ART. XXV.—*The effect of Glaciation and of the Glacial Period on the present Fauna of North America;* by SAMUEL H. SCUDDER.

THE time has perhaps arrived when at least a beginning may be made in an investigation which shall show with some degree of exactitude just what amount of influence the Glacial Period has exerted upon the present distribution of animal life in North America. Within a few years, and with a degree of precision sufficient for our purpose, geologists have mapped the areas which were once completely buried beneath the northern ice-sheet, and which were then absolutely devoid of animal life. With the slow southward advance of the ice, animals were crowded southward; with its recession they advanced again northward to reoccupy the desolated region, until now it has long been repopulated, either with the direct descendants of its former inhabitants or with such limitations to the integrity of the fauna as this interruption of local life may have caused. Precisely what modifications may have resulted, what probable resemblance the present fauna bears to that which preceded it before the interruption of its occupancy of the whole area, is the problem before us, though we shall only attempt a first step toward its solution.

In considering this question it occurred to me that some light might be thrown upon the matter if one were to tabulate separately the animals of the eastern half of the continent now found (1) upon the area once covered by the ice-sheet and (2) upon the driftless area, using the mapped limits of the terminal moraine to separate the two regions; to discover how

many genera and species were common to both, and how many peculiar to each, of the two areas; and finally, to compare these results with those reached by a similar study of the existing fauna of somewhat equivalent areas upon the Pacific coast where, it is claimed, no continental ice-sheet covered the face of the country. Here one would have to choose somewhat arbitrarily a delimitation between the two areas, north and south, which should tolerably correspond climatically with that of the terminal moraine of eastern America. Accordingly, before beginning any tabulation, I selected the following areas for comparison: East of the Rocky Mountains, the "barren ground" of the high north, the immediate vicinity of the Rocky Mts. and the extreme south of Florida and Texas were left out of consideration, and the two areas were separated by the line of the great terminal moraine as mapped by Chamberlin. West of the Sierra Nevadas, the two areas were separated by the northern border of California, and the southern district was limited southwardly by the omission of the region south of Los Angeles; while the northern district was made to include the northern part of Washington and the southern portion of British Columbia, though drift covered, so as to embrace in the lists the numerous collections made on Vancouver Island and the adjoining main land.

Of course it is well understood that the fauna of eastern is far better known than that of western America; but this is no real obstacle, since the comparison is to be made in either section between the northern and the southern districts of that section only, and there no great inequality exists; the special point of enquiry is as to the relative faunal weight of the north, if the expression may be allowed, in the east, where the ground required complete reoccupancy, and in the west, where occupancy had not been interrupted.

This would furnish a gauge, as it were, of the effect of the Glacial Period upon the present faunal distribution of life. For if it should be found that the relative proportion of endemic northern genera and species was distinctly less in the east than in the west, and the relative number of genera and species common to north and south also less; then surely such relative poverty might properly be taken as a gauge of the insufficiency of the time that has elapsed since the glacial period for the fauna to have recovered its ancient territory. If, on the other hand, no sign of such poverty can be discovered, then we may fairly assume that the east has fully recovered from the shock of the Glacial Period, and that, excepting in minor points which special investigation would point out, the present distribution of life is much what it would have been had there been no Glacial Period. I may

venture to add that before beginning this enquiry I had no idea what the result of my tabulation would prove.

In the following discussion of the question, I shall limit myself to the use of insects, and indeed of a single order of insects, as subjects for illustration; not only because some limitation must be made in this place with so large a subject before us, but also, and principally, because insects may rightly be regarded as better tests than any other group of animals or than any group of plants, in nice questions of distribution either in space or time. This is not generally acknowledged, but a single pertinent illustration will suffice.

