ECOLOGICAL STUDIES OF AQUATIC INSECTS. I. ADAPTATIONS OF MAYFLY NYMPHS TO SWIFT STREAMS [1]

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This is the first of a proposed series of papers growing out of studies carried on during several summers in the Colorado Rockies, with headquarters at the Summer Mountain Laboratory of the University of Colorado, at Tolland, Gilpin County, Colorado. The authors are much indebted to Francis Ramaley, Director of the laboratory, for materials and equipment, as well as for a stimulating interest in the work. Our studies in that region have dealt with various phases of the ecological relations of the nymphs of stoneflies and mayflies and the larvae of caddisflies, giving special attention to the means by which these insects have met the difficult conditions of life in the swift streams of the region.

The Laboratory is located in the valley of South Boulder Creek, at 9,000 feet, on the east slope of the Front Range of the Rockies, within four miles of the Continental Divide on the west, and about 15 miles from the plains on the east. It has within easy reach a wide range of topographic, climatic and biotic conditions. The creeks and numerous small lakes of the region are of great interest, and are fully described, together with the important topographic and climatic features, in former papers by one of the authors (Dodds, '17, '20). The most abundant and striking part of the fauna of the lakes and streams is the insect life, including the immature stages of mayflies, stoneflies, and caddisflies, which here are found in an abundance wholly unknown in ordinary lowland portions of the United States, except in the northern tier of states.

We have made special study of the swift streams. It should be clearly recognized that the swift streams of this region are far more than the "babbling brook" or the riffles of streams in level or moderately hilly country, but are in reality often torrential, especially during high water. These streams frequently make a descent of a thousand feet within a distance of a mile, and

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the average fall of South Boulder Creek in a course of 25 miles is nearly 250 feet to the mile. The various tributaries and heads of the streams are small trunks, across which one may easily step or jump, but the main creek has a width of 25 to 50 feet. The stream beds are commonly covered with angular rock fragments of various sizes, but usually so large that they are not moved by the water except during freshets. Among and over these rocks the water rushes with great force, while at places it descends over solid rock ledges in cascades. The water is usually free from sand or suspended mud, is without hardness, on account of the igneous origin of the rocks, and maintains a low temperature, even in summer.

Animals inhabiting standing water have the problems of locomotion in search and pursuit of food and in flight from enemies. They rest at will, either by floating in the water or by standing on the bottom. But animals living in swift streams are confronted with many conditions differing from those of quiet water, problems which have been solved in many different and interesting ways. The swift stream, as a habitat, is more specialized and restricted than the lake, or even the quiet stream, and its inhabitants possess adaptations peculiar to it. The predominating problem in the stream is that of retention, as these animals are in constant danger of being washed away, and must maintain their position by adaptations which either enable them to withstand the current or to avoid it by crawling into crevices or under stones.

The adaptations of mayfly nymphs to swift water may be classified into three groups, namely: (1) those which enable them to swim vigorously through the water; (2) those for withstanding swift current by holding to the bottom; and (3) those for avoiding the current by crawling into crevices. The first two groups of adaptations are much alike in certain of their phases, in that the first solves the problem of moving through the water, and the second of letting the water pass by. It is obvious that specializations which offer least resistance to the water would be of advantage to both of these groups. The fifteen species of mayfly nymphs found in the lakes and streams of the region adequately illustrate the three groups of adaptations mentioned above, and eleven representative species have been selected for detailed consideration in this paper.

Adaptations for Quiet Water

The mayfly nymphs of quiet waters, though by no means independent of the bottom, have developed strong powers of swimming. Two species will be used to illustrate the structural features of this type.

