolaemus montrouzieri} Muls., 4-12; \textit{Cyclonedia sanguinea} immaculata Fabr., 5-27; \textit{Hippodamia convergens}, 14-17 (Miller and Thompson), usually 30 (Palmer); \textit{B. predecipitata}, usually 10-40; \textit{Leis conformis} Boisd., 1-60, average 34; \textit{Pseudoplatystoma japonica} Kuritaeki, one mass of 20 and \textit{Syria melanaria} Muls., 10-16. In general the number of eggs per mass declines as the end of the oviposition period is approached.

The eggs of \textit{Curinus zonatus}, \textit{Coccinella (Psechlatia) zygips} Pall. and \textit{Hyperaspis signata} O. (Ghototay Say) are placed more or less at random in irregular heaps, these containing 5-10, 10-20 and 4 eggs, respectively, in certain instances. On the other hand, \textit{Cryptopus orbitatus} Schönh. and \textit{Scymnus rubes} deposit one egg at a place. \textit{Chilposonus similis} West and \textit{Rodolia cardinalis} lay their eggs either singly or in small clusters.

**TABLE II. OVIPOSITION**

<table>
<thead>
<tr>
<th>Name</th>
<th>Observer</th>
<th>Best eggs observed</th>
<th>Total eggs produced per female</th>
<th>Daily yield per female</th>
<th>Additional data</th>
</tr>
</thead>
<tbody>
<tr>
<td>\textit{Adalia bipunctata}</td>
<td>Hawkes</td>
<td>-</td>
<td>144.0</td>
<td>6.0</td>
<td>Largest individual yields 167,189, 418.</td>
</tr>
<tr>
<td>\textit{Adalia bipunctata}</td>
<td>Fluke</td>
<td>2</td>
<td>273.0</td>
<td>14.3</td>
<td>Range of daily yield 5-23 and 2-49.</td>
</tr>
<tr>
<td>\textit{Adalia bipunctata}</td>
<td>Burgess</td>
<td>1</td>
<td>122.0</td>
<td>3.2</td>
<td></td>
</tr>
</tbody>
</table>

Fig. 97


"Declaration".
<table>
<thead>
<tr>
<th>Name</th>
<th>Observer</th>
<th>Beetles observed</th>
<th>Observed period of oviposition in days</th>
<th>Total eggs produced per female</th>
<th>Daily yield per female</th>
<th>Additional Data</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>A. frigida</em> humeralis</td>
<td>Burgess</td>
<td>2</td>
<td>35.6</td>
<td>175.0</td>
<td>5.0</td>
<td>146 eggs in 40 days; 206 in 51 days.</td>
</tr>
<tr>
<td><em>Anatis quinquecostata</em></td>
<td>Burgess</td>
<td>3</td>
<td>15.7</td>
<td>93.0</td>
<td>5.9</td>
<td></td>
</tr>
<tr>
<td><em>Callinera testudinaria</em></td>
<td>Swezey</td>
<td>3</td>
<td>-</td>
<td>722.0</td>
<td>-</td>
<td>Yields per female: 591, 632 and 944.</td>
</tr>
<tr>
<td><em>Chilocorus similis</em></td>
<td>Nakayama</td>
<td>4</td>
<td>Entire period</td>
<td>16.2</td>
<td>-</td>
<td>Yields per female: 14, 16, 17 and 18.</td>
</tr>
<tr>
<td><em>Coccinella arxyridis</em></td>
<td>Tan</td>
<td>1</td>
<td>-</td>
<td>498.0</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>
| *Coccinella novemnotata*| Palmer   | 4                | 63.0                                   | 731.0                         | 11.6                   | Yields per female: 435, 493, 950 and 1047, in 40, 53, 83 and 76 days, respec-
<p>|                        |          |                  |                                        |                              |                        | tively.                                                                         |
| <em>Coccinella novemnotata</em>| Burgess  | -                | 12.0                                   | 251.0                         | 21.0                   |                                                                                 |
| <em>C. transversoguttata</em> | Palmer   | 3                | 50.0                                   | 458.0                         | 9.1                    | Yields per female: 366, 469, and 836, in 70, 62 and 39 days, respectively.   |
| <em>C. trifasciata</em>       | Burgess  | -                | 89.0                                   | 426.0                         | 4.7                    |                                                                                 |
| <em>Cycloneda sanguinea</em>  | Fluke    | 1                | 20.0                                   | 248.0                         | 12.4                   | Mostly laid at rate of 10-24 per day.                                          |
| <em>C. sanguinea immaculata</em>| Miller and Thompson | 6 | 16.0                              | 126.0                        | 7.9                    |                                                                                 |
| <em>Hippodamia tredescantia</em> | Outright | 5                | Entire period                         | 407.0                         | -                      | Average length of adult life in summer about 30 days.                           |
| <em>Hippodamia convergens</em>| Palmer   | 2                | 32.0                                   | 221.0                         | 6.8                    | Yields per female: 130 and 312 in 20 and 46 days, respectively. Three others laid 190, 296 and 312 eggs, in undetermined periods. |
| <em>Leis coniformis</em>      | Thompson | 1                | 106.0                                  | 904.0                         | 8.5                    |                                                                                 |
| <em>Prospilaena japonica</em> | Kanbe    | 1                | -                                      | 210.0                         | -                      |                                                                                 |</p>
<table>
<thead>
<tr>
<th>Name</th>
<th>Observer</th>
<th>Beetle's observed</th>
<th>Observed period of oviposition in days</th>
<th>Total eggs produced per female</th>
<th>Daily yield per female</th>
<th>Additional Data</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rodolia cardinellus</td>
<td>Bodenheimer</td>
<td>29</td>
<td>11-170: ave. 97</td>
<td>340.8</td>
<td>1.14-13.2: ave. 5.90</td>
<td>The variations are largely traceable to summer and winter conditions.</td>
</tr>
<tr>
<td>Scymnus rubes</td>
<td>Davidson</td>
<td>--</td>
<td>26.4</td>
<td>31.5</td>
<td>1. +</td>
<td>Early in the period they laid about four eggs per day.</td>
</tr>
</tbody>
</table>

Similar data for eight common California species presented in Table III are taken from Clausen ('16). The numbers express the averages in days.

**TABLE III. OVIPOSITION OF CALIFORNIA COCCINELLIDAE**

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of specimens</th>
<th>Length of oviposition period</th>
<th>Percentage of eggs laid in days</th>
<th>Eggs per female during the period</th>
<th>Number of eggs laid per day</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coccinella transversoguttata</td>
<td>10</td>
<td>31.0</td>
<td>69.5</td>
<td>207</td>
<td>8.0</td>
</tr>
<tr>
<td>Coccinella trifasciata</td>
<td>10</td>
<td>29.2</td>
<td>75.0</td>
<td>249</td>
<td>8.4</td>
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<tr>
<td>Hippodamia convergens</td>
<td>11</td>
<td>33.3</td>
<td>63.9</td>
<td>299</td>
<td>8.9</td>
</tr>
<tr>
<td>Hippodamia convergens ambiguas</td>
<td>8</td>
<td>46.1</td>
<td>61.4</td>
<td>312</td>
<td>7.3</td>
</tr>
<tr>
<td>Olla abdominalis</td>
<td>9</td>
<td>37.7</td>
<td>70.3</td>
<td>234</td>
<td>6.3</td>
</tr>
<tr>
<td>Olla oculata F.</td>
<td>9</td>
<td>35.4</td>
<td>89.3</td>
<td>347</td>
<td>9.8</td>
</tr>
<tr>
<td>Adalia bipunctata</td>
<td>10</td>
<td>28.2</td>
<td>69.4</td>
<td>190</td>
<td>6.7</td>
</tr>
<tr>
<td>Cycloneda sanguinea</td>
<td>10</td>
<td>28.8</td>
<td>73.6</td>
<td>201</td>
<td>7.0</td>
</tr>
</tbody>
</table>

While the maximum egg-laying capacity of individual Coccinellidae has obviously not been made known in most species, one female of Hippodamia convergens laid a total of 600, while another, reported by Andrews, yielded 1550 within a period of slightly more than two months (Clausen). The records in Table II show that Coccinella novemnotata and Callineta testudinaria are likewise capable of high yields, having deposited approximately 500 to 1000 eggs per female. It may therefore be supposed that most of the tabulated records do not represent the full capacity in oviposition. However, Chilocorus similis appears normally to produce only a small number of eggs. These instances suggest that the numerical production is to some extent
proportional to the size of the species or individual. But other factors, including seasonal temperature and quantity of food, affect the amount of oviposition. The average number laid per female of Rodolia cardinalis in Palestine in winter, spring, summer and autumn was 198, 320, 535, and 272, respectively, and the daily rate gradually increased up to 2892 (Bodenheimer). When the adult Hippodamia transversa was given five to ten Aphids daily, neither mating nor oviposition took place, but eggs were produced at a maximum rate when fifty or more Aphids were supplied each day. That the duration of the ovipositional process differs greatly among the species is evident from Callinella testudinaria and Chilocorus similis, the first ovipositing at the rate of about 2 eggs per minute while the second required from 20 to 30 minutes to deposit one egg. This difference is traceable in part to the distinct modes of procedure in egg laying. Whereas testudinaria simply places them in masses in the way of most ladybirds, similis stands over the Coccid prey with the ovipositor exerted forward beneath herself and pushed under the edge of the scale.

The color of Coccinellid eggs may depart more or less from the usual orange yellow. These variations are explained first by the approach of the egg to maturity and second by the color of the food consumed by the female, as has been demonstrated in Adalia bipunctata, Coccinella septempunctata and Scymnus nubes. A few hours before the larvae hatch, the eggs turn from yellow to gray and darker as the last of the yolk is consumed (Strouhal). When Scymnus fed on light green Aphids, such as Myzus persicae, she laid light yellowish green eggs, but when the black Aphis rumicis was the food, the eggs were dark amber-colored.

The eggs are laid in a variety of situations, but these are similar in being somewhat hidden and near prey suitable to the species. The egg masses of the larger roaming species such as Adalia, Hippodamia, Coccinella and Cycloneda are found principally on the lower side of leaves near Aphid colonies, while the smaller forms which tend to attack the relatively more sessile mealybugs and other Cocclidae, incline to deposit their eggs nearer to, if not upon or under, the food animal. Thus, Curinus zonatus prefers to oviposit in leaves that are not entirely unrolled; Hyperaspis, Chilocorus and Cryptolaemus montpoulietii on twigs, leaves and bark; H. lateralis places some of its eggs under adult mealybugs; Chilocorus similis inserts them under the scale; Phytocoris ventralis Br., among mealybugs or under the adult female of Saissetia oleae; Cryptognous orbiculus, among the egg masses of Pseudococcus citri or the nymphs of the viviparous P. longispinus; Rodolia cardinalis mostly upon the egg sacs of Icerya purchasi and Scymnus nubes among Aphids in protected situations (Be-sig). Where the species of Brachyacantha, Scymnus and Hyperaspis, inhabitants of the nests of ants, lay their eggs does not seem to have been observed. Coccinella divariaowna oviposits on the underside of pine needles and leaves of other trees above the nests of Formica rufa.

The smaller species above exhibit a noticeable tendency toward a parasitic relationship with the larger Cocclids. This is suggested not only by the habit of ovipositing very near to, upon or under the food animal, but also by the comparatively small discrepancy in the size of predator and prey, the greater specificity in the selection of their food, and, in some cases by the adequacy of a single large Coccid and its newly produced eggs or nymphs to meet the nutritional requirements of the larval Coccinellid. Chilocorus bivulnerus in its food and shelter relationship with Pulvinaria Inquisitor seems to embody somewhat these characteristic features of parasitism.

THE LARVAL STAGE

Incubation. The eggs of the Coccinellidae are not known to serve for hibernation. The incubation period is therefore never of extraordinary length, but, as shown by the records in Table IV, is of relatively brief duration in both temperate and subtropical regions, the majority completing their embryonic development in eight days or less. This generalization is supported also by the following instances of species not included in the table: Callinella testudinaria, 4 days; Crypto- laemus maculatus Fuscella, 4-4; Chilocorus stipitus Say. (bivulnerus Muls.), 13; Coccinella divariaowna, 5-7; C. montspola Muls., 5-6, mostly 4; C. novemnotata, 3-6, mostly 4; C. transversopustulata quinquenotata, 3-5, mostly 3; C. repanda, 3-4; Cycloneda sangui- nas, 3-6, mostly 4; Hippodamia converpensa, 2-6, average 3.6; same, 3-7, mostly 3; H. parenthesis, 3; H. sinuta Muls., 3-6; Lea. conformis, 3-12; Oilla abdominalis sobrina Casey, 4; Propylaea speoia, 4-8; Rodolita cardinalis, 2-8 (Bodenheimer); Thea rigi-
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Hatching. All the larvae from a given mass of eggs hatched within 6 to 10 hours after the first one issued in the instance of Hippodamia tredecimpunctata, according to Cutright. Observations on other species also show that hatching within individual masses is not necessarily simultaneous but may be distributed over a period of several hours. Strouhal ('26a) found egg-bursters on the first instar larvae of Coccinellinae. As a rule these were located on the pronotum and mesonotum, although in some species also on the metanotum, but were always smaller on the second and third segments. They consist of a pair of teeth on the pronotum, and a more prominent bristle arising immediately behind each tooth. When the unhatched larva doubles upon itself longitudinally these processes, whose apices are directed caudad, are probably forced through the egg shell which is thereby ruptured, permitting the issuance of the insect. In hatching, the chordon of H. tredecimpunctata cracks irregularly along the dorsal side (Cutright), and the larva of H. convergens emerges from an irregular aperture across the upper end of the egg (Clausen). The prothorax of tredecimpunctata appeared first, and when bent backward released the head. By vibrating the free part forward and back, the legs and the other thoracic segments were freed in order. The process of hatching to this point required ten minutes. The larva then rested for about an hour, whereupon it employed its strengthened legs to crawl completely out of the shell. The hatching larva of convergens remained for 15 to 30 minutes protruding about two-thirds of the way out of the shell while the body became hardened sufficiently to permit locomotion. Twelve to twenty-four hours usually elapse before feeding commenced in the instance of convergens, the larva in the meantime resting in groups on or near the cluster of empty shells.

Larval Habits. Most Coccinellid larvae crawl actively over the surfaces of plants infested with their food animals, but those of Hyperaspis signata, (Fig. 98) and Chilocorus stigma are sometimes found under Fulvia nervosa. In Europe, larvae of Rhisoclus ventralis live under the egg masses of Pseudococcus, and Rodolia cardinalis in the egg sacs of Isaria. Also other small species at times live similarly under cover of such large prey. The most extreme departure from the usual habitat of the family is represented in several species belonging to Brachyscantha, Symus and Hyperaspis (Wheeler, '11). These seem to have established a rather fixed relationship with the nests of ants and particularly their Homopterous honeydew-producing guests. Wheeler found the larvae of B. quadripunctata Nelson, in the nests of Lasius umbratulus aphidicolus near Boston. Schwarz reported B. ussaria P. abundant in the colonies of L. vagator near Washington, D.C., and Mann had Brachyscantha-like larvae from a nest of Pormion camponotile in Washington state. In Europe, the larvae of Hyperaspis repensae Herbst were discovered in the nests of Tapinoma erraticum nigrum and of Silvestri, and those of Symus formicarius Muls., like the adult, may share the nests of Pormion rufus in Siberia (Wasmann). So far as known, the larval Coccinellidae are more habituated to this mode of life than the adults, but the larvae of Coccinella diversicatae, which Donisthorpe regards as myrmecophilous, do not enter the nest of Pormion rufus as the adults sometimes do. In the more fully studied instances, the nests were moreover inhabited by Homoptera, B. quadripunctatae being found with root-coccids and root-aphids, B. ussaria with Pemphigus, and H. repensae with the Pulgaridae, Tettigometra impressiceps and P. coarctata. This three-fold association of ants, ladybeetles and Homoptera has evidently arisen through the desire of ants for honeydew and the habit of the beetles to prey on the bodies of these same guests of ants.

Fig. 98
Development and Duration. Four instars compose the larval stage in almost all the many species observed. One exception is reported by McKenzie who found the usual four stadia in the spring generation of Hyperaspis laevigata but only three in the fall generation. According to Twats, *Pseudonasonycha japonica* has five stadia in its larval period. In addition to the species listed in Table IV, the following are reported to have the usual number of instars: *Callilus testudinaria*, *Coccinella divaricata*, *C. repanda*, *C. clausata*, *Cryptolaelaps montivarius*, *Leis conformis* and *Syna melanaria*.

It appears from the instance of *H. lateralis* that duration of development is not necessarily proportional to the number of molts. Seventeen larvae having three instars required 21 to 34, or an average of 27, days for their development, whereas thirty with four instars made their growth in the comparatively short period of 13 to 23, or an average of only 16 days. In *Pseudonasonycha japonica*, the larval period was about 2 weeks, the duration of the fourth instar being 2, 2, and 5-6 days, respectively, the last including 2 to 3 days commonly designated the prepupal period. In Table IV, the duration of the first, second, and third instars was 24, 21, and 5-6 days, respectively. The whole numbers represent approximate length, decimals usually signify average duration, and the hyphenated numbers express the high and low extremes of the periods spent in the several instars or stages.

In general, the instars of the *Coccinellidae* are of relatively short duration. In the instance of *Alypia virens*, the second and third instars were frequently passed in less than 24 hours in the warmer parts of the year (Davidson). The second instar is for most part somewhat shorter than the first, and likewise, the third is often passed in less time than the second. In most of the species tabulated, the prepupal period is included with the fourth instar, which in part explains the abruptly longer duration of that stadium. However, after seducing one to five days for prepnupation, there is still left a comparatively long period for the last larval instar. The larval stage, as a whole, is therefore comparatively brief, as is shown also by the following records: *Adalia spp.*, 11-18, mostly 15 days; *Callilus testudinaria*, 11-13; *Coccinella repanda*, 8-9; *C. divaricata*, 25-29; *Cryptolaelaps quinquenotata*, 11-19, mostly 13; *C. monticola*, 16-18, mostly 18; *C. novemnotata*, 10-21, mostly 11-14; *E. styria*, 11-16; *Coccinella maculata fuscula*, 17 (Pluke); *Cyclopedus angusticeps*, 9-16, mostly 11; *Hyperaspis convergens*, 15-26, mostly 18 (Palmer); same, 10-13 (Miller and Thompson); *H. angusticeps*, 21-23; *H. papillifer*, 11; *Propyramus corymbosus*, 46-51 days; *Verania frena*, 16-60; and *L. lineola*, 13-31. The uniform relative brevity of this stage is explained in part by the fact that no species of the family winters in this phase of the cycle. In only a few cases does its duration exceed a month, and usually requires not more than three weeks.

The effect of seasonal weather on duration is reflected in the following instances: *Cyclopedus angusticeps immaculata*, three individuals reared in March developed in 19, 31 and 34 days, respectively; two in April required 18 and 16 days; one in May, 10; one in June, 9; two in October, 17 and 20 days (Miller and Thompson). In *Cyclopedus japonicus*, the first instar lasted 10-12 days in the summer months of November to March, and up to a month in winter. From July to the last of September, the period the average daily temperature was 73 to 69°F, the larval life of *Leis conformis* extended over 10-14 days, whereas in November and December, with temperatures of 65 to 70°F, the stage lasted 13-35 days (Thompson). Bodenheimer showed that the calculated relation between temperature and the development of *Roddio cardinalis* agrees substantially with the empirical data. The extreme developments were 86 days at 13.8°C (56.4°F) and 16 days at 28.2°C (82.7°F),

**PUPATION**

The positions selected by the mature larvae for their pupal life are very often the exposed upper surfaces of leaves, stems and other parts of plants, or inanimate objects, or somewhat sheltered places near the last feeding site of the larvae. The pupae of the smaller species seem more commonly to occur in curled leaves and the crevices of bark. Ensign reports *Cryptolea angustistriga* and *Alypia virens* adopting the shelter of dry clods on the ground, whereas *Hyperaspis signata* and *Cryptogonus orbiculus* sometimes pupate under the remnants of their large Coccid prey. Different kinds of weather were observed by Hawkes to affect the choice of spots in *Adalia bipunctata* which selected the more hidden places in bright warm conditions, and more exposed situations in wet and cloudy times. The larvae of *Brachycentrus quadripunctata* remain in the nest of *Leisus* to transform, and *Hyperaspis
reppensis were found on the lower surfaces of stones or debris covering the nests of Taphronia.

When ready to transform, the Coccinellid larvae seem universally to attach themselves to the support by the caudal end of the abdomen (Fig. 99). So far as observed, this is done also by the younger larvae preceding each molt from one instar to the next. Strohual ('26a) states that the mature larva produces a copious secretion from the anus, but its precise source seems not to have been determined, although Johnssen attributes it to glands in the hind intestine. By means of this fluid the larva is said to secure itself by the tenth abdominal segment. However, other mechanisms for attachment are described. Rhizobius tralis possesses an anal appendage having the shape of a human foot with the toes turned in (Essig), and Rodolia guerini Crotch fastens itself by a posterior adhesive pad (Stebbing). After securing itself, the larva either hangs head downward or lies upon the supporting surface.

The transforming larva may or may not cast its molted skin. Cryptolaemus montrouzieri, Cryptogonus orbiculus, Brachyacantha quadripunctata, Hyperaspis signata, H. lateralis, Rodolia guerini, Scymnus guttulatus v. Leo., and doubtless others, retain the last exuviae unbroken as a covering during the pupal stage. Curinus zonatus breaks its old shell but remains in it exposing only the dorso-median part of its body, and the pupa of E..§... nubes is more or less hidden by the old cuticula and the woolly threads of the larva. S. guttulatus bears a characteristic pair of anal forks on the last abdominal segment which serve to hold the pupa in the larval skin. The practice of retaining the exuviae in these species seems to be correlated with the presence of waxy plates or mealy secretions formed over the body during the larval stage.

But the majority of the species completely shed their last larval cuticula at the time of pupation. The prepupal period varies from several hours to as long as five days, according to species and environmental influences. Within this time the larva gradually arches its back and bends the cephalic end ventrad. The molted skeleton splits dorsally in the region of the thorax and, in some instances, to the apex of the abdomen. By vigorously rocking the body, the pupa of Hippodamia tredecimpunctata crowds the exuviae down about the tip of the abdomen where they remain (Outright). This is also the position of the molted skin in many other species.

