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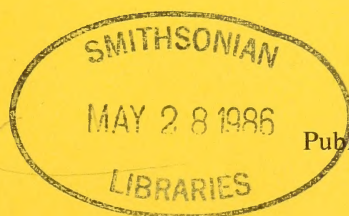
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THE MITE COMPLEX ON THE FOLIAGE OF A PESTICIDE-FREE APPLE ORCHARD: POPULATION DYNAMICS AND HABITAT ASSOCIATIONS

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Abstract

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The population dynamics of the acarid complex inhabiting apple foliage in an orchard in southern Ontario was studied over a 3-year period. Few previous studies have examined the entire acarid complex in the same orchard at the same time. Population dynamics were highly variable from year to year but at no time did pest species reach economic thresholds. *Zetzellia mali* (Ewing) and phytoseiid populations tracked changes in prey abundances; *Z. mali* was more closely linked to eriophyid abundance, and phytoseiids to tetranychid abundance. Certain species were more abundant on particular varieties of apple, but these differences were not always consistent from year to year. *Z. mali* and phytoseiids were more abundant on trees nearer the orchard edge. Implications for pest management are discussed.

Introduction

There is extensive literature describing the dynamics of mite populations on apple foliage, with special emphasis on tetranychids, which are economically important pests in Canada, and their predators, e.g. Hull *et al.* (1978), White and Laing (1977a). Despite the fact that the mite community on apple can be very rich (Berkett and Forsythe 1980; Forest *et al.* 1982) few studies have examined the dynamics of many species concurrently (but see Hoyt and Caltagirone 1971; Oatman 1973; Readshaw 1975) although such studies are essential to a full understanding of interactions within the mite complex.

This paper describes the population dynamics of several mite populations in a pesticide-free orchard over a 3-year period. We then examine the associations of the mite populations with different apple varieties and for individual trees. We also report significant edge effects for predatory mites, which have not been previously reported. Finally, we discuss the management implications of our observations.

Materials and Methods

The study site was a 0.3-ha apple orchard at the Agriculture Canada Research Station farm in Jordan Station, Ontario. The orchard contained 240 trees and was divided by a drainage ditch along its north-south axis. There were 60 trees each of the four varieties, Empire, McIntosh, Red Delicious and Golden Delicious, grown on M26 rootstock and arranged in unequal blocks of 10-20 trees in a Latin square design. The orchard was planted in 1974 and had received only 3 pesticide applications in the six years up to 1981: Ambush in May 1980, Omite in June 1980 and Superior Oil in April 1981. During the course of this study a variety of fungicides were applied (Table I) which are not considered to affect mite populations significantly (Oatman 1973; Meyer 1974; Hagley *et al.* 1980), excepting fungivorous species. The orchard was pruned annually and mowed several times per season.

Table I. Dates of fungicide applications to the Jordan Station orchard 1982-84

Fungicide	1982	1983	1984
Difolatan	28 April	28 April	26 April
Polyram	26 May 9 June	18 May 9 June 28 June	
Cyprex	28 June		
Captan		15 July	

Leaf samples were taken from each of the same 50 trees (randomly selected from all but the outermost rows) at 1-week intervals between 11 May and 7 September 1982, as well as on 25 October 1982, and at 2-week intervals between 3 May and 1 November 1983 and 9 May and 24 October 1984. Sampling was discontinued after the first heavy frost. Each sample consisted of 10 leaves taken from all parts of the canopy of each of the 50 trees. Samples were stored in polythene bags at 5°C and examined within 7 days. Mite counts were made by visual inspection under a binocular microscope. In 1982 we counted only motile stages of tetranychids, stigmatheids, phytoseiids and erythraeids. In 1983 and 1984 we counted all motile stages and also tetranychid eggs.

On 29 August 1984, additional samples were taken from 10 trees selected at random from the outermost rows. These data were used to test for edge effects.

Analysis of habitat associations was carried out by comparing abundances in each sample at the date of maximum abundance for a given population in each year. Data were transformed as $(n + 1, 2)^{1/2}$ where n is number in a sample (Steel and Torrie 1980). The analysis used a 3-way, mixed model, nested analysis of variance incorporating a year effect, a variety effect, a tree effect (a random factor nested within variety) and a year-variety interaction. Where the interaction was significant at the 5% level a one-way analysis of variance against variety was performed separately for each year. Edge effects were examined using a 2-way analysis of variance incorporating a variety effect and a position effect. Position was defined as the number of trees between the sampled tree and the orchard edge. All analyses were carried out using an SAS statistical package (Ray 1982).

Results and Discussion

The mite fauna found during the study period was grouped into 9 taxa (Table II) including several important pests: the European red mite, *Panonychus ulmi* (Koch); the two-spotted spider mite, *Tetranychus urticae* (Koch); and the rust mites (Eriophyidae).

Table II. Common acarids at the Jordan Station orchard 1982-84

Family	Species
1. Tetranychidae	<i>Tetranychus urticae</i> Koch
2. Tetranychidae	<i>Panonychus ulmi</i> (Koch)
3. Eriophyidae	including <i>Aculus</i> sp. (<i>schlechtendali</i> (Nal.)?)
4. Stigmatheidae	<i>Zetzellia mali</i> (Ewing)
5. Phytoseiidae	inc. <i>Amblyseius fallacis</i> (Arman) <i>Typhlodromus caudiglans</i> (Schuster) <i>T. pyri</i> Scheuten
6. Erythraeidae	<i>Balaustium</i> sp. (inc. <i>putmani</i> Smiley)
7. Tarsonemidae	inc. <i>Tarsonemus waitei</i> Banks
8. Tydeidae	<i>Tydeus</i> sp.
9. Tydeidae	<i>Triophtydeus</i> sp.

This list ignores a few rare species which remained unidentified as well as oribatid mites which were considered "incidental" species. The trophic relationships between these taxa are complex and for some taxa, notably the Tydeidae, poorly known (Fig. 1). This makes it difficult to partition out the effects of particular interactions. Several other known mite predators were present: coccinellids, including *Stethorus* sp. (an important tetranychid predator elsewhere (Colburn and Asquith 1971)), chrysopids, syrphids and predaceous mirids. These predators were never common. Of the predatory mites, *Balaustium* sp. and *Zetzellia mali* (Ewing) may attack non-acarine prey, especially small arthropod eggs (Delattre 1971; Cadogan and Laing 1981).

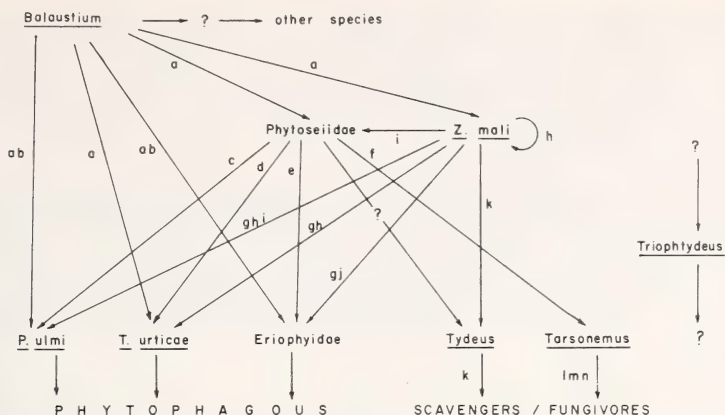


FIG. 1. Trophic relationships among Jordan Station acarid complex. --> = preys upon; ? = uncertain or unconfirmed. Authority: a, Cadogan & Laing (1977); b, Cadogan & Laing (1981); c, Dover *et al.* (1979); d, Johnson & Croft (1981); e, Herbert & Sandford (1969); f, Berkett & Forsythe (1980); g, White & Laing (1977a); h, Santos (1982); i, Santos (1976); j, White & Laing (1977b); k, Readshaw (1975); l, Rasmy & MacPhee (1970); m, Knisley & Swift (1972); n, Forest *et al.* (1982).

Population dynamics. Population dynamics were highly variable from year to year with most populations showing significant differences in annual peak density (Table III) over ranges of up to 2 (*Tydeus sp.*) or even 3 (*P. ulmi*) orders of magnitude. Nonetheless, at no time during this study did pest populations approach economic thresholds, 15-20 mites per

Table III. Temporal and spatial differences in peak mite populations in the Jordan Station orchard 1982-84

Species	Year	Variety ¹	Tree	Edge (29/8/84 only)
<i>T. urticae</i> (motile)	82>83>>84 ***	R>E>G>M	N.S.	N.S.
<i>T. urticae</i> (eggs)	83>84 **	R>E>G>M	N.S.	N.S.
<i>P. ulmi</i> (motile)	82>>83>84 ***	R>E>M>G R>M>E>G E only	* (1982) * (1983) N.S. (1984)	N.S. 0
<i>P. ulmi</i> (eggs)	83>84 ***	E>R>G>M	N.S.	0
Eriophyidae	83>84 N.S.	R>>G>M>E E>M>R>G	* (1983) ** (1984)	N.S. N.S.
<i>Z. mali</i>	83>82>84 ***	E>R>M>G	***	*** (> at edge)
Phytoseiidae	82>83>84 ***	M>G>E>R R>M>G>E M>R>E>G	** (1982) *** (1983) N.S. (1984)	N.S. *** (> at edge)
<i>Balaustium sp.</i>	82>83>84 N.S.	G>M>R>E	N.S.	0
Tarsonemidae	84>83 N.S.	E>M>R>G	N.S.	0
<i>Tydeus sp.</i>	84>83 ***	G>R>M>E R>E>M>G	N.S. (1983) N.S. (1984)	* N.S.
<i>Triophydeus sp.</i>	84>83 N.S.	E>M>R>G	N.S.	N.S.

¹E = Empire, G = Golden Delicious, M = McIntosh, R = Red Delicious.

Where a significant year-variety interaction was found varietal preferences are given by year. N.S. = p > 0.05,

* p < 0.05, ** = p < 0.01, *** = p < 0.001, 0 = insufficient data.

leaf for tetranychids (Dover *et al.* 1979; Parella *et al.* 1981) and 200-300 mites per leaf for eriophyids (Croft and Hoying 1977; Prokopy *et al.* 1980). In addition, no other apple foliage pest (those present included the white apple leafhopper, *Typhlocyba pomaria*; the spotted tentiform leafminer, *Phyllonorycter blancardella*; scale insects; and the rosy apple aphid, *Dysaphis plantaginea*) reached damaging levels, with the exception of a mild outbreak of *Aphis pomi* in July 1982.

Peak tetranychid densities decreased dramatically through 1982-84, *T. urticae* by a factor of 5 (Fig. 2A) and *P. ulmi* by a factor of almost 2000 (Fig. 2B). Outbreaks of *P. ulmi* are characteristic of commercial orchards, and decreases following the cessation of pesticide spraying have been recorded elsewhere (eg. Hoyt and Caltagirone 1971). *P. ulmi* was present on the foliage in early May and peaked in late July in 1982 and early September in 1983; such a range is not unusual (Downing and Moillet 1967; Parent 1967,

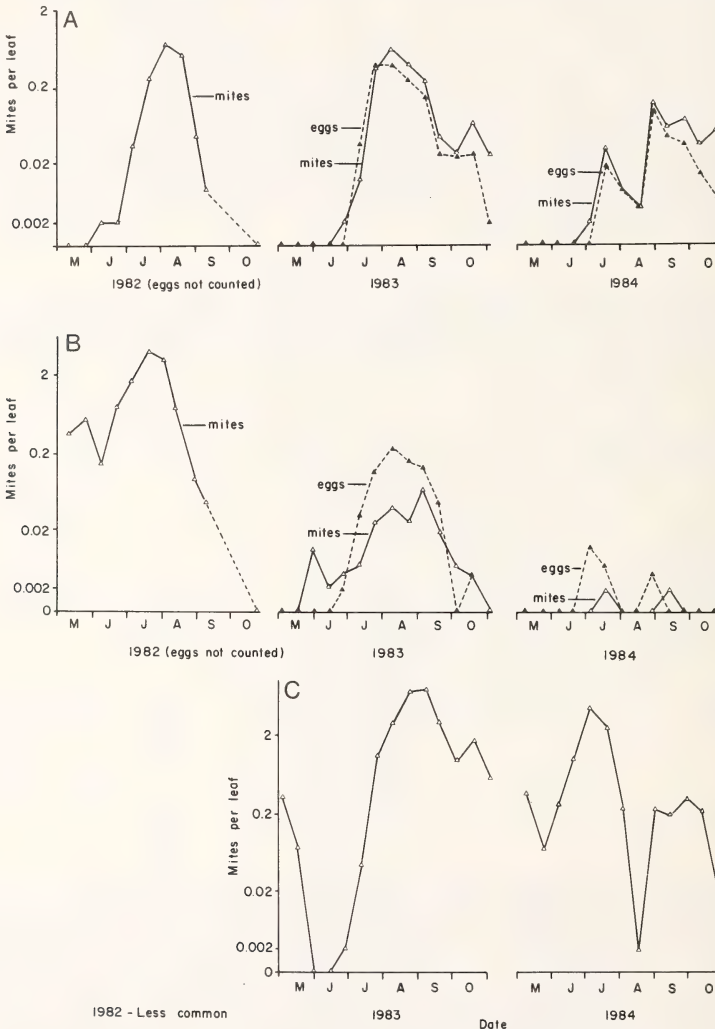


FIG. 2. Fluctuations in population density of acarids in an apple orchard at Jordan Station, 1982-84; (A) *T. urticae* (motile + eggs), (B) *P. ulmi* (motile + eggs) and (C) Eriophyidae.

1973). *T. urticae* appeared on the leaves in June and peaked in August; broadly similar patterns were found by Parent (1967) and White and Laing (1977a).

Peak eriophyid densities were not significantly different through 1983-84 but there were major differences in temporal patterns (Fig. 2C). Eriophyids appeared on the leaves in May but in 1983 crashed in June and recovered to reach peak abundance in early September, whereas in 1984 the population rose rapidly to peak levels in early July, crashed in August and partially recovered late in the season. An early season peak is more characteristic of eriophyid populations (Oatman 1973; Hagley *et al.* 1977) and 1983 patterns may be related to climate; 1983 was an exceptionally dry year in the Vineland area.

Population dynamics of predators and prey will obviously be related. In general, predator populations will track prey populations, although the co-occurrence of several prey species and the existence of time lags make this difficult to follow in the field. Our study was serendipitous in that the vastly different dynamics of prey populations that occurred through 1982-84 allowed us to examine corresponding differences in predator dynamics and to make inferences about predator-prey relationships in the field.

Z. mali shows differences through 1983-84 (Fig. 3A) that correspond to different eriophyid population dynamics with a lag of approximately 2 weeks, as has been reported elsewhere (White and Laing 1977a; Santos 1982). The peak population was slightly higher in 1983 than in 1982 despite a 6-fold decrease in peak tetranychid density. This is consistent with previous reports that *Z. mali* favours eriophyids as prey rather than tetranychids, especially *T. urticae* (White and Laing 1977a; Santos 1982). However, the September 1984 secondary peak occurred when eriophyids are relatively uncommon and may well be associated with the concurrent peak in tetranychid density and/or high levels of tydeids (see below).

The situation is more complicated for phytoseiids because we are dealing with several species which have different prey preferences (Croft and Hoying 1977; Johnson and Croft 1981). Phytoseiids (Fig. 3B) also had different dynamics through 1983-84, which correspond to eriophyid dynamics with a lag of 0-4 weeks. Peak abundances were halved from 1982 to 1983, presumably reflecting specialization of one common species, *Amblyseius fallacis*, on the declining tetranychids (Johnson and Croft 1981). Again the September 1984 peak was most likely associated with high abundances of tetranychids and/or tydeids. Note that predatory mites were found on the foliage until the end of October in all 3 years.

Balaustium occurred as two generations, one in late May-June, the other in August-early September (Fig. 3C) but was never common on leaves, although they also occurred on twigs and branches and on the ground.

Tarsonemids (Fig. 4A) appeared in late August 1983 and mid July 1984. They persisted to the end of the season, but were never common.

Tydeus sp. (Fig. 4B) progressed from virtual absence in 1982 to being the most abundant mite throughout September and October 1984. Peak density reached almost 1 mite per leaf which is higher than in any previous report although Forest *et al.* (1982) describe them as "abundant" in abandoned Quebec orchards and Rasmy and MacPhee (1970) as "common" in Nova Scotia. The importance of *Tydeus* is unclear due to uncertainty as to its feeding behaviour. *Tydeus* species have been classified as predaceous (Rasmy and MacPhee 1970; Knisley and Swift 1972), non-predaceous (Berkett and Forsythe 1980) and fungivorous (Readshaw 1975). It seems probable that *Tydeus* sp. at Jordan Station was a scavenger and/or plant feeder (see Baker 1970). *Triophtydeus* sp. (Fig. 4C) is a small but active mite that may be predaceous (Rasmy and MacPhee 1970; but see Baker 1970). This mite increased from virtual absence in 1982 to almost 1 per 10 leaves in September 1984. Tydeids have been considered prey for stigmataeids (Readshaw 1975); in our study late peaks in abundance of both *Z. mali* and phytoseiids in 1984 are closely correlated with peak tydeid abundances.

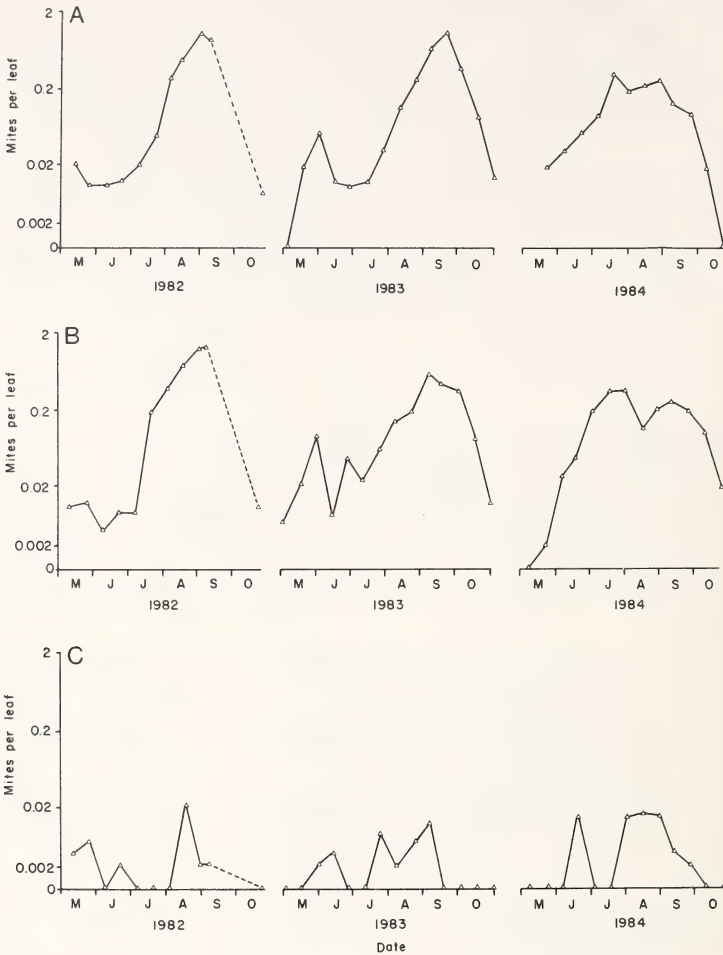


FIG. 3. Fluctuations in population density of acarids in an apple orchard at Jordan Station, 1982-84; (A) *Z. mali*, (B) Phytoseiidae and (C) *Balaustium* sp.

Biotic interactions. Competition, predator-prey interactions and climate may all affect population changes within and between years. Statistical analyses of these factors are extremely difficult due to effects of scale, time lags and functional responses of predators, and such analysis are not presented here. Nonetheless we can make some inferences as to the importance of these factors.

Abundances of phytophagous species were low; abundances of 70 tetranychids per leaf and 200 eriophyids per leaf have been recorded elsewhere on apple in Ontario (Hagley *et al.* 1977) and of 185 and 750 per leaf respectively in Michigan (Croft and Hoying 1977). Dover *et al.* (1979) suggest that tetranychids are not food-limited below 35 mites per leaf and experimental studies suggest that competition between phytophagous mites is significant only at densities higher than 100 mites per leaf (Foott 1962, 1963; Croft and Hoying 1977). Consequently, such competition is unlikely to have been important at our site where densities were at least an order of magnitude below these levels. Competition between

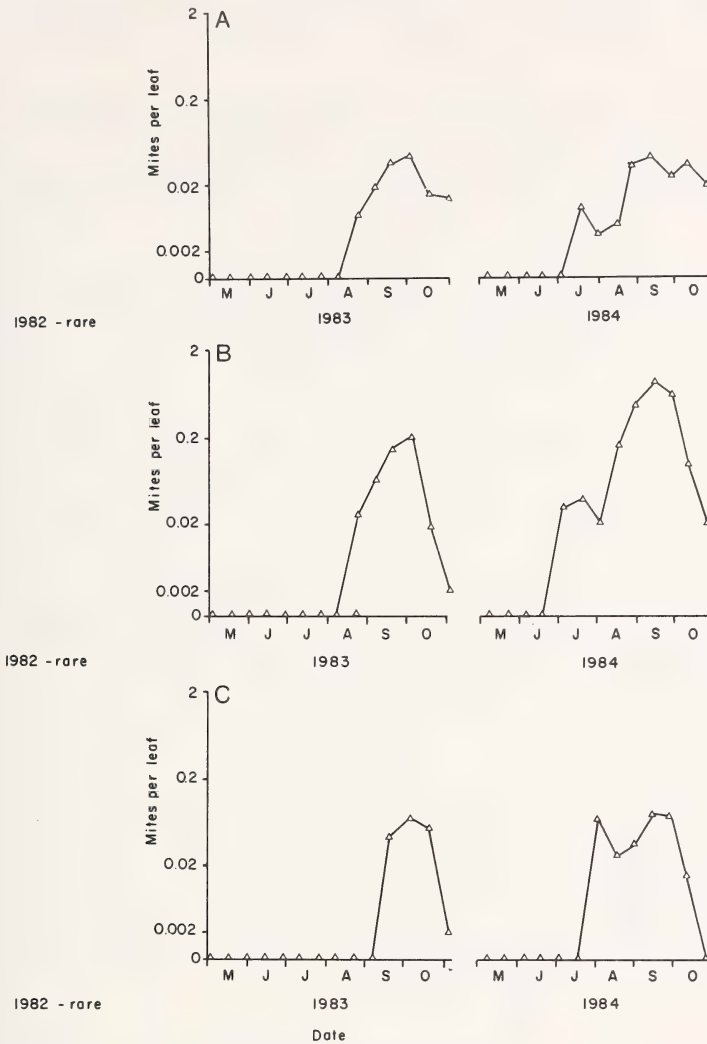


FIG. 4. Fluctuations in population density of acarids in an apple orchard at Jordan Station, 1982-84; (A) Tarsonemidae, (B) *Tydeus* sp. and (C) *Triophthyeus* sp.

predators is more likely because predators often out-numbered their prey, sometimes for several consecutive weeks.

Predators clearly respond to changes in prey abundance (see above) and appear to be exerting natural control over pest populations (see Huffaker *et al.* 1970; MacPhee and MacLellan 1971). The interactions are complex; for instance, low 1984 tetranychid populations are, we suggest, due to high early season predator populations which developed thanks to abundant eriophyid prey in early July.

We also note that climatic effects are doubtless partly responsible for our observed variations in population dynamics. For example, temperature is known to affect *T. urticae* fecundity (Herbert 1981) and *A. fallacis* prey consumption rates (Dover *et al.* 1979);

humidity affects *T. urticae* hatching rates (Ferro and Chapman 1979); wind affects *A. fallacis* dispersal (Johnson and Croft 1981). In this paper, however, we confine attention to the influence of biotic effects on abundances.

Habitat associations. Our analysis examined differences in peak abundance between apple varieties and individual trees, and also for edge effects using data collected 29 August 1984 (Table III). Associations with apple varieties were not always consistent from year to year. We did not examine differences in timing of peak abundance between apple varieties or individual trees, although inspection of the data suggests that such differences are of minor importance.

Tetranychids, both as eggs and motile stages, were consistently more common on Red Delicious and Empire trees though the difference was significant only for motile *P. ulmi*. Previous studies have also found higher abundances of *P. ulmi* on Red Delicious than other varieties (Downing and Moillet 1967; MacPhee and MacLellan 1971; Hagley *et al.* 1977). There were no consistent differences between individual trees nor, for *T. urticae*, was there a significant edge effect. Eriophyids showed inconsistent varietal associations and were most abundant on Red Delicious in 1983 and Empire in 1984. Data from Croft and Hoying (1977) show eriophyids to be more common on Red Delicious than McIntosh. Where varietal associations existed they could be quite marked; *P. ulmi* was 10 times as abundant on Red Delicious as on Golden Delicious in 1982, eriophyids were 12 times as abundant on Red Delicious as on Empire in 1983 but, paradoxically, 11 times as abundant on Empire than Red Delicious in 1984.

Z. mali was most abundant on Empire and Red Delicious, which were favoured by its prey, but did not seem to alter its distribution in response to changing eriophyid distributions. *Z. mali* was more abundant on trees near the edge of the orchard in 1984 (Fig. 5) and also was significantly associated with certain trees, mostly on the west side of the orchard. Patchy distributions of stigmataeids were also reported by Meyer (1974).

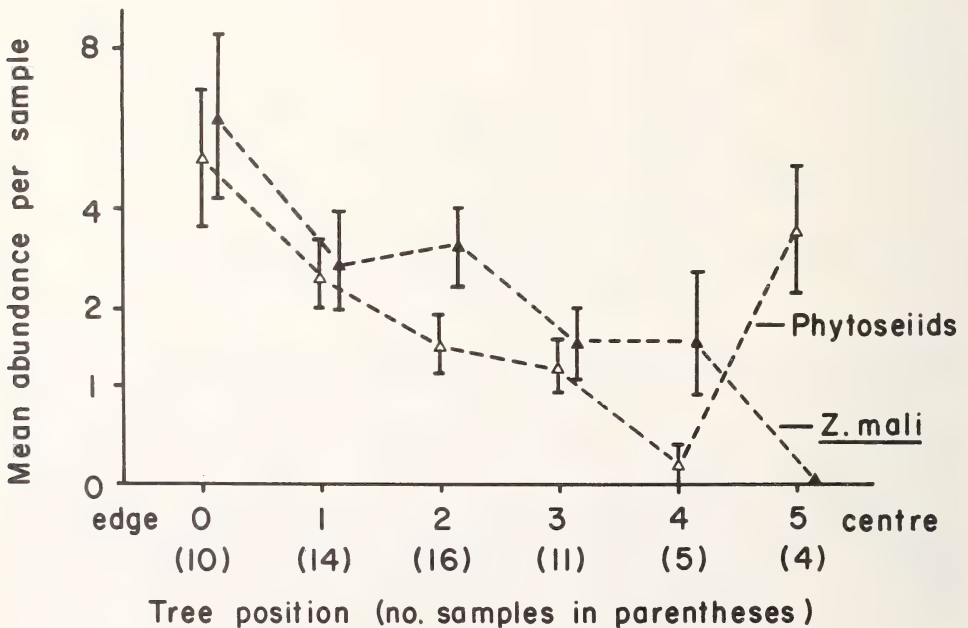


FIG. 5. Relationship of mean transformed count per sample (+ 1 S.E.) to tree position for phytoseiids and *Z. mali* in 1984. Data are pooled over different apple varieties.

Phytoseiids were inconsistently associated with the various varieties but tended to be relatively common on McIntosh, as found by Downing and Moillet (1967). Changing varietal distributions through 1983-84 seem to reflect changing eriophyid distributions but this is equivocal. Phytoseiids were also more abundant at the orchard edge in 1984 (Fig. 5) but were not associated with particular trees. Varietal associations were not as pronounced in phytoseiids (maximum difference: 4.5 times as common on Red Delicious as on Empire in 1983) as in *Z. mali* (maximum difference: 19 times as common on Empire as on Golden Delicious in 1984). Higher predator abundance on certain varieties does not imply that biological control is more effective on these trees. Pest populations were lowest overall on Golden Delicious which supported lowest *Z. mali* and only 'average' phytoseiid populations.

Tarsonemids and tydeids did not show significant varietal associations, although *Tydeus* showed a significant variety-year interaction. *Tydeus* also showed an association with particular trees, especially those in the south-east quadrat. Such associations may be related to the immediate surroundings of the orchard (see Solomon 1982), in this case a managed pear orchard.

The observed distributions of populations among varieties of apple will result from a combination of characteristics of the trees themselves and the distributions of competitors, predators and prey. These relationships may in turn be affected by climate (e.g. Dover *et al.* 1979). We suggest that this type of complexity results in the inconsistent (but nonetheless real) varietal associations shown by several populations during this study. Although additional data would clearly be useful, it may be that the concept of a simple preference of one species of acarid for one variety of apple is not appropriate in so complex a system.

Implications for pest management. This study demonstrates several points relevant to the management of pest mites on apple foliage. Firstly it provides another example of natural biological control. Also, it demonstrates that pest populations tend to be lower on McIntosh and Golden Delicious varieties than on Red Delicious and Empire in a predator-rich environment, sometimes by as much as an order of magnitude. The study demonstrates several differences between *Z. mali* and phytoseiids; the former are more patchily distributed across trees, more unevenly distributed across varieties, and may specialize on eriophyids rather than tetranychids, which is consistent with the view that phytoseiids are more effective control agents of tetranychids (Santos 1976; White and Laing 1977a, 1977b). Tydeids can be common in pesticide-free orchards and might provide a major alternative food source for predators late in the season; more work on tydeid biology is needed. Finally, both *Z. mali* and phytoseiids are more common towards the orchard edge. This implies that acaricide spray programs not including all trees but concentrating on the central portions of an orchard will be less detrimental to predator populations.

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MICROSPORIDIA OF THE EUROPEAN CORN BORER (LEPIDOPTERA: PYRALIDAE) IN SOUTHWESTERN ONTARIO: NATURAL OCCURRENCE AND EFFECTIVENESS AS MICROBIAL INSECTICIDES

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Abstract

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A substantial proportion (4.9 to 24.1%) of adults of the European corn borer, *Ostrinia nubilalis* (Hubner), captured in light traps in a seven-year period at Harrow, Ontario, were infected with a microsporidium. The incidence of infection was not related to numbers of moths captured. Although application of the microsporidia *Nosema pyrausta* and *Vairimorpha necatrix* to plots of sweet corn and field corn did not reduce crop damage in a series of field tests, increased incidence of infection in *O. nubilalis* larvae in treated plots suggested a long-term effect of the microsporidia on the pest population.

