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STUDIES ON THE DISTRIBUTION AND INHERITANCE OF THE RESISTANCE OF THE LARCH SAWFLY TO *MESOLEIUS TENTHREDINIS* MORLEY

by

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CONTENTS

1. INTRODUCTION

A parasite, Mesoleius tenthredinis Morley, was introduced from England into Ontario in 1910 and into Manitoba in 1912. By 1927 it was sufficiently abundant in Manitoba to be redistributed to other parts of Canada. The effectiveness of the parasite declined markedly in Central Canada about 1940. This decline was associated with a resistance mechanism in the larch sawfly whereby the parasite eggs become encapsulated by phagocytic blood cells of the host larvae and embryonic development was inhibited (Muldrew, 1953). Clausen (1958) stated that "this situation has serious implications in biological control of crop pests, though fortunately it appears to be an isolated case, and a comparable loss in field effectiveness of a parasite species has not heretofore been recorded."

2. DISTRIBUTION AND PREVALENCE OF THE IMMUNITY REACTION

The object of this study was to determine the degree to which populations of the larch sawfly in various parts of Canada and the United States possess the ability to encapsulate Mesoleius eggs. A further objective was to determine if the resistance - susceptibility ratios for selected populations showed progressive changes over a period of years.

Two hypotheses that have been advanced to explain the mechanism by which larch sawflies possessing the ability to encapsulate Mesoleius eggs became dominant in Central Canada and the Lake States are:

(1) That the immune form originated in the center of this area,

possibly due to a mutation in one or a few individuals, sometime between 1930 and 1937, and that this form increased in numbers and became dominant in the population because of its superior ability to survive under conditions of relatively intense parasitism by M. tenthredinis. According to this hypothesis the current outbreak is a result of the rapid spread of the resistant form into surrounding areas.

(2) That the immunity reaction is possessed by a few individuals in the majority of populations of the larch sawfly and that this proportion increased greatly and became dominant in localized areas when the selective pressure exerted by M. tenthredinis became high in these areas. There is some evidence that in those areas where the larch sawfly is still highly susceptible to Mesoleius (Newfoundland, Nova Scotia, Pennsylvania, British Columbia), a few individuals (approximately one per cent) possess the ability to encapsulate eggs of M. tenthredinis. According to this hypothesis the distance flown by the adult sawflies is not the important factor in "spread" of infestation but the outbreak is visualized as resulting from the coalescing of the localized infestations in each of which has occurred the release of the resistant portion of the population. It is difficult to judge the feasibility of hypothesis (1) as there is a paucity of information on the dispersal activities of larch sawfly adults. The assumption that the larch sawfly spread from the Maritimes to Saskatchewan during the period 1880 to 1910 requires a dispersal rate of approximately 70 miles per year. Similarly, if sawflies spread from the Riding Mountain National Park, Manitoba, to Prince Albert, Saskatchewan during the period

1938 to 1947, this indicates a dispersal rate of approximately 45 miles per year.

In areas where the larch sawfly populations are at present highly susceptible to M. tenthredinis it is important to determine whether these populations become progressively more resistant to the parasite in the future as it may be that if this should happen it may lead to destructive outbreaks of the larch sawfly in these areas.

2.1 Methods

A. Dissection of prepupae removed from collections of cocoons obtained from various areas.

B. Rearing of collections of cocoons obtained from various areas. Although this provides no estimate of the extent of encapsulation it indicates the degree of successful parasitism by M. tenthredinis and may serve as a check on the accuracy of the dissection estimates.

C. Caging of sawfly adults that emerge from cocoons from various areas for oviposition; rearing of the progeny of these adults, and testing these progeny for degree of resistance by parasitizing them within cages and subsequently dissecting them. This method is particularly useful for collections made from populations in which the evidence of parasitism by M. tenthredinis is very low (e.g. Newfoundland) or where the number of cocoons received is small.

2.2 Variability of Estimates of Percentage Parasitism and Percentage Hatch

In the central region of Canada, where the resistant larch sawfly is found, dissections of samples collected annually by the

Forest Biology Rangers from many locations have shown that both the percentage parasitism by M. tenthredinis and the percentage hatch of the eggs deposited by this parasite vary considerably between areas and from year to year. In this report the term "percentage hatch" refers to the expression:

$$\frac{\text{Total sawfly larvae containing at least one } \underline{\text{Mesoleius}} \text{ larva}}{\text{Total sawfly larvae parasitized by } \underline{\text{Mesoleius}}} \times 100$$

Table 1 shows this variation for four locations. It should be pointed out that the estimated values for percentage hatch are based on a sample size equal to the total number of larvae parasitized by M. tenthredinis rather than the total number of larvae dissected.

The differences between years for each location were analyzed by chi-squares (Table 2). Only the estimates of percentage hatch for Mile 145, No. 10 Highway and Mile 32, P. O. W. Road, indicate no unusual deviations from ordinary sampling variation during the period of study.

Table 2

Chi-Squares for Between-year Differences in Each of Four Locations

Location	Chi-square for per cent parasitism	Chi-square for per cent hatch	Degrees of freedom	$X^2_{.01}$	$X^2_{.05}$
Mile 7 Norgate Road	62.0**	35.0**	12	26.2	21.0
Mile 145 No. 10 Hwy.	124.9**	11.6	9	21.7	16.9
Mile 32 P.O.W. Road	213.6**	15.5	9	21.7	16.9
Nisbet P. F. Home Block	104.2**	30.1**	7	18.5	14.1

** Significant at 1 per cent level

Table 1

Variation in Per cent Parasitism and Per cent Hatch of
M. tenthredinis

Location		1941	1944	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	1955
R. M. N. P. Manitoba Mile 7 Norgate Road Sec. 31, Tp.19 Rge. 17, W.P.	No. of larvae dissected	97	77	297	279	173	48	149	92	97	96	83	191	89
	No. parasitized by *M. tenthredinis*	26	0	44	40	20	8	9	6	4	23	6	29	8
	Per cent parasitism	27.	0.	15.	14.	12.	17.	6.	7.	4.	24.	7.	15.	9.
	Per cent hatch	19.	0.	7.	9.	10.	13.	55.	33.	75.	13.	33.	31.	50.
R. M. N. P. Manitoba Mile 145 No. 10 Hwy. Sec. 26, Tp.21, Rge. 19, W.P.	No. of larvae dissected			313	98	99	43	61	77	196	71	96	162	
	No. parasitized by *M. tenthredinis*			48	8	9	24	8	2	13	4	0	38	
	Per cent parasitism			15.	8.	9.	56.	13.	3.	7.	6.	0.	23.	
	Per cent hatch			17.	13.	22.	4.	25.	0.	38.	50.	0.	29.	
R. M. N. P. Manitoba Mile 32 P.O.W. Road Sec.12, Tp.21, Rge. 21, W.P.	No. of larvae dissected			122	104	200	182	130	35	97	79	94	136	
	No. parasitized by *M. tenthredinis*			84	57	54	41	13	5	4	9	22	27	
	Per cent parasitism			69.	55.	27.	23.	10.	14.	4.	11.	23.	20.	
	Per cent hatch			12.	12.	17.	5.	23.	0.	50.	22.	23.	30.	
Prince Albert Saskatchewan Nisbet. P.F. Home Block Sec.8, Tp.49, Rge. 36, W.2nd	No. of larvae dissected						191	217	80	77	57	93	169	70
	No. parasitized by *M. tenthredinis*						45	124	45	44	40	48	87	9
	Per cent parasitism						24.	57.	56.	57.	70.	52.	51.	13.
	Per cent hatch						9.	27.	40.	14.	53.	29.	22.	22.

Table 3 presents the mean values and ranges for percentage parasitism and percentage hatch over the period of the study. The last column gives the range of percentage hatch considering only samples in which the number of larvae parasitized by Mesoleius was 20 or more.

Table 3

Mean and Range for Percentage Parasitism and Per Cent Hatch

Location	Mean per cent parasitism by *M. tenthredinis*	Range	Mean per cent hatch	Range - based on all samples	Range - based on samples of 20 or more
Mile 7 Norgate Road	13.	0.-27.	19.	0.-75.	7.-31.
Mile 145 No. 10 Hwy.	13.	0.-56.	21.	0.-50.	4.-29.
Mile 32 P.O.W. Road	27.	4.-69.	15.	0.-50.	5.-27.
Nisbet P.F. Home Block	46.	13.-70.	27.	9.-53.	9.-53.

The differences between areas of the means for percentage parasitism and percentage hatch obtained over the period of study were compared by chi-square analysis (Table 4).

Table 4

Chi-Squares for Between-area Differences Based on the Totals for the Period of Study

Locations compared	Chi-square for per cent parasitism	Chi-square for per cent hatch
Mile 7 Norgate Road and Mile 145 No. 10 Hwy.	0.0017	0.26
Mile 7 Norgate Road and Mile 32 P.O.W. Road	95.28 **	1.25
Mile 7 Norgate Road and Home Block Nisbet P.F.	381.57 **	5.01 *
Mile 145 No. 10 Hwy. and Mile 32 P.O.W. Road	75.86 **	2.29
Mile 145 No. 10 Hwy. and Home Block Nisbet P. F.	304.15 **	2.12
Mile 32 P.O.W. Road and Home Block Nisbet P. F.	87.79 **	14.26 **

$X^2_{.01}$ 1 d.f. = 6.63 $X^2_{.05}$ 1 d.f. = 3.84

It can be seen from Tables 2 and 4 that in general the chi-squares for percentage hatch are much smaller than the chi-squares for percentage parasitism. The one exception is the comparison between Mile 7 Norgate Road and Mile 145, No. 10 Highway, two locations that are 14 miles apart. Although the larger samples on which percentage parasitism is based show up smaller differences between the populations, the data may indicate that much of the variability in percentage parasitism is due to factors other than fluctuations in the encapsulating ability of the population (assuming variations in percentage hatch cause variations in percentage parasitism of proportional magnitude).

In the fall of 1954 a study was carried out in the Telford Bog, Whiteshell Forest Reserve, Manitoba (Sec. 17, tp. 10, rge. 16 E. P.) to determine the degree of variation between samples taken within the same stand. Ten samples were collected each of approximately the same size as those collected by the Forest Biology Rangers (100 cocoons) and the method of collection was similar, i.e., the cocoons were collected where they were easiest to find within a small area (25 to 50 square yards). The collection sites were separated by a maximum distance of 300 yards.

Table 5 presents the variance and coefficients of variation of the four types of parasitism and the .95 per cent confidence limits of p based on ten samples. The variance was calculated by the formula given by Cochrane (1953, P. 119) for estimating the variance of a ratio. The confidence limits were calculated both

Table 5

Sampling Variation in Estimates of Parasitism of the Larch Sawfly
Telford Bog, Whiteshell Forest Reserve, 1954

Type of parasitism	$\bar{y}$ (mean No. of parasitized hosts per sampling unit)	cv$\bar{y}$	$\hat{p}$	v (p)	S.D.(p)	cv of p	95% Confidence limits of p: Student's t lower	Student's t upper	Quadratic lower	Quadratic upper	Half-width of student's t interval as a per cent of p
M. tenthredinis encapsulated eggs only	3.9	.185	.0539	.000104	.010173	.189	.0309	.0769	.0316	.0785	43%
M. tenthredinis living larvae	1.1	.268	.0152	.000012	.003464	.228	.0074	.0230	.0051	.0235	52%
Bessa harveyi (at least one living larvae in host)	20.7	.182	.2859	.00111	.0333	.117	.2106	.3612	.1992	.3538	26%
Bessa harveyi (all dead in host)	2.5	.275	.0345	.00009	.00948	.275	.0131	.0560	.0127	.0564	62%

Number of samples (n) = 10
$\bar{x}$ = 72.4 (mean number of sound larch sawfly larvae per sampling unit)
cv$\bar{x}$ = .0838

Table 6

The 95 Per cent Confidence Limits of p based on Student's t for Various Sample Sizes

Type of parasitism	n = 5				n = 2				n = 1			
	cv of p	Confidence limits lower	Confidence limits upper	Half-width as a % of p	cv of p	Confidence limits lower	Confidence limits upper	Half-width as a % of p	cv of p	Confidence limits lower	Confidence limits upper	Half-width as a % of p
M. tenthredinis encapsulated eggs only	.071	.0213	.0864	60%	.422	.0024	.1053	96%	.597	0	.1266	135%
M. tenthredinis living larvae	.104	.0041	.0263	73%	.510	0	.0327	115%	.721	0	.0400	163%
Bessa harveyi (at least one living larva in host)	.027	.1793	.3925	37%	.261	.1174	.4544	59%	.368	.0476	.5242	83%
Bessa harveyi (all dead in host)	.151	.0042	.0649	88%	.614	0	.0825	139%	.869	0	.1024	196%

on the basis of Student's t and the quadratic formula given by Cochrane (1953, p. 121). He suggests that this formula be used when the sample size is less than 30 and the coefficients of $\bar{x}$ and $\bar{y}$ are both less than 0.1 since under these conditions the normal approximation does not apply. In Table 6 the coefficients of variation and .95 per cent confidence limits (based on Student's t) for sample sizes of 5, 2 and 1 are given. The confidence limits for sample sizes of 1 and 2 indicate the accuracy of estimates of the true values of parasitism in this stand that would have been obtained by a typical Forest Biology Ranger collection made in 1954. The chi-squares for the differences in parasitism between samples were as follows:

M. tenthredinis eggs only	=	11.66
M. tenthredinis larvae	=	3.86
Per cent hatch	=	10.90
Bessa harveyi living larvae	=	33.55 **
Bessa harveyi dead larvae	=	16.50
Total Bessa harveyi	=	36.17 **

$X^2_{.01}$ 9 d.f. = 21.67 $X^2_{.05}$ 9 d.f. = 16.92

Only parasitism by living Bessa harveyi larvae showed highly significant differences between samples.

It seems clear that to demonstrate differences in encapsulating ability between populations in different areas or to test for changes in the encapsulating ability of a population over a period of years, large and representative samples are required.

2.3. Parasitization and Encapsulation by Regions

It should be kept in mind that because of small sample size many of the following estimates for percentages of parasitism and hatch are rough approximations only.

