THE NORTHWARD DISTRIBUTION OF ANTS IN NORTH AMERICA

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Abstract

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A study of the ant populations was made through a transect of mid-continent North America from Churchill on Hudson Bay and various localities around the Great Lakes to Iowa and northern Illinois. Data were obtained from extensive personal collecting and from literature sources. The results were assembled and discussed within an ecological framework provided by Merriam's life zones, and showed a regular diminution in the variety and wealth of the ant faunas progressing from south to north. Though the number of species at Churchill is extremely reduced, ants nevertheless do occur there as established reproducing colonies, even in the presumed tundra habitats. These forms which exist so far north represent a highly impoverished remnant of richer faunas further south. Although none of the species is peculiar to the area, each must be tolerant of high boreal environments. A total of 135 species and subspecies are listed for the Carolinian and Alleghenian zones combined, 43 taxa for the Canadian Zone, 4 taxa for the Hudsonian Zone, and 4 also for the Arctic Zone. Comparisons with the recorded ant faunas of the Rocky Mountains of Colorado were made with respect to the corresponding zones, namely, the Plains (Upper Sonoran), Foothills or Submontane (Transition), Montane (Canadian), Subalpine (Hudsonian), and Alpine (Arctic) zones, and appropriate similarities and differences noted.

Although it is well known that the hymenopterous family Formicidae has a cosmopolitan distribution and reaches high latitudes in both the northern and southern hemispheres, the actual northern limits of these insects have not been mapped in accurate detail. Neither has the pattern of species disappearance, in a northward direction, been worked out in more than very broad and general terms. The present paper attempts to contribute to the knowledge of this problem, and new data on species occurrence will be added.

The center of North America from mid-western United States northward toward Hudson Bay probably gives the most representative transect for the temperate and boreal portions of the continent, and is also the region where warmer and colder climatic zones come into closest proximity. The width of the zones appears to be narrower, and the travel distances necessary to traverse several zones are less here than in the west and particularly less than on the west coast, owing to the marked southward displacement of isotherms from Hudson Bay to the Great Lakes (Munroe 1956: figs. 7, 8, 9). Over a period of many years we have had the opportunity to collect ants extensively in certain critical localities of this central North American region, such as the area about the southern end of Lake Michigan and one centering around the western end of Lake Superior. In the summer of 1969 collecting was finally extended to include the Turtle Mountains on the North Dakota - Manitoba border, and northward to Winnipeg, The Pas, and Churchill, The results of this recent field work will be reported presently, but first a consideration of the fauna in the appropriate northern states must provide a foundation for the changes observed in Canada.

Concentrated collecting in the Chicago Region (Gregg 1944) included localities as far north of the city as Volo and Waukegan, Ill., and Lake Geneva and Madison, Wisc.; as far west and south as New Lenox, Momence, and LaSalle, Ill.; and as far east as Bass Lake, Hamlet, and Smith, Indiana, and to Lakeside, St. Joseph, and Three Rivers, Mich. This study provided excellent examples of the ants to be

found in a wide variety of habitats, as is shown by the plant communities and ecological circumstances in the following list which were investigated.

Prairie-meadow-pasture complex Sand dune communities such as

Lower, middle, and upper lake beaches

Foredunes

Cottonwood dunes

Jack pine – white pine dunes

Black oak dunes

Mesophytic dune forest

Mixed oak forest

Oak-hickory forest

Beech-maple forest

Floodplain forest

Bog forest

Forest margin

Marsh

Railway and roadside habitats

Various disturbed situations to be classed as urban steppe¹

Talbot (1934) studied ants in the same region and was able to find 70 species and infraspecific forms, but I found it possible to add 22 forms to the list, making a total of 92 taxa for the area. Several of these were of doubtful identification as the records had to be based on single specimens, and three were introduced species from other parts of the world. As a result of the taxonomic and nomenclatural changes that have occurred in the intervening years, it is necessary to regard at least seven of the taxa recorded in my paper as synonyms, and this would reduce the number of recognizable forms with which I dealt to 85. My work was confined to relatively small areas of four adjacent states, but the ecological diversity was such as to yield a substantial number of ant species and to indicate a tolerably rich fauna for the general region.

At about the same time, a study of the ants for the entire state of Iowa was published by Buren (1944). Iowa, being in the same general latitude as the area about the head of Lake Michigan, presents comparable ecological circumstances, especially in the eastern portion of that state. Buren collected ants in some of the same kinds of habitats as I found near Chicago, notably of the mixed oak and oakhickory type, although in Iowa these communities are usually confined to low places and the bottomlands of watercourses. Upland habitats in Iowa are for the most part grasslands and under natural conditions belong to climax tall grass prairie. Unfortunately, most of the prairies have succumbed to agriculture. Buren collected a total of 97 taxa, and they must certainly be considered very representative of the species of central United States. Both of our investigations turned up many records of the same species, but this is not surprising since most of the ants are wide ranging members of the general fauna of eastern United States. Buren described several new species from Iowa, but as they are rare and local we still know little about their distribution. Of the 97 forms recorded, nomenclatural changes have relegated about eight of them to synonymy, thus reducing the number of valid taxa to 89. This number compares favorably with 85 for the smaller, Chicago area.

As a result of many years of careful field work, the Wheelers (1963) presented an exhaustive survey of the ants of North Dakota. With relatively few exceptions,

¹The term "urban steppe" was applied by Lindroth (1957) to a variety of man-altered or man-produced sites.

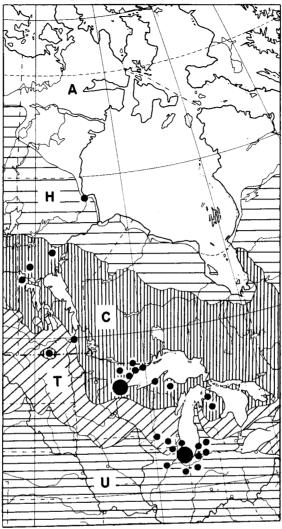


Fig. 1. Longitudinal transect of North America from Hudson Bay to the Great Lakes. Small dots, single collecting localities; large dots, multiple collecting localities (see text). A, Arctic Zone; H, Hudsonian Zone; C, Canadian Zone; T, Transition Zone (Alleghenian); U, Upper Austral Zone (Carolinian), (after Merriam).

the terrain of that state is monotonous, and coupled with a severe continental prairie climate one would suppose that the number of habitats and environmental niches for ants would be minimal. The ants of this region, however, are numerous, considering the adverse conditions, and the Wheelers have collected and recorded a total of 87 taxa, only one of which, *Monomorium pharaonis*, is an introduced species. For many of the forms they have gathered voluminous records. The ant fauna of North Dakota is strategic, being in the approximate center of the continent, and it is moreover of much importance to the present study, for it is probably the best analysis of a transitional assemblage of species between those that are definitely southern in their affinities and those that are boreal. Furthermore, the ecological regimes of the state are about equally divided between fairly humid environments toward the east and semi-arid conditions toward the west.