Siphlurus occidentalis Etn. (Plate I, fig. 3)

This species is typical of those pond-dwelling species which swim moderately well, but are without striking adaptations in this respect. It spends most of its time half buried in the silty bottom of lakes and ponds. When disturbed, it swims rapidly to another place and comes to rest on the bottom. The brownish mottled markings of its body blend admirably with its environment, and it can be located only by the flickering movements of the gill lamellae, which are kept constantly in motion. These lamellae are very large and the two anterior pairs are double. The body is built somewhat on the streamline form, but the abdomen is thick, does not taper very much, and is strongly bowed ventrally. This bow shape causes the abdomen, when the nymph is resting on the bottom, to be partially buried in the silt, while the thorax, supported by the legs, and the upturned tail, are above the surface of the silt. The swimming organ is formed by the three caudal cerci, which are developed into a good-sized paddle, comparable to the tail of a fish. The inner margin of the two outer cerci and both margins of the middle one, are provided with long, stiff hairs, which meet and overlap, forming an excellent oar, which enables the nymph to swim rapidly by dorso-ventral strokes of the well-muscled abdomen. While swimming, the legs are not held close to the body, but extended laterally and backward, in the position assumed while resting on the soft bottom.

Ameletus velox Dodds (Plate I, fig. 1)

This species, though of the same general type as *Siphlurus occidentalis,* is a very much stronger swimmer, with corresponding structural differences. It inhabits ponds and lakes with clean rock or gravel bottoms, and often with a sparse growth of sedges. It also inhabits the edges and quieter portions of streams, and will swim in water flowing two or three feet per second, but it seeks quieter water before coming to rest upon the bottom.

In general structure it is similar to *Siphlurus occidentalis,* but certain significant differences, evidently correlated with its superior swimming powers, must be noted. Comparison of figures 1 and 3, plate I, will show the excellence of the torpedo shaped body of this species compared with that of *Siphlurus.* Note the nicely rounded head, the short, robust thorax, and the long, tapered abdomen, ending in the strong paddle formed by the caudal cerci. It should also be noticed that resistance to passage through the water has been lessened by certain other features in which this species differs from the preceding, namely, the gills are much smaller, as are also the legs, and the latter, when the nymph is swimming, are diverted backward and held close to the body, thus lessening resistance to the water. The whole form of this nymph resembles that of a strong swimming fish such as a mackerel or trout, or a pelagic mammal such as a seal or whale, or one of the modern mechanical devices for rapid motion in air of water, such as a torpedo, the body of a racing automobile or the fuselage of an airplane. The fact that this nymph has caudal propulsion is also of interest, because this is the mode that has proved successful in several groups of animals, past and present, which have adopted the pelagic habit.

The form of body described above is generally called the stream-line form, because in rapid movement through a liquid or gaseous medium it produces a minimum of disturbance of the medium, and hence of resistance to passage of the body. The long, conical form of the posterior end is of importance in allowing the displaced water to return gradually, without creating an eddy with its great retarding effect. No doubt a similarly pointed anterior end would further reduce resistance, as in the case of modern high speed rifle projectile, but such a form would probably be inconsistent with proper mechanical strength and would introduce other serious disadvantages. Moreover, an abrupt slope at the anterior end is of less disadvantage than it would be at the posterior, and a stream-line body offers less resistance when moving with the large end forward than when moving in the reverse direction.

This species, by its strongly developed swimming powers, has made a good beginning of the invasion of streams, but only a beginning. Though it swims very rapidly, and darts about like a small fish, it cannot cope with the current where it is very rapid. It seems to have reached the limit of mayfly possibilities along this line, and the successful invasion of the stream, carried to the extent that there is hardly any part of it too swift for mayfly habitation, has been carried out in a manner in which swimming has no part.

Adaptations for Swift Streams

1. Species which Withstand the Current

Species of the swift stream which do not avoid the current by living in crevices of various sorts, but live upon the exposed surfaces of rocks, where they receive the full force of the strong current, have met the situation in two different ways. Accordingly we have two types of species, (*a*) those with round bodies, and (*b*) those with flat bodies.

(a) Current-resisting Species with Round Bodies

This group is represented in our fauna by three species belonging to the genus *Baëtis,* which represent three grades of ability to withstand strong current, and exhibit three degrees of specialization in the same general direction. These species resemble, in their general form, the swimming species, such as those just described, and have none of the striking modifications of the flat-bodied nymphs, yet, in our observations, they live in swifter water than the flattened and more specialized types.

