

BIOLOGICAL CONTROL AGAINST THE LARCH SAWFLY, PRISTIPHORA
ERICHSONII (HTG.) IN CANADA

by

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TABLE OF CONTENTS

	<u>Page</u>
I INTRODUCTION	1
II THE ORIGIN OF THE RESISTANCE OF THE LARCH SAWFLY TO <u>M. TENTHREDINIS</u> FROM THE STANDPOINT OF EVOLUTIONARY THEORY	
Statement of the Hypothesis and Problem	1
History, Background and Speculation	2
Evidence from Experimental and Survey Studies	25
Geographical Strains of <u>M. tenthredinis</u>	34
Conclusions	
(a) Nature of the immunity reaction	36
(b) Origin of resistance	38
III ADDITIONAL SPECIES OF PARASITES RELEASED AGAINST THE LARCH SAWFLY	41 ✓
IV BIOGEOGRAPHY - THE PROBLEM OF THE ORIGIN OF THE LARCH SAWFLY IN NORTH AMERICA	44
Characteristics of introduced species	44
Origin of North American Larch Sawfly	47
APPENDIX I	64
REFERENCES	66

I. INTRODUCTION

This report is an expanded version of a paper presented at the Twentieth Annual Conference, North Central Branch, Entomological Society of America, Louisville, Kentucky, March 24-26, 1965. It is planned to write up portions of this material in greater detail for separate publication. The first of these is now being compiled and is tentatively titled "A Cartographic History of the Larch Sawfly in North America." The proposed title for the second paper is "The Origin of the Resistance of the Larch Sawfly to its Parasite Mesoleius tenthredinis Morley from the Standpoint of Evolutionary Theory". Since these manuscripts will not be ready for submission until the fall of 1965 at the earliest, it was decided to prepare this interim report for the information of those for whom the subject is of interest at this time.

The first section deals with the history and results of studies on the P. erichsonii - M. tenthredinis relationship; the second is a brief review of the renewed attempt to obtain biological control in Canada involving the importation of additional species of parasites from Europe and Japan, and the final section is a re-examination of the problem of whether the larch sawfly is a native or an introduced species. In this latter section a cursory review is attempted of the literature bearing on the hypothesis that all holarctic species that are not tundra forms (i. e. forms having at least part of their range in tundra) are either introduced species or species which have achieved their present holarctic condition through long-distance dispersal.

II. THE ORIGIN OF THE RESISTANCE OF THE LARCH SAWFLY TO M. TENTHREDINIS FROM THE STANDPOINT OF EVOLUTIONARY THEORY

Statement of the Hypothesis and Problem

In Manitoba, about 1940, an outbreak of the larch sawfly began. Rearing of cocoons revealed that the parasite M. tenthredinis which had been credited as being a very effective parasite in former outbreaks, was present at a very low level. Dissections of larvae were made and it was found that most of the eggs that had been deposited by the parasite were encapsulated by blood cells of the host. Experimental studies showed that the capsules inhibited embryonic development and eventually killed the parasite (Muldrew 1953). It has been postulated that this resistant form of the larch sawfly appeared fortuitously as a mutant which had considerably greater survival power than the susceptible form and which, as a consequence of natural selection, increased rapidly to become the dominant form of the larch sawfly over a large area. This development of a resistance mechanism by the larch sawfly against M. tenthredinis has been cited as an example illustrating that the kinds of mutations observed in Drosophila and other organisms in the laboratory can provide a basis for the type of character change actually observed in populations in the field (Ross 1962 p. 85). The evidence on which this hypothesis

is based is largely circumstantial and should be carefully examined to determine the extent to which it supports the supposition.

Mayr (1963, pp. 432-3) points out that the present state of knowledge concerning speciation and genetic change in populations of uniparental, asexually reproducing animals is poor. He states that with plants, if each morphologically distinct clone is considered to be a microspecies, then a single mutation may indeed produce a new "species". The majority of authors accept the view, however, that even though there are morphological differences between strains that are not bridged by gene flow, there is usually so much morphological agreement among these strains that it is justifiable to treat them as components of collective species. Mayr points out though, that amongst the lower animals not a single case is taxonomically well analyzed and he poses the following as questions for investigation:

"What form of competition is there between strains? How often and under what circumstances do such strains become extinct? If there is continued mutation in such strains, why does it not lead more often to the development of morphologically distinct full species? Why do such strains remain bunched as collective species? From what source do they receive the genetic variability that permits them to cope with natural selection and to continue evolving? Is it possible that a sexual phase does occur in such species under exceptional circumstances and that it provides an equalization of the gene contents of the various diverging strains?"

Recently in the United States, the President's Science Advisory Committee in a report entitled "The Use of Pesticides" (1963) discussed biological control as an alternative to chemical control. They stated that there are two disadvantages of the biological control method that are particularly important; (a) that control of the pest is seldom complete enough to prevent economic damage, and (b) that "the host may become resistant, just as it may develop resistance to chemical controls". As an example of the latter they cite the development of resistance among Australian rabbits to myxomatosis. Swan (1964, p. xiv) cited the resistance of the larch sawfly as the only case on record where a host has become resistant to a parasitoid that had formerly been an effective biological control agent. It is thus important to determine whether the development of the resistance of the larch sawfly to *M. tenthredinis* is fundamentally similar to the development of the resistance of insects to insecticides and whether this case can be cited as an example indicating that resistance of hosts to parasite enemies may become more frequent if the method of biological control is pushed much more intensively in the future than it is at present.

History, Background and Speculation

The first definite records of the presence of the larch sawfly in North America came from Massachusetts and Maine in 1880. During the next six years there was an explosive outbreak throughout the New England States and the Maritime Provinces of Canada. Outbreaks then occurred progressively westward; south of James Bay about 1900; in Minnesota and Manitoba about 1909; in Alberta in 1923, and then on western larch in British Columbia in 1930.

When Dr. C. G. Hewitt was appointed Dominion Entomologist in 1909 he came directly from an investigation of the natural enemies of the larch sawfly in England. The larch sawfly had been a serious pest in the Lake District of England during the period 1904 to 1913. Parasitism of the larch sawfly by M. tenthredinis had reached 62% at Thirlmere in 1910 and 82% at Grasmere in 1912. Hewitt's studies in Canada convinced him that M. tenthredinis was not present in North America, although there is some circumstantial evidence indicating that it may have been present (Appendix I). If it was, it appears that the strain that was present was not a very effective or well-adapted one since there is no unambiguous evidence that it was detected by investigators during the period 1880 to 1910.

Through Hewitt's efforts, parasitized larch sawfly cocoons were obtained and releases of adult M. tenthredinis were made at Ottawa and in Algonquin Park, Ontario, in 1910. Parasitized cocoons were set out near Quebec City and in Algonquin Park in 1911; in Riding Mountain National Park, Manitoba in 1912, and in the Spruce Woods Forest Reserve, Manitoba, in 1913. It should be stressed that the practice of setting out parasitized cocoons, rather than releasing adult parasites only, is no longer carried out because of the danger of releasing hyperparasites. Moreover, the strain of the larch sawfly that is resistant to M. tenthredinis may also have been introduced into Canada from England at that time. Maw (1960) found that the resistant larch sawfly was present in England in 1955. There is no direct evidence that resistance was present in England as early as 1912 but there is some evidence that the effectiveness of M. tenthredinis decreased markedly following the high rates of attack recorded for 1910 to 1912. Wardle (1914) records the trend in percentage parasitism by M. tenthredinis at Thirlmere during the years 1910 to 1913 as being 62, 18, 8 and 2 respectively. In 1913 two other parasites were much more important in terms of percentage parasitism; namely Hypamblys albopictus which emerged from 25% of the cocoons and Myxexoristops stolidus which emerged from 24%. In most plantations the decline in M. tenthredinis parasitism was associated with the decline in the larch sawfly population - but not in every instance. The larch sawfly had ceased to be an important pest in Britain by 1913; the dead and dying trees were felled and, in fact, because of the war, almost all of the older larch stands had been cut by 1918. The insect was not found again in Britain in any numbers until 1948 and up to the present it has not caused any serious damage there. This is inconsistent with the hypothesis that because of the greater survival power of the resistant form, as compared to the susceptible, it increases to outbreak numbers. To fit the facts to the theory one must speculate that in Britain the complex of control factors is keeping the population down in spite of the hindrance to M. tenthredinis caused by the resistance reaction. Parasites apparently do not form an important part of this complex as Maw (1960) found M. tenthredinis to be the only parasite present in 1955.

Thus it may be that the resistant larch sawfly was introduced into Canada rather than arising here fortuitously. One can argue that the original mutation occurred in Britain or, alternatively, in continental Europe, since both the larch sawfly and its host, Larix, are known to be introduced species in Britain. According to the latter view, the susceptible form may have been introduced into Britain first, and the resistant form later. The susceptible

form may have come from the lowlands of Europe since it is known to occur in the plantations of Bavaria at present. This form may have had its origin in the lowland larch stands to the east; perhaps in Asia. The resistant form may have come from the stands of native Larix decidua in the Alps where it is known to occur at the present time. Plans have been made to test the hypothesis that the larch sawfly in Eurasia is comprised of two strains; a lowland one that is susceptible and an upland one that is resistant.

The phenomenon of the encapsulation of M. tenthredinis eggs may be examined in relation to the hypothesis often advanced by conventional parasitologists that a parasite which does not tend to kill its host is a more completely adapted type that reflects a host-parasite relationship of long standing (Wardle and Buckle 1923). Doutt (1960) has emphasized that this view is erroneous when applied to insect parasitoids. He points out that there is a preponderance of evidence indicating that the insect species of an ecosystem tend to evolve toward stable, balanced relationships or increased security of ecological position within the ecosystem. They may be aided in this by natural enemies which, although fatal in their action on the host, are themselves well-adapted species. It seems highly likely that in the initial phases of the larch sawfly — M. tenthredinis relationship, when the parasite was in the process of becoming adapted to this host, that one of the obstacles the parasite had to overcome was the encapsulation of its eggs by this host. It can be argued that with the achievement of this adaptation, M. tenthredinis may have become too successful a parasite and was thus unable to maintain a stable relationship when not held in check by encapsulation or some other similar restraining influence (vide Wynne-Edwards 1962, for a discussion of intrinsic methods of density regulation within species). Evidence can be cited from Bavaria and British Columbia to show that at times both the susceptible larch sawfly and M. tenthredinis populations both seem to virtually disappear. It can also be argued, however, that where there is a high incidence of encapsulation, as in eastern Manitoba, the parasite density has also declined to extremely low levels and this fact tends to negate the hypothesis that encapsulation favors the stability of the host-parasite relationship.

A possibility that should be considered is that resistant individuals of the larch sawfly have always been in existence at least somewhere in the world from the time that M. tenthredinis first became adapted to the larch sawfly. There may be certain regions (Alps?) where the larch sawfly has existed for a long period of time but into which M. tenthredinis has moved only relatively recently. Possibly the place where M. tenthredinis first became adapted to the larch sawfly was Asia and it may be only comparatively recently that the parasite has invaded the Alps, finding there a strain of the larch sawfly to which it was not well-adapted.

Another possibility that should be kept in mind is that what may be occurring in any given region over a long period of time is a sequence of "measures and counter-measures" on the part of the larch sawfly and M. tenthredinis populations. The degree of adaptation of the parasite may

be in a continual state of flux in a given region with changes in host-parasite relationships in different regions probably not being synchronous. An adaptation by M. tenthredinis that allows its eggs to no longer be recognized by the larch sawfly as a "foreign body" may be responded to by an adaptation of the larch sawfly involving a change in its hemocytes such that they acquire a greater sensitivity to detect the parasite eggs as being "non-self" and thus become able to encapsulate them.

On the basis of present facts and supporting evidence, however, it does not seem to be too helpful to carry speculation to this extent, although it does suggest possibilities for further investigation. In terms of the increase of the resistant strain in Canada, however, it probably does not make much difference whether resistance arose as a mutation here or was introduced from Europe.

In Canada, following the original releases of M. tenthredinis from 1910 to 1913, there appears to have been no follow-up program to monitor the establishment, build-up and spread of the parasite in Ontario and Quebec but it was found to be common in these regions 15 to 20 years later and McGugan and Coppel (1962) assume from this that the early releases were successful and that the parasite had spread widely. Criddle (1928) studied the build-up of M. tenthredinis near Treesbank, Manitoba, and found a progressive increase in parasitism from 0% in 1914 to 66% in 1920. The host was scarce there until 1926 and 1927 when an average level of parasitism of 75% was recorded for the area.

No further importations were made from England after 1913 but during the periods 1926 - 1927 and 1934 - 1945 an extensive redistribution program was carried out with releases being made in Newfoundland, Nova Scotia, New Brunswick, Quebec, Ontario and British Columbia. More than 30,000 adult M. tenthredinis were released, most of which were obtained from collections made in southeastern Quebec; indicating a high rate of successful attack for M. tenthredinis in this region at that time. Careful follow-up studies were made in the Maritimes (Reeks 1954) and in British Columbia (McLeod 1952) and parasitism by M. tenthredinis reached levels of 70% in some locations in both regions. The association of high percentage parasitism with declining outbreaks has been interpreted as indicating that this parasite played an important role in reducing host numbers in these areas. Recovery records made by the Forest Insect Survey over the past 25 years show that the parasite is now present over virtually the whole range of the sawfly in North America.

Larch sawfly populations began to increase again in southern Manitoba in 1938. Over 10,000 cocoons were collected in the Spruce Woods Forest Reserve during 1938 to 1940 but no M. tenthredinis were recovered. The parasite was found to be present in small numbers in 1941, however. Since 1940, outbreak conditions have been recorded from a progressively enlarging area now extending to New Brunswick in the east and almost to the limit of occurrence of tamarack in the west (Fig. 2). This figure was prepared mainly from data published by the Forest Insect Surveys of Canada and the Lake States. Only the outer boundaries of light infestations are plotted

for successive years. For purposes of comparison, figure 1 shows the ranges of L. laricina, L. occidentalis and L. lyalli.

The larch sawfly was recently found infesting alpine larch for the first time and tests showed that this material was typically resistant -- indicating an origin from the infestations on tamarack to the east. On the other hand, recent increases in larch sawfly populations on western larch in both Idaho and British Columbia have been found to be completely susceptible -- indicating that they originated by build-up of residual populations deriving from the outbreak of 1930-1949. If this latter outbreak originated from susceptible larch sawflies that crossed the Rockies some time approximately during 1923 to 1928, however, then the resistant larch sawfly may repeat this crossing and eventually appear in the stands of western larch. Certainly every precaution should be taken to ensure that a crossing is not accomplished accidentally through the activities of man.

In figure 2, the spread of light populations through Quebec could not be plotted as no extensive surveys were carried out during this period. It appears that the boundaries of light infestations did not advance north to the limits of the range of Larix laricina in step with the advances to the east and west, but this probably is a reflection mainly of the fact that surveys were not extensively carried out in the north. Figures 3 to 8 differ from figure 2 in that only the moderate and severe infestations are mapped but the full extent of the boundaries are shown rather than simply the outer boundary. It can be seen that as the outbreaks moved east and west the infestations in the central area subsided. The outbreak in Ontario subsided more rapidly than in the west. The moderate and severe infestations in Quebec and Labrador could not be mapped due to insufficient data but it is known that the larch sawfly was abundant and widespread in western Quebec from 1955 to about 1961 and in central and eastern Quebec from approximately 1960 to the present (Bracken and Martineau 1960; Annual Reports, Forest Insect and Disease Survey 1957 to 1963).

The question may well be asked: if the resistant strain that appeared in Manitoba originated from the cocoons placed in the bogs during the parasite releases of 1912 and 1913, why did it not also appear in Quebec and Ontario where similar releases were made in 1911? The answer may be that the material that was placed out in 1911 was collected in different plantations in Britain than was the material placed out in 1912 and 1913 and resistant larch sawflies may not have been present in the earlier collection. Alternatively, if they were present, they may have been comparatively few, or not well-adapted to the new conditions, and may not have survived in Canada.

The encapsulation or resistance reaction that was first noted in central Manitoba was subsequently found to be characteristic of populations from the outbreak areas that developed east and west of Manitoba. This fact, in conjunction with the general appearance of the outbreak boundary as spreading out, with considerable regularity, from one epicenter, supports the theory that it is the larch sawfly adults themselves that are spreading. If resistance has appeared independently in a great many locations, one would not expect such regularity. If climatic release is postulated as an important prerequisite to the outbreak conditions one must demonstrate that

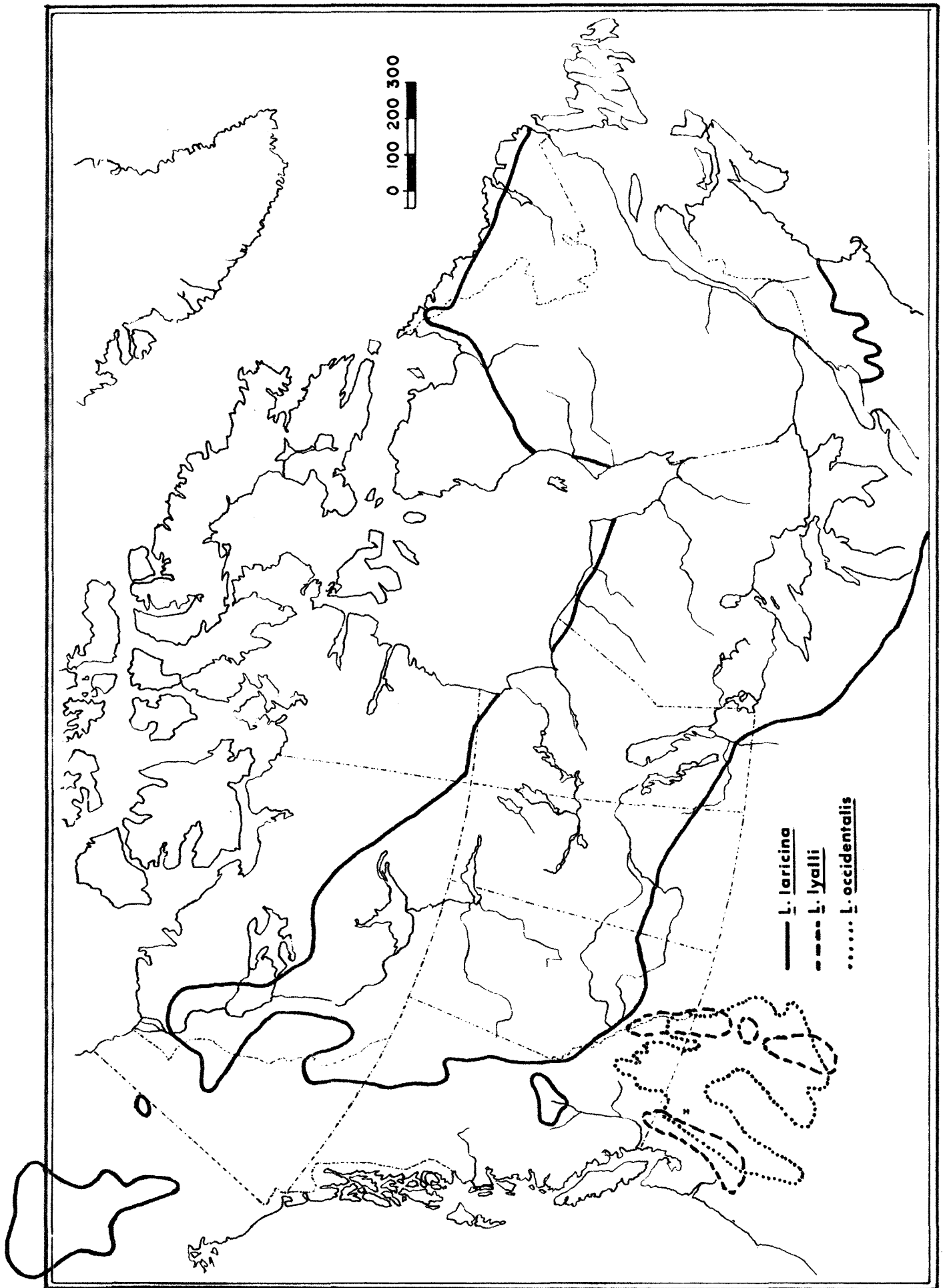


Figure 1.- Ranges of *Larix* species in North America.

