A CONTRIBUTION TO THE BIOLOGY OF MAY-FLIES.*

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I. INTRODUCTION.

This is a study of the habits and structure of May-flies. It describes the situations in which they live and some of the adjustments which they have made to the conditions in them. The two problems which face every organism are those of maintaining its own life and continuing its race. Its youth is devoted entirely to satisfying its individual needs for food and safety; its adult life is devoted to the race, but the necessities of the individual are still satisfied though they may be secured in an entirely different way. The immature life of May-flies is aquatic, and to it all adjustments concerned with food or safety are exclusively confined. The mature or adult life is aerial. It is solely devoted to reproduction. There is no provision for food or for other means of lengthening its life. It gives an opportunity for studying ways of getting a living which have been completely isolated from ways of reproducing. The study which follows has been divided into five sections.

1. The historical sketch, in which the more important papers which have dealt with May-fly biology are briefly discussed.

2. The life cycle which consists of a brief statement of the characteristics of the three stages of life.

3. The evolution of the nymphs in which progress from a generalized to a specialized condition is shown in changes of shape and function of gills, mouthparts, and legs.

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*Contribution from the Limnological Laboratory of Cornell University. This work was done under the direction of Professor James G. Needham, of whose kindly criticism and stimulating interest I wish to express my appreciation. I wish also to thank Miss Anna C. Stryke for her many helpful suggestions regarding the drawings and the photographs from which some of the drawings have been taken.

4. The evolution of the adult in which specialization is shown by changes of function and developments for the furtherance of reproduction.
5. Adjustments for aquatic situations shown in the structures of the eggs.
6. A Bibliography of biological, morphological, and the more important systematic works dealing with this group.

II. HISTORICAL.

In the following historical sketch I have tried to select the more important papers of biological significance. In many cases, however, systematic, morphological, and biological work have been so closely related that such a separation has been impossible.

Swammerdam. 1661. The foundation study of the biology of May-flies was made by Johann Swammerdam, at Culenburg, on the Rhine, in 1661. As a field naturalist, he learned the most important facts concerning the life of Ephemerus, (probably Palingenia longicauda Oliv.). As an anatomist he dissected and studied its internal and external structure with great care. He described the emergence of the nymph, the sub-imago stage in males, and the final or imago stage in which he believed that the eggs and the sperm were deposited separately in the water. He concluded that no food was taken during aerial life, and that copulation did not occur. He examined the eggs and tested their power of dispersal by letting them fall into the water from the end of a knife. His work is a remarkably truthful and interesting record. Later works have added and corrected, but none have contributed better biology.

Reaumur. 1742. In Memoires des Insectes, 1742, Reaumur reviewed much which had already been told by Swammerdam, and illustrated more profusely the life history of a burrowing May-fly, probably also Palingenia. Some of Reaumur's observations were made upon nocturnal species. After he had noticed them swarming about a light near the river bank, he placed a tub of water in his own garden. By holding a light above this, in the evening, he was able to gather great numbers of May-flies and to watch their transformation from the sub-imago to the imago stage, and to see them lay their eggs in the water. He counted the eggs which he found protruding from the abdomens and determined the average number to be 750 to 800 for each female. He disagreed with Swammerdam regarding the fertilization of the eggs, and stated that the males and females probably did mate, and that the forceps of the male were evidently for the purpose of seizing the female.

DeGeer. 1748. In 1748 DeGeer saw the mating* actually take place. Two years later he again saw the mating flight and the mating, and this time was able to give more facts concerning it. The swarm consisted mostly of males. In mating the male was beneath the female with his abdomen recurved upward so that its tip rested against the two openings of the oviducts, between the eighth and ninth segments. Copulation lasted but an instant, and De Geer was not able to observe the process in detail. He described several different varieties of May-flies, distinguishing them by descriptive color names. The double eyes of a diurnal May-fly (possibly a Leptophlebia) were mentioned, the larger eyes being named the turbinate eyes.†

Geoffroy. 1764. Geoffroy, 1764, saw great swarms of May-flies near Paris and noted that there they were called "manne de poissons," because great numbers fell down into the streams to the fishes. He accurately figured and described as a Crustacean,‡ the May-fly, later determined by Vayssiere as Prosopistoma, which he found in the riffles of a stream near Paris.

Newman, 1836. In discussing the transformations of insects, Newman, 1836, wrote of May-flies as follows: "Here then we have the strange fact of an insect's flying before it reaches the imago; that is, flying in the penultimate state. It thus appears that although until the final ecdysis, no insect arrives at perfection; yet before that period, even in the state immediately preceding, it may feed, run and even fly; or it may swim, crawl, barely move, or be without motion."

Bowerbank, 1833. Bowerbank studied the circulation of the blood in young nymphs of Ephemera marginata. He carefully examined the dorsal vessel with its valves and described the circulation of the blood. He was the first to see

*DeGeer, 1748, T. II, p. 644.
†DeGeer, 1748, T. II, p. 651.
‡Geoffroy, Tom. II, p. 658. "Le Binnocle a queue en plumet."

in the setæ the two currents of blood which have since been carefully studied.

Westwood, 1840. In 1840 Westwood discussed the classification of May-flies, following the discussion with some biological facts mostly gathered from previous writers.

Burmeister, 1848. Burmeister made the first real contribution to May-fly embryology. While sitting in his room one evening, many females of Palingenia horaria flew through the open window and began depositing eggs upon his table. Burmeister described these eggs and figured them. He placed some of them in water on July 22 and on August 2 he freed an embryo from the shell. He studied this stage carefully and figured it showing the mouth-parts, legs and gills.

Leuckart, 1858. Ten years later Leuckart carefully described the eggs of three May-flies. This work was followed by

Grenacher, 1868. Grenacher's short, but important paper, "Beitrage zu Kenntniss des Eies der Ephemeriden." He studied eggs similar to those cited by Leuckart and showed that the polar knobs described by him were to be found in various stages within the ovary. So far as known, Leuckart and Grenacher have been the only authors who have made any careful study of these egg structures in May-flies.

Pictet, 1843. The first general study of this group was the monograph in the "Historie Naturelles des Insectes Neuropteres" by Pictet. He classified preceding biological and systematic studies and gave a history of each, reviewing all of the most important contributions from Aristotle to 1840. He described the habits of his four classes of nymphs, fossorial, flattened, swimming and crawling. He discussed the emergence of the nymph and features of the sub-imago and imago stages, but he gave many details less satisfactorily than Swammerdam or Geoffroy.

Dufour, 1849. In 1849 Leon Dufour published a memoire on the different kinds of respiration in insects. In this he classified May-flies with insects breathing by means of external organs. This study was followed by the similar ones of Mueller, 1851, and Milne Edwards, 1857.

Lubbock, 1863–6. After the first contribution to May-fly embryology by Burmeister in 1848, no further investigations were made until 1863–6, when Sir John Lubbock published two papers, "On the Development of Chloeon dimidiatum."

In these two studies he followed individuals through twenty-three successive moults, tracing them to the adult stage. He did not, however, begin his observations at the actual time of hatching as Burmeister had done.

Hagen, 1849–1890. The foundation for the study of May-flies in North America was made largely through the inspiration and contributions of Prof. Hermann Hagen. Although the greater part of his work was systematic, the notes which he sent to Eaton in 1873 show that he made valuable additions to the knowledge of their biology. Hagen identified the nymph of Baetisca which B. D. Walsh described in 1864.

Walsh, 1864. Walsh concluded his paper on Baetisca with a description of the swimming habits of the nymphs which he kept for some time under observation.

Eaton, 1870. About the end of 1870, Rev. A. E. Eaton submitted to the Entomological Society of London the most important work done upon the group since Pictet's monograph. In 1883-86, the completed work was published in the Transactions of the Linnean Society.

Eaton, 1883. In this work the world fauna was reclassified and a great number of forms were described and figured with such accuracy that it at once became and has remained the most important work upon the order. The introduction contained a general account of the biology which included several of Dr. Hagen's* field notes.

N. Joly, 1876. Joly, '76, studied the embryology of Palingenia virgo. He kept eggs in dishes of water and recorded the structures of the developing embryo on the 5th and 6th day. This work was followed by another by N. and E. Joly, which dealt mostly with the structure of the systems in the nymphal and imago stages of certain species.

Vayssiere, 1882. Vayssiere published the first extensive study of the nymphs. This paper was written almost entirely from a morphological view point, but it contains many referances to short biological papers.

The papers of Zimmerman, '79, Eaton, Hagen, Joly, Palmer, '83, Creutzburg, '85, and others were mainly morphological.

*1873. Hagen Notes on the Ephemeridæ. Compiled by Eaton.

Fritze, 1889. Fritze, '89, studied the structure of the alimentary canal. He described and figured a muscular apparatus in the oesophagus, and discussed its changes of function in the adult.

Heymons, 1896. In a paper upon the embryology of Ephemera vulgata, Heymons, '96, stated that the eggs hatched eleven days after they were laid. He traced the development of the nymphs up to the age of four days. He discussed the ancestry of May-flies, and concluded that their life was originally entirely aerial and that the closed tracheal system of the nymphs is an accomodation to aquatic life.

Causard, 1896. Causard noted the birth of living young in Ephemera vivipare and briefly described the development of the nymphs.

Hubner, 1902. Hubner, '02, tested the regenerative powers of nymphs of Cloeon dipterum. Certain nymphs regenerated the last abdominal segment with its appendages. The alimentary canal became functional, and the insect lived for one month.

Tumpel, Needham and Betten, 1901. In the same year two general papers were published. "Die Geradflugler Mitteleuropas" by Tumpel and several complete life histories in "Aquatic Insects of the Adirondacks" by Needham and Betten.

A similar but much more extensive work by Needham followed in 1905 and 1908. In the introduction to this study May-fly nymphs were described as "perhaps the dominant insect herbivores of fresh water." Their herbivorous diet and their importance in the economy of aquatic life were for the first time emphasized.

Sternfeld, '07. Sternfeld, '07, worked upon the atrophy of the mouth-parts and the changes in function of the alimentary canal. He reviewed Fritze's paper and considered the biological significance of the structures much more fully. He concluded that the alimentary canal in imago May-flies is by no means rudimentary and that a muscular apparatus, which is under voluntary control, regulates the supply of air in it. The decrease of specific gravity caused by this "swimming bladder" aids the insects in the mating flight and hence indirectly influences their multiplication.

Drenkelfort, '10. Drenkelfort wrote a general account of the biology of Siphlurus lacustris.

Wodsedalek, '11. Wodsedalek experimented upon nymphs of Heptagenia interpunctata Say and found that they were repelled by light, but that these reactions could be reversed by the addition of certain chemicals to the water.

III. LIFE CYCLE.

The life cycle of May-flies includes the embryonic period within the egg, and the active life which is divided into nymphal, sub-imago and imago stages.

Almost the earliest studies of the embryos were made by Burmeister, '48, who described those of Palingenia horaria twelve days after laying. He noted the rudiments of the mouth parts and legs. According to Joly, '76, embryos of Palingenia virgo take about two months for development. Heymons, '96, found that eggs of Ephemera vulgata kept in a temperature of 20-25 C would hatch in ten to eleven days. At hatching they measured 1 mm. with setæ inclusive. The antennæ and setæ were respectively five and four segmented. External gills were not yet present, but all of the systems were complete except the reproductive. On segments two to seven of the abdomen was a series of lateral hypodermal thickenings. Heymons believed that the gills which arose four days later were outpushings of these thickenings. He held the gills to be lateral projections homologous with the legs and not of dorsal origin as often considered. From the structures in the embryo he concluded that a homology between gills and wings is unfounded.

By nymphal stage is meant the period of life between hatching and emergence from the water. The exact limits of its duration are unknown. Lubbock, '66, followed a Chloeon dimidiatum through twenty-three moults to the imago stage, but his data does not begin at time of hatching. Hexagenia variabilis lays its eggs in April and May, but I have found large and small nymphs abundant in the same locality in the March preceding, so that they must require at least two years to mature. Nymphs of Callibaetis fluctuans mature in about six weeks in mid-summer. As already noted, May-flies quit the egg in a fairly advanced state of development. They are very active and nearly all are voracious herbivores. The nymphal period is one of extreme competition and during it the nymph must find safety, and get food sufficient for its entire life. With the exception of the Diptera, May-flies are the dominant aquatic insect herbivores. They have attained this position by utilization of a vegetable diet and by remarkable adjustments to particular situations. The population about them is divided into two classes, competitors and enemies. Their competitors are mostly insects, which, like the May-flies, live upon herbivorous or nearly herbivorous diet; among them are the larvæ of Caddis-flies (except the Hydrosychidæ), Crane-flies and most of the smaller Diptera. Their enemies are wholly or in part carnivórous. Important among them are the nymphs of Dragon-flies, Stone-flies, many beetles and the Hemiptera and Neuroptera. The adolescence of the nymph is evidenced internally by the development of the reproductive organs, and externally by the growth of rudimentary wings. This stage is terminated by a gradual change in organs of locomotion, respiration and digestion and by the final casting off of the nymphal skin.

The first winged or aerial stage is known as the sub-imago. The general form of body differs little from that of the actual adult insect. The wings are fully expanded and direct respiration through open spiracles is established. All surfaces are dull and in most cases the wings have a prominent marginal fringe of hairs. A few May-flies (females of Palingenia and Campsurus, Eaton '83) never lose the sub-imago skin, but in nearly all it is shed. The duration of the sub-imago stage varies from a few minutes in the most ephemereal species to several days. Needham,* '08, has given this account of Caenis diminuta. "It is the most ephemeral of all Ephemera. It emerges from the water at nightfall, leaving its nymphal skin floating on the surface, and, alighting on the first support that offers, sheds its skin again, and the sub-imago stage is ended."

*N. Y. State Bull. 124, p. 178.