Baëtis tricaudatus Dodds (Plate I, fig. 2)

This species lives in swift and very swift streams where the water is flowing not more than five feet per second [2] but does not venture into the

[2] The velocity of the current in the stream was measured by means of a glass tube bent at a right angle, one limb of which is held horizontally in the water with the

torrents and falls. The nymphs are commonly seen clinging to the upper surface of water-swept rocks, where the current does not excede the above figure. They are also commonly found in clean bottomed lakes, at points of outflow and inflow of streams, provided there is a growth of sedges in the water. This species may be considered a derivative of lake forms that have undergone the minimum structural changes to enable them to live in the current of the stream. The general shape of the body is similar to that of *Ameletus,* with an excellent stream-line form, completed posteriorly by the long cerci with their scant hairs. When compared with the lake-dwelling forms, however, some striking differences become apparent. This species is much smaller than any of the swimming species, being only 7 mm. long, while *S. occidentalis* and *A. velox* measure about 16 mm. The legs of *B. tricaudatus* are also much larger in proportion to the body than those of the the lake dwellers, and the thorax, from which they arise, is also of larger proportional size. The caudal cerci have very scant hairs, which do not overlap to form a swimming organ. These differences are clearly correlated with the mode of life and habitat of the species. It swims very little, and very poorly, but spends most of the time clinging to the exposed surfaces of submerged objects, and moves by crawling from place to place, always with the head up stream.

These habits make the swimming organs of less importance than the legs, which, in addition to being larger in proportion to the body than those of the lake-dwelling nymphs, are also specialized for attaching the nymph to the bottom in swift water. The tibiae are articulated with the femurs in a way which allows them, as well as the tarsal hooks, to be directed forward and placed squarely against the surface to which it is holding. The femurs are dorso-ventrally flattened, and the anterior margins are held closer to the bottom than the posterior, a position which utilizes the force of the current in holding the legs firmly against the bottom, as long as the nymph faces the current. The body itself is not flattened, nor is it pressed against the substratum, but swings freely in the current, held by the stable anchorage of the legs, while its excellent stream-line form offers small resistance to the current.

It is also important, under these conditions, to expose as small a surface of the leg to the current as possible. The two positions of the legs which would offer least resistance would be either straight forward or straight backward. The former position is the only one that would work at all, but it would not give a stable anchorage. In order not to be whipped about by the current, the points of attachment must be close to either side of the body. The requirements of offering the minimum surface and a stable anchorage at the same time, have been met by folding the legs, so that the femurs are

opening up stream, so that the water rises in the vertical limb. The velocity of the current is computed thus: $V = .977 \sqrt{2gh}$, where V is the velocity, g gravity, and h the height in feet of the column of water above the surface of the stream.

directed backward and the tibiae and tarsi forward, causing most of the leg to lie nearly parallel with the current. Moreover, the femurs are so shaped that the water deflected upward by them, has a tendency to flow off at the union of femur and tibia, which causes the leg to be pushed both against the body and the bottom of the stream. Another peculiarity of the legs is seen in the cross section of femurs and tibiae. They are flattened, but thicker at the anterior margin, which is exposed to the current, becoming thinner posteriorly, and fringed with hairs, where the current flows off, thus carrying out in this detail, the general stream-line shape.

Baetis intermedius Dodds (Plate II, fig. 6)

This species is found only in very swift streams, where it is seen clinging to the surface of stones, facing the current, in water flowing as much as eight feet per second. In general appearance it is very much like *B. tricaudatus*, but smaller. Its gill lamellae are decidedly smaller in proportion to the body, the legs are larger, the tarsal hooks longer, and the middle caudal cercus decidedly shorter, all of which differences would serve either to increase its holding powers or to reduce its resistance to the current.

Baetis bicaudatus Dodds (Plate I, fig. 4)

This species inhabits the very swift stream and the torrents, where the water often flows at the rate of ten feet per second, under which difficult conditions, the nymph, by facing the current, is able to cling to the smooth surface of the rocks. It crawls about over the bottom by keeping its head toward the current, the body parallel with it, and by moving sideways, forward and backward. The only marked differences between this species and the two just described are the increased relative size of the legs and thorax, and the further reduction of the gill lamellae and the middle caudal cercus. This nymph lives in swifter water than any other mayfly in these streams.

