

BULLETIN No. 22

1922

ENTOMOLOGICAL SERIES, No. 2

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ENTOMOLOGICAL SERIES, No. 2

NOTES ON THE BIOLOGY OF SOME OF OUR
NORTH AMERICAN SPECIES OF MAY-FLIES.*

HELEN E. MURPHY

- I. The Metamorphosis of May-fly Mouth Parts.
- II. Notes on the Biology of May-flies of the Genus *Baetis*.

*Contribution from the Limnological Laboratory, Cornell University.

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I—The Metamorphosis of May-fly Mouth Parts

I—INTRODUCTION

This paper is a study of the metamorphosis of May-fly mouth-parts. It follows the development of mouth-parts in the embryo, and their changes in form and structure in nymph, subimago and imago.

The life cycle of a May-fly is divided into two main parts: a relatively long period of development spent in the water; and a brief aerial existence devoted entirely to reproduction. The female either drops the eggs at the surface of swift or stagnant water, or, as in *Baetis*, creeps into the water, and deposits them on stones in tiny, single-layered patches. From the time of hatching, nymphal activities are concentrated mainly on food and growth. Indeed, all the eating for a life time takes place during this stage. When nymphal life is completed, the insect usually swims to the surface of the water, sheds its skin, and flutters through the air to some support. There it sits, with wings uplifted, and fore legs thrust stiffly forward, waiting for the subimaginal molt. Then the imago or true adult emerges and joins an assemblage of its own species. A mating dance follows. They rhythmically rise and fall in flight, soaring aloft to various heights and falling ecstatically with wings outspread. Soon the females leave the throng one by one, and fly away to deposit their eggs. The males prolong the joyous revel until exhausted. A little later the dead bodies of all are washed about in the water.

II—TECHNIQUE

EMBRYOLOGY. The principal material used for the study of the embryology of the mouth-parts has been *Baetis posticus*. The eggs were treated as follows:

Hot water	1 minute
Bouin's fluid	12 hours
65% alcohol	72 hours
75% alcohol	24 hours
80% alcohol	24 hours
85% alcohol	24 hours
90% alcohol	24 hours
95% alcohol	24 hours
Abs. alcohol	1 week

The absolute alcohol hardened the embryos so that the outer membranes could be removed without injury to the specimens. The eggs were stained 24 hours with hydrochloric carmine, and differentiated with acid alcohol. Then they were

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transferred to weak glycerine, where dissections were made with No. 12 Sharp's cambric needles under a high power binocular microscope. When mounted in weak glycerine the embryos could be rolled in various directions without injury. For permanent preparations the specimens were dehydrated through the alcohols, cleared in equal parts of absolute alcohol and cedar oil for 12 hours, cedar oil for 6 hours, and xylol for 1 hour. Then they were mounted in balsam.

MUSCULATURE. For a study of the nymphal musculature, dissections of newly molted specimens were made in glycerine. In toto preparations were made by killing the specimens in formalin, dehydrating through the alcohols, clearing in xylol, and mounting in balsam. Serial sections were cut 10 microns in thickness, and stained with Delafield's hematoxylin and picro-fuchsin.

EXTERNAL MORPHOLOGY. Specimens used for study of the external morphology were boiled in 5% KOH until only the chitinized parts were left. Then they were stained with picro-carmin.

INTERNAL METAMORPHOSIS. The material used for the internal metamorphosis of the mouth-parts was *Hexagenia recurvata*.

For histological examination, specimens were treated as follows:

Hot water	1 minute
*Helly's fluid	12 hours
Running water	12 hours
67% alcohol	24 hours
82% + tincture of iodine.....	72 hours
90% alcohol	12 hours
95% alcohol	12 hours
Abs. alcohol	12 hours
Xylol	6 hours
Xylol-paraffin	6 hours
Pure paraffin	3 hours

Sections were cut 9 microns thick, and stained from water with Giemsa's blood stain (1 drop: 1 cc. H₂O) for 45 minutes. They were washed in distilled water until a faint pinkish tinge appeared; then dehydrated through the alcohols, cleared in cedar oil, passed through xylol, and mounted in neutral balsam. Material fixed in Zenker's fluid and stained with Delafield's hematoxylin and eosin gave good results for muscle degeneration, but did not differentiate the plasma cells.

PLASMA SMEARS. For plasma smears from nymph, subimago and imago, a thoracic leg was dipped in 95% alcohol, allowed to dry, and then severed. The

*HELLY'S FLUID: Potassium dichromate, 2.5 gms.; sodium sulphate, 1 gm.; mercuric chloride, 3 gms.; .6% sodium chloride solution, 100 cc.; formalin, 5 cc. added just before using. This fluid preserves the granules in the plasma cells and permits their identification in sections.

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drop of fluid that exuded was touched to a glass slide and the smears made in the usual manner. They were fixed in absolute alcohol for 15 minutes. This has the added advantage of dissolving the fat. Smears were stained with Giemsa's blood stain (1 drop: 1 cc. distilled H₂O) for 20 minutes, and rinsed in distilled water until the better-spread portions had a pinkish tint. Smears were also fixed in Helly's fluid and used as checks on the ordinary smears.

III—HISTORICAL

The earliest work on the embryology of May-fly mouth-parts is probably that published by Burmeister in 1848. He mentions the rudiments of the mouth-parts in *Palingenia horaria* twelve days after oviposition. N. Joly in 1876 wrote a paper on the embryology of *Palingenia virgo*. He figures the mouth-parts during the later stages of development, and says that they are modified considerably before they reach their ultimate form. Heymons, 1896, gives general figures of the mouth-parts of *Ephemera vulgata*. He erroneously calls the mandibular tusk the "morphological equivalent of a mandibular palp."

The greater part of the work on the mouth-parts of May-fly nymphs has been published by systematists. Among the earlier workers, Pictet 1843, Hagen 1849-90, and Eaton 1883-6, stand pre-eminent. Needham 1901-8 published a key for the separation of our common North American genera of May-fly nymphs, and grouped them in three sub-families. A large number of nymphs were also described from bred specimens. His life-history work was followed by that of Morgan 1911, and Clemens 1913-17. Morgan 1913 gives a very complete bibliography and historical review of the entire field. She treats the modifications of the mouth-parts as an adaptation to environment. The main lines of specialization in the three sub-families are sketched, and the details of the mouth-parts. There is a discussion of food, and the function of the individual mouth-parts in feeding.

The atrophy of May-fly mouth-parts during aerial life has long been a matter of observation among students of this group. In 1661 Johann Swammerdam writes: "In the adult condition these insects (Ephemeridae) do not eat, as is the case with various other insects. The mouth-parts and alimentary canal of the winged fly are completely useless and empty." Wolter, 1883, speaks of the fusion of the labial segments in the imago. In 1907 Sternfeld says that degeneration begins in the late nymph. Loss of segmentation is the main difference in the mouth-parts of subimago and imago. He concludes that the form of the mouth-parts is highly variable among the different genera.

MOUTH PARTS OF THE EMBRYO.

IV—MOUTH PARTS OF THE EMBRYO

The eggs of *Baetis sp.* are laid on stones in swift water in single-layered masses of eighty-five to three hundred. They are covered with a thready, viscid substance which causes them to adhere to each other and to the stones. An individual egg (Pl. I, fig. 1) is ovoid in shape and measures .152 mm. x .081 mm. The chorion is yellowish and slightly pitted.

Eggs brought into the laboratory hatched eleven days* after oviposition. The ventral plate (Pl. I, fig. 2, Vp) appears the second day, and differentiates within twenty-four hours into primitive streak and amnion. One day later the head, thoracic and abdominal regions are distinct (Pl. I, fig. 3). Then the mouthpart rudiments appear almost simultaneously (Pl. I, fig. 5). Thoracic legs are differentiated and abdominal segmentation is complete on the sixth day. Embryonic development is finished five days later. Straightening the legs and flexing the abdomen, the nymph emerges through a middorsal slit in the chorion. It begins to eat immediately.

DEVELOPMENT OF THE MOUTH-PARTS.

CLYPEO-LABRUM. The clypeo-labrum arises as an evagination between the procephalic lobes. On the fifth day, at the time of origin of the paired mouthparts, it is a median hemispherical papilla (Pl. I, fig. 5, Clp. Lm). The clypeo-labral suture (Pl. I, fig. 6) is evident on the eighth day. The anterior border of the labrum becomes rounded and emarginate. The sensory hairs appear as tiny papillae (Pl. I, fig. 7) on the tenth day. They are elaborated just at hatching (Pl. I, fig. 8).

MANDIBLES. The mandibles arise as simple cone-shaped papillae during the fifth day of embryonic development (Pl. I, fig. 5, md). A protuberance soon appears at the inner apical region (Pl. I, fig. 9, ia). A little later the mid-apical region is indistinctly divided into two parts (Pl. I, fig. 10, c). As the mandible elongates, the outer lateral region becomes less rounded, and the inner lateral portion slightly bulged. The eighth day the apical portion begins to swing toward the mid-ventral line. At that time the two mid-apical parts, destined to become the nymphal canines, are more distinctly defined (Pl. I, fig. 11, c). Serrations appear at the tips of the canines, and the molar surface is indicated on the inner-lateral bulge by tiny papillae. The ginglymous articulations on the dorsal and the ventral surface are evident, and the inner-apical lobe is movable. The molar papillae increase in size and become confluent to form transverse ridges. These ridges are wedge-shaped, with the apex pointing upward. At hatching the mandible (Pl. I, fig. 12) is dorso-ventrally flattened, and the molar surface (ms.) inclined obliquely ventrad. The two canines (oc., ic.) each possess four teeth at the tip. Molar surface, canines, ginglymous articulation (ga.), and movable inner lobe (il.) are heavily chitinized.

*Twenty-eight days in the cooler water of the creek.

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HYPOPHARYNX. The hypopharynx is evident near the dorsal base of the labium on the eighth day. It then consists of three single papillae: a median papilla between the bases of the two maxillae; and a lateral papilla at either side near the bases of the mandibles. With the forward migration of the mouth-parts, they are crowded together. At hatching, the hypopharynx (Pl. I, fig. 13) is a trilobed structure with sensory hairs.

FIRST MAXILLAE. The first maxillae arise as simple cone-shaped papillae (Pl. I, fig. 5, mx.1.) similar to those of the mandibles, but they elongate more rapidly. A lobe soon appears on the outer lateral region (Pl. I, fig. 14, ol). This is the future palp. The apical region becomes rounded and flattened. Then this area subdivides into two parts (Pl. I, fig. 15, oa, ia). The outer apical region differentiates into the galea; the inner into the lacinia. As the galea-lacinial portion elongates, the cleft between the two parts increases. On the eighth day segmentation in the palp and cardo-stipital region is indicated by notches (Pl. I, fig. 16). Galea and lacinia gradually fuse. The cardo becomes distinct, but neither the palpifer nor the suture between the stipes and galea-lacinia is differentiated. Spines appear as cone-shaped papillae at the distal part of the galea-lacinia on the tenth day. At hatching, hairs are evident on the distal palp segment (Pl. I, fig. 17, Mx. Plp), and the inner galea-lacinial region (Pl. I, fig. 17, Ga Lc). This part is chitinized heavily; the palp very weakly.

