Article V.—ALTITUDE IN COLORADO AND GEOGRAPHICAL DISTRIBUTION

By Frank E. Lutz

It is often desirable in studies of geographic distribution to have some short and usable expression for the general northern-ness or southern-ness, eastern-ness or western-ness of a species or group of species. The "geographic average" has been suggested[1] as such an expression. What was meant may be made clear by the following illustration.

A given species extends from Montana (about 47° N., 110° W.) to British Columbia (about 54° N., 124° W.), Oregon (about 44 N., 121° W.), and Colorado (about 39° N., 106° W.). Its "mid-latitude" is the average of the latitudes (47, 54, 44, and 39° N.) of these corners of its range, or 46.0° N. Its "mid-longitude" is found in a similar way to be 115.25° W. The "mid-range" of the species is, then, 46° N., 115.25° W. The mid-range of a species extending from Virginia to Florida, Louisiana, and Oklahoma is approximately 33° N., 87.5° W. These mid-ranges are directly comparable and we may say that the former species averages 13 degrees more northern and 27.75 degrees more western than the latter. The use of degrees of latitude and longitude instead of geographic names permits us to average also the extents of or limits of ranges.

The "mid-range" should not be confused with "center of population." If a species is very abundant in, say, British Columbia (about 54° N., 124° W.) and is found but rarely southeast to New Mexico (about 34° N., 106° W.), its mid-range would be halfway between these points (about 44° N., 115° W., in Idaho) but the center of population might be very close to, or even in, British Columbia. The "center of population" would probably be much more useful than "mid-range" but it does not seem to be possible to calculate it, for we do not have enough data concerning the density of population in every place of more than a few species.

It should also be kept in mind that, in certain cases, the mid-range is at a point where the species does not in fact occur. For example, if a species has a crescentic range, such as in Canada and southward along the Rockies and the Appalachians, the mid-range would be within the horns of the crescent, say in Iowa. Such a mid-range, however, would indicate a distribution that is in general more northern and more western than that of a species which occurs in the Gulf States and northward along the Mississippi River and the Atlantic coast.

[1]Lutz, Frank E. 1921. 'Geographic Average, a Suggested Method for the Study of Distribution.' American Museum Novitates, No. 5.

Range in Degrees of Longitude	Range in Degrees of Latitude														
	0–2	3–5	6–8	9–11	12–14	15–17	18–20	21–23	24–26	27–29	30–32	33–35	36–38	39–41	Total
0— 8	97	89	41	24	13	3	1								268
9— 17	4	10	24	29	28	11	7		2						115
18— 26			1	6	7	18	14	3		2	1				52
27— 35			1	1	3	4	3		4	2	1	1			20
36— 44					3	3	1	2	6						15
45— 53					1	5	1		6	10	5				28
54— 62				1	1		3	1	2	1	2		1		12
63— 71						3	2	1	2		2			1	11
72— 80								2	2	1					5
81— 89									1				1	1	3
90— 98									13	3	1			1	18
99—107									2	2					4
108—116									9	3	2				14
Total	101	99	67	61	56	47	32	9	49	24	14	1	2	3	565

Table 1.—The relation between the extent of latitudinal range and that of longitudinal range. Based on Colorado plants. Ranges expressed in degrees.

The present paper is an application of the method of geographic averages to certain problems in connection with work which the American Museum's Department of Entomology has been doing in Colorado and adjacent states, but the data used here are for plants, not insects. This is partly because botanists have covered their field much better than have entomologists, so that it is relatively easy to get data concerning the distribution of plants, and partly because it is believed that the distribution of plants is a very important factor in the distribution of even those insects which are not phytophagous.

The data have been secured from Rydberg's 'Flora of Colorado'[1] by tabulating the distribution of species listed from Portulacaceæ to Fabaceæ, inclusive. There was no special reason for selecting this particular part of the flora; all that was wanted in this case was a random sample. Cultivated plants and introduced species were excluded and certain of the plants noted by Cary in his 'Biological Survey of Colorado'[2] were added. It is realized that such a sample would not be the best for all purposes. Selections on the basis of growth-habit (woody or herbaceous, annual or perennial, etc.) or of habitat (aquatic, xerophytic, etc.) or of other distinctions, such as date of flowering, promise interesting results but it is believed that the present selection is satisfactory for the purposes in mind, namely, studies of the general relations between latitudinal, longitudinal, and altitudinal (in Colorado) ranges. An attempt is also made to approximate a concrete expression for the rather indefinite "life zones" as given by Cary for Colorado.

RANGE

Table 1 presents the data concerning the extent of range, latitudinal and longitudinal, of 565 Colorado plants. The ranges of latitude are given in three-degree classes, while those of longitude are in nine-degree classes. There is a strong correlation (0.79 ± 0.01) between the two. In other words, a species that ranges far north and south is almost always wide-ranging in an east-and-west direction and vice versa. While this is what we might expect, the following factors should be taken into consideration.

All the species considered here are Colorado plants. On the one hand, more than a third of the species, as will be shown later, are restricted to the Colorado region and hence, having a small range in both latitude and longitude, greatly increase the correlation. On the

[1] 1906, Agric. Experiment Station, Colo. Agric. College, Bull. 100.
[2] 1911, U. S. Dept. of Agric., Bureau of Biological Survey, North American Fauna, No. 33.

Mid-latitude	Range in Degrees of Longitude													
	0–8	9–17	18–26	27–35	36–44	45–53	54–62	63–71	72–80	81–89	90–98	99–107	108–116	Total
55.0—56.9													3	3
53.0—54.9					1			1	1		2		1	6
51.0—52.9				1		4			1		4		7	17
49.0—50.9		1		2		2	2	1			8		3	19
47.0—48.9		1	2	2	2	12	1	2	3	1	2	4		32
45.0—46.9		9	12	4	3	2	3	2		1	2			38
43.0—44.9		20	20	4		4	1	3		1				53
41.0—42.9	1	19	9	2	3	2	4	2						42
39.0—40.9		11	4	1	4	2	1							23
37.0—38.9		6	3	2			1							12
35.0—36.9		5	1	1	2									9
33.0—34.9		10	1	1										12
31.0—32.9	2	7												9
Total	3	89	52	20	15	28	13	11	5	3	18	4	4	275

Table 2.—The relation between mid-latitude and the extent of longitudinal range, expressed in degrees. Based on Colorado plants having ranges of more than 100 sq. degrees. See also Table 3.

other hand, there is a high correlation, as will be shown later, between altitude and latitude, so that those Colorado plants, all coming from an altitude of at least 4,000 ft., that have a large latitudinal range extend into the north where a degree of longitude is not as large, measured in miles or meters, as it is farther south. Table 2 shows the relation between the mid-latitude and longitudinal range of 275 Colorado plants, each having a range of 100 square degrees or more; the correlation coefficient is .66 and the regression is not linear, as indicated by Table 3, which also shows in tabular form what the correlation coefficient expresses, namely,

Latitude	Kilometers in One Degree of Longitude	Average Longitudinal Ranges	
		Expressed in Degrees	Expressed in Kilometers
56	62.385	112.00	6987.120
54	65.567	80.50	5278.144
52	68.669	86.05	5908.967
50	71.687	76.00	5448.212
48	74.616	59.12	4411.298
46	77.453	34.32	2658.187
44	80.196	25.74	2064.245
42	82.840	26.07	2159.639
40	85.383	25.13	2145.675
38	87.821	22.00	1932.062
36	90.152	22.00	1983.344
34	92.373	15.25	1408.688
32	94.481	11.00	1039.291

Table 3.—The second column shows the length of one degree of longitude at the various latitudes indicated in the first column. The third and fourth columns show the average longitudinal ranges of Colorado plants falling in various mid-latitude classes indicated in the first column. The latter facts are derived from Table 2.

that the more northern the species the greater, on the average, is its longitudinal range when expressed in degrees. It would be difficult to determine the ranges in miles for each of these hundreds of species but Table 3 makes it clear that, on the average, the actual extent of range in the east-west direction is greater for those species whose mid-latitude is northern than for the more southern species. Table 4 confirms this on the basis of the maximum latitude attained by each species.