Introduction

Populations of the European corn borer, *Ostrinia nubilalis* (Hubner), an important insect pest of corn in Ontario, are known to be influenced by several species of parasitic and predaceous arthropods (Wressell 1973). Although pathogens, particularly *Nosema* (= *Perezia*) *pyrausta* and other microsporidia have been found in field populations of the corn borer in several locations in the U.S.A. (Zimmack and Brindley 1957; Van Denburgh and Burbutis 1962; Hill and Gary 1979), it is interesting that Wressell (1973) did not include a microsporidium in his list of parasites of *O. nubilalis* in Ontario. Similarly, Mutchmore (1959) did not report that microsporidia contributed to the high mortality of larvae of the corn borer collected from fields in Ontario.

Infection of *O. nubilalis* adults by *N. pyrausta* reduces longevity and fecundity of adults and may result in a high frequency of deformity (Zimmack and Brindley 1957; Windels *et al.* 1976). Feeding larvae spores of *N. pyrausta* did not increase mortality of larvae in tests by Lewis *et al.* (1983) but adult emergence was significantly reduced. Furthermore, feeding the microsporidium *Vairimorpha necatrix* alone or in combination with *N. pyrausta* was more detrimental to *O. nubilalis* larvae than was *N. pyrausta* alone. These treatments significantly increased mortality of larvae and reduced emergence of adults as compared to the check. Application of *N. pyrausta* or *V. necatrix*, or mixtures of the microsporidia, to field plots of corn in these tests reduced numbers of corn borers per plant and increased percentages of larvae infected with the microsporidia over the natural rate of infection.

The present study concerns incidence of natural infection of *O. nubilalis* adults and larvae by microsporidia. In addition, protection of corn in field plots against the borer by application of *N. pyrausta*, *V. necatrix*, the nuclear polyhedrosis virus of *Autographa californica* (ACNPV), formulations of *Bacillus thuringiensis* (*B.t.*) and two chemical insecticides are compared.

Materials and Methods

Adult European corn borers were captured in black-light Ellisco traps located at the Research Station at Harrow in southwestern Ontario, in a locality in which grain corn and sweet corn are important crops and in which the corn borer is bivoltine. Trapping was begun in May when 1st-generation moth flight began and was continued through September when flight of 2nd-generation moths ceased; peaks of flight of moths of the 1st and 2nd generations usually occur in mid May and August, respectively. The specimens in the trap were identified and enumerated at 1- to 3-day intervals depending on the flight of moths. All adults in the catch or a randomly selected sample from the catch were examined

as wet mounts to determine infection by a microsporidium or other entomopathogen.

Preparations of microsporidia, *B.t.*, ACNPV or a chemical insecticide were applied to field plots to assess effectiveness in protecting sweet corn and grain corn against natural infestations of the European corn borer. Spores of *N. pyrausta* and *V. necatrix* were harvested from infected *O. nubilalis* and *T. ni* larvae and were partially purified by centrifugation, suspended in water, and stored for less than 3 months prior to application. Aqueous suspensions of polyhedral inclusion bodies of ACNPV, propagated in *T. ni* larvae, were partially purified for plot use in each field season. Formulations of *B.t.* were Dipel WP (16.0 BIU/kg) and, in 1983, Bactospeine (9.247 BIU/L). Formulations of chemical insecticides were Ambush 50 E.C. (500 g permethrin/L), and Belmark (300 g fenvalerate/L).

Plots, each consisting of 2 to 4 rows of sweet corn and 4 to 6 rows of grain corn, 6 to 10 m long with 0.2 m between plants, 1 m between rows, and a 2-m nonplanted barrier between plots, were replicated 3 times in randomized blocks. Treatments were applied as dilute sprays (400 to 800 L/ha) to plots using a compressed-air hand sprayer (averaging 275 kPa pressure). A spreader, Plyac (Allied Chemical Company) or, after 1980, Chevron Spray Sticker (Chevron Chemical Company), was included in spray suspensions. Skim-milk powder (0.5% w/v) was added to suspensions of biological materials as a protectant against sunlight.

Ten or more plants of grain corn were randomly selected from each plot and examined for damage by the corn borer to assess protection by the treatments. Ears and stalks were dissected, entry holes and tunnels by corn borers were enumerated, and live and dead larvae were collected for subsequent rearing and/or examination.

Results and Discussion

A substantial proportion of adult European corn borers captured in light traps was infected with a microsporidium (Table I). Annual means of incidence of infection over the 7-year period of observation ranged from 4.9 to 24.1%. In addition, incidence varied with period of capture within the year with higher incidences usually occurring in the month of peak periods of flight of the generations, i.e. during the months of June and August. The

Table I. Numbers of European corn borer adults captured in light traps and the percentage infected by microsporidia

Year	Measurement	Time of Capture					Annual Total
		May	June	July	August	Sept.	
1977	Captured (no.)	35	38	101	287	236	697
	Infected (%)	11	6	17	16	6	9.8
1978	Captured (no.)	-	92	64	2485	72	2713
	Infected (%)	-	1	0	6	10	4.9
1979	Captured (no.)	-	91	14	1106	63	1274
	Infected (%)	-	18	16	19	40	18.6
1980	Captured (no.)	1	47	36	776	154	1014
	Infected (%)	0	30	4	14	13	15.9
1981	Captured (no.)	5	61	88	426	34	614
	Infected (%)	0	21	8	24	8	20.2
1982	Captured (no.)	11	41	92	545	14	703
	Infected (%)	18	26	14	21	7	19.0
1983	Captured (no.)	-	104	64	634	133	935
	Infected (%)	-	19	7	31	27	24.1

Table II. Effectiveness of entomopathogens and chemical insecticides applied to field plots of grain corn and sweet corn to control the European corn borer

Material/ ha/ application ¹		Crop damage ³			Populations of corn borer ³			
		% plants injured	Entries or tunnels / 10 plants		Larvae / 10 plants	Percentage infected and / or killed by:		
			Stalks	Ears		Micro-sporidia	Bacteria	Virus
1978	<i>N. pyrausta</i>	2 x 10 ¹² spores	135	10	92	60	7	0
	ACNPV	7.9 x 10 ¹² PIB ²	130	10	96	28	8	16
	Nontreated check		130	10	98	25	10	0
1979	<i>N. pyrausta</i>	1 x 10 ¹² spores	37	4	8	23	0	0
	Nontreated check		41	3	16	20	0	0
1980	<i>N. pyrausta</i>	2.7 x 10 ¹² spores	29	13	33	63	4	0
		1.3 x 10 ¹³ spores	17	7	17	80	0	0
	<i>B.t.</i> (Dipel)	4 BIU ²	19	9	23	10	1	0
		20 BIU	14	13	19	20	0	0
	Fenvalerate	70 g	17	8	22	13	1	0
	Nontreated check		24	8	26	17	0	0
1981	<i>N. pyrausta</i>	3.9 x 10 ¹² spores	22	4	19	55	0	0
	<i>V. necatrix</i>	3.9 x 10 ¹² spores	22	4	22	45	5	0
		3.9 x 10 ¹³ spores	24	2	17	55	5	0
	<i>B.t.</i> (Dipel)	12 BIU	14	4	11	25	15	0
	Fenvalerate	83 g	3	0	2	0	0	0
	Nontreated check		19	6	13	40	0	0
1982	<i>N. pyrausta</i>	4.2 x 10 ¹² spores	24	5	17	40	0	0
	<i>V. necatrix</i>	4.2 x 10 ¹² spores	19	6	14	18	14	0
		2.1 x 10 ¹³ spores	17	7	19	40	7	0
	Permethrin	140 g	5	0	3	20	10	0
	Nontreated check		27	5	17	15	10	0
1983	<i>N. pyrausta</i>	6.1 x 10 ¹² spores	33	11	25	66	6	0
	<i>V. necatrix</i>	7.7 x 10 ¹² spores	25	8	22	53	13	0
		7.7 x 10 ¹³ spores	20	7	16	63	16	0
	<i>B.t.</i> (Bactospeine)	77 BIU	4	2	3	12	6	0
	Permethrin	140 g	1	2	2	14	7	0
	Nontreated check		21	5	18	40	20	0

¹* Treatments were applied to plots 4 times in 1980, 3 times in 1981, 1982, and 1983, and 2 times in 1978 and 1979.

²** PIB and BIU are polyhedral inclusion bodies and billion international units, respectively.

³*** Data for crop damage and populations of the borer are based on samples from the grain-corn portion of the plots.

percentage infection and the total numbers of moths captured in a month were not related ($r = 0.02$). The incidence of infection was lowest in 1978, the year that the numbers captured were highest but the relationship ($r = 0.25$) was not significant. In addition, the relationships of numbers captured to percentage infected, although not significant, were positive in May and July ($r = 0.51$ and 0.16) at the beginning of the generations and negative in June, August and September ($r = -0.29$, -0.69 and -0.10) in the latter part of the generations.

Entomopathogens were less effective than chemical insecticides in protecting the crop against the corn borer in most field-plot tests in the 6-year study (Table II). Applications of spores of the microsporidia *N. pyrausta* or *V. necatrix* had little or no effect on damage to corn or on numbers of corn borers found in plants. Likewise, ACNPV had no detectable effect. Similarly, applications of *B.t.*, except the heavy dosage of the Bactospeine formulation applied in 1983, did not reduce crop damage or populations of the borer, agreeing with earlier findings (Lynch *et al.* 1977) that spray applications of *B.t.* were not particularly effective. Fenvalerate and permethrin, except in the 1980 test, substantially reduced numbers of entries and tunnels by the corn borer in stalks and ears of corn and correspondingly reduced numbers of larvae found.

Applications of microsporidia to plots did not substantially affect damage to the crop but the applications increased the occurrence of microsporidian infection of larvae found in the plants. Less than 10% of infected larvae were killed. Infection of larvae by microsporidia may adversely affect development and vigor and may affect fecundity of the adults (Hill and Gary 1979; Lewis *et al.* 1982, 1983) suggesting that infection in larvae following application of microsporidia could contribute to suppression of populations of the insect, particularly if substantial areas were treated. The finding of infection by microsporidia in 10 to 24% of adults caught in light traps and in 17 to 40% of larvae found in nontreated check plots indicated a considerable natural occurrence of microsporidia in this insect and a probability that the microsporidia became established in the population following application. Although the incidence was lower than that found elsewhere (Hill and Gary 1979; Lublinkhof and Lewis 1980), further evaluation is warranted. On the other hand, although larvae infected and killed by ACNPV were found in plots treated with the virus, a significant carry-over effect of the virus was not considered to be probable partly because of the low activity of ACNPV against *O. nubilalis* larvae in laboratory tests by Lewis and Johnson (1982) and ourselves.

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INFLUENCE OF SPRAY VOLUMES ON CONTROL OF SAN JOSE SCALE (HOMOPTERA:DIASPIDIDAE)

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Abstract

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Applications of superior oil to small (1.5-2.0 m) plum trees in spray volumes ranging from 787-2360 L/ha indicated that all volumes were equally effective in controlling San José scale, *Quadraspidiotus perniciosus* (Comstock). On larger (4.0-4.5 m) apple trees, tests over four years failed to show any advantage from the application of spray volumes larger than 2400 L/ha. None of the treatments, including combinations of oil sprays during the dormant stage and summer sprays of diazinon, were effective in preventing the resurgence of scale populations.

Introduction

Petroleum oils have been used to control insect and mite pests on tree fruits for over 100 years. San José scale, *Quadraspidiotus perniciosus* (Comstock), has been present in Ontario since about 1893 (Caesar 1914) and oil sprays, which were used almost from the beginning, have remained an important tool in the control of both San José scale and European red mite, *Panonychus ulmi* (Koch). With the development of modern airblast sprayers, spray volumes have been gradually reduced to the point where most growers in Ontario are applying most other pesticides in 100-500 L of water/ha. However, applications of superior oil, ca. 65 L/ha, are still recommended (for apples) in 2200-4500 L water/ha (Anon. 1984). Studies on the influence of spray volumes on control of San José scale have seldom been reported but Meyer and Randell (1973) found that scale control was about equal with volumes ranging from 300 U.S. gallons/acre (2800 L/ha) down to 6 gal/acre (56 L/ha). This paper reports the results of studies over 5 years on the effects of spray volumes on the control of San José scale on apples and plums in the Niagara peninsula of Ontario.

Methods

In 1980, superior oil (70-sec viscosity) at 67.4 L/ha was applied to 1.5-2.0-m-tall, non-bearing plum trees (*Prunus domestica* L.) at water volumes of 787, 1574, and 2360 L/ha. Trees were 5 years old, of mixed varieties and spaced 3.6 x 1.8 m in a seedling variety planting at the Horticultural Research Institute of Ontario, Vineland Station. An area of ca. 0.15 ha was sprayed with each spray volume when buds were at silver tip 23 April 1980, using a Rittenhouse airblast sprayer (M.K. Rittenhouse and Sons Ltd., Jordan Station, Ontario). The nozzles used were Spraying Systems® D5-25 with the pressure set at 1400 kPa. Mortality of scales was based on examination of 200 scales (150 exposed, 50 from under bud scales) selected from 3 branches from each of 6 trees sprayed with each volume. Branches ca. 2-3 cm in diameter were selected and cut from trees with visible infestations on the bark, and were examined in the laboratory under a binocular microscope. Caps on scales were overturned with a sharpened probe. Living scales were orange-yellow in colour and turgid whereas dead scales were darkened, shrivelled and hardened. Scales were examined pre-spray on 22 April, and post-spray on 8, 15 and 22 May 1980.

In 1981, tests were conducted on 20-year-old McIntosh apple trees which were on Malling VII rootstock, 4-4.5 m high, and spaced 8.1 x 8.1 m. Plots were single trees, replicated 4 times. Scale infestations had been untreated for several years and some trees had reduced vigour. Sprays of superior oil at 67.4 L/ha were applied 10 April to dormant trees using a Rittenhouse airblast sprayer. Oil was applied in volumes of 800, 1600 and 2400 L of water/ha. Spray volumes were adjusted by varying the oil concentration in the spray tank, by varying the number of spray nozzles (D8-45) from 3-8, and by changing the

driving speed. Pressure was held constant at 1379 kPa for all treatments. Results were based on examination of 200 scales/plot from twigs and spurs cut from visibly infested scaffold limbs and central leaders 2-3 m high, pre-spray 10 April, post-spray 24 April. The percent fruit infested was estimated on 10 September based on the examination of 100 fruit picked from each plot taking care to include samples from all parts of the canopy. This sample was ca. 10-20% of the total crop remaining on the tree.

In 1982, tests were conducted in the same planting used in 1981. Heavily infested trees were selected, and treatments assigned in a randomized block design, with 3 replicates, using single trees as plots. Prior to treatment on 27 April, estimates of scale populations were made from each of 4 areas (6.45 cm²) on the main scaffold limbs in the field using a 20X hand lens and probe. Treatments were applied 27 April using a Swanson airblast sprayer. Superior oil was applied at ca. 65 L/ha. Three spray volumes were tested; 1600, 2400 and 3370 L/ha. In addition, a second treatment of oil in 3370 L water/ha was followed by an application of diazinon (1.62 kg AI/ha) in 1140 L water/ha on 5 July when crawlers were first seen. Spray volumes were varied by adjusting nozzle size, pressure and driving speed. One other treatment at 3370 L water/ha was applied 27 April using a hand-held spray gun equipped with a Spraying Systems® D-10 orifice. Pressure was set at 1724 kPa and output estimated to be ca. 34.2 L/tree.

Mortality of overwintering scales was estimated 14 days post-treatment with oil sprays (12 May). Sample size and sample area were similar to those of pre-spray samples. At harvest, on 29 September, 100 apples/tree were examined and the percent infested apples and scales/100 fruit estimated.

In 1983, this test was repeated for a second year on the same trees using similar treatments. Applications of oil were made 26 April; diazinon was applied 29 June when the first crawlers were seen. At harvest on 23-25 September, based on a sample of 100 apples, percent infested apples and numbers of scales/fruit were recorded.

In 1984, superior oil sprays (65 L/ha in 3370 L water) applied when trees were dormant on 28 April, were compared with diazinon sprays (1.62 kg AI/ha applied in 3370 L water/ha) applied when crawlers were active on 29 June. Emergence of crawlers was estimated by a degree-day accumulation above 8.9° C as suggested by Anthon (1967) and confirmed with periodic bark examinations. Diazinon sprays were applied to runoff with a jeep-mounted sprayer equipped with a Spraying Systems® gun with a D-6 orifice. Oil was applied 26 April to dormant trees at 65 L/ha in 3370 L water/ha with a John Bean sprayer and gun. Scales were sampled pre-spray 25 April and 4 weeks post-spray 22 May. Samples were from 4 areas (each 6.5 cm²) on scaffold limbs. On 19 September, 100 apples were picked from each plot and percent infested fruit was calculated.

Data, expressed as percent mortality, fruit infested, etc. were transformed using an arcsin transformation. The significance of treatment effects was tested using an analysis of variance and Duncan's Multiple Range Test was used to separate significantly different treatments ($P = 0.05$).

Results

Applications of oil to 1.5-2 m plum trees at all three spray volumes effectively controlled San José scale (Table I). All volumes were equally effective. Mortality increased only slightly from 2 to 4 weeks after treatment. In 1981 sprays applied to larger (4.0-4.5 m) apple trees at about the same volumes reduced the percent living scales to 11-14% but were ineffective in significantly reducing percent fruit infested at harvest (Table II). Reductions were greatest where the highest water volumes (2400 L/ha) were used but the difference between spray volumes were not significant. In 1982 higher volumes (up to 3370 L/ha) and two application techniques were tested (Table III). The percent living scales was lowest where the oil emulsion was applied with the spray gun at 3370 L/ha and highest where the lower water volumes (1600 L/ha) were used but differences were not significant. Post-spray mortalities were highly variable and differences between treatments may have been masked. All treatments significantly reduced the percentage of fruit infested at harvest in

Table I. Effects of spray volumes on control of San José scale on 1.5-2 m plum trees, 1980

Spray volume ¹ (L/ha)	Living scales (%)			
	22 April pre-spray	8 May	15 May	22 May
Unsprayed	73.8 ab ²³	57.3 a	55.0 a	42.2 a
787	79.0 a	1.6 b	0.8 b	0.1 b
1574	69.8 b	1.0 b	0.7 b	0.2 b
2360	73.1 ab	0.8 b	0.4 b	0.2 b

¹ 67.4 L/ha superior oil applied at each spray volume.

² Based on examination of 200 scales/plot.

³ Means followed by the same letter not significantly different (P = 0.05) Duncan's Multiple Range Test.

Table II. Effects of spray volumes on control of San José scale on 4-4.5 m apple trees with superior oil, 1981

Spray volume ¹ (L/ha)	Living scales (%)		
	10 April (pre-spray)	24 April (14 days post-spray)	Infested fruit (%) 10 September
Unsprayed	67.1 a ²³	46.2 a	44.7 a ⁴
800	55.5 a	14.0 b	42.1 a
1600	50.0 a	13.8 b	30.0 a
2400	62.6 a	11.0 b	23.6 a

¹ 65 L/ha superior oil applied at each spray volume.

² Based on examinations of 200 scales/plot.

³ Means followed by the same letter not significantly different (P = 0.05) Duncan's Multiple Range Test.

⁴ Based on examination of 100 apples/plot.

Table III. Influence of spray volumes and application methods on control of San José scale over two years on 4-5 m apple trees

Spray volume ¹ (L/ha)	Application method ²	1982				1983	
		Living scales (%)		Infested fruit (%) 29 Sept.	Scales/ 100 fruit 29 Sept.	Infested fruit (%) 23 Sept.	Scales/ 100 fruit 25 Sept.
		pre-spray 21 April	post-spray 12 May				
Unsprayed	—	33.6 a ³	27.4 a	11.5 a	50.7 a	53.0 a	1261 a
1600	airblast	23.4 ab	16.6 a	3.7 b	20.5 ab	17.3 b	73 b
2400	airblast	15.5 ab	6.8 a	1.1 b	3.3 b	9.6 b	54.5 b
3370	airblast	13.8 b	3.4 a	0.8 b	3.7 b	14.0 b	35 b
3370	gun	17.8 ab	2.1 a	1.7 b	1.3 b	7.5 b	31.5 b
3370 + diazinon ⁴	airblast	19.1 ab	13.1 a	1.3 b	1.3 b	15.0 b	84 b

¹ 65 L/ha superior oil applied at each spray volume.

² Oil applied 27 April 1982, 26 April 1983.

³ Means followed by the same letter not significantly different (P = 0.05) Duncan's Multiple Range Test.

⁴ Diazinon (1.62 Kg A1/ha) applied 5 July 1982, 29 June 1983.

Table IV. Control of San José scale with dormant oils or summer sprays of diazinon on 4-4.5 m apple trees, 1984

Treatment	Rate/ha (in 3370 L water)	Living scales %		Infested fruit (%) 19 Sept.
		Pre-spray 25 April	Post-spray 22 May	
Superior oil ¹	65 L	41.4 a ³	14.2 a	44.1 a
Diazinon 50WP ²	1.62 kg AI	40.5 a	39.2 b	52.3 a
Unsprayed	—	37.2 a	61.1 b	75.5 b

¹ Applied 26 April in 3370 L water/ha with spray gun.

² Applied 29 June in 3370 L water/ha with spray gun.

³ Means followed by the same letter not significantly different ($P = 0.05$), Duncan's Multiple Range Test.

1982-83. However, numbers of scales/100 fruit examined was not significantly different from unsprayed fruit on plots where oil was applied in 1600 L/ha in 1982. A second year of similar treatments did not eliminate infestations (Table III). However, in 1983, all treatments had significantly fewer infested fruit and numbers of scales per fruit than did unsprayed plots. Although numbers of infested fruit and numbers of scales/100 fruit were consistently lower (both in 1982 and 1983) as spray volumes increased, differences were not significant. Where combinations of superior oil and diazinon were used (Table III) in 1982 and 1983, scale numbers and fruit infestations were reduced compared to unsprayed plots but were equivalent to application of oil alone. Where separate applications of oil and diazinon were made in 1984 (Table IV), infestations at harvest were not statistically different. Both treatments reduced the percentage of infested fruit compared to unsprayed controls. Crawlers were found after ca. 1300 degree-days accumulation above 8.9°C, slightly earlier than the ca. 1850 degree-days described by Anthon (1967).

Discussion

Spray recommendations (Anon. 1984) for tree fruit production in Ontario suggest high spray volumes (3500 L/ha on 2.5-3.0 m trees) for control of San José scale. The results obtained in this study do not support that recommendation. We obtained no increase in control on small (1.5-2 m) plum trees as spray volumes increased ranging from 787 to 2760 L/ha. On larger trees, tests over 4 years failed to show any advantage for spray volumes greater than 2400 L/ha. Populations of San José scale had been allowed to reach damaging levels in this orchard and none of the methods tested, including combinations of oil and summer sprays of diazinon, was effective in keeping scale populations below economically damaging levels. Oil alone has been shown ineffective in controlling San José scale in Washington (Howell and George 1984). Perhaps combinations of oil plus insecticides as suggested by Downing and Logan (1977) would be more effective. In commercial plantings, scale populations are unlikely to reach levels which occurred in these tests. Spray coverage was not likely the cause of control failure because application of 3370 L/ha with a gun is equivalent to a spray to runoff. Another approach to control of San José scale might be the use of a preventative program such as that recommended for peaches by Pree *et al.* (1980). This would require the application of superior oil during the dormant stage once every three years to prevent development of damaging numbers. However, the data from this study indicates that application of oil in sprays of more than 2400 L/ha, to trees 2-4.5 m tall does not improve control of San José scale. For smaller trees, volumes as low as ca. 800 L/ha are effective.

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RELATIONSHIP OF FLIGHTS OF EUROPEAN CORN BORER (LEPIDOPTERA: PYRALIDAE) TO TEMPERATURE ACCUMULATIONS AT HARROW, ONTARIO

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Abstract

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Fourteen years of light-trap monitoring of the European corn borer (ECB), *Ostrinia nubilalis* (Hübner) at Harrow, Ontario, indicated the predominance of a multivoltine strain. Comparisons of daily catches with cumulative day-degrees (CDD) made it possible to define the end of first-generation activity as 450 CDD, and the start of second-generation activity as 700 CDD. A scarce but persistent strain of univoltine moths was trapped between these multivoltine flight periods, usually in the period 460 to 650 CDD, but later in some years. About 4% of field-collected, diapausing ECB took over 560 CDD to pupate, consistent with the requirements of the univoltine strain. A third generation of the multivoltine strain was evident in 6 of 14 years.

Introduction

In southwestern Ontario the European corn borer (ECB), *Ostrinia nubilalis* (Hübner), attacks grain corn, sweet corn, peppers, snap beans and potatoes. The degree of infestation depends in part on the density of ECB moths and the attractiveness of the crop to ovipositing females. At the Harrow Research Station a light trap has been used successfully to estimate the abundance of ECB and to provide additional information on the adult sex ratio and mating status of females (Elliott 1977; McClanahan and Elliott 1977). McLeod (1976), in a comparison of seasonal distribution of light-trap catches at a number of Ontario locations, concluded that ECB at Harrow were multivoltine. Recent studies in New York State established the existence of both univoltine and multivoltine strains at 16 of 28 trapping sites (Eckenrode *et al.* 1983). A 9-year study of ECB flight activity at Wooster, Ohio did not indicate the presence of a univoltine strain there (Clement *et al.* 1981).

In order to study the voltinism status of the local population of ECB over the years, and to relate flight activity to temperature accumulations, I examined the data from the Harrow, Ontario light trap, beginning in 1971. I also reared overwintered larvae to determine the day-degrees required for initiation of pupation, which differs for univoltine and multivoltine strains (McLeod 1976).

Method

A light trap was operated at exactly the same location from early May to the end of October, beginning in 1971. Meteorological records for Harrow were used to calculate cumulative day-degrees (CDD) using a base of 10°C and no upper limit (Baskerville and Emin 1969). Since most ECB were caught from 9 p.m. to midnight and counted the next morning, the counts were related to the previous day's CDD. Comparison with earlier literature was possible simply by multiplying DD_{50F} or CDD_{50F} by 0.556 to obtain the equivalent DD_{10C} or CDD_{10C}.

The extensive record of daily catches with corresponding CDD values was reorganized into a table of the number of moths trapped in successive 30-DD intervals. Such intervals included 2 to 7 trapping periods, depending on the season. A composite of the seasonal distribution was obtained by expressing the catch in each interval as a percent of the year's total, then averaging across the 14 years.

Definitive CDD values for the beginning and end of flight activity periods were assembled after examination of the original daily records, then numbers were summed for each generation and peak period noted.

Stalks of sweet corn containing diapausing larvae of ECB were collected in November 1983 and stored in an insectary at field temperature and light conditions. Larvae were dissected from the stalks in late January and early February 1984 and held at a constant 20°C until they completed their development. The incidence of pupation was recorded several times weekly and the number of DD required for pupation was calculated.

Results and Discussion

There were considerable variations from year to year in the period of ECB flight activity, their patterns and their relation to CDD. Yearly catches in the light trap began as early as 110 CDD and continued almost to the end of DD accumulation (Table I). There was an obvious bimodal pattern of activity every year, representing the 1st and 2nd generations of the multivoltine strain. A peak of ECB activity occurred at about 260 CDD and the second, much larger peak varied between 830 and 1070 CDD from year to year. The multivoltine strain of ECB at Eden, NY, close to the east end of Lake Erie, had similar heat requirements (Eckenrode *et al.* 1983). At Wooster, OH the peaks came slightly later, at 400 and 1100 CDD (Clement *et al.* 1981).

At Harrow, Ontario there consistently was some flight activity between the generations of the multivoltine strain. The hypothesis that this portion of the moth catch was due to a remnant univoltine population was supported by the definition of the beginning and end of all flight periods each year (Table II). A substantial gap in flight activity prior to 458 CDD in the years 1973 to 1975 and 1980 to 1984 defined the beginning of mid-summer flight activity. The discreteness of the flight period was evident in 1973 when moths were caught on 9 consecutive nights, preceded by a period of 5 days and followed by a period of 10 days when no moths were caught. The flight period covered a narrower range of CDD when there were low numbers of moths as in 1977, 1980 and 1983.

Relating moth catches to CDD did not eliminate variations from year to year which could be a result of soil moisture conditions or the effect of wind and rain on flight activity. With few exceptions, this mid-summer flight of ECB at Harrow occurred within the period 450 to 710 CDD, and it averaged a span of 170 DD. In areas of New York State where the univoltine strain predominated, it occurred in the period 450 to 768 CDD (Eckenrode *et al.* 1983). Even where a multivoltine strain predominated, as at Eden, NY, some moths were caught in this interval. The summation of moth catches over one-week intervals that were used by these authors could have masked intervals between activity periods, and they provided no indication of the actual numbers caught.

The onset of the flight period of the second generation of the multivoltine strain was clearly defined by a rapidly increasing daily catch of moths beginning some time between 679 and 744 CDD. The mean CDD at the start of activity was 722 and the standard deviation of 22.2 represents less than 2 days of heat accumulation. The mean date marking the start of the second generation of the multivoltine strain, 27 July, had a standard deviation of 4.3 days. Thus 722 CDD is the best predictor for the onset of flight activity of the 2nd generation of the multivoltine strain.

The greatest number of moths was trapped in 1971. The 3 peaks noted in Table II had nightly catches of 494, 845 and 500. A 4-day interval (56.4 DD) separated the 2nd and 3rd generations of ECB moths which had totals of 4292 and 678 respectively. The record catches of 1971 were followed by a very light 2nd-generation flight in 1972, and no evidence of a 3rd generation. There was no consistent relationship between the numbers in consecutive generations, either within or between years.