The following data upon some of the longer lived species shows its average length:

Heptagenia interpunctata	♂	2 days	=	length	of	sub-imago	life
" "	♂	1 "	=	"		"	"
" "	♀	1 "	=	"		"	"
" "	♀	1 "	=	"		"	"
Siphlurus alternatus	♀	2 "	=	"		"	"
" "	♂	2 "	=	"		"	"
Iron fragilis	♂	2 "	=	"		"	"
" "	♂ ♀	2 "	=	"		"	"
" "	♂ ♀	2 "	=	"		"	"

Sub-imagos are very inactive and in nature spend the day-time resting in the shade, often upon the under side of leaves near the stream from whence they emerged. In captivity they are just as inactive, but if confined in very narrow quarters, they almost invariably fail to transform successfully. During this stage the legs, especially the front ones, and setæ are elongated and the reproductive system matures.

That this sub-imago stage is peculiar to May-flies is a well known fact. Little light, however, has been thrown upon its actual significance and analogy to the stages of other orders. Boas, '99, suggested that the sub-imago stage once had a wide distribution among Orthoptera which have now died out; that this corresponds to the pupal stage of holometabolous insects; and that the Ephemeridæ show a transition toward perfect metamorphosis. He believed that there was nothing in the form of Neuropterous pupæ which contradicts the theory that they have been developed out of such sub-imago stage.

The single molt of aerial life is followed by the mature or imago stage. At the beginning of this stage the eyes, legs and setæ attain full size. All surfaces of the body are shiny and the wings are transparent. The duration of this, like the sub-imago stage, varies greatly with the species. It varies also with the individual. Males which have mated are said to live a much shorter time than those kept in captivity.

Imagos are usually active at special times. Those of diurnal species fly freely at all hours of the day, but oftenest are seen in mating flights during the late afternoon. The nocturnal

May-flies must swarm in like manner at night is testified by the great numbers often caught in webs in the early morning. The important functions of this stage are the fertilization and laying of the eggs.

IV. MODIFICATIONS OF STRUCTURES OF THE NYMPH.

Nymphs of Ephemerinæ and Heptageninæ (Needham) live fairly within the limits of two ecological situations. The Ephemerinæ inhabit mud or muddy water exclusively. Most of the Heptageninæ live in riffles of streams or upon the wave washed shores of lakes. The Bætinæ inhabit gentle currents or open waters and intermingle with the mud and cascade dwellers as well. They have become adjusted to very different situations and they show a wide range of specialization.

All of the Ephemerinæ which have been found here live in the same situation and are very similar in their habit of life. Ephemera and Hexagenia are true burrowers in the mud; Polymitarcys occasionally adopts the digging habit and Potamanthus crawls upon silt covered stones and muddy bottoms in the same locality.

The members of the Heptageninæ are also very homogeneous habit. They live in running water, clinging or moving about upon the under sides of stones. Iron and Epeorus dwell in the swiftest water of the current, in riffles and falls; Ecdyurus and Heptagenia live in the gentle currents along the borders of the stream and sometimes beneath the stones in quiet pools.

The Baetinæ dwell in a variety of situations. Siphlurus and Callibaetis clamber upon the aquatic plants or dart about on the alga covered bottoms of still pools and inlets, while Ameletus more often frequents moving waters and nymphs of Blasturus hide among decayed leaves in ponds and brooks. Leptophlebia and Habrophlebia cling closely to the surface of stones, usually upon the under side and often in fairly rapid water. Most members of the genus Ephemerella have a similar habit, but there is a wide divergence among the species of this genus. Two genera, Baetis and Chirotonetes, are dwellers in water falls, and the latter has become remarkably well adjusted to its habitat. Tricorythus and Caenis are adjusted to life in mud and sand and show structures especially well fitted to their surroundings. These two extremes of specialization are examples which show the variety of adjustments within this family. As later discussions will point out, they also show what diverse structures may fit an organism equally well for life in the same of similar situations.

Since the outside of an animal is the first to be influenced by environment, the most important adjustments must be looked for in external structures. In this study only the three most important sets will be considered; those which have to do with respiration, food and motion.

SHAPE OF BODY IN THREE SUBFAMILIES OF MAY-FLIES.

Before attempting to trace the adaption in the three systems just named, it is necessary to briefly describe the general shape of the nymphs in the three subfamilies.

The bodies of the Ephemerinæ are elongate, more or less cylindrical and tapering at either end. Those of Ephemera (Pl. XLIV, Fig. 8) and Hexagenia are almost perfectly cylindrical. The heads are wedge-shaped with the mandibular tusks projecting sharply in front. The bodies of Polymitarcys and Potamenthus (Pl. XLIV, Fig. 7) are flattened. The head of the latter is short and broad with the mandibular tusks barely showing beyond the labrum. A comparison of Ephemera (Plate XLIV, Fig. 8), with Potamanthus, will immediately show Ephemera to be the burrower.

In the Heptageninæ, the head, the body and all its appendages are depressed. In Iron and Epeorus (Pl. XLII, Fig. 4), which inhabit the swiftest water, this depression is greatest, but in Heptagenia and Ecdyurus, it is also very pronounced.

The form of the Bætinæ is various. The most representative is the slender compressed body and rather small rounded head which is characteristic of the active nymphs like Callibætis, Ameletus, (Pl. XLIII, Fig. 5 and Pl. XLII, Fig. 3). All of these nymphs have long legs for running and jumping, but in another type, the body is shortened, more or less flat upon the ventral side, and thickened through the metathorax. Such a form is represented by the majority of the Ephemerellas. It is most marked in the very short stubby bodies of Cænis and Tricorythus, which have become exclusively mud dwellers. In Blasturus (Pl. XLII, Fig. 1) there is a tendency to a depressed form. This is more pronounced in Choroterpes, which is strikingly similar to the Heptageninæ.

ADJUSTMENT TO ENVIRONMENT SHOWN IN THE STRUCTURE OF THE GILLS.

The gills of May-flies are especially susceptible to modification by the character of their surroundings. They are usually large and prominent. In other aquatic insects gills are less directly exposed. Those of stone-flies are generally tucked behind the legs upon the ventral side of the thorax, and those of damsel flies at the hind end of the body. Most May-flies have seven pairs of gills, one borne at each postero-lateral angle of the first seven tergites. They are usually large, sometimes unwieldy and always a conspicuous feature of the body. Situated as they are, they extend along the whole side of the abdomen and brush against everything with which it comes in contact.

The gills of Leptophlebia are the most generalized of any which have been examined. They appear to lack modifications both for respiration in any particular situation or for protection. The seven pairs are identical in shape and nearly so in size. Each one is entire at the base, but deeply cleft into two long narrow divisions which lie in one plane. Their surfaces are without markings or local thickenings. One large trachea enters the gill and sends a branch to each of its divisions. In these there is but a scanty supply of tracheoles. The attachment to the abdomen is exposed above and below so that the only protection for the gill is in the ease with which it may be detached and regenerated.

In Blasturus the first pair of gills are like those of Leptophlebia, but the other six pairs are broadened so that a much greater respiring surface is provided. At the base a trachea enters and splits once, but each arm gives off a good number of branches which supply the whole surface of each gill division or lamella. The two lamellæ do not lie in the same plane, but the outer one is twisted over at the base and lies on top of the inner. A double gill made of two overlapping lamellæ is thus formed. A variation of this same kind of development is shown in the gills of Choroterpes. These gills have neither ribs, nor bands upon their margins. In consequence of this they hang limply from the sides of the body, but the main tracheæ provide some leverage for the muscles, and the gills can be moved a little. The breathing movement is, however, slow and feeble. The nymphs are thus provided with large breathing organs, but also burdened with an unweildy load.

In Siphlurus the gills are double and are stiffened by strong tracheæ and moved by muscles at the base, so that they can be held upright and can also be vibrated with great rapidity. In addition there are narrow spinous bands upon the inner sides of the upper lamellæ. Those of Callibaetis (Pl. XLIII, Fig. 5), are held in upright position, and can be rapidly vibrated like those of Siphlurus. They are much smaller and lie farther dorsad when pulled down close to the body. They are better protected because less conspicuous, and better breathing organs because their rapid vibration enables them to absorb as much oxygen as if they were broad and bulky.

In the gills of Baetis the marginal bands are hardly indicated, but those of Ameletus are broadly bordered by thick spinous bands of chitin. In them the single lamella is fairly supplied by tracheæ. Its base is inserted into a shallow notch in the posterior margin of the tergite. Its attachment is thus slightly protected and at the same time it is allowed to swing freely. Adjustment to the conditions in water falls is always marked by an increase in the tracheal supply. In Chirotonetes (Pl. XLVI, Fig. 13), this has been made by a great increase in the number of fine tracheoles which supply the lamella and by the development of a fimbriate gill at the base main trachea of which is a branch of the main trachea of the lamella. The margins of the lamella are bordered with thickened spinous bands similar to those of Ameletus, but it has also a stiff rib extending from base to tip.

A second group of Baetinæ in which the gills are much specialized includes those which have been adjusted to an environment of mud and sand. Nearly all of these nymphs have the number of gills reduced. In Ephemerella excrucians there are but five pairs of gills and these cover but two abdominal segments. The attachments are in every case protected by lateral spinous extentions of the abdomen. In Ephemerella rotunda and E. excrucians a wide hollow shelf is formed from these spines, upon which the gills rest. Each gill consists typically of a thickened lamella, which completely overlies the delicate fimbriate-lamelliform division beneath.

The thickening of the upper lamella is greatest upon the front gills. This thickening and the reduction in number of the gills is most marked in the two mud dwellers, Caenis and Tricorythus. In these, gills are present upon segments two to six only. In all species of both genera the upper lamella of the first gill is modified into a cover which conceals all of those behind it. They are further protected by a shelf-like extension similar to that just described in Ephemerella. In the slight concavity of this shelf lie the delicate gills of segments 4, 5, 6, protected from the harsh gravel through which the nymphs crawl. When breathing actively the stiff covers are raised enough to allow water to circulate upon the gills beneath, which vibrate freely and create a current.

The gill covers of Tricorythus are scoop shaped, with the concavity beneath, so that even when the cover is closed down the gills are not under pressure, but are enclosed in a protecting box. The edges of the cover and those of the gills beneath are margined with short hairs. This brush of intermingled hairs makes an effective sieve which strains out particles of mud from the incoming current of water. Entrance of water at the base of the gill is prevented by a small triangular extension of the second abdominal segment which fits closely to the inner side of the elytroid cover.

Gills of the Ephemerinæ.

The most homogeneous series of gills is found in the Ephemerinæ which in Fall Creek were represented by Potamanthus, Polymitarcys, Ephemera and Hexagenia. They are single and rudimentary upon segment one, (Pl. XLIX, Fig. 27) and double upon segments 2–7 (Pl. XLIX, Fig. 26). They are long and generally narrow, but this varies slightly with the genus. The upper and lower lamella are both fringed with filaments into which run branches of the tracheæ. The attachments are not protected and the base of the gills appears to be an unbroken continuation of the body wall, which is very flexible and tough. The gills of Potamanthus (Pl. XLIV, Fig. 7) are the most generalized. They are nearly linear, lie limply extended from the sides of the body and except for the scanty fringe of filaments are almost identical with the gills of Leptophlebia.

In the true burrowers, Ephemera (Pl. XLIV, Fig. 8) and Hexagenia (Pl. XLIX, Figs. 26, 27) both lamellae are broader and the number of the marginal filaments is more than doubled. Each lamella is stiffened by a mid-rib of chitin which overlies the main trachea. By the aid of this rib the gills can be held up over the back where they are not exposed to the constant friction as they would be when trailing from the sides.

Gills of the Heptageninæ.

The gills of the Heptageninæ (Pl. XLV, Figs, 10, 11, Pl. XLVI, Fig. 12) show a series of slightly less homogeneous adjustments. They are fitted for breathing in different degrees of rapid water, and at their maximum specialization, they are important aids to the nymph in clinging to surfaces. The gills are double except the last one which in Heptagenia is rudimentary. (Pl. XLV, Fig. 10). The upper division is plate-like and shows greater modification and the lower part is fimbriate-lamelliform or fimbriate, and varies slightly in size and position among different genera. The gills of the Heptagenia and Epeorus have the characteristic abundant tracheation of swift water inhabitants. In Epeorus the lamellæ are large, richly tracheated and lie obliquely recumbent along the sides of the body, (Pl. XLII, Fig. 4), so that the tips and outer edges touch the surface upon which the nymphs rests. Along this edge is a chitinized band thickly beset with spines. When clinging to stones in the rapid current this edge is pressed tightly down to the surface. The bases of the gills are protected by sharp extensions of each tergite, which project backward over them. On the inner margin of each lamella near the base is a shallow notch. When the lamellae are held close to the body the fimbriate gill projects through this notch and receives the full wash of the water. The first pair of lamellae are scoop-shaped and curve inward back of the hind legs so that little water flows beneath the body.

In Iron fragilis there is a similar, but more perfect adhesive apparatus. The outer margins of the lamellae are likewise banded and their position is identical with that just described The first pair of lamellae are much larger, (Pl. XLVI, Fig. 12), and their tips are held almost in contact. The last pair are folded and slightly curved so that the tips of these also nearly touch. When the margins of these lamellae are closely pressed against the surface a sucking disk is formed. In the lamellae and in the fimbriate gill above, the tracheae absorb oxygen from the water constantly flowing over them. An adhesive apparatus is thus coupled with an efficient respiratory organ.

The Food of the May-fly Nymphs.

May-flies are almost entirely herbivorous. Their food consists chiefly of fragments of higher plant tissue, algæ and diatoms. The following table contains the record of an examination of the stomach content of several nymphs. ~~With the exception~~ of Siphlurus and Chirotonetes the examinations ~~were~~ made upon fresh material:

STOMACH CONTENTS OF NYMPHS EXAMINED THROUGH APRIL AND MAY. CROSSES (×) REPRESENT SUBSTANCES FOUND IN MORE THAN TEN SPECIMENS OF A GENUS.

	Siphlurus	~~Heptagenia~~	Blasturus	Hexagenia	Callibaetis	Chirotonetes
1. Fragments of Plant Tissue.						
Stems, decayed leaves	×	×				
Epidermis	×	×				
Epidermis, moss	×	×				
Epidermis, roots						×
2. Filamentous algæ.						
Vaucheria	×					
Spirogyra	×				×	
Mougeotia	×					
Ulothrix	×					
Zygnema	×				×	×
3. Diatoms.						
Navicula	×	×		×		
Fragellaria	×	×	×			
Tabellaria	×	×				
Cocconema		×	×	×		
Meridion			×			
Gonphonema			×	×		×
Synedra						
4. Animal.						
Mayflies	×					×
Other insects						×

The kinds of algæ and diatoms found in the stomach varied a good deal with the locality and date of collection. In certain parts of Cold Brook during March, 1911, every available object was brown with Meridion and the stomachs of nymphs collected there contained little else. Nymphs taken in the same place a month later contained no fragment of Meridion. May-fly food is most abundant in April and May, especially for the running water forms. Later the thick mats of Meridion, Cladophora and Spirogyra begin to decay, there is a diminished supply of water and consequently greater competition for food.