Putting together the findings of these several studies on the myrmecofauna of the central states, we can now compile a rather satisfactory list of the species and subspecies of the region as a whole. This does not presume that each species will be found in all parts of the region, but we may confidently expect to find them in a large percentage of sites examined. The interior lowlands have little topographic relief, no major physical barriers to dispersal, and climates which change only gradually over long distances. Numerous ant species of eastern United States are known to have ranges which extend from the Atlantic seaboard to far beyond the Mississippi River and in some cases to the base of the Rocky Mountains. provisional life-zone classification of Merriam works admirably in the eastern half of the continent, I have no hesitancy in using it to provide the broad ecological background for the objectives of this paper (Fig. 1). It is interesting to note also that Munroe has used the life-zone concept in describing the distribution of many Canadian insects. I have elsewhere (Gregg 1963) discussed Merriam's work in detail, and believe that it is possible to employ life-zones and to coordinate them with the terminology of biomes or plant-animal formations when describing the occurrence of animal species. Accordingly, the list of ants which follows represents the species that are characteristic of the eastern division (typified by higher general humidity) of Merriam's Upper Austral Zone, also called the Carolinian Zone, and his Transition Zone, otherwise called the Alleghenian Zone. An indication is given as to whether the ant occurs in both zones or in only one of either zone. These zones are broad latitudinal belts each several hundred miles in width across The Carolinian characteristically has hot summers and cold central United States. winters, whereas the Alleghenian shows rather cooler summers and very cold winters. Both belts have abundant precipitation, particularly in the eastern portion, with gradually decreasing moisture toward the center of the continent. Iowa, northern Illinois and Indiana, and southern Michigan are situated in the northern section of the Carolinian, and North Dakota is located precisely in the middle of the Transition Zone, whether viewed from north to south or from east to The Wheelers have demonstrated that the Dakota ant fauna has been derived from various sources: some species from the east and some from the west, some from the north and south, others from the northeast and the southwest. It is a composite and a transitional fauna, various elements having come from widely different extremes.

Ants of the Carolinian and Alleghenian Zones²

(C = Carolinian only; A = Alleghenian only; symbol absent = both zones)

Stigmatomma pallipes (Haldeman)—C

S. pallipes subterranea Creighton—C

S. pallipes subterranea Creighton—C

Sysphincta pergandei Emery—C

Concerning Aphaenogaster temesseensis. Creighton writes that this ant definitely occurs in the St. Lawrence Valley where he has had it under observation for a number of years. This serves to further confirm its presence in the Alleghenian Zone.

EDr. Creighton has offered some informative comments on this list of ants. I placed a question mark after the name Harpagoxenus americanus because the ant seemed to belong primarily to the fauna of eastern United States, but since it occurred as far west as Ohio, I thought it advisable to include it in the list on the presumption that its range may yet be found to extend further west. Creighton assures me that he has often collected the species in the Ramapo Mountains, a series of low hills on the New York – New Jersey border, but that the ant is more abundant at the tops of the hills than at their bases, and that beyond the hills americanus does not occur at all. He believes that a similar situation exists in a hilly region of south central Ohio where the Wessons collected americanus in quantity. Those hills reached elevations of 1400 ft. He also pointed out that this ant occurs at sea level in New England and at river level (256 ft) in the St. Lawrence Valley. It thus appears that the range of the species rises slightly as it passes to the south. When this information is coupled with the fact that the ranges of the two host species of americanus (Leptothorax longispinosus and L. curvispinosus) reach into the Gulf Coast States, whereas americanus has not been taken south of Washington, D.C., he draws the tentative conclusion that H. americanus may not properly belong to the Carolinian fauna. We need more data on this problem, and particularly from other unrelated groups of insects showing the peculiar hilltop type of distribution mentioned above. If such could be verified, it might be possible to defend a Transition Zone (Alleghenian) designation for certain isolated ranges of low hills in eastern United States.

Concerning Aphaenogaster temesscensis, Creighton writes that this ant definitely occurs in the St.

Tapinoma sessile (Say) Ponera trigona opacior Forel-C P. coarctata pennsylvanica Buckley Brachymyrmex depilis Emery Camponotus pennsylvanicus (DeGeer) P. inexorata Wheeler-C C. ligniperdus noveboracensis (Fitch) Eciton nigrescens (Cresson)—C C. ferrugineus (Fabricius)—C E. opacithorax Emery—C C. herculeanus (Linnaeus)—A C. americanus Mayr
C. castaneus (Latreille) Myrmica brevinodis Emery M. brevispinosa Wheeler C. nearcticus Emery M. lobicornis fracticornis Emery C. caryae discolor (Buckley)—C M. monticola Wheeler-A C. subbarbatus Emery M. punctiventris Roger—C Paratrechina parvula (Mayr) M. sabuleti americana Weber P. arenivaga (Wheeler)—C M. schencki emeryana Forel Prenolepis imparis (Say) M. hamulata trullicornis Buren-C Lasius alienus americanus Emery Stenamma brevicorne (Mayr)—C L. niger neoniger Emery S. diecki Emery-A L. niger sitkaensis Pergande-A S. impressum Emery-C L. brevicornis Emery S. impar Forel—A L. flavus nearcticus Wheeler S. schmitti Wheeler---C L. umbratus aphidicola (Walsh) Aphaenogaster fulva Roger-C L. speculiventris Emery-C A. rudis Emery-C L. subumbratus Viereck-A A. mariae Forel—C L. claviger (Roger) A. texana Emery—C
A. treatae Forel—C L. interjectus Mayr L. latipes (Walsh) A. tennesseensis (Mayr) L. murphyi Forel Pheidole bicarinata Mayr L. subglaber Emery Ph. bicarinata vinelandica Forel-C L. plumopilosus Buren Ph. pilifera (Roger) L. bureni (Wing)—A Ph. sitarches campestris Wheeler-C L. pubescens Buren-A Ph. morrisi Forel—C L. occidentalis Wheeler—A Crematogaster lineolata (Say) Formica neogagates Emery C. lineolata subopaca Emery—C
C. minutissima missouriensis Emery—C F. lasioides Emery F. limata Wheeler-A Monomorium minimum (Buckley) F. fusca Linnaeus
F. fusca argentea Wheeler Solenopsis molesta (Say) Myrmecina americana Emery-C F. altipetens Wheeler-A Harpagoxenus americanus (Emery) ? F. cinerea lepida Wheeler-A Leptothorax ambiguus Emery F. cinerea montana Emery L. ambiguus foveatus M. R. Smith-C F. marcida Wheeler-A L. curvispinosus Mayr—C F. neoclara Emery-A L. longispinosus Roger-C F. neorufibarbis Emery-A L. schaumi Roger-C F. obscuripes Forel L. rugatulus Emery—A F. obscuriventris Mayr L. tricarinatus Emery F. integra Nylander
F. oreas comptula Wheeler—A
F. dakotensis Emery—A L. texanus Wheeler L. canadensis Provancher-A L. hirticornis Emery-A F. fossaceps Buren L. duloticus L. G. Wesson-C F. reflexa Buren L. provancheri Emery-A L. pergandei Emery-C F. difficilis Emery Tetramorium caespitum (Linnaeus)—C Smithistruma pergandei Emery-C S. pulchella Emery—C S. missouriensis-C S. ornata—C

