AN ECOLOGICAL STUDY OF THE INSECTS OF CRATER CREEK, COLORADO.

by

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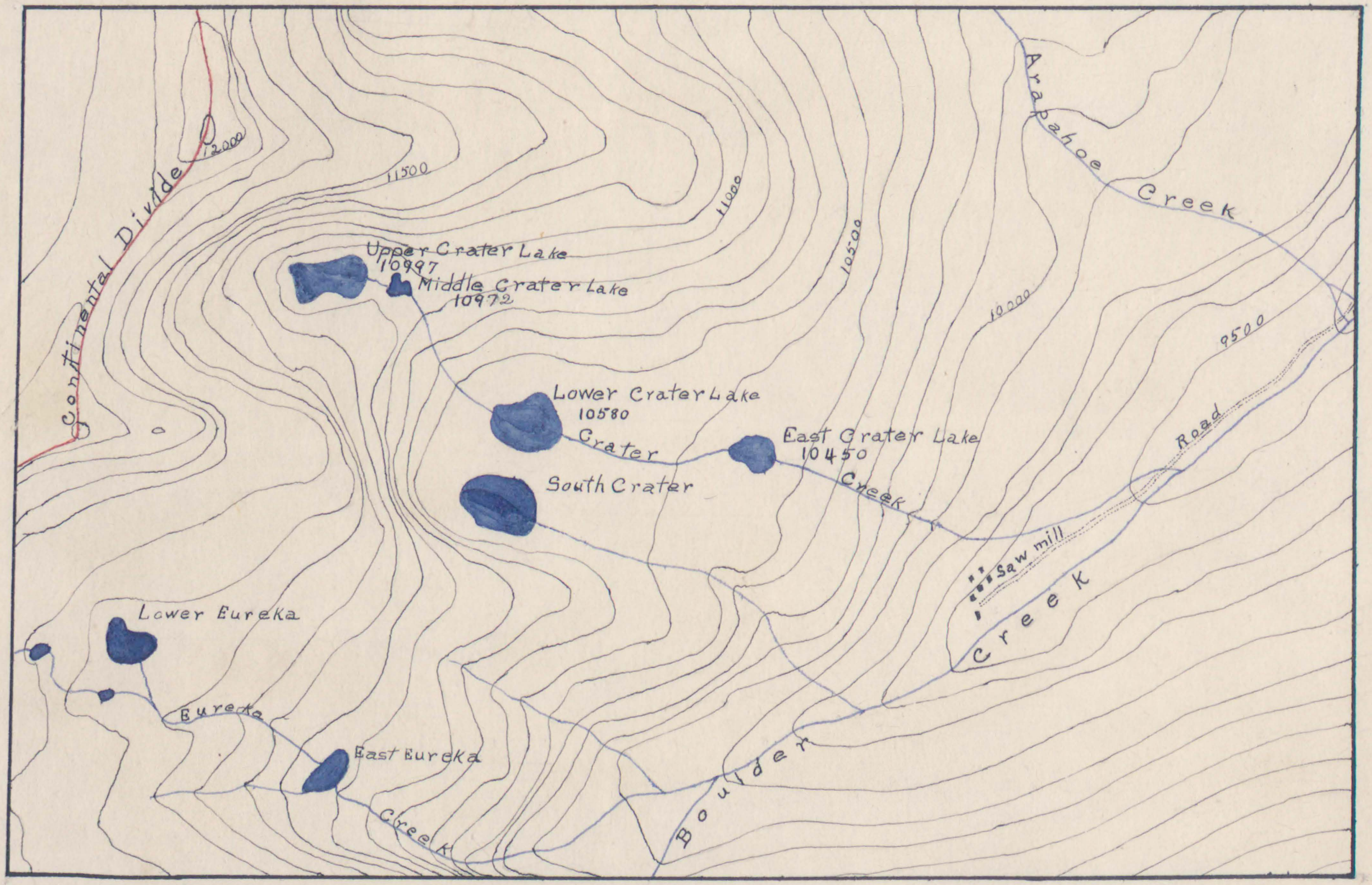
The observations and collections described in this paper were made during the summers of 1914 and 1915, while at the Mountain Biological Laboratory of the University of Colorado, at Tolland, Colorado, and the more detailed studies at the Zoological Laboratory of the University of Missouri. I am indebted to Professor Francis Ramaley, director of the Mountain Laboratory, for the use of the laboratory and equipment during the summers, as well as for a stimulating interest in my work. During these two summers I spent much time in the field with Professor G. S. Dodds, making collections of insects from the lakes and streams in the Tolland region and the region around Boulder, Colorado. The special study of the Crater Lake Stream was suggested to me by him as a part of the general study in this region.

I. THE CRATER LAKE STREAM AND TOPOGRAPHY.

The Crater Lake Stream is a tributary to South Boulder Creek, emptying into it about four and one half miles above the town of Tolland. From source to mouth the stream is one and seven eighths miles long and has a fall of about fifteen hundred feet. In its course is a series of four lakes, the highest of which occupies a cirque on the east side of the Continental Divide about one and seven eighths miles south of Corona. The lakes are not of volcanic origin as suggested by the name, but were formed by the glacier which once occupied the valley. South Boulder Valley has also been glaciated and cut down about five hundred feet below that of the Crater Lake Valley, which thus forms a "hanging valley" with the lower part of its course very steep. There is a second very steep portion of the stream between Middle and Lower Crater Lakes. The accompanying topographic map (Fig. 1) gives a general idea of the topography of the region, and the section (Fig. 2) from the top of the cirque wall above Upper Crater Lake to the lower end of the stream shows the fall of the stream and the elevations of the lakes. The quieter parts of the stream are found just at the outlet of each lake where the valley is relatively level, while in the valley below these places it is very swift, often flowing in torrents or pouring over falls.

The two lower lakes, and the stream for the lower

Crater Creek, Colo.



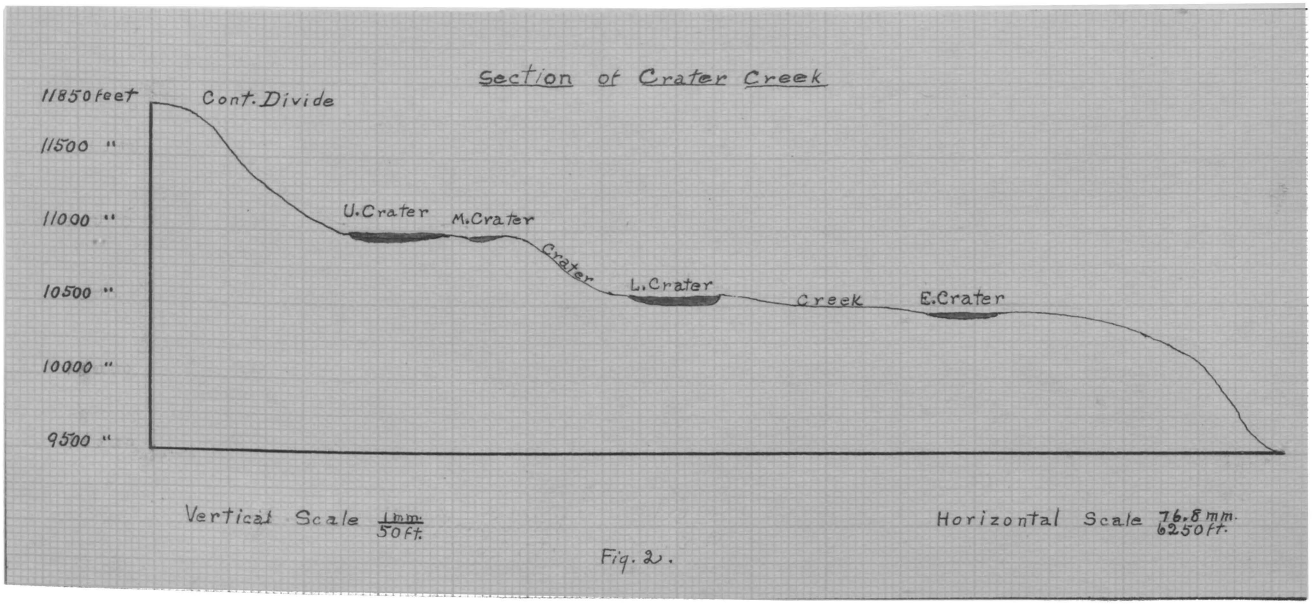
Contour interval 100 feet

Colorado
Central City Quadrangle
U.S.G.S.

Scale $\frac{1}{62500}$

½ mile

Figure 1



Section of Crater Creek
11850 feet
11500 "
11000 "
10500 "
10000 "
9500 "
Cont. Divide
U. Crater
M. Crater
Crater
L. Crater
Creek
E. Crater
Vertical Scale 1mm. / 50 ft.
Horizontal Scale 76.8 mm. / 6250 ft.
Fig. 2.

Figure 2.

three fourths ~~parts~~ of its course, are bounded by an evergreen forest, except in places where the trees have been cut for lumber. In these clearings, and where the trees are thin, the shore is covered with a dense growth of vegetation, while the lake margins are lined with clumps of willows. In contrast to this, the two upper lakes are above timberline. The shores, where they are not too rocky, are covered with a short, stubby growth of sedge and the part of the stream which connects the lakes flows through a dense tangle of willow bushes. Almost the entire shore of Middle Crater Lake has a good growth of sedges or willows but Upper Crater Lake has only a few willows and wind blown spruce "bushes" near the outlet, the remainder of the shore being bordered by talus slopes which extend down into the water. The accompanying photograph (Fig. 3), looking down the valley from the top of the cirque wall above Upper Crater Lake, shows the characteristic features of this part of the stream, while figure 4 shows the creek as seen from the ridge opposite, looking across South Boulder valley and up the Crater valley. This photograph also shows clearly Middle and East Crater Lakes, the cirque in which are Upper and Middle Crater Lakes, and the two very steep portions of the stream, the one just below Middle Crater Lake and the other just before the stream enters South Boulder Creek.