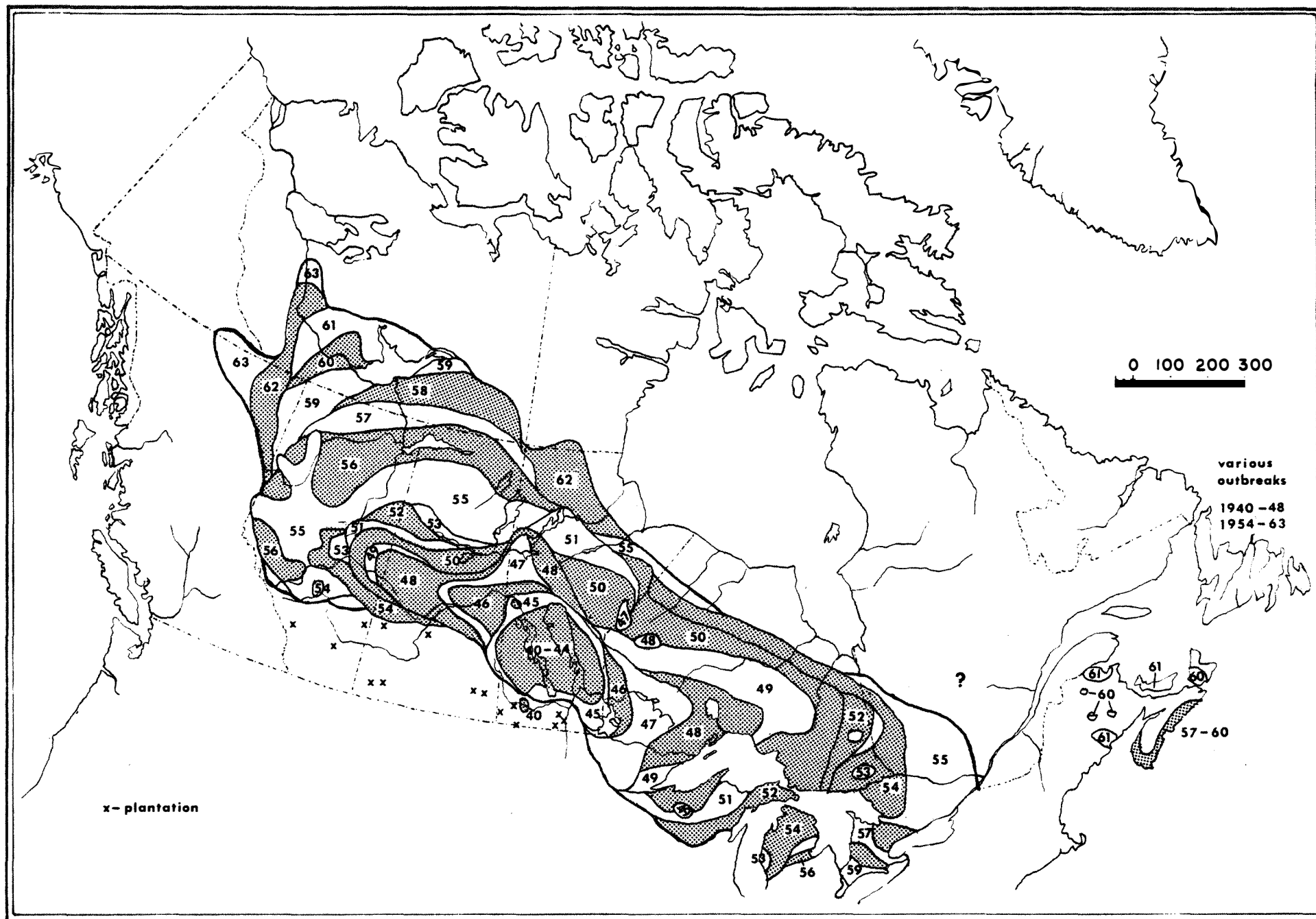


Figure 2.- Boundaries of light infestations of the larch sawfly 1940 to 1963, showing annual extensions.

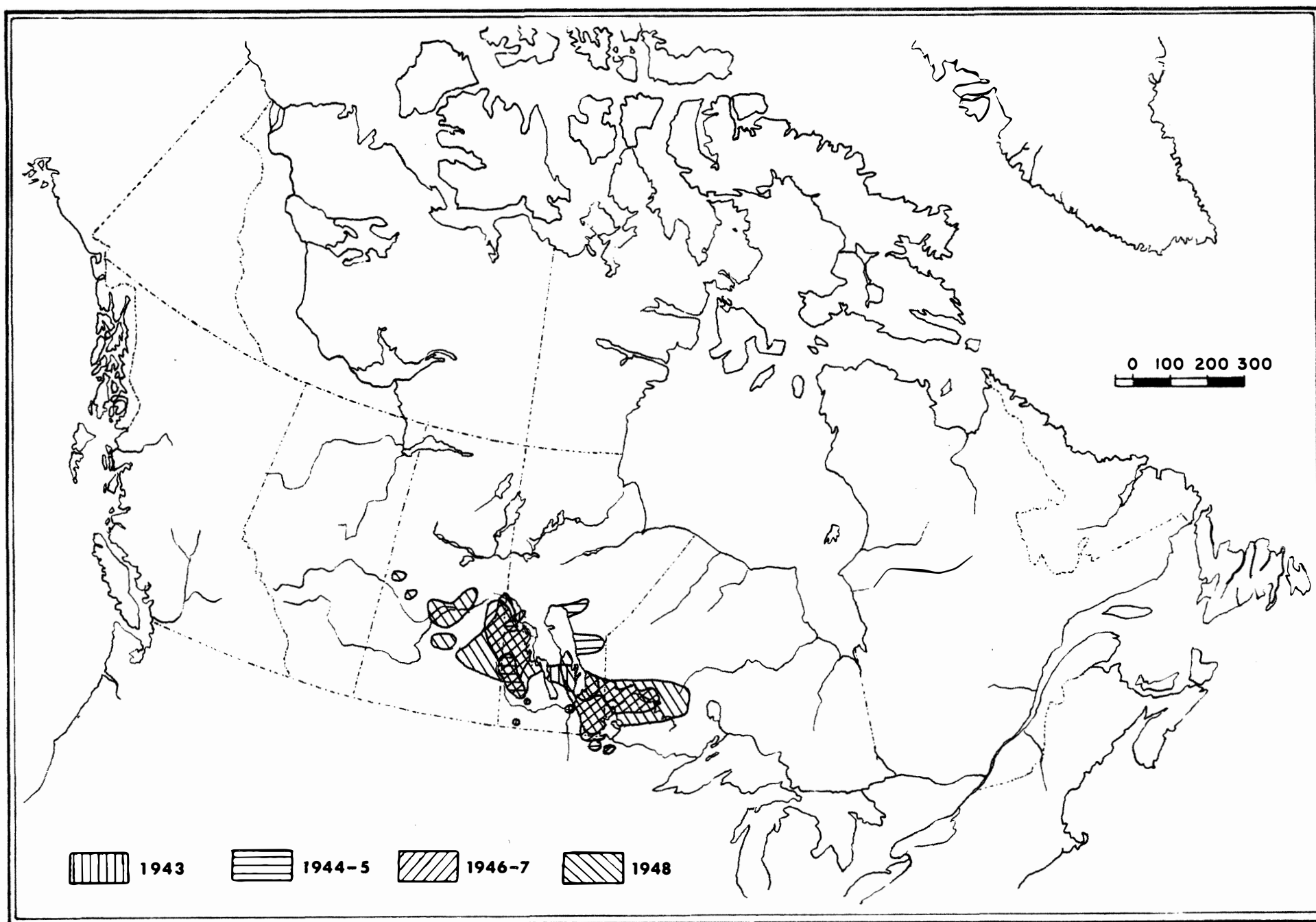


Figure 3.- Combined moderate and severe infestations of the larch sawfly 1943-1948.

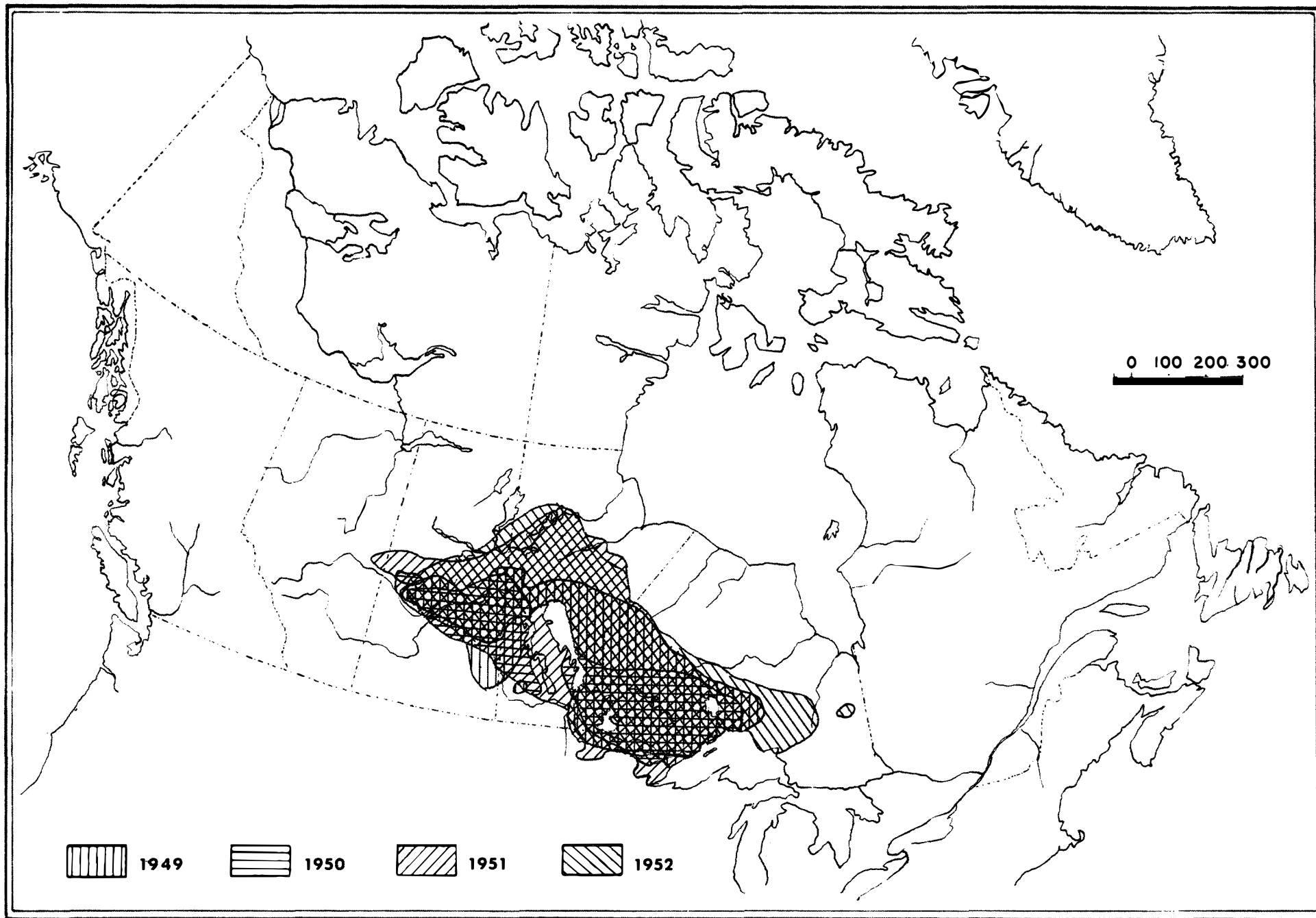


Figure 4.- Combined moderate and severe infestations of the larch sawfly 1949-1952.

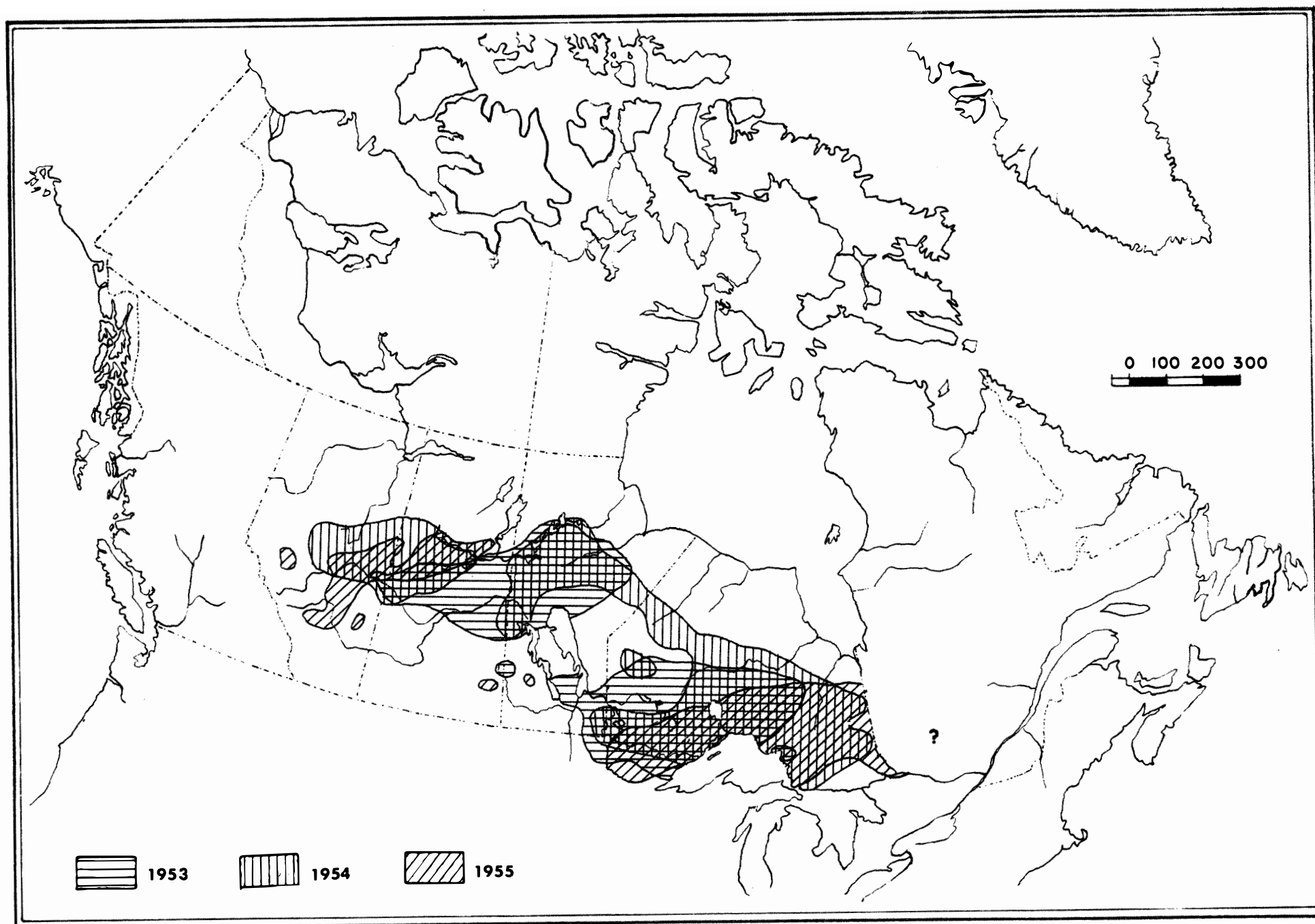


Figure 5.- Combined moderate and severe infestations of the larch sawfly 1953-1955.

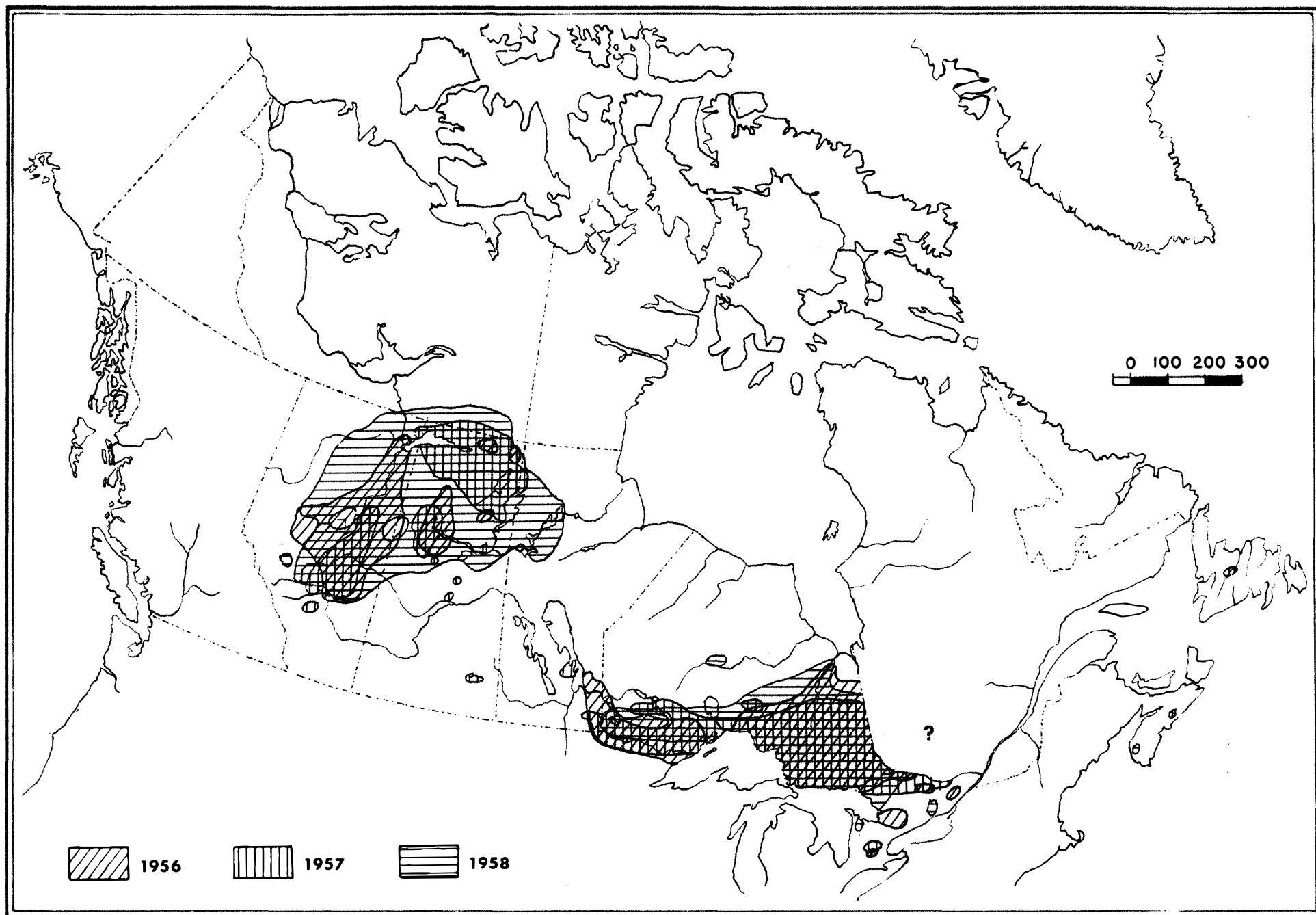


Figure 6.- Combined moderate and severe infestations of the larch sawfly 1956-1958.

