

ALTITUDINAL DISTRIBUTION OF ENTOMOSTRACA IN COLORADO.

By GIDEON S. DODDS,

Of the Department of Zoology, University of Missouri, Columbia, Missouri.

INTRODUCTION.

During the summers of 1908, 1912, and 1913 I made collections of plankton Crustacea from 124 lakes and ponds in Colorado, at elevations from 4,100 to 12,188 feet. I have also received material from Prof. Max M. Ellis and Mr. L. C. Bragg. These collections have yielded 55 species of Entomostraca, which form the basis of this report. I have also made use of all other available records of species previously reported from the State, giving a total of 71 species (Phyllopora, 16; Cladocera, 34; Copepoda, 21).¹

The following list includes the localities where fairly complete collections have been made in the State.

On the plains:	Feet.
La Junta (Dodds), 11 lakes at about	4, 100
Boulder (Dodds), 7 lakes at about	5, 300
Greeley (Beardsley), several lakes at about	4, 600
In the mountains:	
Tolland region (Dodds), 106 lakes	8, 100-12, 188
Twin Lakes region (Juday), several at about	9, 200
Pikes Peak region (Ward), 5 lakes at about	11, 000

Besides these, there are a number of localities from which one or two species have been reported—scattered records in mountains and plains by various men, including some records by early naturalists, chiefly with the Hayden survey.

The interest of this study lies in the fact that here, within a relatively small area, we find a wide range of environmental conditions, physiographic and climatic, with a corresponding diversity of animal and plant life. The eastern two-fifths of the State of Colorado is included within the area of the Great Plains, with a climate, except for its arid nature, essentially like that of the Mississippi Valley generally, while the remainder includes the highest area of the Rocky Mountain region, parts of which have a climate almost arctic.

¹ For list of these lakes, their elevations, and the species collected in each, see Table 8, printed as a folio at the end of the text.

It will be seen from the above that while collections have been made from widely scattered representative localities in the eastern half of the State, the greater part of my own collections are from an area with the city of Boulder as its center, including 7 lakes on the plains east of this city and 106 in the mountain region to the west. This mountain area I will refer to as the Tolland region after the town of Tolland, where, during most of my study, I made my headquarters, at the summer mountain laboratory of the University of Colo-

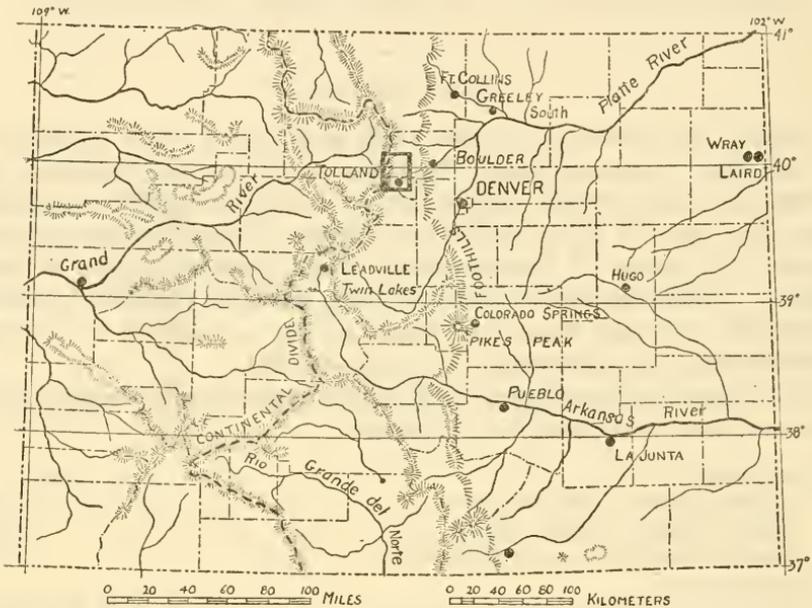


FIG. 1.—MAP OF COLORADO SHOWING LOCALITIES WHERE ENTOMOSTRACA HAVE BEEN COLLECTED. THE BLACK RECTANGLE INCLOSES THE TOLLAND REGION, THE AREA SHOWN IN DETAIL IN FIG. 2.

rado. The lakes of the Tolland and Boulder regions afford especially favorable conditions for the study of altitudinal distribution, because here, within a distance of less than 30 miles, is passed through the whole range of climatic conditions, from temperate to subarctic. To the east of Boulder extend the plains with elevations up to 5,400 feet, while to the west, clearly visible, 20 miles away, Arapahoe Peak with its glacier, rising to 13,506 feet, marks the Continental Divide.

The climatological data presented in the following paragraphs, while in general true for any part of the State, apply particularly to this area.

CLIMATE.

The data regarding climate presented in this paper are, for the most part, from the annual summaries of the Weather Bureau for the Colorado section, though use is also made of data collected by Francis

Ramaley and other members of the biological staff of the University of Colorado, all interpreted in the light of eight years' residence at

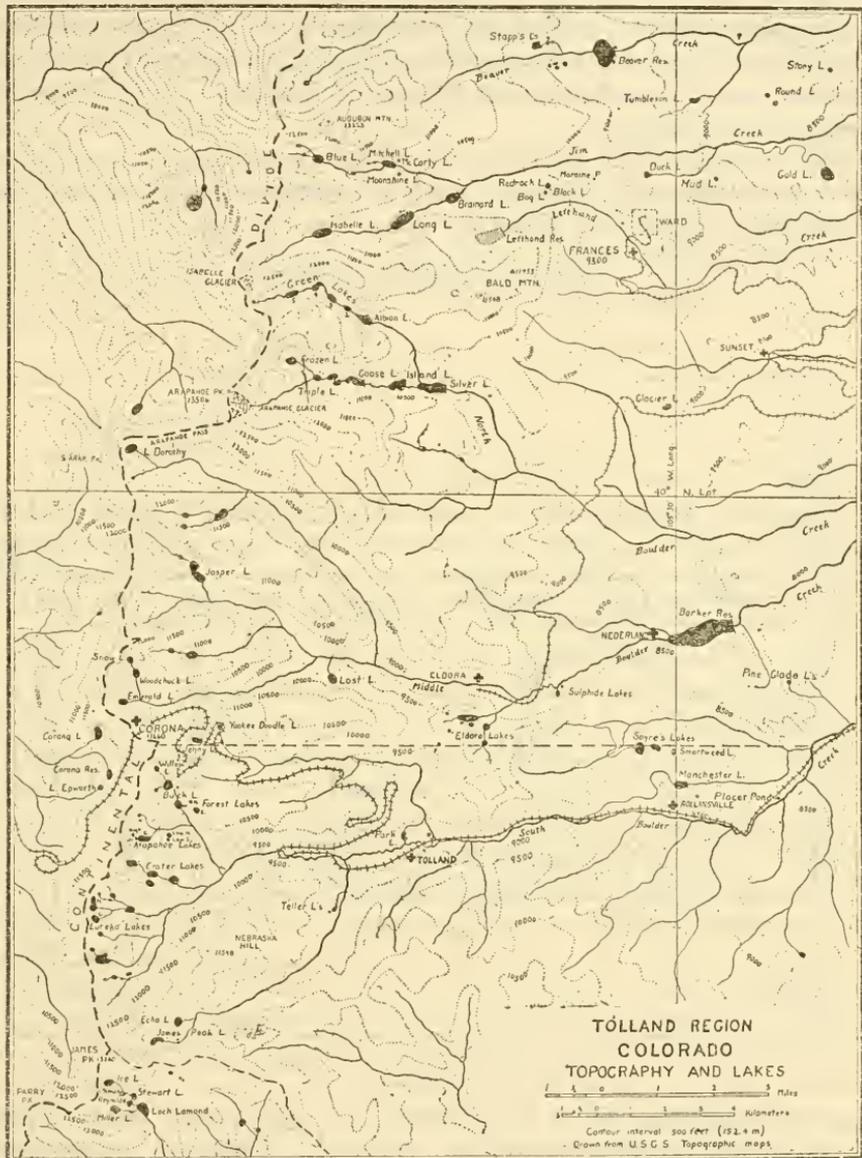


FIG. 2.—MAP OF TOLLAND REGION, THE AREA INCLUDED IN THE BLACK RECTANGLE IN FIG. 1.

Boulder and of several summers spent in whole or in part in the mountains of this region.

Three stations have been chosen as representative of typical conditions in different parts of the area under study:

Denver (5,272 feet), in plains region, records for 41 years.

Frances (9,300 feet), mountains, records for 8 years.

Corona (11,660 feet), high mountains, records for 6 years.

Reference to the maps (figs. 1 and 2) will show that the two mountain stations lie within the Tolland region and that Denver on the plains is also so located as to be of direct use when compared with the other two stations. In discussing climate, special attention has been given to *precipitation* and *temperature*, because these two factors of climate seem to be those most directly of interest in relation to the fauna under study.

Precipitation.—The usual increase of precipitation with elevation is well marked in this region and seems to continue to the highest elevations, as is shown in Table 1.

TABLE 1.—Annual precipitation.

Stations.	Total precipitation.	Snowfall.
	<i>Inches.</i>	
Denver.....	14.02	62.3 inches (5+ feet).
Frances.....	24.16	180 inches (15 feet).
Corona.....	43.69	390.6 inches (32+ feet).