Fig. 3.

The Crater Lake Stream as seen from the Top of the Cirque Wall Above Upper Crater Lake. (Photograph by Dodds and Hisaw)

Fig. 4.

The Crater Lake Stream as Seen from the Ridge Opposite the Lower End of the Valley. (Photograph by Dodds and Hisaw.)

II. CLIMATE.

The difference between the mean annual temperature at the upper and lower ends of the Crater Stream, as estimated from the government reports for Frances, Colorado (9,300 feet) and Corona (11,660 feet), is about 10° F., being about equal to that of two places separated by about one thousand miles of latitude. At the head of the stream, the average yearly precipitation is about forty inches, while at the lower end it is about twenty-four inches. At the higher point the annual snowfall is about thirty feet, at the lower, about fifteen feet. But other conditions than altitude have an important effect on the temperature of both lakes and stream.. From the crest of the Continental Divide there is a gradual slope to the west, but on the east side there are many very steep cirque walls. The immense amount of snow that falls on the west side, above timberline, is blown over by the prevailing west wind, and deposited in these cirques, where it accumulates in great drifts, which are not melted until the summer is well past and occasionally a small portion stays on until the following winter. I have not visited the stream before the middle of June, and so cannot say just what the conditions are in the early part of the year. But by this time the lower lakes are completely open and the upper ones are usually covered with ice which does not go off until the first of August. The late melting of the ice in Upper Crater Lake has a direct influence on the temperature of the stream and the other lakes. After the snow and ice of the lower parts of the stream has melted, the great supply in the upper lake and its cirque is drawn upon during the remaining part of the season, causing its temperature and that of the stream and the other lakes to be lower than it would be were it not for this supply of cold water. (Table I.)

Table I. Temperature of Lakes

Upper Crater Lake			July 3	40 F.------	Aug. 22,		55 F.
Middle	"	"	" "	41 " ------	"	"	58 F.
Lower	"	"	" 17	55 " ------	"	"	61 F.
East	"	"	" "	58 " ------	"	"	62 F.

During the summer the temperature of the water is raised while in the lakes, but does not change to any great extent in the stream between the lakes. The records taken for Boulder Creek at Tolland, five miles lower down on the stream, show that the water in the stream is never warmer, usually a few degrees colder, than that of the lower lakes.

NATURE OF THE WORK.

This is by no means a complete piece of work and should be looked upon as only a few observations which are not conclusive enough in themselves to afford a basis for stable conclusions. Neither does it represent a statement of all the problems that have come up in the work and are as yet unsolved. In this paper only a few of the more striking and perhaps more interesting points will be taken up.

The insects of chief ecological interest are the Ephemerida, Trichoptera, and Plecoptera. The immature forms of the several species of these three groups are important elements of the aquatic communities. As the larvae are more valuable in determining ecological distribution than the imagos, they received particular attention. The manner in which the larvae get into the stream and lakes is also of ecological significance. From observation it seems that the eggs are not always deposited in the habitat to which the larva of the particular species belongs. Although some of the species seem to have a preference for either lake or stream, they do not appear to be particular about the parts of the lake or stream in which they lay their eggs, but drop them promiscuously in both of these places. On hatching, the larvae find the particular part of the stream or lake to which they are adapted, or they die. Just what part the current of the stream plays in the distribution of the eggs is not fully known, but as they are heavier than water, they cannot be washed very far over a rough bottom.

The identification of species has not been completed. The forms found in this collection are, in large part, of species not described in the literature. The printed descriptions are mostly in German, of European forms, and do not fit our species. In a few cases the family could not be determined and the proper species could not be definitely decided upon for any of them. Samples of the material have torrents and falls. Each of these communities will be described in the course of the discussion which is to follow.

A. THE LAKE COMMUNITIES

The four lakes naturally fall into two groups. The discussion of the conditions for East Crater Lake is equally adequate for those of Lower Crater Lake, and the important characteristics of Middle Crater Lake are the same as those of Upper Crater Lake.

1. The lower lakes.

a. Description of the lower lakes. The shores of East and Lower Crater Lakes are covered with a good growth of vegetation (Fig. 5) consisting of sedges, herbaceous plants and trees, which furnish an abundant supply of decaying organic matter which may be either washed or blown into the

Fig. 5.

East Crater Lake. (Photographed by Dodds and Hisaw)

Table II. Distribution of Species.

Elevations	9,500 ft		10,450 ft		10,580 ft		10,985 ft		10,997 ft	
Localities	Saw mill	Stream between	East Crater Lake	Stream between	Lower Crater Lake	Stream between	Middle Crater Lake	Stream between	Upper Crater Lake	
Ephemerida										
N102 Ecyyurus "a"	■	■		■		■	■	■	■	*
N106 Ameletus "a"	▨	■	■	■	■	■	■	■	■	*
N105 Baetis "a"	■	■		■		■				*
N104 Baetis "b"	■	■		■						*
N103 Genus "A" "a"	■	■		■						
N101 Iron "a"....	■	■		■						*
N110 Genus "B" "a"	■	■		■						
N108 Siphlurus "a"			■							
N107 Baetis "c"	■	■								
Plecoptera										
N13 Nemura "a"	■	■		■		■		■		*
N1 Isopteryx "a"									■	
N2 Perlodes "a"						■		■		
N3 Perlodes "b"						■		■		
N11 Isopteryx "b"	■	■		■		■				
N8 Perla "a"	■	■		■		■				
N15 Nemura "b"	▨	■		■		■				
N14 Perlodes "d"						■				
N9 Capnia "b"	■									
Trichoptera										
L204.............			■		■		■	■	■	
L208.............		■				■		■		
L209.............						■		■		
L210.............						■		■		
L207.............				■		■	■	■		
L206.............							■	■		
L205.............							■			
L202.............	■	■		■		■				*
L201.............	■	■		■		■				*
L217.............	▨	■		■		■				*
L221.............						■				
L211.............	▨	■		■		■				
L213.............	▨	■	■	■	■					
L214.............					■					
L219.............					■					
L220.............					■					

each year and the highest temperature reached during the summer is 55°F. In contrast to this, East Crater Lake is free from ice from the first of June to the first of October or later, and reaches a maximum temperature of 64°F. The total number of heat units available during any one season is far greater in the lower lake than in the higher lake.

It may be that an important factor having an influence on altitudinal distribution is the condition of the stream in winter. The water flowing out of the lakes is not over a few inches in depth at any place. The lakes, no doubt, freeze to a much greater depth, which means that the stream must have very little if any water in it during the winter. Also there is no water supply for the upper lakes during the winter as the snow and ice are not melting and consequently the stream would become dry when the level of the water fell to that of the outlet. The larvae living in this part of the stream must be able either to withstand freezing or avoid it by burrowing. It may be that in the lower parts of the stream the bottom does not freeze as deep as that in the parts of higher elevation and it is not likely that the stream is without flowing water, and on this account is a more favorable abode. This if true, is another factor complicating altitudinal distribution, but can be decided only by observations during the winter season.

There are also many local conditions which influence the distribution in any particular locality and make it impossible to draw general conclusions about altitudinal distribution from a single stream. Certain forms require a rock bottom and others mud, some live on rocks where the water is so swift that very little vegetation is able to grow, while others live in quieter places where the rocks are covered with moss. These are some of the physical conditions which must be duplicated at different elevations before the exact distribution of a species can be definitely determined. If the physical conditions of the habitats in the higher altitudes are not to a great extent comparable to those places lower down which the animal inhabits, there is no way to determine the effect of altitude. There are a few species that illustrate this point and their expected distributions in the above table (Table II) are shown by double lines. Some were found in only one place so their extension up or down cannot be determined. Yet there are others about which there is little doubt and a star has been placed in the table to show this.

V. COMMUNITIES.

With these general factors of distribution in mind, collections were made in the stream and lakes, for a comparative study of the communities. To make this easier certain points were picked out at different altitudes, similar as far as possible in other respects, to determine whether there is any change in the composition of the communities with altitude. The four general communities recognized were the lakes, the swift-stream, the very-swift-stream, and the torrents and falls. Each of these communities will be described in the course of the discussion which is to follow.

A. THE LAKE COMMUNITIES

The four lakes naturally fall into two groups. The discussion of the conditions for East Crater Lake is equally adequate for those of Lower Crater Lake, and the important characteristics of Middle Crater Lake are the same as those of Upper Crater Lake.