In the summer of 1911, a few experiments in feeding were made upon Callibaetis fluctuans, one of the most abundant local May-flies in pools and open waters. Six pails about one foot deep and seven inches in diameter were made from strong muslin. A ring of wire was placed at top and bottom to extend them. A string was tied into the upper one for a bale and the pails were fastened to a frame and suspended in a pool where the water was kept constantly fresh. They were numbered 1, 2, 3, 4, 5, 6, and a different food placed in each respective pail.

On June 28, twelve nymphs of equal size were measured and freed in pail. On July 1, nymphs were taken from each pail and the stomach contents examined. For ten days more the same food was given at intervals of two days. Occasionally the pails were rinsed free of stale food. This was especially necessary for the corn meal which soured quickly.

June 28 12 Nymphs in each Pail	July 1 Alive	July 1 Stomach Content	July 10 Alive
1. Fruiting chara	All	Not much food, fragments chara	All
2. Corn meal	All	Half full of meal	6
3. Alfalfa (ground)	All	Not much food, fragments alfalfa	9
4. Spatter-dock (ground)	None	Full of spatter-dock tissue	–
5. Green grass (ground)	7	Half full, green grass	7
6. Fruiting chara (control)	All	Full of chara	All

The mouth-parts of May-fly Nymphs.

Bætinæ

The most generalized mouth-parts occur among the Bætinæ in the species which bite or tear fragments from roots and stems. They consist of labrum, labium, mandibles, maxillæ, hypopharynx, and the epipharynx which is borne upon the labrum. Those of Callibaetis fluctuans (Pl. XLVII, Fig. 14), are typical of this generalized condition. On the concave inner surface of the labrum are two patches of incurving hairs, and these are supplemented by a set of long marginal hairs. When gathering food the edge of the labrum is pressed against a stem or leaf and moved rapidly back and forth. After a few movements its tip is pulled close to the mouth and brushed by the maxillary palpi. The labium sweeps food in from behind as the labrum does from the front. On the maxillæ which lie in front of the labium the lacinia and galea are fused. The lacinia is represented by two teeth on the tip; the galea by the lobe like part behind them. The teeth of mandibles are separated into two distinct groups, the canines (c) and the molars (m). In many cases both of these are very asymmetrical. Both maxillæ and mandibles may be freely extended side wise, but the latter is used less often for biting than for grinding. The epipharynx (cf. Pl. XLVII, Fig. 14b) is an inconspicuous elevation which is borne on the inner surface of the labrum. It is densely covered by short incurved hairs probably sensory. It often extends on to the clypeus and in all the nymphs examined lies a little to the right of the center. Mouth-parts of the type described above are found in nymphs of Siphlurus, Blasturus, Baetis and Leptophlebia. The food getting habits of any of these can be easily observed. They pull off fragments from the stems and leaves by sticking the laciniæ or less often the canines into the tissue, then bracing with the front feet and pulling backward. Upon flat surfaces, they keep the labrum and labium moving rapidly and thus sweep the food into the mouth.

In nymphs of Ameletus ludens a broad plankton rake upon the maxillae formed by a series of arched, regularly graduated, and pectinated hooks borne upon the distal end of the galea and lacinia. When eating, the nymph extends these rakes forward and backward, exactly as one would use a hand rake and by the help of the labium and hypopharynx the food is pulled into the mouth for grinding.

Nymphs of Chirotonetes gather their food upon ledges washed by dashing water. The outer surfaces of the mouth parts are armed with very long bristles. The distal segment of the labial and maxillary palpi are flattened out into broad blades. These blades are used as scrapers upon the algæ covered stones. In the swift current this nymph must of necessity cling to the rocks with its head upstream. In doing this it uses its fore legs little, but they are held up and straight forward close beneath the labium. Armed with long bristles as they are, they help to form an efficient plankton basket which catches the food carried along in the water.

In Caenis, Tricorythus and Ephemerella the mouth-parts are often reduced. In all these the mandibles are stout with very strong canines (Pl. XLVII, Figs. 16, 19, and Pl. XLVII. Figs. 20, 21). Structures like the palpi which extend out from the mouth are much shorter. In Tricorythus (Fig. 22), the body of the labrum is strong, but the palpi are weak and stubby. This reduction is carried to the limit in the maxillæ of Ephemerella deficiens in which the palpi have disappeared, leaving only a little peak of chitin at their attachment place (Fig. 18). If one observes nymphs of Tricorythus or Ephemerella foraging, they will see them continually thrusting their heads through harsh gravel where such appendages would be in the way.

The Bætinæ have the most generalized mouth-parts examined. This group includes species in which there have been modifications of the mouth-parts for rakers and plankton baskets, and great reduction of palpi.

Ephemerinæ

Nymphs of Potamanthus, Polymitarcys and Hexagenia all gather their food in the same places and by the same means. Their relative specialization has been closely correlated with the extent to which they have been modified for burrowing. The mandibles of Potamanthus (Pl. XLVIII, Figs. 23 and 24) show the beginning of this modification. The canines are here in their usual position at the tip of the mandible (c), but upon the outer side of each is a stout pointed process. These processes are not long, and when the mandibles are in natural position only their tips show beyond the labrum. These processes are similar in shape and identical in position with the tusks of the true burrowers, Ephemera and Hexagenia (Pl. XLIX, Figs. 31, 36). In these the processes are long, slightly incurving tusks which are the most conspicuous features of the head. The canines are on the median side of these near the base, and when the mandibles are in natural position, they extend downward and can thus most efficiently grasp food. From them the food is passed inward to the grinding surface of the molars. Upon the left molar (Pl. XLIX, Fig. 34) are eight deep transverse gutters. The upper ends of these are enclosed by irregular teeth and the floors are marked by transverse striations. The right molar (Fig. 35) surface bears seven overlapping ridges, all but one of which is bluntly toothed and enclosed at one end by a prominent jagged process. When in position the ridges of the right molar fit down into the gutters of the left and the terminal teeth fit into the free ends of the gutters. The food brushed into the mouth by the labium and maxillæ is ground in this mill.

In the Ephemerinæ the greatest modification has occurred in the mandibles which have become the strongest structures of the head, important alike to feeding and burrowing.

Heptageninæ.

In the Heptageninæ which have scraping mouth-parts, the labrum is entirely hidden from above. It is freely movable upon the clypeus and has a row of very dense, slightly incurved hairs extending along its margin. The inner surface of the labrum is slightly concave, and bears the epipharynx. When the labrum is extended forward the short hairs upon the inner surface rake in the food and are closely followed by the thick brush upon the margin. Food thus gathered in the concavity of the labrum falls directly between the maxillæ and mandibles.

Legs of Nymphs.

The legs of May-fly nymphs consist of a coxa, trochanter, tibia, tarsus and a tarsal claw. These parts vary in relative size and structure according to the habit of the nymph. The surfaces may be bare, scaly, spinose or hairy. In all of the legs which have been examined there is a small but distinct plate on the inner side at the distal end of each tibia.

Bætinæ.

The Bætinæ includes nymphs which have the most generalized legs, such as those of Siphlurus, Callibætis, Ameletus and Chirotonetes. All of these nymphs can move about upon a heterogeneous footing (Figs. 3 and 5). The legs of Siphlurus are of the most generalized type. They are long and slender and the three pairs are of equal length. The surfaces are sparsely covered with inconspicuous hairs. The tarsal claw is long, slender and without teeth. The tibial plate is well developed, consisting of a thick, flattened projection of the tibia, which bears transverse ridges. The attachment of the legs allows free movement and the nymphs are capable of running very swiftly. The middle and hind legs of Chirotonetes are similar to those which have been described, but the first pair has been modified for food gathering and respiration. At the base of the coxa, there is a large tuft of forked gill filaments. From the tibia an elongate flattened spur extends for more than half the length of the tarsus, and along the inner margin of femur, tibia, and tarsus is a regularly arranged row of very long, stiff hairs. When the legs are sharply bent, these hairs, together with the tibial spur form the bottom of the plankton basket already referred to.

In Cænis, Tricorythus and Ephemerella the legs do not lift the bodies at all. Nymphs of Cænis and Tricorythus clamber upon very uneven surfaces so that the legs do not extend straight out from the body as they do in some of the Ephemerellas later noted. The strain of pulling and climbing comes evenly upon every segment of the leg and there is little difference in their size. In both of these genera the tarsal claws are in constant use and are correspondingly well developed. The same evenly distributed development may be seen in the legs of certain Ephemerellas, which constantly crawl over mud, dead leaves, and small debris. In others in which there are well established clinging habits (Pl. L, Figs. 39, 43), the fore femora are enormously developed by the constant pulling incident to their position. In these legs the hinder part of the femora is greatly thickened by the muscular development, but the front edge is thin and blade-like and often jaggedly toothed or serrate.

Ephemerinæ.

Two stages of modification are shown in the legs of Potamanthus and Ephemera. In Potamanthus, which crawls upon the bottom in a manner similar to the Heptageninæ, the legs sprawl out from the body in the same way. The tibia is prolonged into a flat spine which overlaps the first third of the tarsus. The structure of this fore leg appears to be the fore-runner of the greater modification shown in the fore legs of Ephemera, (Pl. XLIV, Fig. 8), which are perfect digging tools.

V. MODIFICATIONS OF ADULT STRUCTURES.

Reproduction is the sole end of the imago life. Parts of the body which have no function connected with it are reduced or atrophied.

It is probable that, with but few exceptions, May-flies engage in some kind of mating flight. The character of this flight and the time when it occurs vary. The following records show some of these variations. On June 25th a swarm of three or four hundred individuals of Choroterpes basalis were swarming over the water of Fall Creek at about four o'clock on a sunny afternoon. Their average rise must have been thirty feet. From the swarm both males and females were captured, but mating was not observed. On June 29th, at 7:30 in the evening, a female Ephemera varia was captured from a swarm which was rising and falling in flights of thirty to forty feet. Often they descended to within five feet of the ground. Their dance continued until darkness hid them. Mating flights of Leptophlebia præpedita have been seen in the middle of a sunny forenoon, and at two, four and five o'clock of bright afternoons in May and June. None of these rose higher than fifteen feet and two of the swarms did not fiy more than six feet above the ground. One entire swarm which was captured contained forty males and one female.

Actual mating has been observed but a few times. The most satisfactory observation was made in May, 1911, upon a swarm of Bætis, which were flying near Cascadilla Creek just after a shower. Most of the time they were not flying much above the level of the eye so that they could be clearly seen. Large numbers continually settled on bushes and upon my clothing, and there appeared to be about equal numbers of males and females. Many matings occurred, but in only seven could the positions of the insects be seen at all. The male of one of the couples flew up and attached himself beneath a female, pressed the dorsal side of his head against the ventral side of her thorax and extended his fore-legs upward, in order to clutch her prothorax. The setæ of the female extended straight out posteriorly, but those of the male were pointed forward over his back so that their tips projected between the heads of the two insects. The position of the abdomen could not be clearly seen, but judging from that of the setæ, it must have been recurved in order to insert the penes inside the egg valve. Copulation did not last more than half a minute. When in copula, each pair was borne diagonally downward to the ground, but always separated immediately upon touching it.

So far as known, flight is a necessity for copulation and egg-laying in May-flies. The alimentary canal and the legs play a part in flight which is peculiar to this group. It is a well known fact that adult May-flies take no food and that the alimentary canal is inflated with air or gas. Sometime before emergence the nymphs cease to eat and just before it, they push their heads above the surface and appear to be rapidly gulping in air. If dissected at this stage the alimentary canal is found much inflated. It remains thus inflated throughout life. The structure of the alimentary canal of adults was studied by Fritze, '06 and by Sternfeld, '07. Sternfeld found a complicated muscular dilator apparatus in the esophagus. This he concluded to be a pump by which the midgut was filled with air and by which its supply could be voluntarily controlled. He did not discover whether any change occurred in the air taken in. No suggestion was made as to when this pump was used, but it is probable that it functions when the canal is first inflated by the nymph and afterward in controlling the specific gravity during flight. This change of the alimentary canal from its normal function to that of a balloon is very important to flight. The lessening of the specific gravity made possible by this modification makes the work of the wings much easier. Since it is more important that adults mate, than that they live a long time, this function of the alimentary canal exceeds the former one in value.

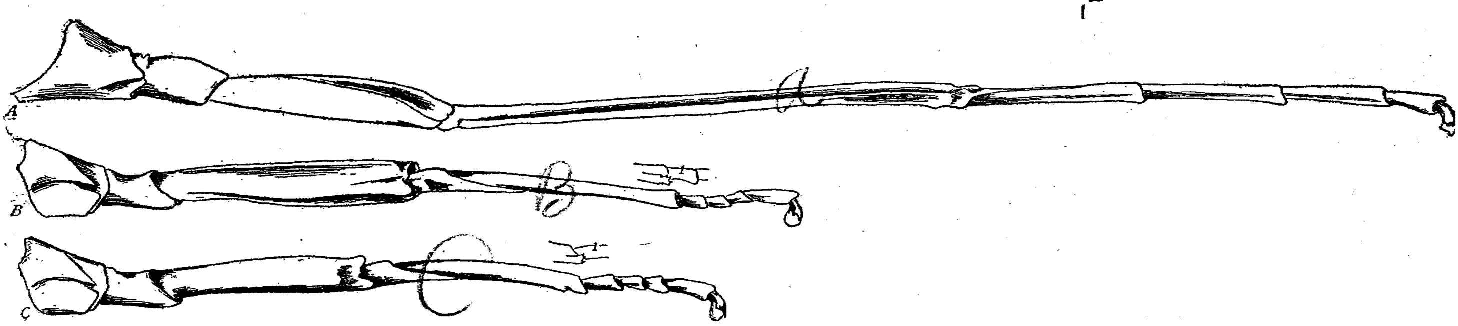

Fig. 1. Legs of male imago of Hexagenia bilineata. A, first leg; B, second leg; C, third leg; 1, opposite side of legs showing tibial spur.