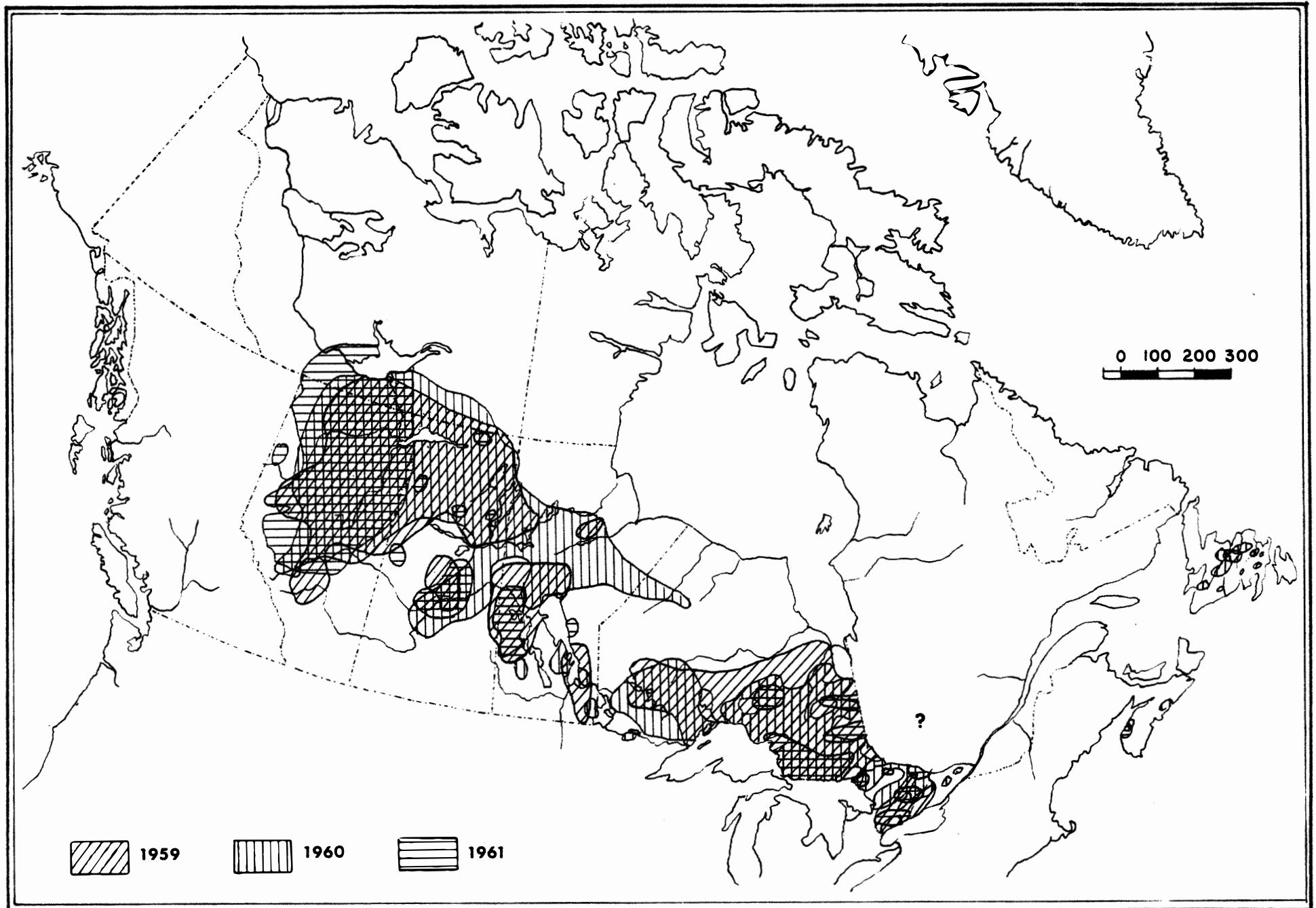


Figure 7.- Combined moderate and severe infestations of the larch sawfly 1959-1961.

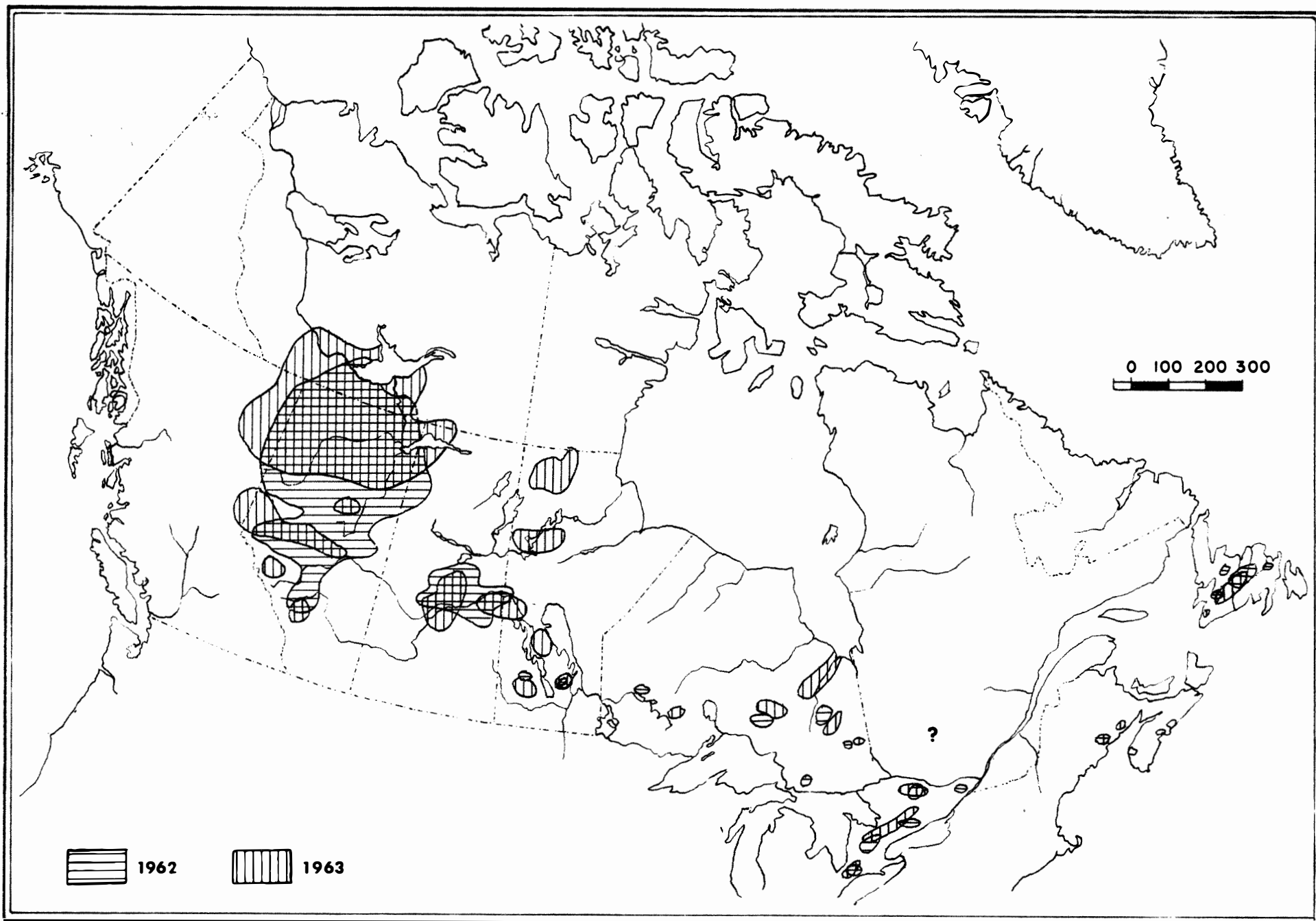


Figure 8.- Combined moderate and severe infestations of the larch sawfly 1962 and 1963.

a period of favorable weather preceded the population build up as it developed eastward and westward over the 20-year period and this seems unlikely although, admittedly, it has not yet been thoroughly studied. An argument against the applicability of the theory of climatic release in this case is that the influence of weather on the larch sawfly is largely exerted through its effect on the fluctuations of water levels in bogs, which determine, to a great extent, the survival of larch sawflies cocooned in these bogs. The water tables in native stands of tamarack and nearby plantations that have been subjected to the same weather conditions have often differed greatly because of differences in elevation and drainage. During the period of outbreak, however, the infestations in both these native stands and the adjacent plantations have occurred roughly contemporaneously.

If the larch sawfly has indeed spread by the dispersal of adults, the evidence indicates that this has occurred at an average rate of 60 to 70 miles per year, unidirectionally, over a period of at least 15 years. Although the dispersal to the west has been against the prevailing winds, it has been almost as rapid as the spread to the east. This is an indication that the larch sawfly has dispersed mainly under its own powers. On the basis of the assumption that dispersal can occur from areas harboring light infestations, the movement of the outbreak may take the form of a 'wave front' as illustrated in Figure 9 (adapted from Skellam 1955, p. 44). There is some indication from Figure 2 that this is a reasonably good representation of larch sawfly dispersal in North America since 1940, allowing for irregularities due to topographic features, lack of stand continuity, etc. Figures 3 to 8 indicate that populations in a given region usually begin to decrease after five or six years of moderate to heavy attack and this is shown in Figure 9.

An alternative assumption is that dispersal occurs from a given region only after populations have built up to a high level in the region. The minimum time between the appearance in a region of the first invaders and the time that heavy defoliation occurs is estimated to be about five years. On this basis, in order to account for an average rate of spread of 70 miles per year we must postulate that some of the adults must travel approximately 350 miles in one year. This hypothesis is illustrated in Figure 10. At the point of origin an initial build up occurs during the first five years. During the fifth year long-distance dispersal occurs into the area bounded by circles of roughly 70 and 420 miles radius. During years 5 to 10 continued dispersal into this region occurs in conjunction with build up in local areas. One would expect that "spot" infestations would appear which would progressively increase in size and coalesce. At the end of the period, infestations near the point of origin begin to decrease. During years 10 to 15, dispersal into, and build up within, would occur in the region bounded by circles of 420 and 770 miles radius.

The cartographic picture (Fig. 2) indicates that the 'wave-front' hypothesis (Fig. 9) is a better representation of what has occurred than is this hypothesis. A certain amount of long-distance dispersal may be

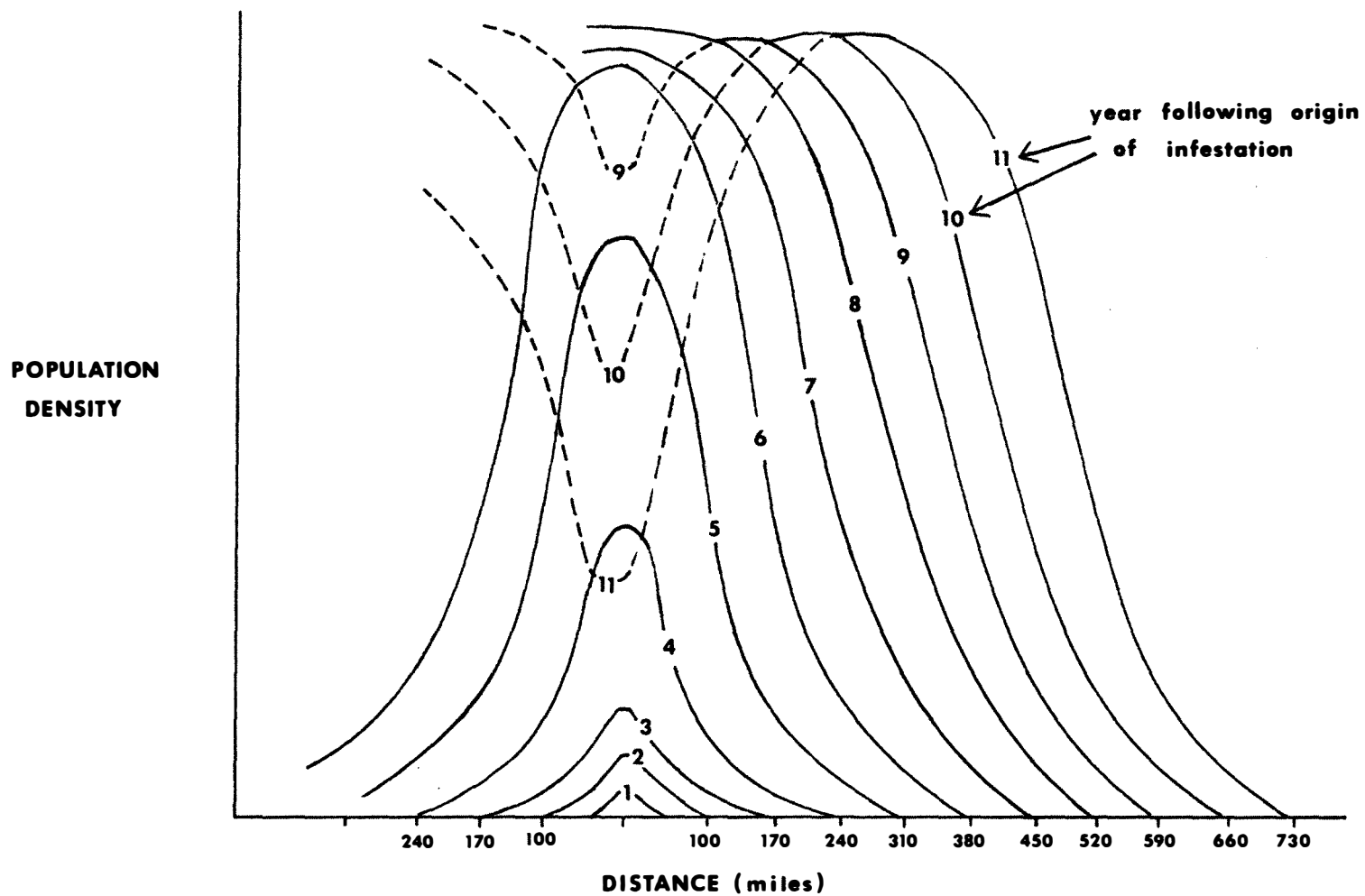


Figure 9.- Hypothetical 'wave-front' spread based on an assumed rate of dispersal of 70 miles per year.

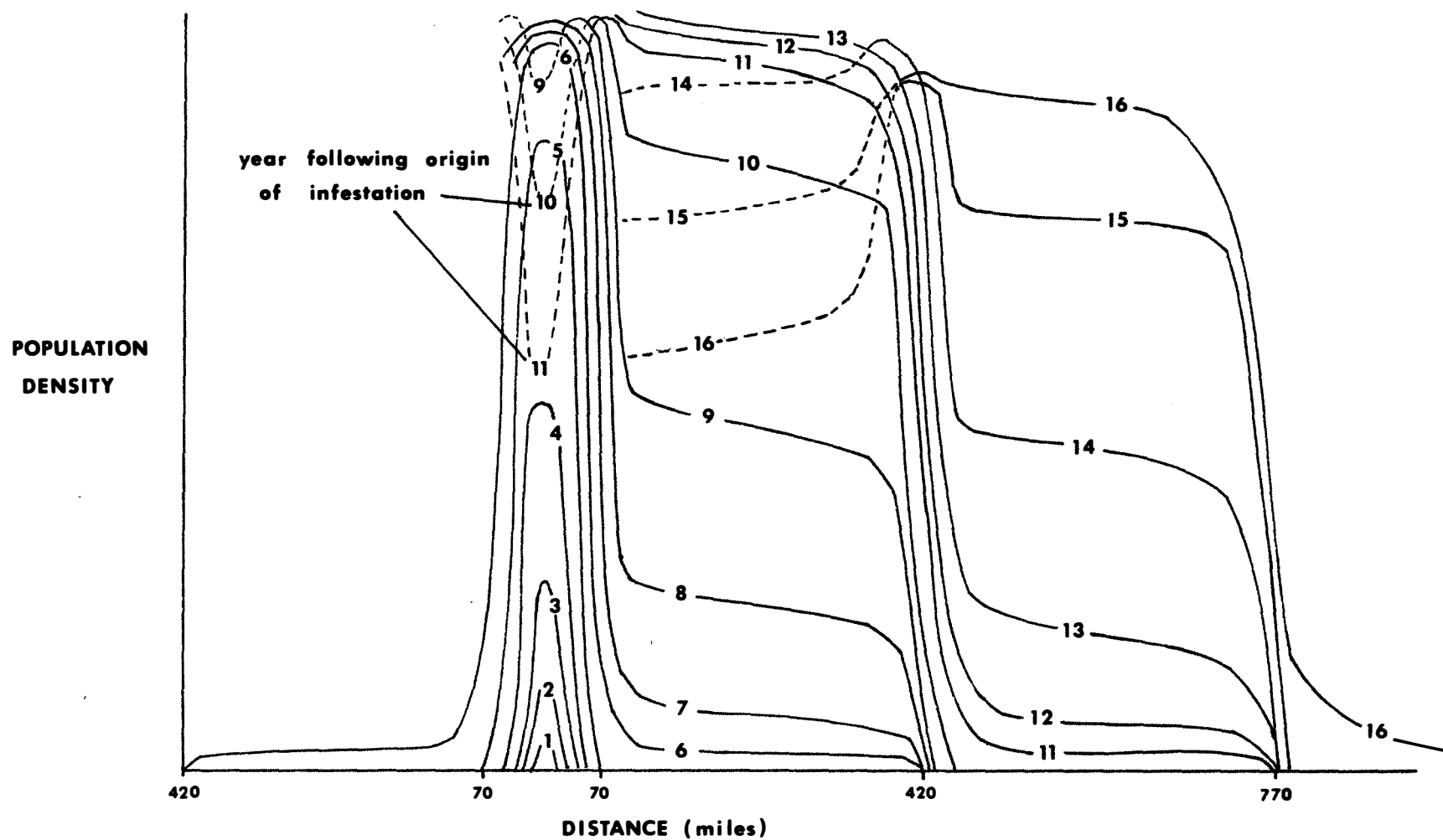


Figure 10.- Hypothetical spread based on the assumption that long-distance dispersal occurs from heavy infestations only.

involved, however, and evidence indicating that it does occur is presented later in the discussion concerning infestations in Larix plantations on the prairies. A third hypothesis is that dispersal is a combination of both 'wave front' and long-distance types of spread. Figure 11 is an attempt to illustrate this. Although populations at the point of origin are still low five years after initiation, some long-distance dispersal is postulated to occur at this time. Many hypothetical constructs could be made intermediate between Figs. 9 and 10 depending on the assumptions concerning the relationship between density and dispersal and the average and maximum distances covered by adults in any one year.

There is little direct evidence that long-distance dispersal of the larch sawfly actually occurs. A number of workers have pointed out, from observational and some experimental evidence, that most of the larch sawfly adults appear to be lethargic and fly only as far as the nearest tree to begin oviposition (Drooz 1955; Turnock 1960, p. 507). A working hypothesis might be that a small proportion of the population differs behaviorally and physiologically, although not necessarily morphologically, from the majority, and these may comprise a dispersal phase of the species.

There are some parallels between the European spruce sawfly Diprion hercyniae (Htg.) and the larch sawfly. Both have the thelytokous habit of reproduction. It is not known when D. hercyniae was introduced but it had spread westward as far as Ottawa by 1922, six years before the first known occurrence of heavy populations in America. These latter infestations occurred in the Gaspé region of Quebec, where, between 1930 to 1938, the area of heavy infestation increased from 2,500 square miles to some 12,000. The annual maps plotting the course of this outbreak (Brown and Fleming, 1938) indicate that spread was not of the 'wave-front' type. The virus disease which appeared in the southern part of the outbreak area in 1938 spread rapidly during the next four years and by 1943 the outbreak was over. The insect continued to spread in spite of low populations, however, and has now almost reached Manitoba. The spread in Ontario since 1940 shows some indication of 'wave-front' movement (Reeks 1963) but the average rate of spread (roughly 10 to 20 miles per year) is considerably lower than that postulated for the larch sawfly. There is no good evidence that the average rate of spread was greater during the period of high populations than it is now. More direct evidence exists for D. hercyniae than for the larch sawfly indicating that long-distance dispersal actually does occur. Balch (1939) stated, concerning D. hercyniae, that -

"in fairly calm weather, and particularly when exposed to direct sunlight, the adults soon take to flight. They fly strongly, and their direction is determined by air currents. A considerable amount of evidence has been obtained to show that the sawfly has an instinct for flight which is, temporarily at least, independent of the proximity of spruce. Large numbers have been observed on the tops of mountains above timberline and a great many adults drop into lakes and rivers. Although the largest distance from the nearest spruce at which adults have been taken from water is one mile, the probability is that many of these came from much

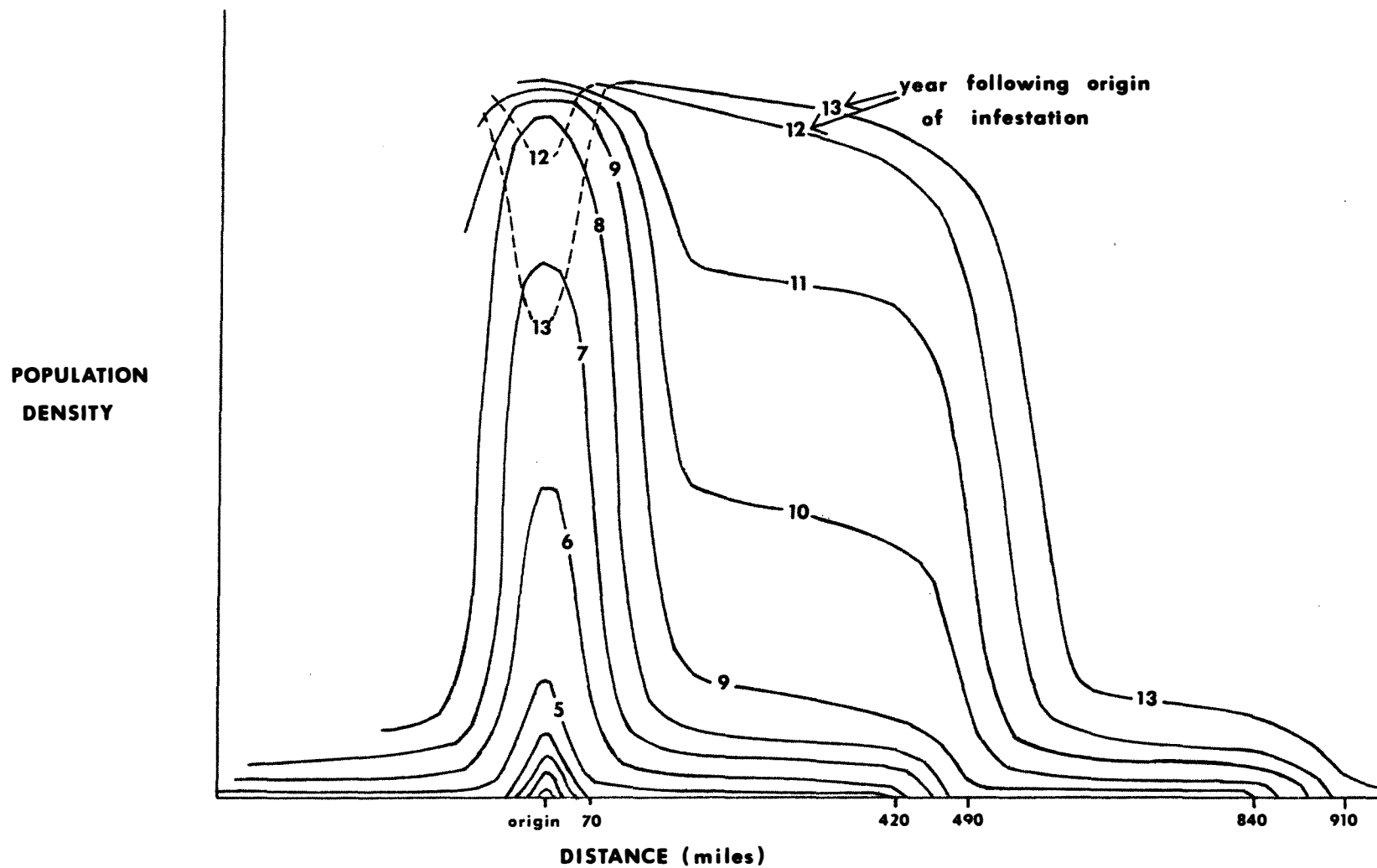


Figure 11.- Hypothetical spread based on the assumption that some long-distance dispersal can occur from light populations.

longer distances. When liberated, such adults again take to the air, flying strongly as soon as they are dried out. Studies of the ovaries of these insects show that nearly all have laid some of their eggs prior to flight but most of them are capable of laying the greater part of their normal complement of eggs after having taken flight."

