

AN ECOLOGICAL SURVEY OF ISLE ROYALE, LAKE SUPERIOR

PREPARED UNDER THE DIRECTION OF
CHAS. C. ADAMS.

A Report from the University of Michigan Museum, published
by the State Biological Survey, as a part of the Report of the
Board of the Geological Survey for 1908.

LANSING, MICHIGAN
WYNKOOP HALLENBECK CRAWFORD CO., STATE PRINTERS
1909

V. Avian Succession.....	20
1. General Remarks.....	20
2. Succession on Isle Royale.....	20
a. The Aquatic Association and Habitat.....	21
b. The Shore and Marsh Association and Habitat.....	22
c. Bog forest Association and Habitat.....	22
d. Aspen-birch Association and Habitat.....	23
e. The Climax Association or Formation and Habitat.....	23
3. Internal Factors.....	24
4. Environmental Factors.....	25
5. Environmental and Associational Convergence.....	25
6. Succession and Environmental Evolution.....	26
7. The Relation of Succession to Organic Evolution.....	26
VI. Some Principles of Succession.....	27
VII. Some Advantages of a Knowledge of the Laws of Succession.....	28

Contents

4. The Fall Migration of Birds at Washington Harbor, Isle Royale, Lake Superior, by Max Minor Peet.....	1
I. Introduction.....	1
II. The Environment.....	2
1. The Clearing.....	2
2. The Forest.....	2
3. Food.....	3
III. The Weather Conditions and Migrants.....	3
1. Weather Conditions.....	3
2. The Bird Migrants.....	3
a. Warblers.....	3
b. Sparrows.....	4
c. Hawks.....	5
d. Owls.....	5
e. Thrushes.....	5
f. Other Birds.....	5
IV. Large Bird Waves.....	6
1. First Wave.....	6
2. Second Wave.....	7
3. Third Wave.....	7
4. Fourth Wave.....	7
5. Fifth Wave.....	8
6. Sixth Wave.....	8
V. The Relation of Weather to Migration.....	8
1. Influence of Wind.....	9
2. Influence of Temperature.....	9
3. Influence of Barometric Pressure.....	9
4. Condition of the Sky.....	9
5. Summary and Conclusion.....	9
VI. The Routes of Migration.....	9
VII. The Perils of Migration.....	10
1. Fatigue.....	10
2. Natural Enemies.....	11
3. Blunders and Fatalities.....	12
5. The Ecological Succession of Birds, by Dr. Chas. C. Adams.....	12
I. Introduction.....	13
II. Representative Literature on Habitats And Succession.....	14
1. Habitat Preference.....	14
2. Succession.....	16
III. The Major Avian Environments.....	16
IV. Minor Avian Environments and their Associations.....	19

6. The Coleoptera of Isle Royale, Lake Superior, and their Relation to the North American Centers of Dispersal, by Dr. Chas. C. Adams.....	31
I. Introductory Note.....	31
II. Notes on the Habitat Relations of Beetles.....	31
III. The Succession of Beetle Associations.....	32
1. The Lake Shore and its Beetle Associations.....	33
2. Rock Openings and Associated Beetles.....	33
3. Lake, Pond and Bog Habitats and Associations.....	33
4. The Forests and Their Beetle Associations.....	34
IV. The General Characteristics of the North American Beetle Fauna.....	34
1. Compiled Generalizations on the Fauna.....	34
2. Comments on the Preceding Generalizations and on the Literature of Geographic Distribution.....	47
V. The Present Centers of Dispersal of the Beetle Fauna.....	47
VI. The General Characteristics and Affinities of the Isle Royale Fauna.....	51
1. Faunal Characteristics.....	51
2. Miscellaneous Notes on the Fauna.....	52
VII. Lists of Isle Royale Beetles.....	52
1. List of Species Collected in 1905.....	52
2. Supplementary List of Isle Royale Beetles, by A. B. Walcott.....	59

THE FALL MIGRATION OF BIRDS AT WASHINGTON HARBOR, ISLE ROYALE, IN 1905. BY MAX MINOR PEET.

I. INTRODUCTION.

Our observations of the fall migrations of birds at
Washington Harbor extended over the period from
August 18 to September 22. A hasty examination was
made of the bird life here before migration had really set
in (August 5 to 8), and the observations gathered at this
time, together with the records obtained the previous

year, gave us an insight into the conditions existing there. This was important, as migration had commenced while we were still at Siskowit Bay.

Isle Royale is situated about fifteen miles from the north shore of Lake Superior, and lies nearly northeast by southwest. Situated as it is several miles from the north shore and with an unbroken stretch of water 100 miles across lying south of it, the island makes an excellent point for the migrants to stop before crossing the lake. The birds seemed to center at Washington Harbor as if focussed there from the north shore, and in all probability the birds observed there represented the avian life of many square miles on the mainland. Records were kept of the species seen each day and are given in tabulated form at the end of this paper.

II. THE ENVIRONMENT.

1. *The Clearing.* Under the head of clearings, we include the three artificial clearings and the narrow roads connecting them. The first of these was situated on the shore of Washington Harbor, near its head and close to the mouth of Washington River. The trees had been entirely cleared away over an area of several acres, making a rectangular clearing which had been seeded to timothy and short grasses. The waves had cut away the soil along the shore leaving a nearly vertical bank two or three feet high, in some places overhanging the water. The land gradually rises from the water's edge, more rapidly at the southern end where a low bluff is formed. On this bluff the Club-house stands, and below, nearer the lake, is a little group of four small houses, the largest of which we used as a camp. Other buildings were also located in this clearing. Part of the clearing was overgrown with brush and small trees. These had been burned and the debris left where it fell. Many small bushes, weeds, and vines sprang up among the fallen logs and branches, forming an ideal retreat for the smaller birds such as warblers and sparrows. The rank growth of the vegetation made it almost impossible to penetrate any distance into it. Here the Lincoln Sparrows were most abundant during their migration. As the soil was very shallow, the timothy grew short and scattering, and probably furnished little protection for the birds, as it was cut about the middle of August. Near the road leading to the second clearing to the north was a small spot cleared for a garden. This bare ground was the favorite feeding place of the Horned Larks. On the short, steep slope which skirted the road to the second clearing, thirty or forty stumps had been left. These were the favorite perches for the Sparrow and Sharp-shinned Hawks, and the tops of many of them were covered with the harder portions of grasshoppers, these insects forming one of the principal foods of these birds. Three narrow roads or trails left this clearing, one to the second clearing, one to the head of Siskowit Bay, and the third to Lake Desor. The first of these was kept open and had originally been much wider than at present, being narrowed by a fringe of alders, birches, and small bushes together with young balsams and spruces.

The second clearing, consisting of 3 acres, was divided into two parts, a grassy tract and a garden in which potatoes, carrots, etc., were grown. From this a road (*Fig. 56*) led to the third clearing, called Wendigo, which was about the same size, and contained two old log houses and two or three decaying sheds. Few of the stumps had been removed and hawks used them as perches. The ground was overgrown with short, nearly dead grass. White-footed mice were abundant in these clearings after nightfall, and many Northern Hares were seen along the roads just at dusk narrow road wound past the clearing and off along the base of the bluffs for a mile or more to several abandoned cuts made by the old mining company. It was along these roads, which ran approximately north-east and south-west, that the bulk of the migrants passed. Even during the heavy migration comparatively few birds were observed in the dense forests, although many passed along the river. It has been generally noticed that many birds, the smaller migrants in particular, as the sparrows and warblers, prefer the borders of clearings, and a long narrow road through heavy timber and bordered by bushes and small trees, appeared to be an ideal place for them. All the clearings were surrounded by the dense, coniferous forest except the first which fronted on the lake.

2. *The Forest.* The forest may be considered to consist of all that portion which has not been entirely cleared of the native trees. The major part consists of balsam and spruce with a heavy undergrowth of ground hemlock, and in places along the river there are dense thickets of alder. The soil in the depressions is damp, with small pools of water standing on the decayed leaves. Washington River flows through the lower portion of the forest. It is a stream sixty or seventy feet wide near its mouth, but it rapidly diminishes in size, so that near Wendigo is not more than five or six feet across. However it becomes much more rapid and the banks are covered with refuse and fallen logs and branches.

Few resident birds were found in the dense, dark forest, and still fewer migrants were found there. During very severe weather the Chipping Sparrow sometimes retreated to the protection of the balsams, but it never wandered far from the open. The White-throated Sparrow was: quite common, breeding in the forest along the river, and even during migration it was found most abundant in the underbrush. The Sharp-shinned and Sparrow Hawks rarely remained here, except during the night, or in very stormy weather. The warblers were scarcely ever found in the heavy timber, but along the more open part of the river and in the alder thickets they were abundant. By far the most common warbler along the river was Grinnell's Water Thrush. This bird was confined almost entirely to the forest, and especially to that portion, bordering the stream where fallen logs and rubbish furnished their favorite haunt. They seemed to be migrating in pairs, but no immature birds were seen with them. During the stormy period lasting from September 2 to 5, the Water Thrush came out into the road and clearings. The Wilson and Olive-backed

Thrushes bred in the forest, but during migration they preferred the open and were only occasionally found in the heavy timber. The path skirting the river was also a favorite route for them. The maple brush which bordered the forest in many places was the favorite habitat of the Hermit Thrush. This and the diminutive Winter Wren were sometimes met with among the very densest conifers. Among the other birds occurring here were the Brown Creeper, Golden-crowned Kinglet, and Red-breasted Nuthatch. Chickadees were nearly always present. This habitat was chosen by nearly all of these birds during migration, probably because it furnished the right kind of food and excellent protection. Many other species were occasionally met with, but they were only wanderers and no particular significance can be attributed to their occurrence here.

3. *Food.* The clearing afforded abundant food for nearly all species. The grassy meadows and dry hillsides were infested with great swarms of grasshoppers which rose up before one as a buzzing cloud. Nearly all the birds taken, among which might be mentioned the Sharp-shinned and Sparrow Hawks, Thick-billed Redwing, Rusty Grackle, Flicker and Nighthawk, fed to a greater or less extent on these pests, as was shown by an examination of their stomachs. Many other species of insects were abundant, blackflies, deer flies, and "no-see-ums" being at times almost unbearable. The Deer Mouse was very plentiful, and also the Northern Hare, as many as twenty or thirty of the latter being seen at one time feeding in the road between the first and second clearings. These animals together with the large number of Red Squirrels found along the edge of the road furnished abundant food for the owls and migrating hawks. Seeds were plentiful and constituted the principal food of the Savannah and other sparrows. Wild red raspberry bushes were common and these berries together with several other kinds were greedily eaten by many of the birds, especially the Cedar Waxwings. A few wild flowers grew in the clearing and these were occasionally visited by the Ruby-throated Humming Bird. Insect life characteristic of coniferous forests was probably abundant because the Brown Creeper, Chickadee, and Golden-crowned Kinglet fed here almost exclusively; otherwise this habitat did not appear to furnish much food for the migrants.

III. THE WEATHER CONDITIONS AND MIGRANTS.

1. *Weather Conditions.* Throughout the period of thirty-five days during which observations were made on migration at Washington Harbor, a daily record was kept of the direction of the wind, temperature, and the general weather conditions. The barometric readings, taken at Port Arthur, thirty-five miles nearly due north from the Harbor, are from the daily weather maps. A comparison of my observations on the weather with those from Port Arthur shows that the conditions at the two places were much the same, so I feel safe in assuming the

barometric pressure at the island to be approximately that recorded just to the north. An examination of the daily weather maps for this period shows that the same isotherms and isobars include both localities. Unfortunately Port Arthur is the most northern station on the daily weather map that could have any appreciable effect on the bird life of Isle Royale. A reference to the areas of high and low pressure indicates that conditions similar to those on the island probably prevailed over a large area to the north of it.

The records for the entire thirty-five days are included in the following table. The readings were made between 7:30 and 8 A. M. Other readings were made during the day and where these are of importance I will give them under the particular discussion upon which they bear. All temperature readings were in Fahrenheit. The dates of the large bird waves are starred.

TABLE.

Date.	Barometer.	Temperature, F.	Wind.	Sky.
Aug. 18.....	29.7	62	S.	Rainy.
19.....	29.7	55	W.	Clear.
20.....	29.7	58	S. W.	Partly cloudy.
21.....	29.6	62	S. W.	Cloudy.
22.....	29.9	52	W.	Clear.
23*.....	29.9	58	N. W.	Clear.
24*.....	30.2	53	N. W.	Clear.
25*.....	30.3	50	None.	Clear.
26*.....	30.2	54	None.	Cloudy.
27.....	30.1	53	None.	Clear.
28.....	30.1	56	S. W.	Clear.
29.....	29.9	61	N. E.	Rain.
30*.....	29.8	56	N. W.	Clear.
31*.....	30.1	46	N.	Clear.
Sept. 1*.....	30.1	52	N. E.	Cloudy.
2.....	30	44	N. E.	Hard rain.
3.....	40	N. E.	Hard rain.
4.....	44	N. W.	Clear.
5*.....	30.1	39	N. W.	Partly cloudy.
6*.....	30.1	42	N. W.	Clear.
7.....	30.1	45	None.	Rainy.
8.....	30.2	52	S. W.	Clear.
9.....	30.1	45	N. W.	Clear.
10.....	30	52	N. W.	Clear.
11.....	29.8	52	N.	Clear.
12*.....	30.2	42	N. W.	Clear.
13*.....	30.4	29	W.	Clear.
14.....	30.2	47	S. E.	Rain.
15.....	29.8	52	None.	Clear.
16*.....	30	50	E.	Cloudy.
17.....	29.9	53	N. E.	Clear.
18*.....	29.8	52	N. E.	Clear.
19.....	29.4	59	N. W.	Cloudy.
20.....	29.8	46	W.	Clear.
21.....	29.5	54	W.	Clear.

*Large bird waves.

2. The Bird Migrants.

a. *Warblers.* Many warblers nest on the island, and so the first indication of migration in this family was the tendency to flock preparatory to the trip south. At first these flocks consisted only of the parent birds and young, but as these wandered about they were joined by other families and, impelled by the gregarious instinct which is so strong after the breeding season, kept together and formed one large flock. Beginning to feel the migratory impulse they were restless and wandered about over considerable territory, probably being joined from time to time by other families, and often by other forms, for a flock of migrating warblers is rarely composed of a single species, as are the flocks of so many birds. Small bands of Myrtle Warblers were seen feeding in the balsam trees on August 18, and on August 19 the first flocks of Tennessee Warblers appeared. However, these were scattered and composed of only a few birds, mostly adults. On August 20 I saw the first Redstarts, and from then on different species were constantly making their appearance. On the 26 the bulk of the Black Poll Warblers began to arrive, only a few adults being seen among the hundreds which came to

the clearing. It is a significant fact that, in all cases where the young were not in company with the adults, the latter and not the former, as some have reported, preceded. In the case of the Tennessee Warblers three days elapsed before there was any noticeable number of young, while toward the last of the migration the young greatly outnumbered the adults. Throughout the entire migration, however, the immature Blackpolls outnumbered the old birds, in fact the latter were very rarely seen. Only two Black and White Warblers were observed, and only four small flocks of Black-throated Green Warblers.

The principal feeding grounds were among the alders, birches and balsams which lined the more open parts of the road. In the narrow strips where the high conifers bordered the path, the bird life was scanty, and when these portions were encountered by the migrating warblers they were quickly passed, often in a single flight. The Myrtle Warblers were the only ones observed to linger among these large trees.

The food of the warblers consisted largely of insects, most of it being gleaned from the leaves and twigs of the bushes, but some was taken on the wing. The open area here afforded a greater supply of insects than the forest, and this may possibly have played a part in the choice of this particular habitat.

On cold mornings, when the thermometer registered about 45° F. or below, the warblers would remain hidden in the dense underbrush, not appearing until about nine o'clock, when the sun would be quite warm and the usual morning fog be dispelled. This fog hung over the harbor nearly every morning and frequently was so dense that Beaver Island, in the harbor, was almost invisible. It was often blown back over the clearings, and until it raised, the majority of the birds remained quiet. The height of the migrating movement seemed to be from the middle of the afternoon until nightfall; how far into the night it extended I was unable to ascertain, but the cries of innumerable birds could be heard until nearly morning. These cries, usually of a single faint syllable, were possibly uttered to help keep the birds together. When the migrating flock had to cross the clearing it was a noticeable fact that they rarely flew directly across, thus exposing themselves to the attack of the numerous hawks, but instead kept near to the ground, making short flights from bush to bush, and where these were scattered they alighted directly on the ground. This was especially noticeable in the case of the Palm Warblers, which, often lingered to feed in the grass.

The Sparrow and Sharp-shinned Hawks were the principal enemies of these birds, devouring many each day. During the large bird wave of September 12, the Pigeon Hawk also played a conspicuous part in their destruction. The influence of the hawks will be taken up under the discussion of that family.

During the first days of migration the warblers moved along very leisurely, the same flocks apparently remaining about the clearings all day, but toward the

latter part of the season the birds hurried forward, taking their food as they moved along. There were several warbler waves or periods of great abundance, the first occurring on August 23. This one was made up almost entirely of Tennessee Warblers, adult and young being about equal in number. For the remainder of the migration, however, the young outnumbered the adults. The second, made up largely of immature Blackpolls, arrived on August 26. The third wave, consisting principally of Palm Warblers, occurred on August 30. The last wave, and by far the largest, occurred September 12. At this time the clearings and roads were full of warblers, nearly every species observed at Isle Royale being represented to a greater or less extent. These waves will be dealt with separately. During the heavy rain and wind storms of September 1, 2 and 3, the warbler migration was at a standstill, the birds keeping under cover as much as possible. The Blackpolls and Palm Warblers were the only species which seemed to be unaffected by the weather. These beautiful warblers were observed feeding in the open clearing during the heaviest rains, but even they did not undertake to migrate against the strong wind, so far as I could determine.

b. Sparrows. The sparrow migration began much later in 1905 than in 1904, some of the most striking examples being Savannah, Aug. 17, White-crowned, Aug. 28 and Lincoln, Sept. 1, 1904. On August 18, (1905) the first day observations were made, Chipping and White-throated Sparrows were seen. The Chipping had gathered into flocks and roamed about the clearings, feeding near the borders, while the White-throated were still in single families hunting about among the dead leaves in the damp underbrush. Many of the White-throated Sparrows were still too young to migrate, some having a little of the first down on them. On August 22, an immature Vesper Sparrow was taken, the only one found on the island. A few Song Sparrows were present, from August 21 to 24. These were the only ones seen and were probably migrating at that time. The next few days the number of both Chipping and White-throated Sparrows was materially increased, large numbers of young of both species making their appearance. Very few of these had moulted the first plumage. Not until August 31 were any other species seen, then large flocks of Savannah Sparrows, both young and adults, came to the clearings. All were in perfect fall plumage. It seems peculiar that none of these birds were seen before this date, because between August 5 and 8, I saw several, and obtained one immature barely able to leave the nest. The food was obtained along the roads, in the meadows, and about the houses, where several lost their lives by entering deserted rooms and not being able to find their way out. The Sharp-shinned Hawks proved to be their worst enemy. The first flocks of Savannah Sparrows to arrive remained for several days, their numbers constantly increasing. On September 5 many of the Chipping, White-throated, and Savannah Sparrows left the island, and for the next two days only a

comparatively few were seen, then others came in from the north and the flocks were rapidly increased.

It was noticeable that most of the birds which migrated from the island on September 5 were adults, the young remaining until a later time. The Savannahs showed the least fear of man during migration of any of the sparrows. On September 12, with the great bird wave, came the Lincoln Sparrows. Throughout this and the next three days hundreds of these birds were seen. As a rule they kept secreted in the burned brush and weeds of the first clearing, but individuals were met with all along the road, where they were seen hunting among the fallen logs and underbrush for insects.

Chipping Sparrows remained throughout the entire period during which observations were made, but probably none of the individuals first seen remained throughout that time. This seems the more likely as on several dates the bulk of the sparrows of all species left, while more came in later from the north.

c. Hawks. During a few days spent at Washington Harbor early in August (Aug. 5 to 8) only a few Sparrow and Sharp-shinned Hawks were seen, but by August 18, many individuals of both species had arrived. These remained here to feed on the swarms of grasshoppers infecting the meadows, and on the small birds, as warblers and sparrows, which were easily caught in the exposed clearing. The first few days the Sparrow Hawks outnumbered the Sharp-shinned about 10 to 1, but as the season advanced their numbers became more equal and toward the last the Sharp-shinned outnumbered the Sparrow Hawks, both because of a steady increase of the former and because many of the latter left the island for the south. When the observations were first made the adult Sparrow Hawks were as numerous as the immature, but toward the last of September the adults had nearly all left and many more immature had taken their places. Some idea of their number may be gained from the statement that more than thirty were counted at one time, sailing over the first clearing. Until the middle of September the immature Sharp-shinned greatly outnumbered the adults. These immature were full size, but did not have the spotted plumage of the adult. The females of both species greatly predominated. Toward the end of September many male Sharp-shinned, both immature and adult, appeared. These two species of hawks fed on grasshoppers to a considerable extent, but many crops of both species were found filled with the remains of Tennessee, Palm and Blackpoll Warblers, Savannah Sparrows and other species not determined. As a rule the older hawks were the ones which destroyed the birds, and this may account for their migration from the island at the same time that the large warbler and sparrow wave passed, while the immature hawks remained. Pigeon Hawks were recorded from time to time, but not until September 12, when the lower end of the island was suddenly flooded with bird life, did they appear in any numbers. On this date several flocks of 6 or 8 were seen in different parts of the clearing. They were preying principally on the sparrows, and were

creating great havoc among them. Coming with the great wave they remained throughout the day and passed on with it that night, only one being seen the next morning.

The migration of the hawks is thus seen to have been intimately connected with the migration of the smaller birds upon which they preyed, and seems to give at least one instance of bird migration being influenced by the food supply.

During cold, rainy mornings the hawks rarely appeared in the open, usually not until about 9 o'clock. This, however, was the time the warblers appeared on such days, and this may also have determined their appearance.

d. Owls. Only two species, the Great Horned and Acadian Owls, were seen. These were residents at this time and only concerned migration in that they sometimes preyed upon the migrants. Their effect was probably slight.

e. Thrushes. Six species were observed migrating, the Bluebird, Robin, Wilson's, Olive-backed, Gray-cheeked and Hermit Thrushes. A pair of Blue Birds nested in a dead Birch at Wendigo, and this family left the island about August 22. On the 24th a small flock probably consisting of two families appeared at the first clearing and remained about the tangled brush until August 31, when they also left. No others were seen except on September 11 and 12. Robins were seen twice during August, but on September 6, the first real migratory movement was initiated, and from then on the number rapidly increased. Small flocks numbering a dozen or so wandered about the clearings and open woodland. Many disappeared on the night of September 12, but the number was soon replenished, and at the time the observations were closed the Robins were quite abundant.

The most common of the Thrushes was the Wilson's. They bred on the island and showed no indications of the migrating spirit until the latter part of August, when they gradually increased in numbers and moved about to a greater extent. After September 6 they became rather scarce, and none were seen after the 14th. Their place was taken by the Olive-backed, and later the Gray-cheeked became abundant. Many immature Olive-backed were seen but this species had nearly disappeared when the great flocks of Gray-cheeked arrived on September 12. They showed little fear and did not seem to be frightened at the report of a gun. The flocks of the Gray-cheeked were made up of immature and adult birds, all in perfect fall plumage.

f. Other Birds. Following the breeding season the woodpeckers wander about the island making what might be called a local migration. Perhaps some of these birds leave the island in the fall and probably others come in from the north. In one instance, that of the Flicker, their numbers are enormously increased during the latter part of August and all through September. It is very improbable that any of these latter

birds winter on the island. Flickers were seen every day, but the number greatly increased toward the last of September, and from the report of residents the number continues to increase until late October when they appear to leave the island. Many were found dead without any apparent cause, and it was reported that in the latter part of October hundreds were found dead each year. The Downy and Hairy Woodpeckers visited the clearings occasionally, as did the Pileated Woodpecker.

Several pairs of Kingfishers frequented the river banks, and one pair nested in a sand bank, rearing 7 young. These birds gradually disappeared, until on September 15 the last ones left. Families of Redbreasted Nuthatches occasionally visited the clearings, often accompanied by Chickadees. During August, Crows were commonly seen, but by the latter part of September they had entirely disappeared, whether to the south or not it was impossible to determine. Several species of flycatchers and vireos were seen migrating, the Alder, Green-crested, and Least Flycatchers being seen several times, while only one Yellow-bellied was found. Both young and adults of the Least Flycatcher were seen, usually together.

One pair of Chimney Swifts was observed circling over the river on August 19. Whether these were migrating I do not know, but they were the only ones noted here in 1905. One of the most conspicuous species during August was the Thick-billed Redwing Blackbird which came to the clearing in flocks numbering from, about 30 to 50. Flocks composed of young and adults arrived nearly every day. The proportion between the two seemed to be about equal, or if anything, in favor of the adults. None were in the black breeding dress, and only a few males had the red on the shoulders out of the pin feather stage. The majority left on August 26, a few were seen on August 29, 31, and September 2, and two young were found on the 8th, 9th and 10th. A single specimen was taken September 16 and another, partially moulted, on the 20th.

There were many instances where only an individual or a single flock of a certain species was seen. Among these might be mentioned the Catbird observed on September 12, which was the only one the expedition noted either in the Porcupine Mountains or Isle Royale during both years, the Philadelphia Vireo, Blue-headed Vireo, Chimney Swift, Vesper Sparrow, Humming Bird, Migrant Shrike, Black-throated Blue Warbler, Black-throated Green and Black and White Warblers, Yellow-bellied Flycatcher, Red-eyed Vireo, and Kingbird. Of these, only two of the Philadelphia Vireo and Chimney Swift were seen, and but single individuals of the Migrant Shrike, Black and White Warbler and Ruby-throated Humming Bird.

IV. LARGE BIRD WAVES.

During the period from August 18 to September 21, six large bird waves passed over the island. Sometimes the waves were composed principally of one species, and again several species occurred in varying numbers. These bird waves were mostly from the north, although small ones, consisting of the birds which had accumulated on the island, took place at various times.

A bird wave may be recognized, first, by a sudden increase of individuals, second, an increase of species, or, third, by a sudden decrease in the number of birds which were residents or had gradually accumulated on the island. During the large wave of September 12, all of these evidences were present, but usually only one or two were recognized, the most pronounced of which was the great increase of birds as they passed along the roads from one clearing to another.

In some cases the bird wave marked the date of first arrival, at other times it simply marked the arrival of the bulk. The bird waves were generally sharply defined, so that their relation to the atmospheric changes could be noted to the best advantage. The bulk of the migration took place during the nights of bird waves, although there was a constant going and coming of certain species throughout the fall. Being almost constantly in the field the writer had excellent opportunities to study the migration when it was most pronounced, that is, during the large waves.

1. *First Wave.* The first wave observed occurred on August 23, and consisted principally of Tennessee Warblers, immature and adults being about equal in number. At 7:00 A. M., the temperature was 58°, a rise of 6° in the last twenty-four hours. The weather was clear, and it was in fact one of the most beautiful autumn days of the season. A light northwest wind prevailed, the barometer standing at 29.9 inches (low). This wave lasted for three days. The day previous the weather conditions had been about the same, except that the thermometer stood at 52°. An area of low pressure (29.75) was advancing towards the island and on this date was central over Assiniboia. On the 23d this area was central over Isle Royale and the area to the north and northeast of it. On August 24 a low area was centered over northeastern Missouri while the high pressure which followed it reached very nearly to Isle Royale, thus lowering the temperature to 53° with a northwest wind and barometer reading of 30.2. On the 25th of August the high (30.3 inches) included the island and the area directly south of it. The weather was clear, no wind, and a fall in temperature to 50°. On this date the beginning of the large wave of Blackpoll Warblers commenced, many large flocks appearing before nightfall. On the fourth day of the wave (August 26) the barometer fell to 30.2 with an increase to 54° in temperature. There was scarcely a breeze, and the day was for the most part humid and cloudy. The bulk of the Blackpolls arrived during the previous night and

throughout the day. The wave lasted for several days, decreasing gradually in volume, so that it was difficult to tell exactly when it stopped, if in fact it did not grade off into the next one.

2. *Second Wave.* On August 30 great flocks of Palm Warblers invaded the island. On the previous day the area of low pressure was central over the region a little to the west of Isle Royale, with a barometric pressure of 29.9, a temperature of 61°, and wind northeast with rain. On the 30th the low area had passed on to the St. Lawrence Valley and the advancing high pressure was over Manitoba. The barometer stood at 29.8 with a northwest wind blowing 4 miles per hour and a temperature of 56°. This wave also lasted three days and might have continued longer but for the severe gales which set in on the night of September 1.

The second day of this wave (August 31) the area of high pressure (30.1) was central over all of Northern Michigan, a considerable area north of it, and south to southern Wisconsin. With the high pressure came a drop in temperature to 46°. The day was clear with a north wind blowing about 4 miles per hour. The Palm Warblers continued to come in large flocks and were by far the most abundant bird at the Harbor. The vanguard of the migrating host of Savannah Sparrows appeared early on the morning of the 31st, and by evening the clearing was fairly covered with them; more came during that night and all the next day large flocks were arriving at the first clearing. There was no appreciable increase during the four succeeding days among the bird migrants. The third day of the wave (September 1) the barometer stood 30.1 inches, temperature 52°, with a northeast wind and a cloudy sky. This day marked the close of this wave both of birds coming to and leaving the island. This wave might have been checked either by the gales which followed or the change of the wind from north to northeast. A few birds attempted to cross during these succeeding days, as many were killed by striking the lighted windows, etc., or were found in an exhausted condition. These were probably part of that steady stream of migrants which continues to pass south during the fall, without any marked wave and in general disregard of the weather conditions.

3. *Third Wave.* This wave was noticed first on September 5 when the bulk of the Chipping, White-throated, and Savannah Sparrows left the island, and on September 6 the first real migration of the Robin commenced. I have considered these two days as parts of one wave, controlled by the same conditions, for probably the same influences acting at the same time caused the sparrows to leave the island and the Robins to leave their more northern home. The weather conditions were such as seem to be most favorable for fall migration. On September 5 the high pressure had advanced to an area lying from Winnipeg on the north to Memphis on the south, and extending east nearly to Duluth. The barometer stood at 30.1 (high) with a northwest wind blowing six miles per hour and a temperature of 39°. The day was partially cloudy, but no

rain fell. On the 6th an area of high pressure had formed over the region directly to the north and northeast of the island. A moderate northwest wind prevailed with the barometer at 30.1 inches, and thermometer 42°, and the weather was clear. A few Robins had been noted before this, but these were only scattered individuals or pairs, but on this date a large number came to the island, both young and adults being seen, although the latter greatly predominated.

4. *Fourth Wave.* On September 12 the largest wave of the season occurred. For number of species as well as individuals it could scarcely be compared to the other large waves, a total of 41 species being observed in actual migration on this day. On the previous day the low area was central over Lake Erie, and a similar area was formed over the Dakotas. The barometer stood at 29.8 inches, the temperature at 52°, with a north wind and a clear sky. It was cloudy, however, on the north shore. On the morning of the 12th the low area was central over New England, while the western one had moved south and had been followed by an area of high pressure central over the Dakotas and Western Minnesota. The island lay between the isobars of 30.1 and 30.2 inches, with a temperature of 42°, and a northwest wind averaging 8 miles per hour. The day was clear and seemed perfect in every way. The birds were so plentiful in the clearing at 6:30 A. M., as to attract my attention from the windows. Unlike the other bird waves, the motion was continuous, scarcely a break occurring in the steady stream of migrants as they passed along the road. There was very little lingering by the way, although when the birds arrived at the first clearing they often scattered about, feeding on the myriads of insects infesting the grass and shrubbery. Many of the birds after collecting into great flocks, sometimes numbering more than a hundred, rose directly from the clearing and taking a southwesterly direction, left the island, presumably for the south shore. As a rule the birds flew directly down the Harbor and the fishermen and tourists at Washington Island reported that never before had they seen such numbers of birds except during the spring migration. These observers reported that the majority of the flocks passed at a considerable height above the island, many of them probably belonging to the same flocks that left the clearing four and one-half miles up the bay. Some species, particularly the warblers and sparrows, flew from the ground in practically the direction they took when on their way, but others as the American Pipit, Rusty Grackle, Horned Lark and Thick-billed Redwing flew around in great circles, often hanging around the border of the clearing for some time, as if not quite decided whether to go or not. No flocks of the last named bird were seen on this day, however. As I passed up the road toward Wendigo that morning I met flock after flock of Palm Warblers, Grey-cheeked Thrushes, and Savannah Sparrows. The progressive movement of the migratory birds was clearly shown as they passed in a southwesterly direction along the road from Wendigo to the clearing at the Club House.

Darting everywhere were Sharp-shinned and Sparrow Hawks, while every few minutes a Pigeon Hawk would dash by. All the birds seemed restless as if impelled by some uncontrollable spirit to keep ever on the move. Warblers, thrushes, sparrows and flycatchers were constantly crossing and recrossing the path in front of me.

During the night of September 12 nearly all the birds left the island. Towards evening the temperature gradually dropped, until at 9 P. M. it was only 38°. The morning of the 13th was one of the coldest I experienced on the island, ice remaining on the water pail until nearly noon. During the night the area of high pressure had advanced until at 7:00 A. M. it was central over Isle Royale with a barometer reading of 30.4, temperature at 26°, and a brisk west wind. The sky was clear, as is usual under high barometric pressure. Many Lincoln Sparrows remained, as well as numerous flocks of Gray-cheeked Thrushes. But the great flood of migrants had passed on the previous night. However, the wave set up by these very favorable conditions was not yet over. Large flocks of Horned Larks numbering from about 60 to 200 or more came to the clearing, feeding on the insects and seeds in the open meadow and on the cultivated ground. On this morning many dead birds were found, among which was an adult male Yellow-bellied Flycatcher, the only one of this species seen.

The following is a list of the 41 migrants which composed this remarkable wave of September 12: Chipping Sparrow, White-throated Sparrow, Sharp-shinned Hawk, Sparrow Hawk, Blue Bird, Flicker, Myrtle Warbler, Tennessee Warbler, Phoebe, Redstart, Least Flycatcher, Hermit Thrush, Spotted Sandpiper, Pigeon Hawk, Robin, Olive-backed Thrush, Golden-crowned Kinglet, Cooper's Hawk, Wilson's Thrush, Solitary Sandpiper, Magnolia Warbler, Palm Warbler, Oven-bird, Bay-breasted Warbler, Blue Headed Vireo, Blackpoll Warbler, Savannah Sparrow, Black-throated Green Warbler, Grinnell's Water Thrush, Marsh Hawk, Catbird, Black-throated Blue Warbler, Nashville Warbler, Philadelphia Vireo, Red-eyed Vireo, Lincoln's Sparrow, Connecticut Warbler, Ruby-crowned Kinglet, Gray-cheeked Thrush, Broad-winged Hawk and White-crowned Sparrow.

The following were seen on September 13: Chipping Sparrow, White-throated Sparrow, Sharp-shinned Hawk, Sparrow Hawk, Flicker, Hermit Thrush, Pigeon Hawk, Robin, Palm Warbler, Blackpoll Warbler, Savannah Sparrow, Marsh Hawk, Lincoln's Sparrow, Gray-cheeked Thrush, White-crowned Sparrow, Horned Lark and Yellow-bellied Flycatcher.

5. Fifth Wave. On September 16 the bulk of the Rusty Grackles arrived. A few had been seen the day previous, but only scattered individuals composing the vanguard of the large, noisy flocks to follow. The area of highest pressure was off the New England states, while the low pressure centered in Kansas. The barometer stood 80.0 inches, temperature 50°, and an easterly wind with a cloudy sky. While this was one of the

smallest of the sharply defined waves, it presents a marked contrast to most of the others. Although the area of highest pressure was not near Isle Royale, as during most waves, the barometer stood at 30.0 inches, which was higher than for the area to the west and south; the wind was from the east and the sky cloudy in contrast to the northwest wind and clear sky of the other waves.

6. Sixth Wave. On September 18 the high area was far to the east (Maine) and the low centered over Kansas. The barometer stood at 29.8 inches, with a clear sky, northeast wind, and a temperature of 52°. Like the last this was comparatively a small wave and only involved a single species, the American Pipit, which came in large flocks numbering from perhaps 100 to 200 birds.

V. THE RELATION OF WEATHER TO MIGRATION.

Cooke ('88, p. 16,) makes the following statement in regard to the relation of temperature and barometric pressure during migration, "The area of the lowest pressure is never stationary but constantly moving, and in an easterly direction. It may be moving northeast, east, southeast, and rarely north or south; but never northwest, west, nor southwest. The usual direction in the Mississippi Valley is a little south of east." Warm waves, which are associated with areas of low pressure, therefore begin in the northwest, and move toward the southeast. "It is a law of the movement of winds that they go toward areas of low pressure, and from an area of high pressure." "But an area of low pressure is followed by one of high pressure, producing an opposite effect, and the isotherms which bent north to welcome the coming of the low area turn rapidly southward before the icy breath which blows from an area of high pressure. Thus the cold and warm waves both come from the same quarter, and both move in the same direction; that is the direction in which the area of low pressure is advancing." It will thus be seen that the temperature and the direction of the wind over any given area are both associated with the barometric pressure and the movement of its high and low areas, and since "low pressure is generally accompanied by clouds and rain, while areas of high pressure are cloudless" it will be seen that this important element is also associated with the barometric pressure. Thus we see that the four striking factors which influence migration, namely temperature, direction of wind, condition of the weather, and barometric pressure are correlated and work together, the same factors being always associated together and giving the same results.

To determine the true relation of these factors to migration we must discover the most favorable conditions for this movement, and then we can correlate the atmospheric changes which are taking place with the corresponding migratory movement. Of course many birds are constantly passing to the south throughout the fall, irrespective of the weather conditions, but the

changes which will set great numbers moving onward simultaneously must be the ideal conditions for migration. If this be true the time to study this relation of the weather is during the great waves.

TABLE OF BIRD WAVES.

Date.	Barometer.	Temperature, F.	Wind.	Sky.
FIRST BIRD WAVE.				
Aug. 23	29.9	58	N. W.	Clear.
24	30.2	53	N. W.	Clear.
25	30.3	50	None.	Clear.
26	30.2	54	None.	Cloudy.
SECOND BIRD WAVE.				
Aug. 30	29.8	56	N. W.	Clear.
31	30.1	46	N.	Clear.
Sept. 1	30.1	52	N. E.	Cloudy.
THIRD BIRD WAVE.				
Sept. 5	30.1	39	N. W.	Partly cloudy.
6	30.1	42	N. W.	Clear.
FOURTH BIRD WAVE.				
Sept. 12	30.2	42	N. W.	Clear.
13	30.4	26	W.	Clear.
FIFTH BIRD WAVE.				
Sept. 16	30	50	E.	Cloudy.
SIXTH BIRD WAVE.				
Sept. 18	29.8	52	N. E.	Clear.