F. prociliata Kennedy & Dennis-C F. impexa Wheeler-A F. indianensis Cole—C F. nepticula Wheeler F. knighti Buren-C F. postoculata Kennedy & Dennis-C Dolichoderus mariae Forel—C F. spatulata Buren F. whymperi adamsi Wheeler-A? D. plagiatus (Mayr) F. exsectoides Forel F. ulkei Emery D. pustulatus Mayr-C D. taschenbergi (Mayr)—A F. rubicunda Emery Iridomyrmex pruinosus (Roger)—C Dorymyrmex pyramicus (Roger) F. subintegra Emery

F. sanguinea subnuda Emery
F. sublucida Wheeler—A
F. pergandei Emery—A
F. puberula Emery—A
F. wheeleri Creighton—A

F. pallidefulva nitidiventris Emery F. schaufussi Mayr Polyergus lucidus Mayr P. bicolor Wasmann P. rufescens breviceps Emery

The foregoing list does not pretend to be absolutely complete, but the commonest and most representative species are included and in addition infrequent, sporadic, and even rare forms will be noted. Though occurring in the appropriate zones, some species seem to be known as yet only from the East Coast and are therefore properly excluded from the area under consideration. Where to draw the western limits for this investigation is difficult owing to the fact that certain well known western ants do seem to penetrate occasionally and locally into more humid portions of the two zones, particularly the Transition Zone in North Dakota. which are widely distributed in the Transition of the Rocky Mountains manage to spread eastward on the plains in these northern latitudes as is evident from a perusal of the records collected by the Wheelers. I have included species or subspecies in this composite list which were not actually found by me in the Chicago area, or by Buren in Iowa, because their distribution is known to blanket the regions involved. For this information I have relied on Creighton's monographic treatment of the ants of North America (1950) which supplies statements about the inclusive ranges of all the taxa up to that date. And since then continued collecting has extended the known occurrence of numerous forms. It has seemed justified to place in the list only those ants that belong typically to the fauna of the eastern half of the United States and to eliminate all which normally occur in the western half of the country, despite the fact that some overlapping has been reported. The 100th meridian serves satisfactorily for this purpose, since it divides the more humid from the more arid sections, but one cannot adhere rigidly to such a line for the environmental changes across it are not abrupt.

This faunal assemblage for the two uppermost zones of Merriam's Austral Region comprises 7 taxa in the Ponerinae, 2 in the Dorylinae, 47 in the Myrmicinae, 7 in the Dolichoderinae, and 72 in the Formicinae. These make a total of 135 species and subspecies for the areas treated, a very substantial fauna of ants for a temperate portion of the northern hemisphere. And while five subfamilies of the Formicidae are represented, two of these, the Myrmicinae and the Formicinae, together account for 88% of the known forms.

Proceeding northward and eastward from the areas so far considered, we enter Merriam's Canadian Zone, a broad ecological belt of relatively uniform conditions from Atlantic to Pacific coasts, contrasting notably with the more southern zones in which important precipitation and humidity differences are recognized between their eastern and western portions. The Canadian Zone can be found, of course, at appropriate elevations in various mountains of the United States as well. transcontinental and most extensively developed in Canada, this zone descends in the central lowlands into the northern parts of the states surrounding lakes Superior, Michigan, and Huron. It is here the zone reaches its most southerly stations at very low elevations. From Chicago to Duluth one passes from Carolinian, through Alleghenian, and into the Canadian Zone over a distance of approximately 500 miles. From northern Iowa to Duluth the distance is considerably less. traverse from the eastern shore of Lake Michigan toward Lake Huron it is possible to change from the Carolinian, through Alleghenian, to the Canadian Zone in the remarkably short distance of about 75 miles. Similar rapid shifts from zone to zone occur northward from Lake Erie into southern Ontario. The climatic moderating effects of the adjacent bodies of lake water are at least partly responsible for these observed changes, which at low elevations are indeed striking. Ordinarily, in lowland regions many miles of latitude are required to produce the ecological changes which in mountainous regions are caused by rapid alterations in the lapse rate of physical factors with increasing altitude, such that zonal differences become evident in a few hundred to a few thousand feet.

The ant populations of typical Canadian Zone habitats were studied extensively in the region of Duluth, Minn., and the north shore of Lake Superior over a period of 3 years (Gregg 1946). It is certain that a representative sample of the boreal ant fauna was collected, and at that time a list of 40 species and subspecies was The city of Duluth affords numerous pockets of natural vegetation, especially steep ravines leading down to the lake where remnants of the original forests are preserved. Minnesota Point, the long sand bar that nearly closes off the end of Lake Superior, retains examples of dune successional vegetation. In addition to these sites within the corporate limits of the city, collections were made also at the following localities in northeastern Minnesota: Jay Cooke State Park at Fond du Lac, Carlton, Holyoke, Rice Lake, Knife River, Knife Island, Gooseberry Falls State Park, Beaver Bay, Hovland, Lake Vermilion north of Tower, and Lake Saganaga on the Canadian border. Other localities in Wisconsin south of the city of Superior were Foxboro and Pattison State Park. Widely separated from Duluth, but nevertheless representative of typical Canadian Zone habitats from which we have collected ants may be added the following stations: Roscommon and Harbor Springs in Lower Michigan, Negaunee and Porcupine Mountains State Park in Upper Michigan, The International Peace Garden in the Turtle Mountains astride the border between North Dakota and Manitoba, Birds Hill Provincial Park at Winnipeg, Man., The Pas, Man., Clearwater Lake, Man., and Thompson, Man. From such a broad selection of locations as the foregoing we have thus been able to observe and sample the ant populations of numerous boreal communities and stands of vegetation. A list of these would include —

Jack-red-white pine forest
Maple-basswood-oak forest
Maple-basswood-pine-cedar forest
Beech-maple-hemlock forest
Spruce-fir forest
Pine-spruce-fir forest
Aspen forest
Tamarack bog forest
Oak-aspen forest
Mixed hardwood – coniferous forest

(involving various combinations of pine, spruce, fir, cedar, tamarack, yew, balsam poplar, aspen, birch, maple, oak, alder, willow, red-osier dogwood, alternate-leaf dogwood, ash, and chokecherry)

Sphagnum bog Meadow-pasture complex Forest margin Brushy woodland Marsh

Railway and roadside habitats

With this varied environmental background from which ants have been collected a composite record for the central part of the Canadian Zone in North America has been assembled. There follows a list of the known species.