Tables 5 and 6 show the relations between altitudinal range in Colorado and the latitudinal and longitudinal ranges. The average altitudinal range, as shown by the data, is 3958 ft. but it should be remembered that this is the altitudinal range in Colorado, a state that

Maximum Latitude	Range in Degrees of Longitude														Average Longitudinal Range
	0–8	9–17	18–26	27–35	36–44	45–53	54–62	63–71	72–80	81–89	90–98	99–107	108–116	Total	
64—66		2	1	7	3	19	4	2	1	3	18	4	14	78	72.9
61—63									4					4	
58—60						1								1	
55—57				1		1	2	6						10	59.8
52—54		20	35	6	7	4	5	3						80	27.3
49—51		1	3		1	1								6	
46—48		31	11	4	3	2	2							53	20.8
43—45		15	1		1									17	15.1
40—42		5												5	
37—39	1	15	1	2										19	14.9
Total	1	89	52	20	15	28	13	11	5	3	18	4	14	273	

Table 4.—The relation between the maximum latitude attained by species and the extent of their longitudinal ranges, expressed in degrees. Based on Colorado plants having ranges of more than 100 sq. degrees.

Range in Feet of Altitude	Range in Degrees of Latitude														Total
	0–2	3–5	6–8	9–11	12–14	15–17	18–20	21–23	24–26	27–29	30–32	33–35	36–38	39–41	
0— 999			1												1
1000—1999	17	9	6	7	6	6		2	5	2			1		61
2000—2999	10	16	9	9	6	7	2		7	4				1	71
3000—3999	20	21	8	11	11	8	10	3	6	1	2			1	102
4000—4999	7	17	14	9	12	1	7	2	7	6	7				89
5000—5999	6	7	6	9	10	7	5	1	10	4	2		1		68
6000—6999	3	5	3	4	6	4	4		3	4	2	1			39
7000—7999	3	1	1	1	1	2	2		1						12
8000—8999	1						1								2
Total	67	76	48	50	52	35	31	8	39	21	13	1	2	2	445

Table 5.—The relation between the extent of altitudinal range in Colorado and that of latitude. Based on plants, including those of restricted range.

Range in Feet of Altitude	Range in Degrees of Longitude													
	0–8	9–17	18–26	27–35	36–44	45–53	54–62	63–71	72–80	81–89	90–98	99–107	108–116	Total
0— 999	1													1
1000—1999	35	12	3	1	1	3		2	1	2			1	61
2000—2999	37	13	3	5	1	5	1	1		1	1		3	71
3000—3999	53	21	12	2	3	3		3			2		3	102
4000—4999	34	22	9	4	2	4	2	1	4		2	1	4	89
5000—5999	21	15	7	2	3	7	6				4	2	1	68
6000—6999	14	5	4	3	4	1	3	1			3		1	39
7000—7999	4	3	3	1								1		12
8000—8999	1		1											2
Total	200	91	42	18	14	23	12	8	5	3	12	4	13	445

Table 6.—The relation between the extent of altitudinal range in Colorado and that of longitude. See Table 5.

Mid-altitude	Range in Degrees of Latitude														
	0–2	3–5	6–8	9–11	12–14	15–17	18–20	21–23	24–26	27–29	30–32	33–35	36–38	39–41	Total
14000–14999									1						1
13000–13999	2					2			2						6
12000–12999	7	3		1				2	2	1	1				17
11000–11999	13	10	4	2	2	1	2		3	2	2				41
10000–10999	9	8	10	3	2	3	3		11	5	3				57
9000– 9999	12	15	9	3	5		6		6	4					60
8000– 8999	20	12	13	10	5	6	4	1	4	3	3			1	82
7000– 7999	16	17	8	9	17	6	5		8	4	3	1	1	1	96
6000– 6999	8	14	9	14	13	13	7	1	3	3	2		1		88
5000– 5999	6	9	5	9	5	3	5	2	4						48
4000– 4999	1	2	2	3	5	3		2	1						19
Total	94	90	60	54	54	37	32	8	45	22	14	1	2	1	515

Table 7.—The relation between mid-altitude in Colorado and the extent of latitudinal range. Based on plants, including those of restricted range. See Table 8.

does not go much below 4000 ft. or much above 14,000 ft. If it were topographically possible, some of these plants would undoubtedly range much farther. This fact doubtless decreases the correlations shown by the data, $0.16 \pm .03$ between extent of altitudinal and latitudinal ranges and 0.13 ± 0.03 between extent of altitudinal and longitudinal ranges. However, it seems safe to conclude that the correlations between altitudinal and geographic ranges is significantly less than between latitudinal and longitudinal ranges. In other words, many species may range widely geographically without being particularly wide-ranging in altitude and vice versa.

		Range in Degrees of Latitude			
		0—8	9—20	21—41	Total
Mid-altitude	12000—14999	12 (50.0%)	1 (4.2%)	11 (45.8%)	24
	10000—11999	40 (40.9%)	23 (23.5%)	35 (35.7%)	98
	4000— 9999	132 (33.6%)	144 (36.6%)	117 (29.8%)	393
	Total	184 (35.7%)	168 (32.6%)	163 (31.7%)	515

Table 8.—An analysis of Table 7. See below.

The curves for both latitudinal and longitudinal ranges (see Table 1) are unilateral. Each starts off with a large number of species having very restricted ranges; each curve then falls until we come to a number of wide-ranging species, where it rises to a secondary peak. This secondary peak is most marked in the case of the extent of latitudinal range and is due to boreal-montane species. Table 7 shows the relation between the extent of latitudinal range and the mid-altitude of a species. One interesting feature of this relation is more clearly brought out in Table 8, where the extent of latitudinal range is given in classes so divided that each class contains approximately one-third of the total number of species. It will be noted that, among the plants having a mid-altitude of less than 10,000 ft., the species are about equally divided among the three classes but with a slight preponderance of species in the class having a moderate extent of latitudinal range. The case is quite different among the plants having a mid-altitude of 12,000 or more feet; 50% have an extremely restricted latitudinal range, 46% have a great latitudinal range, and only 4% are in the moderate class. It would seem that the plants in the higher parts of Colorado fall distinctly into two classes, those of very restricted range and those of very wide range.

These two extremes, however, balance each other to such an extent that there is no significant difference between the average extent of latitudinal range for different mid-altitudes.

Table 9 shows the relation between altitudinal range in Colorado and the mid-latitude for 227 plants having a geographic range of at least 100 square degrees. It will be seen that both extremely northern and extremely southern species have small average altitudinal ranges while the classes of medium latitude have average altitudinal ranges that are fairly uniformly about 4400 ft. It is well known and is further shown in

Mid-latitude	Average Altitudinal Range
53 to 56°	2833 ft.
49 52	4435
45 48	4448
41 44	4386
37 40	4409
33 36	3333
29 32	2900

Table 9.—The relation between mid-latitude and the average extent of altitudinal range in Colorado. Based on 227 plants having ranges of more than 100 sq. degrees.

detail elsewhere in this paper that southern species tend to be found at low altitudes and northern ones at high altitudes. The altitudinal ranges considered here are artificially cut off at about 4000 and 14,000 ft., the altitudinal boundaries of Colorado. It is quite probable that this is the chief explanation of the apparently reduced altitudinal ranges of northern and southern species, a reduction having no particular biological interest.