It is well known that as we pass upward in the Tertiary period there is a growing resemblance of the animals and plants of its different subdivisions to those living at the present time; a resemblance both in general and in particular, an increasing percentage of forms regarded as identical or nearly identical with existing types being found as one passes from the Eocene to the present time. Furthermore the plants and (leaving the mammals out of account) the known animals of the Quaternary are, with extremely rare exceptions, identified altogether with those now living. Nearly all the mammals are extinct. Now, although the main broad features of insect life appear to have been much the same in the early Tertiary as now, not only has not a single Tertiary insect been shown to be living at the present day, whether in Europe or America, but a considerable proportion of Quaternary insects have also been described as extinct. It is true that a few, a dozen or two, Tertiary insects have been listed as belonging to existing forms, but in each such case the determination has been made by one not conversant with insects, or else with no statement of the basis or terms of comparison.

As to the Quaternary insects, I find in Europe 80 Coleoptera which have been studied with more or less care; of these 13 are treated as extinct and 67 identified more or less confidently with existing European forms. This number however, it should be insisted upon, is made up very largely of remains from peat bogs, which are relatively very recent. In our own country, 48 species of pleistocene Coleoptera have been described,* of which only a single one is regarded as probably identical with an existing form, three are specifically indeterminate and 44 are extinct, though in some cases intimately allied to forms now living. I add a list of these.

* Including five species from Hadley, Mass., described in an unpublished memoir.

List of described American Quaternary Coleoptera.

Name.	Locality.	Allied to	From	Resemblance.
Scolytidæ				
Hylastes squalidens	Scarboro, Ont.			
Tenebrionidæ				
Tenebrio calculensis	Greene's Cr., Ont.	T. molitor Linn.	Eur., N. Amer.	general
Chrysomelidæ				
Saxinis regularis	Hadley, Mass.	S. saucia LeC.	Pac. coast to Color.	general
Donacia stiria	Scarboro, Ont.	D. porosicollis Lac.	Lake Sup., N. Engl.	general
pompatica	" "	D. pubicollis Saffr.	Illinois	close
elongatula	Hadley, Mass.	D. lignitum Sord.	Ital. Quaternary	close
Scarabæidæ				
Aphodius præcursor	Port Kennedy, Pa.	A. ruricola Melsh.	Anticosti to La.	close
Phanæus antiquus	" "	A. pluto Har.	Ariz, Mex.	close
Chœridium ebeninum	" "			
Elateridæ				
Corymbites æthiops?	Hadley, Mass.	(Recent)		
Fornax ledensis	Greene's Cr., Ont.	F. calceatus Say	Canada; Mass.	close
Byrrhidæ				
Byrrhus ottawaensis	" "	B. geminatus LeC.	Lake Sup., N. H.	very close
Staphylinidæ				
Arpedium stillicidii	Scarboro', Ont.	A. cribratum Fauv.	Michigan	general
Geodromicus stiricidii	" "	G. nigrita Müll.	North. U. S.; Can.	distant
Bledius glaciatus	" "	B. brevidens LeC.	New York	close
Oxyporus stiriacus	" "			
Lathrobium interglaciale	" "	L. grande LeC.	Lake Sup. to N. Car.	general
Hydrophilidæ				
Hydrochus amictus	Cleveland, O.	H. subcupreus Rand.	Lake Sup., southw.	general
Helophorus rigescens	" "	H. tuberculatus Gyll.	North. U.S.; Scandin	general
Dytiscidæ				
Dytiscidæ sp.	Hadley, Mass.	Matus bicarinatus Say	Canada to Fla.	possible
Carabidæ				
Chlænius punctulatus	Port Kennedy, Pa.	C. laticollis Say.	N. Y. to Fla.; Ariz.	close
Cymindis aurora	" "	C. americana Dej.	New York	close
extorpescens	Hadley, Mass.	C. elegans LeC.	Mass.; Fla.	general
Platynus casus	Scarboro', Ont.	P. rubripes Zimm.	Mid. St. to Kansas	general
hindei	" "	" "	"	general
halli	" "	P. crenistriatus LeC.	Western U. S.	general
dissipatus	" "	"	"	distant
desuetus	" "	"	"	close
harttii	" "			
dilapidatus	" "	P. maculicollis Dej.	Oreg.; Calif.; Ariz.	general
Dicælus alutaceus	Port Kennedy, Pa.	D. dilatatus Say.	U. S. E. of Gr. Plains	close
sp.	" "	D. elongatus Bon.	"	general
Pterostichus abrogatus	Scarboro', Ont.	P. herculaneus Mann.	Pac. coast; Brit. Am.	close
dormitans	Cleveland, Ohio.	P. lætulus LeC.	California	very close
destitutus	Scarboro, Ont.	P. sayi Brullé	Atl. and west. St.	close
fractus	" "	"	"	distant
destructus	" "	P. patruelis Dej.	Mid. St.; N. York	very close
gelidus	" "	P. hudsonicus LeC.	Hudson Bay	close
lævigatus	Port Kennedy, Pa.			
sp.	" "			
Patrobus gelatus	Scarboro', Ont.	P. septentrionis Dej.	N. Eur.; Arc. Amer.	very close
Bembidium glaciatum	" "	B. longulum LeC.	Lake Sup.; N. York	close
fragmentum	Cleveland, Ohio.	B. constrictum Lec.	New England	close
Loricera glacialis	Scarboro', Ont.	L. cærulescens Linn.	Bor. Am. & Eur.; Sib.	general
lutosa	" "			
Elaphrus irregularis	" "	E. viridis Horn	California	close
Cychrus wheatleyi	Port Kennedy, Pa.	C. viduus Dej.	Pennsylvania	general
minor	" "	C. andrewsii Harr.	Centr. Atl. states	general