The three species of *Baetis* just described are of interest because they afford examples of highly successful torrent-dwelling species which differ but little from the most successful lake dwellers. The important changes are a great increase in the relative size of thorax and legs, with a corresponding reduction of the abdomen, including an almost entire disappearance of the hairs of the caudal cerci. The decrease in absolute size of the body is probably also of significance, inasmuch as a small body offers less resistance to the current than a large one. Within the genus *Baetis*, as illustrated by our three species, the progressive adaptation to swift water follows the same line as that which differentiates this type from the swimming type, namely: decrease in the size of the body, without a corresponding decrease in the size of the legs; reduction of size of gill lamellae; reduction of middle cercus from a length two-thirds the other two, to a mere rudiment. The reduction of this cercus is, no doubt, of importance in reducing the pull of the water.

by reducing the exposed surface in this part of the body, while the remaining two, when held close together, as they commonly are, serve to complete the pointed tip of the tapering body.

(*b*) *Current-resisting Species with Flat Bodies*

The species now to be described represent a type of nymph, which, like *Baetis,* live upon surfaces of rocks swept by strong current. They employ the stream-line principle in reducing resistance to the current, but in a modified form. As pointed out by Needham (1916) the body is greatly compressed, resembling half of a stream-line body, which had been divided from end to end, with the flat side closely applied to the substratum. This is commonly spoken of as the limpet-like form.

Iron sp. (Plate II, figs. 8 and 9)

This nymph inhabits clean surfaces of stones in very swift streams and torrents, where the water is flowing about six feet per second, provided the water is gliding smoothly over the surface. Its adaptations, though more spectacular than those of *Baetis bicaudatus,* are not as effective, for the latter species can maintain its position in water up to ten feet per second. *Iron sp.* has a broad, dorso-ventrally compressed body, flat underneath and gently arched above, a form well suited to avoid the full force of the current by hugging close to the bottom. The ability of the nymph to cling close to the bottom is much increased by the formation of a sucking organ from the gill lamellae, which effectively prevents the animal from being lifted from the rock by water running under it.

This sucker is built as follows: The first pair of gill lamellae are much enlarged, and by overlapping under the thorax (Plate III, fig. 9) form a broad, crescent shaped plate, while at the posterior end, the smaller, seventh pair curve inward in a similar manner. The other five pairs extend latero-posteriorly, each one overlapping the one behind it, and in this way forming an elliptical sucker. The thorax is short, so that the sucker extends almost the whole length of the body. The nymphs orient themselves with head against the current and hold the legs in about the same position as *Baetis bicaudatus.* The legs also have about the same shape, and, as in the former species, deflect the water in such a way that part of the force of the stream is used to press them against the bottom.

The head is also strongly flattened, with expanded edges, and when the front margin is pressed against the supporting surface, it completely covers the mouth parts. The anterior margin of the frontal plate is broader than the posterior and bears a dense fringe of hairs, which prevent the water from running under the animal, and aid in deflecting the current over the head. The angle which the front surface of the head makes with the substratum is so low, that a considerable part of the force of the water deflected over the head is utilized in pressing the head downward, a pressure which is added to by the tendency to form a vacuum under the narrower latero-posterior margins of the head, as the water runs off in the region of the eyes. Thus, the flatness of the nymph not only enables it to avoid the full shock of the current, but to utilize part of its force in pressing it against the bottom. This unilateral, limpet-like body is well adapted for avoiding currents which flow in only one direction, but is not suited for resisting an irregular flow, such as found on wave beaten shores. It is not effective on rough bottoms, where the water has opportunity to get underneath it and exert a lifting force.

This species is two or three times as large as *Baetis bicaudatus.* We have found, by repeated observation, that a definite zonation between these two species exists. For example, in a situation where the water glides swiftly over a smooth rock bottom, it is commonly observed that, at the edges of the stream, where the current does not excede six feet per second, both species are found, with the numbers of *Iron* sp. decreasing as the current becomes swifter toward the middle of the stream, until a zone is reached where it is absent, but where there are plenty of *Baetis.* The number of individuals of *Baetis,* is also somewhat reduced in the swifter water.