The plains are decidedly an arid region. Denver is fairly typical of the entire eastern plains of the State, but there are places where

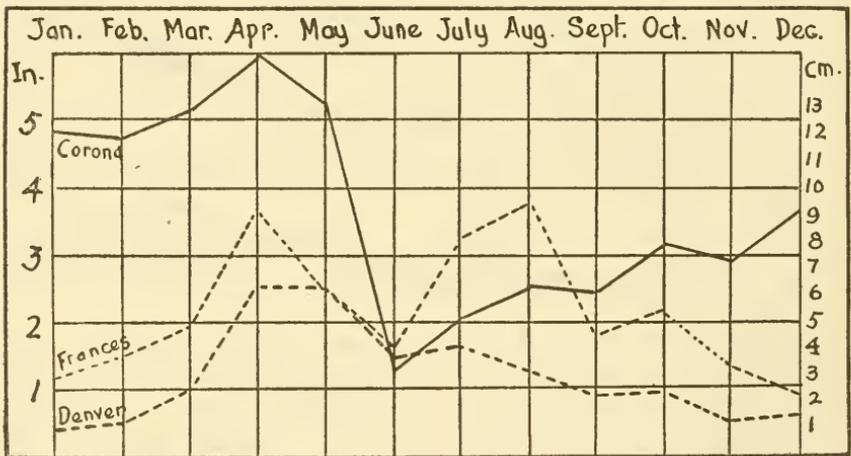


FIG. 3.—MEAN PRECIPITATION BY MONTHS.

the rainfall is only 11 or 12 inches. The arid climate of the plains seems, as will be pointed out later, to play the chief part in determining the nature of their entomotruncan fauna. The greater precipitation of the mountain region is probably of little importance directly, but has its chief significance in the fact that a large proportion of it comes in the form of snow. Reference to figure 3 shows that at Corona the greater part of the precipitation comes in those months when it is entirely in the form of snow (all months but June, July, and August). At the higher lakes, great banks of snow accumulate

on the slopes above, or extend out over the lakes on the ice, and have a great deal to do with keeping the temperature of the lakes low throughout the summer.

Temperature.—Temperature is probably the climatic factor which in this region plays the largest part in determining the distribution of animal life, and it is the factor which within our area is subject to the greatest variation. On the plains we have the conditions which are prevalent throughout temperate latitudes, while in the higher parts of the mountains there is a close approach to arctic conditions. For purposes of comparison between different parts of the area under study, I have made use again of the three stations—Denver, Frances, and Corona—the elevations and temperatures of which are shown in Table 2.

TABLE 2.—Mean annual temperature.

Stations.	Elevation.		Mean annual temperature.	
	Above sea.	Above Denver.	As observed.	Below Denver.
	<i>Fect.</i>	<i>Fect.</i>	<i>° F.</i>	<i>° F.</i>
Denver.....	5,275		49.8	
Frances.....	9,300	4,028	41.0	8.8
Corona.....	11,660	6,385	26.0	23.8

The conditions recorded at Denver are representative of the plains in general, and those at Corona of the highest lakes studied in this region, so that the difference between these two stations expresses the divergence between the two extremes of lakes. It is seen that the mean annual difference between these two stations is 23.8° F., which, allowing 1.35° F. as equivalent to 1° of latitude, corresponds to 17.2° latitude. Thus, though Corona is distant from Denver but 40 miles, it has an annual mean which might be expected 1,200 miles to the north. It is this steep temperature gradient that gives interest to studies in this region.

As a matter of fact, the isotherm corresponding to the temperature of Corona does actually pass through these far northern regions as may be seen by reference to map (fig. 4), while that of Frances, though less extreme, also passes well to the north, at one place touching the Arctic Circle. In this map it is to be noted that the isotherms are drawn as reduced to sea level, so that the effect of elevation is already felt at Denver, where the actual temperature is probably 15° F. below the corresponding sea-level temperature shown on the map. An isotherm map, not reduced to sea level, would show all lines bending far southward over the Rocky Mountain system, as a result of which the isotherm of 26° F. would actually pass through Corona, while at Denver, only 40 miles to the east, would be that of 50° F.

The mean distribution of temperature throughout the year at these three stations is shown in figure 5.

Though the annual mean gives a ready basis for comparison, and furnishes an index of general climatic conditions, it is probably not of itself as effective in determining distribution of aquatic animals as

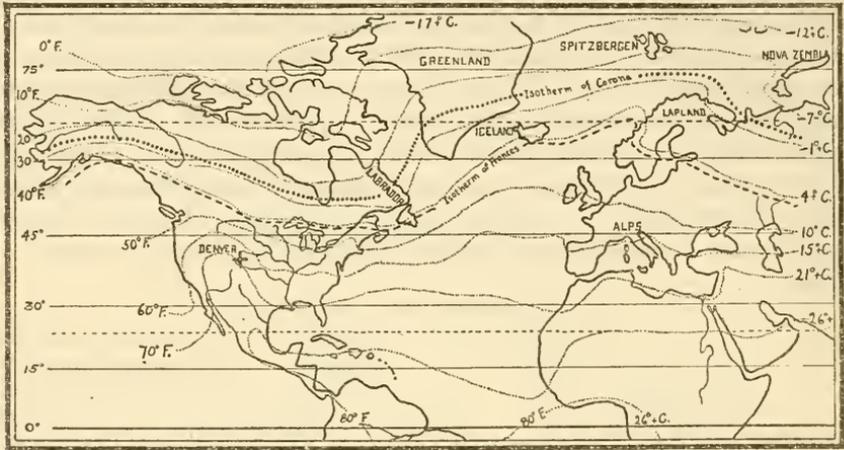


FIG. 4.—ISOTHERM MAP OF THE WORLD, WITH THE ISOTHERMS OF CORONA AND FRANCES DRAWN IN.

other peculiarities of temperature, such as maximum and minimum temperature at certain seasons. Figure 6, a graphic representation of mean monthly minima for the three stations, shows that at

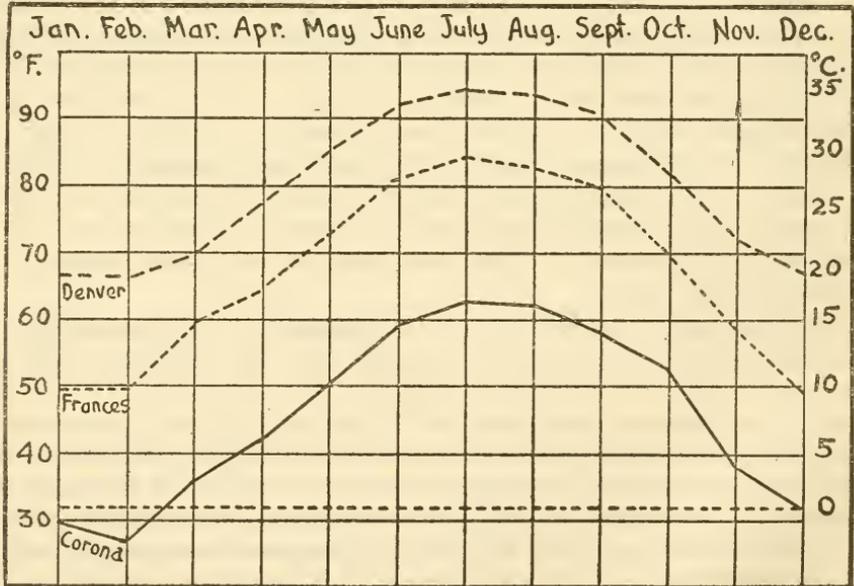


FIG. 5.—MEAN TEMPERATURE BY MONTHS.

Corona there are six months in the year during which zero F. is commonly reached, and that further, during all months, freezing temperatures may be expected. As a matter of observation, frosts are not uncommon during the entire summer in the higher parts of this region.

Figure 7, showing mean monthly maxima, indicates in another way the difference between these three stations. It is seen that at Corona

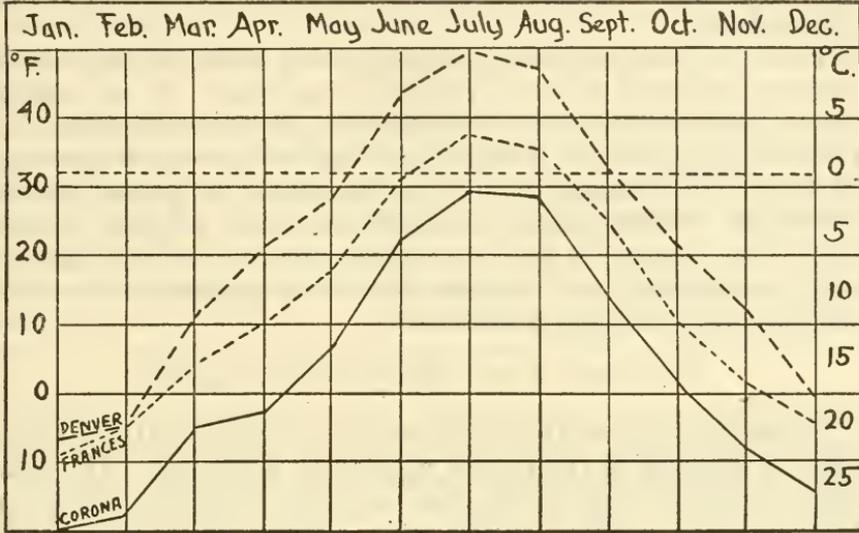


FIG. 6.—MEAN MONTHLY MINIMUM TEMPERATURES.

there are three months—December, January, and February—during which the temperature remains constantly below freezing, while at

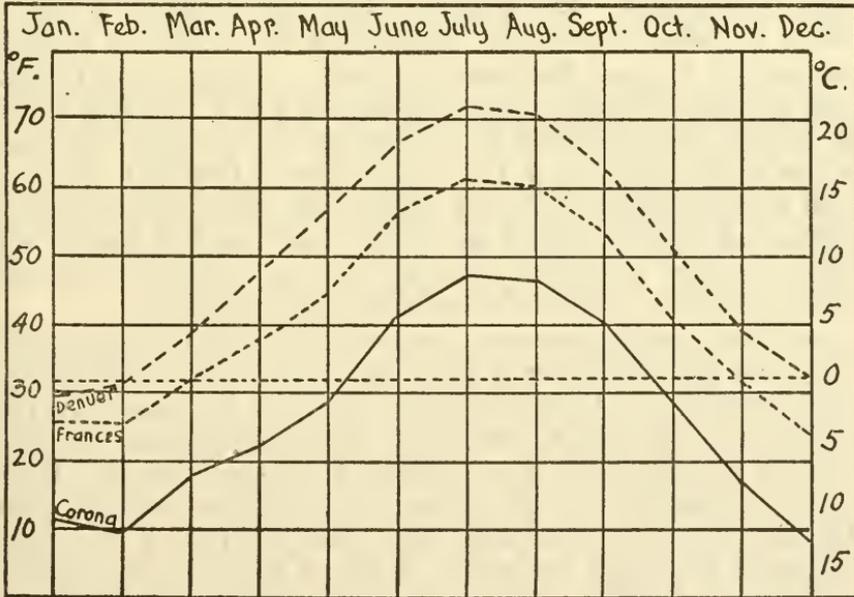


FIG. 7.—MEAN MONTHLY MAXIMUM TEMPERATURES.