The duration of the pupal stage in the several species compares favorably with that of the incubation period and the fourth larval instar. In general it is brief as are the preceding stages of the cycle, the majority of the species pupating in nine days or less. The following records supplement those listed in Table IV: Adalia spp., 5-9 in spring, 3-9 in summer; Collineidae testudinaria, 4-6; Caratopidilus maculicula fuscusdebris, 6 (Fluke); Colloconus stigmus, S. Cocinella coccinellia coccinellia, 9-11; C. monticola, 4-8; mostly 6; C. transversoguttata quinquenotata, 3-6, mostly 4; L. novemnotata, 4-9; Coleophora abalina, 2-7; Cycloneda sanguinea, 3-5; C. sanguinea humicola, 4-8; Hippodamia tredecimpunctata, 5-7 in Florida, 4-9 in Colorado; H. nematodes, 6; H. seraphimia, 6; Hyperaspis lateralis, 15-25, average 17; H. signata, about 2 weeks; H. replessis, 22-30; Lestes conformis, 5-7 in warm weather, 10-15 in cool weather; Olla abdominalis sobrina, 5-6; Prophila épista, 3-18; Pseudonymphus japonicus, 6-8; Coccinella éryptis, 2-7; Rodolia guerini, usually 6-9 and Synia melanaria, 6-7 days. Hawkes gives the following records for three successive years of observation on Adalia bipunctata in England: 9-21, average 13; 3-28, average 17: 16-22, average 20. The lowest record of three days was obtained in a temperature of 101.0°F.

THE ADULT STAGE

When the process of transformation is completed, the new adult remains in the pupal skin for a period of a few hours to several days while its body hardens and takes on its mature color. Considering that the Coccinellidae of the temperate regions always hibernate as adults, this stage is relatively long in the overwintering generations, but is otherwise not disproportionately longer than the other stages. The duration of adult life that includes the period of time spent in hiber-
nation is reported for a few species as follows: Adalia bipunctata, "August and September to the next June (Hawkes); Hippodamia convergens, a male lived nine months and eight days in Colorado (Palmer); H. tridecimpunctata, at least seven months (Outright); Coccinella monticola, captured July 15, 1897 and died August 31, 1908 (Palmer); C. septempunctata, 11 to 14 months, dying between June and early September (Johannsen). On the other hand, the adults of the generations developing in warm seasons lived as follows: Hippodamia tridecimpunctata, an average of 30 days when adequate food was supplied (Outright); H. convergens, 3-4 months; Coccinella transversocincta quinquenotata, 2-3 months; C. monticola, one lived 2 months and 6 days, another 3 months and 12 days; C. septempunctata, 2-3 months; Adalia bipunctata, 1-4 months (Palmer), and Chilocorus simillimus, about 35 days, in Japan. Twenty-nine females of Rodolia cardinalis lived 16 to 178 days in Palestine. Six of these had lifetimes of 107, 109, 112, 131, 176 and 178 days, respectively, under conditions of moderate temperature and relatively high humidity in the months of September, October, November and February, while the instances of shorter duration fall in the warmer and drier season of May to August. The records for 20 males range from 20 to 516 days. The average duration of life of the females was 70 days; that of males, 49 days. It is commonly supposed that the females die promptly after oviposition is completed, those of Scymnus nubes survived the performance of this function about four weeks, and Adalia bipunctata lived as long as two months thereafter.

FOODLY FACTORS

These factors are mostly organic, and affect the Coccinellidae in a variety of ways. A bacterial disease, supplemented by a Cladosporium fungus, played havoc with the larvae of Clypilnea semicirculata during the rainy season in Florida; and a mold flourishing on the honeydew of Aphids fatally attacked the larvae of Adalia bipunctata, according to Hawkes. The mouth parts of the larvae may sometimes be cleared shut or clogged by the fluids from their prey. The smaller and weaker individuals of their kind, and it seems to be common for them to devour their unhatched relatives. The defenseless newly molted larvae and the pupae not infrequently become the victims of their active kin. The cannibalistic tendency is expressed also in the larvae of Epilachna borsellii F., the squash ladybird and in both feeding stages of the fungivorous Thea nigritu suspicata. These in instances it is the egg that is consumed. However, Parlyphora vitiulaculata Fein- data J. Lea., another fungus eater, gave no indications of cannibalism in either stage (Davidson). The practice of consuming their own kind is regarded by Hawkes as a biological advantage in that it preserves the Coccinellidae during periods of lack of other food. It is thought to be of greater value to the larvae, owing to their more limited ability to travel in search of food and their lower resis-
ance to starvation, as was demonstrated in the case of *Adalia bipunctata*.

The *Coccinellidae* are, moreover, harassed by a large number of enemies outside of their own group. Despite their supposed protective secretions, the adults are sometimes eaten by birds, and all the stages suffer commonly from the attack of other predacious insects. Schilider enumerates published records concerning representatives of eight orders that have preyed upon members of this family. While most of these attacked the phytophagous *Epilachna curvata* Nils. in the United States, *Mantis religiosa* was taken eating *Adalia signata*, *Sycus* larvae, the larvae of *Syrphoid fly* (Gage). That the smooth round bodies of ladybeetles may serve to protect one to eight which discharge a malodorous fluid (Gage). That the smooth round bodies of ladybeetles may serve to protect some of the larvae, pupae and adults of *Adalia bipunctata* (Burgees). Jacobs reports finding *Laphria flava*, an Asilid fly, with the beak inserted between the elytra of a living *Coccinella septempunctata*.

The larvae, pupae and adults of *Coccinellidae* are also commonly destroyed by parasites, especially of the Ichneumonidae, *Crypsis* and *Chilocorus*, *Cytophaga*, *Cryptolaemus*, *Coccopternia*, *Hyphastes*, *Hippodamia*, *Hyperaspis*; *Homalotylus* spp. from the larvae of *Adalia bipunctata*. While most writers speculatively regard the secretion is repulsive to natural enemies, it is derived from its bitter taste, high volatility and offensive odor. These qualities, according to McIndoo, seem to be inherent in a peculiar principle called cantharidin which crystallizes into four-sided prisms. The protective value of these devices may, of course, be best judged by their effect on the potential and actual natural enemies of these beetles. Heikertinger, who made a critical examination of the published statements regarding them, points out that ladybeetles are not avoided by various birds, as the study of numerous stomach contents in Europe and the United States shows. Moreover, the complex of invertebrate enemies of adult *Coccinellidae* includes not only chewing and piercing-sucking predators, but also internal parasites. Enemies having almost every conceivable mode of attack are thus not effectively repulsed, and the parasites, which appear to be specific on members of this family, are not all deterred by the odors emitted by the hosts. The larvae, likewise, possess organs commonly looked upon as having a defensive function. These take the form of pairs of pores on abdominal segments one to eight which discharge a malodorous fluid (Legg). That the smooth round bodies of ladybeetles may serve to protect was observed in *Hyperaspis reppensis*. When attacked by *Taxinoma*, the beetle stopped suddenly and attached itself to the surface of stones covering the nest. Ants seemed never to be successful in holding the beetle in their jaws (Baldur). In a similar manner, when prodded by the ovipositor of *Dinocampus coccinellae*, *Coccinella novemnotata* and other staid species responded by clamping the elytra tightly upon the back and squattting close to the floor, thus placing out of reach all parts vulnerable by the ovipositor (*Baldur*).

In certain *Coccinellidae* larvae the waxy coverings, which occur in the form...
of powder, woolly fiber or plates and tufts, are commonly looked upon as protective and doubtlessly serve this and to some degree. Secretions of this kind are produced by Hyperaspis, Curtius, Crypto-
laemus, Cryptococcus, Brachyscentha, Sym-
mat and related forms, and issue from the pore-like apertures of wax glands (Fig. 100). Each body segment of 8, tubae possess six such pores from which come the white woolly threads characteristic of this species (Davidson). As the first
larva of Curtius zonatus grows, the threads emanating from the several adjacent pores flow together to form a thick waxy process at each lateral swelling of the body. In all these species, the waxy excretions are lacking in the newly-hatched larvae, and the molting individuals shed them along with the exuviae, but are secreted rapidly thereafter in sufficient quantity to hide the body more or less completely. But the final exuviae and their waxy substances are generally retained more or less intact and cover the insect during the period of pupation.

That the waxy processes may have protective value is indicated in the instance of Cryptolaemus montrouzieri, whose larvae immediately curl up and expose only the woolly mass when attacked. Essig reports that they are rarely harmed because few predatory insects care to chew through the secretion to reach the body. But the similar coverings of Hyperaspis lateralis do not shield it against heavy parasitism which hinders its beneficial work against Coccid pests.

Not only do the waxy secretions possibly constitute a physical barrier against certain enemies but they sometimes give the larvae a striking resemblance to mealybugs and similar Coccidae. It is conceivable that this resemblance tends to protect the larvae against ants since the latter commonly attend the Coccidae on plants and perhaps defend as well as transport them. If so, it would be especially effective for forms like Brachy-
acentha which habitually inhume the nests of ants and live in more confined association with them than do the free-living Coccinellidae. But, as stated by Wheeler, in no instance does the hypothe-
sis of mimicry seem justifiable if it is meant to imply that the secretions are special adaptations to enable the larvae to live in these nests. It is quite clear that the development of waxy covers is the direct consequence of the habit of feeding on prey that is rich in waxy content. It may be presumed that the wax ingested by these predators is largely eliminated with little chemical change through the cuticular pores instead of being ejected axially in the usual manner of indigestible substances.

FIG. 100

FIG. 101
While Verania in southern Asia are to some known tribes Hippodamiini and Coccinellini, percent of the records for the Chellomenini, former and eighty-five percent in the latter citing Aphids as the food taken. No special groups of Aphids are selected by these. The remaining twenty-three percent of the food of the Hippodamini includes representatives of the orders Coleoptera, Heteroptera, Lepidoptera, Homoptera, Arachnida, Thysanoptera and Dip- tera, and one percent consisted of plants. In the Coccinellini, certain Orthoptera, Acarina, Coccinellidae, Hymoptera, plants. Thysanoptera and Hymoptera compose the other fifteen percent of the food. These food groups are arranged in descending order of their importance in the diet of these tribes. But in the Chilocorini, seventy-nine percent of the records give Coccidae as the food. Aspidiotus, Stictococcus and Gross eat Pseudococcus, as do also Bramus and Lecanium. Seventy-one percent of the food of European and American Coccidae, as do also Bruneus and Lecanidae, but the African forms of Exochomus eat Aphids and the three most plentiful Chilocorus of Europe and America are likewise recorded as aphid eaters.

Feeding Capacity. Unless stated otherwise, the records herewith represent the average number or numerical range of foods provided by Schüller and Schüller demonstrate a far-reaching food specialization among the predacious tribes of the Coleoptera. Aphidophagous insects, seventy-five percent of the records for the Hyperaspini, consists largely of Coccid species belonging to the Coccinea genera Pseudococcus, Phyllococcus and Bacteriidae. While the Microwesmata also eat principally Coccidae, these are chiefly Diaspinae among which Aspidiotus and Chlorops are most often cited. Scales form sixty-two percent of the food of the Seymamini, and the Indian genera seem to have developed an extensive specialization in the selection of prey. Thus, the species of Stictococcus eat Acarina, exclusively; Chlorotomus and Lioxygynus, Aleurodidae; Pectogyne, Aphids; Eriococcus, Nymphus, Parasitida, Sidis and Cryptolaemus largely consume Pseudococcus and its close relatives. The Phalini, Telephantina and Asyntina attack disperse scales, and the Neoelephantina are reported feeding mostly on Icerya and its nearest relatives. All but one of the recorded species of Phtholobini are reported consuming Cocidae, of which 81, 35 and 14 percent were Diaspinae, Coccinea and Le- caninae, respectively. Aleurodidae are said to constitute the exclusive diet of the Gomphini. A few Scymninae also are known to attack white flies. Seventy-two percent of the records for the Chloronemini cite Aphids as the food, but some species take also Cocidae, Aleurodidae and Chermelidae. In the tribe Veranini, species of the African genus Alasca are Aphids eaters, while Veranini in southern Asia are to some grade phytophagous, feeding on Graminae. The Synonymine genera Archonitana and Nada feed on Coccida. The others on Aphids. The majority of the aphis-eating ladybeetles belong to the large and well-known tribes Hippodamini and Chelomini, seventy-six percent of the records for the former and eighty-five percent in the latter citing Aphids as the food taken. No special groups of Aphids are selected by these. The remaining twenty-three percent of the food of the Hippodamini includes representatives of the orders Coleoptera, Heteroptera, Lepidoptera, Homoptera, Acarina, Thysanoptera and Diptera, and one percent consisted of plants. In the Coccinellini, certain Orthoptera, Acarina, Coccinellidae, Hemiptera, plants, Thysanoptera and Hymenoptera compose the other fifteen percent of the food. These food groups are arranged in descending order of their importance in the diet of these tribes. But in the Chilocorini, seventy-nine percent of the records give Coccidae as the food. Aspidiotus, Stictococcus and Gross eat Pseudococcus, as do also Bramus and Lecanium. Seventy-one percent of the food of European and American Coccidae, as do also Bruneus and Lecanidae, but the African forms of Exochomus eat Aphids and the three most plentiful Chilocorus of Europe and America are likewise recorded as aphid eaters.

Feeding Capacity. Unless stated otherwise, the records herewith represent the average number or numerical range of food animals consumed per day. Adult: Adelis bipunctata, 5-8.5 Macrosiphum pisi; Coccuspinus similis, 80-80 Aspil- pis pentagona, or 800-800 in a lifetime of about 35 days; Coccinia novemnotata, 11.8 Macrosiphum pisi; S. transverso- guttata quinquenotata, 200 Aphids, 1001 Exochomus; Coleophora s-wallare albo, 60-70 Aphids; Cylocorus gomphus, two individuals, 15.5 and 73.1 Aphids, respectively; Hyperaspum parthenia, three individuals, 7.4, 8.1 and 9.1 more or less mature Macrosiphum pisi; H. tredecimpunctata, 49.7 W. pisi; H. convergens, a pair ate 150 Chilocorus poppuli in one day and 120 Aphis asteriae in another; same, one male ate Aphids as follows on five consecutive days, 800 Macrosiphum gaureae, 30 W. rubedckeia, 33 Aphids tor- triscuda, 60 Chilocorus gomphus and 70 M. ceresi; same, a female similarly consumed 30 W. rubedckeia, 18 G. neum- dinia, 166 M. ceresi, 110 A. helianthi and 150 A. setiapae in a series of five days; this species accepted 26 kinds of Aphids in captivity (Palmer); Leta con- formis, 100-200 Aphis spiraculata; Propy- laeae repentanse, 78.8 Aphis gossypi or 1486 in an average lifetime; Scymnus nubis, 4 Myrurus perspicus of the fourth instar and at least eight of average size. Individual Rodolia cardinalis devoured from 2.7 to 33 aphids in 24 hours per day in periods of 20 days in Palestine.

In obtaining the data tabulated be-
low, Clausen fed the beetles approximately two-thirds grown Macrosiphum rosae and Phorodon humilis.

### TABLE V. ADULT FEEDING RECORDS (FROM CLAUSEN)

<table>
<thead>
<tr>
<th>Names of Species</th>
<th>Number of specimens fed</th>
<th>Length of Period, days</th>
<th>Maximum Aphids eaten</th>
<th>Minimum Aphids eaten</th>
<th>Period Totals</th>
<th>Averages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coccinella transversoguttata</td>
<td>10</td>
<td>15</td>
<td>661</td>
<td>414</td>
<td>500</td>
<td>34.0</td>
</tr>
<tr>
<td>Coccinella trissecta</td>
<td>10</td>
<td>15</td>
<td>470</td>
<td>383</td>
<td>435</td>
<td>28.9</td>
</tr>
<tr>
<td>Hippodamia convergens</td>
<td>6</td>
<td>8</td>
<td>515</td>
<td>380</td>
<td>449</td>
<td>56.1</td>
</tr>
<tr>
<td>H. convergens ambigua</td>
<td>10</td>
<td>15</td>
<td>420</td>
<td>370</td>
<td>397</td>
<td>26.5</td>
</tr>
<tr>
<td>Olla abdominalis</td>
<td>9</td>
<td>15</td>
<td>534</td>
<td>407</td>
<td>457</td>
<td>30.4</td>
</tr>
<tr>
<td>O. oculata</td>
<td>10</td>
<td>15</td>
<td>672</td>
<td>589</td>
<td>624</td>
<td>41.6</td>
</tr>
<tr>
<td>Adalia bipunctata</td>
<td>10</td>
<td>15</td>
<td>355</td>
<td>215</td>
<td>251</td>
<td>16.7</td>
</tr>
<tr>
<td>Cycloneda sanguinea</td>
<td>10</td>
<td>15</td>
<td>260</td>
<td>205</td>
<td>234</td>
<td>15.6</td>
</tr>
</tbody>
</table>

### TABLE VI. LARVAL FEEDING RECORDS (FROM CLAUSEN)

<table>
<thead>
<tr>
<th>Names of Species</th>
<th>Number of beetles observed</th>
<th>Length of Period, days</th>
<th>Period Totals</th>
<th>Averages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coccinella transversoguttata</td>
<td>13</td>
<td>23.7</td>
<td>600</td>
<td>394</td>
</tr>
<tr>
<td>C. trissecta</td>
<td>12</td>
<td>26.8</td>
<td>365</td>
<td>217</td>
</tr>
<tr>
<td>Hippodamia convergens</td>
<td>12</td>
<td>23.6</td>
<td>490</td>
<td>232</td>
</tr>
<tr>
<td>H. convergens ambigua</td>
<td>8</td>
<td>27.7</td>
<td>396</td>
<td>269</td>
</tr>
<tr>
<td>Olla abdominalis</td>
<td>14</td>
<td>16.7</td>
<td>256</td>
<td>196</td>
</tr>
<tr>
<td>O. oculata</td>
<td>10</td>
<td>22.2</td>
<td>349</td>
<td>299</td>
</tr>
<tr>
<td>Adalia bipunctata</td>
<td>10</td>
<td>21.7</td>
<td>306</td>
<td>220</td>
</tr>
<tr>
<td>Cycloneda sanguinea</td>
<td>10</td>
<td>20.0</td>
<td>427</td>
<td>147</td>
</tr>
</tbody>
</table>

Larvae: Alloiocaria mirabilis in the fourth instar ate four Melasoma Vigintipunctata; Callinidea testudinaria, 131 cane Aphids; Chilocorus similis, most larvae ate 700-800 di-
aspine scales during the larval period; Cocconella transversoguttata quinquenata, 508 Aphis in the larval life-time; S. monticola, 676 Aphis during the larval stage; 0. septempunctata, 50.3 Aphis per day and 665.5 in the entire growth period; Coccinella septempunctata, an average of 15 diaspine Coccids during the entire larval life; Hippodamia convergens, three ate Aphids per day as follows: - 50 Protopulphus fraxinifolii, 33 Necrophorus quadrus, and 106 Chalcidochorus neockii; same, four consumed 364, 309, 576 and 588 Aphids, respectively during the larval life; Hyperaspis lateralis (see Table IV) ate 12-17 new laid mealybugs per day; H. signata: one larva may destroy a large part of several egg masses of Pulvinaria innumabilis; same, an individual estimated to destroy 90 mature Myzus persicae; several of Protopulphus fraxinifolii or 3000 newly hatched scales during its life; Lea conformis, two consumed 141-270 and 75-355 Aphis spiraecola per day, respectively, or an average daily consumption of 161.2 and 220.3 Aphis; Propylea japonica, 107 Aphis spiraecola during the average life which varied from 6 to 29 days; Syneura mohra, 40-80 large M. persicae during the larval stage, but probably 50-100 of average size in mature mealybug; Stethorus pleasii, about 7 Tetanychus per day. The average number of immature Iscerya purchasi consumed by the larvae of Rodolia cardinalis during their entire development varied from 1.3 - 11.0. Early in the mild winter, a Rodolia eats five times more myzal Iscerya than in July, but the consumption per day is lower in the winter season.

Factors Affecting Feeding. The conditions governing the feeding activities of Coccinellidae have been observed only casually in most recorded instances but were made special objectives in the studies of Cressmann and Bodenheimer on Rodolia cardinalis. Here are concerned influences such as size, age and instars of the larvae, age of the adult, sex, season and temperature.

Size of the Larva. The prey attacked is in extreme cases two to three times larger than the predator, but there is mostly not so great a discrepancy in size between them. The small larvae commonly eat the smaller nymphs of Aphids or Coccids or the eggs of the latter. This generalization holds in the above Aphid-eating species described by Clausen, Palmer and others and in the coccidivorous Hyperaspis spp. studied by McKenzie and Risanton. The young larvae of Coccinella zenithus attack primarily the young nymphs of Coccids, especially of Leptosaphes pinetorum. Immediately after hatching, those of Hippodamia convergens consume one or two Aphids per day but the number increases rapidly until near the end of the larval stage, when fifty or more may be eaten each day. The number of Aphis ingested by Adalia bipuncata doubled at about the time the larvae entered the second instar (Olausen). The new young of Hyperaspis lateralis enter the egg masses of Pseudococcus to feed until they reach the third instar and not until then can they overcome the new born mealybug. In a similar way, the first and second instar larvae of H. signata prey upon the smallest nymphs in the broad chamber of Myzus persicae, but in the latter stadium destroy many mature scales.

However, the amount of food taken in the successive instars does not necessarily increase regularly. The four instars of Hippodamia tredaecquata consumed an average of 17, 15, 22 and 58 Myzus persicae, respectively; the second taking slightly less food than the first (Olausen). This condition may prove to be normal rather than exceptional if the data on duration of instars in the species listed in Table IV may be accepted as significant. The presence of one instar shorter than the first, and the larvae accordingly requires less food in the second stadium than its larger size alone would suggest.

Johnsen and Palmer sometimes observed a decline in feeding in the last day before molting and a similar slackening seems to occur just before pupation. On the other hand, the larvae are said to be much more voracious several days preceding the end of this stage (Palmer). But Clausen states that all his species excepting Cocinella transversoguttata Californica fed normally up to the day of pupation, and reports no appreciable diminution in the number of Aphis eaten by Hippodamia convergens upon days when molting takes place. The molt requires only a short time and the larvae immediately thereafter resume feeding very actively.

