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DISTRIBUTION OF INVERTEBRATES IN A HIGH MOUNTAIN BROOK IN THE COLORADO ROCKY MOUNTAINS

BY

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CHIRONOMIDS AND OTHER INVERTEBRATES FROM NORTH BOULDER CREEK, COLORADO

BY

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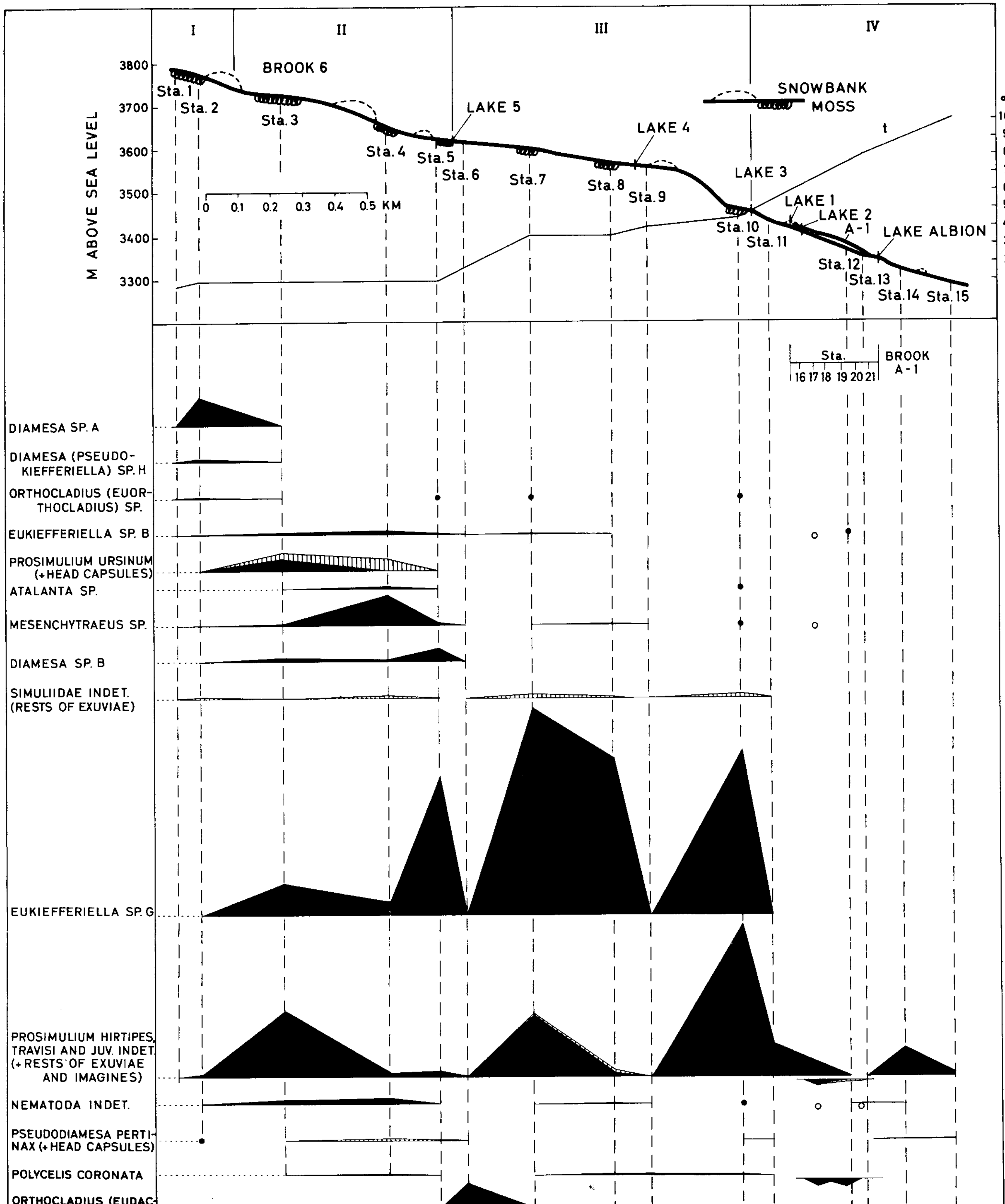
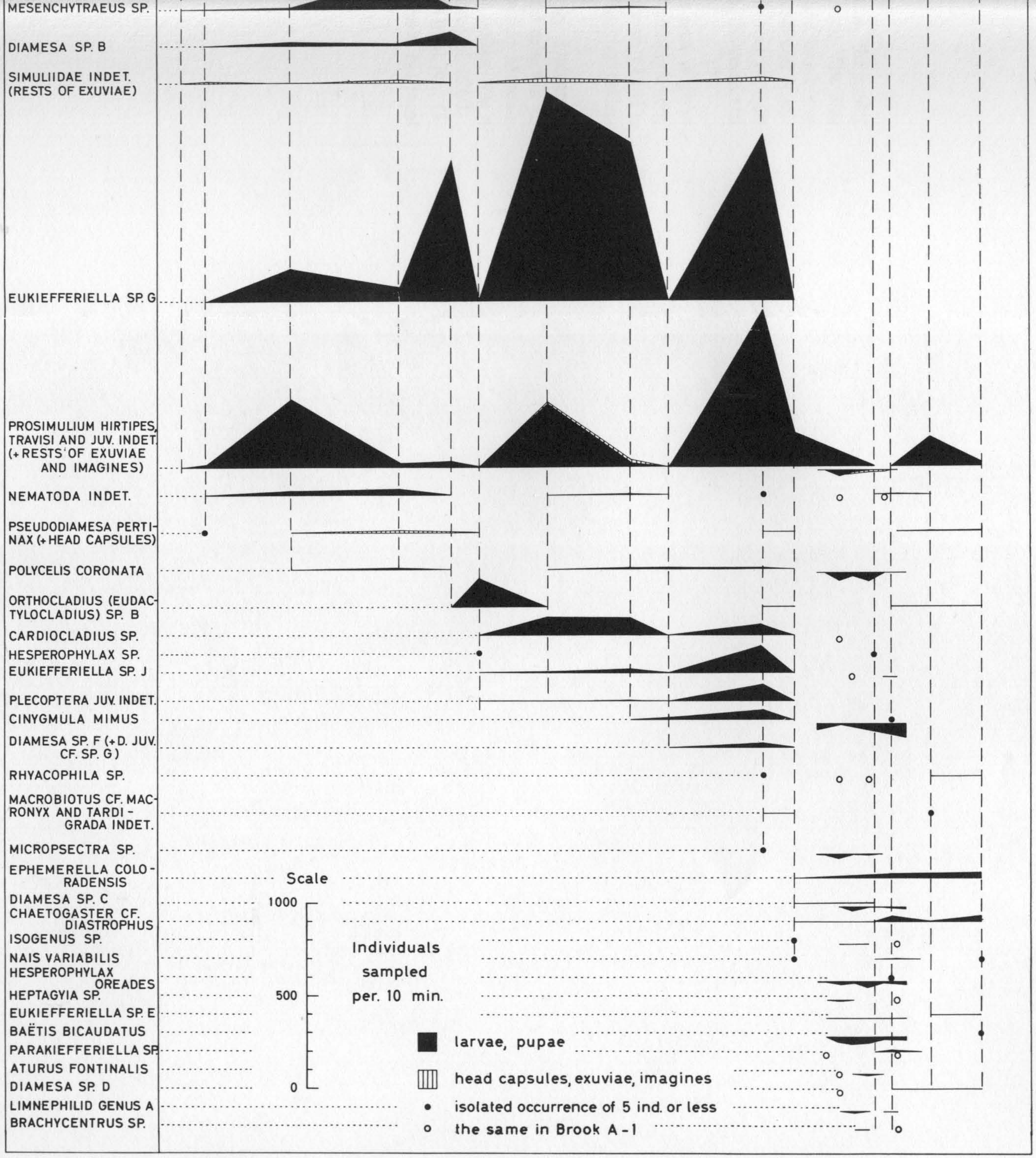


I
II
III
IV
M ABOVE SEA LEVEL
3800
3700
3600
3500
3400
3300
BROOK 6
SNOWBANK
MOSS
°C
t
LAKE 5
LAKE 4
LAKE 3
LAKE 1
LAKE 2
A-1
LAKE ALBION
Sta. 1
Sta. 2
Sta. 3
Sta. 4
Sta. 5
Sta. 6
Sta. 7
Sta. 8
Sta. 9
Sta. 10
Sta. 11
Sta. 12
Sta. 13
Sta. 14
Sta. 15
0 0.1 0.2 0.3 0.4 0.5 KM
Sta.
16 17 18 19 20 21
BROOK A-1
DIAMESA SP. A
DIAMESA (PSEUDO-KIEFFERIELLA) SP. H
ORTHOCLADIUS (EUORTHOCLADIUS) SP.
EUKIEFFERIELLA SP. B
PROSIMULIUM URSINUM (+HEAD CAPSULES)
ATALANTA SP.
MESENCHYTRAEUS SP.
DIAMESA SP. B
SIMULIIDAE INDET. (RESTS OF EXUVIAE)
EUKIEFFERIELLA SP. G
PROSIMULIUM HIRTIPES, TRAVISI AND JUV. INDET. (+RESTS OF EXUVIAE AND IMAGINES)
NEMATODA INDET.
PSEUDODIAMESA PERTINAX (+HEAD CAPSULES)
POLYCELIS CORONATA



FRONTISPIECE. Distribution of abundant forms in relation to environmental factors.

PREFACE

During a high mountain excursion in Swedish Lapland in 1954, the senior author observed a rich aquatic fauna in brooks, even close to glaciers. The idea of studying the zonation of aquatic invertebrates in a high mountain brook was followed up during a short visit to Colorado in the summer of 1960 and is apparently the first investigation of its kind in North America. It was thought that such a study would result in relatively abundant material in the restricted time available for collection.

A survey of previous literature on related subjects in the same area is given by Pennak (1963:362). For more general surveys on the fauna of running water, reference may be made to Illies and Botosaneanu (1963) and Macan (1961).

After the senior author returned to Norway, cand.real. Ole A. Saether undertook the identification and measurement of the specimens.

We are grateful to Dr. Robert W. Pennak, Department of Biology, University of Colorado, for his interest in the project and for his scrutiny and criticism of the manuscript. Dr. William A. Weber of the University of Colorado Museum has kindly identified some mosses found in the brook. The senior author was a visiting investigator in the Department of Biology during the summer of 1960.

The investigation was financed by National Science Foundation Grant No. G-11667, awarded to Kåre Elgmork in 1960, for which he expresses his most sincere gratitude.

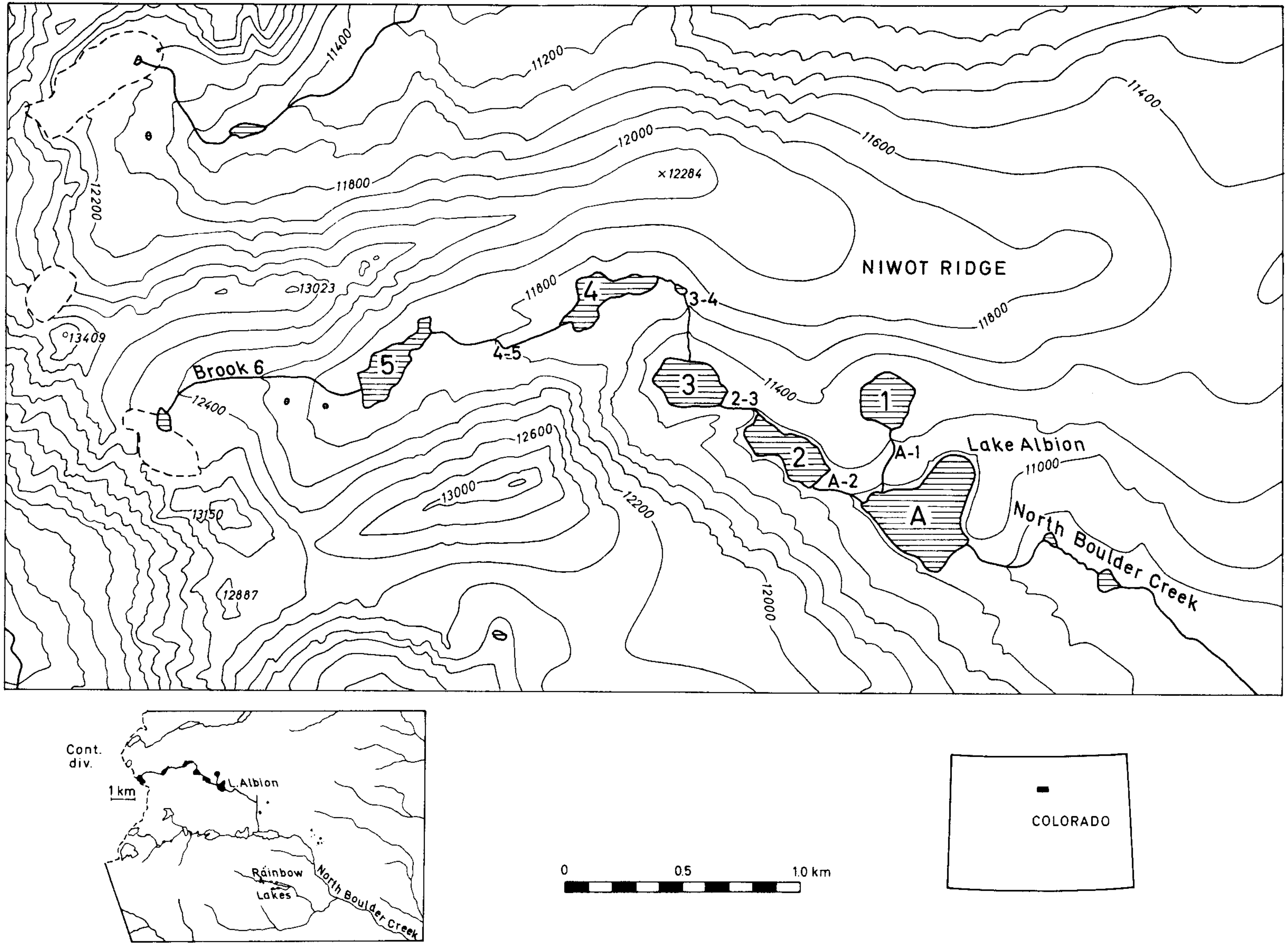


FIGURE 1. Maps showing study area. Elevations in feet.

STUDY AREA

GENERAL SITUATION

The brook chosen for the study was the upper, northern branch of North Boulder Creek, Colorado, running through Green Lake Valley. The study area is situated at about 40°N and the general situation can be seen in Figure 1. The part of the brook investigated extends from its source in a snowbank close to the Continental Divide at an altitude of about 3800 meters down to near the timberline just below Lake Albion at an altitude of 3300 meters. The brook is divided into several parts by Lake Albion and the Green Lakes. The length of the flowage sampled is about 2.7 km, and the difference in altitude is 500 meters. This gives a mean slope gradient of about 1:5. Details on the slope of the brook can be seen on the map in Figure 1 and on the profile at the top of the Frontispiece. A view of the lower part of Green Lake Valley is shown in Figure 2, and the area around Green Lakes 4 and 5 in Figure 3.

GEOLOGY AND CLIMATE

The mountains in the area of investigation are predominantly composed of pre-Cambrian biotite schist of the Idaho Springs Formation, interspersed by Boulder Creek granite and quartz monzonite (Lovering and Goddard 1950). Near Lake Albion and Green Lake 4, formations of intrusive igneous rocks of

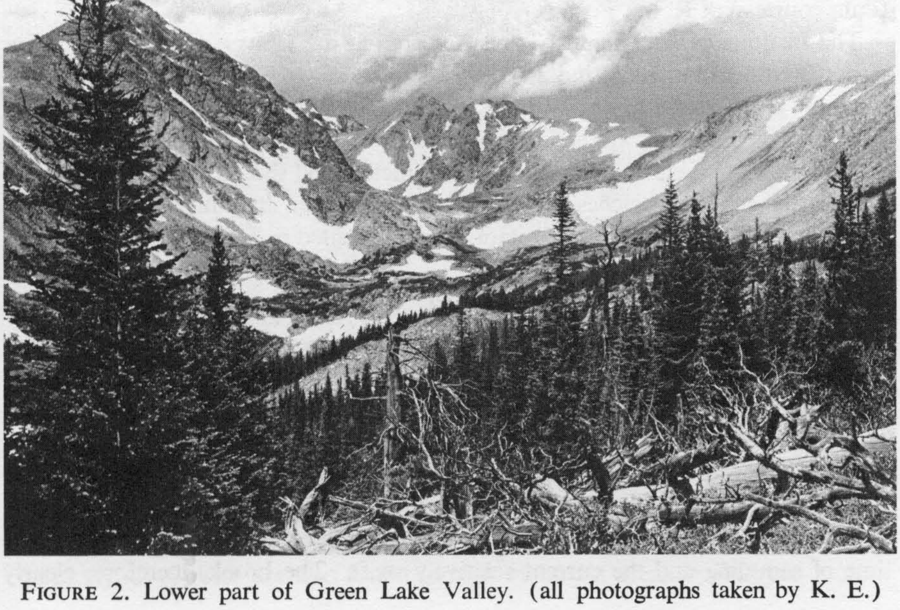


FIGURE 2. Lower part of Green Lake Valley. (all photographs taken by K. E.)

FIGURE 3. Middle part of Green Lake Valley. Green Lake 5 is in the middle.

the Laramide revolution are also present, being mainly composed of monzonite, andesite, and felsite.

No detailed information on the electrolyte content of the water is available, but the general geological background implies a very low level. A water sample taken from Lake Albion in 1941, for example, contained 18.8 milligrams per liter of total solids, of which 13.6 milligrams consisted of inorganic materials (data courtesy of R. W. Pennak).