Denver during the same months it commonly reaches 65° F., a higher figure than the average maximum at Corona during the summer

months. These studies of maxima and minima show more clearly than does the annual or monthly mean the rigorous nature of the climate and short duration of the summer season in the region of the highest lakes.

The above data regarding climate do not touch directly on the medium inhabited by the Crustacea—the water. To an aquatic animal climate means water temperature, not air temperature, and the data just given are of importance only because the temperature of the water is determined by that of the air and by general climatic conditions. Nevertheless it is desirable that data be given concerning the temperature of the water during the summer, the length of time free from ice, etc. Such records will be presented as a part of the account of the lakes themselves.

TOPOGRAPHY AND DESCRIPTION OF LAKES.

The eastern portion of Colorado lies in the region of the Great Plains, with an elevation of from 4,000 to 5,000 or 6,000 feet. The plains have a gradual slope toward the east, the valleys are broad, and the hills gently rolling. In this region natural bodies of water are few and small, being limited almost entirely to transient pools and ponds which are dry for a considerable part of the year. In addition to these natural ponds there are many pools, ponds, and reservoirs which owe their existence to irrigation and are filled periodically from ditches. The largest of these are reservoirs a mile or two in the largest dimension, containing water throughout the year, but subject to great fluctuation in level. Another quite frequent type includes the cattle ponds, depressions 2 to 4 feet deep and 50 to 100 feet across, scooped out to hold water for stock. The water is commonly muddy from the clay bottom, is frequently very foul with the droppings of the stock which water there, and seldom contains much plant growth of any kind. There are long periods with neither outflow nor inflow and they may be entirely dry for considerable periods. Some of these have a very rich fauna.

In drawing conclusions about distribution it must be borne in mind that these artificial bodies of water are of recent origin, and it is entirely probable that their development has been more rapid than the migration of plankton Crustacea, so that an equilibrium has probably not been reached. This condition may account for the absence of certain species from the plains which might be expected there. The climatic conditions of these lakes present no facts of great interest, being essentially like similar bodies of water in other parts of the Mississippi Valley. During the winter months, from the last of November till the close of February, they may be covered with ice, and the water temperature only a little above the freezing point. From May to September the temperature during the day commonly

rises to 90° F. in small bodies of water and probably at times to 100° F. Upper figure, plate 13, illustrates a typical lake of the plains.

A description of the lakes in the mountain region is not so simple a matter, and, in view of the fact that the greatest interest of the present studies centers in the alpine fauna, must be given in greater detail.

At their western border the plains pass, for the most part, abruptly into the mountains, so that the first rank of foothills often rises within a distance of a mile or two from one to three thousand feet above the plains. In sharp contrast to the topography of the plains, the relief in the mountains is great and the streams run in narrow valleys a thousand or more feet in depth. The highest part of the mountains, the Continental Divide, crosses the State from north to south, in much of its course being from 11,000 to 13,000 feet in elevation, with peaks rising to 14,000 feet.

In the mountain region west of Boulder there are very many small lakes, from 106 of which I have made collections. Inasmuch as nearly all of these lakes are of glacial origin, some account of glaciation and glacial topography is necessary. Though no part of Colorado was covered by the continental glacier there were in the higher mountains at the same time very many glaciers, only a few remnants of which remain. In the Tolland region these extended downward from the Continental Divide to an elevation of 8,000 to 9,000 feet, reaching eastward in the valleys as tongues of ice a distance of 5 to 10 miles. On the western slope glaciation in this region was less extensive.

The cirques in which these glaciers had their origins, just below the divide, are now one of the conspicuous topographic features of the higher parts of the mountains. Each cirque, separated from those adjacent to it by high, narrow ridges extending outward from the divide, is shut in on three sides by steep rock walls a thousand feet or more in height. In nearly every cirque is a lake fed by water from the huge snow banks, some of them perennial, which accumulate on its walls in the winter.

These lakes in the cirques at the heads of streams are the highest bodies of water to be considered and present the most extreme alpine conditions. They lie just at or above the upper limits of timber, nearly all of them at elevations above 11,000 feet, the highest one studied being Ice Lake at 12,188 feet. I have designated these as alpine lakes, and those at lower elevations in the mountains will be spoken of as montane, the division, as will be explained later, being made on the basis of faunal as well as physical peculiarities. I have made collections from 24 alpine lakes.

None of these is more than one-fourth mile in length, and, while they are considered locally to be very deep, I suspect that few, if any of them, are over 50 feet, though as boats are not available it can

not be determined certainly. One of them (Yaukiee Doodle Lake), reputed locally to be "bottomless," I found to measure about 25 feet. The rugged inclines surrounding these lakes are covered with large angular fragments of rock, and the bottoms of the lakes are largely of the same material and usually practically devoid of silt and entirely without vegetable mold. The water, derived from melting snow on the slopes above, is very clear, and in many lakes, when viewed from above, presents a brilliant green color.

A striking feature of these lakes is the great amount of snow which accumulates on the cirque walls above, in some of them extending well out over the ice cover of the lake. A lake so covered is long in becoming free from ice and the water remains at a low temperature all summer, so that climatic differences between alpine lakes are determined by the size and position of such snowbanks rather than by elevation.

At the beginning of June, even in warm seasons, all of these lakes are completely covered with ice, and in 1912, a season of heavy snowfall and delayed spring, the breaking up of the ice did not begin until early in July. In those where much snow extends over the ice the process is greatly delayed, as an extreme of which we have Ice Lake (12,188 feet), which on August 28, 1912, was still about half covered with ice and had a temperature of 40° F. (See lower fig., pl. 14.) It is probable that the ice did not entirely melt during the summer and that the temperature did not rise above 45°. I have made no observations of the time of freezing of these lakes in the autumn and have been unable to get definite information, but, judging by general weather conditions in this region, the temperature of the water must begin to decrease early in September and it is probable that by the end of the month they are frozen over. By records made at times of studying each lake it has been learned that, at the time of breaking up of the ice, the surface temperature is 35° to 37° F. and by the time the last floating pieces have melted it has reached about 44°. It then rises rapidly to about 52°, where it remains without much change as long as any considerable mass of snow persists on the cirque walls above to furnish cold water. In all alpine lakes except the few where there is insufficient snow to last well through the summer 52° F. is about the maximum temperature.

The striking conditions then, which characterize the alpine lakes are short season (two to three months free from ice) and the low temperature even during the warmest part of the year (a maximum of about 52° F.). (See fig. 8.)

Though it is not in all cases possible to assign a given lake definitely to one group or the other, yet, for the most part, the alpine lakes form a well-defined group, quite distinct from any of the kinds of lakes which must be included in the montane group.

The lakes which I have designated as montane are of two main types: (1) Rock-basin lakes on the upper courses of the streams, just below the cirques; (2) morainal lakes inclosed by the morainal ridges in the valleys and on the lower hillsides. These lakes are similar to each other and different from the alpine lakes in that they are surrounded by forests (pine, fir, and spruce), and that there is an abundance of other vegetation growing about them and at the water's edge, as a result of which there may be much plant débris and considerable silt on the bottoms of the lakes. There may also be a considerable growth of algae and other aquatic plants. These features, together with the longer season and warmer temperatures,

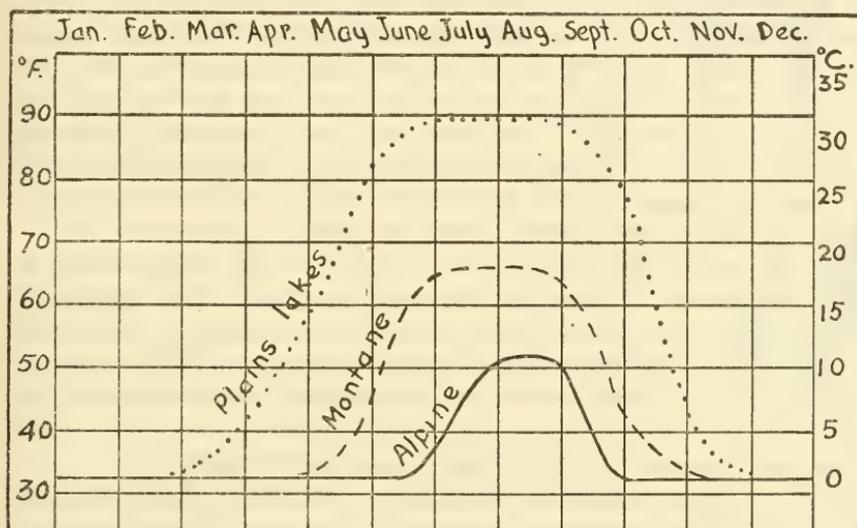


FIG. 8.—CURVES SHOWING THE APPROXIMATE DISTRIBUTION OF SURFACE TEMPERATURE THROUGHOUT THE YEAR IN THREE SORTS OF LAKES.

set them off distinctly from the lakes of the preceding group, and we shall see later that the fauna is also quite distinct.