The peaks tabulated in the last column of Table II were all second generation except for the one at 1282 CDD in 1977. This was an unusually warm summer which resulted in the early appearance of a 3rd generation, with a peak of 101 ECB on 2 September. There were about equal numbers of moths in the 2nd and 3rd generation in 1977. The pattern of flight activity beyond 1200 CDD suggested that moderate 3rd-generation flights occurred in 1971, 1973, 1975, 1977, 1980 and 1983. All of those years had over 1260 CDD on 10 September. The probable limiting factor for the 3rd generation was that a certain CDD

Table I. Light-trap catches of ECB at Harrow from 1971 to 1984 grouped in relation to successive 30-DD intervals

CDD interval midpoint	'71	'72	'73	'74	'75	'76	'77	'78	'79	'80	'81	'82	'83	'84
110	0	0	0	0	0	0	0	0	0	0	2	0	1	0
140	1	0	0	0	0	0	0	0	0	1	3	1	4	4
170	9	1	0	5	0	0	3	6	9	2	10	0	11	6
200	2	2	11	0	0	2	4	2	5	0	7	3	7	3
230	23	10	7	2	0	24	15	4	5	10	7	7	12	24
260	12	25	84	4	3	24	2	4	8	18	9	2	18	29
290	0	3	32	12	1	8	12	16	29	2	5	11	26	5
320	17	6	22	5	0	13	16	26	2	10	10	9	14	13
350	11	19	2	25	1	4	8	8	19	2	0	8	8	4
380	11	23	13	0	3	30	6	18	13	3	7	4	2	1
410	19	36	3	3	1	6	3	2	2	1	2	0	1	1
440	3	19	0	0	0	8	1	3	1	0	4	5	0	0
470	1	3	4	0	2	4	0	5	1	0	0	4	0	0
500	3	12	3	4	0	1	0	0	5	0	0	1	0	0
530	7	6	8	0	1	3	1	2	0	2	0	0	2	0
560	0	0	2	2	2	0	0	0	0	0	0	0	0	0
590	10	2	0	2	0	0	0	1	0	0	0	2	1	0
620	1	5	0	1	2	0	0	0	1	0	5	7	1	3
650	4	1	0	0	1	1	1	1	0	1	1	5	1	6
680	3	0	0	0	0	0	0	0	1	0	8	2	1	6
710	0	4	5	4	0	0	4	13	4	13	3	1	3	17
740	25	0	13	3	1	11	6	13	13	9	6	8	11	15
770	213	9	58	4	1	10	8	7	36	15	31	21	13	44
800	277	14	92	9	4	96	6	173	41	20	28	17	23	58
830	58	3	215	9	4	122	14	143	73	38	19	13	8	143
860	992	46	436	15	41	88	29	264	17	51	32	33	41	54
890	447	27	308	70	63	186	9	276	57	92	65	25	56	75
920	966	81	505	38	125	74	26	677	233	112	36	58	184	79
950	177	157	258	76	177	147	16	480	298	94	66	63	109	55
980	697	265	281	44	173	168	32	195	86	50	42	13	6	51
1010	1	247	153	149	66	27	40	57	117	99	39	143	17	22
1040	45	231	146	90	560	177	37	114	56	49	5	122	92	9
1070	100	233	104	76	488	223	26	74	12	52	49	15	53	1
1100	193	138	89	46	406	92	37	35	22	69	47	41	21	4
1130	99	49	118	21	191	26	21	17	4	34	27	37	9	2
1160	2	63	22	28	73	4	23	6	3	15	5	7	9	5
1190	0	38	84	1	32	1	33	14	0	18	3	0	14	0
1220	66	14	22	6	14	3	7	8	1	21	14	3	11	3
1250	140	4	62	13	41	0	15	26	0	12	12	1	12	0
1280	118	3	46	1	0	5	114	9	0	50	3	4	14	1
1310	15	1	33	3	42	0	53	2	0	9	1	2	5	2
1340	62	0	11	0	45	2	29	2	0	21	1	2	40	0
1370	44	0	17	0	17	4	5	4		12	2	1	10	0
1400	24		44	0	17	0	0	1		13		3	25	0
1430	148		64	0	11		7	0		0		0	17	0
1460	20		148		2		4	0					18	
1490	15		53		29		24						0	
1520	20		108		9		4						4	
1550	6		45		0		0						2	
1580	0*		31		0								1	
1610			0										0	

* The last figure in each column indicates the total CDD for the year.

Table II. Light-trap catches of ECB at Harrow, Ontario from 1971-1984 related to DD₁₀ accumulations

Year	1st generation multivoltine			Univoltine		2nd & 3rd generation multivoltine		
	n	Range	Peak(s)	n	Range	n	Range	Peak(s)
1971	108	136-427	243	29	460-690	4970	740-1540	870, 931, 979
1972	144	168-447	275, 404	33	460-716	162	758-1316	989
1973	174	200-409	266	17	469-574	3571	698-1578	907
1974	56	184-417	293	9	485-614	699	744-1320	901, 1047
1975	9	254-400	—	8	458-639	2632	744-1524	1031
1976	119	200-448	252	9	461-649	1466	726-1380	893, 1069
1977	69	170-417	317	3	453-635	627	710-1530	1043, 1282
1978	88	169-444	280	10	451-654	2610	706-1404	854, 943
1979	92	161-426	282	8	451-613	1074	679-1233	958
1980	49	149-422	260	3	525-645	968	706-1414	894, 964, 1096
1981	66	110-453	305	17	615-702	533	730-1373	983, 1088
1982	45	151-372	232	27	443-704	632	739-1415	1031
1983	90	110-407	313	6	531-675	828	707-1570	934, 1041
1984	104	128-406	248	32	605-708	623	727-1313	845

had to be reached before the daylength fell below 15.5 (Beck and Apple 1961).

At Harrow, both the 1st and 2nd generations appear to be about 100 DD earlier than in Ohio (Clement *et al.* 1981). The trap location at Wooster was 40° 49' latitude, thus it would have a different seasonal pattern of daylengths than Harrow which is at 42° 5' latitude. The late-summer flight in Ohio between 1400 and 1700 CDD, was also analogous to the 3rd generation at Harrow.

The seasonal distribution of moth catches at Harrow was plotted against CDD for the 3 periods 1971-1975, 1976-1980 and 1981-1984. The graphs were all irregular and did not show a change such as the shift shown for the Geneva, NY population (Eckenrode *et al.* 1983). Those authors did not group catches into CDD intervals but took weekly totals and related those to the average CDD at the end of the same week. In the period 1967 to 1971 the peak of the 2nd generation was 22 August which averaged 1005 CDD. For the period 1977 to 1981 the peak appeared on 15 August, but that was not physiologically earlier, since the average heat accumulation was 1002 CDD. Thus comparisons between years are more meaningful on a CDD base.

When the Harrow data were averaged over the 14 years the resulting composite distribution graph was quite uniform (Fig. 1). There was no peak for the univoltine generation because of the small number of moths trapped and the yearly variation in relation to CDD. Similarly, the 3rd-generation peak at 1280 CDD is not well defined, although it can easily be identified in certain years from the data in Table I.

The laboratory data on the length of time taken for post-diapause larvae to pupate supported the conclusion that a small proportion of the ECB population at Harrow was univoltine. Most of 188 larvae pupated between 228 and 504 DD, with an average requirement of 350 DD. Seven, or 4%, of the larvae required between 570 and 672 DD to pupate. McLeod (1976) reported that a univoltine strain took 12 more days, or 240 CDD, to pupate than the Harrow multivoltine strain, when held at 30°C. This difference is comparable to the 257 DD difference between early and late pupations in my experiment.

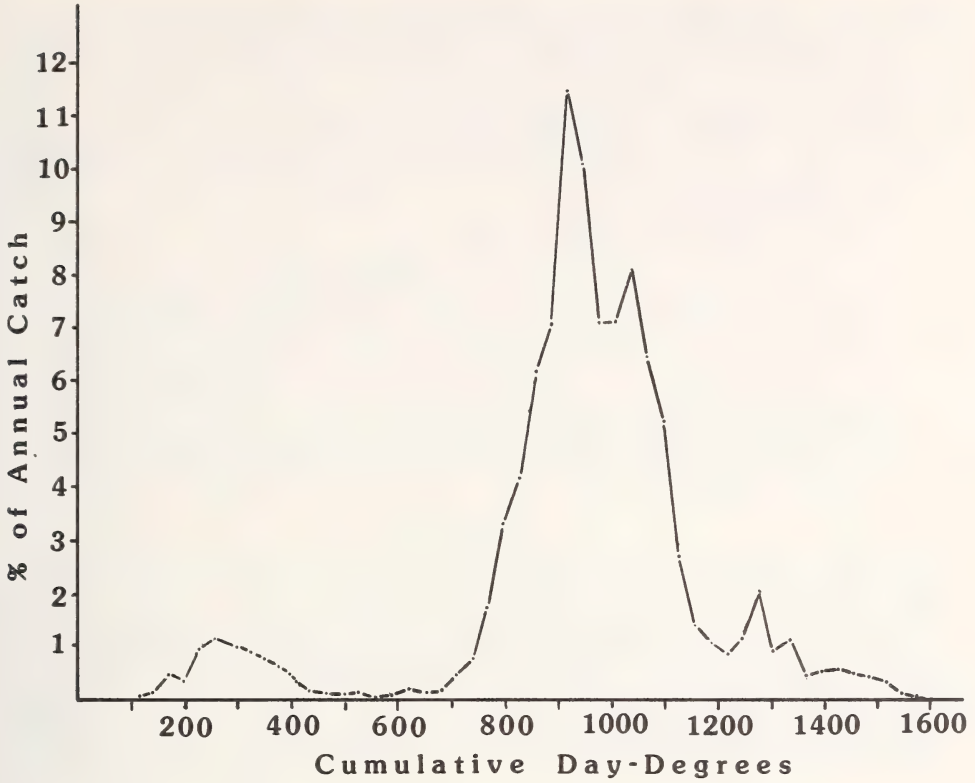


FIG. 1. Flight activity of European corn borer at Harrow, Ontario related to temperature accumulation, base 10° C. Average for 1971 to 1984.

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EFFECT OF BANDING AND INCORPORATION ON THE EFFICACY OF GRANULAR INSECTICIDES FOR CONTROL OF CORN ROOTWORMS (COLEOPTERA: CHRYSOMELIDAE) IN GRAIN CORN

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Abstract

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Several methods of insecticide application for control of corn rootworms were used either with granular applicators attached to commercial corn planters or with a cone seeder pushed by hand along the rows after corn was planted. The tests with commercial equipment compared no spreaders and 15-cm spreaders each with and without drag chains to incorporate the insecticide. Of 4 such tests, efficacy in the treatment with 15-cm spreaders and drag chains was clearly superior in one test and, with respect to some measurements of efficacy, possibly better in two others. Results comparing treatments applied with a cone seeder with 0-, 15-, and 30-cm spreaders, each with and without drag chains, were variable and inconclusive. This was possibly because of soil compaction by the press wheels of the corn planter before the treatments were applied.

Introduction

Corn in North America is attacked by two species of rootworm: the northern corn rootworm, *Diabrotica barberi* Smith and Lawrence, and the western corn rootworm, *Diabrotica virgifera virgifera* LeConte. Recommendations for rootworm control throughout North America generally call for applying granular insecticides at planting time in 15-cm bands and incorporating them into the soil (Anon. 1984). Application in 15-cm bands is practised by 91.8% of Ontario growers while incorporation is practised by only 23.5% (Ellis 1982). The objective of the research reported here was to determine whether these factors influence pesticide efficacy and thus account for some of the reports of poor, on-farm, rootworm control.

Materials and Methods

All experiments were done in southwestern Ontario from 1981 to 1983 in commercial fields of grain corn, each of which had a history of infestation by corn rootworms. All fields were clay loams which were planted at regular planting time in May with commercial corn hybrids not known to be either resistant or susceptible to rootworms. Two experimental methods were used. In one method, designated 'commercial', the insecticides were applied with commercial 6- or 12-row John Deere 7000 Max-Emerge® corn planters which had granular-applicator attachments. In the other, designated 'cone seeder', the corn was planted with similar equipment but no insecticide was applied while planting. Insecticide, in this method, was applied with a cone seeder which was pushed along the corn rows after the corn was planted.

In each case, commercial test plots consisted of 12 rows 200 m long, each subdivided into five 40-m plots. The appropriate insecticides were put in the hoppers of the granular applicators and, after calibration, were applied at recommended rates to rows (main blocks) of the experiments. Five application methods, arranged randomly along each row, were the treatments (subplots) in the split-plot design. Subplots included a control in which insecticide was collected in a bag and returned to the laboratory to confirm actual application rate to the row and to provide a treatment where no insecticide was applied. Insecticide was applied to the other 4 subplots either with or without a 15-cm spreader and with or without drag chains for incorporation. The 5 treatments were tested using 3 insecticides replicated 4 times in 3 trials designated GR81, GR82 and ST82, and using 4 insecticides each replicated 3 times in one trial designated BR81.

In experiments with the cone seeder, 20 treatment combinations, including two

checks without insecticide, were applied to 4-row plots which were 7 m long and arranged in a completely randomized block design. Three insecticides were used in each experiment: carbofuran, terbufos and either disulfoton or fonofos. Each of the 3 insecticides was applied in 3 band widths (without spreaders, with 15- and 30-cm spreaders) and each with and without drag chains for incorporation for a total of 18 treatments with insecticides. The insecticide treatments and 2 checks were replicated 4 times for a total of 80 plots in each trial. This experiment was done 5 times: OL81, MC82, MC83, GR83 and ST83. The MC82 trial had only 2 rows per treatment plot but was otherwise the same experimental design.

The efficacy of the various insecticides and methods of application were assessed by two or more of the following methods: 1, extracting and counting rootworms from soil samples; 2, rating the corn roots for feeding damage; 3, calculating percentage of corn stalks not standing vertically (goosenecking); and 4, estimating the yield.

Larvae were extracted from soil samples which were 15 cm wide by 45 cm long and 15 cm deep and which included the roots of 3 corn plants. One or 2 such samples were taken per plot for a total of 12 to 24 corn roots per treatment. Rootworms were extracted from these samples using the soil-washing apparatus and a flotation method described by Fisher (1981). However, the Calgon® water softener was not used as it did not help break up the soil, and the rootworms were counted directly from the material collected on the sieve. Both northern and western corn rootworms were present in the samples but were not sorted to species. After the soil was washed from the roots, all roots in trials MC82 and GR82 were rated to estimate damage by using a system described by Hills and Peters (1971).

The total number of corn plants and those goosenecked were counted in the fall and the percentage of goosenecked plants was calculated. Corn ears were harvested by hand from the entire 7 m of one of the inside rows of the plots treated with the cone seeder and from 9 m (1981) and 12 m (1982) of row of the plots treated with commercial equipment. Yield of grain at 15% moisture was estimated from the weight of the shelled corn and measurements of the moisture content of the kernels at weighing time. Unfortunately, it was not possible to obtain all measurements of efficacy in each trial. In some fields the soil became too hard to sample and in others the cooperators harvested before the yields could be obtained. Because each of the methods of measuring efficacy have been used in corn rootworm research all were assumed to be equal indicators of efficacy for the purpose of the analysis. To minimize type-I errors, multivariate analysis was executed with Statistical Analysis Systems (SAS) program MANOVA (Helwig and Council 1979). Trials in which MANOVA indicated a significant effect ($P < 0.05$) were further analyzed by comparing treatment means.

Results and Discussion

A comparison of insecticide treatments with the checks for the 5 fully randomized 'cone seeder' trials (Table I) showed little effect from the insecticide treatments on numbers of larvae in two trials, MC82 and MC83. The reason for the poor control at the MC site both years is not known, but the performance of carbofuran, disulfoton and terbufos was not significantly different at this location (Table II). As expected there were no differences in the 4 insecticide treatments at the MC site (Table I).

There was a significant effect in 2 of the remaining 3 trials. In the OL81 trial there was an effect due to banding ($P = 0.03$) which arose partly because of higher larval survival and more goosenecking in treatments with a 30-cm band (Table I). Although more rootworms are potential targets when wider bands are used, the rate per unit of soil surface is reduced. These data show that at presently registered rates, control is more effective if the material is concentrated in a 15-cm band; in fact, wider bands are not recommended for rootworm control. The band effect was not significant when the data were reanalyzed with MANOVA without the data on 30-cm bands.

In the GR83 trial, treatments were significantly different (MANOVA; $P = 0.0001$) and

Table I. Multivariate analysis of efficacy of 6 methods of insecticide application in 5 trials using a cone seeder to apply granular insecticides

Application	Trial														
	OL 81			MC 82			MC 83			GR 83			ST 83		
Band width	Drag chain	Larvae ¹	Goose-necked ² (%)	Yield (t/ha)	Larvae ¹	Goose-necked ² (%)	Root rating	Yield (t/ha)	Larvae ¹	Goose-necked ² (%)	Larvae ¹	Goose-necked ² (%)	Larvae ¹	Goose-necked ² (%)	Yield (t/ha)
0	No	10.6	5.6	4.558	43.9	1.0	2.1	5.080	9.2	2.9	16.6	1.5	0.2	5.706	
0	Yes	11.3	3.7	4.774	37.4	0	2.0	4.958	7.4	4.3	15.8	2.4	0.7	5.553	
15	No	11.3	5.4	5.180	35.0	0	2.3	4.576	9.9	4.7	18.4	0.9	0.4	5.507	
15	Yes	10.6	5.1	4.737	37.4	1.5	1.9	5.485	9.2	2.9	19.3	1.7	0.9	5.550	
30	No	15.8	7.1	5.003	29.3	0.7	2.2	5.255	9.2	0.8	20.2	2.7	1.0	5.604	
30	Yes	14.2	7.6	4.571	40.0	1.7	2.1	4.801	12.7	3.5	15.8	4.0	1.0	5.635	
Check (no insecticide)		27.1	36.1	4.647	29.3	2.4	2.2	4.639	14.2	3.9	31.5	3.8	2.8	5.517	
Manova³															
Treatment			P = .13				P = .12						P = .001*		P = .11
Band			P = .03*				P = .77						P = .15		P = .53
Chain			P = .47				P = .10						P = .47		P = .12

¹ Average numbers of larvae were transformed by $\sqrt{\text{larvae} + 1}$ to normalize data before analysis.

² The angular transformation of the percentage of goosenecked plants was used before analysis.

³ Analysis is only for treatments with insecticide. The probabilities for Hotelling-Lawley Trace, Pillai's Trace and Wilks' Criterion were usually the same and varied by a maximum of 0.02; the maximum probability of the three criteria is presented; * indicates $P < 0.05$.

Table II. Relative performance of corn rootworm insecticides at the various test locations in Ontario from 1981 to 1983

Trial		Measurement of efficacy ¹			
Location	Year	No. of rootworm larvae ²	Corn root ratings	Goose-necking	Corn yield
Commercial equipment					
BR	1981			t d f c	c t d f
GR	1981	t d c		t d c	t c d
GR	1982	c d	c d		t c d
ST	1982			t d c	t d c
Cone seeder					
OL	1981	t c d		c t d	c t d
MC	1982	c t d	c t d	c t d	c t d
MC	1983	t c d		c t d	
GR	1983	c t d		c t d	
ST	1983			f t c	f t c

¹ Insecticides are listed from left to right in decreasing performance. Those with the same line are not significantly different (ANOVA; $P \leq 0.05$). c = carbofuran (11 g AI/ha), d = disulfoton (11.3 g AI/ha), f = fonofos (10 g AI/ha), and t = terbufos (11.3 g AI/ha).

² Includes a few pupae and teneral adults recovered from the soil samples.

were also different after reanalyzing without the data on 30-cm bands. There were more larvae and goosenecking in the treatment with 15-cm bands with chains.

In the 4 trials with commercial equipment, insecticide treatments were always superior to the controls without insecticide for all measurements of efficacy except yield in the GR82 and the ST82 trials (Table III). The 4 application methods were significantly different (MANOVA; $P = 0.05$) in 3 trials. In the BR81 trial, the 15-cm spreaders with drag chains were superior to the other treatments with respect to both less lodging and higher yield. Interpretation of the significant effect in the GR81 and ST82 trials is more difficult. However, the 15-cm band with drag chains resulted in the fewest rootworms in the GR81 trial and the least goosenecking in the ST82 trial.

Efficacy of the insecticides themselves was not significantly different in 3 trials but was different in the remaining 6 trials (Table II). Terbufos and carbofuran were generally superior to disulfoton or fonofos when applied at recommended rates. These data showed that the insecticide used accounted for more variation in efficacy than the method of application. Trials with commercial equipment, which represented actual on-farm practices, showed that the treatment with 15-cm bands and incorporation was clearly superior, considering the various methods of measuring efficacy, to other treatments in one of 4 tests

Table III. Multivariate analysis of efficacy of 4 methods of insecticide application for 4 trials using commercial corn planters with granular applications

Application		Trial									
Band width (cm)	Drag chain	BR 81		GR 81			GR 82		ST 82		
		Goose-necked ¹	Yield (t/ha)	Larvae ²	Goose-necked ¹	Yield (t/ha)	Larvae ²	Root rating	Yield (t/ha)	Goose-necked ¹	Yield (t/ha)
0	No	22.5	6.878	17.5	4.2	7.087	9.9	1.7	5.956	1.2	8.860
0	Yes	23.4	6.632	16.6	4.3	7.763	16.6	1.6	6.433	1.4	8.682
15	No	24.9	6.176	20.2	4.6	7.802	15.8	1.5	5.366	1.4	8.478
15	Yes	15.4	7.579	12.7	5.8	7.261	15.8	1.7	5.996	0.7	8.770
Check (no insecticide)		42.0	—	31.5	55.4	6.395	17.5	2.1	5.773	7.2	8.598
Manova³											
Treatment		P = 0.04*		P = 0.0001*			P = 0.42		P = 0.007*		
Band		P = 0.86		P = 0.91			P = 0.36		P = 0.84		
Chain		P = 0.12		P = 0.31			P = 0.45		P = 0.92		

¹ The angular transformation of the percentage of goosenecked plants was used before analysis.

² Average number of larvae was transformed by $\sqrt{\text{larvae} + 1}$ to normalize data before analysis.

³ Analysis is only for treatments with insecticide. Probabilities for Hotelling-Lawley Trace, Pillai's Trace and Wilks' Criterion were usually the same and varied by a maximum of 0.05; the maximum probability of the three criteria is presented; * indicates $P < 0.05$.

and, although inconsistent, was possibly better in 2 others. Results using the cone seeder, where insecticide was applied after commercial planting equipment had already passed along the rows, were inconsistent and difficult to interpret. In this case treatments, especially drag chains, were expected to produce different results because of previous soil compaction from the press wheels of the planter. The application method affected efficacy in only 2 of 5 tests with the cone seeder. The significance in one of these tests was due to poor efficacy of 30-cm bands. Improved efficacy in some trials with commercial equipment gives some support to North American recommendations to use 15-cm bands and incorporate insecticides for control of corn rootworms.

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DISTRIBUTION OF CAVE-DWELLING SPHAEROCERIDAE (DIPTERA) OF EASTERN NORTH AMERICA

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Abstract

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Terrilimosina racovitzaei (Bezzi), a troglomorphic sphaerocerid previously known only from Europe, is recorded from caves in Ontario, New York, Pennsylvania, Illinois, Iowa, and Wisconsin. *Spelobia tenebrarum* (Aldrich), a troglomorphic species, is shown to be mostly distributed south of the limits of the Wisconsinan glacial maximum. Eight other cave-inhabiting Sphaeroceridae are briefly discussed.

Introduction

A commonly accepted ecological classification of cave organisms defines troglomorphs as species which are specialized for obligate life in caves. Species commonly occupying caves but not specialized for them and which may be occasionally found in similar microhabitats outside caves are termed troglomorphs. Vandel (1965) states that true troglomorphs are rare in the Diptera, and lists the European sphaerocerid *Speomyia absoloni* Bezzi as one of the few known troglomorphic Diptera (see also Matile 1970). Furthermore, according to Papp and Plachter (1976), even true troglomorphs are rare among the European Diptera. In their study of cave-dwelling Sphaeroceridae of Hungary and Germany, they list only *Limosina bequaerti* (Villeneuve) and *Limosina racovitzaei* Bezzi as true troglomorphs. The latter (now *Terrilimosina racovitzaei*) is also known from cellars (Roháček 1982), and is here recorded from North American caves.

Three North American sphaerocerid species have been described from cave-collected specimens. They are *Spelobia tenebrarum* (Aldrich), *Telomerina cana* Marshall and Roháček, and *Telomerina chillcotti* Marshall and Roháček. These species, and other Sphaeroceridae newly recorded from North American caves, are discussed below.

Materials and Methods

Diptera samples from about 100 North American caves were examined. Most of the cavernicolous sphaerocerids were collected by the second author (SBP). This material was supplemented with specimens from the Chicago Field Museum of Natural History (FMNH), United States National Museum (USNM), J.E. Gardner of the Missouri Department of Conservation Cave Inventory Project (MCI), and some material collected by the first author. Unless otherwise specified, all specimens are held in the University of Guelph collection.

Cave Sphaeroceridae and Their Distributions

Terrilimosina racovitzaei (Bezzi) (hypogean-troglomorphic)

This species, previously known only from Europe, is here recorded from the following localities.

Illinois. Henderson Co., Goose Hollow Cave, 13.xi.1965, SBP (1 ♂, 2 ♀). **Iowa.** Jackson Co., Maquoketa St. Pk., Barred Cave, 1-14.xi.1965, SBP (2 ♀). **New York.** Schoharie Co., Onesquethaw Cave, under rotting wood, 6.xi.1982, S.A. Marshall (2 ♂, 4 ♀). **Ontario.**

Mt. Nemo Cave, Burlington, 10.vi.1971, G. Muller (1 ♂). **Pennsylvania.** Berks Co., Wernersville, Hobo Cave, 3.xii.1937, Dierolf Coll. (1 ♂ , 1 ♀ , FMNH); York Co., Lisburn Cave, Dierolf Coll. (1 ♂ , FMNH). **Wisconsin.** Pierce Co., Crystal Cave, July KC379c, side pass, mud floor, K. Christiansen (1 ♀).

The genus *Terrilimosina* includes only 3 other species, all of which are found in hardwood forest litter. Of these 3 species (one Holarctic, one Nearctic, and one European) the one most closely related to *T. racovitzai* (*T. sudetica* Roháček is known only from Beech forest litter in Czechoslovakia. There are too few distributional records for either of these species to suggest their actual ranges, to speculate on their origins, or to explain the relatively few apparently isolated populations so far discovered in northeastern North America (Fig. 1).

Telomerina spp.

The entire genus *Telomerina* (7 species in North America) is characterized by apparently hypogean characters such as reduced eye size. It is thus not surprising that some species of this genus are known from caves. The cosmopolitan, necrophagous, synanthropic *T. flavipes* is very common in epigeal habitats and is not predominantly troglomorphic. It has been recorded from caves in Europe (Roháček) and was collected in Devil's Den Cave, Washington Co., Arkansas (SBP). *Telomerina cana* Marshall and Roháček is known only from caves in Alabama, Tennessee and Oklahoma (full data in Marshall and Roháček 1984). Since species of *Telomerina* are usually associated with cryptic habitats, such as soil interstices under dung pads, it is possible that *T. cana* exists in as-yet undiscovered epigeal populations, and is a facultative troglophile. This is likely to be the case for *T. chillcotti* Marshall and Roháček, also described from cave specimens. This species is known from caves in Tennessee and Texas, but is also represented by a few epigeal specimens from Ontario, New Brunswick, Tennessee and Alabama (Marshall and Roháček 1984). Its habits are not known.