1. *Influence of Wind.* A reference to the table of bird waves shows that on six days of the thirteen during which large waves were observed, the wind was from the northwest. Two days were without appreciable wind, on two, the wind was from the northeast, and upon other days it was from the north, east, and west, but upon none of them was it from the south, southeast, or southwest. A northwest wind prevailed the first two days of the first wave, the third and fourth days being without wind. The second wave commenced with a northwest wind, which changed to north on the second, and to the northeast on the third day. The northwest winds prevailed both days of the third wave, while the fourth started with a northwest wind, and changed to west on the succeeding day. The fifth wave was peculiar in having an east wind and the sixth a northeast one, both of which brought birds of different species, and from a different direction than those with northwest winds. These two waves were also much smaller than the preceding ones. It will thus be seen that the great bulk of migration took place with a northwest wind.

2. *Influence of Temperature.* Since fall migration prevails at a time when the temperature is gradually falling, the records for a wave near the first of the movement would be much higher than those at the last, so this factor can be considered only in a relative way, i. e., we must not compare the temperature at the first and last of the season, but simply consider the temperature immediately preceding and following a wave. The average temperature for the thirteen days was 47°. This low average was partially due to two days of very low temperature. All the waves but one were on a falling temperature, and in this case the mercury had fallen from the day previous. As a falling or low temperature is the cause of the high barometric pressure, which in turn with the passage of the high, causes the northwest winds which are so favorable to migration, it will be seen that a falling or low temperature is perhaps the first requisite for the bird wave. The low temperature also influences the food of the migrants, killing off the insects,

or driving them to shelter, and in this connection may prove to be very important.

3. *Influence of Barometric Pressure.* One of the most striking conditions was the high barometric pressure under which these large waves took place. On ten of these thirteen days the barometer stood at 30 inches, or above, the average of these being 30.17. The lowest pressure was 29.8, the average; for all being 30.09. None of the waves took place on a falling barometer, but where there was a change the pressure was rising as: first wave 29.9, 30.2, 30.3, 30.2; second wave 29.8, 30.1, 30.1; third, 30.1, 30.1; fourth 30.2, 30.4. As before stated the direction of the wind is due to the relation of the areas of low and high pressure to the region under consideration, and it is in this connection that it bears upon the problem of migration phenomena.

Cooke in his discussion of the effects of atmospheric changes on spring migration shows that at this season the large movements took place on low or falling barometers, and stated that it probably would be found that in fall the opposite conditions existed and migration would occur on the rising or high barometric pressures. This was found true at Isle Royale and probably is true for all fall migration.

4. *Condition of the Sky.* It will be noticed that on 9 of the 13 days of bird waves the sky was clear, and on the remaining four it was simply cloudy, no waves occurring during rainy weather. In spring the waves usually occur during cloudy nights; in the fall, as witnessed here, the opposite is the case, and the bulk of the fall migration can be said to take place on clear nights.

5. *Summary and Conclusion.* From the data submitted we see that fall migration as witnessed at Isle Royale occurs, in the majority of cases, with a northwest wind and a falling temperature with its rising barometer, and clear sky. (Cf. Smith, '07, p. 223.) It therefore seems evident that low temperature and high barometric pressure, with the prevailing northwest winds and clear sky which accompany them furnishes the most favorable conditions for the bulk of the fall migration. It will be noticed under the head of Migration Routes that a few birds prefer northeast instead of a northwest wind. The conditions which would be favorable for the migration of these birds would occur after the passage of a high and while the approaching low was still some distance off.

It is desirable that similar observations be carried on at other favorable localities in order to further test these conclusions, and determine whether they are of general application to the fall migration.

VI. ROUTES OF MIGRATION.

From the observations made during the falls of 1904 and 1905, it seems that Isle Royale lies directly in the path of a very strong migratory movement. In the fall there was a great massing of bird life. For some unknown reason the path of densest movement was very narrow, at least appearances pointed to such a condition. This apparent narrowness of the route, through the island was strikingly shown on September 9 when a trip was made across it from Washington Harbor to Siskowit Bay. About 15 miles were traversed, embracing every environment from clearings to high hardwood forests and damp cedar swamps. Nearly a day was spent hunting over the clearing and adjacent forest near the head of the bay, but scarcely any migrants were observed. A few Black-throated and Tennessee Warblers and a few sparrows were seen, while an occasional Sparrow or Sharp-shinned Hawk was met. This was not due to a lack of food, as grasshoppers and other insects were very plentiful. At Washington Harbor the reverse was the case; here on September 9 and 10 I saw many migrants, the majority of which were not seen at Siskowit at all. These observations at the harbor were made in the morning before leaving and in the late afternoon of the following day when I returned from the bay. While at Siskowit scarcely a bird; was heard passing over, although at the harbor they could be heard throughout the night. The path apparently extended lengthwise of Isle Royale with Washington Harbor and the region lying between it and the north shore of the island as its diameter.

In a recent paper, Taverner ('05) makes the statement that perhaps a migration route lies between Isle Royale and Keweenaw Point. From the observations made on the island, I am led to believe that such a route does exist and also one lying much to the west of this point, perhaps to the Apostle Islands and the mainland lying Southwest of them. These conclusions were drawn from a consideration of the following facts. The route taken by the majority of the migrants, both those which passed slowly across the island and those observed flying overhead, whether by night or day, lay nearly southwest. During the latter part of August and parts of September, the nights were unusually bright, so that migrating flocks could often be seen high in the air even when not crossing the face of the moon. The cries of migrating birds, heard mostly on cloudy nights, usually came from a northeasterly direction and died away in a southwesterly one. Certain birds, as the Thick-billed Red-wing Blackbird and Lincoln Sparrow, which were found commonly at the island, are very rare or do not occur at all in the region directly south or southeast of it. The Thick-billed Red-wing has never been taken at any point in southern Michigan. These birds, being of western origin, have gradually worked their way east where they have found suitable breeding grounds, but it seems probable that in their fall migration they move westward and join the throng passing down the migration route traversed by their ancestors. It seems

probable that the greater portion of the migrants which leave Isle Royale, moving in a southwesterly direction, continue thus until they reach the Mississippi Valley, where they are joined by birds from other regions, and all move down this great highway of bird migration.

It was observed that nearly all the large bird waves were associated with northwest winds. As the birds probably take a southwest course this gives them the beam wind which seems to be most favorable for their flight. Of course it was impossible to tell from what direction the birds came to Isle Royale, but it seems reasonable that they should choose a beam wind when leaving the mainland, since they arrived shortly after at the island flying with such a wind. If this proves to be true, the majority of the birds coming to Isle Royale are from the north or northeast.

The data for the supposed route to Keweenaw Point is slight compared with that for the southwestern one. Two species, the Rusty Grackle and the American Pipit, were observed migrating in this direction. During their flight the wind was from the northeast giving them the beam wind which a number of observers have noted to be the one preferred by hawks and gulls during their migration. Under "Perils of Migration" an instance is cited where a number of birds were caught by a storm while crossing to the east of the island and were driven to Washington Harbor. These birds were possibly crossing to Keweenaw Point. Probably the majority of the birds which strike this point are from regions lying to the northeast of it, and arrive there on northwest winds as do those birds which migrate across Isle Royale. The theory that many birds skirt the Great Lakes, as brought out by Taverner, explains the absence of several species from Southern Michigan which is not done by the discussion of the routes from Isle Royale.

VII. THE PERILS OF MIGRATION.

Dixon in his "Migration of Birds," divides the perils of migration into three important classes: first, those arising from fatigue due to the mechanical part of season-flight; second, those arising from the natural enemies of each species; and third, those arising from blunders and fatalities on the way. These three classes were observed in varying degree during the fall migration at Washington Harbor.

1. *Fatigue.* Between the north shore of Lake Superior and Isle Royale, the distance is so short that unless unfavorable winds intercept them the older birds would have little trouble from fatigue due to the simple operation of flight; but the young, which often commence migration soon after being able to fly, would experience considerable strain on their frail bodies in even so short a flight. This was vividly shown in the number of exhausted young found after every bird wave. During September, immature warblers and sparrows were often found in the morning in an almost completely exhausted condition after their night's flight. This was especially evident among the Tennessee and Blackpoll Warblers.

On the morning of September 13, following the day which witnessed the largest bird wave, I picked up many dead birds. Nearly all were warblers, the Tennessee seeming to have suffered most, although the Palm was a close second. A few immature Savannah Sparrows, one adult Yellow-bellied Flycatcher, and several young Flickers were also found dead. These dead migrants were seen in the clearing, along the roads, and on the banks of the stream. An examination of these victims showed no outward indication of the cause of their death. Only a few were emaciated to any extent. It was a noticeable fact, however, that none of the birds found dead were in the prime, fatty condition of most of the other migrants taken. The conclusion therefore seems probable, that the birds must be in the best condition possible to make a successful migration flight, and that the greatest mortality among the migrants lies in that class which for some unknown reason are not in prime condition. As there were no other reasons evident which could have brought on this high death rate, it is probable that death had been caused by severe exertion, coupled perhaps in a few instances with lack of food and unfavorable weather conditions in which to recuperate. This seemed the more plausible considering the fact that in only a comparatively few cases were the victims adult birds, while, as before stated, many of the immature warblers and sparrows had only been able to fly for a, short time.

After heavy storms, especially those from the southeast, many adult as well as young birds were found in an exhausted condition, their plumage presenting a dilapidated appearance, the wing and tail feathers broken, and showing general evidence of a hard struggle with the wind. Some of these birds may have been caught by the storm while crossing from the north shore to the island, but as the birds appeared to be blown before the wind I think that at least part of them were overtaken while crossing the lake considerably to the east of Isle Royale, perhaps toward Keweenaw Point. Overtaken, by the storm and with no place to take refuge they were gradually blown in the direction of the island where they were found the succeeding morning in such an exhausted condition. Some of these birds would even allow themselves to be picked up and handled without showing any fear. The birds which suffered most were the Palm and Tennessee Warblers. Michael Hollinger, a resident on the island for several years, told me that often, especially in spring, he had seen Washington Harbor "literally covered" with floating birds which had succumbed in their struggle against the storms and had drifted in from the open lake. The peculiar shape of the harbor and the lake currents tends to mass floating bodies at this point. But the loss as shown by those collected at the harbor could be but a slight proportion of the vast numbers which must have perished in the open lake.

Several fishermen said that after heavy gales in late fall and early spring, the shore at Washington Harbor would be strewn with the lifeless bodies of birds thrown up by the waves. During the fall of 1905, birds were several

times reported as lighting on the ships coming into the island, and the fishermen secured several which lit on their small boats after a storm, when about two miles from land. They reported the birds as very tame and allowing themselves to be handled freely. The birds secured were several small sparrows, Tennessee and Palm Warblers, a Saw-whet Owl, and one adult Robin. These birds were all encountered near the southwestern end of the island. They had probably been blown out of their course and; were striving to reach the nearest point of land, as no birds would be coming from the south at this time of year nor would any so completely exhausted have attempted to leave the island.

2. Natural Enemies. Without doubt the greatest natural enemies of the birds during migration were the Sharp-shinned and Sparrow Hawks. At times the Pigeon Hawk made great havoc among the smaller birds, and the Owls also played a small part. Probably weasels and minks fed to some extent on the migrants, which they caught while the birds were resting. These animals, however, only destroyed comparatively few, as remains of their victims were seldom found. Likewise the Owls probably destroyed only those which came directly in their path, the abundance of the Varying Hare furnishing a food much easier to procure. This undoubtedly saved a large number of migrants. Of the other animals, the Lynx also fed largely on the Hares and so probably molested the birds very little, while the family of house cats kept at the club-house were more than supplied by the number of small birds which met death striking against the windows, etc.

The early migrants were preyed upon very little by the hawks, principally because the Sharp-shinned Hawk had not arrived in any appreciable numbers, and secondly, the great swarms of grasshoppers furnished an abundance of appetizing food. As the season advanced and both species of hawks grew more numerous, their effect on the bird life increased. None of the smaller birds were safe, away from the protecting boughs of the conifers and alders, and therefore were confined almost exclusively to the edge of the clearings. The Sparrow Hawks fed both on grasshoppers and on warblers and sparrows, while the Sharp-shinned fed almost entirely on the latter. During the bird waves the hawks became more numerous, this being especially true for the great wave of September 12. On this date great numbers of both Sharp-shinned and Sparrow Hawks made their appearance, as well as many of the Pigeon and a few Cooper's and Broad-winged Hawks. The Pigeon Hawks in particular timed their migration to that of their victims, appearing and disappearing with each successive wave, very few remaining on the island. The majority of the Sharp-shinned also kept pace with the retreating birds and by the time the bulk of the warblers and sparrows had passed they too had gone on. Among the birds which suffered most heavily may be mentioned the Tennessee, Blackpoll, and Palm Warblers, the Wilson's, Olive-backed, and Gray-cheeked Thrushes, and the Chipping and Savannah Sparrows. Great daring was shown by the Sharp-shinned Hawks. Sometimes so

I. Introduction.

Almost every observer of animals has noted that certain kinds of birds are usually found associated in certain conditions, as, for example particular species of sandpipers and plovers upon the sandy beach, or the Meadowlark and Dickcissel upon certain prairies; but this is rarely considered a subject worthy of serious scientific study. To discuss the significance and value of such ecological study and suggest phases for investigation is the object of this paper. By the ecological distribution of birds is meant that correlation between environmental conditions and the occurrence and association of certain species of birds. In such study special attention must be devoted to the places of breeding; nevertheless the associations of birds at all seasons of the year are of importance. It is not the isolated occurrence of these species, but their relative abundance, the association of certain species, and their persistent occurrence in such conditions which is significant. In the literature of ornithology there is a vast amount of isolated data bearing on this subject, but very little of it has been organized and systematically studied.

When once the facts and general ecological relations have been determined, so that the representative bird associations or societies of given localities have been correlated with their proper environments it will then be possible to determine how one society becomes transformed into another, whether this is due primarily to other birds or to other environmental influences. A knowledge of the succession of bird societies and of the laws of change will not only lead to new ideas as to the influence of the environment, but will also have a marked influence upon the practical field studies of the bird student. It should lead to a more intelligent understanding of the relation of birds to the world about them, or even better, to the world of which they form a part.

Attention should further be directed to the fact that simply the occurrence of the bird in a definite habitat is not by any means the sole aim of such work. The influence of the environment should be studied in its bearing upon all phases of bird life. Not only should the most favorable habitat or optimum be recognized, but also the influence of the less favorable conditions; thus the nesting site, composition of the nest material, food, abundance, feeding grounds, migrating habits and all like relations are needed for an adequate and exhaustive study of the ecological distribution and succession of birds.

It is therefore not surprising that such requirements will be difficult to meet because the facts themselves are difficult to secure. Then there are further difficulties which are due to the limitations of the student himself,

and are psychological in their nature. As examples of this class of difficulties two may be cited, because they are of frequent occurrence in all kinds of scientific work and not by any means confined to the study of birds. For, contrary to our youthful ideas, naturalists have the same limitations as humanity in general! We may divide naturalists into two classes, depending upon their primary type of mind. First, those who tend to see only the infinite detail of isolated facts and observations. This type of mind is particularly impressed with the multiplicity and variety in nature, and is one to which a general statement is almost a cause of irritation because there are usually exceptions-to any general statement. The constructive imagination seems feebly developed in this type. To this class belongs many extremely valuable and useful students, because of the data which they, often with extreme conscientiousness, collect. They are collectors of facts rather than students of relations. To the second class belongs that type of mind whose primary interest is in generalizations, principles, relations, and which tends to neglect isolated facts and observations. The constructive imagination is liable to be developed in this type. This includes many extremely valuable and useful students on account of their tendency to condense, sift and formulate great masses of isolated facts. They are students of ideas and relations rather than collectors of "facts."

Each class, especially the well-marked types and extremes, often finds it difficult or impossible to understand the point of view of the other class. This frequently leads to misunderstandings and often to mutual contempt. Cope and Marsh clearly illustrate these two types of minds among our American naturalists.

By this time some may wonder why this subject has been introduced. It has been with a definite purpose, because frequently these opposed points of view cause delays in the development of many subjects. Thus a forewarning to students of bird ecology may produce good results if the individual student makes a conscious effort to counterbalance such deficiencies as go with his particular type of mind. In the past, details have tended to produce confusion through the neglect of general ideas. It is rarely that a word of warning on this subject is out of place, because the balanced "golden mean" investigator is never too abundant. The quotations at the head of this article have an immediate bearing upon the subject at this point.

Not only is habitat preference, the association of avian species, their succession, and the laws expressing these relations of much interest, but they are of much importance scientifically as well as in a practical way. It is therefore desirable that naturalists realize the necessity of understanding the "rules of the game" if the true relations of birds are to be studied to the best advantage. No adequate substitute has yet been devised to replace a grasp of general principles.

Throughout this paper emphasis is placed on the *definiteness* of the dominant major environmental

influences and complexes because the irregular features have apparently received undue emphasis and have retarded the recognition of certain important definite relations.

II. REPRESENTATIVE LITERATURE ON HABITATS AND SUCCESSION.

1. *Habitat Preference.* The American literature on habitat preference and succession, as a subject of special investigation, is very limited. By succession is meant the change or replacement at a given place of one or several species (an association) by others; as when a swamp is invaded by a dune and the representative swamp birds are replaced by those of the dune; or even again when the dune becomes fixed by vegetation and is inhabited by still another association of bird life. This is a much neglected subject; however, isolated observations on habitats are abundant in the biographies of the various species. The fragmentary character of these biographies tends to make them composite and they lose what peculiarities they may have which are due to a response on the part of the bird to its particular conditions of life. These unfortunate limitations clearly show that here is an extensive field worthy of careful investigation. The work already done will be a useful guide in many cases, but the student who wishes to develop this subject must turn to the fields and forests rather than to the literature, both for his inspiration and his data.

Perhaps a further word should be added concerning the limitations of the *composite* life-history method, as this will aid in making clear the kind of work needed in the future. This composite or generalized method of describing habitats and life histories and the response of birds to them, tends to lay undue emphasis upon the *average* conditions of life and habits, and tends to neglect those *detailed responses* to the environment which reflect the laws of local influence. These results are similar to those produced by systematic students who are "lumpers" and who do not recognize local races or varieties. Thus a nest may be built upon the ground at the base of a shrub or bunch of grass, or in the brush, but what conditions determine such sites? In a dry meadow a Song Sparrow may build directly upon the ground, but in a swamp, in order to have a dry nesting site, it builds in a willow shrub. In many cases the causes of these differences will be difficult to determine, but in others it is a relatively simple question for any one familiar with the species to solve. There are also geographic variations of habits as well as those of habitats just cited, and for this reason it is necessary not to confuse such variations with those confined to some restricted area. These local and geographic relations are very intimately related, but they are subjects which can only be worked out in detail when local studies give proper attention to local environmental responses.

In the following account of the literature no attempt is made at completeness, but the papers cited are believed to be representative. These papers will help to give

some idea of the kind of observations and records already made, and will be suggestive as to future work. Mention will first be made of the literature on habitat preference, and then of that on succession.

By far the best discussion we have found on habitat preference of the birds of a given region is that by Townsend ('05) on Essex County, Massachusetts. The primary avian environments are described, the representative birds listed, and their preferred habitats are briefly discussed. Thus, the ocean and its birds, the sand beach and its birds, the sand dunes and their birds, the salt marshes and their birds, and the fresh marshes and their birds, give a general idea of the subjects treated. Regarding the birds of the sand beaches, he remarks: "Among the Plover, the Black-bellied, Semi-palmated, and Piping Plovers are above all birds of the beach, although the first two are occasionally found in the marshes, while the last-named rarely strays from the beach and the adjoining sand dunes. The Golden Plover, although at times found on the wet sands, is much more likely to hunt for food on the dry sands above the highest tides, or still farther inland, while the Killdeer generally avoids the beach altogether, preferring the fields" (p. 21). And regarding the birds of the sand dunes he remarks: "Savanna Sparrows nest in numbers at the foot of clumps of tall beach grass throughout the dunes, and on the edges of the tidal inlets from the marsh. The nests of the Red-winged Blackbirds and the Bronzed Grackles are abundant in the bogs and groves of the birches. The Crow, in the absence of tall trees, builds perforce in the stunted pines and birches, at times only ten or twelve feet from the ground" (p. 34). In the case of the Crow, note that he records the response to the dune environment.

While Townsend recognizes changes in the environment, as in the dunes and beach (pp. 21, 30), yet he does not see their relation to the bird life in the definite way in which he sees their habitat preferences, nor does he appear to clearly recognize the fundamental relation of association within the breeding habitat. To him the environment is static. However an excellent feature of his work is the record of seasonal changes in the bird life of the various habitats. In this connection attention should be called to certain papers which will greatly aid in the study of the dynamics or changing environmental factors which influence sea or lake shores bordered by dunes and swamps; conditions represented on the Massachusetts coast. Gilbert ('85) has discussed the general principles and topographic features of lake shores and Gulliver ('99) the shore line of the sea. But in addition to these physiographic forces, the vegetation also has a dominating influence upon bird life. For general principles relating to this subject Cowles ('01) should be consulted for his discussion of the vegetation of inland shores and dunes, and Ganong ('03 and '06) for his treatment of the Atlantic coastal conditions. These authors discuss the succession of the vegetation, a factor of the utmost importance in the study of a vain succession.

While considering Townsend's results, it may be well to outline briefly a general succession of bird life along the shore as indicated by his records. It is evident from the map accompanying his volume that the currents and waves are constantly modifying the coast line and forming spits, bars and islands; and that the barrier beach area is increasing, and thus tending to become continuous at the expense of some of the ocean habitat. As the continuity of the beach develops, the area of swamp land behind it tends to increase and thus to further restrict the open water and increase the swamp habitat. The beach sands, once free from the waves or ground water, are caught up by the winds to form dunes, and may migrate into the swamps and thus transform them. Thus with the extension of the beach the sea birds are replaced in dominance by the shore birds, and a succession is produced.

In a similar manner the dunes encroach upon the swamp, and swamp birds are succeeded by those of the dunes. As the wandering dunes become anchored by vegetation and forests grow upon them, still other birds will invade them. Thus all stages may be expected, from ocean to beach birds, onward to those characteristic of wandering and fixed forested dunes. These relations are outlined simply to indicate the problem and its causes, which need detailed investigation.

In Michigan a few habitat studies have been made. One in the Porcupine Mountains, on the south shore of Lake Superior, and another on Isle Royale. Both are by McCreary; the paper on the latter area is published in this volume. The summer birds of the Porcupine Mountains are listed (McCreary '06) by selected localities and the habitat preferences are discussed as follows: water birds, birds frequenting the shores and banks of streams, birds frequenting grassy meadows and alders, birds frequenting tamarack and cedar swamps, birds frequenting hemlocks and maples, and birds frequenting the cliff and mountain top. In its emphasis upon habitat preference this paper is the only one so far seen which at all approaches Townsend's discussion of this subject. McCreary's work was done without a knowledge of Townsend's.

In southeastern Michigan, Brown ('06) made a locality study and outlines the habitats as follows: birds found in orchards, birds of the open woods, birds of the open fields, birds of the thicket, and birds of the marshes land river. Brown's paper is intermediate in character between the preceding papers and those of an economic nature, to be mentioned later, because the area studied has been so much influenced by man.

There are a few papers which, although primarily faunistic or geographic, contain habitat data. Such, for example, is Ridgway's ('74) discussion of the birds of the Wabash Valley and ('89) the birds of the Illinois prairie (pp. 13-16). An exceptionally good paper of this character on the Louisiana birds is by Beyer, Allison and Kopman ('06), although its aim and method of treatment differs from that of Townsend. The bird life is, however,

closely correlated with the vegetation and the physical conditions of the State.

The papers previously mentioned have been written from a regional standpoint. The study however of all the various conditions frequented by a given species or some natural group is also an important and neglected method, of ecological study which possesses certain important advantages. As an illustration of this method may be mentioned Palmer's ('00) study of the Maryland Yellow-throat. He has shown that different varieties have different habitat preferences. Jacobs ('04) has given us an interesting habitat study of a single species in Pennsylvania, the Golden-winged Warbler.

Let us now turn to another class of habitat studies, those which through man's influence throw only a subordinate light upon "natural" habitats and succession, and are primarily of economic importance but contain valuable habitat data.

An interesting and rather unique paper belonging to this class, based on observations in Southeastern Michigan, is by Watkins ('00). It is entitled 'Michigan Birds that Nest in Open Meadows.' A few of his statements explain his point of view: "To make more plain the limit and scope of this treatise, which, of necessity must be longer than I hoped, I will include in my list only such species as I have found nesting upon the ground in the open fields and meadows, excluding those found nesting upon the boundary fences or ground; also those nesting in the open marsh land which are undrained and boggy to the extent of being unfit for hay or pasture" (p. 67). The paper contains numerous notes on the habitat preference and variations in these traits.

By far the most comprehensive and thorough study of any limited farm area is that by Judd ('02) of a farm in Maryland. In this paper habitat preferences are clearly recognized, and discussed rather fully (pp. 12-20). The birds are associated thus:—birds that nest in the open fields, birds that depend on covers, birds of less limited distribution (consists largely of remarks on haunts), and birds of varied distribution. His last two sections are rather miscellaneous in character and show that the principles of classification for habitats were not clearly defined in his own mind.

The only other paper discussing habitat preference in detail is also the latest upon the subject, and is by Forbes ('07). This is a preliminary report on a bird census across the corn belt of Central Illinois in the early autumn; a study of the feeding grounds and preferences as influenced by the dominant crops of the area traversed, corn, pasture, and stubble. By means of this census, the habitat preferences for different crops and the association of species in them is statistically determined. The paper is particularly suggestive for its bearing on the subject of dominance; however, the suggested method of study has even greater significance when applied during the breeding season. Doubtless opinions will vary as to the validity of the method as applied by Forbes, even by those who would

approve of it for the detailed study of a limited area, or a breeding habitat. For large areas some cooperative method may be necessary.

2. *Succession.* Turning now to the literature on succession, it is found to be extremely limited in amount. So far as known to the writer, only two American authors seem to have realized the existence of succession. In his discussion of the biotic succession in the Porcupine Mountains of Michigan, Ruthven ('06) clearly included the birds, although they did not receive separate treatment, and might for this reason be overlooked. His position is clearly stated (p. 43) as follows: "Owing to the dependence of forms of life on their environment, biotic changes are necessarily closely related to environmental changes. These biotic changes may occur in two ways; the forms must either be able to respond to the new conditions, or be supplemented by other forms. That they tend to become adjusted cannot be questioned, but in many cases at least, this adjustment lags behind the changing conditions, and the forms are replaced by others from adjacent habitats which are adjusted to the conditions toward which the particular habitat is changing, thus bringing about a succession of societies." In speaking of the biota of the hard-wood forest he further says: "This region has been reserved for the last, for the conditions are evidently those toward which the other habitats tend to be changed under the present conditions. . . . This society thus represents the climax society of the region. It consists of the forms that are adapted to or associated with the conditions which prevail in this region in the last stages of the mutual adjustment of all the environmental processes. As the processes become adjusted to one another, the habitat of the climax society is increased at the expense of the other habitats, and the associated biota tends to become of general geographic extent in the region."

The only other paper discussing avian succession is that by Frothingham ('06), and this is not a "natural" succession but one influenced primarily by man. He clearly expresses a bird succession correlated with the reforestation of burned lands. The area studied is the Michigan forest reserve on Higgins Lake. The region was originally covered with White and Norway pine, but repeated fires first killed off the pines, later the oak and maple; and finally the dominant vegetation is sedge, sweet fern, huckleberry and prairie willow. With the fire protection afforded by the reserve, Frothingham anticipates a reversal of the above succession of destruction, and further remarks: "With the types of vegetation which mark the different stages of the plant succession just described there seem to be correlated certain definite bird forms. These forms are for the most part such as frequent observations in northern Michigan have identified as generally characteristic of the respective environments." This is followed by lists of birds characteristic of different kinds of vegetation. While these lists do not correlate perfectly with the implied succession, yet the general statement of the problem is clearly expressed.

The burning of forests has long been known to change the character of the vegetation and fauna of areas, but this is often referred to as the change of a, "life zone." Thus Merriam ('99, p. 47) states that a fire in the Canadian zone on Mt. Shasta is followed by the Transition zone and remarks: "But in the meantime a new growth of Shasta fir has started, and in ten or twenty years is likely to overtop and drown out the Transition zone species, enabling the Canadian zone to reclaim the burn. . . . But on the steeper slopes, especially rock slopes, if the vegetable layer is burned off, the (lower) zone which creeps up to replace the (higher) one destroyed becomes permanent or nearly so. . . . Deforestation of an area therefore tends to lower its zone position." Birds are not mentioned in this discussion nor the relation of "zones" to the general problem of succession. Such "zones" are thus only particular phases of succession.

It is thus seen from the above outline of literature that habitat preferences have been outlined for a few widely separated localities and for some agricultural conditions, but there has been no comprehensive discussion of the problems of habitats and succession, even in a preliminary manner, either from a scientific or economic standpoint. This fact seems rather remarkable in view of the great utility of a knowledge of the general principles underlying economic practice. There are, however, certain phases of biotic succession which have been discussed by a few authors. These subjects have either been discussed in a very general manner or are detailed discussions of special regions or groups of plants and animals. For this reason, perhaps, their bearing upon other groups than those specifically mentioned are very likely to be overlooked by those who take little interest in any subject or discussion which does not specifically mention their specialty or locality. This phase is mentioned in order to show that while avian successions have been considerably neglected, advances have been made elsewhere, by means of which some general principles appear to have been fairly well established. This is particularly true of plant succession, as shown by the writings of Cowles (701), and in considerable detail by Clements (705). The discussion by Clements will be particularly valuable to the student of avian succession.

III. THE MAJOR AVIAN ENVIRONMENTS.

As has been seen in the preceding review of the literature on haunts, no comprehensive discussion has been given of the environmental influences or ecological distribution of (extra-tropical) North American birds. Various authors have discussed their geographic distribution, and certain geographic variations have been referred to certain environmental influences, but a general ecologic treatment, as contrasted with a primarily faunistic one, has not been made. This is remarkable when we recall the fact that the collections of North American birds are, considering the large area concerned, the best in the world both as to quality and as to quantity (Stejneger, '03). This means that there

have been many trained collectors; but what has become of the notes and observations on the environments and conditions of life of these birds, which must necessarily have been known to successful collectors? Part of these observations have been published, and perhaps no one is to blame because more have not; but the point of significance is that we have, in fact, hardly made a beginning in the careful detailed study of the bird environment and its development as a distinct field of study. In common with the remainder of the North American biota, several general principles are known, but they do not appear to be current among ornithologists.

The following discussion and suggestions on the larger environmental units attempt only an outline of certain phases of the problem, in order to call attention to certain principles which seem useful as a background for the intelligent study of bird habitats and succession. From such a standpoint as this, the *dominant* influences of given areas and environments are of particular interest and of fundamental value. By focussing attention upon the importance of recognizing these dominant environmental influences, we may hope to escape some of the confusion which appals those who are keenly impressed with the chaos and complexity of the problem. These dominant factors are usually not single isolated forces, but resultants of several or many influences. Thus, as in the case of the vegetation, it is not one factor, but a complex, which influences different birds in different ways. Nevertheless there is what may be called a mass or dominant effect.

A major habitat unit may be considered as a combination of conditions which are dominant in a certain area. *The very dominance means that a relatively limited number of forces or complexes are operative.* With departure from such a center of influence the dominance changes, as other influences are encountered and other dominants are established.

When we consider that certain ecological groups of birds are worldwide in their environmental relations, it becomes evident that such characters are of fundamental importance. Thus water birds may occur in any part of the world where water is a dominant environmental factor. This is not a simple ecological group of birds, but one of the greater units of association which may be subdivided into many minor classes; as those which frequent the sea, and others the inland bodies of water. The shore birds form another natural ecological group, and also the inland birds a third. There may thus be considered to be three primary ecological groups of birds which are closely correlated with definite and dominant environmental influences: Thus:—

1. Water birds.
Those frequenting the sea and the adjacent rocks on which they nest, and inland waters.
2. Shore and Marsh birds.
Those frequenting shores of all kinds, seas, lakes, swamps and rivers.

3. Inland birds.

Those frequenting deserts, grass lands and forests.

Of course these ecological classes are not sharply defined, and yet they are so distinct that they can be easily recognized. It should be noted that the above groups are closely correlated with certain dominant physical features of the earth—the sea, the shore and the inland environments.

The relative abundance and dominance of these classes of birds will be determined largely by the dominance of such physical conditions as most distinctly favor a particular ecological group. Thus at sea the water birds are dominant; on shore, the shore birds; and inland, still other kinds. The linear character of the shore habitat and the adjacent breeding grounds gives it a rather unique character, as the two other habitats occupy large expanses. However, the swampy, somewhat shore-like conditions of the far north most nearly approach, for the shore birds, the expansive character so usual for water bodies and inland areas.

In the present discussion the emphasis placed upon the inland vegetation does not mean that the dominance of other influences is not recognized, but simply that it makes a convenient and fairly reliable *index to many other environmental influences*, as, for example, the climate and topography. A further important advantage of the plant index is that the science of plant ecology and many of its general principles and methods are applicable to birds. A general knowledge of plant ecology is therefore becoming one of the most valuable tools in the hands of the field ornithologist. Every field naturalist has observed the general correlation of certain birds with certain kinds of vegetation. This relation is clearly expressed by Ridgway ('89, p. 8) as follows: "There is probably no better index or key to the distribution of birds in any country than that afforded by the character of the vegetation; should this vary essentially within a given area, a corresponding difference in the bird-life is a certainty." This phase of the subject clearly illustrates the oft-repeated experience of naturalists that in order to thoroughly understand one subject—perhaps the favorite one—it becomes necessary to study another, or even several. Thus in order to know the bird life of a region it has become necessary to study the ecological relations of its vegetation.

The study of ecological plant geography is an extensive one, but many of the details, so important to the botanist, are of much less concern to the ornithologist, who needs primarily to know the major plant associations or formations and their successional relations. This implies ability to recognize dominance among plant species and the general method of transformation from the dominance of one to that of another.

By a plant formation is meant that association of species (or plant society) which is correlated with those conditions which tend to prevail over a large geographic area in the last stages of mutual adjustment of all

environmental and biotic processes. Such an association or formation tends to occupy such an area to the exclusion of all others, and is thus a climax society.

But absolute dominance of a formation does not occur, because local conditions, break the monotony where streams, water basins, bare rock, and similar influences may interrupt the desert, grassland or forest, and produce minor habitats and associations of both plants and animals.

It is not my purpose to discuss in detail the various plant formations of (extra-tropical) North America, but to outline those which are of evident ornithological utility. The following may be recognized provisionally:—

1. The Arid Deserts of Southwestern U. S. and the Mexican Plateau.
2. The Grasslands of the Great Plains.
3. The Deciduous Hardwood Forest of Southeastern U. S.
4. The Coniferous Forest of Eastern Canada.
5. The Giant Conifer Forest of the Pacific Coast and the Rocky Mountains.
6. The Barren Grounds or Cold Desert
7. The Alpine Deserts.

A mere inspection of this list of avian and vegetational formations shows that the recognition of these large environments is relatively simple. It is also seen that they represent fairly definite physical or environmental complexes of such fundamental importance that there can be no doubt as to their general validity. As to the relative value, influence, boundaries, and the dynamic relations of these formations, much is already known, but not as an organized body of facts and principles. It will also be noted that these regions do not closely correspond with current faunal areas, although there is a very close correlation in some cases. An avian formation may, in general terms, be considered the analogue of a vegetational formation, although this does not imply that they necessarily have the same boundaries.

As the literature treating of the vegetation of these areas is extensive and scattered, a few papers will be cited as an index to others:—

1. Arid Deserts; Bray, '06; Coville and MacDougal, '03.
2. Grasslands or Plains; Clements, '05; Pound and Clements, '00.
3. Southeastern Hardwoods; Cowles, '01; Harper, '06; Transeau, '05.
4. Eastern Canadian Conifers; Whitford, '01; Transeau, '03, '05-'06; Ganong, '03, '06; Harvey, '03.
5. Rocky Mountain and Pacific Conifers; Whitford, '05; Gray and Hooker, '81; Piper, '06; Young, '07.
6. Alpine; Merriam, '90, '99; Coville, '93; Fernald, '07.

These environmental unit areas as found to-day, are the result of many successions which, in some cases at

least, reach rather far back into the past. This is because some occupy ancient land areas, such as much of the Southeastern Hardwood area. On the other hand, some occupy relatively new regions, that is, at least with regard to the dominant factors now in control, as in the glaciated part of North America and on the Coastal Plain. So far as the present is concerned such relations clearly show that these areas are only the end results of extensive past changes or successions which represent the terminal branches and cross sections of development. It is to the study of such regions and associations that we must turn for the fundamental organization or associational relations of the various elements which compose not only the environments but also the associations of animals.

In order to make as definite as possible *the structural and ecological characteristics* of these formations, certain general relations are here formulated. Throughout this paper it should be remembered that the individual birds and associations of given areas: form the units of comparison. Such a distinction is necessary because many species show considerable geographic variation in habits and in the habitats frequented. The writer clearly recognizes the risks and difficulties of such an attempt. They are deliberately put in their present form to *invite criticism and qualification* from field workers. It is desirable to know the validity of these formations, their internal ecological relations and dynamic tendencies, their relation to dominant environmental influences, etc. A complete list is not attempted, and some of the statements may be only fragments of larger generalizations; but it is just such relations as these which will develop if the entire subject is considered critically and synthetically. Some of the leading characteristics of these larger environmental units and their avian *formations* may be briefly outlined as follows:—

1. The dominance of a limited number of physical conditions or complexes, as climate, topography, vegetation, animals, etc., in a given area produces the primary environmental units and formations.
2. Secondary environmental dominance is shown by a secondary avian association. Thus in the Northeastern biotic center there is a secondary dominance due to water basins in the forest area.
3. A formation or climax society is composed of a relatively (and usually absolutely) limited number of species which are dominant in a given environment of geographic extent. Such dominance, in general, implies extensive range, relative abundance, and ability to indefinitely succeed or perpetuate itself under given conditions.
4. Where dominance obtains, avian variety is limited so that the greatest diversity occurs where local influences prevail, and at the margins of the formation.
5. Correlated environmental and biotic dominance produces what may be considered a *biotic base*, stratum, or optimum, from which departures may be

considered less favorable. This is a relative equilibrium, resulting from complete environmental and biotic adjustment, under given conditions.

6. In each formation there is a normal inter-adjustment of the avian species and individuals, in addition to the adjustment with the dominant physical environment. The former is dominated by their structure, habits, and the instincts or behavior; hence the colonial breeding or spacing, migration, etc.

7. Each large environmental area or formation tends to have a full complement or set of species, of diverse but supplementary ecological character, such as water, shore or inland birds. One set is likely to be dominant.

8. Relative stability in an association is correlated with the climax dominance, and generally with extreme and slowly changing local influences. Fluctuation is correlated with intermediate conditions.

9. Diversified associations and isolation are greatest with imperfect dominance, but dominance itself produces isolation of the climax association. This diversification produces associations surrounded by others and hence their isolation.

10. The taxonomic elements in different formations vary much, but there are close analogies in the kinds of taxonomic and ecological groups in different formations,—as the Mniotiltidæ of the New are represented by the Sylviidae of the Old World. Cf. Osborn '02. LeConte, '50, p. 239. Cf. No. 7.

11. The roughly zonal arrangement of societies about the climax society (formation) or the environmental optimum, is primarily due either to local reversals, the lagging influence of local or neutral conditions, or to the influence of adjacent formations. This is a result of the retardation of the complete cycle of successions.