The rock-basin lakes on the upper stream courses are about the same size, on the average, as the alpine lakes in the cirques above but probably have less depth. There may be one or more of these lakes on a stream, which between the lakes usually descends over a steep terrace often several hundred feet high. (See upper fig., pl. 14.) The temperature conditions here are somewhat less rigorous than in the alpine lakes. The cold water flowing out from the higher lakes becomes somewhat warmed, and temperatures from 55° to 60° F. are common, the latter figure about corresponding to 52° in the higher lakes. The time of breaking up of the ice in the spring is about a month earlier than in the higher lakes. Though most of the lakes of this type are above 10,500 feet, and there are none to correspond to them at lower elevations, it seems probable that, if lakes were present on the stream courses lower down, the difference in elevation

would not give to the lakes a decided faunal peculiarity to differentiate them from those just described.

Morainal lakes, from about 40 of which I have made collections, are most abundant between 9,000 and 10,500 feet. These lakes, very numerous in some localities, are inclosed by a network of morainal ridges, usually timbered, varying from a few feet to about 100 feet in height. Most of them are small, many of them mere ponds, and few are more than a few feet deep. They represent all stages of filling with silt and obliteration by growing vegetation. At one extreme are those with clean gravel bottoms and at the other marshes, where the water is entirely hid by plant growth, or meadows and thickets where the process of filling has produced dry land. None of these lakes are on large streams and most of them receive only the surface water from the small basin bounded by the surrounding ridges. Many never have any outflow and others only at times of high water. They are chiefly of a stagnant character, in strong contrast to those on the direct course of the streams, and the water is frequently of a dark brown color, due to the decaying organic matter on the bottom. (See lower fig., pl. 13.)

Climatic conditions are much less rigorous than in the lakes at higher elevations. I have not observed the time of the melting of the ice in the spring, but inquiries among people living in this region place it at about the last of April, and freezing in the fall is probably in October or November. Water temperatures of 55° to 65° F. are common in June, July, and August, while in some of the lower ones 70° or exceptionally 80° have been recorded. (See fig. 8.)

It is to be noted that all of these lakes are included in the western or higher half of the area between the Continental Divide and the plains, and that in the eastern portion (the foothill area), to which glaciation did not extend, there are very few bodies of standing water of any sort. Accordingly data from elevations between 5,400 and 8,000 feet are wanting.

METHODS.

In the plains region no special difficulties are experienced in collecting, but in the mountains, especially in the higher and rougher portions, the work involved in getting from lake to lake is great. Many of them can be reached only on foot, and my practice was to make trips of two or three days, carrying food, blankets, and the necessary collecting materials. For such work I reduced the collecting outfit to a size which was carried in an Army haversack with special pockets sewed in for vials, etc.

A conical net of No. 10 bolting cloth was used. It was 16 inches long, with an opening of 5 inches, supported by a stout wire ring, to which a long cord was attached by three shorter ones. In the bottom of the net, instead of the screw cup of Dr. E. A. Birge, I em-

ployed a small copper funnel of about 40 cc. capacity, which may be stopped with a cork and easily discharged into any suitable vessel. The funnel was loaded with about 2 ounces of lead to give weight to throw the net out from shore and to cause it to sink below the surface of the water. Such a net may be thrown out 50 to 75 feet from shore, or, by means of a long cord, drawn across small lakes or arms of larger ones. In practice I commonly threw out from several places on the shore and made surface collections by drawing the net in promptly, or deeper ones by allowing it to sink to the desired depth before drawing it in (fig. 9).

During three seasons of collecting by this method the question often presented itself whether there is a considerable chance that important species may be overlooked, rendering unreliable any conclusions based upon such material. Comparisons of collections made at different times and at different points on the shore at the same time lead me to believe that there is little danger that any but some of the most infrequent species are likely to be overlooked. One weak point in my collections is that they were all made in the summer, which, while securing the majority of species resident in the lake, fails to get those which may be winter residents only. It is probable that in some lakes in lower altitudes there exist species as winter forms that are part of the summer fauna in the higher ones. From some of these lakes only one collection was made, while from others material was secured at frequent intervals during one or two summers. It seems that in the higher lakes, where the summer season is short, one good collection at the proper time may be relied upon to contain all species; but in those at lower altitudes, where the season is longer, and seasonal succession is more marked, frequent collections are necessary.

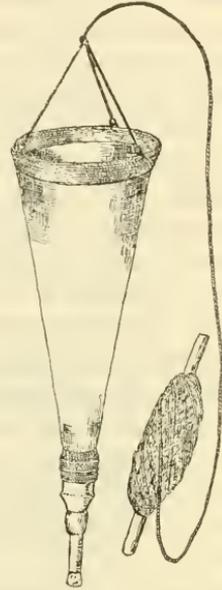


FIG. 9.—DRAWING OF NET USED IN MAKING COLLECTIONS.

THE FAUNA OF THE AREA STUDIED.

General nature and distribution.—A tabulated summary of the results of my collections, by groups of lakes, is given in Table 4, page 76. From this it will appear that they contain 55 species including: Phyllopoda, 10; Cladocera, 28; and Copepoda, 17. As noted in the introductory paragraph, when we add to these species those recorded by other students, we have a list of 71 known for the State. So far as possible I have considered all these records in

drawing conclusions. Figure 10 includes the total list for the State, with a graphic expression of the known range of each. The solid black part of the line represents the range as it appears from my collections and the open part the extension of range from other Colorado records. The broken lines indicate probable extensions of range into elevations not covered by the present records and are based upon the facts of general distribution of each species. The downward extension of many species below the Colorado records means that these are common lowland forms in temperate latitudes and do not in Colorado find their lower limit, inasmuch as even the lowest portions of the State have considerable elevation.

It is at once evident from the above chart that the species in this list fall into three groups—(1) those confined to the plains; (2) those limited to the mountains; (3) those that are not so restricted, but are found at all elevations. The first two of these groups include the stenothermic species, those unable to live except within rather narrow extremes of temperature. The two stenothermic groups differ from each other in that while one of them is unable to withstand high temperatures, the other can not tolerate low. The third group includes the euthermic species—those not so limited by temperature conditions, but able to live about equally well within wide limits, such as those between mountains and plains or between arctic conditions and tropical. In comparing vertical and latitudinal distribution, the first of these groups represents the arctic, or far northern, fauna; the second the more southern forms; while the third is typical of the species which have a wide north and south range. A brief analysis will show to what extent this parallel holds and will also point out that the stenothermic groups are in various respects more narrowly limited than the euthermic.

In the group confined to the mountains there are 16 species, and 3 others, which, though they do extend to the plains, belong primarily in the higher area, making 19 in all. These 19 species fall into two groups: (1) Ten species with a wide range in arctic and subarctic regions (all but one in both old and new worlds), which here range southward along the higher parts of the Rocky Mountains, a true southward extension of a northern fauna; and (2) nine species (some with very narrow ranges), pretty strictly confined to the Rocky Mountain region of the United States, a purely mountain fauna having the characteristics of an arctic fauna but including different species.

The group confined to the plains has somewhat similar components. Of the 28 species assigned to this group (the position of 3 is somewhat doubtful) 5 are found also in the old world and 6 others have quite a wide range in the United States. The remaining 17 species have a rather restricted range on the plains of the western part of the United States, some few extending into Mexico and southern

Canada. The two stenothermic groups have the common characteristic, that each has a considerable proportion of species with a very restricted range.