Age of the Adult. The relatively rapid rate of growth in the Cocinellidae is achieved in part by a prompt inception of feeding by the newly developed adult. Two such individuals of Cocinella septempunctata took their first food within 16 to 17.5 hours, three within 18 to 21 hours, one in 22 and four in 25 to 29 hours after transformation. A similar promptness marks the initial feeding of the group as a whole. Moreover, they consume less food in the first days of their life than during their more mature and actively reproductive periods. The youngest adults of
probably also affects the rate of movement of the virgin females. In the instance of Rodolia cardinalis, the quantity of food was lowest during the first tenth of the adult life span, rose to the maximum in the third tenth, then decreased slightly in the last seven tenths of this period, according to Cressman.

Sex. This investigator further demonstrated that the mated producing females of rodents ate the larger part of the food consumed, while the virgins fed at about the same rate as the males, indicating that there is a correlation between food consumption and the rate of oviposition. Accordingly, the productive females were more effective in combating Icerya than were the males and the virgin females, not only because of their increased progeny, but also because they destroyed more scales during their lifetime. Johnson observed that also the females of Coccinella septempunctata generally consumed more Aphids per day than the males, and in a ten day period the males of Hippodamia convergens consumed a larger net amount of prey in their adult life, despite a lower per diem rate of feeding in the winter (Bodenheimer). The feeding rate in eleven successive generations of this species in Louisiana averaged twenty Aphids daily as compared with forty-two by the females (Cutright).

Season and Temperature. At the beginning of the moderate winter of Palestine, Rodolia cardinalis devours five times more Icerya in the course of its larval development than in July, although the period of growth in winter is only three to four times longer. The larvae therefore consume a larger net amount of prey in their winter generations than do those of the summer cycles, but the average daily feeding rate per larva is lower during the cold season. The adult females likewise live about six to seven times longer in the cool part of the year than in the hot dry mid-summer and, like the larvae, devour a larger total of Icerya in their adult life, despite a lower per diem rate of feeding in the winter (Bodenheimer). The feeding rate in eleven successive generations of this species in Louisiana changed little seasonally from September to October but then increased rapidly to a maximum in early June. Therupon it declined as the summer progressed. While temperature exerted an important direct influence on the rate of oviposition and probably also affects the rate of movement and other forms of conduct in the beetle, its effect on feeding is only an indirect one, operating through the response of these other activities to thermal change (Cressman).

The small species that feed on Coccidae commonly insert their mandibles under the edge of the scale to draw the insect out or may devour it in situ. When attacking Pulvinaria, Pseudococcus and other large Coccidae, they sometimes crawl bodily under their prey and remain as long as the supply of eggs or nymphs lasts. Such are the modes of attack in Entobia ventralis, Hyperaspis and Chilocorus. The adult Rodolia guerini does not always kill its Coccid prey, Monophlebus stebbingi, even by a half hour of feeding, during which time the victim may crawl about and drag the persistent enemy along. When the larva of guerini attacks the Monophlebus it fixes its mouthparts in the soft skin and at the same time anchors itself to the twig by its terminal adhesive pad. Often being the larger and more powerful, the Coccid sometimes stretches the larva full length in making attempts to get away. Some larvae fed contiguously for eight or nine hours and left only the shrivelled skin of the victim (Stebbing). Both the larvae and the adults of Curinus sonatus sit over their Coccid prey, securing themselves with the legs, and stick the tip of the abdomen fast by means of a semi-fluid bit of excrement. After tearing pieces of the waxy covering from the scale's body with the mandibles, the larva cuts into the prey and sucks out the contents. It requires up to twelve hours to drain one Coccid such as Lecanium, Lepidosaphes or Chrysomphalus, of which only the emptied skin is left (Wille).

When Aphids constitute the prey, the adult or larve seize them at various parts of the body but more commonly by the legs or in the caudal region. Davidson found that the Aphid may escape destruction after the adult Scymnus nubes has gnawed off an appendage or even eaten a hole in the skeleton. Smit closely and repeatedly observed Scymnus nubes feeding on Aphids and revealed a procedure suggestive of the precoronal digestion which has been demonstrated in the larvae of some Carabidae and Dytiscidae, and recalls the process described by How and Coccinellidae Feed. The larvae of the predacious ladybeetles possess mandibles provided with two apical dentes and a larger than its enemies, the Aphid, which characterizes them as a piercing type. Such jaws are said to occur also on members of the little-known Lithophilidae. The feeding organs of the adults seem to be the ordinary chewing form. The smaller species that feed on Coccidae commonly insert their mandibles under the edge of the scale to draw the insect out or may devour it in situ. When attacking Pulvinaria, Pseudococcus and other large Coccidae, they sometimes crawl bodily under their prey and remain as long as the supply of eggs or nymphs lasts. Such are the modes of attack in Entobia ventralis, Hyperaspis and Chilocorus. The adult Rodolia guerini does not always kill its Coccid prey, Monophlebus stebbingi, even by a half hour of feeding, during which time the victim may crawl about and drag the persistent enemy along. When the larva of guerini attacks the Monophlebus it fixes its mouthparts in the soft skin and at the same time anchors itself to the twig by its terminal adhesive pad. Often being the larger and more powerful, the Coccid sometimes stretches the larva full length in making attempts to get away. Some larvae fed contiguously for eight or nine hours and left only the shrivelled skin of the victim (Stebbing). Both the larvae and the adults of Curinus sonatus sit over their Coccid prey, securing themselves with the legs, and stick the tip of the abdomen fast by means of a semi-fluid bit of excrement. After tearing pieces of the waxy covering from the scale's body with the mandibles, the larva cuts into the prey and sucks out the contents. It requires up to twelve hours to drain one Coccid such as Lecanium, Lepidosaphes or Chrysomphalus, of which only the emptied skin is left (Wille).

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to appear in the leg of the prey, and three minutes thereafter the fluid was seen moving back toward the larva. After that a steady flow of liquid was maintained alternately up and from the larva, the Aphid being now inflated and then drained to translucency. With the gradual increase in the amount of digestive juice injected, the Aphid was ultimately filled almost to the point of bursting. When successive injection, the liquid became perceptibly darker on account of the increasing proportion of digestive fluid, so that the distended body of the Aphid filled by a coagulated mass of the larval remains of both animal and vegetable food in the intestines of Hippodamia convergens, long known to congregate in large numbers in the United States from New England and westward in the Mississippi Valley. Assemblages are also common in lower levels far remote from mountains. Coccinella septempunctata has appeared in considerable masses under the bark of trees.

In all the above instances, the assemblages occurred in winter dormancy or existed under circumstances indicating a relation to hibernation. But the Coccinellidae appear to assemble also under two other types of conditions. In the first, they exist in a state that suggests aestivation. While Leis conformis tended to congregate during the mild winters of Florida, it also clustered in a dormant state in the warmer days of May and June, suspending both its feeding and reproductive activities (Thompson). Rodolia guerini similarly gathered in large numbers, collecting on the underside of leaves during the heat of the day in India. Also the larvae of this species were found to become gregarious when they had matured and attached themselves to pupae (Steinberg). Second, several species known to winter in mountains have been found moving about actively in high elevation. On warm days of late June and July, a season and observed temperatures indicating that these phenomena bore no relation to wintering. Forms so reported are Coccinella spp.
(Snyder), L. transversoguttata (Piper) and C. septempunctata (Hawkes, '23). The latter swarmed beneath stones in grass in July, and transversoguttata was crawling over the hot bare rock on the summit of a peak 5000 feet high in the same month. When disturbed, they circled about for a few moments then alighted again. No Aphis or other food animals were found in the vicinity. While collecting butterflies at an altitude of about 9000 feet in a Utah mountain on June 30, Snyder observed hundreds of Coccinella passing by him with the wind. Considering that the assemblages seen by Dobzhansky had returned to the valleys during the latter half of May, the presence of these American swarms in high elevations late in June and July probably bore no relation to the hibernation phenomenon.

CIRCUMSTANCES ATTENDING ASSEMBLAGES

The congregations of Ceratomegilla maculata fuscella invariably appear at the margins of woods, along shrubby roadsides, fence rows, ditch banks and other sheltered situations adjoining open fields. Here they assemble gradually in the autumn and may enter cavities in trees or hollow logs, but are often found along the sides of fallen branches, stumps, tree trunks and similar objects lying on the ground. In the level areas of European Russia, the assembling beetles likewise gathered in late summer or early in the fall, sometimes in very large numbers on the shoots of young pine and other plants, then going down to the ground to hibernate under fallen leaves, bark and other superficial surface cover (Dobzhansky).

The species assembling in mountains mostly appear at considerable elevations. Those enumerated by Dobzhansky occurred at about 1500 to 3500 meters; the forms cited by Hawkes were found at 1400 to 7000 feet; by Piper at 5000 feet and by Snyder at a height of approximately 9000 feet. According to Ewing, large numbers of the most common ladybeetles of Oregon tend to move in certain directions or to collect upon flowers late in July or early in August. By the middle of August this movement amounts to a definite migration, the beetles almost simultaneously forsaking the hot dry valleys and passing upward, many of them never stopping until the highest mountain point for miles around is reached. There this observer found thousands move about and swarm repeatedly in September. As winter sets in they settle into their permanent hibernating quarters. Hippodamia convergens is said usually to select the shelter of pine needles on sunny, well-drained slopes in close proximity to running water (Carnes). Here they entered into pockets under large stones and crept beneath rubbish or logs (Ewing). During the winter these situations are covered deeply with snow. The assemblages of Coccinella transversoguttata (Piper), L. septempunctata and Adalia bipunctata (Hawkes) occurred under stones and flat pieces of rock. Dobzhansky found a mass at the base of a shrub, another among the roots of a group of plants and some under stones. One of the largest assemblages discovered by him occurred under a flat rock separated from the soil by the depth of a man's hand. The accumulations in Turkestan were invariably present on unforested peaks kept bare of snow by the unmitigated force of the mountain winds.

The numbers in which the beetles may assemble is indicated by Dobzhansky's estimate that six masses involving several species contained sixty to seventy thousand individuals. In one instance not less than thirty thousand had gathered in a space of one square meter, and the largest assemblage of Hippodamia piromerus might have contained hundreds of thousands. According to the belief of Dobzhansky, there is a strong tendency for the different species and varieties to segregate themselves in their winter quarters, some pockets containing all or more than ninety percent of the typical Hippodamia convergens while in others all or the majority were its spotless variety. However, several species may accumulate in the same assemblage, as is shown by Dobzhansky. While most of the beetles in a certain mass of approximately 6500 were Hippodamia hexaplicita and Hippodamia undecimalis, there was also a considerable number of Brugus piasiformis and Coccinella signata variegata and fewer still of Adonia verticaxis and Platynaspis lutescens.

In the mountain assemblages reported from both Turkestan and the western United States, the proper spots occupied invariably were covered by a substratum of one to two inches thick consisting of the remains of ladybeetles. This fact doubtless signifies that these particular places were made the hibernating quarters of the congregating beetles year after year. Piper estimated that such a mass of Coccinella transversoguttata over a foot square and two inches thick contained over ten thousand dead bodies.

Although the causes of this frequent
gregarioussness has not been carefully investigated, some of the factors operating to produce it may be readily discovered through an analysis of the best known instances. First, it is a phenomenon developing only when the beetles exist simultaneously in extraordinary numbers. Most Coccinellidae have not been found to congregate, and such as are reported doing so invariably belong to the list of the most abundant species. Thus, the larger the number the greater is the chance that they will assemble. Second, the assembling is probably also in part contingent on the familiar and pronounced odor emitted by the adult ladybeetles from the hyperdermal glands. It is perhaps significant that miles away, they hibernate as adults and commonly become as abundant as do our common Coccinellidae, have not been found assembled in the winter. Third, there appears to exist a stimulus which drives the beetles to move from the open fields in which they have developed, to more protected situations. What may be the stimulus producing the migration, and how is the choice of a sheltered spot determined? It is a generally recognized fact that the proportion of fat to water gradually increases in insects during the autumn season. Thereby they seem to reach a bodily state in which hunger causes and the insect becomes possessed with an impulse to move aimlessly from place to place. This has been demonstrated to be true of the mature larvae of Pyrausta nubilalis in North America, and a similar condition probably obtains in the Coccinellidae and many other insects less known. While engaged in this haphazard locomotion, the insect sooner or later discovers a sheltered spot quite by chance. Or, the direction taken in this travel may be determined by the prevailing winds. In the instances of the ladybeetles, the migration is probably accomplished largely by flight, and sooner or later, they encounter a major obstruction on the landscape, such as a building, high brush, or the margin of a forest. So they chance to come into the proximity of other individuals of their species or family, whereupon the characteristic group odor operates to detain and thereby assemble them. With the approach of the lower temperatures of late autumn, the activity of the beetles assembled in the trees or on the sides of buildings declines and they eventually are compelled by the cold to descend to the soil. Here they enter into a state of more or less complete dormancy under the leaves and other surface cover at the base of the trees.

The ascent to the higher elevations of mountains in the late fall is probably not to be looked upon as a phenomenon distinct from the movement of the lowland species from field to forest. The sometimes perplexing fact that they winter over in the cold and wind-swept high mountain levels seems explicable in terms of air currents. Moreover, their occurrence at elevations of five thousand or more feet on hot, rocky, foodless peaks during June and July appears attributable to the same influence. However it may be that a dearth of food, or extraordinary heat, rather than a state of obesity and satiety, disquiets them in their summer habitat and induces flight from the place of their development. The theory of air currents, or rivers of air, flowing up the mountain ravines as the forces that catch the restlessly flying beetles and carry them aloft, has been proposed or implied by Champion, Piper and Snyder. The first writer suggests that the swarms of Coccinella septempunctata on Moncayo had been carried there by the terrific winds then prevailing, and Snyder witnessed numerous Coccinella passing him with the wind at a height of 9000 feet. Garms points out that the colonies of Hippodamia convergens are usually found near running water. Their position may have been determined by currents of air moving up from the lowlands along the ravines in which the water flows. It would therefore appear that careful observations on movements of the beetles with reference to air currents and the topography of the mountain side adjacent to the source of the insect offers the most plausible solution to this fascinating problem.

The Life Cycle

So far as known, the Coccinellidae of regions characterized by cold winters, hibernate exclusively in the adult state. Hulswig, referring to several Coloradoan species of Hippodamia and Coccinella, reports that there did not seem to be any certain fixed generation to hibernate, while Outright found in the instance of Hippodamia tradescantii that individuals of the last two generations of the year overwinter.

The records of duration of development from egg to adult as given in Table IV, and below, exhibit the variations in length of the cycles of various species in different parts of the earth. The length of this period of growth is expressed in days: Adalia bipunctata, 28-56 (Hawkes); A. frigida humeralis, 56 (Burgess); A. frigida frigida, 51-65 (Palmer); Gallissia tabulae-
Coccinella septempunctata: 25-43 (Swezey); Ceratomegilla maculata fusiglabris: average 27.4 (Fluke); Coelocnemia repanda: 26 (Swezey); C. novemnotata: 20-23, and C. monticola: mostly 23 (Palmer); Cycloneda sanguinea: 15-20 (Palmer); C. sanguinea immaculata: 21-44, and Hippodamia convergens: 23-24 (Miller and Thompson); H. convergens: mostly 21, H. sinuata: 32-37 and H. parenthesis: 20 (Palmer); Gila endemina prasina: 33 in April-May (Miller and Thompson); Pseudononycha japonica: about 25 (Iwata); Rodolia cardinalis: 16 days in August to 78 in January in Palestine (Bodenheimer); same: 34 days in California (Coquillett); Verania frena: 21-45, and V. lineola: 25-46 (Swezey).

These data indicate a relatively rapid rate of development in the majority of the species observed. The promptness with which the newly formed adults engage in reproduction, and the comparatively brief duration of the egg, larval and pupal stages, largely contribute to the occurrence of the several generations known to exist annually in most of the species. Callimela testudinaria had practically a generation per month throughout the year in Hawaii (Swezey), and Rodolia cardinalis passed through its cycle eleven times from September to September in Louisiana (Cressman), but completed only 6 to 7 in Palestine (Bodenheimer). Field observations showed that there are rarely more than three generations of Hippodamia tridecempunctata in central Ohio (Outright), and Palmer reared three of Coccinella quinquenotata in cages in Colorado. Hyperaspis lateralis is said to grow very slowly and develops two and possibly three generations annually in California (McKenzie). In the case of Chilocorus simplex, the overwintering adults oviposited in April and those of the first new generation deposited eggs in June, in Japan. Only two cycles were completed in the year. The minimum rate of growth was observed by Johnsen in Germany, where Coccinella septempunctata emerged from hibernation in time to oviposit from May to August, and only one generation was completed. A second generation of Adalia bipunctata seems to appear there only under the most favorable conditions. There is thus a known variation of one to eleven generations annually in the Coccinellidae of the temperate and subtropical areas. While the duration of development is governed to a large extent by local temperatures, it is obviously also regulated by a normal inherent rate of growth that may be more or less characteristic in the several species.
14. SMALLER AND LESS KNOWN FAMILIES

In addition to the foregoing larger families of entomophagous beetles, this order contains a number of smaller groups believed or known to possess, in various degrees, the predatory habit of living. Some of these inhabit the nests of ants as guests, several groups live on wood-boring and bark-beetles, and others prey on miscellaneous insects found on the ground and on plants. The Hygrobiidae and the Helodidae are aquatic.

1. MYRMECOPHILES

A few records and statements indicate a varying degree of predatism in the Pselaphidae, Clavigeridae, Paussidae, Lepitinidae and certain Bremniidae on the brood of their ant hosts. Donisthorpe ('27) discovered the adults of the Pselaphid, Batrisodes delaportei Aub., consuming the brood of an ant in captivity, and cites the observation of Wasmann that E. adnexus Hampe devoured mites in the nest of Acanthomyops brunneus. According to Park ('32), L. globosus (Lec.) may on occasion act as a predator, but more frequently aids in the disposal of dead ant larvae in the nest of Lasius niger. The adult of Claviger testaceus Preyssl. never displayed an aggressive predatism but chewed at, and always killed, the larval ants when these were accidentally wounded (Krüger). According to Wasmann ('12), the adults of Paussus, so far as their habits have been known, lived rather predatorily on ant brood, and the larvae of P. kannegieteri Wasm. are said also to be carnivorous. Lepinus testaceus Mueller has been variously found upon, or in the nest of small mammals in general and in the nests of birds and Vespidae, Bombus and Formica. While its exact relation to the several hosts is not definitely known, Park ('28) suggests the possibility that it, and the Lepitinidae as a whole, "exhibit a facultative parasitism, which would explain many of the differing accounts in the literature, and bring into agreement the finding of testaceus in habitats suggesting phoresy, a guest relationship, an actual ectoparasitism, a scavenger existence, or a chance occurrence." Considering the powerful mandibles of the male Amorphocephalini of the Brenthidae, Kleine ('31) regards these tropical beetles as hostile guests. Neumann established the fact that the related Taphroderes oscillator Sharp and F. neevon- sant Feline bore with their long snouts into the burrows of Xyleborus confusus and prey upon its stages there. Moreover, Stebbing ('14) inclines to believe that some Indian species of Bremniidae may likewise be found to feed upon bark- and wood-boring insects.

2. HYGROBIIDAE

Like the related Dytiscidae, this small family inhabits water. The life history of Hygrobia hermanni Fabr. (Pelo-bius tardus Herbst.) was observed by Bal­four-Browne ('22), in England. Both adults and larvae are predacious.

Habits of the Adult. The adult inhabits the fine ooze at the bottom of ponds where it frequently buries itself with only the apex of the abdomen visible and an air bubble exposed on it. Thus it remains sometimes even more than thirty minutes at a time, then comes rapidly to the water's surface to renew its air supply. This is done in five to ten seconds, whereupon the beetle again descends and disappears into the mud. At intervals the bubble at the end of the abdomen is released and another appears in its place and gradually increases in size. The beetles remained alive for months in aquaria, and in some instances more than a year. Both sexes stridulate squeakily by rubbing the apex of the abdomen against the underside of the apices of the elytra.

When about to oviposit, the female lies along the stem of submerged vegetation, sleeping fit with her legs so that the apex of her abdomen touches the plant surface. The eggs are then laid end to end in rows of eight to ten. Having deposited one egg, the beetle moves forward just far enough to place the next in contact with the end of the first. The gonopores continually remain in contact with the stem and appear to determine how far forward she will move after each deposition. The egg envelope quickly absorbs water and swells into a thick protective covering. During the process of hatching, the larva rips the shell from end to end in an irregular line.

Habits of the Larva. The larvae are heavier than water and obtain oxygen by means of filamentous tracheal gills at the sides of the thoracic and the first three abdominal segments. A single unbranched trachea extends length-
wise in each filament. By vibrating the hairy legs, the larva causes a current of water to pass under its body and bath the gills. To accomplish this end, only the middle leg of one side and the front and hind legs of the other are raised off the support at one time. While some exuviae were shed on the mud floor, other larvae molted in the bottom mud.

The matured larva forsakes the water to pupate, whereupon it digs itself into the earth headfirst to a depth of two to five inches, the distance depending on the character of the soil. There it constructs its pupal cell. By comminuting the particles of soil with the mandibles, and ramming the pellets into the wall with the head, the larva forms practically the whole space of the chamber, and the entrance from the burrows incidentally becomes closed. During the operation, its three caudal appendages are bent forward over the back and wedged against the wall of the cell. On these the body turns about freely in all directions. The work of constructing the cell is usually completed in 12 to 15 hours of continuous energetic activity.

Food and Feeding. The food of the adult consists of immature insects and worms. In aquaria, they readily devoured the naia of Agrionid Odonata, larvae of Chironomidae and Antlids, and other insects. The more active aquatic life like Ohloeon was usually able to escape them. In nature the beetle hunts for its food by swimming over the surface of the bottom mud and poking into the hollows and under stones.

The natural food of the larvae was the Tubifex worms which swarmed in the mud of the ponds. These the larvae sought by moving slowly over the mud bottom, touching it with their antennae and palpi, and on discovering a Tubifex burrow either leaped into it at once or waited watchfully. The larvae of the first instar mostly devoured their prey in its burrow, while the larger individuals usually seized the worm and after a struggle drew it from its case. The victim was apparently always attacked by the end and never at the middle of its body. When feeding, the larva remained motionless with most of the worm projecting from its mouth and wriggling vigorously. Then there follows a series of gulps during which the worm vanishes by degrees down the predator's throat. Whether the tissues of the prey were reduced by chewing or by a digestive secretion poured into the mouth has not been shown.