SECOND MAXILLAE OR LABIUM. The second maxillae arise as cone-shaped papillae on the fifth day (Pl. I, fig. 5, Mx2). They become bi- and tri-lobed (Pl. I, fig. 18) at the same time as the first maxillae. On the seventh day a secondary, lower-median lobe appears (Pl. I, fig. 19, lm) and the two second maxillae migrate toward the mid-ventral line. The secondary lobes fuse first (Pl. I, fig. 20, lm). At that time the galea and lacinia are distinct (Pl. I, fig. 20, Ga, Lc). There are also traces of segmentation in the palp (Pl. I, fig. 20, Lb Plp), and indications of the submentum below the fused lower-median lobes. The large central portion becomes the mentum of the nymphal labium (Pl. I, fig. 21, M), the lacinia the glossa (gl) and the galea the paraglossa (Pgl). A third distal segment of the palp is incompletely differentiated (Pl. I, fig. 21, Lb Plp). Spines and hairs are elaborated at the same time as those of the first maxilla.

The early appearance of the inner lobe on the mandible, and the fact that it is articulated, but has no musculature, suggests the possibility of a primitive structure. It occupies the same relative position on the mandible as the lacinia mobilis of certain crustacea (*Mysis*, *Arolana*). Embryological evidence indicates that the movable inner lobe of the May-fly mandible is a lacinia.

A mandibular palp is present at no stage of embryonic development. *Ephemera vulgata* used by Heymons for his embryological study is a burrowing May-fly. The mandibular tusk, which he calls the "morphological equivalent of a mandibular palp" is a secondary modification appearing at the time of differentiation of the canines and molar region. It is not lateral in origin, but arises from the outer apical region.

MOUTH PARTS OF THE NYMPH.

V—MOUTH PARTS OF THE NYMPH

May-fly nymphs are divided systematically into three sub-families: the Ephemerinae, Heptageninae, and Baetinae. The Ephemerinae (Pl. II, fig. 23) are mud or gravel dwellers. The bodies of those that live in mud are elongate and cylindrical in form, with feet adapted for scooping, and mandibular tusks for lifting. The Heptageninae (Pl. II, fig. 22) are found in running water, generally clinging to the under surface of stones. The head, thorax, abdomen and legs are strongly depressed. The head margins are flaring to deflect the current. The more generalized of the Baetinae (Pl. II, fig. 24) inhabit the still waters of ponds and pools. Some of this group intermingle with the Heptageninae in the swift waters; others associate with the Ephemerinae on the sediment-covered bottom in mud and silt.

The food of May-fly nymphs mainly consists of algae, diatoms, and the dead tissues of higher plants. Members of the Heptageninae have mouth-parts adapted for scraping algae and diatoms from the stones. *Rhithrogena* uses the blade-like distal segment of the maxillary (Pl. V, fig. 69, Mx Plp) and labial palp as a rake. The labrum in front, maxillae at the sides, and labium in the rear brush the food into the mouth cavity. There it falls upon the molar surface of the mandibles, and is ground. The Ephemerinae grind up the mud and silt and digest the diatoms and plant waste. Among the Baetinae, some rasp and strip pieces from roots and stones; some grind the silt in the manner of the bottom-living Ephemerinae; and others have diverse brushes or bristles for use in swift water.

MUSCULATURE.*

I. LABRUM.

Abductor (L'éleveur du labre, Str-D; musculus levator labri, Bauer). The abductors of the labrum (Pl. III, fig. 35, Abd.) are a pair of median muscles originating in the front of the head between the antennae, and inserted in the proximal portion of the labrum by a very short tendon.

Adductor. The adductors of the labrum (Pl. III, fig. 35, ad) are two two-headed muscles inserted by a long tendon, one at either side of the basal angle. They are attached to the front of the head just below the bases of the antennae.

*Owing to the various systems of nomenclature, uniformity in designating the muscles of the mouth-parts is impossible at present. Since the musculature for May-flies is similar to that reported for *Gryllus* by DuPorte (Ann. Ent. Soc. Am. 13:19-23), I have adopted his system to avoid further confusion. Whenever possible, nomenclature previously used is indicated.

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EPIPHARYNX.

The epipharyngeal muscles (Pl. III, fig. 35, epl, ep2) are two cone-shaped muscles attached to the inner surface of the labrum and epipharynx near the median line.

II. MANDIBLE.

Flexor. The flexor of the mandible (Pl. III, fig. 34, F1; Pl. II, fig. 26, F1) is a large three-parted muscle attached to the anterior part of the body of the tentorium (Tn), and inserted at the outer wall of the body of the mandible.

Adductor. (Adducteur des mandibules, Str.-D.; flexor mandibulae, Burm.; musculus flexor mandibulae, Bauer). The adductor of the mandible is a strong pyramidal shaped muscle (Pl. III, fig. 34, ad), its attachment filling the anterior part of the head capsule as far forward as the eye and upper part of the brain. It is inserted by a strong sheath-shaped tendon at the upper, inner angle of the dorsal surface of the mandible (Pl. II, fig. 26, ad).

Abductor. (Abducteur de la mandibule, Str.-D.; extensor mandibulae, Burm.; musculus extensor mandibulae, Bauer). The abductor of the mandible (Pl. III, fig. 34, Abd; Pl. II, fig. 26, Abd) is a slender muscle inserted at the lower outer-angle of the ventral surface by a short tendon, and attached to the postgena at a level with the top of the eye.

The mandible is attached on its dorsal surface to the postgena by a large heavily chitinized articulation (Pl. II, fig. 26, 25 ga.) and ventrally at its lower inner angle by a much smaller ginglymous joint (fig. 25, 26 ga.; fig. 27). With these two articulations as pivots the mandible rocks toward the median line in a dorso-ventral plane.

III. HYPOPHARYNX.

Elevator. The elevator of the hypopharynx (Pl. III, fig. 36, E1) is inserted at the ventral basal angle of the median lobe, and attached to the midlabial apodeme.

Retractor. The retractor of the hypopharynx (Pl. III, fig. 36, R) is a long slender muscle inserted on the dorsal surface at the point of fusion of the lateral and median lobe. It is attached to the base of the central plate of the tentorium at the side of the labial retractor.

Depressor. The depressor of the hypopharynx (Pl. III, fig. 36, d) is a single muscle attached to the midapical region of the median lobe and inserted in the central apodeme (ap.). With the retractor this muscle aids in opening the pharynx.

Compressor. The compressor of the hypopharynx (Pl. III, fig. 36, co) is a mid-lateral muscle attached to the junction of the labium and hypopharynx, and inserted at the central apodeme (ap.). With the elevator it aids in blocking the pharyngeal opening.

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In Ecdyurus, one of the Heptageninae, the hypopharynx (Pl. III, fig. 37) is not heavily chitinized and is relatively large. The compressors form a delicate horizontal sheath (co) around the median lobe (m), and the depressors a vertical sheath (d). The lateral lobe (l) is provided with one depressor (d) and two compressors (co).

In Callibaetis (Pl. V, fig. 67) and Baetis (Pl. I, fig. 13) (Baetinae) no musculature is evident within the hypopharynx.

IV. MAXILLA.

Flexor. (Musculus flexor anterior, Bauer). The flexor of the maxilla (Pl. III, fig. 38, F1) is a two-parted muscle attached to the outer edge of the stipes (St) and inserted at the lower part of the central plate of the tentorium.

Adductor. (Adducteur de la machoire, Str.-D.; flexor maxillae, Burm.; musculus flexor maxillae Posterior, Bauer). The adductor of the maxilla (Pl. III, fig. 34, ad) is a two-parted muscle inserted at the outer and basal angles of the cardo (Cd). It is attached to the lower surface of the central plate of the tentorium.

Abductor. (Musculus flexor superior, Bauer). The abductor of the maxilla (Pl. III, fig. 38, Abd) is a slender two-parted muscle inserted at the lower inner angle of the galea-lacinia (Ga Lc) and attached to the posterior arm of the tentorium.

Flexor of galea-lacinia. The flexor of the galea-lacinia (Pl. III, fig. 38, F1) is inserted at the outer angle of the stipes (St) and attached to the galea-lacinial apodeme (ap).

MAXILLARY PALP.

Extensor. (Musculus extensor palpi maxillaris, Bauer). The extensor of the maxillary palp (Pl. III, fig. 38, e) originates at the stipital apodeme and is inserted at the outer angle of the base of the first palp segment.

Flexor. The flexor of the maxillary palp (Pl. III, fig. 38, f) originates at the stipital apodeme and is inserted at the inner angle of the base of the first palp segment.

The flexor (Musculus flexor articuli palpi maxillaris, Bauer) of the second palp segment (Pl. III, fig. 38, f) originates at the outer basal angle of the first segment, and is inserted by means of a slender tendon into the inner basal angle of the second segment. The extensor of the second palp segment (Pl. III, fig. 38, e) originates at the inner basal angle of the first segment and is inserted into the outer basal angle of the second segment. This system of cross attachments gives greater leverage to the blade-like distal segment. In those forms where

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the palp is not used as a scraper, the attachment is on the same side as the insertion.

V. LABIUM.

Retractor. The retractor of the labium (Pl. III, fig. 39, R) originates at the base of the central plate of the tentorium, and is inserted at the lateral border of the ligula (Lg) near the base of the paraglossa (Pgl).

Adductor. The adductor of the labium (Pl. III, fig. 39, ad) originates in the submentum (Sm) near the median line, and is inserted in the proximal border of the ligula (Lg).

Abductor. The abductor of the labium (Pl. III, fig. 39, Abd) originates at the basal edge of the tentorium, and is inserted at the outer angle of the distal border of the mentum (M).

LIGULA.

Adductor. The adductor (Ad) of the paraglossa (Pgl) is attached at the base of the ligula not far from the median line, and is inserted near the center of the base of the paraglossa. The adductor (ad) of the glossa (gl) originates in the central area of the ligula and is inserted at the base of the glossa.

LABIAL PALP.

Extensor. The extensor of the labial palp (Pl. III, fig. 39, e) originates at the central apodeme (ap) and is inserted at the outer angle of the base of the first palp segment.

Flexor. The flexor of the labial palp (Pl. III, fig. 39, f) originates at the central apodeme (ap) and is inserted at the inner angle of the base of the first segment of the palp.

Within the palp, the extensors (e) arise on the outer side, and the flexors (f) on the inner side of the basal angle, and are inserted into the outer and inner side of the basal angle of the next distal segment.