1. The lower lakes.

a. Description of the lower lakes. The shores of East and Lower Crater Lakes are covered with a good growth of vegetation (Fig. 5) consisting of sedges, herbaceous plants and trees, which furnish an abundant supply of decaying organic matter which may be either washed or blown into the

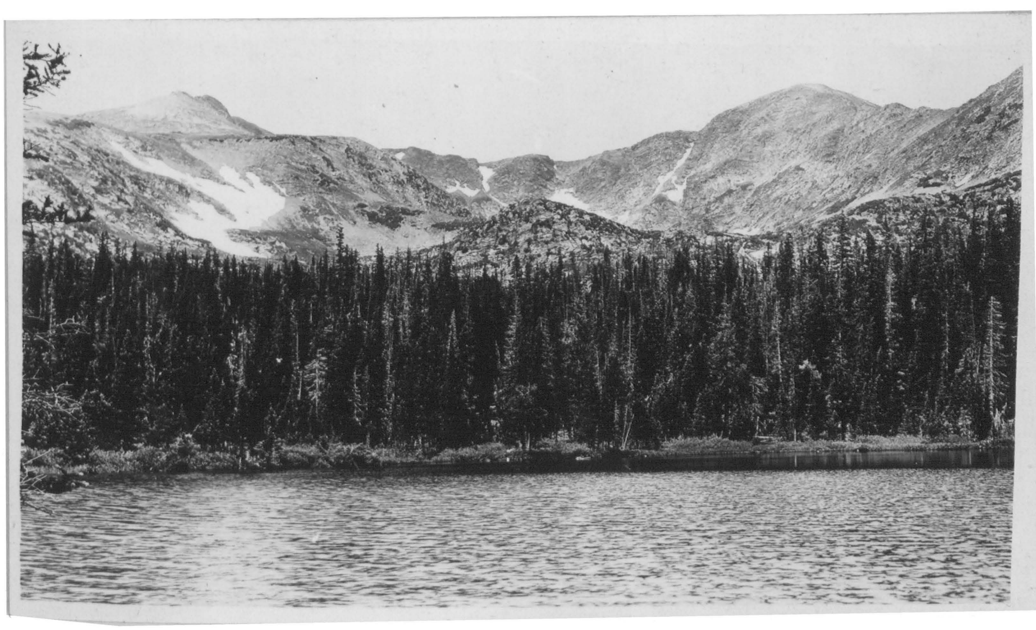


Fig. 5.

East Crater Lake. (Photographed by Dodds and Hisaw) lakes. The immediate region which drains into these lakes also has a covering of loose earth which in time of rains or thaws is washed into the lakes. These two factors give rise to a muddy or silty bottom with much decaying organic debris, and will in time convert the lakes into marshes or bogs. In these lakes, along part of the shore, sedges grow in the water, forming an emerging vegetation, while at other places the bottom near the shore is covered with sand and gravel.

b. Fauna of the lower lakes. In the lower lakes have been collected 10 species, as shown in table III.

Table III. Species of the Lower Lakes.

Species	East Crater Lake	Lower Crater Lake
Ephemerida		
N106 Ameletus "a"	*	*
N108 Siphlurus "a"	*	
Trichoptera		
L204	*	
L213	*	
L214	*	
L219	*	
L220	*	
L205		*
L206		*
L207		*

The caddis-fly larvae inhabiting these lakes, with the exception of one (L204) which uses mica, build their cases out of woody materials. Some use only bits of sedge blades or small pieces of bark, others wood and pine needles, while some weave mica in with these materials. Those which use sedge blades are found in the part of the lakes which have vegetation growing in the water, while those which use pieces of wood and bark are found on the muddy bottoms. The larva which uses mica and very little woody material (L204) lives in the parts of the lakes where the bottom is free from mud.

The may-fly nymphs living in these lakes are without an exception swimming forms. Siphlurus "a" (N108) spends most of its time half buried in the silt, and when disturbed swims for a short distance and scoots into the mud again. Ameletus "a" (N106) is not so dependant on the bottom. It uses the sedge stems, stones and other submerged objects as resting places. These forms will be considered further in the discussion of the upper lakes.

2. The upper lakes.

a. Description of the upper lakes. Although these two lakes (Fig. 3) differ in a few respects, they are near enough alike to be considered together. They differ from the lower lakes in that they are not surrounded by a dense growth of vegetation. Middle Crater Lake has a few willows and wind blown spruce trees on its shores, but not enough to cause its bottom to be covered with an excess of litter. The region which drains into it, although with a shallow covering of soil, is so small that the lake receives very little silt. Upper Crater Lake, as has been mentioned, is surrounded almost entirely by bare rocks. At several places on the shore big talus slopes extend down into the water. Between these piles of boulders, the shallow coat of soil is covered by a short, stubby growth of sedge while only a narrow strip of the shore near the outlet has a reasonably good growth of vegetation. So much of the shore is without a soil coat that the amount of silt washed into it is almost negligible. This causes the bottom to be composed almost entirely of rocks. At no place is there the emerging vegetation which is characteristic of the lower lakes.

Table IV. Species of the Lower Lakes.

Species	Middle Crater Lake.	Upper Crater Lake.
Ephemerida		
N102 Ecdyurus "a"	*	*
N106 Ameletus "a"	*	*
Trichoptera		
L204	*	*
L206	*	
L205	*	
L207	*	
Plecoptera		
N1 Isopteryx "a"		*

b. Fauna of the upper lakes. The caddis larvae of these lakes build their cases mostly of sand grains and mica. None of those forms of the lower lakes which use wood exclusively as a building material are found in the upper lakes, but the one that uses mica and wood (L204) of the lower lakes, is found also in Upper Crater Lake, where its case consists almost entirely of mica. The other two species of caddis larva (L207 and L206) which live in Middle Crater Lake build their cases of sand.

Only two species of may-fly are found in Upper and Middle Crater Lakes. One of them, Ameletus "a" (N106), is a swimming form, while the other, Ecdyurus "a" (N106), crawls on the bottom. Ameletus "a" is found in great numbers in both of the lower lakes, a few were taken in Middle Crater Lake, and only about a half dozen in Upper Crater Lake. This is one of the species which though found in all the lakes, shows a decided decrease in numbers with altitude. Ecdyurus "a" is a species which normally belongs to the stream but enters both of the upper lakes. This is due, probably, to the clean rocky bottom and perhaps it would inhabit the lower lakes if the same conditions prevailed.

Although stone-fly nymphs are seldom found in lakes, one species, Isopteryx "a" (Nl), is found ~~is~~ in great numbers in Upper Crater Lake, It has never been taken in the stream, and would appear to be a true lake form. Yet the imagoes have been taken in different parts of the valley and it is possible that the larvae also live in the stream but for some reason have not been found.

A comparison of tables III and IV shows that the lower lakes have a much greater and more diverse population than the upper ones. The total number of species for the lower lakes is 10 and that for the upper lakes is 7, while East Crater Lake has almost twice as many species as Upper Crater Lake. Six of the ten species found in East Crater Lake do not enter the upper lakes and two of those in the upper lakes are not found in the lower lakes. These two exceptions in the upper lakes are species that have entered from the stream. The difference in population is due to the fact that the lower lakes have a wider variation of conditions and a richer food supply than the upper lakes. These differences are those which distinguish younger from older lakes, and if classified on this basis, East Crater Lake would be the oldest of the series and Upper Crater Lake would be the youngest with the other two as intermediates.

B. STREAM COMMUNITIES

All the communities described for the creek are those of a swift stream, the quieter parts being swifter than most of the places in our ordinary streams. So perhaps it is better to speak of them as swift-stream communities, very-swift-stream communities, and the communities of the torrents and falls. We may also classify the habitats of the stream, on the basis of swiftness of flow, as follows: quieter places and eddies along the shore, surface of stones in the stream, and among and under the stones on the bottom of the stream. These divisions I will call zones, and it is only in the less rapid part of the stream that all three of them are found. In the very-swift-stream community the shore and eddy zone is wanting, while the torrents and falls furnish only the surfaces of the stones as a place for animals to live. These points will be explained more fully and additional peculiarities will be brought out in the discussion of these communities.

1. The swift-stream community.

The quieter parts of the stream are found just below the outlet of each lake, where for a short distance it has relatively little grade. (Fig. 6) The banks are about eighteen inches high and composed of a black, silty soil which rests on a subsoil of coarse rock, mixed with gravel and sand. The bottom is strewn with large stones which occasionally reach to the surface and the intervening space is covered with gravel and sand. The water is not swift enough to prevent the surface of the stones from being covered with a good growth of moss

Fig. 6

Part of the Stream Showing the Habitat of the Swift-Stream Community. (Photographed by Dodds and Hisaw) and algae. The banks are covered with a dense growth of sedges which extend out into the water. It is due to this zone of emerging vegetation that the shore and quieter places were set aside as a part of the stream for special study. Unfortunately this community is not represented in the parts of the stream between Lower and Middle, and Middle and Upper Crater Lakes. The vegetation found in the quieter parts of the swift stream causes it to approach the conditions that are found in the lakes, and, as would be expected, several of the forms that inhabit the lakes are also found in the stream. Out of the ten species of caddis larvae, four are also found in the lakes. Thus half of the caddis-may-fly fauna has representatives in some of the lakes. This does not hold with the stone-flies of the stream, none of which are found in any lake. The one species which lives in the lake is not found in the stream and is restricted to Upper Crater Lake.

A study of the fauna of the swift stream shows considerable overlapping between zones. The surface of the stones has several species in common with the shore zone on the one hand and under the surface of the stones on the other hand. There are, however, no species common to the under surface of the stones and the shore zone. The caseless caddis larvae and stone-fly nymphs which form the greater bulk of the population under the stones, perhaps come out upon the exposed surfaces only in search of food, while it is evident that the surface living may-fly larvae never go under the stones (Table V). The forms living under the stones are also very seldom found along shore.

Table V. Species of The Swift-Stream Community.