The Institute of Arctic and Alpine Research at the University of Colorado has several weather stations in the area of investigation (Marr 1961). One of these stations (D-1) at the top of Niwot Ridge corresponds in elevation to the uppermost part of the brook studied. Another station (D-4) is situated in the valley of the brook at an elevation of about 3550 meters and should thus be representative for the middle stretches of the brook. The mean monthly air temperature and the precipitation at these two stations are presented in Table 1.

DESCRIPTION OF THE BROOK

The Green Lakes, which divide the brook into several parts, have been given numbers as seen in Figure 1. The part of the brook between the lakes is indicated by figures representing both lakes, e.g., Brook 2-3 means the part of the brook between Green Lakes 2 and 3. The brooks connected to Lake Albion are called Brook A-1 and A-2. The uppermost part of the brook above Green Lake 5 is called Brook 6.

In all parts of the brook studied, the water volume was relatively small at the time of sampling and the current relatively swift. The brook, therefore, clearly

TABLE 1. Mean air temperature and precipitation in 1952-53 at two weather stations in the study area. (Figures calculated from Marr 1961.)

	NIWOT RIDGE, STATION NO. D-1 ELEVATION: 3750 METERS		VALLEY, STATION NO. D-4 ELEVATION: 3550 METERS	
	Mean Air Temperature °C	Precipitation mm	Mean Air Temperature °C	Precipitation mm
1952				
October	1.1	8	2.2	10
November	—10.6	33	— 9.4	58
December	—12.2	41	—11.1	61
1953				
January	—10.6	74	— 9.4	81
February	—13.9	33	—12.8	71
March	— 9.4	56	— 8.3	84
April	— 8.3	53	— 6.7	86
May	— 3.3	91	— 2.2	109
June	6.7	71	7.2	71
July	8.9	101	10.0	74
August	6.7	84	7.8	94
September	5.0	20	6.1	18
Year	— 3.3	657	— 2.2	833

belongs to the rhithron in the sense of Illies (1961a) and can be characterized as a typical high mountain brook with a swift current.

The water volume, slope, and current are fairly uniform in the area of investigation. The stretch with the gentlest slope and slowest current is Brook 4-5 (Figure 4), but small stretches in other parts of the brook may have even slower currents than indicated in Figure 4.

The current in the brook was too swift for sand and silt to deposit, and the bottom of the brook was generally made up of stones of variable sizes, quite large at places. Sand was deposited only in the uppermost part of Brook A-1 and in certain places in Brook 6. The stones were often covered by mosses, and areas with a relatively heavy moss cover are indicated on the Frontispiece. The following species of moss were identified by Dr. W. A. Weber:

Station 1: *Drepanocladus exannulatus*
Station 2: *D. exannulatus, Grimmia alpicola rivularis*
Station 3: *Hygrohypnum dilatatum*
Station 4: *H. dilatatum, H. ochraceum*
Station 5: *D. uncinatus, Brachythecium sp., Bryum sp.?*
Station 7: *H. ochraceum, D. exannulatus*
Station 8: *H. dilatatum*
Station 10: *H. ochraceum, H. dilatatum*

Practically all of these are also found in high mountain areas in Europe.

FIGURE 4. Upper part of the brook between Green Lake 4 and 5.

In a few places algae were also observed on the stones, especially on the uppermost plateau of Brook 6 where a filamentous blue-green alga was found. At Station 13 some *Nostoc* colonies were observed.

On the sides of the brook a terrestrial vegetation was generally present, quite dense in places, such as near the lowest sampling locality (Figure 5) and along parts of Brook 4-5. The densest vegetation, however, with shrubs and trees, was found along the tributary Brook A-1, most likely due to its sheltered location and southern exposure. Some conifers were found near Brook A-1. There was no macrovegetation on the shore in the uppermost part of the brook near the snowbank (Figure 6).

In certain places the borders of the brook were covered by snow even in the middle of July (Figure 7), and in some places, indicated on the Frontispiece, the snow banks covered the entire brook.

There was little difference in the water volume in the upper and lower parts of the brook studied. This is most likely due to the fact that no tributary enters the system above Lake Albion and that the precipitation in the area is low. The main source of water is the snow bank at the top. In Lake Albion the tributary Brook A-1 enters the main flowage. This brook was included in the study and the results are specified on the Frontispiece.

The temperature conditions in the water are also given on the Frontispiece. The highest temperature measured in the middle of July was 10°C at the lowest station. There was a gradual decrease in temperature upwards to about 3.5°C at Station 7. Between Stations 5 and 7 there was a radical fall in temperature to 1°C in the area of Green Lake 5. Brook 6 had a fairly constant temperature

FIGURE 5. Brook below Lake Albion near the lowest sampling station.

FIGURE 6. Snowbank at source of the brook.

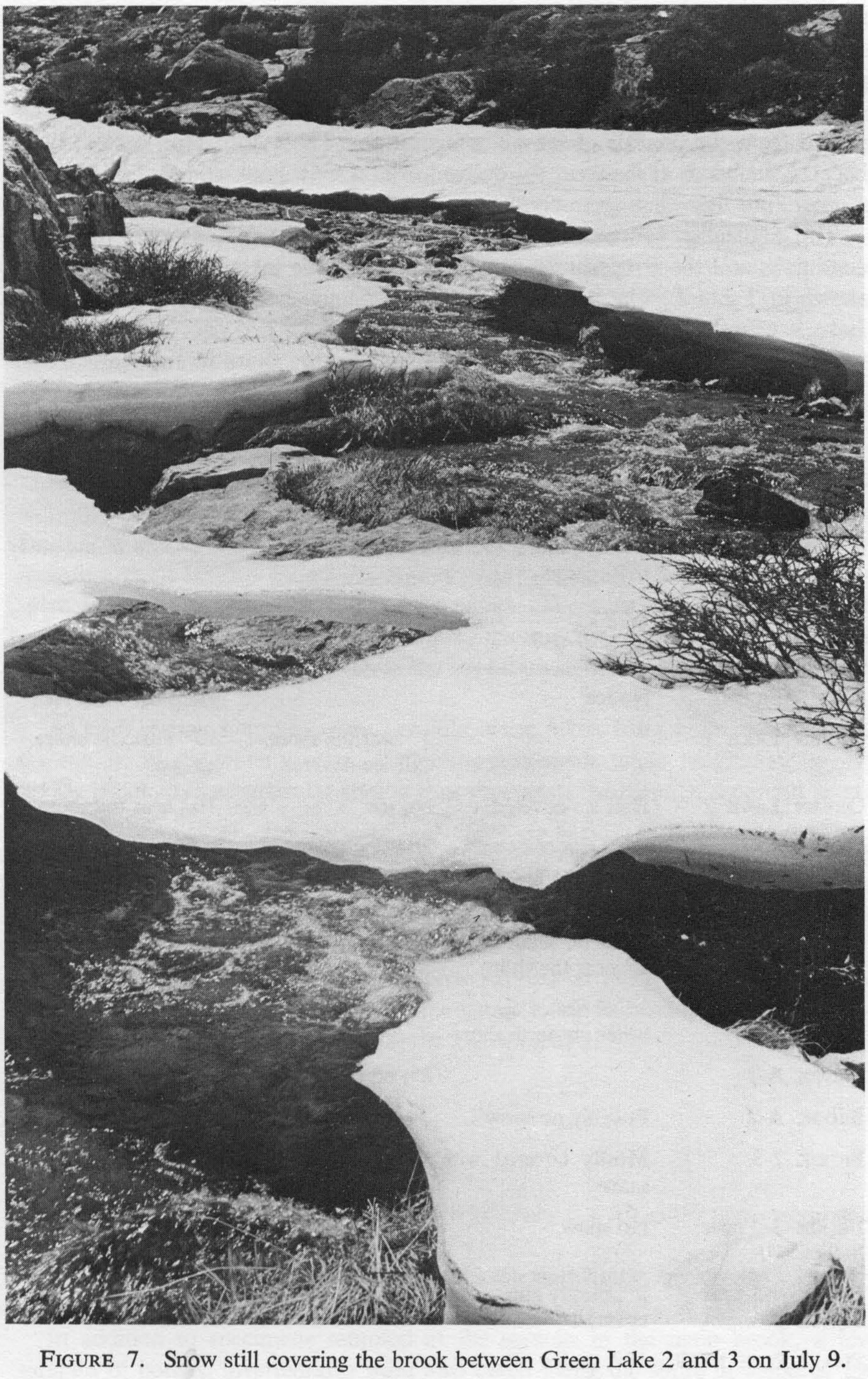


FIGURE 7. Snow still covering the brook between Green Lake 2 and 3 on July 9.

of about 1°C, and the temperature dropped even below 1°C at the uppermost station (Figure 6).

In Brook A-1 the water temperature was 3°C on June 11 and uniformly 10°C on July 8 and 19, higher than in the corresponding parts of the main brook.

The temperature gradient in the brook may seem greater than might be expected from the records of the air temperature (Table 1). This is most likely because the water at the source is derived from a snow bank and thus has a lower temperature than that corresponding to the air temperature at that elevation.

The gradient in temperature along the transect is also demonstrated by the ice conditions and the temperature near the shores of the lakes in the study area as shown in Table 2. On June 7, 1960, Lake Albion had no ice left and Green Lake 2 was about half-covered, while the lakes above had only an open rim of water near the shore. The day temperatures near the shore in July varied from 10° to 2°.

Table 2 gives some additional observations on the ice conditions and temper-

TABLE 2. Records of temperature and ice conditions in lakes and brooks in the study area in 1960. Temperatures in C.

	JUNE 7	JUNE 11	JULY 8-13
LAKE ALBION	No ice		10° near the shore
GREEN LAKE 1		3° near the shore, half ice-covered	10° near the shore, no ice
GREEN LAKE 2	Half ice-covered	No ice	10° near the shore
GREEN LAKE 3	Only rim of open water on south shore	Half ice-covered	9.5° near the shore
GREEN LAKE 4	Only rim of open water on south shore, 4° near the shore		5° near the shore, no ice
GREEN LAKE 5	Small rim of open water on north shore		2° near the shore, one-third ice-covered
BROOK A-1		3°, no snow	10°
BROOK A-2	Possibly no snow		
BROOK 2-3	Mostly covered with snow		
BROOK 3-4 near Station 10	No snow		3.5°
BROOK 4-5 near Station 8	2°, mostly snow-covered		
SMALL POND NEAR GREEN LAKE 4	10°, no ice		

ature in the lakes and in the brook studied. It will be seen that the temperature in the tributary Brook A-1 rose from 3° on June 11 to 10° a month later. The July temperature near the shore in the lakes during the day was several degrees higher than in the brooks nearby in the three lowest lakes, while in Lake 4 it was only slightly higher and in Lake 5 about the same as in the nearby brook. The shores of the lakes, therefore, warm up more rapidly than the corresponding parts of the brooks in the lower range of the study area, as could be expected. The temperature records from both the brook and the shores of the lakes are, of course, only approximations, as most likely daily temperature cycles occur.

Some limnological features of the same brook system have previously been presented by Pennak (1943), but his station was much farther down at the base of the foothills near the city of Boulder at an elevation of about 1600 meters, and his results are therefore not applicable in the present study.

METHODS

As the entire bottom of the brook was stony, the collecting method used was to brush the animals from the stones. Stones of different sizes were taken from the brook, rapidly transferred into a bucket of water, and then brushed thoroughly with a paint brush. To get an approximate quantitative estimation, the time spent in collecting at each station was noted. The time used at each station ranged from 7 to 25 minutes, according to the number of animals present. The numbers of animals found as given in the Frontispiece are corrected to a standard, 10-minute sampling period.

At each station samples, when possible, were taken from both the sides and the middle of the water course. Collecting was made while progressing slowly up the brook, and a particular station thus represents the mean of a certain length of the brook.

After having been brushed from the stones, the animals were concentrated by sieving the water through a fine net and preserved in 4% Formalin. Only the planarians were given special treatment, as proposed by Hyman and Jones (1963).

The collections in the brook were concentrated as much as possible in time to avoid changes likely to occur in the community due to development and hatching. The main brook was sampled on the following dates:

Stations 10-15: July 9, 1960
Stations 6-9: July 12, 1960
Stations 1-5: July 13, 1960

All samples were taken in bright daylight.

The tributary Brook A-1 was sampled on July 8. All collections were thus made within four days.

The weather during collecting was mostly fair and sunny, broken, as usual, by midday thunderstorms.

In addition to specimens sampled at the stations in the main brook, a few samples of bottom invertebrates were also taken along the shore of some of the Green Lakes and in a small pond near Green Lake 4. This pond measured only about 3 meters in diameter and was less than 0.5 meters deep. It was sampled on June 7.

Identification to species was in many cases impossible because only larval and pupal stages were available.

Near Station 10 above Green Lake 3, the brook divides into several parallel channels before going into the lake, and, as a control, samples were taken in two of these parallel brooks. A comparison of the species and numbers of individuals found is presented in Table 3. There is a surprisingly good correspondence between the two brooks, and for most species the numbers of individuals are very close. The few species found in one brook but not in the other were represented by very small numbers of individuals as seen at the end of Table 3.

TABLE 3. Comparison of species and numbers of invertebrates in two parallel brook channels at Station 10.

SPECIES	STATION 10, MAIN BROOK, NUMBER OF INDIVIDUALS	STATION 10a, PARALLEL BROOK, NUMBER OF INDIVIDUALS
Polycelis coronata	9	6
Nematoda indet.	4	3
Macrobiotus cf. *macronyx*	3	1
Mesenchytraeus sp.	2	2
Cinygmula mimus	53	13
Plecoptera juv. indet.	90	123
Rhyacophila sp.	2	1
Diamesa sp.	12	5
Diamesa juv. indet.	11	64
Cardiocladius sp.	57	50
Eukiefferiella sp. G	910	315
Eukiefferiella sp. J	145	38
Orthocladius (*Euorthocladius*) sp.	1	1
Orthocladius (*Eudactylocladius*) sp. A	1	1
Prosimulium esselbaughi (or *travisi*)	842	582
Simuliidae sp. (exuv.)	22	8
Corynoneura sp.	2	0
Atalanta sp.	1	0
Pseudodiamesa pertinax	1	0
Diamesa sp. G	0	5

Altogether, the correspondence between the parallel brooks was close as regards species, and numbers and size distributions of individuals. The data indicate that the method of collecting gives reliable results for the comparison of stations.

COMMUNITY COMPOSITION

Except for the zonation, which will be presented in a following section, few generalizations on the animal community can be made, owing to the unsatisfactory taxonomic status of many of the forms and virtual absence of information on ecology and physiology. The community composition is presented in the Frontispiece and Table 4.

The two most abundant species in the community are clearly *Eukiefferiella* sp. *G* and *Prosimulium esselbaughi,* both Diptera. All other species occur in relatively much smaller numbers.

The great majority of identified species are chironomids. Even though collective groups such as Nematoda, Plecoptera, etc., may include several species, the most common single group is still the chironomids with 34 identified species.

The number of individuals in the main groups of invertebrates present is shown in Figure 8. The biomass present at the time of sampling is totally dominated by the chironomids and the simuliids which constitute 85% of the individuals captured by the method used. The chironomid group is thus the most significant both as regards number of species and abundance of individuals in the brook. The overwhelming majority of chironomids (99.6%) belong to the Orthocladiinae, a group typical of high elevations and rapid stream conditions.

The next most abundant groups are the Vermes and Ephemeroptera, while the Plecoptera and Trichoptera were less well represented. Very few individuals belonged to groups outside those mentioned above.

As to trophic levels in the community, it is difficult to distinguish between herbivores, detritus feeders, and filter-feeders, and the only safe statement that can be made at present is that there are 8 to 10 carnivorous species in the community, most of which occur below Station 5. Most others are primary consumers and detritus feeders.

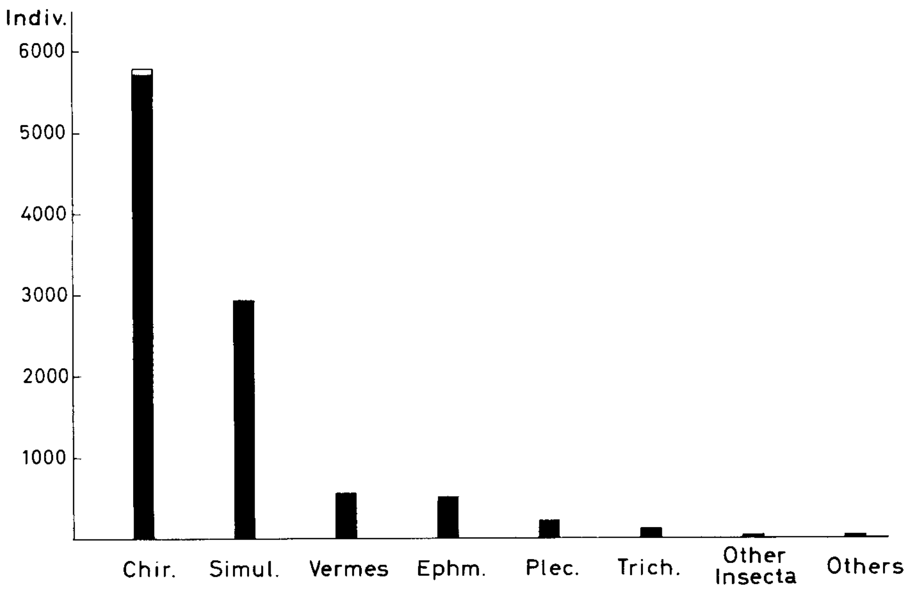


FIGURE 8. Number of individuals in the main groups in the community. White area at the top of the chironomid bar indicates chironomids exclusive of the Orthocladiinae.