EXTREMES OF RANGES

As was shown in the general section on "range," species which extend into high latitudes tend to have wide longitudinal ranges. Figs. 1 to 5 illustrate diagrammatically the extreme ranges for various mid-altitude (in Colorado) classes; for further explanation, see page 350.

The curve for maximum latitude is very irregular, as is shown by Table 4. It may be that there is some biological reason for the accumulation of species at about 38°, 47°, 53°, and 65° latitude and the marked lack of species having northern limits at 50° and 59° latitude, but the irregularity of the curve is doubtless due in large part to the manner of compiling the data for, if a species is said to extend to British Columbia,

Maximum Altitude	No. of Species	Average Latitudinal Extremes	
		Northern	Southern
14000 ft. or more	9	61.0°	37.7°
12000 to 13999 ft.	47	57.7	36.7
10000 to 11999 ft.	72	55.4	36.2
8000 to 9999 ft.	71	51.4	33.8
6000 to 7999 ft.	36	46.8	31.6
Below 6000 ft.	10	45.2	29.9

Table 10.—The relation between the maximum altitude attained in Colorado and the average latitudinal extremes. Based on plants having ranges of more than 100 sq. degrees.

Mid-altitude	No. of Species	Average Latitudinal Extremes	
		Northern	Southern
13000 ft. or more	5	60.8°	38.0°
11000 to 12999 ft.	19	60.2	37.3
9000 to 10999 ft.	54	58.3	37.1
7000 to 8999 ft.	78	54.6	33.6
5000 to 6999 ft.	78	49.5	33.2
Below 5000 ft.	10	45.2	29.9

Table 11.—The relation between mid-altitude in Colorado and the average latitudinal extremes. Based on plants having ranges of more than 100 sq. degrees.

Minimum Altitude	No. of Species	Average Latitudinal Extremes	
		Northern	Southern
13000 ft. or more	1	65.0°	38.0°
11000 to 12999 ft.	4	62.0	38.0
9000 to 10999 ft.	25	60.6	37.2
7000 to 8999 ft.	50	56.0	35.9
5000 to 6999 ft.	48	53.5	35.5
Below 5000 ft.	97	50.8	33.5

Table 12.—The relation between the minimum altitude attained in Colorado and the average latitudinal extremes. Based on plants having ranges of more than 100 sq. degrees.

Maximum Latitude	No. of Species[1]	Average Altitude in Colorado		
		Maximum	Mid-	Minimum
North of 57.9° (Alaska, Greenland)	About 73	11404 ft.	9474 ft.	7688 ft.
49.0 to 57.9° (So. Canada, Labrador)	About 88	10054	7845	5988
37.0 to 48.9° (South of Canada)	About 77	8858	7100	5569

Table 13.—The relation between northern limit of range and average altitudes in Colorado. Based on plants having ranges of more than 100 sq. degrees.

Minimum Latitude	No. of Species[1]	Average Altitude in Colorado		
		Maximum	Mid-	Minimum
37.0 to 40.9° (Not South of Colorado)	About 129	10779 ft.	8844 ft.	7030 ft.
31.0 to 36.9° (So. of Colo., No. of Mexico)	About 57	10464	8110	6179
South of 31.0° (Mexico and Florida	About 55	8133	6352	5115

Table 14.—The relation between southern limit of range and average altitudes in Colcrado. See Table 13.

[1]The number is not the same for each altitudinal class because records of "about" a given altitude were counted as mid-altitude and those of "up to" were counted as maximum altitude.

it was put down as extending to 54° latitude (about the middle of the collected area in British Columbia and falling in the class whose mid-point is 53°), while if it is said to extend to Alaska it was put down as extending to 65° latitude. Now, as a matter of fact, British Columbia and Alaska join each other and, combined, they extend from less than 50° to more than 70° latitude. Doubtless Colorado species are stopping off all along the line but, as the exact northern limit was not given, these mid-points were the only ones that could be used and they are fairly satisfactory when combined in averages with other similar mid-points. The same remarks apply to the data for minimum latitudes.

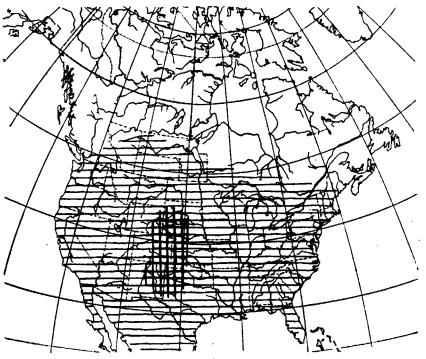
Tables 10 to 12 show the average northern limits and southern limits for the various altitudinal classes. As was to be expected, the higher the altitude the more northern are, on the average, both latitudinal extremes. The correlation coefficients are doubtless large but have not been calculated because of the irregularity of the data upon which they would be based. The averages obtained will be used in the discussion of life zones. Tables 13 and 14 show the complimentary relations.

ALTITUDE AND MID-LATITUDE

The most noticeable thing and the point most emphasized in studies of geographic distribution in mountainous regions is that the more northern species are found in the higher altitudes. Boreal species have southern extensions of their ranges along the north-and-south mountain ranges of North America and, since we take the tips of these often narrow extensions for the southern corners of the range in calculating mid-latitude, we do not get absolutely true expressions of the mid-latitude of the species. It is very desirable to have corrections for altitude in such cases.

It has been suggested, for example, by Hopkins in his papers on the "bioclimatic law," that one degree of latitude is equivalent to 400 ft. of altitude. It seems clear that this, even if it holds true in certain places, is not universal and I understand that Dr. Hopkins takes into account local modifying factors. Without attempting to establish any general law, I have analyzed the data at hand concerning Colorado plants, remembering that mid-latitude was calculated without corrections for altitude and that the altitude data are affected, as regards the minimum altitude of low-altitude plants, by the fact that Colorado does not extend much below 4000 ft.

It is clear that in such an analysis we must not include the species of very restricted geographic range. It has been shown above that half



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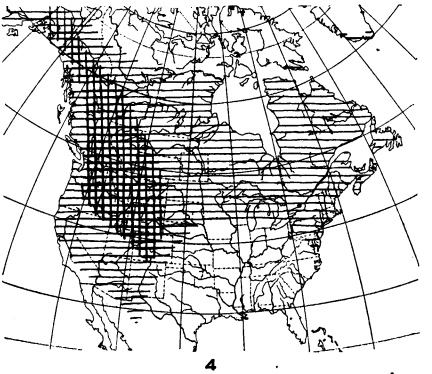

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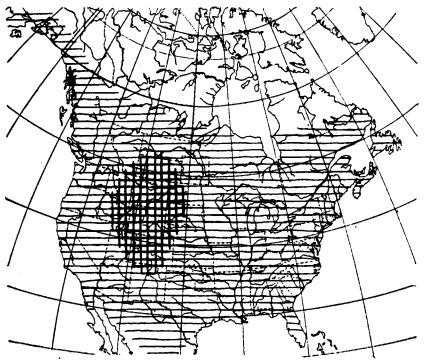

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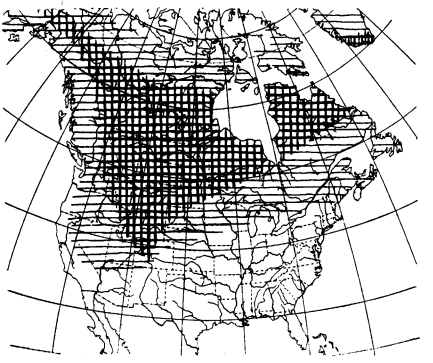