Spelobia tenebrarum (Aldrich) (troglitic)

Spelobia tenebrarum is known only from caves, and is the most abundant of the Nearctic cave sphaerocerids. It was originally described from Wyandotte Cave, Indiana. Comparatively little has been published on its biology. The distribution map (Fig. 1) is based on the following material:

Alabama. Jackson Co., Crossing Cave, 1 mi N Paint Rock, 23-30.viii.1968, SBP (5 ♂ , 5 ♀); Nat. Cave, 1.5 mi SE Paint Rock, 9.vii.1967, rat dung Berlese #77, Peck & Fiske (1 ♂ , 1 ♀); Horseshoe Cave, 6 mi N. Princeton, 30.iv.1967, Peck & Fiske; Shiffman Cave, 27.i.1967 (12 ♂ + ♀), SBP. Madison Co., Byrd Spring Cave, 5 mi S. Huntsville, 5.vii.1967, Peck & Fiske. **Arkansas.** Washington Co., Devil's Den State Park, Devil's Den Cave, 28-31.v.1979, SBP (36 ♂ + ♀); Prairie Grove, Small Delap Cave, and Large Delap Cave, 24.vi.1938, K. Dearolf (FMNH). **Georgia.** Chatooga Co., Blowing Spring Cave, 2.5 mi NE Cloudland, 21.vi.1967, Peck & Fiske (1 ♀). Dade Co., 5 mi NE Rising Fawn, Johnson Crook Cave, 19.vi-3.vii.1967, trap #279, Peck & Fiske (2 ♂ , 6 ♀). Walker Co., Mt. Cove Cave, 1.5 mi E Lookout, 11-20.vi.1967, Peck & Fiske (23 ♂ + ♀); Pettijohn Cave, 5 mi SW LaFayette, trap #272, 10.vi.1967, SBP (2 ♀); Bible Spring Cave, 11.vi.1967, Peck & Fiske (1 ♂). **Illinois.** Calhoun Co., McNabb Hollow Cave, 3 mi W Hardin, 25.xi.1965, on racoon dung, SBP (5 ♂ , 2 ♀). Hardin Co., Cave Spring Cave, 24.x.1965, from *Eurycea lucifuga* (salamander) gut, SBP (7 ♂ , 1 ♀); Layoff Cave, 25.x.1965, SBP (4 ♀). Jackson Co., Cave #1, 24.iii.1966, SBP (2 ♀). Monroe Co., Stemmler's Cave, 28.xi.1968, SBP (2 ♂); Illinois Caverns, 25.vi.1965, SBP (2 ♂ , 1 ♀); Horsethief Cave, 3 mi NE Valmeyer, 16-18.viii.1968, SBP (8 ♂ + ♀); Camp Vanderverter Cave, 27.xi.1965, SBP (3 ♂ , 4 ♀). Pope Co., Frieze Cave, 23.iii.1965, SBP (1 ♂ , 2 ♀). Saline Co., Equality Cave, 23.x.1965, SBP (3 ♂ , 2 ♀). St. Clair Co., Falling Spring Cave, 13.v.1965, SBP (1 ♂ , 1 ♀). Union Co., Saratoga Cave, 4.5 mi ESE Cobden, 16.vi.1966, SBP (1 ♀); Cricket Cave, 3.5 mi SW Dongola, 15.vi.1966, SBP (2 ♂); Sensemeyer Cave, 3.5 mi W Dongola, 15.vi.1966, SBP (2 ♂). **Indiana.** Clark

Co., Springs Cave, 18.vii.1960, H.S. Dybas (30 ♂ + ♀, FMNH); Wyandotte Cave, G. Hubbard (type series of *S. tenebrarum*, USNM, 4 ♂, 3 ♀). **Kentucky.** Carter Co., Carter Caves, Laurel Cave, upper level, 30.viii.1930, H. Morrison (5 ♂, 6 ♀, USNM); Bat Cave, Bat Guano, 3.xi.1979, D.B. Conn (1 ♂, 1 ♀). Edmonson Co., Floyd Collins Crystal Cave, 31.xii.1956, on dung (USNM, 5 ♂, 1 ♀). Hart Co., Mammoth Cave (type series of the synonym *Limosina stygia* Coquillett, USNM). Todd Co., Glover's Cave, 18.vi.1964, SBP (3 ♀). Warren Co., Thomas Cave, 2 mi NE Hadley, 1.i.1957, racoon dung (1 ♂, 1 ♀, USNM); Little Beauty Cave, T.L. Poulson, reared ex. rat dung. **Missouri.** Barry Co., Moonshine Hole Cave, 13.5 mi W Cassville, on floor, on dung, 21.iii.1979, MCI (2 ♂). Carter Co., Mitchell Hollow Cave, 6.5 mi N Freemont, on ceiling, 29.i.1979, MCI (1 ♀). Franklin Co., Mine Cave, 4 mi ENE Sullivan, near entrance in leaf litter, 15.i.1980, MCI (1 ♂); Indian Cave #2, 4.5 mi ENE Sullivan, on floor near rotting wood, 15.i.1980, MCI (1 ♂, 2 ♀); Lone Hill Onyx, 4 mi ENE Sullivan, on dead frog, 9.i.1980, MCI (3 ♂, 1 ♀). Howell Co., Jim Ridge Cave, 14 mi NW West Plains, in leaf litter near entrance, 10.vii.1979, MCI (1 ♀). Jefferson Co., Rices Cave, 3 mi NE Goldman, 20.x.1938, L. Hubricht (5 ♂, 2 ♀, USNM). Laclede Co., Mary Lawson Cave, 22.iv.1955, P.J. Spangler (1 ♀, USNM). Oregon Co., Corbet Cave, 10 mi S Winona, on moist soil beneath dry wood, 24.x.1979, MCI (2 ♀); Willow Tree Cave, 11 mi N Alton, beneath dry wood with eastern wood rat droppings, 6.ix.1979, MCI (2 ♀); White Creek Cave, on fungus in total darkness, 8.ix.1978, MCI (1 ♂). Perry Co., Berome Moore Cave, 14.v.1966, SBP (1 ♂, 1 ♀). St. Genevieve Co., Gegg Cave, 15.vi.1965, SBP (2 ♂, 4 ♀). St. Louis Co., Moss Pit Cave, 4.2 mi N Eureka, 18.vii.1979, MCI (1 ♀). Stone Co., Marval Cave, 27.vi.1938, K. Dierolf Coll. (FMNH). Taney Co., Tumbling Creek Cave, B. Martin (35 ♂ + ♀). **New York.** Sullivan Co., Westbrookville, Surprise Cave, bathroom, 11.ix.1966, SBP (6 ♂, 1 ♀). **Pennsylvania.** Mifflin Co., Aitkin Cave, 4.iv.1947, K. Dierolf (FMNH). **Tennessee.** DeKalb Co., 1.5 mi E Powelltown, Avant's Cave, 23.xii.1956, on dung of cave rat, T.C. Barr (2 ♀, USNM). Dickson Co., Cooks Cave, 0.25 mi N Ruskin, 28.ii.1957, T.C. Barr (1 ♂, 3 ♀, USNM). Van Buren Co., Big Bone Cave, rotting wood, 20.x.1956, T.C. Barr (2 ♀, USNM). **West Virginia.** Greenbrier Co., Organ Cave, 24.ii.1961, L.G. Conrad (1 ♀, USNM).

Like the other cave flies considered here, the eyes of *S. tenebrarum* are greatly reduced and the antennal arista elongated by comparison with other Sphaeroceridae. Although the wings are fully developed, the wing muscles appear to have atrophied and, as Blatchley (1896) observed, these flies leap rather than fly when disturbed. There are no records of *S. tenebrarum* occurring outside of caves, and it is considered here to be a troglobite. This opinion is supported by the coincidence of the northern limit of this species' range with the southern limit of the Wisconsinan glaciation (Fig. 1), which suggests that the distribution of this species has not extended much northward since the Wisconsinan.

According to Banta (1907), *S. tenebrarum* is a polysaprophagous species. This suggestion is supported by the collection data presented above. Barr (1967a) noted that it is most common on racoon feces, but is also found on any sort of decaying organic material in caves. Packard (1888) recorded it (as *Borborus*) from dung and fungi in Kentucky caves. Polysaprophagy and atrophied flight muscles are general attributes of cave-associated sphaerocerids (Papp and Plachter 1976). Eye reduction and appendage elongation are frequent features of sphaerocerids found in caves but also in other dark environments such as forest litter. Unlike the other cave flies considered here, *S. tenebrarum* is both widespread and abundant. Banta (1907) recorded 75-100 per square foot in large areas of Mayfield's Cave, Indiana.

Facultative Cave Sphaeroceridae of Eastern North America

Spelobia semioculata, the sister species to *Spelobia tenebrarum*, is frequently collected in caves but is more frequently found in mammal burrows (Marshall 1985). Cave records for *S. semioculata* are included on Fig. 1.

Other sphaerocerid species are commonly found in caves, but are known to be

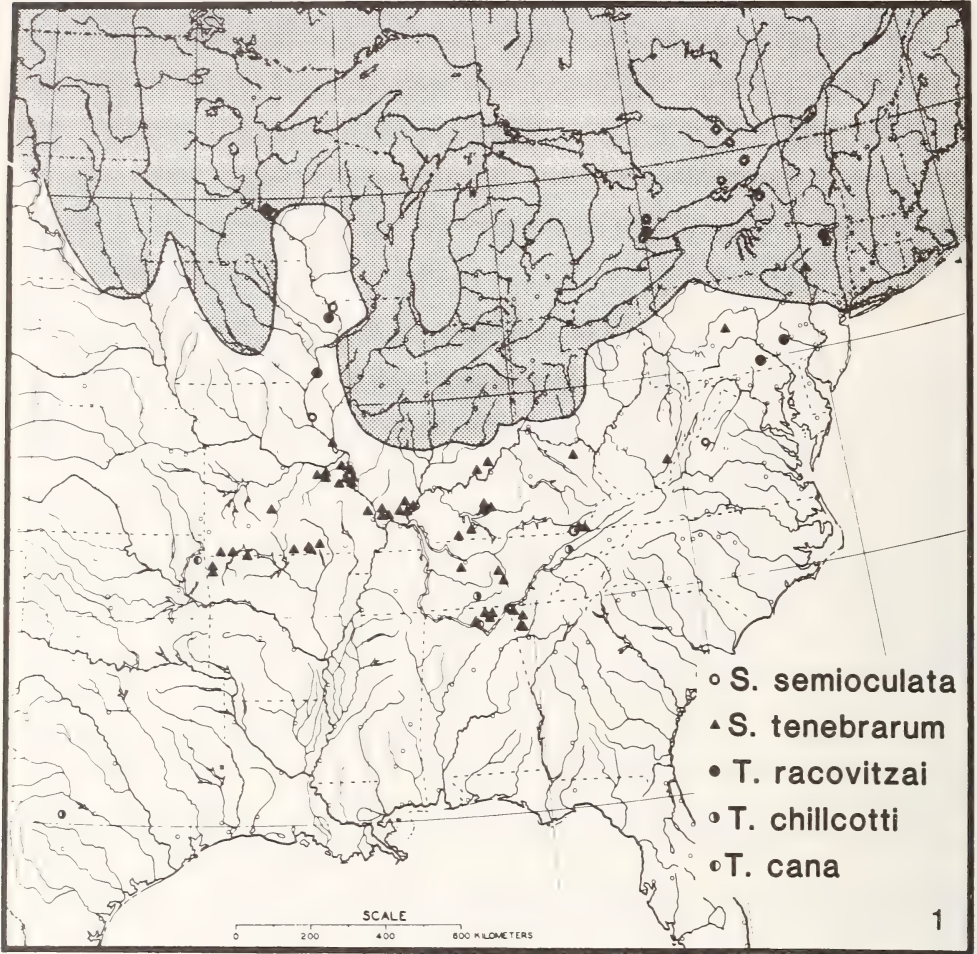


FIG. 1. Collection records of *Spelobia tenebrarum*, *Terrimosina racovitzai* and *Telomerina cana* (known only from caves) and cave records of *Spelobia semioculata* and *Telomerina chillcotti*. Small open circles are major cities. Shaded area represents approximate southern limits of Wisconsin glacial ice sheet.

predominantly associated with other habitats. *Apteromyia claviventris* Vimmer is frequently associated with caves in Europe and has been collected by the first author in New York caves. It is a common but rarely collected fungivorous species. *Opalimosina sordipes* Adams, a common Nearctic species, is associated with large deposits of primarily vegetative, decaying, organic matter and has been found in caves in New York, Texas and Iowa. *Spelobia clunipes* is a ubiquitous Holarctic, polysaprophagous species which turns up in just about every habitat investigated, and is often found in caves.

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SPHAEROCERIDAE (DIPTERA) ASSOCIATED WITH DECAYING FUNGI IN ONTARIO

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Abstract

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The insects attracted to decaying fungi were sampled using mushroom-baited pitfall traps set in the University of Guelph Arboretum during the summers of 1983 and 1984. Over 20 species of Sphaeroceridae were collected, including at least 4 species not normally found on other substrates. The biology of each species is discussed, and a key to the common species is provided.

Introduction

Macrofungi, especially senescent or damaged fruiting bodies of Basidiomycetes, almost always have an associated Diptera fauna. Preliminary sampling of the Diptera occurring on mushrooms, using a vacuum sampling device (Marshall 1982), yielded a number of species of Sphaeroceridae. Although sphaerocerids were the most abundant flies on wild mushrooms, almost nothing was known about North American fungivorous Sphaeroceridae at the inception of this study. The most common species were new to science or not yet recorded from North America, and have since been described in taxonomic papers by the senior author.

Mushrooms are a 45-million-dollar industry in Ontario (Blum 1977), so the insects associated with them are of interest beyond the fact that they form a discrete, interesting community. The impact of Sphaeroceridae on the commercial industry is primarily indirect as they are the major means by which nematodes are introduced into mushroom houses (Haglund and Milne 1973). The species most important in this role are compost-feeding species, such as *Pullimosina heteroneura* (Haliday), rather than the fungivorous species central to the current study. It is possible that specialized fungivorous species such as *Spelobia quinata* Marshall accelerate decay and cause premature senescence, however the impact of Sphaeroceridae as direct mushroom pests is probably minimal.

This paper is a first description of the sphaerocerid fauna associated with mushrooms in North America.

Materials and Methods

Mushroom-baited pitfall traps were used continuously in a Beech-Maple woodlot in the University of Guelph Arboretum from May until September of 1983 and May until October of 1984. During 1984, traps were run concurrently in a Hemlock grove and an old field. The pitfall traps consisted of 9-cm-wide x 11-cm-deep, white plastic tubs sunk into the soil. Mushroom stems (*Agaricus brunnescens*) wrapped in cheesecloth were suspended over the traps as bait. Salt, water and soap formed the trap fluid, and traps were emptied weekly. Similar traps were used elsewhere in Ontario and the eastern United States as opportunity permitted. All flies were critical-point dried and mounted, in preparation for taxonomic study.

Results and Discussion

The data from the University of Guelph sampling program are reported in Table I. Each vertical column represents the pooled data from all pitfall traps during that month. Each species of sphaerocerid is discussed below.

***Spelobia quinata* Marshall:** This is the dominant fungivorous sphaerocerid in the Eastern Deciduous Forest Region (*sensu* Gleason and Cronquist 1964). Full distributional data is given in Marshall (1985a). Mushroom-baited pitfall traps set in Georgia, Indiana, Illinois, New York and Massachusetts yielded large numbers, sometimes several hundreds, of this

Table I. Numbers of Sphaeroceridae collected in mushroom-baited pit traps in the University of Guelph Arboretum

	MAY		JUNE		JULY		AUG		SEPT		OCT	
	1983	1984	1983	1984	1983	1984	1983	1984	1983	1984	1983	1984
<i>Spelobia quinata</i>	18	44	45	8	13	19	16	29	0	9	/	0
<i>Spelobia clunipes</i>	2	11	11	6	11	0	0	5	0	1	/	5
<i>Spelobia luteilabris</i>	0	0	0	0	20	0	22	4	7	1	/	1
<i>Spelobia brevipteryx</i>	16	10	31	4	8	0	35	3	0	0	/	0
<i>Spelobia semioculata</i>	1	0	5	0	7	0	7	3	0	0	/	0
<i>Spelobia maculipennis</i>	0	0	0	0	1	0	0	0	0	0	/	0
<i>Spelobia frustrilabris</i>	0	0	0	0	5	0	0	0	0	0	/	0
<i>Spelobia nudiprocta</i>	0	0	1	0	0	0	1	0	0	0	/	10
<i>Spelobia ochripes</i>	0	6	0	0	0	0	0	0	0	0	1	0
<i>Minilimosina parva</i>	2	0	8	1	4	5	0	10	0	1	/	1
<i>Minilimosina fungicola</i>	0	0	0	0	0	1	0	1	0	0	/	1
<i>Apteryomyia claviventris</i>	0	0	24	1	12	1	10	6	0	4	/	0
<i>Pullimosina pullula</i>	2	1	13	0	8	0	11	0	0	0	/	0
<i>Pullimosina longicosta</i>	1	0	1	0	0	0	0	0	0	0	/	0
<i>Elachisoma atterima</i>	0	0	0	0	0	0	0	0	0	0	/	6
<i>Telomerina flavipes</i>	1	0	8	0	1	0	2	1	0	0	/	0
<i>Telomerina pengellyi</i>	0	0	0	0	0	0	0	1	0	0	/	0
<i>Trachyopella lineafrons</i>	0	0	0	0	0	1	1	3	0	0	/	0
<i>Xenilimosina sicula</i>	0	0	0	0	0	0	0	0	0	0	/	1
<i>Opalimosina sordipes</i>	0	0	0	0	0	0	0	2	0	0	/	0
<i>Opalimosina liliputana</i>	0	0	2	0	7	0	4	0	0	0	/	0
<i>Opalimosina mirabilis</i>	0	1	1	1	1	1	0	2	0	0	/	0
<i>Coproica</i> spp.	0	1	3	4	8	0	25	1	0	4	/	8
<i>Leptocera</i> sp.	0	0	0	0	0	1	0	4	0	0	/	0

species. It has also been collected on fresh mushrooms, especially soft *Pleurotus*-like species. *Spelobia quinata* belongs to the *S. occidentalis* group, which includes the major fungivorous sphaerocerids throughout North and Central America, and also includes the major Palaearctic fungivorous species *S. parapusio* (Dahl). *Spelobia quinata* appears to be strictly fungivorous, and adults are not attracted to other substrates.

***Spelobia clunipes* (Meigen) and *S. luteilabris* (Rondani):** These are common, synanthropic, polysaprophagous species probably introduced from Europe and found almost everywhere.

***Spelobia brevipteryx* Marshall:** Named for its wing polymorphism and tendency towards brachyptery, *S. brevipteryx* is an apparently fungivorous species with a more northerly distribution than *S. quinata*. Full distributional data are given in Marshall (1985a). The sympatry of these two species at Guelph, where both were collected most commonly in the deciduous woodlot, is unusual. Most other records of *S. brevipteryx* are from mushroom-baited traps in wet, cedar-dominated areas where *S. quinata* is absent. *Spelobia brevipteryx* and the closely related western species *S. rimata* Marshall form an isolated species group and are only distantly related to *S. quinata*.

***Spelobia semioculata* (Richards):** This species is most commonly associated with mammal burrows, and its occurrence in mushroom traps is probably spurious.

***Spelobia maculipennis* (Spuler), *Spelobia frustrilabris* Marshall, and *Spelobia nudiprocta* Marshall:** These are probably all coprophagous species, occasionally attracted to fungi as adults.

***Spelobia ochripes* (Meigen):** This Holarctic species is common in open areas, and is occasionally taken in mushroom traps set in meadows or fields. It is probably not fungivorous.

***Minilimosina parva* (Malloch):** This small species, about half the size of *S. quinata*, is most commonly collected on decaying fungi, and tends to outnumber *S. quinata* on older, well rotted mushrooms. Numbers of specimens taken in the Guelph traps were relatively low, but other collection data show that *M. parva* is common throughout North America. Complete distributional data are given in Marshall (1985b).

***Minilimosina fungicola* (Haliday):** In spite of the specific name, this species is rarely found on mushrooms.

***Apteromyia claviventris* (Strobl):** This Holarctic species has been reared from mushrooms (Hackman and Meinander 1979) and is most commonly collected from decaying mushrooms. It was first recorded in the Nearctic by Marshall and Roháček (1982) from specimens taken from an unidentified mushroom in the University of Guelph Arboretum and from coral fungi in the Royal Botanical Gardens, Hamilton. *Apteromyia claviventris* has since proven to be a common species associated with mushrooms in damp, well shaded habitats in eastern Canada. The only United States record of *A. claviventris* is from a cave in New York (Marshall, unpublished). Roháček (1983) records this species from a number of substrates in Europe and considers it polysaprophagous.

***Pullimosina pullula* (Zetterstedt):** Although not previously known from the Nearctic region, this species is common in Europe and has been reared from decaying vegetation (Okely 1974). Most of the North American records are from fungi, but no North American specimens have been reared. *Pullimosina pullula* is primarily parthenogenic (Okely 1974), and known only from females in North America. Like *Spelobia brevipteryx*, *P. pullula* exhibits wing polymorphism, with the brachypterous form most common. It is distributed across Canada and the northern United States.

***Pullimosina longicosta* (Spuler), *Elachisoma atterima* (Haliday), and *Trachypella lineafrons* (Spuler):** These species are common in decaying vegetation and only occasionally associated with mushrooms.

***Telomerina flavipes* (Meigen):** This common, cosmopolitan species has previously been reared from mushrooms (Papp 1973) and has been collected from *Pleurotus* and other mushrooms in eastern North America. It is also frequently collected on dung and carrion and has been reared from house fly medium, so is considered a polysaprophagous species (Marshall and Roháček 1984).

***Telomerina pengellyi* Marshall:** This species was also found on a decayed *Coprinus* species near one of the mushroom-baited pit traps and has been collected on fungi in Manitoba and elsewhere in Ontario. Most known specimens of *T. pengellyi* were collected on dung.

***Xenolimosina sicula* Marshall:** Although this species was taken only once in the Guelph mushroom traps, it is a rare species so the record is considered significant. Species of this genus are known only from late fall and early spring and the larval habitat is unknown. The closely related European *X. setaria* is thought to be fungivorous (Roháček 1983).

***Opalimosina sordipes* (Adams) and *Opalimosina mirabilis* (Collin):** These are polysaprophagous or phytosaprophagous species occasionally found on mushrooms, but more commonly found on other substrates.

***Opalimosina liliputana* (Rondani):** This Holarctic species is most often associated with fungi, but is polysaprophagous and occasionally found on dung, carrion and decaying vegetation.

***Coproica* spp.:** North American species of this genus cannot be identified reliably at this time, but at least 2 species are commonly collected on decaying fungi.

***Leptocera* (*Leptocera*) new species near *caenosa* (Rondani):** This undescribed species was found occasionally on mushrooms in Guelph. Nothing is known of its distribution or biology. The very closely related *L. caenosa* is polysaprophagous.

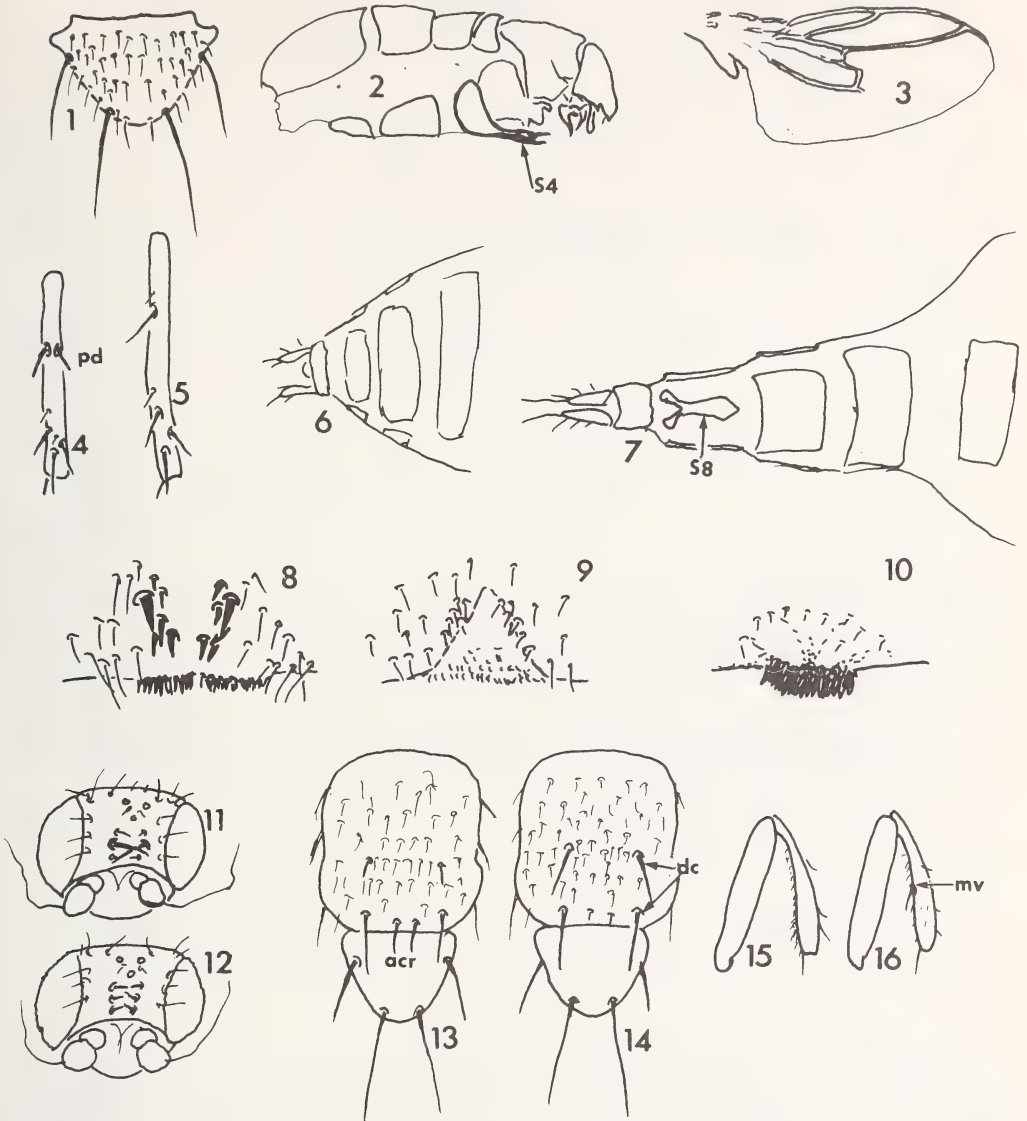
Summary

Damaged or decaying mushrooms attract a wide variety of polysaprophagous species, however the species most often associated with mushrooms appear to be restricted to that habitat. Some, like the common *Spelobia quinata*, are often found on fresh mushrooms and are probably associated with the early stages of decay. Others, like *Minilimosina parva*, are associated with decayed mushrooms. The term fungivorous is used to refer to any sphaerocerid more often found on fungi than other substrates even though, like all Sphaeroceridae, these mushroom-associated species probably feed as larvae by filter-feeding in a microbe-rich substrate. Other than the seasonal mushroom association data presented here, little is known about fungivorous Sphaeroceridae. Oviposition has not been observed, nor have eggs been recovered. Ovipositor structure varies widely between fungivorous species, ranging from the long, telescoping ovipositor of *Minilimosina* species to the broad, short ovipositor of *Spelobia* species. Hopefully, now that the species composition of the fungivorous sphaerocerid community has been ascertained, future investigators will examine such questions as oviposition site, larval behaviour, and the effect of these insects on different mushroom species.

KEY TO THE SPHAEROCERIDAE COMMONLY FOUND ON FUNGI
IN EASTERN NORTH AMERICA

This key is a guide to the most common species only. Other species are keyed and illustrated in taxonomic revisions of the genera as cited above. A key to the genera of Sphaeroceridae in North America is found in Marshall (1985c).

- 1 Disc of scutellum setulose (Fig. 1) *Coproica* spp.
- Disc of scutellum bare, with only marginal bristles (Fig. 13) 2
- 2 Sternite 4 of male projecting posteriorly and ventrally over sternite 5 (Fig. 2). Tergite 8 of female heavily sclerotized, with a shiny posteromedial lobe *Apteryomyia claviventris*
- Sternite 4 of male simple. Tergite 8 of female lightly sclerotized, never with a posterior lobe 3
- 3 Vein R_{4+5} ending well before wing tip, costa ending near wing tip well beyond tip of R_{4+5} (Fig. 3). Known only from females, which have a blunt abdomen *Pullimosina pullula*
- Vein R_{4+5} ending near wing tip. If female with blunt abdomen, then costa ending at tip of vein R_{4+5} 4
- 4 Costa ending at tip of vein R_{4+5} . Mid tibia with a midventral bristle (Fig. 16). Female terminalia blunt, not forming a telescoping ovipositor *Spelobia* 5
- Costa extending beyond tip of vein R_{4+5} . Mid tibia with a row of spines or only minute setulae in midventral region (Fig. 15). Female terminalia telescoping, forming a retractile ovipositor, sternite 8 Y-shaped (Fig. 7) *Minilimosina parva*
- 5 Middle interfrontal bristles strongly cruciate (Fig. 11). Tarsi yellow. Male sternite 5 with a V-shaped pattern of large spines (Fig. 8) *Spelobia quinata*
- Interfrontal bristles equal (Fig. 12). Tarsi brown. Male sternite 5 with a posteromedial cleft or comb but no large spines 6
- 6 Mid tibia with a posterodorsal bristle on proximal third. Sternite 5 of male with a posteromedial cleft (Fig. 9) *Spelobia brevipteryx*
- Mid tibia with only an anterodorsal bristle on proximal third (Fig. 5) Sternite 5 of male with a posteromedial comb (Fig. 10) 7
- 7 Scutum with two pairs of equally long dorsocentral bristles and short prescutellar acrostichal bristles (Fig. 14) *Spelobia luteilabris*
- Scutum with anterior dorsocentral bristles shorter than both posterior dorsocentral bristles and the long prescutellar acrostichal bristles (Fig. 13) ... *Spelobia chunipes*



FIGS. 1-16. 1, setulose scutellum of *Coproica*; 2, abdomen of *Apteromyia claviventris*, male, lateral; 3, wing of *Pullimosina pullula*; 4, mid tibia of *Spelobia quinata*, dorsal; 5, mid tibia of *Spelobia clunipes*, dorsal; 6, general shape of *Spelobia* female terminalia; 7, telescoping terminalia of *Minilimosina parva*; 8, sternite 5 of male *Spelobia quinata*, detail; 9, sternite 5 of male *Spelobia brevipteryx*, detail; 10, sternite 5 of male *Spelobia clunipes*, detail; 11, head with cruciate interfrontal bristles; 12, head with non-cruciate interfrontal bristles; 13, scutum and scutellum of *Spelobia clunipes*; 14, scutum and scutellum of *Spelobia luteilabris*; 15, mid femur and tibia of *Minilimosina*, anterior; 16, mid femur and tibia of *Spelobia*, anterior.

Abbreviations: pd - posterodorsal bristle; S4 - sternite 4; S8 - sternite 8; acr - prescutellar acrostichal bristles; dc - dorsocentral bristles; mv - mid ventral bristle.

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HAZARDS OF CARBARYL FORMULATIONS TO CAGED HONEYBEES (*APIS MELLIFERA*) FORAGING ON FLOWERING CANOLA (*BRASSICA NAPUS*) IN ONTARIO

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Abstract

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Two formulations of carbaryl, Sevin® 80S and Sevin® XLR were applied to blooming canola (*Brassica napus* L. Brassicaceae) in screen tents into which honey bee (*Apis mellifera* L. Hymenoptera: Apidae) colonies were introduced. Both formulations had deleterious effects on the bee populations; although Sevin XLR caused less mortality than did Sevin 80S, both caused significantly more deaths than were found in the untreated controls. Both Sevin XLR and Sevin 80S entered the hives in pollen loads collected by the foraging bees. The levels of insecticides recovered from the pollen loads were not significantly different between insecticide treatments and were sufficient to cause long-term toxic effects in the hive. Very small amounts of residues of carbaryl were found in nectar collected by the bees. We conclude that Sevin XLR is less hazardous to bees foraging in the field than is Sevin 80S, presumably because the former formulation has a "sticker" which prevents the bees from becoming dusted with the insecticide. However, both formulations are dangerous to bees and should not be applied to blooming crops. The insecticide can enter the hive with pollen collected by foragers, especially from flowers with exposed anthers and long availability of pollen, vis a vis alfalfa and corn with which comparisons are made.

Introduction

Carbaryl (1-Naphthyl Methylcarbamate) is one of the most toxic insecticides to honeybees (*Apis mellifera* L.) (Morse 1961; E.L. Atkins unpublished manuscript; National Research Council of Canada 1981) and is one of the major causes of bee poisoning throughout North America. In 1981, P. Burke, Ontario Provincial Apiarist, reported that 75% of insecticide poisonings of bees involved carbaryl (Burke personal communication). In 1979, carbaryl was removed from the list of recommended insecticides for application on alfalfa in Ontario because of the risk of bee poisoning. For application on corn against armyworm and European corn borer, carbaryl applications are suggested with explicit warnings regarding hazards to bees. Incidents of severe bee poisoning involving carbaryl in Quebec in 1981 resulted in court injunctions against aerial application of this insecticide (C. Ritchot personal communication). The hazards which carbaryl poses to honeybees depend on many factors, including the formulation, time of application, mode of application, and the visitation rate of bees to the treated crop. This paper reports on a comparative test conducted in 1982 on the hazards of a new formulation of carbaryl, Sevin® XLR,

versus Sevin® 80S, both manufactured by Union Carbide Agricultural Products Co., Inc.