Williams (1958) cites as examples of migration among sawflies; Athalia rosae Linn. which in England is an occasional immigrant from the continent but which may at times arrive in large numbers, and Athalia cordata Lip., which was seen in vast numbers by R. B. Benson in August, 1945, in South Devon flying to the east against a light east wind. Few such observations have been made for the larch sawfly but occasionally an adult has been seen flying strongly about four feet above the ground in cleared areas. Jarvis (1904) found adults floating down the Porcupine River in Ontario during an outbreak and noted that the shore of Night Hawk Lake (48° 30', 80° 00') was covered with them.

Evidence supporting the long-distance dispersal hypothesis appears to be provided by the manner in which the isolated plantations of larch south of the native stands became infested by the larch sawfly. Some of these are shown by x's in figure 2. The ones in the Cypress Hills Provincial Forest and Dollard, Saskatchewan are over 200 miles from the nearest native tamarack. Some of these are very small plantations, for example the one at Cypress Hills consists of only about a dozen Siberian larch trees. Most of these plantations were set out as small trees between 1910 and 1916. The records showing the shipments of tamarack from the Indian Head Forest Nursery Station were kindly supplied by L. O. T. Peterson (pers. comm. Sept. 9, 1963) and are shown in Table I.

Table I

Numbers of small tamarack trees shipped from the Indian Head Nursery Station, 1910-1916

Year	Manitoba	Saskatchewan	Alberta
1910	8,950	24,050	4,925
1911	1,450	5,975	1,995
1912	3,625	15,190	3,675
1913	None	None	None
1914	925	26,940	9,000
1915	None	None	None
1916	None	400	300
Totals	14,950	72,555	19,895

In addition 1,050 Siberian larch were shipped to Manitoba during 1910-1915 and 810 during 1931-1935 (Walker 1945). The records on the numbers of Siberian larch shipped to Saskatchewan and Alberta were not found but Ross (1912, 1913, 1914) reported that 3,820, 514, and 8,880 respectively, were available for distribution from the Indian Head Station in these years. Peterson reports that the reason that larch was discontinued as a shelterbelt species in 1916 was that larch seedlings flush so early in the spring that fall planting is required which is unsatisfactory to farmers.

By 1942 the trees that had survived in these plantations were quite large. Larch sawfly attack prior to 1942 is recorded for only two plantations, namely those at the forest nursery stations at Indian Head and Sutherland. The larch sawfly was first recorded at Indian Head in 1914 but 'large numbers' were present at this time and spraying was carried out. This larch sawfly may have come from the Spruce Woods Forest Reserve, Manitoba. Coxe (1910) reported that in 1908 he collected 30,000 small tamarack trees and also a carload of moss in the Spruce Woods Forest Reserve for shipment to the Indian Head Station. Nairn et al (1962, p. 248) present evidence indicating that the larch sawfly was probably present in fairly high numbers in the Spruce Woods Forest Reserve by 1908 and its cocoons may well have been present in the moss collected there. Only a few larvae were found at Indian Head in 1915 but the trees were sprayed again. The subsequent sequence of events was as follows:

<u>Year</u>	<u>Degree of Attack</u>	<u>Spraying</u>
1916 - 1920	no larvae found	no
1921 - 1926	moderate to heavy	each year
1927 - 1934	scarce	no
1935	moderate	no
1936	heavy	yes
1937 - 1942	no larvae observed	no
1943 - 1960	light to heavy	1943, 1946, 1950 - 1960

The first record of the presence of the larch sawfly at the Sutherland Nursery Station was made in 1924. In all probability the insect arrived in material shipped from Indian Head.

Reports of the attack on plantations other than the above two began to appear in 1941. The attacks occurred roughly contemporaneously with the westward advance of the outbreak in native tamarack to the north as is shown in Table II.

Table II

Records of larch sawfly attack on plantations in the agricultural
area of the Prairie Provinces

(locations in parentheses are near stands of native tamarack)

Year	Manitoba	Saskatchewan	Alberta
1941		(Crystal Lake)	
1942		Lemberg	
1944	Dauphin Dropmore Reston		
1945		Gerald	
1946	Dropmore	(Archerwill) (Armley) Dollard Saltcoats	
1947	Brandon Clearwater Franklin Gladstone Hamiota Killarney Morden Morris (Russell) Shoal Lake Sperling Waskada	(Archerwill) (Armley) (Dahlton) Dollard Gerald Langenburg (McKague) Quill Lake (Tisdale) Yorkton	
1948		Buchanan	
1950			Provost Consort
1951			Consort (Wetaskiwin)
1952			(Wetaskiwin) (Ponoka)
1953	Decker Clanwilliam McConnell Rackham Turtle Mountain Forest Reserve	Scott	(Innisfail) (Calmar) (Lacombe) Lloydminster (Oliver) (Ponoka) Provost (Red Deer) Sedgewick Three Hills Wainwright (Wetaskiwin)

Table II (Concl.)

Year	Manitoba	Saskatchewan	Alberta
1954	Carman Isabella Pilot Mound St. Elizabeth Waskada	Saskatoon Battleford	
1955-59		Cypress Hills Provincial Forest (Battle Creek Ranger Station)	
1960		Cypress Hills Provincial Forest (Battle Creek Ranger Station)	Seebe Brooks
1962			Auburndale East Kootenay fire trail (on western larch) Radium (on western larch)

(Thanks are here given to Messrs. L. O. T. Peterson and C. E. Brown for checking the records and supplying additional information.)

By 1954, Brown et al reported for Alberta that

"south of the North Saskatchewan River, from Edmonton east, larch sawflies were present wherever larch occurred."

From Figure 6 we note that moderate infestations of the larch sawfly reached southern Ontario about 1956. During the period 1957-1960 the attack of isolated plantations by the larch sawfly was commonly reported for this region.

An alternative hypothesis to that of long-distance dispersal is the postulate of build up from a residual population. Turnock (1960), for example, stated that "although the recent outbreak extended westerly from southern Manitoba there is no evidence to suggest that dispersion played any part in this movement. The rapid extension of outbreaks, the scattered nature of host stands, the lethargic behaviour of the adults, and the subsequent independent population fluctuations in adjacent stands indicate the presence of a small residual population which responded to some generally favourable condition." However, there could not have been a residual population in these planted trees prior to 1890. The insect may have been introduced as cocooned larvae hidden in the roots of the small trees distributed from Indian Head during 1910-15. It seems likely, however, that if the larvae had been common in the nursery beds containing the small trees the damage would have been severe and would have been noticed. Moreover, if the larch sawfly had been present in all the plantations listed above since the

time of planting, surely it would have been noticed during the 20 or more years prior to the time of attack. Moreover, one would expect the susceptible strain of the larch sawfly to be present rather than the resistant strain. In this connection, also, L. O. T. Peterson (pers. comm.) stated that "the practice at Indian Head of washing the roots of the tamarack seedling before dipping them in a mud bath prior to packing would go a long way towards excluding insects that might have reached the seedling plots." He also is of the opinion that if some sphagnum was shipped with the small trees in the earlier years "the probability of the adult emerging from the discarded sphagnum, laying eggs on the newly planted seedlings, and the larvae surviving to produce subsequent generations seems rather remote."

Another hypothesis is that larch sawfly adults may have been accidentally introduced into these isolated plantations by being transported in vehicles (car, train, etc.), but it seems to be pushing chance too far to propose that this is the explanation for the origin of infestation in all of the plantations. The most probable explanation thus appears to be that the larch sawfly adults flew into these plantations.

A larch sawfly outbreak occurred on western larch in British Columbia from approximately 1933 to 1949. This population was a susceptible one and M. tenthredinis became very abundant. During the later stages of the outbreak large numbers of cocoons were collected and almost 75,000 adult M. tenthredinis were obtained and released in the area between Prince Albert, Sask., and northwestern Ontario. These releases, however, failed to increase the effective parasitism significantly. No difference was found between the respective abilities of the B. C. and the central Canadian M. tenthredinis to overcome or avoid the encapsulation reaction of the resistant larch sawfly (Muldrew 1953).

In certain areas of central Canada the density of M. tenthredinis is currently at a very low level. In a life-table study plot near Rennie, Manitoba, the average density of adult M. tenthredinis for the period 1956 to 1963 was approximately 225 per acre as compared to a density of 75,000 per acre for larch sawfly adults.¹ Percentage parasitism has averaged about 0.3 in this plot. In such areas, where selection pressure exerted by this parasite is negligible, there is no evidence as yet that the susceptible strain of the larch sawfly is increasing in frequency. This situation differs from what generally occurs when insecticidal pressure is removed from field populations of a species that has developed resistance to a particular insecticide. Here there has usually been a significant and often rapid decline in resistance (Keiding 1963; but for an exception see Perron 1965). The findings indicating that reversion from resistance to susceptibility typically occurs following release from selective pressure derive from studies on cross-breeding or Mendelian populations whereas the larch sawfly exhibits thelytokous parthenogenesis and this may be an important difference.

¹ From data of the Life Table Study Group on file at the Forest Entomology Laboratory, Winnipeg.

The spread of the resistant strain of the larch sawfly appears to offer additional support to the evolutionary theorists who stress that with non-sexually reproducing forms, there is competition between lineages each descended from a single ancestor and only the most efficient lineages survive. If there is no opportunity for the spread of mutations from one lineage to another, the species must depend entirely for its evolution on the occurrence of mutations in the separate lineages. If this has actually occurred in the larch sawfly, it can be seen that it can happen with great rapidity and perhaps such species, in spite of the lack of cross breeding, can evolve as rapidly as Mendelian species.

This speculation, however, is based on the assumption that fertilization never occurs in the larch sawfly and it is important to bear in mind that this may not be correct. We know that an abundance of sperm is produced in the male; that the males often react vigorously to the presence of females when they are placed together in cages or vials and that mating occasionally occurs. It is quite possible that it occurs more readily in the field than it does in the laboratory since this is known to be the case for many other insects. It is not known whether sperm is transferred to the female or whether effective fertilization (gene-exchange) occurs. More work is evidently required on this important point. Smith (1955) has stated that if the males are nonfunctional and if mutation and structural rearrangement of chromosomes does not occur, then the abandonment of heterozygosity is progressive and irrevocable and the benefits associated with heterosis are thereby excluded. Fertilization of eggs in the larch sawfly thus might have important evolutionary consequences even if the rate at which it occurred was very low, say in one female of every thousand produced (see Dobzhansky 1951, p. 302-3). Smith (1955) implies that only the fertilization of an egg destined to be a male larch sawfly (i.e. one in which there is a failure of auto-fertilization) produces a fertile adult female since the triploids would be sterile. Thus in the larch sawfly only one or two per cent of all eggs fertilized by sperm would produce fertile adult females unless auto-fertilization were preceded or circumvented by sperm-fertilization in some way. One wonders whether such a low rate of gene exchange could have evolutionary significance. On the other hand one wonders whether the production of males would not have already disappeared through natural selection acting over a very long period of time if they are completely inutile. The larch sawfly undoubtedly evolved from a normal bisexual form as evidenced by the occasional production of males (Smith 1955) and it is assumed that it has had its present method of reproduction for at least several million years.

Evidence from Experimental and Survey Studies

During the period 1954 to 1958 an attempt was made to investigate the hypothesis that the larch sawfly populations in the Prairie Provinces were composed of a mixture of both the 'resistant' and 'susceptible' strains of the larch sawfly and that the 'resistant' form was competing successfully with the 'susceptible' one and gradually replacing it because of its postulated greater survival power. Many larch sawfly adults were obtained from

central Alberta in 1954, during the initial stage of the outbreak in this region. The split-family technique was used in which the progeny of each female sawfly selected was divided into two portions; the larger being tested for resistance by cage-parasitization and subsequent dissection and the smaller being overwintered to maintain the clone for further testing the following year. On the basis of the 1955 results some clones were designated as being comparatively resistant and others as being comparatively susceptible. However, it was later found that these differences between the clones did not persist if a sufficient number of families were tested over a series of years; all clones eventually being classified as resistant. An example is shown in Table III. Clones A and B in this table both originated with females collected at Prince Albert, Saskatchewan, but similar results were obtained for the Alberta material.

Table III

Change in rating of susceptibility to M. tenthredinis of two clones when reared over a four year period

	<u>1955 results</u>		<u>cumulated 1955-1958 results</u>		<u>cumulated 1956-1958 results</u>	
	<u>clone A</u>	<u>clone B</u>	<u>clone A</u>	<u>clone B</u>	<u>clone A</u>	<u>clone B</u>
No. of families tested	11	6	28	22	17	16
Hosts parasitized by <u>M. tenthredinis</u>	Number 92	69	305	193	213	124
	Susceptibility 47%	22%	27%	19%	17%	18%
Designation of clone	Comparatively susceptible	resistant	resistant	resistant	resistant	resistant

The term "susceptibility" used in the above table is synonymous with the term "per cent hatch" and signifies the number of hosts containing at least one living M. tenthredinis larva expressed as a percentage of the total number of host larvae parasitized by M. tenthredinis. Estimates of per cent hatch have shown considerable variability within various regions over the years but the long-term averages are mostly within the range 15% to 30%. The term "effective parasitism" by M. tenthredinis is defined as the percentage of the total number of host larvae dissected in any given collection that contain living M. tenthredinis larvae. The rate of effective parasitism in resistant populations has usually been less than 5%. 'Total parasitism' by M. tenthredinis refers, of course, to the percentage of the total number of host larvae dissected that contain either living M. tenthredinis larvae or encapsulated eggs. Estimates of the percentage of the total eggs deposited that hatch correspond to 'susceptibility' only in instances where there has been no superparasitism. If the latter occurs this estimate can cause confusion for the first larva to hatch usually

kills the remaining eggs.

It was found in this study that both susceptible and resistant individuals usually occurred within the same family as shown in Table IV. Many families were found to have only four or fewer individuals parasitized since the incidence of attack and also the survival from egg to co-cooned larva was often low. Only families in which five or more individuals were parasitized are considered in Table IV.

Table IV

Distribution of resistant and susceptible individuals within families of central Canadian origin

	No. of families	Total no. of resistant individuals	Total no. of susceptible individuals
Families containing both resistant and susceptible individuals	64	762	290
Families containing resistant individuals only	33	323	-
Families containing susceptible individuals only	1	-	5

The susceptibility rating for the total 1,380 parasitized larvae included in this table is 21%.

A fairly large degree of variability in per cent hatch was found between the various families tested even within each clone, but in spite of this it was concluded that the population as a whole in this region was relatively homogeneous with respect to resistance to M. tenthredinis. It is known that the early infestations in Central Canada began in areas in which the larch sawfly had been very scarce during the preceding 10 or more years. It is felt that the evidence supports the view that the resistant sawfly moved into such areas and built up with little or no competition from the residual, susceptible population. Supporters of the hypothesis that resistance has arisen independently in many locations might argue that the competition took place when the density of the larch sawfly was very low and by the time that 'light' populations were widespread, the proportion of susceptibles was negligible. If this mutation has occurred so commonly in central Canada, however, it should also have occurred by now in Newfoundland, Pennsylvania, British Columbia, Bavaria and other areas where the

susceptible strain has been present for periods of up to 50 years or more. In some of these areas M. tenthredinis pressure has been high at times and yet no resistant form has been 'selected out' to date.

As mentioned above there was much variability in per cent hatch even between families belonging to the same clone when these were tested at different times under different conditions. There is evidence that this variation is largely environmentally controlled. It was found that when M. tenthredinis eggs were deposited in 'unhealthy' larch sawfly larvae most of them hatched successfully. This 'unhealthiness' could be caused by partial starvation, excessive parasite attack or disease. An experiment was carried out in which groups of larvae were first exposed to M. tenthredinis attack in cages and then reared under a series of constant temperatures. The results are shown in Figure 12. Per cent hatch is higher at the lower temperatures.

There is some evidence that per cent hatch is higher in larch sawfly larvae collected in late August or early September (Muldrew 1953, fig. 2).

A working hypothesis for this aspect of the problem might be that both the rate of encapsulation and the rate of embryonic development of M. tenthredinis vary with temperature. At higher temperatures the relation between these rates is such that the capsule is sufficiently developed by the late germ band stage of embryonic development that further development (dorsal closure and succeeding stages) cannot proceed. As temperature decreases, the rate of encapsulation slows down faster than does the rate of embryonic development and at low temperatures capsule development is too slow to effectively inhibit embryonic development. A study attempting to measure these two rates at various temperatures has not yet been carried out.

Environmental conditions may account for some of the variability that occurs within the resistant strain, but since encapsulation occurs only exceedingly rarely in populations of the susceptible strain, and since the environmental conditions to which the susceptible and resistant strains are exposed are roughly similar, the difference between the two strains seems most likely to have a genetic basis.