12. The primary environmental conditions tend to encroach upon all others. The local conditions thus tend to become transformed in the direction of the dominant environment and to be appropriated by it. The corresponding avian associations are thus given a definite dynamic trend.

13. The mobility of birds during the breeding season is very generally overestimated. The presence of the nest and young renders them for a time relatively sedentary. There are many causes influencing this, such as other individuals, proximity of food for young, homing, instinct, etc.

IV. Minor Avian Environments and their Associations.

We have seen that the larger geographic environments or formations are characterized by definite conditions and associations, and at the same time that even throughout these favorable regions the climax association is not distributed with absolute uniformity because of local variations in the physical features, such

as vegetation, water basins, streams, mountains, etc. For the student of local bird life the real work begins when one attempts to examine into the causes and influences exerted by these conditions which break the monotony of the formation and make possible a diversified avifauna. But birds do not always respond as closely to slight local influences as does the vegetation, and for this reason one must learn by experience just what size of units must be used. Thus in the forest a few wind-falls will attract but little attention, but a burn of a few acres will have a noticeable influence in harboring those species of birds which frequent openings; while swifts and swallows ignore many local influences which dominate other species.

It should also be noted that whenever possible it is of distinct advantage to examine all habitats in their original state, uninfluenced by man.

Instead of discussing the leading features of local conditions and their societies or associations in detail, only an outline of them will be given, and that in a form to facilitate use and revision.

1. Minor environments are primarily dependent upon local conditions, and are thus in a sense correspondingly independent of the dominant forces of the region. This is, of course, a relative condition,

2. Minor environments are, as a rule, relatively limited in area. In general their limited area favors their short duration, but age is primarily a result of the rate of change.

3. Marked isolation, even when of extensive linear extent,—as a shore line, along a stream, or an elongate rocky ridge,—is also characteristic of minor environments.

4. Minor environments tend to become encroached upon by the dominant regional influences and ultimately to become extinct. The succession of societies in local habitats is a declining one, while that of the geographic or climax habitat is an increasing and ascending one.

5. Local habitats produce most of the variety within the dominant area, and make possible a diversified avifauna. The structural differentiation within a formation (zones, etc.) is thus largely, in addition to variations in the formation itself, of local origin.

6. Local associations or societies, in general, furnish the essential clues as to their earlier successions which have attended the evolution or development of regional dominance. The variations in these are due both to the kind of life and to the influence of adjacent associations and centers of dominance.

7. Marginal societies are particularly liable to variation in composition, due to the combined influences of adjacent formations or centers of dominance as well as to local conditions.

8. Comparative studies of local habitats will form the most general and practical guide in the determination of the successions in the formation.

9. Local habitats and societies, in common with the larger environmental complexes, are characterized by the dominance of few physical and biotic factors, and by a limited number of species.

V. Avian Succession.

1. *General Remarks.* Since the breeding grounds are fundamental importance in the ecology of birds, the study of them in such situations furnishes the greatest source of insight into their life relations. By an avian association, formation or society is meant different combinations of species which *regularly occur together in the same breeding habitat or area*. These breeding grounds must be considered broadly, and include not only the nesting site but also the feeding grounds, even when they are physically very different, because ecologically these conditions form a unit during the breeding season.

It is well known that when a given set of physical conditions are dominant, as in a dense conifer forest, a swamp or an extensive orchard, relatively few individuals and kinds of breeding birds are characteristic of such conditions, except in the case of those nesting in colonies. The field relations of these colonial and isolated breeders are quite different. It is also of importance to recall that abundance is a relative term, with a very different meaning in the case of seed-eating and predaceous species.

Bearing in mind these conditions, bird succession means a change from the dominance of certain species or associations to that of others. Thus in the beginning a slight change in abundance of a species may be noted, with a corresponding decrease in another; and this proportion may continue to change until the intruder becomes dominant and the rival form may disappear entirely. This process of change, as a rule, is not limited to a single species, but usually involves several or all of the members of the association, as when a dune invades a swamp and the swamp birds are completely replaced by those frequenting the sand dunes.

2. *Succession on Isle Royale.* With these preliminary considerations in mind, we will turn to the ecological succession of bird life upon Isle Royale, Lake Superior. The field work upon the island was carried on by a party from the University Museum of the University of Michigan, under the direction of the writer. Aside from succession, the general ecological relations of the birds were studied by Otto McCreary and Max M. Peet, and elsewhere detailed descriptions of the region and detailed notes will be published. The writer has based his main records of habitat preference upon their work. For this outline of succession only the primary features of the location need be given.

In the present treatment an attempt will be made to follow the genetic succession, at least in its broader outlines. Various qualifications and reservations have been made, and others will follow, so it is hoped that no confusion will be produced by this method of treatment.

Geographically, Isle Royale, Michigan, is an island in Lake Superior, near the North Shore, not far from Port Arthur, Ontario. The *topography* forms a part of an ancient peneplain of moderate relief, glaciated and with an abundance of elongated low ridges and valleys with numerous water basins. The *soil*, which is locally absent, is generally humic or mixed in character, bordering and in the depressions; but is mineral, stony and residual elsewhere. The combined shore and beaches are extensive, largely stony and gravelly, and contain but little sand; much of the shore line is rocky and precipitous; many outlying islands. *Vegetation*, herbaceous in shallow inland waters and as a ground cover except where the shade is too dense, and upon rocks; shrubs on protected beaches, in more open places in the forest and in burns; the forest consists of Tamarack, Black Spruce and Arbor Vitæ in bogs; and elsewhere in mesophytic conditions of Balsam Fir, Arbor Vitæ, White and Yellow Birch, and rarely Sugar Maple. Upon the dry ridges, Jack Pine; and in burned areas, Aspen and Paper Birch. *Climate*, seasonal changes very pronounced; winters very long and cold, and summers short and cool; a relative humidity of about 80% in December and of about 70% in July (*cf.* Johnson, '07); a mean temperature for January 7.97° F.; and for July, 62.24° F. (Port Arthur data). Early, deep snows. *Predaceous* animals, as the Lynx, Marten, weasels, Red Squirrel and bats are directly in competition with the birds for food, or prey upon the birds.

The above environmental factors are dominant features and give us a general picture of the conditions, largely in terms of common experience. In the life of the birds, however, a complete reassortment and change of intensity in these factors occurs when they are combined as habitats. The surrounding lake, the numerous bays, small lakes and ponds compose the aquatic habitat and make it a characteristic feature. The very irregular and extensive shore line and limited beach area characterize the coastal border, while inland, excepting the main bodies of the few larger lakes, the encroachment of the bog vegetation upon the shores is such as to prevent an extensive development of sandy open beaches. The above mentioned habitats are open unforested areas; the remainder of the island, with the exceptions of the bare rocky ridges, the clearings and burned over areas, are fostered. Very extensive swamp forests abound in the elongate valleys and the borders of the water bodies, and are composed of Tamarack, Black Spruce and Arbor Vitæ. The mesophytic forest occurs on drained areas and is characterized by Balsam Fir, White Spruce and Paper Birch; the burned areas by second growths of aspens and Paper Birch. Then there are also influences which are exerted upon the bird life in general, as for example, migration. In this case, undoubtedly both external conditions and the habits and the behavior must be correlated. Another general and dominant influence should be reiterated here, and that is that all open areas tend to become invaded with vegetation and finally forested, whether they are lakes, ponds, bogs, rock openings on the ridges, burns or clearings. The

mesophytic Balsam-spruce forest tends to monopolize *all* habitats, and gives a definiteness to all succession upon the island.

From a genetic standpoint the past and present dominance of the surrounding Lake must be recognized. This formerly stood at a level much above that of the highest ridges upon the island, as is clearly evidenced by the abandoned beaches on the north shore of Lake Superior. Such relations prove that Isle Royale was once a rocky reef in the lake, which, as the Lake level was lowered (it is quite unlikely that the island has been materially elevated) became exposed as a wave-washed beach. These conditions are approximated to-day by the low outlying islands. The beach or shore is thus the *original* habitat upon Isle Royale, and in general, all others have been derived or developed from it. To discuss these as a truly genetic series would require that these be described *simultaneously*, as the differentiation took place. These habitats did not develop as isolated phenomena, but several developed at the same time, or abreast. Thus as soon as enough of the land surface had become exposed so that its inequalities began to have an influence, the ridges would be the parts best drained, and certain depressions would tend to accumulate the drainage. This process would lead to a simultaneous development or differentiation of the well, moderately, and poorly drained habitats. Almost all of the residual soil formed as the region was baseleveled was probably cleared away by the glaciers; or later, as the waves fell from the island, by the pounding of the waves. Thus the relative absence of a soil must characterize all habitats. At what period life first reached the island in post-Glacial time is not definitely known; but it is likely that the pioneer vegetation of lichens, mosses and low herbaceous vegetation reached it soon after its exposure. If the biota reached the island about the time of the formation of the Algonquin beach, which, roughly speaking, may have been at about the present elevation of 475 feet above the Lake surface, it has since spread upward and downward from that level. The composition of the initial societies is not liable to as much variation at the later ones. Thus if the Herring Gulls returned to the region at this early period of the exposure, they were probably the pioneer birds; but if only at a much later date, still other species might have accompanied them. While such variations as this may be expected, and due allowance must be made for them, yet there can be little reasonable doubt but that *water birds* and those frequenting *open places* tended to become the pioneers, and that later, with the development of a soil and forests, other associations of birds became established.

There are at least five important factors which enter into the composition of the past and present conditions which have moulded and are even now moulding the formation of the habitats upon Isle Royale. These five are:—*first*, past climatic changes; *second*, the local topography; *third*, the falling lake surface; *fourth*, dynamic tendency of the vegetation; and *fifth*, the habits and structure of the birds. With these guiding principles, let us now turn to certain details of the resultant succession.

a. The Aquatic Association and Habitat.

The expanse of Lake Superior, the irregular shore line producing coves, the inland water bodies and streams, together furnish an extensive and expansive area of habitat. The cutting of the Lake waves encroaches upon the land habitat, and the deposition by them elsewhere causes minor extensions of the land habitat (as at Rock Harbor where a sand spit furnishes a nesting site for a Kingfisher). Inland the encroachment of the vegetation tends to restrict the water areas, as the falling Lake level has, in the past, tended to increase the land habitat. These processes must be recognized in order to grasp the dynamic tendencies of the habitat.

The *characteristic* aquatic society is composed of the Herring Gull, Loon, American and Hooded Mergansers, and the Pied-billed Grebe; mainly fish eaters and scavengers. Other species, of greater inland tendencies, are attracted by the fish food, as the Eagle, Osprey and the Kingfisher. The Gulls show a decided preference for the great Lake, and the Loon for the inland waters. The presence of the Kingfisher was influenced by the harbor with its attendant sand banks and bars. As all these water bodies near Isle Royale freeze over in winter, the strictly aquatic birds must normally migrate to secure food. Of course none of these birds nest in the open waters, but on the island beaches (Gulls), near the mouths of streams, and inland in marshy places; but all, as a rule, nest near the water. The very young soon attend their parents, and are thus in the water at an age when many land birds are yet helpless in the nest, thus confirming their aquatic habits and habitat. During migrations many other species frequent this habitat.

Where Isle Royale now is, once rolled the open Lake; and it is not improbable that as the island appeared the Herring Gull was one of the first species to discover it. Such a bird might even reach the island under climatic conditions of the Ice Age, for the species now ranges far north along the shore of the Arctic Sea. A species of such extensive chronological and geographical range will tend to give much stability to succession. The present range of the Mergansers and the Loon is not so far north, and for this reason they may have arrived under milder climatic conditions. But if the island became exposed under mild post-Glacial conditions, all of these species may have arrived at much the same time. But even with the chances for such variations the general succession seems to have been initiated with the aquatic association as the pioneer society.

In following the genesis of the habitats and associations from this point onward, divergence and differentiation becomes so marked that it is impossible to develop all lines abreast. A linear treatment becomes necessary, and therefore certain general relations are liable to become obscured unless specifically mentioned in advance.

The aquatic and beach habitats possess a marked tendency toward a zonal arrangement. From the

Superior beach the transition is through open or shrub zones into the climax forest. The topography of the island with its longitudinal ridges and valleys form a dominant factor in impressing this zonal structure upon the biotic associations. The series,—from the water, through the beach, open and shrub marginal zone, into the climax forest,—may be considered as the genetic vegetable succession. They change simultaneously and are due to the same general cause,—the falling Lake surface, which transforms the water area into beach, the beach into forest margin, and forest margin into the climax association. But as mentioned, it is manifestly impossible to discuss all these transitions at once, and each ecological unit must therefore receive separate genetic treatment.

This tension line or marginal zone between the Lake and the forest shows such a wonderful diversity and complexity in its conditions, that several plant and animal associations are formed within this zone. With its onward march there are simultaneous changes in several associations which, while they will vary in their changes, yet all tend to converge in harmony with the dominant factors. These conditions migrate or radiate from the highest land. On the other hand, the inland marginal zones, which border the smaller water bodies, migrate inwardly; and being closed areas, tend to become extinct. This marginal zone, particularly beyond the upper beach, forms one of the most interesting and complex conditions found upon the island. It is not an ecological unit, but is composed of several of them. This is where most of the confusion arises in actual field work of habitat studies.

b. The Shore and Marsh Association and Habitat.

As the area of the islands expanded and the shore line was lengthened, the habitat for shore birds increased; but the steep and rocky shores were unfavorable for the development of beaches because loose rock, as tools for the waves, was limited in amount. The local character of the shingle and gravel to-day found in the various coves clearly indicates their local origin; and much the same conditions have obtained in the past. On account of these conditions, the sandy beaches are very conspicuously absent. The dynamic tendencies of the beach are those which cause the extension or restriction of the aquatic and beach habitats, supplemented by the drift which is tossed upon the shore. Where there is shallow water, and mud accumulates, favorable conditions are furnished for invertebrate food for birds. Inland, the numerous lakes, ponds and marshes furnish shore conditions which tend to become extinct through drainage or overgrowth of the vegetation, except in those parts of the larger lakes where wave action tends to scatter such accumulations as rapidly as formed, or to prevent its formation altogether.

Although observations on this subject are quite limited, yet it seems fairly safe to consider the Spotted and Solitary Sandpipers as characteristic birds of this association. Upon such a rocky coast, sandy and

gravelly beaches are quite exceptional and are confined to protected coves. Additional diversity is produced where small streams enter these coves and produce deltas.

Little is gained by sharply segregating the marsh and shore birds, although the marsh birds show a preference for conditions better represented or correlated with topographically older coasts, protected and inland conditions. Attention should be directed, however, to the significant fact that successions initiated with such diversity will produce a variation in the composition of the associations. Also that so far as possible these variations should be considered comparatively and synthetically in reconstructing and anticipating successions.

The American Bittern, Lesser Yellow-legs, Swamp Sparrow and Marsh Hawk belong to this society of marsh birds. As in the case of the aquatic association, these birds generally nest in close proximity or entirely within these shore or marsh conditions. Still other species frequent this belt to feed, as it is an open area; but their presence is mainly conditioned by the adjacent shrubs or forest. The very limited number of species in the aquatic and shore associations is worthy of particular mention.

The Yellow-legs, Spotted Sandpiper, Bittern and Marsh Hawk range far to the north, even to the Barren Grounds, and thus suggest chances, as in the case of the aquatic association, of an early arrival and succession upon the island.

With the growth of the island, there has been a corresponding extension of the outer and inner shore habits, although the encroaching vegetation has had a marked tendency to restrict the area of the inland habitat. The dominant environmental influences in this habitat appear to be, 1, the physical character of the shore and beaches; 2, the dynamic forces of the water bodies and streams; 3, the encroachment of the vegetation; 4, the downward migration of the shore; and 5, the habits and structure of the birds.

As a general rule, we may say that the beach of the outer lake tends to be succeeded by either the bog or upland associations, and those inland by the bog association.

c. Bog forest Association and Habitat.

As just stated the outer coast or an inland one may develop into a marsh or bog habitat or association. In the bog, the Tamarack, Black Spruce and Arbor Vitæ are the pioneer trees in transforming the open marsh into a forested one; while upon the outer shore the alders and aspens tend to precede the conifers as a general rule. From the bog forest the transition to the Balsam-White Spruce forest may be perfectly continuous, and thus there will be a series characterized by the dominant conifers. In places Arbor Vitæ may form the dominant swamp forest, but this is only a variation in the conifer dominance. With improved drainage or the

accumulation of vegetable debris, these habitats become converted into the Balsam-spruce climax forest and hence the environmental dynamic tendency.

As the forest encroaches upon the open bogs the Tamarack, Black Spruce, Arbor Vitæ, Cassandra, Labrador Tea and alders are accompanied by birds characteristic of this early stage; such as the Red-breasted Nuthatch, Yellow-bellied Flycatcher, Golden-crowned Kinglet, Cedar Waxwing, Chickadee, Canada Jay, White-winged Crossbill. Where alders abound the conditions are favorable for the Redstart and the White-throated Sparrow. But later, as the bog conifer forest becomes continuous and dominant, the Waxwing, Redstart and White-throated Sparrows diminish in numbers and finally disappear. Still later, as the swamp becomes eliminated with the development of the climax forest, the Yellow-bellied Flycatcher will also become excluded.

This is perhaps the simplest succession from the water to the climax forest, via the bog forest. This series is very perfectly preserved in all stages and has an extensive range. The number of species in the association is rather large when compared with the preceding associations.

d. Aspen-birch Association and Habitat.

This series develops from the beach and the waves fall from the ridges or low rock surfaces and leave the bare expanses. As the rock disintegrates, decomposes, and humus accumulates, a soil is formed, mainly in depressions or at the bases of the ridges, and from these it tends to encroach upon the open places with a zone of Jack Pine, aspens, or White Birches. These areas are largely strips along the crests of ridges or small park-like openings on rather level rock. In no case are these single areas large, so that the habitat is only extensive in the aggregate. With the presence of the open aspen and birch woods, the following society is likely to be characteristic:—Junco, Oven Bird, Red-eyed Vireo, Chipping Sparrow, White-throated Sparrow, Flicker, Cedar Waxwing, Wilson's Thrush and the Chickadee. As the deciduous trees are replaced by the open encroaching conifer forest, the Song Sparrow, the Nashville, Myrtle and Black-throated Green Warblers and Wilson's and Olive-backed Thrushes, which frequent the forest margins, increase in abundance. The Oven Bird has an extensive northern range from Labrador into the Yukon Valley and may well have been a very early pioneer upon the island as the aspens and birches were probably the first broad-leaved tree arrivals. From the above it is seen that this means an extensive variety, but as the dominance of the climax forest encroaches this number again becomes reduced.

The composition of the society varies somewhat, depending upon the surroundings, as proximity of the present shore or distance from it. Many of these openings are continuous with the present beach. It is not improbable that this was a prominent society whenever the waters fell rapidly from the island between,

rather stationary levels. This has been a society decidedly on the decline with the encroachment of the forest.

Probably this association varies considerably in its composition, and has done so in the past; but its main features are fairly constant. These variations seem likely, through the influence of openings produced by fires which, when extensive, may have caused a new equilibrium among those species frequenting openings.

The Burned Area Association.

This phase should perhaps be considered as supplementary to the aspen-birch association just considered. A fire brings about a reversal of conditions through the destruction of the forest, and in some cases, a part of the soil as well. As there are all degrees of extent and completeness in this process, there is a corresponding variation in the details of the resulting succession, at least in its early stages. It is only when there is a very complete destruction of the vegetation that the continuity with former occupancy is wholly broken.

The easily inflammable character of these conifers, even when in a green condition, makes it likely that natural causes, such as lightning or marsh gas (*cf.* Penhallow, '07), may have been influential. The proximity of the gas supply and the conifers is of interest as this may influence their liability to fire and thus to this sort of reversal of conditions. Thus liability to fires is rather characteristic of the region, and man's influence has tended merely to reinforce rather than to introduce this feature. Thus it seems probable that fires have been a factor in supplementing the natural park-like openings. In, addition to the burned areas found upon Isle Royale, other limited open areas are due to cultivation and are kept open.

The birds characteristic of the more open situations are the Sharp-tailed Grouse, Song and Chipping Sparrows, Flicker, and the Purple Finch. The Grouse is a Plains form, is near its eastern limit, and is perhaps a late arrival upon the island. The other species are wide ranging in the Canadian coniferous forests but are not of such northern range as the aquatic and shore associations. There is nothing in their range to suggest their arrival earlier than the forest association. Taking all the birds of the openings together, it is not improbable that they arrived at about the same time as those of the forests, but frequented different situations,—the forest kinds occupying the slopes and drier valleys, and the others the openings.

e. The Climax Association or Formation and Habitat.

The climax association should not be considered in such a way as to lead one to think that it is *distinct* from the other associations. It belongs to *all* of them as the end of their series under existing biotic and environmental conditions. Thus the aquatic association, through the bog conifers, is transformed into the Balsam-spruce association; and from the beach through the aspen-birch

association again to the balsams and spruces. The climax association is the condition of adjustment toward which all societies move under the present conditions. For this reason the earlier stages, conditions and associations of the climax have been outlined in the preceding discussion.

In the dominant forest the dense shade prevents an extensive ground cover of herbaceous plants; and although Ground Hemlock is abundant locally, yet in places the forest floor is quite open and free from lower shrub growth. The remarkable preservation of trails or roads through such tracts shows clearly how slowly changes take place. Such a habitat must be relatively equable in its temperature and moisture relations.

Geographically speaking, the primary characteristic of the climax is its *relative stability*, due to a dominance or relative equilibrium produced by the severe environmental and biotic selection and adjustment throughout the process of succession.

At this point attention should be called to the fact that dominance is a resultant of an equilibrium produced by neutralizing or overcoming other forces and influences. We may think of the process of succession as a stream of forces whose development may be compared with the transformation of a drainage line,—such as, for example, that of a rivulet into a creek, and then into a river. The stream and the character of the ground mutually influence each other and the course followed is a resultant of the mutual adjustments. The stream is; deflected by one condition and then another, just as succession varies with local conditions; yet the water continues to run down grade and seeks an equilibrium, and similarly, biotic succession continues on its course deflected here and there by local influences, yet forever tending toward a state of biotic equilibrium. The dominance of the climax society or formation, considered as a process rather than a product, has much in it that is analogous to the dominance produced by the process of base-leveling.

The characteristic birds of the climax forest are:—the Chickadee, Golden-crowned Kinglet, Red-breasted Nuthatch, Canada Jay, Downy, Hairy, Arctic Three-toed and Pileated Woodpeckers, and the White-winged Crossbill. Here again the association becomes small in variety of species and comparable with the small society which must have been associated with the complete dominance of the Lake waters. Thus there has been a development of diversity from simplicity, with later a return to simplicity. To these birds of the forest should also be added those species of general distribution, as the Eagle, Swift, Swallows, etc., a class of birds whose predaceous, insect-feeding and wide ranging habits make them particularly difficult to properly associate. A careful study of this class of birds will be necessary before they can be satisfactorily correlated with their proper avian associations.

But let us not overlook the fact that even this dominance is only *relative*, for since the Ice Age even this *entire*

formation has migrated northward, and a true succession has been produced with its attendant changes in the conditions and in the composition of the associations. Just as upon Isle Royale a definite dynamic trend was given to the complete environment by the falling Lake surface, so in the post-Glacial northward migration there was a northward migrating climate. These conditions determined that on the *north side* of this immense succession or migration habitats and associations were developed which are comparable to those attending the downward march of the Isle Royale beach; and even today, by passing from Isle Royale to the tree limit with its zone of aspens and birches, one may find representatives of the various kinds of associations which in all probability moved north, just as today in passing from the forest to the rocky beach balsams and spruce are encountered before the aspens and birch. If, however, this is only another case of convergence and not at bottom the same or a comparable process, we are then certainly far from an understanding of even the general nature of the problem.

3. *Internal Factors.* With the idea of succession, as exemplified by Isle Royale, let us turn to other factors which influence the internal relations of the birds within an association or society, because such relations are also necessary to an intelligent understanding of succession. Some of these general relations have been outlined, but certain others are needed which have been well expressed by Brewster ('06, p. 62-63): "Many if not most birds show a marked preference for breeding in certain regions, throughout which they are more or less evenly and generally distributed, but within which their numbers do not seem to increase beyond fixed maximum limits no matter how carefully the birds may be protected or how successful they may be in rearing their young * * * I have observed—as, indeed, who has not!—that few birds—excepting those which, like Swallows, Terns, Herons, and Gulls, are accustomed to nest in colonies—tolerate very near neighbors of their own species during the season of reproduction. At its beginning each pair takes possession of a definite tract of woodland, orchard, swamp or meadow, which the male is ever on the alert to defend against trespassers of his own kind and sex, although he often seems quite willing to share his domain with birds of other and perhaps closely related species. The extent of the area thus monopolized varies exceedingly with birds of different species. An apple orchard which affords sufficient room for—let us say—two pairs of Yellow Warblers, two pairs of orioles, three or four pairs of Chippies and four or five pairs of Robins, seldom or never harbors more than a single pair of Kingbirds or crested Flycatchers. * * * As a rule, the species which roam over the most ground in the course of their daily wanderings claim and maintain the broadest preserves, while those of sedentary habits often content themselves with very modest freeholds. Whatever the extent of the domain, the birds who occupy it as a summer home evidently regard it as exclusively their own. The

readiness and celerity with which trespassing birds are accustomed to retire when attacked or even merely threatened by the established tenants, has seemed to me to indicate that the claims of temporary ownership are respected by all right-minded birds. * * * In my opinion the desire for exclusive possession so conspicuously shown by the male, and often by him alone, is usually the direct result of *sexual jealousy*. This, as is natural, makes him intolerant, during the breeding season, of the near presence of rival males. If his concern were chiefly in respect to the food supply, it would be equally manifested at every season and towards all birds who subsist on the same food that he and his mate require—which is, certainly not the case."

The tendency of pairs and species to *space themselves* and to become *relatively sedentary* is thus a characteristic condition in an association, and is an important element in an understanding of succession because it shows the internal organization and habit with which an invader or pioneer from another association has to contend. As Dixon ('97, p. 91) has pointed out, this spacing tendency is an important factor in the extension of range of species and is intimately related to the location of nesting sites. These facts clearly show that both these internal influences and the environmental ones must be distinguished if we wish to determine the relative influence of each and their bearing on succession. The above quotation from Brewster clearly shows that in general not only a greater number of birds can live in a given area, but also that they can live closer together, if they vary in kind. Then again, within the association there are marked differences in habitat preference. Thus in the forest there are those birds which nest in the trunks or among the topmost branches of the trees, or even upon the ground; and these are differences largely distinct from the spacing of the pairs of the same species. These influences must be recognized among the dominant influences within the association, and upon which much emphasis must be placed.

4. Environmental Factors. Then in addition to these internal factors, there are the dominant physical factors. In the following discussion primary emphasis will be placed upon succession as found in the Northeastern Biotic or Conifer Center, because successions at other centers with different biotic components and other dominant physical conditions must possess a certain amount of individuality, in addition to those features common to succession in general. The dominant biotic tendency or dynamic trend of this center, as a *resultant of all internal and environmental influences*, is for the conifer biotic association to *encroach upon all other societies and habitats and to become the dominant or universally distributed association*. Thus, in general, all habitats produced by local influences tend to become transformed into the dominant biotic association or formation. In general also, small bodies of water are rapidly encroached upon by inwash, vegetation or drainage, and tend to become extinct and forested. All other openings, as the rocky ledges and ridges or burns,

are encroached upon as soil accumulates or fires are prevented, and the forest biotic association spreads over the entire area.

From such relations it will be seen that our knowledge of the causes and conditions of succession must largely result from the study of these *local environments or habitats and their biotic succession*, because, where dominance is established the succession is almost completely obliterated. *Each minor habitat and society is to be looked upon as simply a stage, more or less temporary, in the onward wave toward the dominant or climax association*. Thus in the marshes, birch or aspen woods, rock openings and ponds may be "original" conditions which are becoming cumulatively transformed in the direction of the final dominance of the climax biotic type.

The relatively slow rate of change in many environmental processes and the relative stability of the climax biota,¹ is doubtless the basis for the current view that such conditions are relatively constant or fixed; but that change and not constancy is the normal and usual condition in nature is quite evident upon a moment's reflection. Almost every one notices these changes after an absence of a few years from a region. Thus intimacy tends to blind us to changes unless a *habit* of giving attention to them is deliberately cultivated. For this reason some find it almost impossible to recognize environmental changes or to comprehend their significance. It is therefore of practical value to recognize clearly under what conditions changes may be most readily perceived. Therefore the importance of the study of *local influences* is emphasized, and the necessity recognized of distinguishing the dominance of geographic and relatively stable conditions or formations as contrasted with those due to local and often relatively changeable conditions. Then among these changes we must distinguish those which are mere fluctuations and those which are indicative of the true progressive succession. This is mainly accomplished by attention to general relations and the subordination of minor details.

¹For the migrations of climax societies, cf. Adams, '05.

5. Environmental and Associational Convergence. At the present imperfect stage of ecological development, comparison must furnish us the most important and general clues to the processes of succession; and undoubtedly this method must long remain as our main guide on account of its comprehensive application and the magnitude of the problem to be solved. It is therefore desirable that the limitations of the method should be clearly borne in mind. It is often assumed that the implied successions of a given place are the same as those which have developed at that place in the evolution of the present climax. But as we positively know that *many different causes are able to produce the same or very similar results*, such conclusions must be received with due caution. That the dominant geographic conditions tend to override local influences seems very fairly established because *diverse local or original conditions are*

transformed into the climax or dominant type. This clearly shows that in time diverse local influences have flowed into the general environmental trend or current and have become a part of it. There is thus a very strong *convergent* tendency. By convergence is meant the independent production of the same kind of association from diverse starting points or habitats and associations. Quite minor ecological units may show similar but temporary convergent tendencies in their succession. It is therefore not surprising that any marked environmental dominance will tend to produce similar or convergent results, even in local areas. Under such circumstances similar associations or societies may be independently and repeatedly formed by the selecting environmental influences, such as, for example, are found in the numerous small lakes scattered throughout the coniferous forests. This convergent phenomenon is certainly a fertile source of confusion throughout all phases of science. Perhaps the best guide through such a labyrinth will be to clearly bear in mind the relative value of general and local influences, and watch with an "eternal vigilance" for convergent results due to diverse causes. This convergent phenomenon is particularly liable to occur in the case of environments produced by reversible physical conditions. It should further be stated that a study of these problems from a genetic and dynamic point of view will aid in recognizing such results. Under such circumstances attention is primarily directed toward the dominant causes and conditions of change rather than to the stages, products, and results produced by them. Convergence thus viewed is the result of several causes and should be considered a product rather than a process. This same distinction may be made for all societies, associations and formations. *Convergent phenomena are thus particularly liable to confuse wherever products rather than genetic processes receive primary emphasis.*

6. Succession and Environmental Evolution. The relation of succession to general biological problems is very intimate. This opens up a very extensive field which is only mentioned to indicate its general relation to succession. The facts of succession and evolution must ever remain far in advance of our knowledge of their causes. If, however, one turns to the standard evolutionary treatises and searches for a discussion of the evolution of the environment, as correlated with animal evolution, only the most general, or the elementary and superficial phases, are as a rule discussed. To be sure, certain papers and treatises take up special phases of the problem, and the broadest phases are treated by the geologists; but none of them seem adequate as a comprehensive treatment of so important a subject. Succession, broadly and genetically considered (dynamic rather than static), is a phase of environmental evolution.

7. The Relation of Succession to Organic Evolution. Mention has been made of the relation of succession to environmental evolution, but its relation to the organic evolution of birds should also be indicated.

The mutual relations of organic and environmental evolution have been and will continue to be the battleground of biological thought for an indefinite length of time. Here lies the tension line between the two main schools of biological interpretation.

One school maintains that all *causes* of evolution are *internal*, and that the environment is only a *condition*, not a cause. From this point of view the fundamental causes are internal and therefore environmental conditions can only indirectly influence evolution through the weeding out of those forms not in harmony with the conditions; and hence it has a *selective* rather than an *originative* influence. From this point of view succession and environmental evolution can contribute nothing to the elucidation of the *causes* of organic evolution, though they may to an understanding of the selection produced by the succession of conditions in which organic evolution has taken and is taking place. In harmony with this point of view, succession, broadly treated, should furnish a fundamental method of treatment for the process of selection, and the detailed principles of its working. This would certainly be an important advance because natural selection has frequently been reproached for its indefinite methods and lack of definite treatment. Succession from this point of view is primarily related to the Darwinian factors of evolution. No doubt this is: one reason why Darwin himself put such high value upon the study of ecological relations of animals, *i. e.*, their relation to their complete environment, or their struggle for existence.

If, however, all causes are internal and not directly subject to external influences, they must be beyond experimentation to a corresponding degree. Under such conditions evolution becomes a *descriptive* rather than a *causal* science, and all that investigation can do is to describe the succession of forms produced by these internal causes.

On the other hand the rival school maintains that both internal and external conditions may be real *causes* of organic evolution. This is thought to be brought about by the direct or indirect influence of the environment upon the germ cells, by environmental selection, or even by both combined. From such a point of view the environment may thus be either a *cause* or a *condition* of organic evolution, or both. From such a standpoint the evolution of the environment receives increased importance, as under such conditions organic and environmental evolution are causally related, and thus intimately correlated. Viewed thus, environmental evolution is more than the description of the succession of conditions, but may be explanatory as well.

The particularly significant feature is that environmental evolution and biotic succession are of great value and can contribute either to the causes or conditions, or to both, of evolutionary advancement.

VI. Some Principles of Succession.

By succession is meant the progressive change (= adjustment) in the composition of the associations at a given place. If a swamp becomes filled with dune sand, the birds characteristic of the swamp will be replaced by those of the dunes, and thus succession is initiated. But in addition to changes due to local influences there are those produced by very extensive or geographic influences, as in the case of a climatic change. Attention should also be directed to the fact, that biotic succession is only a particular phase of 'the general law of change which we see operating wherever a complex of forces are tending toward a condition of mutual adjustment. That succession is a process which, from its very nature, must be as extensive as are the causes of change does not appear to have been clearly recognized by all students of biotic succession. For this reason there are certain principles of succession which are well established in other sciences, but which have not been applied to biotic succession. In human society, for example, there are many institutions whose formation, development and perpetuation clearly illustrate the laws of succession) which also apply, not only to plants and animals, but to geologic phenomena as well. It is not at all surprising therefore that under these various guises their common features are easily overlooked and even denied by some students.

In the study of the animal environment some knowledge of the general principles of succession, not worked out in detail for birds but already well established elsewhere, ought to be suggestive and possibly valuable in the study of avian succession. Though such generalizations are primarily of a provisional and suggestive character, yet investigation should be stimulated rather than retarded by them. Such descriptive characteristics and principles are stated briefly in a form convenient for testing and criticism and should be useful as are criteria in the study of geographic origin. So far as known to the writer only two authors have attempted to formulate principles of biotic succession, and these have been limited to plants. The first is by the Danish ecologist Warming ('96, *Oekologische Pflanzen Geographic*, pp. 360-361), and the second by Clements ('05), whose treatment merits special attention. Cowles ('01) has done much to put the idea of succession upon a genetic basis. In the present outline only those features and principles are mentioned which are thought to be of a more or less general character, and those particularly applicable to animals. This list needs to be greatly prolonged, and the interrelations of these characteristics must be determined as well as their relative value and application to various ecological groups and in diverse regions. The following suggestions can only outline the problems involved. At this stage, differentiation is particularly desirable. Processes and products bear the same names and must be understood accordingly; thus the *processes of dominance* lead to the *product* dominance. Dynamically considered, the process is primary, but used in a structural sense such terms refer to products.

1. Starting with any given set of environmental conditions and organisms, these become a cause and condition of future changes. All changes are cumulative and form a continuous series or process.
2. No sharp line can be drawn between cause and conditions in succession as their relations are often reversible. A cause at one time may be a condition at another, and *vice versa*.
3. The formation or association itself must be considered as an essential part of the complete environment, and should be so understood when reference is made to the environment. cf. No. 1.
4. A given formation in its dominance tends to encroach upon all minor habitats and associations. These minor habitats tend to become cumulatively changed convergently toward the climax environment or formation. This is a process of eliminating diversity and thus establishing dominance.
5. Where complete environmental and biotic adjustment has taken place, the dominance of the biotic formation is most complete. This may be considered a geographic or environmental optimum. This, in general, implies complete succession and the dominance of the climax formation.
6. From the standpoint of causes and processes, the succession of societies and formations is the expression or result of the environmental process moving toward an equilibrium.
7. The lack of a uniform rate of succession throughout large areas is the rule, on account of the slowness with which extreme conditions are transformed into those of the average.
8. The slowly changing extreme conditions tend to preserve many of the most important early stages of conditions and succession; hence the utility of these belated changes in validating succession as determined by the comparative method.
9. Other things being equal, the slower the succession the greater the chances for variation in the details and composition of the societies.
10. The formation or climax society is only the most conspicuous case of convergence, reached by all routes and successions, at a given environmental center.
11. The succession of societies within a formation is liable to be more stable in its main features than the composition of its societies. Probably the general features of such a succession most nearly approximate that which the region passed through in the development of the formation. Adams, '05, p. 67.
12. Formations of different geographic centers will vary in their *dominant dynamic tendencies*, yet open (unforested) formations will have certain features in common, as will also forest formations. Thus, not only will the compositions of the societies vary, but also the climax formations and their dynamic trends.

13. The stability of the climax environmental factors and their biotic formations is only relative. They may themselves migrate or change by a progressive succession in the direction of the dominant environmental trend. This migration involves a true succession, as is well illustrated by changes and successions attending the Glacial influences and the elevation of the Coastal Plain of the United States. (Cf. Adams, '05).

14. The stability of dominance is due to a complete biotic and environmental adjustment brought about by the repeated selections of the preceding succession and resulting in a "pure culture." Dominance may be likened to the static social condition of China or to a monopoly.

15. Succession is a form of complete or entire environmental selection, certain species or associations receiving an environmental approval while others are excluded. This is a particular and extensive form of natural selection. Successional selection in its broadest ecological aspect includes the evolution of the organisms, particularly as members of *associations* in their most intimate environment.

16. Any association not a climax is in unstable equilibrium and in a condition unfavorable to its permanence. The climax society is in a state of biotic and environmental equilibrium. (Cf. Warming, No. 6 and Clements V; also cf. No. 13, 14).

17. Widespread physically uniform conditions favor a dominant biotic formation. Climate may neutralize topographic diversity, or topography the climate. Base leveling and other geological processes which favor the production of uniform conditions will favor dominance. (Adams, Amer. Nat., 35, p. 842).

18. From an evolutionary standpoint the earlier stages of succession are liable to be struggles with the physical environment; later, in the intermediate state of "storm and stress," the competition is most diverse and intense, and may thus be a fertile source of adaptive changes and individual adjustments, through severe selection; and finally in the stage of dominance, the competition is also biotic and physical, but under relatively simpler conditions. Permanence of new characters may be favored by habitat isolation and thus favor polytypic or divergent evolution.

19. In succession the adjustments and modifications of species may be accomplished by a change from one society to another as well as by individual modifications or adjustment within the society.