The extreme development of labial musculature is found among the Heptageninae. The palp muscles are enormously increased in size and their insertion shifted to give greater leverage. The extensor of the palp (e) of *Ecdyurus* (Pl. III, fig. 40) is inserted far out on the lateral surface of the basal segment. It has no opponent. Within the palp the attachment of the flexor (f) of the second segment extends across the base and along the outer lateral surface of the first segment. The adductors (ad) and abductors (Abd) of the labium are sheath-like bands extending across the fused ligula and mentum. Glossa (gl) and paraglossa (Pgl) each possess one abductor (Abd) and two adductors (ad).

MOUTH PARTS OF THE NYMPH.

SURVEY OF THE MOUTH-PARTS.

A survey of the mouth-parts of representatives of the various genera* reveals striking variations in form, and diverse adaptations to similar ecological situations.

LABRUM (Pl. IV).

The main variations in the labrum of May-fly nymphs are in the form of the anterior border, and in the cuticular appendages. Judged from embryological evidence, the more primitive form of border is straight, like that of *Ephemerella* (fig. 57) and *Chirotenetes* (fig. 42). There are two lines of deviation from this condition. In the one, the border is notched in the center (*Callibaetes*, fig. 43; *Baetis*, fig. 44). In the other, it is extended laterally and incurved like that of *Ecdyurus* (fig. 46) and *Hagenulus* (fig. 47). The cuticular appendages consist of hairs and spines. Some forms possess both hairs and spines (*Polymitarcys*, fig. 41); some like *Chirotenetes* (fig. 42) have spines only; and others but hairs (*Oligoneuria*, fig. 45). Spines are characteristic of those forms exposed to swift water. Hairs are peculiar to burrowers or sprawlers in the mud.

The labrum of *Hagenulus* (fig. 47), one of the *Baetinae*, is strangely adapted for life in swift water. It is flattened and has an extraordinary lateral extension far beyond the head capsule, simulating the flaring, depressed head of the *Heptagenine* associates. Among these, the mouth-parts are retracted beneath the outgrowth of the head; in *Hagenulus* it is the labrum that protrudes, and the head capsule is small. The backward projecting spines at the free posterior margins in *Hagenulus* doubtless serve for protection.

MANDIBLE (Pls. II, IV).

Molar surface. The primary function of the May-fly mandible is to grind food. For this purpose a molar surface is developed. Among the *Ephemerinae* there is one prevailing type. The left molar surface of *Ephemera* (fig. 31) bears eight transverse ridges, the anterior edge of each provided with teeth. Between these ridges are deep gutters. The right molar surface (fig. 32) has seven transverse ridges toothed at the anterior edge. The molar surfaces (fig. 28) move in a dorso-ventral plane, rubbing together the transverse ridges. The teeth extending out into the gutters doubtless serve as strainers for the food. Cast skins show many of the transverse ridges worn smooth, but the teeth still sharp, and clogged with ground food. Among the *Baetinae* and *Heptageninae* are two main types of molar surface. In one, the transverse ridges are irregularly serrated (fig. 33), with stiff bristles acting as strainers across the gutters. In the other, the transverse ridges are rounded and knobbed (fig. 29, 30). They

*The exotic specimens were very kindly loaned me by Dr. J. G. Needham.

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are broad at the posterior portion, but fray out anteriorly. This is the prevailing type among those forms inhabiting streams with gravel or sand bottom.

The molar surface reaches its maximum of development in *Lachlania* (fig. 56) and *Homeoneuria* (fig. 62). Eaton's nameless Chilean nymph (fig. 63) has no molar surface. He suggests that it is predatory.

Lacinia. The lacinia of the May-fly mandible has been variously named. Eaton, 1883, writes: "The endopodite is often represented by a slender jointless movable appendage attached to the inner base of the inferior lobe, or sometimes by a tuft of hairs." Folsom, 1900 (p. 107) states: "It is an interesting fact that Heymons '96, distinctly represents a mandibular palp for the larva of *Ephemera*,—a rare condition; indeed Packard, '98, terms this appendage of nymphal *Ephemerids* a 'lacinia-like' process, although Heymons states that it is lateral in position, and so figures it." Lestage, 1917, states that a "prostheca" is present. In fig. 1, p. 219, he erroneously labels it a canine and states that the prostheca is absent in that form.

Many varieties of mandibular lacinia exist among the different genera. There are well developed forms. Many of these are articulated at the base (*Baetis*, fig. 60; *Polymitarcys*, fig. 50; *Siphylurus*, fig. 51; *Euthyplocia*, fig. 59). Others are ankylosed (*Choroterpes*, fig. 55; *Leptophyes*, fig. 52; *Heptagenia*, fig. 53). Some laciniae bear teeth at the apex (*Polymitarcys*, fig. 50; *Leptophyes*, fig. 55; *Euthyplocia*, fig. 59). Long brush-like bristles are present on the lacinia of *Leptophyes* (fig. 52), *Polymitarcys* (fig. 50), and *Choroterpes* (fig. 55). In *Siphylurus* (fig. 51) and *Euthyplocia* (fig. 59) the lacinia is covered with short hairs. Sometimes the lacinia is reduced to a slender lobe (*Ameletus*, fig. 61, Lc), or is absent entirely (*Rhithrogena*, fig. 48). Among the *Heptageninae* the lacinia is diminished in size. In *Heptagenia* it is present on the left mandible (fig. 53, Lc) and absent on the right (fig. 54). A row of hairs is often found on those forms where the lacinia is weak or absent. In *Rhithrogena* (fig. 48) the hairs are pectinate. These hairs are cuticular appendages, and entirely different in origin from the lacinia.

Canines. A generalized May-fly mandible possesses two teeth at the apex (Pl. I, fig. 12, oc, ic) known as outer and inner canine. When in position, they are more or less ventrally directed. The two canines of the right mandible of *Hexagenia* (Pl. II, fig. 28) dovetail between the outer and inner canine of the left mandible. The raised surface of the epipharynx fits into the anterior cavity formed by the two outer canines. This explains its position a little to the right of the center in many forms (Pl. III, fig. 34; IV, 43, 44, Ep). In the *Baetinae* and *Ephemerinae* the canines are toothed and used for tearing or holding. In the *Heptageninae* they are more or less scoop-shaped.

A survey of the mandibles of our North American forms confirms the systematic grouping of the three sub-families and reveals generic characters as

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definite as are furnished by other organs. These are summarized in the following key:

- | | |
|--|----------------------|
| I. MANDIBLE WITH TUSK. | <i>EPHEMERINAE.</i> |
| A. Tusk shorter than mandible proper, tf.* 23. | <i>Potamanthus.</i> |
| AA. Tusk longer than mandible proper. | |
| (a) Tusk with spines, and out curved | |
| (b) Outer edge serrated, tf. 12. | <i>Pentagenia.</i> |
| (bb) Outer edge not serrated, tf. 17. | <i>Ephemera.</i> |
| (aa) Tusk without spines | |
| (b) Tusk incurved | |
| (c) Outer edge serrated, tf. 24. | <i>Polymitarcys.</i> |
| (cc) Outer edge not serrated; hairs long and abundant, tf. 21. | <i>Euthyplocia.</i> |
| (bb) Tusk nearly straight, very slightly out curved at tip, tf. 14. | <i>Hexagenia.</i> |
| II. MANDIBLE WITHOUT TUSK. | |
| A. Outer canine with large teeth. | <i>BAETINAE.</i> |
| (a) Outer canine with 5 teeth, tf. 19; inner canine with 4 teeth. | <i>Ameletus.</i> |
| (aa) Outer canine with 4 large teeth. | |
| (b) Inner canine with 5 teeth, tf. 18. | <i>Callibaetis.</i> |
| (bb) Inner canine with 4 teeth, tf. 22. | <i>Baetis.</i> |
| (bbb) Inner canine with 3 teeth. | |
| (c) Outer edge of mandible straight, or nearly so, tf. 3. | <i>Siphylurus.</i> |
| (cc) Outer edge of mandible distinctly curved. | |
| (d) Outer edge of mandible with a distinct curve from base to apex, tf. 8; lacinia bluntly cone-shaped, with short hairs at tip. | <i>Caenis.</i> |
| (dd) Outer edge of mandible with a distinct curve at the apex; lacinia with long hairs at the tip, tf. 10, 25. | <i>Blasturus.</i> |
| (bbbb) Inner canine with 2 teeth. | |
| (c) Outer edge of mandible with a distinct curve near the base, and with long spines, tf. 13. | <i>Tricorythus.</i> |

*tf., text figure.

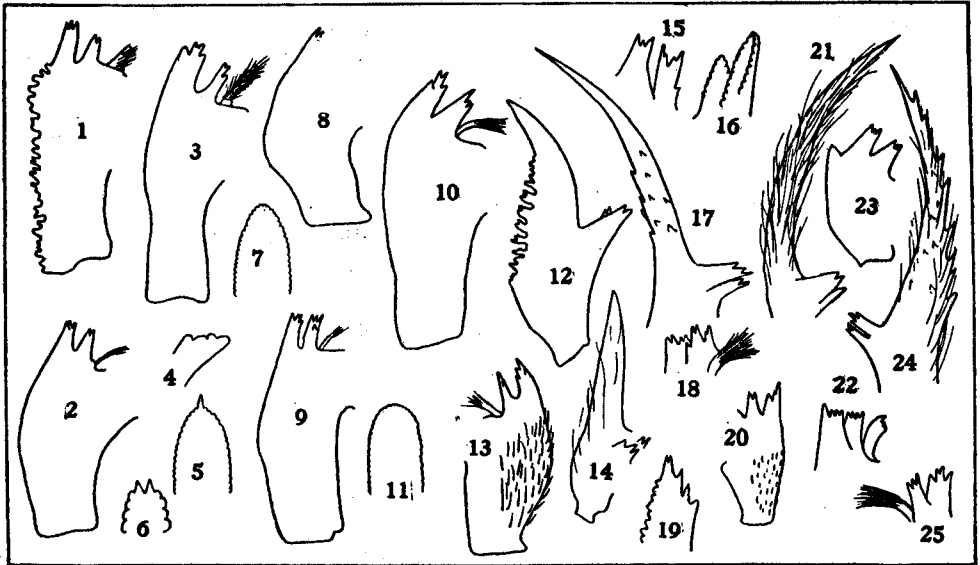
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II. MANDIBLE WITHOUT TUSK—*Continued.*

- (cc) Outer edge of mandible with a gentle curve midway between base and apex, and with short spines, tf. 20. *Ephemerella.*
- (aaa) Outer canine with three large teeth.
- (b) Inner canine with 4 teeth, tf. 15. *Chirotenetes.*
- (bb) Inner canine with 3 teeth. *Choroterpes.*
- (bbb) Inner canine with 2 teeth.
- (c) Outer edge of mandible serrated; lacinia broad at base, and cone-shaped, tf. 1. *Baetisca.*
- (cc) Outer edge of mandible not serrated; lacinia slender, tf. 2. *Leptophlebia.*
- AA. Outer canine without large teeth, more or less scoop-shaped; edge crenated. *HEPTAGENINAE.*
- (a) Outer canine with small teeth at apex.
- (b) Outer canine, with 1 small tooth at apex, tf. 5. *Heptagenia.*
- (bb) Outer canine with 2 small teeth at apex, tf. 6. *Ecdyurus.*
- (aa) Outer canine without small teeth at apex; edge finely crenated.
- (b) Inner canine not more than $\frac{1}{2}$ length of outer canine (Pl. IV, fig. 48). *Rhithrogena.*
- (bb) Inner canine more than $\frac{1}{2}$ length of outer canine.
- (c) Inner canine but little over $\frac{1}{2}$ length of outer canine; edge coarsely crenated, tf. 4; outer canine sharp at tip, tf. 7. *Epeorus.*
- (cc) Inner canine almost as long as outer canine, tf. 16; edge finely crenated; outer canine blunt at apex, tf. 11. *Iron.*

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TEXT-FIGURE I.