It should be noted that this series, in contradistinction from the European, does not include any forms from the peat, regarding which nothing has yet been published. I may however add that I have studied a very large collection of peat insects from Massachusetts and have so far separated over 60 species of Coleoptera, of which 27 are identified with existing forms, 10 are probably the same as species now living, and only one, a Hydrocanthus, is certainly different from anything yet known. The study of the remainder has not been concluded.

In our own country, then, the coleopterous fauna of the peat is practically identical with that now living; while that of deposits further removed from the present, but laid down *since* the beginning of the Glacial Period, is practically entirely extinct. When the early Quaternary Coleoptera of Europe have been attentively studied, I believe that the same conclusion is likely to be drawn from them. It thus appears that in this country the Coleoptera are at least as sensitive standards of climatic or faunal changes as are the Mammalia, which have hitherto been regarded as the only group of animals any considerable portion of which have become extinct in quaternary times; and that they are more sensitive tests than other groups of animals or than plants.

Having for these reasons selected insects as the best subjects for investigation, I have further restricted myself to Coleoptera, as the order which has been longest studied, is best known, and is most numerous in described species, the greater part of which have had the benefit of monographic revision. The main difficulty, that the catalogues give no indication of the geographical distribution of the different species, has been completely removed by the signal kindness of my friend Mr. Samuel Henshaw, who has liberally allowed me the freedom of his manuscript catalogue, in which he has placed against each species every published indication of special locality or general range, besides those furnished by his own knowledge.

The following table gives in detail for each family of Coleoptera the result of my examination of Mr. Henshaw's catalogue, and includes over 7500 species. For brevity, I have designated the drift-covered area of the east as D; the driftless area of the same as E; the northern portion of the Pacific region as N; and the southern as S. The first figure in each column indicates the number of genera, the second of species. The sign $>$, as in S$>$N, indicates that the numbers in that column are the number of genera found in S and not occurring in N, and the number of species in those same genera occurring in S. The sign $+$, as in S$+$N, means the number of genera common to both S and N and the number of species

of those genera occurring in one or the other or in both (which is usually fully twice the number of species common to both). Although beside my immediate purpose I have added the middle set of three columns for the sake of comparison.