TABLE 4. Less abundant species from North Boulder Creek not given in Frontispiece.[a]

Stations	Brook 6					Brook 4-5				Brook 3-4		Brook 2-3	Brook A-2		Brook 0		Brook A-1					
	1	2	3	4	5	6	7	8	9	10	10a	11	12	13	14	15	16a	16	17	18	19	20
[*Copidosoma* (*Litomastix*) *naevia* Saeth.]*	5.0		4.0							1.0												
Podura aquatica L.		1.3																				
Metriocnemus sp. B		2.5																				
cf. *Epoicocladius* sp.		4.0											3.0									
Metriocnemus sp. A			1.3																			
[*Platynothrus* sp.]				1.4																		
Lebertia atelodon Saeth.				1.4																		
[*Heptathela* sp.]				1.4																		
Thienemannia cf. *gracilis* Kieff.				3.0																		
Diamesa (*Pseudokiefferiella*) sp. J				1.4				0.7														
Diamesa sp. E				3.0	1.0			0.7														
Sciaridae sp. A, larva indet.				1.4																		
(*Cyclops* sp.)				1.4																		
(*Orthocladius* s.str., imago)					1.0								1.0									
Oligochaeta, cocoons					2.5								1.0									
Nemoura sp. (without gills)						1.0																
(*Diaptomus* sp.)							5.0				0.4											
[*Parasitus* sp.]								0.7														
(*Cressoniella montana* Saeth., imagines)*								0.7	3.0	0.7												
[*Smittia* sp., imago]								0.7														
Paraphaenocladius sp.								0.7								0.7						
Eukiefferiella sp. H								0.7														
(Sciaridae sp. B, ♀ imago)*								0.7														

TABLE 4 continued.

	Brook 6					Brook 4-5			Brook 3-4			Brook 2-3	Brook A-2		Brook 0		Brook A-1					
STATIONS	1	2	3	4	5	6	7	8	9	10	10a	11	12	13	14	15	16a	16	17	18	19	20
[Thelaxinae indet.]								4.0										1.0				1.0
Ephemeridae indet.								0.7														
(*Daphnia* sp., ephippium)								0.7														
Corynoneura sp.										2.0			1.0									
Orthocladius (*Eudactylocladius*) sp. A											1.0								2.0			
Diamesa sp. F											5.0	0.7										
(*Lycoriella* (*Hemineurina*) sp., ♀ imago)*											0.4											
(*Aedes* (*Ochlerotatus*) *impiger* Walk., im.)											0.8											
Ephemeroptera juv. indet.													1.0									
(*Plumatella* sp., statoblast)													1.0									
Hydra sp.*													9.0	17.0		0.7						
Hydrachnellae indet.														1.4								
Microcricotopus sp. *parvulus* type														1.4		2.8						
Rheocricotopus sp. *effusus* type														2.8		0.7						
(*Gammarus lacustris* Sars)														1.4			6.0					
(*Psectrocladius octomaculatus* Wülk., exuv.)															1.2	0.7						
(*Chironomus anthracinus* group, exuviae)															0.6							
[cf. Adelgidae sp. A]															0.6							
[cf. Adelgidae sp. B]															1.8							
Baetis intermedius Dodds															1.2							
Baetis cf. *rusticans* McD.															0.6							
(*Pisidium* sp.)																	3.0					
Rheocricotopus sp. *atripes* type																1.4						
Eukiefferiella sp. A																		3.0				

TABLE 4 continued.

	Brook 6					Brook 4-5			Brook 3-4			Brook 2-3	Brook A-2		Brook 0		Brook A-1					
Stations	1	2	3	4	5	6	7	8	9	10	10a	11	12	13	14	15	16a	16	17	18	19	20
Eukiefferiella sp. C																		5.0				
Eukiefferiella sp. D																		1.0				
Eukiefferiella sp. F																		1.0				
Thaumalea sp.																		3.0			0.9	
Nemoura (*Zapada*) *haysi* Rick.																			1.0			
Alloperla sp. A																			1.0	0.8		
Sperchon glandulosus coloradensis Saeth.																				0.8		
Alloperla sp. B																				0.8		
Oligochaeta indet., in dissolution																						1.0

[a]Figures = number of individuals calculated per 10 minute sampling period; ( ) = regarded as drift from lakes and as imagines with aquatic larvae; [ ] = of terrestrial origin; * = habitat not known for certain.

ZONATION

DIVISIONS OF THE COMMUNITY AND THE BROOK

The community of invertebrates in the part of the brook studied showed considerable zonation, as illustrated in the Frontispiece. Less abundant forms are presented in Table 4. Such zonation is fundamentally due to gradients of environmental factors and may be exaggerated by competitive exclusion (Hutchinson 1953:7). Influence of biotic factors on the zonation of running water communities has also been emphasized by Macan (1962).

In the present study, which represents conditions in midsummer only, there is a clear sequence from species occurring only in the extreme upper part of the brook, through more eurytopic forms occurring over most of the range studied to forms inhabiting only the lower, warmer part of the brook.

Five groups may be distinguished along the transect:

Group 1: Chironomids found only in the upper two stations at temperatures slightly below 1°. The most abundant species in this group are *Diamesa* sp. *A*, and *Diamesa* (*Pseudokiefferiella*) sp. *H*.

Group 2: Species found mainly in the upper part of the brook at Stations 3, 4, and 5 at temperatures about 1°. The most abundant forms in this group are Enchytraeida, *Prosimulium ursinum*, and *Diamesa* sp. *B*.

Group 3: Species found mainly in the middle part of the brook between Stations 6 and 10 inclusive, at temperatures of 2 to 5°. Typical species in this group are *Cardiocladius* sp. and *Eukiefferiella* sp. *J*.

Group 4: Species restricted to the lower part of the brook below Station 10, at temperatures from 5 to 10°. Forms belonging to this group mostly all occur in relatively smaller numbers than those in the groups above.

Group 5: Forms occurring at most of the stations investigated throughout the whole temperature range from 1 to 10°. The most typical representative of this group is *Prosimulium esselbaughi*. It is probable that *P. travisi* was present in small numbers only in the upper part of the brook and should thus belong to Group 1 or 2, but *P. esselbaughi* was present throughout the whole range.

It is noteworthy that the two clearly most abundant species in the community, *Eukiefferiella* sp. *G* and *Prosimulium esselbaughi*, both belong to Group 5.

* * *

The distribution of both the two most abundant forms, *Eukiefferiella* sp. *G* and *Prosimulium esselbaughi*, showed a discontinuous pattern with alternating maxima and minima. Except for a large concentration of only *Eukiefferiella* at Station 5 and of *Prosimulium* only at Station 14, the maxima and minima in the two groups followed each other closely, indicating regulation by common factors. Maxima were found in both forms at Stations 3, 7, and 10, and minima at Stations 4, 6, and 9. Very small numbers were found in general at Station 9, while some other forms occurred in relatively dense populations at Stations 4 and 6. The general paucity of fauna at Station 9 can best be explained by its proximity to a large snowbank. At this station there was a patch of open water of only about 10 to

12 meters between Lake 4 and the snowbank, and the ice may have just recently thawed. At Station 6, *Orthocladius* (*Eudactylocladius*) sp. *B* was almost the only form found. This station was atypical, however, as the brook had recently been artificially widened, and the whole bottom community had been disturbed. This part of the brook was also relatively deep with a slow current.

The large number of individuals of certain species found in particular stations may be related to the presence of a cover of moss on the stones. A moss cover can most likely accommodate a much larger number of individuals than a bare stone, and it is noteworthy that all the pronounced maxima were found at stations with a dense cover of moss on the stones (Frontispiece). It should be noted, however, that Station 4, with relatively few of the two predominant species, was also rich in mosses. The relative paucity here may be due to a prolonged ice cover indicated by the proximity of two snowbanks.

When considering faunal distribution along the transect, it should be kept in mind that most of the species found are larvae of insects and that absence of individuals from a certain area may be due to a species having hatched and left the brook at the time of sampling. The extent to which this error may influence the pattern of distribution is difficult to assess, however, as samples are available for a restricted time only.

The zonation in the part of the brook studied showed a more radical change in community composition in certain stations than in others. This is most obvious between Stations 10 and 11, an area which constitutes the upper limit for many species in Group 4 and the lower limit for the occurrence of many species in Group 3, and also for *Eukiefferiella* sp. *G* in Group 5. This juncture is identical with Green Lake 3, which thus constitutes the area of the most pronounced change in community composition.

It is difficult to explain why this should be so. There was no change in gradient or in temperature except that the temperature seemed to fall a little slower above Lake 3 than below. Another factor that might contribute to a change at this point is the greater abundance of mosses on the stones above Lake 3 than below. But these factors do not explain the prominent change found in a restricted area. A tentative explanation may be proposed that a temperature in July of about 5° is an upper temperature limit for one fraction and a lower limit for another fraction of the community.

Another marked division line in the community seems to exist between Stations 5 and 6. This is the lower limit for the most abundant species in Group 2 and the upper limit for Group 3. The boundary here is also represented by a lake, Green Lake 5. This disjunction corresponds better to a change in temperature, since below Lake 5 there is a gradually rising temperature, whereas above this lake the temperature is constant at about 1°. Green Lake 5 also represents the first interruption of the brook on its way down from the source in the snowbank.

Another less distinct boundary may be distinguished between Stations 2 and 3, which divides Groups 1 and 2. The brook above this line is characterized by a slightly lower temperature and a slower current close to the source.

From the zonation of the community of invertebrates, the brook can thus be divided in four main sections, indicated by roman numerals in the Frontispiece.

These four sections correspond to the first four groups of invertebrates that have been established.

CHARACTERIZATION OF THE DIFFERENT ZONES

In this section the community composition *within* each of the sections established will be considered, followed by the relative occurrence of each of the main groups of invertebrates *along the entire transect* represented by the successive zones. These relations are presented in Figure 9 to the left and right, respectively.

The community composition within each section shows a clear change between Zones III and IV, corresponding to the main division line between Stations 10 and 11 as discussed above. The upper three zones, and especially the uppermost, are dominated by chironomids, while the simuliids constitute the dominant group in Zone IV. Ephemeroptera, Plecoptera, and Trichoptera are all lacking in the two upper zones and are only seldom represented in Zone III. The Trichoptera and Plecoptera occur between Stations 5 and 6 and are present in the whole of Zone III, while the Ephemeroptera occur between Stations 8 and 9 and are thus present only in the lower part of Zone III. In Zone IV the Ephemeroptera show a clear relative increase. *There is thus a clear tendency towards a relative increase in the number of chironomids within each zone as one goes upwards, and in the number of simuliids and Ephemeroptera as one goes downwards.*

Along the transect (the tributary Brook A-1 is included as an additional zone in the transect), chironomids, simuliids, and Plecoptera have their relative maximum occurrence in Zone III, while the Vermes have their maximum occurrence in Zone II, and Ephemeroptera in Zone IV. All groups are represented in relatively large numbers in more than one zone except the Plecoptera, which are practically restricted to Zone III. This is due to the exceptionally large number of unidentifiable small larvae occurring in Station 10.

On the whole, the relatively largest number was found in Zones II and III, a problem that will be given further consideration below.

NUMBER OF INDIVIDUALS AND SPECIES

The number of individuals per station and per 10 minutes sampling time is shown in comparison with the number of species in Figure 10, represented by the mean for each of the zones. The number of species is to be regarded as a minimum, as some of the groups, especially the Nematoda and Plecoptera juv., may contain more than one species.

The number of individuals per station shows a clear maximum in Zone III and is also relatively large in Zone II, but very small and about equal in Zones I and IV. *There is thus a clear maximum with respect to the total number of individuals in the middle part of the brook.*

A glance at the Frontispiece shows that this result may be primarily due to the overwhelming majority of two species, *Eukiefferiella* sp. *G* and *Prosimulium esselbaughi*. The distribution when these dominant species are excluded may therefore be of interest and is shown as curves c and d in Figure 10. The curves become more flattened, but the maximum number is still in the middle part of the

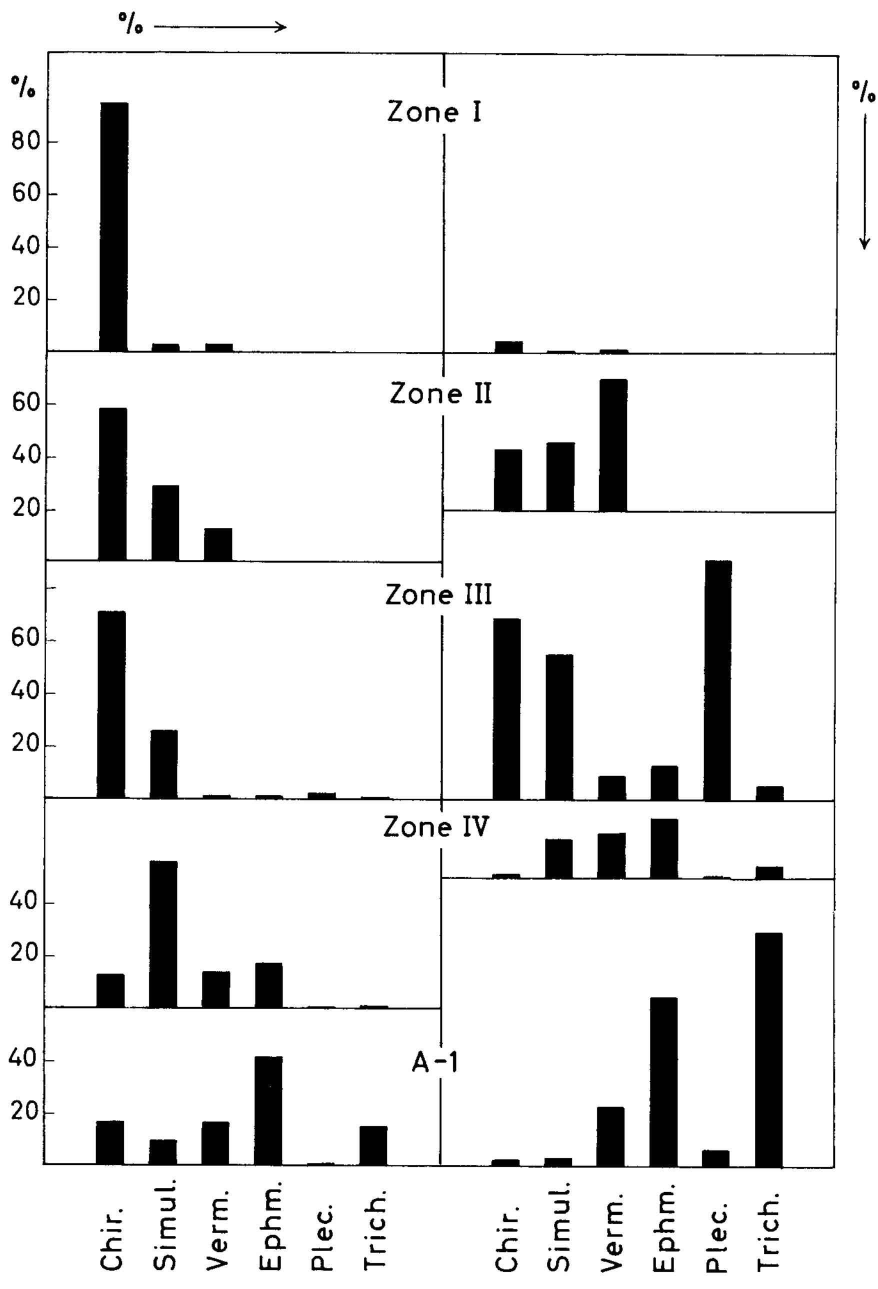


FIGURE 9. Relative distribution of the main groups of animals. *Left*: Percentage variation within each zone; *right*: Percentage variation along the brook, tributary A-1 inclusive.

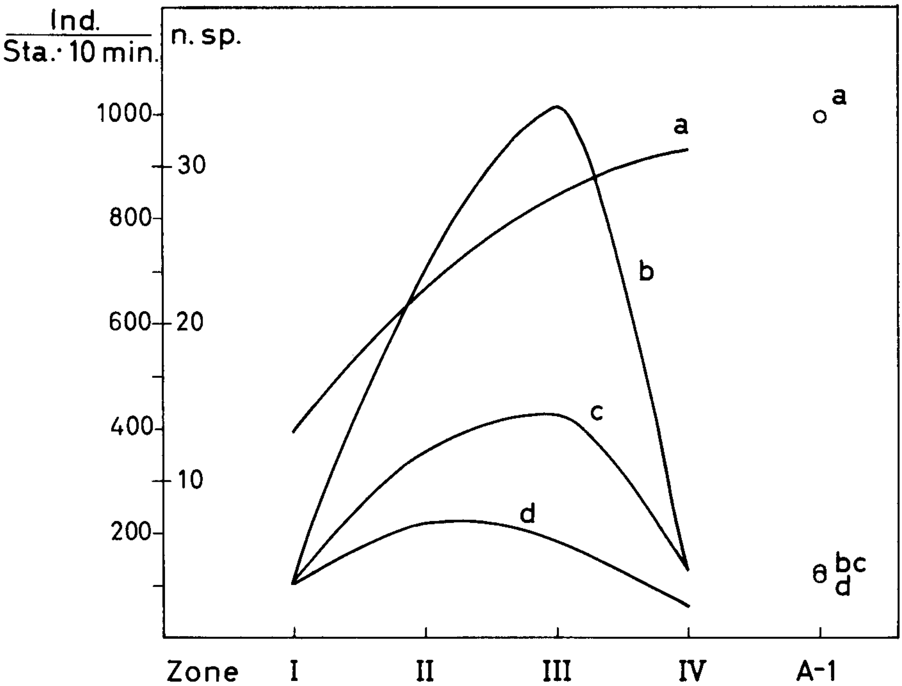


FIGURE 10. Variation in number of species (*a*) and the total number of individuals (*b*). *c*: Total number of individuals exclusive of *Eukiefferiella* sp. *G*, *d*: total number of individuals exclusive of *Eukiefferiella* sp. *G* and *Prosimulium esselbaughi* and *travisi.*

brook; the emphasis, however, is gradually shifted from Zone III to Zone II. The occurrence of a maximum in the middle of the brook is therefore not due to the distribution of the two dominant species alone, even though these strongly accentuate this tendency.