Types of May-fly Mandible. 1. Baetisca, molar surface removed. 2. Leptophlebia, molar surface removed. 3. Siphylurus, molar surface removed. 4. Epeorus, inner canine. 5. Heptagenia, outer canine. 6. Ecdyurus, outer canine. 7. Epeorus, outer canine. 8. Caenis, all tips removed. 9. Callibaetis, molar surface removed. 10. Blasturus, molar surface removed. 11. Iron, outer canine. 12. Pentagenia. 13. Tricorythus, molar surface removed. 14. Hexagenia, molar surface removed. 15. Chirotenetes, outer and inner canine. 16. Iron, canines. 17. Ephemera, molar surface removed. 18. Callibaetis, canines and lacinia. 19. Ameletus, outer canine. 20. Ephemerella, molar surface removed. 21. Euthyplocia, tusk and canines. 22. Baetis, canines and lacinia. 23. Potamanthus, molar surface removed. 24. Polymitarcsys, molar surface removed. 25. Blasturus, canines and lacinia.

Among the exotic genera are some rather aberrant forms. In the nameless Chilean nymph figured by Eaton (Pl. IV, fig. 63, c), the canines are extremely well developed, and certainly suggest carnivorous habits. This region in *Palinogenia* (fig. 49, c) is not distinctly differentiated. *Lachlania* (fig. 56, c) possesses but one canine on the mandible, and that is no longer apical in position. The canines of *Homeoneuria* (fig. 62) and *Lachlania* are covered with scale-like teeth.

HYPOPHARYNX (Pl. V).

The hypopharynx of May-fly nymph is a relatively large tongue-like process at the dorsal base of the labium. As with the labrum, the chief variations are in the form of the anterior border. The free edge of the median lobe of *Ameletus*

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(fig. 65, m) is straight; while that of *Habrophlebia* (fig. 66) is notched. In *Callibaetes* (fig. 67) this lobe is produced in the center. The lateral lobe (l) of *Habrophlebia* (fig. 66) is emarginate at the anterior border. In *Polymitarcys* (Pl. III, fig. 36) it is notched at the posterior border. The hairs on the outer border of both lobes of the hypopharynx are incurving, and doubtless aid in retaining food.

MAXILLA (Pl. V).

The main adaptations to environment in the nymphal maxilla involve loss of segmentation, and peculiar cuticular appendages.

Reduction in segmentation in the body of the maxilla is primarily a consolidation for strength. Galea and lacinia are fused, although in some forms, as *Hagenulus*, (fig. 85) faint traces of the suture remain. The articulation between the stipes (St) and galea-lacinia (Ga-Lc) is differentiated in *Lachlania* (fig. 83), but in most cases indistinctly (*Hagenulus* fig. 85; *Hexagenia* fig. 77; *Blasturus* fig. 75), or not at all (*Baetisca* fig. 78). The palpifer also shows gradations in fusion. That of *Blasturus* (fig. 75, Plf) or *Rhithrogena* (fig. 69) is well defined. In *Hagenulus* (fig. 85) or *Hexagenia* (fig. 77) it is not so clearly differentiated. The cardo is distinct.

Reduction in segmentation in the maxillary palp takes place by fusion, by incomplete differentiation, and by loss of segments. Where there is consolidation, the parts are heavily chitinized. This condition is found in the first segment of the palp in *Lachlania* (fig. 83). It is fused proximally with the palpifer. There is incomplete differentiation of the distal segment in some forms. In these (*Blasturus* fig. 75; *Hagenulus* fig. 85; *Hexagenia* fig. 77) the chitinization is weak. Entire loss of segmentation is found in *Ephemerella deficiens* Morgan (fig. 82), where there is no palp at all. Members of this genus are found in streams with gravel bottoms. The mouth-parts are small, retracted, and heavily chitinized. Loss of the palp is the extreme of specialization in this line.

The reduced multiarticulate palp (fig. 68, 72) of the nameless Chilean nymph figured by Eaton is an aberrant form.

The cuticular appendages of the maxilla mainly consist of bristles, rakers and heavy spines. Bristles are best developed in those forms among the Baetinae that inhabit swift water. They serve as diatom brushes and plancton strainers (*Hagenulus* fig. 85). This is a specialization for food getting which parallels the labial diatom rakers of the Heptageninae. On the ventral surface of the blade-like distal palp segment of one of these (*Rhithrogena*, fig. 69) are countless numbers of tiny toothed spines (fig. 70). Mixed with these combs at regular intervals are crook-shaped hairs. Spines are present on the galea-lacinia of those forms of the Baetinae that dwell in rocky streams (*Ephemerella* fig. 82; *Baetisca* fig. 78). The greatest development in this line is the teeth-like spines on Eaton's nameless Chilean nymph (fig. 68).

Tracheal gills (G) are present on the maxilla of *Lachlania* (fig. 83) and some other swift water forms.

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LABIUM (Pl. V).

Since the primary function of the labium is to prevent the escape of food, and to sweep it into the pharyngeal cavity, the main adaptations are found in the ligular region. The greatest changes in this region are found among the Baetinae dwelling in swift water. There are two lines of specialization. In the one are forms with reduced mouth-parts. The glossa (gl) and paraglossa (Pgl) lose their segmentation in part as in *Ephemerella* (fig. 71) or entirely as in *Tricorythus* (fig. 64). In the other line of specialization are forms with the mouth-parts more or less enlarged and depressed. The ligula is expanded and constitutes the greater part of the body of the labium. The glossa of *Lachlania* (fig. 76) is not differentiated from the ligula. The paraglossae (Pgl) are enlarged and produced anteriorly until their tips are contiguous. The whole labium resembles a scoop. The same result is obtained among the Heptageninae, but by a different specialization. There, as in *Lachlania*, the ligula (fig. 84, Lg) forms the main bulk of the labium; but the glossa and paraglossa, though small, are distinct. It is the basal portion of the ligula that is expanded.

The main adaptations in the labial palp involve reduction in segmentation, or decrease in size. In those swift water forms that have mouth-parts depressed and the palp flattened and blade-like, there may be a consolidation of segments. This condition is found in *Epeorus* (fig. 84). The second palp segment is small, heavily chitinized, and incapable of independent movement. No musculature is developed for this segment. The palp of *Oligoneuria* (fig. 76) is two-segmented. In those swift water forms where the head is small and the mouth-parts retracted, there is a reduction in the size of the entire palp, particularly the distal part. The second and third segments of the palp of *Tricorythus* (fig. 64) are very reduced, and weakly chitinized. In *Baetis sp.* (fig. 73), the distal portion of the second palp segment is enlarged and bears an inner prolongation. The third segment is knob-like and fits down into the enlarged tip. It is weakly chitinized and the articulation is incompletely differentiated. Specimens of this genus which do not inhabit rocky places in swift water show a less knobbed distal segment, and better differentiated articulation. Greater specialization in this line is found in the labial palp of *Baetisca obesa* (fig. 74). There the inner prolongation of the second segment is longer and tooth-like. The third segment is small and pointed, giving a forceps-like appearance. However, this segment is weakly chitinized and shows no musculature.

The cuticular appendages of the labrum are similar to those of the maxilla of the same forms. *Baetisca obesa* (fig. 74) has chitinized papillae on the ligula and submentum.

The labial palp of Eaton's nameless Chilean nymph (fig. 80) is multiarticulate. The addition appears to result from secondary division of the distal segment.

MOUTH PARTS OF THE SUBIMAGO AND IMAGO.

VI—MOUTH PARTS OF THE SUBIMAGO AND IMAGO

May-fly mouth-parts are vestigial during the life of the subimago and imago. External evidences of degeneration are shown in reduced size, asymmetrical form, and general lack of chitinization. Internally there is a degeneration of the musculature.

EXTERNAL METAMORPHOSIS.

A comparison of the functional mouth-parts of a *Hexagenia* nymph (Pl. III, fig. 34) with the atrophied mouth-parts of the subimago of the same species (Pl. VI, fig. 98) shows the change of form with loss of function. Molar surface, canines, and lacinia of the mandible (Md) are not differentiated. The large chitinized tusk (Pl. II, fig. 26, T) is soft, irregular and thread-like (Pl. VI, fig. 98, T). The maxillae (Mx) show no segmentation, although the labium (Lb) does contain traces of a suture between the mentum and submentum. The labrum is visible only after dissection. It is a tiny misshapen protuberance retracted beneath the nose-like clypeus (Clp). A shapeless papilla drawn back into the pharyngeal opening is the only remnant of the hypopharynx. There are no hairs or spines. All the mouth-parts are diminished in size, irregular in form, and very weakly chitinized.

Atrophy of the mouth-parts is progressive during the aerial life of an individual (Compare figs. 88, 90, 93, with figs. 95, 96, and 97). It also varies in extent among members of a species. (Compare figs. 88, 89, 90; 91, 92; 93, 94).

INTERNAL METAMORPHOSIS.

Internal evidence of the metamorphosis of Ephemeroptera mouth-parts is shown in the degeneration of the musculature. In the mouth-parts proper there is a gradual regressive process during aerial life.* The part of the head capsule occupied during nymphal life by the strong mandibular adductors, is filled by the large compound eyes after transformation. Although these eyes have been developing internally since mid nymphal life, they attain the greater part of their enormous size just at transformation. Specimens observed to feed one-half hour before emergence show no traces of mandibular adductors one hour later. There are, then, two physiological types of degeneration: a simple progressive atrophy of the mouth-parts proper; and a rapid degeneration of the mandibular adductors. Histologically degeneration is the same in both cases.

*Specimens of *Hexagenia recurvata* emerged in mid-afternoon May 31; spent two days as subimago; mated at sundown two days later, and died that evening.

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NORMAL MUSCLE. A normal muscle of the mouth-parts in longitudinal section shows the dark bands relatively broad and deep blue staining. The light bands are narrow, with Krause's membrane showing as a distinct dark line. The nuclei are oval and lie just under the sarcolemma. Their chromatin is coarse, dark purple staining, and lies chiefly about the periphery. In cross section Cohnheim's areas are evident.