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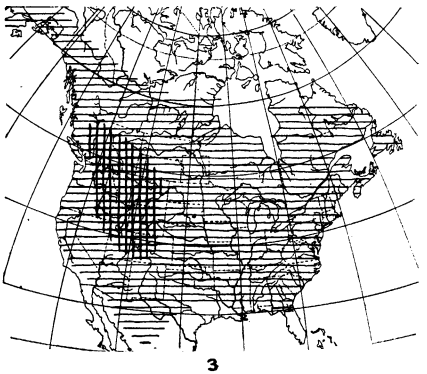

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Figs. 1–5.—Diagrams showing the relation between geographic range and mid-altitude in Colorado. Horizontal lines indicate the area containing at least one species of the given mid-altitude class. Heavier shading indicates the area containing at least half of the species of a given mid-altitude class. Fig .1: average mid-altitude, 4500 ft. Fig. 2: 6500 ft. Fig. 3: 8500 ft. Fig. 4: 10,500 ft. Fig. 5: at least 12,000 ft.

of the high-latitude plants in Colorado are confined to that region; that is, they have a mid-latitude of approximately 39°. If they were included, it would mask the real facts concerning the boreal nature of the other half of the montane species. The same is true of plants of very restricted geographic range occurring at other altitudes. After careful consideration of the frequency curves for extent of ranges and because round numbers appeal to one's sense of the fitness of things, I have confined the following analysis to those species having a geographic range of at least 100 square degrees, as determined by multiplying the extent of latitudinal and that of longitudinal range.

Figs. 1 to 5 illustrate diagrammatically the areas covered by plants having mid-altitudes in Colorado of about 4500, 6500, 8500, 10,500 and at least 12,000 ft. respectively. These diagrams were made up by connecting by straight lines the corners of the ranges as given by Rydberg. Of course the actual ranges do not have straight-line boundaries but the picture obtained by such a process indicates certain features of the actual facts. The diagrams of the areas (indicated by a combination of vertical and horizontal ruling) having at least 50% of the species contained in a given group seem to be most interesting. Such an area for the group of plants having a mid-altitude in Colorado of at least 12,000 ft. spreads out fan-like from Colorado to Alaska and Greenland. The corresponding area for the 10,500-foot group does not go to the East but follows the mountains to Alaska. Going to the other extreme, the corresponding area for the 4500-foot group is confined to the plains and in the eastward direction stops rather abruptly at 100° longitude. These diagrams should not be mistaken for "life-zone" maps and it should be remembered that they are based on straight-line diagrams of the ranges of from only ten to fifty-two plants in each altitude group. Rather more significant conclusions may be reached by the following use of mid-ranges and the correlation methods long employed in the statistical study of variation.

Table 15 shows the relation between mid-latitude and the maximum altitude attained in Colorado by each of 248 plants having a range of at least 100 square degrees, including species concerning which Rydberg merely says that they extend "up to" a given altitude. The correlation is 0.609 ± 0.027.

Table 16 shows the relation between mid-latitude and the minimum altitude at which 227 such plants are found in Colorado. The correlation is 0.515 ± 0.033.

Maximum Altitude	Mid-latitude													
	32	34	36	38	40	42	44	46	48	50	52	54	56	Total
14500						1	1		2	1	3		1	9
13500						1		6	2	1	4	2		16
12500			1		1	2	9	3	6	6	2	1		31
11500					2	1	3	3	4	3			1	17
10500				3	4	9	11	9	10	5	4	1		56
9500	1	2		2	6	9	12	7	1	2	1			43
8500	3	1		1	4	4	8	5	4					30
7500		2	4	2	6	3	1	4						22
6500	1	4	2	2		3	1							13
5500	2	2	1	2		3	1							11
Total	7	11	8	12	23	36	47	37	29	18	14	4	2	248

Table 15.—The relation between the maximum altitude attained in Colorado and the mid-latitude. Based on plants having ranges of more than 100 sq. degrees.

Minimum Altitude	Mid-latitude													
	32	34	36	38	40	42	44	46	48	50	52	54	56	Total
13500													1	1
12500							1							1
11500										1	1	1		3
10500								3	3	1	3	1		11
9500						1	2	1	5	3	1		1	14
8500	1				1	2	9	6	3	3	4	2		31
7500				2	1	4	4	3	2	2	1			19
6500					3	2	4	2	4	4				19
5500	3	1	2	1	4	3	4	6	1	2	2			29
4500	2	8	5	8	12	22	20	11	8	2	1			99
Total	6	9	7	11	21	34	44	32	26	18	13	4	2	227

Table 16.—The relation between the minimum altitude attained in Colorado and the mid-latitude. Based on plants having ranges of more than 100 sq. degrees.

Mid-altitude	Mid-latitude 32	34	36	38	40	42	44	46	48	50	52	54	56	Total
14500												1		1
13500							1		1				2	4
12500									1	2	3			6
11500						2		4	3		2	2		13
10500						1	8	4	6	5	5	1	1	31
9500					2	2	6	4	3	3	2	1		23
8500	1		1	2	1	6	8	3	4	5				31
7500	1		1	1	8	7	8	9	7	2	3			47
6500	3	4	1	2	5	11	15	8	3	1				53
5500		3	4	4	5	6	1	1	1	1				26
4500	2	2	1	2		3	1							11
Total	7	9	8	11	21	38	48	33	29	19	15	5	3	246

Table 17.—The relation between mid-altitude in Colorado and mid-latitude. Based on plants having ranges of more than 100 sq. degrees.

Table 17 shows the relation between mid-latitude and mid-altitude in Colorado of 246 such plants, considering that when Rydberg says a plant occurs at "about" a given altitude this is the mid-altitude in Colorado of that plant. This relation seems to be the most interesting of these three. The correlation is 0.602 ± 0.027, and, as the correlation ratio is 0.615, the regression may be considered to be linear.

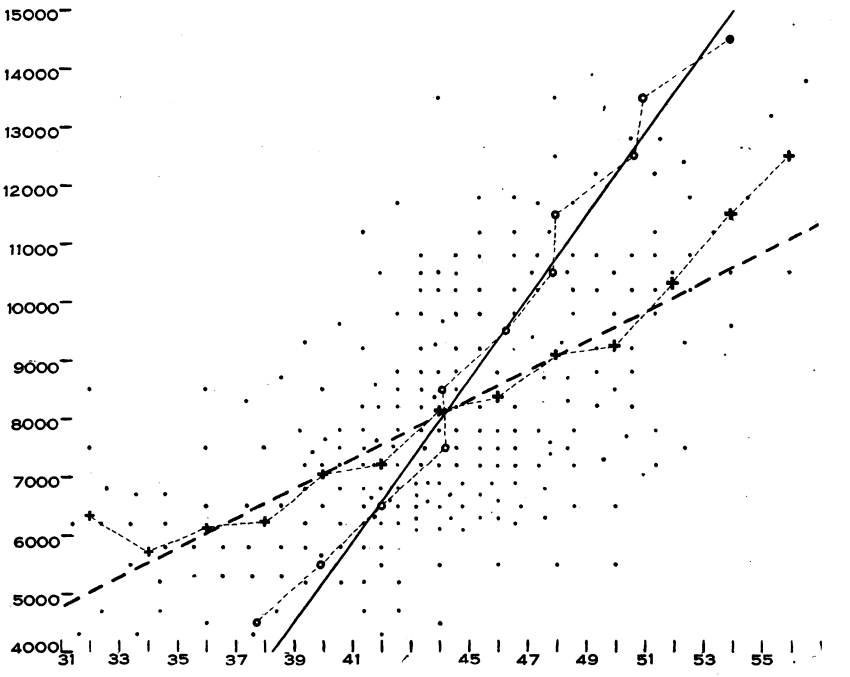

Fig. 6.—The relation between mid-altitude in Colorado and mid-latitude. Dots stand for individual species; circles and crosses, for averages. The heavy lines are regression lines drawn from the formulæ given below.