2.3.1 Newfoundland

Collections made in four locations in Newfoundland in the fall of 1954 were forwarded to Winnipeg. These cocoons were subdivided as follows:

Location	No. of cocoons received	No. discarded	No. opened	No. of prepupae dissected	No. of cocoons reared
Glenwood	267	41	100	100	126
Random Island	126	2	75	60	49
Gander	138	4	85	84	49
Notre Dame Junction	255	42	100	99	113
Total	786	89	360	343	337

One of the discarded cocoons from Notre Dame Junction was a cocoon spun in 1953 or earlier which had what appeared to be a typical *Mesoleius* emergence hole and a typical thin *Mesoleius* cocoon inside.

Dissections of field-collected cocoons are shown in the following synopsis:

Location	No. of prepupae dissected	Parasitized by *M. tenthredinis*	Parasitized by *Bessa harveyi* No.	Parasitized by *Bessa harveyi* Per cent
Glenwood	100	0	0	0.
Random Island	60 (2♂♂)	0	19	32.
Gander	84 (2♂♂)	0	6	7.
Notre Dame Junction	99	0	2	2.
Total	343	0	27	8.

Rearings of field-collected cocoons are summarized in the following text table:

Location	No. of cocoons reared	*P. erichsonii* ♀♀	*P. erichsonii* ♂♂	*M. tenthredinis*	*B. harveyi* No.	*B. harveyi* Per cent*	Dead in cocoons	Hold-overs
Glenwood	126	87	2	0	1	1.	36	-
Random Island	49	4	0	0	5	55.	40	-
Gander	49	36	0	0	3	8.	10	-
Notre Dame Jct.	113	79	2	0	10	11.	21	1
Total	337	206	4	0	19	8.	107	1

*based on total adult emergence

In the fall of 1958 three collections of approximately 200 cocoons each were made at Dawe's Farm, Corner Brook; Little Barachois Brook, St. George's District and Badger-Millertown Road. These were forwarded to Winnipeg. To date 22 prepupae have been examined. Four were parasitized by an unknown small external parasite; none by *M. tenthredinis*.

Parasitization of Reared Families

Data are presented in the following summary only for those families in which at least one member was found to be parasitized at the time of dissection.

Source of parent female	Family designation	Year family reared	No. of prepupae Reared	No. of prepupae Dissected	Parasitized by *M. tenthredinis* Unhatched eggs	Parasitized by *M. tenthredinis* Living larvae	Parasitized by *M. tenthredinis* Per cent hatch
Glenwood	B	1955	61	25	0	23	100.
Glenwood	C	1955	64	39	1*	23	96.
Glenwood	D	1955	106	16	1**	14	93.
Glenwood	D.3.7	1957	18	13	0	3	100.
Glenwood	F.	1958	15	8	0	1	100.
Gander	A.	1955	58	27	1***	22	96.
Gander	B.	1955	12	2	0	2	100.
Notre Dame J.	A.	1955	121	72	0	9	100.
Notre Dame J.	C.	1955	76	3	0	1	100.
Notre Dame J.	D.	1955	102	2	0	2	100.
Total			633	207	3	100	97.

*a very thin capsule around this egg
**1 unencapsulated egg - 5 dead larvae, 0 living larvae in this host
***17 unencapsulated eggs - 3 dead larvae, 0 living larvae in this host

The writer knows of no records of high recovery of *M. tenthredinis* from the larch sawfly population in Newfoundland. Thus, although over 7,500 *M. tenthredinis* adults were liberated in Newfoundland between 1941 and 1947, the parasite has apparently failed to become successfully established in spite of the fact that the sawfly larvae have shown the least degree of resistance of any tested in this study. It may be that there is some unknown harmful factor in the tamarack-bog environment in Newfoundland that militates against *M. tenthredinis*.

2.3.2 Nova Scotia

The larch sawfly has been increasing in numbers in Nova Scotia since 1955. The last major outbreak of this insect occurred there from 1933 to 1942. From 1943 to 1953 only six isolated colonies were found. Evidence was obtained in 1934 and 1935 that *M. tenthredinis* was not present in New Brunswick and liberations were made there beginning in 1935. The average parasitism by *M. tenthredinis* increased progressively from 0 to 50 per cent during the period 1935 to 1939 in New Brunswick. Although several thousand larvae were dissected encapsulation was not observed (Reeks, 1954).

Dissection of Field-collected Cocoons

Cocoons collected at Pope's Harbour, Halifax County, and Hassett, Digby County, N. S., in the fall of 1958 were forwarded to Winnipeg for dissection. The results follow:

Location	No. of cocoons received	No. of cocoons discarded	No. of prepupae dissected	Parasitized by M. tenthredinis: Eggs	Larvae	% parasitism	% hatch	Parasitized by B. harveyi: No.	Per cent
Pope's Harbour	174	16	142*	0	4	3.	100.	2	1.4
Hassett	171	35	136	0	13	11.	100.	1	0.7

* 16 prepupae were parasitized by an unknown ectoparasite

Rearing of Field-collected Cocoons

The following data are the combined results from the survey collections, which were made at many locations, except in 1955 when all cocoons were collected at Black Point, Halifax Co.:

Year Collections made	No. of cocoons received	P. erichsonii ♀♀	♂♂	M. tenthredinis ♀♀	♂♂	% based on total emergence	Bessa harveyi	Eclytus ornatus
1955	21	5	0	0	0	0	0	0
1956	1111	124	1	8	12	14.	0	0
1957	1610	516	9	22	24	8.	0	4
Total	2742	645	10	30	36	9.	0	4

Parasitization of Reared Families

The origin of the parent female of each of the following lines was Black Point, Halifax Co.

Year cocoons collected	Family designation	Year family reared	No. of prepupae: Reared	Dissected	Parasitized by M. tenthredinis: Encapsulated eggs	Larvae	Per cent hatch
1955	N.S.A.	1956	44	32	11	2	15.
1955	N.S.B.	1956	24	13	10	2	17.
1956	N.S.C.	1957	64	33	2	9	82.
1956	N.S.D.	1957	32	21	2	2	50.
1956	N.S.F.	1957	19	3	0	3	100.
1956	N.S.P.	1957	8	5	0	2	100.
Totals			191	107	25	20	44.

The dissection of field-collected cocoons indicates that the larch sawfly populations at Pope's Harbour, Halifax Co., and Hassett, Digby Co., are highly susceptible to M. tenthredinis as no encapsulated eggs were found in a total of 278 prepupae dissected, 17 of which were parasitized by M. tenthredinis. The data for the populations at Black Point, Halifax Co., obtained by dissection of prepupae parasitized in cages in Manitoba using M. tenthredinis of Central Canadian origin, indicate a fairly high degree of resistance. Possibly the Black Point population is quite different from those at Pope's Harbour and Hassett because Black Point is approximately 70 miles south of Pope's Harbour and 80 miles north-east of Hassett. The evidence for Black Point, however, is based on only six females originating from this location and cocoons should be field-collected at Black Point and dissected to check on the encapsulating ability of this population.

The fact that the larch sawfly of British Columbia and Newfoundland origin showed high susceptibility when parasitized by M. tenthredinis of Central Canadian origin indicates that it is not the source of the parasites that influence the encapsulating ability of the Black Point larvae. Contamination of the families seems unlikely because encapsulation was found in four of six families tested in 1956 and 1957. Moreover, in 1956, the parent females emerged on June 6, by which time fewer than four per cent of the adults had emerged in the field at Red Rock Lake. New shoots placed in oviposition cages were always carefully checked for eggs and/or larvae as was tamarack foliage given to the larvae during rearing. It was noted that the capsules formed by the Black Point larvae appeared to be thinner on the average than those formed in Central Canadian larch sawfly larvae.

2.3.3 New York State, U. S. A.

Drooz (1957) dissected 95 larch sawfly prepupae removed from cocoons collected from a stand of Japanese larch near Coventry, Chenango County, New York. He found that 50 per cent contained living larvae of M. tenthredinis and none contained encapsulated eggs although four encapsulated "foreign bodies" were observed.

2.3.4 Pennsylvania, U. S. A.

Drooz (personal communication, October 6, 1958) reported that parasitism by M. tenthredinis of sawfly prepupae in a Japanese larch plantation at Renova, Pennsylvania, was 7 per cent by dissections and 10 per cent by rearing in 1957. Dissection of 100 cocoons in 1958 revealed parasitism to be 14 per cent. On August 15, 1958, 1136 cocoons were collected by Drooz and shipped to Winnipeg on October 6. A sample of 100 prepupae removed from these cocoons was dissected. Eighteen contained living M. tenthredinis larvae; one contained an unhatched unencapsulated egg and one contained an egg enclosed in a light brown, typical capsule.

2.3.5 Quebec

In 1954 collections of cocoons were received from La Sarre and La Ferme. (see Fig. 1 for these locations.) They were treated as follows:

Location	No. of larvae collected	No. of cocoons obtained	No. of cocoons discarded	No. of cocoons opened	No. of larvae dissected	Cocoons retained for rearing
La Sarre	200	31	5	0	0	26
La Ferme	200	136	22	50	47	64

LEGEND FOR FIGURE 1

1 - Robson Tp.

2 - Hemlo

3 - Hunt Tp.

4 - Dog Lake

5 - Panet Tp.

6 - Casgrain Tp.

7 - Homuth Tp.

8 - Evelyn Tp.

9 - Denton Tp.

10 - Noble Tp.

11 - Sault Ste. Marie

12 - Gauthier Tp.

13 - Ville Marie

14 - Gillies Limit Tp.

15 - Strathy Tp.

16 - La Sarre

17 - La Ferme

18 - Senneterre

19 - Mt. Laurier

20 - Grand Remous

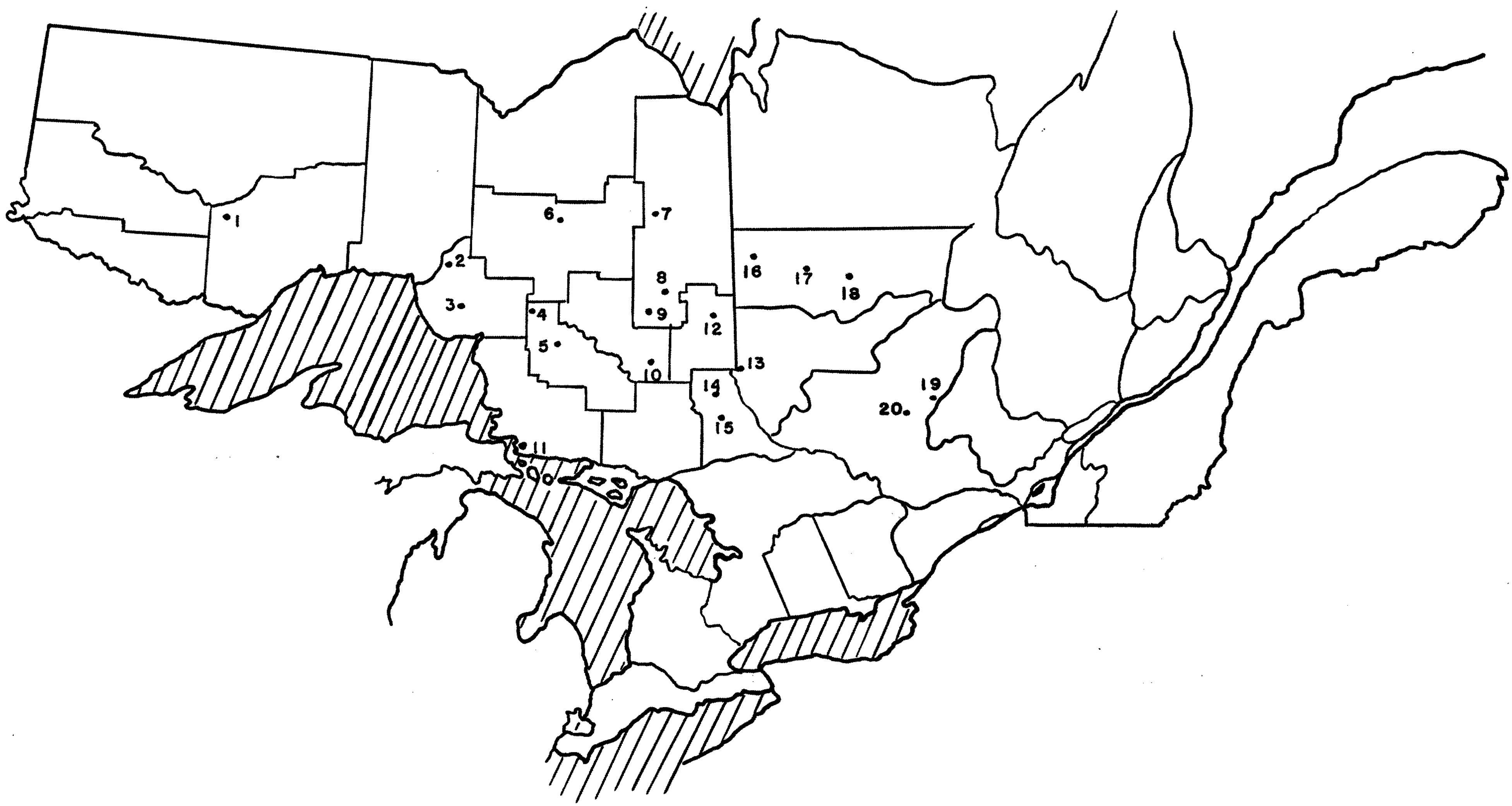


FIG. 1. LOCATION OF COLLECTION POINTS IN QUEBEC AND ONTARIO

Dissections of a sample of the above are shown in the following synopsis:

Location	No. of larvae dissected	No. parasitized by *M. tenthredinis* Eggs	Larvae	% parasitism	% hatch	*B. harveyi*
La Ferme	47	0	2	4.	100.	0

Another sample lot was reared, with the following results:

Location	No. of cocoons reared	*P. erichsonii* ♀♀	♂♂	*M. tenthredinis* ♀♀	♂♂	% parasitism	*B. harveyi*
La Sarre	26	17	1	0	1	5.	0
La Ferme	64	24	0	0	0	0.	0

In 1955, a collection of 110 sawfly cocoons was made at Ville Marie, Quebec (see Fig. 1) and forwarded to Winnipeg. A total of 51 adult female larch sawflies emerged from these cocoons in 1956 but no *M. tenthredinis* or *B. harveyi*.