PLASMA CELLS. In the body plasma from the first instar through imaginal life there are five varieties of cells (Pl. VI, fig. 87), which intergrade with no sharp lines of demarcation:

A. Little cells with a small amount of deep-blue staining, homogeneous cytoplasm; nuclear chromatin evenly distributed, deep-purple staining, and coarsely reticular. These cells show very slight ameboid movement.

B. Cells 1.5 to 3 times the size of variety A, with a large amount of homogeneous cytoplasm varying from dark to light blue; nuclear chromatin deep-purple staining, coarsely reticular and evenly distributed. These cells show mitotic division and active ameboid movement.

C. Cells 2 to 3 times the size of variety A; with light blue staining vacuolated cytoplasm; nuclear chromatin finely reticular and light-purple to dark-blue staining. Spindle forms are common. Ameboid movement is active.

D. Cells 2 to 3 times the size of variety A; with small pink staining areas or a few pink granules; cytoplasm light blue staining and vacuolated, similar to variety C. Spindle forms are common. Ameboid movement is active.

E. Cells 1 to 4 times the size of variety A; with many deep-pink staining granules; cytoplasm staining a very light reticular blue, or not at all; nucleus light purple, with coarsely reticular chromatin, and light staining ground substance.

Smears made from the abdominal cavity of the nymph and subimago just after molting show many degenerating plasma cells. The most common form is vacuolated, with the nucleus crowded to the periphery (fig. 87, w). Some of the vacuoles contain pink granules or diffuse pink areas.

DEGENERATING MUSCLE. Not all the muscles of the mouth-parts degenerate simultaneously; neither is an entire muscle at the same stage of degeneration. This process is evident in portions of some of the mouth-part muscles of *Hexagenia recurvata* five days before emergence. In all the specimens examined cross-striations were visible in portions of the muscle just before transformation.

Early in degeneration the dark bands stain lighter and irregularly (Pl. VI, fig. 86, I). The light bands increase in width, and Krause's membrane is no longer evident. The muscle nuclei (n) are swollen and stain faintly. There is also slight evidence of fibrillation. Then the muscle substance changes from blue to

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pink in color, and the cell contents (II), begin to liquify. The nuclei (n) assume a spherical shape and their chromatin becomes diffuse. Plasma cells of the five varieties (A, B, C, D, E) increase in the proximity of the degenerating muscle. In cross section (IV) Cohnheim's areas are not evident, and many of the fibers are vacuolated. As degeneration increases, the dark bands disappear (III) and the muscle substance stains more and more faintly. The sarcolemma is no longer evident, and the nuclei (n) rupture. Finally nothing remains but a formless mass (V), and that soon ceases to stain. There is no evidence of phagocytosis.

During the muscle degeneration no plasma cells are present that do not occur in a first instar nymph. The following differential count from smears of the plasma of nymph, subimago and imago shows a proportional increase in varieties D and E after transformation, and a decrease in varieties A and B.

* % OF PLASMA CELLS IN DIFFERENTIAL COUNT.

VARIETY	NYMPH	SUBIMAGO	IMAGO
A	25.0	1.3	1.5
B	12.5	2.3	1.5
C	27.5	16.7	22.0
D	5.0	11.7	26.0
E	30.0	68.	49.0

Tracheae (Pl. VI, fig. 86, Tr.) and tracheoles (tr) persist after the muscles have entirely lost their identity. These cells have a finely granular dark purple staining cytoplasm, and a densely staining finely reticular nucleus.

DISCUSSION.

The nature of the cells present in the vicinity of metamorphosing muscles among holometabolic insects has long been a subject of discussion. Berlese and Terre contend that the cells are not leucocytes, but are developed from the nuclei of the larval muscles; Anglas and Perez, that they do not arise from the nuclei of larval muscles, but are leucocytes. Deegner says that spindle-shaped cells whose origin is uncertain, appear in the late larva of *Hydrophilus*. Breed, 1913, in a very complete work on the metamorphosis of the muscles of a beetle writes: "Mesenchymal cells arise singly from the tracheae or hypodermis, and give rise to tracheae, leucocytes, and other related tissues (p. 353)—It is probable that some of these tracheal cells become leucocytes—Certainly the large vacuolated leucocytes which have persisted from the larva, disappear in old pupae, and their

*100% = 500 plasma cells.

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places are taken by smaller less vacuolated cells. These new leucocytes grow in size and soon are characteristically vacuolated (p. 355)."

That the same cells may appear very unlike with different fixers is possible. None of the authors quoted have used a technique which permits a direct comparison of plasma cells in section and in smear.

In the metamorphosis of the muscles of May-fly mouth-parts, I find no evidence of a proliferation of free tracheal cells. There is a rapid increase in tracheal cells just after the various nymphal molts, but they form tracheoles. The varieties of plasma cells in the vicinity of the degenerating muscles are the same as those found in the first instar nymph. The muscle nuclei clearly degenerate. There is no evidence of phagocytosis.

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EXPLANATION OF PLATES

Unless otherwise stated, the figures are original and made with the aid of the camera lucida.

ABBREVIATIONS

A—variety of plasma cell	L—leg
Ab—abdomen	l—lateral lobe
Abd—abductor	Lb—labium
ad—adductor	Lb Plp—labial palp
am—amnion	Lc—lacinia
Ant—antenna	Lg—ligula
ap—apodeme	lm—lower median region
B—variety of plasma cell	M—mentum
C—variety of plasma cell	m—median lobe
c—canine	md—mandible
Cd—cardo	m s—molar surface
c.h.—Cohnheim's area	Mx—maxilla
Clp—clypeus	Mx Plp—maxillary palp
co—compressor	n—nucleus
D—variety of plasma cell	oa—outer apical region
d—depressor	oc—outer canine
E—variety of plasma cell	ol—outer lateral region
e—extensor of palp	Pcl—procephalic lobe
El—elevator	Pgl.—paraglossa
Ep—epipharynx	Plf—palpifer
ep—epipharyngeal muscle	Plg—palpiger
F—fat	R—retractor
f—flexor of palp	St—stipes
Fl—flexor.	T—tusk
Ga—galea	Th—thorax
ga—ginglymous articulation	Tn—tentorium
Ga Lc—galea-lacinia	Tr—trachea
gl—glossa	tr—tracheole
H—head	Vm—vitelline membrane
ia—inner apical region	Vp—ventral plate
ic—inner canine	I, II, III, IV, V—degenerating muscle
il—inner lobe	

PLATE I

- Fig. 1. Egg of *Baetis posticus*.
Fig. 2. Embryo, 2 days.
Fig. 3. Embryo, 4 days.
Fig. 4. Embryo, 9 days.
Fig. 5. Head region, embryo, 5 days.
Fig. 6. Clypeo-labrum, 8 days.
Fig. 7. Labrum, 10 days, ventral aspect.
Fig. 8. Labrum, 11 days, ventral aspect.
Fig. 9. Right mandible, 6½ days.
Fig. 10. Right mandible, 7½ days.
Fig. 11. Right mandible, 9 days.
Fig. 12. Left mandible, 11 days.
Fig. 13. Hypopharynx, 11 days.
Fig. 14. Left 1st maxilla, 6 days.
Fig. 15. Left 1st maxilla, 6½ days.
Fig. 16. Left 1st maxilla, 8 days.
Fig. 17. Left 1st maxilla, 11 days.
Fig. 18. Left 2nd maxilla, 6½ days.
Fig. 19. Left 2nd maxilla, 7 days.
Fig. 20. Labium, 9 days.
Fig. 21. Labium, 11 days.

PLATE I

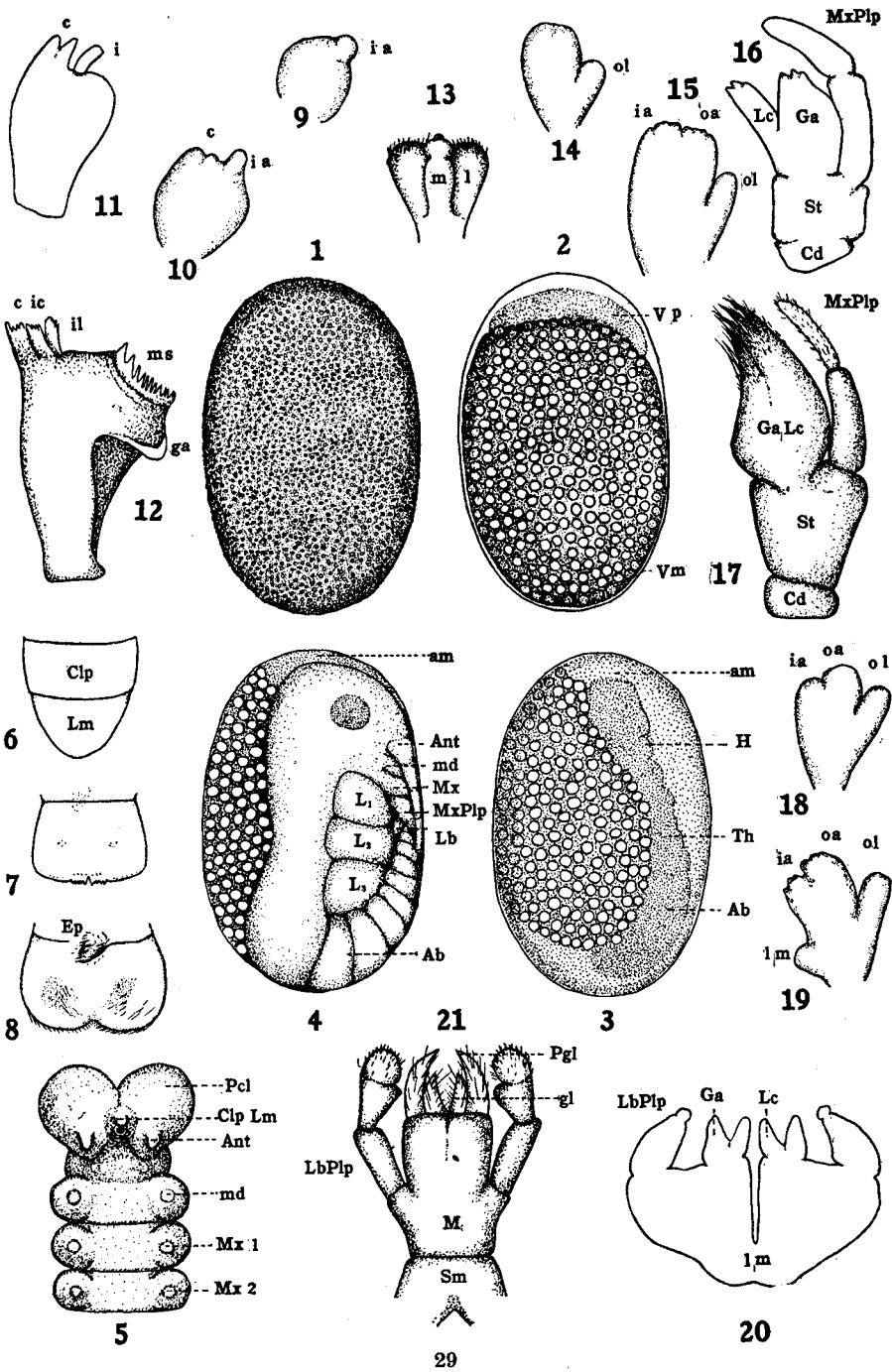


PLATE II

- Fig. 22. Nymph, *Epeorus humeralis*.
Fig. 23. Nymph, *Hexagenia bilineata*.
Fig. 24. Nymph, *Baetis posticus*.
Fig. 25. Diagram of portion of postgena, Hexagenia nymph.
Fig. 26. Right mandible, Hexagenia nymph.
Fig. 27. Diagram of cross-section of ginglymous articulation of mandible, Hexagenia nymph.
Fig. 28. Diagram of body of right and left mandible of Hexagenia nymph, dorsal aspect.
- Fig. 29. Diagram of right molar surface, Ephemerella nymph.
Fig. 30. Diagram of left molar surface, Ephemerella nymph.
Fig. 31. Diagram of left molar surface, Ephemera nymph.
Fig. 32. Diagram of right molar surface, Ephemera nymph.
Fig. 33. Diagram of cross-section of right molar surface, Ameletus nymph.