Iron longimanus Etn. (Plate II, fig. 7)

This species is found on the surface of stones where the water is flowing from one to three feet per second, and also between and under the stones. It is much like the species of *Iron* just described, but with certain differences which probably explain its smaller current-resisting powers. It is somewhat larger, and the sucker formed by the gill lamellae is less perfect, inasmuch as the two anterior gill lamellae are smaller than in the former species, and lack much of meeting in the mid line, as do also the posterior pair (compare figs. 7 and 9, plate III). This arrangement is evidently less effective in preventing currents from running between the nymph and the substratum. Moreover the longer thorax and smaller anterior gill lamellae of *Iron longimanus* causes the sucker not to extend as far toward the head, leaving the anterior end of the body unprotected from the lifting effect of the current. In respect to other adaptations for strong current, the two species of *Iron* are very similar, so that we may conclude that it is the differences in the suckers that determine the difference in ability to withstand the current.

2. Species which Avoid the Current by Living in Crevices and under the Stones

The population of the stream also includes a number of species which avoid the current by living under and among the stones. These species comprise a rather miscellaneous assemblage of forms, having little in common except the absence of well developed adaptations, either for swimming in quiet water or for resisting the current of swift streams. While some have bodies somewhat flattened, none approach *Iron* in this respect, and though three well developed caudal cerci are present, none of them are provided with the interlacing hairs of the swimming forms. Some of them have bulky bodies and large, sprawling legs. They move about by walking, and are all very awkward swimmers. Certain of these species, however, do, in certain respects, approach the torrent dwelling type, and probably make excursions, to a certain extent, upon the exposed sides of rocks.

Ecdyurus ramaleyi Dodds (Plate II, fig. 10)

This species has a very wide distribution, being the commonest nymph living under the stones in all parts of the stream. It is also found in some of the higher lakes, which have clean, rocky bottoms. This wide distribution, in both streams and lakes, is probably due to the constant conditions which exist under the stones, both in streams and lakes. There is very little or no current beneath the rocks, and the oxygen content here has been found to be about the same in the lakes as in the streams. A species living under these mild current conditions would be expected to have conservative current resisting adaptations. An examination of the nymphs of *Ecdyurus ramaleyi* shows this to be the case. The body, while flattened, is less so than *Iron,* the head is more rounded, and its expanded margins do not cover all the mouth parts. Neither is the anterior margin of the head fringed with hairs, nor can it be held closely against the bottom in a manner which will effectively divert the water over the head. The tibiae and tarsi are almost cylindrical and do not have a row of marginal hairs, while the femurs are less flattened than those of *Iron,* though they have a row of short hairs on the posterior margin. The legs are also very delicately articulated with the body, which would prevent them from being of much use in resisting the shock of water. This fragility is strikingly shown by the fact that it is hard to find a complete specimen of *E. ramaleyi* in our collections, while almost every individual of *Iron* is in perfect condition.

Drunella grandis (Etn.) (Plate II, fig. 11)[3]

This is a striking nymph of unique form and large size which lives under the stones in very swift streams. The body is flattened on the ventral side, and highly arched above, especially in the thorax, making a very thick body. The head is small in proportion to the body and the narrow frontal plate forms an angle of about 45 degrees with the surface on which the nymph rests, a position much less effective in avoiding the shock of the water, than that of the flatter head of *Iron*. The femurs are flat, with tooth-like projec-

[3] This is the nymph described by Eaton in his Monograph, under the heading "Nameless Nymph Allied to Ephemerella, No. 3" and figured in his plate 39. We refer it to the above species after rearing the imago from the nymph.

jections on the anterior edges, and the two posterior pairs are slanted so that when the nymph is facing the stream, the force of the current pushes them against the body.