Samples of both the La Sarre and La Ferme stock were used for family rearings. The parasitization and encapsulation of dissections of family lots are shown as follows:

Source of female parent	Family designation	Year family reared	No. of larvae Reared	Dissected	Parasitized by *M. tenthredinis* Encapsulated eggs	Larvae	Per cent hatch
La Sarre	L.S.A.	1955	11	6	0	3	100.
La Sarre	L.S.B.	1955	46	14	0	8	100.
La Sarre	L.S.C.	1955	29	15	9	2	18.
La Sarre	L.S.E.	1955	38	7	6	1	14.
La Ferme	L.F.G. 1.1.	1957	60	42	18	2	10.
Total			184	84	33	16	33.

In the fall of 1958, 243 cocoons collected at Seneterre, 150 at Mont Laurier and 150 at Grand Remous were forwarded to Winnipeg (see Fig. 1 for locations). The majority of these will be dissected at a later date.

2.3.6 Ontario

Cocoon collections received in the fall of 1954 from Ontario were subdivided as follows:

Location (see Fig. 1)	No. of cocoons obtained	No. of cocoons discarded	No. of cocoons opened	No. of larvae dissected	No. of cocoons retained for rearing
Hemlo	252	1	100	97	151
Homuth Tp.	381	8	100	98	273
Casgrain Tp.	332	15	100	97	217

The dissected field-collected cocoons from Ontario contained:

Location	No. of larvae dissected	Parasitized by *M. tenthredinis*				Parasitized by *B. harveyi*	
		Encapsulated eggs	Larvae	Per cent parasitism	Per cent hatch	No.	Per cent
Hemlo	97	0	1	1.	100.	2	2
Homuth Tp.	98	18	18	37.	50.	2	2
Casgrain Tp.	97	1	0	1.	0.	4	4

Rearings of field-collected cocoons produced:

Location	No. of cocoons reared	*P. erichsonii*		*M. tenthredinis*			*B. harveyi*		*Eclytus ornatus*	
		♀♀	♂♂	♀♀	♂♂	% parasitism	No.	Per cent	No.	%
Hemlo	151	116	1	3	1	3.	3	2.4	1	1
Homuth Tp.	273	184	3	22	22	19.	0	0	0	0
Casgrain Tp.	217	138	1	1	0	1.	8	5.4	0	0

Cocoon collections were received in the spring of 1957 from the following locations (see Fig. 1):

Chapleau District, Dog Lake, Sec. 69, Tp. 46, Grid 5-053-226
Chapleau District, Golf Course, Sec. 69, Panet Tp., Grid 5-061-218
Gogama District, P. S. Plot 55-1, Sec. 72 Noble Tp., Grid 5-082-215
Cochrane District, 16 miles south west of Timmins, Sec. 43, Denton Tp., Grid 5-081-227
North Bay District, Latchford, Sec. 64, Gillies Limit Tp., Grid 4-009-209

The adults that emerged from these cocoons in 1957 were as follows:

Location	No. of cocoons received	P. erichsonii		M. tenthredinis			B. harveyi		Hold-overs	Found dead in cocoons
		♀♀	♂♂	♀♀	♂♂	%*	No.	%*		
Dog Lake	314	129	3	2	3	3.2	17	11.0	11	148
Panet Tp.	311	208	1	0	2	0.9	1	0.5	4	95
Noble Tp.	530	340	1	7	4	3.1	6	1.7	29	143
Denton Tp.	765	505	4	10	7	3.2	7	1.3	18	214
Latchford	684	390	4	16	11	6.4	0	0.0	69	194
Total	2604	1572	13	35	27	3.9	30	1.8	131	704

* based on total adult emergence

In the fall of 1957 collections of cocoons were received from the following locations:

Swastika District, Gauthier Tp.
North Bay District, Strathy Tp.
Sault Ste. Marie District, near Sault Ste. Marie

The adults that emerged from these cocoons in 1958 were as follows:

Location	No. of cocoons reared	P. erichsonii		M. tenthredinis			B. harveyi		
		♀♀	♂♂	♀♀	♂♂	%*	♀♀	♂♂	%*
Gauthier Tp.	780	425	4	15	12	5.7	11	4	3.2
Strathy Tp.	1394	803	6	25	21	5.3	14	8	2.5
Sault Ste. Marie	631	380	0	7	11	4.5	1	2	0.7
Total	2805	1608	10	47	44	5.2	26	14	2.3

* based on total adult emergence

Approximately 200 cocoons were received in the fall of 1958 from each of the following locations: White River District, Hunt Tp.; Cochrane District, Evelyn Tp.; and Port Arthur District, Robson Tp. The majority of these will be dissected at a later date.

Parasitization of Reared Families

The results of dissections are presented in the following table:

Source of parent female	Family desig-nation	Year family reared	No. of larvae		Parasitized by M. tenthredinis		
			Reared	Dissected	Encapsulated eggs	Larvae	% hatch
White R. (near Hemlo)	W.R.A.	1955	95	26	1	12	92.
"	W.R.B.	1955	72	26	15	9	38.
"	W.R.E.	1955	50	10	0	2	100.
"	W.R.H.	1955	28	2	0	2	100.
Homuth Tp.	Coch.A.	1955	65	22	0	2	100.
Strathy Tp.	Strathy B.	1958	62	10	4	0	0.
Total			372	96	20	27	57.

2.3.7 Manitoba and Saskatchewan

The Forest Biology Rangers have dissected samples of cocoons collected annually at numerous locations in Manitoba and Saskatchewan during the current outbreak. Table 7 presents the average values for percentage parasitism and "per cent hatch" for selected locations.

Table 7

Average Percentages Parasitism and Hatch in Manitoba and Saskatchewan

Location	Sec.	Tp.	Rge.	Mer.	No. of years samples collect-ed	Total No. of prepupae dissect-ed	M. tenthredinis	
							Per cent parasitism	Per cent hatch
				Manitoba - Southern District				
Sprague East	8	1	14	E.P.	5	448	3.1	50.0
Braintree	33	7	14	E.P.	6	722	4.3	54.8
Sandilands	5	8	10	E.P.	6	676	4.3	48.3
Sandilands	31	7	11	E.P.	6	748	4.0	26.7

Table 7 cont'd

Location	Sec.	Tp.	Rge.	Mer.	No. of years samples collected	Total no. of prepupae dissected	M. tenthredinis Per cent parasitism	M. tenthredinis Per cent hatch
				Manitoba - Eastern District				
West Hawk Lake	29	9	17	E.P.	6	600	7.8	48.9
Telford	17	10	16	E.P.	9	1204	10.9	35.9
Red Rock Lake	8	12	15	E.P.	7	945	4.2	35.0
Rennie	22	10	15	E.P.	5	881	2.7	41.7
Hoctor	10	11	13	E.P.	7	956	11.6	35.6
Seddon's Corner	3	13	9	E.P.	12	1412	2.4	20.6
Riverton	32	23	4	E.P.	9	1088	7.9	24.4
				Manitoba - Western District				
R.M.N.P. Norgate Rd.	31	19	17	W.P	14	1957	12.4	18.5
R.M.N.P. Mile 145	26	21	19	W.P.	10	1216	12.7	20.8
R.M.N.P. L. Audy	15	20	19	W.P.	9	1032	11.4	23.7
R.M.N.P. P.O.W.Rd.	12	21	21	W.P.	10	1179	26.8	15.2
Cowan	11	35	23	W.P.	7	611	11.9	34.2
Renwer	15	36	23	W.P.	10	949	13.1	33.9
				Manitoba - Northern District				
Mafeking	19	44	21	W.P.	6	718	12.4	32.6
Mafeking	16	46	25	W.P.	5	606	7.8	21.3
"The Bog"	2	52	27	W.P.	3	275	2.9	75.0
The Pas	24	57	26	W.P.	5	652	13.0	33.7
Cormorant	31	60	21	W.P.	3	313	16.0	30.0
Cranberry Portage	18	65	26	W.P.	4	511	10.8	53.6
				Saskatchewan - Hudson Bay District				
Pelly	15	34	32	W.P.	7	527	17.6	22.6
Madge Lake	27	30	30	W.P.	5	453	7.9	44.4
Hudson Bay	29	45	3	W.2nd	5	645	3.1	35.0
Armit Rd.	6	44	2	W.2nd	4	573	9.2	13.2
Armit Rd.	6	44	32	W.P.	4	345	8.6	50.0
Armit Rd.	14	44	31	W. P.	5	478	1.3	66.7
Greenbush	21	45	5	W.2nd	4	397	2.0	62.5
Fort a la Corne	4	50	20	W.2nd	4	419	25.8	36.1

Table 7 cont'd

Location	Sec.	Tp.	Rge.	Mer.	No. of years samples collect-ed	Total no. of prepupae dissect-ed	*M. tenthredinis* Per cent parasitism	*M. tenthredinis* Per cent hatch
Saskatchewan - Prince Albert, Meadow Lake and Northern Districts								
Steep Creek	28	48	23	W.2nd	4	328	41.5	26.5
Home Block	8	49	26	W.2nd	8	954	46.3	26.7
Red Rock Block	27	49	25	W.2nd	7	864	29.7	24.1
McDowall	21	46	1	W.3rd	4	255	42.3	16.7
Crutwell	27	49	1	W.3rd	9	880	26.6	31.2
Holbein	13	49	2	W.3rd	4	337	28.5	42.7
Canwood	33	50	4	W.3rd	4	330	33.3	36.4
Mayview Road	24	53	2	W.3rd	7	576	22.2	32.8
Turtle Lake	34	53	18	W.3rd	4	362	10.8	25.6
Big River	32	55	7	W.3rd	4	412	29.1	21.7
Candle Lake	13	56	24	W.2nd	4	374	13.1	3.9
Waskesiu River	28	57	1	W.3rd	3	435	26.9	31.6
Loon Lake	16	59	22	W.3rd	5	498	5.0	48.0
Green Lake	5	61	12	W.3rd	4	380	2.1	37.5
Pierce-land	14	62	26	W.3rd	5	469	1.9	11.1

A collection of 203 cocoons was made at Keith Lake, Sask. (Tp. 80, Rge. 22 W.2nd, Grid 8-081-359) on August 19, 1955 by W. Turnock and parasitism by M. tenthredinis based on a total adult emergence of 183 was 1.6% (parasitism by B. harveyi was 6.0%). Some of the adult female sawflies were caged and their progeny tested with the following results:

Source of female parent	Family designation	Year family reared	No. of larvae Reared	No. of larvae Dissected	Parasitized by M. tenthredinis Encapsulated eggs	larvae	Per cent hatch
Keith L.	K.L.A.1	1957	73	46	18	2	10.
Keith L.	K.L.A.3	1957	66	43	1	0	0.
Keith L.	K.L.A.4	1957	51	37	4	3	43.
Keith L.	K.L.Q.1	1957	74	35	1	0	0.
Keith L.	K.L.T.6	1957	21	13	2	0	0.
Keith L.	K.L.V.1	1957	39	35	17	1	6.
Total			324	209	43	6	12.

Larch Plantations in Southern Saskatchewan

In the fall of 1954 cocoons received from Wolseley (*Larix laricina* (Du Roi, K. Koch) and Indian Head (*Larix decidua* Mill.) were subdivided as follows:

Location	No. of cocoons received	No. discarded	No. opened	No. dissected	No. reared
Wolseley	183	5	100	93	78
Indian Head	247	0	100	82	147

The results of the dissections were:

Location	No. of prepupae dissected	Parasitized by M. tenthredinis Encapsulated eggs	Larvae	% parasitism	% hatch	Parasitized by B. harveyi Number	Per cent
Wolseley	93	1	5	6.5	83.3	4	4.3
Indian Head	82	19	5	29.3	20.8	26	31.7

The results of the rearings were:

Location	No. of cocoons reared	P. erichsonii ♀♀	P. erichsonii ♂♂	M. tenthredinis ♀♀	M. tenthredinis ♂♂	M. tenthredinis % parasitism *	B. harveyi Number	B. harveyi Per cent parasitism*
Wolseley	78	56	0	0	2	3.3	2	3.3
Indian Head	147	39	0	0	3	5.0	18	30.0

* based on total adult emergence

The progeny of a number of adult sawflies that emerged were tested with the following results:

Source of female parent	Family designation	Year family reared	No. of larvae Reared	Dissected	Parasitized by *M. tenthredinis* Encapsulated eggs	larvae	Per cent hatch
Wolseley	W.A.	1955	47	13	9	1	10.
Indian Head	I.H.B.	1955	34	3	2	1	33.
Indian Head	I.H.B.	1955	4	3	3	0	0.

A survey collection of cocoons made by Forest Biology Ranger K. Mortensen on August 31, 1956 revealed the following data when dissected:

Location	No. of cocoons examined	No. of prepupae dissected	*M. tenthredinis* Eggs	Larvae	% parasitism*	% hatch	*B. harveyi* No.	%*	*T. klugii* No.	%**
Wolseley	200	177	34	8	23.7	19.0	15	8.5	0	-
Indian Head Plot 1	75	3	0	0	-	-	0	0	50	94.3
Indian Head Plot 2	150	118	5	1	5.1	16.7	29	24.6	11	8.5

* based on number of prepupae dissected
** based on total number of sound cocoons

Two larger collections of cocoons made in October, 1956, were examined. Those parasitized by *T. klugii* were removed by submerging the cocoons in water and examining over a light box. All "doubtful" cocoons were opened. Those found to be sound were placed in gelatin capsules and reared along with the unopened "apparently sound".

The data on parasitism follow:

Location	No. of cocoons collected	Parasitized by T. klugii No.	Parasitized by T. klugii %*	No. of cocoons reared	P. erichsonii ♀♀	P. erichsonii ♂♂	M. tenthredinis ♀♀	M. tenthredinis ♂♂	M. tenthredinis %**	B. harveyi ♀♀	B. harveyi ♂♂	B. harveyi %**
Wolseley	1107	1	0.001	1106	359	5	25	22	9.5	42	40	16.6
Indian Head Plot 2	5463	2057	37.7	3406	1391	4	13	12	1.2	354	358	33.4

* based on number of "sound" cocoons collected
** based on total adult emergence

The mortality in the unopened cocoons was 33 and 24 per cent and in the opened cocoons was 83 and 50 per cent for Wolseley and Indian Head, respectively.