ANTS OF THE CANADIAN ZONE

Ponera coarctata pennsylvanica Buckley Myrmica brevinodis Emery M. brevispinosa discontinua Weber M. sabuleti americana Weber M. schencki emeryana Forel M. lobicornis fracticornis Emery M. monticola Wheeler

M. monticola Wheeler Stenamma diecki Emery

Leptothorax canadensis Provancher

L. provancheri Emery

Harpagoxenus canadensis M. R. Smith

Dolichoderus taschenbergi (Mayr) Tapinoma sessile (Say)

Camponotus herculeanus (Linnaeus)
C. ligniperdus noveboracensis (Fitch)

C. ligniperdus noveboracensis (F C. nearcticus Emery Lasius niger neoniger Emery L. niger sitkaensis Pergande L. alienus americanus Emery L. subumbratus Viereck L. umbratus aphidicola (Walsh)

L. claviger (Roger)

L. interjectus Mayr
L. latipes (Walsh)
L. subglaber Emery
L. pubescens Buren
L. plumopilosus Buren
Formica neogagates Emery
F. lasioides Emery
F. fusca Linnaeus

F. fusca argentea Wheeler F. neorufibarbis algida Wheeler

F. integra Nylander
F. dakotensis Emery
F. obscuriventris Mayr
F. reflexa Buren
F. impexa Wheeler

F. whymperi adamsi Wheeler

F. ulkei Emery

F. sanguinea subnuda Emery

F. pergandei Emery Polyergus bicolor Wasmann P. rufescens breviceps Emery

The bulk of these forms have been collected by us from habitats of the Canadian Zone, and the few which have not been obtained directly from this zone were added from literature sources (Creighton 1950; Wing 1968). It will be observed that the fauna comprises 1 taxon in the Ponerinae, 10 in the Myrmicinae, 2 in the Dolichoderinae, and 30 in the Formicinae. Thus a total of 43 species and subspecies may be regarded as definitely present in the Canadian Zone. This figure compares very favorably with the one mentioned above (40) that were recorded 26 years ago, despite the fact that a number of nomenclatural changes and corrections of misidentifications have been necessary. Several species were listed in my paper of 1946 which have been omitted here. They were all based on minimal amounts of material, and their presence in boreal localities is certainly open to doubt. Aphaenogaster tennesseensis was represented by one individual from Hovland, Minn. How it came to be there is still unexplained. Leptothorax texanus was also based on one specimen, and though its identity has been rechecked, I cannot account for its presence in Duluth. Formica cinerea montana was taken once at Duluth, quite unexpectedly, and the explanation offered earlier seems still to be the most plausible, namely, that as the result of destruction of continuous dense forest in the Lake Superior district, and the growth of many open grassland areas, this ant may have extended its distribution from its normal range further south. Specimens of ants previously identified as Formica fusca gelida are now known to be the same as Formica neorufibarbis algida, a common ant in the forests of northern Minnesota, Michigan, and southern Canada. Gelida is a western subspecies which occurs as far east as Saskatchewan and may make contact with the eastern algida somewhere in Manitoba. Finally, Formica emeryi was reported from one individual collected at Saganaga Lake, Minn., on the Canadian border. This species is very problematical, and the one example of it we have from northern Minnesota is so far removed from its type locality, Colorado Springs, Colo., that the difficulties are thereby compounded. It is very rare and practically unknown except for type material. Some persons question the validity of its existence as a species. I have

Table I. Comparative zonation of ant faunas

Subfamilies	Mid-continent		Colorado*	
	No. species	%	No. species	%
	Arctic		Alpine	
Formicinae	2	50	5	83
Myrmicinae	$egin{array}{c} 2 \ 2 \ 4 \ \end{array}$	50	1	17
TOTAL	4		. 6	
	Hudsonian		Hudsonian	
Formicinae	2	50	20	77
Dolichoderinae	0	-	1	4
Myrmicinae	2	50	5	19
TOTAL	4		26	
	Canadian		Canadian	
Formicinae	30	69	44	75
Dolichoderinae	2	4.6	1	2
Myrmicinae	10	23	13	22
Ponerinae	1	2.3	0	
TOTAL	43		58	
	Alleghenian		Transition	
Formicinae	63	73	70	60.2
Dolichoderinae	2	2.34	5	4.3
Myrmicinae	20	23	39	33.5
Ponerinae	1	1.17	2	1.72
TOTAL	86		116	
	Carolinian		Upper Sonoran	
Formicinae	52	48.4	65	51
Dolichoderinae	6	5.6	6	4.8
Myrmicinae	40	37.2	52	41
Dorylinae	$\frac{2}{7}$	$\overset{2}{6.5}$	1	0.8
Ponerinae		6.5	3	2.4
Total	107		127	

*Alternative terminology for altitudinal zones in these mountains from the higher to the lower elevations is: Alpine, Subalpine, Montane, Submontane (or Foothill), and High plains,

omitted it from the present list as not typical of the Canadian Zone fauna, but inasmuch as we know so little about the ant and its distribution (for adequate samples have never been collected) and cannot tell actually what *emeryi* represents, I prefer to withhold it from synonymy. The ant has been discussed before and reasons given for its continued tentative recognition (Gregg 1963).

Of the 43 taxa listed above as characteristic of the Canadian Zone, 30 of these, or 70%, belong in the Formicinae, and 10 forms, or 23%, are myrmicine. Thus 93% of the fauna is made up of ants in the two largest subfamilies, with a very poor representation in only two of the other subfamilies of ants. The dominance of these two groups, formicine and myrmicine, is here even more striking than in the Carolinian and Alleghenian zones. For a numerical comparison of the species in all three zones see Table I.