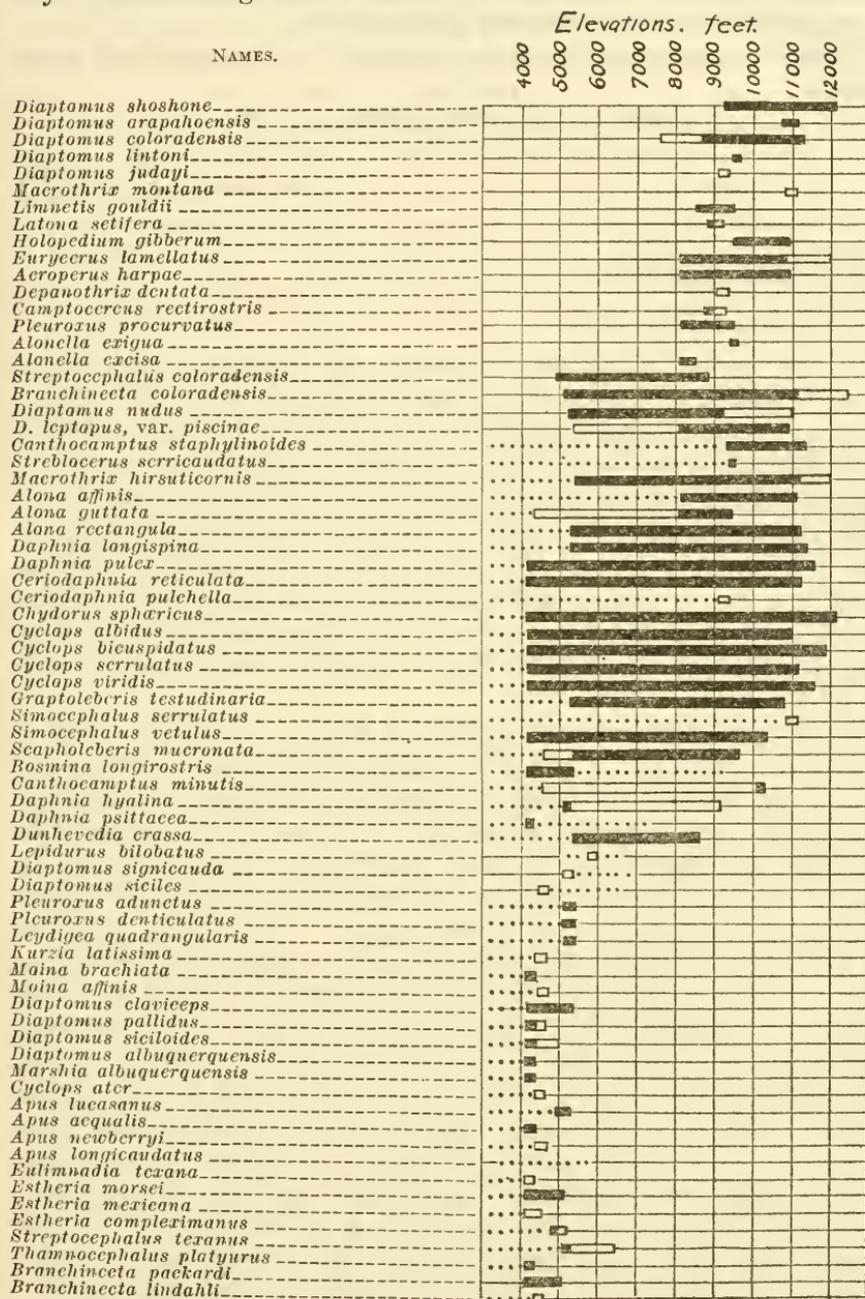


FIG. 10.—GRAPHIC REPRESENTATION OF ALTITUDINAL RANGES OF ALL SPECIES OF ENTOMOSTRACA KNOWN TO OCCUR IN COLORADO. SOLID BARS INDICATE THE RANGE AS SEEN IN THE COLLECTIONS OF THE WRITER; OPEN PORTIONS, EXTENSIONS OF RANGE FROM OTHER RECORDS; DOTTED PORTIONS, PROBABLE EXTENSIONS OF RANGE INTO ELEVATIONS NOT COVERED BY COLORADO RECORDS, ESPECIALLY INTO LOWER ELEVATIONS THAN THOSE FOUND IN THE STATE.

In strong contrast is the third group, including 24 species which seem about equally at home in either mountains or plains. Of these there are 22 common to both old and new worlds, and only two have a range restricted to the western United States.

Table 3 summarizes the facts presented in the preceding paragraphs.

TABLE 3.—*Distribution of species by groups.*

	Mountains.	Plains.	Mountains and plains.
Number species in each group.....	19	28	24
Confined to western United States.....	9	17	2
Confined to North America.....	1	6
World-wide.....	9	5	22

In the above comparisons between the euthermic and stenothermic groups of species there have doubtless been some mistakes made in assigning certain species to a given group, but, even allowing for some error from this source, it is quite evident that the stenothermic forms found in this region have a much less extended range than the euthermic. Of course, inasmuch as stenothermic species are of necessity shut out from large areas by unsuitable temperatures, it is not to be expected that such species should have as wide ranges as do those forms not so limited, but such differences as those just pointed out can hardly find a complete explanation in this set of conditions.

In this connection it is of interest to compare the genera *Cyclops* and *Diaptomus*, each of which is world-wide, forming an important part of the fresh-water plankton Crustacea everywhere. *Cyclops* is characterized by having a relatively small number of species, most of which are euthermic in nature and have a wide geographical range, while *Diaptomus* includes a multiplicity of species, usually stenothermic and with very limited ranges. Of the five species of *Cyclops* found in Colorado, four are very common at all elevations and are also practically world-wide in distribution; while of the 13 species of *Diaptomus* about half belong strictly to the mountains, the other half to the plains, and not one of them has a range extending beyond North America, most of them being confined to a narrow area in western United States. Moreover in the entire genus there is not known a single species common to Eastern and Western Hemispheres. The apparent correlation between stenothermic habit and restricted range is striking, but to what extent it is of general application and whether there is any necessary relation between the two conditions must at present be left unanswered.

Zonation.—If we can recognize among plants or animals ranging through different climatic conditions a zonation, we have an instructive method of analysis of use in bringing out significant points in

their distribution. Thus we recognize on the basis of latitude a very striking zonation of both animal and plant life and in a similar way a definite zonation on the basis of altitude. In the region of the Rocky Mountains from which my collections were made, Ramaley (1907) has defined and limited the plant zones on the basis of distribution of forest growths as follows:

Plains zone: Up to 5,800 feet. Grassland with trees and shrubs along water courses only.

Foothill zone: 5,800–8,000 feet. An open forest chiefly of rock pine (*Pinus scopulorum*).

Montane zone: 8,000–10,000 feet. Close forest of lodge-pole pine (*Pinus murrayana*).

Subalpine zone: 10,000–11,500 feet. Forests chiefly of Engelmann spruce (*Picea engelmanni*).

Alpine zone: Above 11,500 feet. Above timber line, where conditions are so extreme that trees will not grow.

Such a zonation gives a definite datum to which other animals or plants may be referred. This expresses much more significantly their true position than to place them between such and such elevations, because on the basis of zonal position we at once have suggested the environmental conditions and associates.

A study of the plankton Crustacea in my collections, and comparison with the records of others, so far as they can be applied to this problem, indicate three pretty well defined zones, which I shall call alpine, montane, and plains zones, the first and the last corresponding in the main with Ramaley's zones of the same names, and the montane zone covering pretty much the same range as his three middle ones. Whether these shall prove to be of general application to other parts of the Rocky Mountains or not, they afford an instructive method of pointing out the significant features of distribution in the region under study.

Alpine zone.—This zone includes lakes, nearly all of which are above 11,000 feet. The bodies of water that I have assigned to this zone (43 in all) include the lakes that I have designated as "alpine" lakes (together with a very few of these on upper stream courses, though not at the head), 32 in number, and 11 shallow pools at the same general elevation, all of them at or above timber line. Their general characteristics have already been pointed out.

The fauna of these lakes, while less abundant in species and individuals than that of the lower lakes, is by no means meager and includes 17 species, some of which were found in certain lakes in considerable abundance. The fauna of this zone is characterized by (1) the greater abundance here of certain species than in other zones, and (2) the absence of a considerable number of species that are present in lower zones.

TABLE 4.—Summary of the writer's collections by groups of lakes, giving number of records in each zone, the total number of localities, and the altitudinal range of each species.

Names.	Plains zone.	Montane zone.	Alpine zone.		Total.	Altitudinal range (feet).	
	22 lakes and ponds up to 5,400 feet.	49 stagnant lakes and ponds 8,100-10,950 feet.	14 flowing lakes 8,200-11,350 feet.	32 lakes 10,580-12,188 feet.			11 pools 10,500-11,900 feet.
<i>Branchinecta coloradensis</i> Packard.....	1	1			5	7	5,100-11,200
<i>B. packardii</i> Pearse.....	2					2	4,100-5,100
<i>Thamnocephalus platyurus</i> Packard.....	1					1	4,100
<i>Streptocephalus coloradensis</i> Dodds.....	1	3				4	4,900-8,850
<i>S. texanus</i> Packard.....	2					2	5,100-5,300
<i>Apus aequalis</i> Packard.....	1					1	4,100
<i>A. lucasanus</i> Packard.....	2					2	4,900-5,300
<i>Estheria complerimanus</i> Packard.....	1					1	4,900
<i>E. morsei</i> Packard.....	2					2	4,100-5,100
<i>Limnætes gouldii</i> Baird.....		2				2	8,500-9,500
<i>Latona setifera</i> (O. F. M.).....		1				1	8,850
<i>Holopedium gibberum</i> Zaddach.....		9	1	1		11	9,500-10,950
<i>Daphnia hyalina</i> Leydig.....	1	(*)				1	5,200
<i>D. longispina</i> O. F. M.....	1	39	8			48	5,250-11,350
<i>D. psittacea</i> Baird.....	6					6	4,100
<i>D. pulxer</i> De Geer.....	3	14	4	20	7	48	4,100-11,650
<i>Scapholeberis mucronata</i> (O. F. M.).....	1	12	1			14	5,400-9,650
<i>Simoccephalus vetulus</i> (O. F. M.).....	3	22	1			26	4,100-10,300
<i>Ceriodaphnia reticulata</i> Jurine.....	3	17		1	1	22	4,100-11,185
<i>Moina brachiata</i> (Jurine).....	7					7	4,100
<i>Bosmina longirostris</i> (O. F. M.).....	3					3	4,100-5,400
<i>Streblocerus serricaudatus</i> (Fischer).....		1				1	9,500
<i>Macrothrix hirsuticornis</i> Norman and Brady.....	1	5	3	2		11	5,400-11,250
<i>Eurycerus lamellatus</i> (O. F. M.).....		8	2			10	8,100-10,850
<i>Campocercus rectirostris</i> Schoedler.....		2				2	8,880
<i>Acroporus harpae</i> Baird.....		11			1	12	8,100-10,950
<i>Graptoleberis testudinaria</i> (Fischer).....	3	4				7	5,200-10,800
<i>Leydigea quadrangularis</i> (Fischer).....	1					1	5,200
<i>Alona rectangularis</i> Sars.....	3	10	2	7		22	5,250-11,250
<i>A. affinis</i> (Leydig).....		11	3		1	15	8,100-11,185
<i>A. guttata</i> Sars.....	(*)	4				4	8,100-9,500
<i>Dunhevedia crassa</i> King.....	2	1				3	5,400-8,675
<i>Pleuroxus procurvatus</i> Birge.....		4	1			5	8,150-9,500
<i>P. adunctus</i> Jurine.....	1					1	5,250
<i>P. denticulatus</i> Birge.....	3					3	5,250-5,400
<i>Alonella excisa</i> (Fischer).....		2				2	8,100-8,475
<i>A. exigua</i> (Lilljeborg).....		1				1	9,500
<i>Chydorus sphaericus</i> (O. F. M.).....	6	32	9	15	9	71	4,100-12,188
<i>Diaptomus albuquerqueensis</i> Herrick.....	8					8	4,100
<i>D. arapahoensis</i> Dodds.....				4		4	10,750-11,165
<i>D. claviceps</i> Schacht.....	2					2	4,100-5,400
<i>D. coloradensis</i> Marsh.....		19	1	8	1	27	8,675-11,350
<i>D. leptopus</i> , var. <i>piscinae</i> Forbes.....	(*)	27				27	8,100-10,950
<i>D. lintoni</i> Forbes.....		2				2	9,575
<i>D. nudus</i> Marsh.....	2	5		(*)		7	5,200-9,300
<i>D. pallidus</i> Herrick.....	1					1	4,100
<i>D. shoshone</i> Forbes.....		5	1	26	7	39	9,250-12,188
<i>D. siciloides</i> Lilljeborg.....	2					2	4,100
<i>Cyclops albidus</i> Jurine.....	3	10	1	2		16	4,100-11,000
<i>C. bicuspidatus</i> Claus.....	5	13	10	6	4	38	4,100-11,900
<i>C. serrulatus</i> Fischer.....	5	18	3	3	1	30	4,100-11,150
<i>C. viridis</i> Jurine.....	12	24	1	4	4	45	4,100-11,600
<i>Marshia albuquerqueensis</i> Herrick.....	1					1	4,100
<i>Gnathocamptus minutus</i> Claus.....	(*)				1	1	10,200
<i>C. staphylinoides</i> Pearse.....		3		1		4	9,250-11,350