Parasitization of Reared Families

The progeny of adult females that emerged in the spring of 1955 were tested with the following results:

Source of parent female	Family designation	Year family reared	No. of larvae Reared	No. of larvae Dissected	M. tenthredinis Encapsulated eggs	M. tenthredinis Larvae	M. tenthredinis % hatch
Wolseley	W.A.	1955	47	13	9	1	10.
Indian Head	I.H.B.	1955	34	3	2	1	33.
Indian Head	I.H.C.	1955	4	3	3	0	0.

A collection of 200 cocoons made in the fall of 1958 by K. Mortensen, Forest Biology Ranger in the Wolseley plantation were parasitized as follows:

No. of "sound" cocoons	T. klugii No.	T. klugii %	No. of prepupae dissected	M. tenthredinis Eggs	M. tenthredinis Larvae	M. tenthredinis Per cent parasitism*	M. tenthredinis Per cent hatch	B. harveyi No.	B. harveyi %*
133	50	37.6	83	9	2	13.3	18.2	3	3.6

* based on number of prepupae dissected.

2.3.8 Minnesota and Wisconsin

Drooz (1953) reported that in a collection of cocoons made at Aurora, Minnesota, from which 155 prepupae were dissected, total parasitism by M. tenthredinis was 23.9 per cent. Of the 37 host containing Mesoleius, 5 or 13.5 per cent contained living larvae; the rest encapsulated eggs. Drooz (1957) also reported that encapsulated M. tenthredinis eggs were found in larch sawfly larvae collected in Wisconsin.

Collections of cocoons made in Minnesota in July, 1955, were sent to Winnipeg through the kindness of A. Drooz. These cocoons were partly desiccated when received. The collections were consolidated into four groups. The rearing results are presented in the following text table:

Location	No. of cocoons received	No. of cocoons reared	P. erichsonii ♀♀	P. erichsonii ♂♂	M. tenthredinis ♀♀	M. tenthredinis ♂♂	M. tenthredinis % parasitism*	B. harveyi No.	B. harveyi Per cent*
Lake of the Woods and Koochiching Counties	814	711	46	0	6	5	18.6	2	3.4
Itasca, Cass and Hubbard Counties	2255	2039	82	0	2	4	6.4	6	6.4
St. Louis and Lake Counties	599	499	11	0	3	0	15.0	6	30.0
Unknown	779	763	10	1	0	0	-	0	-

* based on total adult emergence

2.3.9 Alberta

The Forest Insect Survey collections of larch sawfly larvae made in Alberta in 1954 were reared to the cocoon stage and the cocoons were forwarded to Winnipeg. These collections were consolidated into five groups on the basis of area collected as shown in Fig. 2. The total

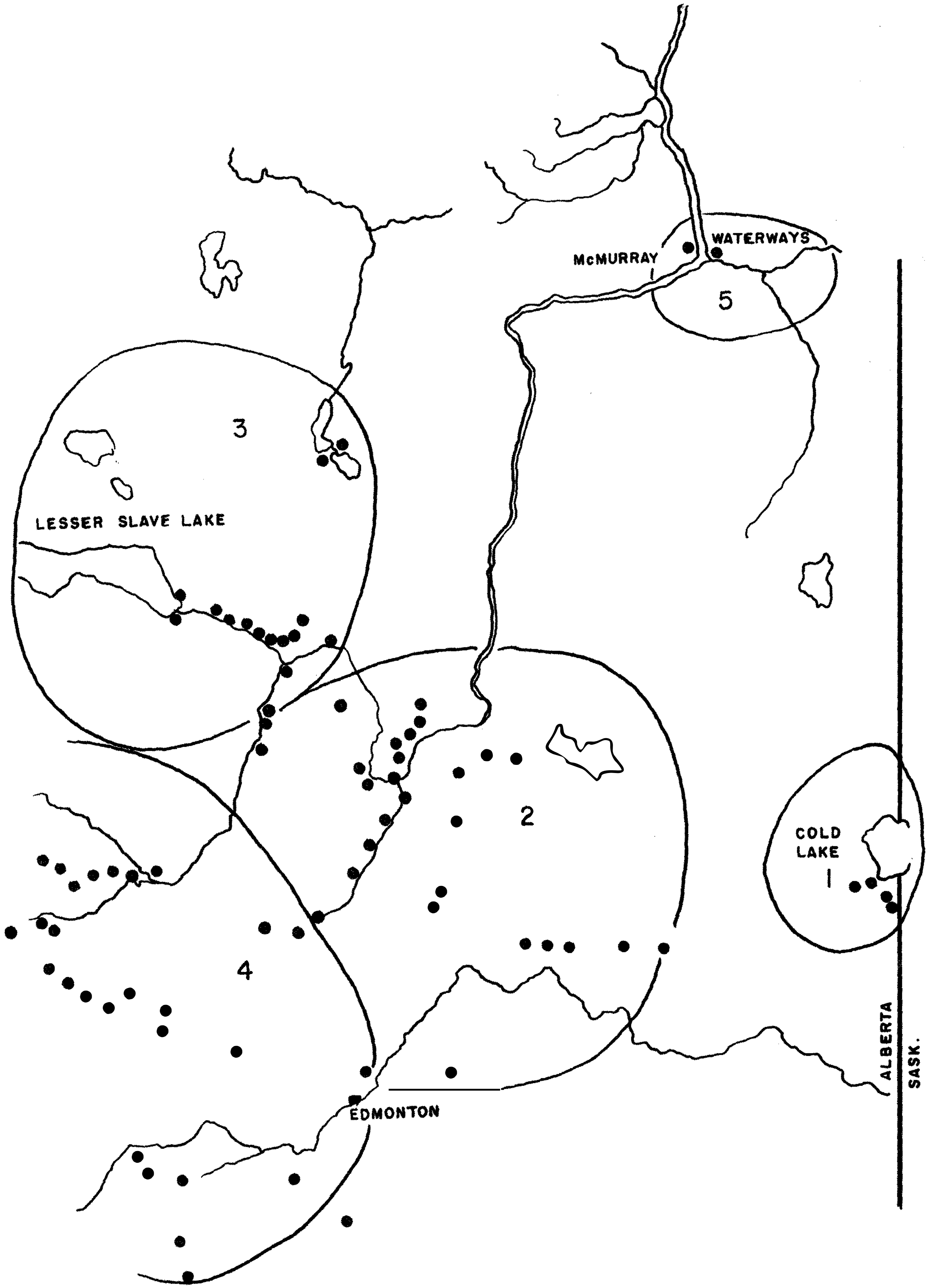


FIG. 2. LOCATION OF SURVEY COLLECTIONS OF LARCH SAWFLY IN ALBERTA, 1954.

number of larvae collected was 4380. Each group of cocoons was subdivided as follows:

Location	No. of cocoons received	No. of cocoons opened	No. of prepupae dissected	No. of cocoons reared
Area # 1	71	48	37	23
Area # 2	380	190	169	190
Area # 3	362	253	215	109
Area # 4	294	150	122	144
Area # 5	11	0	-	11
Total	1118	641	543	477

Since these larvae did not receive full exposure to parasite attack, percentage parasitism is probably less than it would have been had the samples been field-collected cocoons. Parasitism as determined by dissections was:

Location	No. of prepupae dissected	*M. tenthredinis* Encapsulated eggs	Larvae	Per cent parasitism	Per cent hatch	*B. harveyi* No.	Per cent
Area # 1	37	4	0	10.8	0.0	2	5.4
Area # 2	169	0	0	0.0	0.0	4	2.4
Area # 3	215	5	1	2.8	17.0	4	1.9
Area # 4	122	0	0	0.0	0.0	1	0.8
Total	543	9	1	1.8	10.0	11	2.0

A total of 228 ♀♀ and 5 ♂♂ adult *P. erichsonii* emerged from the 477 cocoons reared (emergence - 49 per cent) but no adult parasites emerged from these cocoons. A considerable number of the adult female sawflies were used to start lines for testing in the study on the inheritance of resistance and the results for each family parasitized will be presented in that section. A rapid build up of the larch sawfly occurred in Alberta from 1952 - 1954 and these adults were thus representative of the initial phase of an infestation. The table below presents the results of parasitization of reared families consolidated on the basis of area of origin of parent female:

Source of parent female	No. of larvae		Parasitized by M. tenthredinis		
	Reared	Dissected	Encapsulated eggs	Larvae	Per cent hatch
Area # 2	1359	655	212	122	36.5
Area # 3	476	285	64	11	14.7
Area # 4	280	132	87	4	4.4
Area # 5	815	409	154	24	13.5
Total	2930	1481	517	161	23.7

The chi-square for differences between areas was 62.72 which is highly significant ($X^2_{.01}$ 3 d.f. = 11.34).

2.3.10 British Columbia

The larch sawfly was first reported in 1930 on Larix occidentalis near Fernie. Cocoon samples obtained in 1933 showed no evidence of parasitism. A total of 4,976 M. tenthredinis were released in the southern interior of British Columbia during 1934 to 1936 and 1941 to 1942. Percentage parasitism by living M. tenthredinis larvae was 66.2 in 1948; 61.5 in 1949; 54.9 in 1950 and 68.0 in 1951 (based on samples of 1252, 496, 388 and 1098 prepupae dissected, respectively). The percentage parasitism based on the rearing of 1181 cocoons collected in 1949 was 69.2 per cent (McLeod, 1952, 1954). From 1948 to 1950 over 237,000 cocoons were collected for redistribution of Mesoleius to other parts of Canada. By 1952 the larch sawfly population had subsided to the extent that it was impractical to collect cocoons to determine parasitism.

The progeny of adult female sawflies emerging from cocoons collected in the southern interior of British Columbia in 1950 were tested for resistance in Manitoba with the following results:

Source of parent female	Source of adult M. tenthredinis used	No. of sawfly prepupae parasitized	M. tenthredinis Encapsulated eggs	Larvae	% hatch
British Columbia	British Columbia	12	0	12	100.
British Columbia	Saskatchewan	41	2	39	95.1
Total		53	2	51	96.2

Cluculz Lake, B. C.

In 1955 a collection of larvae made by J. Grant and R. Tocher of the British Columbia Forest Service at Cluculz Lake, was forwarded to Winnipeg. This area is approximately 35 miles west of Prince George, B. C. (elevation 2,600). The collectors reported that "this is a small and apparently relict stand of *Larix laricina* - the only area where it occurs west of the Rockies in Central British Columbia. The larch sawfly was found here for the first time in 1953." From the 55 cocoons that were reared during 1956, 16 adult female sawflies emerged and 4 *M. tenthredinis* (20 per cent of the total adults that emerged).

The progeny of some of the adult female sawflies were tested with the following results:

Source of female parent	Family designation	No. of larvae Reared	Dissected	M. tenthredinis Encapsulated eggs	Larvae	Per cent hatch
Cluculz Lake	B.C.-A	10	6	0	6	100.
Cluculz Lake	B.C.-D.6	48	5	0	1	100.
Total		58	11	0	7	100.

The evidence for this population is scanty but it does indicate that the larch sawfly here is highly susceptible to *M. tenthredinis*.

3. THE INHERITANCE OF THE RESISTANCE OF THE LARCH SAWFLY TO *M. TENTHREDINIS*

3.1 Introduction

The question has been posed as to whether the development of resistance in larch sawfly populations is a selection process whereby the susceptible elements in the population have been progressively eliminated and is therefore analogous to the development of resistance to insecticides by many pests. Ordinarily, evolution is so slow that changes within a human lifetime cannot be seen in wild species but the development of resistance to insecticides constitutes an important exception to this and perhaps in the best proof of natural selection yet obtained. The appearance of DDT-resistant houseflies in widely separated parts of the world supports the view that such mutants occur frequently in natural populations. For some insecticide-resistant species (e.g. California red scale, Smith, 1941) there is evidence that the relative proportion of resistant and susceptible individuals in any population is related to the frequency and intensity of application of the insecticide. Since the susceptible individuals are dominant prior to application they are believed to be superior to the resistant ones in "adaptive value" in the absence of insecticide pressure. "Adaptive value" refers to the ability of a given genotype, relative to that of other genotypes, to transmit their genes to future generations (Lewontin, 1955).

With intense selective pressure the resistant individuals become dominant but when this pressure is relaxed or stops, the susceptible part of the population usually gradually recovers its original dominance. This process is termed reversion. Reversion may be slow if the genes causing resistance are only mildly deleterious from a survival standpoint in respects other than resistance to insecticides.

With the larch sawfly, if the resistant part of the population becomes dominant due to intense Mesoleius pressure, this should reduce the relative numbers of the parasite and bring about relaxed selection. If reversion to susceptibility occurs, this should allow an increase in the relative numbers of Mesoleius, the system thus being homeostatic or self-regulating, with feedback.

Much work has been done on the housefly in an attempt to determine if differences exist in the adaptive value of resistant and susceptible strains. The length of the larval period has been found to be longer in some resistant strains than in comparable susceptible strains. Some workers have found that resistant strains developed in the laboratory have low fertility. Milani (1958), however, believes this is mainly due to excessive homozygosis brought about by inbreeding. A number of workers have been unsuccessful in attempts to correlate degree of resistance with such factors as duration of egg, larval, pupal and adult stages; number of eggs laid and percentage hatch; average weight of pupae and adults; sex ratio; pre-oviposition period; survival within the life cycle; susceptibility to heat and cold, etc. Varzandeh et al (1954) compared three susceptible and four resistant strains of houseflies and concluded that the considerable differences in biological characteristics which they found were correlated with general vigor and origin of the strain rather than resistance. When resistant strains as a whole are compared with susceptible strains there are no consistent differences in their bionomics and Brown (1958) points out that such comparisons should be restricted to resistant and susceptible strains having the same origin. This was done by Bøggild and Keiding (1958) who reared mixed cultures of strains susceptible and resistant to knockdown from DDT and found that under conditions of severe competition the resistant strain survived better than the susceptible in the absence of the insecticide.

When the environment of two genotypes is changed their relative adaptive values may be changed or even reversed since the adaptive value is a function of the environment and, ideally, comparison studies should be carried out in a natural environment.