It has already been noted that adult May-flies use their legs little or none in walking and in many instances the fore legs are not even used for support. In most males the fore legs are enormously lengthened and when the insects are at rest, they are often extended out from the head (Pl. XLIV, Fig. 9). The middle and hind legs brace the body, but they usually lift only the front part, while the abdomen rests upon the supporting surface (Pl. XLIII, Fig. 6). The fore legs are necessary structures in copulation and males of Palingenia which have very short legs mate not in mid-air, but close to the surface of streams. (Eaton). The legs of some May-flies have been enormously specialized. The fore-legs of a South American Campsurus are very long, (see Fig. 2), while the middle and hind ones are but short stubs. In the fore legs there is a twist in

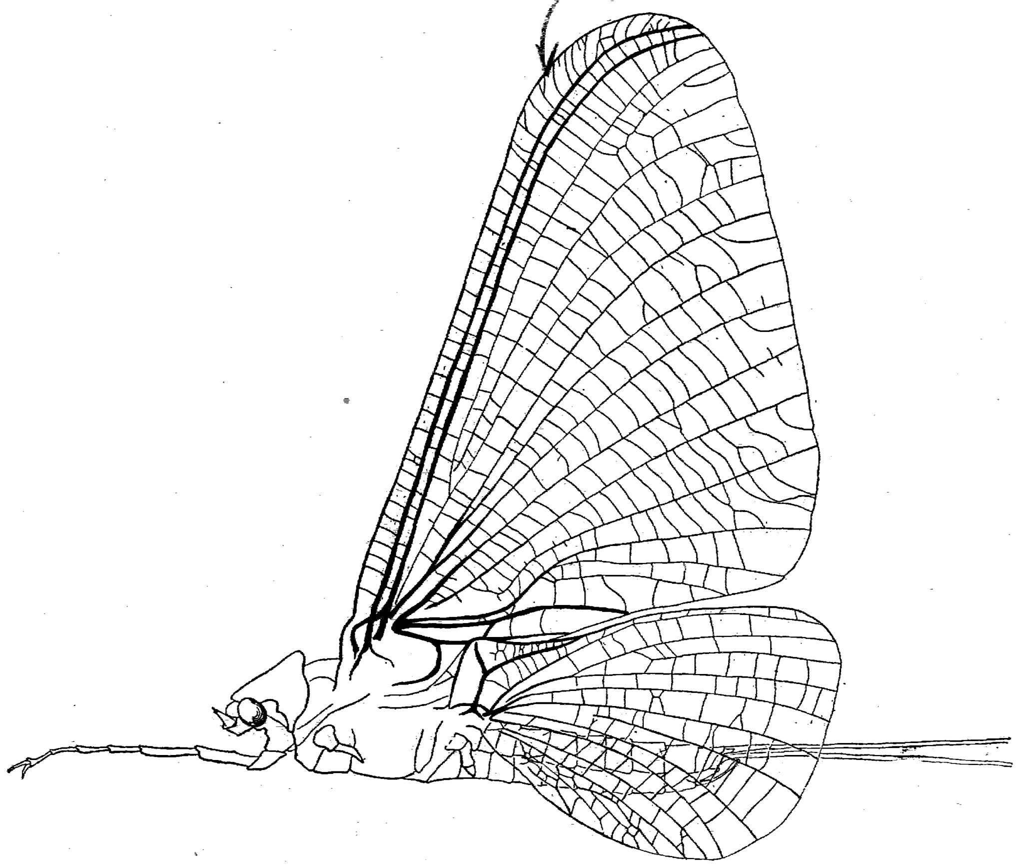

Fig. 2. Male imago Campsurus (South America) showing rudimentary middle and hind legs. The setæ not represented at full length here, are about three times the length of the body.

the joint which articulates the tarsus with the tibia. This admits the supination of the tarsus and is evidently a modification for clutching the female.

External Genitalia of the Male.

The external genitalia of the male consists of a pair of forceps, jointed except in Cænis and Campsurus, and two penes, each with a distinct opening. The forceps are incurved appendages of the tenth segment, by which the male grasps the abdomen of the female. The genitalia of Hexagenia

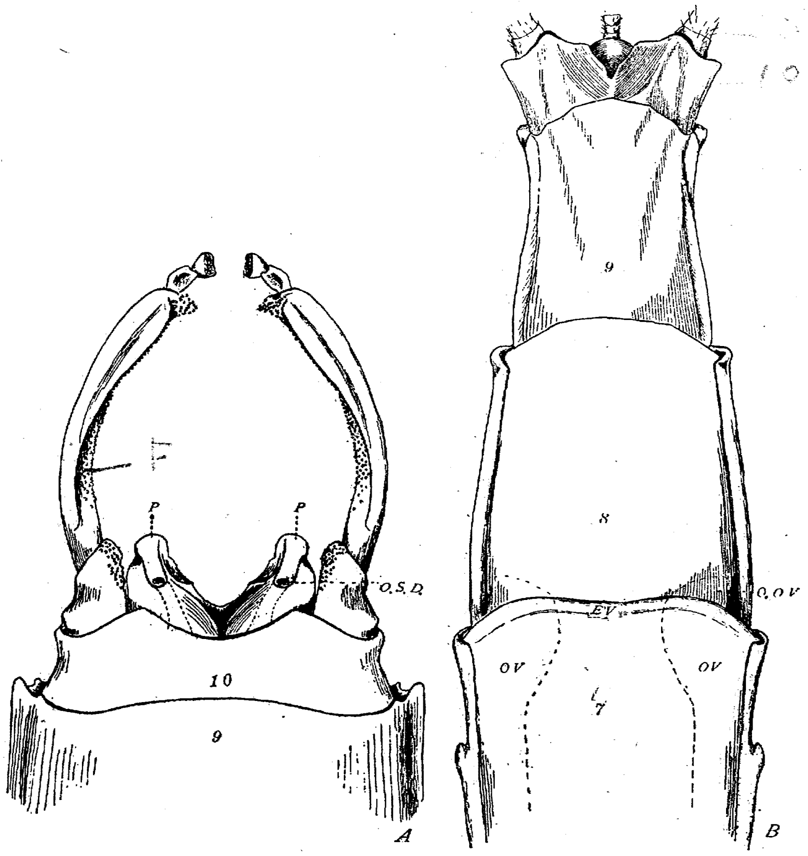

Fig. 3. A, external genitalia of Hexagenia sp.? ♂; p, penis; o. s. d., opening of seminal duct; f, forceps. B, ventral view of rear abdomen of Hexagenia sp.? ♀, showing ov, outline of oviduct seen through body-wall; o. ov., opening of oviduct; e. v., egg-valve; 7, 8, 7th and 8th sternites.

sp.?* are of the simple type. The forceps are three jointed, with a stout basal piece. The two distal segments are concave on the inner surface and tip. These concavities, the flap like extension upon the main segment and the inner surface of the basal piece are thickly covered with small papillæ, which are characteristic of nearly all forceps examined. The roughened surface produced by them probably

This is a species Hexagenia recurrata in manuscript which I have to be published.

helps to hold the female. The penes are the intromittent organs. In Hexagenia they consist of two chitinous funnels whose larger ends open inside the body, and whose smaller ends are slender tubes bent down ventrally. Between the penes is a thin chitinous plate, and beneath they are supported by the tenth sternite. In each penis the seminal duct can be clearly traced to its termination at the end of the bent tube.

Of the more complicated condition which exists in most May-flies, the genitalia of Siphlurus alternatus is fairly typical (Pl. LI). The forceps are similar to those of Hexagenia. Their origin from the ninth sternite is shown in Figures 48 and 49. The penes (P) are wholly hidden from beneath by the tenth sternite, but they are attached only at their bases, and in copulation may be freely projected within the (Fig. 50, EV) egg valve, while the tenth sternite remains outside it. Essentially they consist of the funnels just described in Hexagenia with secondary structures added. The larger ends of the funnels open into the body (Fig. 49, A). In Figure 49 the penes are shown in dorsal view, separated off from the dorsal part of the abdomen with the large ends of the funnels exposed (A). The small end of the funnel (B) extends outside the body and turns downward as in Hexagenia, but the opening of the seminal duct is enlarged and trumpet-shaped. From the dorsal side only the backs of these trumpets can be seen, but when the penes are completely removed from the ninth sternite and turned with their ventral sides up, one can look directly down into their openings, (Fig. 52, O. S. D.) and the seminal ducts can be traced from the testes directly to them. Lying dorsal and lateral to each seminal tube are two prominent, heavy chitinized processes (Fig. 49). The raised apex of the upper process (C) is pointed toward the middle, that of the lower (D) is pointed outward toward the side and the prominent spines upon each are directed in different directions. If the supposed position of the penes in copulation, be correct, the dorsal or spinose surface of these processes must be in contact with the inner surface of the egg valve (E. V. Fig. 50). When inserted they would thus hook over its soft lip and pull it down, allowing the seminal tubes to discharge their contents at the mouth of the oviducts.

Genitalia of the Female.

In the simple condition each oviduct lies well to the side of the abdomen and opens between the seventh and eighth sternites (Hexagenia). Each opening is perfectly distinct (see dotted line Fig. 3, B) and there is no sign of an open passage or vestibule between the two.

In Siphlurus alternatus (Pl. LI, Figs. 53, 55) the lower ends of the oviducts approach each other and open into a common vestibule (C. V.) just inside the egg valve. Opening into this vestibule is a soft membraneous sac (S. R). In fresh specimens this sac shows prominently between the bases of the oviducts (Figs. 53, 55). In figure 55 the sac and oviducts are shown viewed from the inside; the nerve chain has been severed so as to fully expose the sac. In the specimens thus far examined, no spermatozoa have been found within this sac. It is extremely probable, however, that this is a true seminal receptacle, and that this is a specialization which nearly approaches the unpaired opening found in other insects.

VI. THE EGGS.

Under the ordinary conditions of their life a large proportion of May-fly nymphs regularly perish before reaching maturity. A great excess of young must be produced in order to meet this loss and the success of different groups in maintaining their existence becomes more than usually dependent upon the number of eggs produced and the structures which aid in their dispersal and safety during incubation.

In insects whose lives are so brief as these, the eggs are well developed even at emergence, and may then be readily counted, the difference in size between the developed eggs and the egg rudiments being very marked. It is easy, therefore, in mature nymphs, sub-imagos or imagos to determine the actual fecundity.

The first count of May-fly eggs was made by Reaumur* to determine the fecundity of some specimens which he captured in his garden. He found egg masses protruding from the abdominal openings, counted the eggs and found about 400 in each mass. His results have been several times quoted by later workers, but no references has been found to any

*Reaumur 1742. T. VI, Mem. XII, p. 495.

other actual determination of the fecundity of May-flies since that time.

In this study the eggs of seventeen May-flies have been counted and examined. They were taken from imagos which had been kept in cages until they showed signs of old age. Usually a count was made of the eggs in several individuals and an average taken. They were examined and counted upon a glass slide in a mixture of water and glycerine which formed a convenient medium in which to manipulate them. The results of the counting are given in a table which follows.

All of the eggs are viscid. When laid in dishes they adhere to the bottom, as do those of Bætis to stones. When twigs or algæ are introduced, they become attached to them. There are two kinds of structures found upon them; micropylar structures and knob or thread-like extensions of the chorion, both of which are important to the egg; and there is also a variety of chorionic sculpturings which have no apparent significance.

Examples of the more important structures were long ago pointed out. Polar knobs (micropylar structures) were figured by Burmeister '48, and described by Leuckart '55. The latter believed that the knobs were composed of masses of spermatozoa and it remained for Grenacher, '68, to find many stages of them upon developing eggs in the egg-tubes and to point out their true nature. Micropylar structures were also shown in Palingenia virgo by Joly, '71 and '76, and in Bætis sulphurea by Joly, '76. Grenacher, '68, also pointed out (upon an unnamed May-fly egg) some little threads which were continuous with the chorion and which bore tiny spheres upon the ends. He figured these with remarkable accuracy. Of the eggs here figured, three bear a micropylar apparatus, five have thread-like extensions of the chorion and nearly all are more or less elaborately sculptured.

The eggs of closely related forms may be very different. This is well shown by a comparison of those of Ephemerella excrucians and E. rotunda (Pl. LIV, Figs, 66, 67). The eggs of Ephemerella excrucians are pure white, and slightly dumb-bell shaped, with a distinctly sculptured chorion, but with no micropylar apparatus. Those of Ephemerella rotunda are yellowish and oval with a prominent mushroom shaped cap about the micropyle. If examined in the body or when first extruded, two small knobs may be seen upon either side of the egg, near its lower pole. Each knob is attached to the distal end of a thread-like extension of the chorion, which lies beneath it, tightly coiled like a watch spring. Upon coming in contact with the water these threads spring out like elaters. The little knobs thus extended probably act as floats or anchors for the egg. An even greater difference between the eggs of closely related forms may be seen in the eggs of Heptagenia interpunctata (Pl. LIII, Fig. 65) and Heptagenia pulchella (Fig. 64). The former has a pure white oval egg without sculpturings or extentions of any kind. The latter is white and slightly rounder with small regularly arranged bosses upon the chorion. At each pole there is a skein of fine bright yellow thread. These skeins are also prominent upon the poles of developing eggs, even in the tips of the egg-tubes. Upon a glass slide they are easily seen with the naked eye and the threads may be pulled out with needles to a length of two or three inches. As soon as the eggs float free in water the skeins begin to unroll and if shaken a little they quickly uncoil altogether and become entangled with any object near them. In nature the eggs are deposited upon the surface of moving water. The threads just described probably wind about sticks or plants and thus anchor the eggs and keep them from being buried with silt during incubation.