Species	Along Shore	Surface of stones	Under Stones
Ephemerida			
N102 Ecdyurus "a"			*
N104 Baetis "a"	*	*	
N105 Baetis "b"		*	
N106 Ameletus "a"	*	*	
N107 Baetis "c"	*		
N110 Genus "B" "a"		*	
Plecoptera			
N2 Perlodes "a"			*
N3 Perlodes "b"			*
N8 Perla "a"			*
N11 Isopteryx "b"			*
N13 Nemura "a"			*
N15 Nemura "b"			*
Trichoptera			
L201		*	*
L202		*	*
L203	*		
L204		*	
L207		*	
L208		*	*
L209			*
L210		*	*
L213	*		
L217	*	*	
L221			*

a. Shore Zone. Clinging to the submerged portion of the vegetation, which is the chief characteristic of the shore zone, are found such lake-inhabiting forms as L203, L213, and *Ameletus* "*a*" (N106), (Table V). In addition to these, a caddis larva (L217) and a may-fly nymph (*Baetis* "*a*" (N106) found only in the stream, constitute an important part of the shore population. The caddis larvae build their cases of the sedge on which they live and the pieces of wood which occasionally lodge or float past them. The may-fly nymphs are of the swimming type. The marginal hairs on the three caudal setae form a paddle which serves as an efficient organ for propelling them through the water.

b. Surface of stones. This zone seems to be a region of general overlapping, including certain species found also in the shore zone, certain others found also under the stones, together with some forms entirely confined to the surfaces of the rocks. *Baetis* "b" is a typical surface larva and is very seldom taken along shore and never under the stones. (Table V). L207, a caddis larva, which was recorded as being found under the stones, is perhaps strictly a surface-living species. In the lakes it goes under the stones only in time of pupation and the fact that most of the specimens taken from the stream were pupae, lends itself as a possible explanation. The caddis larva L202, which lives only in the stream, furnished further evidence that this is the probable explanation. The entire larval period is spent on the exposed surfaces but at the time of pupation it fastens itself to the lower side of the stones.

c. Under the stones. The stone-fly larvae form the greater part of the population in this zone. They are represented by six different species, found almost exclusively under the stones whence they make short excursions to the more exposed parts but return when disturbed. Judging from their relation to the stones in the upper lakes, it is doubtful if they use the silty bottom to any great extent. The caseless caddis larvae, as has been mentioned, also make this part of the stream their headquarters.

2. The very-swift-stream community.

This habitat differs from that of the swift stream in several respects, the most important of which is the absence of a shore zone. The bottom is very rough, being composed mostly of large boulders many of which project above the water. The stream has a fall of about twenty to twenty five per cent and is so swift that very little vegetation is able to grow on the surfaces of the stones. This type of habitat is represented in all sections of the stream except that between Upper and Lower Crater Lakes. Figure 7 shows most of the peculiarities of such a stream, but unfortunately the photographs were taken during the latter part of the season when the amount of water was considerably reduced.

We have noticed that in the swift stream about half of the total number of species making up the caddis- and may-fly population were also found in some of the lakes. This is not true to such a great extent of the very swift stream. All of the six species of caddis larvae of this community are restricted to the stream, while only two of the six species of may-fly larvae (N106 and N102) have representatives in the lakes. Another marked difference is the absence of the large caddis larvae which build their cases out of wood and stone, and the abundance of the caseless species.

Fig. 7.

The Habitat of the Very-Swift-Stream Community. (Photographed by Dodds and Hisaw)

Table VI Species of the Very Swift Stream Community

Species	Surface of Stones	Under Stones
Ephemerida		
N101 Iron "a"	*	
N102 Ecdyurus "a"		*
N103 Genus "A" "a"		*
N104 Baetis "a"	*	
N105 Baetis "b"	*	
N106 Ameletus "a"	*	
Plecoptera		
N8 Perla "a"		*
N2 Perlodes "a"		*
N9 Capnia "b"		*
N11 Isopteryx "b"		*
N13 Nemura "a"		*
N15 Nemura "b"		*
Trichoptera		
L201		*
L202	*	
L203	*	*
L209	*	*
L211	*	
L217	*	

a. Surface of stones. The species occupying the surfaces of the stones (Table VI) are Iron "a" (N101), Baetis "b" (N105), Ameletus "a" (N106), Baetis "a" (N104), and caddis larvae L217 and L202. Iron "a" lives in the swiftest parts of the stream, on the clean surfaces of the stones, and is found only in the part of the creek below Lower Crater Lake. The factor that prevents its entering the swift stream community seems to be the growth of vegetation which covers the bottom. Ameletus "a" is found in the quieter places along the shore and does not venture into the swifter parts. This is also true to a great extent, of Baetis "a" but Baetis "b" is a typical surface species and may be taken from both the quieter and swifter places. The two species of caddis larvae which bear cases (L202 and L217) are very small, a quarter of an inch or less in length. The head of larva L217 is round and antero-posteriorly compressed, so that the frontal part is perpendicular to the supporting surface. The case is short and cylindrical and is built of fine woody fiber. This species seldom ventures into the swifter parts of the stream where the stones receive the greatest shock from the water. Species L202 which has a small cylindrical head and builds a long, tapering case of fine sand grains and mica, lives in both the quieter and swifter parts.

b. Under the stones. The conditions under the stones are about the same as those for the swift stream habitat and the species represented are about the same. The few differences are shown in table VI.

3. Community of the torrents and falls.

The community of the torrents and falls is the most spectacular and in a few respects the most interesting of all. Here the animals are subjected to the most rigorous conditions and it is only by means of special adaptations that they are able to maintain their positions in the stream. Here, not only is a shore zone wanting but the rocky bottom is entirely free from exposed surfaces, also have a very poor growth of algae and in many places are worn perfectly smooth. This kind of habitat is found only in the steepest parts of the stream between Middle and Lower Crater Lakes and below East Crater Lake.

The caddis larvae inhabiting this community are caseless, (Table VII) except the two species (L202 and L217) which do enter the swifter parts of the stream, and were spoken of in some detail under the discussion of the very-swift-stream community. The three species (L208, L211 and L218) which do not build cases inhabit the milder parts of the torrent where the bottom is rough. A marked characteristic of these larvae is the absence of gill filaments. In the swift-stream community, there was only one species of this type (L208) which did not have well developed gill filaments, while half of those in the very swift stream had gills. It is also observed that L208 and L211 are representatives of the very-swift-stream community while L218 is the only larva confined to the torrents.

Table VII Species of the Torrents and Falls Community.

Species	Surface of Stones
Ephemerida	
N101 Iron "a"	*
N104 Baetis "a"	*
N105 Baetis "b"	*
Trichoptera	
L202	*
L208	*
L211	*
L217	*
L218	*

Iron "_a_" (N102), _Baetis_ "_b_" (N105) and a few individuals of _Baetis_ "_a_" are the may-flies of this community. (Table VII) _Iron_ "_a_" is strongly dorso-ventrally compressed and the gill lamellae are used as a sucking organ for holding to the bottom. It does not enter the swiftest parts of the stream and is found only in the region below Lower Crater Lake. Baetis "b" is small, has a round body, and is found in all parts of the stream, Baetis "a", which also has a round body, is larger and is found in small numbers only in the quieter places. Iron "a" and Baetis "b" each has its own way of maintaining its position in the swift water. Iron avoids the current by hugging the bottom with its flat body and Baetis "b" depends wholly on its ability to hold on. Of these two methods the latter is the most efficient, and this difference in ability causes a zonation that is very striking in both the torrents and falls.

Figure 8 represents a typical torrent which flows down a steeply inclined, crooked, trough-shaped crevice. This was studied in some detail. At a and b only the round may-fly nymph (Baetis "b") is found, while both it and Iron "a" live at c which is an eddy. The rock at a receives the full force of the water which is thrown across towards b causing an eddy at c. Then the water glides off over a smooth surface with the swifter part d, which is partly hidden, against the right bank. In this part both species occupy the places at e and f and only the round ones are at d. The flat ones (Iron "a") seem to be able to stay where the water is moderately swift provided it does not fall on the rock at an angle that would have a tendency to lift them off the bottom.

This susceptibility to current is also shown where the

Fig. 8

The Habitat of the Torrent Community.
(Photographed by Dodds and Hisaw)

water flows down smaller, crooked, trough-shaped crevices found in places along side the main torrent. When the water flows down one of these crevices it is reflected from side to side as shown in figure below. The water traveling along some such line as c strikes at a and is thrown across to the opposite side a'. These places receive the full force of the

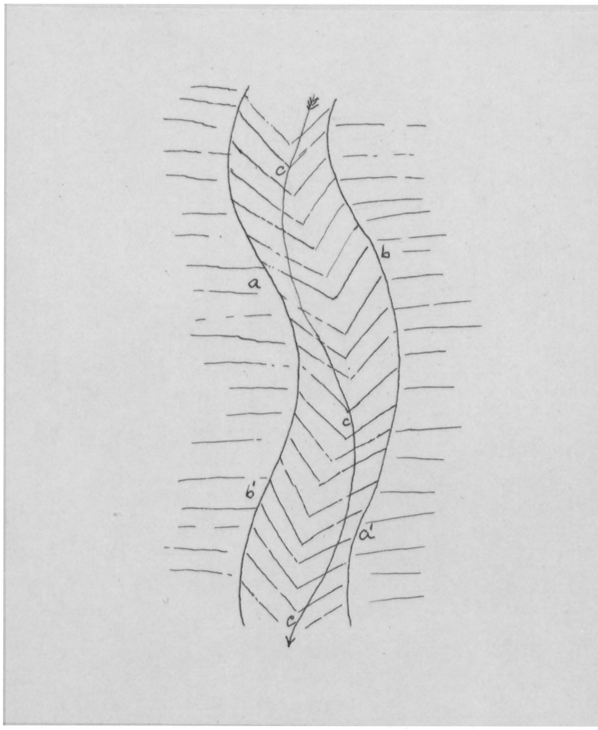


Diagram showing the flow of water in a crooked, trough shaped crevice.

water, while such places as b and b' do not. Neither is the bottom of the crevice opposite b and b' washed as hard as the sides at a and a'. Both the round (Baetis "b") and the flat (Iron "a") live at these places which do not receive the direct flow of the water while at such places as a and a' only the round ones are found. In the less swift places as b and b' the tusk-shaped caddis larva (L202) also inhabits the bottom of the crevices.