If the adaptive value of the susceptible strain is only slightly superior to that of the resistant a large number of individuals might have to be tested to demonstrate that the differences are statistically significant yet such differences might still be large enough to allow the susceptible strain to become dominant over a period of ten to fifteen generations in the absence of strong selection pressure.

A major difference between the genetic aspects of the resistance of such insects as houseflies, mosquitos, *Drosophila*, etc., to insecticides and the resistance of the larch sawfly to *M. tenthredinis* stems from the obligatory parthenogenetic mode of reproduction of the larch sawfly which imposes restrictions on the possibilities of genetic experimentation. It is not known whether the rare male is functional in gene exchange although an abundance of sperm is produced and mating has been observed (Coppel and Leius, 1955).

Segregation of genetic differences in the larch sawfly is probably brought about by auto-fertilization, i.e. the fusion of the second polar body with the female pronucleus, with chromosome pairing and presumably crossing-over occurring (Smith, 1955). Commenting on this, Smith (personal communication, 1957) stated that assuming re-fusion

> "Daughters will be homozygous for all genes lying between the centromere and the nearest (proximal) chiasma in each chromosome. If the site of this chiasma is rather strictly localized and if the chiasma frequency per chromosome is usually one, essentially all daughters will carry the same combination of distal genes as the mother did ... If, then, encapsulation is the result of a single dominant gene (E) lying in this distal region, heterozygous females (Ee) will segregate, besides progeny like themselves, susceptible daughters (ee) and resistant daughters (EE) with a grouped frequency that will depend on the incidence of failure of the proximal chiasma to be formed. Obviously, if two or more pairs of chromosomes carry such genes in similar positions, the segregation of susceptible daughters will be correspondingly rarer. Chiasma frequency and localization may be under the control of the genotype and/or the environment.
>
> "At the other extreme, if the ability to encapsulate is controlled by numerous polygenes with cumulative effects, the tendency to increasing homozygosity inherent in obligatory parthenogenesis might be expected to produce a graded series of clones with characteristic degrees of resistance. How many distinct clonal types could exist would depend on a number of factors: their disposition on and between chromosomes; the integrity of blocks of polygenes; threshold value, etc."

Apparently, whether control is by major genes or polygenes, the change to homozygosity is progressive and irrevocable in the absence of mutations and structural rearrangement of chromosomes (Smith, 1955).

3.2 Objectives

(a) To determine the degree to which the factor of resistance to *M. tenthredinis* is heritable and the extent to which the expression of resistance is influenced by environmental conditions.

(b) To determine whether resistance, if heritable, is due to major genes or polygenes and perhaps gain some information on the degree and process of gene segregation in thelytokous parthenogenesis.

(c) To determine whether field populations will revert from resistance to susceptibility in the absence of *M. tenthredinis*, and if so, the rate of this reversion. This involves an attempt to measure the adaptive value of resistant and susceptible forms in the absence of *M. tenthredinis*.

3.3 Method

Larch sawfly families were reared from individual adult females of differing categories with respect to area collected or degree of resistance, etc., The progeny of these adults, where practicable, were split into two groups; the larger group being exposed to parasitization by *M. tenthredinis*, reared to the cocoon stage and subsequently dissected and the small group retained to carry on the line.

An attempt was made to select for lines of high and low resistance and to measure some of the characteristics that might influence adaptive value such as longevity and survival of the various life stages; fecundity; average width of head capsule;

weight of prepupae and cocoon; resistance to disease, etc.

A rearing method based on one developed by A. P. Randall was tested in 1957 and used exclusively in 1958. Oviposition and rearing of larvae (to approximately the fourth instar) were carried out in plastic cages (lucite in 1957 and polyethylene in 1958) that enclosed tamarack twigs having their cut ends immersed in water. Prior to this the adult females had been caged in the field on branches bearing six or more new shoots. These cages were brought to the insectary when the majority of the larvae were in the third and fourth stadia and rearing was completed there using clean quart oil cans, one-third full of moist sphagnum moss and containing cut twigs of tamarack. The top was covered by a square of unbleached cotton held in place by an elastic band.

3.4 Results

Data are presented only for those families in which at least one member was found to be parasitized by M. tenthredinis at dissection.

3.4.1 Clone P. A. 1.

The parent female emerged in 1954 from cocoons collected in the fall of 1953 at Prince Albert, Saskatchewan. A family comprising 31 cocoons was obtained from this female and parasitization was obtained in 11 of the families produced by females that emerged in 1955. Fig. 3 shows the relationships and designation of the families parasitized. The figures in brackets show number of cocoons carried through the winters. Some of the smaller families obtained in 1958 are omitted. Table 7 presents the results of the dissections indicating the degree of encapsulation within each family.

Table 7

Encapsulation Within Families of Clone P. A. 1.

Family designation	Year family reared	No. of larvae Reared	Dissected	Parasitized by *M. tenthredinis* Encapsulated eggs	Larvae	Per cent hatch
1.1	1955	39	19	14	0	0.0
1.21	1956	5	2	1	0	0.0
1.3	1955	55	9	9	0	0.0
1.4	1955	21	9	3	4	57.1
1.5	1955	52	32	8	5	38.5
1.6.1.1	1957	66	28	20	7	25.9
1.6.2.1	1957	74	50	28	7	20.0
1.6.2.2	1957	52	27	9	14	60.9
1.6.2.3	1957	61	14	6	0	0.0
1.6.2.4	1957	58	22	9	2	18.2
1.6.2.6	1957	44	37	12	1	7.7
1.6.2.7	1957	40	27	17	1	5.6
1.6.2.8	1957	86	13	5	0	0.0
1.7	1955	52	5	0	5	100.0
1.7.1	1956	13	6	5	0	0.0
1.7.3.3	1957	63	39	23	1	4.3
1.7.4.1	1957	89	49	16	3	15.8
1.7.4.5	1957	60	1	1	0	0.0
1.7.5.2	1957	33	27	7	1	12.5
1.7.6.1	1957	43	29	13	1	7.1
1.8	1955	20	8	2	6	75.0
1.9	1955	10	4	2	1	33.3
1.10	1955	33	16	4	11	73.3
1.11	1955	12	7	3	3	50.0
1.12.2	1956	15	12	1	0	0.0
1.13	1955	25	8	3	4	57.1
1.13.2.1	1957	82	37	2	0	0.0
1.14	1955	23	7	1	4	80.0
Total		1226	544	224	81	26.6

In 23 of these 28 families there were five or more members parasitized and between these the chi-square indicating variability in resistance within the clone was 100.96** ($X^2_{.01}$ 22 d.f. = 40.29).

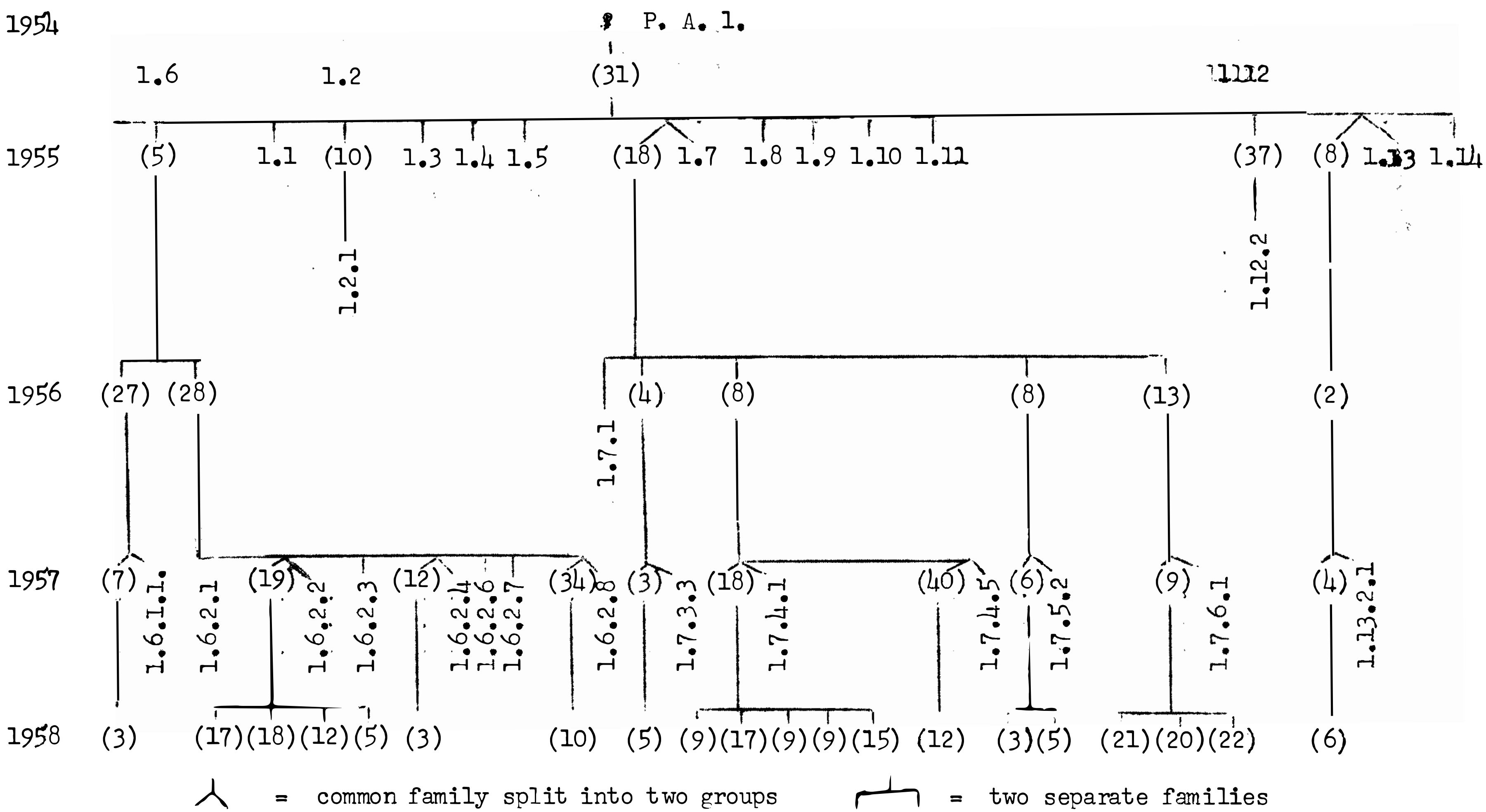


Fig. 3 Relationship and Designation of Families in Clone P. A. 1.

Families 1.10, 1.7, 16.2.2 and 1.8 contributed 16.41, 13.52, 13.43 and 9.43 respectively. Omitting these from the calculations gives a chi-square of 52.85** ($X^2_{.01}$, 18 d.f. = 34.81). To this latter total 13.2 was contributed by family 1.14; 7.4 by family 1.13 and 7.4 by family 1.4.

For the eight parasitized families in the line that began with female 1.6 the chi-square was 27.03 ** ($X^2_{.01}$, 7 d.f. = 18.48). The chi-square for this line when family 1.6.2.2 is omitted from the calculation is 6.76 ($X^2_{.01}$, 6 d.f. = 16.81).

For the six families in the line beginning with female 1.7 in which five or more larvae were parasitized the chi-square was 32.89** ($X^2_{.01}$, 5 d.f. = 15.09) but 29.25 of this value was contributed by family 1.7.

3.4.2 Clone P. A. 2.

The parent female emerged in 1954 from cocoons collected in the fall of 1953 at Prince Albert, Saskatchewan. A family comprising 24 cocoons was obtained from this female and parasitization was obtained in six of the families produced by females that emerged in 1955. Fig. 4 shows the relationships and designation of the families parasitized. Table 8 presents the results of the dissections indicating the degree of encapsulation within each family.

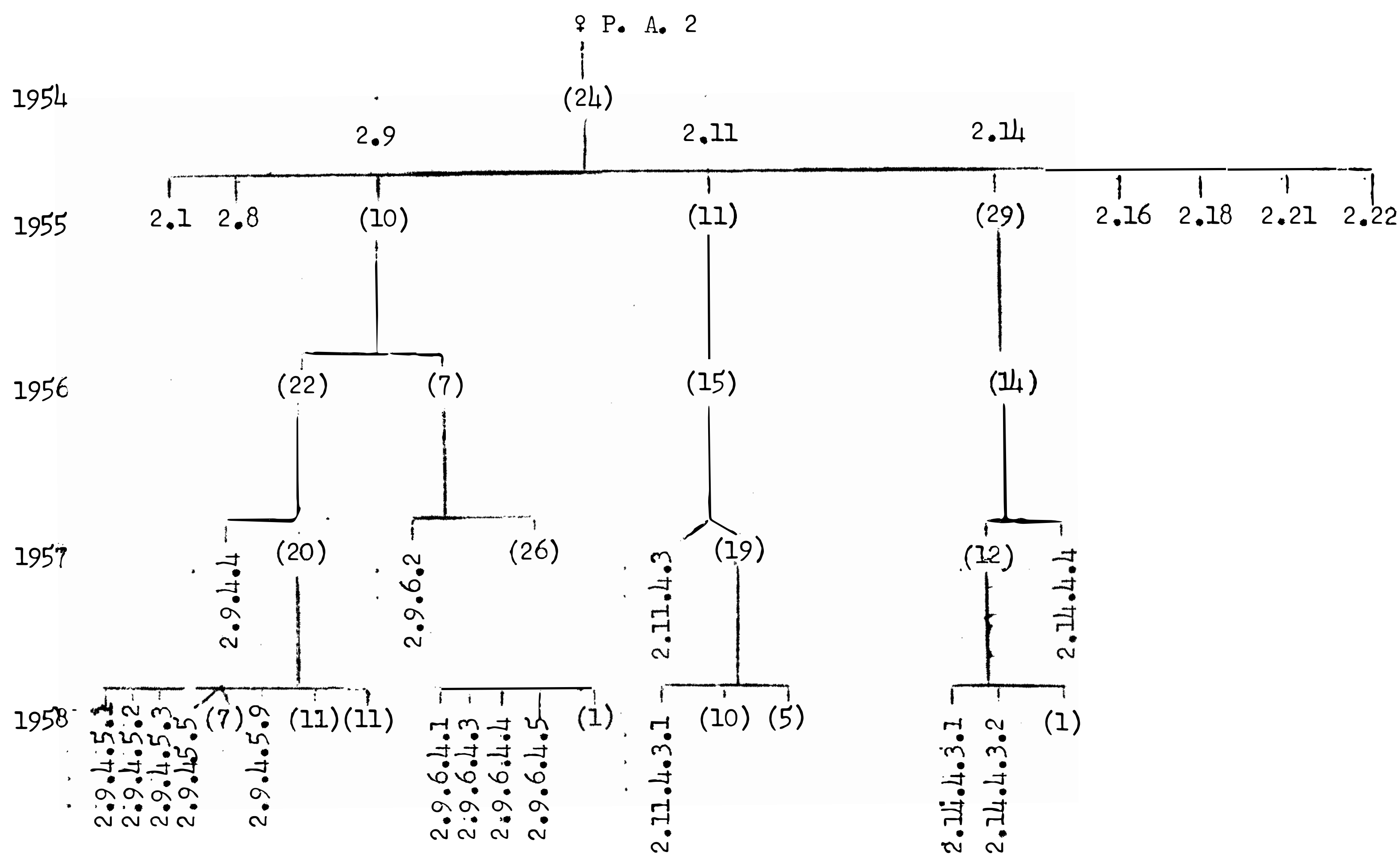


Fig. 4 Relationship and Designation of Families in Clone P. A. 2

Table 8

Encapsulation Within Families of Clone P. A. 2.