The most remarkable feature of this species is a sucker on the ventral side of the abdomen, formed by the hairy sterna of seven of the abdominal segments. Each of these segments bears a dense growth of fine hairs, which are shorter on the median portion and become longer laterally, where they are situated on a low ridge. The sucker is completed anteriorly by a similar hairy ridge which follows the curved anterior margin of this segment to form a crescent-shaped area, while on the last two segments of the sucker, the hairs are of about uniform length, and distributed over the entire surface of the sternum. This is an adhesive organ of considerable power, as shown by the strength with which nymphs adhere to rocks or aquaria, strongly resisting efforts to remove them. In spite of this, the species is not one of those inhabiting very swift water, and has never been found anywhere except under the stones, where current resisting devices of a high order are not needed. It is possible that the nymph at times visits the upper surface for food, though we have not observed this, and it is unlikely on account of the absence of adequate current resisting devices other than the sucker. An obvious disadvantage of a sucker in such a situation is that it must be released for the animal to move, leaving it at the mercy of the water, unless, as in *Iron,* there are also other good current resisting devices. In the case of *Drunella,* however, the great size and thick form of the body, the shape of the head, the form of the legs, and the presence of three well developed caudal cerci, are departures from an effective current resisting type.

Ephemerella coloradensis Dodds (Plate I, fig. 5)

This species lives under and among the stones in the stream, especially on gravelly bottoms. It is an awkward, long legged species, obviously suitable only for a life where the current is not an important factor. The thorax is long and well developed, giving ample support for the strong legs. The femurs are provided with short, stout spines, which are suited, possibly for pushing between stones. The tibiae of the first pair of legs have, at the distal end, a thumb-like extension, useful, perhaps, in digging. The whole structure of this nymph is quite unsuited to life in very swift water, or for swimming in ponds, or even for creeping into small crevices between rocks, but rather for fighting its way among the small stones or gravel, where it commonly lives.

Ephemerella sp. (Plate II, fig. 12)

This is a sluggish, sprawling species which inhabits root mats and masses of debris along the banks of streams. The thorax is longer than in most mayfly nymphs, and the legs, accordingly, distributed along the body, a condition, probably useful in crawling among the roots in which the nymphs live. The legs are adapted for walking, and unlike those nymphs which face a strong current, have hairs on both anterior and posterior margins of femur and tibia. Not only are the caudal filaments undeveloped into a swimming organ, but the swimming instinct is nearly lacking, for when a nymph is released at the surface of an aquarium, it makes no effort to swim, but curls the abdomen over the thorax and sinks to the bottom.

Discussion

The observations recorded in the preceding pages, based upon our work in mountain torrents, have led us to certain conclusions somewhat at variance with certain views commonly held concerning the significance of the limpet-like form among aquatic insects. We have also found support for our conclusions in observations we have made in some lakes and streams in Wisconsin.

It seems generally agreed that the flattened species have developed as an adaptation for life upon rocks exposed to strong currents or the action of waves, and that they represent the highest perfection for life in such situations. In many instances this is doubtless the case, but the conditions which we have observed seem to demand a different interpretation. The most successful species of mayfly nymph in the invasion of swift streams we have not found to be any of the flattened forms, but one with a round body (*Baetis*) which manifests very conservative departures from the ancestral walking or swimming forms. Only one of our flattened genera (*Iron*) approaches *Baetis* in ability to hold its position in swift water. The other flattened forms, *Ecdyurus* and *Drunella,* do not live upon exposed surfaces, but seek the protection of crevices, along with *Ephemerella.* Certain genera of mayfly nymphs of a more or less flattened type, such as *Ecdyurus, Heptagenia, and Ephemerella,* are usually spoken of as inhabitants of wave-beaten shores and swift streams. We have searched such situations repeatedly, and though these and other flattened forms, such as the water penny, are found on exposed shores and in swift streams, we do not find them upon the exposed surface of the stones, but beneath them, where they can be found only by turning over the stones, even on lake shores in quiet weather.

This leads us to the conclusion, that among mayfly nymphs, flattened bodies are probably primarily utilized for creeping into narrow crevices under the stones, and only in a few species, *e.g., Iron,* has the flat body been utilized, by the addition of strong adhesive structures, to allow its possessor to live upon exposed surfaces.