Concerning the question of whether the species of food plant influences the resistance of the larch sawfly, there is considerable information which shows that susceptible sawfly larvae remain susceptible when reared on Manitoba tamarack foliage (from the egg to the mature larval stage). The sources of these larvae have been: B. C. (from western larch); Newfoundland (from eastern larch); Pennsylvania (from a plantation of Japanese larch) and from Bavaria (from Japanese or European larch). The evidence also indicates that the larch sawfly present in central Canada prior to 1938 was susceptible. With regard to the converse, namely whether the immunity of resistant larch sawfly larvae changes when fed on a different species of host plant, we have the evidence that the larch sawfly in-

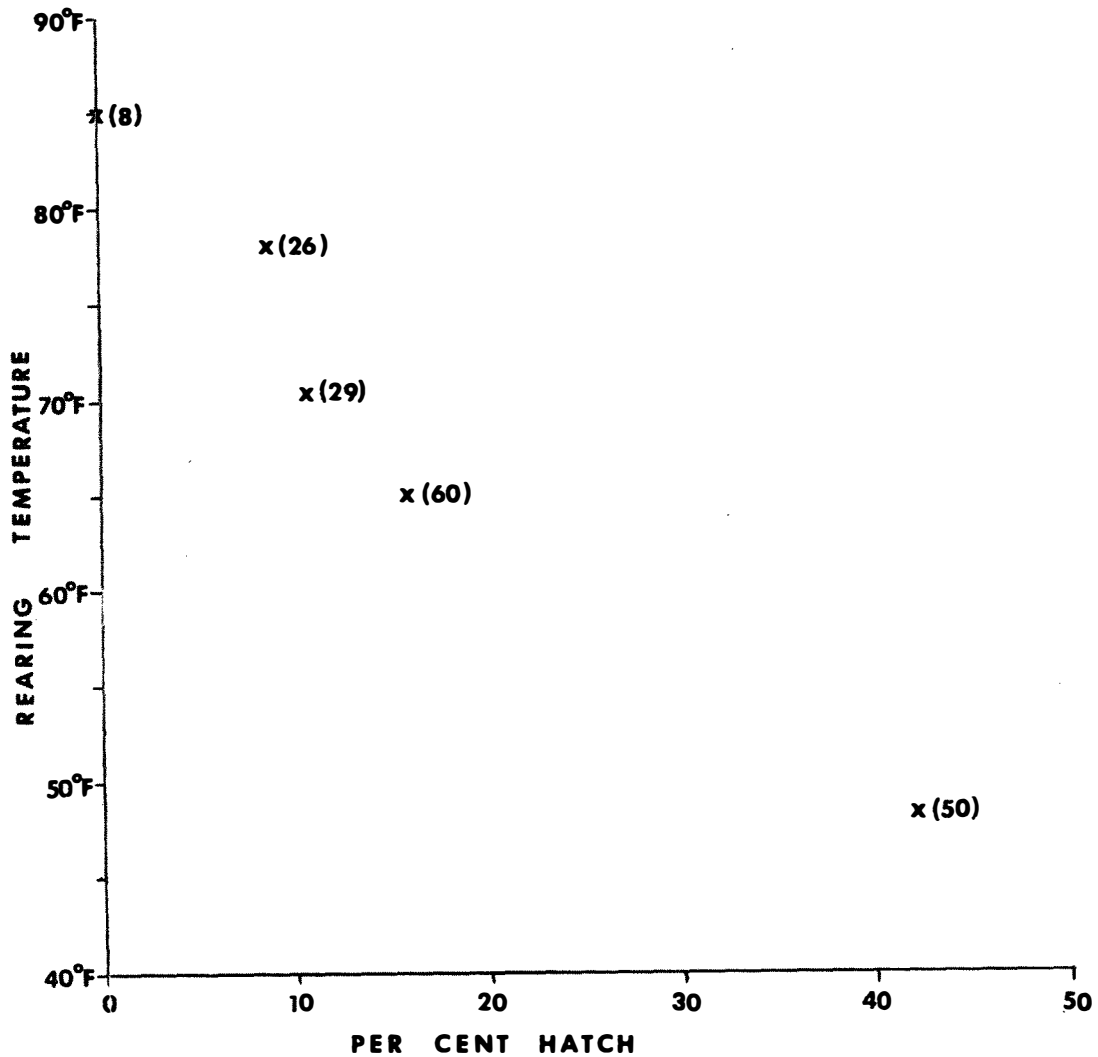


Figure 12.- Per cent hatch of M. tenthredinis eggs in resistant larch sawfly in relation to rearing temperature following parasitization.

(Numbers in parentheses show numbers of parasitized hosts obtained from rearings.)

festing plantations of L. decidua Mill and L. sibirica Ledeb. at Indian Head, Sask., since 1954 has been found to be typically resistant.

Robert van den Bosch in a recent paper (1964) describes a case of host resistance by encapsulation very similar to the larch sawfly - M. tenthredinis relationship, and proposes that the explanation "may lie in the biochemical nature of the blood ... as influenced perhaps by nutrition ... which in turn could influence the encapsulating capacities of the populations". He points out that this explanation "does not involve a genetically determined factor but rather factors in the external environment." In proposing this, van den Bosch is attempting to explain why it is that in both his study and in the case of the larch sawfly in B. C., a low incidence of encapsulation is found in the susceptible populations and yet, in spite of heavy selective pressure, there is no trend toward greater expression of this advantageous characteristic in the population over the years. In commenting on the possibility that the few M. tenthredinis eggs found to be encapsulated in B. C. sawfly larvae might have been nonviable or of such a nature that they incited the same encapsulating reaction as do "inert objects" in B. C. larvae (which explanation I believe to be the most probable) he states that this "is quite tenuous in light of the fact that Muldrew (1953) has found that apparently non-viable eggs of M. tenthredinis are not encapsulated by P. erichsonii". On the top of page 320, however, where I referred to such eggs, I pointed out that they were all found in hosts in which at least one living M. tenthredinis larva was present. This shows that B. C. sawfly larvae which allowed a Mesoleius egg to hatch due to inability to encapsulate, also could not encapsulate the supernumerary eggs that were killed by this first larva to hatch. In addition there is considerable evidence showing that the first M. tenthredinis larva to hatch in those "resistant" hosts in which the immunity reaction fails, often has a detrimental effect on the haemocytes that form the capsules. In such hosts "dead capsules" are commonly found. These capsules are relatively opaque and lack the gelatinous, translucent appearance of a living capsule. They had undoubtedly formed in these hosts before one of the eggs managed to hatch and were almost certainly healthy and functioning until this event occurred.

A point that should be kept in mind is that although there is considerable evidence indicating that the characteristic of resistance to M. tenthredinis was an important factor in enabling the resistant strain of the larch sawfly to become dominant over a large area, particularly in the early stages of the process, this may not be the only difference involved or even the most important. In the genetic study outlined above, an attempt was made to determine if such other differences existed; and measurements were made of weight of cocoon plus enclosed larva, weight of larva only, weight of cocoon only, width of head capsule of fifth-instar larva, fecundity, viability of eggs, incidence of disease and other mortality during larval rearing. Due to a high degree of variability in these characteristics, largely due no doubt to environmental differences during rearing, no significant differences between clones that were originally designated as 'comparatively resistant' or 'comparatively susceptible' were found when

measurements were made over a series of years. Most of these measurements, however, were made on material originating from central Canada and, as stated above (Table III), it was later concluded that all these clones belonged to the resistant strain. Some of the clones studied, however, originated from Newfoundland and other areas where the susceptible larch sawfly was known to occur and it was noted that some of the larch sawflies received from these regions were larger than sawflies collected in central Canada. For example the average weight of cocoon plus contained larva for 147 sawflies collected at Notre Dame Junction, Newfoundland, in 1954 was $92.8 \pm .8$ mg. and for 157 sawflies collected at Glenwood, Newfoundland, it was $88.5 \pm .9$ mg. The average weight of central Canadian cocoons plus enclosed sawflies is 75-80 mg. A third of 25 Newfoundland females caged for oviposition deposited over 100 eggs; a figure that was encountered only rarely with central Canadian females caged under similar conditions. Data supplied by R. J. Heron indicate that mean fecundity values for various populations in Manitoba are usually within the range of 70 to 90, although extreme values as high as 130 are occasionally recorded. Butcher (1951) dissected adults reared in Minnesota in 1949-1950 and found a mode of about 68 with a range from 40 to 90 but these estimates are probably low by a factor of about 10% based on the assumption that he failed to account for the development of some of the immature oocytes during adult life. Reeks (1954) records that six adults collected in Nova Scotia in 1937, and thus presumably the susceptible strain, deposited an average of 115 eggs with a range of 60 to 206. Graham (1956) dissected 23 adults reared from cocoons collected in the field in Minnesota in 1928 (and therefore probably the susceptible strain) and found that 6 of the 23 contained over 100 eggs with a maximum of 130. This evidence thus indicates that the superiority of the 'resistant' larch sawfly does not lie in either larger size or greater fecundity for, if anything, the susceptible strain appears to be superior in these respects. There may, however, be more subtle differences that are more difficult to measure, such as resistance to extremes of temperature, flooding, disease, etc.

Reeks (1954) studied the parasitism of the larch sawfly in Nova Scotia and New Brunswick during an outbreak that occurred from 1933-1942 and concluded that the populations at that time were highly susceptible; encapsulation not being encountered in several thousand sawfly larvae that were dissected even though M. tenthredinis was relatively abundant. The larch sawfly was very scarce in Nova Scotia until 1956 when an increase occurred in parts of the southern and western counties along the coast. Rearing of cocoon collections each year since 1956 has revealed an effective parasitism by M. tenthredinis fluctuating between 8% and 27%; a rate considerably higher than the five per cent or less that is usually found in central Canada. Prior to 1962 most of this material was reared at Winnipeg so that the adults could be used for experimental purposes. Between 1958 and 1962, however, a total of 780 field-collected hosts had been dissected and in the 80 larvae parasitized by M. tenthredinis that were found in this group, none contained an encapsulated egg of this parasite. The first encapsulated eggs were found in 1963 as shown in Table V.

Table V

Parasitism of Nova Scotian Larch Sawfly Larvae by M. tenthredinis

	1958-1962 material	1963 material	Breakdown of 1963 material according to region		1964 material	Breakdown of 1964 material according to region	
			Three counties near Chignecto Isthmus	Other counties		Four counties near Chignecto Isthmus	Other counties
No. of hosts dissected	780	831			1,193		
No. parasit- ized by <u>M.</u> <u>tenthredinis</u>	80	156	40	116	103	68	35
No. containing encapsulated eggs	0	37	27	10	56	53	3
Per cent con- taining en- capsulated eggs	-	24%	67%	9%	54%	78%	9%

The incidence of encapsulation was much higher in the three countries near the Chignecto Isthmus (Cumberland, Colchester and Pictou) than in the rest of the province both in 1963 and 1964 indicating perhaps that the main invasion of the resistant form has occurred through this isthmus. In 1964 the above three counties plus the county of Hants were considered as a group for comparison with all other counties combined.

The populations in Nova Scotia appear to be composed of a mixture of both the susceptible and resistant strains. Concerning the 1963 results -- in 22 locations all of the parasitized hosts found harbored M. tenthredinis larvae only; in five locations all of the parasitized hosts contained encapsulated eggs only, and in only four locations were both M. tenthredinis larvae and encapsulated eggs found. In 1964 the corresponding numbers of locations in each of these three categories was 15, 10 and 5 respectively. A mixture of encapsulated eggs and living larvae is what is usually found in collections made in central Canada as shown in Table IV. The data in Table IV refer to separate families of larvae whereas the Nova Scotia data refer to collections from specific locations, most of which are probably composed of a mixture of individuals originating from different families. If only separate families had been collected in Nova Scotia, the separation into 'all resistant' and 'all susceptible' categories would probably be even more marked.

In New Brunswick the larch sawfly was not found during the period 1941 to 1958. Progressively larger numbers have been found since then in scattered locations. From the material collected in 1962, 410 larvae were dissected and 8 were found to be parasitized by M. tenthredinis. In 1963, 505 larvae were dissected and 12 had been attacked by this parasite. All parasitized hosts contained encapsulated eggs only; the absence of living M. tenthredinis larvae probably being due to small sample size in addition to a comparatively high incidence of resistance. In 1964, 18 parasitized larvae were found in 323 hosts dissected. Of these, 14 contained encapsulated eggs and 4 contained living parasite larvae, giving a susceptibility rating of 22%.

The situation in New Brunswick and western Nova Scotia thus appears to be similar to that postulated for central Canada, namely; resistant larch sawfly adults have invaded an area in which the residual and presumably susceptible population was either absent or of negligible importance. The resistant strain also appears to have invaded those regions of Nova Scotia where the susceptible strain and also M. tenthredinis have been present in comparatively high numbers since 1957. An opportunity thus exists to determine, in the first reasonably well-defined instance of this kind, if competition occurs between the two strains in this region and whether the resistant strain will become dominant as postulated by theory.

Geographical Strains of *M. tenthredinis*

In 1959 studies were initiated to determine the extent to which various *M. tenthredinis* populations in North America differed in their ability to overcome or avoid encapsulation in 'resistant' hosts. Various combinations of larch sawfly and *M. tenthredinis* originating from Pennsylvania, Nova Scotia, Ontario, Manitoba and Saskatchewan were tested but no marked differences between these parasites were detected, although an insufficient number of parasitized hosts was obtained to differentiate small differences that might exist.

As part of a renewed cooperative effort to obtain biological control of the larch sawfly in North America, which is discussed in section III of this report, *M. tenthredinis* adults collected in Europe were shipped to Canada. The results of studies on this European material are included here for purposes of continuity.

In 1959, a few *M. tenthredinis* of Austrian origin were received at Winnipeg and were used in cage experiments to parasitize resistant larch sawfly from Manitoba. Dissections showed that over 90% of 84 parasitized hosts were successfully parasitized. Larger numbers of Austrian and Bavarian *M. tenthredinis* were received in 1961 and 38 groups of resistant host larvae originating from eight locations in Manitoba and Saskatchewan were experimentally parasitized. No evidence of encapsulation was found in 60% of these groups and parasitism of 594 larvae in which eggs were deposited was again approximately 90% successful. In controls parasitized by Canadian *M. tenthredinis* the parasitism was 25% successful.

Studies on the Bavarian-Canadian and Austrian-Canadian reciprocal crosses of *M. tenthredinis* showed a high degree of successful parasitism when the female parent was European (61 of 76 parasitized hosts in 1961 and 29 of 31 parasitized hosts in 1962) and a lower degree of successful parasitism when the female parent was Canadian (13 of 34 parasitized hosts in 1962). Some evidence was obtained that the characteristic conferring greater success in hatching was transmitted to female progeny from the male parent in Bavarian male X Canadian female crosses.

Because of these promising results, Bavarian *M. tenthredinis* were released near Riverton, Manitoba, in 1963 and in the Whiteshell Provincial Park in 1964. Austrian *M. tenthredinis* received in 1963 were not released because European workers had found encapsulated eggs in certain Austrian larch sawfly populations but not in Bavarian populations.

Simmonds (1963) considers that "the most important factor ... in the material liberated for biological control (is) the maximum possible genetic variability, from which, by natural selection in the given environment, the most suitable strain for that environment would be developed". The release of the Bavarian genotype of *M. tenthredinis* is an attempt to increase the genetic variability of this parasite in Canada.

The detection of whether the establishment of Bavarian M. tenthredinis has occurred is more difficult than for the other species of parasites that have been released, since no way is known at present of distinguishing it morphologically, from the local populations of M. tenthredinis. It is assumed that establishment will be followed by an otherwise inexplicable increase in total parasitism by this species coupled with an increase in the per cent hatch of the parasite eggs. The release point chosen in 1963, near Riverton, Man., harbored a comparatively high larch sawfly population. Unfortunately, there were no past records showing effective parasitism and per cent hatch for M. tenthredinis for this particular stand. It was felt that the benefits of releasing the parasites where there was a plentiful supply of hosts outweighed this disadvantage. Past records were available for a stand seven miles to the east of the release point but here larch sawfly density was low in 1963. These records, which were gathered by Forest Insect Survey personnel, are as follows:

	1945	1946	1947	1948	1949	1950	1951	1952	1954	1959	1960	1961	1962	1963
Per cent)Total	15.5	17.3	10.9	1.4	2.2	1.3	1.7	5.0	2.4	0.5	1.0	4.5	6.5	5.4
parasitism) Effect-														
by <u>M. ten-</u>) ive	2.5	4.3	2.9	0.0	2.2	0.0	1.2	1.3	0.8	0.0	0.5	2.0	4.9	2.9
<u>thredinis</u>)														
Per cent														
hatch	16	25	26	0	100	0	100	33	33	0	50	44	75	45

(sampling was not carried out in the years omitted.)

The mean total parasitism by M. tenthredinis was 5.5%, the mean effective parasitism was 1.8% and the mean per cent hatch was 33%. Some of the high estimates for per cent hatch for particular years are due to small sample size. Also, in years where the dissection was carried out by an inexperienced technician, there may be a bias due to the ease with which M. tenthredinis larvae can be found as compared to encapsulated eggs.

Table VI presents dissection data for material collected at the release plot and two check plots. Check plot #1 is approximately seven miles east of the release point and is in the same stand as is the plot from which the F. I. S. data presented above were obtained. Check plot #2 is approximately 10 miles from the release point and 4.5 miles north of check plot #1.

Table VI

Results of study made to monitor effects of release of Bavarian
M. tenthredinis

Location	Year	No. of hosts dissected	Parasitism by <u>M. tenthredinis</u>		
			Total	Effective	Per cent hatch
Release Plot	1963	355	12.1%	5.8%	48%
	1964	223	8.9%	4.4%	50%
Check Plot #1	1963	89	9.0%	2.2%	25%
	1964	89	4.5%	2.2%	50%
Check Plot #2	1964	188	15.9%	7.4%	47%

It can be seen that because of the relatively high values of M. tenthredinis parasitism obtained in the check plots no conclusion can yet be reached as to whether the release of the Bavarian strain has resulted in an increased incidence of attack by this parasite. It is conceivable, although highly unlikely, that the Bavarian adults dispersed as far as the check plots in 1963 when over 3,000 were released. In addition to the lack of knowledge concerning extent of dispersion, interpretation is hampered by lack of information on the density and effectiveness of M. tenthredinis in the release plot and check plot #2 prior to 1963. The history of parasitism in the release plot in the Whiteshell Provincial Park is well documented and since 'native' M. tenthredinis is very scarce here, interpretation of the effect of the 1964 release should not be as difficult.

It is possible that certain characteristics of the Bavarian parasites may be so unfavourable in the Canadian environment as to outweigh the large competitive advantage that should result from their greater effectiveness in parasitizing the resistant larch sawfly. If the favourable genes manage to persist in the gene pool, however, a favourable combination may eventually be produced.

Conclusions

(a) Nature of the immunity reaction

The weight of evidence appears to support the view that although environmental influences (temperature, quality of food, etc.) may affect the incidence of encapsulation in the resistant strain, the important difference between the susceptible and resistant strains is a genetic one. That this difference may be very slight is indicated by the studies of Salt (1960, 1961). He has proposed that the reactions of haemocytes to foreign bodies can be explained in terms of surface characteristics and states that "Evidence has accumulated which seems to show that most, if not all of the internal surfaces of an insect are coated with a substance laid on them by the haemocytes... The surface thus applied to the organs and tissues does not attract aggregations of haemocytes." Salt carried out experiments in

which he altered the surface layer of larvae of the parasite Nemeritis canescens which, when deposited naturally into their normal host Ephestia sericarium, stimulate no reaction. He immersed these larvae in various solutions and found that when they were treated briefly with fat solvents, of which octane was particularly efficient, and then injected into host larvae by means of an artificial ovipositor, they were then encapsulated. He states that before injection, the treated eggs were washed for some hours in insect saline but it is a moot point whether all traces of the chemical were removed. The parasite larvae were not killed by the treatment and could be seen to move inside the capsules. He concluded that the removal of a lipid constituent from the surface of these parasites also removed the specific properties that provided its immunity to the haemocytic reaction of its host.

As a working hypothesis based on Salt's theory we might assume that the adaptation of M. tenthredinis to the larch sawfly lies in its ability to produce eggs whose surface constituents 'mimic' the constituents of the internal surfaces of the larch sawfly to the extent that the larch sawfly haemocytes cannot detect the differences in molecular construction. For the purpose of this discussion we might set up the following categories:

- S = surface type of susceptible larch sawfly larvae (more particularly, probably the lipid constituent of the internal surfaces).
- R = surface type of resistant larch sawfly larvae.
- B = surface type of Bavarian M. tenthredinis egg (probably the lipid constituent on the external surface of the chorion).
- C = surface type of Canadian M. tenthredinis egg.

The following assumptions appear to be consistent with the evidence collected to date: (a) that the differences between S, R, and C are such that the haemocytes of R react to C but the haemocytes of S do not. This implies that the difference between R and C is greater than the difference between S and C. Thus the degree of chemical difference between S and R would be directly related to the sensitivity of the haemocytes to detect minute chemical differences. The sensitivity may or may not differ between R- and S-type haemocytes. An alternative possibility to consider is that R and S are identical but the haemocytes of R differ from those of S in that they have a greater sensitivity to detect minute chemical differences between surfaces; (b) that B is more closely similar to R than C is and the reaction of the R type haemocytes to B is less than it is to C with a consequent lower degree of encapsulation being manifested.