Family designation	Year family reared	No. of larvae		Parasitized by M. tenthredinis		
		Reared	Dissected	Encapsulated eggs	Larvae	Per cent hatch
2.1	1955	36	28	6	4	40.0
2.8	1955	35	27	12	0	0.0
2.9.4.4	1957	72	54	15	3	16.7
2.9.4.5.1	1958	37	6	1	0	0.0
2.9.4.5.2	1958	16	16	1	0	0.0
2.9.4.5.3	1958	13	11	2	0	0.0
2.9.4.5.5	1958	41	24	2	1	33.3
2.9.4.5.9	1958	24	20	14	0	0.0
2.9.6.2	1957	42	17	9	0	0.0
2.9.6.4.1	1958	5	1	1	0	0.0
2.9.6.4.3	1958	50	35	22	1	4.3
2.9.6.4.4	1958	37	31	5	0	5.0
2.9.6.4.5	1958	21	16	0	1	100.0
2.11.4.3	1957	52	23	11	2	15.4
2.11.4.3.1	1958	26	14	2	0	0.0
2.14.4.3.1	1958	6	4	3	1	25.0
2.14.4.3.2	1958	13	12	6	1	14.3
2.14.4.4	1957	28	23	8	12	60.0
2.16	1955	60	19	3	0	0.0
2.18	1955	43	36	26	10	27.8
2.21	1955	7	1	0	1	100.0
2.22	1955	32	7	7	0	0.0
Total		696	425	156	37	19.17

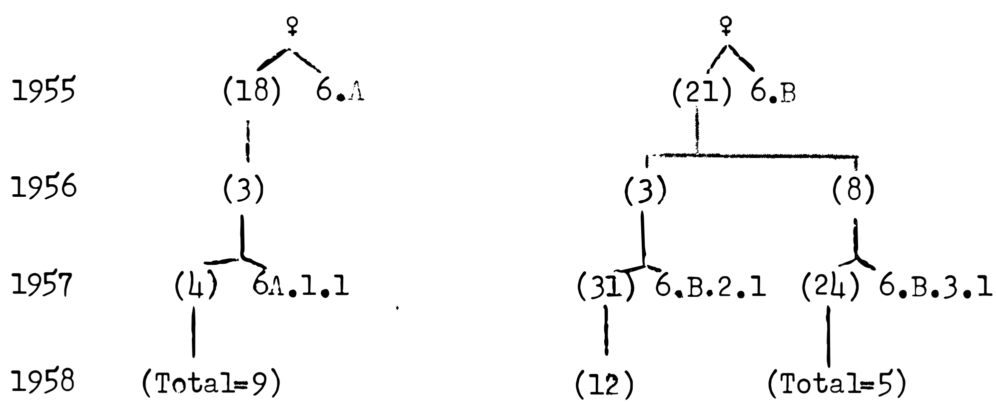
In 12 of these 22 families there were five or more members parasitized and the chi-square indicating variability in resistance between them was 40.97** ($X^2_{.01}$, 11 d.f. = 24.72). The component for family 2.14.4.4 was 21.94 and eliminating this family from the calculations gave a chi-square of 21.16* ($X^2_{.01}$, 10 d.f. = 23.21 $X^2_{.05}$, 10 d.f. = 18.31).

For the five families in the line beginning with female 2.9 in which five or more larvae were parasitized the chi-square was 5.73 ($X^2_{.01}$, 4 d.f. = 13.28 $X^2_{.05}$, 4 d.f. = 9.49).

Comparing clone P. A. 1. with P. A. 2 gave a chi-square of 3.57 ($X^2_{.05}$, 1 d.f. = 3.84) indicating a high likelihood that the probability of encapsulation in the two clones having their origin from the same stock (Prince Albert, Sask.) is similar to what would be expected in groups randomly drawn from a population with constant probability of encapsulation.

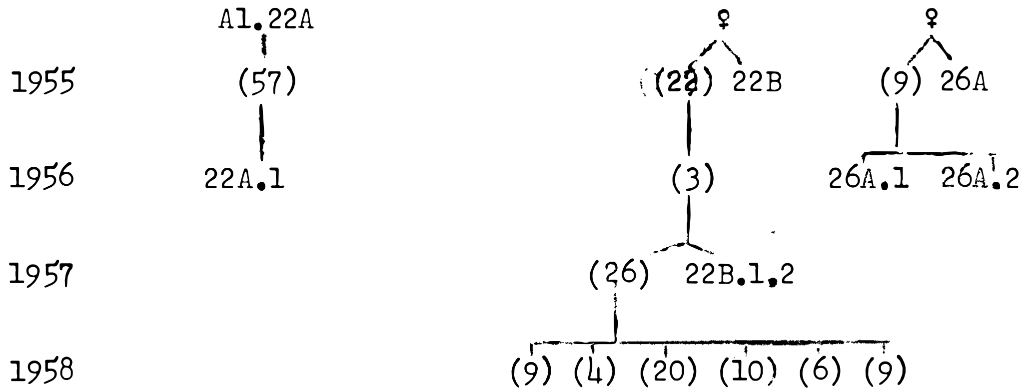
3.4.3 Alberta Lines

These lines originated with females emerging from cocoons received from Alberta in the fall of 1954. The family relationships and designations are presented in the following diagrams and the dissection results are presented in the following text-tables, with the results of chi-square analysis given for each line in which at least two families had five or more members parasitized.



Family designation	Source of parent female	Year family reared	No. of larvae		M. tenthredinis		
			Reared	Dissected	Encapsulated eggs	Larvae	% hatch
A1.5	Baptiste Lake	1955	21	9	4	1	20.0
A1.6A	Boyle	1955	61	36	9	0	0.0
A1.6A.1.1	Boyle	1957	76	60	12	0	0.0
A1.6B	Boyle	1955	68	45	6	0	0.0
A1.6B.2.1	Boyle	1957	86	34	16	5	23.8
A1.6B.3.1	Boyle	1957	73	23	10	1	9.1

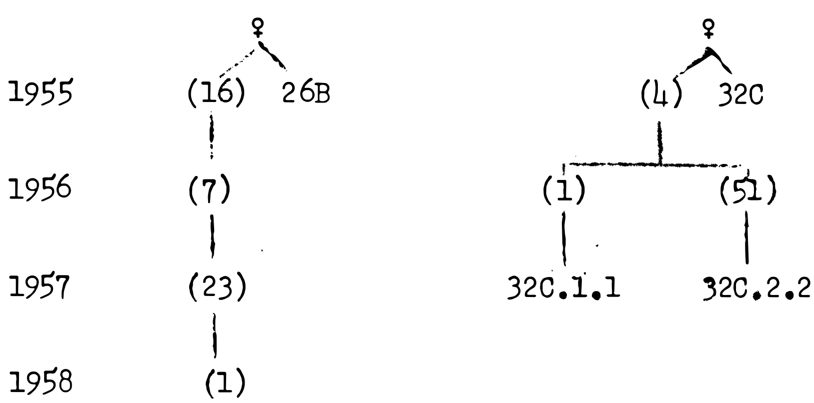
The chi-square for line 6B is 2.51 ($X^2_{.05}$, 2 d.f. = 5.99)



Family designation	Source of parent female	Year family reared	No. of larvae		*M. tenthredinis*		
			Reared	Dissected	Encapsulated eggs	Larvae	% hatch
A1.22A.1	Nestow	1956	8	7	2	4	66.7
A1.22B.	Nestow	1955	56	21	2	17	89.5
A1.22B.1.2	Nestow	1957	51	2	0	1	100.0
A1.23A.	Plamodon	1955	63	20	0	2	100.0
A1.23B.	Plamodon	1955	28	14	7	7	50.0
A1.26A.	Baptiste L.	1955	31	7	1	6	85.7
A1.26A.1	Baptiste L.	1956	7	3	3	0	0.0
A1.26A.2	Baptiste L.	1956	19	13	11	0	0.0

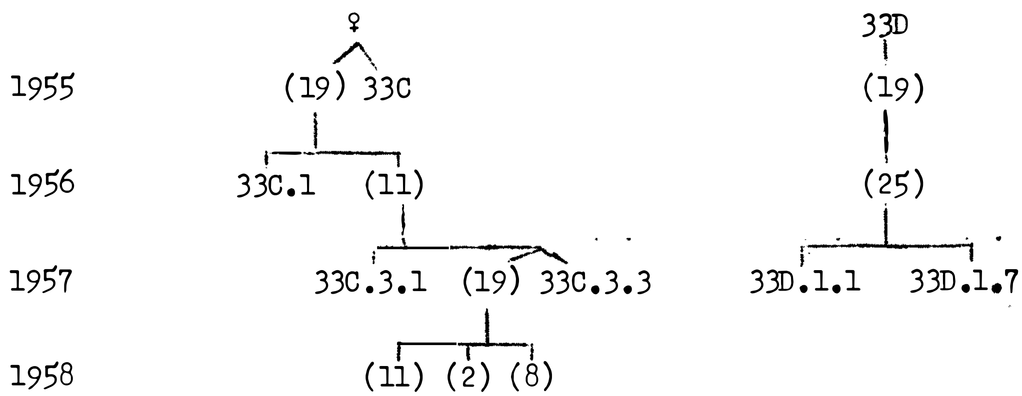
The chi-square between families 26A and 26A.2 is 14.17**

($X^2_{.01}$, 1 d.f. = 6.63)



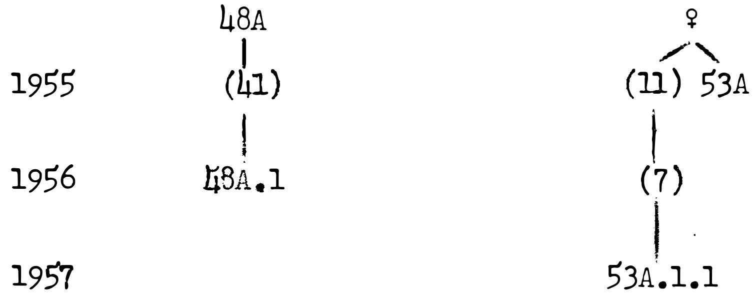
Family designation	Source of parent female	Year family reared	No. of larvae		*M. tenthredinis*		
			Reared	Dissected	Encapsulated eggs	Larvae	% hatch
Al.26B	Baptiste Lake	1955	76	39	21	16	43.2
Al.32A	Westlock	1955	52	8	2	1	33.3
Al.32C	Westlock	1955	27	15	12	0	0.0
Al.32C.1.1	Westlock	1957	54	30	10	10	50.0
Al.32C.2.2	Westlock	1957	63	49	2	0	0.0

The chi-square between families 32C and 32C.1.1 is 8.73**



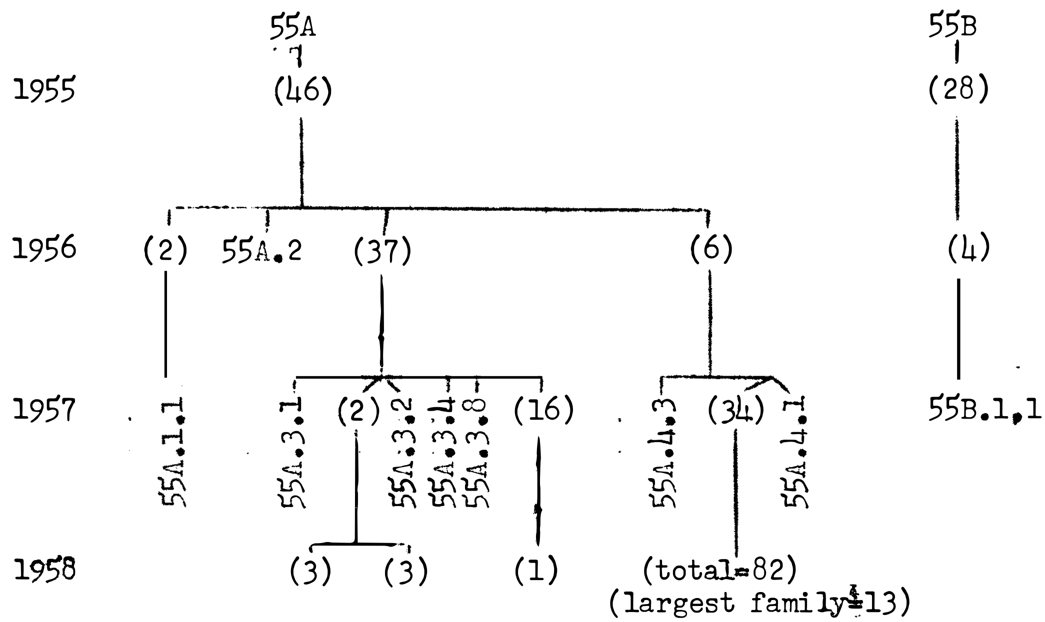
Family designation	Source of parent female	Year family reared	No. of larvae		*M. tenthredinis*		
			Reared	Dissected	Encapsulated eggs	Larvae	% hatch
Al.33A	Smith	1955	98	49	18	7	28.0
Al.33B	Smith	1955	71	6	1	2	66.7
Al.33C	Smith	1955	81	45	9	18	66.7
Al.33C.1	Smith	1956	5	2	1	1	50.0
Al.33C.3.1	Smith	1957	55	47	17	11	39.3
Al.33C.3.3	Smith	1957	39	4	0	4	100.0
Al.33D.1.1	Smith	1957	43	33	20	8	28.6
Al.33D.1.7	Smith	1957	47	34	16	0	0.0

The chi-square for the comparison of families Al.33C and Al.33C.3.1 is 4.13* ($X^2_{.05}$, 1 d.f. = 3.84) and the chi-square for families Al.33D.1.1 and Al.33D.1.7 is 5.59* ($X^2_{.01}$, 1 d.f. = 6.63).