Table of the regional distribution of North American Coleoptera.

Families.	S>N	S+N	N>S	N>D	N+D	D>N	D>E	D+E	E>D
Cicindelidæ	2:2	2:23		1:2	1:32	1:1		2:73	1:1
Carabidæ	24:39	22:172	5:6	3:4	26:382	47:132	12:15	64:679	33:69
Amphizoidæ		1:3		1:3	1:3				
Haliplidæ	2:2	2:2			2:9			2:13	
Dytiscidæ	8:12	10:51	2:2		12:129	13:24	2:3	23:171	3:3
Gyrinidæ	2:2	1:5			1:18	2:5	1:1	2:6	
Hydrophilidæ	6:7	4:28			4:33	10:32	3:4	12:84	5:5
Leptinidæ					2:2	2:2	2:2	2:2	
Silphidæ	1:1	10:22	4:4	6:9	10:60	6:13		13:62	4:4
Scydmænidæ	1:1	1:4			1:15	5:6	3:4	3:29	1:1
Pselaphidæ	3:3	2:10	1:1	1:1	15:104	14:35	1:1	14:103	11:14
Staphylinidæ	24:54	21:142	9:9	9:9	22:311	55:138	13:20	61:519	33:51
Trichopterygidæ		3:17		1:1	2:14	3:6		5:29	5:6
Sphæriidæ	1:1	1:1							
Scaphidiidæ	1:1	1:1			4:9	4:9	1:1	3:14	2:3
Phalacridæ	1:2	1:1	1:1		2:8	1:5		3:24	6:11
Corylophidæ	2:2		1:1		1:1	5:9	3:4	3:10	
Coccinellidæ	2:2	9:37	1:1	1:1	9:66	11:20	2:2	18:109	2:3
Endomychidæ	2:4	1:3			1:3	6:6		7:9	3:8
Erotylidæ	1:2	1:1			1:11	6:16		7:42	
Colydiidæ	4:4	5:11	1:1	4:5	2:3	8:9		10:20	10:14
Rhyssodidæ	1:2		1:1		1:2	1:1		2:2	
Cucujiidæ	3:8	3:4	1:1	2:2	2:5	6:18		8:35	6:8
Cryptophagidæ	2:3					7:9	1:1	6:14	2:2
Mycetophagidæ	1:1	2:4			2:8	4:7		6:20	
Dermestidæ	5:10	3:8			3:11	6:10		9:27	3:3
Histeridæ	4:5	3:21			3:58	8:16		12:128	7:8
Nitidulidæ	3:4	4:9	2:2	2:2	4:20	14:30		18:60	6:6
Latridiidæ	4:15					4:22	2:2	3:37	2:2
Trogositidæ	2:2	3:7	1:2		3:16	4:8	1:1	6:24	2:2
Derodontidæ					1:1	1:1		1:1	
Byrrhidæ	2:7	1:3	2:2	1:2	2:5	4:12	4:12	2:12	1:1
Georyssidæ	1:1					1:1		1:1	
Parnidæ	2:2	1:4			1:9	5:10		6:24	2:2
Heteroceridæ		1:2			1:9			1:13	
Dascyllidæ	6:6	1:2	2:2	1:1	2:8	9:13	3:3	8:24	2:2
Rhipiceridæ	1:1					3:5		3:5	
Elateridæ	14:18	17:100	3:4	1:1	19:200	29:53	5:8	42:269	14:20
Throscidæ	1:1	1:5			1:6	1:2		2:11	
Buprestidæ	6:14	6:37	1:1	1:1	6:61	12:41	2:2	16:146	9:14
Lampyridæ	8:14	8:36		1:1	7:66	18:43	2:2	23:13	10:11
Malachidæ	5:9	5:35		3:4	1:8	5:9	1:1	6:35	5:8
Cleridæ	4:5	4:12			4:17	11:20	2:4	13:53	3:4
Ptinidæ	15:23	4:9	1:1		4:13	22:36	2:3	24:77	12:18
Cupesidæ			1:1	1:1		1:2		1:2	
Lymexylidæ						3:3	3:3		
Cioidæ	1:1					3:6		3:11	
Sphindidæ	1:1					3:3	3:3		
Lucanidæ		3:8		1:1	2:6	3:6		5:10	
Scarabæidæ	14:22	8:46	2:3	1:1	9:80	31:80	3:3	37:247	16:24

[TABLE continued.]