Sevin® XLR is of smaller particle size (3-5 microns) than the most commonly used preparations of carbaryl (e.g. Sevin® 80S with particles of 8-10 microns) and contains a "sticker" which provides wash-off resistance. For this to be effective the spray must dry, which may take more than 1 hour depending on atmospheric humidity (Union Carbide 1981, 1982). The "sticker" in this formulation not only provides wash-off resistance, but is suggested to make the insecticide less available, when dried, to honeybees than the more easily removed powdery formulations. Dried Sevin XLR is less effective than other formulations as a contact insecticide, but is just as effective as an ingested one. It is just as toxic to honeybees as other formulations of Sevin, but because the bees do not eat leaves and cannot become dusted with the dried material, it is probably less hazardous (E.L. Atkins unpublished manuscript; R.D. Nelson unpublished manuscript; Hanny and Harvey 1982). However, Sevin XLR must dry to meet this expectation, and furthermore could enter the humid environment within flowers and contaminate nectar or stick onto the anthers or pollen. Thus, the material could be transported to the hive by foraging bees, thereby causing poisoning. The aim of this study was to elucidate the relative hazards of Sevin XLR and Sevin 80S in terms of bee deaths in experimental hives, and to determine whether the carbaryl from either or both formulations could enter hives through nectar and pollen collections by the bees foraging at flowers with exposed and easily contaminable anthers and nectar.

Material and Methods

Experiments were conducted near Arthur, Ontario. Three plots of blooming canola (*Brassica napus* L., Brassicaceae var. Tower) were chosen, treated, and then covered under screen tents (3 x 3 x 2.5 m high) into each of which a small hive of honeybees (1 standard Langstroth super with 5 frames of honeybees) was placed. The experiment was conducted twice for treatments of Sevin XLR, Sevin 80S, and the control. In the first trial, the colonies of bees were of similar, but not equal strength and constitution of brood, honey, and pollen stores. In the second trial, the hives were equalized prior to use. The carbaryl was applied from a back-pack sprayer at the rate of 1.5 kg AI/ha. (i.e. in the range of active ingredient recommended for control of armyworm (Ontario Ministry of Agriculture and Food 1985)). The ratio of water to Sevin XLR concentrate used was 5:1 (the maximum adherence of Sevin XLR occurs when water volume ratio is < 9:1 (Union Carbide 1982)). The same volume of water was used for the application of Sevin 80S. The experimental hives were placed in the sprayed plots after the Sevin deposits had dried, i.e. within 2 hours. Each hive was equipped with a Todd dead-bee trap (Atkins *et al.* 1970; Atkins 1975) and an OAC pollen trap (Smith 1963) for collecting dead bees and pollen respectively. Nectar, recently collected by the bees, was collected by shaking it out of uncapped cells onto chromatography paper (Whatman®). Samples of pollen and nectar were returned to the Ontario Provincial Pesticide Laboratory, University of Guelph, for residue analysis.

The experiment was done twice, the first beginning on 1 July 1982, and the second on 13 July 1982. For the duration of the experiments the weather remained generally sunny, warm, and dry. For each hive we monitored the following daily, for 10 days: numbers of dead bees collected in the Todd dead-bee trap (absolute count), numbers of bees in the hive (approximate count by 100's), and the estimated areas of capped honey, uncapped honey, pollen, eggs, young larvae, old larvae, and sealed brood. These were estimated visually as tenths (and as hundredths for items occupying small and discrete areas) of each side of each frame and summed (i.e. 5 frames = 100/10ths). The pollen was collected each day and uncapped nectar was collected at the end of each experiment.

Statistical analysis for the mortality of bees under various treatments and trials was according to the methods described in Zar (1974:296) for differences between proportions. A one-way analysis of variance, followed by t tests, was used to examine data on the differences between the amounts of carbaryl found as residues in pollen collected by bees in the experiments.

Results

In the control tents, the numbers of living bees in the hives increased (2,200-4,100 in trial 1) or remained fairly constant (2,400-2,600 in trial 2) over the duration of the experiment. The results from the 2 trials were not significantly different from each other ($z = 3.45$; $p > .05$). In the second trial, the amount of sealed brood declined, reflecting the emergence of the bees as adults (from 3.1% of the comb area to 0.67%), whereas in the first trial the amount of sealed brood fluctuated slightly, but with no apparent pattern (0.75 to 1.25%). The numbers of eggs laid in each control fluctuated slightly (0.38 to 1.08% in trial 1 and 0.21 to 1.12% in trial 2 of the total comb area). The numbers of dead bees collected from the control hives were low (averages: 5.6/day in trial 1 and 17.4/day in trial 2).

By contrast, in the Sevin 80S-treated plots the numbers of living bees dropped from 1,400 to 800 in trial 1 (43% decline) and from 2,500 to 1,800 in trial 2 (28% decline). These results are highly significantly different from those from the controls ($z = 69.4$ for trial 1 and $z = 43.0$ for trial 2; $p < 0.0001$) and significantly different between trials ($z = 16.8$; $0.002 < p < 0.005$). The amount of sealed brood declined from 2.22 to 0.6% in trial 1 and from 2.95 to 0.55% in trial 2. Despite the addition to the worker force by the emergence of the capped brood within the hives, numbers of workers declined; thus our figures for percent decline are an underestimate of mortality. Egg laying continued in both trials at about the same level as in the controls (0.37 to 0.88% in trial 1 and 0.20 to 0.70% in trial 2). The numbers of dead bees collected averaged 483.3 and 276.2 per day for trials 1 and 2, respectively.

Treatment of canola with Sevin XLR affected the hives to an intermediate degree. The number of living bees increased from 800 to 1400 in trial 1, due to the relatively large amount of sealed brood which was ready to emerge (2.25% of the total comb area, i.e. over 1,300 cells); this occurred within the first 2 days of the experiment when the population reached 1,100 bees. However, in the second experiment the number of bees declined from 4,300 to 2,200. These results are significantly different from those from the controls ($z = 15.5$ for trial 1 and $z = 24.17$ for trial 2; $0.002 < p < 0.005$ and $p \approx 0.002$, respectively), from those from the treatment with Sevin 80S ($z = 34.3$ for trial 1 and $z = 31.0$ for trial 2; $p < 0.001$), and between trials ($z = 10.2$; $0.005 < p < 0.01$). During the experiment the amount of sealed brood remained about the same (1.75 to 0.61%) Egg laying also fluctuated in a manner similar to that seen in the controls and in the Sevin 80S treatment (0.19 to 1.20% in trial 1 and 0.15 to 0.57% in trial 2). The number of dead bees collected averaged 78.6 and 82.9 per day for trials 1 and 2, respectively. Because all the hives were not of exactly even strength and composition our findings are summarized in terms of ratios, which provide a means of comparing the relative effects of the treatments (Table I).

Table I. The effects of carbaryl formulations on honeybees on flowering canola in screen tents near Arthur, Ontario. Ratios of live bees at the end of the experiment to live bees at the beginning (change in the number of bees), of the number of dead bees collected over the experimental period to the number of living bees at the beginning of the experiment (proportion of bees dying), and of the number of dead bees collected over the experimental period to the number of living bees at the end of the experiment

Treatment	No. live bees at end/ live bees at beginning		No. dead bees/ live bees at beginning		No. dead bees/ live bees at end	
	Trial 1	Trial 2	Trial 1	Trial 2	Trial 1	Trial 2
Control	1.90	1.06	0.02	0.01	0.01	0.01
Sevin 80S	0.59	0.71	2.24	0.99	4.88	1.40
Sevin XLR	1.32*	0.51	0.64*	0.22	0.46	0.37

* These values are based on the population after the relatively large emergence of capped brood (see text); these values are 1.82 and 0.83 if this effect is not taken into account.

Analyses of the pollen and nectar collected from the hives showed that carbaryl was entering the hive by these routes (Table II) and that Sevin 80S entered in greater amounts. The small amounts of carbaryl found in one sample of each of pollen and nectar from control hives are not understood. They may represent minor contamination picked up in the laboratory. Small amounts of carbaryl also were detected from samples of chromatography paper of the type used for collecting nectar. There were significant differences between formulations in the amounts of carbaryl in pollen ($F = 9.13$; $p = 0.002$). The amount of Sevin detected from both the Sevin XLR and Sevin 80S treatments was significantly different from that found in the controls ($t = 3.80$ and 4.15 for $p = 0.0035$ and 0.0013 , respectively) but the amount of Sevin found in samples of pollen from the Sevin XLR treatment was not significantly different from that found in the Sevin 80S treatment ($t = 1.32$; $p = 0.22$).

Table II. Carbaryl in pollen and nectar taken from honeybee hives on flowering canola in screen tents near Arthur, Ontario

	Carbaryl residues in pollen (ppm)			Carbaryl residues in nectar (ppm)		
	range	mean	N	range	mean	N
Control	ND — 7.1	1.79	7	ND — 0.005	—	3
Sevin 80S	7.1 — 94	47.4	7	0.003 — 0.07	0.047	3
Sevin XLR	7.4 — 53	27.9	5	0.003 — 0.06	0.037	3

Discussion

Our results indicate that Sevin XLR is less hazardous to caged bees foraging on canola than is Sevin 80S; but that bees in contact with Sevin XLR or Sevin 80S experienced significantly higher mortality rates when compared with untreated controls. By all criteria used, the controls showed the least effects, while Sevin 80S showed, significantly, the greatest deleterious effects on the colonies over the period of the experiment. Furthermore, carbaryl entered the hive with canola pollen (Table II). These amounts would suffice to cause a high mortality (see Moffett *et al.* 1970). Even in the Sevin XLR treatment, the mean amounts are above the LD50 level reported for honeybees (Georghiou and Atkins 1964).

Winterlin *et al.* (1973) reported that carbaryl residues in bee bread (i.e. mostly pollen) correlate well with the levels of residues found in bees. They also reported that the LC50 for carbaryl in sugar solution is between 3.8 and 4.5 ppm. Thus, we conclude that nectar from canola flowers sprayed with carbaryl is unlikely to be sufficiently contaminated to cause bee mortality (Table II). However, our nectar samples were collected from the hives at the end of the experiment, by which time the flowers which would have been exposed to carbaryl applications would have withered and been no longer attractive to bees. Thus dilution of the contaminated nectar by uncontaminated nectar from later flowers in the comb would have taken place. Canola flowers last about 3 days, suggesting that a maximum of about 2/3 of the nectar collected was uncontaminated. If this were the case, the concentrations of carbaryl in nectar from freshly treated flowers could be as much as 3 times higher than indicated in Table II, but would still not pose a serious hazard to honey bees.

Although Sevin XLR is less hazardous than Sevin 80S to foraging bees, as has been demonstrated in this study by E.L. Atkins (unpublished manuscript) on alfalfa, R.D.

Nelson (unpublished manuscript) on apples, and Hanny and Harvey (1982) on corn, it still must be regarded as dangerous, with the potential for causing considerable immediate mortality of contaminated bees. It can also enter hives in large quantities on contaminated pollen, and possibly nectar, thereby causing long-term, chronic poisoning of larval and adult bees within the hive. Attention has been drawn to these potential hazards of carbaryl for bees foraging on corn (Moeller 1971; E.L. Atkins unpublished manuscript; Hanny and Harvey 1982), alfalfa (Stanger and Winterlin 1975), apples and other fruit crops (Johansen and Brown 1972; R.D. Nelson unpublished manuscript) as well as in areas being treated with carbaryl for pest insects such as gypsy moth (Connola *et al.* 1966; Matthenius 1973; Martin 1974).

Hanny and Harvey (1982), in comparing the amounts of Sevin XLR and Sevin 80S which honey bees, foraging for corn pollen, were returning to their hives, showed that less carbaryl from Sevin XLR-treated corn than from Sevin 80 S-treated corn entered the hives. This difference can be explained through floral morphology and pollen production of corn. In corn tassels, new florets open each morning at about 09:00 hrs (Mason and Tracewski 1982); 3 anthers emerge from each floret and dehisce, releasing all their pollen at the same time. Thus, anthers with mature pollen are usually not exposed to carbaryl applications made early in the morning, or in the evening. In contrast to the dried and adhering deposits of Sevin XLR, the Sevin 80S dust is readily dislodged from leaves and florets onto the bodies of foraging bees throughout the day.

Atkins (unpublished manuscript) noted reduced honey bee kills in alfalfa fields treated with Sevin XLR as compared with those treated with Sevin 80S. Again, the difference can be explained, in large part, by floral structure. The nectar, anthers and pollen of alfalfa, with its enclosed flowers, are not exposed directly to insecticide deposits, unless the flowers have been tripped by pollinators so that the anthers are exposed; but by then much of the pollen has been removed.

In contrast to the flowers of corn and alfalfa, the open, upright flowers of canola (and apple (R.D. Nelson unpublished manuscript)) expose the anthers and nectar continually for a 3- to 4-day period. Contamination of canola pollen with direct applications of Sevin 80S and Sevin XLR would be greater than in either corn or alfalfa. During our study, white deposits of Sevin XLR and Sevin 80S were visible on the pollen of canola anthers. The Sevin XLR, in drying, often bound a number of pollen grains together into a conglomerate which could be teased from the anther with a needle. Foraging bees were observed to collect these Sevin XLR-pollen conglomerates from canola flowers. This situation, with open flowers, exposed anthers, and uninterrupted pollen availability to bees, probably accounts for the relatively high levels of carbaryl residues from Sevin XLR in bee-gathered canola pollen (Table II). Nelson's (unpublished manuscript) findings from a study of the mortality of bees foraging at apple flowers in orchards treated with Sevin XLR or Sevin 50WP showed that the former was significantly less hazardous than the latter. However, the mortality in hives in orchards treated with Sevin XLR was the same as that in hives in untreated areas (average 109 and 110 dead bees/day/hive for 5 days), and the latter may have been due to the control colonies having been exposed to pesticide poisoning elsewhere. The question of validity of the controls makes it difficult to interpret the effects of Sevin XLR, but Nelson's implication is that Sevin XLR did cause more mortality than would have been expected in unequivocal controls.

Canola is a major bee pasture plant for nectar and pollen in western Canada where 2-3 million ha are grown annually (Statistics Canada 1984). In Ontario, canola is becoming increasingly important; presently, 10,000 ha are grown (D.J. Hume personal communication; Statistics Canada 1984) and predictions indicate that this will rise ten-fold over the next few years. If control of pest insects is required on flowering canola, an insecticide which is less hazardous to honey bees than either Sevin 80S or Sevin XLR should be used.

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HABITAT DISTRIBUTION OF ADULT MOSQUITOES IN SOUTHERN ONTARIO

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Abstract

Proc. ent. Soc. Ont. 115: 55-59 (1984)

The abundance of females of 11 mosquito species was related to the placement of New Jersey and CDC light traps and a New Jersey suction trap in specific habitats. Females of *Culex pipiens* L., *Culex restuans* Theo., *Culiseta morsitans* (Theo.), *Aedes vexans* (Meigen) and univoltine *Aedes* spp. were collected in significantly larger numbers in a woodlot and a transition zone between a woods and a field. Females of *Anopheles walkeri* Theo. were collected in largest numbers in the field whereas those of *Mansonia perturbans* (Walker) were evenly distributed among all habitats.

Introduction

The estimation of mosquito populations can be influenced by a variety of factors including habitat. Host-seeking mosquitoes of particular species often occur more frequently in specific habitats (Bidlingmayer 1971; Trimble and Thorsteinson 1974; Howard *et al.* 1983). This study was designed to determine the best habitat for the collection of particular species of mosquitoes and to allow for comparisons between traps operated in different habitats. It was expected that this work would eliminate non-productive sampling and reduce the costs of mosquito monitoring in Ontario.

Materials and Methods

A portion of the University of Guelph Arboretum located at Guelph, Ontario (43° 30' N, 80° 20' W), was selected for this study. This area had 3 distinct habitat types, i.e. a deciduous forest (woods), an old field (field) and the transition zone between these habitats (interface) (Fig. 1).

The woodlot (ca. 20 ha) was a swampy area containing many snow-melt pools which served as breeding sites for spring *Aedes* spp. *Betula lutea* Michx. f. (yellow birch) and *Thuja occidentalis* L. (eastern white cedar) were the most common trees. A dense shrub layer of *Rhamnus frangula* L. (glossy buckthorn), *Rhamnus cathartica* L. (European buckthorn), *Ulmus americana* L. (American elm) and *Salix* spp. (willow) was present. The ground cover consisted primarily of *Solanum dulcamara* L. (climbing nightshade).

The field habitat contained mostly low growing (ca. 60 cm) *Bromus inermis* Lyess (brome grass) and *Solidago* spp. (goldenrod).

The interface consisted of *Pyrus communis* L. (wild pear), *Crataegus* spp. (hawthorn), *Lonicera* spp. (honeysuckle) and *Rhamnus frangula* L. (glossy buckthorn). *Convolvulus arvensis* L. (field bindweed), *Plantago lanceolata* L. (narrow-leaved plantain), *Dactylis glomerata* L. (orchard grass) and *Solidago* spp. (goldenrod) made up the ground cover.

The New Jersey light trap (Mulhern 1934) with a 25-watt bulb and the Center for Disease Control miniature light trap (CDC) (Sudia and Chamberlain 1962) were used in this study. When operated, approximately 1.5 kg of dry ice (CO₂) wrapped in paper was suspended adjacent to the top of the CDC trap. In addition, a non-attractant suction trap constructed from a New Jersey light trap (Bidlingmayer 1967) provided a baseline of

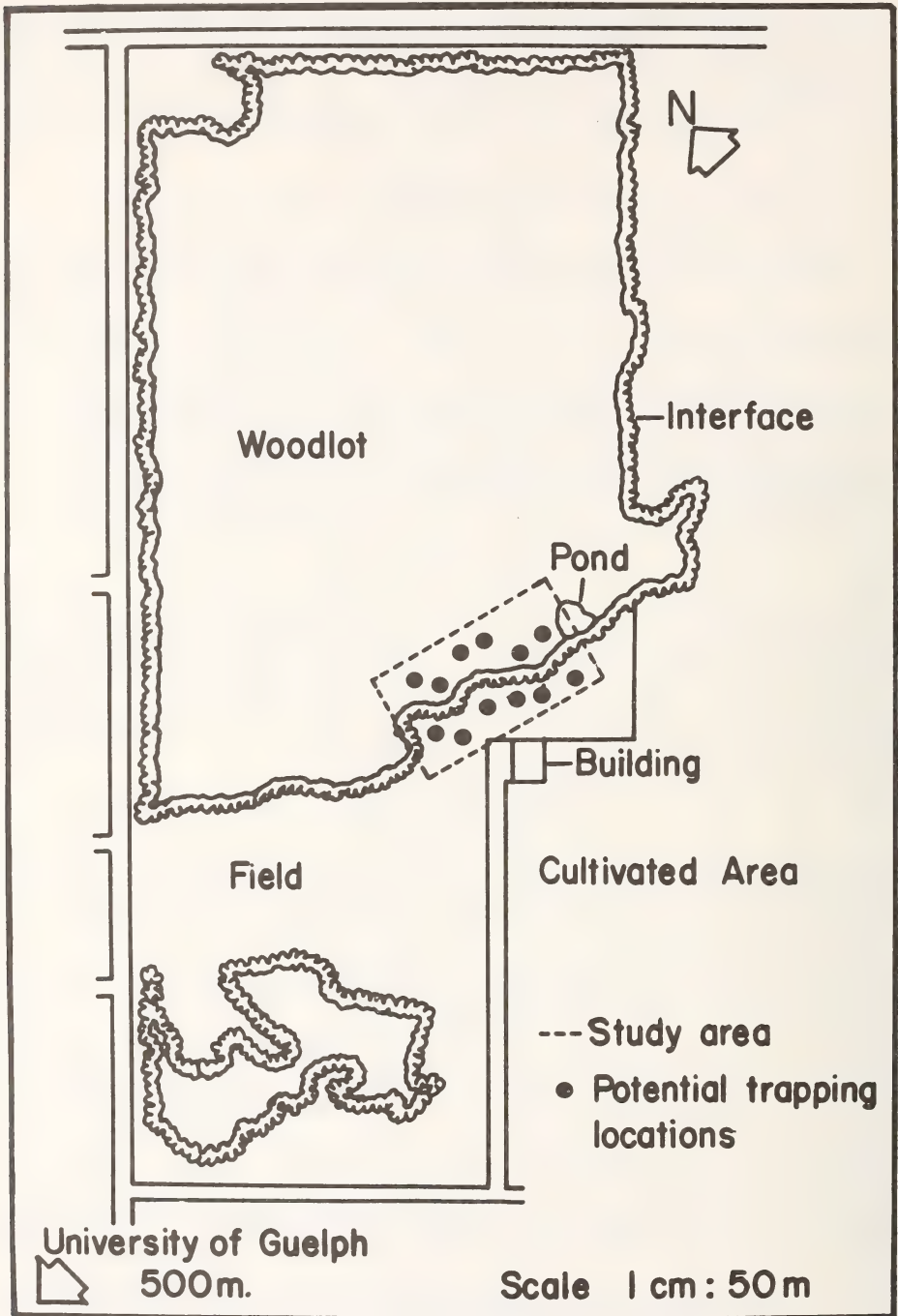


FIG. 1. Study area showing trapping locations at University of Guelph Arboretum, Guelph, Ontario.

mosquito activity. The light source was removed and the cover was raised to a height of 50 cm from the top of the cylinder using an aluminum lamp chain.

A total of 9 samplers were operated, i.e. 3 traps (one of each type) in each of the 3 habitats (field, interface and woods). Once a week, the traps were randomly interchanged to different positions within each habitat. At intervals of ca. 4 weeks, traps were also interchanged between habitats. All positions were at least 25 m apart. The traps were suspended 1.2 m above the ground to avoid the effects of vertical stratification (Mitchell and Rockett 1979). Trapping was conducted from 26 May to 28 August 1981 and from 17 May to 26 August 1982. Traps were operated from 1700 h to 0900 h (Daylight Saving Time) 4 nights a week. Mosquitoes were identified to species if possible using the keys of Wood *et al.* (1979) and Darsie and Ward (1981).

All collection data were transformed to the logarithm ($X + 1$) before performing an analysis of variance (ANOVA) to identify significant ($P \leq 0.01$) habitat effects. Duncan's Multiple Range Test was used to determine significant differences in mean numbers of mosquitoes per habitat ($P \leq 0.05$).

Results and Discussion

Culex pipiens and *Culex restuans* were collected more frequently in the woods habitat than in the interface or field (Table I). More *Culiseta morsitans* were collected from the woods than from the field or interface zones. Females of these 3 species are ornithophilic (Mattingly *et al.* 1951; Morris *et al.* 1976; Morris and Zimmerman 1981) which may explain their greater association with the woods. In Florida, Bidlingmayer (1971) recorded a similar result with other ornithophilic species. In upstate New York, females of *C. morsitans* were more common on the forested edge of a swamp (Morris *et al.* 1980; Morris and Zimmerman 1981). However, in a later study this species was found to be more prevalent in an open field habitat, whereas *C. pipiens* and *C. restuans* were collected most often in a tree row (Howard *et al.* 1983).

Although habitat did not significantly effect trap catches of *Anopheles walkeri* during 1981 (Table I), significantly more *Anopheles walkeri* were collected from the field than from the interface or woods during 1982 (Table I). Magnarelli (1975) concluded that the higher incidence of this species in open marshy areas was probably due to the proximity of

Table I. Mean number of female mosquitoes captured per week in 3 habitats using both New Jersey and CDC light traps at Guelph, Ontario during 14 weeks of trapping in 1981 and 15 weeks of trapping during 1982

Species	1981 Habitat type			1982 Habitat type		
	Field	Interface	Woods	Field	Interface	Woods
<i>Culex pipiens-restuans</i>	2.9a ¹	3.6a	8.5b	2.7a	4.3b	9.1c
<i>Culiseta morsitans</i>	1.0a	3.3b	8.4c	4.7a	9.8b	19.5c
<i>Anopheles walkeri</i>	5.9a	3.4a	2.2a	135.1a	59.0b	19.8b
<i>Mansonia perturbans</i>	12.7a	11.4a	18.5a	64.3a	44.3b	43.1a
<i>Aedes vexans</i>	27.4a	40.1b	67.1b	43.4a	55.4a	41.1a
Spring <i>Aedes</i> spp. ²	16.0a	70.3b	72.0b	54.2a	200.2b	166.0b
Total mosquitoes ³	67.9a	134.9b	178.6b	308.8a	380.8a	306.0a

¹ For each year, within a species, means followed by the same letter are not significantly different, Duncan's Multiple Range Test ($P < 0.05$).

² Includes all univoltine *Aedes* spp. (see Table II).

³ Also included are 492 specimens (1981) and 1707 specimens (1982) of *Culiseta inornata*, *Anopheles punctipennis*, *A. quadrimaculatus*, *A. earlei*, *Aedes triseriatus*, *A. trivittatus* and unidentifiable mosquitoes.

breeding sites within the marsh. Because larval breeding sites were not located in the field habitat, more females of *A. walkeri* likely immigrated into the field from outside the immediate study area.

Numbers of *Mansonia perturbans* (taxonomic status as per Wood *et al.* 1979) caught in each habitat during 1981 or 1982 were not significantly different (Table I). *M. perturbans* frequent large permanent marshes in southern Canada and the northeastern United States (Magnarelli 1975; Wood *et al.* 1979; Allan *et al.* 1981). Such breeding sites were not present in the immediate vicinity of the study site at Guelph. Because females of this species are general feeders (Downe 1962), they appeared to forage without preference to habitat. Howard *et al.* (1983) noted a definite association of this species with an open field.

In 1981, fewer females of *Aedes vexans* were collected in the field than in the interface or woods (Table I) but in 1982 no significant habitat association was observed (Table I). These results were similar to those of Trimble and Thorsteinson (1974) who collected large numbers of *A. vexans* from both deciduous and coniferous forests although larvae of this species were not found in these habitats. Females of *A. vexans* were attracted to the forest edge upon dispersal from breeding sites and remained in the interface and woods habitats. In another study, Brust (1980) found large numbers of *A. vexans* in a shelterbelt that rose above flat cultivated land. He concluded that the trees provided a focal point for dispersing male and female adults.

Significantly more spring *Aedes* spp. were caught in the woods or interface than the field irrespective of species (Table I). The *Aedes stimulans* complex constituted the majority of spring *Aedes* spp. collected (Table II.) These mosquitoes remained in the woods and did not disperse far from breeding sites located within this habitat. Similar findings were recorded in Manitoba by Trimble and Thorsteinson (1974).

Table II. Numbers and species of female spring *Aedes* spp. mosquitoes identified in collections from all traps at Guelph, Ontario in 1981 and 1982

Species	1981		1982	
	No. caught	% of total caught	No. caught	% of total caught
<i>Aedes cinereus</i>	153	2.3	131	0.7
<i>A. canadensis</i>	1629	24.6	235	1.3
<i>A. excrucians</i>	440	6.6	467	2.5
<i>A. stimulans</i> , <i>A. fitchii</i> , <i>A. euedes</i>	4081	61.7	15154	82.1
<i>A. provocans</i>	77	1.2	1943	10.5
<i>A. punctor</i>	166	2.5	85	0.5
Unidentifiable	72	1.1	433	2.3
Total	6688		18448	

The habitat preference of a particular host-seeking species of mosquito must be considered when positioning mosquito monitoring equipment. Females of *C. pipiens*, *C. restuans*, *C. morsitans*, *A. vexans* and univoltine *Aedes* spp. were collected in the largest numbers in the woods and transition zone. Those of *A. walkeri* were collected in the greatest numbers in the field while females of *M. perturbans* were abundant in all habitats studied.

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AN ASSESSMENT OF SAMPLING TECHNIQUES FOR ADULT MOSQUITOES IN SOUTHERN ONTARIO

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Abstract

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A comparison of 7 trapping devices for collecting female mosquitoes at Guelph, Ontario is presented. The traps compared were: New Jersey suction, New Jersey light, CDC light trap baited with dry ice, *Culex* spp. oviposition pools, Ehrenberg bird-baited traps, a rabbit-baited trap and a Trinidad mouse-baited trap. New Jersey light and CDC light traps, baited with dry ice, collected statistically similar numbers of *Culex pipiens* L., *Culex restuans* Theo. and *Culiseta morsitans* Theo. when evaluated over 2 years in 3 habitat types. An oviposition sampler was the most useful method for monitoring *Culex* spp. populations. The CDC light trap collected the largest numbers of *Aedes* spp. (86% in 1981 and 84% in 1982 of all mosquitoes collected) and *Mansonia perturbans* (Walker) (83% in 1981 and 87% in 1982). Pigeon-, quail-, rabbit- and mouse-baited traps collected few mosquitoes. Indices of effectiveness for the various traps were calculated by comparing numbers of females collected in each trap to numbers of females collected in a non-attractant suction trap. These indices could be used to aid in comparing mosquito populations sampled by different methods.

Introduction

The success of a mosquito control program can depend on accurate monitoring of mosquito numbers. Many sampling techniques have been used to quantify adult mosquito populations. Bidlingmayer (1974) and Service (1976) have indicated the value of simultaneously using various trapping methods. Although methods can vary depending on the objectives of control agencies (Gilles 1974), greater standardization in the techniques used to monitor adult mosquito populations has been advocated (Muirhead-Thomson 1968). Many of the variables, (e.g. species biases of traps, biases due to locations of traps, influence of meteorological conditions, etc.) affecting the validity of different sampling techniques have been reviewed (Muirhead-Thomson 1968, 1982; Service 1976, 1977; Southwood 1978).

The objective of this study was to determine the most efficient trapping method for adult mosquitoes in southern Ontario and to use this information to standardize mosquito problem assessment. Indices of effectiveness for various traps were developed to allow comparisons of mosquito numbers between municipalities using different trapping techniques. This information could be used when comparing pest problems on a provincial scale, from different municipalities using different trapping techniques, and indicating areas of concern during potential disease outbreaks.