20. Pioneer invaders, except in social species, are generally isolated and increase progressively with dominance. Cf. Warming, No. 1.

21. Species and individuals in the early stages of succession or of societies are relatively few, increase in the intermediate stage, and are again reduced in number with dominance and in the climax society. Cf. Warming, No. 2. Clements VI. (3, 5).

22. The species of open (unforested) formations are only pioneer societies in forested formations and *vice versa*. Cf. Warming, No. 5.

23. The less sedentary species, those less inclined to regularly return to old nesting sites, and young birds tend to become pioneers and thus extend the breeding range. Cf. Warming No. 4. Dixon, '97, p. 91.

24. Pioneers generally come from near by and from similar conditions. Cf. Clements III, (3).

25. Extension of range takes place mainly at the unoccupied margin. This may mean unilateral or radiate extension. Cf. Clements V, (5).

26. The succession from the aquatic association to the forest is probably an ancient one. In this there is a general succession from the less to the more specialized kinds of birds. Cf. Warming No. 2; Clements VI (4).

VII. Some Advantages of a Knowledge of the Laws of Succession.

The study of succession implies a detailed knowledge of the field relations of birds, and as this has received so little attention as a subject of special study, it is perhaps worth while to mention briefly some of the practical and scientific advantages which we may reasonably expect will result from the development of this phase of investigation.

The current discussions of environments are generally very fragmentary and chaotic, and the careful study of bird habitats and succession will greatly improve this phase of ecology. Here is a field of study in need of distinct recognition as a subject worthy of detailed investigation, in addition to those lines already current. When once this field is developed, then and only then will it be possible to intelligently discuss the evolution of avian environments and to correlate them with the evolution of birds themselves. It is quite probable that one of the main conditions which prevents a more rapid advance along evolutionary lines is in a large measure due to the almost utter failure to analyze dynamically environmental complexes. Succession, studied in its broader aspects, should greatly aid in the formulation of the laws governing the "struggle for existence," which is frequently condemned for its indefinite character.

From another point of view there are very important reasons for urging extensive studies of this character at a relatively early date, because the encroachments of civilization, which by the destruction of the forests, the drainage of the land, irrigation, farming and grazing of the grasslands, are rapidly destroying original environmental conditions before they are studied ecologically. Much of Europe has already gone through this stage of demolition, and it is only to new and relatively unmodified countries that we can look for an adequate statement of these problems and their relations in their original and primarily evolutionary and developmental form. It is not improbable that the next generation may wonder why some subjects, the

investigation of which might have been delayed, have received detailed attention, while others equally or perhaps even more important have been almost ignored and must forever remain unknown because of this neglect to secure the "vanishing data." (Cf. Haddon, '03.)

Such ecological studies may be expected to have a valuable reflex influence upon the naturalist himself. We may hope that the future re-visor of a group of birds will consider a knowledge of the field relations of his specimens as an essential qualification, just as at the present time a large series of specimens is held necessary. Fifty years ago a limited series was considered no disqualification, just as to-day the lack of a knowledge of their ecological relations is not so considered. Perhaps our ideas of relative values must change. In this connection a statement from Tristram ('94, p. 472) is to the point:—"The closet systematist is very apt to overlook or take no count of habits, voice, modification and other features of life which have an important bearing on the modification of species. To take one instance, the short-toed lark (*Calandrella brachidactyla*) is spread over the countries bordering on the Mediterranean; but along with it, in Andalusia alone is found another species, *Cal. baetula*, of a rather darker color, and with the secondaries generally somewhat shorter. Without further knowledge than that obtained from a comparison of skins, it might be put down as an accidental variety. But the field naturalist soon recognizes it as a most distinct species. It has a different voice, a differently shaped nest; and, while the common species breeds in the plains, this one always resorts to the hills. The Spanish shepherds on the spot recognize their distinctness, and have a name for each species."

Many examples of similar character might be cited to show the scientific value of a knowledge of the environmental relations of birds, and a moment's reflection will show that the problem of succession is only a small part of the general problem of environmental relations of plants and animals. Attention has already been directed to the relation which this general subject bears to evolutionary problems.

It is not at all unlikely that succession is very closely related to some of the causes of bird migration, and that with advance in this subject much light would be thrown upon migration. Migration is doubtless another illustration of convergent phenomena. In all probability, migration has originated not only independently in very diverse kinds of birds, but perhaps repeatedly, from different causes, even in the same group. The causes of migration must be numerous, varying with different ecological groups, which appear to be the true natural units for study and comparison. Thus the comparative study of migrations of different kinds of associations, as formations and societies, should lead not only to a better understanding of the various associations, but should also contribute to the general subject of migration which seems to have shown a tendency toward stability in the current methods of study. It scarcely seems probable

that with the diverse formations inhabited by birds, and with their ecological diversities there should be only a few causes of the phenomena.

To keep pace with successions animals must either adjust themselves, change their habitat, or migrate. From such relations it is evident that various supposed environmental responses must be *tested primarily within the association and environment to which the animal normally belongs*. To this class belongs protective coloration and allied phenomena. To be of fundamental value, the influence must have some permanence and this may be sought in the *dynamic* trend and dominant influences of different associations. It is difficult to conceive of other more reliable methods of approach to such problems.

In addition to the scientific value of this line of investigation, there are important economic applications of the laws of avian environment. This is particularly true of forestry and agriculture. The forestry problem is continually becoming more important, but the relation of bird life to forests and forest succession has received little attention. As agents for scattering seeds of trees and shrubs, birds are very important. Here is where the interests of the avian ecologist and forest ecologist overlap. The student of bird life will wish to know how a region is to be reforested, and what succession of bird life will attend the succession of the forest as reforestation progresses. On the other hand, the forester will wish to know how birds will aid or retard him in the process of reforestation. Then, in guarding or protecting the forest, what help can be secured from birds with regard to insect pests? These are only samples to show that here is a field which, as time advances, will become of more and more importance, and that these problems will eventually call for specially trained men to handle them.

In connection with forestry and agriculture we have quite exceptional conditions for extended experimental studies in bird succession as related to forest succession, crop rotation, etc. The relation of birds to agriculture appeals to a much larger number of people than does their relation to forestry. There are several reasons for this; first, because more persons are interested in farm and horticultural crops than in forests; and second, because birds are soon attracted in such large numbers by the food supply of grains and fruits which these crops so greatly increase, that the extensive destruction by birds readily attracts attention. And while we hear much of the great reduction of certain species of birds in parts of the country, it is not at all improbable that with the destruction of the forests (which were dense and dominant and tended to *limit* the abundance of many species frequenting the open), and the increase of food in cultivated fields, there has been an increase in the total number of birds, even in spite of the great numbers killed by man.

But to the phase of succession with which we are primarily concerned, almost no attention has been given, in spite of its fundamental relation to crop rotation and

the corresponding avian succession attending this. Indeed there seems to be a very decided need of a thorough investigation and discussion of the general principles underlying all these economic problems, that they may be brought into harmony with the advances made in some other phases of ecology.

References.

- Adams, Chas. C.**
1905. The Postglacial Dispersal of the North American Biota. *Biol. Bull.*, 9, pp. 53-71.
- Beyer, G. E., Allison, A., and Kopman, H. H.**
1906. List of the Birds of Louisiana. Part 1, *The Auk*, 23, pp. 1-15.
- Bray, W. L.**
1906. Distribution and Adaptation of the Vegetation of Texas. *Bull. Univ. of Texas*, No. 82.
- Brewster, W.**
1906. The Birds of the Cambridge Region of Massachusetts. *Mem. Nuttall Ornith. Club*, No. IV.
- Brown, R. A.**
1907. A Study of the Birds of the Overflow, East of Ann Arbor, Michigan. Eighth Ann. Report Mich. Acad. Sci., pp. 162-174.
- Burns, F. Z.**
1901. A Sectional Bird Census. *The Wilson Bull.*, N. S., 8, pp. 84-103.
- Clements, F. E.**
1905. *Research Methods in Ecology*. Lincoln, Nebraska.
- Coville, F. V.**
1893. Botany of the Death Valley Expedition. *Cont. U. S. Nat. Herbarium*, IV.
- Coville, F. V., and MacDougal, D. T.**
1903. Desert Botanical Laboratory of the Carnegie institution. Carnegie Institution.
- Cowles, H. C.**
1901. Plant Societies of Chicago and Vicinity. *Bull. Geog. Soc. Chicago*, No. 1.
1901. The Physiographic Ecology of Chicago and Vicinity; a Study of the Origin, Development and Classification of Plant Societies. *Bot. Gaz.*, 31, pp. 73-108, 145-182.
- Dixon, Chas.**
1897. *The Migration of Birds*. London.
- Fernald, M. L.**
1907. Soil Preferences of Alpine Plants. *Rhodora*, 9, pp. 149-193.
- Forbes, S. A.**
1907. An Ornithological Cross-Section of Illinois in Autumn. *Bull. Ill. St. Lab. Nat. Hist.*, 7, pp. 305-335.
- Frothingham, E. H.**
1907. Notes on the Michigan Forest Reserve. Eighth Rep. Mich. Acad. Sci., pp. 157-161.
- Ganong, W. F.**
1903. The Vegetation of the Bay of Fundy Salt and Diked Marshes; an Ecological Study. *Bot. Gaz.*, 36, pp. 161-186, 280-302, 349-367, 429-455.
1906. The Nascent Forest of the Miscou Beach Plain. *Bot. Gaz.*, 42, pp. 81-106.
- Gilbert, G. K.**
1885. The Topographic Features of Lake Shores. Fifth Ann. Rep. U. S. Geol. Surv., pp. 69-123.
- Gray, A., and Hooker, J. D.**
1881. The Vegetation of the Rocky Mountain Region. *Bull. U. S. Geol. and Geogr. Surv. of Terr.* (Hayden), 6, pp. 1-77.
- Gulliver, F. P.**
1899. Shoreline Topography. *Proc. Am. Acad. Arts and Sci.*, 34, pp. 149-258.
- Haddon, A. C.**
1903. The Saving of Vanishing Data. *Pop. Sci. Mo.*, 62, pp. 222-229.
- Harper, R. M.**
1906. A Phytogeographical Sketch of the Altamaha Grit Region of the Coastal Plain of Georgia. *Ann. N. Y. Acad. Sci.*, 17, pp. 1-359.
- Harvey, L. H.**
1903. A Study of the Physiographic Ecology of Mount Katahdin, Maine. *Univ. of Maine Studies*, No. 5.
- Jacobs, J. W.**
1904. The Haunts of the Golden-Winged Warbler. *Gleanings*, No. 3. Waynesburg, Pa.
- Johnson, K. S.**
1907. Mean Monthly and Annual Relative Humidity Charts of the United States. *Rep. South African Assoc. Adv. Sci.*, 1906, pp. 161-168.
- Judd, S. D.**
1902. Birds of a Maryland Farm. *Bull. No. 17, Div. of Biol. Sur. U. S. Dept Agr.*
- LeConte, J. L.**
1850. General Remarks upon the Coleoptera of Lake Superior. *Agassiz, "Lake Superior,"* pp. 201-242.
- McCreary, O.**
1906. The Ecological Distribution of the Birds in the Porcupine Mountains, Michigan. *Mich. Geol. Surv. Ann. Rep.*, 1905, 56-67.
- Merriam, C. H.**
1890. Results of a Biological Survey of the San Francisco Mountain Region and Desert of the Little Colorado, Arizona. *N. A. Fauna*, No. 3, Div. Ornith. and Mammalogy, U. S. Dept. Agriculture.
1899. Results of a Biological Survey of Mount Shasta, California. *N. A. Fauna*, No. 16, Div. Biol. Surv., U. S. Dept. Agriculture.
- Osborn, H. F.**
1902. The Law of Adaptive Radiation. *Amer. Nat.*, 36, pp. 353-363.
- Palmer, W.**
1900. Ecology of the Maryland Yellow-throat, and its Relatives. *The Auk*, 17, pp. 216-242.
- Penhallow, D. P.**
1907. A Blazing Beach. *Pop. Sci. Mo.*, 70, pp. 557-564.
- Piper, C. V.**
1906. Flora of the State of Washington. *Cont. U. S. Nat. Herbarium*, XI.
- Pound, R., and Clements, F. E.**
1900. The Phytogeography of Nebraska. *Bot. Surv. of Nebraska. General Survey*, 1.

Ridgway, R.

1874. The Lower Wabash Valley, Considered in Its Relation to the Faunal Districts of the Eastern Region of North America; with a Synopsis of Its Avian Fauna. *Pro. Bost. Soc. Nat. Hist.*, 16, pp. 304-332.
1889. The Ornithology of Illinois. *Ill. Nat. Hist. Surv.*, 1, Springfield, Ill.

Ruthven, A. G.

1906. An Ecological Survey of the Porcupine Mountains and Isle Royale, Michigan. *Geol. Surv. Mich., Ann. Rep.*, 1905, pp. 17-55.

Stejneger, L.

1903. A Reply to Recent Strictures on American Biologists. *Science*, N. S., 19, pp. 371-376.

Townsend, C. W.

1905. The Birds of Essex County, Massachusetts. *Mem. Nuttall Ornithol. Club*, No. 3.

Transeau, E. N.

1903. On the Geographic Distribution and Ecological Relations of the Bog Plant Societies of Northern North America. *Bot. Gaz.*, 36, pp. 401-420.
1905. Forest Centers of Eastern America, *Amer. Naturalist*, 39, pp. 875-889.
1905-'06. Bogs and Bog Flora of the Huron River Valley. *Bot. Gaz.*, 40, pp. 351-375, 418-448; 41, pp. 17-42.

Tristram, H. B.

1894. Field Study in Ornithology. *Smith. Rep. for 1893*, pp. 465-485.

Watkins, L. W.

1900. Michigan Birds that Nest in Open Meadows. First Report of Mich. Acad. of Sci., pp. 66-75.

Whitford, H. N.

1901. The Genetic Development of the Forests of Northern Michigan; A Study in Physiographic Ecology. *Bot. Gaz.*, 31, pp. 289-325.
1905. The Forests of the Flathead Valley, Montana. *Bot. Gaz.*, 39, pp. 276-296.

Young, R. T.

1907. The Forest Formations of Boulder County, Colorado. *Bot. Gaz.*, 44, pp. 321-352.

kindly furnished certain records of distribution, as indicated in the text.

The field notes and collections were largely made by Dr. H. A. Gleason; some were made by the writer; and specimens were also collected by B. F. Savey. The geographic range of all the species taken is given in some detail, as a basis for geographic conclusions. Time limitations have prevented a full discussion of these.

The geographic relations of the fauna have been discussed in more than customary fullness. The entire subject of the geographic relations of the North American beetle fauna had to be gone over; and as the work advanced, it became evident that a general account of these faunal relations was desirable from a standpoint somewhat different from that generally expressed. Undoubtedly many important papers and statements have been overlooked, so that it will be desirable for others to further extend this treatment of the subject.

Attention should also be called to the fact that in the past studies of the distribution of insects have been largely irrespective of their habitats, associations and such ecological relations. This has been one of the many defects of distributional studies, as it is of the present study. It is for this reason that an attempt is made to briefly discuss the habitat relations and successions of beetle associations. Life history, food habits and other ecological phases need detailed investigation and discussion so that all these phases can be related to the causes and conditions which affect distribution. The economic advantage of a knowledge of the laws of succession of beetle associations has largely been neglected, but ultimately must become one of the main general principles in much economic practice. This will probably become more conspicuous when forests assume a higher value, and the relation of beetles to reforestation, etc., demands careful attention.

THE COLEOPTERA OF ISLE ROYALE, LAKE SUPERIOR, AND THEIR RELATION TO THE NORTH AMERICAN CENTERS OF DISPERSAL.

BY DR. CHAS. C. ADAMS.

1. Introductory Note.

The beetles secured in 1905 by the Museum expedition were collected during July and August by various members of the party. We are indebted to Prof. H. F. Wickham, of the University of Iowa, Iowa City, for the determination of most of the species; the remainder were determined by Mr. E. A. Schwarz, of the U. S. National Museum, through Dr. L. O. Howard and Mr. E. S. Titus. To these gentlemen we wish to express our appreciation for these favors. Mr. A. B. Wolcott has

II. Notes on the Habitat Relations of Beetles.

The beetles collected by our party were tabulated by Stations to determine if marked habitat preferences were evident. The tabulation shows that at most stations only a relatively few species were found. At those stations where the largest variety was found, as at our camps, the conditions were exceptional. The occurrence of the flowers of the Cow Parsnip attracted many species. It is quite evident that these flower frequenting species did not breed there, so that in a strict sense they do not belong to these open areas, as the breeding places of insects must furnish the only substantial basis for the determination of insect habitats. In many cases only provisional habitats can be assigned with our present incomplete knowledge of life histories. In many species the larval and adult habits are very different, particularly with regard to their food. For this reason error is very liable to occur and caution is necessary. In the present

provisional discussion the haunts frequented by the adults have been primarily utilized. This is an unfortunate limitation, but it is hoped that this will not confuse the main feature of the problem.

On the Lake Superior beach (I, 1) the following 14 species were found: *Calosoma frigidum*, *Bembidium* (five species), *Rhantus binotatus*, *Anatis 15-punctata*, *Macropogon rufipes*, *Corymbites medianus*, *Podabrus diadema*, *Malthodes niger*, *Sericea vespertina* and *Leptura chrysocoma*. It is evident that some had been washed up by the waves (*Calosoma* and *Anatis*) while others normally frequent sandy beaches (*Bembidium*) or the beach pools (*Rhantus*), while still others were here because of the open character of the beach and the proximity of the forest. Hayward ('97, p. 37) says concerning the habitat of *Bembidium*: "Most of them are riparian in their habits, occurring under stones and refuse near the water's edge along streams, the shores of ponds, or on the seamoss, while a few occur almost anywhere."

The clearing about the Light-house (I, 7) had the greatest variety of beetles found at any station. It included 37 out of the 89 species found at all stations. There were several circumstances which combined to make this number large. The greater opportunity of those about camp to make collections; the season of the year (July); the presence of the Cow Parsnip in large numbers (which acted as insect traps, and upon which beetles congregated in such numbers that they were easily brushed into the cyanide bottles in large numbers); and the presence of logs, stumps, brush, etc. The flowers were a very conspicuous factor, and on these *Leptura chrysocoma* gathered in large numbers. The open space was favorable to the Carabids, the flowers, for the Coccinellids, Elaterids, Buprestids, *Trichias* and the Cerambycids. The two latter frequent also the logs and stumps. The wandering, tramp-like existence of these adult wood-boring beetles should not confuse one as to the true habitat of the immature stages which is in the forest. The surrounding forest was mainly composed of White or Paper Birch, Balsam and Spruce.

At the camp on Siskowit Bay (V, 3) somewhat similar conditions were found to those at the Light-house (I, 7), but there were fewer flowers, more cut timber, furnishing logs, stumps, brush; a log shack was very thoroughly infested with beetles and their Hymenopterous parasites. The surrounding forest was largely White Spruce and Paper Birch. *Xylotrechus* was particularly abundant at this place.

Other open places, as those bordering the beach (V, 2) or the small openings on the ridges (I, 2), produced, in addition to the wandering flower feeders *Buprestis striata* and *Mordellestina scapularis*, a few Carabids, as *Harpalus megacephalus* and *Pterostichus femoralis*.

In the Balsam, White Spruce and White Birch forests (I, 3 and V, 4) the Staphylinids, *Grophoema*, *Boletobius cincticollis*, the Erotylids, *Tritoma* and the Carabids,

Calathus and *Blechnus*, are characteristic. The moist conditions which favor fleshy fungi show a marked influence. Here in the forest, of course, must also belong a great number of wood and bark boring beetles, which our limited collecting found assembled in the sunny openings on flowers.

Along the Desor trail (III, '04), through the hardwood forest of Yellow Birch, aspen and Sugar Maple, two other Staphylinids were found, *Quedius fulgidus* and *Tachinus memnoius* and the Scarabaeid *Geotrupes Blackburnii*.

If now we turn to the lakes and bogs, a very different kind of beetle life is found. On the surface of Siskowit Lake (V, 6) were found *Gyrinus minutus* and *picipes* and in the water-lily margins of ponds and lakes were found (III, 5 and IV, 3) *Donacia proxima*, *cincticornis* and *Galerucella nymphaeae*. In the tamarack and arbor vitae swamps (I, 4, 6 and V, 5) the following species of water beetles were found: *Haliphus ruficollis*, *Hydroporus tristis*, *Agabus congener* and *Scutopterus hornii*.

These may seem very elementary and commonplace observations, but the principles which underlie the correlation of certain (even common) species and their environmental conditions are very generally ignored by students of local faunas, except for collecting purposes. To know the exact habitat of certain species in one locality does not by any means prove that the subject is exhausted for other localities. No general ecological treatment of our beetle fauna has been attempted, not even of the smaller groups, such as families or genera, or even for a local area. The nearest approach we have to such work is found in certain economic papers, devoted to insects affecting some particular plant. Here is an excellent field for investigation.

Before leaving the subject of habitats, attention should be called to certain publications which are of particular use in the study of the life histories of insects in these northern forests. The first is Packard's "Forest Insects," and the second is Felt's "Insects Affecting Park and Woodland Trees."

A few suggestions are added as to methods of ecological collecting which may aid similar surveys. When the time for a survey is limited some system of ecologic trapping will prove of great advantage. Thus for aquatic beetles traps, like those planned by Needham, may be very useful, and still others are needed for the ground fauna and those frequenting trees and shrubs. Sweeping and beating as usually practiced, while securing many species, certainly produce little ecological data. It may be suggested that systems of trapping may be devised which will contribute much valuable ecological information.

III. The Succession of Beetle Associations.

The subject of succession is a relatively new one in entomology. The only other paper treating of beetle succession known to the writer is that by Shelford ('07). Our points of view are very similar but have been independently conceived. Broadly speaking succession means the change, in time, of the insect life at any given habitat or place. Our aim is to note the changes in the composition of the beetles found *associated in a given breeding habitat or region*. The method is first to determine what species of beetles are associated or found together in the same habitat, and then to determine their mutual and environmental relations, so that their laws of change may be determined. Habitats and their associated insects have very rarely been considered as worthy subjects for special study. Even in very excellent local lists, but little attention is given to this subject. This is well exemplified by Wickham's Bayfield list. In one case he says: "A peat-bog of several acres in extent also proved very productive of peculiar species." But unfortunately he does not indicate the kinds.

In spite of the lack of a detailed study of the problem of beetle succession, however, certain general relations are apparent. We will only attempt an outline of the problem as found on Isle Royale. This involves an idea of the history of the island as the Lake formerly stood at a much higher level, which as it fell exposed Isle Royale. We are thus given, as a natural starting point, the Lake shore and beaches.

1. The Lake Shore and its Beetle Associations.

Topographically the shore is very diverse in its character, and all stages are to be found, from a cliff to a low rocky shore and on to the gravelly and sandy beach. When the shore lies at a low angle, so that beach pools are developed by the waves and rain, certain water beetles as *Rhantus binotatus* at Tonkin Bay (I, 1) and Scovill Point (IV, 1) find a habitat. Upon topographically older beaches, where gravel and sand have accumulated, various species of *Bembidium* are to be found, as previously listed. Such a sandy beach often contains a mixed lot of beetles, and may contain examples of a large number of species from all habitats, which have been tossed up by the waves. It is probable that many of these come from a considerable distance. Upon the upper parts of such a beach, where soil accumulates and annuals grow, certain flower beetles, as *Leptura* and *Trichias* are liable to be found feeding. In such a soil may be expected Carabids, as *Pterostichus femoralis* was found upon the heath beach (V, 2) on the south shore of the island.

The transition from the upper beach to the rock openings is often a gradual one; all stages of which were found preserved.

2. Rock Openings and Associated Beetles.

These park like rock openings and open oak ridges furnish a transition from the beach into the forest conditions. They are characterized by the absence of soil or the presence of only a shallow one, and by the reindeer moss and heath plant society. The shallow soil and low open vegetation favors the continuation of some of the Carabids found upon the upper beach, as *Pterostichus*. Under such conditions were found *P. femoralis* and *Harpalus megacephalus* (1, 2; V, 2). The flower feeders also continue to maintain their position, but the *Bembidiums* have largely been eliminated.

These open sunny spots, surrounded by dense shady forests, in their attractiveness for insects, remind one of electric lights where insects congregate in such vast numbers. As representative of these conditions the great variety of beetles found about the camps should be recalled.

3. Lake, Pond and Bog Habitats and Associations.

From the park-like rock openings let us turn to another series of open habitats: those which are initiated by inland water bodies. The water beetles to be found in the open lakes were not given special attention but there can be no doubt as to their existence in such places, but in general we may say that water beetles increase in number and kind nearer the margins and in shallow water. Here the *Gyrinids* (V, 63), *Donacia* (III, 5), and *Galerucella* (VI, 3) abound, while farther inland at the bog margins and in the bogs occur Haliplids and Hydrophilids, *Halipplus*, *Hydroporus*, *Agabus* and *Scutopterus* (I, 4, 6; V, 5). Even this brief series outlines the main features seen in the transition from the strictly open water conditions and species to those of the bog. But this succession may even be safely carried a step farther, as is clearly shown by an important observation by Wickham ('97, p. 126) at Bayfield, Wisconsin. He states that "The Water Beetles were not found in such abundance as I had hoped from a perusal of lists from northern localities, and of those named in the present report a great part were taken not in water but under moss in damp spots;—a peculiarity which I have noted in some species of *Agabus* collected on a previous trip to Alaska." Under such conditions as this the bog association of water beetles may even be able to spread beyond the bogs and invade the forest, a *change of habitat* which has been recognized, among plants but has been largely overlooked by students of animals. It is only by the detailed study of habitats that the significance of such facts can be understood and the peculiarities of succession determined for different regions.

There is thus seen to be a very perfect transition from the bog forest into that of the balsam and spruce, and the dominance of conifer trees clearly shows that the beetles frequenting such forests will be on the increase as the aquatic association of beetles declines in dominance. The methods and detailed order of this

succession awaits investigation, but it is clearly dominated by the forest succession.

4. *The Forests and Their Beetle Associations.*

The gradual and perfect character of the transition from the bog to the balsam-spruce forest has just been indicated. This is paralleled by a corresponding transition from the park-like openings and the bare ridges to the forest. These habitats change as rapidly as soil, humus, and shade increase at the margins of the openings; and as shrubs and young trees encroach upon the open. Thus as the bogs fill up, and as the soil increases on the rock surfaces, both habitats tend to become transformed toward and invaded by the balsam-spruce forest conditions and association. Here is a clearly defined convergent tendency, the exposed ridges and the water basins both tending to become forested. Corresponding with these environmental changes are corresponding ones in the beetles. The Carabids, as previously mentioned, continue in the humus from the rock openings as the water beetles may in the damp moss. As the vertical extent of the forest increases and the forest crown migrates upward, the intervening trunk, bark and branch habitat for beetles enlarges and the leaf eating inhabitants of the forest crown rise upward. This crown fauna retains, or rather continues some of the characteristics found at the marginal zone, with which it retains direct continuity. The marginal zone of trees is likely to be birches (yellow or white) or aspens, in the rock opening succession, and conifers in the bog series, a feature which influences the beetle fauna. With a dominance in the forest of Balsams, Paper Birch and White Spruce, the beetles (and many other insects as well) are likely to be much influenced, not only by the plant food, but also by the physical conditions associated with the forest. As one plant or forest society replaces another, the *unfavorable conditions* of the *declining* society may be expected to favor insect injury as it is well known that in general vigorous trees suffer less from such attacks than those which are defective. Under such circumstances as this insect injury may be a useful index of succession, as well as a factor hastening it. Under such circumstances the climax of insect abundance or dominance may lag behind the climax of the development of the plant society upon which it depends. Insects may also initiate a plant succession, through a period of extreme abundance by doing damage to the food plant, thus permitting the invasion of other forms. If, however, the hardwoods, the yellow birch-sugar maple forest, is the climax type, then the balsam-spruce-paper birch association will be succeeded by it in lime; and a further change in the beetles may be expected. But here also, as in the coniferous forest, a dense forest stand appears to be unfavorable for the abundance and variety of beetles (as is generally the case with many other animals). This scarcity of beetle life in the dense forests of the Lake Superior region has been commented upon by LeConte ('50, p. 201) as follows: "The whole country being still almost in a primitive condition, the specimens are

equally distributed throughout a large space; the woods will not therefore be found very productive to the collector. In fact nearly all the species were adjacent to small streams; or else were driven on shore, particularly on sand beaches, by the winds and waves after being drowned in the lake."

Throughout the preceding discussion the intimate relation of the beetles and the vegetation has been assumed. There seems to be a good reason for this. Ulke ('02, p. 3) has well expressed this dependence as follows: "Now, as about half of all the beetles depend upon plants for their food, the greater variety of food plants the larger we find the number of species of beetles." In this we also see why so few species (relatively) are found where a climax plant society has become dominant, because such societies are, as a rule, composed of but relatively few species. At the same time it is seen why at an intermediate stage, with a diversified vegetation, we may expect the greatest variety of beetles. From such relations as these it follows that a knowledge of plant succession will furnish a very important basis for the study of beetle succession.

While these remarks have been primarily intended for beetles, it is equally evident that they have a much more extended application to other plant feeding insects and certain other invertebrates as well.

IV. The General Characteristics of the North American Beetle Fauna.

In attempting to form some idea of the general faunal affinities of the Isle Royale beetle fauna, the literature was searched for a general account of the distribution of North American beetles. As no recent comprehensive account of the subject could be found, various general statements and generalizations were compiled. On account of their scattered occurrence in the literature and their value and suggestiveness to students of other groups of insects, it has been thought desirable to assemble and publish them. An effort has been made to quote only the more important statements. Several of the older statements by LeConte, before he accepted the theory of evolution, are omitted. A similar selection has also been exercised in the case of some other writings. The main aim has been to bring together the most comprehensive generalizations which have been made upon our beetle fauna, so that they may have greater utility, further extension, and revision. Supplementary data from other groups of insects has largely been omitted, although this should be given due weight in a comprehensive study of this subject. The references should be consulted in connection with the compiled abstracts.

1. *Compiled Generalizations on the Fauna.*

Carpenter, W. L. 1875, pp. 539-542: "The principal and most interesting result obtained from the study of this collection, is the demonstration of the fact that the alpine insect-fauna of the Rocky Mountains, is nearly identical

with that of Mount Washington (New Hampshire), Labrador, and Alaska; and that insects which are found upon mountains at great elevations will likely occur in a much higher latitude at a less elevation.

"Insect-life, with the exception of the grass-hoppers, is more abundant in the foot-hills than the plains near the foot of the mountains. An altitude of about seven thousand feet appeared to produce the greatest variety of species." p. 540.

Cockerell, T. D. A. 1893, pp. 305, 306, 309, 310-311, 312, 313-314, 315, 316, 317, 319-320-322.

"The insect fauna of the mid-alpine zone of Custer County [Colorado] presents some elements which are sufficiently diverse; but taken as a whole, it is a natural fauna, belonging to a well-defined region, and hence available for comparison with other like faunas. It is, indeed, truly characteristic of the mid-alpine, that besides its ordinary elements, it contains species coming up from the sub-alpine, and down from the high alpine; but although it thus happens that *Junonia coenia* and *Parnassius smintheus* have been taken in the same zone, it does not follow that either are truly characteristic of it, or that they belong to the same fauna. All faunal lists contain such exceptions or deviations from the average; but when, as in the case of Colorado as a whole, there is no uniformity about the range of the various species, and the majority do not occur throughout the territory, it is impossible to treat the region as containing a single fauna." p. 305.

"The mid-alpine zone, as I have defined it,* extends from about 6,500 feet to 10,000 feet. It is essentially the zone of oak-scrub (*Quercus undulata*) and quaking asp (*Populus tremuloides*). Its most characteristic conifer is *Pinus ponderosa* var. *scopulorum*, but with the high-alpine zone it shares *Picea engelmanni*, with the sub-alpine, *Pinus edulis*, and *Juniperus virginianus*." p. 306.

"Among the Coleoptera it will be noticed at once how many of the species are boreal extending to Canada (*sens, lat.*) and often to the New England States. The Southern element is but slight although distinct if looked for; and there is also a fair number of species endemic in the Rocky Mountains. The Tenebrionidae, characteristic of the Western prairies, are fairly numerous. The Coleopterous fauna, as a whole, is strikingly distinct from that of the Mississippi region and the Eastern States generally, except as regards the boreal element. Mr. Wickham has published a list of the beetles found in the vicinity of Iowa City, and on comparing it with the present list. I was astonished to find how few were the species common to both. This result is brought about in large measure, no doubt, by the different character of the forests—those of Iowa containing a great variety of deciduous trees, those of Colorado mainly conifers, with very few deciduous species. Thus, it happens that not one species of Cerambycidae is common to the Custer County and Iowa City lists, although six species are common to our district and the much more distant State of New Jersey." p. 309.

"The high-alpine zone in Custer County extends from 10,000 feet on the Sangre de Cristo range to summits of the mountains (Gibb's Peak, wrongly called Gibson Peak, 13,729 feet; Horn's Peak, 13,447 feet; Humboldt Peak, 14,041 feet, etc.). A list of the high-alpine species so far as observed, is given in "Can. Ent." 1890. Although the number of records is not great, they show that the high-alpine and mid-alpine zones are sufficiently distinct." p. 310.

"Of the high-alpine Coleoptera, 25 species are recorded, and a 26th may be added, namely, *Coccinella trifasciata* L., from near the Micawber Mine in October. It extends to Canada, Lapland, etc. Of these 26, seven genera are not mid-alpine, namely, *Orsodachna*, *Dichelonycha*, *Chrysobothris*, *Zeugophora*, *Athous*, *Dasytes* and *Glyptina*. Eleven of the species are wanting in the mid-alpine collections." p. 310.

"These statistics would undoubtedly be altered by further research, but I do not think they can be without significance. That the high-alpine and mid-alpine fauna are largely of different derivation seems to be proved by the large proportion of generic difference. Thus, 25 distinct species of Hymenoptera include no less than 16 genera; and eleven Coleoptera include eight genera. The high-alpine, therefore, is not, as regards its peculiar features, derived from the mid-alpine or lower; contrasting in this respect with the high-alpine of Ecuador, which is so derived.

"The affinities of the high alpine not being with the mid-alpine, they could only be with the far North. Alberta being a suitable region for comparison, I wrote to Mr. Thomas E. Bean, asking him to tell me how many of my high-alpine species occurred with him. He most kindly replied, giving me the following interesting information:

"Of the Coleoptera, he finds at Laggan *Dolopius lateralis*, *Podabrus lateralis*, *Orsodachna atra*, *Cicindela longilabris*, *Adoxus vitis*, *Chrysobothris trinervia*, *Coccinella transversoguttata*, *Trichodes ornatus*, *Acmaeops pratensis* and *Mordella scutellaris*. He adds: "That is a good sprinkling considering that I derive the facts from a small lot I sent Mr. Fletcher several years ago, presumably the commoner species.' * * * The timber line at Laggan is at, 7,000 ft. p. 311.

"Thirty-six Coleoptera were found and identified in the sub-alpine zone, and of these twenty-two, or nearly two-thirds, were not found in the mid-alpine. These include the following eleven genera not found in the mid-alpine: *Pityophagus*, *Batyle*, *Ditylus*, *Badister*, *Serica*, *Diabrotica*, *Tomicus*, *Polyphylla*, *Euryomia*, *Listrus* and *Desmaris*. Of the thirty-six species, only one, *Hippodamia convergens*, was observed to range up to the high-alpine.

*See "Entomological News," 1892, p. 203.

"Thus, in both Coleoptera and Orthoptera, the difference between the two zones is seen to be very marked, not only as to species, but also as to genera, showing that we have to deal with distinct fauna. p. 312.

"So far as I am able to judge, the suppression of the central region is entirely justified, but I cannot agree as to the proposed Sonoran region. An analysis of the insects of the Colorado Rocky Mountains shows that the high-alpine and mid-alpine elements, although sufficiently distinct, are both essentially boreal. If we follow Dr. Merriam's arrangement, it appears that the high-alpine is truly boreal while the mid-alpine belongs to the transition region, containing a considerable number of strictly American types. The sub-alpine, on the other hand, is southern or Sonoran.

"Dr. Horn has kindly given me his opinion as follows: 'My ideas of the distribution of the Coleoptera in the mountainous region of Colorado, which is a good center of the Rocky Mountain chain are as follows: The high region seems to have been populated from the Canadian through the H. B. T. region. A collection made above 8,000 feet in Colorado is almost identical with one made in the Lake Superior region. The same fauna runs down to N. M. and Arizona, and again appears, mixed, of course, in the Mexican Mountains.

"The sub-alpine region is one that continues from Washington to New Mexico, as shown by such striking forms as *Ergates*, *Melanophila miranda*, *Iphthimus serratus*, *Galeruca externa*, *Calosoma lunatum* in varieties.

"The lower region, foot hills, etc., is a mixture of New Mexico forms with those of the Eastern United States, with some peculiar forms allied more to the southern regions.

"California is a peculiar region, and, in many respects, allied to Europe (in general). I think California supplies us with more species of genera peculiar to Europe than does the Eastern region.' (In litt., July 14, 1892.)

"According to the facts now recorded it seems that there is, firstly, a circum-polar and strictly boreal element; secondly, a boreal but modified or Canadian element; and thirdly, a southern element belonging to the arid portion of Dr. Merriam's Sonoran region. I do not think any distinct faunae except these can be recognized, and the central region accordingly falls. But there is, sprinkled among the ordinary types, a *distinct element of endemic species*, to which I shall refer later. There also seems to be a few surviving fragments of an ancient fauna, of which *Anthracoptyx* is a good example.

"There seems to be a small California element, but the species falling under this head are perhaps rather Southern than properly Californian. pp. 313-314,

"The resemblance between the Colorado fauna, and that of the Mississippi basin and further East, always, excepting the boreal element that comes from the North, is very slight indeed. The great plains to the east of the Rocky Mountains have been as much a barrier as the sea would have been. p. 314.

"*A Method for Defining Faunal Regions*. It appears from a consideration of what has been written on faunal regions, that it would be desirable if some rules could be laid down, so as to leave the matter less to the discretion of the individual writer. It would require a good deal of research to determine what rules could be laid down, that would work, but as regards insects, at all events, I have thought it possible that the following rule might answer for secondary faunal divisions:

"*Any two districts shall be regarded as in the same secondary faunal division if the number of species common to both exceeds the number of genera in common.* p. 315.

"*Equigeneric Areas*. For minor divisions, to be used in relation to particular groups, I have devised what may be termed equigeneric areas.

"*Equigeneric areas are areas throughout which the genera of the group under consideration are identical.*

"These areas are sometimes large, sometimes small. When two genera overlap, the region where they both occur, however small, makes a separate equigeneric area. This might be thought a disadvantage; but really, I believe it to be an advantage in the method, since it is important to recognize these intermediate or overlapping areas. p. 316.

"*Origin of the Rocky Mountain Fauna*. The numerous fossils of Colorado bear testimony to the fact that the region of the Rocky Mountains has in the past been peopled by a highly remarkable and numerous fauna. This fauna, however, does not appear to be ancestral to that of the present day. Nor has the present fauna any special connection with that of the high regions to the far South—the Andes. In order to arrive at just conclusions, it will be needful to consider these points in some further detail.