Families.	S>N	S+N	N>S	N>D	N+D	D>N	D>E	D+E	E>D
Spondylidæ		1:1			1:1	1:1	1:1	1:2	1:1
Cerambycidæ	27:32	22:90	12:14	8:8	23:170	55:95	8:11	67:258	51:74
Chrysomelidæ	20:30	21:75	8:12	3:4	25:144	40:95	6:8	60:431	22:34
Bruchidæ	2:9					1:7		1:32	3:4
Tenebrionidæ	26:37	12:54	4:4	9:15	8:33	22:30	5:5	28:97	34:72
Aegialitidæ	1:1	1:1							
Cistelidæ	2:3					7:22		7:33	2:6
Othniidæ		1:1						1:2	1:2
Lagriidæ								1:1	1:3
Melandryidæ	1:1	3:6	2:2	2:2	5:11	23:33	7:8	19:37	3:3
Pythidæ	5:5		1:1	1:1	1:1	5:5		2:3	1:2
Oedemeridæ	3:3	2:6	1:1		3:9	3:3	1:1	5:12	2:3
Cephaloidæ			1:1		1:3	1:2			
Mordellidæ	2:4	1:3			1:4	2:14		4:100	3:4
Anthicidæ	3:16	1:6	1:1	1:1	1:6	6:35	1:1	6:69	4:7
Pyrochroidæ			1:1		1:3	3:3	1:1	3:7	
Meloidæ	7:11	4:33		1:4	4:25	5:8		8:69	7:20
Rhipiphoridæ	2:3					3:11		3:19	
Stylopidæ						2:2	1:1	1:1	
Rhinomaceridæ	1:1	1:3			1:2			1:2	
Rhynchitidæ	1:1	1:5			1:3	3:7		4:14	
Attelabidæ					1:3	1:3		1:4	
Byrsopidæ								1:1	
Otiorhynchidæ	12:16	6:11	3:4	9:12		11:15	3:4	8:13	23:33
Curculionidæ	17:22	16:77	10:11	5:5	19:138	52:80	14:19	56:411	28:44
Brenthidæ								1:2	1:1
Calandridæ	6:7	2:7			3:19	5:7		7:36	13:17
Scolytidæ	1:1	9:34	2:2		10:58	12:22	2:2	22:99	4:5
Anthribidæ	2:2		1:1		1:1	9:11	2:2	8:18	7:10
Totals	334:521	281:1300	88:101	81:104	307:2355	690:1446	129:169	844:5072	432:673

Translating these totals into percentages we shall reach the following figures:

Districts.	S>N	S+N	N>S	N>D	N+D	D>N	D>E	D+E	E>D
Percentages	48:27	40:68	12:5	8:3	28:60	63:37	9:3	60:86	31:11

Or, if we place the percentages of the west and the east in parallel columns, we shall have the following:

	West	East
North	12 : 5	9 : 3
In common	40 : 68	60 : 86
South	48 : 27	31 : 11

Here it will be seen that in the northern percentage of both genera and species, the East lags a little behind the West, but it is only a very little, and it is much more than made up by the considerably larger percentage in the East of the genera common to North and South.