PLATE III

Fig. 34. Diagram of ventral aspect of head of *Hexagenia* nymph, portion of left side removed.

Fig. 35. Diagram of labrum, *Ephemerella*.

Fig. 36. Diagram of hypopharynx, *Polymitarcys*.

Fig. 37. Diagram of hypopharynx, *Ecdyurus*.

Fig. 38. Diagram of right maxilla, *Ecdyurus*.

Fig. 39. Diagram of right half of labium, *Ephemerella*.

Fig. 40. Diagram of labium, *Ecdyurus*.

PLATE III

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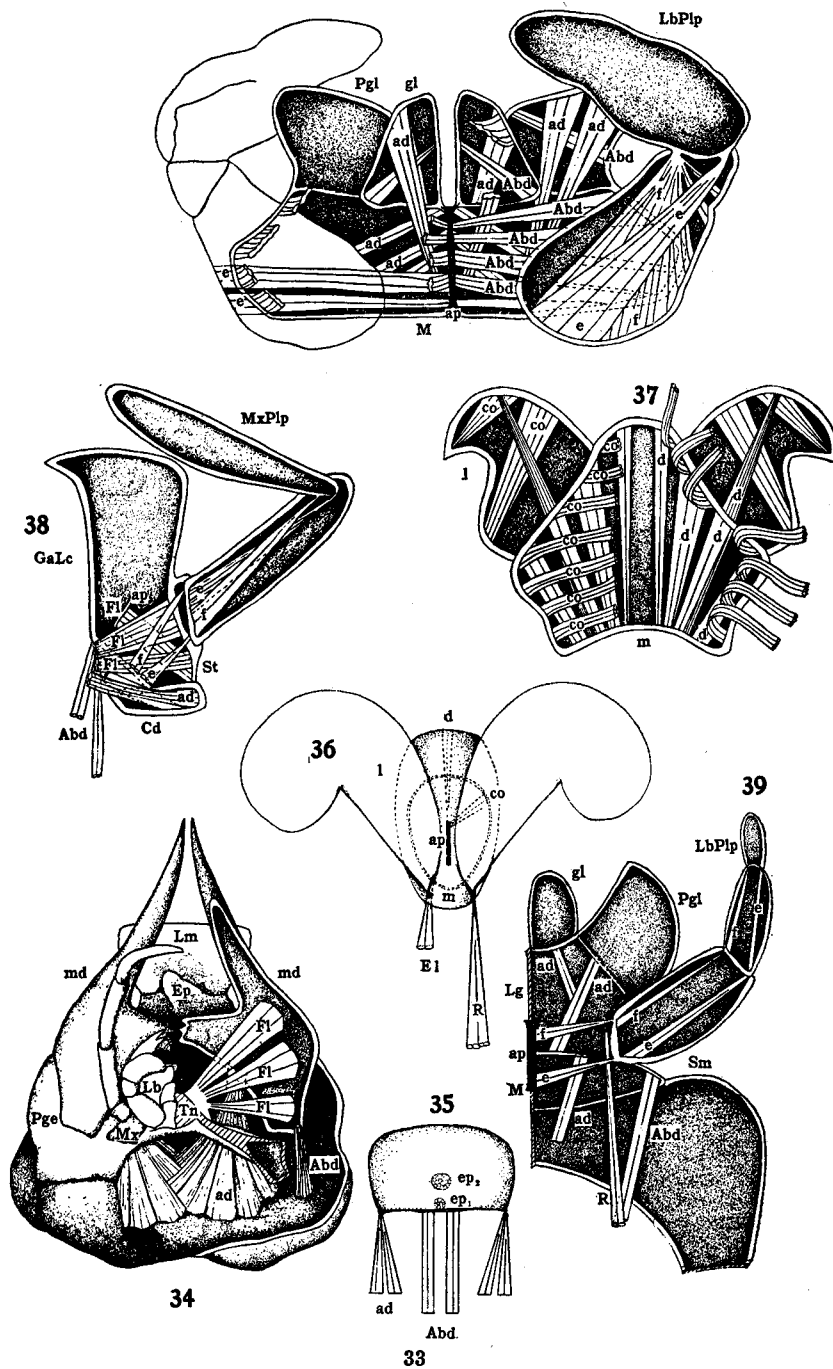


PLATE IV

- Fig. 41. Labrum, *Polymitarcys*, dorsal aspect.
Fig. 42. Labrum, *Chirotenetes*, dorsal aspect.
Fig. 43. Labrum, *Callibaetis*, ventral aspect.
Fig. 44. Labrum, *Baetis*, ventral aspect.
Fig. 45. Labrum, *Oligoneuria*, dorsal aspect.
Fig. 46. Labrum, *Ecdyurus*, ventral aspect.
Fig. 47. Labrum, *Hagenulus*, ventral aspect.
Fig. 48. Canines, *Rhithrogena*.
Fig. 49. Right mandible *Palingenia*, after Eaton.
Fig. 50. Lacinia, mandible *Polymitarcys*.
Fig. 51. Lacinia, mandible *Siphurus*.
Fig. 52. Lacinia, mandible *Leptophyes*.
Fig. 53. Lacinia, left mandible *Heptagenia*.
Fig. 54. Lacinial region, right mandible *Heptagenia*.
Fig. 55. Lacinia, mandible *Choroterpes*.
Fig. 56. Right mandible, *Lachlania*.
Fig. 57. Labrum *Ephemerella*, ventral aspect.
Fig. 58. Right mandible *Prosopistoma*, after Eaton.
Fig. 59. Lacinia, mandible *Euthyplocia*.
Fig. 60. Lacinia, mandible *Baetis*.
Fig. 61. Apex right mandible, *Ameletus*.
Fig. 62. Left mandible, *Homeoneuria*.
Fig. 63. Left mandible, nameless Chilean nymph, after Eaton.

PLATE IV

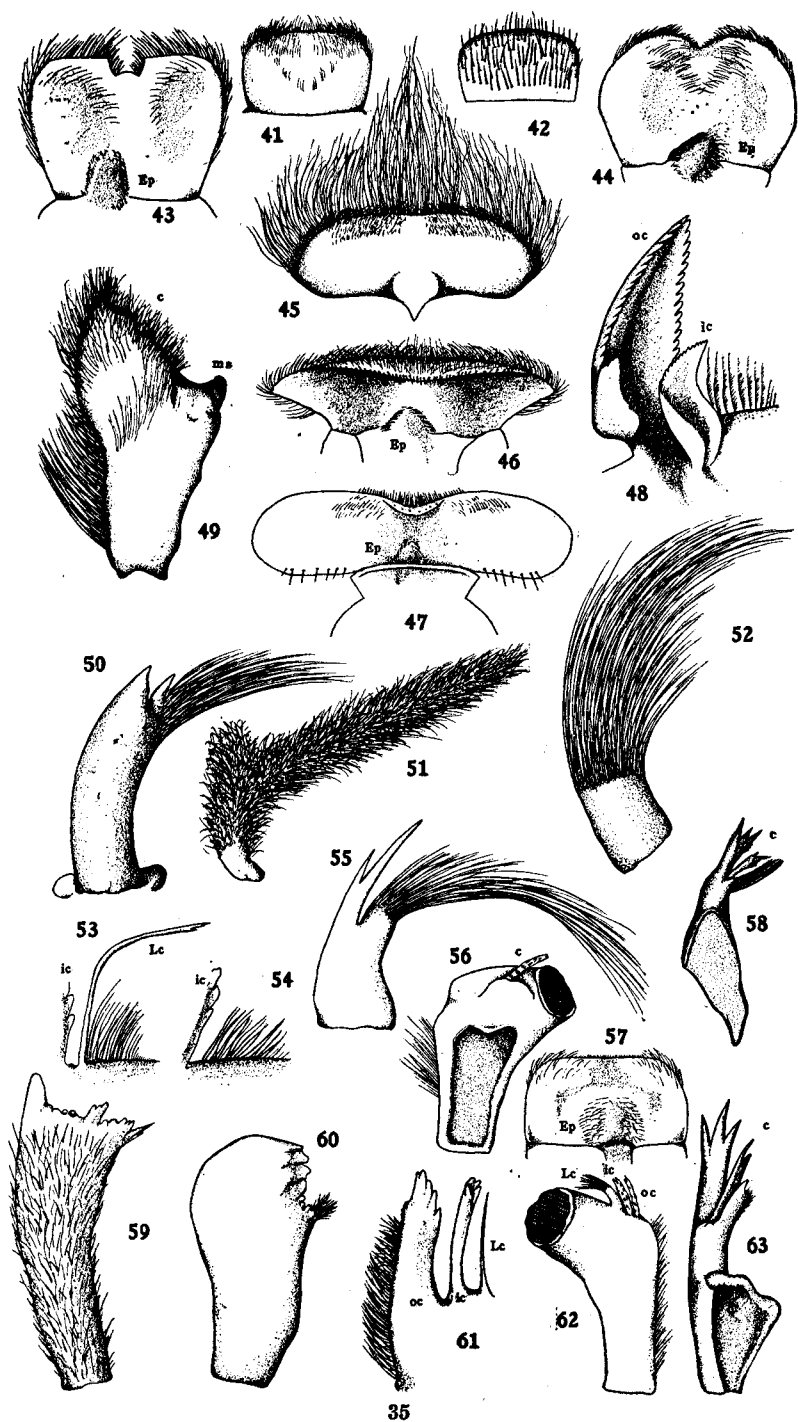


PLATE V

- Fig. 64. Labium *Tricorythus*, ventral aspect.
Fig. 65. Hypopharynx, *Ameletus*.
Fig. 66. Hypopharynx, *Habrophlebia*.
Fig. 67. Hypopharynx, *Callibaetis*.
Fig. 68. Right maxilla, nameless Chilean nymph, after Eaton.
Fig. 69. Left maxilla *Rhithrogena*, in part.
Fig. 70. Diatom raker from maxillary palp, *Rhithrogena*.
Fig. 71. Labium of *Ephemerella*, ventral aspect.
Fig. 72. Maxillary palp, nameless Chilean nymph, after Eaton.
Fig. 73. Labium *Baetis*, ventral aspect.
Fig. 74. Labium *Baetisca*, ventral aspect.
Fig. 75. Left maxilla *Blasturus*, ventral aspect.
Fig. 76. Labium *Oligoneuria*, ventral aspect.
Fig. 77. Left maxilla *Hexagenia*, ventral aspect.
Fig. 78. Left maxilla *Baetisca*, ventral aspect.
Fig. 79. Diatom raker, maxilla *Rhithrogena*.
Fig. 80. Labium, nameless Chilean nymph, after Eaton.
Fig. 81. Left maxilla *Caenis* in part, ventral aspect.
Fig. 82. Left maxilla *Ephemerella deficiens*, ventral aspect.
Fig. 83. Right maxilla *Lachlania*, ventral aspect.
Fig. 84. Labium *Epeorus*, ventral aspect.
Fig. 85. Left maxilla *Hagenulus*, ventral aspect.