This zonation is very striking in the falls, as shown in figure 10. The water at a falls on the flat surface of the rock below. That at b being the quietest and that at c the swiftest. Both the round and flat may-fly nymphs are found at b, at c only the round ones, and between these places all stages in the eliminating process can be found. A few of the round nymphs were also taken from the surface of the boulder at d which receives the full force of about a four foot fall. The little wooden-cased and the tusk-shaped caddis larvae (L217 and L202) live in the stream at such places as e and f where the water is only moderately swift.

The above examples of the torrent and fall community were taken from the region below East Crater Lake, but the descriptions for the conditions and the inhabitants could be applied equally well to the parts of the stream below Lower Crater Lake except that Iron "a" does not extend into this part of the stream.

Another form that has not been mentioned is a small black dipterous larva, which has not been identified, which inhabits all parts of the stream. It is found under all conditions from the most rigorous to the mildest. A species of black-fly larva also lives in all three communities but does not enter the more trying conditions of the torrents and falls.

Fig. 10

The Habitat of the Falls Community.
(Photographed by Dodds and Hisaw)

In the discussion of the stream communities it was pointed out that there is an overlapping of the zones in each community. The tables showing the distribution of the members in each community may be considered as cross-sections of the stream which show the relations existing between the species in the different parts of each habitat. A point of equal ecological interest is the relation between the larvae of the different communities. To make this comparison the habitats have been arranged on the basis of the difficulties they offer the larvae which inhabit them. (Table VIII). The most rigorous conditions are found in the torrents and falls where there is only one species that is not also found in the very-swift-stream community, while all except two of those in the very-swift-stream community, have representatives in the swift stream. The overlapping between the swift-stream community and that of the lake is not so striking, primarily because the stone-flies do not enter the lakes. In contrast to the tables showing the distribution in the particular habitats, Table VIII could be thought of as a longitudinal section of the stream showing all the ecological conditions in the several habitats and the overlapping of the species which live in them.

VI. THE ADAPTATIONS OF AQUATIC INSECT LARVAE.

A. ADAPTATIONS OF MAY-FLY NYMPHS.

The many problems presented by the widely varied environment in which the different species of may-flies live have been solved in several interesting ways which sometimes ap-

Table VIII. The Fauna of the Lakes and Stream Showing Overlapping Between Different Habitats.

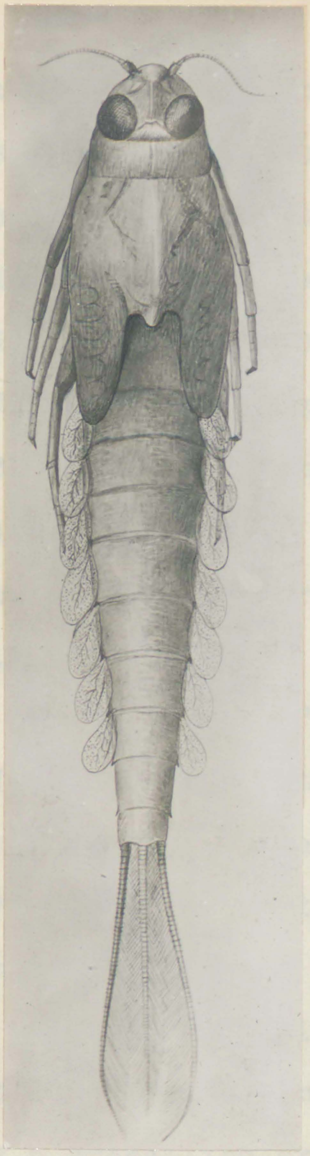
Names of species	Lakes	Stream: Swift	Stream: V.Swift	Stream: Torrent
L318				■
L211			■	■
N101 Iron "a"			■	■
N105 Baetis "b"		■	■	■
L208		■	■	■
L202		■	■	■
L217		■	■	▨
N104 Baetis "a"	▨	■	■	▨
N106 Ameletus "a"	■	■	■	
N102 Ecdyurus "a"	■	■	■	
N103 Genus "A" "a"			■	
N9 Capnia "b"			■	
L301		■	■	
L209		■	■	
N107 Baetis "c"		■	■	
N2 Perlodes "a"		■	■	
N8 Perla "a"		■	■	
N11 Isopteryx "b"		■	■	
N13 Nemura "a"		■	■	
N15 Nemura "b"		■	■	
N3 Perlodes "b"		■		
L231		■		
L210		■		
N110 Genus "B" "a"		■		
L203	■	■		
L204	■	■		
L207	■	■		
L213	■	■		
L205	■			
L206	■			
L214	■			
L219	■			
L220	■			
N108 Siphlurus "a"	■			
N1 Isopteryx "a"	■			

proach the bizarre. In general the conditions both in the lakes and the streams, resolve themselves into two problems which are closely allied. Those that swim in the quieter water have the problem of getting through the water, while those that walk or cling to the bottom in the torrent have the problem of letting the water past them while retaining the same position on the bottom. One is the difficulty of propulsion and the other retention.

Doctor Needham has found by experimenting with different shaped bodies of the same weight and volume that those which have the form of a cone offer less resistance to the water when drawn blunt end first than when drawn in the reverse direction. This is due to the fact that the water which is pushed away by the blunt end is allowed to close in behind without a tendency to form a vacuum which would tend to pull the object back. The resistance is further reduced if the forward end is also bluntly conical. A study of the swimming forms shows that they are constructed on the general plan of a cone with the head forming the larger, somewhat rounded end. It is evident that if this shape is beneficial to an animal which swims through the water it is of equal advantage to one which remains stationary and lets the water flow past. The former condition is that found in the lakes; the latter in the stream.

1. Ameletus "a" (N106)

Ameletus "a" (Fig. 10) is a typical swimming species which has a long tapering body and lives in the lakes and quieter parts of the stream. The three caudal setae are de-



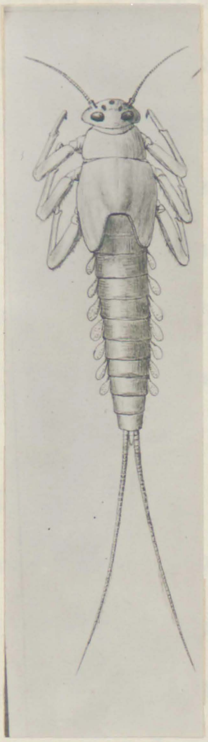


Fig. 10. Ameletus "a" (N106) (Left-hand figure) A typi- lake species which has the caudal setae devel- oped into a paddle. (Photograph from drawing made by G. T. Kline.)

Fig. 11. Baetis "b" (N103) (Right-hand figure) A round- bodied, torrent species which maintains its position in the current by holding on with its legs. (Photograph from drawing made by G. T. Kline.)

veloped into a great paddle which, like the tail of a fish, serves as a propeller. The two outer setae have long hairs on their inner margins which meet and form a lattice work with those of the middle one, which is fringed on both sides. The legs are used primarily for support when the animal is at rest; only secondarily as walking organs, and when swimming they are directed backwards and held close against the side, thus giving the least resistance to the water. The detailed structure will be brought out more fully in connection with the stream forms.

2. Baetis "b" (N103)

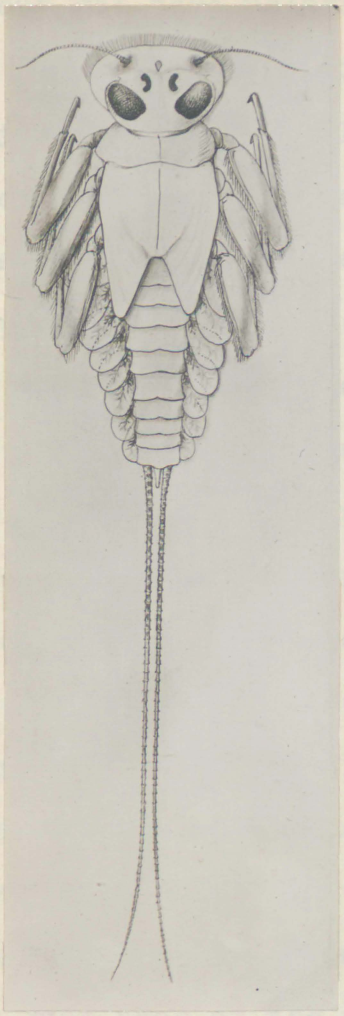
This larva (Fig.11) as has been mentioned, belongs to the torrent and fall community, and is an example of the type which clings to the rocks with its head up stream instead of swimming. The shape of the body is, in general, like that of Ameletus "a" but there are certain marked differences between them. The caudal setae are not modified into a paddle, as there is little need of a propelling organ. The conditions are such that if an attempt were made to swim, it would end disastrously. The middle caudal seta is reduced to an unsegmented rudiment which enables the outer two to be pressed closely together, thus forming a more perfect apex to the cone-shaped body. The legs are also quite different from those of Ameletus "a". They are very much larger in proportion to the body and the tibia is articulated in a way which enables it, as well as the tarsus and hook, 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 ones. This position causes the leg, and consequently the animal, to be held firmly against the bottom. That is, when the nymph is situated in the current with its head up stream the water which is caught by the anterior margin of each femur is deflected upwards causing pressure to be exerted on the dorsal surface, and as a result, the leg is pushed against the rock. Yet it is important, under these conditions, to expose as small a surface of the leg to the current as possible. With the relation the nymph has to the current the two positions of the leg which would offer the least resistance would be when they were held straight ahead or behind. The former is the only one of these two that could work, but neither of these positions would give the body a stable anchorage. In order not to be washed about the points of attachment must be close to either side. Both of these requirements have been met by folding the legs so that the femurs are directed backwards and the tibiae and tarsi forwards, thus causing most of the leg to be nearly parallel with the current, moreover the water caught by the small lateral expanse is used to hold the leg to the bottom. Another peculiarity of the legs is shown in the cross-sections of the femurs and tibiae. This shows that they are also built on the general principle of a cone. They are flattened, but thicker on the anterior margin which is exposed to the current, become thinner posteriorly, and are fringed with hairs suggesting the tapering end of the body with its caudal setae. These points are, no doubt, the most interesting and obvious adaptations which enable Baetis "b" to withstand the great force of the current to which it is exposed, but the exact way in which some of them work is not fully understood and are problems which require further investigation.