I have also tabulated the species reported as found common to the northern and southern districts on each side of the continent and find that about 16 per cent of all the western species are common to the two districts, while about 35 per cent of all the eastern are common to the drift-covered and driftless areas. I append a table of these numbers. One difference between this table and the previous one is that here the common species form the base, while in the previous one the common genera form the base; hence a genus represented in the two districts, but only by *distinct* species, does not appear in this table, but only in the previous one. Seven families in which there are no species recorded as found in two regions are omitted from the list.

Table of the species common to pairs of regions.

Families.	S+N	N+D	D+E	Families.	S+N	N+D	D+E
Cicindelidæ	2:5		2:22	Throscidæ			2:5
Carabidæ	20:46	14:25	62:245	Buprestidæ	5:10	4:6	16:62
Amphizoidæ	1:1			Lampyridæ	5:6	3:3	22:65
Haliplidæ			2:6	Malachidæ	3:3		5:12
Dytiscidæ	8:12	4:7	22:67	Cleridæ	2:3	2:2	12:18
Gyrinidæ		1:2	2:10	Ptinidæ	3:3		23:28
Hydrophilidæ	4:6	2:2	11:37	Cupesidæ			1:2
Silphidæ	13:17	7:12	15:43	Cioidæ			3:3
Scydmænidæ	1:1		2:7	Lucanidæ	3:3		5:8
Pselaphidæ	1:1		14:36	Scarabæidæ	6:9	2:3	36:106
Staphylinidæ	15:29	13:27	57:189	Spondylidæ	1:1	1:1	1:1
Trichopterygidæ	1:1		3:5	Cerambycidæ	17:20	12:13	66:155
Scaphidiidæ			3:7	Chrysomelidæ	15:19	12:14	59:164
Phalacridæ	1:1		2:5	Bruchidæ			1:7
Corylophidæ		1:1	3:5	Tenebrionidæ	10:14	1:1	28:45
Coccinellidæ	8:10	6:7	17:45	Cistelidæ			7:11
Endomychidæ	1:1		7:8	Lagriidæ			1:1
Erotylidæ			7:20	Melandryidæ	1:1	2:2	19:26
Colydiidæ	3:3	1:1	10:11	Pythidæ		1:1	1:1
Rhyssodidæ			2:2	Oedemeridæ			4:5
Cucujidæ	3:3		8:19	Mordellidæ	1:1		4:31
Cryptophagidæ			6:6	Anthicidæ			5:24
Mycetophagidæ	1:1	1:1	6:12	Pyrochroidæ		1:1	2:2
Dermestidæ	3:5	3:3	8:16	Meloidæ	3:4		7:15
Histeridæ	2:5	1:1	11:51	Rhipiphoridæ			1:5
Nitidulidæ	4:4	4:4	18:33	Stylopidæ			1:1
Latridiidæ			3:6	Rhinomaceridæ			1:1
Trogositidæ	3:3	1:1	6:16	Rhynchitidæ	1:1	1:1	4:8
Derodontinæ			1:1	Attelabidæ			1:5
Byrrhidæ	1:2		1:1	Byrsopidæ			1:1
Georyssidæ			1:1	Otiorhynchidæ	5:5		6:6
Parnidæ			6:13	Curculionidæ	10:16	7:7	47:117
Heteroceridæ	1:1	1:1		Brenthidæ			1:1
Dascyllidæ		1:1	7:12	Calandridæ	1:1	1:1	6:16
Rhipiceridæ			3:5	Scolytidæ	7:10	6:6	21:39
Elateridæ	9:14	10:15	41:119	Anthribidæ		1:1	6:7
				Totals	205:302	128:174	794:2083

These figures indicate, it seems to me, that on the whole the fauna of the East has nearly or quite recovered from its enforced removal from the northern States and Canada at the time of the Glacial Period, and that whatever influence the past existence of a Glacial Period may now exert upon the distribution of animal life in North America should be sought only in minor features, such as the remnants of boreal faunas lingering in favorable spots amid temperate surroundings, and the similar features induced by the latitudinal trend of our great mountain chains.