Similar extensions of the chorion are found upon the eggs of Tricorythus allectus and Ecdyurus maculipennis. The eggs of Tricorythus (Pl. LII, Fig. 60) are bright green and oval with a prominent shingle-like surface. Upon each side of the egg toward the lower pole are two threads very similar to those of Ephemerella rotunda, but without any knobs upon the ends. At the other pole is a prominent smooth yellowish micropylar apparatus. The eggs of Ecdyurus (Pl. LIII, Fig. 62) are roundly ovate and pure white. Their entire surface is covered with minute pits and scattered between these are numerous short blunt projections. When the egg is first removed from the body, a small coil of thread may be seen in the depression on the top of each projection. As soon as the egg has been in the water a little while, each coil unwinds with a sudden spring. At the end of each thread is a tiny viscid button.

The eggs of Leptophlebia sp.? (Pl. LII, Fig. 58) are elongate ovoid, distinctly brownish and thickly covered with short hairs, so that they look like ciliated protozoans. Those of Choroterpes basalis (Pl. LIII, Fig. 63) which are laid in the same or similar situations have no extensions of the chorion. They are pure white, elongate, with an elaborate design in the sculpturing. The eggs of Blasturus cupidus (Pl. LIV, Fig. 68) are slightly flattened and tablet-like. Upon these flattened areas are irregularly scattered pits and bosses which appear shining white in the glycerine and about the longitudinal circumference is a shelf-like extension which bears a large number of strap-shaped pegs. The eggs of Polymitarcys albus (Pl. LIV, Fig. 69) are roundly ovate and white. The body of the egg is nearly smooth, but the prominent yellow micropylar apparatus has a distinctly shingle-like surface. The eggs of Callibætis fluctuans and Chirotonetes albomanicatus were perfectly smooth and pure white.

Nymphs of Hexagenia variabilis and Polymitarcys albus live in the same situations but the eggs of the former are only a little roughened, while Polymitarcys has the prominent micropylar apparatus just described. The roughness due to chorionic sculptures may be of some slight service in helping to lodge the eggs, but its significance is probably slight. The extensions of the chorion, on the other hand, are no doubt of much importance in the dispersal and safety of the eggs. The anchors upon Ephemerella rotunda and Tricorythus allectus hang the eggs upon sticks and stems and prevent them from being buried in the mud; the many viscid threads upon those of Leptophlebia and Ecdyurus maculipennis accomplish the same result in a different fashion. Those which probably have the most important function are the long threads upon the eggs of Heptagenia interpunctata. A number of these were shaken about in water strewn with chara and the threads immediately became closely entangled upon its stems. Eggs thus hung upon stems in natural conditions would be safeguarded and prevented from being buried in the mud.

	Number of egg in both ovaries	Color of egg	Length (Fresh eggs measured in glycerin)	Width
Ameletus ludens	670	Light brown	.276 mm.	.153 mm.
Blasturus cupidus	3700	White	.177 mm.	.093 mm.
Callibaetis fluctuans	500	White		
Chirotonetes albomanicatus	2500	Pale green	.200 mm.	.138 mm.
Choroterpes basalis		White	.174 mm.	.085 mm.
Ecdyurus maculipennis	1000	White	.170 mm.	.133 mm.
Ephemerella excrucians	1950	White	.200 mm.	.125 mm.
Tricorythus allectus	750	Green	.189 mm.	.122 mm.

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EXPLANATION OF PLATES.

Plate LXII.

Fig. 1. Mature nymph of Blasturus cupidus.
Fig. 2. Male imago of Blasturus cupidus just after transforming. The cast sub-imago skin shows the dark wing-pads.
Fig. 3. Ameletus ludens.
Fig. 4. Nymph of Epeorus humeralis. The hind wing-pads may be seen through the transparent front ones.

Plate XLIII.

Fig. 5. Nymphs of Callibaetis fluctuans, climbing about in their natural habitat.
Fig. 6. Male sub-imago of Callibaetis fluctuans just emerged.

Plate XLIV.

Fig. 7. Half grown nymph of Potamanthus bettini.
Fig. 8. Mature nymph of Ephemera.
Fig. 9. Male imago of Hexagenia bilineata showing a posture of the fore legs characteristic of the males of many May-flies.

Plate XLV.

Fig. 10. Right gills of Heptagenia interpunctata. The first gill is turned with the lower side up and the fimbriate division is fully exposed; in the others it is indicated through the transparent lamella.
Fig. 11. Right gills of Epeorus humeralis, upper surfaces. When in the natural position the spinose border is in contact with the surface upon which the nymph rests.

Plate XLVI.

Fig. 12. Right gills of Iron fragilis, upper surface, gills turned backward in natural position.
Fig. 13. Right gills of Chirotonetes albomanicatus, under surface, gills turned forward.

Plate XLVII.

Fig. 14. Mouth-parts of Callibaetis fluctuans. a, right, and d, left mandible; b, labrum; c, hypopharynx; e, right maxilla; f, labium.
Fig. 15. Maxilla of Tricorythus allectus.
Figs. 16 and 19. Right and left mandibles of Ephemerella lata.
Fig. 17. Left maxilla of Ephemerella serrata.
Fig. 18. Left maxilla of Ephemerella deficiens.

Plate XLVIII.

Figs. 20 and 21. Right and left mandibles of Tricorythus allectus.
Fig. 22. Labium.
Figs. 23 and 24. Right and left mandibles of Potamanthus bettini.

Plate XLIX.

(Structures of nymph of Hexagenia).

Fig. 25. Maxilla.
Fig. 26. Second right gill.
Fig. 27. First right gill.
Fig. 28. Labrum (La) and Clypeus (Cl), outer aspect.
Fig. 29. Labrum (La) and Clypeus (Cl), inner aspect, showing the epipharynx lying partly upon the clypeus and partly upon the labrum.
Fig. 30. Antenna.
Fig. 31. Right mandible, outer aspect.
Fig. 32. Right mandible, inner aspect.
Fig. 33. Hypopharynx, under side, showing lingua and superlinguæ.
Fig. 34. Grinding surface of left molar.
Fig. 35. Grinding surface of right molar.
Fig. 36. Left mandible, inner aspect.
Fig. 37. Left mandible, outer aspect.
Fig. 38. Labium outer aspect.

PLATE L.

Fig. 39. Right legs of Ephemerella lata.
Fig. 40. Right fore leg of Ephemerella serrata.
Fig. 41. Right fore leg of Ephemerella rotunda.
Fig. 42. Right leg of Ephemerella deficiens.
Fig. 43. Right fore leg of Ephemerella tuberculata.
Fig. 44. Right fore leg of Ephemerella cornuta.

PLATE LI.

(Genitalia of imagos of Siphlurus alternatus.)

Fig. 45. Rear abdomen of male, F, forceps, ventral view.
Fig. 46. Right forceps, showing roughened inner surfaces.
Fig. 47. Rear Abdomen, dorsal view, showing c. s., caudal setae; pp, penes and 10s. 10th sternite.
Fig. 48. Rear of abdomen, side view.
Fig. 49. Dorsal view of penes resting upon the 10th sternite. The white surface, c. e., represents the cut surface of the body wall. The large bases of the penes, a, lying inside the body have been exposed by cutting away the dorsal part of the abdomen.
Fig. 50. Part of the abdomen of the female. e. v., egg-valve, with the opening of the vestibule directly beneath.
Fig. 51. Inner view of the 7th and 8th sternites with the oviducts, o. v., and the seminal receptacle turned backward to show the ventral side of the receptacle.
Fig. 52. Penes removed from the 10th sternite and viewed from the ventral side. o. s. d., opening of seminal duct.
Fig. 53. Egg valve, common vestibule and outline of receptacle and oviducts, from without.
Fig. 54. Rear abdomen of female, dorsal view.
Fig. 55. Dorsal view of dissection of oviducts and vestibule. The top of the vestibule has been cut away and pulled off with the 7th sternite, so as to expose the inner surface of the common vestibule, c. v., and seminal receptacle, s. r.
Fig. 56. Rear abdomen, female, ventral view.
Fig. 57. Rear abdomen of female, side view, e. v., egg valve.

PLATE LII.

Fig. 58. Egg of Leptophlebia.
Fig. 59. Egg of Ameletus ludens.
Fig. 60. Egg of Tricorythus allectus.
Fig. 61. Egg of Chirotonetes albomanicatus.

PLATE LIII.

Fig. 62. Egg of Ecdyurus maculipennis.
Fig. 63. Egg of Choroterpes basalis.
Fig. 64. Egg of Heptagenia pulchella.
Fig. 65. Egg of Heptagenia interpunctata. Needham.

PLATE LIV.

Fig. 66. Egg of Ephemerella rotunda.
Fig. 67. Egg of Ephemerella excrucians.
Fig. 68. Egg of Blasturus cupidus.
Fig. 69. Egg of Polymitarcys albus.
Fig. 70. Egg of Siphlurus alternatus.

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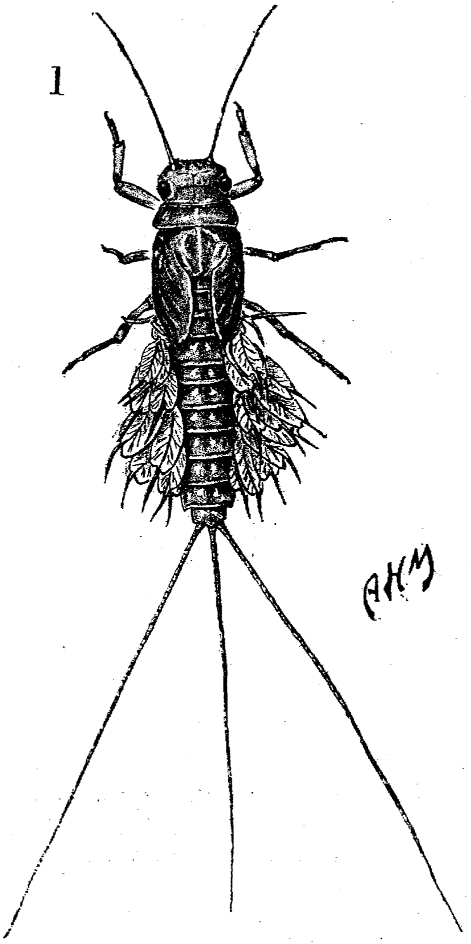

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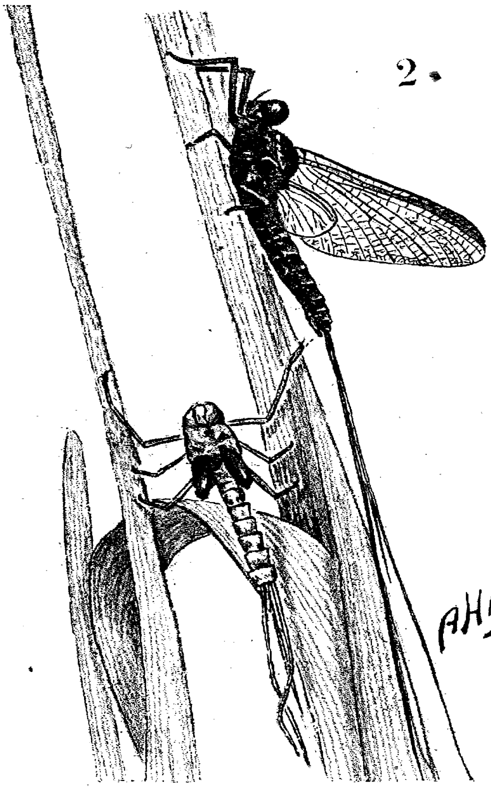

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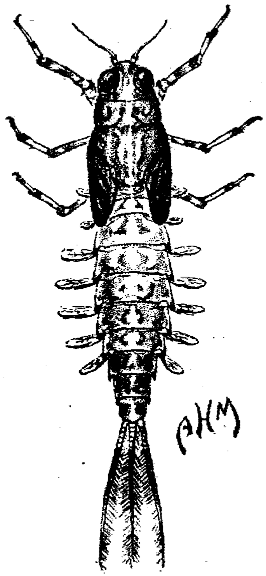

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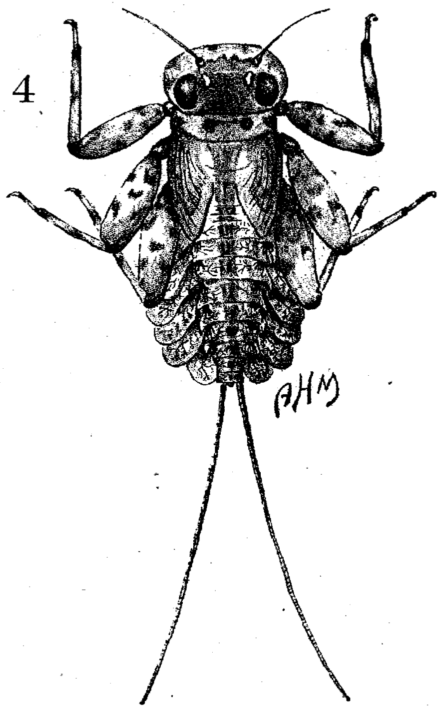

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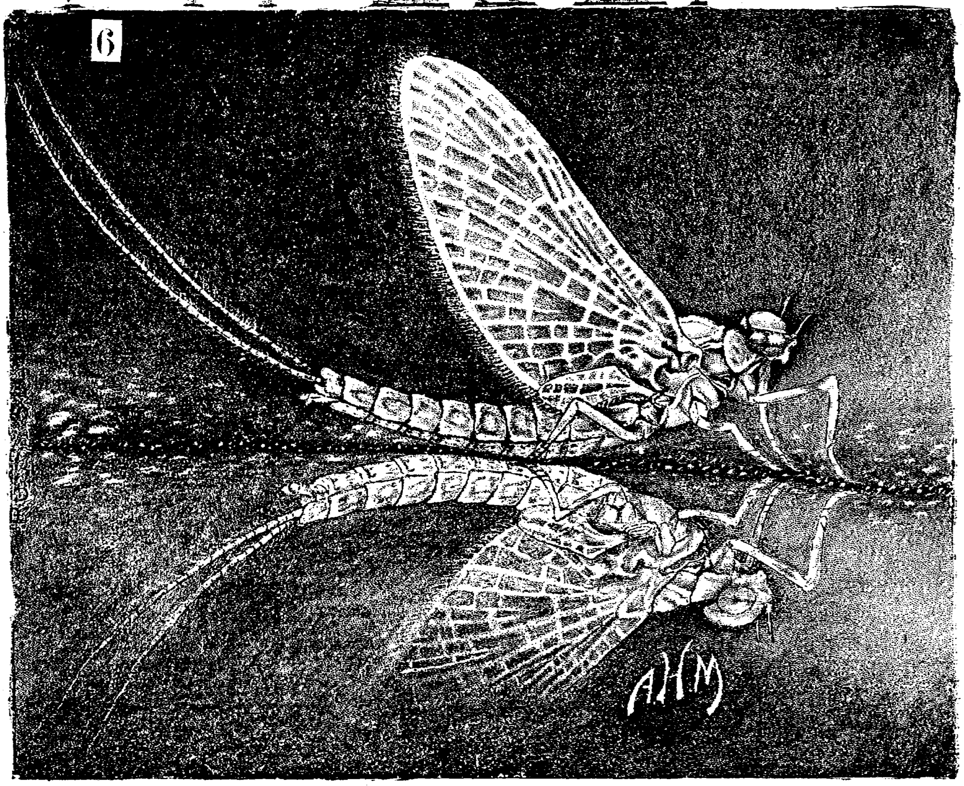