"*Alpine Insects of the Andes*. The recently-published 'Supplementary Appendix' to Mr. Whymper's work on his travels amongst the Andes of Ecuador, containing an account of his captures, includes some very valuable information about the insects of high altitudes in that country. The late Mr. H. W. Bates has written the introduction, in which the following passages occur:

"If there had been any distinct element of a North Temperate or South Temperate Coleopterous Fauna on the Ecuadorian Andes the collections he made, inexhaustive though they may be, would have shown some traces of it; but there are none. A few genera belonging to temperate latitudes, though not found in the tropical lowlands, do indeed occur, but they are forms of almost world-wide distribution in similar climates, and there is no representative of the numerous characteristic and common genera of the North or South. Even the Northern genera, more or less abundantly found on the Mexican highlands, are absent.

"One feature of the fauna is of great interest. It is the occurrence of apterous species of genera which at lower levels are always winged.

"It seems to me a fair deduction from the facts here set forth that no distinct traces of a migration during the lifetime of existing species, from North to South, or *vice versa*, along the Andes, have as yet been discovered, or are now likely to be discovered.'

"Going through the list of insects taken at high altitudes in Ecuador, the following points may be noted. There are four new species of *Pterostichus* from 12,000 feet upwards, but they represent a new subgenus. There is not a single *Amara* or *Harpalus*. pp. 317-318.

"*The Glacial Epoch*. It can readily be imagined that such a state of affairs [Prestwick's account of the Amer. Ice Age] would lead to the destruction of a large part of the fauna, the remainder either surviving along the northwest coast-line, or going southward to the Gulf States and Mexico. The eastern fauna, with which we are not now particularly concerned, would largely survive, owing to there being a considerable area of unglaciated territory available. This, indeed, has been the case. The Californian fauna would survive in part to the north, and also in lower California and the western coast region of Mexico. But the fauna of the central region would be almost annihilated, because the warm winds being cut off by the coast ranges, the country would become extremely cold, even far down into the higher lands of Mexico. The arid region where not actually glaciated would be a frozen desert, and the migration of the fauna southward would be far from easy.

"In the eastern province the species of the moist Northern States would find little difficulty in migrating southward into the equally moist Southern States. The isotherms would shift southward over moderately uniform country. In the central region, however, this would not be the case. There is no place available to the South, except the moister coast line, and the interior uplands, which latter were undoubtedly glaciated. The great plains between the Rocky Mountains and the Mississippi would have made an impassable barrier for most species, preventing migration in that direction.

"But, it may be urged, at some point to the southward the mountains or central uplands would cease to be glaciated, and why should not migration take place into the neotropical region. That it did not take place at all events beyond the isthmus, is evidenced by the facts above quoted from Mr. Whymper's 'Appendix;' and the reason of this no doubt is, that the isthmus itself was submerged, and all connection between North and

South America cut off. This question of the submergence of the Isthmus of Panama, has been fully discussed by various naturalists, and need not be enlarged upon here.

"It is impossible in the present paper to give more than this bare outline of the subject, but I believe the conclusion is justified, that the central region fauna was practically stamped out during the glacial epoch; and that the present fauna is derived from the boreal faunae which survived to the east and to the west, and the southern fauna which survived in Mexico. This view seems to be supported by a consideration of the present distribution of species, as well as by geological evidence. pp. 319-320.

"*Post-Glacial Developments*. Excepting the remnants of the ancient fauna, all the strictly endemic element in the Rocky Mountains is of *post-glacial* origin—that is, according to the views here set forth. This means a good deal, if it is actually the case, as I believe. Under certain circumstances, species develop quickly, and we have, at least among insects and flowering plants, a great array of new species coming into existence. Such species are closely allied to species from which they sprang, and to each other, so as to give rise to much dispute as to their validity—as an example, one may cite the genus *Argynnis*, which has been very productive of post-glacial species in America. In such a case it matters little whether we term all these diverse forms true species, or subspecies or races,—but to lump them under a common name obscures the facts, and leads us to ignore one of the most interesting phenomena that are presented to a zoologist. pp. 320-321.

"*Species-Forming Areas*. It is well known that the genera commonly accepted are unequal in value, but most of those whose validity could not be questioned, are evidently of considerable antiquity.

"But the curious thing is, that these wide-ranging genera are not equally productive of species over their whole areas. p. 321.

"Among insects, *Argynnis* and *Colias*, and several genera of Noctuae, exhibit strong species-forming tendencies in the Western States of North America. *Catocala*, in the Eastern States, has a very strong species-forming area. And so on in many other instances which will occur to the reader. This phenomenon is a most remarkable one, since it affects chiefly old and almost cosmopolitan genera, and does not occur in the same districts in all the genera. Two cosmopolitan genera, as we have seen, may have their species-forming areas on opposite sides of the world. It would seem, indeed, as if there were causes at the bottom of it, that we do not yet understand." p. 322.

Fall, H. C. and Cockerell, T. D. A. 1907. pp. 150-151, 152-153: "Comparing the beetles of New Mexico with those of Colorado, one is struck by the large amount of difference in the lists. Colorado has not, of course, the important and characteristic Middle Sonoran element, but the higher elevations are continuous from north to south, and one would expect a practically identical fauna. Botanical investigations, however, have revealed striking differences in the plants of the northern and southern Rocky Mountains, and a degree of endemism among those inhabiting the mountain ranges which is quite surprising. The oaks (*Quercus*) are abundant in New Mexico¹, and have a luxuriant development as far north as Manitou, Colorado, and even beyond. But at Boulder, and north of Denver, generally, they are totally absent. On the western slope they go farther north, and one species just enters Wyoming; but there are none at all in Wyoming, with this

exception, and none in Montana. This alone would explain the northward limitations to the distribution of the numerous species of Coleoptera which are attached to the oak, and various similar cases could be cited. It appears probable that the oaks were driven south during the glacial period, and owing to the unsuitability of their seed for being carried great distances, have been unable to recover their lost ground. Under these circumstances, the ample powers of flight of certain of the oak feeding beetles are of no service for promoting migration northward of the slowly moving line of oaks. pp. 150-151.

"It will be noted that New Mexico shows a greater proportion of non-Colorado genera than species; or, in other words, the species found in New Mexico but not in Colorado are more likely to be of non-Colorado genera than in the reverse case. This is explained by the fact that the desert fauna in nearly all groups is rich in peculiar genera, but these are represented so far up as New Mexico by comparatively few species. On the other hand, the boreal fauna, so strongly developed in Colorado, is largely characterized by the abundance of species of circumpolar genera.

"In Colorado the eastern plains region has been little searched for beetles, and the corresponding region of New Mexico is also poorly known. There is no doubt that the plains will furnish many species additional to the lists, and most of these will doubtless be common to both. The following are characteristic eastern species which are known to reach New Mexico, but have not yet been found in Colorado: *Scarites subterraneus*, *Clivina bipustulata*, *Clivina ferrea*, *Aspidoglossa subangulata*, *Panagaeus fasciatus*, *Tachys xanthopus*, *Pterostichus sayi*, *Dynastes tityus*, *Anomala undulata*, *Alindria teres*.

"The New Mexico list contains over 135 species, indicating that the eastern fauna is really crossing the plains to some extent, and not only reaching us by way of the northern mountains. There are strong reasons for believing that a considerable part of this migration is recent, and has been assisted involuntarily by man. This affords, of course, a strong argument in favor of the speedy exploration of western regions, in order that their original fauna may be ascertained before it is unduly contaminated by introduced forms. Fortunately for the naturalists, the desert will not quickly or easily accommodate alien elements, but it is quite otherwise in more ordinary localities; and as Perkins has shown in the Hawaiian Islands the result may be destruction as well as confusion.

"The number of species common to New Mexico and Southern California, but not known from Colorado, is over 160, indicating a wide-spread southwestern fauna; but in general, the species of the Southern California coast region are not those of the Rocky Mountains.

"We find over 30 names of New Mexico species listed from the Lower Rio Grande, but not in the Colorado, Southern California or District of Columbia lists. Such for example: *Cincindela circumpecta*, *Cindela severa*, *Dyschirius terminalis*, *Philophuga viridicollis*, *Helluomorpha ferruginea*, *Oodes cupraeus*, *Ischiodontus ferreus*, *Ludius texanus*, *Agrilus addendus*, *Mastinocerus texanus*.

"The following are examples of characteristic southern genera which reach New Mexico, but do not enter Colorado: *Thalpius*, *Hololepta*, *Sandalus*, *Thrincopyge*, *Lycus*, *Plusiotis*, *Aphonides*, *Strategus*, *Allorhina*, *Derobrachus*, *Tylosis*, *Dendrobias*.

"Because of the conspicuous place which these southern genera occupy in the fauna, an entomologist arriving from the

north or east is very likely to assume that the Middle Sonoran of New Mexico contains precisely the same elements as the Lower Sonoran of Arizona just as it has been assumed that Florida is typically West Indian, because its numerous West Indian genera attract attention, and the *absence* of innumerable West Indian types is not so readily observed." pp. 151-153.

Hamilton. '94 a. pp. 408-415. Cf. also Fauvel '89. Hamilton gives the following lists of species indicative as to their nativity:

1. Species equally native in North America and in northern Asia not yet observed as occurring in Europe—49 species.
2. Species native in North America and Northern Asia occurring in Europe—277 species.
3. Species native in North America and Europe not at present known to occur in northern Asia—50 species.
4. Species probably introduced into North America now acclimated occurring in Europe, and those marked with a likewise in Asia. Many of these are cosmopolite, or becoming so, through commerce—216 species.
5. Species cosmopolite or subcosmopolite.

Horn, G. H. 1872. pp. 383-384. "As is well known to all collectors, various species of *Eleodes* occur in great numbers in all parts of the west of our continent, and the species themselves occur over a wide range of territory, and are not limited, as might be inferred from their apterous condition, to regions of small extent. As we pass from east to west over a given line, we find variations of average temperature, and of course great differences in altitude. These two causes, combined with, of course, the botanical changes, have tended to produce variations from a given type to a greater or less extent. *Eleodes obscura* Say affords a beautiful illustration of the extent to which this divergence may be carried. As a general rule I find, not only in *Eleodes*, but also in many other genera, that the higher the elevation or the colder the climate, the rougher and more deeply sculptured is the species. The smoother forms of *E. obscura* may therefore be expected in the southern regions in which it occurs; for example, var. *dispersa* is New Mexican, elytra with scarcely any traces of striae; var. *obscura*, elytra distinctly sulcate, but not deeply, is from Colorado and Southern Idaho. As we advance to the west the elytra are more deeply sulcate, as in var. *arata*, while var. *sulcipennis*, from nearer the Pacific Coast, has deeply sulcate elytra, with very convex interspaces. The same variation of sculpture occurs in *Calosoma luxatum*, Say, which starts in Colorado with comparatively smooth elytra, until in Vancouver we find the elytra covered with lines of granular elevations, forming the variety known as *C. pemelioides*, Walker. The two extremes of each series above noted appear to differ widely from each other, and to be entitled to rank as a distinct species. In the foregoing remarks reference only has been made to variations within specific limits. The same law appears to hold between different species. In the genus *Omus* the most roughly sculptured species occurs in Washington Territory, (*O. Dejeanii* Reiche) and the smoothest (*O. laevis*, Horn) from near Visalia, California. The object of the preceding remarks is to explain what appears to be a law of variation for our western slope, and thus cause the unnecessary multiplication of species, founded on slight characters, to be avoided.

"Species everywhere in our fauna appear to be distributed on lines of country presenting as nearly as possible similar meteorologic conditions. Thus many Oregon forms extend southward into California, gradually seeking a higher mountain

habitat as the region becomes warmer. Two species illustrate this—*Tragosoma Harrisii* and *Phrygan-ophilus collaris*. Both extend their habitat from Maine to California following the cooler regions westward from Maine through the Canada and Red River region, thence northward nearly to Sitka. From the latter point southward to Oregon both occur at ordinary level, and rising as a more southern region is reached until at the latitude of Visalia they occur only a short distance below the snow-line, at an altitude of from ten to twelve thousand feet. p. 383.

"As might be expected each new region visited yields new *Meloidae* of the genera *Epicauta* and *Lytta*; in fact, each species of *Astragalus* has its peculiar *Lytta*; and whenever any of that genus of plants is found in flower, an accompanying visitant may always be looked for." p. 384.

LeConte, J. L. 1850. pp. 239-239*, 240*: "First, the entire absence [in Lake Superior region] of all those groups which are peculiar to the American continent. Thus, there is no *Dicaelus*, no *Pasimachus* among the Carabica; the *Brachelytra* are represented only by forms common to both continents. Among the *Buprestidae* is no *Brachys*; in the *Scarabaeidae*, the American groups (except *Dichelonycha*) are completely unrepresented; in brief, there is scarcely a genus enumerated which has not its representative in the Old World. p. 239.

"Secondly, the deficiency caused by the disappearance of characteristic forms, is obviated by a large increase of the members of genera feebly represented in the more temperate regions, and also by the introduction of many genera heretofore regarded as confined to the northern part of Europe and Asia. Among these latter are many species which can be distinguished from their foreign analogues only by the most careful examination. p. 239.*

"When a species in one district is paralleled by another in a different region so closely allied that upon a superficial glance they would be regarded as the same. These are called *analogous species*; e. g., the *Olisthaeri*, *Spondyli*, *Bembidia*, *Helophori*, etc., etc., of the preceding catalogue, as compared with European species.

"Where several species in one region are represented by several others of the same genus, which perform a similar part in the economy of nature, without, however, displaying any further affinity to each other. These are called *equivalent species*; e. g., most of the species of *Cicindela*, *Brachinus*, *Clytus*, *Donacia*, etc., of America, as compared with those of the eastern world. p. 239.*

"Notwithstanding this approximation to a uniform, subarctic standard, we still find in these boreal regions, a prevailing character of North American fauna—the extreme paucity of *Curculionidae*. The *Donaciae* too, although numerous, do not afford any prominent parallelism." p. 240*.

LeConte, J. L. 1851. pp. 249-250, 251, 252, 253-254. "The first fact observed by the collector [in California], is the very small number of species which can be obtained at any single locality. Day after day he meets with a continual repetition of a few common forms, with an occasional admixture of rare species; so that at the end of two or three months a single locality will have furnished him with about 200 species of *Coleoptera*, and a rather less number of other orders. It will be here remembered that the contrary is true of the eastern part of the continent, where each locality furnishes a large number of species, extending over a large area, and represented by comparatively few individuals.

"On removing to another locality, the same thing is again observed, with this difference: the species of the first place, even the most abundant, are replaced by others, many of which are true representative species, approaching as closely as those of Eastern America and Europe; while others belong peculiarly to their own district, and are without any representatives in the other parts of the country. pp. 249-250.

"It must be observed that the localities east of the Sierra, (Vallecitas, Colorado and Gila) show more resemblance in their productions than the maritime regions of California: the desert nature of the country undoubtedly produces this effect, by presenting conditions unfavorable to animal life; yet even in this uniformly sterile tract, great differences are observed among the smaller species which abound only in moist places. p. 250.

"The first point worthy of notice in this list is the extremely small number [compared with Europe] of Scarabaei, Elateridae and Longicornia: this might have been predicted, as these insects derive their food for the most part from large plants. The Curculionidae and Chrysomelidae are not in the same proportion as in the more wooded countries. The saprophagous Coleoptera, with the exception of Histeridae, are almost wanting: and these latter are not in larger proportion than with us. Thus the only effect, so far as observed, is the paucity of species in tribes for which the country affords but little food. The Staphylini and Carabica bear the same proportion to the whole, that they do with us; while the deficiency caused by the small representation of the tribes mentioned above, is made up almost entirely by the Tenebrionidae, which, as is well known, are but slightly developed in Eastern America. The Malachidae are also in larger proportion than in other parts of the continent." p. 251.

"The Tenebrionidae, from being the group most characteristic of the country, might be supposed capable of giving us the most certain data with regard-, to the law of distribution. The great majority of the genera of this tribe are apterous; and of those which are not apterous, all the genera found in California are cosmopolitan (Phaleria, Platydema, Helops, Uloma, Tenebrio, Upis, etc.), except Blapstinus, which again occurs in tropical America. Of the apterous genera, only three are found in eastern temperate America: two of these are peculiar, and one (Nosoderma) which exists in California is also found in Brazil. Of this group, there are in California about 28 genera, of which 5 or 6 extend into the tropics.

"The Histeridae, though not in undue proportion, exhibit a peculiarity: they nearly all belong to the genus Saprinus, which, in Eastern America and Europe, forms scarcely one-fourth of the group.

"Thus the only manner in which the insect fauna of California approaches that of Europe, is in the great abundance of apterous Tenebrionidae. But in this respect it does not differ from a large part of South America and by the very form of these Tenebrionidae, which bear no resemblance at all to those of Europe, the greater relation of the Californian fauna to that of the rest of America is clearly proved. It will be seen, too, that the resemblance to European forms in the other tribes is only indirect, proceeding solely from universal or zonal forms, while the greater relation is again with the rest of America. It will moreover be seen, that while the stronger relation of the fauna is continental, yet a sufficient number of individual peculiarities are introduced to prove that it constitutes a system of its own, bearing no relation to that of Eastern America, except the slight continental resemblance proceeding indirectly through the tropics. pp. 251-252.

"The principles shown by the preceding analysis may be expressed briefly as follows:

1. California constitutes a peculiar zoological district, with sufficient relation to the other districts of America to prove that it belongs to the same continental system.

2. This zoological district is divided into several sharply defined sub-districts, having a very close resemblance to each other.

As the same mode of distribution obtains in the group of islands adjacent to the western coast of America, we are led to believe.

3. That the local distribution of a small number of species is the characteristic of the eastern Pacific region, as the extensive distribution of a large number is the prevailing feature of the Atlantic.

4. The genera occurring in, but not peculiar to, this district, belong to two classes: either they occur on the Atlantic slope of both continents, or they are peculiar to America, and are also found within the tropics." pp. 253-254.

1859. pp. III-V. "Before proceeding to consider the special material used in the preparation of this memoir, it will be proper to give a short sketch of the general results thus far obtained regarding the geographical distribution of Coleopterous insects in the territory of our republic.

"The whole region of the United States is divided by meridional or nearly meridional lines into three, or perhaps four, great zoological districts, distinguished each by numerous peculiar genera and species, which, with but few exceptions, do not extend into the contiguous districts. The eastern one of these extends from the Atlantic Ocean to the arid prairies on the west of Iowa, Missouri, and Arkansas, thus embracing (for convenience merely) a narrow strip near the sea-coast of Texas. This narrow strip, however, belongs more properly to the eastern province of the tropical zoological district of Mexico.

"The central district extends from the western limit of the eastern district, perhaps to the mass of the Sierra Nevada of California, including Kansas, Nebraska, Utah, New Mexico, Arizona, and Texas. Except Arizona, the entomological fauna of the portion of this district west of the Rocky Mountains, and in fact that of the mountain region proper, is *entirely* unknown; and it is very probable that the region does in reality constitute two districts bounded by the Rocky Mountains, and southern continuation thereof.

"The western district is the maritime slope of the continent to the Pacific, and thus includes California, Oregon, and Washington territories.

"These great districts are divided into a number of provinces, of unequal size, and which are limited by changes in climate, and therefore sometimes distinctly, sometimes vaguely defined.

"The Atlantic district may be divided into: 1, a northern province, including Maine, Eastern Canada, Nova Scotia, Newfoundland, etc., and extending westwardly from Lake Superior to Lake Winnipeg and Western Canada, which fades insensibly into the great Arctic district; 2, a middle province, limited westwardly by the Appalachian chain, and extending to Southern Virginia; 3, a western province, including Minnesota and the States of the valley of the Mississippi, as far as the State of that name; 4, a southern province, including the States south of Virginia and Kentucky; 5, a subtropical province,

including the point of the peninsula of Florida; 6, a subtropical province, including the sea-coast of Texas.

"The Central district, as far as known, may be thus divided: 1, a northern province, comprising the regions north of the Missouri, the plains of the Saskatchewan, etc.; 2, a middle eastern province, divided into two subprovinces, including: a, Kansas, and Nebraska; b, northeastern New Mexico; 3, a southeastern province, including Texas, with the exception of province six of the Atlantic district; 4, a southwestern province, including the upper part of the valley of the Gila; and 5, a south-southwestern province, including the lower Gila and Colorado. The unexplored portions of this district will indicate middle western, and northwestern provinces, or perhaps the necessity of constituting with them and the southwestern province a district to be called the Interior district.

"The Pacific district may be divided as follows: 1, a hyperborean province, consisting of Sitka and the neighborhood; 2, a northern province, including Eastern Oregon and Washington; 3, a middle province, including California, probably as far south as Santa Barbara; 4, a southern province, including California from Santa Barbara to San Diego, extending to the crest of the Sierra. Southern, or lower California is also, perhaps only in part, a province of this district;* but, as yet, no collections of magnitude have been received therefrom. Other provinces will, from the peculiar method of distribution of species in that portion of America, be defined when more full collections are made, but at present cannot be indicated.

"At the north, the Atlantic and Central districts seem to merge imperceptibly together, about the valley of the Athabasca, and Winnipeg rivers, and finally to disappear in the limited Arctic fauna; the hyperborean province of the Pacific district also fares into this Arctic fauna, without, however, losing itself so perfectly in the northern provinces of the other districts. We have thus evidence that the American Arctic district may be divided into two provinces, an eastern and a western.

*"A few species, collected by John Xantus, Esq., at Cape San Lucas, though all new, indicate a greater resemblance to the fauna of the lower Colorado, than to that of maritime California; this province may therefore be found eventually to belong to the interior district."

"At the south, the Atlantic district merges through Florida into the Caribbean tropical province, and through maritime Texas into the Mexican lower eastern province. In the same direction the Central district merges into the Mexican upper or central province, and the Interior district, towards the Gulf of California, into the Mexican western province. Regarding the southern affiliations of the Pacific district we know absolutely nothing; scarcely a single species found at San Diego had been found in Mexico.

"The method of distribution of species in the Atlantic and Pacific districts, as already observed by me in various memoirs, is entirely different. In the Atlantic district, a large number of species are distributed over a large extent of country; many species are of rare occurrence, and in passing over a distance of several hundred miles, but small variation will be found in the species obtained. In the Pacific district, a small number of species are confined to a small region of country; most species occur in considerable numbers, and in travelling even one hundred miles, it is found that the most abundant species are replaced by others, in many instances very similar to them; these small centers of distribution can be limited only after careful collections have been made at a great number of localities, and it is to be hoped that this very interesting and important subject of investigation may soon

receive proper attention from the lovers of science on our Pacific shores.

"In the Central district, consisting, as it does to a very large extent, of deserts, the distribution seems to be of a moderate number of species over a large extent of country, with a considerable admixture of local species; such at least seems to be the result of observations in Kansas, Upper Texas, and Arizona." pp. III-V.

1860. pp. 2-4. "The distribution of species in the northern part of the region which furnishes the materials for this report [Pacific R. R. Report], presents no remarkable phenomenon. As in other northern lands, certain tribes like Aephegata, Staphylinidae, and Elateridae assume a greater predominance in the fauna, from the fading out of the groups more characteristic of warmer climates, while a greater number of species are found common to both continents. Of these latter, about one-half are found on the Atlantic slope of America, while the other half have not yet occurred there.

"The number of species occurring on both sides of America is also largely increased in these northern regions, but with the exception of *Epiphania cornutus* and *Priognathus monilicornis*, the genera of such species are distributed on both continents.

"On proceeding southwards to Oregon (and Washington Territory, which is, for purposes of convenience, always included when Oregon is referred to in these pages), similar phenomena may be observed, though on a diminished scale. The species of the eastern continent, not found on the Atlantic slope of America, have entirely vanished, and of the species common to both sides of both continents, but four remain. The number of species common to the Atlantic and Pacific slopes of America has greatly diminished, and among them *Haplochile pygmaea*, *Ligyris gibbosus*, *Alaus myops*, and *Microrhopala vittata* are the only representatives of America genera.

"Finally reaching California, the species common to the two continents are reduced to *Silpha lapponica* and *Dermestes vulpinus*, the species common to Atlantic and Pacific America have not diminished absolutely in number, but from the more complete and copious fauna known to their relative proportion is much lessened. Among them, however, are found but few which extend their range to the Atlantic States proper, while the greater proportion are not found east of Kansas. Of American genera, *Amblychila cylindriciformis*, *Lachnophorus elegantulus*, and *Eurmetopon atrum* are found in Kansas, or New Mexico, while *Ligyris gibbosus* and two species of *Diabrotica* also extend to the Atlantic."

"In Russian America the genera seems to follow to a certain extent the course already pointed out of the species, that is: the genera common to both continents have a much greater relative proportion, and among them a by no means insignificant part have not yet been found in Atlantic America; but as some of them are characteristic of high northern latitudes, there is reason to believe that the number will be reduced by more thorough explorations in Labrador, Newfoundland, and the regions near Hudson's Bay.

"Of genera confined to America, but six or seven occur in Russian America; of these but three, *Pristodactyla*, *Epiphania*, and *Priognathus*, have been detected on the Atlantic slope. *Pristodactyla* might, indeed, be for the present excluded from the list of peculiar American genera, for two reasons: 1, a certain number of species classed by Dejean, with *Agonum*, and remarkable for having but two dorsal punctures, are in reality *Pristodactylae*, and until the species of Siberia are thoroughly revised, we are warranted in supposing that some

of them may also be included; but, 2, because the distinctions between *Calathus* and *Pristodactyla*, as observed by Lacordaire, are hardly sufficient to warrant the retention of the latter genus.

"In Oregon the eastern genera, not found in the Atlantic States, have diminished in number, but among them occurs *Callisthenes*, which is found in Kansas. The number of American genera has largely increased, even with our limited collections; of them 14 are found in the Atlantic States, 2 in Kansas, while 8 are peculiar to Pacific America; of the 14 found in the Atlantic States, *Haplochile*, *Dichelonycha*, *Anelastes*, and *Alaus* are the only ones not found within the tropics.

"In California the genera of the eastern continent have increased absolutely, from more extensive collections, over those found in Oregon, but do not attain the same relative proportion as those found in Russian America; among them is one, *Tryssus*, a genus heretofore known only from Madagascar, and is thus far the sole representative of the tribe of *Scarabaeidae*, to which it belongs on this continent.

"The number of American genera has greatly increased, partly by the addition of genera found within the tropics, and partly by the introduction of a few peculiar genera; the most remarkable addition, however, is that of eighteen genera of *Tenebrionidae*, of which but two, *Nosoderma* and *Blapstinus*, extend into the Atlantic States, while only four others extend into Kansas or New Mexico. The genera found in the Atlantic States, and not in the tropics, are *Thalpius*, *Axinopalpus*, *Dichelonycha*, *Anelastes*, *Perothops*, and *Melanactes*.

"Another fact of great interest is the distribution of species within narrow limits observed in California. I am not able to exhibit the results in a tabular form, as collections have not been made with minuteness at a sufficient number of localities to give any definite results, but I can merely state my own experience, that but few species occurred at more than one place, and call attention to the fact that, in every collection made at a fresh locality, a large proportion of new species is found, while in Oregon, at points equally distant from each other, a greater uniformity is seen.

"The analysis, therefore, conducts to the same results announced by me, in 1851, at the meeting of the American Association for the Advancement of Science; the fourth proposition was, unfortunately, announced in too absolute terms, as the only two genera then known to me, *Thalpius* and *Axinopalpus*, were not considered as of sufficient importance to modify the result. *Thalpius*, indeed, is too closely allied to *Diaphorus*, that we may well expect some of the species of the latter genus to belong to it, while *Axinopalpus* is by many entomologists not separated from *Dromius*. The other four American genera common to California and Atlantic America, not found in the tropics—*Dichelonycha*, *Anelastes*, *Perothops*, and *Melanactes*—upon which I am now obliged to modify the assertion, were subsequently obtained.

"The four propositions mentioned by me in the essay mentioned are:

1. California constitutes a peculiar zoological district, with sufficient relation to the other districts of America to prove that it belongs to the same continental system.
2. This zoological district is divided into several sharply-defined sub-districts, having a very close resemblance to each other.

As the same mode of distribution obtains in the groups of islands adjacent to the western coast of America, we are led to believe—

3. That the local distribution of a small number of species is the characteristic of the eastern Pacific region, as the extensive distribution of a large number is the prevailing feature of the Atlantic basin.

4. The genera occurring in, but not peculiar to, this district belong to two classes; either (with the exception of *Ergates*) they occur on the Atlantic Slope of both continents, or, if peculiar to America, they are (with the few exceptions above noted) also found within the tropics." pp. 2-4.

This paper is accompanied by four tables as follows:

- I. Genera Common to the Eastern and Western Continents.
- II. Genera Peculiar to America.
- III. Species Common to the Atlantic and Pacific Slopes of the Continent.
- IV. Species Found in Russian America and in the Eastern Continent, not Introduced and not Found in Atlantic America.

1862. p. 336. "Some of the more conspicuous and peculiar species are described below: enough has been stated to show that the affinities of the fauna [of Lower California] are with that of the region extending from the Colorado Desert across to the Rio Grande valley, thereby confirming the results obtained by Prof. Baird and Mr. Cope from the study of the vertebrata collected by Mr. Xantus.

"The limited number of species of these two classes precludes the possibility of the occurrence of many new forms in the region here treated of; but in the number of peculiar species of the much more extensive class of insects seen in Mr. Xantus' collections, we recognize that lower California constitutes one or more provinces of the Interior district, as defined by me in the introduction to my synopsis of the *Coleoptera* of Kansas and New Mexico.

"The preponderance of *Tenebrionidae*, both in genera and species seen in the fauna of Upper California and Arizona, has here been partially destroyed. The genera which survive are, however, such as are already known from the last mentioned region. None of those peculiar to maritime California have as yet occurred." p. 336.

1878. pp. 447-448. "The elevated interior region of North America presents peculiarly favorable opportunities for the study of some of the most interesting questions connected with geographical distribution of animals and plants.

"If the materials at our hands be, as indeed they yet are, a very scanty representation of the organic forms now living in that part of the continent, they are, at least, sufficient to indicate the direction in which investigations should be pushed, in order to arrive at definite and final results.

"The peculiarly favorable circumstances to which I chiefly refer at present are dependent on the following points in the development of the region: —

- 1st. The gradual enlargement of the land-surface at the expense of the circumambient seas during the latest Mesozoic periods.
- 2d. The gradual elevation of the middle of the continental mass during post-Cretaceous times, so as to greatly modify the climate in respect to both moisture and temperature. These changes have been so gradual, that we may say with certainty

(excluding the local eruptive phenomena, which were more numerous, but not remarkably different from those of the present age) there has been no great or paroxysmal disturbance destructive of the land-surface in the elevated plains east of the Rocky Mountains since the deposition of our early Cretaceous strata (Dakota Group).

3rd. While, during the Glacial epoch, the valleys of the mountains were filled with glaciers of moderate size, and the line of permanent ice streams and fields brought to a much lower level, there was an absence of the extensive ice sheets and flooded areas, which in Eastern America destroyed entirely the terrestrial organized beings of the former period.

"It must be inferred from the first and second of these premises that the new land exposed by this gradual development of the continent received its colonies of animals and plants from the conterminous older land-surfaces in various directions, and that the subsequent elevation of the continental mass, by which the moisture was diminished, caused a later invasion of the territory by those genera and species which are characteristic of arid regions.

"We may also conclude, from the third premise that the glacial displacement of species in the Rocky Mountains has been much less than in Eastern America, and that a very small area would be left bare of life on the return to a normal temperature; consequently, the previous occupants of the higher mountains would again return to their former domain, increased by refugees from the circumpolar continent of temperate climate, driven southward by the increasing cold.

"Such being the case, it ought to be possible, with well-prepared lists of the insects of the plains and mountain regions, by comparison with lists of the local fauna of other zoological districts of the continent, to ascertain, with reasonable probability, the invasions from different directions by which, in the first place, the newly emerged land was colonized; and, in the second place, the modifications, either in distribution or in structure, which have subsequently occurred.

"I have on an other occasion¹ expressed my belief that the study of the distribution of existing insects could give much information concerning former topographical and geographical changes in the surface of the earth, I then gave several examples to show how the distribution of species peculiar in their habits and structure confirmed what was already known by geological investigation of the gradual evolution of the middle part of the continent. I will now advance the additional thesis, that we may obtain somewhat definite information of the sequence, extent, and effects of geological changes in the more recent periods by a careful study of the insect fauna in its totality."

1878a, pp. 470-471. Includes lists of Florida Coleoptera:

1. Florida species also found in the Antilles.
2. Common to Florida and Mexico and partly found in Texas.
3. Common to Texas, Arizona, and southern California.
4. Anomalous common to Florida and South America.
5. Distribution of anomalous species.

Murray, A. 1870. pp. 7, 8, 11-12, 32-33, 36-37, 38, "The position I am about to maintain then is, that, subject to modifications to be afterwards mentioned, all the Coleoptera in the world are referable to one or other of three great stirpes. These three no doubt originally sprung from one stirps, and acquired their distinguishing features by long-continued isolation from each other, combined with changes in their

conditions of life. But now we have three, and only three, great strains, sometimes intermingling with each other, sometimes underlying or overlying each other, and sometimes developed into new forms, but always distinguishable and traceable to one or other of the three sources.

"These are—1, the Indo-African stirps; 2, the Brazilian stirps; and 3, what, for want of a better name, I shall call the microtypal stirps, in allusion to the general run of the species composing it being of a smaller size, or, more strictly speaking, not containing such large or conspicuous insects as the others. It is not altogether a satisfactory name, because the stirps does contain some large species, and it is not peculiar to it to abound in small ones. But, taken as a whole, its ingredients are smaller and more modest in appearance than those of the others. The fauna and flora of our own land may be taken as its type and standard. pp. 7-8.

"The Indo-African stirps, as its name implies, inhabits Africa south of the Sahara, and India and China south of the Himalayas, also the Malayan district, the Indian archipelago, and the New Guinea group. This range is less modified by the general introduction of foreign elements than that of the next stirps.

"The Brazilian stirps inhabits South Central America east of the Andes, and north of the River Platte, and furnishes, moreover, a large share in the constitution of North America, but has also received in return a very perceptible tinge from the microtypal stirps.

In the microtypal stirps I include the fauna of Europe, Asia north of the Himalayas, Eastern North America, so far as not modified by the Brazilian element, and, what has less of this strain, the whole of North-west America, California, part of the Mexican fauna, Peru, Chill, the Argentine Republic south of Tucuman, Patagonia, Tierra del Fuego, Polynesia, New Zealand, and Australia. p. 8.

"Let us now turn to the three great stirps, and pass each of them in review, trace their course, and determine their limits. I shall begin with the microtypal stirps (with which we are most familiar). It is the most extensive of the whole, being distributed over the whole world with the exception of the Indian, African, and Brazilian regions; and even they, from various exceptional causes, have a greater or less tinge of it in their faunas. It contains some minor faunas, and these, again, a number of subfaunas. The Europeo-Asiatic region is one of these minor faunas, and of it the Atlantic islands, the Mediterranean, and the Monoglian are subfaunas. Taken as one fauna, the Europeo-Asiatic extends from the Azores east to Japan, the whole of that vast space being inhabited entirely by the same type and, for the most part, by the same species, a few only dropping off here and there, and being replaced by others of the same general character. p. 11.

1. Trans. Am. Assoc. Adv. Science, 1875, Detroit, President's address. [cf. Le Conte, 76.]

"The Europeo-Asiatic Beetle-fauna¹ does not stop even at Japan; it passes over into North America by Behring's Straits, or rather, I should say, it is found in North America on the other side of Behring's Straits. In Russian America we have a fresh crop of Europeo-Asiatic form, genera and species; and here another noteworthy circumstance presents itself. It is generally taken for granted that there is a uniform homogeneous arctic fauna which extends all around the arctic circle. It is so, and it is not so. It is so on the large scale, but not so on the small. The arctic fauna is subject to the laws of spreading by continuity and stoppage by barriers just the same as any other fauna. I have elsewhere endeavored to show that the

mammalian fauna of Greenland is Europeo-arctic as distinguished from Americano-arctic. I maintain that the homogeneity of a fauna depends on other causes than uniformity of condition of life within its limits. I cannot doubt that if there had been an isolated communication between the indo-African districts and the North-Pole, we should there have had a fauna related to and developed out of that fauna, and wholly distinct from the other faunas of the arctic regions. It is continuity of soil or freedom of intercommunication which has produced the present uniformity of fauna in the arctic regions; but were minor interruptions exist, or old barriers or conditions equivalent to a barrier formerly existed, there are also subdivisions in the character of the fauna, and in the position of these minor divisions we see the operation of these laws and are able to trace the existence and former position of the barriers. Thus we find two minor subfaunas in Arctic America, an eastern and a western one. Two causes may have produced these. One of these may have been the sea which, it can scarcely be doubted, formerly existed between the Gulf of Mexico and the Polar Sea, in the line of the Missouri and Mackenzie rivers; another may have been that the ground now occupied by one of these subfaunas was under water at a later period than the other, so that it was peopled at a different date from it. Probably both contributed to produce the present arrangement of the subfaunas to the east and west of the Mackenzie River. That there was a barrier there, and that that side was still supplied with the same general type (though with minor deviations), is to be explained by their having received their species from the same general stock, but coming to it from different directions, the one from the east, the other from the west. That the minor differences to which I allude are, in the case of North America, to be referred this cause, and not to mere gradual increase of variation arising from increase of distance, seems to be a legitimate inference from the fact that while the whole of the north of North America, without exception, belongs to the Europeo-Asiatic type, there are a number of European genera which occur in North-east America, and not in the North-west, and a few which occur in the North-west, and not in North-east America. pp. 32-33.

"Returning to the Asiatic terminus of the microtypal stirps, let us now endeavor to trace its further course. The genus *Blaps*, which is a characteristic feature in the Coleopterous fauna of Central Asia, will furnish us with the means. It may be taken as a representative case applicable to other species also, although it is the most striking instance which occurs to me. Upwards of 100 different species of *Blaps*, out of a total of about 150, have been described as inhabiting the country between Southern Russia, Mongolia, and Mantchouria. Now if we cross to California in continuation of the same line we have not *Blaps*, but we have *Blaps*'s brother and he has been a twin. We have *Eleodes*, its perfect counterpart and representative; and it is to be observed that while the facies of the species actually inhabiting California is entirely that of *Blaps*, a number of species which are found in Kansas and on the eastern flanks of the Rocky Mountains have a somewhat different facies; and I should add that the supposition that these are stragglers from the Californian shores is strengthened by the fact that the genus does not occur to the east of the Missouri; other Heteromerous forms, reminding us of Mediterranean and Asiatic species, occur in California, and the whole of the north-west of America has a greater preponderance of the microtypal stirps than perhaps occurs east of the Rocky Mountains. pp. 36-37.

"¹ I was unable in my 'Geographical Distribution of Mammals' to adopt Dr. Sclater's terminology of Palaearctic, Neoarctic, &c., because we did not agree in the extent and limits of our regions; and now, of course, in this paper I can still less do so, as a principal effect of my hypothesis, if it be sound, must be to still further break down their limits and destroy their solidity."