Proceeding north of the Canadian Zone, one enters what Merriam termed the Hudsonian Zone, and which may also be called the Subarctic Zone. An opportunity to collect in a typical subarctic habitat, where trees are definitely dwarfed in stature, was not afforded, but samples were obtained in Hudsonian forest (composed of tall trees) in the vicinity of Churchill, Man. In view of the fact that our far northern collecting was done in the vicinity and close to Churchill, it will be treated

as a unit (Fig. 2). Churchill is situated in arctic tundra, but the boundary between tundra and forest is a very few miles south of the town. In fact the forest-tundra ecotone is an extremely irregular line, penetrating far inland in some places and extending, especially along river valleys, almost to the coast of Hudson Bay in other places. Observations along the railroad showed that a gradual dwarfing of the spruce trees making up the bulk of the forest occurred over a distance of about 100 miles, with occasional clumps or stands of trees that seemed to approach normal Trees generally became fewer and further apart, and muskeg or tundra heath slowly became more and more dominant until only they occupied the scene, and conditions were apparently truly arctic. But it must be emphasized that these changes were not abrupt, and in no way closely resembled the timberline krummholtz that typifies the transition between subalpine forest and alpine tundra on high mountains of western United States, where the changes are rapid and occur over a distance of a few hundred feet of elevation. As indicated above, subarctic forest follows the watercourses, and since Churchill is located at the mouth of the Churchill River, a major drainage channel, the forest grows along this valley and almost reaches the sea. This forest was visited at a point approximately 4 miles south of Churchill, and undisturbed forest as well as forest margin conditions along an abandoned roadway, were available. Composition of the forest included black spruce, tamarack, willow, and birch as trees, with an understory of Labrador tea, grasses, and thick mats of mosses and lichens, particularly cushions of the large fruticose Cladonia sp. Open areas were occupied by muskeg. We had not anticipated finding many ants, if any, at Churchill, but were happily surprised to discover a few species in this forest, and considering its latitude (58°45′ N.), in moderate abundance. The species of ants collected are as follows:

Myrmica brevinodis Emery (3) Leptothorax canadensis Provancher (4) Camponotus herculeanus (Linnaeus) (9) Formica neorufibarbis algida Wheeler (5)

The mature tundra vegetation they describe as a *Cladonia-Ericaceae* Climax, apparently in equilibrium with, and adapted to, the regional climate. Their map (Fig. 1, p. 48) shows clearly that such climax occurs at Churchill, but that numerous other seral communities are present as well. The plants of this climax include lichens of the genera *Cladonia*, *Cetraria*, etc., ericaceous plants such as Labrador tea (*Ledum*), various species of *Vaccinium* (squawberry, blueberry), the shrub Andromeda (*Andromeda*), and such other plants as the crowberry (*Empetrum*), salmonberry (*Rubus*), several bushy dwarf willows (*Salix* spp.), and the dwarf birch (*Betula glandulosa*). This analysis accords well with the general classification of the climax tundra as "tundra heath".

tundra as "tundra heath".

The authors studied the animal constituents of these communities (both vertebrate and invertebrate) with a view to their proper allocation. They concluded that most animal species must be regarded as permeant, that is to say, the animals occur and move about in various seral stages and in the climax, during the course of their respective life-histories. Few seem to be closely or critically associated with the climax alone or any other community. The barren-ground caribou, for example, appears to feed mainly in the climax, and the arctic hare breeds there by preference. The musk ox feeds mostly in seral stages where grasses and sedges are more abundant, but all of these animals move about freely over the tundra. The insects are generally wide-ranging in the adult flying stage. It was suspected that they may show greater limitations during developmental (larval and nymphal) stages owing to specific food requirements, but this could not be investigated in detail and information of this nature remains virtually unknown.

*Number of records obtained.

[&]quot;Shelford and Twomey (1941) published a detailed investigation of the plant-animal communities of the Tundra Biome in the vicinity of Churchill. Their study over several summer seasons (1931, '32, '33, '34, '36, and '39) revealed a good many details about the tundra in mid-continent North America, and involved work on various successional or seral stages all leading to climax tundra. The sand-gravel sere, the rock sere, and the clay sere were recognized as important terrestrial successions, and such stages or associes as the Elmus or wild rye, the Poa sp. or bunch grass, and the Dryas or arctic dryad communities were analyzed. Communities and successions in lakes and ponds of the region were studied to some extent also. The climax tundra is shown to develop eventually whether succession starts on any of the above substrata, including the hydrosere. Rather than having a deep soil with characteristic profile, as is so often associated with climax communities farther south, the substratum essential for climax tundra is a thick mat of peat (climatically retarded partially decayed accumulations of dead plant remains). This mat will develop on sand, clay, rock, or frozen masses of sphagnum moss. The mat must reach at least 10 cm. in depth in order to support climax vegetation. Raw mineral soil (or bed rock) will continue to exist under it, in about the condition it was left after recession of the glaciers.

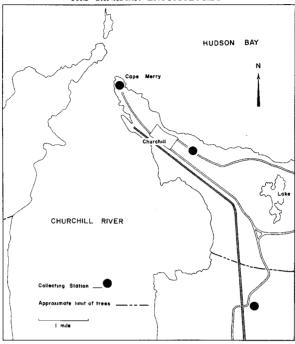


Fig. 2. Churchill, Man., and vicinity.

The microsites in which these ants were found showed considerable variety. The samples of *Myrmica* occupied the moss mat, a hummock above the general mat surface, and a mid-stage decaying log which I have elsewhere described as "log stage 3." Larvae and pupae were abundant in one colony. The *Leptothorax* all occurred in well-rotted logs, again of stage 3 decomposition, and one nest contained a very large number of larvae and pupae. *Camponotus* was found under wood (one case, a deälated female presumably starting a colony), in log stage 3 (3 colonies and 1 founding female), log stages 3 and 4 (1 colony), and one very populous colony in a stump (log stage 4). Larvae and pupae were present in abundance for all female castes in the latter sample. The records of *Formica* were from a soil hummock, log stage 2 and log stage 3. A male pupa and the larvae and pupae of both female castes were obtained. All collections were made on 8 August 1969, which was one of several very warm days. Temperature measurements at this forest site gave the following results:

Air (1 ft above soil) — 92°F Soil (surface of mat) — 95° to 96°F Soil (4 in. depth) — 69° to 70° F

Two tundra sites in the immediate vicinity of Churchill were visited, one a short distance east of town, and the other at Cape Merry, a peninsula restricting the mouth of the Churchill River. Both of these locations are on a ridge of exposed

^{**}Scoggan (1959) provides certain climatic data with respect to the Churchill area. Thirty year records of temperature and precipitation at this town show that the monthly averages of daily mean temperature range from a low of -19°F in January to a high of 54°F in July, and that the annual average for this period of records is 18°F. A 15 year period of observation shows the average monthly minimum temperature for January, the coldest month, to be -40°F, and the average monthly maximum temperature for July, the warmest month, to be 82°F. The average of maximum temperatures without regard to the month in which they occurred was 84°. The very highest temperature recorded was one for July at 96°. Our isolated readings, then, are in line with these records. The average monthly precipitation at Churchill ranges from a low of 0.48 in. in January to a high of 2.69 in. in August. The annual average is 15.96 in. of which 10.27 in, is in the form of rain, and the remainder forming an annual average snow depth of 56.9 in.