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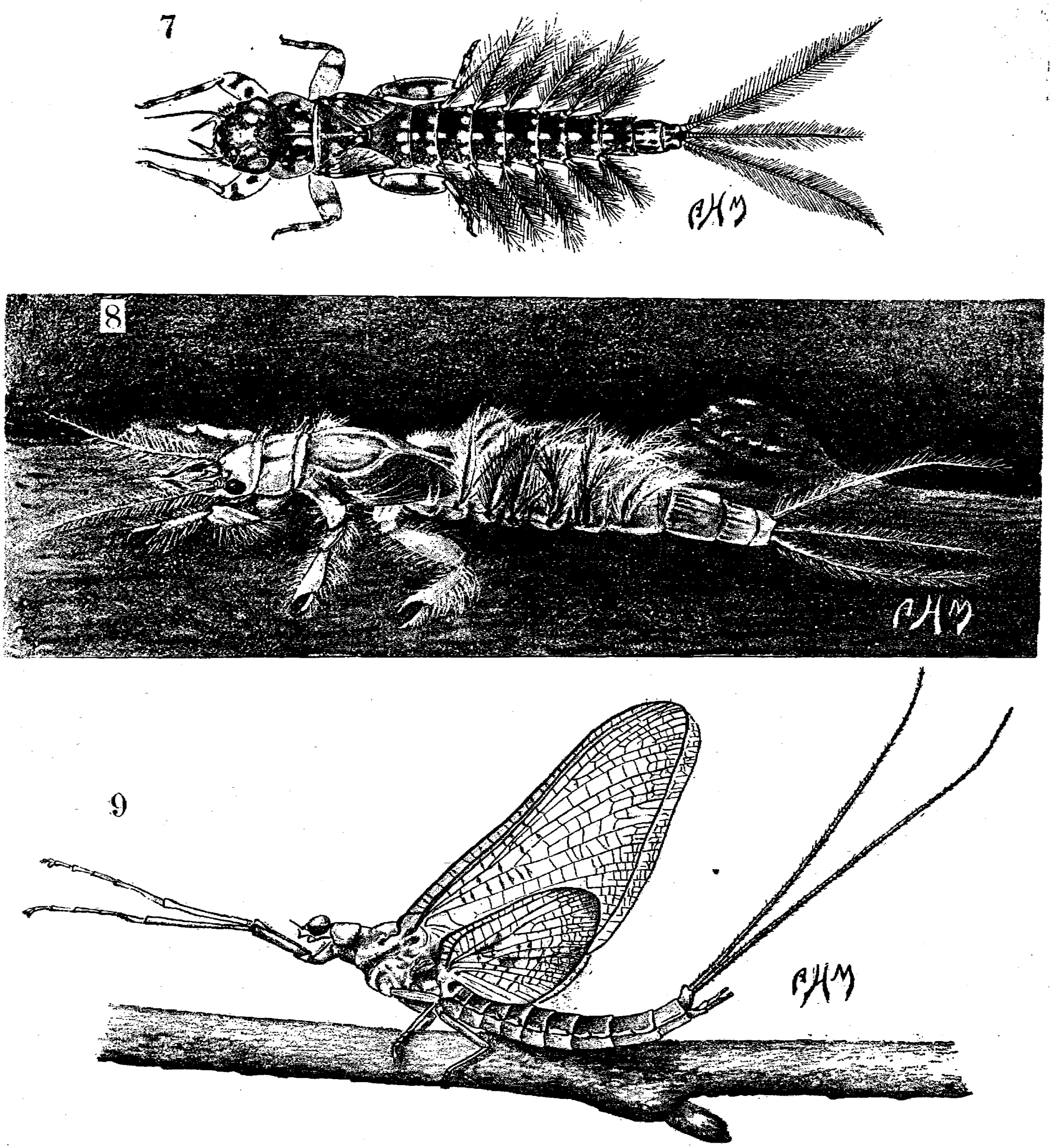

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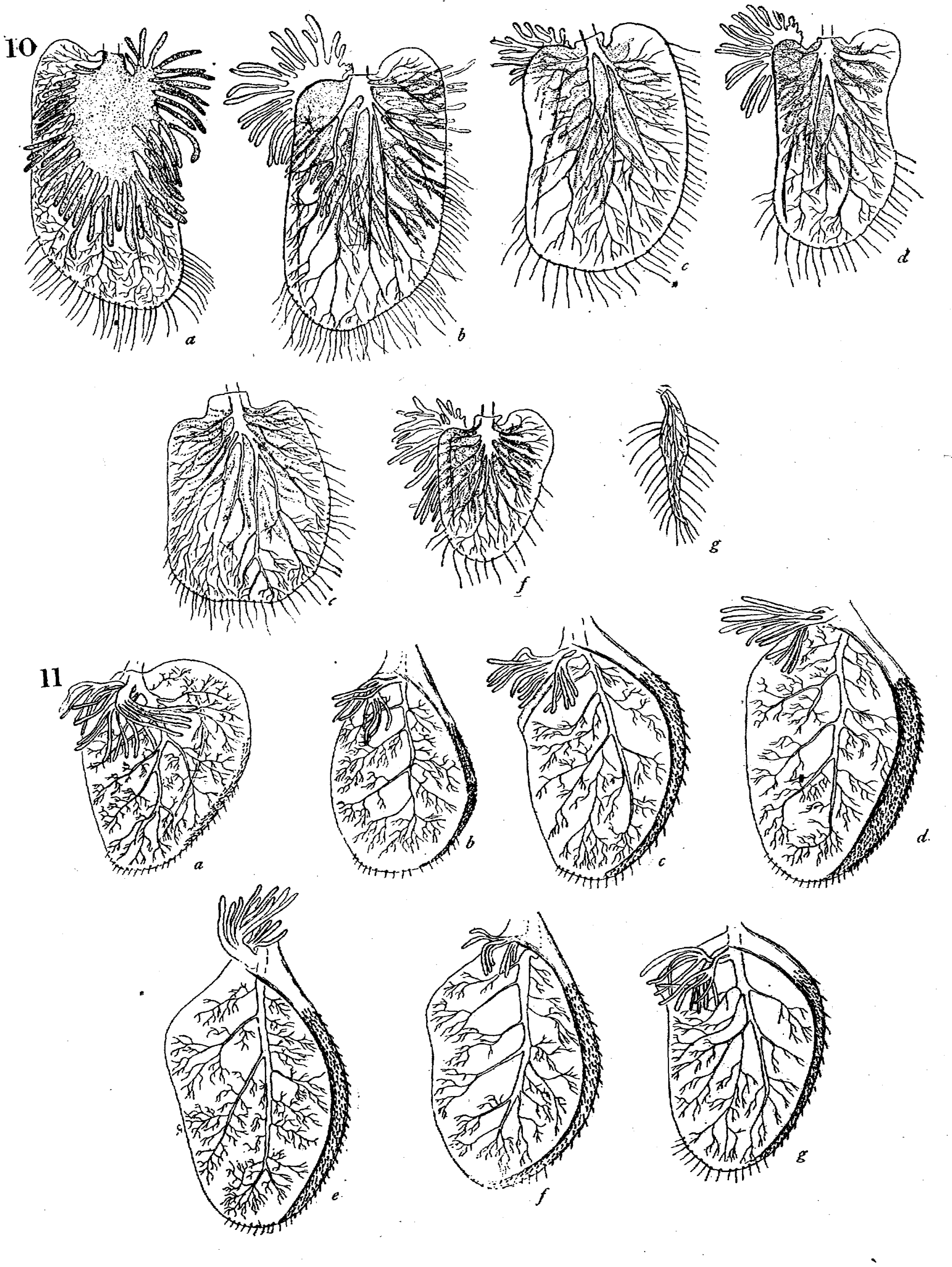

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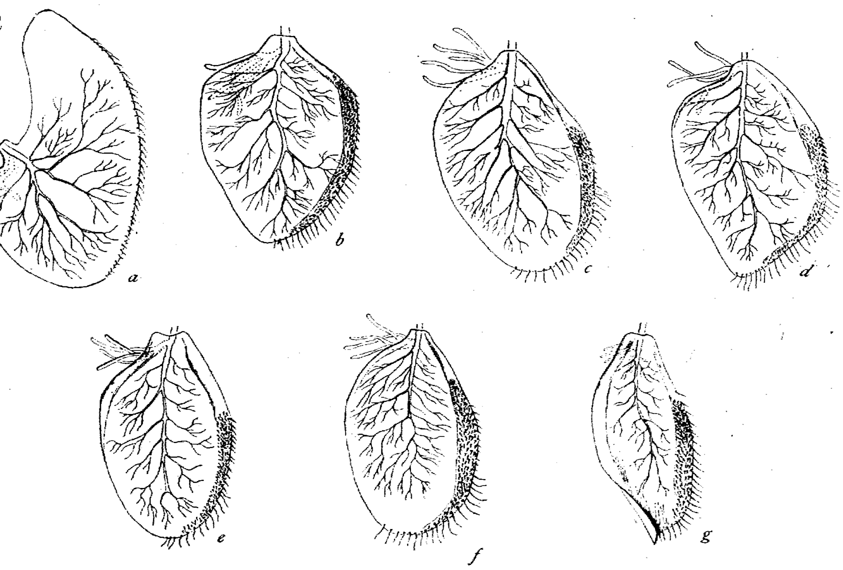

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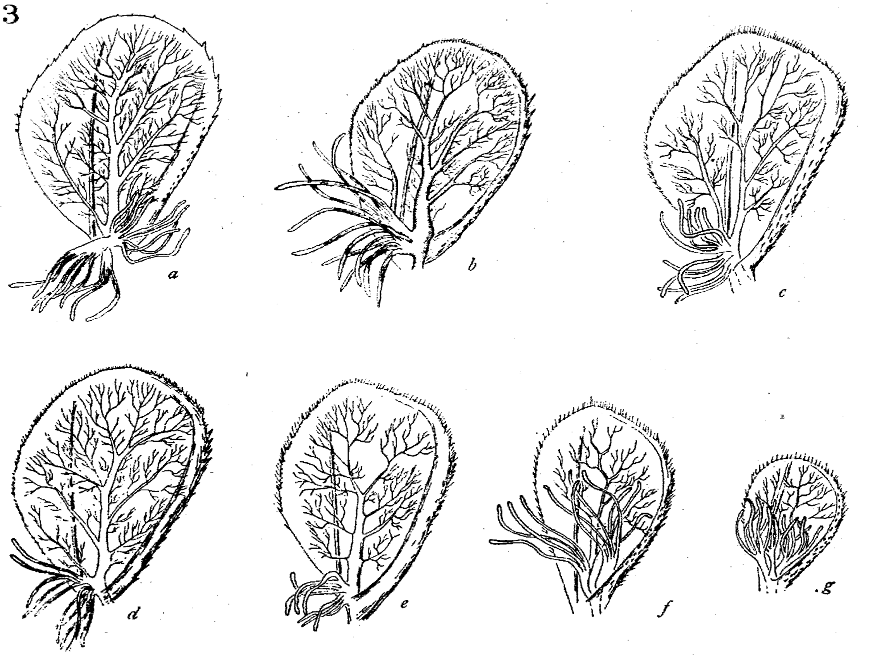