"Next step to the south of California comes Mexico. It also is largely supplied with *Eleodes*; and although some of the showiest and finest non-microtypal Coleoptera in the whole world come from Mexico, they have no bearing on this part of my inquiry; for they come from parts of Mexico which are in direct communication with another stirps, the rich Coleopterous fauna of Brazil and Venezuela; and the vast multitude of small European-looking species which occur on the high lands and western side is quite sufficient for my purpose. The collections made by Truqui in Mexico show this thoroughly microtypal character in a very marked way, Staphylinidous genera, such as *Falagria*, *Homalota*, &c., abounding. Mexico, being a sort of halfway house between Europe and Australia, might be expected to contain species both from the north and the south which have got thus far. *Eleodes* is an instance of this from the north, *Philonthus* another; both reach as far as Chili, but not into Australia, *Zopherus*, on the other hand, is an instance of a species which occurs in Australia, and runs up into Mexico, where it is in strength, and goes even a little further. Mexico may, indeed, have been its starting-point, but the connexions and relations of it and the allied genus *Nosodendron* decidedly indicate a separation between the eastern and western type of both; and the western type extends into Australia and New Caledonia." p. 38.

Schwarz, E. A. 1888. pp. 166-167, 168-170, 171-172. "After a study of this peculiar fauna of Key West which I also found on many other localities farther north and which constitutes the semitropical fauna of Florida, I have come to the conclusion that it is entirely of West Indian origin, and that the region I shall hereafter circumscribe as Semitropical Florida does not contain any endemic forms. In other words, the distinctive fauna of Southern Florida is a permanent colony of West Indian forms, much more numerous in species than it has hitherto been supposed; the number in Coleoptera alone amounting, according to a very low estimate, based upon my collection, to at least 300 species not yet in our catalogues. pp. 166-167.

"Before entering on a discussion of the character and extent of this West Indian colony in Florida it seems worth while and instructive to give a glance at the south-western extremity of North America where our fauna comes also in contact with a semitropical fauna. The great faunal regions known as Nearctic and Neotropical are connected or divided by the Central American fauna which from the nature of the conditions participates in the characters of both regions, but is more nearly allied to the latter than to the former. It is again divided into the fauna of the Central American continent and the Insular fauna of Central America, more commonly called the West Indian fauna; these two faunal regions being related to each other in the same degree as is the fauna of our Atlantic slope to that of the Pacific slope. At the zone of contact between the North American fauna and that of Mexico the conditions are as follows: The ocean current along the Pacific coast of North America runs from north to south, thus facilitating the spread of more northern species southward. It loses its force and disappears before reaching southern California and thus the North American fauna along the coast does not come into contact with that of the Mexican coast. On

the mainland we find between California and the largest portion of Arizona on the one side and Mexico on the other, a broad tract of the most barren and sterile* country which proves to be a most effectual barrier between the two faunal regions. Farther east, and more especially along the Rio Grande, a complete intermingling of the two faunas takes place in such a way that species of all families participate in this intermingling. It is thus impossible to decide whether a collection of insects comes from Texas or the State of Tamaulipas, or whether it comes from southern New Mexico, from south-eastern Arizona, or from Sonora. The Morrison collection, for instance, has been distributed among North American entomologists as coming from south eastern Arizona and is worked up in the 'Biologia Centrali-Americana' as coming from Sonora, Mex. pp. 167-168.

*See Dr. G. H. Horn's "Notes on the 'Biologia Centrali-Americana,'" Trans. Amer. Ent. Soc., Vol. XIII, Month. Proc., p. VII.

"In looking for the original home of this colony of West Indian insects and plants we have been hitherto too much accustomed to consider the island of Cuba as the only place from which this immigration has taken place. In the task of determining my South Floridian Coleoptera it was found over and over again that these immigrants may have been described not only from Cuba, but from any other of the West Indian islands, or from the Central American continent south of Yucatan, or even from Columbia and Venezuela—in other words from all parts of Central America which come under the influence of the Gulf stream. As can be seen from any physical atlas, the warm equatorial current enters the Caribbean Sea through the Windward Islands and attaining by this contraction a considerable velocity forms the Gulf Stream which flows between the southernmost chain of the West Indies and the Leeward Islands and strikes the Central American continent, flowing northward along the coast. Deflected by the projecting peninsula of Yucatan, the stream turns eastward and reaches the coast of Cuba and the southernmost part of Florida. Thus the West Indian colony of insects in Florida may come from any part of this vast area swept by the Gulf stream, although the largest proportion comes of course from Cuba since this island is the nearest to Florida. This immigration by the aid of the Gulf stream explains the following interesting phenomenon in geographical distribution. We have seen that insects from the coast of Central America south of Yucatan may occur in Southern Florida; but the same species often had the power of extending their geographical distribution northward on the Central American mainland through Mexico, thus reaching the south-eastern limits of the United States. Certain species may occur, therefore, in the United States, in Western Texas or South-eastern New Mexico and in Southern Florida, being however, absent in the intervening Southern States, viz: Eastern Texas, Louisiana, Alabama, Georgia, and Northern and Central Florida. This curious distribution has never been pointed out so far as I am aware but can be exemplified by numerous species, not only among the Coleoptera but also other Orders of insects,

"The distance between Cuba and Florida is not very great, the current of the Gulf stream is very swift, and logs and other debris swept out to sea from, the rivers of Cuba may reach the coast of Florida within three or four days; from Yucatan in about double that time. It is evident that within that short time all such insects may safely be carried from the West Indies to Florida which, in the imago or preparatory stages, live under bark, or within the wood of trees, or within seeds and similar sheltered conditions, or whose eggs are firmly attached to trees and covered with viscous liquid. But it is evident that this

sea voyage is too long for all such insects as do not live in such sheltered positions. As a consequence, all adepagous Coleoptera, further all those living under old leaves, in the ground, in very rotten wood and similar places, and finally most of the *Chrysomelidae* which lay their eggs either onto the leaves or in the ground are not brought over from the West Indies. There are, therefore, no West Indian *Carabidae*, *Lampyridae*, *Staphylinidae* and other rhyphagous Clavicorn families and very few West Indian *Scarabaeidae* and *Chrysomelidae* to be found in Southern Florida.* This is a most characteristic feature of the semitropical Coleopterous fauna of Florida, strikingly contrasting with the state of affairs in the southwestern extremity of North America. I have stated before that along the Texan and New Mexican frontier there is a perfect intermingling of the North and Central American faunas so that it is impossible to decide whether a miscellaneous collection of Coleoptera comes from Western Texas or the adjacent parts of Mexico. A miscellaneous collection, consisting only of about 100 species but made promiscuously in semitropical Florida can at a glance be distinguished from a similar collection made in Cuba or any other part of the West Indies. Further, the peculiar composition of this fauna at once precludes the assumption that any agencies other than the current of the Gulf stream could have been active in assisting the Immigration from the West Indies. pp. 168-170.

** The absence of fresh water in the coral region of the keys and the mainland south of Miami River necessitates the absence of *Dytiscidae* and most other aquatic or semi aquatic families. Even the Everglades and the rivers draining the same at the northern end of Biscayne Bay seem to be almost destitute of aquatic Coleoptera."

"Most of the more southern Keys are covered with semitropical forest, i. e. forest covered with composed of West Indian trees, while, as I stated before, the true Floridian fauna and flora are almost entirely absent. These islands are, therefore, by no means favorable to a study of the relation of semitropical to the true Floridian fauna. However, a stay of a few weeks on the shores of Biscayne Bay fully sufficed to settle this question. Here, as well as on the mainland farther south and the northernmost Keys (Key Largo and Elliott's Key) the Floridian flora largely infringes upon the semitropical forest and reduces the same to smaller or larger island-like patches lying close to the shore or occupying similarly isolated patches on the shore of the Everglades and the few islands in the Everglades. The bulk of the mainland is covered by pine woods† with an undergrowth composed almost entirely of true Floridian plants. There are further vast stretches of what is called 'the prairie,' i. e. land quite recently formed, partly by the accumulation of seaweeds swept ashore by the waves, and partly by the advance of the Mangroves. This prairie is covered with the same herbaceous vegetation which we see in similar places in Central Florida and does not contain a single semi-tropical plant. Even the hammock is invaded by several Floridian trees: the Live Oaks, several Palmettos, the Hackberry and others make their appearance and, on higher ground we find plenty of *Persea carolinensis*. Now on all these trees in the pine woods and on the prairie, in short wherever there is the Floridian flora we meet the true Floridian insect fauna whereas the semitropical fauna is confined to the semitropical forest.* This fact once recognized, it becomes evident that the northward extent of this fauna is identical with that of the semi-tropical forest, a fact fully borne out by subsequent experience." pp. 170-171.

"I desire to emphasize here once more as one of the principal characteristics of this flora and fauna, that north of the Everglades they nowhere appear inland but always close to

the shore. Even along the inner bank of the Indian River there are—or rather were—but a very few spots covered with semitropical forest, viz: on the mouth of the St. Lucie and Sebastian Rivers, at the southern end of Merritt's Island and perhaps some others; but they are now mostly destroyed by cultivation." p. 172.

1890. pp. 186-187.

"The mountain ranges in America run in the direction from north to south, and the colonies of circumpolar insects upon their summits have thus been able to preserve their connection and specific identity with the arctic forms; whereas in, Europe, where the mountain ranges run from east to west, the alpine colonies have generally undergone changes and, by isolation, lost their specific identity with the arctic species. There is, therefore, in the Old World an abundance of distinct alpine forms, none of which are identical with North American species; while we, on our high mountains, have but few, if any, alpine, but more arctic forms. pp. 186-187.

"Among the strictly circumpolar Coleoptera the predaceous families predominate over the phytophagous families; the *Carabidae*, *Dytiscidae*, *Staphylinidae*, and *Coccinellidae* are well represented, the *Chrysomelidae* and *Rhynchophera* are tolerably well, and the *Cerambycidae* and *Elateridae* are poorly represented. The *Buprestidae* are absent although this family contains numerous boreal species in every region. The phytophagous *Scarabaeidae* do not, or barely extend into the arctic regions; the coprophagous *Scarabaeidae* (*Aphodius*) are well represented there, still none of them (with the exception of *Aphodius rufipes*, which doubtfully belongs here) is on the list of circumpolar Coleoptera." p. 187.

"*Species not Belonging to the Circumpolar Fauna.*—This division comprises endemic species of probably intratropical origin, which have spread, by natural dispersion, into the temperate zone of North America." p. 187.

1890a. pp. 170-171.

"Turning now to the bulk of the species in the list [St. Augustine, Florida] we find that they consist of the usual admixture of more or less widely-distributed species and true Floridian forms, the proportion being but little different from that of the other localities, e. g., Crescent City, Enterprise, Tampa. . . But the St. Augustine list contains another element, viz: species belonging to the faunal region lying directly north of eastern Florida and comprising lower Georgia, the lower Carolinas, and eastern Virginia. This is an ill-defined region with very few, or no, peculiar species, and only characterized by a certain combination of a number of southern species. The existence of this faunal region will become evident to any one who, on a summer day, goes from here [Washington] down to Fortress Monroe, Va. The difference between the Washington fauna and that of Fortress Monroe will then be found quite striking. Of this fauna I noticed about twenty species in the St. Augustine list not previously known from Florida." pp. 170-171.

1901. pp. 1, 2, 3.

"Still, southwestern Texas belongs, at least as far as the insects are concerned, to the lower Sonoran fauna, of which it forms a marked subdivision, but with marked affinities to the austroriparian region.

"† While it is true that the pine of Southern Florida, *Pinus Cubensis*, is also of West Indian origin, its distribution in Florida is quite different from the rest of the semitropical flora and its introduction is evidently of very ancient date. Its fauna does not differ from that of the Yellow Pine, (*P. palustris*)."

"* There is, in addition, in Southern Florida a maritime fauna of semitropical character, but the number of species composing the same (about 12 in Coleoptera) is so small that it is hardly worth while considering. Its northern extent is still uncertain but it is safe to say that on the eastern coast it does not reach beyond Mosquito Inlet at New Smyrna."

"Collections made at Laredo, San Diego, Corpus Christi and in the lower Nueces river valley prove that, with few exceptions, no tropical forms occur in that section, and the trip on the stage from Alice to Brownsville shows that the character of the country does not change southward until the black alluvial soil of the delta of the Rio Grande is reached. Here, within the bends of the river, as well as along the various backwaters and old river arms (resocas) which dissect the delta, isolated areas or strips of larger or smaller extent are covered with a dense forest having thick undergrowth of varied shrubbery and a rich vegetation of lower plants, the like of which is not seen at any other place in Southwestern Texas. The forest jungles (in Florida they would be called hammocks) are the home of the semitropical insect fauna of Texas, which, so far as known to me, has, previous to the year 1895, never been investigated by any entomologist, since even many of the most abundant species are either entirely new or not yet recorded from the United States. If, confining myself to Coleoptera found by Prof. Townsend or myself near Brownsville, I mention the genera *Agra*, *Dasydactylus*, *Physorhinus*, *Achryson*, *Gnaphalodes*, *Amphionycha*, *Megascelis*, *Plectrotreta*, *Brachycoryne*, *Listronychus*, *Polypria* (quite a number of others are not yet determined, or undescribed), no one can deny the existence of a semitropical insect fauna along the north bank of the lower Rio Grande. The number of species composing this fauna is very large; in Coleoptera alone I estimate that, after proper exploration, between 300 and 400 species will be added to our lists.

As stated above, these semitropical thickets occur in isolated patches in the lowest parts of the delta; wherever the ground is a little more elevated, the usual mesquite and spiny chaparral, liberally interspersed with *Opuntias*, make their appearance, and with them the general fauna of southwestern Texas."

Scudder, 1895. pp. 27-28.

"The Post-pliocene deposits have proved the most prolific with thirty-two species, though here only seven families are represented, of which the *Carabidae* and *Staphylinidae*, but especially the former, very largely predominate. The greatest interest attaches to the interglacial locality near Scarboro, Ont., which alone has yielded twenty-nine species,* and is the largest assemblage of insects ever found in such a deposit anywhere. These clays have been studied and their fossils collected by Dr. G. J. Hinde,† who sets forth the reasons why he regards them as interglacial, lying as they do upon a morainal till of a special character and overlain by till of a distinct kind. The elytra and other parts of beetles found by him, represent five families and fifteen genera; they are largely *Carabidae*, there being half-a-dozen species each of *Platynus* and *Pterostichus*, and species also of *Patrobus*, *Bembidium*, *Loricera* and *Elaphrus*.

The next family in importance is the *Staphylinidae*, of which there are five genera, *Geodromicus*, *Arpedium*, *Bledius*, *Oxyporus* and *Lathrobium*, each with a single species. *Hydrophilidae* are represented by *Hydrochus* and *Helophorus*, each, with one species, and the *Chrysomelidae* by two species of *Donacia*. Finally a species of *Scolytidae* must have made the borings under the bark of a juniper described below.

"Looking at the assemblage of forms as a whole and noting the distribution of the species to which they seem to be most

nearly related, they are plainly indigenous to the soil, but would perhaps be thought to have come from a somewhat more northern locality than that in which they were found; not one of them can be referred to existing species, but the nearest allies of not a few of them are to be sought in the Lake Superior and Hudson Bay region, while the larger part are inhabitants of Canada and the northern United States, or the general district in which the deposit occurs. In no single instance have any special affinities been found with any characteristically southern form, though several are most nearly allied to species found there as well as in the north. A few seem to be most nearly related to Pacific forms, such as the *Elaphrus* and one each of the species of *Platynus* and *Pterostichus*. On the whole, the fauna has a boreal aspect, though, by no means so decidedly boreal as one would anticipate under the circumstances." pp. 21-28. Cf. Scudder '94.

"*This statement includes four species (*Hydrochus amictus*, *Helophorus rigescens*, *Pterostichus dormitans*, and *Bembidium fragmentum*), found by Dr. Hinde near Cleveland, Ohio, on the shores of Lake Erie, in clay beds very similar to those found near Scarboro', on the shores of Lake Ontario, but not found at Scarboro' itself. They undoubtedly belong to the same category."

"†Can. Journ. Sc., N. S., xv, 388-413 (1887)."

Ulke, H. 1902. p. 3.

"The appearance of northern and southern forms are here controlled [Washington, D. C.] by the change of seasons, so in early spring we may always expect more northern types, while in midsummer the southern ones predominate."

VanDyke, E. J. 1901. pp. 198-199.

"The California faunal region proper includes practically all the lowlands of the State, the fertile valleys of southern California and the extensive valleys of the San Joaquin and Sacramento, the lesser valleys along the coast and the foot hills bordering them. The fauna prevailing throughout these portions are so affiliated with Sonoran forms, particularly toward the south as to warrant the designation of such portions as Sonoran sub-regions, and by the extension of these forms into the foot hills where they have interbred with Boreal types through a series of ages, genera characteristic of both parent regions have been evolved. *Omus*, *Brennus* (a cychrid subgenus), *Metrius*, *Promecognathus*, *Pleocoma*, and *Rosalia* with others while more or less related to adjacent northern forms probably developed from a rich circumpolar fauna under the influence of adaptation to environment. *Omus* occurs rather generally throughout the state, and *Metrius* and *Promecognathus* similarly but less frequently in the moist timber belt of the Coast Range, although an Alpine variety of *Metrius* is found in the Sierras, and *Brennus* is confined to the coast. Many other examples of restricted location could be given. In earlier periods California was more isolated particularly from the Sonoran region, and northern influences prevailed. Then such genera as *Omus* and *Pleocoma* became first established. Subsequently a few southern forms such as *Coniontis* and its congeners gained access. These constituted the old California fauna, but when the southern isolation ceased, followed by the invasion of Sonoran forms, a new and later fauna was developed. This theory is partially supported by the fact that in the islands off the coast and in certain still isolated areas are faunas which are largely *sui generis*, and typical of the old California fauna above described."

Wickham, H. P. 1902. pp. 221-222.

"The phenomena of distribution in Colorado are of much interest. Within a radius of a few miles we may find assemblages of species representing at least three distinct

fauna. The first, that of the great plains surrounding the mountains, is marked by a great development of wingless or imperfectly winged forms, probably largely invaders from the south where we may suppose that the arid deserts first made their appearance and where this characteristic feature is more in evidence among the beetles. Good examples may be found among the Meloidae, Tenebrionidae and epigaeal Rhynchophora. Occasionally these forms leave their natural haunts and extend for long distances up the river valleys. Thus *Eleodes* may sometimes be met with at altitudes exceeding ten thousand feet. As we enter the timbered country on the higher foot-hills and lower mountain sides, we encounter a fauna which while not unmixed with species that have come up from the plains, shows a strong affinity to the life about our Great Lakes. Higher still—that is to say from about eight thousand to nine thousand feet, according to the exposure, presence or absence of near-by snow-fields and so on—we meet with many species of genera still more boreal in habits. We may mention *Nebria* with its many species, usually taken along the coldest mountain streams, the flattened *Bembidia*, and the large *Aphodii*. Above timber line the peaks sustain a few beetles which seem to be of arctic origin, left, probably, by the retreating ice-sheets of the Glacial period.

"I cannot agree with Prof. Cockerell* who claims that the Glacial epoch would, for the time being result in the almost complete extermination of the insect fauna of Colorado and the adjacent table-lands. He assumes that the arid region 'where not actually glaciated would be a frozen desert,' something which I think is not indicated by such geological evidence as we possess. The glaciation of Colorado was apparently not particularly extensive. Neither does it seem likely that the western ice-sheet went so far south as San Diego; at any rate the indications seem to show that along the highlands of Southern California only the loftier mountains were glaciated at all. Today great glaciers exist in the immediate vicinity of well-wooded districts rich in animal life. The same phenomenon may have occurred during ancient times."

*Transactions of the American Entomological Society, Vol. XX, p. 319.

1893. pp. 232-233.

"1. That the fauna of southern Alaska is less closely related to our alpine, northern inland, or north-east coast faunae than is that of the Stikine Canon or of Glenora.

2. That the Stikine Canon fauna is more closely allied to that of the North and East than is that of the coast, and about the same as is that of Glenora.

3. That the chief relations of all three are in the direction of Lake Superior: with larger lists this affinity might turn to the Rocky Mountains, especially in the case of Glenora.

Regarding the affinities of the faunae of the Coast, the Stikine Canon and Glenora among themselves we find:

4. That one-sixth of the Coast species extend up to the Canon while only one-thirtieth reach Glenora.

5. That the last-named fauna is much more closely allied to that of the Canon than to that of the Coast; nearly one-fourth of the Glenora species are found also at the Canon while only about one-eleventh extend to the Coast.

6. That the fauna of Glenora is apparently less related to that of the Coast than to that of the interior or the East.

"Reference to the accompanying maps will throw some light on the problems here suggested. Glenora is on the inside of the

great Coast Ranges while the Little Canon is regarded by Dr. Dawson as marking the head of the old salt-water inlet that has been silted up. This would account for much in the distribution of the species in question. The climate of the country above the Canon is also much dryer and with greater extremes of heat and cold than on the Coast. Aside from the influence of the barrier of the Coast Mountains interposed between faunae which might tend to intermingle, the change of plants consequent upon difference in climate on opposite sides must also have its effect on the insects dependent on vegetation for food." pp. 232-233.

1905. p. 46.

"My proposed explanation, correlating the briefly outlined geological history with the facts offered as to the distribution of the insects [shore insects of the Great Basin], may be summarized as follows:

1. The shore beetles under consideration are confined to the Great Basin or its immediate borders, and have, in general, no allies in other districts from which they could have been recently developed. This in itself is strong presumptive evidence that they are endemic, not immigrants.
2. Within the Basin, recent conditions are such that the present distribution cannot possibly be a matter of modern origin. The small lakes now remaining in the Basin are separated by great tracts of arid desert, impassable to beetles depending on a moist soil for their development and food supply. The nature of these insects is such that they cannot be carried long distances, as eggs or larvae, on the feet of birds or other animals.
3. Ancient conditions, as shown by the geological history through the Pleistocene, were favorable to the diffusion of shore-loving insects through the Basin, because of the much greater extension of the lakes in those times.
4. The insect most thoroughly studied, *Cicindela echo*, is entirely confined, in its present range, to the neighborhood of lakes, from which their size and the presence of nearby springs, may be presumed to have lasted in some form from a remote period—even through times of severe drought. Other littoral forms follow the same general law, though some of them are less sensitive to local conditions.

"From these facts, I think we can come to but one conclusion—the beetles under consideration are types that have inhabited the Basin during the Pleistocene times when the shores of the great lakes stretched over hundreds of miles of what are now desert sands. As the lakes shrunk during times of drought, the insects followed the retreating beaches. Those which attached themselves to bodies of sufficient size or permanence were able to sustain their specific existence, while such as were dwelling on the edges of pools of a transient nature were exterminated altogether. Thus we have the phenomenon of discontinuous distribution, presented not by one species alone but by an entire assemblage." p, 46. Cf. Wickham, 1904.

2. Comments on the Preceding Generalizations and on the Literature of Geographic Distribution.

The American authors who have given special attention to the study of the geographic distribution of our beetle fauna are few in number, but they are very representative men. First and foremost is Dr. J. L. LeConte, the most remarkable and "exceptional" of American entomologists. A man who, had he devoted himself to subjects of more general interest than insects or to more general problems would, in all probability,

have been generally recognized as one of the greatest of American naturalists. Other students who have devoted much attention to distribution, although none have given as much attention to the general principles of the problem as did LeConte, are: Schwarz, Hubbard, Hamilton, Wickham and Cockerell. Then there are several authors of local lists which must furnish the basis for comparisons, but only in a few cases do the authors of these local lists attempt to discuss the *general characteristics* of their fauna or compare them with those of other localities. This is certainly an unfortunate omission, particularly so as, in general, the authors of such lists should be the most competent to discuss the main features of their fauna. Of the various local lists, two are to be particularly commended for the ecological notes which they contain: those by Schwarz in Hike's Washington list, and those by Hamilton, in the Pittsburg list. It is through the ecological influences upon distribution that we must expect the greatest advances in the future study of distribution. In this connection there should be mentioned the studies by Webster on the routes of dispersion of certain species, particularly those of economic importance. A very useful bibliography of local lists of beetles has been published by Hamilton and Henshaw ('91-'92), and still other recent local lists will be found in the bibliography accompanying this paper, although no attempt at completeness is made.

Limited time has prevented a detailed discussion of the quotations as originally intended, but in their present form they are much more accessible than when scattered.

V. The Present Centers of Dispersal of the Beetle Fauna.

The general characteristics of the Isle Royale beetle fauna can only be appreciated through a comparison with other areas, particularly with those of boreal regions and the remainder of the North American continent. Only the major features can here be outlined. It has been thought desirable to consider the subjects from the standpoint of centers of dispersal, rather than from the current taxonomic standpoint because of the emphasis thus put upon the genetic side of distribution and its ecological relations.

In a former paper, (Biol. Bull., 1902, 9, p. 122) the writer listed certain criteria which may be used to determine biotic centers of dispersal and centers of origin. As is well known, centers of origin and centers of dispersal do not necessarily coincide, although all established centers of origin must be centers of dispersal. Centers of origin are very often difficult or impossible to determine with the present state of knowledge; and many are likely to remain so indefinitely. Then there is the possibility, or even probability, that some forms have originated at more than one place, and independently. This certainly complicates the subject of origins, increases the importance of determining them, and means that this method must be repeated in such cases, but not that such determinations are impossible. Centers of origin,

either single or multiple, at once become centers of dispersal, and by means of dispersal new centers become established so that there may be numerous centers of dispersal in wide ranging forms. It should also be again stated that centers of dispersal while not necessarily centers of origin, are likely to become such with age, particularly if favored by diverse environmental conditions.

It is desirable to understand clearly what is meant by criteria. As understood by the writer, they indicate the kinds or convenient classes of evidence to which we may turn for suggestions and proof as to the origin and dispersal of organisms. Their value is largely relative, so that they vary much in value, and in their application to various groups. In some cases a criterion may have great weight, while in another taxonomic or ecologic group it may have no value or so little as to be merely suggestive. *Each case must be tested on its own merits.* The main advantage of criteria is the definite form in which they present the problems and in the definiteness which it gives to such inquiries as to origin. The number of criteria needs to be greatly increased by the formulation of those restricted to groups of peculiar taxonomic or ecologic character. It should be clearly emphasized that it is the convergence of evidence from many criteria which must be the final test in the determination of origins rather than the dependence upon any supposedly absolute criterion.

The development of criteria has been largely along taxonomic lines, because taxonomy has been based largely upon structural characters rather than upon the convergence of all kinds of affinities and evidence. For this reason ecological criteria have been largely overlooked. With their increase in number, certain origins and dispersals may be established which otherwise could not be determined.

It should be understood that the breeding range only is of fundamental value in the use of criteria, in the determination of origins and the centers of dispersal. Of course only natural dispersal is considered when criteria and natural centers are involved. Dispersal as influenced by man has peculiarities of its own which have not yet been carefully formulated. Species introduced by man may thus secure many new centers of dispersal.

Aside from historical and paleontological evidence the following criteria, may be listed as those which will probably be of value in the study of beetles. They have also furnished the basis for the determination of centers of dispersal and origin of the North American beetle fauna.

1. Location of great or maximum taxonomic differentiation of a type or types.
2. Location of synthetic, primitive or closely allied taxonomic forms or groups possessing convergent affinities.

3. Location of maximum size of taxonomic forms or groups.
4. Continuity and convergence of lines of dispersal.
5. Direction indicated by seasonal appearance; vernal suggesting boreal or montane origin, and aestival as austral or lowland derivation.
6. Direction indicated by continuity and directness of individual variations or modifications along highways of dispersal.
7. Location where the succession of beetle associations or societies reaches the relative equilibrium of a climax association or formation.
8. Location of dominance and great abundance of individuals.
9. Direction indicated by biogeographical or ecological affinities,
10. Location of least dependence upon a restricted habitat, except humid types in arid regions, and analogous cases.
11. Location (when both a center of origin and dispersal) of maximum ecological differentiation in habits, habitats, food, etc. "Adaptive radiation," in part, of Osborn.

By various combinations many additional criteria may be produced. By sorting into groups most of the above criteria will readily fall into either a taxonomic or ecologic class. But it will readily be seen that no sharp distinction can be drawn between the two groups; and further, no particular advantage is gained by such a classification.

The necessarily condensed character of such formulations makes further expansion and discussion desirable, but certain criteria are so well known and easily understood that their discussion is not necessary as in the case of No's. 1, 2 and 4; the remainder will be briefly considered.

3. Maximum size. This should be expected to apply to the larger taxonomic units as well as to the smaller ones. In certain families, genera, etc., there can be no question but that this criterion has great value, although it might not apply to allied groups. The broader outlines of the relationship must be borne in mind and should not outweigh exceptional cases. This relation of large size and centers of origin seems to be supported in part, by Murray's (70, pp. 7-8) primary strains of beetle descent. Two of the three strains, the Indo-African and the Brazilian centers, contain the largest beetles. But this entire subject needs critical study before its value and limitations can be fully understood.
5. Seasonal distribution. Although familiar with this criterion, it was, by an oversight, omitted from my former list of criteria. The northern affinities of the vernal flora have long been known. My attention to this oversight was called by my friend, Mr. A. B. Wolcott. Recently Ulke ('02, p. 3) formulated this, in part, for beetles. But it should perhaps be extended to include montane forms

also, as the vernal fauna of the mountains may be expected to extend their breeding range downward, where they will appear as vernal forms at lower altitudes. At the same time the fauna at lower altitudes might tend to spread up the mountains where they would occur at the height of the summer season. I do not know that this subject has been investigated.

The late fall feeding habits and the lack of ability to resist low temperature on the part of certain species which are extending their range, may be indicative as to their direction of origin. Many plant feeding insects, acclimated to northern localities, tend to cease feeding some time before the fall frosts and are thus better able to resist low temperatures (cf. Bachmetjew, '99, Zeit. wiss. Zool., 46, p. 600) than those which feed late and are well fed. Chittenden ('01, p. 74) has recognized this general tendency, but has not correlated it with Bachmetjew's results.

It is highly probable that there are many other seasonal phenomena which indicate, in a general but more or less definite manner, the direction of origin.

6. Continuity and directness of individual variations. The continuity and directness or definiteness of individual variations along routes of dispersal may give very definite information as to the direction of origin. This is perhaps not of universal application but carries much weight under certain conditions. For example, continuity of variations, as dwarfing or increasing size, have a certain definiteness which clearly points in a limited number of directions, when correlated with highways of dispersal (cf. Horn '72, p. 383). This is particularly so when a route is of a restricted character, as a drainage line, or a valley. If these variations were entirely promiscuous along lines of dispersal, there could be no idea of direction; but by taking into consideration the entire range, as one is perfectly justified in doing, continuity and directness clearly point in a given direction. It is mainly when the animals along a route are uniform or promiscuous that direction cannot be determined by the character of the variation. This criterion, as restated, like most other criteria should not be used independently. Compare Tower '06, pp. 12-13.

7. Geographical centers and climax associations. To apply this ecological criterion it is necessary to understand the principles which underlie the succession of beetle associations or societies. By a beetle association is meant that combination of beetles which occur associated in the same breeding habitat. As the environmental conditions upon which beetles depend change, the beetles also change and thus a succession is produced. The same general principle holds for a beetle association. Thus as the conditions change the association also changes and a *succession of beetle associations* is produced. When, however, a relatively complete adjustment or equilibrium is acquired, and changes become slight, a self perpetuating or climax, association or formation has become established. Areas occupied by formations, through their abundance and dominance, become centers of dispersal, although they

are probably more productive or originative, at an intermediate stage, before the dominance of the climax association is fully established.

Members, therefore, of such climax associations may be expected to point in the direction of such centers as include their associated species. If such a relation is valid, the various characteristics of climax associations will aid in the determination or location of centers of origin and dispersal. Such criteria may have more value in determining centers of dispersal than those of origin. This criterion will probably apply to secondary societies, but with attenuated force.

8. Dominance. This is a fundamental criterion in the determination of ecological associations. The tendency for certain associated species to obtain exclusive possession of any given area implies the abundance of individuals and their dominance. This idea is prevalent and fundamental in ecologic studies. This is also a relative term, and like all other criteria, has its limitations. Dominance in a desert must in general have a different meaning than in a humid area.

9. Biogeographical or ecological affinities. In its broader application this criterion is applicable to general biotic relations and to large areas. It is one of the oldest criteria used in the determination of faunal and floral affinities. In some respects it is closely related to No. 7. This criterion can be illustrated by reference to the Ajax Butterfly (*I. ajax*). The sole food plant of the Ajax larva is the Pawpaw, a shrub clearly of tropical origin. The allies of *Ajax* are also tropical; thus the associated biogeographic (plant and animal) affinities clearly point to the tropics. It is this combination of certain ecological relations or associations which show biogeographic affinities. Thus food and other habits and instincts become of special value. Here also belongs a large class of ecological relations, particularly those related to the succession of insect associations. The great dependence of Insects, as a class, upon vegetation necessitates a close relation between the succession of plant associations or societies and certain species of beetles. If certain members of a biotic (plant and animals) association or society have certain geographic affinities, others associated with them are likely to have similar affinities (cf. Horn '72, p. 384). This phase is not identical with the idea of faunal or floral affinities, it includes them and the relation of *biotic association*, particularly as members of a climax association or formation, when geographic affinities are to be determined.

This criterion is of very extensive application. It is really a group of criteria and not a single one, because associations include not only organisms in close proximity, but also commensals, symbiots, parasites, etc. Seasonal phenomena might well be included within this class.

10. Least dependence upon a restricted habitat. From the standpoint of animal associations this is a criterion which may be expected to have a rather extensive

application. Its most conspicuous application is to that of dispersal. Out-lying colonies tend to have a limited or restricted range. At the same time such colonies are particularly liable to become extinct, as they are usually near the limit of favorable conditions. Often beetles in such a location are dependent upon a single food plant, etc. This is true of the "boreal islands" in swamps within the glaciated portion of the continent. For example, members of the tamarack bog association, toward their southern limit, have very restricted or local range; but to the north, the bog forest conditions, as it were, spread from the bogs proper and become of extensive geographic range, as the water beetles invade the damp mosses (Wickham, '97, p. 126). The outlying tropical "islands" bordering the Rio Grande, as described by Schwarz ('01) and Wickham ('97a), apparently illustrate the same phenomena. These restricted, attenuated, or isolated colonies, dependent upon special conditions, are clearly indicative that they are pioneers or relicts, which point toward the region where their range is spread out and becomes of geographic extent. But it does not follow that every isolated habitat has such a meaning. In general, a study of succession in the region will determine to which class the colony belongs, pioneer or relict.

There is an exception to this criterion in the case of semi-aquatic or aquatic animals in an arid region. In such regions the springs, streams, and water basins are so limited in extent that their isolation is conspicuous; and yet these conditions may be very favorable to the formation, or at least preservation, of new variations and species. Thus an arid region may be particularly favorable, in a sense, to the formation of varieties and species, although individuals may not be numerous. In such cases the amount and kind of differentiation within the area should carry more weight than abundance of individuals. But by the proper correlation of criteria, such cases will not be confusing. This sort of differentiation is well shown among beetles by Wickham, '04, '03.

This criterion evidently does not apply, at least in part, to the fauna now found in glaciated North America. This is made probable through origin elsewhere and a later expansion in the glaciated area as the Ice Age declined.

11. Ecological differentiation. Ecological and taxonomic differentiation need separate recognition, although they are frequently not distinct because of their intimate genetic relations. With great taxonomic diversity, within a group, there is almost certain to be ecologic diversity; but generally much less attention is given to the ecological diversity. Compare No. 1.

The following outline of the centers of beetle dispersion must be considered provisional and suggestive, as it is a subject which has received but little attention from the standpoint here presented. The preceding criteria, of taxonomic and ecologic nature, have been given much emphasis in locating the present centers of dispersal. Throughout this section references are given to significant papers, but this does not imply that the views here presented are approved by the authors to whom

reference is made. These references also apply to the quotations already given in detail.

1. *The American Tropical Center.* From Panama northward to the Mexican plateau is the main body of the tropical center. Narrow elongations extend coastwise on each side of the plateau, and on the Gulf Coast to the Rio Grande river. William Wickham '97a; Schwarz '01; Townsend '95, '97; Tower '06. Outlying colonies are found on the Pacific coast of Mexico and at the Southern extremity of Lower California; at the mouth of the Colorado river (Schwarz); and in southern Florida (LeConte '78a; Schwarz '78, '88). The fauna of the West Indian Archipelago probably belongs with this great composite center.

A vast number of beetles are characteristic of this complex area. The *Biologia Centrali-Americana* devotes thirteen volumes to the description of beetles from part of this area. Within the United States the attenuated tropical element has been most carefully studied and its faunal affinities determined by Schwarz ('88) and Wickham (97a).

This tropical center is composed of several distinct units. This is an ancient center of origin, preservation and of dispersal. The routes of dispersal into the United States have been along both coasts of Mexico and via the West Indies. It was practically uninfluenced by the Ice Age.

2. *The Mexican Plateau and the Southwestern Dry Desert.* This center includes the Mexican Plateau; most of Lower California; the deserts of southwestern United States; the low lands of California; the Great Basin and the Great Plains northward into Canada and east to the forests. LeConte '51, '50, '60, '62; VanDyke '01; Wickham '96, '98, '04, '05; Tower '06; Fall and Cockerell '07.

Characterized by numerous desert species; wingless Tenebrionidae (Horn '71), and Cicindellidae. A given locality is characterized by a limited number of species which are individually abundant; numerous local faunae. Contains the characteristic desert fauna of North America. Influenced markedly by glaciation only at the extreme north, and possibly in the Great Basin, but certainly by the great fresh water lakes formerly occupying this basin (Wickham '04, '05). An old (pre-Glacial) center of origin, preservation, and center of dispersal.

3. *The Southeastern Humid Hardwood Forest Area.* This area includes much of eastern United States east of the plains (exclusive of southern Florida), and north to the Canadian conifers. The Coastal Plain (and possibly the Mississippi Embayment area) may form a sub-center through the influence of its conifers (Schwarz '90; Chittenden '00, '01).

Local lists within this center: Summers '74; Schwarz '78; Ulke '02; Dury '02, '06. cf. LeConte '78a.

Characterized by the abundance of forest insects, particularly those infesting hardwoods; species of

extensive range; few local fauna; a large number of species found in a given locality, often but few individuals.

An ancient centre of origin, preservation and dispersal. Glaciated on the north, and post-Glacially repopulated, as was also the Coastal Plain and Embayment, with the elevation of the Coastal Plain.

4. *The Transcontinental Conifer Area.* This area includes the remainder of forested North America, and includes all of the higher mountain ranges. Its relation to the Coastal Plain conifer belt has not been determined.

Characterized by conifer feeding beetles, Cerambycids, Scolytids; numerous Carabids and Staphylinids, and thus shows a decided subarctic circumpolar affinity. Few endemic elements and local faunae. Extensive range of species, except in the high mountains. Largely a new land surface through glaciation; largely repopulated at a relatively late date; apparently characterized by dispersal or diffusion of forms rather than for their origin or preservation, except the mountain areas of the United States, which were areas of preservation and origin.

The very different history of its eastern portion, with much more extensive glaciation, is to be contrasted with the moderate western glaciation. The differences in the character of the forests is also marked; the giant western conifers are to be contrasted with the smaller conifers of the Northeast. The Mackenzie Basin and the Plains mark the line of division between these subcenters. This division is so marked that it may yet necessitate a complete severing of the transcontinental conifer belt. (cf. Murray '70, pp. 82-33.)

a. The Eastern Canadian Conifer Fauna.