Life Cycle. The adults enter the mud at the bottom of the pond in October to hibernate, and reappear to begin ovipositing toward the end of March, the eggs becoming common in nature in about the second week of April. Oviposition extends to July, and the period of incubation varies from 22 days in early spring to 9 to 10 days in June. The larval stage comprises three instars, the first requiring 6 to 11, but usually 7 or 8, days, the second lasted 9 to 13, and the third about 22 days. After completing its pupal cell, the matured larva rests from 6 to 11 days before changing to the pupal state. Transformation to the adult required about 16 days and the new beetle remained inactive in the cell for a week or more before breaking out. Development from hatching to the appearance of the adult from its pupal chamber occupied from 9 to about 15 weeks. The earliest adults should therefore appear about the middle of June. Perhaps one generation is developed in a year.

3. MELYRIDAE

Food and Feeding. In a general assertion covering the family, Xambeau ('08) states that the agile larvae of Melyridae live either in dead animal bodies, under bark, or in tree trunks, where they consume the larvae of other insects (Fig. 102). In a number of specific instances recorded by this writer, the larvae fed as follows:

![Fig. 102](image-url)
Neateleus, small worms in dead fish and other aquatic animals; Hyobiaeus, in galleries of wood-borers; Rhoeus, both stages preying on the digger wasp, Passaloceus; Antholinus, around pine trees, feeding on worms, molluscs and insect larvae; Antino- tapus, under bark of oak devouring wood-borers; Apalochus, small worms, Arthropods, Molluscs and insects under rubbish; Malachius genus L., insect larvae in grass and stubble; M. insortanus Kust., wood boring larvae; M. marginellus 01., preying on insect larvae under bark and in wood; M. bipustulatus L., on insects in logs and under bark; M. lusitanicus Krs., in tree trunks consuming the Cerambycid, Cattallus vulitilus; M. paralis Krs., worms, Molluscs and larvae under bark; M. dilatior cornis Germ., on the Cerambycid, Exocentrus, in dead wood and M. viridis Fab., on the larvae of Cerambycidae. Urban repeatedly cut the larvae of Cerambycidae from the stems of Artemisia Vulgaris that were also inhabited by the larvae of Mordellistena parvula. The latter were attacked only when other food was scarce. While some writers state that it eats dead larvae and pupae, others have regarded it an an enemy of Cerambycidae, but Urban looks upon it as a scavenger in the burrows of the bark beetles.

Collops quadrimalatus (Fabr.) (Fig. 103) was found by Albert Reebel.

Fig. 103

Both the adults and larvae of C. vittatus (Say) were rather numerous preying on the larvae and pupae of Burymys suryphes, the alfalfa catertpillar, in Arizona (Wilder-muth). As many as 20 beetles were found attacking as many chrysalises in a single day. They appear to exhibit no preference between living and dead Burymys. In attacking, the beetle gradually makes a hole in the exoskeleton, thereby killing the prey. Only the exuding juices of the body are ingested, and being relatively small, the beetle consumes but little of any one victim. When hungry again, it attacks another, and thus kills many.

Seasonal History. The adults of Malachius bipustulatus L. generally make their appearance in the second half of May and disappear again during July. On June 6, a captive female deposited 42 reddish yellow eggs in a cone-shaped cavity in sand. Incubation has been found to require 14 to 20 days and the duration of the first instar was 18 days. According to Heeger, exuviation occurs at long intervals and at least five months are spent in the third instar. The larva is said to winter, and pupation takes place in the spring (Urban).

4. MORDELLIDAE

The somewhat common belief that the larvae of this family are predacious on other insects in old wood and the stems of plants seems to have originated in the discovery by Coquillett, and also Webster (Ol), both of whom reared Mordellistena pustulata Wels. from stems of plants in-
habituated by other insects. According to Xambeau ('08a), the larvae of Anaspis prey on xylophagous larvae and their excrement, while those of Scaptia, Tomoxia, Mordellia, and Mordellistina are not predatory. Hill ('22) found a few M. erythroderes Hill associated with termites in rotten wood but his claim that the beetle preys on the Isopteron is not well supported by the facts cited. On the other hand, Schwarz ('90), Buddenberg ('31), Webster ('03), Phillips ('11), Ring ('15), von Lengerken ('20), French ('33), and doubtlessly others, definitely report certain species of Mordellistina feeding on plant tissues. The form of Mordellid larvae, so far as they are known, does not suggest the aggressive mode of life that characterizes a predator.

5. ANTRICILLAE

Notoxus mono don Fabr. was found on two different occasions feeding on the pupae of Archips argyrospila in rolled-up leaves (Gill, while both the larvae and adults of Anthicus haldemani Lec. were taken in the large egg masses of Corydalus cornutus on rocks along the Potomac river (Fig. 105). In the laboratory the larvae of haldemani pupated in sand (Howard, '96). Chobaut ('97) and Rouval ('12) found species of Notoxus and Anthicus feeding on dead adult Meliidae, whereas Notoxus constrictus Casey and N. calcaratus Horn sometimes feed on fruits in California (Essig).

6. ELATERIDAE

Although present knowledge indicates a predominance of phytophagism among the larvae of click beetles, not a few species are known to feed upon the larvae of other insects and apparently also small worms. Like their phytophagous relatives, the predatory forms live under cover in soil or in wood. The larvae of Alaus oculatus L., formerly believed to eat decaying wood, feed instead on the larvae of wood-boring beetles. Feeding also on xylophagous insects are the larvae of Adelocera punctata Hbst., Athous furus Deg., A. nigerr L., Corymbites tessellatus L. (Xambeau, '14) and Proctopera cantori Hope (Stebbing).

Lacon murinus L. eats phytophagous insects in fields and gardens. Selastoma mus melanohylotus F. feeds on subterranean larvae, and Corymbites cupreus F. particularly consumes the grubs and pupae of Aphodius, according to Xambeau. Poultou found a female adult of C. viras Bhr. preying on the living caterpillars of Vanessa urticae on a mountain road, and the larvae of Conoderus pallipes Bth. are fairly important as predators on the white grubs of the Melolonthidae, Rhopaea vestituta (Weitch and Orpen). Other Elaterid genera containing predacious species are Adelocera, Agrypnus, Chaloolepidius, Hemmerhypus, Melanotua, Pyrophorus and probably others (Thomas).

In addition, some species exhibit a tendency toward cannibalism. Not only did the larvae of Monoceropinus vesparinus (Fabr.) destroy the pupae and soft molting larvae of Mordallonotus uneri Horn, according to Conradt and Eagerton in South Carolina, but others of their own kind whenever the infestation was heavier than five larvae per square inch of surface. Cannibalism was also observed among Agriotes larvae in Russia, and the larvae of Monoceropinus luteus (Deg.) and Alaus oculatus frequently feed on other wireworms, especially in experimental cages (Thomas). The carnivorous forms are said by Xambeau to become detritivorous or saprophagous in the absence of prey. The larvae of Lacon stricticollis Fairm. and Simocastlyus cinnamomeus Bold. attack the roots and young shoots of Secale arvensis but also feed on the grubs of Rhopaea vestituta.
7. HELODIDAE

The larvae of Microcara testacea L., Prionocyphon serricorns Will. and P. limbatus Lee. are said not to be predacious (Benick, '24; Good), and those of Ariltes tibialis Guer. feed upon Lemna minor, a duckweed, in Ohio (Kraatz, '18). However, those of A. grandis Mots. in India are said to prey upon other aquatic insects but are not adverse to consuming also dead specimens (Nowrojee). They cling to, or move quickly over the sides or bottoms of drains, particularly in dark places. Being much lighter than water, they must cling to some support to remain below the surface. Air is taken from the atmosphere by elevating the tip of the abdomen above the water level. The larvae then carry a bubble, which is attached to the caudal end and when they go down again. Several slender finger-shaped, thin-walled sacs on the apex of the abdomen are believed to have a respiratory function.

The larval stage of S. tibialis consisted of seven instars. In both species of this genus, the mature larvae come out of the water and enter the mud, where they make a pupal cell. The duration of the pupal period in grandis was 8 to 10 days in August. While the adult of tibialis is non-aquatic, it is common near the larval habitat.

8. DERMESTIDAE

Rüschkamp ('21) observed the feeding habits of seven species of five genera, confirming the generally accepted statements that Dermestidae live in dead animal or plant materials. But the larvae of some species of Thaumaglossa have been reported from the living egg clusters of Mantidae. Among these is T. dimaculata Arrow from the egg masses of Sphodromantis guttata in Pretoria. The larvae appear to eat both the eggs and the membranous substance enveloping them, hollowing out the interior of the cluster without destroying the outer layer (Arrow, '15).

9. OSTOMIDAE

Representatives of several genera prey upon other insects living in trees. The adults of Temnochila virescens (Fabr.) destroy wood-boring and bark beetles (Essig, '26), and T. coerulea Oliv. is a most useful forest species in destroying Tomionus and Polygraphus in Pinus (Stebbing, '14) (Fig. 106). Schwarz ('90a) found the larvae of Corticosterna cylindrica (Lec.) frequent in the galleries of Pityophthorus and other Scolytidae infesting deciduous trees, and Kleine ('08) lists Xenosoma elongatum L. as an enemy of the bark beetles, Philegesinus and Phileopus. According to Stebbing ('24), Alloniscus orientalis Reit., its variety parallelistus Lev., Melanoplus crenicollis Gyll. and Tenebrionides philochryssoides Walt. prey upon the wood-borers, Xylocyton grandis and S. minutus. The caddie, T. maartentus (L.) breeds in stored grains and cereal products, feeding both on these materials and on other insect pests that infest them.

Fig. 106

10. MITIULIDAE

According to Kleine ('08) and Imms ('34), the larvae of certain Philegesinus, Nitidula and Pityophagus prey upon bark beetles in Europe. Kleine specifically lists Pityophagus ferrugineus L., Nitidula rufipes L., Philegesinus depressus F., N. ripipes Gyll., N. bipunctatus F., N. nitidulus F. and R. paralleloccalis yull. as enemies of Scolytidae. R. paralleloccalis has also been looked upon as a scavenger on human corpses, but Blair ('22) observed that it probably lives on the larvae of Phora atrorius associated with it.

11. CUCUJIDAE

Several species, including Oryzaephilus surinamensis (L.), the sawtoothed grain beetle, breed in stored grain and the cereal food materials of man, but many others live under the bark of trees where they are predacious or parasitic on other insects, chiefly Coleoptera.

Predation. Both feeding stages of Cucujus clavigerus Fabr. destroy wood borers and bark beetles in the United States (Essig, '26) (Fig. 107), and according to Schwarz ('90b), the larvae of Inopeplus immunda Reit. probably prey on those of Pityophthorus pulicarius under the bark of pine. Schwarz ('90a) regards also the following species as enemies of Scolytidae:
Dymerus basalis, in galleries of P. concentrica, P. annectens and P. consimilis. Narthicus grandiceps Lee. from twigs of Liquidambar, and Lampyrophagus angustatus Lee. from Musa glabra infested with P. consimilis. Champion considered it probable that Pediacus depressus Hbst. fed on the larvae of the Mycetophagid, Typhastus, and the Labridid, Cononimus and Corbicula. This observer also looked upon Silvanus undentatus F. as a certain predator. The larvae of S. gemellatus Duval was frequently found feeding upon stages of Anthonomus grandis (Pierce, Cushman, Hood). According to Stebbing, Hecthrum heros Fabr. preys on Sinoxylon, Platypus and other wood-inhabiting beetles, and like its relative, H. uniforme Waterh., also feeds upon termites. Imm and Chatterjee ('15) cite the larvae of Berginus maindroni Grouv. and Silvanopsia iyeri Grouv. as common enemies of Tachardia in India, devouring both the insect and its secretions.

Parasitism. Craighead ('20) regards Scelidia and Catogenus as parasites, but little data concerning the former has been published. Schwartz ('90a) found S. linearis Lee. in the galleries of Pityophthorus concentrica. Dismuck ('82) and Fiske ('05) have reared C. rufus under circumstances having all the earmarks of entomophagous parasites. Dismuck observed a newly formed pupa of the Cermatobium, Hypermaulius parallellus, attacked by the small white larva of rufus in March. During its growth, the parasite consumed all but a few shreds of the pupal host. The larva became mature about May 20, and the adult beetle issued about July 1. Fiske reared this species on three occasions from insects living in trees, once from a Cerambycid pupa, which was possibly that of Goes punctatus, and in two instances from the cocoons of Brason dorsatus Say, a well known parasite of Cerambycidae. Where Goes was concerned, the Catogenus larva was very minute on April 17 and clung to the ventral surface of the pupal host. It gave no evidence of feeding until May 8, when it molted, whereupon it fed freely and grew rapidly. By May 20 it had completely destroyed the host, without showing signs of further eddies. Pupation followed on June 5, and the adult stage was reached by July 3.

In all these instances, the larva appeared to live as a true external parasite and always made most of its growth in May, at first exhibiting no perceptible increase in size and thereafter feeding and developing rapidly. The four individuals reared by the several investigators transformed to the beetle stage on July 1, 3, 5 and 9 respectively. Further details of the life history are lacking.

12. COLYDIIDAE

Studies by Craighead ('20) on representatives of the genera Bitoma, Philocoenus, Synchita, Sycophorus and Aulonium show that these feed purely on decaying vegetable matter, but Colydium may possibly be predacious. Aulonium trisulcum Geoffr. was listed by Klein ('08) as an enemy of the Scolytid, Raccottogaster multistriatus. Aglenus brunneus (Gyll.) is destructive in commercial mushroom beds (Essig, '26).

So far as known, members of the tribes Deretaphrini and Bothridiini attack other beetles inhabiting wood and bark. Some of these have recently been regarded as sustaining a parasitic relation to their food animals, but were formerly considered predators. Oxylaamus cylindricus Panz. is an enemy of the Scolytid, Pteleobius vitatus (Klein, '08), and Bothrides andrewsi Grouv., preys upon the Bostrychid, Sinoxylon, while Trachypollia basalis Weber and T. decorata Grouv. live beneath bark infested with Platypus and other lignicolous beetles upon which they are undoubtedly predacious (Stebbing, '14). Individuals of Lithocyctus suscinctus Pac., reared by Craighead, fed upon the Cerambycidae, Acerophon monocular, Ptilion tormensvit and Crucom angulatum, and Bothridius porosus Walk. preys upon the long-
horned borer, *Rhytidodera simulans* in Malaya (Corbett and Miller, '33). *Parasitio Colydiidae*. The species of *Deretaphrus* and *Bothrideres* studied by Burke ('19) and Craighead ('20) parasitized principally wood-borers of the groups Cerambycidae and Buprestidae. *Deretaphrus oregonensis* Horn is well known to inhabit trees and to feed on a number of insect hosts (Fig. 108). Its cocoons have been taken from the pupal cells of *Trachycolea opulenta*, the adults from the cell of *T. nimbosa* and from the bark of pines harboring *Buprestis laeviventris*, *B. aurulenta* and the brood of the Scolytids, *Dendroctonus jeffreyi* and *D. monticolae*. The hosts of *Bothrideres geminatus* (Say) were larvae of *Saperda discoidea* and the pupae of *Chariessa* and *Chrysobothris*. Large numbers of the larvae of *Oactophagi* Schwarz occupied the cocoons of the cactus weevil, *Cactophagus validus* on which it is undoubtedly parasitic.

The larvae of *Deretaphrus oregonensis* superficially resembles an Ichneumonid larva in having a whitish fleshy body that tapers to the rather small head. But the legs are well developed and the cauda bears a pair of recurved hooks. Moreover, the discrepancy in the size of host and parasite seems to enable the latter readily to derive all its sustenance from a single food insect. It appears, further, that *Bothrideres geminatus* is at times not only an internal, but a supernumerary parasite as well, considering the discovery of several larvae in a single pupa of *Chrysobothris*. The hosts of both *geminatus* and *Deretaphrus oregonensis* were killed by their parasites after the larval mines had been completed, and, in the instance of *Oregonensis* the hosts had constructed their pupal cells before they were overcome (Craighead).

**D. oregonensis**, *Lithophorus succineus* and *Bothrideres geminatus* pupate in cocoons attached to the wood on the side of the larval mine of the host. The cocoons probably consist of a chitinous material, but whether this is produced from the mouth or from anal glands has not been determined. Those of *Bothrideres* and *Lithophorus* have a silky appearance and waxy texture as though composed of minute threads. The cocoon of *Deretaphrus* consists of a considerably harder substance of uniform texture, and in the instance of *D. oregonensis*, it is elongate hemispherical, the flat side being joined to the rounded sides with a heavy seam or rim. The longitudinal and transverse dimensions of the known cocoons range from 6 by 3 millimeters in *Lithophorus* to approximately 14 by 4 mm. in *Deretaphrus* and *Bothrideres*. *D. oregonensis* hibernates as an adult in the cocoon and probably parallels its host in having one generation in two or more years.

13. TENERBRIONIDAE

These beetles feed largely on decaying organic matter, but some species eat cereals and living plants, and a few may perhaps be predacious. Stebbing ('14) claims that some species investigated in India undoubtedly are predators. Among these are the larvae of *Amarygmus* inhabiting the galleries of the Scolytidae, *Polygraphus*, *Tomicus* and *Pityogenes*, and *Kleine* ('08) cites some species of this genus which are likewise regarded as enemies of bark beetles. Moreover, Stebbing inclines to regard the larvae of *Amerygnus cuprarius* Weber, *Tribolium ferrugineum* Fabr., and perhaps other forms of *Tribolium*, as predators on xylophagous beetles. On the other hand, Buxton ('14) states that there is no good evidence to indicate a predatory food habit in this family, and Struble ('30) found that both the adults and the larvae of *Ephyphinae subsatratius* Lec. feed on fungi under the bark of trees.

14. CERAMBYCIDAE

Schwarz ('90a) reported the interesting instance of *Leptostylus aculifer* (Say) whose larvae preferably burrowed through the colonies of *Pityophthorus annector* in the branches of *Liquidambar*. By so doing, the comparatively large *Leptostylus* completely obliterated the galleries and crushed the larvae and pupae of the bark beetle. Similarly, the larvae of *Astylus nepula* (Say) and *Hyperplatys aspera*.
(Say) run their galleries over those of *Thysanodes fimbriicornis* in hickory. It is thought that the Scolytids somewhat loosen the bark from the wood, thereby creating a condition more favorable to the burrowing of the Cerambycid larvae. Such destruction of the bark beetle brood is obviously accidental, does not fall strictly within the pale of entomophagism and is of doubtful value inasmuch as the Cerambycidae concerned may prove as destructive as their victims.

15. OTHER SMALL FAMILIES

The activity and arboreal habit of the adult Othniidae has suggested the possibility of a predatory feeding habit. The small Lathridiid beetle, *Entomus minutus* L., occurred commonly on a beech tree on which Morley ('09) witnessed their masticating individuals of *Cryptococcus fagus*. While the larvae of the Platystomidae principally inhabit dead wood, woody fungi and smuts, the adult *Brachytarsus kuwanai* Yuasa feeds on the eggs of *Kermes* in Japan (Yuasa, '31). Also other species of this genus are known to prey on *Coccidae* (Imms). Kleine ('08) regards the Pythid, *Rhinosimus planticostalis* Fabr., as an enemy of the Scolytid, *Eccoptogaster intricatus*, and the Carabid-like form of *Salpingus* and *Lissodema* may also signify a predatory life. The linear-bodied *Rhyssoidae* inhabit wood where, it is believed, they may exist at the expense of other insects.
LITERATURE CITED

1. CICINDELIDAE


Criddle, Norman ('07), Habits of Some Manitoa "Tiger beetles" (Cicindela), Can. Ent., 39, 1907, 100-114.


Docters van Leeuwen, W. ('10), Ueber die Lebensweise und die Entwicklung einiger holzbohrenden Cicindeliden Larven, Tijd. voor Entomologie, 53, 1910, 100-114.


Fletcher, T. B. ('07), Cicindela biramosa and ~ trilunaris, Spolia Ze ylandica, Colombo, 5, 1907, 62-63.


Horn, Walther ('08), Coleoptera Adephaga, Carabidae, Cicindelinae, Genera Insectorum, Fasc. 82, 1908, 1910, 1915, 1-486. Many plates.


Shelford, R. ('07), The Larva of Collurius emarginatus Dej., Trans. Ent. Soc. Lond., 1907, 83-90, Pl. III.

Shelford, V. E. ('06), Life-Histories and Larval Habits of the Tiger Beetles, Jour. Linn. Soc. Lond. (Zoology), 30, 1907-1910, 187-184, 3 pl. (58 figs.).


Vuillermont, H., Note sur deux Cicindelides d'Indo-China, Insecta Nemesis, 2, 1915, 04-06.


Williams, F. X. and Sungerford, H. B. ('14), Notes on Coleoptera from Western Kansas, Ent. News, 25, 1914, 1, 16 figs.

2. CARABIDAE


Macnaghten, Charles ('22), Tiger Beetle Larvae, Can. Ent., vol. 54, 1925, 221-246, 3 figs.


Shelford, R. ('07), The Larva of Collurius emarginatus Dej., Trans. Ent. Soc. Lond., 1907, 83-90, Pl. III.

Shelford, V. E. ('06), Life-Histories and Larval Habits of the Tiger Beetles, Jour. Linn. Soc. Lond. (Zoology), 30, 1907-1910, 187-184, 3 pl. (58 figs.).


Vuillermont, H., Note sur deux Cicindelides d'Indo-China, Insecta Nemesis, 2, 1915, 04-06.


Agr., 1896, 412-426, 5 p.l.s.


Salt, George ('28), Notes on the Life History of Pleceteria sulcatus Guérin, Psyche, 35, 1928, 131-134.


4. GYRINIDAE


Buhl, P. ('10a), Stridulationsapparat bei Spercheus emarginatus Schall, Zeits. Wiss. Insektenbl., 6, 1910, 342-346, 1 fig.

Donisthorpe, Horace ('00), Notes on the coagulation of Hydrophilus piceus L. Entomologist's Rec. and Jour. Variation, 12, 1900, 291-292.

114, tbl.


Smith, H. B. ('26), Notes on the behavior of Dineutus americanus, Psych. 33, 1926, 166-167, 1 fig.


Wickham, F. H. ('26), On some aquatic larvae, with notice of their parasites, Can. Ent., 26, 1894, 39-41.


Matheson, Robert (1914), Notes on Hydrophilus triangulifer Say, Can. Ent., 46, 1914, 337-343, 1 pl. and 3 figs.


Nowrojee, D. (1912), Life histories of some aquatic Rhynochota and Coleoptera, Mem. Dept. Agr., India, Ent. Ser., II, 9, 166-341, 6 pls. and 3 figs.