On the basis of linear regression in each case, we get the following regression formulæ.

Maximum altitude = 266.12 mid-latitude − 1644 ft.
Mid-latitude = 29.90 + .00140 maximum altitude.

Minimum altitude = 216.08 mid-latitude − 3156 ft.
Mid-latitude = 36.23 + .00123 minimum altitude.

Mid-altitude = 250.94 mid-latitude − 2991 ft.
Mid-latitude = 32.47 + .00145 mid-altitude.

The fit of the last set of regression lines to the averages is shown in Fig. 6.

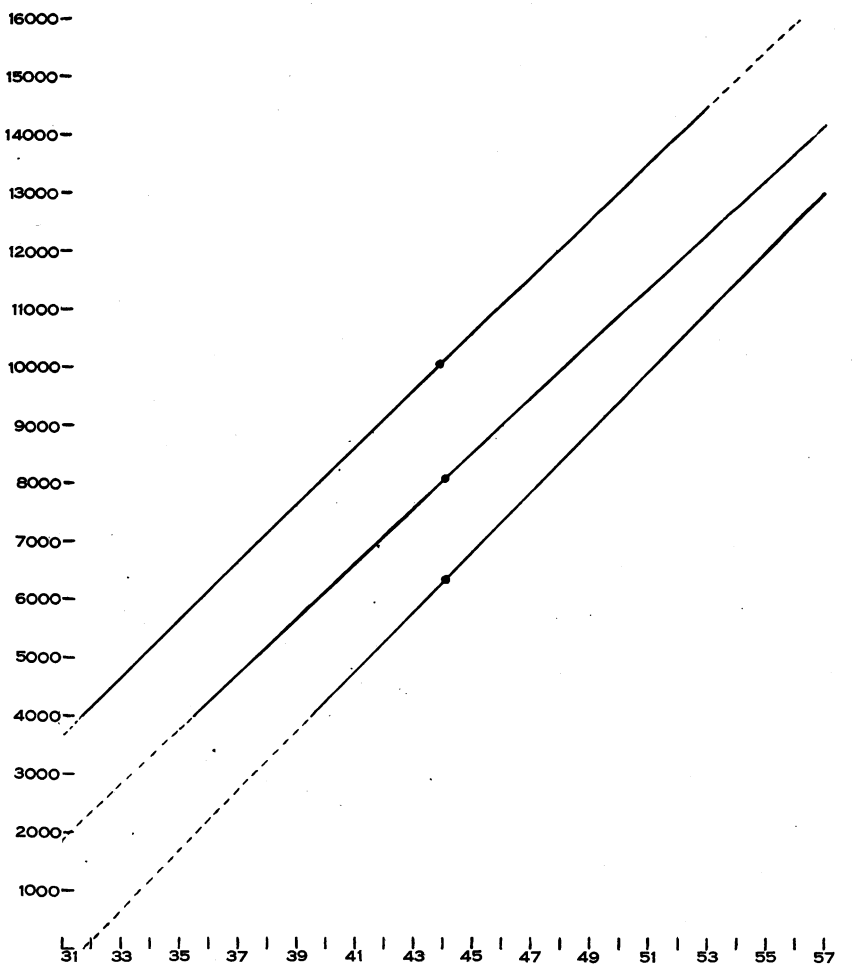

Fig. 7.—Diagrammatic representation of the relation between the maximum altitude (upper line), mid-altitude (middle line), and minimum altitude (lower line) in Colorado and the mid-latitude. See below for further explanation.

It is perhaps permissable to average the two formulæ of each of these sets in order to get the formulæ of single lines that will fit fairly well the averages of both rows and columns. Such averages are

Mid-latitude = .002035 Maximum altitude + 23.48 degrees
= .001943 Minimum altitude + 31.69 degrees
= .002121 Mid-altitude + 27.00 degrees

Mid-altitude	Mid-longitude											
	127	123	119	115	111	107	103	99	95	91	87	Total
14500						1						1
13500							1	1		1	1	4
12500				1			1	1	2	1		6
11500		2		4	1	2		1	3			13
10500	1	4	1	7	3	3	3	5	4			31
9500		3	2	9	3	1	3		1		1	23
8500		3		9	8	3	3	2		2	1	31
7500		1		8	9	14	7	4	3	1		47
6500		1	1	10	4	13	9	6	5	2	2	53
5500		1		1	2	7	7		3	3	2	26
4500						1	3	4	2	1		11
Total	1	15	4	49	30	45	37	24	23	11	7	246

Table 18.—The relation between mid-altitude in Colorado and mid-longitude. Based on plants having a range of more than 100 sq. degrees.

The formula of a line referred to the average mid-altitude and mid-latitude of this material and based on one degree of latitude being equivalent to 400 ft. of altitude is

Mid-latitude = .0025 Mid-altitude—23.93 degrees.

This is not nearly as good a fit to the facts as the formula for mid-altitude given above.

The three formulæ supposed to represent fairly well the facts concerning the conditions in Colorado, as found by a study of these plants, give the lines shown in Fig. 7. In this figure I have taken the liberty of extending the lines to altitudes which do not exist in Colorado. If such extensions are justified, they indicate that, were a portion of Colorado

Mid-altitude	Average Mid-latitude	Average Mid-longitude
13500 ft.	51.0°	95.0°
12500	50.7	99.7
11500	48.0	108.8
10500	47.9	109.1
9500	46.3	111.9
8500	44.1	109.3
7500	44.2	107.1
6500	42.0	105.3
5500	39.9	102.4
4500	37.7	99.4

Table 19.—Showing the average mid-latitudes and mid-longitudes for various classes of mid-altitudes in Colorado. Based on 246 plants having ranges of more than 100 sq. degrees.

at sea-level, the plants there would have a mid-latitude of about 31.7°. Unpublished data in my possession concerning plants near sea-level from Texas to Lower California indicate that this is probably true. In the Merriam system they would represent the Lower Sonoran flora, not, in fact, considered by the Biological Survey to be present in Colorado. If the Colorado mountains ran much higher than they actually do, there would doubtless be plants at 16,000 ft. altitude and the extension of the maximum-altitude line indicates that they would have a mid-latitude of about 50°. Of course, it is never safe to extend generalizations far beyond our facts but, if the facts are determined for a large number of mountainous regions, the determinations being based in each case on a large number of species, we may be able to arrive at a safe generalization.

ALTITUDE AND MID-LONGITUDE

Table 18 gives data based on 246 Colorado plants, each having a geographic range of at least 100 square degrees, for the relation between their mid-altitude in Colorado and their mid-longitude. The correlation

is only +0.16 but the regression is not linear and the correlation ratio is about .39. The average mid-longitude for each thousand-foot class of mid-altitude (disregarding the highest, as one species is manifestly too few to form the basis of an average) is given in Table 19 and they indicate the existing relation. On the average, the plants of low altitudes have mid-longitudes of about 100° in other words, about the eastern border of Colorado. As we go up the mountains the species become more western until we reach about 9500 feet and then they become progressively more eastern until, on the average, they reach about 95°.