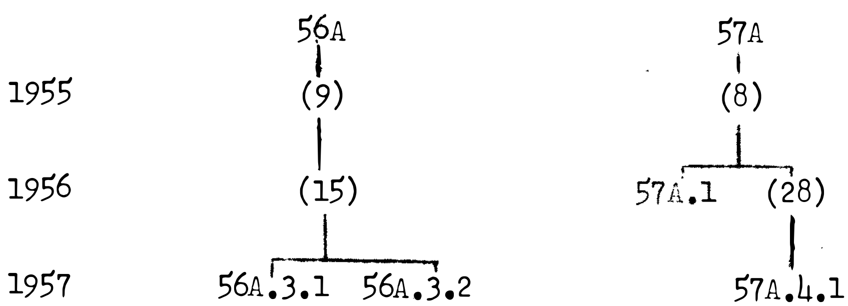
Family designation	Source of parent female	Year family reared	No. of larvae		*M. tenthredinis*		
			Reared	Dissected	Encapsulated eggs	Larvae	% hatch
Al.48A.1	Wabiskaw	1956	28	22	2	0	0.0
Al.48B	Wabiskaw	1955	13	8	3	3	50.0
Al.48D.1	Wabiskaw	1956	18	13	2	0	0.0
Al.50A	Slave Lake	1955	103	40	18	3	14.3
Al.53A	Berrymoor	1955	65	34	28	1	3.4
Al.53A.1.1	Berrymoor	1957	58	24	21	3	12.5

The chi-square for the comparison between families Al.53A and Al. 53A.1.1 is 1.55 indicating high similarity in degree of resistance.

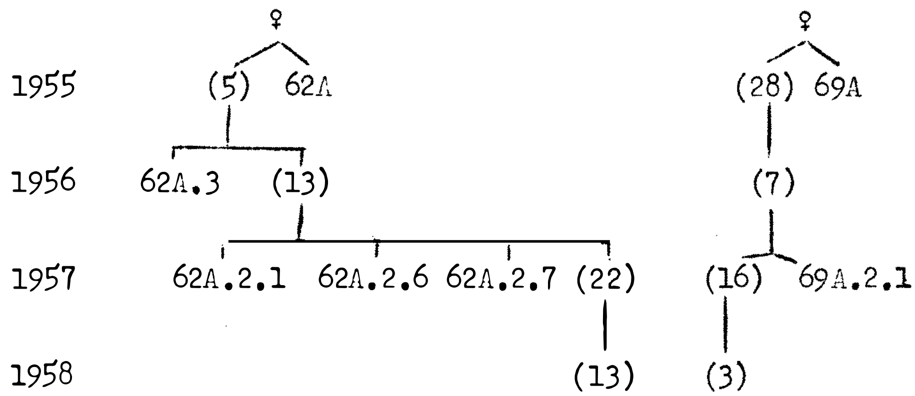


Family designation	Source of parent female	Year family reared	No. of larvae		*M. tenthredinis*		
			Reared	Dissected	Encapsulated eggs	Larvae	% Hatch
A1.55A.1.1	McMurray	1957	68	59	21	2	8.7
A1.55A.2	McMurray	1956	11	10	3	2	40.0
A1.55A.3.1	McMurray	1957	114	63	13	7	35.0
A1.55A.3.2	McMurray	1957	47	43	20	1	4.8
A1.55A.3.4	McMurray	1957	63	14	6	2	25.0
A1.55A.3.8	McMurray	1957	35	13	4	2	33.3
A1.55A.4.1	McMurray	1957	123	63	30	3	9.1
A1.55A.4.3	McMurray	1957	19	3	3	0	0.0
A1.55B.1.1	McMurray	1957	85	16	9	1	10.0
A1.55C	McMurray	1955	46	19	18	1	5.3

The chi-square for the comparison of the first seven families listed in the above table is 13.13* ($X^2_{.01}$, 6 d.f. = 16.81; $X^2_{.05}$, 6 d.f. = 12.59)



Family designation	Source of parent female	Year family reared	No. of larvae		*M. tenthredinis*		
			Reared	Dissected	Encapsulated eggs	Larvae	% hatch
A1.56A.3.1	Hoadley	1957	81	31	27	0	0.0
A1.56A.3.2	Hoadley	1957	76	43	11	0	0.0
A1.57A.1	Wabiskaw	1956	32	25	5	0	0.0
A1.57A.4.1	Wabiskaw	1957	27	13	1	1	50.0

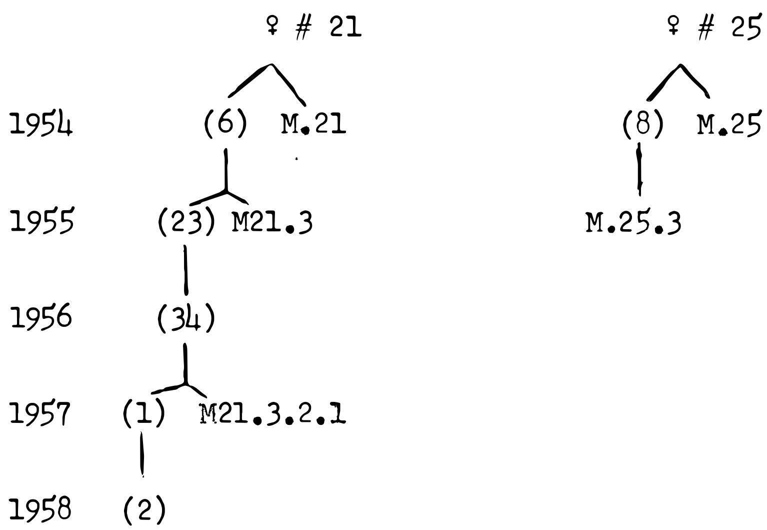


Family designation	Source of parent female	Year family reared	No. of larvae		*M. tenthredinis*		
			Reared	Dissected	Encapsulated eggs	Larvae	% hatch
A1.62A	Wabiskaw	1955	31	4	2	2	50.0
A1.62A.2.1	Wabiskaw	1957	60	26	19	2	9.5
A1.62A.2.6	Wabiskaw	1957	58	33	2	0	0.0
A1.62A.2.7	Wabiskaw	1957	84	53	7	0	0.0
A1.62A.3	Wabiskaw	1956	22	21	3	0	0.0
A1.69A	Waterways	1955	39	10	1	0	0.0
A1.69A.2.1	Waterways	1957	53	27	2	0	0.0

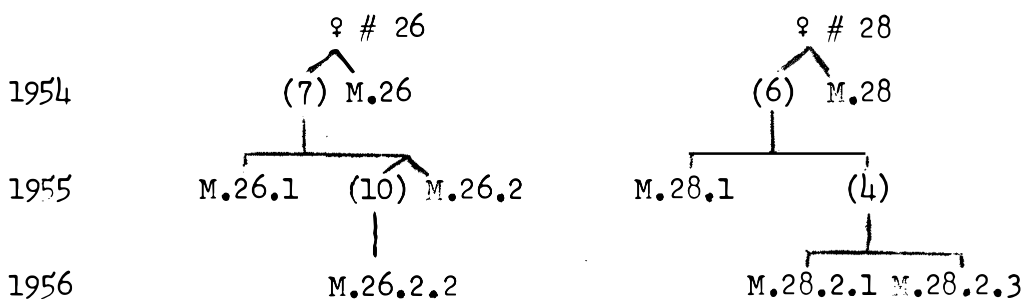
The chi-square for the comparison between families A1.62A.2.1 and A1. 62A.2.7 is 0.72 indicating no significant difference between them in resistance.

3.4.4. Manitoba Lines

Each of these lines was started as a field-collected colony of second- or third-instar larch sawfly larvae found in various locations in the Whiteshell Forest Reserve, Manitoba in the summer of 1954. These colonies were reared until the majority were early fifth-instar larvae at which time each colony was divided into approximately equal portions; one of which was exposed to parasite attack and later dissected and the other retained to carry on the line.

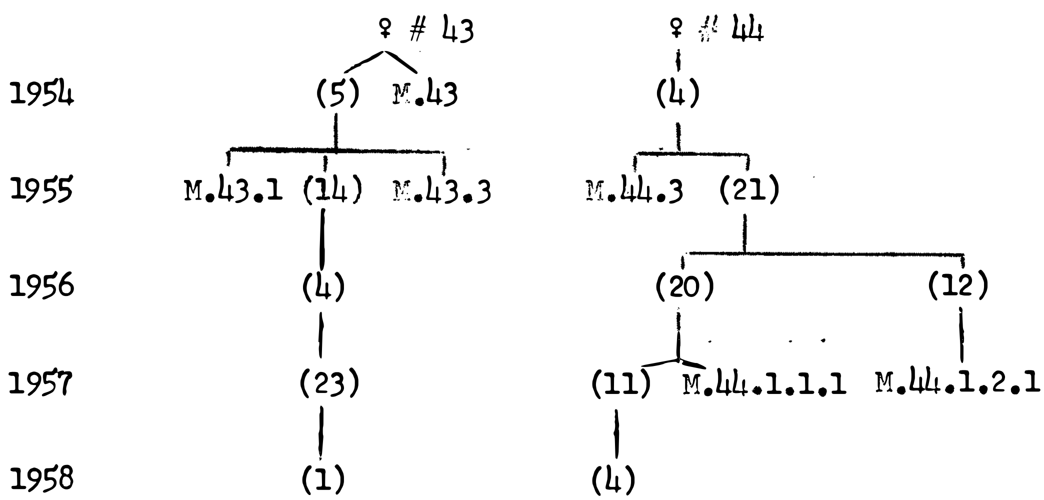


Family designation	Source of parent female	Year family reared	No. of larvae Reared	No. of larvae Dissected	*M. tenthredinis* Encapsulated eggs	*M. tenthredinis* Larvae	*M. tenthredinis* % hatch
M.15	Telford	1954	22	10	1	0	0.0
M.16	Telford	1954	14	4	1	2	66.7
M.17	Red Rock L.	1954	9	1	1	0	0.0
M.19	"Picnic Bog"	1954	11	5	5	0	0.0
M.21	Mile 30	1954	13	3	0	2	100.0
M.21.3	Mile 30	1955	47	3	0	3	100.0
M.21.3.2.1	Mile 30	1957	31	27	8	0	0.0
M.22	Mile 30	1954	24	3	2	1	33.3
M.23	Picnic Bog	1954	10	1	1	0	0.0
M.24	Picnic Bog	1954	20	1	1	0	0.0
M.25	Picnic Bog	1954	13	2	1	1	50.0
M.25.3	Picnic Bog	1955	36	10	4	0	0.0



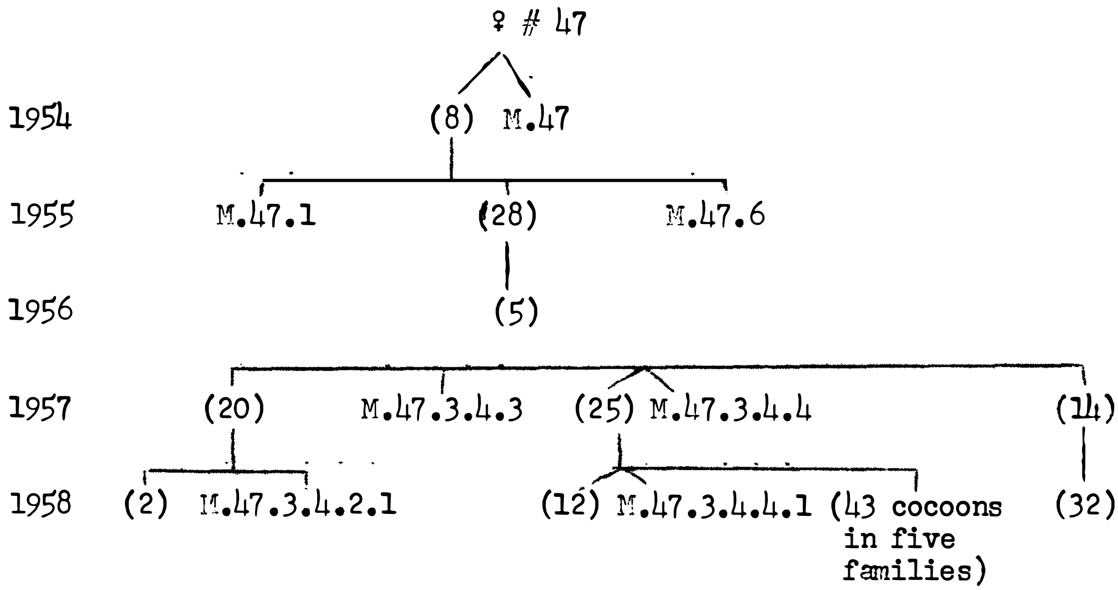
Family designation	Source of parent female	Year family reared	No. of larvae		*M. tenthredinis*		
			Reared	Dissected	Encapsulated eggs	Larvae	% hatch
M.26	Picnic Bog	1954	18	1	0	1	100.0
M.26.1	Picnic Bog	1955	46	22	10	0	0.0
M.26.2	Picnic Bog	1955	20	7	1	1	50.0
M.26.2.2	Picnic Bog	1956	29	6	2	3	60.0
M.27	Mile 30	1954	22	1	1	0	0.0
M. 28	Mile 30	1954	26	12	6	6	50.0
M.28.1	Mile 30	1955	7	3	0	1	100.0
M.28.2.1	Mile 30	1956	6	4	1	3	75.0
M.28.2.3	Mile 30	1956	17	15	2	0	0.0
M.29	Telford	1954	17	4	2	1	33.3
M.30	Red Rock L.	1954	11	2	1	1	50.0
M.31	Mile 30	1954	18	3	3	0	0.0
M.32	Picnic Bog	1954	12	1	1	0	0.0
M.33	Mile 30	1954	11	6	4	1	20.0
M.34	Mile 30	1954	9	3	1	1	50.0
M.35	Picnic Bog	1954	13	2	1	1	50.0
M.36	Picnic Bog	1954	15	2	1	1	50.0
M.37	Picnic Bog	1954	10	4	1	3	75.0
M.38	Picnic Bog	1954	14	2	1	1	50.0
M.39	Mile 30	1954	7	1	1	0	0.0
M.40	Mile 30	1954	10	5	4	0	0.0
M.41	Picnic Bog	1954	35	16	2	0	0.0
M.42	Picnic Bog	1954	13	5	2	3	60.0