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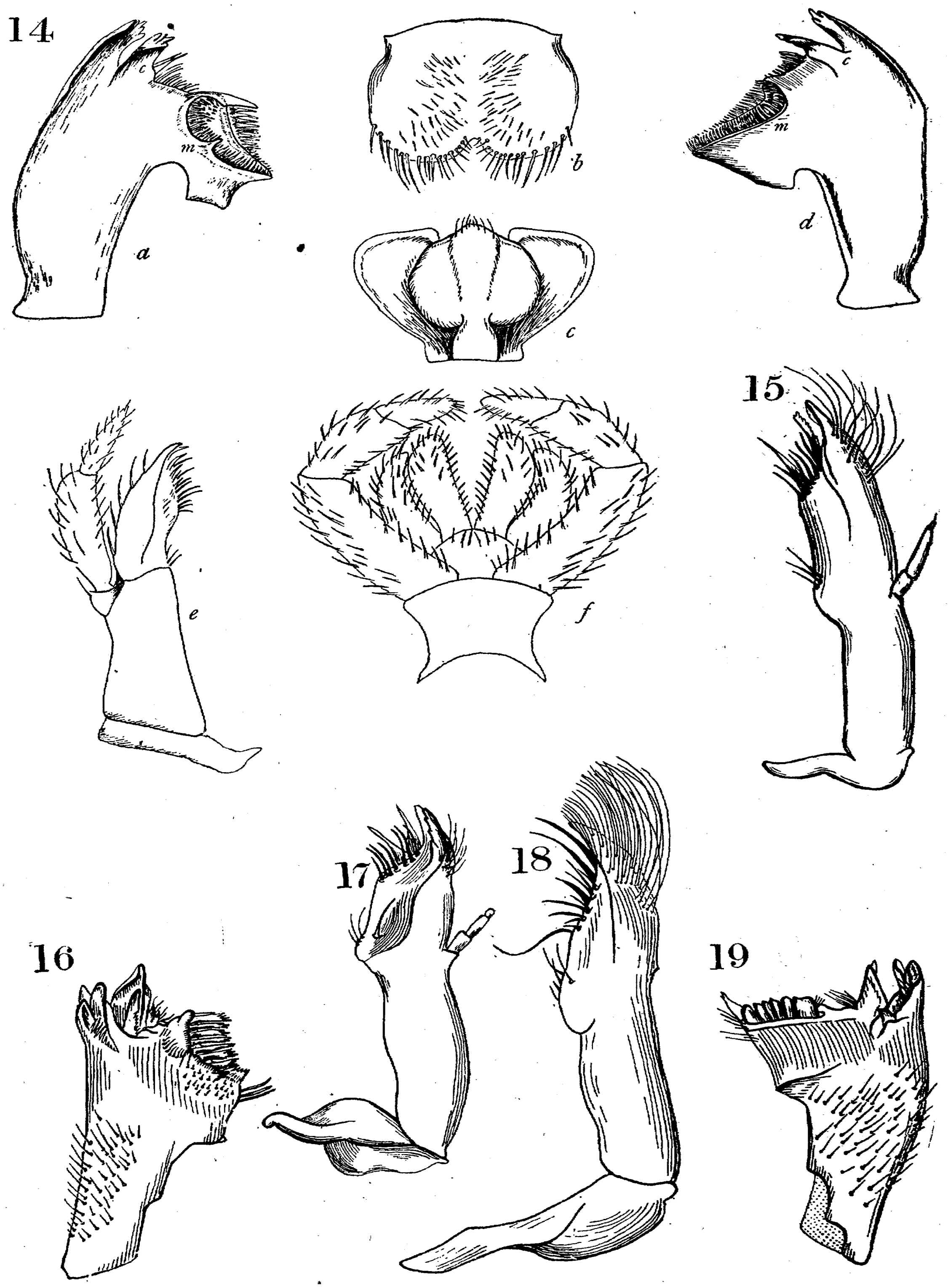

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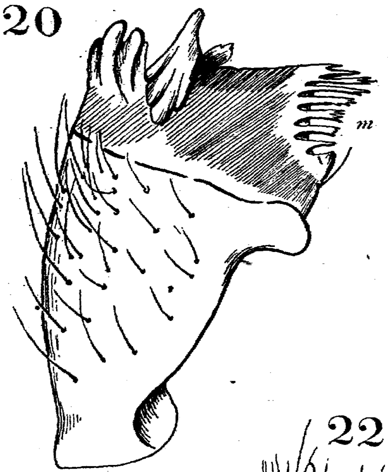

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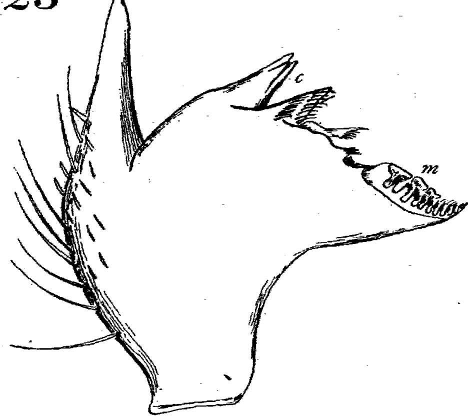

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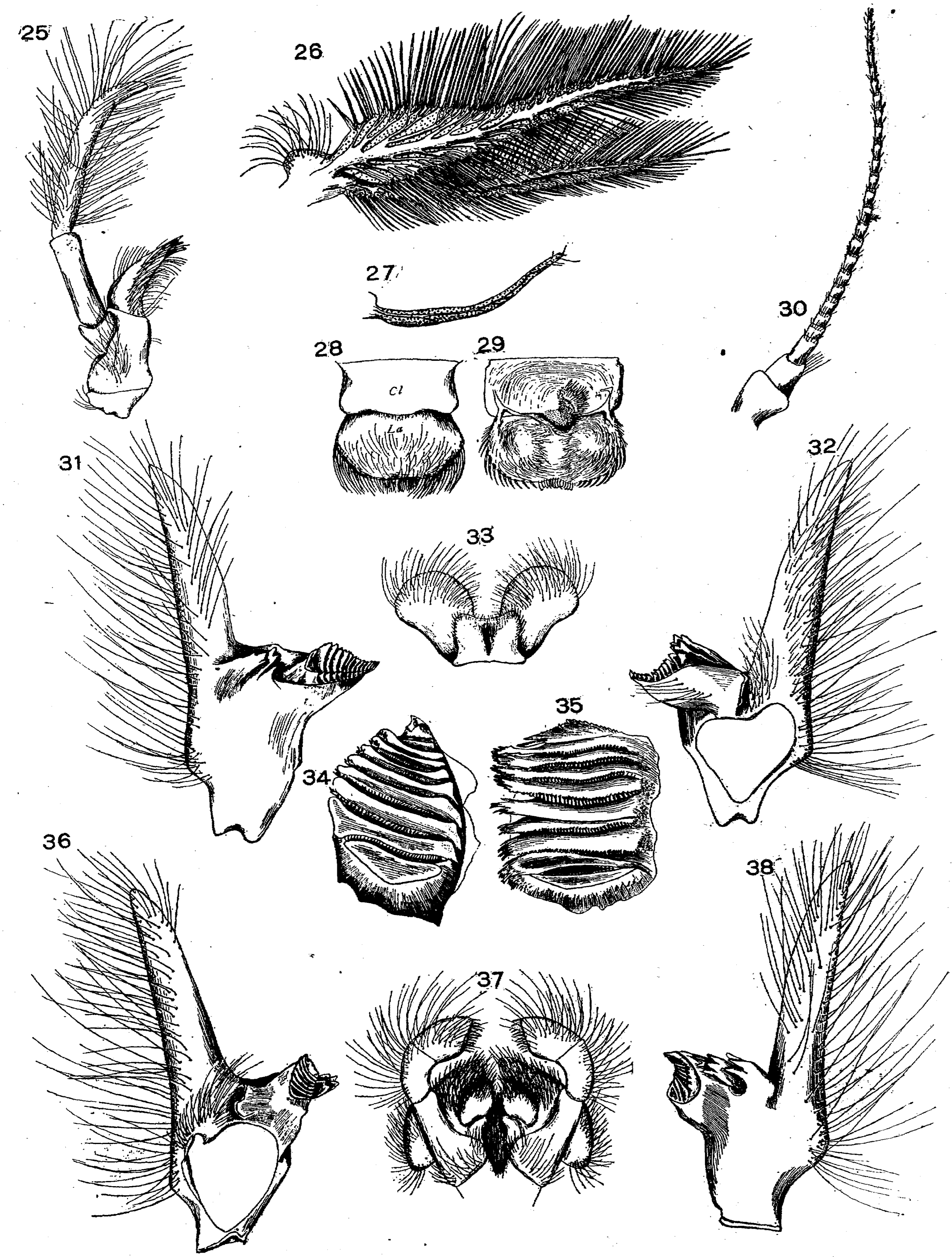

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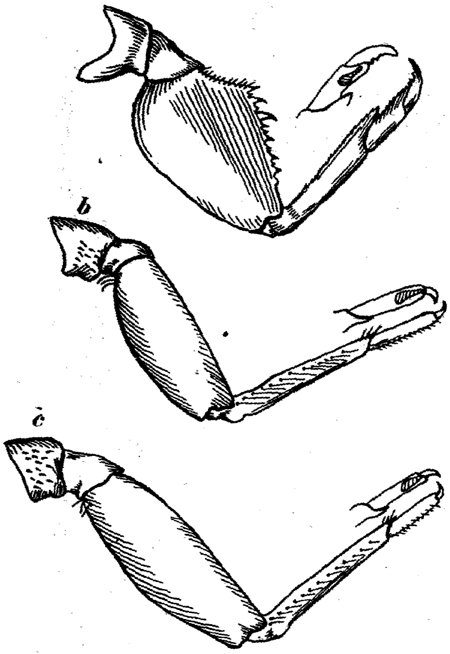

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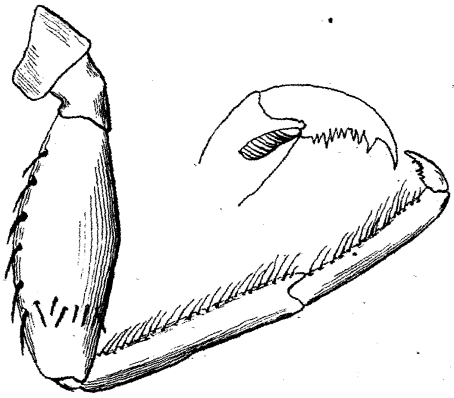

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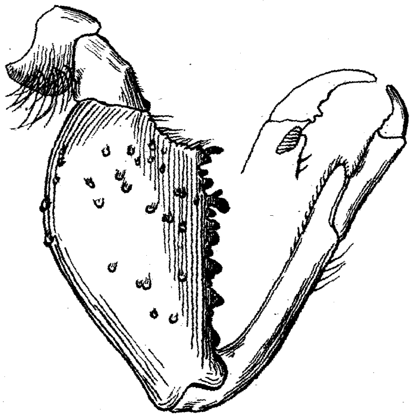

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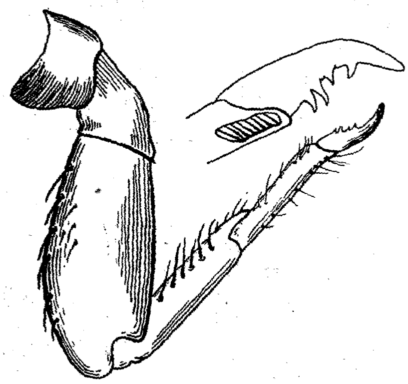

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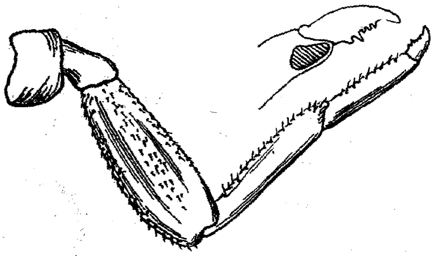

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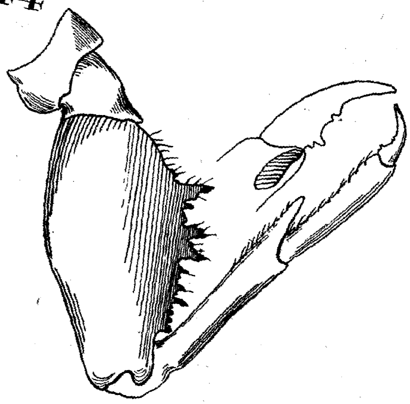

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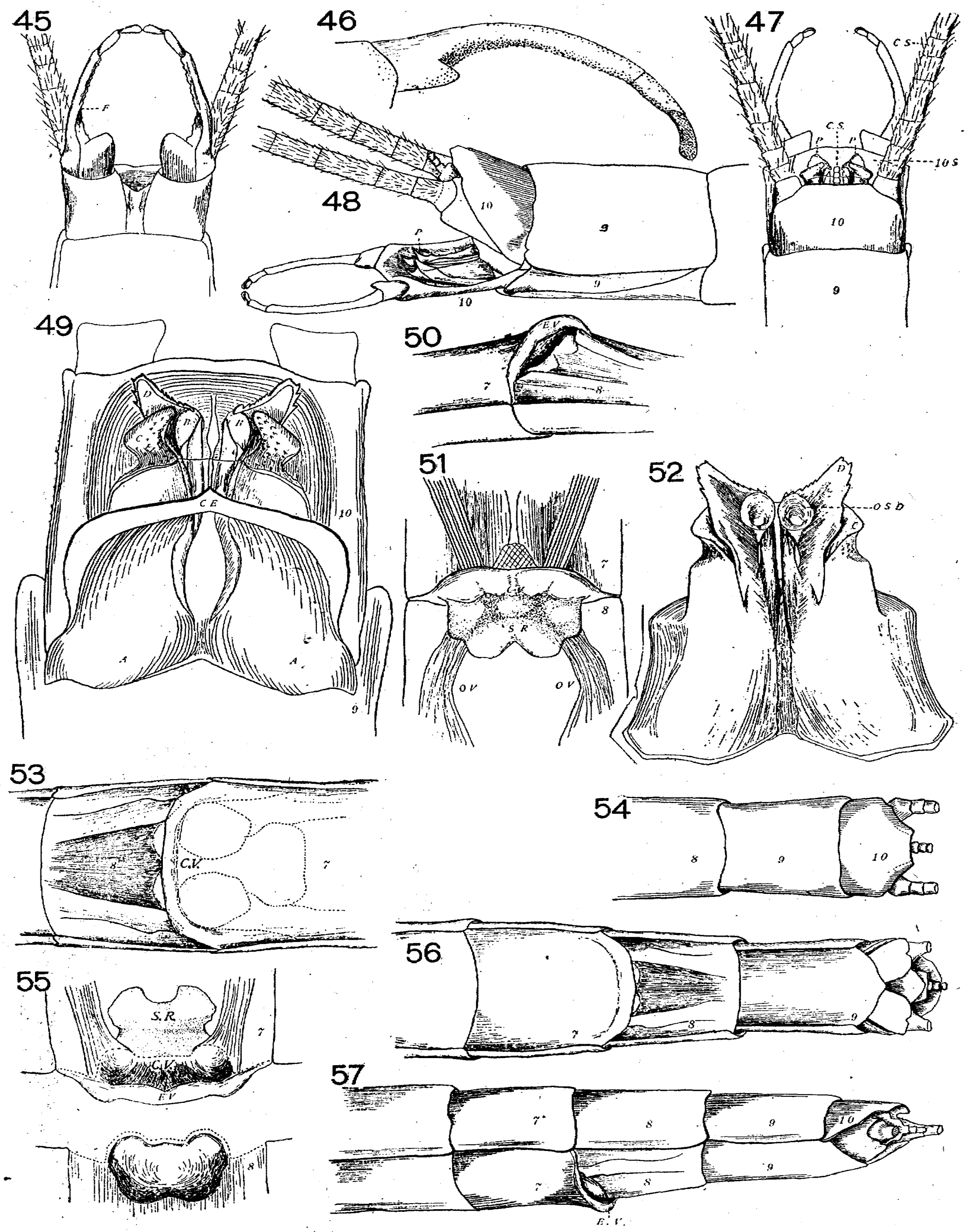