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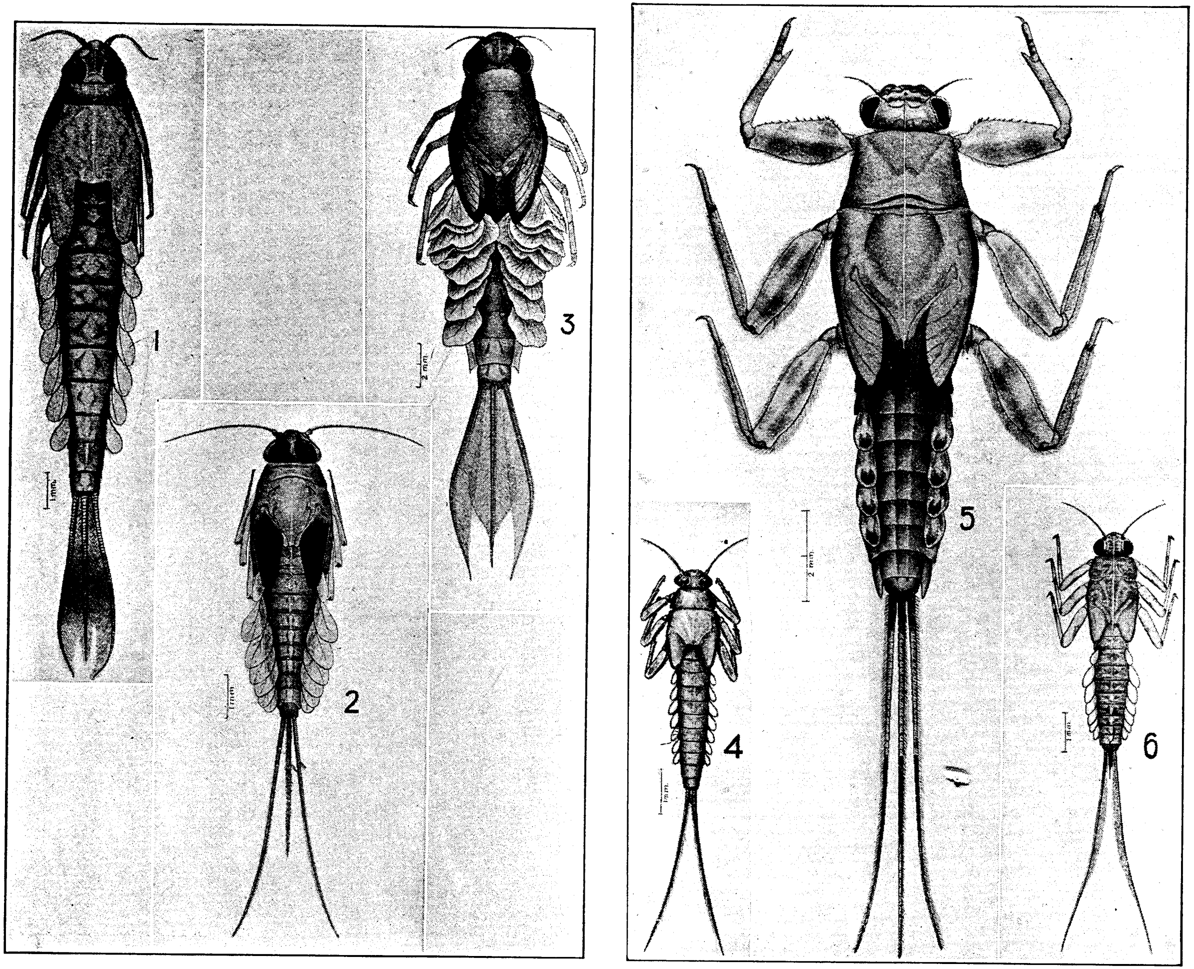
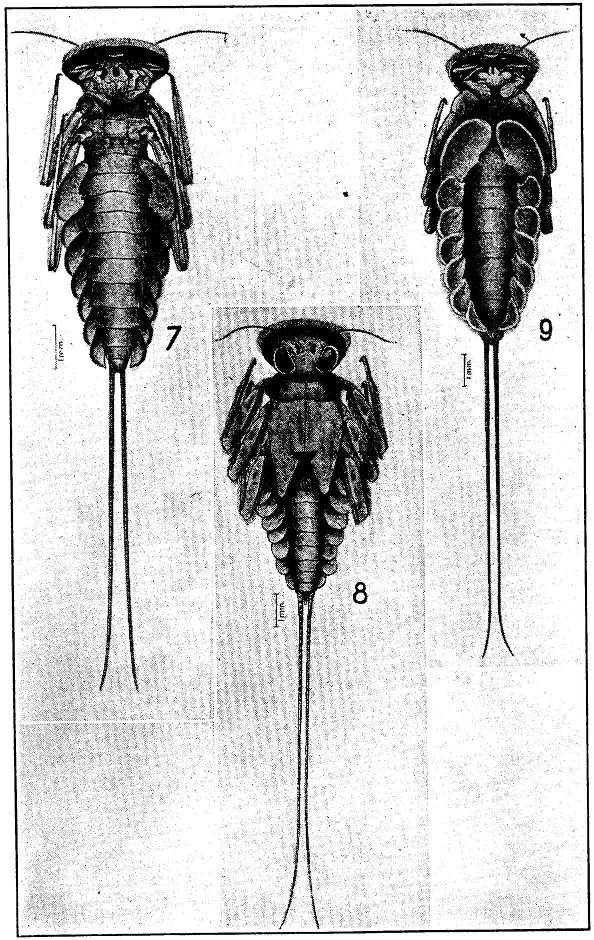
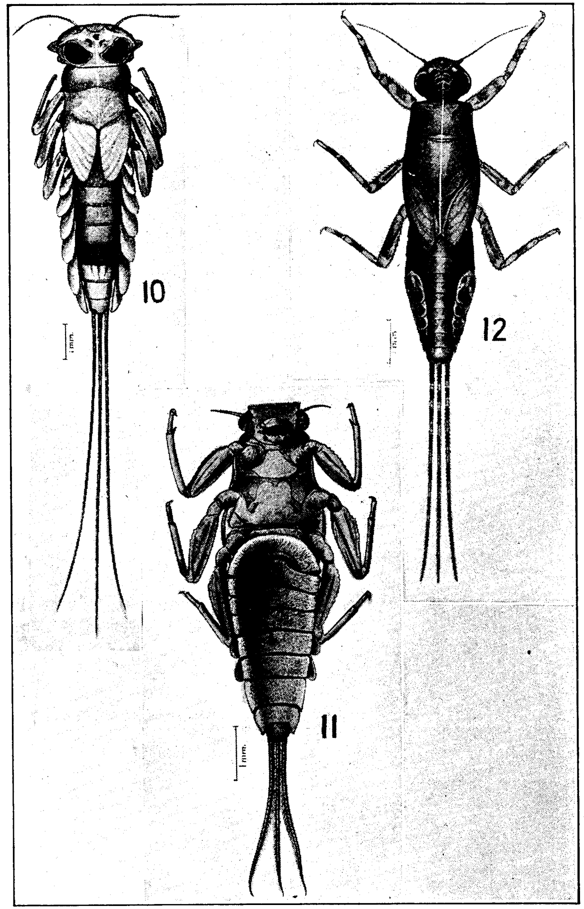


All drawings were made by aid of camera lucida, and the magnification is indicated on each figure.

1. *Ameletus velox.* Lives in lakes and quiet portions of streams.
2. *Baetis tricaudatus.* Lives in streams up to five feet per second.
3. *Siphlurus occidentalis.* Lives on silty lake bottoms.
4. *Baetis bicaudatus.* Lives in streams up to ten feet per second.
5. *Ephemerella coloradensis.* Lives under stones in streams.
6. *Baetis intermedius.* Lives in streams up to eight feet per second.





7. *Iron longimanus.* Lives in streams up to three feet per second.
8. *Iron sp.* Dorsal view. Lives in streams up to six feet per second.
9. *Iron sp.* Ventral view.
10. *Ecdyurus ramaleyi.* Lives under stones in streams and on rocky shores of lakes.
11. *Drunella grandis.* Lives under stones in swift streams.
12. *Ephemerella sp.* Lives in root mats along bank of swift stream.