PLATE V

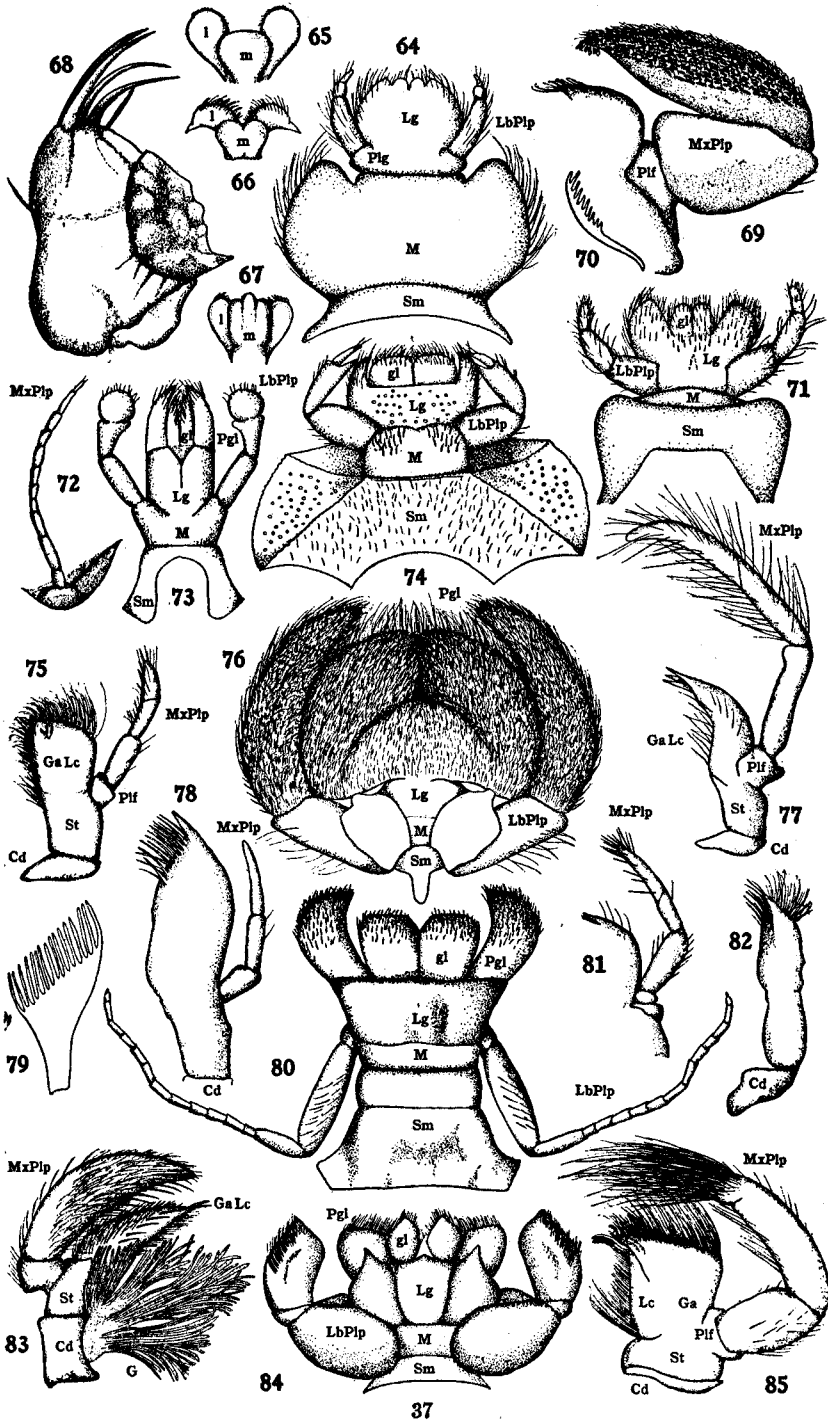


PLATE VI

Fig. 86. Muscle degeneration *Hexagenia* subimago of 24 hours, cross-section from mandible.

Fig. 87. Plasma cells from smear.

Fig. 88. Mandibles, subimago *Hexagenia recurvata*.

Fig. 89. Mandibles, subimago *Hexagenia recurvata*.

Fig. 90. Mandibles, subimago *Hexagenia recurvata*.

Fig. 91. Maxillae, subimago *Hexagenia recurvata*.

Fig. 92. Maxillae, subimago *Hexagenia recurvata*.

Fig. 93. Labium, subimago *Hexagenia recurvata*.

Fig. 94. Labium, subimago *Hexagenia recurvata*.

Fig. 95. Labium, imago *Hexagenia recurvata*.

Fig. 96. Labium, imago *Hexagenia recurvata*.

Fig. 97. Mandibles, imago *Hexagenia recurvata*.

Fig. 98. Head, subimago *Hexagenia recurvata*, ventral aspect.

II—Notes on the Biology of Mayflies of the Genus *Baetis*

While gathering material for a study of May-fly embryology, some observations were made on the habits of a species of *Baetis*. This led to rearing experiments that were carried through successive generations for two and one-half years. A comparative study was made of two other species of the same genus.

The determination of these species as *B. posticatus*, *B. pygmaea*, and *B. propinquus* was made by detailed comparison with specimens in the Cornell University collection.

BAETIS POSTICATUS.

The mating flight of *B. posticatus* was observed late in the afternoon of May 6, 1918. Males and females flying together rhythmically rose and fell in vertical lines. In numbers varying from hundreds to two or three, they danced fitfully up and down; sometimes rising short distances above the surface of the water; sometimes soaring exultantly out of sight. Then they dropped with wings out spread. A female left the throng followed by a male. He flew up from below and grasped her prothorax with his forelegs. The posterior of his abdomen was flexed up and forward. His tails were extended on either side of the head of the female. Then he seized the seventh segment of her abdomen with his forceps. The egg-valve was pushed open and the penes inserted into the sperm receptacle in the seventh segment. The female continued to fly, carrying the male along with her. In this manner they copulated for about a minute; then the male rejoined the dance, and the female flew away to deposit her eggs. She alighted on a partially submerged stone, wrapped her wings about her abdomen, and crawled into the water. After walking about feeling the stone with the tip of her abdomen, she suddenly stopped and braced her legs. As the abdomen swayed from side to side, the eggs came from the oviducts. They were pressed to the surface of the stones. The masses are irregularly ovoid (Fig. 21), and contain from eighty to three-hundred eggs. These eggs are covered with a sticky substance which causes them to adhere to each other and to the stones. Some of the females were washed away while ovipositing; others managed to crawl weakly out of the water. The males continued their flight until exhausted. Shortly after sun-down the dead bodies of all floated away in the current.

A stone coated with freshly laid egg-masses was covered loosely with a piece of china silk, and submerged in the running water of the creek. Nymphs hatched in twenty-eight days. They were left in the silk covering until too large to escape through fine wire mesh. Then they were transferred to cylindrical

BIOLOGY OF MAYFLIES OF THE GENUS BAETIS.

breeding cages of wire cloth, six inches long and three inches in diameter. These cages were covered top and bottom with canvas. A small stone with algae was placed in the bottom, and the cage, half submerged, was anchored in the stream. As the nymphs neared maturity, they were separated into groups of four to a cage.

For a more detailed study, an egg-mass was carefully loosened from a stone and transferred to a Syracuse watch glass in the laboratory. The water was changed twice daily. Nymphs appeared in eleven days as contrasted with twenty-eight days in the cooler water of the creek. As soon as hatched, the nymphs were transferred to Syracuse watch glasses, ten nymphs to each glass. The water was changed twice daily, and fresh bits of green algae added every other day. When the fifth instar was reached, the nymphs were separated into groups of two per dish. The cast skins of each specimen were kept separate. Table A is a summary of the number and length of the stadia.

A nymph of the first instar (Fig. 8) is .74 mm. in length including antennae and tails. It has no gills and no middle tail. The nymphs are very active, and start eating almost immediately. The food consists of diatoms at first; then green algae and decaying higher plant tissue are added in gradually increasing quantities.

A nymph of the fifth instar is 1.5 mm. long including antennae and tails. Gills show as tiny outpockets of the body wall, and the middle tail is evident for the first time. The color pattern is faintly visible. As the nymph grows older, this color pattern is more clearly defined. There is however, much individual variation in the differentiation of the pattern. At the seventh instar the gills reach their full relative size, and are freely moved.

Nymphs of the same instar are not uniform in length. This becomes apparent at the fifth stadium. The critical stage is at molting. This takes place generally during the warmer part of the day.

Specimens kept in cages and nymphs free in the stream began emerging October 22, 1918. The main pulse started October 25, and continued for four days; stragglers appeared even ten days later.

A nymph ready to transform (Fig. 20) swims to the surface of the water. Strong pulsations in the dorsum of the prothorax cause a rent in the nymphal skin. The subimago emerges and flutters through the air to some support. There it sits with wings uplifted and forelegs thrust stiffly forward, waiting for the subimaginal molt. This takes place from eighteen to twenty-four hours later. Then the imago or true adult emerges and the mating flight follows.

A mass of eggs laid October 28, 1918, was brought into the laboratory for the purpose of rearing the nymphs. These specimens emerged during the second week in May. There were again twenty-seven stadia (Table A).

Nymphs reared in the creek from eggs laid October 28, 1918, did not emerge until August, 1918. A new cycle started in August was completed the following May.

BIOLOGY OF MAYFLIES OF THE GENUS BAETIS.

It is evident that the cycle started October 28, 1918, was completed in the laboratory in the same length of time as that of the previous cycle extending from May-October in the creek; but that the corresponding cycle (Oct. 28) in the creek was completed three months later.