Materials and Methods

The research area is described by Copps *et al.* 1984. The following traps were used in this study:

- (1) The non-attraction trap (NJS, Fig. 1a) was a New Jersey light trap modified by removing the light source and raising the cover 50 cm above the cylinder. The trap was suspended 1.2 m above the ground using a tripod.
- (2) The standard (25-watt incandescent bulb) New Jersey light trap (NJL, Fig. 1b)

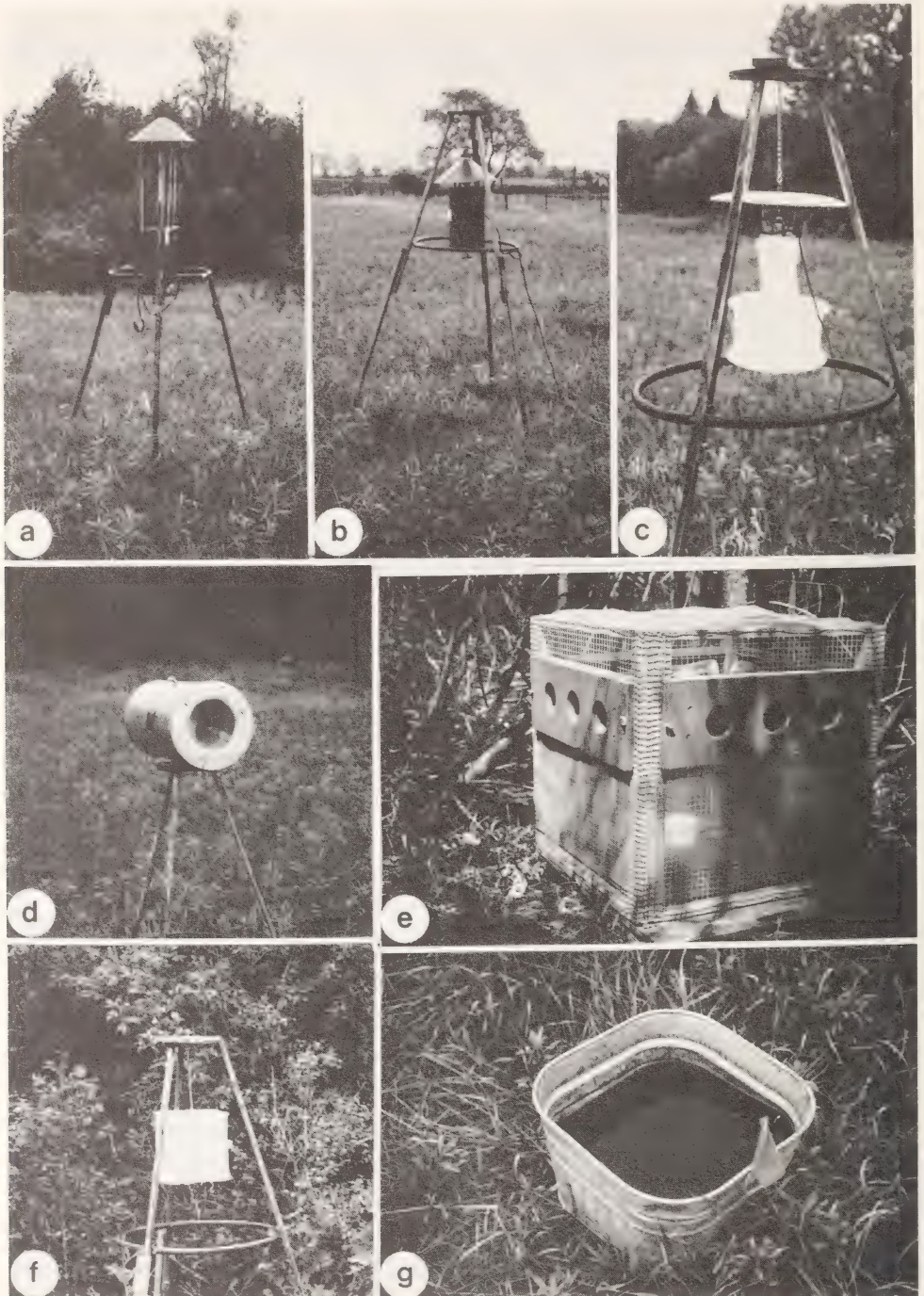


FIG. 1. Traps used to monitor populations of adult mosquitoes at Guelph, Ontario during 1981 and 1982. (a) Suction Trap; (b) New Jersey Light Trap; (c) CDC Light Trap; (d) Ehrenberg Bird-Baited Trap; (e) Rabbit-Baited Trap; (f) Mouse-Baited Trap; (g) Oviposition Sampler.

(Mulhern 1934) was employed because this model has been used most often by municipalities in Ontario.

(3) The Center for Disease Control miniature light trap (CDC, Fig. 1c) (Sudia and Chamberlain 1962). When operated, approximately 1.5 kg of dry ice (CO₂) wrapped in paper was suspended adjacent to the top of the trap.

(4) A bird-baited trap (Ehrenberg 1966) was tested using 2 different bait sources (Fig. 1d). One Japanese quail per trap (EHBq) was used in 1981 and one pigeon per trap in 1982 (EHBp).

(5) A rabbit-baited trap (RB, Fig. 1e) consisted of a hardware cloth cage (50 x 50 x 50 cm) covered with 22-mesh screening which contained the rabbit. Four removable, screened (22-mesh) sleeves (10 x 10 x 50 cm) were located in the top sides of the cage. Mosquitoes entered these sleeves through any one of 3 funnel-shaped entrances on each sleeve (10-cm-diameter plastic funnels). Mosquitoes were aspirated from each collection cage through an access hole. This trap was used in 1981 only.

(6) The Trinidad Regional Virus Laboratory Number 17 Trap (MB, Fig. 1f) (Davies 1971) was used in 1982. Two mice were placed in each trap.

(7) A modification of the artificial oviposition sampler (OVP, Fig. 1g) (Madder *et al.* 1980) was used to monitor *Culex* spp. This sampler consisted of a galvanized metal washtub lined with sod and filled to a depth of 15 cm with water. Egg rafts were collected from the water's surface, counted and taken to the laboratory for subsequent identification of first-instar larvae (Dodge 1966). One egg raft was considered equivalent to one female mosquito to permit comparison with other trapping techniques.

A total of 18 samplers were operated, i.e. 6 traps (one of each type) in each of the 3 habitats (field, interface and woods). The influence of habitat on the numbers and species composition of trap catches has been discussed by Copps *et al.* (1984). Once a week, the traps were randomly assigned to different positions within each habitat. At intervals of ca. 4 weeks, traps were also interchanged between habitats. All positions were approximately 25 m apart to minimize the influence of one trap on another (Gilles and Wilkes 1969, 1970, 1974). The NJL, NJS, CDC light, Ehrenberg bird-baited and mouse-baited traps were suspended at the same height (1.2 m) above the ground to avoid the effects of vertical stratification (Mitchell and Rockett 1979). The rabbit-baited and oviposition samplers were at ground level.

Trapping was conducted from 26 May to 28 August 1981 and from 17 May to 26 August 1982. Traps were operated from 1700 h to 0900 h (Daylight Saving Time) 4 nights a week. This schedule was selected to correct for potential trap failures and permitted an allowance for poor weather conditions. If a trap failed (i.e. bulb burned out) or heavy rains occurred, trapping was repeated on another night so that four complete samples were taken each week. Loomis and Hanks (1959) reported little difference in indices of mosquito populations based on light-trap collections made 4 or 7 nights a week.

The rabbit-baited and bird-baited (quail) traps were operated during the first 10 weeks of sampling in 1981. In 1982, the mouse-baited and Ehrenberg bird-baited (pigeon) traps were used during the initial 8 weeks of trapping. All other traps were used for 14 weeks (1981) and 15 weeks (1982).

Mosquitoes were identified to species if possible using the keys of Wood *et al.* (1979) and Darsie and Ward (1981). Weekly totals were accumulated and an index of 'trap effectiveness' was calculated for each trap in every habitat using a method similar to that of Graham (1969). This index was obtained by dividing the catch per week in each type of trap by the catch in the suction trap during the same period. Indices per week were then averaged for the entire season. The suction trap was chosen as a standard because it was a non-attractive sampling device and provides less bias than other sampling methods (Service 1976).

All trap-catch data were transformed to the logarithm ($X + 1$). The following procedures were used to analyze the data: Bartlett's test for homogeneity of variance ($P \leq 0.01$), ANOVA for differences attributable to sampling method and Duncan's Multiple Range Test for significant differences between sampling methods ($P \leq 0.05$).

Results and Discussion

Suction and Light Traps. The suction traps are believed to provide the best estimate of non-biased baselines of mosquito activity (Service 1976). However, these traps collected few *Anopheles walkeri* Theo., other *Anopheles* spp. and spring *Aedes* spp., particularly *Aedes cinereus* Meigen and *A. punctor* (Kirby) (Tables I and II). In 1981 and 1982, the suction traps captured only 4.2% and 3.5%, respectively, of total female mosquitoes collected in the CDC light traps and 26.9% and 23.4% of those caught in the NJL traps. A more powerful type of suction trap (Bidlingmayer 1964) might have captured more mosquitoes.

During 1981, the mean number of females collected per week (all species) was 49.4 for NJL traps and 318.7 for the CDC light traps. In 1982, these means were 126.2 and 839.6 (Table III). The index of effectiveness for all mosquitoes using the New Jersey light trap was 3.7 in 1981 and 4.3 in 1982. For the CDC trap baited with CO₂ the indices of effectiveness were 23.2 and 28.4 in 1981 and 1982, respectively. Thus if 2 municipalities with equal mosquito numbers (as determined by suction traps) were comparing total mosquitoes collected, one using New Jersey light traps and one using CDC light traps baited with CO₂, the municipality using the CDC trap should theoretically expect to trap 6.3-6.6 times as many mosquitoes per unit trapping time as the municipality using the NJL trap. The larger numbers of mosquitoes in the CDC traps were believed due to the CO₂ attractant. Similar results were reported by Carestia and Horner (1968).

The NJL trap and CDC light traps baited with CO₂ collected similar numbers of ornithophilic mosquitoes (*Culex* spp. and *Culiseta morsitans*) (Table III) and had indices of effectiveness of 2.0 to 4.0 (Tables I and II). Municipalities using CDC traps or New Jersey light traps would report statistically similar numbers of ornithophilic mosquitoes (Table III). However, the NJL traps collected approximately 66,600 and 40,600 extraneous insects (mostly Lepidoptera and Diptera) in 1981 and 1982, respectively, compared to 6,500 and 6,400 for the CDC light traps. Further, specimens from the NJL traps were often damaged, making identification difficult. Specimens from the CDC light traps were alive, identifiable and therefore suitable for arbovirus studies. These findings and those of Magnarelli (1975) support the conclusion that CDC light traps are more useful for arbovirus surveillance programs.

For nuisance, spring *Aedes* spp., (i.e. *Aedes stimulans* group) the CDC trap had an index of effectiveness of 17.5, whereas the NJL trap had an index of 2.3. Thus the CDC trap should collect approximately 7.6 times more females than the NJL trap. For summer *Aedes* spp. (i.e. *Aedes vexans*) which are major pests of man (Wood *et al.* 1979), the CDC trap had a combined index of effectiveness of 60.6, whereas the NJL trap had an index of 8.1. The CDC trap collected 7.5 times the number of females as the NJL trap. For *Mansonia perturbans* the CDC trap had an index of effectiveness of 172.4 compared to 27.9 for the NJL trap. The CDC trap collected 6.2 times the number of *M. perturbans* females as the NJL trap.

Host-Baited traps. The mouse-baited traps collected predominantly *Culiseta morsitans* (64% of all females captured in host-baited traps) (Tables I and II). Hayes (1961) reported that *Culiseta morsitans* fed readily on small mammals but Morris *et al.* (1976) found the species primarily ornithophilic. However, much larger numbers of this species were collected in the NJL and CDC light traps. The Ehrenberg traps baited with pigeon or quail and the rabbit-baited traps collected few mosquitoes of any species.

A general paucity of *Culex* spp. at the study site was believed to have adversely affected the success of the Ehrenberg traps. The failure may also have been due, in part, to the size and species of the host bird. In Africa, when these traps were baited with chickens, ducks, or pigeons, mosquitoes oriented to a trap from distances as great as 7 m (Gilles and Wilkes 1974). Japanese quail which are smaller than pigeons may not have had this range of attraction. Dow *et al.* (1957) found smaller birds attracted fewer *Culex tarsalis* Coq. than larger birds. In addition, the 'passive' (i.e., without fans or other collection aids)

Table I. Weekly numbers of female mosquitoes and indices of effectiveness for different traps at Guelph, Ontario, 1981

Species	Trap type ¹					
	NJS	NJL	CDC	EHBq	RB	OVP
<i>Culex pipiens-rexuans</i> complex	7.1 (1.0) ²	18.7 (2.6) ²	19.0 (2.8) ²	7.3 (1.0) ²	0.2	34.0 (4.8) ²
<i>Culiseta morsitans</i>	4.9 (1.0)	15.2 (3.1)	18.0 (3.7)	6.8 (1.4)	0.1	0.0*
<i>Culiseta inornata</i>	0.5 (1.0)	1.5 (3.0)	0.8 (1.6)	0.1 (0.2)	0.0*	0.0*
<i>Mansonia perturbans</i>	0.5 (1.0)	20.8 (41.6)	106.6 (213.2)	0.5 (1.0)	0.0*	0.0*
<i>Anopheles walkeri</i>	0.4 (1.0)	4.1 (10.25)	30.2 (75.5)	0.0*	0.0*	0.0*
Other <i>Anopheles</i> spp. ³	0.3 (1.0)	1.6 (5.3)	3.4 (11.3)	0.0*	0.0*	0.0*
<i>Aedes cinereus</i>	0.1 (1.0)	2.5 (25.0)	8.9 (89.0)	0.0*	0.0*	0.0*
<i>A. canadensis</i>	2.1 (1.0)	7.7 (3.7)	93.8 (44.7)	0.0*	2.3 (1.1)	0.0*
<i>A. excrucians</i>	1.9 (1.0)	3.8 (2.0)	30.8 (16.2)	0.0*	0.9 (0.5)	0.0*
<i>A. stimulans</i> , <i>A. fitchii</i> , <i>A. euedes</i>	15.5 (1.0)	22.8 (1.5)	242.9 (15.7)	0.1	6.9 (0.4)	0.0*
<i>A. provocans</i>	0.3 (1.0)	0.4 (1.3)	4.6 (15.3)	0.0*	0.0*	0.0*
<i>A. punctor</i>		0.9	10.8	0.1	0.1	0.0*
<i>A. vexans</i>	5.4 (1.0)	42.9 (7.9)	355.7 (65.9)	0.3 (0.1)	1.6 (0.3)	0.0*
Other <i>Aedes</i> spp. ⁴	0.3 (1.0)	1.1 (3.7)	11.7 (39.0)	0.2 (0.7)	0.3 (1.0)	0.0*
Total <i>Aedes</i> spp.	25.6 (1.0)	82.1 (3.2)	759.2 (29.7)	0.7	12.1 (0.5)	0.0*
Unidentifiable	1.2 (1.0)	5.7 (4.75)	55.4 (4.5)	0.6 (0.5)	0.1 (0.1)	0.0*
Total	40.5 (1.0)	149.7 (3.7)	943.5 (23.2)	16.0 (0.4)	12.5 (0.3)	34.0 (0.8)

¹ For NJS, NJL, CDC and OVP, N = 14 weeks. For EHBq and RB, N = 10 weeks. Total number of females per week in 3 traps of each type.
² The index of effectiveness is the number of mosquitoes per week taken in a trap divided by the number of mosquitoes per week in the NJS trap for each species averaged over the sampling period.
³ *Anopheles earlei*, *A. punctipennis*, *A. quadrimaculatus* and unidentifiable *Anopheles* spp.
⁴ *Aedes triseriatus*, *A. trivittatus* and unidentifiable *Aedes* spp.
 * Trap operated but no specimens collected.

Table II. Weekly numbers of female mosquitoes and indices of effectiveness of different traps at Guelph, Ontario, 1982

Species	Trap type ¹					
	NJS	NJL	CDC	EHBq	MB	OVP
<i>Culex pipiens-restuans</i> complex	5.8 (1.0) ²	21.9 (3.8) ²	20.5 (3.5) ²	5.3 (0.9) ²	2.3 (0.4) ²	27.5 (4.7) ²
<i>Culiseta morsitans</i>	14.0 (1.0)	40.1 (2.9)	34.5 (2.5)	13.0 (0.9)	15.9 (1.1)	0.0*
<i>Culiseta inornata</i>	0.9 (1.0)	8.3 (9.2)	9.0 (10.0)	1.8 (2.0)	2.1 (2.3)	0.0*
<i>Mansonia perturbans</i>	3.1 (1.0)	44.1 (14.2)	407.9 (131.6)	7.3 (2.4)	4.3 (1.4)	0.0*
<i>Anopheles walkeri</i>	1.0 (1.0)	45.7 (45.7)	595.2 (595.2)	3.1 (3.1)	0.0*	0.0*
Other <i>Anopheles</i> spp. ³	0.5 (1.0)	7.1 (14.2)	20.4 (40.8)	0.0*	0.0*	0.0*
<i>Aedes cinereus</i>	0.2 (1.0)	0.6 (3.0)	8.2 (41.0)	0.0*	0.0*	0.0*
<i>A. canadensis</i>	0.1 (1.0)	0.5 (5.0)	14.7 (147.0)	0.9 (9.0)	0.0*	0.0*
<i>A. excrucians</i>	4.3 (1.0)	5.8 (1.3)	21.3 (5.0)	0.0*	0.0*	0.0*
<i>A. stimulans</i> , <i>A. fitchii</i> , <i>A. euedes</i>	43.7 (1.0)	133.7 (3.1)	841.9 (19.3)	2.0	0.4	0.0*
<i>A. provocans</i>	1.1 (1.0)	4.1 (3.7)	123.7 (112.4)	2.6 (2.4)	0.0*	0.0*
<i>A. punctor</i>	0.2 (1.0)	0.7 (3.5)	5.1 (25.5)	0.0*	0.0*	0.0*
<i>A. vexans</i>	6.5 (1.0)	53.0 (8.2)	360.4 (55.4)	0.3	0.0*	0.0*
Other <i>Aedes</i> spp. ⁴	4.8 (1.0)	10.5 (2.2)	35.7 (7.4)	1.0 (0.2)	0.1	0.0*
Total <i>Aedes</i> spp.	60.9 (1.0)	208.9 (3.4)	1411.0 (23.2)	6.8 (0.1)	0.5	0.0*
Unidentifiable	2.6 (1.0)	5.2 (2.0)	22.5 (8.6)	2.4 (0.9)	0.1	0.0*
Total	88.8 (1.0)	381.3 (4.3)	2520.9 (28.4)	32.9 (0.4)	24.7 (0.3)	27.5 (0.3)

¹ For NJS, NJL, CDC and OVP, N = 15 weeks. For EHBq and MB, N = 8 weeks. Total number of females per week in 3 traps of each type.
² The index of effectiveness is the number of mosquitoes per week taken in a trap divided by the number of mosquitoes per week in the NJS trap for each species averaged over the sampling period.
³ *Anopheles punctipennis*, *A. quadrimaculatus*, *A. earlei* and unidentifiable *Anopheles* spp.
⁴ *Aedes triseriatus*, *A. trivittatus* and unidentifiable *Aedes* spp.
 * Trap operated but no specimens collected.

Table III. Mean number of female mosquitoes captured per week (N = 14, 1981; N = 15, 1982) in 3 types of traps at Guelph, Ontario in 1981 and 1982

Species	1981 Trap type			1982 Trap type		
	NJS	NJL	CDC	NJS	NJL	CDC
<i>Culex pipiens-restuans</i> complex	2.4 a ¹	6.0 b	6.6 b	1.9 a	7.3 b	6.8 b
<i>Culiseta morsitans</i>	1.7 a	5.1 b	6.0 b	4.9 a	15.3 b	13.8 b
<i>Anopheles walkeri</i>	0.1 a	1.4 b	10.0 c	0.3 a	15.2 b	198.4 c
<i>Mansonia perturbans</i>	0.2 a	6.9 b	35.5 c	1.1 a	14.7 b	136.0 c
<i>Aedes vexans</i>	1.8 a	14.3 b	118.6 c	2.1 a	17.7 b	120.1 c
Spring <i>Aedes</i> spp. ²	6.8 a	13.3 b	138.3 c	18.2 a	52.0 b	350.2 c
Total mosquitoes ³	13.3 a	49.4 b	318.7 c	29.5 a	126.2 b	839.6 c

¹ Within a species, means followed by the same letter are not significantly different ($P \leq 0.05$).

² Includes all univoltine *Aedes* spp.

³ Also included are 492 specimens (1981) and 1707 specimens (1982) of *Culiseta inornata*, *Anopheles punctipennis*, *A. quadrimaculatus*, *A. earlei*, *Aedes triseriatus*, *A. trivittatus* and unidentifiable mosquitoes.

nature of the host-baited traps may have contributed to the poor performance of these devices. Rotary-mounted lard-can traps and host-baited CDC traps were more effective than passive traps in the collection of ornithophilic species (Hayes 1961; Edmord and Morris 1982).

A poor design for the rabbit-baited (RB) trap likely caused the low numbers of mosquitoes which were captured. Mosquitoes had difficulty entering the traps. Large numbers of mosquitoes were seen on the outside of the trap but these did not enter.

This study does not support the conclusions of Graham (1969) that small mammal-baited traps provide an approximation of human biting rates and permit an estimation of the nuisance level of mosquitoes. However, traps baited with a specific host may be useful for arbovirus studies, particularly if they are 'active' (i.e., fan-type) designs.

Oviposition Sampler. The oviposition sampler had an index effectiveness of 4.75 for *Culex* spp. during 1981 and 1982 (Tables I and II). Collections of *Culex* spp. in NJL and CDC light traps were only slightly lower than oviposition collections. A week-to-week comparison of collections in the NJL, CDC light and oviposition traps (Fig. 2) showed that these traps provided a similar pattern of *Culex* spp. activity. The reduced numbers of *Culex* spp. in August as estimated by the oviposition trap is believed due to *Culex* spp. entering reproductive diapause (Madder *et al.* 1980). Similar results were obtained by Madder *et al.* (1980) and Leiser and Beier (1982). The oviposition trap also provided the best overall method for monitoring populations of *Culex pipiens* L. and *C. restuans* Theo., potential vectors of St. Louis Encephalitis (Madder *et al.* 1980). Larvae from only 3 of 489 egg rafts (1981) and 2 of 428 (1982) were identified as *C. pipiens*; the remainder, except 23 (1981) and 16 (1982) which did not hatch, were *C. restuans*.

This work demonstrates the superiority of the CDC light trap baited with CO₂ over passive animal-baited traps and New Jersey light traps for monitoring mosquito activity in southern Ontario. This is particularly important because Slaff *et al.* (1983) have shown that data collected from CDC traps closely approximates biting activity on humans. A particular type of sampling device (e.g. oviposition sampler) may be useful for monitoring a specific mosquito (e.g. *Culex* spp.) population. The indices provided in Tables I and II should be useful for comparing numbers of mosquitoes collected by municipalities using different techniques. Overall numbers of mosquitoes collected by CDC traps were ca. 6.5

times that of New Jersey light traps but numbers of ornithophilic species, i.e. *Culex* spp., were similar in either trap.

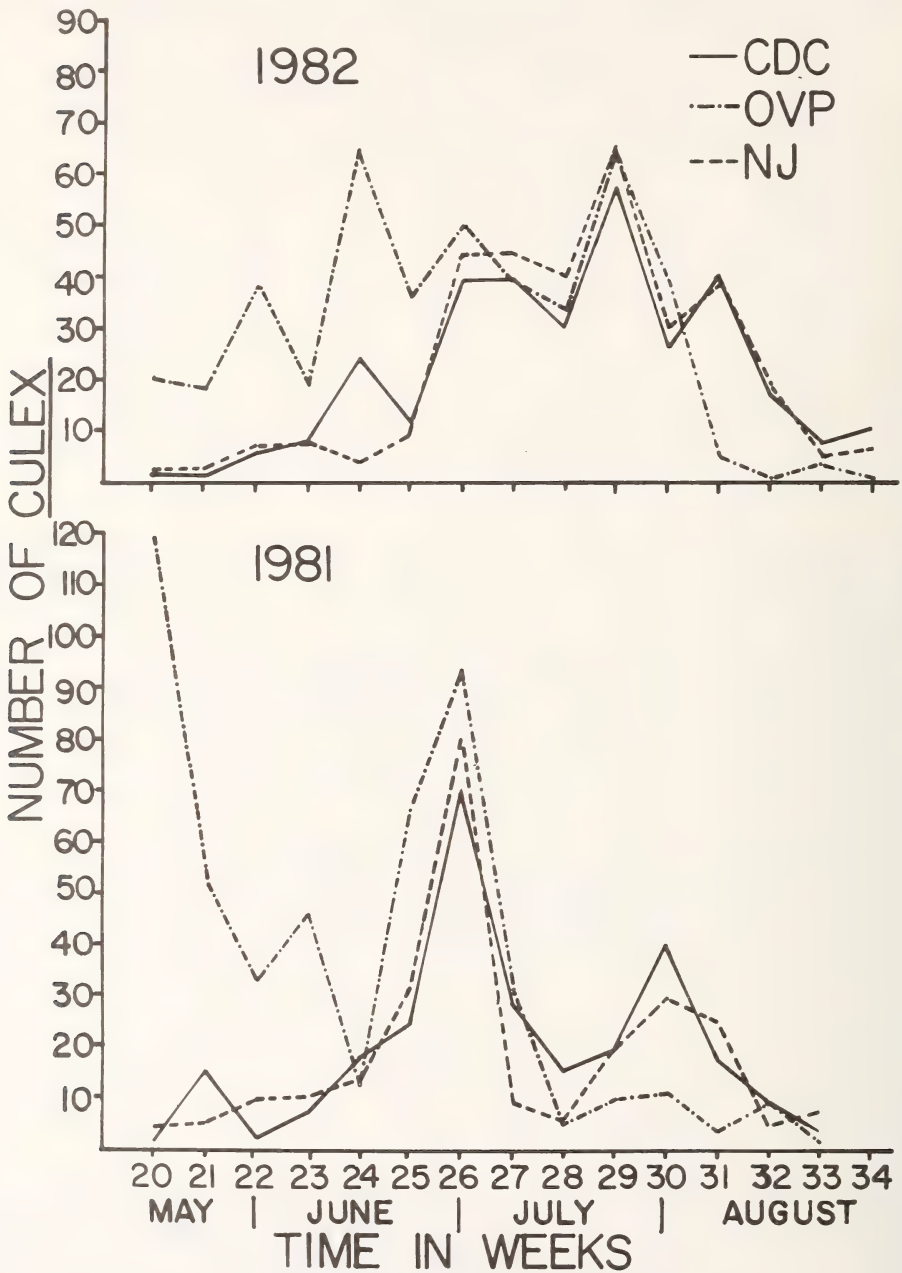


FIG. 2. Mean number of *Culex restuans-piapiens* females collected using three sampling devices, Guelph, Ontario, 1981-82. (CDC—Centre for Disease Control trap, OVP—Oviposition trap, NJ—New Jersey light trap).

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THE TRANSMISSION AND EFFECTS OF *NOSEMA FUMIFERANAE* AND
PLEISTOPHORA SCHUBERGI (MICROSPORIDA) ON
CHORISTONEURA FUMIFERANA (LEPIDOPTERA: TORTRICIDAE)

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Abstract

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The microsporidian parasites *Nosema fumiferanae* and *Pleistophora schubergi* were not transmitted congenitally through the male of the spruce budworm at doses tested. Mating of infected males with healthy females did not reduce fecundity or egg viability. The fecundity of females infected with *P. schubergi* was reduced. The adverse effects of the microsporidia on weight and adult longevity were more pronounced in the females than males.

Introduction

The spruce budworm, *Choristoneura fumiferana* (Clem.), is readily infected by the microsporidia *Nosema fumiferanae* (Thomson) and *Pleistophora schubergi* Zwölfer. The effects of *N. fumiferanae* on spruce budworm, particularly the females, are well documented (Thomson 1958a; Wilson 1977, 1983); these include reduced pupal weights, longevity and fecundity. Less information is available on the effects of *P. schubergi*. Surface treatment of the diet with spores of this microsporidium (Wilson 1982a) did not allow precise determination of the number of spores ingested. This problem was largely overcome with the development of a better dosing technique (Wilson 1983).

There is conflicting information on whether infected spruce budworm males can transmit either of the microsporidia to their offspring or if mating infected males with healthy females affects fecundity. This report attempts to answer these questions and to provide further data on the effects of *P. schubergi* on the spruce budworm.

Materials and Methods

Maintenance of insects and spore production. The methods used in rearing insects, spore production and dosing the experimental insects have been reported previously (Wilson 1983). Healthy (i.e., microsporidia-free) 4th instars (14 days out of the hibernacula) were supplied by the rearing facilities of the Forest Pest Management Institute, Sault Ste. Marie, Ontario. All larvae were reared on a synthetic diet (Grisdale 1973) using a photoperiod of 16:8 L:D, at $23 \pm 1^\circ\text{C}$ and 60-80% RH.

Spores of *N. fumiferanae* and *P. schubergi* were obtained from laboratory-infected spruce budworm. Infected insects were macerated in tap water and the resulting homogenate was filtered through two layers of cheesecloth and purified by a modified method of Cole (1970). Spore concentrations were determined by using a hemocytometer.

Treatment of larvae. Spore suspensions containing 0.5% (V/V) Nu-Film, a spreader-sticker (Miller Chemical and Fertilizer Corp., Hanover, Pennsylvania, USA) were applied at a volume of $5 \mu\text{L}$ to tips of individual balsam fir (*Abies balsamea* [L.] Mill.) needles. One larva and one treated needle were confined in a Beem embedding capsule (Ladd Research Industries, Burlington, Vermont, USA). Spore dose per needle was 5×10^2 , 5×10^3 , or 5×10^4 *P. schubergi* or 5×10^4 and 5×10^5 *N. fumiferanae* spores. Control larvae were given needles treated with $5 \mu\text{L}$ of distilled water containing 0.5% (V/V) Nu-Film. Insects were allowed to feed on the needles for 72 h, and only those that consumed the entire treated area were reared to maturity on the synthetic diet. Experiments were repeated once.