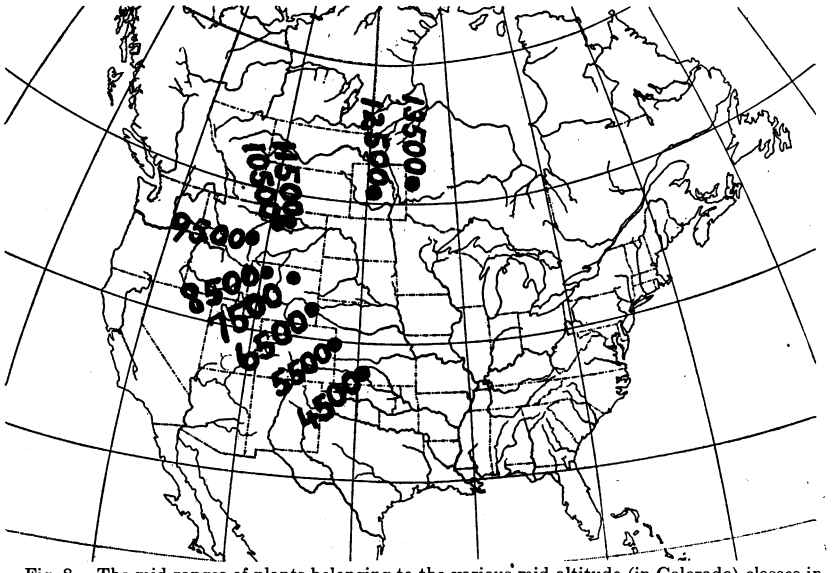

Fig. 8.—The mid-ranges of plants belonging to the various mid-altitude (in Colorado) classes indicated by the numerals.

ALTITUDE AND MID-RANGE

Table 19 and Fig. 8 shows the average mid-range of the species in each thousand-foot class of mid-altitude from 4500 to 13,500. Compare also Figs. 1 to 5, which show diagrammatically the extent of ranges. All of these show that, as we go upward in Colorado from a basic elevation of about 4000 ft., the species become more northwestern in their distribution until we reach an elevation of about 9500 ft. This is probably due to the influence of distinctly Rocky Mountain species. Then there is a sudden turn in the trend, the species becoming more and more northeastern, due, apparently, to the influence of transcontinental boreal-montane species.

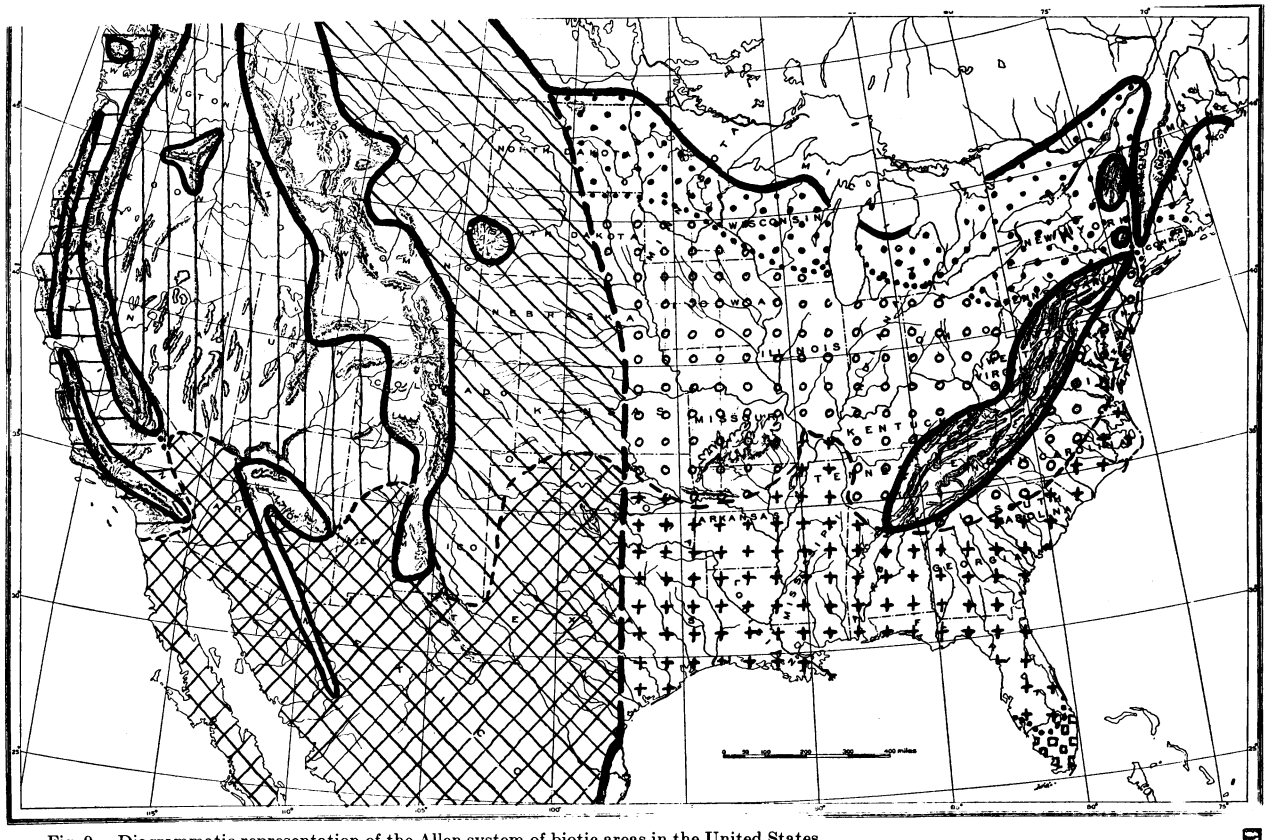

Fig. 9.—Diagrammatic representation of the Allen system of biotic areas in the United States.

Only the Warm Temperate Subregion (boundaries indicated by heavy solid lines) is subdivided in this map and locations of the areas are only approximate, especially in mountainous regions. The Humid Province is shaded by various kinds of dots and the Arid Province by lines (boundary between them indicated by heavy broken line). Boundaries between Subprovinces are indicated by light broken lines. Appalachian Subprovince: Alleghanian Fauna, plain dots (found also south on the mountains); and Carolinian Fauna, circular dots. Austroriparian Subprovince: Louisianian Fauna, cross dots; and Floridian Fauna, square dots. Campestrian Subprovince; Great-Plains District, sloping lines; Great Basin District, vertical lines; Pacific Coast District, horizontal lines. Sonoran Subprovince: lines sloping in two directions.

LIFE ZONES

Livingston and Shreve[1] have recently published a most excellent study of the distribution of vegetation in the United States and of certain climatic factors that are undoubtedly important in connection with it. In the concluding pages they say (p. 528):

> From the preceding discussion, and from considerations presented in Part II, it appears that the system of life-zones worked out by Merriam and now rather widely used in a descriptive way, especially by the United States Biological Survey, will require much modification before it may become at all satisfactory to a serious student of etiological plant geography. It is extremely unfortunate that the actual data on which this system was originally based, and on which its applications are based in current descriptions, do not exist in the published literature. Neither Merriam nor any of his followers has thus far attempted to present the actual basis for the system in form such that a critical study of its good and bad features may be undertaken. Perhaps this may be a main reason why the whole subject of the climatic relations of floral and faunal areas has received so little attention at the hands of students who are able and willing to undertake the complex analyses which are involved in such a subject. The publication of the charts without the data on which they were based, together with the general and official adoption of the system by the United States Biological Survey, have given this important problem the appearance of having been satisfactorily solved—of being a closed subject. Those who have employed this zone system have either refrained from any discussion of its good and bad characteristics, or else they have merely taken the standpoint of advocates, and the lack of the numerical data that are absolutely necessary for a critical study has tended strongly to discourage such inquiries. Also, a sort of authoritative atmosphere that seems to hang over government publications in general, together with the apparent authority and dogmatism that invariably go with well-printed (and especially colored) charts, to the exoteric reader, tend in the same direction, to retard real progress.