3. Baetis "a" (N104)

In the discussion of Ameletus "a" and Baetis "b" two extremes have been considered. One represents a lake form which is subjected to the mildest of conditions, the other may be thought of as a lake species which has undergone the minimum modifications which would enable it to meet the rigorous requirements of the torrents. Baetis "b" represents a mean between these two extremes, both in habitat and adaptations. It inhabits the surfaces of the stones in the swift and very swift stream communities, but does not enter the swiftest parts of the torrent. The three caudal setae are well developed but the marginal hairs are not long enough to form an efficient paddle. The legs and tarsal hooks are smaller in proportion to the body than those of Baetis "b", and perhaps cannot hold as closely to the bottom. Baetis "a" also occupies an intermediate position with relation to size, which is, no doubt, an adaptation. The relation between size of body and legs is not so much of a problem for the forms living in the lakes as it is for those living in the stream. In the stream the legs or other organs of attachment must be built in accordance with the size of the object which they are to hold. Baetis "a" is larger than Baetis "b" and, as mentioned, its legs are smaller in proportion to the body, so if it should ever enter the torrent community it would, among other things, have to either decrease the size of the body or increase the size of the legs. But under the present conditions it does not need a body which is adapted for the swiftest water or legs that can be so perfectly adjusted to the bottom, and as it swims very little, a well developed paddle is not a necessity.

4. Iron "a" (N101)

This nymph (Fig. 12) inhabits the clean surfaces of the stones in the very swift stream and torrents but is found only in the portions which do not receive the direct shock of the water. Its adaptations, although in many respects more spectacular, are not as effective as those of Baetis "b". Instead of depending on adaptations which would offer the least resistance to the water, as in the round bodied forms, Iron "a" avoids the current by having a broad body that is strongly dorso-ventrally compressed, thus enabling it to hug close to the bottom. The gill lamellae are modified into a sucking organ. The first pair by overlapping under the anterior end of the abdomen (Fig. 13) forms a very broad half-moon shaped plate, and the seventh pair forms a similar arrangement at the posterior end. The other five pairs extend latero-posteriorly, each one overlapping the one behind and in this way forming an eliptical sucker. The legs are all well adapted for holding to the bottom. The nymphs orient themselves with the head up stream as does Baetis "b", and



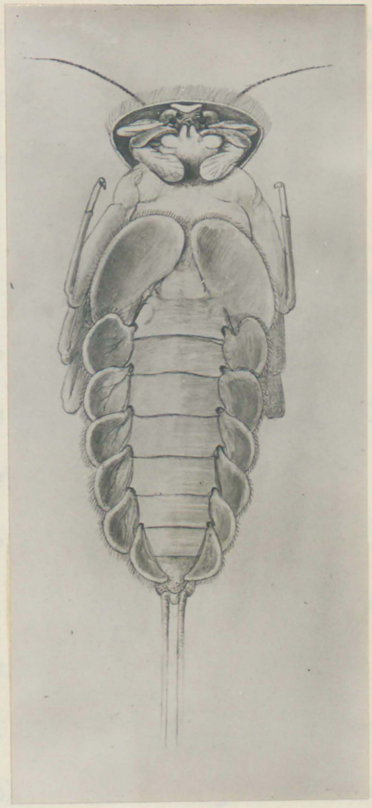


Fig. 12. Iron "a" (N101) (Left-hand figure) A flat-bodied, torrent species which has the gill lamellae developed into a sucker. (Photograph from drawing made by G. T. Kline.)

Fig. 13. Iron "a" (N101) (Right-hand figure) Ventral view showing the sucker. (Photograph from drawing made by G. T. Kline.)

the legs have about the same relation to the body. The tibiae are flattened on the anterior margin in a way which forms a sharp edge that is held close to the bottom and causes the water to be directed over the dorsal surface. The general plan of a cone is formed by a ridge just back of the anterior edge and to the posterior surface of this is attached the marginal hairs. These hairs are long and extend well over the posterior margin, thus preventing an eddy behind the legs. The head is also very strongly compressed. The frontal plate is broader in front than behind, and when pressed against the supporting surface, it completely covers the mouth parts. The slightly curved anterior margin bears a dense fringe of hairs which prevent the water from running under the animal by directing it over the top of the head. This in itself would cause pressure on top of the head which would help to hold it to the bottom, but at the same time there is an additional means provided. Just back of the anterior edge where the head becomes narrower the water that was caught by the broader part begins to flow off laterally and has a tendency to form a vacuum in the region ventral to the eyes. All of the adaptations mentioned so far are quite different from those of the round bodied forms, and are of such a nature that the force of the current presses the insect close against the rock. There is, however, a similarity between _Iron_ "_a_" and _Baetis_ "_b_" in the structure of the caudal setae. In both species the middle seta is reduced to a rudiment and the remaining two serve to bring the posterior end of the body to a more perfect point. Although the abdomen of Iron "a" is considerably flattened it would end bluntly if it were not for the two caudal setae.

Iron "a" is considerably larger than Baetis "b" but its adaptations enable it to live in very swift current provided the water flows smoothly over the stones on which the nymph rests, but if the bottom is rough it is limited to the parts where the water does not fall on the rocks with enough force to lift it off. The marked zonation between this nymph and Baetis "b" in the torrents and falls is, to a great extent, due to the lifting tendency of the water as well as its swiftness.

Another group of adaptations, which are not directly connected with the problem of resisting the current, are those of the mouth parts. The palpi of the first and second maxillae of this species are develped into four brushes which work laterally, protected by the front margin of the head, and are used, no doubt, for sweeping food material from the bottom. These structures are very different from those of the species which have been described. Baetis "a" and "b" have sharp chisel-shaped mouth parts which are used for nibbling the scant vegetation on the rocks where they live, while the first maxillae of Ameletus "a" are provided with sharp hook-shaped spines which are perhaps used for catching plankton.

5. Genus "A" "a". (N103)

Genus "A" "a" (Fig. 14) is a large robust nymph which lives under the stones in the very swift stream. The body is

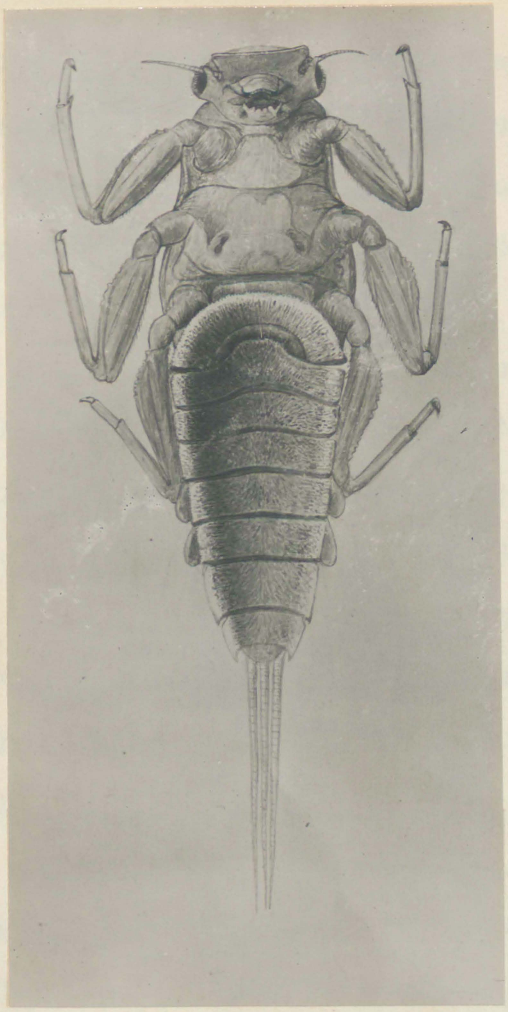


Fig. 14. Genus "A" "a" (N103) A nymph which lives under the stones in the very swift stream. Ventral side of abdoman forms sucking disc. (Photograph from drawing made by G. T. Kline.)

dorso-ventrally compressed but not so much so as that of Iron "a". The head is small in proportion to the body and the narrow frontal plate forms an angle of about forty five degrees with the bottom. The anterior edge of the frontal plate is fringed with hairs which, no doubt, work in the same way as the corresponding structures in Iron "a", but its shape and the great angle at which it is held to the bottom allows it to receive the full force of so much water that its efficiency is greatly reduced. The femurs are flat with saw-tooth projections on both the anterior and posterior edges and are slanted in a way that the force of the stream would push them against the body. The tibiae are flat but are not held in a position that would cause their flatness to be of advantage in swift water.