One possible approach to this problem would be to remove the lipid constituents from the various surfaces involved and analyze them by spectrophotometric or other means to determine if chemical differences can be detected. Another, and perhaps simpler, approach would be to carefully separate the chorions from both Canadian and Bavarian M. tenthredinis embryos and (after washing in a physiological solution) inject them into type R and S hosts singly and in various combinations and compare the reactions of the haemocytes to them.

(b) Origin of resistance

Workers who were involved in assessing the effects of M. tenthredinis on the larch sawfly in Canada prior to the appearance of the resistant larch sawfly generally concluded that this parasite was an important factor in reducing populations in certain regions and keeping them at a low level. Sporadic outbreaks did occur, however, for example in Manitoba in 1924-27, and in Ontario and Quebec in the late 1930's and early 1940's, but these were not well studied from the standpoint of parasitism and it is unknown whether M. tenthredinis was present in the localities where the outbreaks occurred, during the initial stages at least. There is some evidence that the parasite was important in bringing some of these infestations to a close but it may have spread into these areas during the course of the outbreak. In other words it is possible that these outbreaks of the presumably susceptible strain of the larch sawfly were due to the fact that M. tenthredinis was not uniformly distributed throughout the whole range of tamarack in America at this time. On the other hand, outbreaks have occurred in areas where the susceptible larch sawfly and M. tenthredinis have co-existed for a considerable period; for example, Newfoundland, parts of Nova Scotia and Idaho. An intensive study might reveal reasons why M. tenthredinis cannot operate efficiently in these areas. In spite of this adverse evidence, however, most of the facts seem to be consistent with the postulation that prior to 1938 the larch sawfly in America, with the exception of central Manitoba, was susceptible to M. tenthredinis and that a resistant form appeared in Manitoba which built up rapidly after 1938 and spread widely.

If these assumptions are accepted as valid, three hypotheses concerning the origin of resistance to M. tenthredinis can be made:

Hypothesis 1 - that resistance has arisen by mutation independently in Canada and Eurasia in many different locations.

The implication here is that this mutation occurs at a particular rate that can be measured (as is commonly done for mutations in Drosophila, etc.). I believe that the bulk of the evidence, particularly that provided by the maps, is against this hypothesis. Moreover, if this hypothesis is true, one would expect that by now the resistant larch sawfly would have appeared in such regions as Newfoundland, Pennsylvania, British Columbia, Idaho, Bavaria, etc., where the sawfly populations have remained highly or completely susceptible for many years. The evidence concerning the infestations in plantations may also be cited. Populations from these plantations that have been tested have been found to be resistant. Proponents of the hypothesis that the larch sawfly has survived in these stands since establishment must also assume that the mutation conferring resistance has also occurred in each stand, since the evidence indicates that the larch sawfly that was present in Central Canada when the small trees were set out was the susceptible strain.

Hypothesis 2 - that the resistant strain in Canada originated by mutation but that this occurred only once, apparently somewhere in Manitoba prior to 1935.

Probably before we can estimate the likelihood of this we need to know more about the process of inheritance in the larch sawfly. For example: does a rare effective mating ever occur?; how do genetic differences segregate out in the process of auto-fertilization that occurs in the larch sawfly?; is the encapsulating ability controlled by a single dominant gene or by numerous polygenes with cumulative effects?; etc. Various possibilities to be considered are: (a) that the ability to encapsulate is due to a mutation that occurs exceedingly rarely, (b) that the rate of mutation for this characteristic is fairly high but that a special set of environmental conditions must be present at the time it occurs in order for the resistant form to become dominant, and (c) that a combination of mutations must occur or be brought together in the same individual in order for a resistant strain to develop.

The studies on the genetic aspects of this problem cited above were without much success in obtaining answers to the above questions. The main difficulties were uncontrolled environmental conditions and inability to obtain a high incidence of attack for each clone without coincident excessive superparasitism and/or high mortality in many clones during the rearing from egg to cocoon stage. In the early stages of the study some time was spent attempting to adapt the use of the artificial ovipositor developed by G. Salt (1955) to this problem. M. tenthredinis eggs for injection purposes were obtained by dissecting them out of susceptible larch sawfly hosts previously parasitized in cages but insufficient work was done to perfect the technique to the stage where it was certain that the adverse effects on both the eggs and the host larvae were slight enough to approximate normal parasitization, encapsulation, etc. In future studies on genetic aspects more attention should be given to utilizing this technique.

Hypothesis 3 - that the resistant strain of the larch sawfly in Canada is a distinct variety that was introduced into Manitoba at the time M. tenthredinis was liberated there in 1912-1913.

The apparent spread of the resistant form from an epicenter as shown by figures 2-8 may be taken as support for this hypothesis. There is a strong resemblance to other cases where the spread of animals definitely known to be introduced has been studied (vide Elton, 1958, pp. 22, 25, 53, 113, etc.). It may be argued, however, that a similar spread would occur following the appearance of a mutation having a high selective advantage, and although there appear to be few examples of this in the literature, Kettlewell (1961) has stated that industrial melanics are characterized by rapid spread.

The implications of this hypothesis are (a) that the resistant strain required a 25-year period (1913-1938) during which a slow process of adaptation to the conditions of the new environment occurred that enabled this strain to build up rapidly to become the dominant form in central Manitoba; (b) that the larch sawfly material collected in Great Britain in the years 1910-1912 for parasite release purposes was mainly the susceptible strain but included some representatives of the resistant strain.

This, in turn, implies that the susceptible strain had been present in Great Britain for many years and was the dominant form (as indicated by levels of successful parasitism by M. tenthredinis up to 80%) and that the resistant form was a more recent introduction (Wardle noted a reduction in the effectiveness of M. tenthredinis during his studies from 1910 to 1913 and Maw in 1955 found a total parasitism by M. tenthredinis of 54% but an effective parasitism of 39%); and (c) as a necessary condition for the above that the two strains occurred in Europe at that time and that the susceptible one (lowland strain?) was introduced at an early date and the resistant (alpine form?) at a later date. Maw (1960) states that larch trees from both alpine (Tyrol) and lowland sources had been introduced into Britain before 1860, the year the larch sawfly was first recorded for Britain and, presumably, small trees from upland sources at least, were being introduced in the early part of the present century.

Although the evidence at present is insufficient to choose between these hypotheses with any great degree of certainty the following argument appears to support the third hypothesis. If resistance is due to a mutation as proposed in hypotheses 1 and 2, one can accept the suggestion that it would become dominant fairly rapidly as a result of selection due to Mesoleius pressure. In some regions, however, this pressure has been virtually of no importance for a considerable period of time and there is as yet no indication that the susceptible larch sawfly is replacing the resistant in these areas. It is difficult to see why the resistant strain should remain dominant unless one also postulates that other mutations also occurred in Canada that endowed this strain with superiority in other characteristics. It is easier to conceive that an introduced strain would be different from the 'native' one in a number of characteristics of which resistance to M. tenthredinis may be the most easily detected but not necessarily the most important.

Smallman (1963) in discussing the drawbacks of chemical control and the alternatives to it stated that "there are grounds for supposing that as we push the development of these alternatives ... we will encounter many of the same difficulties. For one thing any method that threatens the existence of a population seems certain to meet resistance of some sort." The example of the resistance of the larch sawfly to M. tenthredinis does not appear to provide strong evidence supporting the view that resistance to parasitoids will commonly arise with increasing use of these agents. In most cases where insects have developed resistance to insecticides the genes conferring resistance were present in the population at a low level prior to the use of the insecticide as part of the 'hidden genetic variability' of the species and these genes increased rapidly in frequency due to intensive selective pressure. A corollary of this is the usual decline in frequency of these genes upon the removal of the pressure. In the case of the larch sawfly it would seem that the resistant genes, whether they arose by mutation or were introduced, were not widely distributed in Canada before 1938 and additionally, it appears that resistance persists in larch sawfly populations even after the disappearance of the selective pressure.

Since the resistant strain of the larch sawfly appears to be almost identical with the susceptible in its morphology, behavior, etc., its introduction into America, or its appearance there if due to a mutation, would not be comparable to the introduction of an organism that is a completely new element. Since the resistant larch sawfly would have to compete with other members of the same species its success can probably be considered to be a legitimate case of 'evolution in action'. The evidence indicates that the competition between the two strains and the initial achievement of dominance of the resistant strain occurred in a localized area following which there was rapid dispersal and build up and in which competition did not appear to play an important role. Perhaps a similar evolutionary process occurs more commonly than is generally accepted when a strain (or perhaps even species) replaces another over an extensive area.

III. ADDITIONAL SPECIES OF PARASITES RELEASED AGAINST THE LARCH SAWFLY

The biological control program against the larch sawfly entered a new phase in 1957 when agreement on a cooperative effort was reached between the Forest Entomology and Pathology Branch, Department of Forestry; the Entomology Research Institute, Bellville, and the Commonwealth Institute for Biological Control. Surveys were begun in Europe in 1958 and ecological studies were started in 1959. Since 1960, material from overseas has been shipped to Canada and the adult parasites have either been released or studied in cages. Collections have been made in Austria, Bavaria, Switzerland and Japan. Alternate hosts harboring parasites or potential parasites of the larch sawfly have also been collected. The numbers of parasites released to date are shown in Table VII.

Table VII

Additional parasites released in Manitoba since 1961

Species	Locality and Numbers			
	Pine Falls		Riverton (except where noted)	
	1961	1962	1963	1964
<u>Ichneumonidae</u>				
<u>Mesoleius tenthredinis</u> (Bavarian material)			3,021	816 (Rennie, Man.)
<u>Holocremnus</u> sp. nr. <u>nematorum</u>	214	217	2,155	39 (P.A., Sask.)
<u>Hypamblys albopictus</u>			214	

Table VII (Concl.)

Species	Locality and Numbers			
	Pine Falls		Riverton (except where noted)	
	1961	1962	1963	1964
Tachinidae				
<u>Hyalurgus lucidus</u>	99	109	692	462
<u>Myxexoristops stolidus</u>		281	77	29
<u>Vibrissina turrita</u>			149	521

All of these parasites were obtained from Europe except Vibrissina turrita, which came from Japan.

In addition to the above species, other parasites exist which attack the larch sawfly in Europe and Japan. None of these have been released. Those marked with an asterisk have been studied in cages in Winnipeg.

Additional parasites of the larch sawfly not released

- Europe: * Polyblastus tener
 * Rhorus lapponicus
Trematopygus sp.
Eclytus ornatus
Eclytus exornatus
Cteniscus hofferi
 * Eudiaborus pedatorius
Erromenus sp. nr. haemorrhoeus
Bessa selecta
Tritheptis klugii
- Japan: * Mesoleius sp.
Bessa sp. (fugax?)
Aptesis (Pleolophus) sp.
Drino gilva aurora
Mastrus sp.

* studied in cages at Winnipeg

As Pschorn-Walcher (1963a) has pointed out, the parasite complex in Europe is much richer than in America, there being half a dozen species showing a relatively high degree of abundance and constancy. He concludes that "without doubt the larch sawfly is not indigenous to the Nearctic Region and must be considered an alien element". He prefers the view, however, that the

larch sawfly entered America by the Bering bridge in the Pleistocene; its rarity in Europe militating against the view that it was imported by settlers.

The tachinids have been obtained largely from the alternate hosts rather than the larch sawfly. Some of these alternate hosts feed on species of plants other than Larix and it is a moot question whether these species of parasites may not be comprised of a number of biotypes having different preferences for the various species of plants on which they search for hosts. The biotypes emerging from alternate hosts may leave the tamarack stands after release in search of willow, alder, etc.

Only one of the recently introduced parasites is known to be established at present. This is the ichneumonid Holocremnus sp. nr. nematorum. This species is apparently almost completely specific to the larch sawfly in Europe and has one generation per year on this host. It is reported to attack the first- and second- and probably third-instar host larvae. The size of the egg is stated to be slightly larger than the egg of M. tenthredinis which is approximately 0.8 mm. when deposited. For comparison purposes, the larch sawfly egg (3 days after deposition) is approximately 1.3 mm. long and the mean length of the first-instar larva is roughly 2.8 mm.

In Europe this parasite is usually second in importance to M. tenthredinis in terms of percentage parasitism of the overwintering larvae, being present in up to 20-30%. Its efficiency in Europe, however, is adversely affected by the hyperparasite Mesochorus sp. nr. crassicus Thomson. This species deposits its eggs in the embryo or first instar larva of H. sp. nr. nematorum. It has commonly been found attacking 40 to 70% of the H. sp. nr. nematorum in Europe. The primary parasite may prove to be much more efficient in Canada than in Europe in the absence of this secondary parasite.

The data showing the release and recovery records for H. sp. nr. nematorum in Manitoba are presented in Table VIII.

Table VIII

Estimated number of adults of Holocremnus sp. nr. nematorum following release

Date	Pine Falls	Riverton	
		at release point	at study plot 580' away
1961	(158♀, 56♂ released)		
1962	?	152♀, 65♂ (released)	
1963	351/acre	(1,245♀, 910♂ released)	353/acre
1964	675/acre		279/acre
1965	10,700/acre*		779/acre*

* (Number of small (parasitized) cocoons present in the fall of 1964) x mean survival in cocoon stage 1961 - 1963.

It was found to be characteristic of larch sawflies parasitized by H. sp. nr. nematorum that both the feeding larvae (in the fourth and fifth stadia at least) and the cocoons are significantly smaller than they are for non-parasitized larch sawflies (Muldrew and Turnock 1965). The weight of the larvae removed from cocoons is smaller by a factor of about 50%. There is a tentative indication that Bessa harveyi, a native tachinid parasite, and M. tenthredinis attack a smaller percentage of Holocremnus-parasitized hosts than non-Holocremnus-parasitized hosts. The ability of H. sp. nr. nematorum to reduce the size of this host may thus be an adaptation to avoid competition with other parasite species. In Europe, cases of multiple parasitism involving H. sp. nr. nematorum and M. tenthredinis occurred about three times less commonly than would be expected if parasite attack by M. tenthredinis were random (Pschorn-Walcher 1963).

There are indications that the Holocremnus population in Pine Falls, at least, is entering an 'explosive' phase of growth, and the fact that there are life-table plots, both here and to the southeast, for which there exists a body of population data, collected over a ten-year period in some cases, makes this a unique opportunity to study the impact of this introduced parasite. The Forest Insect Survey of the Winnipeg Laboratory has also initiated studies to determine the rate of spread of this parasite and this should provide information that will enable the determination of the optimum distance between release points if future results indicate that a redistribution program would be beneficial.

IV. BIOGEOGRAPHY - THE PROBLEM OF THE ORIGIN OF THE LARCH SAWFLY IN NORTH AMERICA

Characteristics of introduced species

Most of the successful cases of biological control that have been achieved have been directed against organisms that have been introduced into a country through various trade channels, etc. within historic times. These usually arrived without the natural enemies that attack them in their native home. Since, on empirical grounds, introduced pests offer the best chance of success, it is important to be able to distinguish between introduced and native species where this is in doubt. As Balch (1955) has written, "this is essential if we are to attempt generalizations about the epidemiology of introduced versus native species".

Clausen (1956) stated that most of the major pests of agricultural crops in the United States are of foreign origin. A good many, if not most, of the major pests of stored grain, forest trees and species of importance in medical entomology are also known to be introduced. The difficulty in deciding whether a particular species is exotic or native usually concerns species that may have been introduced before the native fauna of the region had been well studied. Some of the introduced species rapidly became abundant and widespread, while others remained scarce and localized in distribution. Some of the criteria suggested by various authors as characterizing

introduced species apply to both of these categories while other criteria apply to one or the other of the two groups.

(a) Criteria that apply to both groups:

- (i) The species is identical morphologically, physiologically and cytologically with a species belonging to another region of the world or differs only very minutely.
- (ii) There is evidence of a restricted center of origin in the new region.
- (iii) The species feeds on a host that was itself introduced.
- (iv) The species is anomalous taxonomically, and in terms of evolutionary history, with the native fauna.
- (v) The species was not found in the new region in reasonably thorough surveys made there prior to the date of first discovery.
- (vi) The species has an incomplete or anomalous complex of natural enemies, in particular of specific parasites. If natural enemies brought from the suspected native home establish themselves readily, this provides additional supporting evidence. Graham (1963, p. 225) points out that this criterion does not apply to forms such as wood borers, seed-infesting insects, etc., which normally have few enemies.
- (vii) The species is most likely to find a niche in a simple ecosystem. Elton (1958) argues that simple ecosystems are more vulnerable to invasions than are the more complex ones. The tundra is usually considered to be a simple ecosystem as compared to the complex tropical rain forest. Tropical islands, however, are usually low in numbers of indigenous species and have been successfully invaded many times. Crops, or other man-made monocultures (orchards, tree-plantations, etc.) can also be considered to be simple ecosystems. The simplification is often increased by intensive management. Certain introduced weed species thrive where the soil is regularly broken by man but are unable to penetrate habitats having unbroken soil.
- (viii) Species reproducing by thelytokous parthenogenesis are more readily introduced than forms in which mating is obligatory, since one individual can give rise to an infestation, the potential rate of increase is high and there is not the risk, during the initial phase of invasion, of extinction due to the failure of mating to occur because of low population density.
- (ix) Species reproducing by thelytokous parthenogenesis show genetic uniformity in the new region since the populations are composed of

pure lines, each of which accumulates a complex of mutations differing from those of other lines. The difference is usually proportional to the duration of the period of separation between the populations in the new region and the country of origin.

All of these criteria except (iii) and perhaps (vii) apply to the larch sawfly to a greater or lesser degree, although the analysis of genetic uniformity in North America versus Eurasia and also the cytological analysis on a world-wide basis have not been thoroughly studied.

(b) Criteria that apply to species that have flourished in the new region:

(i) The initial build up and spread of the immigrant is often of an 'explosive' nature. Elton (1958) states that when a species reaches the 'flood' stage its movement is seldom absolutely checked except by the natural limits of the environment. This high rate of increase is usually attributed to an absence of the restraints which exist in the native home. Such introduced species are often scarce in the country of origin; sometimes so rare that an intensive search must be made to find the native home of an introduced pest. It is conceivable that some pests now considered to be 'native' are in fact species that were introduced at an early date and have not yet been discovered in their true native home. With some of the early invaders of foreign lands the explosive phase has been followed by a decline to lower average densities and to what has been termed a 'balanced' relationship (e.g., the Canadian water weed, Elodea canadensis, in Britain). If the larch sawfly is an introduced species this process may be occurring in North America as it seems to be less destructive now than it was near the turn of the century.

(ii) The invader successfully competes with native species often replacing them in the region invaded. Elton (1958) points out that it is often difficult to determine what happens here since replacement sometimes seems to occur without direct interference or "when one species decreases through pure coincidence from independent causes during the increase of the other." Sometimes an invading species finds an ecological niche that is unoccupied by any similar form, the end result being the addition of one species to the faunal list. Elton believes that the interior causes involved in the process of replacement constitute the "single most important problem underlying all the facts" given by him in his book.

- (iii) The progressive enlargement of the range in the new region is shown by the collection records. With some of the earlier introduced species, collecting was not extensive enough to demonstrate this. The Hessian fly, for example, was introduced into America from Europe prior to 1780. Anomalies are likely to be found with species capable of comparatively rapid spread and also where spread may have been unintentionally aided by the activities of man.

Criteria (i) and (iii) apply to the larch sawfly. Concerning criterion (ii), the initial introduction appears to have been the filling of an unoccupied niche while the appearance of the resistant strain as the dominant form may be an example of replacement.

- (c) Criteria that apply to species restricted in numbers and range in the new region:

Many of these species appear to have been introduced in ship's ballast. Brown (1940) listed 47 species of Coleoptera, many of which were probably introduced in this way and over half of which still have restricted distributions near the coastal ports of eastern North America. These 47 species all are widely distributed in Europe. This method of entry was extensively documented by Lindroth (1957), especially for the Carabidae.

- (i) Species with 'immature' or 'unnatural' distributions, usually near a coastal port. There appears to be no limitation imposed by soil, vegetation type, climate, etc., preventing such species from increasing their range.
- (ii) Species limited to open, dry (artificially drained) land in and around ports, often surrounded by a differing vegetation type (forest, marsh, etc.). Lindroth (1957) terms such land the 'culture steppe'.
- (iii) Synanthropic species restricted to the more densely populated parts of the new region and thus occupying discontinuous ranges.