Pupation and mating of adults. As pupation occurred, pupae were removed from the diet and placed in screw-capped, glass shell vials (diameter 2 cm, length 6 cm) lined with paper

towel, until eclosion. In the case of *N. fumiferanae*-treated larvae, only male pupae were collected. However, for *P. schubergi* both male and female pupae were reared. In both cases the infected adults that emerged were mated with healthy adults. These healthy individuals were obtained as pupae from the rearing section of F.P.M.I. A male and female were placed in a 250-ml styrofoam container with a balsam twig containing needles for oviposition. A piece of moistened absorbent cotton was wrapped around the end of the twig to prevent rapid desiccation. Containers were closed with a plastic lid containing a small hole for air. Adults were allowed to remain in the styrofoam container until death, when smears of each individual were examined microscopically for the presence or absence of microsporidian spores.

After seven days the containers were examined for eggs. Only those matings that resulted in fertile eggs were used in the experiment. Eggs were then set-up and the resulting F₁-generation larvae were placed in cold storage (2 ± 1°C) according to the method of Stehr (1954). After diapause requirements were satisfied, the larvae were reared for 21 days after emergence from hibernacula before examination for the presence of microsporidia. This allowed time for possible low levels of microsporidia to develop. Infection was based on the presence of spores or vegetative stages (Giemsa-stained material) using phase contrast and bright field optics.

Larval and pupal mortality, days as pupae and adults, pupal weights and microsporidian infection in the F₁ generation were recorded. Results were analyzed using the Student's t-test.

Results

Pupal mortality, longevity and weight. Spruce budworm larvae treated with 5 x 10⁴ spores of *P. schubergi* or 5 x 10⁶ spores of *N. fumiferanae* suffered 38 and 55% pupal mortality, respectively (Table I). Therefore, the dose chosen for further studies was 5 x 10³ for *P. schubergi* and 5 x 10⁵ for *N. fumiferanae*.

Table I. Pupal mortality as a result of ingesting various doses of *Nosema fumiferanae* and *Pleistophora schubergi* spores by mid-4th instars of the spruce budworm

Treatment (spores/larva)	Microsporidia			
	<i>Nosema fumiferanae</i> ^a		<i>Pleistophora schubergi</i>	
	Number	Mortality (%)	Number	Mortality (%)
0	37	0	95	1
5 x 10 ²	--	--	87	4.6
5 x 10 ³	--	--	74	20.2
5 x 10 ⁴	56	3.6	60	38.3
5 x 10 ⁵	39	10.2	--	--
5 x 10 ⁶	11	55.0	--	--

^a Male pupae only.

In no case did the dose of microsporidia tested affect pupal duration; however, pupal weight was reduced (Tables II and III). A dose of 5 x 10³ *P. schubergi* significantly reduced the pupal weight of females and 5 x 10⁴ had the same effect on the pupal weights of males.

Longevity and fecundity of adults. Female adults died sooner when they had ingested (as 4th instars), 5 x 10³ or more spores of *P. schubergi* (Table III). Table II shows that when healthy females were mated with males infected with *N. fumiferanae* there was no effect on fecundity or the number of eggs that hatched. However, this was not the case when *P.*

Table II. Effects of *Nosema fumiferanae* spores on male longevity and pupal weight, and fecundity of healthy female spruce budworm mated with infected males^a

Treatment (spores/larva)	No. insects	Mean days as pupa	Mean pupal wt (mg)	Mean days as adults	Mean eggs/ mating ^b	Hatch (%)
0	33	9.0	81.1	9.2	158 (22)	80.8
5 x 10 ⁴	50	9.1	74.8*	9.3	170 (33)	79.0
5 x 10 ⁵	31	9.1	64.9*	8.9	167 (8)	75.6

^a Larvae were treated with spores during the 4th instar.

^b Individual matings in parentheses.

* Different from the control (P = 0.05).

Table III. Effects of ingestion of *Pleistophora schubergi* spores by 4th instars of spruce budworm on pupal weights and longevity

Treatment (spores/larva)	Mean days as pupa ^a		Mean pupal wt (mg) ^a		Mean days as adults ^a	
	♀	♂	♀	♂	♀	♂
0	8.0 (42)	8.1 (49)	125.4 (42)	78.2 (49)	11.6 (42)	8.3 (49)
5 x 10 ²	8.8 (25)	8.5 (37)	119.5 (25)	83.7 (37)	10.6 (25)	8.1 (37)
5 x 10 ³	9.0 (20)	8.8 (31)	89.7 (20)**	73.0 (31)	9.3 (20)**	8.2 (31)
5 x 10 ⁴	9.5 (10)	8.9 (24)	86.9 (10)**	69.5 (24)**	8.8 (10)**	8.0 (24)

^a Sample size in parentheses.

** Different from the control (P = 0.01).

schubergi-infected females were mated with healthy males. In this instance the mean number of eggs laid by females, resulting from 4th instars treated with 5 x 10² or 5 x 10³ *P. schubergi* spores was 91 and 97, respectively. This compares to 171 for healthy adults. There was about a 12% reduction in hatch for those eggs laid by infected females. Because of the relatively few matings for the infected adults (5 pairs for each dose) these reductions need to be confirmed.

Congenital transfer of microsporidia to F₁ generation.

***Pleistophora schubergi*.** Fifty-two infected spruce budworm males were mated with microsporidia-free females. From these matings 694 offspring were examined and none were infected with *P. schubergi*. Nine infected females were mated with microsporidia-free males and none of the 168 individuals of the F₁ generation examined was infected.

***Nosema fumiferanae*.** Thirty-seven infected males were mated with microsporidia-free females. A total of 1060 individuals of the F₁ generation were found to be free of microsporidia.

Discussion

The sub-lethal effects of reduced pupal weight, fecundity and adult longevity of *N. fumiferanae* on the spruce budworm have been described earlier (Thomson 1958a; Wilson 1977, 1983). Transmission of this parasite to its host can occur in at least three ways; perorally, transovarially and by injection into its host (Wilson 1982b). Infected females readily transmit the microsporidium to their offspring. Thomson (1958b) demonstrated

schizonts of *N. fumiferanae* in developing eggs of the spruce budworm. In fact, spores have been detected in eggs just prior to hatching, in 1st instars and also in 2nd instars inside the hibernaculae. Thomson (1958b) also suggested that infected males are sometimes capable of transmitting the parasite to some of their offspring. Spores can be observed lying among the bundles of sperm. Various stages of the microsporidium *Nosema heliothidis* have been observed in the caps of gelatinous material in which the heads of the bundles of sperm of the corn earworm are inserted (Brooks 1968). It was therefore suggested that transmission of the microsporidium during copulation was possible. Kellen and Lindegren (1971) studied the mode of transmission of *Nosema plodiae*, a pathogen of *Plodia interpunctella*. The microsporidium invaded the reproductive organs of both sexes. They reported that diseased males may transmit spores to healthy females and subsequently to their offspring. However, only in one incident did such an infected female produce infected progeny. In this particular system, infected males, mated with healthy females, did reduce fecundity. Wilson (1982b) examined 540 offspring from 17 matings of *N. fumiferanae*-infected males with microsporidia-free females and no infection in the offspring was observed. In this present report 37 similar matings involving some 1060 offspring showed no detectable infection. It is therefore doubtful if male budworm can transmit this parasite to their offspring. Infected males mated with healthy females produce normal numbers of progeny.

The results with *P. schubergi*-infected males are similar to those with *N. fumiferanae*. In no case did the males transmit the microsporidium to their offspring. However, in contrast to *N. fumiferanae*-infected females of spruce budworm, females infected with *P. schubergi* did not produce infected progeny. This agrees with the findings of Lipa (1963) who reported that the main (if not the only) mode of infection of *P. schubergi* is *per os*. This microsporidium had a definite effect on spruce budworm fecundity, but again only if the females were infected. In this study fecundity was reduced by about 45%.

There is no information on the effects of *P. schubergi* on fecundity of other insects but other effects have been noted. *Porthetria dispar* larvae become passive, lose weight and moulting is retarded. If pupation occurs, pupae usually die or eclose as deformed adults that are unable to copulate and lay eggs (Weiser 1961). Similar effects on other insects have also been reported (Kaya 1973; Simchuk 1980). *P. schubergi* definitely reduced the pupal weight and adult longevity of female spruce budworm, i.e., a dose of 5×10^3 spores fed to 4th instars reduced pupal weights by almost 30% and adult longevity by 2½ days.

In conclusion, male spruce budworm do not transmit either *N. fumiferanae* or *P. schubergi* to their offspring. The detrimental effects of the microsporidia are more severe on female budworm than on males.

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PHORID FLIES (DIPTERA: PHORIDAE) ASSOCIATED WITH MUSHROOMS IN SOUTHERN ONTARIO

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Abstract

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Phoridae associated with mushrooms were sampled using light traps in commercial mushroom farms, by rearing from wild mushrooms, by using mushroom-baited pitfall traps in the University of Guelph Arboretum, and by vacuum collecting from wild mushrooms. The pitfall traps collected mostly saprophages, but the economically important species *Megaselia nigra* (Meigen) and *M. halterata* (Wood) were reared from wild mushrooms. No fungivorous phorids were collected in commercial mushroom houses.

Introduction

Phorid flies are a major pest of the commercial mushroom-growing industry throughout the world. Four species of *Megaselia* Rondani have been responsible for most of the damage in North America and western Europe, namely *Megaselia agarici* (Lintner), *M. bovista* (Gimmerthal), *M. nigra* (Meigen), and *M. halterata* (Wood) (Robinson 1979); of these, all except *M. bovista* occur in North America. *M. halterata* is the most damaging species, and has probably been spread worldwide with cultured mushroom spawn from Europe (e.g. Cliff 1978).

In addition to the above economically important species, *M. eisfelderiae* Schmitz, *M. flava* (Fallén), *M. fungicola* (Coquillett), *M. longipennis* (Malloch), *M. lutea* (Meigen), *M. pulicaria* (Fallén), *M. pygmaeoides* (Lundbeck) and *M. straminipes* (Malloch) have been reared from fungi in North America, while many other species have been collected on or with fungi (Robinson 1971).

This paper describes the phorid fly fauna associated with mushrooms in southern Ontario.

Methods and Materials

The Diptera fauna of mushrooms was sampled using 4 methods in the summers of 1983 and 1984. Light traps were placed in 3 commercial mushroom houses near Waterdown, Ontario and were emptied every week during the summer of 1983. Infested mushrooms, collected in the field, were placed on a layer of vermiculite in 20 X 14 X 10 cm clear plastic trays, sprayed with water, and covered tightly until adult flies emerged. Pitfall traps, baited with decaying *Agaricus bisporus* (Lange), were placed in the University of Guelph Arboretum from May to September 1983 and May to October 1984. The mushrooms were hung in cheesecloth bags over 9 X 11 cm plastic tubs sunk into the ground, with soap, salt and water used as a trapping and preserving agent. These traps were placed in a wet beech forest in 1983, and in a dry beech/maple forest, a hemlock grove and an old field in 1984. Finally, adult flies were collected from mushrooms in the field using a vacuum aspirator (Marshall 1982).

All specimens were preserved in 70% ethanol, critical-point dried and mounted by gluing them to the side of an insect pin using water-soluble white glue. Some specimens were later remounted on slides following the methods of Disney (1983). Identifications were made by the senior author using the monographs of Borgmeier (1963, 1964, 1966), the work of Robinson (1977) and by comparison with specimens in the collection of the National Museum of Natural History, Washington, D.C.

Results and Discussion

Only one phorid fly, *Megaselia aequalis* (Wood), was collected from light traps in the 3 mushroom houses. This species develops in slug eggs (Robinson and Foote 1968), and its presence is no doubt accidental. In contrast, thousands of *Lycoriella* sp. (Diptera: Sciariidae) were collected each week, showing that flies had access to the houses. Phorids can be abundant and serious pests in mushroom houses (Thomas 1942; Hussey 1972) but have not yet been recorded from Ontario mushroom farms (D. Rinker, Horticultural Research Institute Ontario, Vineland, pers. comm.).

The pest species are, however, present in Ontario. Six *M. nigra* were reared from *Agaricus campestris* Fries from a lawn in Guelph (viii. 1982), 3 *M. chaetoneura* (Malloch) were reared from *Pleurotus* sp. from the University of Guelph Arboretum (9.vii.1984), and approximately 25 *M. halterata* and over 100 *M. rufipes* (Meigen) emerged from *Agaricus campestris* from Meaford, Ontario (12.viii.1984). The presence of the economically important (and presumably introduced from Europe) *M. halterata* and *M. nigra* is significant to mushroom growers, since there is the possibility of future infestations from these feral populations. Hussey (1959) showed that *M. nigra* bred only in mushroom beds that are exposed to direct sunlight, a situation that is rare today with efficient ventilation systems replacing open doors as a cooling method. The presence of *M. halterata* is more important, as this species still causes considerable damage in Delaware and southeastern Pennsylvania (Cantelo 1980). Also, feral populations may be a reservoir for the disease-causing *Verticillium* sp. bacteria that attacks mushrooms (White 1981). Previously, *M. halterata* was known only from mushroom farms, and was assumed to be unable to compete with the native *M. agarici* (Lintner) in wild mushrooms (Robinson 1978). The rearing of *M. chaetoneura* from *Pleurotus* is more difficult to interpret, as the only previous record of its larval food is decaying Lepidoptera larvae and pupae (Robinson 1971), possibly placing it in the polyphagous saprophage group. However, with recent attempts to culture *Pleurotus* spp. in Ontario (Patrick *et al.* 1983), this record could have importance to growers in the future.

The pitfall traps in the Arboretum collected 29 species of *Megaselia* and 7 other genera of phorids (Table 1). Of these, only the 5 species *M. brevicostalis* (Wood), *M. longipennis*, *M. pulicaria*, *M. rufipes*, and *M. setacea* (Aldrich) occurred in large numbers (20 or more specimens). Disney (1983) cautioned workers not to accept rearings from media such as carrion, fungi, and dung as proof of saprophagy, since there is increasing evidence that many *Megaselia* species are highly specialized predators or parasitoids (examples in Disney 1983; Robinson and Wisseman 1983). Conversely, species commonly regarded as parasitoids, like *M. giraudii* (Egger), *M. rufipes*, and *M. scalaris* (Loew), may be true saprophages that facultatively prey on inactive or dying insects (Disney 1983). *M. brevicostalis*, *M. longipennis*, *M. pulicaria*, and *M. setacea* may also belong to the latter group, as they have all been recorded as emerging from insect larvae or pupae (Robinson 1971). Most of the other species of phorids trapped are likely to be spurious records, species that are caught in any type of trap set out (e.g. *Diplonevra nitidula* (Meigen)), or generalized saprophages (e.g. *Puliciphora occidentalis* (Melander and Brues), *Dohrniphora incisuralis* (Lowe)).

Adults of *M. compressa* Borgmeier were the only phorids vacuumed from mushrooms. In Guelph, 6 specimens were collected from an unidentified species of mushroom growing from a rotten log, while in Meaford over 100 specimens were collected from *Coprinus* sp. on a lawn. This phorid is named for the chitinized, compressed ovipositor that is usually indicative of a parasitic lifestyle. The large numbers occurring on mushrooms could be due to adults feeding on the dissolved flesh of these mushrooms (commonly known as "inky caps") rather than oviposition.

Table I. Phorid flies collected in mushroom-baited pitfall traps in the University of Guelph Arboretum, Ontario

Species	No. trapped	
	1983	1984
<i>Conicera barberi</i> (Malloch)	1	2
<i>Diplonevra nitidula</i> (Meigen)	2	18
<i>Dohrniphora incisuralis</i> (Loew)	3	4
<i>Metopina fenyesi</i> Malloch	1	2
<i>Metopina subarcuata</i> Borgmeier	—	1
<i>Megaselia aequalis</i> (Wood)	3	—
<i>agarici</i> (Lintner)	2	—
<i>albibasis</i> Borgmeier	—	3
<i>aristalis</i> (Malloch)	6	2
<i>brevicostalis</i> (Wood)	—	20
<i>breviterga</i> (Lundbeck)	1	—
<i>brunnipes</i> (Malloch)	3	—
<i>crinifrons</i> Borgmeier	—	1
<i>decussata</i> Borgmeier	—	1
<i>femoralis</i> (Enderlein)	1	7
<i>fisheri</i> (Malloch)	9	3
<i>flava</i> (Fallén)	7	7
<i>hesperia</i> Borgmeier	—	1
<i>juli</i> (Brues)	—	1
<i>limburgensis</i> (Schmitz)	1	—
<i>longipennis</i> (Malloch)	3	23
<i>minuta</i> (Aldrich)	8	—
<i>nasoni</i> (Malloch)	5	—
<i>nigriceps</i> (Loew)	—	1
<i>nubilipennis</i> Schmitz	1	—
<i>postcrinata</i> Borgmeier	1	—
<i>procera</i> Borgmeier	1	—
<i>pulicaria</i> (Fallén)	99	22
<i>pygmaeola</i> Borgmeier	—	1
<i>retardata</i> (Malloch)	4	—
<i>ruficornis</i> (Meigen)	5	1
<i>rufipes</i> (Meigen)	18	67
<i>setacea</i> (Aldrich)	93	76
<i>straminipes</i> (Malloch)	1	5
<i>subpleuralis</i> (Wood)	1	—
unidentified	23	6
<i>Phora</i> sp. females	2	—
<i>Puliciphora glacialis</i> Malloch	—	4
<i>Puliciphora occidentalis</i> (Melander and Brues)	—	12
<i>Spiniphora excisa</i> (Becker)	4	—

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DEVELOPMENT OF THE POTATO STEM BORER, *HYDRAECIA MICACEA* (LEPIDOPTERA: NOCTUIDAE) IN THE LABORATORY AND FIELDR.J. WEST¹ and J.E. LAING

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Abstract*Proc. ent. Soc. Ont.* 115: 81-87 (1984)

The development of all immature stages of *Hydraecia micacea* (potato stem borer) in the laboratory and field was examined. Eggs required a minimum of 8 weeks of storage at 2°C before a high percentage (86%) hatched. Fifty percent of eggs exposed to -29°C for one week survived. Thermal constants and developmental thresholds, calculated by linear regression analysis, were 130.4°D_{7,5} for cold-treated eggs, 432.9°D_{8,7} for male larvae, 427.4°D_{9,2} for female larvae, 303.9°D_{5,6} for male pupae and 298.5°D_{5,5} for female pupae. In the field, eggs hatched about one week earlier than predicted whereas pupation and adult emergence occurred a few days later than the forecasted dates. The method used predicted 50% pupation and 50% adult emergence within a few days but was inadequate for predicting the time of hatching.

Introduction

The potato stem borer, *Hydraecia micacea* Esper, a polyphagous noctuid introduced from Europe ca. 1900, has become a pest of potato, rhubarb and corn in southern Ontario (Deedat *et al.* 1982). In spring, eggs hatch and larvae initially feed on grasses bordering cultivated fields and later attack crops, primarily those near field margins. Pupation, mating and oviposition occur during the summer while overwintering occurs in the egg stage. Studies concerning this pest have included aspects of its life history (Jobin 1963; Deedat *et al.* 1983) and its control (Deedat *et al.* 1982), but not its thermal requirements for development. Such information would be useful in timing applications of appropriate controls against susceptible life stages.

Materials and Methods

Development in the Laboratory. *H. micacea* were reared on a combination of corn leaf and artificial diet (West 1984) using a 16:8 L:D photoperiod and various constant temperatures which varied no more than ±0.5°C. Eggs, following 14 weeks of exposure at 2±1°C, were incubated at 12°, 15°, 17°, 23° and 25°C and checked daily to determine the time of hatch. Larvae and pupae were reared at 15°, 17°, 19°, 21°, 23°, and 25°C and checked every 12 hours to determine the time to complete development.

Because eggs of *H. micacea* will not hatch unless subjected to a period of cold (Chawla *et al.* 1975), it is probable that they have an obligatory diapause. To test this hypothesis, newly laid eggs were held for one week at 25°C, 3 weeks at 17°C (16:8 L:D) and 3 weeks at 10°C (0:24 L:D) before storage at 2°C (0:24 L:D). Eggs were removed from storage after 1, 2, 3, 4, 5, 6, 7 and 8 weeks and held at 25°C (16:8 L:D) for 2 weeks to promote hatching.

Developmental thresholds (t) and thermal constants (K) were determined for each immature stage by regressing developmental rate against temperature. The threshold temperature was approximated by the intersection of the regression line with the X axis and the thermal constant was calculated as $K = 1/b$, the inverse of the line's slope (Arnold 1959). Standard errors of t and K were determined following the method of Campbell *et al.* (1974).

The effect of freezing temperatures on the egg stage was tested. After storage at 2°C, eggs were exposed to short periods (1, 3 and 7 days) of extreme cold (-18° and -29°C) then were returned to 2°C for 12 weeks before removal for hatching at 25°C.

¹Present address: Newfoundland Forest Research Centre, Canadian Forestry Service, Box 6028, St. John's, Nfld. A1C 5X8

Development in the Field. The predictive value of thresholds and thermal constants determined in the laboratory was tested by accumulating degree-days in the field and noting the date of 50% hatching, pupation and adult emergence. Studies were undertaken during 1983 in a corn field near Guelph, Ontario. Eggs used were laid in the laboratory during 6 to 9 August 1982 by field-collected *H. micacea*. Eggs were held for one week at 25° C, acclimated to cold (17° C for 3 weeks followed by 10° C for 3 weeks) and then were held at 2° C for 18 weeks until they were transferred to the field on 17 February 1983. Approximately 200 eggs were placed in each of 3 petri dishes (9 X 50 mm) with tight-fitting lids, and placed either inside or outside a Stevenson screen located in a thatch of reed canary grass adjacent to the corn field. This was done because Stevenson screens may moderate climatic influences (Rahn and Brown 1971). One petri dish was placed in the Stevenson screen 5 cm above the soil surface and the remaining dishes were placed within the thatch also 5 cm above the soil surface. Although these dishes were shaded by the thatch, sunlight was expected to heat their interiors and so one of the dishes was fitted with a screened lid.

Mature larvae and pupae of *H. micacea* were collected from the field during 28 June to 8 July 1983 and placed in a walk-in cage adjacent to the field. *H. micacea* were held at ground level in ventilated plastic vials (3 X 7 cm) containing 10 cm³ of moistened vermiculite. Larvae were fed pieces of corn stem which were changed as needed. Larvae and pupae were observed daily to record the incidence of pupation and emergence.

Temperatures throughout the study were recorded by a Weather Measure[®] thermo-graph¹ in the Stevenson screen and by a Omnidata[®] degree-day accumulator². The temperature-sensitive probe of the degree-day accumulator was placed within the thatch during the period of egg hatch. During the period of larval and pupal activity the Omnidata[®] recorder accumulated degree-days inside the Stevenson screen. The Omnidata[®] recorder accumulated Fahrenheit degree-days every 10 minutes above programmed thresholds of 39°, 45°, 46°, 48° and 50° F (corresponding to 3.9°, 7.2°, 7.8°, 8.9° and 10.0° C, respectively). In addition, an estimation of the accumulated number of degree-days was calculated using the method of Allen (1976).

Results and Discussion

Development in the Laboratory. Hatching occurred within 7 to 10 days at 25° C but could be delayed by up to one month by rearing at 12° C (Table I). Development of larvae and pupae was also affected by temperature with developmental times at 25° C being approximately one-half of those at 15° C (Table II). At 15° C larval development for males was significantly faster than for females but at 17° and 25° C pupal development for females was significantly faster. Because of these differences, t- and K-values for pupation and emergence were determined using data for each sex (Table III). However, given the standard errors of t and K for larvae and pupae (Table III), it is concluded that there is little difference in developmental rate between sexes.

An estimate of the number of degree-days accumulated below the egg developmental threshold during cold storage (N), here defined as 'cooling degree-days', was determined by:

$$N = n(t - S)$$

where n = number of days of storage
 t = developmental threshold
 S = storage temperature (°C)
 for S < t.

¹Model T-610, Weather Measure Corporation, Box 41257, Sacramento, Calif. 95841, U.S.A.

²Model TA51, Omnidata International, Box 3489, Logan, Utah 84321, U.S.A.

Table I. Developmental time (days) of eggs of *Hydraecia micacea* at 6 constant temperatures¹ following 14 weeks at $2 \pm 1^\circ\text{C}$

	Temperature ($^\circ\text{C}$)					
	12	15	17	19	23	25
n	188	143	157	188	172	261
\bar{x} (days)	24.3	17.7	15.7	10.5	9.0	7.4
S.E.	0.1	0.1	0.1	0.1	0.1	0.1
Range	21-32	16-20	14-17	9-13	8-11	7-10

Table II. Developmental time (days) of larvae and pupae of male and female *Hydraecia micacea* reared at 5 constant temperatures¹

Stage	Sex	Temperature ($^\circ\text{C}$)				
		15	17	21	23	25
Larva	n	26	53	59	33	54
	\bar{x} (days)	64.4*	53.0	36.8	32.6	26.1
	S.E.	1.0	1.0	0.7	0.6	0.4
	Range	56-76	43-69	28-55	27-42	22-35
Males	n	53	53	47	44	39
	\bar{x} (days)	71.8*	56.0	38.6	33.1	25.7
	S.E.	1.9	1.3	0.9	0.7	0.5
	Range	57-121	43-89	30-52	23-47	22-36
Females	n	26	47	52	33	53
	\bar{x} (days)	32.4	27.9*	19.0	17.5	16.0*
	S.E.	0.5	0.2	0.2	0.2	0.1
	Range	28-38	25-32	16-23	15-20	15-20
Pupa	n	49	52	45	40	39
	\bar{x} (days)	31.2	26.7*	19.4	17.1	15.4*
	S.E.	0.3	0.3	0.2	0.1	0.1
	Range	25-37	21-32	16-23	16-20	14-18

* Denotes a significant difference ($P < 0.05$) in development at same temperature between sexes (Student's t-test using Satterthwaite's approximation where variances were unequal).

¹ photoperiod = 16:8 L:D.

Table III. Developmental thresholds and thermal constants determined for the immature stages of *Hydraecia micacea* using individual developmental rates. Eggs were stored for 14 weeks at 2° C before their development was examined

Stage Sex	n	t± S.E. (°C)	K±S.E. (degree- days)*	r	Equation
Egg	1109	7.5±0.09	130.4± 1.0	0.97	Y = -0.05751 + 0.00767X
Larva					
Males	223	8.7±0.35	432.9±12.3	0.92	Y = -0.02013 + 0.00231X
Females	237	9.2±0.32	427.4±12.4	0.91	Y = -0.02151 + 0.00234X
Pupa					
Males	210	5.6±0.32	303.9± 6.9	0.95	Y = -0.01849 + 0.00329X
Females	225	5.5±0.25	298.5± 5.3	0.97	Y = -0.01848 + 0.00335X

* Requirement for completion of life stage in 50% of the population.

Three weeks of storage at 2° C (115.5 cooling degree-days accumulated) were required before any hatching occurred, but 8 weeks of storage (308.0 cooling degree-days accumulated) were needed before a high percentage (86.4%) of eggs hatched (Table IV). This suggests that a period of near-freezing temperatures lasting a minimum of 2 months is necessary to terminate diapause.

The majority of eggs exposed to periods of extreme cold hatched although those held at -29° C for 7 days suffered considerable mortality (Table V). Temperatures as low as this are unlikely to be experienced for appreciable periods by *H. micacea* in the field, especially in southern Ontario. In addition, eggs normally are insulated by snow cover during the coldest months of the year.

Development in the Field. The location of eggs in the field influenced the time of hatching. Those in the ventilated dish in the thatch hatched first and those in the closed dish in the Stevenson screen hatched last (Table VI). The dishes in the thatch probably received more radiation and thus accumulated degree-days faster. There was little difference in the accumulation of degree-days between 14 and 17 May, the respective dates of 50% hatching for eggs in the ventilated and closed dishes in the thatch. However, temperatures during the day may have been warmer in the thatch than were recorded by the Omnidata® recorder or by the thermograph in the Stevenson screen. If this study were to be repeated, overwinter-

Table IV. Effect of storage¹ on percent hatching of *Hydraecia micacea* at 25° C²

Weeks of storage at 2° C	No. eggs	% eggs hatching	Accumulated cooling degree-days
1	221	0.0	38.5
1	220	0.0	77.0
3	260	0.7	115.5
4	231	0.4	154.0
5	232	5.6	192.5
6	217	18.4	231.0
7	217	39.2	269.5
8	214	86.4	308.0

¹ After oviposition, eggs were held for 1 week at room temperature, 3 weeks at 17° C and 3 weeks at 10° C prior to storage at 2° C.

² photoperiod = 16:8 L:D.

ing eggs should be observed *in situ* and a more sensitive method of recording temperatures is recommended. Fine constantan-copper thermocouples placed within leaf sheaths of grasses where eggs overwinter might be used to advantage in such a study.

The occurrence of hatching was not accurately predicted by Allen's (1976) method or with the Omnidata® recorder. One source of error may have been instrumentation. The Omnidata® recorder was powered by penlight batteries which may have been adversely affected by cold temperatures during the period of embryonic development in the eggs

Table V. The effect of exposure to extreme cold for 1, 3 and 7 days on the survival of eggs of *Hydraecia micacea*. Eggs were held at 2°C for 3 weeks prior to freezing and for 12 weeks after freezing before removal for hatching at 25°C¹

Temperature	Period held (days)	Number of eggs treated	Percentage of eggs hatching
-18°C	1	303	76.6
	3	336	70.0
	7	267	80.9
-29°C	1	217	81.1
	3	263	75.3
	7	314	50.6

¹ photoperiod = 16:8 L:D.