Apparently Livingston and Shreve had overlooked, as have so many others, the work of Dr. Allen. A part of the Allen system is diagrammatically shown in Fig. 9. The question as to Dr. Allen's share in originating the zones which have since been worked out in such detail by the U. S. Biological Survey as a result of Dr. Merriam's stimulating influence is, I am sure Dr. Allen would say, of little importance. In his paper read before the Tenth Congress of the American Ornithologists Union, held in Washington, D. C., November 15–17, 1892, he spoke with his characteristic kindness and modesty as follows.[2]

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[1]1921. 'The Distribution of Vegetation in the United States, as Related to Climatic Conditions.' Carnegie Inst. of Washington, Publication No. 284.

[2]Quoted from The Auk, X, pp. 143, 144. The 1871 paper to which reference is made was in Bull. Mus. Comp. Zool., II, No. 3; the 1878 one was Bull. U. S. Geol. and Geogr. Survey (Hayden), IV, pp. 338–344. In 1892 Dr. Allen published a detailed study on 'The Geographical Distribution of North American Mammals,' Bull. Amer. Mus. Nat. Hist., IV, pp. 199–243, Pls. v–viii (colored distribution maps). Dr. Merriam's papers appeared at approximately the same time: 1890, North American Fauna, No. 3; 1891, North American Fauna, No. 5; 1892, Proc. Biol. Soc. Wash., VII, pp. 1–64, with colored map.

In comparing the present scheme of faunal areas of North America with those employed by Dr. Merriam in his recent well-known admirable papers on the geographical distribution of North American mammals, so frequently cited in the preceding pages, it will be noticed that there is a striking agreement in their number and boundaries, although a few new minor divisions have here been introduced; yet the terms employed for their designation are to a great extent different. As already intimated, the present system of classification and nomenclature is a further development of that first instituted by me in 1871, and used later in 1878, and now carried out in greater detail and extended to the whole North American Continent. The present revision of the subject is therefore not to be looked upon as unfriendly criticism of Dr. Merriam's classification and nomenclature, which he evidently adopted provisionally, selecting such terms as would suffice to clearly indicate the areas under discussion; his attention was given mainly and most successfully to an elucidation of the facts of distribution; a detailed consideration of the nomenclature of the subject was outside of his special field.

Much more important for the science of distribution are the differences between the two systems as published. Of these, Dr. Allen said in the same paper (pp. 147–148):

The first discrepancy between Dr. Merriam's classification and my own that requires notice is in respect to the primary divisions of the North American Region, which he first termed "Provinces" and later "Regions," with the prefixes "Boreal" and "Sonoran" respectively for the "Cold Temperate" and "Warm Temperate" *Subregions* of the present writer. The use of Boreal, however, as shown above, was not an innovation; but the term "Sonoran" was used in a new and greatly extended sense, the term Sonoran being applied to a region identical in geographical extent with the Warm Temperate,—a designation previously used for the same area,—and hence including the region east of the Mississippi (as well as that west of it), from the Great Lakes and southern New England south to Florida and the Gulf Coast. The terms "Sonoran" and "Sonoran Province" were used as early as 1866 by Prof. Cope, and also later by Cope, Heilprin, and others, for a region of comparatively small extent, consisting of Sonora and adjoining portions of Arizona and New Mexico. In 1887 Heilprin extended the region to include "the peninsula of Lower California, the State of Sonora in Mexico, New Mexico, Arizona, and parts, not yet absolutely defined, of Nevada, California, Texas, and Florida," and modified its title by calling it the "Sonoran Transition Region." The Sonoran Province or Region of these authors is thus not at all the "Sonoran Region" of Merriam, which is an area of much greater extent and of higher rank. The term Sonoran, used in this extended sense, seems at least inappropriate if not misleading, as there are few if any strictly "Sonoran" types represented in that portion of the United States situated to the eastward of the Mississippi River. The more descriptive and appropriate designation of "Warm Temperate" is therefore preferred for the region in question, since it not only has priority, but is in harmony with the terms Arctic, Cold Temperate, and Tropical, used currently for other coördinate areas of the continent.

Another, and perhaps the only other, important discrepancy between Dr. Merriam and myself is in respect to the primary subdivisions of the Warm Temperate or "Sonoran" Subregion. Here the difference is in respect to classification, Dr. Merriam dividing the Warm Temperage into two transcontinental divisions which he

terms respectively "Upper" and "Lower Sonoran"; while according to my best judgment the primary division is in a meridional line into an eastern and a western division, which I have termed respectively Humid and Arid Provinces, borrowing the terms from Dr. Merriam, who has used them in the same geographical sense but not in the same nomenclatural relation, as already shown in preceding pages. As the evidence, pro and con, has already been submitted (see *antea*, pp. 128–131, and Bull. Amer. Mus. Nat. Hist., IV, pp. 230–232), it is unnecessary to rediscuss the matter here.

The interesting difference pointed out in the last quoted paragraph may be expressed by saying that, according to the Allen system, humidity is considered to be a more potent factor controlling distribution within the borders of the United States than is temperature, at least outside of the higher mountains. Dr. Allen also divided his Campestrian subprovince longitudinally into Great-Plains, Great-Basin, and Pacific-Coast districts, a point that the Biological Survey apparently considers of minor importance. I am attempting to analyze, with these points in mind, the distributions of more than a thousand species and, although the analysis has not yet reached a point that will permit definite statements, the indications are that Dr. Allen was right in each case.

However, to return to the quotation from Livingston and Shreve, it may be that these authors were so engrossed in their important work on climatic factors that they have naturally failed to recognize fully the importance of other sorts of work. The early theories as to the climatic bases of the life zones that have been adopted by the Biological Survey may be left out of account. What has been accomplished is that the Survey's field men have done an unsurpassed piece of work in accumulating data concerning the distribution of mammals and birds (incidentally other forms also), especially in western United States. They have correlated these data with their accepted zones and these are the data upon which the zones are now based.

It is true that apparently the Biological Survey zones are now based on species primarily, leaving future work to discover the exact climatic factors controlling the distribution, rather than mapping climatic factors first and subsequently discovering the way in which these factors have, if they have, influenced distribution. Really, this method of attacking the problem seems rather logical. What seems more serious is that these zones are primarily nothing but an indefinite expression of the northernness or southern-ness (in mountains the highness or lowness) of a species or of a fauna or flora.

In suggesting[1] the geographic average as a method for the study of distribution I said:

[1]1921, American Museum Novitates, No. 5.

Students of the distribution of animals and plants have divided North America, especially United States, into sections, within each of which the fauna or flora, or both, is believed to be more or less homogeneous and more or less distinct from other, corresponding sections. I must confess that these sections seem to me less distinct than they once did. It is characteristic of human psychology that we classify and make categories where there are no definite classes or categories. We speak of north, east, south, and west. When we go more deeply into the subject we speak of northeast, southeast, and so on. At sea, however, we box the compass by such gradual steps that we have a continuous circle with no separate divisions. This does not mean that "north," "east," and so on are not convenient and useful conventions but, as a matter of fact, they are only very general terms. In the same way, there is no definite "arctic-alpine," "austral," and so on, and a definiteness can only be maintained for these zones by a special selection of "indicator species" or something of that sort. If this procedure be accepted, almost any sort of system of zones may be devised by selecting appropriate "indicators."

On the other hand, some system is convenient and useful. The carefully investigated system of Merriam, based on the fundamental studies of Allen, has been widely accepted. Can we take the proposed biotic areas and get some concrete expression for them that will be based on the biota as a whole? This expression should, if possible, be something that will help us to say with a fair degree of assurance that a given limited area or a given species belongs in this section or that.