The number of species in the different zones, on the other hand, shows an increase as one goes down the brook. At lower altitudes more ecological niches become available, and in the upper three zones there is an increase downwards both in the number of individuals and species. In Zone IV, however, there is a radical drop in the number of individuals while the number of species continues to rise.

The number of individuals per species also shows a maximum in Zone III, especially due to the simuliids. The chironomids also have a relatively large number of individuals per species, while the other groups, especially the Trichoptera, Ephemeroptera, and Plecoptera, show considerably lower values.

COMPARISON WITH A TRIBUTARY BROOK

The only tributary to the main brook in the study area was the short Brook A-1 between Lake Albion and Green Lake 1. Brook A-1 differs from the main brook primarily in the presence of a denser vegetation along the sides. The temperature of the water was quite uniform at about 10°. This is higher than in the main brook at the same altitude and time, due to a more southern exposure.

The Brook A-1 was sampled quite exhaustively on July 8, 1960. The results for the more common forms are specified in the Frontispiece where they can be compared with those from the main brook. The less common forms are given in Table 4.

The most abundant species in Brook A-1 were *Cinygmula mimus, Polycelis coronata,* and *Baetis bicaudatus.* The last two occurred more abundantly in Brook A-1 than in the main brook, as did also *Micropsectra* sp. and *Diamesa* sp. *C.* Except for *Polycelis coronata,* all these species occurred only in the lowest part of the main brook. Their greater abundance in Brook A-1 may therefore be connected with a higher temperature.

The population density was generally low in Brook A-1 and never reached the high values found in the main brook.

Of the 58 species found in the main brook, 16 were also found in Brook A-1. In addition, 16 other species were found only in Brook A-1, giving a total of 32 forms. The relatively large number of forms found only in A-1 reflects the difference in ecological conditions. Of the more abundant species found only in Brook A-1 are *Hesperophylax oreades, Pseudostenophylax edwardsi, Brachycentrus* sp., *Eukiefferiella* sp. *A* and *C,* and *Boreoheptagyia* sp.

The tributary Brook A-1 was generally characterized by an abundance of Trichoptera and Ephemeroptera. These groups had a much higher frequency in the tributary than in the main brook (Figure 9).

The community of Brook A-1 resembled most closely that of the lower part of the main brook. In Zone IV, situated at the same altitude as Brook A-1, about two-thirds, in the two middle zones about one-half, and in the uppermost zone about one-quarter of the species were common to both brooks. The similarity with Zone IV is also emphasized by comparing the community composition within the zones and the total number of individuals and species as shown in Figures 9 and 10. The results for Brook A-1 in all these comparisons resemble Zone IV much more closely than any of the other zones. On the whole therefore, *the fauna of the tributary was most closely related to the community structure of the main brook at the same elevation.*

DISCUSSION

The division of the brook into zones as described above corresponds remarkably well with the division of mountain brooks proposed by Thienemann (1954) based on genera of chironomids. The chironomids of North Boulder Creek are compared with the system of Thienemann in Table 5. It will be seen that the upper part of the brook, corresponding to Zones I and II, down to Green Lake 5, corresponds well to Thienemann's "Gletscherbach" (Glacier Brook), and Zone III between Green Lake 5 and 3 to his "Hochgebirgsbach" (High Mountain Brook); Zone IV of the present brook below Green Lake 3 does not correspond so well to Thienemann's next category, "Übergangsbach" (Transition Brook), but is rather a mixture of a High Mountain Brook and a Transition Brook.

Most species found in North Boulder Creek are closely related to Thienemann's European species and form species pairs that are found on the same line in Table

5. High mountain brooks on different continents thus seem to be inhabited by related communities with respect to the chironomid fauna.

Other groups found in North Boulder Creek are also represented by related species in the same genus in European mountain brooks and even by identical species such as *Aturus fontinalis* and *Nais variabilis*.

TABLE 5. Comparison of species in the system of Thienemann (1954) and North Boulder Creek. Closely related forms are placed on the same line.

EUROPEAN SPECIES (Thienemann 1954) *Glacier brooks*	NORTH BOULDER CREEK *Glacier brook (Brook 6)*
Diamesa steinböcki	
Diamesa sp. *cinerella*—group	*Diamesa* sp. A
Diamesa aberrata	*Diamesa* sp. B
Diamesa latitarsis and *lindrothi*	*Diamesa* sp. E
Diamesa tyrolensis	
Pseudodiamesa branicki	*Pseudodiamesa pertinax*
Orthocladius (*Eudactylocladius*) sp.	(*O.* (*Eudactylocladius*) sp. B present at Station 6)
Dyscamptocladius	
Eukiefferiella sp.	*Eukiefferiella* sp. B and G
	Diamesa (*Pseudokiefferiella*) sp. A
	Orthocladius (*Euorthocladius*) sp.
	Thienemannia cf. *gracilis*
	Metriocnemus sp. A and B
	cf. *Epoicocladius* sp.
HIGH MOUNTAIN BROOKS	HIGH MOUNTAIN BROOK (BROOK 4-5 and 3-4)
Eutanytarsus inermipes—group	
Micropsectra sp.	*Micropsectra* sp.
Phaenopelma sp.	
Diamesa steinböcki	
Diamesa latitarsis	*Diamesa* sp. E, F, and G
Diamesa insignipes	
Diamesa davisi	
Diamesa sp.	*Diamesa* sp. E, F, and G
Onychodiamesa macronyx	
Boreoheptagyia sp.	*Boreoheptagyia* sp.
Cardiocladius sp.	*Cardiocladius* sp.
Eukiefferiella sp. cf. *calvescensslobulifera*	(*Eukiefferiella* sp. A, only in Brook A-1). Same type, different subtype: E. sp. B, C, and D
Eukiefferiella sp. cf. *minor-montana*	*Eukiefferiella* sp. G, and H
Eukiefferiella brevicalcar, cf. *hospita*, and *alpestris*	
Eukiefferiella sp. cf. *devonica*	*Eukiefferiella* sp. J
Parorthocladius nudipennis	

TABLE 5 continued

HIGH MOUNTAIN BROOKS	HIGH MOUNTAIN BROOK (BROOK 4-5 and 3-4)
Orthocladius (*Eudactylocladius*) *bipunctellus*	*Orthocladius* (*Eudactylocladius*) sp. A and B.
Orthocladius (*Euorthocladius*) *rivicola, rivulorum, thienemanni,* and *saxosus*	*Orthocladius* (*Euorthocladius*) sp.
Orthocladius (*Orthocladius*) *rhyacobius*—group	*Orthocladius* (*Orthocladius*) sp.
Cricotopus spp.	
Rheocricotopus sp. *effusus*—group	*Rheocricotopus effusus*—group *Rheocricotopus atripes*—group
Microcricotopus sp. cf. *bicolor*	*Microcricotopus* sp.
Parametriocnemus boreoalpinus *Thienemanniella? vittata*	*Paraphaenocladius* sp.
Corynoneura sp.	*Corynoneura* sp.

This general correspondence is in accord with the statement of Illies (1961b) that high mountain brooks all over the world constitute biotopes that are physiographically identical and have acquired the same general types of communities.

In the system of classification of running waters proposed by Illies and Botosaneanu (1963), the part of North Boulder Creek studied fits best with their zones I Eucrenon, II Hypocrenon, and III Epirhithron. These zones, however, do not closely correspond to the division of the present brook, as Zones III and IV must both be included in the Epirhithron. The division of the brook studied is compared with the system of Thienemann, based on the chironomid fauna, and with that of Illies and Botosaneanu in Table 6.

TABLE 6. The divisions of North Boulder Creek in relation to the systems of Thienemann and of Illies and Botosaneanu.

NORTH BOULDER CREEK ZONES	STATIONS	THIENEMANN (1954)	ILLIES AND BOTOSANEANU (1963)
I	1 - 2	Glacier	III Epirhithron
II	3 - 5	Brooks	II Hypocrenon
III	6 - 10	High Mountain Brooks	I Eucrenon
IV	11 - 15	High Mountain-Transition Brooks	

AUTECOLOGY AND ZOOGEOGRAPHICAL NOTES

In Table 4, which includes the less important forms not presented in the Frontispiece, some terrestrial forms and some forms that may have drifted from lakes are in brackets. Most of these are not mentioned in the following section.

The length distribution is given for some of the more abundant forms.

Descriptions of color are made on material preserved for four years in 4% Formalin.

COELENTERATA

Hydra sp.

It is difficult to tell whether all the hydras found were really living in the brook or were washed out from the lakes. Their numbers indicate that these specimens really belonged to the running water community.

Preserved hydras cannot be identified except by the embryonic thecae in some cases, and such thecae were not present in the collected specimens.

TURBELLARIA

Polycelis coronata (Girard)

As seen in Figure 11, specimens measuring from 1 to 12 mm occurred together in almost all parts of the creek, and especially in the lower parts. *P. coronata* is known to reach 15 to 20 mm, but the present specimens were somewhat contracted.

The species is known in hill and mountain streams from the Black Hills of South Dakota westward to the Pacific Coast (Hyman and Jones 1959).

NEMATODA

The undetermined nematodes seem to belong mostly to the family Tylenchidae. As it will appear from the Frontispiece, they had their maxima in the upper stations together with the greatest abundance of moss. Nematodes were, however, found in all parts of the brook.

TARDIGRADA

Macrobiotus cf. *macronyx* Duj.

Specimens measuring 630 to 650 μ in length were found.

This cosmopolitan species lives mainly among algae, but may also be found in *Fontinalis* beds and other more or less submerged mosses. It has been found in high alpine waters to an elevation of 2640 meters, and in the Himalayas up to 2700 meters (Marcus 1928).

OLIGOCHAETA

Chaetogaster cf. *diastrophus* (Gruith.)

Single individuals measured 215 to 1100 μ in length.

According to the keys of Sperber (1950) and Goodnight (1959), this species seems to be *C. diastrophus*. However, the latter, according to Ude (1929), is found in different kinds of waters, but not in cold springs and creeks. As no dissections or sections were made, the determination is doubtful, but among the species mentioned by Ude, Sperber, and Goodnight, no other corresponds to the present species. The food of *C. diastrophus* is mainly detritus (Ude 1929). It has been found in Europe, India, China, and North and South America. The genus *Chaetogaster* as a whole is cosmopolitan (Sperber 1948).

Nais variabilis Piguet

Five specimens found at Station 11 measured 2.5 to 3.5 mm; four individuals at Station 13 reached 4 mm; four specimens at Station 15 measured 5 mm.

N. variabilis has been found in all kinds of waters, including brackish waters. In Peru it has been found up to an elevation of 5140 meters. The food of this species is algae (Ude 1929). *N. variabilis* is cosmopolitan (Sperber 1948).

Mesenchytraeus sp. (Saether 1970.)

Among the known species, *M. hydrius*

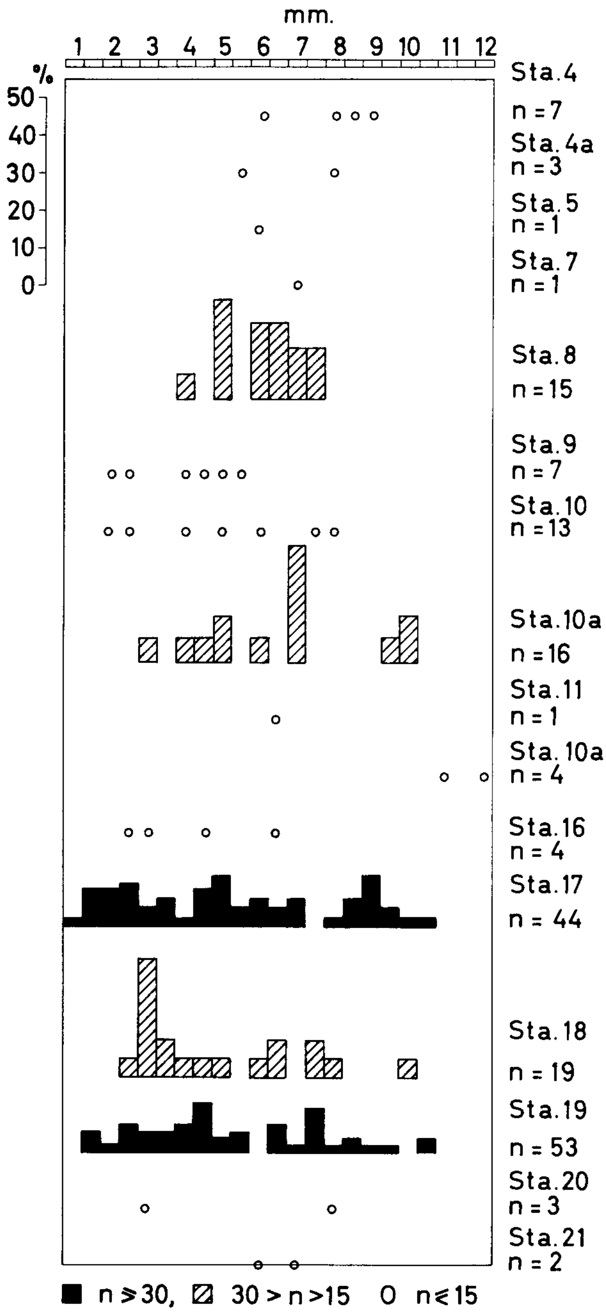


FIGURE 11. Length distribution of *Polycelis coronata*. Lengths computed to the nearest half mm; "n" is the number of animals measured.

Welch (Welch 1919) seems closely related. This species is one of the few enchytraeids found in fully aquatic habitats. *M. hydrius* was found in the Mt. Rainier National Park at an altitude of 3400 feet (about 1000 meters). The worms were found in slowly moving water in close proximity to melting snow (Welch 1919). This means that *M. hydrius* is found in the same type of habitat as the present species of *Mesenchytraeus*.

COLLEMBOLA

Podura aquatica L.

One specimen was found at Station 2. *P. aquatica* is a cosmopolitan species found on stagnant water (Scott 1956). *Podura* is one of the commonest genera in the edges of small melt torrents of the Himalayas, where it has been found at elevations up to 4267 meters (Mani 1962).

EPHEMEROPTERA

Ephemerella coloradensis Dodds

This species is widespread in the higher mountains of the western states. Dodds and Hisaw (1925b) and Dodds (1923) found imagines from 9000 to 9500 feet (2750-2900 meters) and nymphs from 6700 to 9500 feet (2050-2900 meters) in the valley of South Boulder Creek, Colorado. In the present investigation a few specimens were found up to about 3400 meters, i.e., at considerably higher elevations. *E. coloradensis* lives under and among stones and gravel rather than in mud. The whole structure of the nymph seems not to be adapted to life in swift waters, but rather for maintaining its position among the small stones or gravel (Dodds and Hisaw 1924a). In North St. Vrain Creek, Boulder, Colorado, Pennak and van Gerpen (1947) found 49 specimens of *Ephemerella* per square meter on coarse gravel, 48.2 on rubble, only 3 specimens per square meter on the bedrock, and 1.9 on the coarse sand. In Logan River *E. coloradensis* was not found in the swiftest water, but only in rapids where the current was moderate (Needham and Christenson 1927).

There seemed to be three size groups that may indicate a two-year cycle (Figure 12).

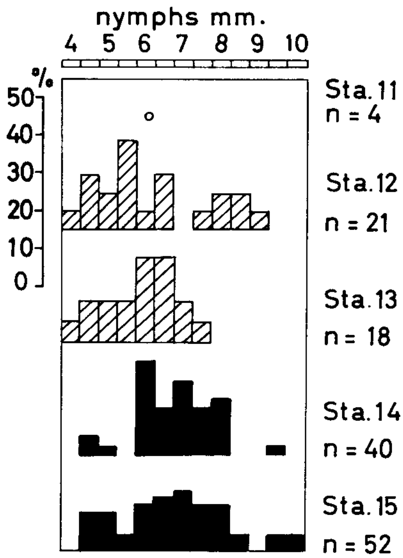


FIGURE 12. Length distribution of *Ephemerella coloradensis* (for explanation see Figure 11).

Baetis bicaudatus Dodds

According to Needham, Traver, and Hsu (1935) and Dodds (1923), the species found belongs to *bicaudatus*. Dodds and Hisaw (1925b) and Dodds (1923) found imagines at an elevation of 10,500 to 11,000 feet (3200-3350 meters), and nymphs from just below 9000 feet up to 11,000 feet (2750-3350 meters). According to Edmunds and Allen (1957), however, *B. minimus* Dodds is a synonym of *B. bicaudatus*. Imagines of *B. minimus* were recorded from an altitude of below 7000 feet up to 10,500 feet (2100-3200 meters). In the present investigation, nymphs were collected up to 3400 meters in Brook A-1 and below Lake Albion in the main brook.

B. bicaudatus inhabits very swift water and torrents where the flow often reaches 10 feet (3 meters) per second. The nymph lives in swifter water than does any other mayfly in the streams examined by Dodds and Hisaw (1924a) and Dodds (1923). Dodds and Hisaw (1924b) found the species at velocities of 6 to 10 feet (1.8-3 meters) per second in water containing 7.3 cc of oxygen per liter or about 150% saturation at the prevailing temperature and pressure. Pennak and van Gerpen (1947) found that specimens of *Baetis* in North St. Vrain Creek preferred rubble and bedrock.

The nymphs of the genus as a whole are very adaptable, living in open waters of streams in currents ranging from slow to very swift (Day 1956).

The length distribution appears in Figure 13.

Baetis intermedius Dodds

Two specimens measuring 6.0 mm

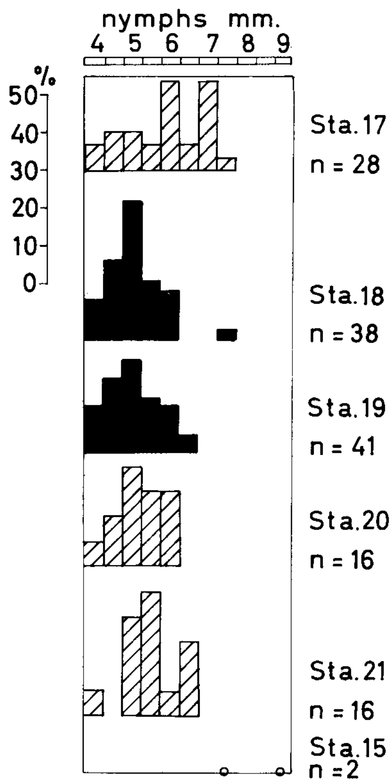


FIGURE 13. Length distribution of *Baetis bicaudatus* (for explanation see Figure 11).

and 2.0 mm in length were collected at Station 14.