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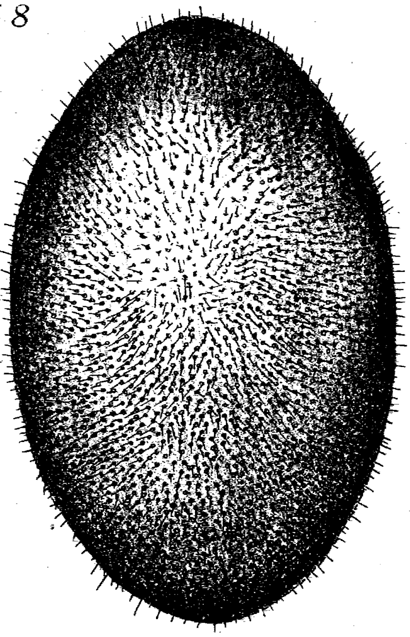

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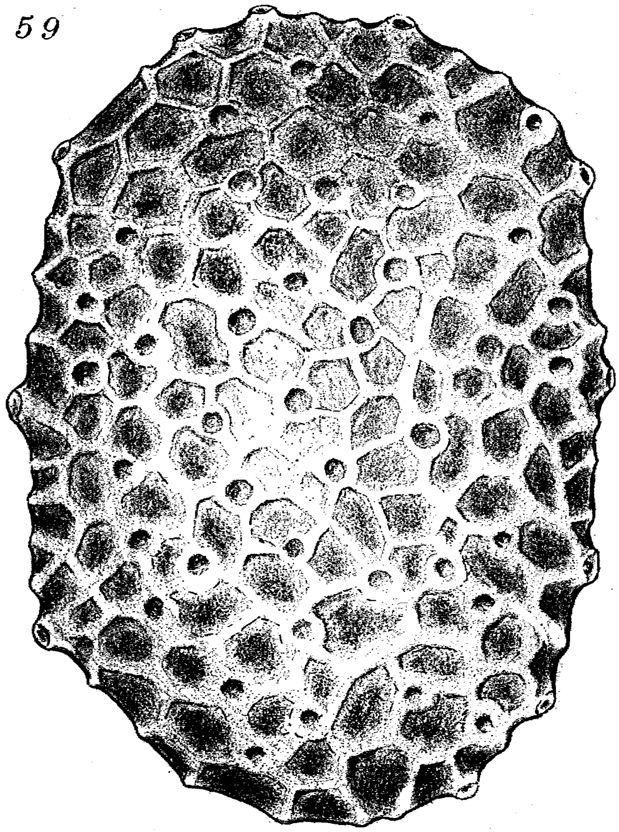

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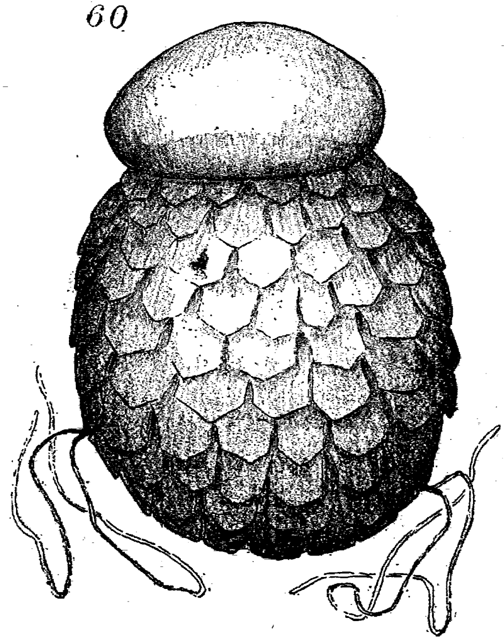

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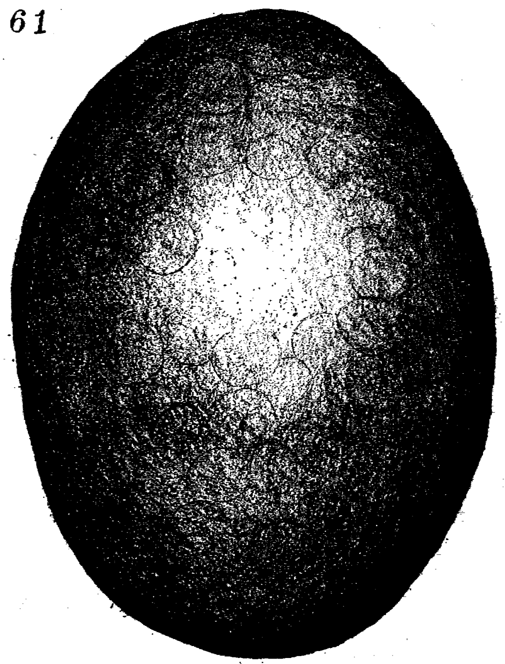

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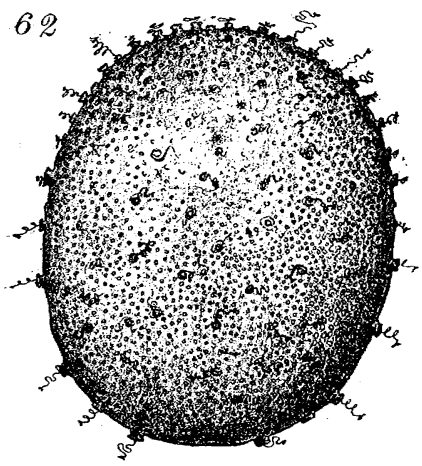

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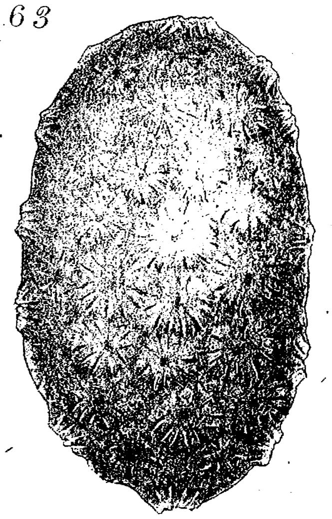

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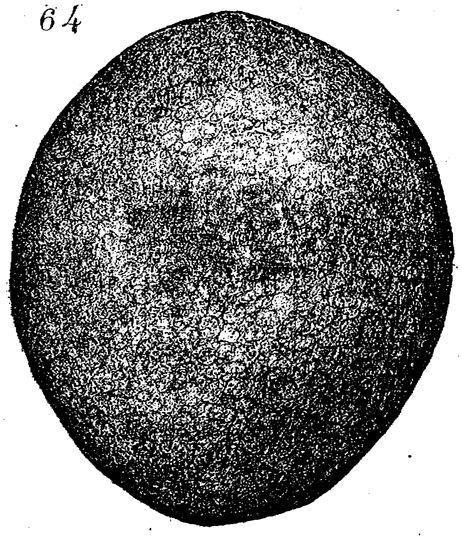

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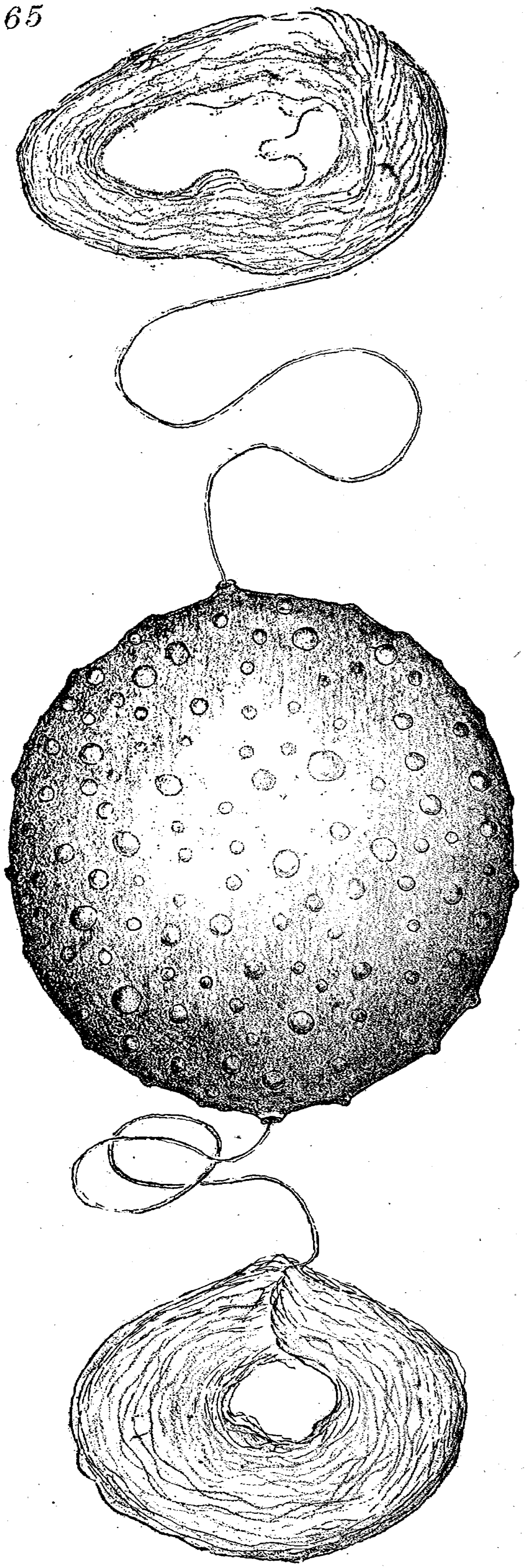

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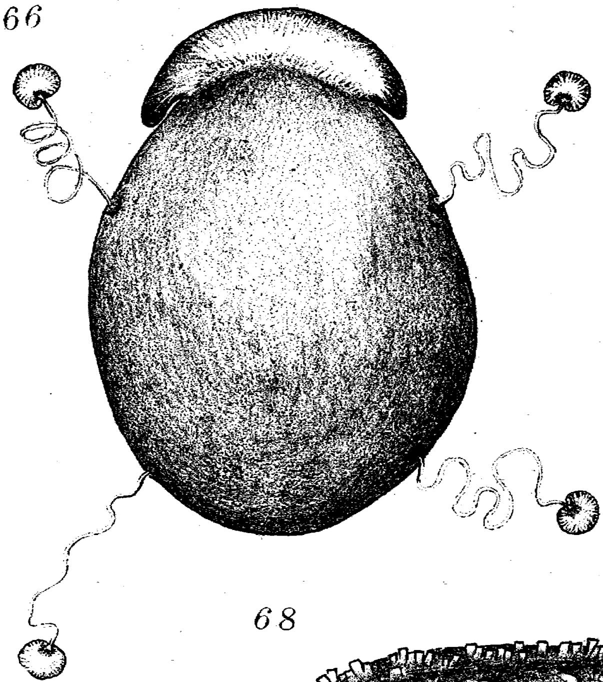

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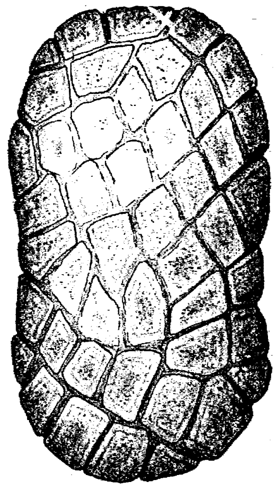

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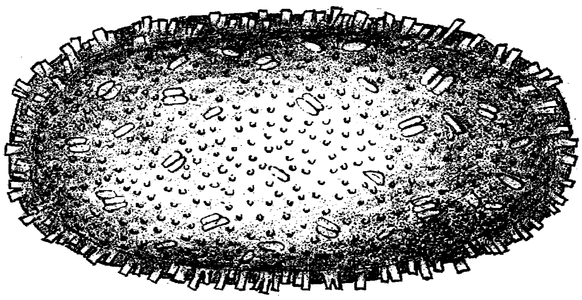

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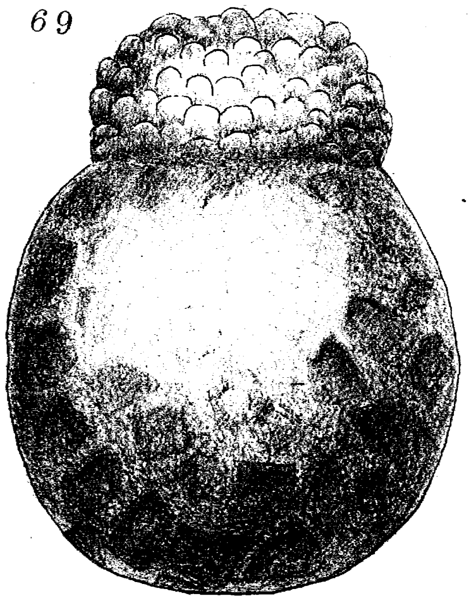

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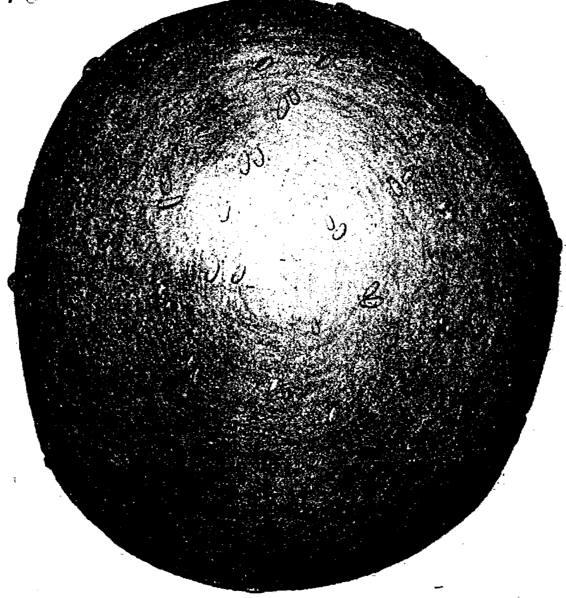

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