Wesenberg-Lund, C. (1911), Uber die Respirationseinrichtungen bei einigen Tiere, Fig. 132, 1911, 467-468.


Wintersteiner, Fred (1913), Environment of Hydrophilidae, Jour. N. Y. Ent. Soc., 21, 1913, 64-84.

6. SILPHIDAE


Blatchley, W. S. (1910), An illustrated descriptive catalogue of the Coleoptera or beetles known to occur in Indiana, 1910, 1385 pp. Indianapolis, Indiana.

Clark, Charles U. (1901), On the food habits of certain dung and carrion beetles, Jour. N. Y. Ent. Soc., 9, 1895, 61.

Davis, W. T. (1913), Silphidae turbinensae and Hydrophilus villosus as predacious insects, Jour. N. Y. Ent. Soc., 25, 1915, 100-100.


(1927) - II. Pherogyna atrata L., 9, 1927, 271-312.

(1926) - III. Xylodrepa quadrifasciata L., 10, 1926, 330-352.


(1930) - V. Silpha tylus L. 17, 1920, 282-287.

(1930) - VI. Bililophagus undata R. 18, 1920, 170-188.

(1931) - VII. Caepepoma thoracica L., 20, 1931, 601-706.

(1932) - VIII. Allocerta laevigata F., 24, 1932, 259-287.

(1932) - IX. Silpha carinata L., 25, 1932, 534-546.

(1933) - X. Silpha tristis L., 28, 1933-34, 469-479.


7. STAPHYLINIDAE


Bischoff, --- ('09), Note on Velleius dilatatus F. Berl. Ent. Zeits., 54, 1909, 45.


Loderswall, R. ('17), Biologisches über brasilianische Staphylinidae, Zeits. Wiss. Insektil., 15, 1917, 9-14, 44-47.

Mann, W. M. ('23), New genera and species of Termitophilous Coleoptera from northern South America, Zoologica, N. Y., 3, 1923, 323-366, 13 figs.

McIndoo, N. E. ('28), Glandular structure of the abdominal appendages of a termite guest (Spirachtha). Zoologica, N. Y., 3, 1923, 367-368. 1 fig. and 9 pls.


Quayle, H. J. ('13), Some natural enemies

Scott, Hugh ('20), Notes on (I) the parasitic Staphylinid Aleochara algarum Fauvel, and its hosts, the Psococentrid flies; (II) A case of supposed parasitism in the genus Homalota, Ent. Mo. Mag., 55, 1920, 143-147, 2 figs.


Clark, G. S. ('16), On the food habits of certain dung and carrion beetles, Jour. N. Y. Ent. Soc., 3, 1895, 61.


A. Lycidae

Mjöberg, E. (’25), The mystery of the so-called "trilobite larvae" or "Per- ty's larvae" definitely solved, Psyche, 32, 1925, 119-157, 4 pls., 2 figs.


B. Phengodidae


C. Lampyridae


Allard, H. A. (’31), The photoperiodism of the firefly Photinus pyralis Linn., its relation to the evening twilight and other conditions, Proc. Ent. Soc. Wash., 33, 1931, 49-88, Fig. 2.


Blatchley, W. S. (’10), An illustrated descriptive catalogue of the Coleoptera or beetles known to occur in Indiana, 1910, 1385 pp., Indianapolis, Ind.


Elmhirst, Richard (’14), Some observations on the glowworm (Lampyris noctiluca L.), Societé, 16, 1915, 190-192.

1912, 256-272, refs.

McDermott, F. Alex. ('10), A note on the light-emission of some American Lampyridae, 42, 1910, 357-363.

McDermott, F. Alex. ('11), Some further observations on the light-emission of American Lampyridae: the photosensitive function as a mating adaptation in the Photinini, Can. Ent. 43, 1911, 299-306.


E. Cantharidae


Essig, E. O. ('26), Insects of Western North America, 1926, 1035 pp., 766 figs., Macmillan Company, N. Y.


Chapman, Murray and Smith ('70), Discussions of Rhipiphorus paradoxus, Zoological Record, 7, 1870, 301-302.

Chapman, T. A. ('91), On the oviposition of Metoecus (Rhipiphorus) paradoxus, Ent. Mo. Mag., 27, 1891, 18-20.


Crawshay, George A. ('05), A note on Metoecus paradoxus L., Ent. Mo. Mag., 61, 1905, 45-46.


12. MELOIDAE


Belajavsky, A. G. ('22), Elater beetles and their relation to the honeypot bee, Bee World, Camberley, Surrey, 14, 1935, 31-34, 4 figs.


Fabbre, J. H. ('19), The glowworm and other beetles, 1919, 488 pp., Dodd, Mead and Co. Translation by A. T. de Mattos.


13. COCCINELLIDAE


Coquillett, D. W. (1909), The imported Australian ladybird, Insect Life, 2, 1889-90, 70-74, figs. 9, 10.


Donisthorpe, Horace (1927), The guests of British ants, their habits and life histories, 244 pp., 16 pis., 55 text figs., London, 1927.


Fluke, C. L. ('29), The known predacious and parasitic enemies of the pea Aphid in North America, Univ. Wis. Agr. Exp. Sta., Research Bull. 92, 1929, 47 pp., 6 pls., 2 figs.


Girault, A. A. ('07), Biological notes on Marsupata (Mulsant), Proc. Zool. Soc. Lond., 1907, 193-197, 3 tables.


McKenzie, H. L. ('32), The biology and feeding habits of Hyperaspis (Coccinellidae) of North America, Univ. Calif. Publ. Ent. 6, 2, 9-20, 2 pls., 4 figs.


Miller, C. L. and Thompson, W. L. ('27), The life histories of ladybeetle predators of the citrus Aphid, Florida Entomologist, 11, 1927, 1-6, 5 figs.


Muller, C. L. and Thompson, W. L. ('27), The life histories of ladybeetle predators of the citrus Aphid, Florida Entomologist, 11, 1927, 1-6, 5 figs.


Stebbing, E. P. ('04), On the life history of a new Monophlebus from India, with a note on that of a Vedalia predacious on it, Jour. Linn. Soc. Lond., 29, 1904, 142-161.

Stebbing, E. P. ('14), Indian forest insects of economic importance, Coleoptera, London, 1914, 448 pp., 401 figs., 63 pls.

Steinhoff, E. ('04), On the life history of a new Monophlebus from India, with a note on that of a Vedalia predacious on it, Jour. Linn. Soc. Lond., 29, 1904, 142-161.

Stenbock, E. P. ('14), Indian forest insects of economic importance, Coleoptera, London, 1914, 448 pp., 401 figs., 63 pls.


Stroehel, Hans ('26), Pilzfressende Coccinelliden (Tribus Psylloborini), Zelts Wiss. Insaktivol., 21, 1926, 131-143, 4 figs., refs.


Cogito ergo sum.


Thompson, W. L. (26), A life history study of important ladybeetle predators of the citrus Aphid, Florida Entomologist, 10, 1926, 40-46, 57-59, 1 fig.


14. SMALLER FAMILIES OF ENTOMOPHAGOUS COLEOPTERA


Blair, K. O. (22), Notes on the life history of Rhizophagus paralleloscol-
<table>
<thead>
<tr>
<th>Author</th>
<th>Title</th>
<th>Source</th>
<th>Volume/Issue</th>
<th>Pages</th>
</tr>
</thead>
<tbody>
<tr>
<td>Morley, Claude ('09)</td>
<td>Enicmus minutus Linn., attacking Cryptococcus fagi</td>
<td>Ent. News, 44, 1933, 149-152</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Park, Orlando ('29)</td>
<td>Ecological observations upon the myrmecocoles of Formica rufa Emery,</td>
<td>Psyche, 30, 1923, 285-287, 1 Text figs.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>


INDEX

Abeille de Perrin, E., 112
Adelastria laevigata Fabr.
Duration of cycle, 71
Egg bursters, 71
Food of adult, 68
Food of larva, 70
Hibernation, 74
How it overcomes snails, 68
Incubation, 71
Mode of overcoming prey, 70
Oviposition, 71, 74
Predation, 68
Prepupal period, 71
Structure of jaws, 68
Temperature vs. growth, 71
Anastasia bulum of males
Dytiscinae, 34, 35
Function, 36
Development, 40
Structure, 34, 35
Aloeta bulum
Flight, 31
Life cycle, 50
Parasite, 29
Protection, 30
Season of oviposition, 50
Swimming fringes, 41
Submerged larvae, 41
Winter under ice, 47
Anilus femoralis Aeh.
Food of adult, 34
Food of larva, 45
Oviposition, 37
Undersurface larvae, 41
Ani.lis aeneus Lin.
Chewing jaws of larva, 45
Duration of stay at surface, 35
Food of larva, 45
Hibernation, 47
How larvae catch prey, 44
Life cycle, 50
Oviposition, 37
Ovipositor, 37
Periods of submersion, 33
Respiration of larva, 42
Activities
Adult Carabidae, 13
Adult Dytiscidae, 30
Adult Hydrophilidae, 57
Carabid larvae, 21
Colembelidae, 2
Dytiscid larvae, 39-48
Oryzid larvae, 54
Hydropid larvae, 61-65
Meloidae, 116-118
Nerophorus larvae, 75, 76
Adalia
Duration of larva, 146
Life cycle, 168
Pupation, 146
Where eggs are laid, 142
Adalia bipunctata L.
Advantage of cannibalism, 148
Cannibalism, 147
Color of eggs, 142
Egg masses, 159
Parasites affecting feeding, 154
Feeding capacity, 152
Generations, 159
Gregarious, 156, 157
Length of adult life, 147
Life cycle, 158
Mating, 158
Natural enemy, 147, 148
Oviposition, 159
Pupation, 145, 146
Adalia frigida humeralis (Say)
Egg masses, 159
Life cycle, 158
Adalia signata
Natural enemy of, 148
Adephaga, 4
Adonia variegata (Goeze)
Gregarious, 157
Aestivation
Carabus nemoralis, 18
Dytiscidae, 47, 48
Acanthocaris
Aestivation in mud, 49
Creeping larvae, 41
Dermal respiration, 42
Flight, 81
Food of larva, 45
Hibernation, 49
Life cycle, 50
Larvae in host plant, 59
Oviposition, 37, 38
Protection, 30
Swimming larvae, 41
Agabus bipustulatus L.
Duration of stay at surface, 33
Periods of submersion, 33
Pupal cell, 49
Agabus chalconotus Fahl.
Hibernation, 48
Agabus fasciculatus Payk.
Hibernation, 48
Agabus guttatus Payk.
Hibernation, 48
Agabus nubilus Sehr.
Oviposition, 27
Posture in mating, 36
Process of oviposition, 36
Acanthocaris pallipes (Fabr.)
Flight, 12
Oviposition, 19
Plant food, 16
Alocaecia mirabilis Mot.
Egg masses, 159
Feeding capacity of larva, 153
Alocaecia
Form of third larva, 80
Alocaecia algarum (See Polycestus)
Alocaecia nubilus Sehr.
Cropulation, 62
Development, 80
Food of adult, 80
Hosts, 79
Instars, 82
Mating season, 83
Oviposition, 57, 83
Parasite, 79
Pupal case, 80, 85
Rate of parasitism, 80
Relation to host, 79, 80
Seasonal development, 85
Alocaecia latreillei Gr.
Food of adult, 80
Food of adult, 58
Hibernation, 67
How egg case is made, 60
Locomotion of larva, 62
Inspiration of larva, 63
Spinning process, 60
Nerous epinure Sten.
Egg case, 60
Nerous spinus (Boy).
Egg case, 61
Food of adult, 58
Hibernation, 67
Locomotion of larva, 62
Inspiration of larva, 63
Spinning process, 60
Beroe a spinosus Stev.
Egg case, 59
Berosus striatus (Say)
Egg cases, 1
Food of adult, 58
Hibernation, 67
Locomotion of larva, 62
Respiration of larva, 63
Spinning process, 60
Beroe a spinosus Stev.
Egg case, 59
Berosus striatus (Say)
Egg cases, 1
Food of adult, 58
Hibernation, 67
Locomotion of larva, 62
Respiration of larva, 63
Spinning process, 60
Betis, L., 132
Bettin, C., 38
Black, R. F., 84, 86
Blinder
Locomotion, 30
Bliss, G. E., 72
Blightey, W. G., 17, 18, 34, 69, 73, 100, 105
Vesuvius, 66
Blundell, P. E., 22
Bollo, F., 40, 42, 43, 44, 45, 46, 47, 48, 49, 50, 57
Bodenheimer, F. S., 138, 142, 154, 155, 159
Boldoni, Leonida, 19, 20
Borchmann, 131
Benn, Paul, 28
Bothriopogon clorogynclata F.
Feeding on blister beetles, 17
Food of adult, 16
Best, R. R. B., 61, 62, 63, 64
Böting, A. S., 57, 87, 103, 104, 105, 106, 111, 120, 134, 135, 146, 147, 148, 149, 150, 151, 152, 153, 154, 155, 156, 157, 158, 159, 160, 161, 162, 163, 164, 165, 166
Brachytrus, 1
Brachytrus Parasitism, 24
Protection, 22
Brachymus Parasitism of Dineutes
Enemy, 13
Oviposition on plant, 19
Position of egg cases, 20
Brachymus Parasitism (Boy.)
Parasitism on Thrips, 24
Brachycentrus
Habitat, 138, 144
Ministry of Entomology, 149
Myrmecophilous, 139, 144
Oviposition, 142
Protection against ants, 149
Protective wax cover, 149
Brachycentrus parasitism Boul.
Exuviae of pupal cases, 149
Habitat of larva, 144
Myrmecophilous, 144
Pupation, 148
Brachycentrus urtica F.
Habitat of larva, 144
Myrmecophilous, 144
Britton, W. E., 159, 160
Brocker, Frank, 29, 32, 41
Brother parasitism Boul.
Food of adult, 18
Bruni pseudoplagiochroa Geh.
Dagre, 127, 128
Buscher, 163
Bunton, F. S., 99, 99, 100
Bunz, F., 58, 59, 60
Burges, A. F., 12, 13, 15, 17, 18, 19, 20, 22, 24, 25, 26, 147, 148, 150, 156, 158
Burke, R. E., 156
Burrows
Adults of Cicindelidae, 2
Hibernation burrows, 2
Larvae of Cicindelidae, 1, 6, 7
Process of burrowing, 2
Butler, F. Y., 68, 69
Callabates pseudopersica Del.
How adult feeds, 15
Callimorpha spargani Chom.
Food, 108
Callineura tusculuminaria McLe.
Duration of larva, 145
Size masses, 129
Incorporation, 143
Life cycle, 150, 150
Hatching, 150
Nesting vs. fertilization, 138
Inclusion eggs laid, 141
Number of instars, 145
Oviposition, 139
Pupation, 145
Rate of oviposition, 139
Cullopterus fasciatus Lea.
Food of larvae, 15
Massing of larvae, 97
Calosoma
Carnivolae, 22
Duration of cycle, 26
Economie importance, 23
Food of larvae, 23
Preoral digestion, 23
Calosoma calicis Fabr.
Bomiers, 17, 18
Food of adult, 15
Food of Larvae, 23
Instars, 25
Calosoma cancellatum Eich.
Food of adult, 15
Calosoma clavipes Say
Arboricola, 12
Calosoma criptomene Say
Amount of food, 24
Calosoma griseocollum Say
Food of adult, 25
Calosoma hemipterus Say
Amount of food, 24
Calosoma junciperoides Lea.
Food of adult, 15
Calosoma junciperoides Say
Food of adult, 25
Calosoma maricosta Mon.
Food of adult, 15
Calosoma pergaminator Guer.
Food of adult, 15
Catacosma sayi Dej.
Food of adult, 15

Catacosma serratator Fabr.
Adult attacking nesting birds, 18
Arboreal, 12
Attraction to light, 12
Food of adult, 15

Catacosma semilaeve Lec.
Food of adult, 15

Catacosma sycophanta L.
Age and food vs. oviposition, 20, 21
Age vs. food and reproduction, 17
Crawling of larva, 12
Duration of adult life, 26
Hibernation, 12
Flight of adult, 12
Food of adult, 16
Food vs. longevity, 26
Growth vs. temperature, 22
Habitat of larva and adult, 12
Hibernation, 13
How adult attacks prey, 14
Incubation, 21
Mating, 22
Life cycles, 26, 27
Longevity, 26
Mating, 19
Mating, 22
Mortality in hibernation, 18
Oviposition, 20, 26
Protracted dormancy, 18
Publisher, 22, 26
Quantity of food eaten, 16
Sex vs. mortality, 16
Starvation experiments, 17
Submersion in water, 12
Temperature vs. incubation, 21
Tolerance of poisoned and diseased prey, 17

Callosoma willcoxii Lee.
Arboreal, 12

Cameron, Malcolm, 81
Cantharidae
Food, 103, 104
General features, 103
Generations, 104, 106
Habitats, 104
Hibernation, 104, 108
Incubation, 106
Larval growth, 105
Life cycles, 104, 106
Life history, 104, 108
Occurrence of adults, 106
Oviposition, 106
Pupation, 106
Spring development, 104

Cantharis
Food, 103
Habitats, 103
Cantharis abdominalis Fabr.
Hibernation, 105
Cantharis bilineatus Say
Food of larvae, 104
Season of adult, 108
Cantharis carolinus Fabr.
Food of adult, 103
Season of adult, 108
Cantharis consors Lec.
Food of adult, 103
Cantharis dusceides Aub.
Hibernation, 105
Life cycle, 106

Pupation, 106
Cantharis divisa Lec.
Food of adult, 103
Season of adult, 108
Cantharis imitator Lec.
Season of adult, 108
Cantharis imitator Fabr.
Food of adult, 104
Hibernation, 106
Cantharis lineola L.
Season of adult, 105
Cantharis rectus Fabr.
Season of adult, 108
Cantharis fulvus Lec.
Season of adult, 108
Cantharis scitulus Say
Season of adult, 105
Cantharis tuberculatus Lec.
Season of adult, 105
Cantharoidea, 87
Cantharidae, 103-106
Drilidae, 100-103
GeneraL features, 87
Lepiopidae, 87-100
Lycidae, 87
Phaenopidae, 87
Photogenial organs, 87
Predation, 87
Sexual dimorphism, 87
Cantharidae
Activities of adults, 13
Activities of the larva, 21
Aestivation, 12
Arboreal, 12
Cannibalism of larvae, 22
Cheating mode of feeding, 22
Distribution, 12
Drinking, 17
Egg cases, 19, 20
Extraneous digestion, 14
Extraesophageal digestion, 14
Flight, 12
Flightless forms, 12
Food and feeding of adult, 13-17
General features, 13
Gregariousness in hibernation, 19

189
Habitat, 1

Termitophilous, 1

Cicindela campestris L.

Burrow and burrowing of larva, 6
Drinking, 5
Food of larva, 6
How larva seizes prey, 6, 9
Life cycle, 10, 11
Oviposition, 5
Pupal cell, 10

Tropisms of adult, 3

Cicindela cuprascens Dej.

Habitat, 1

Termitophilous, 1

Cicindela dyspunctata Dej.

Burrow of adult, 2

Cicindela flavomaculata rectilatata Chad.

Food of adult, 4
Mating, 5

Cicindela geminata Dej.

Life cycle, 10, 11

Pupal cell, 10

Cicindela formosa manitoba Leng.

Burrow of adult, 2

Burrows of adult, 2

Combat, 3
Drinking of adult, 5
Food of adult, 5

Cicindela hybrida L.

Burrowing of adult, 2

Burrows of adult, 2

Combat, 3
Drinking of adult, 5
Food of adult, 5

Cicindela lugenda Dej.

Burrow of larva, 7

Life cycle, 10, 11

Cicindela lima Dej.

Burrow of adult, 2

Life cycle, 11

Cicindela mitrata Latr.

Burrowing of adult, 2

Burrows of adult, 2

Combat, 3
Drinking of adult, 5
How adult feeds, 4
Quantity of food, 5

Cicindela punctulata Olivier.

Burrow, 2
Food of adult, 4
How adult feeds, 4
Life cycle, 10, 11
Pupal cell, 10
Quantity of food, 5

Cicindela purpurea Olivier.

Burrow and burrowing of larva, 6, 7, 8
How adult feeds, 4
Larval molts, 9
Life cycle, 10
Mating, 5
Oviposition, 5
Pupal cell, 10
Quantity of food, 4

Cicindela purpurea purpurea Casey

Life cycle, 10

Cicindela remigia Dej.

Burrowing of adult, 2
Combat, 3
Drinking of adult, 5
Duration of feeding, 4, 5
Food of adult, 4
How adults feed, 4
Oviposition, 5
Play, 5
Tropisms of adult, 3

Cicindela sanctalewia laconotil, Hald.

Burrow of adult, 2

Burrow of larva, 7

Cicindela segetisata Fabr.

Habitat, 1

Cicindela xanthonota L.

Food of adult, 4

Cicindela oryptic crest.

Burrows of larva, 7, 8

Cicindela transversa Hbst.

Burrow of adult, 2

Burrow of larva, 7

Food of adult, 4

Cicindela truncata L.

Duration of feeding, 4, 5
Food of adult, 4
How adults feed, 4
Oviposition, 5
Play, 3
Tropism of adult, 3

Cicindela trinervia Klug.

Locomotion on water, 1
Semiaquatic, 1

Cicindela laevipennis Dej.

Habitat, 2

Cicindela venustana LeC.