In that paper I made provisional suggestions as to the latitudinal averages for life zones along the Atlantic Coast. It was necessary there to make guesses as to how the Biological Survey would place certain species or areas. In Colorado we have the advantage of a published Biological Survey report. Although what follows was intended to be held until our report on the western work of the American Museum's Department of Entomology had been completed, it may be of interest to publish in this connection the analysis, as far as made, of at least the mid-latitudes for the Colorado zones.

Cary in his report on 'A Biological Survey of Colorado'[1] defines the life zones of that state in two ways: (1) by a table showing the extreme altitudinal limits of zones in Colorado, and (2) by citing what he considers to be typical animals and plants of each zone. The table of altitudes seems to be very carefully worked out, different limits being given for northeast and southwest exposures as well as for northern and southern Colorado. Furthermore, this table was doubtless drawn up as the result of many observations in the field in which the record made in each case was that of the general impression created by the environment. It is quite probable that the table represents the Biological Survey's ideas of life zones more accurately than do the individual species of plants which were doubtless selected as typical species by men who were not specialists in botany and who had not given careful attention to the distribution of these plants outside the area covered by their field work.

[1]1911, U. S. Dept. of Agriculture, Bureau of Biological Survey, North American Fauna, No. 33.

	Data from Cary's	Upper Sonoran	Transition	Canadian	Hudsonian	Arctic-Alpine
Maximum Altitude	Table	6600 ft.	8175 ft.	10475 ft.	11425 ft.	
	Plants	7196	9240	10750	12500	13087 ft.
Mid-altitude	Table	**5300**	**7388**	**9325**	**10950**	**12700**
	Plants	**5718**	**7346**	**8813**	**10477**	**10940**
Minimum Altitude	Table		6600	8175	10475	11425
	Plants		5500	6906	9364	8714

Table 20.—Altitudinal averages for various "life-zones" in Colorado. Based on Cary's table of altitudes and Rydberg's data concerning Cary's "typical" plants.

		Upper Sonoran	Transition	Canadian	Hudsonian	Arctic-Alpine
Averages based on regression lines and Cary's table of altitudes	Maximum Latitude	46.5°	52.7°	56.0°	58.8°	61.0°
	Mid-latitude	**39.7**	**43.0**	**45.6**	**47.8**	**50.6**
	Minimum Latitude	31.5	34.2	36.0	37.0	37.9
Averages based on Rydberg's data concerning Cary's "typical" plants	Maximum Latitude	47.9	51.9	59.2	57.7	60.9
	Mid-latitude	**39.4**	**42.7**	**46.4**	**46.1**	**49.2**
	Minimum Latitude	30.7	34.3	36.4	36.7	37.0

Table 21.—Latitudinal averages for various "life-zones." Based on data as indicated in the table.

Averaging the altitudinal limits given in Cary's tables for the various zones and estimating average mid-altitudes, we get the results shown in Table 20. The table also shows for comparison the average altitudes of the plants cited by Cary as typical of each zone, the averages being calculated from data given by Rydberg in his 'Flora of Colorado.' It will be seen that there is fairly close agreement in the lower zones but not in the upper, strengthening the belief that the Survey's field men were not altogether fortunate in their selection of "indicator" or "typical" plants, especially in the higher zones which were doubtless not studied by them as thoroughly as were the lower ones.

Given the average altitude in Colorado of a group of species, it is easy to calculate the average mid-latitude of that group from the regression formulæ given on page 355. The results of such calculation are given in Table 21. This table also shows the average mid-latitudes of the plants which Cary cited as typical of the various life zones in Colorado. It will be noticed that, on the average, the plants cited as typical of Hudsonian are not more northern than those cited as typical of the Canadian. Believing that, as stated above, Cary was not particularly fortunate in the selection of certain of these plants, I would be inclined to lay greater stress on the mid-latitudes derived from the altitudes given in his table.

Table 21 also suggests probable average maximum and minimum latitudes for the various zones, based on both altitude and indicator plants. As explained in the section on Extremes of Ranges, the data on which these averages are based is not entirely satisfactory and I have not worked out the formulæ of the regression lines. The figures given are probably, however, fairly close approximations.

If the reasoning followed here be justified, it seems possible to make a "first approximation" to a definition of the latitudinal element involved in the conception of these zones. It may be said that species in a typical Upper Sonoran region have an average mid-latitude of about 40°; Transition, 43°; Canadian, 46°; Hudsonian, 48°; Arctic Alpine, 50° N. The average for the Arctic Alpine is based on rather too few cases to be good even for a first approximation; probably 52° is nearer right and, since the "zones" themselves are convenient conventions rather than real entities, we might agree to move "Hudsonian" up to an average mid-latitude of 49° N. Then we could easily remember that, starting with Upper Sonoran at 40°, the average mid-latitude of each succeeding zone is three degrees more northern. Judging from the average mid-latitude (31° N.) of 69 plants cited by Bailey as typical of the Lower Sonoran in New Mexico, the break in average latitude between it and the Upper Sonoran of Colorado is as great as that between Upper Sonoran and Hudsonian in Colorado. Upper Sonoran sweeps

boldly to Canada in the survey maps, while Lower Sonoran is not recognized as a zone in Colorado although a number of Bailey's typical Lower Sonoran plants do occur there. Perhaps there is a distinct break between the distribution of species to which Allen, in the paper quoted above, insisted the term Sonoran should be restricted (a large part of the Lower Sonoran of Merriam) and what Merriam called Upper Sonoran. On the other hand, it may be that the conception of zones in Bailey's 'Biological Survey of New Mexico' is different from that in Cary's 'Biological Survey of Colorado,' a point which is being investigated.

It happens that 68 of the plants considered in this paper are recorded from Fort Collins, Colorado, by Rydberg. They have an average mid-latitude of 42.5° N. This is, on the scale just suggested, rather close to typical Transition. Cary's map puts Fort Collins in Upper Sonoran near its junction with Transition. "Samples" which I have in the same way from other Colorado points show the following average mid-latitudes. Grand Junction, 39.2°; Lamar, 39.8°; both close to the suggested typical Upper Sonoran. Trinidad, 40.3°; Boulder (plains), 40.6°; Durango, 40.8°; Colorado Springs, 41.0°; slightly northern but still good Upper Sonoran. Mancos, 41.6°; getting on toward Transition. Walsenburg, 42.1°; more southern that Fort Collins (42.5°) but verging on Transition. Ouray, 44.4°; Pagosa Springs, 44.6°; more northern than typical Transition but not yet Canadian. Steamboat Springs, 45.3°; fairly good Canadian. Tennessee Pass, 47.9°; either typical Hudsonian or a little too southern, depending on the convention adopted.

Now, each of these averages is based on too few species to give good statistical results but they will serve as illustrations. It will be noted also that mid-longitude has not been considered but neither does the Merriam system take it into account except for the secondary division along the 100th meridian. The illustrations clearly show how gradually one zone merges into another and indicate that few places are typically one zone or another. Such being the case, some may doubt the desirability of retaining the zonal names at all. If we want an expression for the northern-ness or southern-ness of the group of species living in a given place, for the purpose of telling farmers what crops are likely to succeed there or for any other purpose, it might be better to go directly and rather more accurately at the task and determine the average mid-latitude of the group. Such average mid-latitudes could be plotted on a map and places having mid-latitudes of about the same value could be connected by iso-some-name-or-other lines. Such a map would be more definite than one painted in five colors, but whether it would be of greater practical use than a pentamerous system would depend somewhat on the purpose in mind.