At least the smaller of these two specimens seems to belong to *B. intermedius* as described by Dodds (1923) and Dodds and Hisaw (1924a). The larger specimen may very well belong to another species, as all caudal filaments were broken. Other characteristics, however, were identical.

Dodds and Hisaw (1925b) and Dodds (1923) recorded the species at an elevation of 8800 up to 11,000 feet (2700-3350 meters). According to Dodds and Hisaw (1924a), the species is found only in very swift streams clinging to the surface of stones, facing the current, in water velocities up to 8 feet (2.4 meters) per second.

Cinygmula mimus (Eaton)

According to Needham, Traver, and Hsu (1935), this species belongs to the *ramaleyi-mimus* group; according to Day (1956), it is *C. mimus*. Dodds and Hisaw (1925b) and Dodds (1923) found that this species had the highest altitudinal range of the 25 species of mayfiies collected in the valley of South Boulder Creek. The imagines were taken at an elevation of 10,500 to 11,650 feet (3200-3550 meters). In North Boulder Creek the nymphs were collected up to about 3550 meters. As in South Boulder Creek, this species had the highest altitudinal range of the mayflies present. Fragments of gills of an ephemerid, however, were found at about the same elevation (Table 4).

The distribution of size groups is shown in Figure 14. The most reasonable interpretation is that there is a two-year life cycle. This seems especially evident at Stations 19-21 with a clear bimodality in the lower part of Brook A-1. At Stations 9-13 there may be a retarded development. There were still a few large nymphs left, which may be two years old. The nymphs measuring about 2 to 5 mm are one year old and correspond to the largest fraction measuring 5 to 10 mm farther down the stream. A very few small nymphs are most likely the brood of the year. These correspond to the smallest fraction farther down.

PLECOPTERA

Isogenus sp. (Saether 1970). This species is closely related to *I. expansus* Banks known from Colorado to Montana (Ricker 1959).

The only species of *Isogenus* found by Dodds and Hisaw (1925b) among the 27 species of stoneflies was *I. elongatus* with an altitudinal range from just below 6000 feet to nearly 11,000 feet (1850-3350 meters).

Alloperla sp. *A*

One nymph, 8.5 mm in length, was found at Station 18, and one nymph measuring 10 mm at Station 19.

The nymphs of *Alloperla* resemble one another very closely, and few have been described. These specimens seem to be identical with the nymph of *pacifica* (syn. *A. spatula* Needham and Claassen) described by Claassen (1931). *A. pacifica,* however, is known from Washington, British Columbia, and Montana to California, but has not been reported from the Colorado Rockies (Jewett 1956, Gaufin 1964). Among the other species of the subgenus *Sweltsa* (with *pacifica*) with similar coloration of the imago, occurring in the Colorado Rockies and with a flight period in the

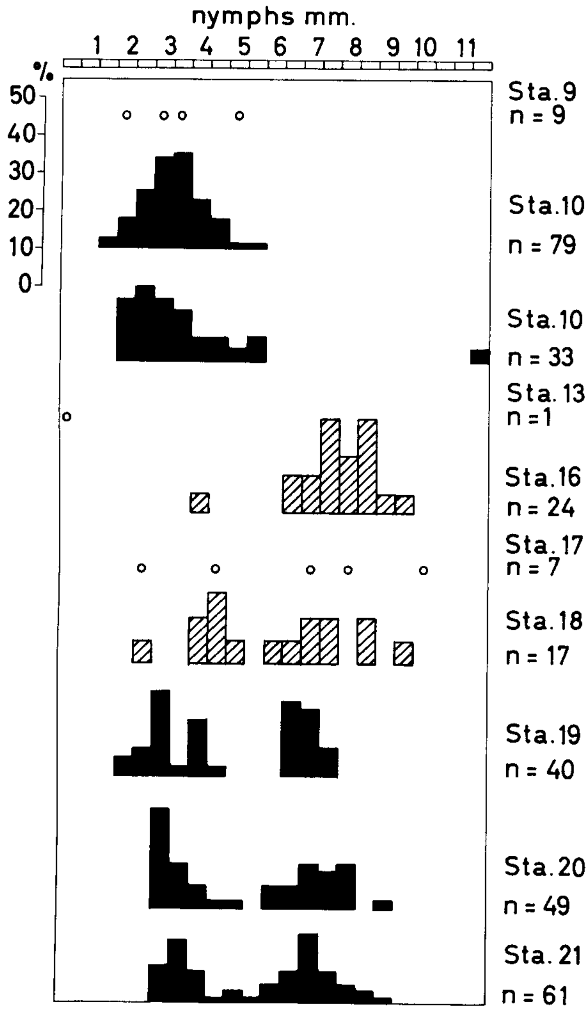


FIGURE 14. Length distribution in *Cinygmula mimus*. (for explanation see Figure 11).

middle of July or later, there is only one related species, *Alloperla pilosa* Needham and Claassen. This species is rare, but its type locality is South Boulder Creek, and it has an altitudinal range from just above 9000 feet to 11,500 feet (2750-3500 meters) above sea level (Dodds and Hisaw 1925b). The species has the highest altitudinal range of the 27 species of stoneflies from the investigations of Dodds and Hisaw.

Alloperla sp. *B*

One nymph measuring 9 mm in length was found at Station 19. The distinct color pattern on the dorsum of the mature nymph corresponded to the pattern of the imago of *A.* (*Sweltsa*) *oregonensis* Frison (Frison 1935, Gaufin 1964). This species, however, is not found in the Colorado Rockies, but is common from British Columbia to Oregon (Gaufin 1964).

The only known species of *Alloperla* from Colorado with a yellowish coloration and a dark V-shaped mark over the ocellar triangle is *Alloperla borealis* (Banks). This species is common from Alaska to Colorado and California (Gaufin 1964). Description of the nymph is given by Claassen (1931). As mentioned above, the color pattern of the present specimen seems to be more in accordance with that of *A. oregonensis.* Dodds and Hisaw (1925b) found *A. borealis* from 5500 to 11,000 feet (1700-3350 meters).

Nemoura (*Zapada*) *haysi* Ricker

One nymph reaching only 3 mm in length was found at Station 18. The species is known from Alaska to California, Montana to Utah and Colorado (Ricker 1959, Jewett 1956). In Colorado it has been found at an elevation of 11,000 feet (3350 meters) near Lake Agnes, at 9400 feet (2850 meters) in Rocky Mountain National Park and in Mt. Boy Park (Ricker 1959).

Nemoura sp. (without gills) (Saether 1970)

One nymph was found at Station 5. This species from North Boulder Creek may be identical with *N. delicatula* Claassen (Saether 1970). *N. delicatula* was the second in number of the stoneflies in South Boulder Creek and had an altitudinal range of 8000 feet to more than 11,000 feet (2450-3350 meters) (Dodds and Hisaw 1925b).

Plecoptera juv. indet.

Several nymphs measuring less than 1.5 mm, and thus not identifiable, were found. As will appear from the Frontispiece, this species is, together with *Cinygmula mimus,* the dominating non-dipterous insect in the study area. The species may be identical with the above-mentioned species of *Nemoura,* but probably not with any of the other species on the basis of their size and distribution in the brook. The most numerous stoneflies in the investigation of Dodds and Hisaw (1925b) were *Alloperla lamba* and *Nemoura delicatula,* the latter probably identical with the above-mentioned species.

TRICHOPTERA

Rhyacophila sp. (cf. *Rhyacophila* sp. in Dodds and Hisaw 1925a fig. 10b) (Saether 1970)

The specimens found at Stations 10, 10a, 17, and 19 measured 4 to 5.5 mm in length; those at Station 14, 8.5, and 9 mm; and at Station 15, 13, and 14.5 mm.

The larvae of *Rhyacophila* are especially abundant in cold running water in mountain streams. There are 70 known North American species, but very few larvae are known and described (Ross 1959).

Brachycentrus sp. (Saether 1970)

The specimen at Station 18 measured 18 mm in length; that at Station 19 reached 7 mm, and those at Station 21, 5.5 to 6.5 mm. The only species of *Brachycentrus* found by Dodds and Hisaw (1925b) was *americanus* (Banks) (syn. *similis* Banks), which has an entirely black head, while this species has a dark brown head with blackish spots.

Pseudostenophylax edwardsi Banks (syn. Limnephilid)

Limnephilid Genus *A* in Ross (1959 p.

1044). Type 9c L. 243 of Dodds and Hisaw (1925a, p. 127) (Saether 1970)

Ross (1959) mentions the form only from Lobster Valley, Alsea, Oregon, but it must be identical with Type 9c of Dodds and Hisaw, who collected the species in upper Arapahoe Creek, Colorado, at a little over 11,000 feet (3350 meters) (Dodds and Hisaw 1925a). Here it was found clinging to steep or vertical rock faces, over which a little water was flowing, i.e., in the same type of habitat as the present specimens of larvae. The larvae, mentioned by Dodds and Hisaw, were clinging to the rocks with their legs, while the flat surface of the head was pressed closely against the surface of the rock, presumably acting as an organ of adhesion.

Hesperophylax oreades Saether (cf. syn. *H. designatus* Dodds and Hisaw (1925a) nec. Walk.)

The length distribution of this new species described by Saether (1970) appears in Figure 15.

Dodds and Hisaw (1925a,b) found *H. designatus* and *H. occidentalis* in South Boulder Creek (*H. occidentalis* only recorded once). *H. designatus*, which probably here is identical with *H. oreades*, was collected between 2750 and 3350 meters. Dodds and Hisaw (1925a) mention the larvae from the sedge zone of swift streams, where the current flows at about two or three feet (0.6-0.9 meters) per second, and also from certain clean-bottomed lakes at high altitudes. The larvae from the lakes, however, may belong to another species, probably the following.

Hesperophylax sp. (Saether 1970)

Besides 5 larvae at Station 6 and 2 at Station 12, 2 were found on the shore of Lake 5 and 11 on the shore of Lake 4.

The species may be identical with *H. consimilis* Banks, first described from South Park, Colorado (Banks 1900). It may also be identical with the lake specimens of *H. designatus* Dodds and Hisaw (1925a,b) nec. Walk. (see above.)

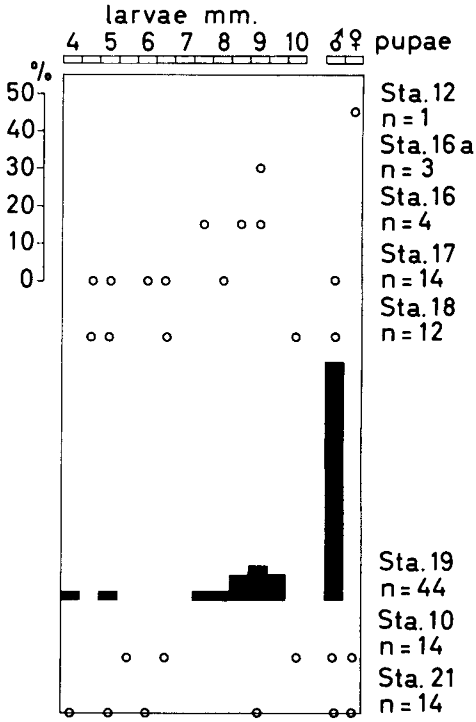


FIGURE 15. Length distribution of larvae of *Hesperophylax oreades* n.sp., and the relation between numbers of larvae and pupae. (for explanation see Figure 11).

Limnephilus sp. (Saether 1970)

Thirteen larvae were collected together with larvae of *Aedes excrucians* in a little pond near Lake 4.

Dodds and Hisaw (1925b) found imagines of *Limnephilus kincaidi* Banks (syn. *L. clausa* Banks) in 39 collections from an elevation of 6000 to 11,000 feet (1850-3350 meters) in the valley of South Boulder Creek, Colorado. This species was the most abundant caddis fly in the survey. *L. kincaidi* is transcontinental (Ross 1944). Other species of *Limnephilus* found by Dodds and Hisaw (1925b) were *L. abreviatus* Banks at 8500 to 11,000 feet (2600-3350 meters), *L. coloradensis* (Banks) at 8500 to 9500 feet (2600-2900 meters), *L. sansoni* Banks, and *L. extensus* Hagen (syn. *L. oslari* Banks), just below 9000 feet (2750 meters).

HYMENOPTERA

Copidosoma (Litomastix) naevia Saeth. (Saether 1970)

Some wasps of the super family Chalcidoidea are known to be parasitic on aquatic dipterous larvae. Chalcid flies belonging to the family Encyrtidae, however, have never been found on aquatic larvae. As members of the subgenus *Litomastix* Thoms. of the Encyrtidae are parasitic on hemipterous, lepidopterous, and dipterous larvae, the imagines found may possibly have been caught while depositing their eggs (Saether 1970).

DIPTERA

FAMILY CULICIDAE

Aedes (Ochlerotatus) excrucians Walk.

Several larvae of this Holarctic species were found together with *Limnephilus* larvae on June 7 in a small pond near Lake 4.

The larvae of this species are most abundant in unshaded sedge marshes, bog pools, and in vegetated rock pools with much humic and organic detritus. The typical vegetation is sedge and grass and occasionally sphagnum moss.

Taxonomy, distribution, and ecology are discussed in Natvig (1948), and Jenkins and Knight (1950).

Aedes (Ochlerotatus) impiger Walk. (syn. *nearcticus* Dyar)

Two female imagines were found below the waterfall in Brook 3-4.

This species is a typical arctic and alpine mosquito limited to the arctic tundra and high mountain habitats in more southern latitudes. The most typical habitats of larvae and pupae are small bog pools and melting water pools above timberline in meadows.

Taxonomy, distribution, and ecology are discussed in Natvig (1948), and Jenkins and Knight (1950).

FAMILY SCIARIDAE

One single larva measuring 4.75 mm in length was found between two small snowbanks at Station 4. Two female imagines, one clearly, and the other probably, belonging to *Lycoriella (Hemineurina) (sensu Tuomikoski* 1960) found at Station 10a and Station 8 have been described (Saether 1970).

Several sciarids are found in arctic and high mountain regions. They are mostly dark with blackish and brownish colors, which have given the family its German name, Trauermücken ("mourning gnats"). The black coloration may be connected with the life in arctic and alpine surroundings as it is known that several alpine insects tend to melanism (Mani 1962).

In early stages, members of the family are almost exclusively terrestrial. There are a few, however, living in a semi-aquatic environment (Hennig 1948). The habitats of the immature stages are described by Lengersdorf (1930) and Hennig (1948). The phenomenon of larval procession has been found in many species.

FAMILY THAUMALEIDAE

Thaumalea sp. (Saether 1970)

The larvae of Thaumaleidae are hygropetric in mountain brooks. They are always found in places irrigated by a thin layer of water, with their stigmata rising above the water. *T. testacea* prefers rocks lacking or almost devoid of vegetation and exposed to the sun, and lives on organic particles (Lindner 1930, Hennig 1950, Johannsen 1934). Such a niche seems to be present at Station 17. The larvae of *Boreoheptagyia* and probably those of *Micropsectra* and Limnephilid Genus *A*, found at Station 17, are also hygropetric.

Most species of *Thaumalea* are restricted to the Alps, but a few have an Holarctic distribution. They are not found in Northern Europe, however (Lindner 1930). The larvae show many similarities to those of *Boreoheptagyia.*

FAMILY CHIRONOMIDAE

Subfamily Chironominae

Tanytarsariae genuinae

Micropsectra sp. (Saether 1970)

In mountain brooks *Micropsectra* larvae are especially found in sand, silt or mud; a few species occur in aquatic moss, but no species belong to the fauna

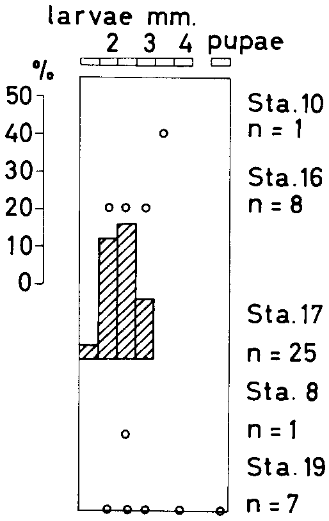


FIGURE 16. Length distribution in *Micropsectra* sp. (for explanation see Figure 11).

of the stones. Larvae of *Micropsectra* are also represented, however, in the hygropetric fauna (Thienemann 1941, 1954). As the maximum of this species occurs together with that of *Thaumalea* and *Heptagyia,* and at a place were neither mud nor sand and probably little moss occurred, the larva is most likely hygropetric.

The length distribution in larvae and pupae (Figure 16) is not inconsistent with a life cycle of two generations a year, such as observed for instance in *M. heptameris* K. (Thienemann 1954) and in *M. groenlandica* And. (Brundin 1949), but the numbers are too small to be significant.

The genus *Micropsectra* is known from all over the Holarctic region and from the Cape Province, but does not occur in South America, Australia, and on the East Indian Islands (Thienemann 1954, Brundin 1956b, Freeman 1958, 1961). (An asterisk is missing for the genus *Micropsectra* in Brundin 1956b.)

Subfamily Diamesinae
Tribe Diamesini
Diamesa—group
Pseudodiamesa pertinax (Garrett)

Description of immature stages is given by Johannsen (1937a) and Saether (1970).

Two head capsules were found at Station 2; nine at Station 4; one larva (12.5 mm in length) at Station 10; one larva (1.5 mm) at Station 11; two larvae (both 7 mm) at Station 13; four larvae (2-9 mm) at Station 14, and seven larvae (2.5-8 mm) at Station 15.