The chi-square for the comparison of families M.26.1 and M. 26.2.2 is 7.5**



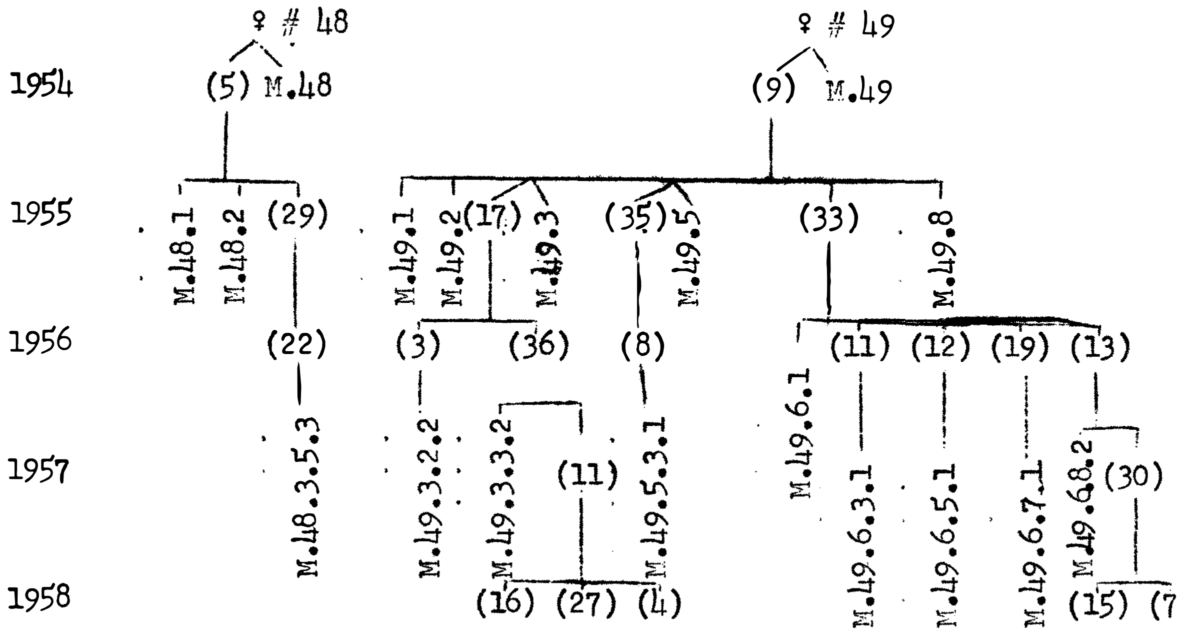
Family designation	Source of parent female	Year family reared	No. of larvae Reared	No. of larvae Dissected	M. tenthredinis Encapsulated eggs	M. tenthredinis Larvae	M. tenthredinis % hatch
M.43	Picnic Bog	1954	13	3	0	2	100.0
M.43.1	Picnic Bog	1955	12	4	0	4	100.0
M.43.3	Picnic Bog	1955	21	3	2	1	33.3
M.44.1.1.1	Picnic Bog	1957	59	16	10	2	17.0
M.44.1.2.1	Picnic Bog	1957	84	72	13	0	0.0
M.44.3	Picnic Bog	1955	31	18	8	0	0.0

The chi-square for the three families in line M.44 is 3.70 indicating no significant difference between them. ($X^2_{.05}$, 2 d.f. = 5.99)



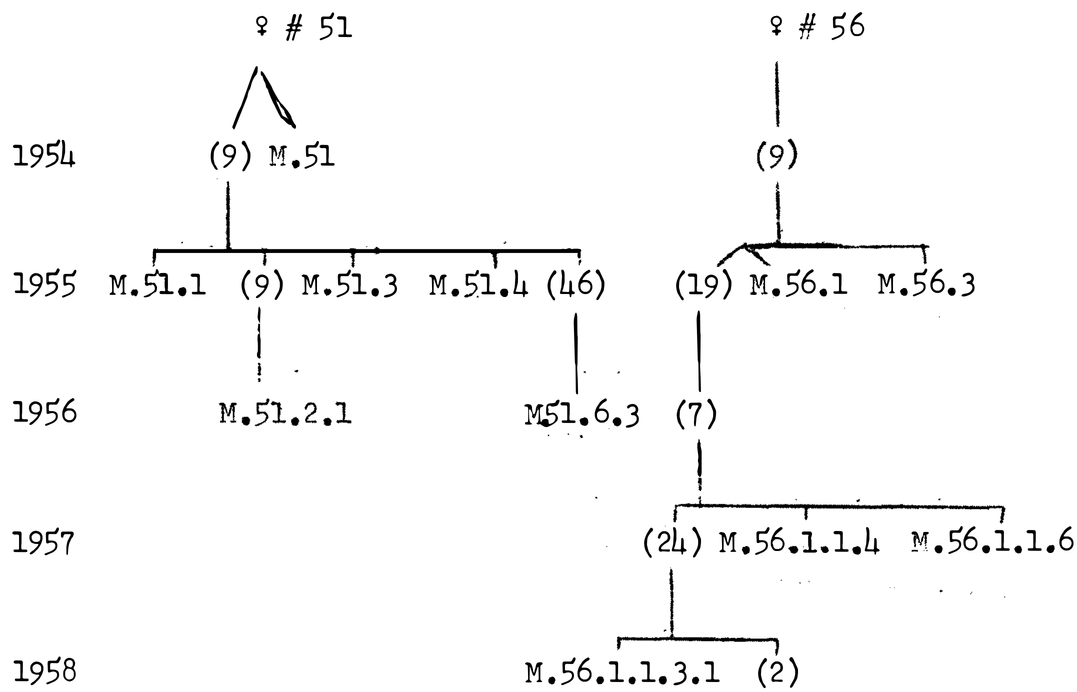
Family designation	Source of parent female	Year family reared	No. of larvae Reared	No. of larvae Dissected	M. tenthredinis Encapsulated eggs	M. tenthredinis Larvae	M. tenthredinis % hatch
M.45	Picnic Bog	1954	12	6	3	3	50.0
M.47	Telford	1954	16	6	6	0	0.0
M.47.1	Telford	1955	26	2	1	1	50.0
M.47.3.4.3	Telford	1957	34	33	16	0	0.0
M.47.3.4.2.1	Telford	1958	7	5	1	0	0.0
M.47.3.4.4	Telford	1957	112	69	24	3	11.1
M.47.3.4.4.1	Telford	1958	29	21	1	0	0.0
M.47.6	Telford	1955	29	9	7	0	0.0

The chi-square for families M.47, M.47.3.4.3, M.47.3.4.4 and M.47.6 was 3.39 indicating no significant difference. ($X^2_{.05}$, 3 d.f. = 7.81)



Family designation	Source of parent female	Year family reared	No. of larvae		*M. tenthredinis*		
			Reared	Dissected	Encapsulated eggs	Larvae	% hatch
M.48	Telford	1954	13	4	4	0	0.0
M.48.1	Telford	1955	81	37	21	2	8.7
M.48.2	Telford	1955	28	4	1	0	0.0
M.48.3.5.3	Telford	1957	15	12	1	0	0.0
M.49	Telford	1954	22	7	5	0	0.0
M.49.1	Telford	1955	6	5	3	0	0.0
M.49.2	Telford	1955	19	17	4	0	0.0
M.49.3	Telford	1955	31	5	1	1	50.0
M.49.3.2.2	Telford	1957	70	52	27	7	20.6
M.49.3.3.2	Telford	1957	36	25	11	2	15.4
M.49.5	Telford	1955	43	1	1	0	0.0
M.49.5.3.1	Telford	1957	47	20	1	0	0.0
M.49.6.1	Telford	1956	20	18	1	0	0.0
M.49.6.3.1	Telford	1957	46	36	7	0	0.0
M.49.6.5.1	Telford	1957	46	31	17	1	5.6
M.49.6.7.1	Telford	1957	25	24	2	0	0.0
M.49.6.8.2	Telford	1957	36	30	16	0	0.0
M.49.8	Telford	1955	24	4	2	2	50.0

The chi-square for families M.49, M.49.3.2.2, M.49.3.3.2, M.49.6.3.1, M.49.6.5.1 and M.49.6.8.2 is 7.59 indicating no significant difference in encapsulating ability between them ($X^2_{.05}$, 5 d.f. = 11.07)



Family designation	Source of parent female	Year family reared	No. of larvae: Reared	No. of larvae: Dissected	*M. tenthredinis*: Encapsulated eggs	*M. tenthredinis*: Larvae	*M. tenthredinis*: % hatch
M.50	Telford	1954	17	7	7	0	0.0
M.51	Red Rock L.	1954	23	9	8	1	11.1
M.51.1	Red Rock L.	1955	46	5	2	0	0.0
M.51.2.1	Red Rock L.	1956	10	8	1	0	0.0
M.51.3	Red Rock L.	1955	16	9	2	4	66.7
M.51.4	Red Rock L.	1955	16	2	1	1	50.0
M.51.6.3	Red Rock L.	1956	14	11	4	0	0.0
M.52	Red Rock L.	1954	24	1	0	1	100.0
M.53.1	Red Rock L.	1955	44	1	0	1	100.0
M.56.1	C.N. Bog	1955	63	5	2	0	0.0
M.56.1.1.3.1	C.N. Bog	1958	18	16	2	0	0.0
M.56.1.1.4	C.N. Bog	1957	51	42	9	0	0.0
M.56.1.1.6	C.N. Bog	1957	46	21	9	0	0.0
M.56.3	C.N. Bog	1955	17	8	7	1	12.5

The chi-square for families M.51 and M.51.3 is 5.0*
($X^2_{.05}$ 1 d.f. = 3.84)

The chi-square for families M.56.1.1.4, M.56.1.1.6 and M.56.3 is 2.3 indicating no significant difference in encapsulating ability between them.

The chi-square for the comparison between the five locations in the Whiteshell Forest Reserve is 32.33 indicating a highly significant difference between them ($X^2_{.01}$ 4.d.f. = 13.28)

The following table presents the chi-square comparisons of all the parasitized prepupae obtained in the inheritance study subdivided on the basis of origin of parent females.

Areas Compared	Total parasitized prepupae	Chi-square
Whiteshell Forest Reserve, Manitoba X Prince Albert, Saskatchewan	918	3.92*
Whiteshell Forest Reserve, Manitoba X Alberta	1098	4.48*
Prince Albert, Saskatchewan X Alberta	1176	0.00043

$X^2_{.05}$ 1 d.f. = 3.84 $X^2_{.01}$ 1 d.f. = 6.63

This analysis thus indicates that the differences between the Whiteshell Forest Reserve, Manitoba material and both the Prince Albert, Saskatchewan and Alberta material are significant at the five per cent level but that there is no significant difference between the Saskatchewan and Alberta material.

4. DISCUSSION AND SUMMARY

The chi-square analyses of the lines tested show significant differences between families at the one per cent level in five instances; significant differences between families at the five per cent level in four instances and no significant differences between families in ten instances. In some lines (e.g. P. A. 2.) one or a few families showed a considerably different degree of encapsulation than the majority of the other families in the line. Possibly more consistency in the resistance reaction within lines would have been obtained had temperature and perhaps other variables been kept reasonably constant during the rearing and parasitization of the families. (see Muldrew, 1952)

Concerning the hypotheses presented on pages one and two, the following points should be considered:

(a) Although M. tenthredinis pressure has been at a very low level in Central Canada for the past ten to twenty years, no evidence has been obtained indicating a marked reversion of the population as a whole to a condition of greater susceptibility.

(b) Although M. tenthredinis pressure was high in British Columbia from 1948 to 1951 and in the Maritimes from 1938 to 1942 (approximately), the evidence indicates that the resistant portion of the population in these areas did not become dominant as a result of selection by the parasite.

Section 3 of this report summarizes the data obtained to date on the inheritance of the immunity reaction. Subjects still to be written up include the following:

(a) Two by two chi-square comparisons of all lines in which five or more parasitized prepupae were obtained.

(b) Relation of actual percentage of parasitism in individual families with theoretical percentage based on the assumption of a random distribution of eggs.

(c) Influence of various factors on degree of parasitization obtained. (e.g. - temperature, humidity, cloud cover, barometric pressure, average age of parasites, relative density of hosts, etc.)

(d) Comparison of measurements obtained for members of "resistant" and "susceptible" lines in the attempt to determine the relative adaptive values of the two forms. (e.g. - fecundity, weights of prepupae, head-capsule widths, etc.)

(e) Production of males in relation to temperatures during the oviposition period of the parent female sawfly (see Smith, 1955 for a discussion of the possibility of obtaining females that produce only males; the males to be used in an attempt to obtain exchange between different gene pools).

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APPENDIX 1

(Table 4 condensed for future reference)

Chi-Squares for Between-area Differences Based on the Totals for the Period of Study

Areas Compared	Chi-square for per cent parasitism	Chi-square for Per cent hatch
Three locations in R. M. N. P., Manitoba	122.27 **	2.573
The combined totals for three locations in R. M. N. P. with Nisbet P. F. Home Block	396.20 **	13.38 **

$X^2_{.01}$ 2 d.f. = 9.21 $X^2_{.05}$ 2 d.f. = 5.99

$X^2_{.01}$ 1 d.f. = 6.63 $X^2_{.05}$ 1 d.f. = 3.84