An (*) indicates that the species has been collected in the zone by other investigators though not appearing in the collections of the writer.

One species in my collections, *Diaptomus arapahoensis* (four lakes), is confined to the zone, though its frequency is insufficient to be of importance as a characteristic species. *Diaptomus shoshone*, though not

strictly confined to the zone, belongs primarily here and is the chief differential form. It was found in 33 out of the 43 bodies of water in the alpine zone and only in 6 of the 63 lakes of the montane zone. It was first described from Yellowstone Lake by Forbes, and has since been collected at Pikes Peak by Ward at 11,000 feet, and in the Tolland region, and may be taken as a typical alpine form. I have not found it below 9,250 feet. The species of second importance is *Daphnia pulex* (27 lakes), which, though present in all zones, and having a general distribution throughout the world, seems to have a particular significance in this zone. The variety found here is a very large form with long straight spine and more than the usual number of anal spines and of teeth in the pecten. The striking condition is the frequency with which these two species, *Diaptomus shoshone* and *Daphnia pulex*, are associated together in this zone, so that the two rather than either one may be said to characterize the fauna of the zone. In 39 out of the 43 lakes assigned to this zone, one or both of these species are found, and in 22 cases both of them. This association, as we shall see presently, gives place, in the montane zone, to another equally stable one. Third in frequency of occurrence is *Chydorus sphaericus* (24 lakes), but as it is common in all zones and in all parts of the world it does not seem to have any special significance in this zone. Next in importance comes *Diaptomus coloradensis* (nine lakes), which appears to belong in the lower part of this zone, whence it extends into the montane zone, where it has its greatest abundance. This species, said by Marsh to be common in the mountain lakes of Colorado, is closely related to *D. tyrelli*, a common mountain form in the western United States. Only one other species need be mentioned particularly, *Branchinecta coloradensis* (five pools). This phyllopod characterizes the pools of this zone and in them makes a third member of the *pulex-shoshone* combination. This species, common in the pools of the alpine region, has only once (9,575 feet) appeared in my collections from the montane zone, and this was in a pond where were also the two primary members of the alpine fauna. The species was described from material near Grays Peak at 12,000 feet, has been collected near Leadville at 12,500 feet, and on the slopes of Pikes Peak at 11,000 feet, and ranks as a typical example of a mountain species with a restricted range. One record, however, necessitates somewhat of a changed notion on this point. I have recently received from Prof. Max M. Ellis a collection from St. Vrain, Colorado (5,100 feet), dated May 30, 1912, in which are a considerable number of specimens of this species. This record at once extends its range to the plains, where it is possible that it is found in the early spring, though not during the entire summer. The record does not, however, take away from its significance in the alpine zone, where it is much more common than at any other elevation. The remaining species of

this zone, as may be seen from Table 4, are, for the most part, euthermic forms ranging up from the plains.

Montane zone.—To this zone I have assigned 63 bodies of water, nearly all below 11,000 feet (the great majority below 10,500 feet). In spite of peculiarities of different types of lakes, the faunal characters of this zone are well defined and quite distinct from those of either of the others. In this zone I have collected 35 species, 11 of which are confined to the zone, though on the basis of general distribution 3 of these may be expected in the plains. Three other species, evidently belonging primarily to this zone, are found in one or two lakes each, at Boulder, just at the edge of the plains, but not in plains lakes more remote from the mountains. In addition to these species there are the usual euthermic forms, common at all altitudes, which make a large part of the fauna of all zones. On account of the absence of lakes in the foothill region of the mountains (between 5,400 and 8,100 feet) there are certain points about the fauna of this zone in doubt, especially the nature of the transition between montane and plains zones. In describing the fauna of this zone it will be well to treat first the 49 lakes of the morainal type, more or less stagnant in their nature, and later those directly on the stream courses (14 in number).

In the morainal lakes there have been found 34 species (including all but one of those found in the zone), and in this region I think of the morainal lakes as being typical of the zone. The characteristic species, *Diaptomus leptopus*, var. *piscinae* (27 of the 49 lakes), is confined to the zone except for one record by Marsh of its occurrence in the lake on the university campus at Boulder. The most abundant species is *Daphnia longispina* (39 lakes), which, though it is a widespread species in temperate lowlands throughout the world, in our region seems to belong, primarily, to the montane zone, for it is not found at all in the alpine lakes, and on the planes of the State it has so far been found in only one lake near Boulder, close to the mountains. Here, as in the alpine zone, the frequent association of two species (a copepod and a cladoceran) is conspicuous, and the two above mentioned form a pair which, in the montane zone, replaces the *pulex-shoshone* group of the alpine zone. In 43 lakes one or both are found and in 23 both. Though neither member of this pair has been found in any alpine lake, the members of the alpine pair have been found in this zone, *Daphnia pulex* (14), *Diaptomus shoshone* (5 times), but there is only one case where all four species have been collected from the same lake.

In spite of this and other cases of partial mixing of these two faunas the fact is quite evident that the two arrangements (*pulex-shoshone* and *longispina-leptopus*) are very much more frequent than either of the other possible combinations of these four species, and it is

equally clear that one pair belongs primarily to the alpine and the other to the montane zone. These two sets of species are nearly mutually exclusive, the conditions necessary for the one being so different from those demanded by the other that it amounts essentially to mutual repulsion. This is especially true of the two species of *Diaptomus* and to a marked degree also of *Diaptomus shoshone* and *Daphnia longispina*. A third species of importance is *Diaptomus coloradensis* (19 lakes), found also in the alpine zone, which seems about equally well at home in either zone and to have about equal relations to each of the two combinations. It is to be noted, however, that in neither zone is it so abundant as the definitive *Diaptomus* of that zone.

The significance of such combinations of species as the above is that they may be used as a measure of ecological conditions. In our area *Diaptomus shoshone* and *Daphnia pulex* are ecologically similar, as are also the corresponding members of the montane pair, and the two pairs are ecologically dissimilar, though the lack of similarity is not the same in degree between all of these species. Though we are unable to measure in physical and chemical units the complex of conditions required for any of the above species, the frequency of their association together gives us an index for the measurement of the similarity of the conditions demanded. Conditions required by two species may be so similar that one is seldom found without the other, or they may be so unlike that they are as mutually exclusive as if one actually repelled the other. I have reduced to percentages the frequency of association of the members of these two pairs and also of *Diaptomus coloradensis*, which is a frequent associate of both. In Table 5 are shown the association percentages of each of these species in the alpine and montane zones. It is read as follows: *Daphnia pulex* is found in 45 lakes, in 27 per cent of which *Daphnia longispina* is found, in 20 per cent *Diaptomus leptotus*, etc.

TABLE 5.—Association percentages.

Name.	<i>Daphnia pulex</i> .	<i>Daphnia longispina</i> .	<i>Diaptomus leptotus</i> .	<i>Diaptomus shoshone</i> .	<i>Diaptomus coloradensis</i> .	Number of lakes.
<i>Daphnia pulex</i>	27	20	58	25	45
<i>Daphnia longispina</i>	25	49	8	34	47
<i>Diaptomus leptotus</i>	33	85	4	26	27
<i>Diaptomus shoshone</i>	66	10	3	30	39
<i>Diaptomus coloradensis</i>	38	55	24	45	29

From the above table the high association percentages between the two members of each pair are evident as well as the low correlation between the two species of *Diaptomus* or between *Diaptomus shoshone* and *Daphnia longispina*. Such figures as the above are useful in giving other sorts of information about the inter-relations

of the several species, as for instance, the less restricted nature of *Daphnia pulex* and *Diatomus coloradensis*, evidenced by their more uniform correlation percentages, contrasted with the wide variability of correlation of each of the other three species. In using such figures care must be exercised not to attach to them greater significance than is justified on the basis of the number of localities collected and the frequency of occurrence of the various forms, but in this table I suspect that the significance of the figures is less, rather than greater, than the actual facts, because, in some cases, two species are computed as living in the same lake when one of them is plainly the dominant form and clearly belongs there, while the other one is present in small numbers and barely manages to exist.

In a similar manner I computed correlation percentages between all the species in my collections, and though such figures when arranged in the form of a table were useful in the analysis of my data they do not seem of sufficient importance to publish. I merely suggest this as a possible means of analysis for other data of this sort.