Burrow of adult, 2

Burrow of larva, 7

Life cycle, 11

Cladinaidae

Activities of adults, 1
Activities of larva, 6
Adaptations of larvae, 6
Arboreal, 1, 5, 8
Burrows, 2
Burrowing, 2, 6
Combat, 3
Drinking of adults, 5
Feeding of adults, 3, 4, 5
Food of adults, 3, 4, 5
General features, 1
Habitats of adults, 1
Hibernation burrows, 2
How larva seizes prey, 8, 9
Inactivity of larvae in summer, 8
Larval burrows, 1, 6
Larval molts, 9
Life cycle, 10, 11
Locomotion, 2
Mating, 5
Mozesephalus, 6
Natural enemies, 3
Oviposition, 5
Play, 3
Protective form and coloration, 3
Pupation, 9, 10
Semidiapause, 1
Termitophilism, 1
Tropisms of adults, 2, 5

Cicindelidae, 1

Habitats of adults, 1

Classens, F. W., 19, 22
Clark, K. H., 69, 84
Clade, C. F., 12, 138, 139, 141, 144, 153, 154
Clavicornia, 1
Clavigeridae, 160
Cleridae, 161
Economiidae, 109
Food and feeding, 107-109
Food of adults, 107-108
General features, 107
Generations, 111
Habits, 107
Hibernation, 110
Larval life, 110
Life history, 109-111
Mating, 109, 110
Mode of attacking prey, 107
Occurrence of adults, 110, 111
Oviposition, 109, 110
Parallelism between predator and prey, 111
Pupal cell, 110
Pupation, 110
Search of larvae for prey, 109
Specificity of food habit, 111
Clivina impressifrons Lec.
Plant food, 15
Coarctate larva of Meloidae, 120
Coccinella
Where eggs are laid, 124
Coccinella esvividia Fall.
Duration of larva, 124
Gregariousness, 126
Incubation, 126
Oviposition, 126
Coccinella davidiata Oliver.
Duration of larva, 126
Habitat of larva, 126
Incubation, 126
Instar, 126
Myrmecophilous, 126, 127
Oviposition, 126
Pupation, 126
Coccinella monticola Bliss.
Duration of larva, 126
Incubation, 126
Length of adult life, 127
Life cycle, 129
Mating, 128
Coccinella nevadensis M.
Duration of larva, 126
Oviposition, 126
Coccinella septempunctata L.
Duration of larva, 126
Egg masses, 129
Feeding capacity, 129
Length of adult life, 127
Life cycle, 129
Pupation, 129
Studies of stomach contents, 150
Coccinella septempunctata L.
Natural enemy, 147
Coccinella septempunctata L.
Natural enemy, 147

Factors affecting feeding, 154, 155
Feeding capacity, 156
Gregariousness, 156, 157
Length of adult life, 147
Mating, 148
Natural enemy, 147, 148
Oviposition, 150
Why they congregate, 158
Coccinella stimulans (margarita) Feld.
gregarious, 156, 157
Coccinella sp.
Gregariousness, 156, 157
Coccinella transversoguttata californica Mann.
Factors affecting feeding, 154
Gregarious, 156, 157
Rating, 158
Oviposition, 159
Coccinella transversoguttata quinquemaculata Kirby
Duration of larva, 145
Egg masses, 139
Feeding capacity, 157, 158
Gregarious, 157
Incubation, 142
Length of adult life, 147
Life cycle, 142
Preoviposition period, 139
Pupation, 146
Studies of stomach contents, 150
Coccinella trifasciata L.
Egg masses, 139
Pupation, 146
Coccinella
terrestrial, 146
Adult stage, 146-147
Advantage of cannibalism, 147, 148
Advantage of dual food habit, 150
Aestivation, 156
Aphids and Cicadas as food, 149
Attachment for pupation, 146
Cannibalism, 147
Circumstances attending gregariousness, 157, 158
Color of eggs, 132
Daily rate of oviposition, tables, 139-141
Data on oviposition, tables, 139-141
Development of eggs, 149
Development of pupae, 149
Duration of larval stage, 145, 149
Duration of prepupa, 146
Duration of pupa, 145, 146
Duration of stages and instars, tables, 142
Egg bursters, 146
Egg masses, 139
Factors affecting feeding
Age of adults, 154, 155
Season and temperature, 155
Size of larvae, 156
Factors determining oviposition, 142
Feeding capacity of adult, 152-153
Feeding capacity of larva, 148-149
Feeding habits of adults, 153-154
Food records of species, 150-152
Food specialization among the tribes, 152
Frequency of copulation, 139
Fungus-eaters as cannibals, 147
General features, 139
Genetics, 139
Habitats of larvae, 144
Hatching, 144
Hibernation, 156, 157, 158
Hostile factors, 147-148
How Coleomelinae feed, 155-156
Hypodermal secretion as protection, 148
Incubation, 142, 143, 144
Larval Life, 142-145
Length of oviposition period, 141
Life cycle, 142-149
Life of adult, 138-144
Manner of laying eggs, 139
Mating, 134-139
Mating vs. fertilization, 138, 139
Maximum egg-laying capacity, 141
Means of attachment for pupation, 144
Molt to pupate, 146
Number of instars, 145
Numbers in congregations, 159
Oviposition, 139-141
Parasites of Coleomelinae, 148
Period of oviposition, table, 139-141
Places of pupation, 148
P:opular names, 138
Prepupation, 145, 146
Prey of Coleomelinae, 146-150
Protection and defense, 143-149
Pupation, 143, 145-146
Summaries of prep, 148
Total eggs per female, tables, 139-141
Where eggs are laid, 142
Why do lady beetles congregate? 157-158
Cocolinellinae
Egg bursters, 144
Food habit, 138
Coccinellini
Summary of prey, 152
Coeiostoma orbiculare F., egg case, 59, 61
Coleophora swinhoei C., feeding capacity, 152
CollinS, C. W., 12, 15, 17, 18
Collins, C. W., 12, 15, 17, 18
Colyris
Activity, 2
Archoreal, 2
Colyris
Surrounding of larvae, 6
Burrows of larvae, 6
Food of larvae, 9
Natural enemies, 5
Colyris canaliculii Gyll.
Food of adults, 4
Food and feeding of larva, 8
Life cycle, 10
Oviposition, 6
Wasp cell, 9
Pupation, 9
Colyris earamasensis Thomas.
Resemblance to Spyroa, 5
Colyris tuberculosis Mels. I.
Food of adult, 4
Food and feeding of larva, 8
Oviposition, 6
Colyrisidae
Cocoon of Derataspheus, 166
Food habits, 165-166
Habits of parasitic forms, 166
Hosts and prey, 165-166
Coleotes
Creeping larvae, 40
Parasite, 79
Subepiastal air chamber, 37
Winter under ice, 47
Coleotes flavicollis
Climbing larvae, 40
Food of larvae, 16
Hatching moisture, 38
Hibernation, 47
How larvae catch prey, 44
Instars, 39
Life cycle, 30
Oviposition, 37
Perforation in mating, 36
Cook, A. R., 156
Corylogara
Form of third larva, 80
Corylogara hilligiana, Qyl., development, 80
Food of adults, 80
Generations per year, 83
Host, 39
Incubation, 82
Instars, 62
Parasite, 79
Prepupal and pupal period, 82
Relations to host, 79
Corylogara omaria
Corylogara venom Say
Host, 39
Parasite, 79
Corylogara venom venom Say
Host, 39
Parasite, 79
Coptolobus
Cannibalism, 46
Oviposition, 37
Swimming larvae, 41
Coptolobus interruptus (Fabr.)
Food of adult, 46
Food of larvae, 46
Oviposition, 38
Preoral digestion of larva, 45
Respiration by cilia, 42
Structural changes on leaving water, 48
Copulation (See mating.)
Coullet et al, 13, 139, 146, 167
Coullet, D. W., 13, 140, 154, 193
Coullet, D. W., 13, 140, 154, 193
Copulipus maxillosus L.
Food of adult, 46
Food of larva, 23
Number of eggs, 20
Oviposition, 19
Copepodidae
Dobsonflies, 18
Corynodes
Termitepilus, 78
Corimetopus, DON, 109
Craighed, Jr., C. V., 15, 203, 104, 113, 114, 144, 181, 104, 105, 165, 168
Cratopolys armillata Schaum
Food of adult, 78
Food of larva, 23
Habitat, 12
Number of eggs, 20
Oviposition, 19
Ctenoplectus d'Apres Bennet.
Enemy, 12
Crawley, L. S., 201, 102, 112
Ctenoptilus maculatus L.
Parasite of, 76
Ctenoplectus villosus (Grum.)
Food of adult, 80
Cressmann, A. A., 156, 159
Cridder, Norman, 1, 2, 3, 4, 5, 6, 7, 10, 11
Cros. A., 140, 141, 142, 143, 144, 145, 146, 147, 148, 149, 150
Ctenonemus
Protective waxy cover, 140
Specificity of food relation, 111
Entomophageous beetles, 1

Epimetus
Activity of later instars, 126
Cannibalism among larvae, 124
Generations, 128
Life cycle, 135
Observations by Riley, 121
Oviposition, 126
Scara baeoid larvae, 120

Epicauta cinerea Forst.
Larval cells, 125
Epicauta cinerea varians V.
Early observations, 121
Life cycle, 135
Epicauta mutata Say
Incubation, 118
Larval cells, 125
Life cycle, 135
Oviposition, 117
Search for hosts, 122
Epicauta nemorum Disc.
Generations, 126
Life cycle, 135
Oviposition, 117
Epicauta rufidens 111.
Cocoon larvae, 126
Duration of first instar, 125
Duration of scolytoid larvae, 127
Feeding of primary larvae, 124
Larval cells, 125
Non-feeding instars, 126
Oviposition, 117
Quantity of food, 120
Search for hosts, 122
Tenacity of life, 125
Epicauta sericans J. Lec.
Life cycle, 135
Epicauta sibirica Pall.
Xiphidium as host, 131
E. vittata Fab.
Activities of primary larvae, 121, 122
Change to coarctate form, 129
Concrete larvae, 120
Diagram of life cycle, 137
Duration of first instar, 125
Duration of later instars, 127
Early observations, 121
Feeding of primary larvae, 124
Habits of scolytoid larvae, 126
Hibernates as coarctate larva, 127
Importance as enemy of locusts, 123
Invasion, 119
Life cycle, 135
Non-feeding instars, 126
Oviposition, 117
Function, 124
Scaphoideous larva, 125
Scolytoid larvae, 121
Search for hosts, 120
Six larval instars, 121
Tenacity of life, 125
Euplatus borealis F.
Cannibalism, 147
Sphacelodea
Sphytophasus, 138
Sphexidae

Remotes picipiens L.
Duration of transformation, 48
How it seizes prey, 33, 34
Preoral digestion of larva, 45
Respiration of larva, 42
Scaphoidea, 12
Food of adults, 15
Hering, H. E., 126, 127
Respiration
Summary of prey, 152

Fabre, J. B., 71, 116, 117, 119, 120, 123, 124, 125, 131, 134, 146
Furhinger, Josef, 15, 69
Fiedler, Aug., 15
Filamentous algae, 1
Flake, W. P., 165
Flashing of lampryidine
Attraction of other species, 94, 95
Biological significance, 92
Population, 96, 97
Pastors causing periodicity, 92
Flash pattern, 90, 91
Flight and flashing, 91
Periodicity of, 92
Synchronous flashes, 91
Time of day, 92
Fletcher, T. H., 1, 4
Fluke, C. L., 103, 116, 117, 119, 120, 121, 122, 146, 150, 151, 159
Food and feeding
Cantharidae, 102, 104
Carabidae, 13-17, 22
Cicindelidae, 3, 4, 5, 8
Coleoptera, 107-109
Oecolus, 145-146
Belliidae, 103
Eptidae, 33, 34, 43-47
Oryctidae, 53, 54
Histeridae, 84, 92
Hydrophilidae, 66, 68
Lampryidae, 94, 95, 96
Plagiodontidae, 87
Silphidae, 69-70
Staphylionidae, 80-82
Smaller families, 160-167
Frogbatt, W. W., 108, 109
French, A. M., 163
Frost, C. A., 12
Gage, J. H., 148, 166
Gaines, J. C., 120, 121
Galerita binocular Brady
Method of defence, 13
Galerita tarsus Pab.

General features
Carnivorous, 12
Cannibalism, 103
C. tarsus, 87
C. latens, 107
Ectopsoboe, 138
Delitae, 100
Euplatus, 20
Histeridae, 94
Hydrophilidae, 97
Lyctidae, 97
Graphoderes
Hibernation, 48
Inquiline of Hydrous, 67
Oviposition, 37
Underconcentrated larvae, 41
Graphoderes bilineatus Dec.
Hibernation, 47
Life cycle, 55
Oviposition, 38
Green, R. H., 254
Greenwood, W., 163
Ground Beetles, 12
Orydidae, 4
Activities of adult, 51
Activities of larvae, 52
Adaptations for surface life, 52, 57
Cambellia, 55
Copulation, 52, 59, 66
Divis of adults, 52
Duration of incubation, 55
Ecological groups, 51
Eggs, 54
Factors affecting floating, 58
Failure of adults to collide, 62
Feeding of larvae, 55
Flight, 51
Floating of adults, 52
Food and feeding, 53
Food in captivity, 55
Food in nature, 56
Food of larva, 55
Generations per year, 56
Gills, 54
Gregariousness of adults, 51
Gregariousness of adults, 51
Habitat, 52, 54
Hibernation, 66
How eggs are laid, 54
How pupal cells are built, 66, 66
Insulation, 66, 66
Johnson's organ, 62
Larval food and feeding, 66
Life cycle, 56
Locomotion, 51
Locomotion of larvae, 54
Mandibles of larvae, 66
Melanosis prevents eclosion, 53
Mixed congregations, 51
Modifications for air storage, 52
Oviposition, 53, 54, 56
Preoral digestion, 55
Prey of Hydrous, 55
Protection, 51
Pupal case, 56
Pupation, 55
Respiration of larvae, 54
Respiration under water, 52
Scavenger food habit, 51
Stream inhabitants, 51
Structure of mandibles, 63
Subaquatic respiration, 52
Tracheal gills, 56
Where eggs are laid, 54
Corydalis
Building pupal cell, 66, 66
Flight, 53
Food of adults, 56
How larva swims, 64
Material of pupal cell, 56
Pupal case, 56
Pupation, 55
Respiration of larvae, 54
Structure of pupal case, 55
Swarm, 51
Swarm of larva, 54
Tracheal gills, 56
Corydalis marina Gyll.
Experiments, 63
Johnston's organ, 56
Corydalis mixtus substratus Steph.
Animal food of adult, 63
Building pupal cell, 68
Copulation in water, 64
Food of adult, 56
Food of larva, 66
Hibernation, 66
Incubation, 54
Larva leaves water, 66
Life cycle, 66
Material of pupal cell, 55
Mating, 53, 54
Oviposition, 55
Position of pupal cell, 55
Transformation, 66
Habitats
Carabidae, 12
Cathartidae, 107
Cicindelidae, 1, 2
Coccinellidae, 130
Dytiscidae, 28
Orydidae, 51, 54
Nisteridae, 94
Hydrophilidae adults, 57
Lampyridae, 90, 91
Larvae of Hydrophilidae, 62
Silphidae, 68
Haldane, Kathleen, 96
Haliplidae, 1
Haliplis, 1
Hemmidae, C. C., 1
Harpalus alaschanicus (Pabhr.)
Food of adult, 15
Food of larva, 56
How adult feeds, 16
Method of defense, 13
Harpalus pensylvanicus Deg.
Enemy, 12
Food of adult, 15
How adult feeds, 15
Harpalus, B. M., 94
Hatch, Melville, H., 51, 52, 54, 56
Hawkes, O. A. M., 138, 146, 148, 149, 156, 157, 158
Heeger, E., 152
Heikertinger, F. E., 148
Halobates
Egg case, 59, 61
Eggs carried by female, 59
Pupation, 65
Meloidae, 116
Rhipiphoridae, 112
Silphidae, 68
Gibson, Arthur, 15, 80
Gill, J. B., 163
Goe, Milton T., 71
Goodart, 171
Goldenith, R. M., 9
Good, R. G., 164
Gowdy, C. C., 151
Gouveia, Ch., 150
Graells, 110
Graphoderes
Hibernation, 48
Inquiline of Hydrous, 38
Oviposition, 37
Underconcentrated larvae, 41
Graphoderes bilineatus Dec.
Hibernation, 47
Life cycle, 55
Oviposition, 38
Green, R. H., 254
Greenwood, W., 163
Ground Beetles, 12
Orydidae, 4
Activities of adult, 51
Activities of larvae, 52
Adaptations for surface life, 51, 57
Cambellia, 55
Copulation, 52, 59, 66
Divis of adults, 52
Duration of incubation, 55
Ecological groups, 51
Eggs, 54
Factors affecting floating, 58
Failure of adults to collide, 62
Feeding of larvae, 55
Flight, 51
Floating of adults, 52
Food and feeding, 53
Food in captivity, 55
Food in nature, 56
Food of larva, 55
Generations per year, 56
Gills, 54
Gregariousness of adults, 51
Gregariousness of adults, 51
Habitat, 52, 54
Hibernation, 66
How eggs are laid, 54
How pupal cells are built, 66, 66
Insulation, 66, 66
Johnson's organ, 62
Larval food and feeding, 66
Life cycle, 56
Locomotion, 51
Locomotion of larvae, 54
Mandibles of larvae, 66
Melanosis prevents eclosion, 53
Mixed congregations, 51
Modifications for air storage, 52
Oviposition, 53, 54, 56
Preoral digestion, 55
Prey of Hydrous, 55
Protection, 51
Pupal case, 56
Pupation, 55
Respiration of larvae, 54
Respiration under water, 52
Scavenger food habit, 51
Stream inhabitants, 51
Structure of mandibles, 63
Subaquatic respiration, 52
Tracheal gills, 56
Where eggs are laid, 54
Corydalis
Building pupal cell, 66, 66
Flight, 53
Food of adults, 56
How larva swims, 64
Material of pupal cell, 56
Pupal case, 56
Pupation, 55
Respiration of larvae, 54
Structure of pupal case, 55
Swarm, 51
Swarm of larva, 54
Tracheal gills, 56
Corydalis marina Gyll.
Experiments, 63
Johnston's organ, 56
Corydalis mixtus substratus Steph.
Animal food of adult, 63
Building pupal cell, 68
Copulation in water, 64
Food of adult, 56
Food of larva, 66
Hibernation, 66
Incubation, 54
Larva leaves water, 66
Life cycle, 66
Material of pupal cell, 55
Mating, 53, 54
Oviposition, 55
Position of pupal cell, 55
Transformation, 66
Habitats
Carabidae, 12
Cathartidae, 107
Cicindelidae, 1, 2
Coccinellidae, 130
Dytiscidae, 28
Orydidae, 51, 54
Nisteridae, 94
Hydrophilidae adults, 57
Lampyridae, 90, 91
Larvae of Hydrophilidae, 62
Silphidae, 68
Haldane, Kathleen, 96
Haliplidae, 1
Haliplis, 1
Hemmidae, C. C., 1
Harpalus alaschanicus (Pabhr.)
Food of adult, 15
Food of larva, 56
How adult feeds, 16
Method of defense, 13
Harpalus pensylvanicus Deg.
Enemy, 12
Food of adult, 15
How adult feeds, 15
Harpalus, B. M., 94
Hatch, Melville, H., 51, 52, 54, 56
Hawkes, O. A. M., 138, 146, 148, 149, 156, 157, 158
Heeger, E., 152
Heikertinger, F. E., 148
Halobates
Egg case, 59, 61
Eggs carried by female, 59
Pupation, 65
Helochares griseus P.  
Food of adult, 88  
Food of larva, 84  
Locomotion in water, 97  
Mandibles of larva, 83  
Posture in feeding, 83  
Helochares manuelliata.  
Eg. cases, 61  
Food of larva, 64  
Generations, 67  
Life cycle, 67  
Oviposition, 67  
Helochares sp.  
Eg cases, 61  
Helodidae  
Nature of food, 164  
Helophorus lacustris Lec.  
Eg cases, 59, 61  
Hibernation, 67  
Heteromoea (Say;  
Nature of host, 131  
Herman, W. C., 15  
Hesperobium californicum Lec.  
Food of adult, 80  
Hess, Walter N., 89, 90, 91, 93, 94, 95, 96, 97, 99, 100  
Heterocerus brunneipennis Rand  
Ant host, 84  
Foods, 84  
Myrmecoophilous, 84  
Trichomes, 84  
Heterocerus ferrugineus 01.  
Myrmecoophilous, 84  
Trichomes, 84  
Heymons, R., 68, 70, 71, 74  
Hibernation  
Adult Carabidae, 17, 18  
Burrowing of adult Cincinelididae, 2  
Burrows of Cincinelididae, 2  
Cemharda, 104, 106  
Cleridae, 110  
Dytiscidae, 47, 48  
Ephydridae, 67  
Lampyridae, 100  
Larvae of Carabidae, 10  
Molcidae, 127, 130, 136  
Situations of Carabidae, 18  
Hidman, J. R., 1  
Hill, G. F., 163  
Hippodamia  
Where eggs are laid, 142  
Hippodamia convergens.  
Eg. cases, 139  
Factors affecting feeding, 124  
Feeding capacity, 132, 134  
Gregariousness, 136, 137, 138  
Hatching, 144  
Incubation, 124  
Length of adult life, 147  
Life cycle, 125  
Molt to pupate, 146  
Pupation, 146  
Hippodamia rickmersi Ws.  
Gregarious, 156, 157  
Hippodamia sinata.  
Duration of larvae, 146  
Incubation, 142  
Life cycle, 159  
Pupation, 146  
Hippodamia tricolor.  
Summary of Food, 152  
Hister  
Food of larva, 84  
Habitats, 85  
Hister bispinatus Lee.  
Food of adult, 84  
Hister euryrhachis 0.  
Food of adult, 84  
Hister companus 0.  
Food of adult, 84  
Hister interrugosus Say.  
Food of adult, 84  
Hister pusillatus Genz.  
Food of adult, 84  
Hister quadrinaculatus L.  
Food, 84  
Hister parvulorum Orm.  
Food, 84  
Hister sazercestus Lee.  
Food of adult, 84  
Hister trivitalis Rbs.  
Food of larva, 84  
Histeridae  
Adaptation for life under bark, 84  
Coleoptera as food, 84  
Diptera as food, 84  
Enemies of Scolytidae, 84  
Food and feeding, 84, 85  
General features, 84  
Generations per year, 85  
Guests of ants, 84  
Habitats, 84, 85  
Hibernation, 86
Life history, 86
Myrmecophiles, 84
Oviposition, 88
Predation on xylophagous beetles, 85
Scavengers or predators, 84
Seasonal development, 86
Symeothrans, 84
Symeketes, 84
Hoffer, E., 112
Hololepta
Habitat, 86
Prey, 85
Holste, G., 13, 15, 19
Hopkins, A. D., 85
Horn, Walther, 2, 4, 5
Hornia
--flightless, 116
Hornia tigantea (Weilln.)
Carried by bees, 122
Enemy of Anthophora, 133
Hornia minutipennis Riley
Activities of primary larva, 122
Horrus, J., 117
Howard, L., 118
Hungerford, H. B., 7, 9, 133
Hutson, J. C., 100
Hydatidella seminiger Der.
Hibernation, 47
Oviposition, 38
Hydaticus transversalis Pontopp.
Hibernation, 47
Oviposition, 38
Hydaticus
Cannibalism, 46
Food of larvae, 45
Hibernation, 48
How larvae catch prey, 44
Life cycle, 60
Oviposition, 37
Parasites, 33
Quantity of food, 45
Season of oviposition, 50
Undercompensated larvae, 41
Hydaticus seminiger Der.
Hibernation, 47
Oviposition, 38
Hydatiscus transversalis Pontopp.
Hibernation, 47
Oviposition, 38
Hydronoera pallipessee Say
Food of larva, 115
Hydronoera subhaemae L.
Food of larva, 109
Hydronoera verticalis Say
Food of larva, 119
Hydronoera
Egg cases, 59
Insemination, 62
Hydranga pennsylvanica Kies., 67
Hydrophilidae
Egg cases, 58
Hydrophiinae
Egg cases, 59, 61
Pupation, 60
Hydrobius Fuscipes L.
Cannibalism, 86
Copulation, 58
Drumming in copulation, 58
Early larval life, 62
Egg cases, 50, 61
Enemies, 67
Floating, 62
Food of larva, 64
Generations, 67
Habitat of larva, 62
Hatching, 62
Hibernation, 67
Insemination, 62
Instars, 63
Larval instars, 63
Life cycle, 67
Locomotion of larva, 62
Mandibles of larva, 63
Manner of feeding, 63, 64
Oviposition, 67
Plant food of adult, 50
Position of pupa in cell, 66
Posture in copulation, 58
Posture in feeding, 63
Prepupation, 66
Prophases of puation, 66
Prey, 66
Spinning eg cases, 59
Strident sound, 58
Hydrobius globosus (Say)
Cannibalism, 46
Locomotion of larva, 62
Hydrophila
Egg cases, 59
Hydrobius aquarius Lea.
Egg cases, 67
Hibernation, 67
Hydrophilidae, 47
Activities of adult, 57
Adults as scavengers, 58
Antennae in respiration, 57, 58
Asymmetry of mandibles, 63
Aquatic forms, 57
Cannibalism of larva, 65
Constructing pupal cells, 65
Dorsal air chamber, 57
Duration of larval life, 63
Early larval life, 63
Egg cases, 57, 58, 59
Egg cases, 57
Feeding of larva, 63
Fish food of Hydrobius, 65
Fitness for aquatic life, 57
Floating, 66
Food and feeding of adults, 58
Food of larva, 64
Function of max, 61
General features, 57
Gregariousness of larvae, 62
Habitat of adult, 67
Habitat of larva, 62
Hairy tracts in respiration, 57, 58
Hatching, 62
Hibernation, 67
How Dytiscidae swim, 57
Instars, 63
Larval activities, 61, 65
Larval food, 65, 64
Larval growth, 63
Life cycle, 67
Locomotion of adult, 57
Locomotion of larvae, 62
Mandibles of larvae, 63
Manner of swimming, 67
Mantle of egg cases, 61
Mating, 58
Metamorphic larvae, 62
Natural enemies, 66
Number of eggs, 61
Operation of spinnerets, 59
Oviposition, 68
Plant food of adults, 66
Position of pupa in cell, 66
Preoral digestion, 64
Prepupal state, 66
Process of feeding, 64
Protection, 66
Pterostichus larvae, 62
Pupation, 65
Respiration, 57, 58
Respiration of larvae, 63
Respiratory organs, 57
Respiratory process, 58
Ribbons of egg cases, 61
Shape of egg cases, 61
Silk glands, 59
Size of egg cases, 61
Spermatophore, 58
Mandibles of adult larvae, 63
Mast of egg cases, 61
Mode of feeding, 65
Morphology of spinning apparatus, 60
Nest, 67
Nymph process, 60
Oviposition, 37
Parasitic larvae, 62
Pupation, 65
Pupal stage, 66
Hydrophilus obtusatus Say
Duration of larval life, 63
Early larval life, 62
Egg cases, 61
Food of adult, 68
Food of larva, 64
Hatching, 62
Hibernation, 67
Parent, 66
Hydrophilus sp.
Locomotion of larvae, 62
Mandibles of larvae, 63
Method of feeding, 66
Position of pupa in cell, 66
Pupation, 66
Hydrophilus
Crepis larvae, 40
Insect, 50
Pupal cell, 49
Subelytral air chamber, 53
Hydrophilus (Percnidae) depressus Fabr.
Length of larval stage, 40
Oviposition, 37
Position of pupa cell, 50
Pupal cell, 49
Hydrophilus latens Grnig. Pupa
Food of larva, 43
Length of larval stage, 40
Oviposition, 57
Pupal cell, 49
Hydrophilus piger Say
Crawling larvae, 40
Instar, 34
Food of larva, 45
Respiration in water, 42
Hydrophilus picturatus Fabr.
Duration of stay at surface, 33
Periods of submersion, 35
Hydrophilus septentrionalis Odcill.
Shape of pupal cell, 49
Where they pupate, 48
Hydrophorus
Egg cases, 69
Hydrophilus
Antennae in respiration, 57
Egg cases, 59, 61
Floating egg cases, 59
Food of larva, 64
Incubation, 62
Mantle of egg case, 61
Nymph, 63
Prey of Hydrophorus, 64
Protection, 67
Rectal ampulla, 67
Respiration, 57
Subelytral reservoir, 57
Swimmers, 57
Hydrophilus caraboides L.
Early larval life, 62
Egg cases, 59, 61
Food of adult, 58
Food of larva, 64
Generations, 67
Hibernation, 57
How egg cases are made, 59
Life cycle, 67
Mandibles of larva, 63
Mantle of egg case, 61
Mode of feeding, 64
Posture in feeding, 63
Preoral digestion, 64
Pupal stage, 66
Spermatophore, 58
Hydrophilus sp.
Locomotion of larvae, 62
Mandibles of larvae, 63
Method of feeding, 66
Position of pupa in cell, 66
Pupation, 66
Hydrophilus obtusatus Say
Duration of larval life, 63
Early larval life, 62
Egg cases, 61
Food of adult, 68
Food of larva, 64
Hatching, 62
Hibernation, 67
Parent, 66
Hydrophilus sp.
Locomotion of larvae, 62
Mandibles of larvae, 63
Method of feeding, 66
Position of pupa in cell, 66
Pupation, 66
Hydrophilus obtusatus Say
Duration of larval life, 63
Early larval life, 62
Egg cases, 61
Food of adult, 68
Food of larva, 64
Hatching, 62
Hibernation, 67
Parent, 66
Hydrophilus sp.
Locomotion of larvae, 62
Mandibles of larvae, 63
Method of feeding, 66
Position of pupa in cell, 66
Pupation, 66
Hydrophilus obtusatus Say
Duration of larval life, 63
Early larval life, 62
Egg cases, 61
Food of adult, 68
Food of larva, 64
Hatching, 62
Hibernation, 67
Parent, 66
Supporting spines of pupa, 66