A summary of the corresponding yearly cycles (Table B) and the continuous cycles (Table C) for the years 1918-1920 inclusive, together with the average monthly temperatures, shows a striking ratio between the length of cycle and the temperature. One six month cycle confined entirely to the warm months, is followed by two nine month cycles extending through the winter. Two years are necessary to complete three continuous cycles (Fig. 3). There are three periods of emergence during a year.

Four females captured during a mating flight October 28, 1918, were found to be parasitized. Each imago contained a single nematode coiled up in the body cavity (Fig. 16). The hosts appeared natural in flight, and it was not until the specimens were preserved that the presence of the parasite was observed. The abdomen, normally conspicuously filled with eggs, seemed to contain nothing except the nematode.

B. PYGMAEA AND B. PRONPINQUUS.

Associated with nymphs of *B. posticatus* are nymphs of *B. pygmaea* and *B. propinquus*. An examination of a series of reared specimens of these three species fails to reveal specific characters which are valid at any given instar. Mature and fully colored nymphs may be separated by the relative characters given in Table D. A microscopic examination of the mouth-parts shows slight variations in the form of the labial palp (Figs. 13, 14, 15), and in the maxilla (Figs. 17, 18, 19).

The venation of the hind wing of the male (Figs. 4, 5, 6) and female, and the genitalia of the male (Figs. 1, 2, 12), furnish definite specific characters in the imago. There is also a variation in the relative length of the first and second leg in the males of these species (Figs. 9, 10, 11).

The oviposition of *B. pygmaea* is described by Morgan in 1911 (3); the mating flight of a species of *Baetis* by the same author in 1913 (4).

The life cycle of *B. pygmaea* reared in the creek extending from August, 1919 to August, 1920; that of *B. propinquus* from September, 1919 to August, 1920. Change of residence prevented further rearing experiments to determine the number of stadia in these two species, and whether there are overlapping cycles.

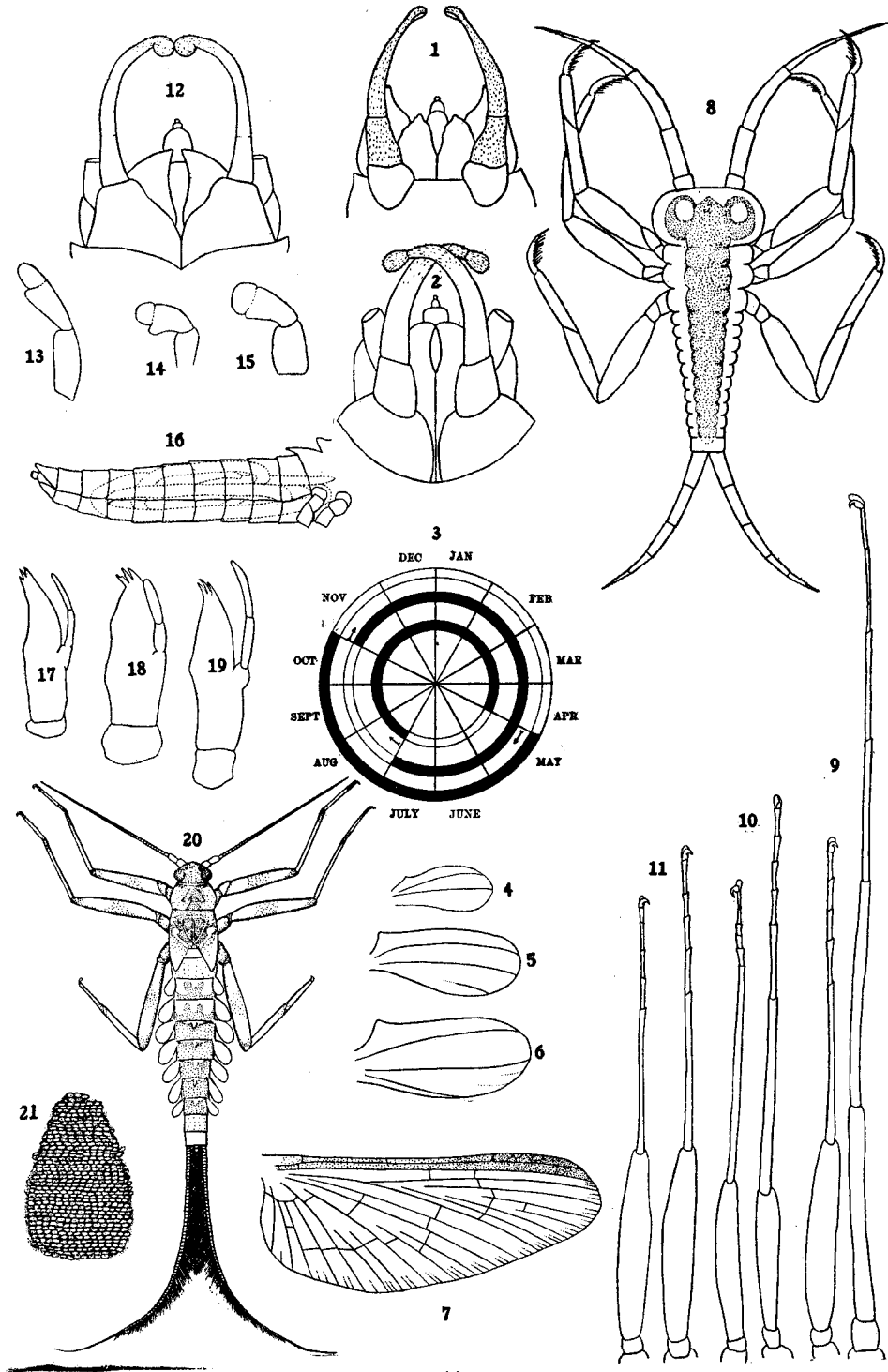
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- (3) Morgan, A. H. Ann. Ent. Soc. Amer., 4:116. 1911.
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EXPLANATION OF PLATE

1. Diagram, genitalia σ imago, *B. pygmaea*.
2. Diagram, genitalia σ imago, *B. posticus*.
3. Diagram, life cycle, *B. posticus*, May, 1919-May, 1920.
Arrows indicate three successive broods.
4. Venation, hind wing σ imago, *B. pygmaea*.
5. Venation, hind wing σ imago, *B. propinquus*.
6. Venation, hind wing σ imago, *B. posticus*.
7. Venation, fore wing σ imago, *B. posticus*.
8. Diagram, 1st instar nymph, *B. posticus*.
9. Diagram, 1st and 2nd leg σ imago, *B. propinquus*.
10. Diagram, 1st and 2nd leg σ imago, *B. pygmaea*.
11. Diagram, 1st and 2nd leg σ imago, *B. posticus*.
12. Diagram, genitalia σ imago, *B. propinquus*.
13. Diagram, labial palp nymph, *B. pygmaea*.
14. Diagram, labial palp nymph, *B. posticus*.
15. Diagram, labial palp nymph, *B. propinquus*.
16. Diagram, nematode in σ imago, *B. posticus*.
17. Diagram, maxilla nymph, *B. propinquus*.
18. Diagram, maxilla nymph, *B. posticus*.
19. Diagram, maxilla nymph, *B. pygmaea*.
20. Diagram, mature nymph, *B. posticus*.
21. Diagram, egg mass, *B. posticus*.

BIOLOGY OF MAYFLIES OF THE GENUS BAETIS.



BIOLOGY OF MAYFLIES OF THE GENUS BAETIS.

TABLE A

Summary of Number and Length of Stadia, *B. posticatus* Laboratory Reared Specimens

STADIUM	DAYS		LENGTH BODY		PER CENT. DEATH RATE	
	(1) May 1918- October 1918	(2) October 1918- May 1919	May 1918- October 1918	October 1918- May 1919	May 1918- October 1918	October 1918- May 1919
1	2	2	.30	.30	2.4	1.2
2	2-3	2	.40	.40	1.2	0.6
3	4-6	3-5	.50	.50	0.9	0.3
4	4-6	4-5	.60	.60	3.1	0.0
5	6-7	4-6	.71	.70	0.0	0.8
6	7-8	4-7	.84	.82	0.6	0.4
7	6-10	5-7	1.3	.95	0.0	0.2
8	6-10	6-8	1.7	1.2	0.2	0.2
9	6-10	6-8	2.1	1.5	0.3	0.0
10	6-11	6-9	2.5	1.8	0.2	0.0
11	7-10	8-11	2.9	2.1	0.1	0.0
12	7-11	8-10	3.3	2.4	0.3	0.0
13	6-10	8-11	3.7	2.7	0.0	0.3
14	7-10	8-11	4.0	3.0	0.0	0.1
15	7-10	7-10	4.3	3.3	0.0	0.0
16	7-10	7-10	4.6	3.7	0.0	0.0
17	7-10	8-10	4.9	4.0	0.0	0.1
18	7-10	8-10	5.1	4.3	0.0	0.0
19	7-10	8-10	5.4	4.7	0.0	0.0
20	7-10	8-10	5.6	5.0	0.0	0.0
21	7-10	8-10	6.0	5.3	0.1	0.0
22	7-10	8-10	6.3	5.7	0.0	0.0
23	7-10	8-10	6.6	6.1	0.0	0.0
24	7-10	8-10	6.9	6.3	0.0	0.0
25	7-10	8-10	7.2	6.5	0.0	0.0
26	7-10	8-10	7.5	6.8	0.0	0.0
27	7-10	8-10	7.8	7.0	0.0	0.1

TABLE B

Summary of Corresponding Yearly Cycles, *B. posticatus*, at Ithaca, N. Y.

CYCLE	MONTHS	AV. MON. TEMP.
May, 1918-October, 1918.....	6	60.7
May, 1919-October, 1919.....	6	63.5
May, 1920-October, 1920.....	6	62.4
August, 1918-May, 1919.....	9	45.0
August, 1919-May, 1920.....	9	41.4
October, 1918-August, 1919.....	9	47.9
October, 1919-August, 1920.....	9	43.3

(1) 376 Specimens.

(2) 237 Specimens.

BIOLOGY OF MAYFLIES OF THE GENUS BAETIS.

TABLE C

Summary of Continuous Cycles, *B. posticatus*, at Ithaca, N. Y.

CYCLE	MONTHS	AV. MON. TEMP.
Brood 1—May, 1918-October, 1918.	6	60.7
Brood 2—October, 1918-August, 1919.	9	47.9
Brood 3—August, 1919-May, 1920.	9	41.4
Brood 4—May, 1920-October, 1920.	6	62.2

TABLE D

Distinguishing Characters of Species of *Baetis* at Ithaca, N. Y.

Species	NYMPH			IMAGO		
	Length Body	Tail		Length		
		Length	Color	Hind Wing	Body	Tail
<i>pygmaea</i>	4-5	2.3-2.5	3 dark bands	0.6	3-5	7
<i>propinquus</i>	6	2	3 dark bands	1.0	4-5	7.5-10.2
<i>posticatus</i>	6-8	4-5	no bands	1.3	8	19