Pre-Cambrian rocks which in general are well drained. A search for ants was at first without success, but later a number of nests were revealed under stones. The circumscribed distribution of these colonies was particularly notable on the ridge east of town. Level areas and those with slight depressions were boggy, the soil saturated and cold. Though several hundred rocks were turned, not a single ant Where the surface sloped away, the soil was gravelly and drier, and was covered with an abundance of cobbles and boulders. The exposure was generally to the south so that microclimatic conditions were doubtless much warmer. Temperature measurements should have been taken, but were omitted owing to the almost intolerable hoards of black flies. Nevertheless, it was precisely in this gently sloping site that, within a few minutes after commencing to work, we secured colonies of ants beneath the rocks. It appeared that rocks of small to moderate size were the most productive, and this can be attributed probably to the greater speed at which they are heated during the daylight hours. Larger stones and boulders lie deeper in the soil and remain permanently cold underneath. Below the ridge, where the land levels off and the general topography is very flat, muskeg is present and large areas are covered with melt water. Such locations are probably the least attractive to ants. None was found there.

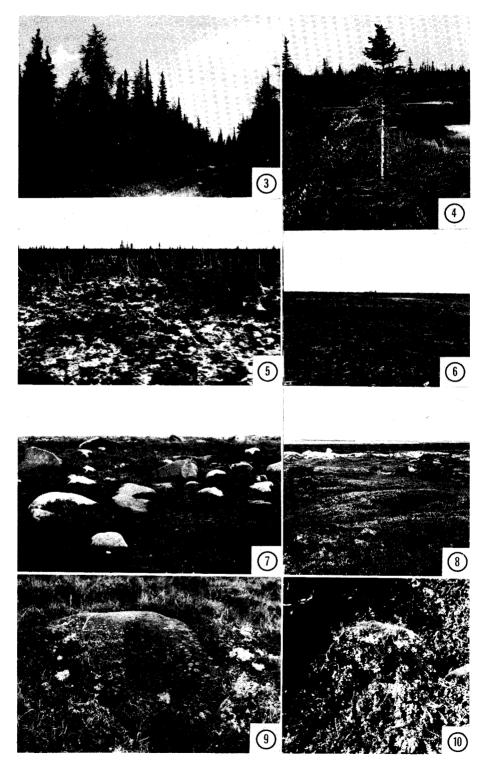
Away from the muskegs and in the areas where ants were collected, the vegetation is in general described as tundra heath. The stature of the plants is, of course, very low, in keeping with the usual nature of tundra vegetation. Most species are only a few inches high, but others may grow a foot or more, and several of the dwarfed and shrubby tree species may reach 2 to 21/2 ft. The floristic composition includes arctic dryad, arctic blueberry, crowberry, Labrador tea, arctic sunflower, arctic daisy, arctic laurel, arctic cotton, arctic birch, several arctic willows, bearberry, grasses, sedges, mosses, and crustose, foliose, and fruticose Ten collections of ants were secured from the tundra heath represented by the following forms:6

Leptothorax canadensis Provancher (1) L. canadensis kincaidi Pergande (5) Camponotus herculeanus (Linnaeus) (1) Formica neorufibarbis algida Wheeler (3)

eIn their work on the tundra at Churchill, Shelford and Twomey (1941) so far as ants are concerned make only brief mention of these insects. Ants were encountered during the 1939 season and turned up in a soil quadrat survey involving five seral stages and the climax. They accounted for 18% of the insects collected from soil (others were Diptera 59%, Coleoptera 10%, and beetle larvae 12%), but no information was given as to what or how many were in each community, and none of the ants was identified to genus or species. For insects in general, and especially the flying insects, the order Diptera vastly outnumbered all other types, accounting for 80% and more of the fauna.

Although the majority of tundra animals are classed as permeant, it would appear that in ants we may have examples of species that are truly associated with climax or other communities. Ants are sedentary as colonies, and except for their colonizing flights, do not range far as individuals. In this regard they are somewhat like plants, having relatively fixed locations, and therefore may be useful in characterizing communities along with the dominant plants. The species we collected seemed to be in what Shelford would regard as climax lichen-heath tundra, or at least late subclimax. Certainly they were associated with coarse-grained, rocky, well-drained ground where some heat is available, and were always under rocks rather than clearly in the thick vegetation mat or peat. They were conspicuous by their absence from wet, soggy, cold ground of any type, even where rocks were available. Shelford's experience would indicate that ants are present also in the bunchgrass associes on a sandy substratum. Unfortunately, he did not supply names for these ants.

Figs. 3-10. 3, subarctic, spruce-tamarack forest, 4 miles south of Churchill, Man. (collecting site). 4, subarctic forest and muskeg south of Churchill. Alternating ridges and marshy swales. Note snow-protected skirt of lower branches on small spruce. 5, subarctic pygmy forest of conifers north of Herchmer, Man. Light areas are cushions of the lichen Cladonia. 6, tundra heath with a few scattered islands of remaining subarctic forest at Belcher, Man. 7, tundra heath on rocky ridge east of town, Churchill, Man. (collecting site). 8, tundra heath with dwarf willows, at Cape Merry and the mouth of the Churchill River (collecting site). 9, tundra heath encroaching upon lichen encrusted boulder. Cushion lichens, grasses, sedges, and several woody flowering species compose the vegetative mat. 10, tundra heath. Moss covered boulders surrounded by mat composed mostly of crowberry.



It appears from these few records that Leptothorax canadensis and its subspecies kincaidi overlap at Churchill. In the forest all the samples belong to the typical canadensis, and one colony was found in tundra heath. But the clear majority of nests in the tundra are referable to kincaidi. This form is a western subspecies being known from Alaska to British Columbia, Alberta, and Washington State. However, there seems to be no doubt about the determination of the specimens from Churchill, which means that this ant has a noteworthy eastern extension at high latitude. All examples were nesting under rocks, and most of them were rearing numerous larvae and pupae. The single specimen of a Camponotus minor worker was under a rock on Cape Merry, but we could not locate the colony. it came to be there remains unanswered. It should be emphasized, however, that the abundant material of herculeanus taken from the spruce-tamarack forest south of town contrasts strongly with the virtual absence of this ant from the tundra in and around Churchill. No doubt, its well known habits as a carpenter ant and requirement of wood for nesting material exclude it from the treeless tundra. Under natural conditions, this situation would act to sharply limit the distribution of carpenter ants, but in the vicinity of human habitations discarded pieces of wood might enable Camponotus to enter the tundra for short distances. Driftwood brought down the rivers and washed ashore could have the same effect. The three good samples of Formica were found under rocks, and all three had brood of larvae, or larvae and pupae, of both female castes. Collections of tundra ants were made east of town on 11 August and at Cape Merry on 12 August 1969.