Told food of larvae, 65

Hydrous triangularis, (Say)

Antennae in respiration, 67

Cannibalism, 65, 67

Constructing pupal cell, 65, 66

Early larval life, 62

Economie importance, 47

Egg case, 60, 61

Enemies, 67

Fish food of larvae, 65

Food of Sisyphus, 45

Food of larva, 64, 65

Generations, 67

Hatching, 62

How egg case is made, 60

Instars, 63

Larval instars, 63

Life cycle, 67

Mandibles of larva, 63

Menace to fish, 68

Method of feeding, 64

Molt, 63

Position during respiration, 58

Position of pupa in cell, 66

Posture in feeding, 63

Prepupal state, 66

Process of respiration, 63

Proteids in food of adult, 68

Pupal case, 65

Respiration of larva, 63

Respiration while ovipositing, 58

Respiratory mechanism, 63

Respiratory process, 58

Spiracles, 57

Stomach contents, 65

Structure of egg case, 50, 61

Sugarers of male, 58

Supporting spines of pupa, 66

Swimming larva, 62

Transformation, 66

Hydrbia hexamand Fab.

Food and feeding, 161

Habits of adult, 160

Habits of larva, 160, 161

Life cycle, 161

Oviposition, 160

Pupation, 163

Respiration of larva, 160

Hydrbiidae

Life history, 169, 161

Hydraspini

Summary of prey, 182

Hydraspis

Factors affecting feeding, 154

Habitat, 138, 144

Mode of feeding, 165

Myrmechophila, 118, 144

Oviposition, 145

Pupation, 144

Respiration of larva, 160

Hyphroscaphinae

Means of production, 148

Myrmechophila, 144

Pupation, 145, 146

Hexapoda sigillata, 61

Hydraspis sigillata, 61

Hygrophila, 147

Hexeidae as pupal cases, 146

Feeding capacity, 154

Habitat of larvae, 144

Natural enemy, 143

Oviposition, 139

Pupation, 140, 146

Hypsometamorphosis

Drilidae, 102

Melioidae, 79, 80

Hypopyriidae

Crawling larvae, 40

Subelytral air chamber, 32

Winter under ice, 47

Hypopyris weissi

Duration of stay at surface, 33

Hibernation, 47

Life cycle, 60

Periods of hibernation, 33

Hypopyris weissi

Duration of transformation, 49

Life cycle, 60

Preoral digestion of larva, 45

Pupation, 48

Hypopyris weissi

Duration of transformation, 49

Life cycle, 60

Pupation, 48

Hypopyris weissi

Egg cases, 58

Hybribus

Climbing larvae, 41

Dermal respiration, 42

Flight, 31

Hibernation as larvae, 48

Life cycle, 40

Natural enemy, 29

Oviposition, 37

Hygrobiidae

Entomocorpus P.

Food of larva, 40

Hibernation as larva, 48

Oviposition, 38

Hymenoptera

Carabidae, 21

Cantharidae, 105

Dorcididae, 145, 144

Drilidae, 102

Ephemeridae, 62

Elytra, 57

Eustressa tabida (Leo.,)

Food of larva, 109

Imuta, X., 126, 126, 128, 130, 146, 150, 151, 159

Jacobs, W., 148

Jangue, H. R., 89

Jarykov, A. A., 157, 168
Laophobius agilia Rand
Egg cases, 59
Enemies, 67
Incubation, 62
Plant food of adult, 58
Laophobius agilis Rand
Crawling larvae, 62
Necro cases, 61
Not cannibalistic, 65
Laophobius
Cannibalism, 46
Oviposition, 37
Prey of Hydrosys, 65
Swimming larvae, 41
Laophobius maculatus (Germ.)
Duration of transformation, 49
Food of larva, 46
Natural energy, 60
Preoral digestion of larva, 45
Respiration of larva, 45
Laophobius obesus Pant.
Duration of stay at surface, 33
Periods of submersion, 35
Laophobius proximus Say
Food of larva, 66
Preoral digestion of larva, 45
Ladybeetles, 138
Lamborn, 24
Lamprophorus
Synchirites, 76
Lamprophorus angustatus Dr.
Food of adult, 60
Host relations, 78
Lamprophorus
Habitat and structure, 97, 98
Sexual uniformity, 97
Lamprophorus
Sexual dimorphism, 98
Lamprophorus tuberosus (Wlk.)
Attracton to prey, 96
Caudal filaments of female, 96
Caudal filaments of larva, 96
Color of light, 90
Copulation, 96
Dimorphism in size, 98
Fasting of larva, 95
Flashing habits, 91, 95
Food of adult, 94
Food of larva, 96
Glow of female, 91
Incubation, 97
Instars, 98, 99
Larval development, 98, 99
Life cycle, 100
Light of prepupa, 89
Luminosity of larva, 89
Manner of laying eggs, 97
Oviposition, 97
Preoral digestion, 95
Pupation, 99, 100
Quantity of food, 96
Sexual dimorphism, 96, 98, 99
Survival after mating, 97
Lampyridae
Appearance of larval light organs, 88
Biological significance of flashing, 92
Cannibalism, 94, 96
Caudal appendages of larva, 98
Circumstances attending synchronous flashing, 92
Construction of pupal cell, 99
Copulation, 96, 97
Copulation and flashing, 92
Daylight vs. flashing, 91
Defense, 96
Defensive secretion, 96, 98
Description of eggs, 97
Development of light organs, 90, 93, 94
Dimorphism vs. luminousness, 88
Duration of mating, 97
Duration of pupation, 99, 100
Elytra, 97, 98
Enemies, 95, 98
Exclamation of synchronous flashing, 92
Eyes, 97, 98
Feeding, 94, 96
Feeding of larvae, 94, 96
Feeding process, 96
Flash curves analyzed, 94
Flash patterns, 90
Flight and flashing, 90, 91
Food of adult, 94, 96
Food of larva, 96, 98
Pupa of larva, 97
Generations per year, 100
Gradations in structure, 81, 88
Gregariousness among larvae, 96
Growth of larvae, 96, 99
Habitat, 90, 91, 97, 98
Hibernation, 100
Incubation, 97
Larval life, 97, 99
Life cycle, 100
Life history, 96
Location of light organs, 89, 90
Luminous stages, 88
Nature of light, 94
Nocturnal larvae, 95
Origin of dimorphism, 97, 98
Origin of light organs, 95, 94
Origin of median light organs, 90
Oviposition, 97
Paired light organs, 89
Paralyzing the prey, 96
Periodicity of flashing, 91
Photogenesis, 68
Photogenic organs, 87, 88
Photogenie process, 94
Predation of larvae, 95, 96
Preoral digestion in larvae, 96
Process of producing light, 94
Pupation, 99, 100
Search for food, 94
Seasonal activities, 100
Seasonal occurrence, 100
Sexual dimorphism, 87, 88
Shape of light organs, 90
Snails as food, 95
Structure of larval mandible, 95
Structure of light organs, 93, 94
Synchronous flashing, 91, 92
Theories of light production, 94
Use of mandibular canals, 95
Where eggs are laid, 97
Wings, 87, 88

Lampyris noctiluca L.
Caudal filaments of larva, 98
Chemical dissolution of prey, 96
Color of light, 90
Copulation, 96, 97
Flight and flashing, 91, 93
Food of larva, 96
Incubation, 97
Life cycle, 100
Method of attacking prey, 96
Oviposition, 97
Paralyzing its prey, 96
Position of larval light organs, 88, 89
Position of light organs of adult, 90
Preoral digestion, 96
Pupation, 100
Quantity of food eaten, 95
Sexual dimorphism, 88
Significance of flashing, 95
Structure of light organs, 83, 94
Structure of mouth, 96
Survival after mating, 97
Larvae, 96

Larval life and growth
Carabidae, 22
Cantharidae, 105
Cleridae, 112
Dytiscidae, 89, 90
Hydrophilidae, 63
Lampryidae, 98, 99
Meloidae, 118
Mecoptera, 73, 94
Meliponinae, 124, 123
Silphidae, 74

Leptinaeidae
Food habits, 160

Leptopelus restrictus Fab.
Incubation, 118
Oviposition, 117
Tenacity of life, 122
Letten, 13
Lewis, G., 85
Lichtenstels, 108

Life cycle
Carabidae, 26, 27
Cantharidae, 105
Cleridae, 111
Dytiscidae, 80
Gyrinidae, 66
Hydrophilidae, 67
Lampryidae, 100
Meloidae, 134, 136
Silphidae, 74

Life History
Cantharidae, 104, 106
Cleridae, 109, 111
Lampryidae, 96, 100
Meloidae, 134, 136
Lightning beetles, 87

Light organs
Appearance on larva, 88
Development, 90, 93, 94
Embryonic development, 93, 94
Lampryidae, 89, 90
Locust, 89, 90
Origin of median, 90
Paired and unpaired, 89
Shape, 89
Structure, 93, 94

Limnebiinae
Egg cases, 59
Limnebius
Antennae in respiration, 57
Limnebius diastolor Casey
Egg case, 59

Limnophus
Food of larva, 64
Limnophus oblongus Hbst.
Food of adult, 58
Food of larvae, 64
Mandibles of larvae, 63
Posture in feeding, 63
Limnus, 121

Lepismatidae
How larvae feed, 52

Lithophleba
Predatory 133

Locomotion
Adaptations in dytiscidae, 30
Adult Gyrinidae, 61
Adult Hydrophilidae, 87
Carabidae, 12
Cleridae, 2
Dytiscidae, 2
Dytsilid larvae, 40
Flightless Carabidae, 12
Flight of Dytiscidae, 31
Gyrinid larvae, 84
Hydrophilid larvae, 62
Overcompensated larvae, 40
Undercompensated larvae, 40

Lopophorus
Defense glands, 76
Host of, 78
Instars, 83
Lambychus elongatus Gray.
Copulation, 81
Effect on ant colony, 78
Food of adult, 77
Food of larvae, 77
Generations per year, 81
Larvae embedded by ants, 83
Larval period, 83
Method of defense, 76
Oviviparous, 83
Pupal period, 83
Season of adults, 83
Season of larvae, 83
Trichomes, 77
Laphroaegus
Hemiagaulis, 12
Lapidotes
Food of adult, 94
Habitat of larvae, 97
Habitat and structure, 87, 88
Manner of laying eggs, 17
Respiration in water, 94
Sexual uniformity, 87
Lapidotes atra (Poir/)
Luminescent organ, 89
Non-luminescent adult, 89
Position of larval light organs, 88
Pupation, 99
Season of adult, 100
Lapidotes corrusus (L.)
Position of larval light organs, 88
Pupation, 99
Season of adult, 100
Lapidotes fenestralis (Melsh.)
Attacking earthworms, 96
Copulation, 96
Food of larvae, 95
Frequency of mating, 97
Incubation, 97
Larval light organs, 88
Oviposition, 97
Preoral digestion, 96
Pupation, 99
Season of adult, 100
Lapidotes puntilata (L.)
Non-luminescent adult, 89
Luminescent organ, 89
Lapidus cruciatus (L.)
Caudal filaments, 98
Color of light, 90
Food of larvae, 98
Habitat of larvae, 98
Light of pupa, 89
Position of larval light organs, 88
Preoral digestion, 96
Respiration in water, 98
Lapidus cruciatus viticoilla Kiefer
Position of light organs, 80
Lapidus corrallinus Ritz.
Food of larvae, 96
Position of larval light organs, 88
Preoral digestion, 98
Lapidus denticulatus
Significance of flashing, 91
Lapidus denticulatus Mots.
Caudal filaments, 98
Color of light, 90
Food of larvae, 96
Habitat of larvae, 97

Light of pupa, 89
Position of larval light organs, 88
Preoral digestion, 98
Respiration in water, 98
Lapiolita australis (Charp.
Caudal filaments, 98
Food of adult, 98
Incubation, 97
Larval life, 98
Life cycle, 100
Position of larval light organs, 88
Pupation, 99
Sexual dimorphism, 88
Lapiolita parvula (Fair.
Habitat of larvae, 97
Respiration in water, 97, 98
Ludermidt, E. C., 82
Lucbeck, 15
Lund, E. J., 84
Lydae
Calopteron fasciatum, 87
Duliticola paradoxus, 87
General Facts, 67
Sexual dimorphism, 87
Lygaeus aequalis (L.)
Duration of first instars, 124
Feeding experiments, 124
Lygaeus viridissimus (L.)
Activities of primary larva, 122
Feeding experiments, 124
Oviposition, 117
Lyconet, 81
Lyttia vestitia A. Cantarini, 116
Ny larvae find host, 122
Oviposition, 117
Lyttinella
Hosts, 131
Lyttinia
Hosts, 151
McDermott, F. Alex., 90, 91, 94, 97, 98
McIndoe, B. E., 78, 148
McKenzie, E. L., 144, 151, 154, 159
Maclean, Charles, 7, 8
Macrobius
Activities of later instars, 125
Cannibalism among larvae, 124
Generations, 135
Life cycle, 136
Observations by Riley, 121
Oviposition, 116
Searabaeoid larva, 120
Macrobius: immature Say
Activity of scolytoid larva, 127
Change to coarctate form, 126
Coarctate Larva, 125
Diagram of life cycle, 137
Emergence of new adult, 134
Hibernates as coarctate larva, 127
Incubation, 118
Larval cells, 125
Life cycle, 136
Non-feeding instars, 125
Oviposition, 117
Pupal cell, 156
Searabaeoid larva, 126
Search for hosts, 122
Macrobius minor (Say)
Seasonal distribution, 135
Feeding habits of larvae, 126
Fifth instar larvae, 120, 121
Fourth instar larva, 120
Duration of coarctate larva, 126
General features, 126
Fourth instar larva, 120
Habit of later instars, 126
Habits of, 116
Hazards of primary larva, 122
Hibernation, 135, 136
History of primary larva, 121
Hymenopterous hosts, 130, 131
Hypermetamorphosis, 118
Inubation, 117, 118
Importance as enemies of locusts, 133
Instar B, 118-121
Larvae as enemies of bees, 133
Larval activities, 121
Life cycle, 134-136
Male bees as carriers, 124
Non-feeding instars, 126
Origin of coarctate larva, 126
Origin of parasitism, 132, 133
Orthopterous hosts, 120-123
Oviposition, 116, 117
Parasitism, its rise, 132, 133
Phytophagous parasitism, 125
Primary larva, 118, 119
Pseudochrysaelis, 120
Pseudolarva, 120
Pseudopupa, 120
Pupation, 127, 128
Seasonal development, 134-136
Second instar larva, 119
Sixth instar larva, 121
Third instar larva, 120
Triungulin, 118, 119
Mylabris
Hosts, 131
Mylabris camptodonthes among larvae, 124
Cantabricis, 116
Hosts of, 131
Importance as enemies of bees, 131
Oviposition, 116, 117
Searabectis larva, 120
Mylabris callida Fall
Hosts of larva, 131
Mylabris erythroneura Fall
Importance as enemy of locusts, 133
Xiphidium as host, 131
Mylabris partula Thunb.
Activities of primary larva, 181, 132
Activity of later instars, 125
Coarctate larva, 126
Duration of later instars, 127
Duration of sooyloid larva, 127
Feeding of primary larva, 124
Importance as enemy of locusts, 135
Inubation, 118
Larval cells, 126
Non-feeding instars, 126
Oviposition, 117
Quantity of food, 125
Search for hosts, 122
Tenacity of life, 122
Mylabris quadripunctata L.
Inubation, 118
Mylabris schreibersi Heise
Inubation, 118
Mylabris Wagneri Chevr.
Incubation, 118
Oviposition, 117
Pupation, 134
Myrmecophiles
Brepinnes, 180
Clavigeridae, 180
Coscinellidae, 188
Histeridae, 96
Leptinidae, 180
Psephidae, 180
Psocophila incognita, 96
Psilophidae, 180
Stephanidae, 78-78
Myrmecophili
Parasitic myrmecophiles, 76
Stephanidae, 78-78
Symphiles, 76, 77
Symesthrans, 76, 77
Symesthecetes, 76-78
Symphytina incognita, 16
Mycnema
Copulation, 82
Defense glands, 76
Host relations, 78
Symesthrans, 78
Mycnema communis Bl.
Host relations, 78
Mycnema communis communis Bl.
Method of defense, 78
Mycnema communis communis Bl.
Host relations of, 78
Mycnema laticollis Bl.
Habitat, 78
Mycnema lugens Bl.
Host relations, 78
Mycnema phalerata Bl.