The larvae mentioned by Johannsen (1937a) were taken from fish-hatchery troughs at Yellowstone Lake, Wyoming. *P. pertinax* occurs in the Rocky Mountains and the Canadian arctic (Oliver 1959). On the glaciers one can often find small ponds. The only chironomid which lives in this habitat is *Pseudodiamesa branicki* (Now.). This species also occurs regularly in the moss of the middle mountain creeks, in the litoral of oligotrophic lakes, and has been found together with *P. nivosa* (Goetgh.) in Tibet in the highest lakes in the world where limnological studies have been undertaken (Pagast 1947, Thienemann 1954). The full distribution of *P. nivosa* and *branickii* is given by Pagast (1947), Oliver (1959), and Wülker (1959). North American species of *Pseudodiamesa* are *P. pertinax, P. branickii, P. diastena* Dendy and Sublette, and *P. (Pachydiamesa) arctica* (Mall.) (Oliver 1959, Dendy and Sublette 1964).

P. branickii and *P. nivosa* have a boreo-alpine distribution. Thienemann (1950, p. 550) writes: "Jedenfalls lässt es sich für die boreoalpinen Arten unserer Liste nicht wahrscheinlich machen, dass sie an Ort und stelle die Eiszeit überdauert haben. Mit einer Ausnahme: *Pseudodiamesa nivosa* und *Branickii.*" The same may be the case with *P. pertinax.*

P. pertinax seems to occupy the same ecological niche as *P. branickii* and *P. nivosa.* It was found everywhere in the creek as well as near Yellowstone Lake. It is omnivorous as are other known *Pseudodiamesa* larvae. In the present study the guts were filled with pollen of fir and a few remnants of small Plecoptera. It has tubuli anales varying in lengths and constrictions, also known in other members of the genus (Fittkau 1954). Its flight period seems to be rather prolonged as indicated by great differences in length of larvae. [(Imagines of *P. nivosa* are observed in March, May, July, and August; imagines of *P. branickii* are observed from February to August (Pagast 1947)]. In the upper colder parts of the North Boulder Creek the period of flying seems, however, to be less prolonged than in the lower, warmer parts.

Diamesa sp. *A*. (Saether 1970)

The species was found only at Stations 1 and 2, and seems to be a strictly cold water form. It is closely related to the *cinerella*-group. The larvae, however, are distinct in having only one short bristle instead of procerci. Larvae of the *cinerella*-group have been found in glacier brooks in central and northern Europe, and in the Arctic islands and have a typical boreo-alpine distribution (Edwards 1935a, Pagast 1947, Thienemann 1950, Wülker 1959, Serra-Tosio 1964, Saether 1966d). The group may also include a few Japanese species (Saether 1966d).

The length distribution appears in Figure 17. The development seems to have been more rapid at Station 2 than at Station 1. At Station 2 more than 72% of the specimens were larvulae, while at Station 1 only pupae, exuviae, and

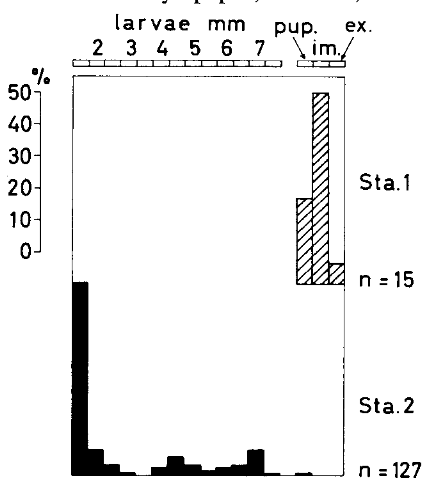


FIGURE 17. Length distribution in *Diamesa* sp. *A*. (for explanation see Figure 11).
The relation between larvae, pupae, exuviae, and imagines is also given.

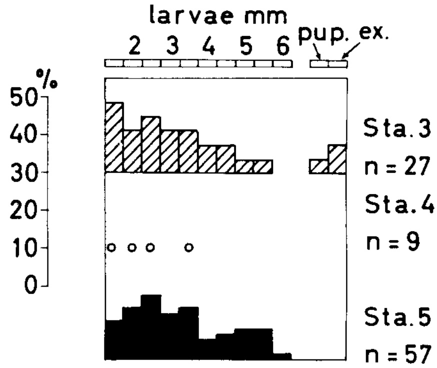


FIGURE 18. Length distribution in *Diamesa* sp. *B*. (for explanation see Figure 11).

imagines were found. The lack of large larvae at Station 1 may not be significant due to the small number of specimens found at this station. The group of larvae measuring 4 to 7.5 mm seems to indicate a prolonged flight period as is usual in species of *Diamesa* (Pagast 1947), but the majority seem to have been undergoing the flight period at Station 1 and to have finished it at Station 2.

Diamesa sp. *B*. (Saether 1970)

The species, especially the pupa, seems to be closely related to *D. aberrata* Lundb. and *D. incallida* (Walk.) Edw. It is not certain, however, that the larvae belong to the same species as the pupa. *D. aberrata* has been found in glacier brooks in the Alps (Thienemann 1954). It is furthermore recorded from Eastern Greenland, Spitsbergen, Bear Island, Ian Mayen, Scandinavia, Schwarzwald, Spain, and Morocco (Wülker 1959, Oliver 1962, Serra-Tosio 1964). *D. incallida* is known from Swedish Lapland, Iceland, England, Estonia, the Rhone, the Vosges Mountains, and the Schwarzwald (Wülker 1959). These two species together with *Diamesa* sp. *B* may form a "triple-species" with two European and one Rocky Mountain species.

As in *Diamesa* sp.*A*, development seemed to have gone further in the lower parts of the brook, and the flight period seemed to be even more prolonged (Figure 18).

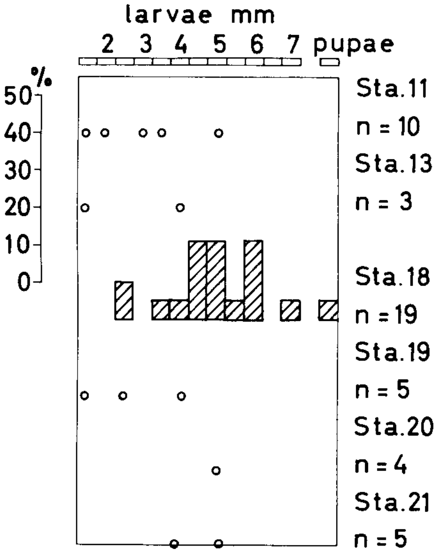


FIGURE 19. Length distribution in *Diamesa* sp. *C.* (for explanation see Figure 11).

D. latitarsis Goetgh.-group
Diamesa sp. *C, D, E, F,* and *G* (Saether 1970)

Diamesa sp. *C* does not seem to be such a strictly cold-stenothermic species as the species mentioned above. The *Diamesa* spp. *C* to *G,* however, seem all related to the *D. latitarsis*-group and may, although this is unlikely, be one species, with several stunted or senescent forms.

The *latitarsis* group, consisting of *D. latitarsis* Goetgh., *D. lindrothi* Goetgh., *D. goetghebuèri* Pag., *D. wuelkeri* Ser.-Tos., *D. laticauda* Ser.-Tos., *D. berardensis* Ser.-Tos., and *D. valkanovii* Saeth., are boreo-alpine species (Thienemann 1950, Serra Tosio 1964, Saether 1968), known from glacier brooks, high mountain brooks, "transition" brooks ["Übergangsbäche" of Thienemann (1954)], and middle mountain brooks, where they belong to the stone fauna as most species of *Diamesa.* [The northern *D. lindrothi,* however, is also observed in stagnant waters) (Thienemann 1954, Styczynski and Rakusa-Suszcewski 1963)].

The length distribution of sp. *C* (Figure 19) indicates that development has proceeded further in Brook A-1 than at Stations 11 and 12 of the main brook, owing perhaps to differences in temperatures.

The smaller larvae of sp. *F* (≦ 1.5 mm) may belong to another species, although this is unlikely. The different length distributions in Figure 20 are not easy to explain. They may not be significant due to the very small numbers at Station 10. The flight period seems to be more restricted than in the other *Diamesa-species observed.* It is unlikely that this species is identical with *Diamesa* sp. *C, but* it obviously belongs to the *latitarsis*-group.

The larvae of the *latitarsis*-group are extremely rheobiontic and live on stones in strong current without making tubes. They have very elongated posterior prolegs that make it easier to adhere to the stones. The reduction of the procerci with their bristles seems to be a similar adaptation, making the current resistance less (Thienemann 1954). All the *Diamesa* larvae found in this investigation have these characteristics. The larvae of

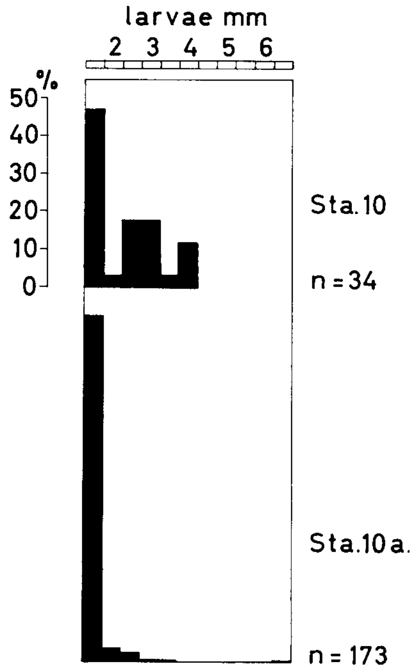


FIGURE 20. Length distribution in *Diamesa* sp. *F.* (for explanation see Figure 11).

Diamesa sp. *A* and *Diamesa* sp. *B* are more adapted to a rheobiontic life than their European relatives (*D. cinerella*-group and *D. aberrata*-group).

Diamesa (*Pseudokiefferiella*) sp. *H* (Sather 1970)

The species was found at Stations 1 and 2 where the temperature of the water ranged from 0.5°-1.5°.

The larvae measured 9-10.5 mm in length, and the pupa reached 6 mm in length. This indicates that the species was in process of hatching. Farther down in the creek they may have developed further and as no larvae, pupae, or larvulae were found, the flight period is likely very short. But the species may well be present in the upper parts only, constituting, together with *Diamesa* sp. *A*, the most stenothermal cold water species.

The larvae and pupae are closely related to *Diamesa* (*Pseudokiefferiella*) *parva* Edw. (syn. *Diplomesa lapponica* Pag. (1947) and *Pseudokiefferiella* sp. Zavrvel (1941)). This form differs, however, in several respects. The length in mature larvae of *D.* (*Pseudokiefferiella*) sp. *H* reaches 10.5 mm, while larvae of *D.* (*Pseudokiefferiella*) *parva* only reach 6 to 7 mm in length. *D.* (*Ps.*) *parva* lives in the moss of creeks and springs as well as on hygropetric places. It is found in Swedish and Finnish Lapland, Finse in Norway, Scotland, the Tatra Mountains, the Schwarzwald, the Vosges Mountains, the Alps, the Pyrenees up to 2200 meters, and the Northwest Territories of Canada (Wülker 1958, Oliver 1959, Serra-Tosio 1964, Saether 1968). It is a typical boreoalpine species. *Diamesa* (*Ps.*) sp. *H* and *Diamesa* (*Ps.*) *parva,* according to our knowledge, seem to constitute a boreoalpine species and a Rocky Mountain species, which may be regarded as a species pair.

Diamesa (*Pseudokiefferiella*) sp. *J* (Saether 1970)

One larva, measuring 4 mm in length, was found at Station 8; one larval skin was recorded at Station 4.

This species, together with the second species of *Pseudokiefferiella* mentioned by Zavřel (1941), seems to form a species pair.

Tribe Boreoheptagyini

Boreoheptagyia sp. (Saether 1970)

The lengths ranged from 2.5 to 6 mm. This larvae does not belong to Boreoheptagyia lurida* Phil., the only previously described North American larva of the genus, but the eversible papillae on the abdominal segments are in *B. lurida* and thus different from the described European and Japanese species. These short, soft, protrusible papillae that Saunders (1928) believes to be respiratory blood gills are not considered respiratory by Thienemann (1954). The larvae of *B. lurida,* like their European relative, live in high mountain brooks on the stones splashed by the water, which is an environment very rich in oxygen (Tshernovskij 1949, Thienemann 1954).

Thus, striking similarities between the larvae of *Boreoheptagyia* and those of *Thaumalea* (see p. 76) may be convergent adaptations to life in the same type of hygropetric habitat, rather than evidence of phylogenetic relationship. The genus is reported from southern Europe, North America, Chile, Patagonia, Japan, and Australia (Pagast 1947, Thienemann 1954, Freeman 1961).

Subfamily Orthocladiinae

Tribe Orthocladiini

Cardiocladius sp. (Saether 1970)

These larvae were among the predominant chironomid larvae of North Boulder Creek.

Cardiocladius has a worldwide distribution and is one of the purported ancestral genera of Orthocladiini (Brundin 1956a, Freeman 1961).

Development seems to be more advanced at Station 7 than at Station 8, and still more so at Station 10 (Figure 21). The discrepancy between Stations 10 and 10a is peculiar. The stations are situated very close together, and the temperature at Station 10a is only a half degree higher than at Station 10, owing to a smaller volume of water. There is perhaps a better supply of food at Station 10a as the simuliids, which compose the diet of *Cardiocladius,* are smaller.

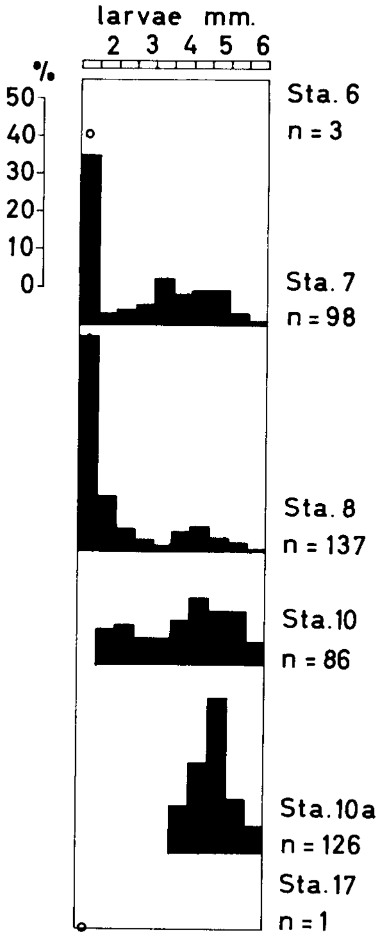


FIGURE 21. Length distribution in *Cardiocladius* sp. (for explanation see Figure 11).

But the differences in the environment seems too small to account for the much more rapid development at Station 10a, and it seems likely that the smaller individuals at Station 10 may have been carried along with the somewhat swifter current there. A similar influence of current, however, is not indicated by size distribution in the other organisms. More rapid development at Station 10a than in its neighboring station, however, is also observed in the other chironomids.

The distribution of size groups could be explained by the occurrence of a one-year cycle in the upper part and two generations a year farther down. The smallest larvae at Stations 7 and 8 may be the brood of the year, and the larger ones may be those from last year that are now developing to adults. The relatively large larvae at Station 10 may be the brood of the year that later in the season will give rise to a new generation, indicated at Station 17, which may survive the winter. The distribution may also be explained, however, as a two-year cycle at Stations 7, 8, and in part, at 10, and a one-year cycle in the lower parts.

Eukiefferiella Thien.
Type: *discoloripes*
Subtype: *discoloripes* s. str.
Eukiefferiella sp. *A*

There seem to be no discrepancies between these larvae and those of *E. discoloripes* Goetgh. (Zavřel 1939). However, as the larvae were small (1.5-2 mm in length), they may belong to another species.

E. discoloripes Goetgh. belongs to the fauna of the moss, and has been found both in transition brooks ("Übergangsbäche" of Thienemann), in moderately elevated brooks ("Mittelgebirgsbache") and in lowland creeks, and are also recorded from hot springs with a water temperature of 23°C (Thienemann 1954). The species has previously been found only in central Europe (Thienemann 1936, 1954). The subtype is new to North America.

Subtype *bavarica*
Eukiefferiella sp. *B, C,* and *D.* (Saether 1970)

Eukiefferiella sp. *B* was the only *Eukiefferiella* species found on the upper shelf of Brook 6.

E. bavarica Goetgh., a closely related species, is reported from the Alps and from Swedish Lapland. It lives in the same localities as *E. discoloripes* and in the Lunz area has two generations a year (Thienemann 1954).

The length distribution (Figure 22) may indicate two generations a year, but the numbers are too small to give significant results.

Type: *longicalcar*
Subtype: *longicalcar* s. str.
Eukiefferiella sp. *E* and *F* (Saether 1970)

The lengths of sp. *E* ranged from 5 mm (at Station 17) to less than 1 mm (at Station 15). The single larva of sp. *F* (at Station 17) measured 4 mm in length.

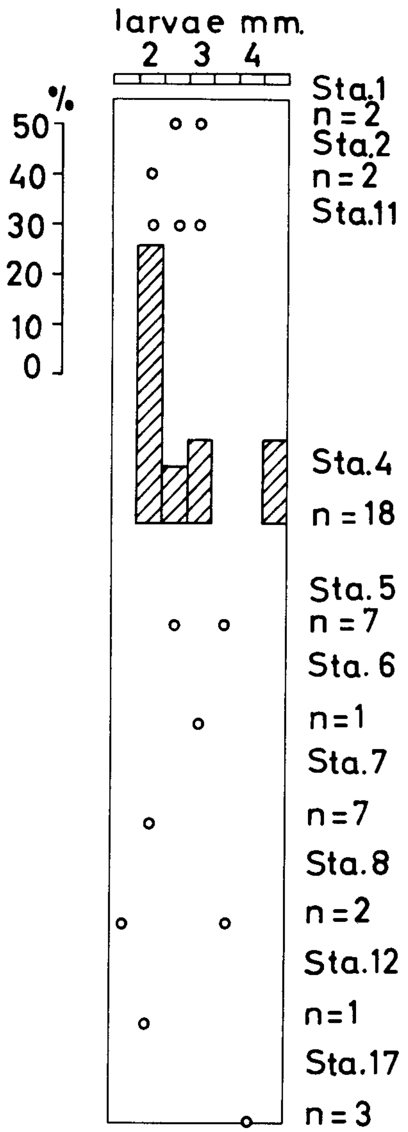


FIGURE 22. Length distribution in *Eukiefferiella* sp. *B*. (for explanation see Figure 11).