The most remarkable adaptation of this species is a sucker on the ventral side of the abdomen (Fig. 14). Each segment of the abdomen bears a dense tuft of hairs on the outer margin of the sterna. These tufts are situated on a ridge which is well developed on the anterior segments but is less prominent on the posterior ones where the hairs are scattered over the entire surface of the sterna. The efficiency of this sucker and its exact importance to the nymph may be judged from the conditions under which it lives. It has never been found anywhere except under the stones, where it is obvious that the most excellent current resisting devices are not needed. Perhaps these adaptations are used when the nymph ventures out into the swift stream in search of food but its great size would prevent it from entering the more rigorous conditions. Moreover, although the sucker enables the insect to hold quite firmly to any smooth surface, it appears that it must be released when the nymph moves. In spite of the apparent excellency of this sucking organ the nymph cannot resist as strong a current as can Iron "a" or Baetis "b".

6. Ecdyurus "a" (N102).

This species (Fig. 15) has a very wide distribution, being found under the stones in all parts of the stream where such a zone exists, and it is also found in Upper Crater Lake, which has a bottom free from decaying organic matter. This wide distribution is perhaps due to the constant conditions which exist under the stones, while there is little difference between lake and stream. The oxygen content of the water under the stones in the lakes is probably about the same as that of this zone in the quieter parts of the swift stream and the current is not an important factor in either place. In harmony with these conditions it should be expected that the species found living here should also be conservative in its adaptations.

In several respects the adaptations of Ecdyurus "a" seems to be a combination of those found in Iron "a" and Baetis "b". The body is dorso-ventrally compressed but not nearly so much as that of Iron "a". The head is more rounded and its expanded margin does not cover all of the mouth parts, neither can its anterior margin be held closely against the bottom. The tibae and tarsi are almost cylindrical and do not have a mar-

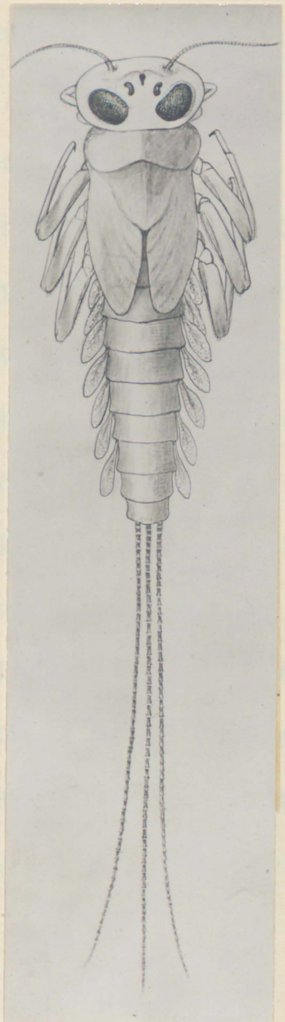


Fig. 15. Ecdyurus "a" (N102) Flat-bodied nymph living under the stones in stream and clean bottomed lakes. (Photograph from drawing made by G. T. Kline.)

ginal row of hairs. The femurs have a short row of hairs on the posterior margin but are not flattened as much as those of Iron "a" or Baetis "b". The legs are also very delicately articulated with the body which would prevent them from being of much use in resisting the shock of the swift stream. This difference in fragility is very strikingly shown by the fact that it is very hard to find a complete specimen of Ecdyurus "a" in my collection, while almost every individual of Iron "a" is perfect. This conservatism is again shown in the development of the caudal setae. All three are well developed and the middle one prevents the outer two from being pressed close together, which is the means used by the torrent species for perfecting their cone-shaped bodies. Thus in no way would these imperfect adaptations enable the owner to meet the difficult conditions under which certain other species live.

7. Relation of Gill Area to Body Weight.

It was observed that some of the forms living in the lakes had very large gill lamellae while those living in the stream did not have them so well developed, and assuming, as is probably the case, that the oxygen content in the lakes is less than in the stream, investigations were made to find the relation between respiratory surface and body weight. If the oxygen content of the water in the lakes is less than that in the stream, it should take a larger respiratory surface per unit body weight for those species living in the lakes than for those living in the stream. The results of this investigation, while of considerable interest, should not be taken as conclusive, because the data were obtained from preserved material and because a sufficient number of species have not been studied.

Assuming that the body fluid of the nymphs was about the same density as water, the alcoholic specimens were soaked in distilled water until the alcohol had been removed. Then the specimens were quickly dried with filter paper, in order to remove excess water on the surface. The weights were taken on a chemical balance which weighed to the fourth place. The container in which the nymphs were weighed consisted of a vial, with a tightly fitting cover, and was filled about half full of water. This was weighed a number of times in order to determine the evaporation rate. After the contain--er had been weighed, a nymph was placed in the vial and the total weight recorded. In this manner a number of specimens were weighed, and their average taken as that of the species. The gill lamellae were removed and outlined under known magnification and their areas were determined by means of a planimeter. In this case also, the average for several specimens was taken as the area for the species.

Table IX, a tabulation of the results, seems to show that in some cases there is a direct relation between gill surface and the probable amount of oxygen in the place where the species lives. Siphlurus "a" which lives on the silty bottom of East Crater Lake, where on the account of the great amount of decaying organic matter the oxygen content of the water would be expected to be low, has a very large

Table IX. Relation of Gill Area to Body Weight.

Species	Ration grams to sq. cm.	Habitat
Siphlurus "a"	1 " 28.4	Silty bottom of lake.
Callibaetis "a"	1 " 20.4	Vegetation in lakes.
Baetis "a"	1 " 17.0	Quieter parts of stream.
Baetis "b"	1 " 10.3	Torrent.
Iron "a"	1 " 24.1	Torrent.
Ecdyurus "a"	1 " 28.8	Under stones.
Ameletus "a"	1 " 9.3	Lake and stream.

gill area. When at rest the posterior end of the abdomen is almost completely covered with silt and the gill lamellae are very much smaller than those on the anterior end, which is well above the mud. The gill surface is also increased on the anterior end by having the first two pairs of lamellae doubled. Callibaetis "a" (not found in the Crater Lakes) lives on the vegetation and rocks where the oxygen content is probably greater than on the muddy bottom of the lakes, and as would be expected, its ratio of respiratory surface to body weight is smaller than for Siphlurus "a".

Baetis "a" is taken from the vegetation and the surface of stones in the swift and very swift stream communities. These conditions are intermediate between those of the lakes and torrents and it has been pointed out that the adaptation of the nymph for resisting the current are also intermediate between those of the forms living in these two extremes. The same also holds for the ratio between body weight and respiratory surface. That of Siphlurus "a" being 1 : 28 and that of Baetis "b" 1 : 10, while for Baetis "a" it is 1 : 17.

Iron "a" (Fig. 12) which is a torrent species and has a ratio of 1 : 24 seems to be an exception. However this large gill area can be accounted for if the specialization of the gill lamellae to form a sucking organ is taken into consideration. When thus used only the upper surface comes into contact with the water, so that the functional gill area is really reduced one half. There is also an additional specialization which must be considered. At the base of each lamella there is a bunch of well developed gill filaments which are exposed to the water and are, no doubt, functional respiratory organs. Perhaps when the gills were specialized into a sucking apparatus these filaments were developed to take the place of the respiratory surface that was lost. If these filaments are counted in with half of the gill surface, the ratio would be about 1 : 12.7, just a little greater than that for Baetis "b".

The very large gill area of Ecdyurus "a" (Fig. 15), another stream species, can also be explained by the conditions under which it lives. The oxygen content of the water under the stones where this nymph lives cannot be as great as that for the other parts of the stream, but whether there is enough decaying organic matter to reduce it to the level that is found in the lakes remains to be proven. But if this is the case, the large gill area of Ecdyurus "a" is an adaptation which enables it to live under these conditions.

Ameletus "a" (Fig. 10) is found in the lakes and quieter parts of the stream. This species has a very small gill area, the reason for which cannot be explained on the theory that the oxygen content of the water in the lakes and quieter parts of the stream is less than that of the swifter parts of the stream. Yet there are a few things that may lead to something definite. The mouth parts, as described, seem to be specialized for catching plankton, which is strained out of the water while the nymph is swimming. From observation it is known that Ameletus "a" is very active, spending a great part of its time swimming near the surface where the water is fairly well saturated with oxygen, but whether or not the hooks on the first maxillae are used for catching food is not known. If it is found that this point is true it will have an important place in the explanation of the small gill area.

This study of the adaptations throws some light on the probable evolution of the may-flies. It would be expected that the ancestral forms first entered the lakes or quieter parts of the stream and from here gradually worked their way into the swifter parts. There were two possible lines of evolution. They could either avoid the current by living under the stones or adapt themselves to resist the current on the surfaces of the stones. Evidently the nymphs took advantage of both these possibilities. The round bodied forms meeting the conditions on the surfaces have their climax represented in Baetis "b", those which specialized for the conditions under the stones acquired large gill areas and flat bodies. These forms are, perhaps, the ancestors of Iron "a" which has used its flat body and large gill area for a sucking organ. These two lines of evolution are particularly emphasized by the development of the caudal setae. It was pointed out that all of the species belonging strictly to the quieter places had three caudal setae while those living in the torrents had only two. For the round bodied forms the disappearance of the middle seta can be traced directly from Ameletus "a" through Baetis "a" to Baetis "b". For those species which live under the stones there is little necessity for losing the middle seta, so all of them are well developed though the marginal hairs are missing. When such species as Iron "a" entered the torrent from under the stones, the middle caudal seta degenerated and allowed the posterior end of the body to become more pointed. That these are the true lines of development is further evinced by the structure of the caudal setae of Baetis "b" and Iron "a", the two caudal setae of Baetis "b" having rudimentary hairs resembling those of the other round species while those of Iron "a" do not have marginal hairs and resemble those of the flat species.