This includes Canada east of the Rocky Mountains, north to the tree limit and the interior of Alaska; northeastern United States; and southward on the Appalachians.

Characterized by forms of extensive subarctic range, very few endemic elements or those peculiarly American; individuals abundant, variety moderate; beetles feeding on conifers, birches, and aspens. LeConte '50, '59, '78b. There is a possibility that this fauna has North European affinities stronger than Asiatic ones; the reverse from the western conifer center.

Local lists including this fauna: Hubbard and Schwarz '78; Harrington '84; Wickham '97; Hamilton '94, '94a, '95, Klages '01.'

b. The Western Canadian Conifer Fauna.

This includes the western mountains northward and upward to the tree limit, eastward to the Great Plains and the eastern Conifers. North of the United States this area has been extensively glaciated but within the United States the glaciers were local.

On account of this moderate glaciation in the mountains of the United States, this old land surface has been a

center of origin, preservation and dispersal. It contains more endemic elements than the-eastern conifer center, and more local faunae. Beetles feeding upon conifers and aspens are fairly characteristic. The Asiatic affinities of the fauna are much more pronounced than those of the eastern conifer center. Part of the apparently European influence may more truly be considered Asiatic—both the Western and European—having been derived from Asia. Elements of this fauna probably survived the Ice Age on the Pacific Coast north of the United States, but the humid interior has been invaded from the south, or is endemic. LeConte '76; Wickham '96; Cockerell '93; Hamilton '94, '94a; Fall and Cockerell '07; Keen '95.

5. *Alpine and Arctic.* This fauna occupies the area north of the tree limit, and above the tree limit on the mountains. This fauna is very imperfectly known and is limited in variety and in the number of individuals. Many species are of circumpolar range in the Arctic regions. Composed of very diverse elements and of diverse origin. The unglaciated arctic areas are probably centers of origin as well as of dispersal, as also slightly or moderately unglaciated alpine areas. The glaciated portions have been repopulated and show incipient endemism but are mainly characterized by the extensive dispersal of species, as is apparently true of unglaciated Asiatic Siberia. Both of these centers (Alpine and arctic) have been much confused with regard to whether they are centers of origin or of dispersal. These types are currently stated as of boreal origin, but this is very improbable for perhaps the majority of the population. They may be of alpine origin on the western mountains with an extensive post-Glacial dispersal favored by climatic conditions, and the low topographic relief of the northern land areas. Schwarz '90; Murray '70, pp. 32-33.

Eastern Alpine, Scudder '74; Bowditch '96.

Western Alpine, Carpenter '75; LeConte '78, '79; Schwarz '90; Cockerell (including Horn) '93; Wickham '03; Fall and Cockerell '07.

VI. The General Characteristics and Affinities of the Isle Royale Fauna.

1. *Faunal Characteristics.* The accompanying list of beetles collected in 1905 includes 89 species. The only previous list is that by Hubbard and Schwarz ('78) in which they list 123 species. A surprising feature of our 1905 collections is that of our 89 species, 66 are not listed by Hubbard and Schwarz. Such species are indicated by the letter A. following the scientific name. On the basis of these two lists, 206 species are now recorded from the island. It is not improbable that other species have been recorded in the scattered literature, but no effort has been made to search for them. Undoubtedly only a fair start has been made in the study of the beetle fauna. Careful detailed collecting, covering several years, would probably increase the number about five times, or bring it up to about 1,000 or 1,100

species; that is, judging from other northern localities. Pettit has recorded from Grimsby, Ontario 1,143 species and Harrington ('84) from Ottawa 1,003 species. On the other hand it is not improbable that the present known 206 species give a fair sample of the dominant features of the beetle fauna. Wickham's ('97) Bayfield, Wisconsin list contains 691 species (six weeks collecting by an expert). Such statistics mean but little, beyond showing the reduction in variety toward the north when compared with southern localities. The two best local southern lists—the best in America—are those by Ulke for Washington, D. C., with 2,975 species, and by Dury for the region about Cincinnati with 2,290 species. Two important intermediate locality lists between these northern and southern ones are from the vicinity of Allegheny and Pittsburg by Hamilton, in which 2,153 species are listed or 2,500 as given by Klages; and at Buffalo, where about 1,424 species are listed by Keinecke and Zesch. The variety in beetle life is thus seen to drop off about ½ or more in passing from the latitude of Washington and Cincinnati to that of Lake Superior and the St. Lawrence valley.

2. *Miscellaneous Notes on the Fauna.* In the present list there are included 6 species which in the Hubbard and Schwarz list are indicated as "Species found by Dr. LeConte, mostly catalogued in Agassiz' Lake Superior, p, 203-239, which have not since occurred." These species are as follows: *Carabus serratus*, *Calthus gregarius*, *Blechnus nigrinus* (*linearis* Lec), *Harpalus ruficollis*, *Pachyta liturata*, *Donacia proxima*. All these and other rare species turned up in our collection.

LeConte and Horn describe the following three new species from Isle Royale specimens in the Hubbard and Schwarz paper: *Habroceras magnus* Lec., p. 598; *Phymatodes maculicollis* Lec., p. 614 (from one specimen); *Orchestes canus* Horn, p. 620. None of these species were found in our collection. LeConte ('78, p. 463) described *Magdalis alutacea* (*armicollis* Say) from Colorado and Isle Royale specimens.

As numbered in the accompanying list of species collected during 1905, the following are not to be found in the Bayfield list by Wickham; No's. 2, 6, 7, 10, 12, 15, 16, 17, 18, 20, 21, 22, 25, 27^ 30, 34, 36, 41, 50, 52, 53, 55, 56, 59, 60, 62, 64, 73, 76, 77, 79, 81, 85, 86,—35 species.

VII. LISTS OF ISLE ROYALE BEETLES.

1. LIST OF SPECIES COLLECTED IN 1905.

Cicindelidae.

1. *Cicindela longilabris* Say. A. One specimen of the dark form was taken from the clearing about Neutson's resort (IV, 5) on July 21 (G. 121).

Geographic Range. Newfoundland; Ottawa, Canada; Hudson Bay; Nova Scotia; Quebec; Mt. Washington (summit), N. H.; Michigan; Wisconsin; Nebraska; New

Mexico; Colorado (10,000-12,000 ft.); Utah; Idaho; Montana; Alberta; California; Oregon; Alaska.

Carabidae.

2. *Carabus serratus* Say. A. A single specimen was found crawling over and through the tufts of *Cladonia* in the rock opening near camp on Siskowit Bay (V, 3) on August 5 (G. 208).

Geographic Range. Saskatchewan Basin, Canada; Mt. Washington, N. H.; W. Penna.; Michigan; Indiana (A. B. Wolcott); Chicago, Ill. (Wolcott); Kansas; Colorado; New Mexico. Hamilton 794a, p. 354.

3. *Calosoma frigiduni* Kby. A. A single specimen was found on July 7 among the drift on the beach (I, 1) near Tonkin Bay (A. 7).

Geographic Range. Drummond's Island, Ottawa, Canada; Mt. Washington (summit) N. H.; New York; Chicago, Illinois (Wolcott); W. Penna.; Michigan; Indiana; Wisconsin; New Mexico; Texas.

4. *Bembidium carinula*. Chaud. A. "Very abundant July 8 on the sandy beach at the head of Conglomerate Bay (I, 1). Running rapidly over the sand and fine gravel just back of the wet strip along the shore." (G. 30), Gleason.

Geographic Range. New Hampshire; Mass.; Adirondack Mts., New York; Port Arthur, Ontario; Saskatchewan Basin, Canada; Georgia; Ohio; Michigan; Indiana (Wolcott); Illinois; Wisconsin; Arkansas; Colo. (8,000 ft.); Oregon; Brit. Columbia. Hayward, '97, p. 46.

5. *Bembidium transversale* Dej. Two specimens were taken about the camp at the Light-house (I, 7) on July 11 (G. 49).

Geographic Range. Canada; Gulf of St. Lawrence; Lake Superior region; Mich.; Wisconsin; Nebraska; Kansas; Colo.; New Mexico; Arizona; Wyoming; Utah; Pacific Coast from So. Calif. to Alaska.

6. *Bembidium grapii* Gyll.=*nitens* Lec. A. "On a low bare rock on the shore near the Lighthouse at Rock Harbor (I, 1). On July 11, early in the morning, with air temperature of 51° F. and surface temperature about the same, no specimens were seen; but as the surface grew warmer, up to 95° F., the beetles became abundant. They probably conceal themselves in crevices in the rock when the temperature is low." (G. 46.) Gleason.

Geographic Range. Greenland; Hudson Bay region, Saskatchewan and Mackenzie Basins; Isle Royale, Michigan; White Mts., N. H.; New York; southward on the mountains of the west to Colorado, New Mexico and Nevada; Alaska; Siberia; Northern Europe. Hamilton, '94, p. 8; '94a, p. 351.

7. *Bembidium variegatum* Say.=*patruelle* Dej. "In debris cast up on the beach at the head of Tonkin Bay (I, 1) with *B. versicolor* and *Platynus*." (G. 21). Gleason.

Geographic Range. Nova Scotia; New England States; New York; New Jersey; Penna.; Maryland; Distr. Columbia; Texas; Ohio; Michigan; Lake Superior region;

Wisconsin; Illinois; Iowa; Missouri; Nebraska;
Saskatchewan Basin, Manitoba; Colorado; Nevada;
Calif. to Brit. Columbia.

8. *Bembidium versicolor* Lec. A. "In debris at the head of Tonkin Bay (I, 1) with *B. variegatum* and *Platynus 4-punctatus* (G. 21)." Gleason.

Geographic Range. General distribution in Canada and United States; from Anticosti, Quebec to Florida, Texas and California and north to Colorado and Manitoba; Pine, Ind. (Wolcott).

9. *Pterostichus coracinus* Newm. A. A specimen of this species was taken in the Lighthouse clearing (I, 7) on July 11 (G. 49) and on July 28 (G. 1.79).

Geographic Range. Ottawa, Canada; Mt. Washington (summit) N, H.; Vermont; New York; New Jersey; W. Penna.; Maryland; Virginia; Dist. Columbia; Tenn.; Ohio; Mich.; Northern Illinois; Iowa; Wyoming.

10. *Pterostichus femoralis* Kby. A. A specimen of this ground beetle was found under *Cladonia* upon a sloping rock shore (V, 2) just beyond the reach of the waves, on August 16 (A. 130).

Geographic Range. Ottawa, Ontario; Saskatchewan Basin; Mass.; Mich.; W. Penn.; New York; Ohio (Dury); Colo.; New Mexico; No. Ill. and Ind. (Wolcott).

11. *Calathus gregarius* Say. A. A specimen was taken on or in leaf mould in a deeply shaded balsam-spruce forest (I, 3) on July 24 (G. 140), and (V, 4) on August 14 (G. 236).

Geographic Range. Ottawa, Ontario; Quebec; Saskatchewan Basin; Vermont; New York; New Jersey to Florida and Texas; W. Penna.; Ohio; Mich.; No. Illinois (Wolcott); Wisconsin; Iowa; Kansas; Nebraska; New Mexico.

12. *Calathus advena* Lec. A. "One was found crawling through soft decayed wood in the balsam-spruce forest (I, 3) on July 24 (G. 142)." Gleason.

Geographic Range. Maine; Vermont; Mt. Washington; N. H.; Michigan; Colorado; New Mexico; So. Alaska. Hamilton, '94, p. 11.

13. *Platynus 4 punctatus* DeG. A. A single specimen of this species was found about camp at the Lighthouse (I, 7) on July 11 (G. 49), also in debris cast up on the beach at the head of Tonkin Bay (I, 1) where it was found alive (G. 21).

Geographic Range. Ottawa, Ontario; Canada; Hudson Bay and Lake Superior regions; Mt. Washington, N. H.; New York; W. Penna.; Mich.; Wisconsin; Idaho; Colorado; New Mexico; Montana; Alaska; Kamchatka; Siberia; Northern and Alpine Europe. Hamilton, '94, p. 11.

14. *Blechrus nigrinus* Mann.=*linearis* Lec. "In the debris under mats of bearberry on the rock ridge north of the Lighthouse at Rock Harbor (I, 3), (G. 64)." Gleason.

Geographic Range. Saskatchewan Basin, Canada; New York; New Jersey; Mich.; Iowa; Wisconsin; Missouri; Dakota; Wyoming; Colorado; New Mexico; Calif.; Brit. Columbia; possibly Siberia and No. Europe. Hamilton, '94a, p. 355.

15. *Harpalus megacephalus* Lec. "In rock crevices and under debris from bearberry on the jack pine ridge (1, 2) on July 13 (G. 72)." Gleason.

Geographic Range. Lake Superior; Isle Royale, Michigan.

Haliplidae.

16. *Haliphus ruficollis* DeG. A. "At the bottom of small pools in the partially drained sphagnum bog near Conglomerate Bay (I, 6) on July 18 (G. 116), and at the bottom of a small stream flowing from a tamarack swamp near Siskowit Bay (V, 5) on August 12 (G. 230). In each case the water was shallow and the bottom composed of sphagnum covered with dead leaves." Gleason.

Geographic Range. Canada; Hudson Bay region; Mt. Washington; New Hampshire; Vermont; New York; New Jersey; Mich.; W. Penna.; Ohio; Ill. (Wolcott); Iowa; Colo.; New Mexico; Texas; Wyoming; Kansas; Western Siberia; Europe; Turkestan. Hamilton, '94a, p. 355.

Dytiscidae.

17. *Hydroporus tristis* Payk. A. "In the bottom of small streams draining a tamarack swamp (V, 5), (G. 237)." Gleason.

Geographic Range. Ottawa, Ontario; Vermont; Mass.; Mich.; Lake Superior region; Hudson Bay; Colorado; British Columbia; Alaska; Arctic Siberia; Northern Europe to Finland. Hamilton, 794, pp. 13, '94a, 357. Sharp, '82, p. 472.

18. *Hydroporus modestus* Aube. A. Taken at Benson Brook clearing (II, 1) on July 29 (A. 81).

Geographic Range. Ottawa, Ontario; Mt. Washington, N. H.; Mass.; W. Penna.; New Jersey; Dist. Columbia; "Carolina"; Wis.; Mich.; Ohio (Dury). Sharp, '82, p. 480.

19. *Ilybius pleuriticus* Lec. A. "In the water near the shore at camp on Siskowit Bay (V, 1) on August 7 (G. 213)." Gleason.

Geographic Range. Penna.; New York; Isle Royale, Mich.; Bayfield, Wis.; Iowa; Colorado.

20. *Agabus stridulator* Sharp. A. Taken in a clearing (II, 1) on July 29 (A. 81).

Geographic Range. Isle Royale, Mich.; Hudson Bay; Canada. Sharp, '82, p. 509.

21. *Agabus congener* Payk. A. "In the bottom of streamlets draining a tamarack swamp (V, 5), (G. 237)." Gleason.

Geographic Range. Greenland; Labrador; Hudson Bay; White Mountains N. H.; Mass.; Penna.; Mich.; Missouri;

Arctic and Western Siberia; Central and Northern Europe. Hamilton, 794a, p. 358. Sharp, '82, p. 513.

22. *Scutopterus hornii* Cr. A. "In small pools in the tamarack and arbor vitae swamp (1, 4) on July 28. These pools were under fallen logs and at the bases of trees; seldom more than 1.5 dm. in depth and with a bottom of sphagnum and vegetable debris (G. 181, 182)." Gleason.

Geographic Range. Canada; Isle Royale, Michigan.

23. *Rhantus binotatus* Harr. A. Two were found in rock pools on the beach at the entrance to Tonkin Bay (I, 1) on July 13 (G. 73, 74) and at Scovill Point (IV, 1) on July 19 (G. 130). The beetles usually remained on the bottom except when they came to the surface for air.

Geographic Range. Labrador; Ottawa, Canada; Hudson Bay region; Brit. Columbia; Mt. Washington, N. H.; New York; New Jersey; Mich.; Wisconsin; Kansas; Nebraska; Colorado; New Mexico; So. Arizona; Utah; Nevada; Calif.; Lower Calif.; Mexico; Guatemala. Sharp, '82, p. 614.

Gyrinidae.

24. *Gyrinus minutus* Fab. A. "In sheltered coves of Siskowit Lake (V, 6) on August 9, where the water was quiet. Most numerous near the shore under the overhanging alders where they congregated in large flocks (G. 219)." Gleason.

Geographic Range. Labrador; Canada; Hudson Bay region; Saskatchewan basin (Evans '03); Vermont; W. Penna.; Michigan; Wisconsin; Washington; Oregon; Siberia; Central and Northern Europe. Hamilton, '94a, p. 360.

25. *Gyrinus picipes* Aube. A. In large numbers near the shore of Siskowit lake (V, 6) with the preceding species (G. 219).

Geographic Range. Labrador to Brit. Columbia; Vermont; Michigan; Idaho; Oregon; So. Alaska. Hamilton '94, p. 14.

Staphylinidae.

26. *Gyrophaena* species. "Several specimens (G. 229) were taken from a shelf fungus, *Pleurotus ostreatus*, on August 11 (V, 4)." Gleason.

27. *Quedius fulgidus* Fab. A. Two were taken from leaf mould or under decayed bark in the maple forest (III, '04) on August 21 (A, 142).

Geographic Range. Greenland to Alaska; south to No. Georgia and La. and Central Calif.; Peru; Mich.; West Siberia; Europe; Asia Minor; No. India; Java; Tasmania; Australia; New Zealand. Hamilton, '94, p. 18, '94a., p. 366.

28. *Philonthus politus* Linn.=*aeneus* Rossi. A. Hamilton, '94a, p. 19. One specimen was taken about camp at the Lighthouse (I, 7) on July 7 (G. 26).

Geographic Range. Isle Royale, Mich.; Nova Scotia; Hudson Bay region; British Columbia; New York; Mass.; Penn.; New Jersey; La.; Ohio; Illinois (Wolcott); Wisconsin; Iowa; Kansas; Colorado; New Mexico; Queen Charlotte Island; Alaska; Siberia; Amur region; Europe.

29. *Lathobium simplex* Lec. A. One specimen (A. 24) was taken July 17 on a jack pine ridge (I, 5).

Geographic Range. Canada; Mass.; New York; Michigan; Wisconsin, Am. Ent. Soc., '80, p. 176.

30. *Tachinus memnonius* Grav. A. One beetle was found under the bark in the hardwoods along the Desor trail (III, '04) on August 24 (A. 149).

Geographic Range. Dist. of Columbia; W. Penna.; Ohio (Dury); Wisconsin; Michigan; Ill. (Wolcott).

31. *Boletobius cincticollis* Say. "In fresh plants of the bracket mushroom *Pleurotus* sp. growing in the balsam-spruce forest (V, 4) on August 11." Gleason. One specimen (G. 229).

Geographic Range. Canada; New York; W. Penna.; New Jersey; Dist. of Columbia; Ohio; Wisconsin; Iowa; Mich. to Brit. Columbia; Calif. and Arizona; cf. Hamilton, '94, p. 21, Alaska.

Coccinellidae.

32. *Hippodamia 13-punctata* L. A. Taken about camp at Rock Harbor (1, 7) on July 14 (G. 98).

Geographic Range. "All America north of Mexico;" West Indies; Alaska; throughout Europe and Central Asia; Siberia. Hamilton, '94a, p. 378.

33. *Anatis 15-punctata* Oliv.=*ocellata* L. A. Found among drift-cast up on the beach at the head of Tonkin Bay (I, 1) on July 6 (G, 21).

Geographic Range. Ottawa, Saskatchewan basin, Canada; Nova Scotia; New York; New Jersey; West Indies; W. Penna.; Ohio; Illinois; Mich.; Wisconsin; Iowa; Siberia; Europe. Hamilton, '94a, p. 379.

Erotylidae.

34. *Tritoma macra*, Lec. A. "One specimen (G. 229) found August 11 in a shelf fungus *Pleurotus ostreatus* (V, 4)." Gleason.

Geographic Range. Maine; Michigan; Illinois; W. Penn.

35. *Tritoma thoracica* Say. A. From fresh specimens of *Pleurotus* growing in the balsam-spruce forest (V, 4) on August 11 (G. 229).

Geographic Range. Hudson Bay region; Saskatchewan basin; Ottawa, Canada; Vermont; New York; New Jersey; Va.; Georgia; Florida; Texas; W. Penna.; Ohio; Illinois; Mich.; Wis.; Iowa; Colo.; New Mexico; Washington.

Dascyllidae.

36. *Macropogon rufipes* Horn. A. One specimen was found upon the beach of Lake Superior (I, 1) on July 12 (G. 60).

Geographic Range. Illinois; Isle Royale, Mich.; White Mts., N. H.; Horn, Amer. Ent. Soc., '80, p. 80.

Elateridae.

37. *Adelocera brevicornis* Lec. A. One taken about camp at the Lighthouse (I, 7) on July 18 (G. 117).

Geographic Range. Ottawa, Canada; Mich.; Wisconsin; Lake Superior.

38. *Elater hepaticus* Mels. A. Two taken about the camps both at the Lighthouse (I, 7) on July 13 (G. 86), and at Siskowit Bay (V, 3) on Aug. 7 (G. 212).

Geographic Range. Canada; Vermont; W. Penna.; New Jersey; Ohio; "Western States;" Wisconsin; Michigan.

39. *Elater apicatus* Say. A. One taken at the camp on Siskowit Bay (V, 3) on August 3 (G. 195).

Geographic Range. Saskatchewan basin; Ottawa, Canada; New Hampshire; Vermont; New York; Mich.; Wis.; Duluth, Minn. (Wolcott); Colo.; Arizona; New Mexico; Idaho; Wash.; Oregon; Calif.; "Northern U. S. generally."

40. *Agriotes limosus* Lec. Taken on flowers of the Cow Parsnip (*Heracleum lanatum*) in the clearing at the Light-house (I, 7) on July 17 (G. 105) and on July 23 (G. 136). Five specimens.

Geographic Range. Newfoundland; Mt. Washington (summit), N. H.; Ottawa, Canada; Lake Superior; Saskatchewan basin; Michigan; Wisconsin.

41. *Melanotus paradoxus* Melsh. A. One taken about the camp at the Lighthouse (I, 7) on July 11 (G. 49), and near Lake Desor (VII, '04) on August 21 (A. 139).

Geographic Range. Isle Royale, Mich.; Colorado; New Mexico (Snow).

42. *Corymbites medianus* Germ. One taken on the beach south of Tonkin Bay (I, 1) on July 10 (G. 41), "crawling over the sand in a shaded place near a rock cliff." Gleason.

Geographic Range. Ottawa, Canada; Mt. Washington (summit); N. H.; New York; W. Penna.; Michigan; Wisconsin.

43. *Corymbites aeripennis* Kby. One taken at Scovill Point (IV, 1) on July 19 (G. 130).

Geographic Range. Ottawa, Canada; Nova Scotia; Maine; Mt. Washington, N. H.; New York; Mich.; Wis.; Colo.; New Mexico; Idaho; Oregon; Brit. Columbia.

44. *Corymbites aratus* Lec. On July 19 one was taken at Tobin Harbor (A. 29).

Geographic Range. Canada; Lake Superior; Michigan; No. Wisconsin.

Buprestidae.

45. *Dicera prolongata* Lec. A. Two were taken about camp at the Light-house (I, 7) on July 10 (G. 45) and on July 15 (G. 86).

Geographic Range. Saskatchewan basin; Ottawa, Canada; New Hampshire; Mass.; New Jersey; Mich.; Wisconsin; Nebraska; Kansas; Colo.; New Mexico; Idaho.

46. *Dicera tenebrosa* Kby. Taken about the camps at the Lighthouse (I, 7) on July 25 (G. 153), and at Siskowit Bay (V, 3) on August 7 (G. 212), and 15 (G. 239).

Geographic Range. Ottawa, Canada; Lake Superior; Mt. Washington, N. H.; Mass.; Mich.; Duluth, Minn. (Wolcott); Wisconsin; Colorado.

47. *Buprestis maculiventris* Say. A. This was the most abundant species of the family, and was very abundant about the camp on Siskowit Bay (V, 3) during August; others were taken at the Light-house clearing (I, 7) during July (G. 86, 117, 179, 195, 212, 222, 231), (A. 152).

Food plants. Beetles have been found on balsam and spruce, and emerging from pine timber. (Felt, 1906, p. 674.)

Geographic Range. Newfoundland; Ottawa, Canada; Lake Superior region; Mt. Washington (summit), N. H.; Vermont; Mass.; New York; Penna.; Mich.; Wisconsin; Nebraska; Kansas; Colo.; New Mexico; Utah. (Washington; Oregon, cf. Bethune, '76, p. 65).

48. *Buprestis fasciata* Fab. (and varieties). Like the preceding species, this was also taken in large numbers; at the Light-house (I, 7) during July and at camp on Siskowit Bay (V, 3) during August. (G. 117, 133, 153, 166, 195, 212, 231). This is a large metallic green species which shows considerable variation in the amount of the light-colored spots on the elytra. In some Isle Royale specimens the spots are well developed, in others completely lacking. The var. *langii* is credited to Isle Royale in the Hubbard and Schwarz list ('78). This is a western and northwestern variety, Alaska, Brit. Columbia and western mountains.

Food plants. Found on poplars, and the larva bores in maple. (Felt, '06, p. 459.)

Geographic Range. Ottawa, Canada; Nova Scotia; Northeastern U. S. generally; W. Penna.; Ohio (Dury); Michigan; Wisconsin; Colorado.

49. *Buprestis striata* Fab. A. Taken on the open rock ridge north of the Light-house (I, 2) on July 13 (G. 68). One specimen.

Food plants. Occurs on pine and spruce, the buds of which the beetles are said to eat; may also feed upon, dead wood. (Felt, '06, p. 655).

Geographic Range. Ottawa, Canada; New York; Mass.; New Jersey; Penna.; Ohio (Dury); Michigan; Wisconsin.

50. *Melanophila accuminata* DeG.-*longipes* Say. A. Two specimens were taken at the Light-house (I, 7) on July 7 (G. 26) and on July 11 (G. 49).

Geographic Range. Canada; Hudson Bay south to Virginia, and Kentucky; W. Penna.; Mich.; Wisconsin; Colo.; New Mexico; So. Calif.; Brit. Columbia; Alaska; Europe; China.

51. *Melanophila drummondi* Kby.=*guttulata* Gebl. A. Taken about the camps at the Light-house (I, 7) during July (G. 98), and on Siskowit Bay (V, 3) during August (G. 212, 231, 239). Five specimens.

Food plant. Found on spruce logs. (Blanchard, Ent. Amer., 5, p. 30).

Geographic Range. Maine to Alaska (Yukon); Mt. Washington (summit), N. H.; Mich.; Wisconsin; Idaho; Colo.; New Mexico; Utah; Calif.; Washington; Oregon; Alaska; Siberia. Hamilton, '94, p. 29, '94a, 391.

52. *Chrysobothris trinervia* Kby. Found at the Light-house (I, 7) during July (G. 166) and very abundant at the camp on Siskowit Bay (V, 3) during August (G. 212, 222, 231, 239).

Food plant. Found on spruce logs. Blanchard, Ent. Amer., 5, p. 31.

Geographic Range. Lake Winnipeg; Alberta; Hudson Bay region; Ottawa, Ontario; N. H.; W. Penna.; North Carolina; Mich.; Colo.; New Mexico; Washington; Oregon. Hamilton, 794, p. 29.

53. *Agrilus acutipennis* Mann. A. One specimen from the clearing at the Light-house (I, 7) on July 26 (G. 166).

Food plant. Found on Oak. Blanchard, Ent. Amer., 5, p. 32.

Geographic Range. "Mass, to Kansas, Florida and Texas"; W. Penna.; Ohio (Dury); Mich.; Glendon Park, Ill. (Wolcott). Horn, Trans. Am. Ent. Soc., 18, p. 309.

Lampyridae.

54. *Podabrius diadema* Fab. A. Found about the camp at the Lighthouse (I, I) on July 23 (G. 133), and among beach drift at the head of Tonkin Bay (I, 1) on July 7 (A. 7). Two-specimens.

Geographic Range. Ottawa, Canada; Mt. Washington, N. H.; Vermont; New York; New Jersey; W. Penna.; Mich.; Wisconsin; Iowa.

55. *Podabrus tomentosus* Say. A. Taken at the camp on Siskowit Bay (V, 3) on August 4 (G. 201.).

Geographic Range. W. Penna.; Mich.; Illinois (Wolcott); Colorado.

56. *Malthodes niger* Lec. Found in a small rock pool on the Lake shore (I, 1) on July 12 (G. 75).

Geographic Range. Isle Royale, Marquette, Mich.; Lake Superior region; Mt. Washington, N. H.

Scarabaeidae.

57. *Geotrupes Blackburnii* Fab. A. Two of these beetles were taken about horse dung on the Desor trail (III, '04) on August 21 (A. 143).

Geographic Range. Ottawa, Canada; New York; New Jersey; Dist. Columbia; Ohio; Mich.; Wis.

58. *Serica vespertina* Gyll. A. One specimen found on the gravelly beach near the Light-house (I, 1) on July 10 (G. 43).

Geographic Range. Ottawa, Canada; Nova Scotia; Saskatchewan basin; Vermont; New York; N. J.; Dist. Columbia; Fla.; W. Penna.; Ohio; Mich.; No. Illinois and Indiana (Wolcott); Wisconsin; Iowa; Nebraska; Kansas; Colorado; New Mexico.

59. *Diploptaxis liberta* Germ. A. A single dead specimen (G. 102) was found under a flat rock on a jack pine ridge (I, 5).

Geographic Range. Isle Royale, Mich; W. Penna.; New Jersey; Dist. of Col.

60. *Lachnosterna arcuata* Smith. A. Taken at the Light-house camp (I, 7), on July 26 (G. 166).

Geographic Range. W. Penna.; Dist. Columbia; Michigan; Elliot and Carbondale, Ill. (Wolcott).

61. *Trichius affinis* Gory. Very abundant in the flowers of the Cow Parsnip (*Heracleum lanatum*) in the clearing at the Light-house (I, 7) during July (G. 26, 45, 49, 105, 133, 136, 137).

Geographic Range. Saskatchewan basin; Ottawa, Canada; Nova Scotia; N. H.; New York; New Jersey; Virginia; W. Penna.: Ohio. Mich.; No. Illinois (Wolcott); Wisconsin; Iowa; Colorado; New Mexico.

Cerambycidae.

62. *Phymatodes variabilis* Fab. A. Two specimens were taken on Siskowit Bay (V, 3) on August 15 (G. 239) and August 16 (A. 152).

Food plants. Larva feeds on the inner bark of dead and dying oaks and hickory. Probably has other food plant as hickory was not found on the island and oak is of very rare occurrence. (Felt, '06, p. 433.)

Geographic Range. Mass. to Alabama; W. Penna.; Ohio (Dury); New York; Mich.; Wisconsin; Kansas; Colorado; Arizona. Hamilton, '97a, p. 395. Probably introduced.

63. *Xylotrechus undulatus* Say. This active beetle was exceedingly abundant about the camps at the Light-house (I, 7) during July and on Siskowit Bay (V, 3) during August. There is considerable variation in the yellow elytra! markings in the series secured. (G. 86, 212, 222, 231, 239), (A. 5, 152).

Food plants. Has been found on hemlock and spruce, but as hemlock is not found on the island, spruce is probably the food plant. (Felt, '06, p. 671).

Geographic Range. Ottawa, Canada; Lake Superior; New Hampshire; New York; New Jersey; W. Penna.; Mich.; Wisconsin; Iowa; Nebr.; Kansas; New Mexico; Northwest Terr.; Colorado; British Columbia.

64. *Pachyta liturata* Kby. A. The one specimen is from the camp at Rock Harbor (1, 7) on July 31 (G. 191).

Geographic Range. Vermont; Hudson Bay region; Mich.; Colo.; New Mexico (Psyche 9, p. 303); Washington; Idaho; British Col. Hamilton, '94, p. 31."

65. *Acmaeops proteus* Kby. One taken at the Siskowit camp (V, 3) on August 15 (G. 239).

Geographic Range. Labrador; Ottawa, Ontario; "common through Canada;" Hudson Bay; Saskatchewan basin; Mt. Washington (summit), N. H.; Mass.; New York; Mich.; Wisconsin; Kansas; New Mexico; Montana; Colo.; Oregon; Brit. Columbia.

66. *Bellamira scalaris* Say. A. A single specimen of this slender beetle came from the Light-house camp (1, 7) on July 22 (G. 133).

Food plants. Beetle and larva have been found under the bark of the Yellow Birch. (*B. lutea*) and has been found ovipositing on maple. (Beutenmuller, '96, p. 77.)

Geographic Range. Saskatchewan basin; Ottawa, Canada; N. H.; New York; W. Penna.; New Jersey; Maryland; Va.; La.; Ohio (Dury); Mich.; Wisconsin.

67. *Leptura subargentata* Kby. One specimen from the Lighthouse camp (1, 7) on July 11 (G. 49).

Geographic Range. Canada; Hudson Bay and Lake Superior region; N. H.; Mass.; New York; Dist. Columbia; Georgia; Mich.; Ohio (Dury); Wisconsin; Montana; Colo.; New Mexico; Nevada; Utah; Calif.; Washington; Brit. Columbia; Alaska.

68. *Leptura nigrella* Say A. A single specimen was taken at the Siskowit camp (V, 3) on August 7 (G. 212).

Geographic Range. Ottawa, Canada; Hudson Bay region; Maine; Georgia; W. Penna.; Mich.; No. Illinois (Wolcott); Wisconsin; Colo.; New Mexico; Nevada; Washington.

69. *Leptura sexmaculata* L. A. Taken on the flowers of the Cow Parsnip in the clearing at the Light-house (1, 7) during July (G. 105),

Geographic Range. Hudson Bay to Lake Superior; Ottawa, Canada; Quebec, Mt. Washington (summit), N. H.; Mich.; Wisconsin; Colo.; Brit. Columbia; eastern; and western Siberia; Alps and Europe. Hamilton, '94, p. 396.

70. *Leptura canadensis* Fab. A. Only two specimens of this red shouldered beetle were taken, one from the camp on Siskowit (V, 3) on August 7 (G. 212), and the other on August 13 (G. 232) from near the head of Siskowit Bay (VIII, '04).

Food plants. Larva burrows in spruce and hemlock. (Beutenmuller, '96, p. 78).

Geographic Range. Ottawa, Can.; Nova Scotia; N. H.; Vermont; Mass.; New York; Penna.; Virginia; Ga.; Mich.; Wisconsin; Mo.; Colo.; New Mexico; No. Arizona; No. Idaho; Brit. Columbia; eastern and western Siberia; Japan; Russia; Germany. Hamilton, '94a, p. 396.

71. *Leptura chrysocoma* Kby. This bright yellow beetle was the most abundant Cerambycid, occurring in great numbers in the flowers of the Cow Parsnip in the clearing at the Light-house (1, 7); also found in the flowers of the Wild Rose on the beach (I, 1); and on the flowers of *Opulaster opulifolius*, at the mouth of Benson brook (II, 1) during July. Also taken at the Siskowit camp (V, 3) on August 5. (G. 37, 45, '49, 105, 133, 137, 148, 191.)

Geographic Range. Ottawa, Can.; Hudson Bay region; Nova Scotia; Maine; N. H.; New York; Mich.; Wisconsin; Colo.; New Mexico; No. Arizona; Priest's Lake, Idaho, (Wolcott); Utah; Nevada; Calif.; Brit. Columbia.

72. *Leptura proxima*. Say. A. Two specimens were found on the flowers of the Cow Parsnip (I, 7) in July (G. 105, 179), and another specimen at the camp on Siskowit Bay (V, 3) on August 3 (G. 195).

Food plant. Reared from maple. (Wickham. Can. Ent., 29, p. 192.)

Geographic Range. Ottawa, Can.; Vermont; N. H.; Mass.; New York; W. Penna.; Virginia; Ga.; Dist. of Columbia; Ohio; Mich.; No. Ill. (Wolcott); Wisconsin; Iowa; Missouri.

73. *Leptura tibialis* Lec. A. The one specimen is from the camp on Siskowit Bay (V, 3) on August 16 (A. 152).

Geographic Range. Mt. Washington, New Hampshire; Michigan; Oregon.

74. *Leptura mutabilis* Newm. Four specimens were taken at the Light-house (I, 7) during July (G. 49, 105, 137, 166). Some of these were taken on the flowers of the Cow Parsnip.

Geographic Range. Saskatchewan basin; Ottawa, Can.; Mt. Washington (summit), N. H.; New York; Dist. Columbia; Mass.; New Jersey; W. Penna.; Ohio (Dury); Mich.; Wisconsin; New Mexico.

75. *Monohammus scutellatus* Say. A. Six specimens of these large beetles were taken: one at the Light-house (I, 7) on July 24 (G. 152), and the others on August 7, 12 and 16 at the Siskowit camp (V, 3). (G. 212, 231; A. 152).

Food plant. Taken on white and hard pine; beetle girdles branches and the larva bores in spruce trunk. (Felt, 706, p. 364.)

Geographic Range. Ottawa, Can.; Hudson Bay region; Saskatchewan basin; W. Penna.; St. Joseph (Wolcott); Isle Royale, Mich.; Wisconsin; Duluth, Minn. (Wolcott); Colo.; New Mexico; Brit. Columbia; Alaska; extensive N. American range in "pine regions." District of Columbia.

Chrysomelidae.*

76. *Donacia proxima* Kby. A. "In the water-lily zone of Sunnier Lake (III, 5) on July 27 (G. 171). The beetles fly low, dragging the tip of the abdomen in the water, and apparently alight only on leaves of the waterlily." Gleason. Also taken July 29 (A. 184).

Geographic Range. Ottawa, Can.; Lake Superior; N. H.; Mass.; New York; Penna.; Mich.; Wis.; Hudson Bay Terr.; Idaho; Calif. Leng, Trans. Am. Ent. Soc., 18, p. 167.

*cf. Chittenden ('93) for food habits of this family.

77. *Donacia cincticornis* Newm. A. "Three specimens were taken on July 27 and 28 at Simmer Lake (III, 5), associated with the preceding species and with the same habit." Gleason. (G. 171, 175).

Geographic Range. Canada; Vermont; New Hampshire; Mass.; New York; Michigan; No. Illinois; Texas.

78. *Orsodachna atra* Ahr. var.=*childreni* Kby. Two specimens were taken at the Light-house (I, 7) on July 11 (G. 49). Horn, Tr. Am. Ent. Soc., '92, pp. 6-7. Ent. Amer., I, p. 9.

Geographic Range. Saskatchewan basin; Ottawa, Canada; New England and south on the mountains to N. Carolina; W. Penna.; Mich.; Wisconsin; No. Ill. (Wolcott); Iowa; Alberta; Colorado; New Mexico; Arizona; California. Psyche, 9, p. 303; Brit. Columbia.

79. *Galerucella nymphaea* L. A. These leaf beetles were taken in a small bayou (IV, 3) connected with Tobin Harbor on July 21 (A. 42). Larvae, pupae, freshly emerged and fully covered adults were all represented in very large numbers. The lily leaves were riddled by the innumerable larvae. Cf. Cliittenden, '05, p. 58 and Mac Gillivray, '03, p. 325 for the life history of this species.