The *E. longicalcar*-group is known from the same localities as *E. bavarica* and *E. discoloripes* (Thienemann 1954). *E. longicalcar* Kieff. has been found in Sweden, England, Germany, and Austria (Brundin 1956a). The subtype is new to North America.

Subtype: *Minor*
Eukiefferiella sp. *G* and *H* (Saether 1970)

The larvae of species *G* was the predominant chironomid in North Boulder Creek as a whole.

E. minor Edw. is present in Norway, Sweden, Latvia, England, the Alps, and the Tatra Mountains (Brundin 1956a). The subtype is new to North America.

Eukiefferiella sp. *G* is characterized by having longer posterior prolegs and shorter tubuli anales than the abovementioned other known species of *Eukiefferiella,* except *E. cyanea.* This may, according to Thienemann (1954), be an adaptation to a more rheobiontic life. *Eukiefferiella* sp. *G,* however, does not have reduced procerci, and the bristles of the procerci are not reduced even where they are shorter than the long prolegs.

The species show a clear sequence in size distribution (Figure 23) from two fractions in the upper part of the brook to one intermediate fraction farther down. Two generations a year have been observed in *E. bavarica* Goetgh., *E. coerulescens* (Kieff.) (Thienemann 1954), and *E. hospita* Edw. (Brundin 1949). It seems reasonable to suppose that there are two generations a year in all *Eukiefferiella* wherever environmental temperatures are not too low. Several interpretations of the size distribution are possible, but the ones below seem to fit the data best and allow for two generations a year in the lower parts.

In July, only one generation may be present in the lower reaches, corresponding to the single fraction found at Stations 10 and 10a. This may be the second generation of the year that will pass the winter as larvae and hatch next spring. At the intermediate Stations 7 and 8, the smallest larvae, 2 mm long, correspond to those at Station 10, and the larger ones are of the first generation

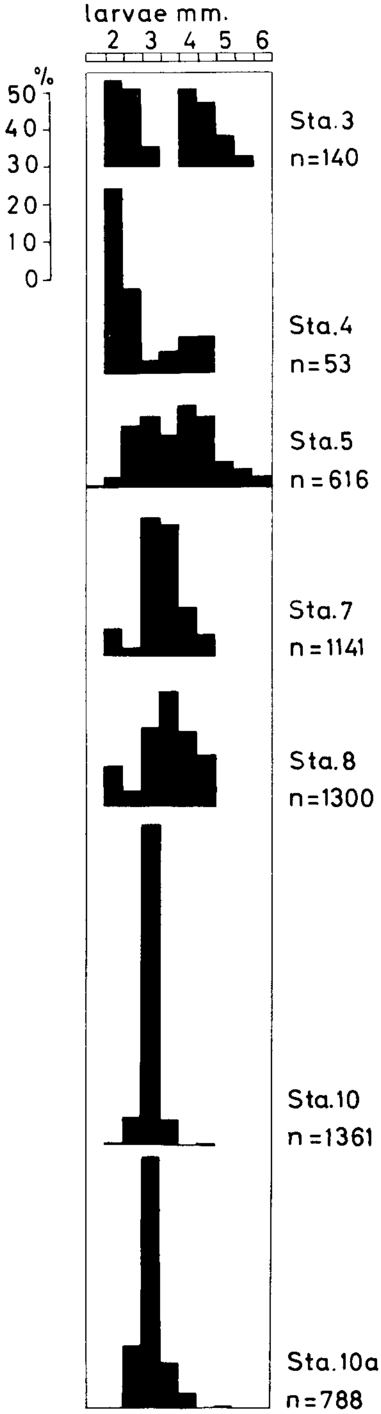


FIGURE 23. Length distribution in *Eukiefferiella* sp. *G*. (for explanation see Figure 11).

hatching in spring. In the uppermost part of the brook the largest specimens represent individuals hatched in the year before, which have just reached maturity and have given rise to a new generation represented by the smaller specimens. At Stations 3 and 4 there is thus only one generation a year. At Station 5 there seem to be some individuals that may reach two generations a year, while others only have one generation.

The distribution pattern in Figure 23, however, can also be explained by the occurrence of a one-year cycle in the lower part and a two-year cycle in the upper part. Still other interpretations are possible, and the question can only be solved by collecting at various times of the year.

Eukiefferiella sp. *H* was represented by a single larva at Station 8, measuring 1.5 mm (Saether 1970).

Type: *Rectangularis* (syn. *Akiefferiella* Type *Abisko* Thienemann 1941, 1944)

Eukiefferiella sp. *J* (Saether 1970)

The group is previously known from England, Ireland, central Europe, Sweden, and Norway (Thienemann 1941, Brundin 1956a).

A slower development is indicated in upper parts (Figure 24). There seem to be two generations a year, at least in the lower stretches of the brook. (See *Eukiefferiella* sp. *G*.)

Orthocladius (V.D. Wulp) Brundin

Subgenus *Eudactylocladius* Thien.

Orthocladius (*Eudactylocladius*) sp. *A* (Saether 1970)

Two larvae measuring 5.5 mm in length were found at Station 17, three reaching 4.5 to 5 mm at Station 10a, and one larva less than 1 mm in length at Station 10. These measurements suggest that this species may have been hatching at the time of collection.

Most species of *Eudactylocladius* belong to the rock fauna in glacier brooks, transition brooks, and brooks at medium

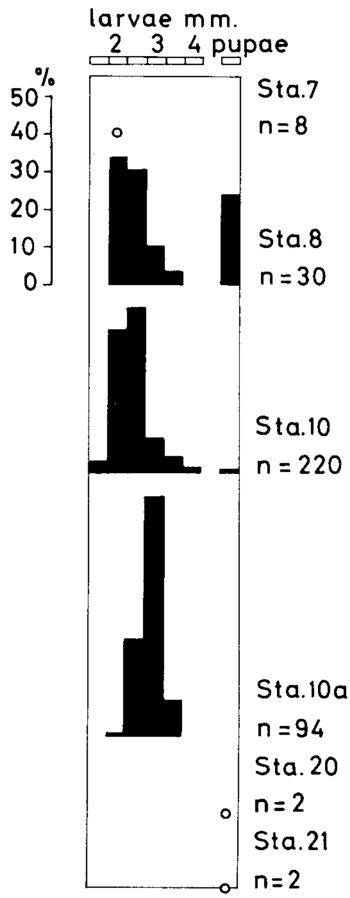


FIGURE 24. Length distribution in *Eukiefferiella* sp. *J*. (for explanation see Figure 11).

elevation, but some may belong to the moss and hygropetric fauna and, in northern areas, may live in stagnant waters (Thienemann 1935, 1954; Brundin 1956a). The subgenus is Holarctic and Ethiopian (Thienemann 1935, Goetghebuer 1940-50, Brundin 1956a, Freeman 1956).

Orthocladius (*Eudactylocladius*) sp. *B* (Saether 1970)

The larvae from Station 6 were all caught just before pupation, as indicated by the thoracic segments. A one-year cycle seems clear, the old generation being present only at Station 6 and the new generation only lower down (Figure 25).

Station 6 is different from the other stations in being artificially deepened (about 1 meter). Along the edges there are stones only, most of which are bare and sharp. The current here is also very slight. *Eudactylocladius* is among the less rheophilous larvae in brooks, which may explain the distribution; or perhaps the species prefers the bare stones. The subgenus has a Holarctic and Ethiopian distribution (Johannsen 1937a; Thienemann 1944, 1954; Freeman 1956).

Subgenus *Euorthocladius* (Thien.) Brundin

Orthocladius (*Euorthocladius*) sp. (Saether 1970)

The larvae measured 4.5 to 6 mm in length at Stations 7, 10, and 10a; 3.5 mm at Station 5; 1.5 to 3 mm at Station 2; and 4 mm (only one larva) at Station 1. A larva of the same type was also found in Rainbow Lake Brook. The length distribution clearly indicates a

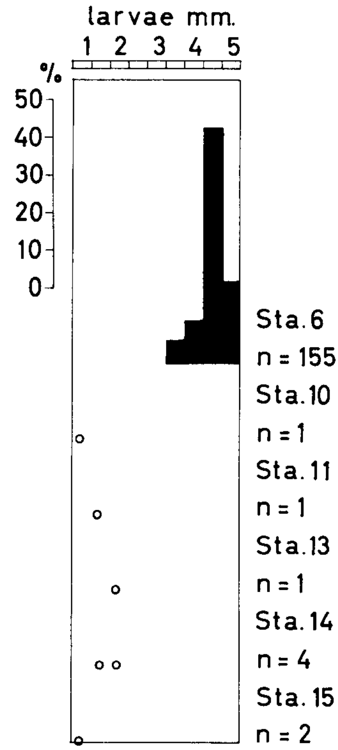


FIGURE 25. Length distribution in *Orthocladius* (*Eudactylocladius*) sp. *B*. (for explanation see Figure 11).

slower development in the upper parts and possibly two generations a year in the lower reaches, as in *E. rivicola* K. (Thienemann 1954).

Euorthocladius larvae are known from bare stones in high mountain brooks, transition brooks, and lower brooks where the current is strong (Thienemann 1954). The subgenus has a Holarctic and Ethiopian distribution (Thienemann 1944, 1954; Freeman 1956).

Subgenus *Orthocladius* (V.D. Wulp) Brundin (syn. *Rheorthocladius* Thien: *rhyacobius*-group, *lignicola*-group)

A damaged male imago was found in Station 5.

The subgenus is known as well from high mountain and lower brooks as from springs and stagnant waters (Thienemann 1954, Brundin 1956a). It has a Holarctic distribution (Thienemann 1944, Brundin 1956a).

Rheocricotopus Thien. et Harn.
Rheocricotopus sp. *effusus* (Walk.) (syn. *fuscipes* Kieff.) type (Saether 1970)

One larva, measuring 4 mm in length, was found at Station 15; two larvae reaching 5 mm in length were found at Station 13.

The *effusus* group lives among plants or mosses on stones in high mountain brooks, lower creeks, or springs. Some of the species are typical members of the Palaearctic hygropetric fauna (Thienemann 1954). The genus as a whole is reported from Europe, North America, Japan, Java, and Africa (Thienemann 1954, Freeman 1956, (Saether 1970).

Rheocricotopus sp. *atripes* Kieff. type (Saether 1970)

Two larvae, measuring about 2 mm in length, were found at Station 15.

This group is similar to the preceding group in its way of life and distribution. It is also known to occur in Indonesia where the above-mentioned group is not recorded (Thienemann 1954).

Microcricotopus Thien. et Harn.
Microcricotopus sp. *parvulus* Kieff. type (Saether 1970)

Two larvulae and one pupa with attached larval exuvia were found at Station 15; one larva, reaching 4 mm in length, was caught at Station 13.

The genus has been found in Europe, Japan, Indonesia, and Africa. *M. parvulus* is known from the fauna of stones in moderately elevated creeks, while *M. bicolor* has been found in the moss of high mountain creeks (Thienemann 1954, Freeman 1956).

Tribe Metriocnemini
Metriocnemus group
Thienemannia cf. *gracilis* Kieff. (*clavaticornis* Kieff.) (Saether 1970)

Only one larval skin was found between two small snow banks in Station 4.

T. gracilis is previously known from Germany, Belgium, England, Sweden, Iceland, and the Faroes. It is hygropetric or belongs to the moss fauna of mountain creeks (Thienemann 1954, Brundin 1956).

Metriocnemus sp. *A* (Saether 1970)

One larva measuring 7.5 mm in length was found at Station 3.

Metriocnemus is a genus rather rich in species, of which several are arctic. These may belong to the forms from the northern glaciated margins ("nördliche Gletscherrandformen") (Thienemann 1950). Many of the species, however, have a terrestrial or semi-terrestrial life. The larvae are found high up in the littoral of lakes, in the moss of mountain brooks, and hygropetric in brooks, hot springs, cold springs, phytotelmata, pools, bogs, caves, brackish waters, water purification works, etc. (Thienemann 1954).

Metriocnemus seems to be a plesiomorph genus (Hennig 1948) among the Metriocnemini (Brundin 1956a). Recent species are known from the Cretaceous (Thienemann 1954). The genus is cosmopolitan (Thienemann 1944, Freeman 1956, 1961). In the Tyrol *M. fuscipes* MG., *M. picipes* MG., and *M.* sp. *hygropetricus* group have been found close to the margin of glaciers (2550-2490 meters) (Thienemann 1954), i.e., in biotopes similar to those of the present Colorado specimens.

Metriocnemus sp. *B* (Saether 1970)

Two larvae reaching 7.5 and 8 mm in length were found at Station 2.

Paraphaenocladius sp. (Saether 1970)

One larva each was found at Stations 15 and 8. Both measured 2 mm in length.

The larvae of *Paraphaenocladius* are mostly terrestrial, but they are also found in caves, bogs, moss of mountain creeks, and especially in cold springs. *P. impensus* Walk. belongs to the glacial fauna of springs (Thienemann 1950, 1954). Members of the genus are previously known from Europe, Ellesmere Island, Canada, and Africa (Strenzke 1951, Freeman 1956, Saether 1968, 1969, Oliver 1963).

Parakiefferiella group
cf. *Epoicocladius* sp.

The only visible feature in the three very small larvulae (< 1 mm in length) found at Station 13 and on the three head capsules found at Station 2 was the labium, which was of the type described by Johannsen (1937a, figure 269). The larva has been found clinging to the gills and legs of *Hexagenia recurvata* (Johannsen 1937a). No ephemerids, however, were found in Brook 6. In Brook A-2 there were several specimens of *Ephemerella coloradensis,* one juvenile *Cinygmula mimus,* and one very small indeterminable ephemerid nymph. The genus is Holarctic (Thienemann 1954).

Parakiefferiella sp. (Saether 1970)

Three larvae measuring 2 mm in length were found in Brook A-1 (Stations 16 and 21). Seven larvae ranging from 1 to 2 mm in length were found at Station 13.

The genus has been found mostly in lakes and pools, but is also recorded from the moss of mountain brooks. It is Holarctic (Thienemann 1944, Oliver 1963, Saether 1969).

Corynoneura group
Corynoneura sp. (Saether 1970)

One larva measuring 2.5 mm in length was found at Station 12. Three larvae of same length were recorded from Station 10.

Corynoneura is characteristic of submerged moss and, uncommonly, mud in mountain brooks. It may also live among plants in lakes, in pools, springs, bogs, rock pools, and brackish waters.

Corynoneura has a worldwide distribution, and some North American species are identical with European ones (Thienemann 1954).

FAMILY SIMULIIDAE (BLACKFLIES)
Prosimulium Roubaud.

All specimens of larvae and imagines observed belong to this genus. Remnants of one type of exuviae were always lacking the posterior parts, and these may belong to another genus (Saether 1966b).

While *P. esselbaughi* Sommerm. and *P. travisi* Stone are especially difficult to distinguish, the smaller specimens were usually determined only to genus, except for a few larvae and head capsules of *P. ursinum* (Edw.). The imagines as well as the *Prosimulium* exuviae were all of *P. esselbaughi.*

The distribution in numbers and lengths of *P. esselbaughi* and *P. travisi* are shown in Figure 26 and the Frontispiece. It seems probable that the numbers of *P. travisi* are too small to have any influence on the distribution, except perhaps in Stations 1-5.

P. ursinum is known from North America, East Greenland, Bear Island, and Jotunheimen and Svartisen in Norway (Edwards 1935a, 1935b; Stone 1952; Carlsson 1962). According to Carlsson (1962), the species has one generation a year with a flight period in Jotunheimen during late August and September. It is doubtful if the females take any food (Carlsson 1962).

P. esselbaughi is known from western Canada, Alaska, Oregon, and Washington. The species is univoltine (Peterson 1970).

P. travisi Stone has been collected in Alaska and at Loveland Pass, Colorado. Pupae were found from the middle of July to the end of September (Stone 1952).

According to Sommerman (1953) and Peterson (1970), the mature larvae of *travisi* reach 7.75 mm in length, those of *ursinum* 8.5 to 9.5 mm, and the larvae of *esselbaughi* 5.8 to 8.1 mm. A few of the present Colorado specimens of *esselbaughi,* however, measured 9.5

mm in length. Perhaps a longer growth period coupled with a later hatching period gave rise to larger larvae.

The length distribution (Figure 26) indicates an extensive hatching period. Stations 1, 3, 4, and 5 give a different picture from that of the lower stretches. This may be due to slower development in the colder, upper parts, or to the presence of a two-year cycle. Distribution may be caused chiefly by larvae of *P. travisi*. *P. esselbaughi* and other blackflies have not been observed to have a two-year cycle, and *P travisi* seems to be very scarce. The first interpretation is therefore the most likely one. At Station 10a development had been slower than at Station 10, in contrast to the case in other species found. Larvae of blackflies are filter-feeders. In the main brook the current is stronger and thus more food is carried along and may consequently give larger simuliids. Station 11 differs distinctly from those nearby. The only abundant species was *P. esselbaughi.* No specimens of *Eukiefferiella* or even the simuliid-eating *Cardiocladius* were present. As will appear from the map (Figures 1 and 7), Station 11 lies more in shadow and is covered by snow for a longer period than the neighboring stations, which may be the cause of the slower development.