Conclusion

The adaptations of the may-fly nymphs may be summarized as follows:

1. The adaptations of the may-flies are for two purposes.
    a. For propelling the animal through the water as shown by the species living in the lakes and quieter parts of the stream, e.g. Ecdyurus "a"
    b. For resisting the current. This was met in two ways:
        1. By decreasing in size and having a body shaped in a way that offers the least resistance to the water, e.g. Baetis "b"
        2. By avoiding the shock of the water by having a flat form and using the gill lamellae as a sucker, e.g. Iron "a"
2. There seems to be a definite relation between body weight and respiratory surface which is, perhaps, governed by the oxygen content of the water in which the animal lives.
3. The ancestral forms of the may-flies first lived in the lakes and quieter parts of the stream and became adapted for living in the torrents along two diverging lines of development:
    a. Some developed an elongated cone-shaped body which would offer the minimum resistance to the water.

b. Some developed a flat body and a large gill area for living under the stones and later used these adaptations for sucking to the exposed surfaces of the rocks.

B. THE ADAPTATIONS OF THE CADDIS-FLY LARVAE.

One of the most interesting adaptations of the caddis-fly larvae is the case, and more particularly the materials used in its construction (Fig. 16). The species living in the lower lakes build their cases almost entirely of woody material while those living in the stream and the upper lakes use mica or sand grains. The advantage of wood over sand particles for the forms living in the lakes which have a muddy bottom is that of lightness. This enables them to crawl over the soft bottom or climb up and down the submerged vegetation more easily. Those living in the upper lakes and stream are not handicapped by having a case composed of mica or sand grains because it can be easily dragged over the stony bottom. Most of the caddis larvae also shape their cases in a way which will give the least resistance to the surface over which they crawl. They are not straight, but arched so that the anterior and posterior ends touch the bottom. Most of the weight of the anterior end is borne on the legs while only the tip of the posterior end drags.

Fig. 16. L205. This caddis larva lives in the lakes and builds its case out of wood and mica during the early larval stage and later adds sand grains. (Photograph from drawing made by G. T. Kline.)

The ecological importance of the materials of which caddis larvae build their cases is not fully understood. It is not definitely known whether they use the objects which are most available or are capable of selecting a particular kind of material and have become so intimately associated with it that its absence would keep them from entering a community where it is not found. The data gained by this investigation seem to substantiate the latter view. Part of the evidence offered is the fact that some of the lake species are also found in the stream where other materials are equally available and they do not choose them. The ability to select building materials is also demonstrated by the queer way in which some of the larva living in the upper lakes and stream construct their pupa cases. The larval case is entirely of mica (L204) or mica and wood (L205) and as the time for pupation approaches sand grains are added to its anterior end. (Fig. 16) After a cylinder long enough to hold the ~~work~~ insect has been built the mica part is cut off and the larva, after sealing both ends of the stone case, pupates. This is a unique way of obtaining a relatively light case during the active, feeding, larval period and a heavy stable one for the helpless, inactive pupa. These species show a selective ability, at two different times during their larval period, between the materials used in building their cases.

The caddis larvae have also acquired adaptations which enable them to live in the very-swift-stream and torrent communities. The larva with the tapering tusk-shaped case (L202) is able to live on the exposed surfaces of the stones in almost the swiftest parts, while the other case-bearing larva (L217) which also enters the torrent is confined to the crevices along the edge of the water. The shape of the case is the most important factor which accounts for this difference in distribution. The case of L202 is elongated and cone-shaped while that of L217 is almost cylindrical and less slender. The value of a cone-shaped body was emphasized in connection with the adaptation of the may-flies and it is very probable that this is also the most important factor which gives L202 the advantage over L217. It has also been shown that those species which maintain their positions in the torrent by grasping rather than sucking or by fastening themselves with webs, are small. This may explain the absence of the larger species in the torrent community.

The caseless caddis larvae (Fig. 17 and 18) are also of interest on account of their adaptations, the most important of which is that of the gill filaments. The species living in the quieter parts of the stream have well developed gill filaments, while those species which live in the torrent are almost completely without them. There seems to be a direct relation between the swiftness of the water and the amount of respiratory surface. The loss of the gill filaments of the torrent forms was perhaps due to one or both of two factors. They were rendered of less importance

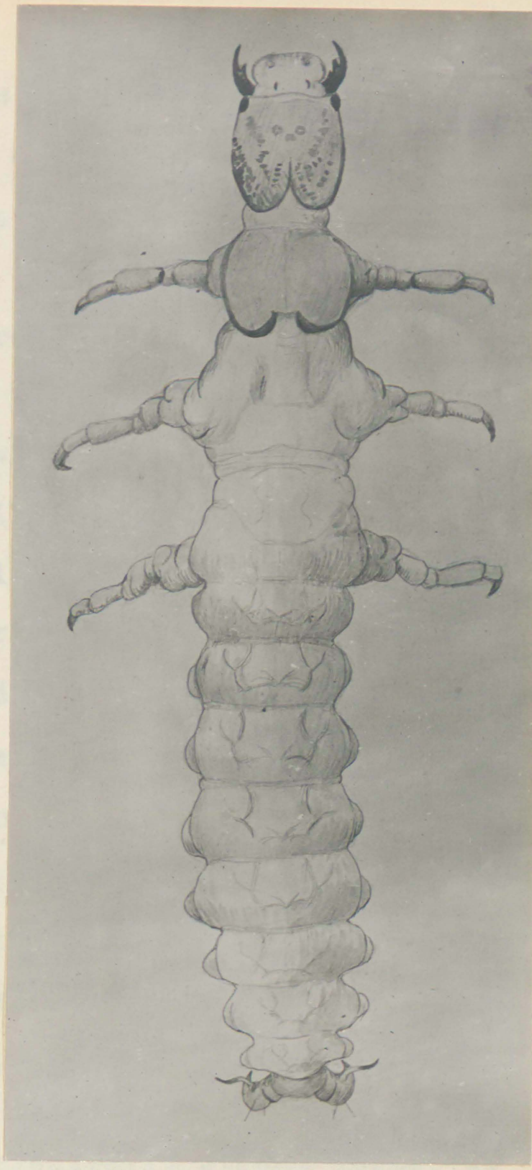


Fig. 17. L201. (Left-hand figure) Caseless caddis larva which lives in the quieter parts of the swift stream and has the gill filaments well developed. (Photograph from drawing made by G. T. Kline.)

Fig. 18. L211. (Right-hand figure) Caseless caddis larva which lives in the very swift stream and does not have gill filaments. (Photograph from drawing made by G. T. Kline.)

because the water of the torrents contains a greater amount of available oxygen or they were a disadvantage to the owner because of their added resistance to the water which flowed over them.

These few facts may also throw light on the probable evolution of the caddis larvae. The first caddis-larvae were, in all probablilty, forms which lived in still water where they developed the case building instinct, and as they entered the streams their evolution took place along two divergent lines. Some lost their cases and used the abdominal hooks, (originally developed to hold the case in place) as instruments for holding to the surface of the bottom, and in time when some came to live in the torrents the gill filaments were discarded. Those which followed the other line of development retained their cases and met the problems of the torrent by decreasing in size.

C. ADAPTATIONS OF THE STONE-FLIES.

The stone-flies which are principally stream forms, do not have any striking adaptations for resisting the swift water, but live under the stones where they are not subjected to the current. The members of the different species do not live under widely varied conditions which would cause each species to have its particular adaptation, but occupy habitats which have about the same requirements and consequently have adaptations which are quite similar.

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UNIVERSITY OF MISSOURI
COLUMBIA

COLLEGE OF AGRICULTURE
AGRICULTURAL EXPERIMENT STATION
DEPARTMENT OF ENTOMOLOGY

May 22 1916.

Dean Walter Miller,

Academic Hall.

Dear Professor Miller:

I have just completed hurried review of F. L. Hisaw's thesis and it occurs to me that this is an unusually fine piece of investigation. It represents work in practically a new field and it seems to me that the thesis presented completely meets the general standard which has been established for the Master's dissertation.

There is only one question that occured to me during my review of the paper and that is with reference to the naming of the particular species of the insects discussed. If it were possible to have had each species of insect identified and named where the species proved to be new, it would have been of considerable value to the thesis. It is a little difficult to follow the discussion where letters and numbers are given for the species in question. It realize, however, that Mr.Hisaw's insects are probably entirely new species and I presume he did not have time to have them named and described.

Very truly yours

L. Haseman

ENTOMOLOGIST

LH:RG.

UNIVERSITY OF MISSOURI

COLUMBIA May 19, 1916

ZOOLOGICAL LABORATORY

Dean Walter Miller,

211 Academic Hall.

Dear Dean Miller:-

I send you herewith the thesis of Mr. F. L. Hisaw, with the title, AN ECOLOGICAL STUDY OF THE INSECTS OF CRATER CREEK, COLORADO. I have examined this thesis and find it satisfactory.

Very truly yours

G. S. Dodds

This thesis is never to leave this room.
Neither is it to be checked out overnight.