Origin of North American Larch Sawfly

There are three schools of thought on the origin of the larch sawfly in North America: (a) that it was accidentally introduced from Europe probably sometime between 1800 and 1875; (b) that it entered America via the Bering land bridge sometime between the Miocene of the Tertiary, some 25 million years ago and the final disappearance of the bridge at the close of the last ice age of the Pleistocene, some 15,000 years ago, or, alternatively that it crossed the Bering Strait by long distance dispersal in post-glacial times -- most likely during the period of the climatic optimum; and (c) that there is insufficient evidence as yet to allow the conclusion that either hypothesis is more probable than the other.

In support of the hypothesis that the larch sawfly is a recently introduced species it can be mentioned that during the period from at least 1846 to the time of the discovery of the larch sawfly in America in 1880, small European larch trees, approximately one foot high, were being imported from England by the thousands, without quarantine restrictions, and planted in the New England region (Hough 1878). Larch sawfly cocoons, some harboring parasites, may have been present in the soil around the roots or in the packing material.

Some of the larch sawfly outbreaks that occurred in Europe during this period were:

Denmark - 1827-29; 1839-48 (a severe outbreak on the island of Bornholm)
Sweden - 1835-??
Germany - 1835-40 in the Holstein district; 1874 at Kiel

Rehder (1940) states that Larix sibirica Ledeb. was introduced into America in 1806 and L. leptolepis (Sieb. and Zucc.) Gord. in 1861. He was unable to find the records for the first introduction of European larch, L. decidua Mill., and he refers to it only as being 'long cultivated' in America.

The first authentic record of the larch sawfly in North America was made by Prof. C. S. Sargent who found larvae on European larch at the Arnold Arboretum, Massachusetts. Packard (1890) presents evidence that the sawfly was also present in East Turner Maine, about 150 miles north of the Arnold Arboretum, in 1880. The Arnold Arboretum has occasionally been held responsible for having brought the pest in, for example Strickland (1934) states that "it was accidentally imported into the Arnold Arboretum"; Fletcher (1906) stated "the larch sawfly was imported into America, probably with trees sent to the Harvard Arboretum and Botanic Garden at Cambridge, Mass.", and Fyles (1907) believed the insect "was imported at Boston in the cocoon stage hidden in the roots of young larch or spruce trees obtained from Norway". However, Dr. R. A. Howard, the present director of the Arboretum, writes that the Arboretum could not have been responsible (pers. comm.). Nurseries were first established about 1875, and L. decidua and L. sibirica were first brought in as seed in 1882; L. leptolepis as seed from a supplier in Massachusetts in 1872, and Picea abies as young plants from a supplier in New Jersey in 1878.

Audubon (1926) is often quoted as having stated that an insect, presumably the larch sawfly, destroyed tamarack in Maine early in the 19th century. Droege (1960) pointed out, however, that Audubon simply recorded statements by a lumberman to the effect that a green caterpillar, three-quarters of an inch in length, not only killed tamarack but "spruces, pines, and other firs." This insect referred to was probably the spruce budworm since Swaine and Craighead (1924) report that a spruce budworm outbreak of

great intensity began in eastern North America about 1806. The only other report indicating the possible presence of the larch sawfly in America before 1880 is the hearsay evidence given by Jack (1887) whose father had told him that about 1835 the tamarack woods near Chateauguay, Quebec, "were entirely defoliated, and looked as though scorched by fire" and "it was more noticeable at that time as there were large tracts of tamarack forest that have now entirely disappeared." Graham (1956), studied the ring pattern of large tamaracks growing in Michigan and concluded that periods of defoliation, which he strongly suspected were due to larch sawfly attack, occurred in addition to the periods 1906-1913 and 1917-1929, during the following periods: 1877-1885, 1864-1867, 1849-1854, 1835-1841, 1819-1823, 1791-1799, 1781-1786, 1752-1754, 1745-1749 and 1734-1741. Nairn et al (1962), however, concluded that growth reduction in tamarack due to insect attack could not be differentiated from that due to other adverse factors, at least in trees growing in Manitoba and Saskatchewan.

Another approach to the problem is to examine the state of knowledge of insects attacking larch prior to 1880. The following table gives the species listed by Packard (1881), their present names, the date of the original description, an indication of their specificity and an indication of their average abundance. The figures in parentheses show the number of times the Forest Insect Survey of Canada has collected the species from tamarack (from Forest Lepidoptera of Canada Vols. 1-3) over a period of approximately 20 years.

In Packard's subsequent compilation (1890), made after he and others had examined larch closely while studying the distribution and habits of the larch sawfly, the following species were added to the list: a sphinx caterpillar (probably *Sphinx gordius* Cram (37)); *Orgyia antiqua* L. (148); *Orgyia leucostigma* J. E. Smith (72); *Platyserura furcilla* Packard; *Biston cognataria* Gn. (80); three *Eupithecia* spp.; *Coleophora laricella* Hübner; a *Selandria* sp. (possibly *Anoplonyx* sp.?); *Neophasia menapa* F. & F. (on western larch); *Dendroctonus* sp. (probably *simplex*); *Hylesinus opaculus*; *Tetranychus telarius*, plus an *Apatela* sp., seven unnamed geometrids and two unnamed tortricids. The fact that the first four species listed in Table IX were known at least 15 years before the larch sawfly was first discovered in America signifies that this host tree had not been neglected by entomologists during this period. Graham (1956) postulated from tree-ring studies that there were ten outbreaks of the larch sawfly, in Michigan at least, that occurred before the severe outbreak at the turn of the century. The duration of these outbreaks averaged five years and the abundance of the sawfly must have been high in order to produce the moderate to severe defoliation necessary to reduce the growth of the tree. If the larch sawfly was so prevalent in Michigan prior to 1880 one would expect it to occur at similar levels of density periodically in the other parts of the range of tamarack. It seems highly unlikely that entomologists would miss this species and yet find the much less noticeable species listed in Table IX. Moreover, as Coppel and Leius (1955) and others have pointed out, tamaracks of large size were apparently common throughout the swamp areas before 1880 but are of rare occurrence at present, indicating perhaps that long-continued growth is now being repressed by a new element in their environment; the larch sawfly.

Table IX

Insects Known to Attack Larch Prior to 1880

Name in Packard (1881)	Present Name	Year of original description	Specificity	Abundance
<u>Samia columbia</u> (Caulfield)	<u>Hyalophora columbia</u> Sm.	1865	Specific on tamarack	Rare (14)
<u>Lachnus laricifex</u> Fitch	<u>Cinara laricifex</u> Fitch	1859	Specific on tamarack	Rarely abundant enough to cause noticeable injury
<u>Chermes laricifolia</u> Fitch	<u>Sacchiphantes laricifolii</u> Fitch	1859	Forms "pine-apple galls" on spruce - the young feed on larch	Occasionally common (but not conspicuous) on larch
<u>Tolyte laricis</u> Fitch	<u>Tolyte laricis</u> Fitch	1856	Many hosts but probably first described from larch	Rare (31)
<u>Eacles imperialis</u> Hübner	<u>Eacles imperialis</u> Drury	1773	Many hosts	Not listed in Lepidoptera of Canada
<u>Lophyrus abietis</u> Harris	<u>Neodiprion abietis</u> (Harris)	1841	Rarely found on larch	Not common on larch
<u>Tomicus pini</u> Leconte	<u>Ips pini</u> (Say)	1826	Pines and spruces	Hopping (Can. Ent. 96: 976) does not list larch as a host

Table IX (concl.)

Name in Packard (1881)	Present Name	Year of original description	Specificity	Abundance
<u>Loptocampa caryae</u> Harris	<u>Halisidota caryae</u> Harris	1841	Many hosts	Not collected from larch by Canadian Forest Insect Survey
<u>Arctia quenselii</u> (found in Labrador).	<u>Apantesis quenselii</u> Paykull	1793	?	Rare. (Apparently a northern Holarctic species) not listed in Lepidoptera of Canada

The other main proposal concerning the origin of the larch sawfly in North America is that it entered via the Bering Bridge. The difficulty with the land-bridge hypothesis is that during the Pleistocene, according to present evidence, the bridge only existed during times of maximum cold when the sea level had dropped about 500 feet as a result of the transfer of water from the oceans to the ice caps (Hopkins 1959). The evidence from pollen analysis (Colvinaux 1963, 1964) shows that although the region was unglaciated during the last ice age, only tundra vegetation grew on it. Insects that feed on trees would thus have remained as isolated in the two continents during the glacial periods as they were during the interglacials. Tundra forms, however, could either cross the bridge and occupy a new region or if they already occurred on both continents they could migrate onto the bridge and exchange genes if reproductive barriers had not developed during the period of isolation of the previous interglacial or perhaps longer period. Gilmore (1946) appears to have been the first to propose the hypothesis that the only intercontinental migrants between Asia and America during the Pleistocene were those species that occupied Beringia during the Glacial Ages - when the species occurring in the continental centers were blocked by ice sheets. He suggested that "the four bridges of the Pleistocene allowed only the survivors in the bridge area to gain access to the other continent and to spread farther when the ice melted". Some modern forms with almost continuous holarctic distributions have "survived in the refuges, and have subsequently repopulated former ice-covered areas, and have recontacted their continental populations with subsequent fertility". There are many species which have the greater part of their range south of the tundra but which can exist under tundra conditions, and presumably, with these, periodic gene flow between the Asiatic and North American populations during the glacial periods was sufficient to prevent speciation from occurring. Gilmore documented his case by a study of the Microtus populations of the Beringian region. Simpson (1947) considered Gilmore's hypothesis to be an interesting one but he cautioned that "many complicated details remain to be worked out". He referred to an extensive unpublished manuscript of Gilmore's on this subject but I have been unable to find this paper in the literature. Simpson's objections appear to be based mainly on his conclusion that certain "non-tundra" animals apparently crossed the bridge during the Pleistocene (Lagurus, Felis, Bison, Pitymys, Camelidae, etc.) but one wonders whether these are actually Tertiary migrants for which the fossil evidence is incomplete. On the basis of this evidence Simpson concluded that the Bering land bridge persisted throughout the early and middle Pleistocene and that the actual migrations were mainly interglacial. However, the most northerly point at which Tertiary terrestrial fossil vertebrates have been found is southern British Columbia; the majority of such fossils in North America having been found in Wyoming, Montana, etc. MacNeil, et al (1961) have commented that "it is as puzzling as it is lamentable that not even fragmentary remains of terrestrial vertebrates have been found in the coal-bearing or other non-marine deposits of Tertiary age, despite the seemingly favorable lithologic character of the beds over large areas of Alaska." Fossil invertebrates of the Tertiary are also virtually absent in this region although fossil plants are commonly found.

from Asia to America under present conditions is highly unlikely. During the warmer periods of post-Wisconsin time, however, it appears that this gap was greatly reduced. Pschorn-Walcher (pers. comm.) favors the view that the larch sawfly crossed the Bering Strait at this time. He points out that Frenzel's (1960) vegetation map for Siberia during the climatic optimum period shows a larch-cembra pine-spruce taiga all around the Chukotka Peninsula as far east as Cape Dezhneva and a 'forest tundra' with larch and even Alnus on the southern New-Siberian Island at 73° N. latitude. He also mentions that even in the period of the Russian-American Company, larch forests were still common at the mouth of the Anadyr River, in an area which is pure tundra today; the forests having been exterminated by man since then. The gap between larch in Siberia and Alaska during the climatic optimum thus may not have been much wider than the Bering Strait itself. If the larch sawfly occurred on Dahurian larch in Siberia at this time, then dispersal to Alaska over a distance of approximately 100 miles is certainly a possibility.

There is no evidence in the form of specimens showing that the larch sawfly is present in the disjunct area of tamarack that is now present in Alaska although verbal descriptions of an insect found feeding on these trees in 1964 correspond to the larch sawfly. If the larch sawfly is present there, proponents of the hypothesis that the insect was introduced into America during the 1800's must assume that the sawfly jumped the approximately 200-mile gap that separates this disjunct area from the main area of tamarack.

The existence of this disjunct area was one of the main reasons for E. Hulten's (1937) proposal that tamarack survived the Wisconsin glaciation both in the Bering refugium and south of the ice-sheet. He proposed that spread has occurred from both refugia but the advancing boundaries have not yet met. I have been unable to find any report of fossil wood or pollen indicating the presence of Larix in the Bering refugium during the Wisconsin ice age although J. C. Ritchie of the University of Manitoba believes it may have survived there on the basis of the presence of associate species. I believe a fairly strong case can be made that tamarack from refugia south of the ice followed close behind the ice-sheet as it retreated northwards and spread into Alaska sometime after the corridor between the Cordilleran and Laurentide ice-sheets opened up about 12,000 years ago, and reached its most northwesterly penetration during the climatic optimum. Its range may have broken into the present disjunct areas following the onset of colder climatic conditions. The Larix in Alaska was originally placed in a separate species, L. alaskensis, (Wight 1907) but it was later shown that the distinguishing characteristics of this population also occurred in the northerly populations of L. laricina from Great Slave Lake, Lake Athabaska, Churchill, Manitoba, etc., indicating that it is a geographic variety (Raup 1947, p. 105).

Some workers have proposed that the larch sawfly crossed to North America before the ice ages of the Pleistocene. Throughout much of the Tertiary the climate in the north was warmer than at present and a forest similar to the boreal forest of today existed in the regions where tundra now occurs. The Bering land bridge was at times a wide connection

about 1,000 miles from south to north and was well forested. The ranges of the ancestors of many of the species of plants and animals characteristic of the taiga or boreal forest of today occupied ranges comprising portions of both Eurasia and America. With the onset of colder conditions during the Pliocene i.e., near the end of the Tertiary about 6 million years ago, this biota migrated south resulting in the isolation of many conspecific populations of plants and animals in the two continents. It is believed that the evolution of these populations along separate lines has resulted in the multitude of "twin species" or "sister species" that occur in the respective continents today. It is believed that the following arguments will show that unless the larch sawfly has evolved exceptionally slowly, the populations in Eurasia and North America would have achieved varietal, if not specific, status by now if these populations had been isolated this long.

At present the great majority of the species of tundra plants of northwest Alaska are also present in northeast Siberia, but no tree species are common to both continents. Rausch (1963) has listed 21 species of mammals that are found on both continents. Eighteen of these are tundra forms; two (the beaver and moose) are characteristic taiga forms but are often found north of the tree line, and one (Cervus elaphus, the wapiti of America or red deer of Eurasia) is more southerly but is considered by many workers to be two separate species. The most northwesterly part of its present range in North America is in the Upper Liard River in British Columbia but Murie (1951) has stated that "it is certain that a wapiti quite similar to the living animals occupied interior Alaska in the Pleistocene. Churcher (1959) analysed the dentition of the holarctic red fox, Vulpes vulpes, and found a clinal gradation from Europe across to eastern America with greater differences occurring between both the European and Siberian biotypes and the Alaskan and eastern American biotypes than between the Siberian and Alaskan forms.

In a study of the fresh-water fishes of the Beringian region, Walters (1955) found that 20 species occurred in northeast Siberia and 20 in northwest Alaska and that 19 of these were common to both continents. The minnow, Phoxinus phoxinus, occurred in Siberia only and the lake trout, Salvelinus namaycush, occurred in Alaska only. These had apparently migrated into these regions in post-glacial times. Walters concluded that the 19 common species, with the possible exceptions of the hump-backed and dog salmon which may have entered both continents from the sea post-glacially, survived the last glaciation on the Bering land bridge.

Ross (1956) discussed the evolution of mountain caddisflies. He noted that some species have evolved very slowly being very similar to forms found in Baltic amber (formed about Eocene times - 40 to 60 million years ago). However, in spite of the fact that extensive dispersal occurred between Asia and North America during the Tertiary, only one living species, Glossosoma intermedium, is Holarctic. This species is not truly mountain, however; existing successfully in cold springs in flat country, and it is undoubtedly this characteristic that enabled it to cross the

Bering bridge during the Pleistocene. Moore and Ross (1957), in their discussion of the genus Macrosteles in Illinois, state that "in the case of living species of Holarctic distribution, it is reasonable to suppose that each evolved in either Eurasia or North America and has spread into the other continent during relatively recent time, most likely during the last ice age. Otherwise, based upon what has happened in other branches of the group, populations of these Holarctic species on the different continents would have evolved into discreet entities by this time."

Acton (1962) has approached the problem through a study of the banding pattern of the giant chromosomes of Chironomus tentans Fabricius which he believes to be ideally suited to a study of speciation since they are not affected by environmental variables. The larvae of the European and North American populations of this species are identical and the adults differ only minutely but there are striking differences in chromosomal banding patterns between the two populations. An Alaskan population was found to resemble the European one. Acton suggests that the Alaskan population survived the last glaciation in the Beringian refugium and the North American population in the eastern United States and the gap has not yet been closed. He states that "C. tentans may have reached America in either the last interglacial period, about 130,000 years ago, or the one before that, between 250,000 and 450,000 years ago." He suggests that the two groups are destined to become full species and that it has taken this long for them to reach the halfway point. Crosses between the two groups produced eggs that were almost all viable. One might argue with his suggestion of an interglacial crossing, however, since he implies that because of the weak flight, short life and restricted habitat of this species, long-distance migration is unlikely. Unless a land bridge existed during the last or next-to-last interglacial, a crossing at this time therefore seems improbable. The species, moreover, occurs at Churchill, Manitoba, and thus appears capable of crossing during a glacial period.

The situation is not so clear when the evidence from other groups of insects, smaller plants, etc., is examined. For example, Townes (1963) discusses the ephialtine ichneumonids in this regard. He states that the ranges of most of the species extend over two or three life zones (Merriam's). In much of his discussion he considers only the zone occupied by the northernmost representatives and here, of 4 Arctic ("mostly tundra") species, 2 (50%) are Holarctic; of 26 Hudsonian ("transitional") species, 15 (58%) are Holarctic; of 69 Canadian ("mostly taiga") species, 23 (33%) are Holarctic and none of the 83 species having their northern limits south of the Canadian Zone are Holarctic. He also states, however, that

"we may question whether the Bering Strait is even now an important barrier to migration. In regard to ichneumonids, probably it is not. One hundred kilometers is not a great distance for an ichneumonid to fly, if it has a good tail wind; and so far as a species is common in the Bering area, individuals will cross with some regularity. At present the Bering area is Hudsonian and Arctic in climate. A slight

warming trend would bring the Canadian zone forests to the strait; and during a warmer interval, crossing of the Nearctic ephialtine species that range as far north as the Canadian zone would be easy, even without a land bridge."

A similar situation occurs with respect to plants. H. J. Scoggan in his Flora of Manitoba (1957) presents the following summary for the 270 Manitoba plants, exclusive of 193 introduced species, that are circumpolar (out of a total of 1,417 species):

1 Arctic circumpolar	96) 57%
2 (Arctic) subarctic circumpolar	58	
3 Subarctic circumpolar	84	31%
4 (Subarctic) temperate circumpolar	23	9%
5 Temperate circumpolar	9	3%

Groups 1 and 2 extend north of the tree line; group 3 extends north to the northern limit of the Northern Conifer Forest or Hudsonian Biotic Province; groups 4 and 5 extend north to the southern boundary of the Northern Conifer Forest (group 4 differing in that it includes southern Labrador, Newfoundland, and the northern parts of the western provinces).

Chillcott (1960) discussed 105 nearctic species of Fanniinae of which 32 are Holarctic. Seven of these latter are cosmopolitan and probably introduced; 20 occur in Alaska and five occur in other parts of North America. The species that occur in Alaska are mainly forest inhabitants although some, apparently, can also exist in tundra. The species groups which are scarcely or not at all represented in the Palaearctic are Lower Austral to Neotropical in distribution.

In the above discussion it is difficult to determine whether (a) the conspecific populations in Asia and America have existed unchanged for long periods of time; (b) there has been a considerable degree of long-distance dispersal, or (c) the taxonomic criteria by which species are differentiated are less stringent, i.e., species in these groups may correspond to genera in other groups. Chillcott has pointed out "that species and species groups do not necessarily evolve at the same rate, and a group showing considerable evolutionary divergence may have simply had a higher mutation rate or had more opportunities to diverge into new ecological niches What appear to be closely related species, because of a lack of differentiating characters, may actually have diverged much longer ago than postulated, and subsequently undergone a period of very slow evolution." Omdeco (1963) compares the chronology of mammal evolution with that of oligochaete evolution diagrammatically as shown in Figure 13.

Arctic plants are notoriously plastic and Polunin (1955) suggests this is due to: (a) periodic isolation and remingling of populations during the glacial and interglacial stages; (b) wide ecological amplitude of the species and associated wide morphological variation; (c) multiplicity of micro-habitats; and (d) frequent introgressive hybridizations due to continual disturbance of the arctic habitat. This great variation tends to blur distinctions that probably have arisen due to long separation of populations in various areas.