FAMILY EMPIDIDAE (DANCEFLIES)
Atalanta sp. (Saether 1970)

Two larvulae (1.5 mm in length) were found at Station 10; 1 larvula was found at Station 5; and 11 larvae were found in an open space between two snow banks (Station 4). At Station 4, specimens measuring 8.0, 7.5, 6.5, 5.5, 4.5, 3.5, and 2.0 mm were taken. This would seem to indicate an extended hatching period. The species was also found in Rainbow Lake Brook.

Vaillant (1952) distinguishes three ecological groups of Atalantinae-larvae: the rheophilous larvae, the less rheophilous larvae, and the "almost limnophilous" larvae. As shown by Saether (1970), the present larvae belong to the second group, although related to the rheophilous forms.

The genus *sensu latu* has a worldwide distribution. It has, for instance, been reported from South America and New Zealand. Most species are in mountainous regions, and the genus seems especially well represented in northern Europe and in the Alps (Engel 1918).

FAMILY EPHYDRIDAE (SHORE FLIES)
Cressoniella montana Saeth. (Saether 1970)

One imago was collected at Station 8, two imagines at Station 9, and one imago at Station 10.

Most species of shore flies burrow in water plants. Some have peculiar habitats, living in petroleum, salt water, urine, plant juices, etc. (Becker 1926).

ACARINA

HYDRACHNELLAE
Sperchon glandulosus coloradensis Saeth. (Saether 1966a)

One male was found at Station 19.

The larvae of the *Sperchon* usually live in the larval cases of Orthocladiini. Most likely the larvae crawl from the larva to the pupa and, when the insect hatches, from the pupa to the imago (Viets 1936). The species seems to be adapted to a rheophilous life and to need cool water. The *thienemanni* form, which is nearer to *S. g. coloradensis* than *S. glandulosus* s. str., is usually connected with brooks, while the typical *S. glandulosus* is most abundant in springs (Viets 1936). Exceptionally, *S. glandulosus* is also found in the littoral and sublittoral of lakes (Lundblad 1927). The species may be said to be eurythermal (Lundblad 1927). *S. glandulosus* has a Holarctic distribution and is probably the most common water mite in the lotic biotopes of central and southern Europe. It has been found up to an elevation of 2300 meters in the Alps (Lundblad 1927, 1956; Viets 1936). In West Lost Trail Creek, Colorado, Bergstrom (1953) found the species up to 10,325 feet (3150 meters)[1]

[1]After this paper was submitted for publication W. C. Young, 1969: Ecological distribution of Hydracarina in North Central Colorado. *Amer. Midl. Naturalist,* 82: 367-401 appeared.

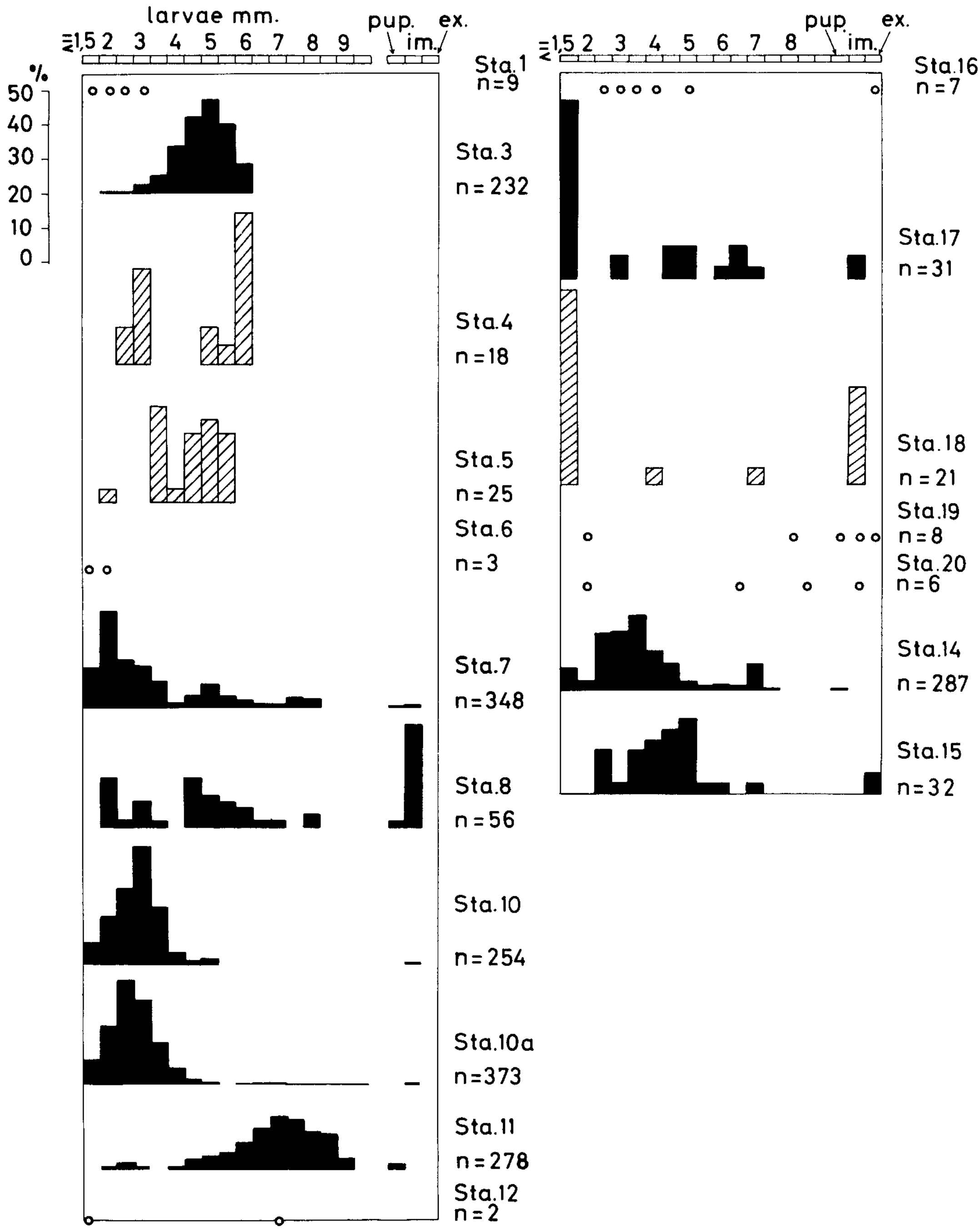


FIGURE 26. Length distribution in *Prosimulum esselbaughi, P. travisi* and juvenile larvae belonging to either *esselbaughi* or *travisi*. At Station 1-5 probably mostly *P. travisi* present, below Station 6 probably exclusively *P. esselbaughi*. The relation between larvae of *Prosimulium* and pupae, exuviae, and imagines of *P. esselbaughi* is also given. (for further explanation see Figure 11).

Lebertia (Pseudolebertia) atelodon Saeth. (Saether 1966a)

Two males were found at Station 4.

The species, together with *L. groenlandica* Lettev. (Lettevall 1962) and *L. convergens* Thor from Kamchatka (Thor 1911), form triplet species. According to Thienemann (1950), the genera *Sperchon, Lebertia,* and *Aturus* (all found in the investigated creek), with numerous closely related species, mainly seem to have evolved during and after the glacial age. The European *L. glabra* Thor and *L. zschokkei* (Koen.) are also closely related to the above-mentioned triplet species.

The genus *Lebertia* is, next to *Sperchon* and *Atractides,* the most abundant genus in the lotic biotopes of central and southern Europe. Specimens have been found in the Alps up to an elevation of 2543 meters (Lundblad 1956). In Rocky Mountain National Park, Colorado, Bergstrom (1953) found *Lebertia* at a height of 11,000 feet (3350 meters).

Aturus fontinalis Lundbl.

Two males and nine females were found, which constitute the first record of this species from North America. (See Frontispiece.)

The species occurs only in running water, but may accidentally be found in springs. It is eurythermic (Lundblad 1927). *A. fontinalis* has been recorded from Scandinavia and central Germany. It may, therefore, be regarded as a form from the northern margin of the glacial sheet (Lundblad 1927).

GENERAL REMARKS ON ZOOGEOGRAPHY

In mountains a great variety of habitats are to be found, and the sharp zonation creates isolated areas, thereby favoring speciation. The North American Cordilleras of the Tertiary mountain ranges have existed long enough to allow for species evolution, but not for development of higher taxa (Lindroth 1957).

As will appear from Table 7, most types and groups of species and genera found in the area investigated are members of the Holarctic fauna. A few of these forms, mostly cosmopolitan, also occur in South America. *Cardiocladius, Corynoneura,* and *Parakiefferiella* may be said to be characteristic members of the South Andean fauna (Brundin 1956b). *Boreoheptagyia* and *Cardiocladius* are plesiomorph genera. In Europe, *Boreoheptagyia* belongs to the forms from the southern glacial margins, i.e., those not found in northern Europe. Many water mites and, among the Diptera, the blepharocerids, also known from the Rocky Mountains, have a similar distribution. Many of these are rheobiontic, rheotactic, and petrophilous torrential forms, and it was impossible for them to pass the central European plain. The species that remained in the same area during and after the Ice Age changed less than those that dispersed in postglacial times and had to adjust to variable conditions. This may explain why the southern glacial margin genera and species are closer to the ancestral forms.

According to Brundin (1966) the genus *Boreoheptagyia* and a major group comprising the tribes Diamesini and Protanypini, for instance, are all boreal apomorph sister groups of austral plesiomorph groups. In these instances the bipolar distribution pattern is obviously a consequence of transtropic dispersal northwards. There are, however, also several examples of bipolarity among chironomids caused by transtropic dispersal southwards. The Tanypodinae, for

TABLE 7. Zoogeography of the animals found.

SPECIES, SPECIES GROUPS, AND GENERA FOUND BOTH IN NORTH AMERICA AND IN EUROPE		
Cosmopolites:		
Hydra	Aedes	Metriocnemus
Macrobiotus macronyx	Lycoriella	Corynoneura
Chaetogaster	Chironomus anthracinus group	Atalanta
Nais variabilis	Cardiocladius	Sperchon
Podura aquatica		Aturus
In Europe, boreo-alpine:		
Pseudodiamesa	D. (Pseudokiefferiella) parva type	*E. longicalcar subtype
*Diamesa cinerella group	Eukiefferiella bavarica subtype	*E. minor subtype
D. aberrata group		*E. rectangularis type
D. latitarsis group		
In Europe, forms from the northern glacial margins:		
Aedes impiger (arctic)	Prosimulium ursinum	*Aturus fontinalis
*Psectrocladius octomaculatus	*Lebertia convergens-groenlandica-atelodon group	
In Europe, forms from the southern glacial margins:		
Boreoheptagyia	Thaumalea (mostly)	
Others, or not known for certain:		
Polycelis	*Diamesa (Pseudokiefferiella) sp. 2 of Zavřel type	Psectrocladius
Chaetogaster cf. diastrophus	Orthocladius subgen. Eudactylocladius	*Thienemannia cf. gracilis
Mesenchytraeus	O. subgen. Euorthocladius	*Thienemannia
Ephemerella	O. subgen. Orthocladius	Paraphaenocladius
Baetis	Microcricotopus	Smittia
Isogenus	Rheocricotopus effusus type	Epoicocladius
Nemoura	R. atripes type	Parakiefferiella
Rhyacophila	Rheocricotopus	Prosimulium
Brachycentrus		Sperchon glandulosus
Limnephilus		*Lebertia subgen. Pseudolebertia
Aedes excrucians		Lebertia
Micropsectra		Pisidium
GENERA COMMON TO NORTH AMERICA AND ASIA, BUT NOT EUROPE		
Alloperla		
EXCLUSIVELY NEARCTIC SPECIES, SPECIES GROUPS, AND GENERA (UNIDENTIFIED FORMS FROM THE INVESTIGATED AREA EXCLUDED)		
Polycelis coronata	Isogenus subgen. Pictetia	Hesperophylax oreades
Ephemerella coloradensis	Alloperla subgen. Sweltsa	Hesperophylax
Baetis bicaudatus	Nemoura haysi	Copidosoma naevia
B. intermedius	Nemoura subgen. Zapada	Prosimulium travisi
Cinygmula mimus	Pseudostenophylax edwardsi	P. esselbaughi
		Cressoniella montana

* = New to North America.

instance, is a chironomid group of boreal origin fairly well represented in the southern temperate zone. The most plesiomorph groups among chironomid groups are found, according to Brundin, among cold-adapted mainly austral groups as the Podonominae, the Aphroteniinae, and the Diamesinae. If the transtropic dispersal northwards has been over a transtropic highland bridge between North and South America, probably in the late Cretaceous (cf. Brundin 1956b, Darlington 1957), it must be presumed that the most plesiomorph boreal species of the migrated plesiomorph austral groups can be expected to be found in North America, and in parts which changed not too much during the Glacial Age, i.e., as these parts of the Rockies (see below). Unfortunately, phylogenetic analysis of the present material cannot be carried out at present as the imagines of most of the chironomids found are unknown.

In the investigated area, forms were found, which in Europe belong to the southern glacial margins, as well as forms, for instance *Aedes impiger,* which in Europe are recorded only from north of the Arctic Circle. The last mentioned forms may be interglacial elements in Europe, northeastern immigrants, or, in the case of the chironomids, special cold-stenothermic species. They may have been littoral stenobathic (or restricted to brooks) and present farther south in late glacial times, but became extinct as the climate changed, and they could find no refuge in the profundal of lakes (Brundin 1949). In the Rocky Mountains, they may be postglacial immigrants, as the North American cordilleras form a continuous route; or they may be preglacial or interglacial elements, since, in these parts of the Rockies, according to Flint (1957), the snow line never extended more than 4000 feet (1220 meters) below the present snow lines.

The *Lebertia convergens-groenlandica-atelodon* group is composed of a species from Kamchatka, one from Greenland, and a third from the investigated brook (Saether 1966a). These three species seem to be closely related, more so than other water mites belonging to the *Lebertia* (Ps.) *glabra* group, and may be said to form a triplet species. Pairs of species, triplet species, and larger groups of species are especially well known among boreo-alpine groups. The majority of chironomids in the investigated area belong to such groups, but they do not seem to be the same species as found in Europe. They thus seem to have been isolated for a longer time from their relatives in Europe than these relatives have been separated from each other. In Europe, *Pseudodiamesa nivosa* and *branickii, Diamesa aberrata,* and *Diamesa* (*Pseudokiefferiella*) *parva* are, for instance, identical in the Alps and in northern Europe (Thienemann 1950). The relatives in the Rocky Mountains of these species are closely related, but most likely different species. A few of the *Eukiefferiella* spp. may, though this is unlikely, be identical to European species. *Diamesa* sp. *A* and *Diamesa* sp. *B* seem to have developed a better adaptation to a rheobiontic life than their European relatives (Saether 1970). As shown in Table 7, many of the European boreo-alpine species groups have not previously been recorded from North America.

The Colorado part of the Rocky Mountains is somewhat isolated from the rest and has had its own local glaciation (Flint 1957). Many of the species found, therefore, may not be identical with species from other parts of the North American Cordilleras. Racial differentiation in a Rocky Mountain form is known, for instance, in the moose with the local subspecies *Alces alces shirasi* (Lindroth 1957).

The Rocky Mountains form a continuous bridge from north to south in the Nearctic temperate and arctic region. There is thus no formation of species from northern and southern glacial margins or parallel to the boreo-alpine species in Europe. Forms, which in Europe would belong to these different groups, are sympatric in the Rocky Mountains.

SUMMARY

The midsummer distribution of invertebrates in North Boulder Creek in Colorado was studied from the brook's source in a snowbank at about 3800 meters above sea level down to near the timberline at about 3300 meters. The brook is a typical high mountain brook with a small water volume and a rapid current. The temperature of the water in July, the warmest month, varied from slightly below 1 °C near the snowbank to about 10° in the lowest part.

The brook can be divided into four zones based on the distribution of the fauna. The clearest break is at Green Lake 3 at a temperature of about 5°. This is a limit for many species, either downwards or upwards. Another clear zonal boundary is constituted by Green Lake 5 where the temperature drops to 1°.

Of the various groups of invertebrates represented, the chironomids are the most abundant both in number of individuals and species. The second most abundant group is the simuliids. The other groups present are relatively far less numerous. The largest number of individuals was generally found in the middle part of the brook, while the number of species showed an increasing trend downwards. There was a relative increase in the number of chironomids within each zone going up the brook, and in the simuliids and Ephemeroptera going down.

The community of a tributary brook was most closely related to that of the corresponding part of the main brook at the same elevation.

The community of chironomids corresponds closely to those in the system of Thienemann (1954). Many species and genera have closely related or identical forms in other high mountain areas of the world.

The length distribution is given for some of the more abundant forms. Slower development in the colder, upper parts and at stations close to snow banks is clearly indicated in most of the species. In *Eukiefferiella* sp. *G* of the *minor* group and probably also in *Cardiocladius* sp., there seem to be two generations a year in the lower stretches of the brook, one generation a year in the upper. In *Prosimulium esselbaughi* there may be a two-year cycle at the upper stations, a one-year cycle in the lower reaches. A two-year cycle is indicated in *Ephemerella coloradensis* and *Cinygmula mimus*.

All species from the creek belong to the moss fauna, e.g., *Eukiefferiella* spp., or to the stone fauna, e.g., most of the *Diamesa* spp. and the *Prosimulium* spp. A few species, however, such as *Pseudostenophylax edwardsi, Thaumalea* sp., *Boreoheptagyia* sp., and *Micropsectra* sp., seem to belong to the hygropetric fauna of the stones.

The majority of types and groups of species and genera found in the area investigated are members of the Holarctic fauna. Most, however, are probably not identical to European species. Pairs of species and larger species groups are well known among boreo-alpine forms. The majority of chironomids in the investigated area belong to such groups but seem to have been isolated for a longer time from their relatives in Europe than these relatives have been separated from each other.

The Rocky Mountains create a continuous bridge from north to south. Forms, which in Europe would belong to the species from northern glacial margins, from southern glacial margins, or to the boreo-alpine groups, are therefore sympatric in the Rocky Mountains.

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