Myrmeoophilous, 84
Nemognatha
Food of adult, 80
Host relations, 78
Hymenoptrans, 76

Natural enemies
Carabidae, 12
Cicindelidae, 3
Coccinellidae, 147, 148
Melyridae, 59, 59
Hydrophilidae, 66, 67
Lampyridae, 96, 98
Silphidae, 74

Necrobioe
"Cocoon", 110
Economic Importance, 108
Food of larva, 108
Habitat, 107
Pupal cells, 110

Necrophorus
Food of adult, 108
Food of larva, 106

Necrophorus humator Goose
Depth of shaft, 73
Hibernation, 74
Maggots as food, 69, 70
Reproductive season, 72, 74

Nemognatha investigator Zett.
Hibernation, 71, 74
Maggots as food, 70
Reproductive season, 72

Nemognatha orbicollis Say
Maggots as food, 70

Nemognatha vespillidae Lewis
Depth of shaft, 73
Eggs in gallery, 73
Enemies of larva, 74
Hibernation, 74
Maggots as food, 69, 70
Reproductive season, 72, 74

Nemognatha vespillidae Hbst.
Burying carcass, 73
Hibernation, 74
Maggots as food, 70
Male feeds larva, 74
Quantity of food, 70
Season of reproduction, 72, 74
Needham, J. G. 93, 31
Nelochnea lacticornis Say
Food of larva, 109
Generations, 111
Oviposition, 110
Pupation, 110
Specificity of food relations, 111

Nemognatha
Host parts, 116
Nemognatha ezenecamella F.
Inubation, 118
Oviposition, 117
Nemognatha
Hosts, 131
Nevermann, 160
Newell, Wilson, 16
Newport, George, 83, 116, 117, 119, 121, 123, 134
Nickel, G. 26
Nigroius andre- Shutt Lewis
Food of larva, 85
Nigroius canalisolita Lewis
Frey, 85
Nitidulidae
Predacious species, 164
Frey, 164
Witsch, 87
Noterus
Locomotion of larva, 40
Oviposition, 37
Noterus slaviscornis Dej.
Chewing jaws of larva, 85
Duration of stay at surface, 85
Hibernation, 47
Seasonal occurrence, 85
Noterus grabrigerosus MM.
Durinat stay of larva, 65
Hibernation, 47
Notman, Howard, 76
Nudobius
Food of adults, 81
Nudobius sylvestris Casey
Duration of stay, 85
Food of adult, 81
Generations per year, 85
Hibernation, 85
Incubation, 82

Nudobius
Food of adults, 81
Nudobius sylvestris Casey
Duration of stay, 85
Food of adult, 81
Generations per year, 85
Hibernation, 85
Incubation, 82
Pelecium
Parasitism, 24

Peleciu m sulcatum Guer.
Parasitism, 24

Pupation, 26

Pelechus tarsus Host. (see Cyclorhina)
Paratriata
Termitiphiles, 78

Pharini
Summary of prey, 163

Phausis delarouzei Duv.
Caudal appendages of larva, 90

Food of adult, 94
Food of larva, 96
Incubation, 97
Life cycle, 100
Light organs, 99
Oviposition, 97
Pupation, 98
Sexual dimorphism, 88

Phausis splendidula L.
Caudal filaments of larva, 98

Instars, 98
Life cycle, 100
Position of light organs, 99
Preoral digestion, 95
Sexual dimorphism, 88

Phengodes
Food Habit, 87

Phengodes fasciatus Lec.
Copulation, 87
Life cycle, 87
Luminosity, 87
Oviposition, 87

Phengodes plumosus (Oliv.)
Luminosity, 87
Phengodidae
Form of mandibles, 87
Luminosity, 87
Predators, 87

Phillips, W. J., 16, 163

Philonthus
Food of adults, 81
How larvae feed, 82

Philonthus semispinosus L.
Food of adult, 81

Philonthus promusculus Gr.
Food of larva, 61
Larval period, 83
Prepupal and pupal period, 83
Pupal position, 88

Philonthus flavimarginatus Gr.
Food of larva, 61
Prepupal and pupal period, 83
Pupal position, 88

Philonthus degusclus Gr.
Prepupal and pupal period, 83

Philonthus flavimarginatus Gr.
Food of adult, 81

Philonthus longicornis Steph.
Food of larva, 61
Prepupal and pupal period, 83
Pupal position, 88
Philonthus nitidus W.
Food of larva, 61

Philonthus sp.
Food of adult, 80
Food of larva, 61

Philonthus splendidulus Gr.
Prepupal and pupal period, 83

Pholasia
Flightless, 115

Phosphena
Sexual dimorphism, 88

Phosphena hamiltonus Guenee
Courtship, 98
Life cycle, 100
Sexual dimorphism, 88

Phosphena narvaizae Lea.
Air swallowing, 71
Copulation, 71
Dormancy in July, 75
Duration of cycle, 71
Duration of instars, 71
Egg hatching, 71
Egg laying season, 75
Feeding habits, 88
Feeding rate, 89
Food of adult, 88
Food of larva, 70
Hibernation, 74
How it overcomes snails, 68, 69
How larvae feed, 70
Incubation, 71
Mode of overcoming prey, 70
Oviposition, 71
Predators, 68
Prepupal period, 71
Process of hatching, 71
Structure of jaws, 68

Phosphena subtrudata Leach
Feeding, 68
Food of adult, 68
How it attacks snails, 68
Structure of jaws, 63

Photinus
Copulation, 96, 97
Flash pattern, 97
Food of adult, 94
Food of larva, 96
Habitat of larva, 97
Manner of laying eggs, 97
Oviposition, 97
Predators, 88
Sexual dimorphism, 88

Photinae
Feeding, 68
Food of adult, 68
How it attacks snails, 68

Photinus angulatus Say
Flash pattern, 90

Photinus australis Lec.
Copulation, 97
Flash pattern, 90
Locomotion, 89
Position of light organs, 90
Sexual dimorphism, 88

Photinus consanguineus Lec.
Flash pattern, 90

Photinus marginatus Lec.
Flash pattern, 90
Flight and flashing, 93
Oviposition, 97
Position of light organs, 90
Season of adult, 100
Sexual dimorphism, 88
Significance of flashing, 93

Photinus marginatus Lec.
Copulation, 97
Flash pattern, 90
Flight and flashing, 93
Position of light organs, 90
Prey of Photuris, 94, 95

212
Pupation, 105
Season of adult life, 105
Psocidius unicolor Say
Air swallowing, 21
Cannibalism, 22
Oviposition, 19
Psocidius lucublandus Say
Food of adult, 15
Polyphaga
Form of third larva, 80
Polyphemus piger and P. pygmaeus L., 21
Cannibalism, 22
Oviposition, 19
Poecilus lucublandus Say
Food of adult, 15
Polyphaga
Form of third larva, 80
Polyphemus piger Say
Hibernation, 82
Hosts, 79
Parasite, 79
Polypus, 1
Polyphemus piger Say
Form of third larva, 80
Polyphemus piger Say
Hibernation, 82
Hosts, 79
Parasite, 79
Popenoe, G. H., 106
Portohinsky, I. A., 117, 118, 131, 133
Portier, P., 41, 58, 59, 61
Poulton, E. B., 4, 163
Predatory diving beetles, 28
Predation, 1
Predation among Elateridae, 103
Predatory groups, 1
Preoral digestion
Coccinellidae, 155
Dytiscidae larvae, 43, 44, 45
Gyrinidae larvae, 44
Hydrophilidae larvae, 64
In adult Carabidae, 14
Lampyridae, 56
Oligota urticae, 82
Priest of Coccinellidae, 118-119
Primary larvae of Melolonthinae, 118, 119
Propylea japonica Tt.
Duration of larvae, 145
Feeding capacity, 152, 154
Immature, 142
Natural enemy of, 148
Pupation, 146
Propylea quatuordecimpunctata Reitt.
Mode of feeding, 156
Protection or defense
Adult Carabidae, 15
Adult Oryctes, 61
Coccinellidae, 148, 149
Dytiscidae, 28
Gases and liquids, 13
Hydrophilidae, 96, 97
Lampyridae, 96, 97
Milky secretion, 90, 91
Protective resemblance
Coccinellidae, 3
Pelecaphoda, 160
Pseudogyme
Origin of, 78
Pseudolama di Melolontha, 120
Pseudonomophaga japonica Kuriki
Duration of instars, 146
Instars, 146
Life cycle, 149
Pupation, 146
Pylilaborini
Pragivorus, 128
Psocidium
Food of newly hatched larva, 22
Psocidius lucublandus Say
How adult feeds, 15
Psocidius multiventralis Dej.
Oviposition, 19
Metamorphosis, 19
Number of eggs, 20
Psocidius Sayi Bruull
How adult feeds, 15
Pokorný, K. M., 69, 70, 71, 72, 73, 75, 81
Pupation
Carabidae, 26, 26
Cicindelidae, 104, 106
Coccinellidae, 9, 19
Cleridae, 110
Coccinellidae, 148, 149, 146
Dytiscidae, 49, 49, 50
Oryctes, 86
Hydrophilidae, 66
Lampyridae, 99, 100
Prochnophora
Phyllocladinae, 2
Pyrrhotoma
Cantharidae, 104, 105
Cleridae, 110
Coccinellidae, 143, 145, 146
Dytiscidae, 46, 49, 50
Gyrinidae, 55
Hydrophilidae, 66
Lampyridae, 99, 100
Quayle, H. J., 01, 02, 155
Quadus
Syncrothrips, 76
Quadus urv'rs Dr.
Host relations, 78
Rabe, F. von, 82, 83
Randshofer, K. A., 112
Rea, Phil., 91, 92, 116, 117, 122
Reamur, 121
Rental ampulla
Dytiscidae, 30, 31, 34, 39
Hydrophilidae, 67
Regeneration
Dytiscid larvae, 40
Regimbart, 54
Reichenberger, August, 84
Reiseck, Georg, 7
Rengel, C., 58, 62, 64, 65, 66
Reptillum
Adult Dytiscidae, 33, 32, 33
Adult Oryctes, 62
Adult Hydrophilidae, 57
Dytiscid larvae, 41, 42, 43
Gyrinidae larvae, 54

In water, 31, 32, 52

Larvae of Hydrophilidae, 63

Larvae of Lampyridae, 97, 98

Modifications in Gyrinidae, 52

Tracheal gills, 54

Food, 105

Habitats, 105

Food, 103

Habitats, 103

Rhagonycha

Food of larva, 104

Generations, 105

Hibernation, 105

Incubation, 105

Oviposition, 105

Pro-larva, 105

Season of adult, 105

Rhantus

Climbing larvae, 41

Food of larvae, 45

Hibernation, 46

Life cycle, 50

Oviposition, 37

Rhipidius

Rhipidius boissyi Ab.

Rost, 112

Rhipiphoridae

Carriers of larvae, 113

Development, 114, 115

Hosts, 112

Habits, 112

Host, 112

Habits of larva, 112, 113

Mode of feeding, 113

Natural enemy of, 113

Parasite of social wasp, 113

Seasonal development, 114

Structure of larva, 113

Rhipiphorus

Host, 112

Rhipiphorus paradoxus L.

Feeding of larvae, 113

Habits of larva, 115

Hosts, 112

Instars, 113

Life cycle, 114

Metamorphosis, 113

Parasite of social wasp, 113

Seasonal development, 114

Structure of larva, 113

Rhipiphorus solidae (Pierce)

Carriers of larvae, 112

Host, 113

Larval life, 113

Life cycle, 114

Mortality among larvae, 115

Parasite, 112

Rhipiphorus

Hosts, 112

Rhipiphorus sordidus B.

Feeding of larvae, 113

Habits of larva, 113, 115

Hosts, 112

Instars, 113

Life cycle, 114

Metamorphosis, 113

Parasite of social wasp, 113

Seasonal development, 114

Structure of larva, 113

Rhipiphorus sordidus

Carriers of larvae, 112

Host, 113

Larval life, 112

Life cycle, 114

Seasonal development, 114

Rhipiphorus sordidus

Host, 112

Life cycle, 114

Oviposition, 112

Seasonal development, 114

Structure of larva, 112

Rhipiphorus

Summary of prey, 153

Rhizophorini

Summary of prey, 153

Rhizophorini

Attachment mechanism, 146

Habitat of larva, 144

Mode of feeding, 146

Natural enemy of, 146

Position of eggs, 142

Rhyzyphorina, 1

Rhyzobius cardinale Muls.

Emerges as pupal cases, 146

Factors affecting feeding, 134, 135

Factors influencing oviposition, 142

Feeding capacity, 152, 154

Feeding vs. season, 153

Generations, 159

Ingestion, 142

Length of adult life, 147

Life cycle, 150

Mating, 150

Oviposition, 129, 142

Preoviposition period, 139

Temperature vs. adult life, 147

Temperature vs. growth, 145

Rhyzodes paradoxus L.

Attachment mechanism, 146

Gregariousness, 156

Mode of feeding, 155, 156

Puparium, 146

Roeper, W., 116, 122

Rondelet, 28

Rosenberg, E., 25

Roush, J., 103

Rove beetles, 76

Rusinsky, P. A., 92

Ruschkamp, F., 101, 102, 103, 104, 164

Salt, George, 24

Saprinus

Habitat, 85

Saprinus sexdens F.

Food of adult, 84

Saprinus ridibundus Pk.

Food of adult, 84

Saprinus patruellus Lec.

Food of adult, 84

Saprinus solidaginis (Pierce)

Carriers of larvae, 113

Food of adult, 15

Saprinus guttulatus Leo.

Habitat, 85

Saprinus nauticus Payk.

Food of adult, 84

Scarabaeoid larva of Meloidae, 120

Sarcites subterraneus Fabr.

Food of adult, 120

Schilder, F. A., 15, 146, 162

Schilder, M. 10, 146, 162

Schmitz, 103

Schmitt, 101

Schmitt, E. A., 12, 85, 106, 108, 109, 162, 164

Scolytid larva of Meloidae, 121

Scott, Hugh, 79, 108

Seymerrini

Summary of prey, 152

Seymernini

Summary of prey, 152

Seymernini

Habitat, 138, 144

Myrmecomphus, 138, 144

Oviposition, 142

Protective waxy cover, 149

Seymernini castaneum Muls.

Mode of feeding, 125

Seymernini formicarius Muls.

Habitat of larva, 144

Myrmecomphus, 144

Myrmecomphus, 144

Seymernini calcuttensis Lee.
<table>
<thead>
<tr>
<th>Diagram of life cycle, 137</th>
<th>Duration of first instar, 125</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duration of larval life, 127</td>
<td>Knowles, 120</td>
</tr>
<tr>
<td>Vastbre limits choice of hosts, 132</td>
<td>Feeding experiments, 124</td>
</tr>
<tr>
<td>Fifth instar larva, 125</td>
<td>Hibernation, 126</td>
</tr>
<tr>
<td>How larvae find hosts, 125, 124</td>
<td>Incubation, 126</td>
</tr>
<tr>
<td>Larva spins down, 126</td>
<td>Larva vs. egg of host, 124</td>
</tr>
<tr>
<td>Life cycle, 135, 136</td>
<td>Male bees as carriers, 124</td>
</tr>
<tr>
<td>Male bees as carriers, 124</td>
<td>Non-feeding instars, 125</td>
</tr>
<tr>
<td>Oviposition, 117</td>
<td>Pupal covering, 131</td>
</tr>
<tr>
<td>Pupal covering, 134</td>
<td>Second instar larva, 119</td>
</tr>
<tr>
<td>Sixth instar larva, 121</td>
<td>Tenacity or life, 122</td>
</tr>
<tr>
<td>Third and fourth larvae, 121</td>
<td>Tenacity or life, 122</td>
</tr>
<tr>
<td>Trogodendron fascigulatum Schreib.</td>
<td>Triungulin, 118</td>
</tr>
<tr>
<td>Food of adult, 108</td>
<td>Tropisema, 2, 3</td>
</tr>
<tr>
<td>Tropisternus</td>
<td>Tropisema, 2, 3</td>
</tr>
<tr>
<td>Cannibalism, 64</td>
<td>early larval life, 62</td>
</tr>
<tr>
<td>egg cases, 59, 61</td>
<td>Anemies, 67</td>
</tr>
<tr>
<td>Food of adult, 58</td>
<td>How egg case is made, 60</td>
</tr>
<tr>
<td>How egg case is made, 60</td>
<td>Heart of egg case, 61</td>
</tr>
<tr>
<td>Plant food of adult, 56</td>
<td>Pupation, 66</td>
</tr>
<tr>
<td>Pupation, 66</td>
<td>Swimmers, 57</td>
</tr>
<tr>
<td>Tropisternus planae (Ehret.)</td>
<td>Urban, C., 162</td>
</tr>
<tr>
<td>Cannibalism, 62</td>
<td>Valery-Mayet, M., 116, 126</td>
</tr>
<tr>
<td>Duration of pupal stage, 66</td>
<td>van der Heyde, H. C., 28, 32, 33</td>
</tr>
<tr>
<td>Food of larvae, 64</td>
<td>Veth, K., 163</td>
</tr>
<tr>
<td>Hibernation, 67</td>
<td>Velleius dilatatus Fabr.</td>
</tr>
<tr>
<td>Pupal cell, 65</td>
<td>Copulation, 62, 63</td>
</tr>
<tr>
<td>Pupation, 66</td>
<td>Hibernation, 63</td>
</tr>
<tr>
<td>Swimming larva, 62</td>
<td>Sexual activity, 85</td>
</tr>
<tr>
<td>Trogisternus lateralis (Fabr.)</td>
<td>Verruca gremata M.</td>
</tr>
<tr>
<td>Cannibalism, 65, 66</td>
<td>Duration of larva, 145</td>
</tr>
<tr>
<td>Feeding, 63</td>
<td>Incubation, 144</td>
</tr>
<tr>
<td>Food of larvae, 64</td>
<td>Life cycle, 159</td>
</tr>
<tr>
<td>How egg case is made, 60</td>
<td>Verruca linearis F.</td>
</tr>
<tr>
<td>Incubation, 62</td>
<td>Duration of larva, 145</td>
</tr>
<tr>
<td>Mode of feeding, 64</td>
<td>Incubation, 144</td>
</tr>
<tr>
<td>Posture in feeding, 65</td>
<td>Life cycle, 159</td>
</tr>
<tr>
<td>Pupation, 66</td>
<td>Oviposition, 149</td>
</tr>
<tr>
<td>Respiration during prophase, 66</td>
<td>Verbeek, F. A. T. M., 116, 118, 120, 122, 125, 133</td>
</tr>
<tr>
<td>Respiration of larva, 65</td>
<td>Verhoeff, R. W., 13, 14, 20, 21, 22, 76, 81, 98, 104, 106</td>
</tr>
<tr>
<td>Spinning egg case, 60</td>
<td>Vogel, R., 95, 96, 98, 100</td>
</tr>
<tr>
<td>Swimming larva, 62</td>
<td>Wulst, A., 6</td>
</tr>
<tr>
<td>Trogisternus planae (Ehret.)</td>
<td>Trogisternus planae (Ehret.)</td>
</tr>
<tr>
<td>Cannibalism, 65, 66</td>
<td>Cannibalism, 65, 66</td>
</tr>
<tr>
<td>Food of larvae, 64</td>
<td>Food of larvae, 64</td>
</tr>
<tr>
<td>Gregarious larvae, 62</td>
<td>Gregarious larvae, 62</td>
</tr>
<tr>
<td>Transformation, 66</td>
<td>Transformation, 66</td>
</tr>
<tr>
<td>Tylotus tribulatus Mars.</td>
<td>Art host, 64</td>
</tr>
<tr>
<td>Art host, 64</td>
<td>Myrmosphillus, 84</td>
</tr>
<tr>
<td>Myrmosphillus, 84</td>
<td>Trichomes, 84</td>
</tr>
<tr>
<td>Xantholinus amylonum Say</td>
<td>Xantholinus bracteatus Beer</td>
</tr>
<tr>
<td>Food of adult, 80</td>
<td>Host relations, 79</td>
</tr>
<tr>
<td>Xantholinus semileatus Say</td>
<td>Food of larvae, 80</td>
</tr>
<tr>
<td>Xantholinus hamatus Say</td>
<td>Food of adult, 80</td>
</tr>
<tr>
<td>Xanthopyga symphoniae Ehr.</td>
<td>Food of larvae, 80</td>
</tr>
<tr>
<td>Xenoecus</td>
<td></td>
</tr>
</tbody>
</table>
Host relation, 78
Hosts of, 79
Xenogaster, 78
Xenogaster Termitophilus, 78
Xenopelta Termitophilus, 78
Xenopygus analis Kr.
Food habit of larva, 82
Xylophorus quadripunctatus L.
Air swallowing, 71
Conduct in old age, 75
Copulation, 71
Death rite, 71
Defense of larva, 71
Duration of cycle, 71
Duration of instars, 71
Food of adult, 69
Inhibitation, 76
Incubation, 71
Oviposition, 71, 74
Predacious, 68
Pupal period, 71

Yuasa, E., 287

Zabrus tequestre Goze

Army of, 13
Zarapkin, G. P., 158
Zonabris picta (Goeze) Luminous stages, 67
Zonabris rivesi Horn Luminosity, 87
Zonabris Canibalism among larvae, 134
Zonabris strausse (Chevre.) Incubation, 118
Oviposition, 117
Zonabris subaextimulata Mars. Incubation, 118
Oviposition, 117
Tenacity of life, 122
Zonitis Mating, 116
Zonitis immonapla G1. Incubation, 118
Oviposition, 117
Zonitis pallida Pabr. Activities of later larvae, 125
Feeding of later larvae, 126
How larvae reach host, 132
Life cycle, 126
Zonitis puehita P. Incubation, 118
Oviposition, 117
Zonitis puehita analis Ab. de Per. Feeding experiments, 124
Incubation, 118
Oviposition, 117

220