The following northern species, which range southward along the mountain range, are entirely or nearly confined to these lakes, and belong primarily to the montane zone: *Limnetis gouldii* (3 lakes), *Latona setifera* (1), *Holopedium gibberum* (9), *Eurycerus lamellatus* (8), *Acroperus harpae* (11), *Camptocercus rectirostris* (2), *Alonella excisa* (2), and *Alonella exigua* (1). Two other species worthy of mention are *Diatomus lintoni* (2), described from the Yellowstone region, and *Diatomus nudus* (5), described from lakes at Pikes Peak at 11,000 feet, apparently under alpine conditions, but in the Tolland region not found above the montane zone. *Simocephalus vetulus* (22), the dominant Cladoceran in marshes and weedy pools of this zone, is widespread and common in all zones except the alpine, from which it may be shut out by the lack of plant growth rather than by extreme climatic conditions, an indirect rather than a direct effect of altitude. *Chydorus sphaericus* and four species of *Cyclops* are common here but have no significance as they are met with everywhere. Other species not of special significance may be learned by reference to Table 4.

Of the other lakes of this zone, the 14 on stream courses, it is difficult to give a good characterization. At first I was inclined to place them in a separate zone, the subalpine, but because of the lack of lakes of this type in elevations below 10,000 feet it is not possible to tell which of their faunal characters are due to altitude. Barker Reservoir (8,200 feet), a lake of the same sort, has somewhat similar faunal characters, a fact which leads me to suppose that their fauna does not give place to a different one in lower altitudes.

That these lakes are definitely distinct from those of the alpine zone is clearly indicated by the fact that while the dominant forms

of the alpine lakes are constantly being carried into these lakes by the streams, yet they do not find a footing here, *Daphnia pulex* being found in small numbers in three of them and *Diaptomus shoshone* in but one. It is equally conspicuous that not only the definitive species, but also other important and common forms of the montane morainal lakes are either wanting or very scarce here, *Diaptomus leptopus* being wanting and *Diaptomus longispina*, though found in 8 of the 14, was never abundant. On the positive side we may say that the fauna of these lakes comprises 18 species, usually present in very small numbers, most of which are euthermic forms, found at all altitudes. The only species which attains anything like abundance is *Cyclops bicuspidatus*, found in 10 of the 14 lakes, in 5 of which it is abundant. Not only does it seem more at home here than does any other species, but it is more abundant here than in any other type of lake studied. The reasons for assigning these lakes to the montane zone are unwillingness, on the basis of the present data, to constitute them a separate zone; evident separateness from the alpine lakes; their geographical relations; and the fact that most of their species are also found in the morainal lakes of the montane zone.

These two kinds of lakes I have taken as constituting the montane zone, and because those of the morainal sort are more abundant I have come to think of them as the representative type of the zone, to which I have referred the others. If the latter kind were the more abundant the faunal characters of the zone would be defined quite otherwise than they have been; but in either case, the distinctness from those above and from those on the plains would remain, and the differences seem in either instance to be due to altitude rather than to peculiarities which might equally well be duplicated at any elevation.

As already pointed out, the absence of lakes in the lower portion of the mountain region, a strip about 12 miles wide, makes it impossible to get data to show the nature of the fauna in the foothill region and the transition between montane and plains faunas. The small evidence we have bearing on this question seems to indicate that probably the chief species of the montane zone continue to be the dominant forms through the foothill area, wherever there are bodies of water. The finding of *Diaptomus leptopus*, var. *piscinae* (1), *D. nudus* (2), and *Daphnia longispina* (1), montane forms, in lakes near Boulder, just at the edge of the plains, though not in plains collections more remote from the mountains, seems to indicate that these species, in the foothill region as in the higher lakes, may continue to be important forms.

Plains zone.—My own data concerning the plains lakes are somewhat meager, due to the loss, before I had studied them, of a con-

siderable number of collections. My records are from only 7 lakes in the Boulder region and 11 near La Junta. To get a fairly adequate notion of the fauna of the plains I have, accordingly, had to supplement my own records with all others available, chiefly those of Beardsley from the Greeley region, and still our knowledge of the plains fauna is less complete than of that of the mountains. My own collections from lakes on the plains include 36 species. The total list is 50, and 5 others, though collected only in the mountains, are to be expected also on the plains, making a total considerably larger than that of both mountain zones combined. Of these 55 species, 28 have been collected only in the plains, though a few of these, on the basis of general distribution, are to be expected in the mountains also. The remaining 27 range upward into mountain zones. The few lakes collected in the Boulder region, just at the border between mountains and plains, but really in the plains, seem to have a fauna somewhat resembling that of the montane zone, indicating, as is to be expected, that there is not a sharp dividing line, and that these lakes belong as much to the mountains as to the plains.

Concerning the composition of the fauna it is unnecessary to go into detailed description, as it is made up chiefly of species which are common members of lowland faunas in America and to a considerable extent in Europe and other Old World areas. This is particularly true of the euthermic members of this fauna, but as pointed out previously (Table 3), it is not true to a large extent of the stenothermic members, those 28 species found only in the plains area, of which 17 are confined to the western part of the United States and 6 others to North America. This condition indicates that like the fauna of the mountain lakes, that of the plains is also considerably specialized. This is a condition contrary to expectation, for we are accustomed to think of the plains conditions as the "ordinary" and the mountains as the "exceptional" and so calculated to produce the exceptional fauna. It appears, however, that in the great plains of this country, especially their western portion (probably on account of their arid climate) there exist conditions of a quite specialized nature, differing decidedly from those of lowland countries in general. This may furnish an explanation for the restricted range of a considerable proportion of the species of the plains zone in Colorado. A conspicuous feature of this fauna is the large proportion of Phyllopods (12 species) confined exclusively to the plains zone, none of which has a range extending beyond the semiarid plains of western United States, northern Mexico, and southern Canada, and most of them are much more restricted than that. Though Phyllopods are universally distributed and every portion of the world is likely to have the group represented in its

fauna, it is very unusual for so large a proportion of a fauna to fall within this group. Of the 42 North American species of Phyllopo-
ds, 16 have been found in Colorado (12 confined strictly to the plains)
and 25 are confined to the area west of the meridian of Kansas City.
These species are the part of the fauna which differentiates it from
that of most lowlands in temperate regions. This type of fauna finds
a suitable home in the transient pools of the arid plains, from which
the species unable to endure these conditions are excluded. Because
other types of lakes and ponds were almost unknown here until the
development of irrigation produced them, the more generalized por-
tion of the fauna has not had the same chance to develop, and it is
probable that even with the facility of dispersal which characterizes
plankton organisms, an equilibrium has not yet been reached, so that
we may expect the next period of years to produce considerable changes.

Though the exploration in no part of the area studied has been
anything like complete (especially deficient in the plains area) it is
pretty evident that three well-defined zones exist, and while farther
investigations may change many details, it seems safe to assume that
what has been presented here expresses fairly well the main facts.
Table 4, page 76, expresses briefly the facts about zonation. It would
be of interest to learn how far this zonation may be applicable to
other portions of the Rocky Mountain region, and to what extent the
dominant species may be the same in other localities, but up to the
present, in other mountain areas in this country, insufficient work has
been done to give a very definite notion of its plankton Crustacea.

COMPARISON WITH OTHER MOUNTAIN FAUNAS.

Though no extensive work on mountain plankton Crustacea has
been done in this country, there has been accomplished in Europe
some work of considerable importance, notably in two regions, the
Alps and the mountains of the Scandinavian Peninsula.

Important among work in the Alps is that of Zschokke (1900)
treating other European mountains as well. Much of his descriptive
matter dealing with the nature of lakes and streams, and his photo-
graphs of lakes in the Alps, might well be used to illustrate conditions
in the higher part of the mountains of the Tolland region. His
description of a typical alpine lake essentially describes lakes of our
own alpine zone, so that we are justified in making a direct compari-
son of the fauna. The only conspicuous difference is that in the Alps
corresponding conditions are reached at a lower elevation than in the
Colorado Rockies. A comparison of the plankton Crustacea beings
out a striking similarity also, for though so far separated geographi-
cally, a comparison of the 63 species from the Alps with the 44
reported from our own mountains shows 19 species in common
(Table 6). Zschokke's data are not presented in such a way as to

make it possible to determine if there is a zonation similar to that just described for our own mountains, and a comparison of the greatest recorded elevations for each of the 19 common species, while showing a general agreement, also presents some striking differences which make comparisons on this basis of little direct use. The average difference in greatest elevations is approximately 3,500 feet, which probably expresses the relative values of altitude in the two regions as affecting plankton Crustacea.

TABLE 6.—Species common to the three mountain regions.

Name.	Colorado Mountains.	Swiss Alps.	Swedish Mountains.	Name.	Colorado Mountains.	Swiss Alps.	Swedish Mountains.
<i>Holopedium gibberum</i>	*	*	*	<i>Alona guttata</i>	*	*	*
<i>Daphnia longispina</i>	*	*	*	<i>Alona quadrangularis</i>	*	*	*
<i>Daphnia pulex</i>	*	*	*	<i>Alonella excisa</i>	*	*	*
<i>Daphnia hyalina</i>	*	*	*	<i>Alonella erigua</i>	*	*	*
<i>Simocephalus vetulus</i>	*	*	*	<i>Pleurozus truncatus</i>	*	*	*
<i>Ceriodaphnia pulchella</i>	*	*	*	<i>Chydorus sphaericus</i>	*	*	*
<i>Ceriodaphnia quadrangula</i>	*	*	*	<i>Cyclops albidus</i>	*	*	*
<i>Scapholeberis mucronata</i>	*	*	*	<i>C. bicuspidatus</i>	*	*	*
<i>Streblocerus serricaudatus</i>	*	*	*	<i>C. serrulatus</i>	*	*	*
<i>Macrothrix hirsuticornis</i>	*	*	*	<i>C. strenuus</i>	*	*	*
<i>Bosmina longirostris</i>	*	*	*	<i>C. vernalis</i>	*	*	*
<i>Eurycerus lamellatus</i>	*	*	*	<i>C. viridis</i>	*	*	*
<i>Acroperus harpae</i>	*	*	*	<i>Diaptomus denticornis</i>	*	*	*
<i>Alona affinis</i>	*	*	*	<i>Canthocamptus minutus</i>	*	*	*
<i>Alona costata</i>	*	*	*				

Ekman (1905), in an extensive account of the plankton Crustacea of the high mountains of northern Sweden, lists 49 species, 15 of which are also in the Colorado mountain list and 19 of them in Zschokke's list from the Alps. In the three mountain lists there are 12 common species, certainly a strikingly large duplication considering the wide separation of the areas. Ekman recognizes three zones, birch, willow, and lichen, which he makes the basis of faunal zones. The limits and characters are shown in Table 7, compiled from his data.