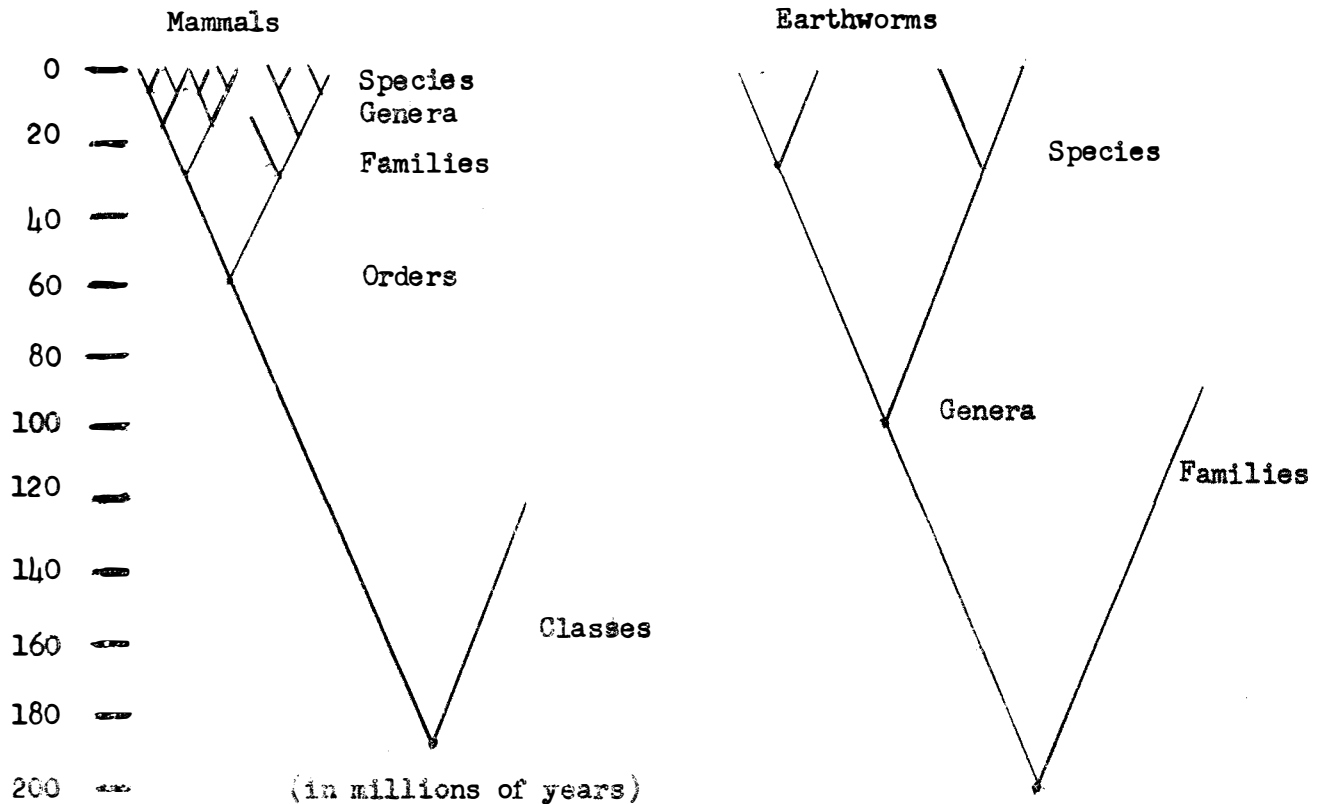


Figure 13.- Chronology of mammals and terrestrial oligochaeta (after Omcdec, 1963)

The great plasticity of arctic plant species may also be due in part to wind pollination. If pollen is transported from North America to Asia or vice versa then gene exchange may be sufficient to prevent speciation from occurring in the two continents. Polunin (1955) stated that "even a single pollen grain finding its stigmatic billet in a millenium might serve to establish a subspecies, genetically speaking, in an entirely new region." Gene exchange due to long-distance dispersal of plants and seeds seems less likely. Dahl (1963) indicates that plant species adapted to long-distance dispersal by wind comprise roughly 20% of the total species in most North Atlantic assemblages and analysis shows that in the 'Amphi-Atlantic' element of these assemblages the anemochorous species are less numerous in Iceland, Greenland, etc., than would be expected as compared to species having no adaptations for wind dispersal. D. Love (1963) concluded that the distributions of only a small fraction of the plant species showing North Atlantic disjunctions could be explained by wind- water- or animal dispersal of plants and seeds over the present distances. She concludes that "these plants ... must have come to the Atlantic islands over land connections, or over a system of landmasses at considerably shorter distances from each other than at present," probably in pre- or early-Pleistocene time.

It thus appears that each group of animals and plants (Order, Family, etc.) must be examined separately with respect to the prevalence within the

group of species having Holarctic distributions and the nature of these distributions to determine, for any given Holarctic species, whether its distribution can be used as a criterion indicating the nature of its origin in a particular region. The Tenthredinidae were recently examined by Benson (1962) who lists 134 sawfly species that are Holarctic (out of a total of approximately 1,000 sawfly species that occur north of Mexico in America). Thirty two species are listed as arctic or alpine and could conceivably have crossed the Bering Bridge under tundra conditions. Most of these species feed on Salix, Carex, Rumex, Vaccinium, etc. Seventy one species are listed as circumboreal but about 25 of these also occur in subarctic and arctic regions. This leaves about 46 species that might be classed as "non-tundra" but of these 6 feed on Equisetum; 5 on Graminae; 3 on Salix; 2 on Alnus, etc., and it may be that if their distributions were better known many might be found capable of existing under tundra conditions. He lists only six Holarctic sawfly species that feed on conifers: the larch sawfly; three Siricids (Sirex cyaneus, Urocerus gigas flavicornis and Xeris spectrum) (---because these feed in wood and are long lived the chances that they are introduced species seem fairly high) and two xyelids (Xyela alpigena and X. obscura). The latter two species were discussed by Burdick (1961) under the names X. middlekauffi and X. pini. The first is transcontinental and feeds on many pines while the second occurs only in eastern America and has but one host - white pine. Considering the total number of sawflies that attack conifers in Eurasia and North America, it would seem that if the Bering Bridge was ever forested during the Pleistocene or if long-distance dispersal of forest species across the Bering Strait has been an important means of entry to America --- there should be a greater number of Holarctic species of sawflies that feed on conifers than there are. Pschorn Walcher (pers. comm.), however, believes this argument is not fully convincing since a number of the Holarctic sawflies (e.g., Pontania, Phyllocolpa and Euura) feed on Salix and other shrubs which occur side by side with larch in the Alps in an association that might be termed "forest tundra" (intermediate between taiga and tundra). The implication that these species are equivalent to the larch sawfly in that they are restricted to regions south of the tree line may not necessarily be true, however, and the point that remains for further investigation is whether they also exist in the tundra of the Beringian region where larch is absent.

The rate of evolution in the various groups of organisms under discussion is basic to the problem of whether populations of a given species could have survived since the Tertiary in completely isolated regions and still remain conspecific. It has already been mentioned that some insect species found in Baltic amber (ants, caddisflies, etc.) are very similar to forms living today indicating almost no evolutionary change for approximately 50 million years. Evidence indicating such long periods of stability, however, is not provided by studies on animal populations that have remained disjunct over this length of time. From studies on long-standing disjunctions made on many groups of insects, including Neodiprion sawflies, Ross (1962) came to the conclusion that 35,000 to 50,000 years was sufficient time for distinctive sister species of insects to evolve in isolated habitats. Zimmerman (1960) presents

evidence that five species of obligate feeders on the introduced banana in Hawaii evolved from endemic species of the pyraustid Hedylepta within the course of 1,000 years. It may be that populations of certain boreal forest species on the two continents have remained conspecific during periods up to five million years but if true, these must be rare cases. Pertinent in this regard is the statement of Carter (1961) that "the stability or instability of environmental conditions is the most important factor in the control of the rate of evolution" and the boreal forest has certainly been an unstable environment during the last million years. It has long been known (Gray 1889; Dansereau 1957, p. 24) that certain plant species occur in both eastern Asia and eastern North America; the separated populations having remained similar for 15 to 20 million years without exchanging genes. These are all deciduous forest species, however, and this forest has probably been a more stable biome than has the taiga. The absence of tree species in this group seems paradoxical in view of the conclusion of paleobotanists that some existing species (of Pinus, Quercus, etc.) are almost identical with species of Miocene times (Stebbins 1950; 521, 551). As with insects, fossil evidence indicates slower evolution than does evidence from disjunctions. Possibly the species known as fossils did not have a Holarctic distribution in Miocene times. Examples of comparatively rapid evolution of plants are also known; in the genus Crepis active evolution of new, highly specialized species has been going on throughout the Pleistocene and Recent epochs (Babcock 1947). Stebbins (1950) believes that "given selective forces acting at their maximum intensity, a normal rate of mutation, and the possibility of occasional hybridization ... a new species could evolve in 50 to 100 generations."

In the case of the larch sawfly, two species of its parasites Tritoneptis klugii (Ratz.) and Ecolytas ornatus Holmgr. which occur in both Europe and America did not achieve their present distribution as a result of deliberate introductions by man. There is evidence also that Mesoleius tenthredinis may have been in America before the earliest releases of this species were made in 1910 (Appendix I). To be consistent, if one rejects the hypothesis that the larch sawfly was introduced by man, one must also reject it for these parasites, and must then postulate that all three or four of these insects have existed unchanged in both Eurasia and North America for at least the last few million years. Since each such instance appears to be of rare occurrence this seems less probable than the hypothesis that they were all accidentally introduced. The larch sawfly, however may have been able to cross the Bering Strait by long-distance dispersal when Larix in both Siberia and Alaska grew north of present tree lines. Could these parasites also have crossed at that time? T. klugii must spend a good part of its adult life searching for host cocoons in moss or soil and it is difficult to imagine this small insect dispersing over great distances. The latter comment, however, can also be made in relation to the hypothesis that T. klugii has spread across North America within the last hundred years or so. It was found west of the Rockies six years before the larch sawfly was first found there. The host in Idaho and Montana was a species of sawfly feeding on lodgepole pine (probably Neodiprion burkei or N. nannulus contortae). One may speculate that the parasite transferred from the larch sawfly to this host in western Alberta where the ranges of tamarack and lodgepole

pine overlap, thus facilitating its spread through the Rockies. The following list presents the year of first collection for various localities (based on data from Peck (1963) and Gahan (1938)).

<u>Year</u>	<u>Locality</u>	<u>Host Insect</u>
1883	Maine	Larch sawfly
1885	Quebec	Larch sawfly
1910	Minnesota	Larch sawfly
1911	Ontario	Larch sawfly
1923	(probably Lake States)	<u>Neodiprion pratti banksianae</u>
1924	Idaho	A sawfly on lodgepole pine
1926	Montana	A sawfly on lodgepole pine
1934	Oregon	Unnamed host on <u>Tsuga hetero-</u> <u>phylla</u> (probably <u>Neodiprion tsugae</u>)
1935	British Columbia	Larch sawfly
1935	Oregon	<u>Neodiprion tsugae</u>
1957	California	<u>Neodiprion abietis</u> complex (white-fir sawfly)

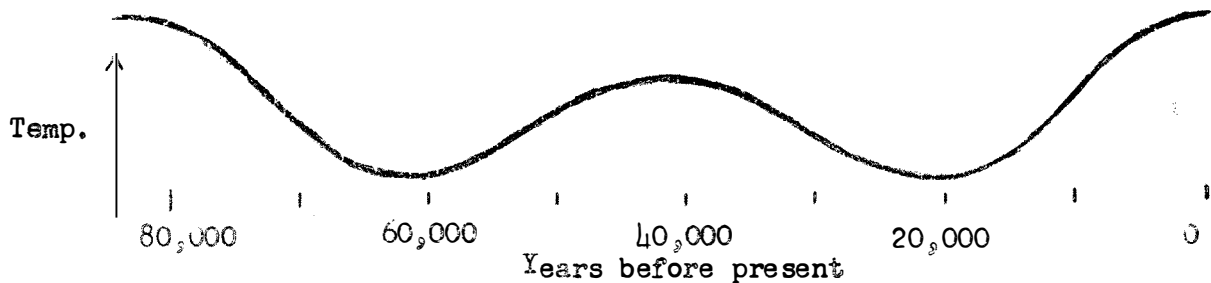
The comment made by Nairn et al (1962) in relation to the larch sawfly may also apply to T. klugii but with less force, namely: "The argument that the apparent westward spread of this insect may be largely a reflection of increasing observation and entomological interest may have some validity with respect to regions in northwestern Canada ... but is less convincing with respect to southern areas of the western provinces. Careful study of the natural history of this region by eminent observers and entomologists ... is a matter of record and it may be assumed that this insect would hardly have escaped notice had it occurred in abundance."

T. klugii has not been found in England and this may be an indication that, if it was introduced from Europe, it came in with larch sawfly material originating from the continent. On the other hand proponents of an entry via the Bering bridge might cite this as evidence supporting their case. Pschorn Walcher (pers. comm.) believes it may have entered thus under tundra conditions. He writes that "cocoon parasites are generally not very specific and Nematid sawflies feeding on dwarf willows, Vaccinium, Carex, etc. may have served as hosts for Tritneptis and may have allowed this parasite to cross the bridge step by step rather than by flight across an open strait." It remains for further investigation to determine whether T. klugii actually does parasitize hosts that occur in the tundra.

Concerning Eolytus ornatus, the distributional evidence is in favor of its being a species that has been introduced from Europe. It is fairly common in Newfoundland, Nova Scotia, New Brunswick and eastern Quebec; rare in Ontario and virtually absent west of Ontario. To fit

this case to the hypothesis of entry via the Bering Bridge one must speculate that it survived the Wisconsin ice age only in a refugium along the Atlantic seaboard and has spread westward extremely slowly during the last 12,000 years. Another possibility, however, is that the larch sawfly (and T. klugii?) entered via the Bering Bridge whereas E. ornatus was recently introduced from Europe. These problems could perhaps be solved by research along morphological and cytological lines to determine if clines exist.

A final point for discussion concerns the suggestion that has occasionally been made that perhaps man may have been instrumental in transporting the larch sawfly across the tundra of the Bering Bridge in the form of cocoons hidden in moss. Sphagnum moss may have been used then, as it is today amongst the indigenous peoples, for such purposes as a substitute for baby diapers, etc. The Wisconsin ice age was composed of two glacial stadia separated by an interstadial period. This can be roughly illustrated as follows:



Hopkins et al (1965) state that sea level rose during the interstadial and the Bering Strait may have been open. The evidence indicates that the ice sheet was continuous across North America only during the glacial stadia. Man apparently crossed the Bering Bridge during the first glacial stadium and dispersed southward with the opening of a corridor through what is now western Alberta about 50,000 years ago. A few traces of his presence dating back to 37,000 years ago have been found in Texas and Nevada. With the closing of the corridor about 30,000 years ago a culture developed in the Alaskan part of Beringia characterized by the fluted "Clovis" projectile points. This culture was based on the hunting of big-game animals (mammoth, etc.) and apparently developed in situ with little or no influence from Asian sources (Mason 1962, Vance Haynes 1964). With the re-opening of the corridor along the foothills of the Rockies about 12,000 years ago these people dispersed rapidly and occupied almost the entire United States in less than 1,000 years. Mason believes that the adaptation to big-game hunting "resulted in the opening up to man of the varied environments of the New World ... He was formed by his environment; but that section of his environment with which he was in closest articulation was mobile --- he had only to follow it". Giddings (1960) states that the

archaeology of Beringia "refuses to divulge the short term sites of people on the move ... It shows rather the slowly changing record of several groups of indigenous hunters and fisherman whose interests were as local as the shores and river banks on which they dwelt ... We need not give up the search for evidence of the migration of small bands, or even of uneasy hordes; yet the emphasis can be for a time, on the cultural stability of a Bering Strait which is a centre, rather than a way station of circumpolar ideas."

Even if Larix did exist in the Beringian refugium during the glacial stadia its range would probably be reduced in comparison to its present range since glaciers occupied considerable areas in the mountainous regions and vast portions of the lowlands were covered by a deep layer of windblown silt (loess). Thus the transportation of infested sphagnum or other moss from the range of Larix in Siberia to that in Alaska seems unlikely. It is possible, however, that Larix grew farther north than at present in the glacial periods. According to Goradkov (in Berg 1950) trees die in the tundra not from winter frosts but as a result of evaporation in summer, since little moisture reaches the shoots by way of the root system from the very cold soil. It may be that moister summers than now prevailed in Beringia during the glacial periods. Goradkov also states, however, that forest vegetation in the tundra avoids areas where there is permanently frozen soil and this was probably more extensive during the glacial periods than at present in the Beringian region.

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APPENDIX I

Evidence of the possible presence of *M. tenthredinis* in North America prior to 1910

The following evidence is not conclusive proof of the presence of this parasite in America prior to 1910 but in sum it is probably sufficient to cast a reasonable doubt on the assertion that *M. tenthredinis* was first introduced here in 1910:

(a) Lintner (1889) reared a small sample of larch sawfly cocoons collected at Cherry Valley, New York State. Following the completion of adult emergence he opened the remaining cocoons and found in addition to some dead larch sawflies "a pale yellow-green pupa of a large ichneumon fly within a slight inner cocoon". He believed this to be a *Pimpla* but this genus has not been recorded as a parasite of the larch sawfly and it seems certain that this was not the correct identification. Experience has shown that parasites of the larch sawfly that spin a thin cocoon inside that of the host, other than *M. tenthredinis*, have not been commonly found in North America.

(b) Fletcher (1885) studied the larch sawfly during a visit to Dalhousie, New Brunswick, in 1884. He mentions that he found *Podisus modestus* destroying the larvae and "two other species of insects harassing them; ... a larger Hemipteron and a species of Ichneumon fly about half an inch long, black, with red legs." Although there are, in addition to *M. tenthredinis*, undoubtedly numerous ichneumons of this size and coloration, it is very uncommon for forms like this, other than *M. tenthredinis*, to be observed actually harassing larch sawfly larvae.

(c) S. A. Graham (1956) states that in his work in Itasca Park, Minnesota, in 1914 some parasites were reared from cocoons. These were apparently destroyed by fire while in storage but he recalled that some ichneumonids were reared. He also stated (pers. comm., letter of Sept. 6, 1963) that "as I recall there were some specimens of about the size and appearance of *M. tenthredinis*. I suspect that the parasite may have been present, but no one will know for sure." If it was present, it seems highly unlikely it could have had its origin in the releases of English material made in Quebec, Ontario and Michigan in 1910 and 1911 or in Manitoba in 1912 and 1913. Griddle (1928) found no *M. tenthredinis* present in the cocoons he collected at the release point in Manitoba in 1914.

(d) Hopping, Leach and Morgan (1945) presented evidence, obtained from the rearing of about 7,000 cocoons, indicating that *M. tenthredinis* was not present in British Columbia in 1933. In 1934, 393 ♂♂ and 280 ♀♀ *M. tenthredinis* were liberated near Fernie, B. C. In 1935, 1,157 ♂♂ and 815 ♀♀ were liberated there. Dowden (1937) reported the recovery of *M. tenthredinis* from larch sawfly cocoons collected in 1935 along the north fork of the Flathead River in northern Montana and stated that it was present "in appreciable numbers." This infestation was part of the

one that was present in B. C. and the collection point was only 40 miles from Fernie but it seems certain that the M. tenthredinis found in Montana cannot be derived from the releases made in B. C. Even though a few adults may have dispersed 40 miles in 1934 it is highly unlikely they could have built up to "appreciable numbers" in one year. I believe it is possible that the parasite may have spread westward from Manitoba following the 1912-1913 releases there, perhaps crossing the Rockies shortly after its host accomplished this (assuming it did). No populations west of Winnipeg were examined for parasitism during this period. Graham (1931), however, found that the parasite had spread eastward at least 200 miles by 1928.

If M. tenthredinis was present in North America prior to 1910 it may have been accidentally introduced with the larch sawfly during the 19th Century and, conceivably, it could have spread with its host across the continent as Eclytus ornatus appears to be spreading now, even though it apparently did not reach high levels of abundance. There is certainly a good deal of evidence to indicate that the releases made during 1910-1914 and the intra-continental transfers made thereafter were highly effective. Perhaps a superior strain was introduced at that time. Alternatively, some workers may prefer the explanation that both the host and M. tenthredinis have existed in North America for at least several thousands of years.

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