At high boreal localities and even in the arctic ants are thus known to exist, but their numbers and diversity of species are extremely reduced as compared to regions much further south. The fact that established colonies, rearing brood including reproductive castes, were easily collected (providing one looked in the right places) demonstrates that ants do range to far northern portions of the continent, but in the region of northern Manitoba they would appear to have reached, or nearly reached, the limits of their distribution. Only two subfamilies manage to achieve these limits: in the forest, 50% of the species are myrmicine and 50% are formicine; in the tundra again 50% are myrmicine and 50% are formicine. One might have expected the ubiquitous and very adaptable *Formica fusca* to be present at Churchill, but it was not seen. Further and more intensive search may show that it is present.

This study has utilized the general zonal classification of ecological conditions, and has been concerned with the pattern of change at low elevations through the center of the northern half of North America. It will therefore be of interest to compare these results with those of an intensive study of zonal distribution of ants in regard to altitude in the southern Rocky Mountains (Gregg 1963). In fact the use of life zones makes such a comparison easier and more meaningful than if the correlations had to be made solely on the basis of plant formations or communities which differ so much in the austral and transitional zones of the two areas under consideration. In my study of the Colorado ant fauna the data are summarized in table II (p. 192), and pertinent figures will be drawn from this table. Although the Transition Zone is, as its name implies, intermediate between the Austral Region and the Boreal Region, it is much richer than the boreal because it shares such a large number of species with the austral and many fewer with the boreal. be noted that Merriam included the Transition Zone with his two Austral zones to make up the Austral Region as distinct from the Boreal Region. The latter was

F. fusca was taken by us as far north as Thompson, Man., in Canadian Zone forest.

composed of the Canadian, Hudsonian, and Arctic zones. For these reasons, my first list of taxa in this paper combines the ants of both the Carolinian and the Alleghenian zones, but in the accompanying tabular presentation the totals for each of these zones are given separately (Table I). There follows then a numerical comparison of the ants in this study with those of the Colorado mountains.

It is quite evident that a steady decline in numbers of species and subspecies of ants occurs as one proceeds northward from the Carolinian toward the Arctic Zone, and this parallels the same phenomenon from lower to higher altitudes in the The exact number of taxa differ in the two situations, as would be expected, since the regions are not precise replicas of each other, either ecologically or historically. The mid-continent transect represents mid-western United States and corresponding parts of Canada. The species listed for this transect are those known to occur in it, but those forms which appear only in eastern and northeastern United States and Canada are omitted, properly, and those that are characteristic of the drier western portions of the Austral and Transition Zones are also omitted. The fauna of the mid-continent transect is then made more manageable and more comparable to that of the Rocky Mountains in Colorado. The total square mileage of the former is many times that of the latter (which is 103,000 sq. miles), but it must be recalled that zonal changes are spread over a much vaster area and take place more gradually in lowland regions, whereas the zones of mountains are usually concentrated in relatively smaller areas and change abruptly in rather short distances. Even so, as the table shows, the mountain fauna is richer in species When analyzed by subfamilies, there is a close correspondence than the lowland. among all the zones, except in the Dolichoderinae of the Hudsonian where one species, Tapinoma sessile, does occur in the subalpine forests but is absent from the subarctic of Canada. The variety of species in the subalpine and alpine zones of the mountains is much greater than in the high boreal parts of Canada. I presume this is a result of the fact that such habitats in Canada are hundreds of miles removed from sources of supply in warmer regions to the south, and in contrast the upper altitudinal zones of mountains are only a few miles and a few thousands of feet in elevation separated from rich lowland faunas, that have doubtless been the source from which some new species have evolved to fit the environments of high Other factors probably also play a part in this complex situation, such as the differences in the Pleistocene and post-Pleistocene history of the two regions. It is, however, beyond the scope of this paper to enter into a discussion of the effects of glaciation on North American ant faunas.

Another interesting feature is revealed by the table concerning the numbers and percentages of Formicinae of the Transition Zone as compared to zones adjacent to it. In both the Alleghenian lowland and the Transition of mountains there are more formicines than in either the Austral zones or the Canadian. This seems to reflect the fact that the Transition Zone everywhere is augmented by some of the thermophilous species from warmer regions, as was mentioned earlier. When the Canadian Zone is reached, a marked drop in ant species is manifest, and this trend continues to the northern limit of their ranges.

The number of species in the Hudsonian of Canada appears to be very impoverished as compared to the Hudsonian of Colorado (4 vs. 26), but this may be due to the fact that we had very little time to collect in the high latitude forest. Further collecting may reduce the disparity, but I doubt that the two faunas would approach equality. As Munroe pointed out (p. 463), the most notable feature of the Hudsonian Zone as compared with the Canadian is the impoverishment of its

fauna, and stated further that a large proportion of its species are tolerant Canadianzone forms whose ranges extend northward. The same situation probably applies to the ants of the arctic and alpine tundras. The fact that ants actually occur in tundra at all is of no small consequence, especially since they comprise a group of insects noted for its intolerance of cold and wet habitats. The species collected at Churchill have been listed above, and it will be useful here to cite the species that are known definitely from the Colorado alpine tundra to show the similarities and the differences. Six species have been found there as compared to three at Churchill (leaving out Camponotus herculeanus which does not truly belong to areas beyond timberline). Ants from the alpine tundra are as follows:

Leptothorax canadensis Provancher

Lasius niger neoniger Emery

L. niger sitkaensis Pergande

Formica neorufibarbis gelida Wheeler

F. whymperi alpina Wheeler

F. sanguinea subnuda Emery

Although ants have been found in environments at Churchill that can be classified as arctic tundra, we do not yet know how much further north these insects The tundra which follows closely the southern shores of Hudson Bay is not far beyond the present timberline, and there is some question as to whether the northern limit of trees has been stabilized, after the retreat of the glaciers. extent to which ants penetrate into high arctic tundra north of Churchill remains to be investigated.8

Munroe (1956, p. 424) cites certain evidence (from Dansereau) concerning the existence of the arctic region and particularly its southern border. The isotherm of 50°F (10°C) for the warmest month is one factor, the Nordenskiöld Line is another, and the southern limit of continuous permafrost in the soil as a third factor are believed to be critical in determining the distribution of tundra. Furthermore. Porsild is credited with pointing out that insufficient summer precipitation and extreme winter dryness occasion the disappearance of trees over much of the tundra or barren grounds. He quotes Raup to the effect that the forest-tundra border, or the northern limit of trees, is still mostly an observed fact, without a completely clear explanation as to why or where it occurs. It is a boundary that reflects climate, supposedly, but how the climatic factors operate is very poorly understood.