Geographic Range. In Canada westward to the Mackenzie Basin and into Alaska; New York; Va.; Ohio (Dury); W. Penna.; Mich.; Colorado; Texas; Oregon; Calif.; Siberia into Europe. Hamilton, '94a, p. 398.

Tenebrionidae.

80. *Upis ceramboides* L. A. A single specimen was taken at the Light-house (I, 7) on July 23 (G. 153).

Geographic Range. Ottawa, Can.; Hudson Bay; Saskatchewan basin; Lake Superior; Nova Scotia; Maine; Mt Washington, N. H.; Vermont; New York; New Jersey; W. Penna.; Mich.; Wisconsin; Estherville, Cass Co., Minn. (Wolcott); Colo.; Montana; Manitoba; No. Asia; Siberia; No. Europe; Germany. Hamilton, '94a, p. 400.

Cistelidae.

81. *Cistela sericea* Say. A. Found under loose stones on the jack pine ridge (I, 5) on July 14 (G. 81).

Food plants. Has been found on pine, oak and basswood. (Felt, '06, p. 518.)

Geographic Range. Michigan; W. Penna.; New Jersey; New Mexico,

Melandryidae.

82. *Serropalpus barbatus* Schall. A. One specimen was taken at Tobin Harbor on July 19 (G. 129).

Food plant. Larva bores in sap and heart wood of balsam and spruce. (Felt, '06, p. 671).

Geographic Range. Canada; Lake Superior and Hudson Bay regions; Maine; Vermont; New York; W. Penna.; West Virginia; Colorado; Rocky Mts. south to New Mexico; Manitoba; Oregon; Brit. Columbia; Alaska; Siberia; Europe.

Mordellidae.

83. *Anaspis rufa* Say. A. Many specimens of this species were taken about the camp at the Lighthouse (I, 7) on July 28 (G. 179).

Geographic Range. Ottawa, Can.; lit. Washington (summit), N. H.; Vermont; New York; New Jersey; Dist. Col.; Florida; Ohio; Michigan; Wisconsin; Wyoming; Colo.; Utah; Lower Calif.; New Mexico; Mexico; Washington; Brit. Columbia; Alaska.

84. *Mordellistena biplagiata* Helm. A. One specimen was taken on flowers in the clearing at the Lighthouse (I, 7) on July 11 (G. 40).

Geographic Range. New York; Dist. of Columbia; Ohio; Mich.; Illinois; Wis.

85. *Mordellistena scapularis* Say. A. Two specimens were taken at the Lighthouse (I, 7) on July 28 (G. 179).

Geographic Range. Dist. of Columbia; "Middle and Western States"; Mich. (Isle Royale); Ottawa, Canada.

Curculionidae.

86. *Hylobius pales* Hbst. A. A single specimen was taken at the Lighthouse (I, 7) on July 13 (G. 86).

Food plant. Larvae live in bark of white pines. (Felt, '06, p. 664).

Geographic Range. Ottawa, Canada; Maine to Florida; Michigan; W. Penna.; Duluth, Minn. (Wolcott).

87. *Hypomolyx pineti* Fab. A. This large snout beetle (G. 179) was taken July 28 in the Lighthouse clearing (I, 7).

Geographic Range. Canada; Hudson Bay region; Saskatchewan basin; Mich.; Wisconsin; Siberia; Europe.

88. *Magdalis*. "Apparently new," Wickham.; Taken at the Lighthouse camp (I, 7) on July 23 (G. 136), at Siskowit (V, 3) on August 15 (G. 230).

Calandridae.

89. *Cossonus subareatus* Boh. A. Taken at the Siskowit Camp (V, 3) on August 7 (G. 212).

Geographic Range. Mt. Washington, N. H.; Michigan; Wisconsin; Glendon Park, Ill. (Wolcott); Iowa; Kansas; Nebraska; Colorado; New Mexico; "Middle States."

2. SUPPLEMENTARY LIST OF ISLE ROYALE BEETLES.

BY A. B. WOLCOTT.

Field Museum of Natural History, Chicago.

This supplementary list of species records from Isle Royale all the species taken by Hubbard and Schwarz ('78, pp. 627-643) but not found in the 1905 collections. These two lists make a complete catalog of the species so far found on this island, excepting those species which are scattered in the literature and have thus been overlooked. The general geographic range of each species is given.

Carabidae.

1. *Bembidium concolor* Kby. New York; Maine; Canada; Michigan (Michipicoton River); Wyoming; Maine to the Pacific coast.
2. *Bembidium planatum* Lec. Michigan (Isle Royale); Colorado; Wyoming; Nevada; Oregon; Washington to British Columbia.
3. *Patrobium longicornis* Say. New Jersey; Vermont; New York; Dist. Columbia; Ohio; Pennsylvania; Canada; Michigan (Escanaba); Wisconsin; Illinois; Indiana; Iowa; Colorado; Texas; New Mexico.
4. *Pterostichus punctatissimus* Rand. Massachusetts; New Hampshire; Vermont; Maine; Canada; Hudson Bay region; Michigan (Michipicoton Island); Arctic Siberia; the Amur; Dauria.
5. *Pterostichus mandibularis* Kby. var. New Hampshire; Vermont; Massachusetts; Canada; Wisconsin; Michigan (Marquette, Michipicoton River); Hudson Bay region; Alaska; Arctic Siberia.
6. *Amura latior* Kby. New Jersey; New Hampshire; Canada; Michigan (Escanaba, Ann Arbor); Wisconsin; Illinois; Nebraska; Colorado; Idaho; New Mexico; Arizona; Vancouver Island.
7. *Amara impuncticollis* Say. Dist. Columbia; Ohio; Michigan (Detroit); Wisconsin; Canada; Montana; Colorado; New Mexico.
8. *Calathus advena* var. *mollis* Mots. Vermont; Maine; Michigan (Michipicoton River, Michipicoton Island); Alaska.
9. *Platynus aeruginosus* Dej. Dist. Columbia; Indiana (Pine); Illinois (Chicago); Michigan (Escanaba, Detroit); Wisconsin.
10. *Dromius piceus* Dej. New Jersey; New York; Dist. Columbia; Massachusetts; Ohio; Michigan (Marquette, Detroit); Wisconsin; Canada; Iowa; California.
11. *Harpalus fulvilabris* Mann. Michigan (Marquette, Michipicoton River).

12. *Harpalus rufimanus* Lec. Michigan (Escanaba, Marquette); Wisconsin; Canada; British Columbia.

13. *Harpalus laticeps* Lec. New Hampshire (Summit Mt. Washington); Michigan (Escanaba, Marquette, Lake Huron); Wisconsin; Canada (Ottawa); Colorado.

14. *Bradycellus cordicollis* Lec. New Hampshire (Mt. Washington); Michigan (Marquette).

Hydrophilidae.

15. *Crenophilus (Hydrobius) digestus* Lec. Michigan (Marquette, Detroit).

Silphidae.

16. *Necrophorus vespilloides* Hbst. New Jersey; New Hampshire (Mt. Washington); Michigan (Escanaba, Michipicoton Island); Wisconsin; Hudson Bay Territory; Nova Scotia; Ontario; Manitoba; British Columbia; Alaska; Washington; Oregon; East Siberia; Kamtschatka; Amurland; Europe; China.

17. *Choleva basillaris* Say. New Jersey; New Hampshire (Mt. Washington); Ohio; Michigan (Sault de Ste. Marie, Detroit); Wisconsin; Nebraska; Kansas; Canada; Hudson Bay Territory; British Columbia; Alaska; Nevada to Colorado; California.

18. *Choleva (Catops) terminans* Lec. Virginia; New Jersey; Massachusetts; Dist. Columbia; Ohio; Illinois; Michigan (Bachewanung Bay, Michipicoton Island); Wisconsin; Canada (Ottawa).

19. *Anistoma assimilis* Lec. Dist. Columbia; New Hampshire (Summit Mt. Washington); Michigan (Marquette, Michipicoton River); Wisconsin; Canada; Colorado; Vancouver Island.

20. *Liodes globosa* Lec. New Hampshire (Mt. Washington); Michigan (Marquette); Canada (Ottawa); Colorado; New Mexico.

21. *Agathidium revoivens* Lec. Canada (Ottawa); British Columbia; New Mexico.

22. *Clambus gibbulus* Lec. Florida; Dist. Columbia; Michigan (Marquette, Detroit); Colorado; S. Arizona.

Pselaphidae.

23. *Tychus longipalpus* Lec. Florida; Dist. Columbia; Michigan (Marquette); Canada (Ottawa).

24. *Reichenbachia (Bryaxis) propinqua* Lec. Canada (Ottawa); Michigan (Marquette, Point aux Pins); Colorado (species doubtfully identical).

Staphylinidae.

25. *Quedius laevigatus* Gyll. Georgia; New Hampshire (summit Mt. Washington); Massachusetts; Pennsylvania; Ohio; Illinois; Michigan (Marquette, Bachewanung Bay, Detroit); Canada; British Columbia; Alaska; Oregon; Nevada; Colorado; Kansas; New Mexico; California; eastern Siberia; northern and Alpine Europe.

26. *Stenus semicolon* Lec. Dist. Columbia; Michigan (Escanaba, Marquette, Bashewanung Bay, Michipicoton River).

27. *Lathrobium terminatum* Grav. (*punctulatum* Lec.). Florida; Georgia; Dist. Columbia; New Jersey; W. Pennsylvania; Ohio; "Eastern States"; Massachusetts; Michigan (Escanaba, Marquette, Detroit); Wisconsin; Iowa; Canada; Kansas; Colorado; Europe and Siberia,

28. *Tachinus fumipennis* Say. Florida; Dist. Columbia; Michigan (Marquette); Wisconsin: Colorado.

29. *Bolitobius cingulatus* Mann. Virginia; New Jersey; New Hampshire (Mt. Washington); Pennsylvania; Michigan (Sault de Ste. Marie, Bachewanung Bay, Detroit); Wisconsin; Canada; Oregon; Queen Charlotte Island; British Columbia; Alaska; Caucasia; Europe.

30. *Hobrocerus magnus* Lec. Michigan (Marquette). The type of this species came from Isle Royale.

31. *Olisthaerus megacephalus* Zett. Michigan (Michipicoton Island); Canada; Alaska; California; Siberia; Lapland; Sweden; Hungary; Arctic and Eastern Siberia.

32. *Olisthaerus substriatus* Payk. (*nitidus* Lec.). Massachusetts; Michigan (Michipicoton, Eagle Harbor); Wisconsin; Sweden; Germany; France; Arctic and Eastern Siberia.

33. *Ancyrophorus planus* Lec. New Hampshire (Mt. Washington); Michigan (Isle Royale).

34. *Anthophagus verticalis* Say. Michigan (Marquette, Detroit).

35. *Acidota creanta* Fabr. (*seriata* Lec.). Massachusetts; Common on Islands and shores of Lake Superior; Michigan (Marquette, Michipicoton River, Detroit); Canada; central and northern Europe; Siberia.

36. *Arpedium* sp. Michigan (Marquette).

Phalacridae.

37. *Phalacrus politics* Melsh. Florida; Dist. Columbia; Ohio; Illinois; Michigan (Marquette, Detroit); Canada (Ottawa); Iowa; Colorado.

Coccinellidae.

38. *Coccinella perplexa* Muls. (*trifasciata* Linn.). New York; New Hampshire (Mt. Washington); Canada; Hudson Bay Territory; Michigan (Detroit, Marquette, Au Train Falls, St. Joseph); Wisconsin; Illinois (Chicago, taken by Wolcott); Alaska; Vancouver Island; Oregon; Washington to California; New Mexico; Kamtschatka through northern Siberia and Europe to Lapland. Circumpolar.

39. *Coccinella transversoguttata* Fald. var. *transversalis* Mills. The typical form or its varieties are known from New Hampshire (summit Mt. Washington); Greenland; Hudson Bay region; various places in Canada; British Columbia; Northwest Territory; Alaska; Illinois (Chicago, Wolcott coll.); Michigan (Bachewanung Bay, Chatham;

Wisconsin; Minnesota (Duluth, Wolcott coll.); Nebraska; Nevada; Colorado; New Mexico; California; Rocky Mountains and Pacific regions to mountainous Mexico; eastern Siberia; Japan; northern China; Dauria; Lapland. Circumpolar.

40. *Cycloneda sanguinea* Linn. Florida; West Indies; "United States and Canada generally"; Michigan (Michipicoton River, Chatham); Wisconsin; Illinois; Indiana; Ohio; New Jersey to Colorado; New Mexico; N. Arizona; Texas; Baja California; Europe.

41. *Cleis (Harmonia) picta* Rand. Dist. Columbia; Pennsylvania; Canada to Colorado; New Hampshire (summit Mt. Washington); Michigan (Escanaba, Marquette); Minnesota (Duluth, Wolcott coll.); New Mexico.

42. *Scymnus lacustris* Lec. Michigan (Escanaba, Marquette); Colorado; Arizona.

Endomychidae.

43. *Lycoperdina ferruginea* Lec. Dist. Columbia; New Jersey west to Colorado; New Hampshire (Mt. Washington); New York; "Middle and Southern States"; Ohio; Illinois (central and northern); Michigan (Bachewanung Bay, Detroit); Canada; Wisconsin; Iowa; Colorado; New Mexico.

Histeridae.

44. *Hister basalis* Lec. Ohio; Michigan (Marquette).

45. *Plegaderus sayi* Mars. "Middle States"; Michigan (Sault de Ste. Marie, Marquette); Canada; Wisconsin; Colorado; New Mexico.

Nitidulidae.

46. *Omosita discoidea* Fabr. Canada; Michigan (northern); Colorado; New Mexico; Europe and the Pacific States, east to Colorado.

Lathridiidae.

47. *Stephostethus (Lathridus) liratus* Lec. Dist. Columbia; Ohio; Canada (Ottawa); Michigan (Detroit); Queen Charlotte Islands, British Columbia.

48. *Lathridius minutus* Linn. "Nearly all North America"; Dist. Columbia; Michigan (Detroit); Wisconsin; Colorado; "Alaska to Louisiana and to Massachusetts and eastern Canada"; all Europe and northern Asia to Kamtschatka.

49. *Corticaria serricollis* Lec. Michigan (Michipicoton River, Detroit); British Columbia.

Byrrhidae.

50. *Byrrhus geminatus* Lec. New Hampshire (summit Mt. Washington); Michigan (Isle Royale only).

Dascyllidae.

51. *Macropogon piceus* Lec. Michigan (Isle Royale only).

52. *Eurypogon niger*. Michigan (Michipicoton River).

53. *Euscinetus terminalis* Lec. New Jersey west to Colorado; New York; Vermont; Ohio; Illinois; Michigan (Escanaba, Marquette, Detroit); Canada.

Elateridae.

54. *Cryptohypnus bicolor* Esch. This species is believed to be merely a variety of *nocturnus* Esch. which is recorded with the variety from the following localities;—Labrador; Hudson Bay regions; New Hampshire (summit and alpine regions Mt. Washington); Canada; Michigan (Marquette, Sault de Ste. Marie); Dakota; Wisconsin; Utah; Colorado; Montana; Idaho; New Mexico; Oregon; British Columbia; Alaska; Kamtschatka; eastern Siberia.

55. *Cryptohypnus tumescens* Lec. Michigan (Sault de Ste. Marie); Colorado; New Mexico.

56. *Elater nigrinus* Payk. var.? *Elater nigrinus* occurs in Vermont; Canada (Ottawa); Michigan (Escanaba, Marquette, Detroit); Alaska; Vancouver Island and Queen Charlotte Island; British Columbia; New Mexico; northern and central Europe; west Siberia; Amurland.

57. *Elater mixtus* Hbst. Dist. Columbia; New Hampshire (summit Mt. Washington); Canada (Ottawa); Michigan (Marquette, Michipicoton Island); Colorado.

58. *Betarmon bigeminatus* Rand. Dist. Columbia; Canada (Ottawa); Michigan (Marquette).

59. *Melanotus Leonardi* Lec. Michigan (Marquette, Detroit).

60. *Melanotus castanipes* Payk. (*scrobicollis* Lec.). "Middle States to Canada"; New York; Vermont; New Hampshire (summit Mt. Washington); Dist. Columbia; Ohio; Pennsylvania; Canada; Michigan (Escanaba, Marquette, Detroit); Wisconsin; Colorado; Europe; West Siberia; Amurland.

61. *Limonus aeger* Lec. New Jersey; New Hampshire (Mt. Washington); Canada (Ottawa); Michigan (Marquette); Wisconsin.

62. *Campylus denticornis* Kirby. New Hampshire (summit Mt. Washington); Maine; Pennsylvania; Canada (Ottawa); Ohio; Michigan (Marquette, Port Huron); Wisconsin.

63. *Paranomus costalis* Payk. New Hampshire (summit Mt. Washington); "The northern shore of Lake Superior"; Labrador; Europe (Sweden, Finland, Lapland); Amurland.

64. *Sericosomus incongruus* Lec. Canada (Ottawa); Michigan (Marquette); New Hampshire (Mt. Washington).

65. *Corymbites resplendens* Esch. Newfoundland; Maine; Lake Superior region northward to 56°; Vermont; Canada (Ottawa); Michigan (Michipicoton Island, Marquette); New Hampshire (summit Mt. Washington); Wisconsin; Queen Charlotte Island; British Columbia; Alaska.

66. *Corymbites spinosus* Lec. New Hampshire (summit Mt. Washington); Canada (Ottawa); Michigan (Escanaba, Marquette); Wisconsin; Iowa.

67. *Corymbites mendax* Lec. Michigan (Eagle Harbor).

68. *Corymbites insidiosus* Lec. New Hampshire (Mt. Washington); Michigan (Marquette).

69. *Corymbites falsificus* Lec. New Hampshire (summit Mt. Washington); Canada; Michigan (Marquette); Wisconsin.

70. *Corymbites triundulatus* Rand. New Hampshire (summit Mt. Washington); Maine; Vermont; Michigan (Marquette); Canada (Ottawa); Wisconsin; Colorado.

71. *Corymbites propola* Lec. New York; Vermont; New Hampshire (summit Mt. Washington); Canada; Michigan (Michipicoton River, Marquette); British Columbia.

72. *Corymbites nigricollis* Bland. Michigan (Marquette); Colorado.

73. *Corymbites splendens* Ziegl. Dist. Columbia; Ohio; Canada (Ottawa); Michigan (Marquette).

74. *Corymbites nigricornis* Panz. New Jersey; New Hampshire (summit Mt. Washington); Massachusetts; Illinois (Ft. Sheridan, Wolcott); Michigan (Marquette, Detroit); Canada; Iowa; Wisconsin; Colorado; central and boreal Europe and Siberia.

Buprestidae.

75. *Melanophila fulvoguttata* Harr. New Hampshire (summit Mt. Washington); Canada (Ottawa); Michigan (Escanaba, Marquette, Port Huron); Kansas.

Lampyridae.

76. *Plateros (Eros) modestus* Say. Florida; Dist. Columbia; New Hampshire (summit Mt. Washington); Ohio; Michigan (Detroit, Marquette); Canada (Ottawa); Iowa (McGregor, Wolcott); New Mexico.

77. *Ellychnia (Photinus) corrusca* Linn. "Common in Canada and most of the United States east of the Rocky Mountains"; Dist. Columbia; Virginia; Georgia; New Jersey; New Hampshire (summit Mt. Washington); New York; Ohio; Indiana (Wolcott); Illinois; Michigan (Michipicoton River, Detroit); Iowa; Wisconsin; Nebraska; Kansas; Colorado; New Mexico; Arizona; Canada (Ottawa); Nova Scotia; Northwest Territory.

78. *Podabrus modestus* Say, Georgia; New Jersey; New York; New Hampshire (Mt. Washington); Pennsylvania; Ohio; Michigan (Escanaba, Marquette, Detroit); Canada (Ottawa); Iowa; Wisconsin; Colorado.

79. *Podabrus laevicollis* Kby. New Hampshire (Mt. Washington); Michigan (Marquette, Michipicoton River); Colorado.

80. *Telephorus Curtisii* Kby. New Hampshire (summit Mt. Washington); Michigan (Marquette, Michipicoton River); Wisconsin; Iowa; Hudson Bay region; British Columbia.

81. *Malthodes laticollis* Lec. (*transversus* Lec.). Michigan (Isle Royale only).

82. *Malthodes concavus* Lec. Dist. Columbia; Michigan (Marquette, Detroit); Colorado.

83. *Malthodes fragilis* Lec. Michigan (Detroit).

Cleridae.

84. *Thanasimus (Clerus) undatulus* Say. New York; Vermont; Maine; New Hampshire (summit Mt. Washington); Canada; Michigan (Marquette, Escanaba); Minnesota; Hudson Bay north to lat. 65°; Kansas; Colorado; New Mexico; variety *nubilus* occurs in Northwest Territory and Alaska.

Ptinidae.

85. *Dinoderus substriatus* Payk. New Hampshire (summit Mt. Washington); "Northern States"; Canada; Pennsylvania; Michigan (Escanaba, Marquette., Bachewanung Bay); Alaska; eastern and western Siberia; Europe.

Cioidae.

86. *Cis creberrimus* Mellié. Florida; Dist. Columbia; Ohio; Michigan (Marquette, Detroit).

Cerambycidae.

87. *Tetropium cinnamopterum* Kirby. New Jersey; New Hampshire (summit Mt. Washington); Vermont; Pennsylvania; Canada; Michigan (Marquette); Wisconsin; Colorado; New Mexico; northern and mountainous Arizona; California; Oregon; Washington; Northwest Territory; British Columbia; Alaska; "north to 55°".

88. *Phymatodes maculicollis* Lec. New Hampshire (Mt. Washington); Michigan (Isle Royale-type locality); Colorado (7-9000 ft. el.).

89. *Microclytus gazellula* Hald. (*Cryptophorus gibbulus* Lec.). Dist. Columbia; New Hampshire (Mt. Washington); Canada (Ottawa); Michigan (Detroit).

90. *Pachyta monticola* Rand. New York; New Hampshire (summit Mt. Washington); Vermont; Maine; Massachusetts; Pennsylvania; Michigan (Marquette); Wisconsin; Canada (Ottawa); Anticosti Island; Alaska.

91. *Leptura rufula* Hald. Michigan (Isle Royale only).

92. *Pogonocherus mixtus* Hald. Dist. Columbia; New Jersey; New York; New Hampshire (summit Mt. Washington); Indiana (Clarke Junction, Dune Park, Wolcott coll.); Canada; Michigan (North Muskegon, Marquette, Michipicoton River, Port Huron); Kansas; New Mexico; Colorado; Northern Arizona.

Chrysomelidae.

93. *Zeugophora varians* Cr. New Jersey; New Hampshire; Pennsylvania; Indiana (Pine-Wolcott coll.); Illinois (Glen Ellyn, Wolcott coll.); Canada; Michigan (Detroit); Wisconsin; Kansas; Washington.

94. *Syneta ferruginea* Germ. Dist. Columbia; Maryland; New Jersey; New York; New Hampshire (Mt. Washington); Vermont; Massachusetts; Ohio; Illinois (central and northern); Michigan (Marquette); Canada (Ottawa); Wisconsin; Nebraska; Colorado; Newfoundland.

95. *Bassareus mammifer* Newm. var. *sellatus* Suffr. (*Cryptocephalus sellatus* Suffr.). Dist. Columbia; New Jersey; "Middle and Western States"; Ohio; Indiana (Clarke, Hessville, Wolcott coll.); Michigan (Escanaba, Marquette, Detroit, North Muskegon, Holland); Wisconsin; Iowa; Canada; Colorado.

96. *Pachybrachys* sp. Michigan (Sault de Ste. Marie, Marquette).

97. *Gonioctena pallida* Linn. New Hampshire (summit Mt. Washington); Michigan (Marquette, Bachewanung); Minnesota; Wisconsin; Colorado; Hudson Bay region generally; Europe and Siberia.

98. *Phyllodecta vulgatissima* Linn. Virginia; New Jersey; New Hampshire (summit Mt. Washington); New York; Pennsylvania; Ohio; Illinois (central); Michigan (Detroit); Wisconsin; Iowa; Canada (Ottawa); Iceland; Siberia; China; Turkestan; Canaries. Perhaps also in Alaska.

Cistelidae.

99. *Hymenorus niger* Melsh. Florida; Texas; Dist. Columbia; New York; New Hampshire (Mt. Washington); Pennsylvania; Ohio; Canada (Ottawa); Michigan (Escanaba, Marquette, Detroit); Wisconsin; Colorado.

Melandryidae.

100. *Emmesa connectens* Newm. New Hampshire (summit Mt. Washington); Michigan (Marquette).

101. *Scotochroa basalis* Lec. Canada (Ottawa); Michigan (Escanaba, Marquette); Colorado.

Pythidae.

102. *Lecontia (Crymodes) discicollis* Lec. New Hampshire (summit Mt. Washington); Michigan (Marquette); Manitoba; Canada; (Ottawa); Idaho; Colorado; New Mexico.

103. *Boros unicolor* Say. Dist. Columbia; Michigan (Marquette); Canada (Ottawa).

104. *Rhinosimus viridiaeneus* Rand. (*nitens* Lec.). Dist. Columbia; Michigan (Detroit, Marquette).

Curculionidae.

105. *Pissodes dubius* Rand. New Hampshire (Mt. Washington); Canada; Michigan (Marquette); Wisconsin.

106. *Dorytomus brevicollis* Lec. Dist. Columbia; New Jersey; New York; New Hampshire (Mt. Washington); Ohio; Michigan (Marquette, Detroit); Colorado; New Mexico; Canada; Vancouver Island.

107. *Trichalophus alternatus* Say. Michigan (Michipicoton River); Wyoming (Laramie); Colorado.

108. *Apion* sp. Michigan (Marquette).
109. *Magdalis hispidoides* Lec. Dist. Columbia; Michigan (Marquette, Port Huron); Colorado; British Columbia.
110. *Magdalis gentilis* Lec. Michigan (Marquette); Colorado; California.
111. *Magdalis armicollis* Say (*Magdalis alutacea* Lec. Bul. U. S. Geol. and Geogr. Surv. Terr., 4 p. 463, 1878). LeConte described *alutacea* from Isle Royale, Lake Superior (Mr. E. A. Schwarz) and Leavenworth Valley, above Georgetown, Colorado, specimens; the species is not given in Hubbard and Schwarz's list. It has since been found at various places in the mountains in Colorado; Ohio; Canada (Ottawa); New Hampshire (Mt. Washington); and a species doubtfully referred here occurs in New Mexico.
112. *Anthonomus corvulus* Lec. Dist. Columbia; Ohio; Illinois C River Forest, Bowmanville, Wolcott coll.); Michigan (Marquette, Detroit).
113. *Pseudanthonomus (Anthonomus) crataegi* Walsh. Florida; Dist. Columbia; Ohio; Illinois (central and northern); Michigan (Detroit, Marquette).
114. *Orchestes pallicornis* Say. "Nova Scotia to Texas, and to Puget Sound" (LeConte); Dist. Columbia; New Hampshire (Mt. Washington); Ohio; Michigan (Escanaba, Marquette, Detroit).
115. *Orchestes canus* Horn. Ohio; Type locality given thus: "Specimens are before me from Isle Royale and Escanaba, Michigan, and from San Juan, Colorado" Horn. Also known from Marquette, Michigan.
116. *Cnemogonus epilobii* Payk. Michigan (Marquette); British Columbia; Great Slave Lake, Northwest Territory; Colorado; northern and central Europe.

Scolytidae.

117. *Dendroctonus rufipennis* Kby. Alaska; "Vancouver to Anticosti, New Brunswick and southwest to Florida and New Mexico"; Western Pennsylvania; Michigan (Marquette).

REFERENCES.

- Bethune, C. J. S. (compiled by).
1876. Insects of the Northern Parts of British America. Ent. Soc. Ontario, pp. 1-156, Supp. pp. 1-14.
[From Kirby's Fauna Boreali-Americana; Insecta.]
- Beutenmuller, W.
1893. On the Food-Habits of North American Rhyncophora. Jour. N. Y. Ent. Soc., I, pp. 36-43, 80-88.
1896. Food-Habits of North American Cerambycidae. Jour. N. Y. Ent. Soc., 4, pp. 73-81.
- Blanchard, F.
1889. List of Buprestidae of New England. Ent. Am., 5, p. 29-32.
- Bowditch, F. C.
1896. List of Mt. Washington Coleoptera. Psyche, 7, Supp. pp. 1-11.
- Caudell, A. N.
1903. Some Insects from the Summit of Pike's Peak, Found on Snow. Pro. Ent. Soc. Wash., 5, pp. 74-82.
- Carpenter, W. L.
1875. Report on the Alpine Insect-Fauna of Colorado. Ann. Rep. U. S. Geol. Survey Terr, for 1873. (Hayden). pp. 539-542.
- Chittenden, F. H.
1889. Notes on the Habits of Buprestidae. Ent. Am., 5, pp. 217-220.
1893. Notes on the Food Habits of Some Species of Chrysomelidae. Pro. Ent. Soc. Wash., 2, pp. 261-267.
1900. Insects and the Weather: Observations During the Season of 1899. Bull. 22, N. S. Div. of Entomology, U. S. Dept. Agric., pp. 51-64.
1901. Insects and the Weather During the Season of 1900. Bull. 30. U. S. Div. Entomology, U. S. Dept. Agr., pp. 63-75.
1905. The Pond-Lily Leaf-Beetle. Bull. Bureau of Ent., No. 54, 58-60.
- Cockerell, T. D. A.
1893. The Entomology of the Mid-Alpine Zone of Custer County, Colorado. Trans. Am. Ent. Soc., 20, pp. 305-370.
- Coleman, A. P.
1906. Interglacial Periods in Canada, Inter. Geol. Congress, Mexico, 1906, reprint, pp. 1-26.
- Dury, C.
1902. A Revised List of the Coleoptera Observed near Cincinnati, Ohio, etc. Jour. Cinn. Soc. Nat. Hist., 20, pp. 107-196.
1906. Additions to the List of Cincinnati Coleoptera, Jour. Cinn. Soc. Nat. Hist., 20, pp. 251-260.
- Evans, J. D.
1903. List of Canadian Coleoptera. Can. Ent., 35, pp. 239-243, 288-292, 317-320.
- Fall, H. C.
1902. Some Insects of the Hudsonian Zone in New Mexico—Coleoptera. Psyche 9, p. 303.
- Fall, H. C., and Cockerell, T. D. A.
1907. The Coleoptera of New Mexico. Trans. Am. Ent. Soc., 33, pp. 145-272.
- Fauvel, A.
1889. Liste des Coleopteres Communa a l'Europe et a l'Amerique du Nord. Rev. D'Entomologie, 8, pp. 92-174.
- Felt, E. P.
1905-06. Insects affecting Park and Woodland Trees. Mem. 8, N. Y. St. Mus., Vol. 1, 1905; Vol. 2, 1906.
- Hamilton, J., and Henshaw, S.
1891-92. A List of Some of the Catalogues and Local Lists of North American Coleoptera. Psyche, 7, I (A.-G), pp. 160-162; II (H.-P), pp. 188-193; III (R.-Z.), pp. 205-209. (Contains an index of localities.)
- Hamilton, J.
1894. Catalogue of the Coleoptera of Alaska, with the Synonymy and Distribution. Trans. Am. Ent. Soc., 21, pp. 1-38.
1894a. Catalogue of the Coleoptera Common to North America, Northern Asia and Europe, with Distribution and Bibliography. Second edition.

- Trans. Am. Ent. Soc., 21, pp. 345-416. (First edition 1. c., '89, 16, pp. 88-162.)
1895. Catalogue of the Coleoptera of Southwestern, Pennsylvania, with Notes and Descriptions. Trans. Am. Ent. Soc., 22, pp. 317-381.
- Harrington, W. H.
1884. List of Ottawa Coleoptera. Trans. Ottawa Field Natur. Club, No. 5, pp. 67-85.
- Hayward, R.
1897. On the Species of Bembidium of America, North of Mexico. Trans. Am. Ent. Soc., 24, pp. 32-143.
- Henshaw, S.
1885. List of the Coleoptera of America, North of Mexico. Amer. Ent. Soc.
1895. Third Supplement to the List of Coleoptera of America, North of Mexico. Amer. Ent. Soc.
- Horn, G. H.
1871. Revision of the Tenebrionidae of America. Trans. Amer. Phil. Soc., N. S. 14, pp. 253-404.
1872. Coleoptera, Fifth Ann. Rep. U. S. Geol. Surv. Montana and Portions of Adjacent Territories (Hayden), pp. 382-392.
- Hubbard, H. G., and Schwarz, E. A.
1878. Coleoptera of Michigan. Pro. Amer. Phil. Soc., 17, pp. 593-669.
- Keen, J. H.
1895. List of Coleoptera collected at Massett, Queen Charlotte Islands, B. C. Can. Ent., 27, pp. 165-172, 217-220.
- Klages, H. G.
1901. Supplement to Dr. John Hamilton's List of the Coleoptera of Southwestern Pennsylvania. Ann. Carnegie Museum, I, pp. 265-294.
- LeConte, J. L.
1850. General Remarks upon the Coleoptera of Lake Superior, pp. 201-242*. Agassiz' Lake Superior. Boston.
1851. On the Geographical Distribution of Animals in California. Pro. Am. Assoc. Adv. Sci., 6, pp. 248-254.
1859. The Coleoptera of Kansas and Eastern New Mexico. Smith. Cont. Knowl., 11, pp. 1-58.
1860. Report upon Insects Collected on the Survey. Rep. Expl. And Surv. from Miss. River to the Pacific Ocean, 12, Pt. 3, pp. 1-72.
1862. Notes on the Coleopterous Fauna of Lower California. Pro. Acad. Nat. Sci. Phila. for 1861, pp. 335-338.
1876. Presidential Address. Pro. Am. Assoc. Adv. Sci., 1875, pp. 1-18. (Also Pop. Sci. Mo., 8, pp. 285-299; Amer. Nat., 9, pp. 481-498.)
1878. The Coleoptera of the Alpine Regions of the Rocky Mountains. Bull. U. S. Geol. and Geogr. Surv. Terr., 4, pp. 447-480.
1878a. Remarks on Geographical Distribution. [Florida Coleoptera.] Pro. Am. Phil. Soc., 17, pp. 470-471.
1878b. Description of New Species [from Michigan]. Pro. Am. Phil. Soc., 17, pp. 593-626.
1879. The Coleoptera of the Alpine Rocky Mountain Regions—Part II. Bull. U. S. Geol. Survey. Terr., 5, pp. 499-520.
- MacGillivray, A. D.
1903. Aquatic Chrysomelidae and a Table of the Families of Coleopterous Larvae. Bull. 68, N. Y., St. Mus., pp. 288-327.
- Murray, A.
1870. On the Geographical Relations of the Chief Coleopterous Faunae. Jour. Linn. Soc. Zool. 11, pp. 1-89.
- Packard, A. S.
1890. Forest Insects. Fifth Report U. S. Ento. Comm. U. S. Dept. Agr.
- Riley, C. V.
1880. Food Habits of the Longicorn Beetles or Wood Borers. Amer. Ent., 3, pp. 270-271, 237-339.
- Schwarz, E. A.
1878. The Coleoptera of Florida. Pro. Am. Phil. Soc., 17, pp. 353-469.
1888. The Insect Fauna of Semi-tropical Florida with Special Regard to the Coleoptera. Ent. Amer., 4, pp. 165-175.
1890. On the Coleoptera Common to North America and Other Countries. Pro. Ent. Soc. Wash., 1, pp. 182-195.
1890a. On a Collection of Coleoptera from St. Augustine, Florida. Pro. Ent. Soc. Wash., 1, pp. 169-171.
1901. Semi-tropical Texas. Pro. Ent. Soc. Wash., 4, pp. 1-3.
- Scudder, S. H.
1874. The Distribution of Insects in New Hampshire. Final Report Geol. New Hampshire, I, pp. 331-380.
1894. The Effects of Glaciation on the North American Fauna. Am. Jour. Sci., 48, p. 180.
1895. The Coleoptera Hitherto Found Fossil in Canada. Cont. to Can. Paleon. II, Pt. I, pp. 27-56; Can. Geol. Surv.
1900. Additions to the Coleopterous Fauna of the Interglacial Clays of the Toronto District, With an Appendix by A. D. Hopkins on the Scolytid Borings from the Same Deposits. Cont. to Can. Paleon. II, Pt. II, pp. 67-92.
- Sharp, D.
1882. On the Aquatic Carnivorous Coleoptera or Dytiscidae. Sci. Trans. Roy. Dublin Soc., (2), 2, pp. 176-1003.
- Shelford, V. E.
1907. Preliminary Note on the Distribution of the Tiger Beetle (Cincindela) and its Relation to Plant Succession. Biol. Bull. 14, pp. 9-14.
- Skinner, H. (editor).
1903. A List of the Insects of Beulah, New Mexico. Trans. Am. Ent. Soc., 29, pp. 35-117.
- Smith, J. B.
1900. Insects of New Jersey. Supp. Twenty-seventh Ann. Rep. N. J. St. Bd. Agr., 1899, pp. 167-367.
- Summers, S. V.
1874. Catalogue of the Coleoptera from the Region of Lake Pontchartrain, La. Bull. Buffalo Hoc. Nat. Sci., 5, pp. 78-99.
- Tower, W. L.
1906. An Investigation of Evolution in the Chrysomelid Beetles of the Genus Leptinotarsa. Carnegie Institution.
- Townsend, C. H. T.
1897. On the Biogeography of Mexico and the Southwestern United States. Trans. Texas Acad. Sci., 2, pp. 33-86.
- Ulke, S. 1902. A List of the Beetles of the District of Columbia. Pro. U. S. Nat. Mus., 25, pp. 1-57. No. 1275.

- VanDyke, E. J.
1901. Observations upon the Faunal Relations of California from the Standpoint of a Coleopterist. *Jour. N. Y. Ent. Soc.*, 9, pp. 197-199.
- Wickham, E. F.
1893. Report on an Entomological Reconnaissance of Southern Alaska. *Bull. Lab. Nat. Hist., Univ. of Iowa*, 2, pp. 202-233.
1896. A List of Coleoptera from the Southern Shore of Lake Superior, With Remarks on Geographical Distribution. *Pro. Davenport Acad. Sci.*, 6, pp. 125-169.
1896. A List of Some Coleoptera from the Northern Portions of New Mexico and Arizona. *Bull. Lab. Nat. His. Univ. Iowa*, 3, pp. 153-171.
1897a. The Coleoptera of the Lower Rio Grande Valley. *Bull. Lab. Nat. His. Univ. Iowa*, 4, pp. 96-115.
1898. The Beetles of Southern Arizona. *Bull. Lab. Nat. His., Univ. Iowa*, 4, pp. 295-312.
1902. A Catalogue of the Coleoptera of Colorado. *Bull. Sci. Lab. Nat. His. Univ. of Iowa*, 5, pp. 217-310.
1904. The Influence of the Mutations of the Pleistocene Lakes upon the Present Distribution of Cicindela. *Amer. Nat.*, 38, pp. 643-654.
1905. Insect Distribution in the Great Basin Considered in the Light of its Geological History. *Thirty-fifth Ann. Rep. Ent. Soc. Ont.* pp. 42-46.