TABLE 7.—Table of zonation in Swedish mountains.

Name of zone.	Elevation.	Time open.	Average maximum temperature.	Number of lakes.	Number of species.
Birkenregion (subalpine).....	Up to 700 meters (2,300 feet).	3½ to 4 months.	{ 10 to 12 C. 50 to 54 F. }	48	45
Grauwelderregion (lower alpine).	{ To 1,000 meters (3,250 feet).	2 to 3½ months.	{ 10 C. 50 F. }	89	39
Flechtenregion (higher alpine) ..	To 1,350 meters (4,350 feet).	2 months and less.	(?)	43	26

Above 1,350 meters depressions are filled with permanent snow. No fauna.

In determining the character of the entomostracan fauna of a lake, Ekman considers that temperature is of prime importance. He finds that in all zones the smaller bodies of water open earlier in the

spring and attain a higher temperature during the summer, so that for temperature conditions and faunal characters the smaller lakes at higher elevations resemble the larger ones at lower altitudes. As a result of this condition, faunal zones can not be drawn definitely on the basis of altitudinal limits, but there is overlapping due to the size difference of lakes. In lakes of the Colorado Rockies I find the temperature difference above referred to, but have been able only indefinitely to correlate it with faunal differences. It is not easy to compare zone for zone with the Colorado lakes, but it is probable that his birch zone agrees with the upper part of my montane zone, and that his other two correspond to my alpine zone, although I have not encountered conditions as severe as those of his highest lakes.

PLACE OF COLORADO FAUNA IN WORLD DISTRIBUTION.

Wesenberg-Lund (1908), in summarizing the present knowledge of the fresh-water plankton of the earth, classifies lakes under the following zones:

(1) Arctic lakes: Those in Arctic America, Greenland, Franz Joseph Land, Spitzbergen, Nova Zembla, and Arctic Siberia.

(2) North European lakes: Scotland, Iceland, Norway, Sweden, Finland, etc.

(3) Central European lakes of the level country.

(4) The Mediterranean lakes.

(5) Tropical lakes: Those of Central Africa and places of similar climate.

To these zones he adds (6) the Central European alpine lakes.

He describes the physical and climatic characters in each zone, and so far as possible gives the constitution of the plankton.

Though a detailed comparison can not be made, it is possible to assign some elements of our Colorado fauna to certain of Wesenberg-Lund's zones. The lakes of the alpine zone, though less extreme than the northernmost of those, belong very close to the arctic lakes. Though there are few common species, the general similarity of the fauna is evident. *Holopedium gibberum*, which he considers as very nearly confined to the arctic regions, is found in our alpine and montane zones. Other species considered as arctic by him are *Daphnia longispina*, *Bosmina longirostris*, *Ceriodaphnia pulchella*, and *Chydorus sphaericus*. All these range southward from the arctic regions. In Colorado they are not by any means the most important nor the highest of our alpine forms, but they do range high in the mountain region. The importance of *Diaptomus* in both faunas is marked, though it is not surprising that there are no common species of this genus. The essential agreement of the climate of our alpine zone to that of the zone occupied by the arctic lakes has been pointed out in the section on climate.

Our montane zone seems to correspond to the North European lakes. The isotherm indicating the mean annual temperature at this elevation in the mountains of Colorado passes through the countries he assigns to this zone. The agreement of faunas is also evident. Certain species, most of which do not reach into the arctic regions, are common in the North European lakes and also in our montane zone. Chief among these are the following: *Latona setifera*, *Daphnia longispina*, *Ceriodaphnia reticulata*, *Simocephalus vetulus*, *S. serrulatus*, *Scapholeberis mucronata*, *Streblocerus serricaudatus*, *Eurycerus lamellatus*, *Camptocercus rectirostris*, *Acroperus harpae*, *Graptoleberis testudinaria*, *Alona guttata*, *Depanothrix dentata*. These species are common in our montane zone, though not confined to it, and do not commonly reach into the alpine zone. Thus it seems that our two well-defined mountain zones correspond to the two most northerly zones recognized by Wesenberg-Lund. It is probable, however, that the most extreme conditions met with in our alpine zone are less extreme than the most extreme of the arctic zone.

If we carry the comparison further, we may compare the plains zone with the Central European lakes of the level country, except so far as our conditions are specialized and local in their nature due to the arid climate. Wesenberg-Lund comments on the very great similarity (large number of common species) between the plankton of Central Europe and temperate North America.

The above writer is unable, because of the relatively small amount of data, to clearly recognize in America zones corresponding to those of Europe. Judging partly by the mean annual temperatures and partly by the available records of the distribution of plankton Crustacea it appears that the Hudson Bay region and Labrador correspond to the arctic zone, and that the region from Lake Superior and eastward to Newfoundland represents the zone of the North European lakes. Just where lines should be drawn between zones in the western portion of Canada and in Alaska is not clear except that the mountainous nature of this area causes the lines to curve far southward. It is accordingly not possible definitely to refer the different zones represented in the Colorado mountains to their position in the scheme of general distribution on this continent. This much is certain, that the alpine zone is a true southern extension of arctic condition and of arctic fauna along the higher parts of the Rocky Mountains.

The great similarity between the fauna of the higher Rocky Mountains and that of the Alps has already been pointed out. Each resembles the fauna of arctic regions. There is this difference: While the alpine fauna of the Colorado Rockies is a direct southern continuation, without interruption, of an arctic fauna, that of the Alps is separated from the corresponding arctic fauna by intervening

lowlands, and rises as an island, surrounded by faunas of warmer climates. This difference of situation does not, however, make any apparent or significant difference in the nature of the two faunas. The conditions and fauna in both cases, as pointed out by Zschokke, are glacial in their nature—in the Alps as a remnant left at the retreat of the glacier, and in the Rockies as a direct southern extension of present glacial conditions in the north.

BIBLIOGRAPHY.

- BEARDSLEY, A. E. Notes on Colorado Entomostraca, *Trans. Amer. Micros. Soc.*, vol. 23, 1902, pp. 40-48.
- COCKERELL, T. D. A. The Fauna of Boulder County, Colorado, II. *Univ. of Colorado Studies*, vol. 9, 1912, pp. 41-52.
- DODDS, G. S. Descriptions of Two New Species of Entomostraca from Colorado, with Notes on other Species. *Proc. U. S. Nat. Mus.*, vol. 49, 1915, pp. 97-102.
- Key to the Entomostraca of Colorado. *Univ. of Colorado Studies*, vol. 11, 1915, pp. 265-299.
- EKMÁN, SVEN. Die Phyllopoden, Cladoceren und Freilebenden Copepoden der nord-schwedischen Hochgebirge. *Zool. Jahrb. Abth. System*, vol. 21, 1905, pp. 1-170.
- JUDAY, CHANCEY. A Study of Twin Lakes, Colorado, with especial Consideration of the Food of the Trouts. *Bull. Bureau of Fisheries*, vol. 26, 1907, pp. 147-178.
- PACKARD, A. S. Monograph on the Phyllopod Crustacea of North America, with remarks on the Order Phyllocarida. 12th Ann. Rept. U. S. Geol. Surv. (Hayden), vol. 1, 1883, pp. 295-592.
- PEARSE, A. S. Contributions to the Copepod Fauna of Nebraska and other States. *Studies from Zool. Lab. Univ. of Nebraska*, No. 65, 1905, pp. 145-160.
- Notes on Phyllopod Crustacea. *Michigan Acad. Sci.*, 14th Report, 1912.
- RAMALEY, FRANCIS. Plant Zones in the Rocky Mountains of Colorado. *Science*, N. S., vol. 26, 1907, pp. 642-643.
- SHANTZ, H. L. Notes on the North American Species of Branchinecta and their Habits. *Biol. Bull.*, vol. 9, 1905, pp. 249-264.
- WARD, HENRY B. A Biological Reconnaissance of Some Elevated Lakes in the Sierras and the Rockies. *Studies from Zool. Lab. Univ. of Nebraska*, No. 60, 1904. Report on the Cladocera, by E. A. Birge. Report on the Copepoda, by C. Dwight Marsh.
- WESENBERG-LUND, C. Plankton Investigations of the Danish Lakes. General Part; The Baltic Fresh-water Plankton, its Origin and Distribution, 1908, 391 pp., 46 tables.
- ZSCHOKKE, F. Die Tierwelt der Hochgebirgseen. *Neu. Denkschr. allg. Schweiz. Ges. ges. Nat.*, 1900, 400 pp., 8 pls., 4 maps.



LAKE AT SEMPER, COLORADO (5,400 FEET)

A lake of the plains with the mountains in view in the background



REDROCK LAKE (10,000 FEET)

A montane lake of the morainal type



CRATER LAKES AS SEEN FROM THE CONTINENTAL DIVIDE

Shows an alpine lake in a cirque at timber line (11,000 feet) and several Montana lakes at lower elevations



ICE LAKE (12,188 FEET)

A lake of the alpine zone. Photograph taken August 1, 1914