Evidently, the question as to whether the presumed tundra at Churchill is actually true arctic tundra, is open to debate. One reviewer states that it is a sort of preclimax community sustained by strong cold winds from the ocean. I cannot deny the accuracy of this description of the conditions along the shores of Hudson Bay, and the fact that timberline there may be as yet not in equilibrium with regional climatic averages, communities seem to bear the unmistakable traits

plant growth.

Scoggan (1959) discusses the present timberline in the vicinity of Churchill in regard to whether it is as yet stabilized, and also the question of whether Churchill is situated in an area of climatically true arctic tundra. The July isotherm of 50°F (10°C) is taken by many biologists and geographers as the southern limit of the true arctic. The average daily mean temperature of 54° for July at Churchill places the town definitely south of that isotherm. The 50 degree isotherm is said to occur in most localities considerably north of the present polar limit of trees, the inference being that the forest has not yet expanded to its normal climatic limit, and that the tundra at Churchill will be invaded eventually by forest. The "Nordenskjöld line" (an isotherm based upon both mean temperature of the warmest month and the coldest month) is believed to show a much closer correspondence with the northern tree line. He concludes that probably a more accurate picture of the influence of temperature on plant growth can be obtained by combining information on summer and winter temperatures than by use of summer records only.

Scoggan also cites Thornthwaite's belief that in cold climates, growth is restricted much more by low temperatures than by reduced precipitation, and that ordinarily moisture is not a limiting factor for plants in arctic and subarctic regions. Support for this conclusion comes from studies in several arctic areas which demonstrate that tree rings are remarkably uniform in width with an absence of incomplete or stunted rings such as are often seen in regions subject to drought. The uniformity of rings is supposedly correlated with rather uniform mean monthly temperatures and soil moisture sufficient to supply the requirements for plant growth.

of an arctic environment. Regardless of how they are maintained, these communities lack trees, forests are absent, and the resident plants that do occur are those of the tundra. The areas could in no sense be classed as subarctic forest. This is to say, that although the tundra at Churchill may owe its existence to very special circumstances and may be quite impermanent, so far as ants and other insects are concerned, they are living under arctic environmental control at the For all practical concerns the ants are living in tundra. present time. geologic times tundra existed at much lower latitudes, but the fact that the tundra of those times, was a climax vegetation, was slowly on the move, and the fact that these latitudes are no longer clothed with arctic plants, does not justify a claim that the regions, at the time in question, did not support arctic tundra. We do not look for ants to occur much further north of Churchill as conditions no doubt become far too severe for them. If this proves to be true, it can then be said that these insects tolerate low arctic situations, or the mildest of the arctic areas, but are rapidly excluded from the vast stretches of tundra toward the pole. It should be further emphasized that in our studies of Colorado ants, most of the alpine tundra records are from the lower elevations of this zone, approximately from 11,500 to 12,500 ft. Some go to 13,000 ft, but these are few and ant populations disappear before the highest altitudes and mountain summits are reached. It is to be expected that a comparable pattern of distribution will be demonstrated for the high latitude or arctic tundra.

The writer is keenly aware of the fact that our records of ant occurrence in northern Manitoba are decidedly fewer than those for more southerly regions, but the reasons are obvious. Ants as a group are generally thermophilous, and they are especially intolerant of cold and wet situations and dark forests. The boreal ant fauna is widespread but is composed of a monotonously small number of species, which therefore does not attract much attention and myrmecologists have tended to carry out their studies elsewhere. Collections which include ants have been made at various stations in far northern localities, it is true, but these records are mostly the by-products of other investigations. In the case of Shelford and Twomey the identity of the species was not even reported. I believe it is correct to say that the present study represents the first effort to concentrate on the ant fauna of high boreal and arctic stations in central Canada, and was performed by those whose primary interest is in the taxonomy and distribution of ants. Inasmuch as the number of species in the far north is very small, the paucity of records is much less serious than it would be in the more variable and faunistically rich austral regions. Admittedly, a great deal more information is needed about the ants of northern Canada, and it is hoped that new records will steadily accumulate. However, this report on the subject as it now stands seems fully justified.

The nomenclature used in this report is consistent with that which I employed in 1963, therefore it is not necessary here to repeat a taxonomic synopsis complete with subgeneric allocations. It will be advantageous, however, to indicate the subfamilies in which the various genera involved in this study belong, so that the discussions concerning zonal distribution of ants may be clarified.

FORMICIDAE (with subfamilies and genera)

Ponerinae Stigmatomma

Stigmatomma Proceratium Sysphincta Ponera DORYLINAE Eciton

MYRMICINAE
Myrmica
Stenamma
Aphaenogaster
Pheidole
Crematogaster
Monomorium
Solenopsis
Myrmecina
Harpagoxenus
Leptothorax
Smithistruma
Tetramorium

DOLICHODERINAE

Dolichoderus

Iridomyrmex

Dorymyrmex

Tapinoma

FORMICINAE

Brachymyrmex

Camponotus

Paratrechina

Prenolepis

Lasius

Formica

Polvergus

It may be noted that 28 genera are reported for the mid-continent area. A similar number of genera (total of 29) comprise the Colorado ant fauna, but there are a number of differences between the two regions. Present in the mid-continent but absent from Colorado are: Proceratium, Sysphincta, Harpagoxenus, Smithistruma, Tetramorium, Dolichoderus, and Paratrechina. In contrast, those present in Colorado but absent from the midlands are: Manica, Pogonomyrmex, Veromessor, Epipheidole (now regarded as synonymous with Pheidole), Sympheidole, Forelius, Liometopum, and Myrmecocystus.

The use of subspecies terminology has been retained. There is a tendency by some myrmecologists to elevate every recognizable infraspecific form to full species rank, and in certain instances this would appear to be justified, but it does not follow that the subspecies as a category is non-existent among ants. Each case needs to be judged on its own merits. There is a good deal of intergradation between closely related forms, and it seems incredible that all such mixing is taking place among fully differentiated species. While interspecific hybridization in animals is known, on the whole species are regarded as reproductively isolated populations, and if the amount of intergradation observable among ants, resulting from supposed interbreeding, is occurring with numerous full species, such a condition puts a severe strain on the cardinal criterion of the species status.

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