Table VI. Predicted and actual occurrence of 50% hatching, pupation and emergence of *Hydraecia micacea* at Guelph, Ontario, 1983

Stage	Starting date for degree-day accumulations	Method	50% occurrence		
			Predicted date	Actual date (accumulated degree-days)	% Error (E) ¹
Egg ² Batch A	Feb. 17	Allen	May 25	May 14 (86.6)	33.6
		Omnidata®	June 4	May 14 (69.4)	46.8
Batch B	Feb. 17	Allen	May 25	May 17 (89.1)	31.7
		Omnidata®	June 4	May 17 (77.8)	40.3
Batch C	Feb. 17	Allen	May 25	May 21 (108.9)	16.5
		Omnidata®	June 4	May 21 (91.7)	29.7
Larva Males	May 15	Allen	July 8	July 15 (533.9)	23.8
		Omnidata®	July 17	July 15 (403.3)	6.8
Females	May 15	Allen	July 9	July 16 (523.5)	22.5
		Omnidata®	July 18	July 16 (399.4)	6.6
Pupa Males	July 15	Allen	Aug. 1	Aug. 4 (362.4)	19.2
		Omnidata®	Aug. 4	Aug. 4 (301.1)	0.0
Females	July 16	Allen	Aug. 2	Aug. 4 (343.5)	15.0
		Omnidata®	Aug. 5	Aug. 4 (276.7)	7.3

¹ E = (AC - K)/K, where AC = accumulated degree-days on date of 50% occurrence; K = thermal constant.

² Batch A = ventilated dish in thatch; Batch B = closed dish in thatch; Batch C = closed dish in Stevenson screen.

prior to hatch. Other possible error sources are the t - and K -values derived from laboratory experiments. Extrapolation of the regression line to estimate t can lead to errors when temperature conditions tend toward the extremes under variable conditions (Stinner *et al.* 1974). As noted by Wilson and Barnett (1983), this method may over-estimate t because the relationship between developmental rate and temperature is non-linear at low temperatures. In addition, changes in the relationship between developmental rate and temperature at temperatures near the threshold for development would result in corresponding changes in the value of K . Because temperatures near t persisted for several months before egg hatch in the present study, it is not surprising that calculations using the linear degree-day method resulted in errors. Finally, the amount of chilling that eggs experience during diapause may affect the rate of post-diapause development. Therefore, it would be worthwhile in future studies to use eggs that overwinter in the field.

May 15 was chosen as the date to begin degree-day accumulations for larvae as 50% hatching was observed in the thatch between 14 and 17 May (Table VI). The Omnidata® recorder predicted 50% pupation and emergence within 1 to 2 days (Table VI), a very accurate estimation considering that a broad range in developmental times was observed for larvae and pupae in the laboratory (Table III). Degree-days were accumulated every 10 min. by the Omnidata® recorder and thus results were expected to be superior to those using Allen's (1976) method which required only daily maximum and minimum temperatures. Nevertheless, the Allen (1976) method predicted 50% pupation within 7 days and 50% emergence within 2 to 3 days (Table VI).

The accuracy in prediction of 50% pupation and 50% emergence in the field suggests that the thresholds calculated for larvae and pupae of *H. micacea* are realistic and that developmental times of laboratory-reared individuals are similar to those reared under field conditions. It should be noted, however, that larvae feed above and below the soil surface within a variety of non-cultivated and cultivated plants (Deedat *et al.* 1983). Since the nutritional quality of plants varies for insects (Friend 1958) and since microclimate near the ground is very subject to perturbation (Geiger 1965), developmental rates of *H. micacea* in the field are expected to vary. This may explain why, as observed by Deedat *et al.* (1983), adults are present in southern Ontario from late July to early September.

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**TOXICITY OF INSECTICIDES TO THE ASTER LEAFHOPPER,
MACROSTELAS FASCIFRONS (HOMOPTERA: CICADELLIDAE)
IN THE LABORATORY AND FIELD**

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Abstract

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Twelve insecticides currently registered for use or with potential for use in Ontario on carrots and lettuce were tested, using a Potter tower, for toxicity to the aster leafhopper (ALH), *Macrostelus fascifrons* (Stål.), vector of aster yellows. The synthetic pyrethroids, deltamethrin, permethrin, cypermethrin, and fenvalerate, were ca 3.3 to 67 times more toxic than carbaryl, currently the standard insecticide for ALH control in Ontario. Carbaryl was less toxic than carbofuran, but more toxic than other insecticides used on carrots, i.e., phosmet, parathion, mevinphos, malathion, and diazinon. Acephate was the least toxic insecticide tested. In field trials, permethrin reduced the incidence of aster yellows in lettuce, and was as effective as ca 10 to 20 times the concentration of carbaryl.

Introduction

The aster leafhopper (ALH), *Macrostelus fascifrons* (Stål.), is an important pest of several vegetable crops grown in Ontario, mainly because it is the vector of the mycoplasma-like agent causing aster yellows (AY) (Kunkel 1924). ALH adults are usually present in Ontario from June until September (Miller 1960) and, therefore, repeated applications of insecticides may be necessary to protect susceptible vegetable crops against AY. DDT was very effective for control of ALH (Chapman 1973), and malathion and carbaryl have been used extensively since the use of DDT was discontinued. Various systemic insecticides, applied to soil in granular formulations at time of seeding, are also effective (Henne 1970; Chapman 1973). Systemics generally are less effective on organic than on mineral soils (Chapman 1973), so growers in Ontario's Holland Marsh usually rely on spraying to control leafhoppers, most commonly using carbaryl or malathion, (M. Valk, personal communication).

Serious outbreaks of AY on lettuce and celery in Ontario in 1981 and 1983 suggested that currently recommended insecticides for ALH control on these crops were inadequate. Moreover, the development of integrated pest management for carrots in the Holland Marsh (Stevenson 1981) required that the efficacy against ALH of insecticides recommended for control of the carrot rust fly, *Psila rosae* (Fabr.), and the carrot weevil, *Listronotus oregonensis* (LeConte), be determined. This paper reports the results of laboratory bioassays of the toxicity to ALH adults of the insecticides most likely to be used on carrots and lettuce in the Holland Marsh. The results of 2 field trials evaluating permethrin for control of AY in lettuce are included.

Materials and Methods

Laboratory Bioassays. ALH adults were obtained from a colony maintained on barley (*Hordeum vulgare* L.) seedlings in a greenhouse (minimum temperature 21°C). Barley seedlings, ca 7 to 10 cm high, grown in 10-cm pots, were placed in cages containing ovipositing ALH adults. After about 1 week of exposure to adults, the pots of seedlings were removed and held in the greenhouse. When the eggs began hatching, the seedlings were shaken over sheets of paper to collect young nymphs at intervals of 24-48 hours. Nymphs were then placed onto fresh barley seedlings. Adults to be used for bioassay were collected when they were 3-5 days old. They were aspirated, in lots of 10, into 336-ml glass jars fitted with metal lids that had a center hole plugged with cotton. Leafhoppers were first anaesthetized in the jars with CO₂, 3.5 L/min, for 15 sec and within 2 min transferred to a

7-cm Whatman No. 1 filter paper in a 9-cm glass petri dish. They were then placed in a Potter tower and treated with technical grade insecticides in 5 ml of analytical grade acetone. Materials were applied for 10.5 sec at an air pressure of 150 mm mercury and allowed to settle for 5 sec. Six concentrations of each insecticide were used, each replicated 10 times. After treatment, the adults were returned to clean 336-ml glass jars and the lids replaced. Two leaves of barley (ca 6 cm long) were placed in the jars to sustain the adults. Mortality was determined after holding the jars for 24 h in a room at $20^{\circ} \pm 1^{\circ} \text{C}$, 60% RH and a 14:10 L:D photoperiod. Natural mortality of ALH handled by these procedures was ca 2%. Data were subjected to probit analysis using an Agriculture Canada Time Sharing (ACTS) program, adapted from Finney (1971), which incorporates Abbott's (1925) correction for natural mortality.

Field Trials. In 2 field trials, the "standard" insecticide for ALH control on lettuce, carbaryl, was compared to permethrin at 2 rates of application to lettuce, cv Ithaca. In 1978, 4 replicates of 3-row (7.5 m) plots were seeded 15 May. In 1980, plots were 3 rows, 14 m long, replicated twice and seeded 12 May. Sprays were applied in ca 560 L/ha water, using a push-cart sprayer designed by Menzies and Fisher (1975) that delivered 1100 L/ha at ca 2100 kPa. Each year, 6 sprays were applied at ca weekly intervals. When lettuce was ready to harvest, all plants in the centre row (1978) or in each of the 3 rows (1980) of each plot were examined *in situ*, and the numbers of healthy plants and those showing symptoms characteristic of AY were recorded. Percentages of plants infected were transformed by the arcsine method (Little and Hills 1972), analysis of variance was performed, and means were compared using Duncan's Multiple Range Test.

Results and Discussion

In the laboratory, the pyrethroids, generally, were much more toxic to ALH than any of the non-pyrethroids (Table I). The carbamate insecticides, carbofuran and carbaryl, were more toxic than the organophosphorous insecticides. Carbaryl was more toxic than any of the other insecticides currently registered for use on carrots (diazinon, parathion, phosmet) or lettuce (malathion, parathion, mevinphos) in Ontario, suggesting that this material probably remains the best choice among available materials for use against ALH. Phosmet, which is used to control the carrot weevil, was about one-third less toxic than

Table I. Toxicity of insecticides to adults of the aster leafhopper in the laboratory

Treatment	Concentration (%) ¹			Equation of Log-probit line
	LC ₅₀	Fiducial limits		
		Lower	Upper	
Deltamethrin	0.000045	0.000039	0.00005	$Y = 3.1x + 6.1$
Permethrin	0.00015	0.00014	0.00017	$Y = 2.5x + 4.6$
Cypermethrin	0.00024	0.00019	0.00032	$Y = 2.5x + 4.0$
Fenvalerate	0.00090	0.00082	0.00097	$Y = 2.8x + 2.3$
Carbofuran	0.00102	0.00081	0.00123	$Y = 4.4x + 0.6$
Carbaryl	0.00302	0.00273	0.00332	$Y = 3.0x + 0.5$
Phosmet	0.00429	0.00317	0.00515	$Y = 3.5x - 0.7$
Ethyl parathion	0.00518	0.00484	0.00558	$Y = 3.7x - 1.4$
Mevinphos	0.00528	0.00444	0.00619	$Y = 4.9x - 3.4$
Malathion	0.00640	0.00544	0.00715	$Y = 5.4x - 4.7$
Diazinon	0.00723	0.00634	0.00808	$Y = 6.1x - 6.3$
Acephate	0.01487	0.01358	0.01604	$Y = 4.1x - 4.0$

¹N = 100

carbaryl. Field tests are needed to determine whether or not phosmet would provide adequate control for ALH on carrots when it is applied for control of the carrot weevil. Acephate, which is recommended for ALH control in New York state, was the least toxic compound tested.

In field trials, the amount of AY in untreated plots was not more than 10%, however, this level of infection is probably typical of the Holland Marsh in a "normal" year. In 1978, permethrin, at 0.14 kg AI/ha, reduced the % infection by AY significantly ($P < 0.05$) (Table II). Carbaryl, applied at one-half the rate normally used in the field, did not reduce AY significantly.

Table II. Efficacy of carbaryl and permethrin applied 6 times¹ at weekly intervals at Bradford, Ontario for control of aster yellows in lettuce

Treatment ²	Rate (kgAI/ha)		Mean percent of lettuce with symptoms of aster yellows ³	
	1978	1980	1978	1980
Carbaryl	1.5	3.3	5.4 a	2.3 b
Permethrin	0.07	0.085	7.6 a	1.0 b
Permethrin	0.14	0.175	0.6 b	1.4 b
Check			10.0 a	8.1 a

¹ Dates of application, 1978: 20,28 June; 5,11,18,25 July; 1980: 17,24,30 June; 8,15,23 July.

² Carbaryl (Sevin 50W); permethrin, Ambush 50E (1978), 25W (1980).

³ Means within a column followed by the same letter were not significantly different ($P < .05$), Duncan's Multiple Range Test.

In the 1980 trial, all treatments reduced the incidence of AY significantly ($P < 0.05$) (Table II) with no differences between treatments. These findings indicate that increasing the rate of application of permethrin above 0.17 kg AI/ha would not be economically advantageous.

The laboratory bioassays, together with the field testing of permethrin, suggest that the pyrethroid insecticides are effective against the ALH-AY complex in the field. These materials need to be tested in the field under conditions of severe AY infection, such as occurred in 1981 and 1983 to determine if they will provide economic control of the disease under such conditions.

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**DOSE-MORTALITY RESPONSE OF *CHORISTONEURA FUMIFERANA*
(LEPIDOPTERA: TORTRICIDAE) TO A MICROSPORIDIUM,
*PLEISTOPHORA SCHUBERGI***

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The microsporidium, *Pleistophora schubergi* Zwölfer, can infect a wide range of insects including the spruce budworm, *Choristoneura fumiferana* (Clem.) (Wilson 1981, 1982). In past experiments, spores of *P. schubergi* were applied as surface contamination to the host's diet, making a precise determination of the spores ingested difficult, and calculation of dose-mortality response impossible (Wilson 1982). In this note the dose-mortality response is reported for spruce budworm larvae when treated as fourth instars with a known number of *P. schubergi* spores. Maintenance of the insects, construction of the bioassay capsule, and the technique of spore production were the same as those used for determining the dose response of spruce budworm to the microsporidium, *Nosema fumiferanae* (Thom.) (Wilson 1983). Spores of *P. schubergi* were counted in suspension using a hemacytometer and dilutions were made to give concentrations of 10^7 , 10^8 , 10^9 and 10^{10} spores/ml. These suspensions, which each contained 0.5% (v/v) of the spreader-sticker Nu-Film® (Miller Chemical and Fertilizer Corp., Hanover, Pennsylvania), were applied at a rate of $5 \mu\text{L}$ to individual needles of balsam fir, *Abies balsamea* (L.) Mill. Each needle thus had a deposit of 5×10^4 , 5×10^5 , 5×10^6 or 5×10^7 spores/needle. Each fourth instar was allowed to feed on a treated needle for 72 h; only those that consumed the entire treated area of the needle were used in the test. These larvae were returned to cups containing artificial diet and reared at $23 \pm 1^\circ\text{C}$ (16:8 L:D) and 60-80% R.H. Control insects were fed balsam fir needles treated with $5 \mu\text{L}$ of distilled water containing 0.5% (v/v) Nu-Film® and were reared in a similar manner. The tests were replicated three times with 15-25 larvae/dose used each time, for a total of 45-75 larvae/dose. More larvae were used for spore-treated needles than for controls to insure sufficient numbers of infected insects. Dead larvae were air-dried for a minimum of 7 days at 32°C , and weighed. Spores were counted using the method of Cantwell (1970) and the median lethal dose (LD_{50}) was determined by probit analysis (Finney 1971).

Larval mortality exceeded 80% after ingestion of 5×10^5 spores or more. A dose of 5×10^7 caused 100% mortality (Table I). When probits were plotted against the logarithm of the doses, the regression line was ($y = -0.33 + 1.11x$) with a slope and standard error of 1.11

Table I. Mortality, survival time and number of spores following ingestion of various doses of *Pleistophora schubergi* by fourth-instar spruce budworm

Dose (spores/ larva)	Number in test	Larval mortality (%)	Mean survival time \pm S.D. (days)	Pupal mortality (%)	Mean spores/ mg tissue $\times 10^6 \pm$ S.D.
Control	42	2	—	0	—
5×10^4	67	47	$22.9 \pm 10.7\text{a}$	43	$195.9 \pm 66.4\text{a}$
5×10^5	69	81	$22.6 \pm 9.9\text{a}$	84	$194.4 \pm 85.7\text{a}$
5×10^6	58	97	$17.9 \pm 8.2\text{b}$	100	$192.8 \pm 92.7\text{a}$
5×10^7	73	100	$13.9 \pm 5.7\text{c}$	—	$134.6 \pm 91.8\text{b}$

Means within columns followed by the same letter are not significantly different ($P = 0.05$, Student's t test).

± 0.18 . The LD_{50} was 6.3×10^4 spores per larva with 95% lower and upper fiducial limits of 3.6×10^4 and 1.0×10^5 spores per larva, respectively.

Survival times were not significantly different between doses of 5×10^4 and 5×10^5 ; however higher doses caused a significant decrease in survival time. Spore production in infected larvae, as indicated by mean spores per mg of tissue, was significantly lower when larvae ingested a dose of 5×10^7 spores. This decrease in production probably resulted from the shorter survival time of these insects as compared to those insects treated with lower doses (Table I). Kaya (1973) tested *P. schubergi* against fourth instars of *Anisota senatoria* (J.E. Smith) and found that death occurred somewhat earlier in this species than in infected spruce budworms. He found that a dose of 10^5 spores per larva resulted in death 19 days after treatment whereas larvae fed 10^6 spores died after 13 days. The mean survival time of fourth-instar spruce budworms ranged from 14 to 23 days depending on the dose.

In general, *P. schubergi* kills many insects under laboratory conditions. Infected larvae are usually smaller, display reduced vigor and feed less than healthy larvae. Although the period of lethal infection is relatively long, this may be advantageous for transmitting the microsporidian parasite to healthy larvae. More research is needed on the environmental persistence of this parasite and its effects on beneficial insects. However, due to its high degree of pathogenicity for spruce budworm, *P. schubergi* may have promise as a biological control agent for this forest pest.

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**OBSERVATIONS OF ADULT *CURCULIO CARYAE* (HORN)
(COLEOPTERA: CURCULIONIDAE) ON A PERSIAN WALNUT,
JUGLANS REGIA, IN SOUTHERN ONTARIO.**

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The pecan weevil, *Curculio caryae* (Horn), an important pest of commercial pecan orchards, (Harris 1983) was recently found attacking Persian walnut, *Juglans regia*, in southern Ontario (Foott and Timmins 1984). Several aspects of the bionomics of *C. caryae* on *J. regia* in southern Ontario not mentioned in the previous report are reported here.

A 0.5-m-wide band of Tanglefoot® was placed 1.2 m above ground level around a previously infested Persian walnut tree in Harrow, Ontario on 15 July 1984, to estimate adult emergence and activity. The Tanglefoot® was reapplied weekly or as needed and trapped adults were sexed and removed from the tree daily. We believe that the trapped individuals developed on the Persian walnut and not on other hosts as no pecan weevils have been observed within 2 km of the study area. Dissections of walnuts have shown that the tree studied has been parasitized (*sensu* Price 1977) by *C. caryae* since 1980 (Foott and Timmins 1984; Timmins and Quiring unpubl. data) which also supports this assumption.

Thirty-two males and 46 females were trapped between 29 July and 3 September with 50% of the males and females being caught by 13 and 19 August, respectively. These captures indicate that emergence of *C. caryae* adults infesting Persian walnut in southern Ontario starts at approximately the same time but terminates earlier than in more southern populations which attack pecan (Raney *et al.* 1970; Harris and Ring 1979; Alverson 1984). An examination of oviposition punctures in 50 nuts showed that the oviposition behavior of *C. caryae* on Persian walnut was similar to its oviposition behavior on pecan (Harris and Ring 1979) in that females usually only punctured a fruit once (48 of 50 nuts had only one oviposition puncture, $X^2 = 42.3$, $P < .001$) and the puncture was usually in the distal third of the nut (86.5% of all punctures, $N = 52$, X^2 on count data = 27.8, $P < .001$).

The presence of a substantial *C. caryae* population, sustained on Persian walnut for at least 2 generations (*i.e.*, 4 years), indicates that the pecan weevil is well adapted to this alternative host plant.

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FRASS DROP AS A METHOD FOR EVALUATING INSECTICIDE EFFICACY IN FORESTS

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Traditionally, feeding by insects following the application of insecticides has been measured by the quantity of damage done to the host plant. This damage is one measure of efficacy. Few experiments use the weight of frass that drops as a measure of feeding activity and thus of efficacy. The collection of frass was used to assess the effects of various insecticides on the feeding of treated larvae (Rhumbler 1929; Schwerdtfeger 1930) and to study the influence of weather upon feeding and development of forest insects (Monro 1935). Green and de Freitas (1955) reviewed studies where frass samples were used indirectly to measure populations of forest insects and Morris *et al.* (1975) collected frass to estimate the feeding activity of larval spruce budworm, *Choristoneura fumiferana* (Clem.) on white spruce, *Picea glauca* (Moench) Voss, which was sprayed with *Bacillus thuringiensis* Berliner combined with Orthene.

Other investigators have found frass drop useful for evaluating the impact of treatments with nuclear polyhedrosis virus (NPV) on both feeding activity and on the survival time of treated insects (Cunningham 1982). More recently Volney *et al.* (1983) used larval droppings to determine the timing of insecticide applications to treat California oakworm, *Phryganidia californica* Packard, in urban oaks. Our objective was to determine if a postspray collection of frass could be used to assess the efficacy of an insecticide for *C. fumiferana*.

The study was conducted in May and June 1981 near Bathurst, New Brunswick, as part of larger field trials which were designed to determine the efficacy and environmental impact of 2 formulations of aminocarb. Matacil 180F®, a flowable insecticide, and Matacil® 1.8D, an oil-soluble concentrate, 2 treatments with each formulation; a treatment with Atlox 3409F®, the emulsifier used in the aqueous mix; and an untreated control (Table I) made 6 study plots. Treatments were applied using a Cessna 188 Ag Truck® aircraft fitted with 4-AU3000 Micronair® rotary atomizers.

A plastic container (39 by 33 by 15 cm deep; 1287 cm² surface area) containing 1 L of 1.0% Formalin solution was placed on the ground at the drip circle of each of 10 balsam fir trees, *Abies balsamea* (L.) Mill., in each plot approximately 1 h before the spray was applied. Containers were collected 24 h after the spray.

Frass which had fallen into the containers was removed with an aquarium dip net having 100- μ m-diameter mesh, was placed into jars and air dried in the field. The samples were then stored in a freezer at -20°C and at a later date oven dried at 150°C for 4 h. The frass was separated from any extraneous materials and its dry weight measured with a Mettler Model 54 analytical balance.

Populations of larval insects were monitored from 3 to 30 June. Two 46-cm branches, one from the upper third section of the crown and one from the midcrown, were taken from each of the same 10 sample trees under which frass was collected. The living insects on each branch were recorded and the number of budworms per branch per tree was determined. From these data, budworm populations which infested the trees during the frass-collecting period were estimated. These numbers were then used to investigate correlations between budworm populations and weight of frass collected. It was established that *C. fumiferana* accounted for ca 99% of the larvae counted. Defoliation was evaluated by taking 2 46-cm branches from each of the 10 sample trees and assessing the damage using Fettes' method (Fettes 1950).

The quantity of frass excreted by insects is directly related to their number and the amount of food ingested per individual. Because both of these parameters can be influenced by an insecticide, the frass collected in this study was expected to measure the

Table I. Summary of treatment and weather data, Bathurst, New Brunswick, 1981

Block	Treatment	Application		Average weather conditions during application			
		Dates (June '81)	Times	Temp. (°C)	Wind (kph) and direction	Cloud cover (%)	R.H. (%)
1	Matacil 180F ¹ + Atlox 3409F ² + water	12	2005	13.0	0.2	10	83
		18	0635	10.7	2.0 SW-W	10	96
2	Matacil 180F + I.D. 585 ³	12	2100	10.0	0.0	0	96
		18	0720	13.7	5.0 W	10	73
3	Matacil 1.8D + Sunspray 6N ⁴	13	2024	17.2	0.0	0	69
		18	2034	20.7	1.0	0	56
4	Matacil 1.8D + I.D. 585	16	0610	10.0	0.5 S-SW	100	79
		19	0724	18.0	1.0 W-NW	0	87
5	Atlox 3409F + water	15	2030	12.5	1.0 SE-E	100	77
		19	0608	13.7	0.0 SW	0	85
6	Untreated control	N/A	N/A	-	-	-	-

¹Matacil supplied by Chemagro Ltd., Mississauga, Ontario, applied at 70 g AI/ha.

²Atlox 3409F supplied by Atlas Chemical Industries, Brantford, Ontario.

³Insecticide Diluent 585 supplied by Shell Canada Ltd., Toronto, Ontario.

⁴Sunspray 6N oil supplied by Sun Oil Co. Toronto, Ontario.

- All treatments applied at 1.5 L/ha and spray times averaged 15 min/application.

- Lower dates refer to 2nd applications.

efficacy of the treatments. In the 4 plots treated with aminocarb there were less than 5 larvae/tree as compared to 45 in the control and 14 in the plot treated with emulsifier (Table II). There was only one intermediate value, however correlations were found between frass and budworm populations ($r^2 = 0.80$) and between frass and defoliation ($r^2 = 0.98$). The initial size of the populations, initial defoliation, and initial levels of frass drop were unknown, but not necessary because change in population was not being measured. However, these data suggest that if an insecticide significantly reduces budworms or their feeding, this reduction will be measurable as a reduction in frass deposited. Random or systematic collections of this frass can then be used to estimate the effectiveness of the treatment.

Table II. The relationship between dry weight of frass collected, mean number of spruce budworm larvae (SbW) and percent defoliation

Block	No. of SbW ¹ /tree (X ± S.D.)	Wt. of frass ² (gms)	% Defoliation (X ± S.D.)
1	2.00 ± 2.9	0.209	13.9 ± 11.2
2	1.70 ± 1.2	0.381	9.5 ± 6.5
3	0.20 ± 0.6	0.466	23.2 ± 13.6
4	5.00 ± 7.3	0.510	20.7 ± 13.9
5	14.40 ± 6.5	4.247	62.3 ± 15.4
untreated control	45.1 ± 17.2	5.234	75.5 ± 16.6

¹Taken 3 to 7 days after the 2nd application.

²Total frass collected from 10 sample trees 24 h after the 2nd application.

We are fully cognizant that localized microweather conditions within the forests could have introduced variability in larval responses and/or dissemination of windblown frass; however, we believe that these differences were inconsequential. Frass from insects other than budworm was not considered a source of error because the larval populations in the study consisted almost entirely of *C. fumiferana*.

We believe the frass-drop method is better suited to situations where destructive sampling of the host plant is undesirable, and where a single or numerically dominant insect species is the problem. Since most lepidopterous larvae produce pellets which are often specific to species, genus or family (Volney *et al.* 1983), the method could still be applicable to infestation involving several species of caterpillars. Morris and Moore (1983) reported that surviving spruce budworms in plots sprayed with *Bacillus thuringiensis* weighed significantly less than those in untreated plots, thus it appears that frass-drop could be used to augment measurements of insect biomass when evaluating sublethal or slow-acting compounds.

In conclusion, this work has shown that a collection of frass can be used, especially by forest managers, to estimate the effectiveness of an insecticide applied to control spruce budworm.

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DEDICATION**The Proceedings of the Entomological Society of Ontario
Volume 116**

It is with great pleasure that we dedicate this issue of the Proceedings to Professor D.H. Pengelly, who devoted countless hours to the Entomological Society of Ontario. Moving from Director to Secretary-Treasurer of the Society in 1966, "D.H." filled that double position until 1975, then served as Treasurer of the Society until 1979. It is particularly fitting that this issue be dedicated to Dr. Pengelly, since it contains the major papers of his last three graduate students in the Department of Environmental Biology at the University of Guelph, where he was on faculty from the inception of the department until his retirement in 1982. D.H. is now in his second career, as a farmer in Manitoba—we wish him the best!

A REVISION OF THE NEW WORLD SPECIES OF *MINILIMOSINA* ROHÁČEK (DIPTERA: SPHAEROCERIDAE)

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Abstract

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The genus *Minilimosina* is revised for the New World, with the description of a new subgenus, *Amputella* and the following 21 new species: *intercepta*, *vixa*, *bipara*, *archboldi*, *contrasta*, *masoni*, *ternaria*, *digitata*, *bistylus*, *priapismus*, *erecta*, *curvistylus*, *sclerophallus*, *zeda*, *baculum*, *longisternum*, *intermedia*, *lepida*, *tuberculum*, *pulpa*, and *accinta*. The following new synonymies are established: *M. dissimilicosta* (Spuler) for *M. hackmani* (Roháček); *M. niveipennis* (Malloch) for *Limosina varicosta* Malloch and *Limosina mollis* Richards; *M. vitripennis* (Zetterstedt) for *Leptocera albifrons* (Spuler). *Minilimosina parvula* (Stenhammar), *M. trogeri* Roháček, *M. gemella* Roháček, *M. fungicola* (Haliday), *M. albinervis* (Duda), and *M. vitripennis* (Zetterstedt) are recorded from the Nearctic region for the first time. A key is provided to New World species and the phylogeny of the entire genus is discussed.

Introduction

The genus *Minilimosina* was erected by Roháček (1983) to include 22 Palaearctic species and is equivalent (in part) to the *Limosina fungicola* group of Richards (1930). Roháček (1983) divided *Minilimosina* into three subgenera: *Minilimosina* Roháček, *Allolimosina* Roháček and *Svarciella* Roháček. All three subgenera are recorded here for North America in addition to a distinctive fourth subgenus, *Amputella*, new subgenus.

The subgenus *Minilimosina* includes 15 species in the New World, five of which are also found in Europe. The subgenus *Allolimosina* includes only two New World species, one of which is also found in Europe. There are nine New World species in *Svarciella*, only two of which are known from Europe. *Amputella* is a primarily Neotropical subgenus. One of the six *Amputella* species described here has a range extending north into Canada, but no species occurs outside the New World.

Little is known about the biology of most *Minilimosina* species, even though some species are common. *M. parva* (Malloch) is among the most common fungivorous Diptera in North America, and *M. fungicola* (Haliday) is a common, synanthropic species. Several species are phytosaprophagous and tend to be collected rarely. Most specimens considered in this study were collected by use of dung or carrion traps.

Minilimosina species can be separated from other Limosiniinae by the combination of a mid tibia which lacks a mid-ventral bristle, a long telescoping female abdomen, and the simple wing venation, in which the costa extends beyond the tip of R_{2+4} . Similar taxa are the genus *Xenolimosina* Roháček, in which the hind tibia has a long dorsal bristle, and the species *Aptilotus spatulatus* Marshall. *A. spatulatus* is clearly part of the *Aptilotus pulex* group on the basis of the male abdomen, but the female retains a primitive, *Minilimosina*-like habitus (Marshall 1983). As suggested by this sort of similarity between genera, the diagnostic features for *Minilimosina* are plesiomorphic for the subfamily Limosiniinae. There are no outstanding synapomorphic characters for the genus as a whole, however there is no positive evidence that the group is not monophyletic. Unless such evidence is found in the form of synapomorphies between part of *Minilimosina* and another genus, the genus *Minilimosina* should be retained as a convenient grouping of generally similar insects. Each of the subgenera are more clearly defined on the basis of synapomorphic characters.

Materials and Methods

Many of the specimens on which this paper is based were collected in baited pitfall traps set by Dr. A. F. Newton of the Museum of Comparative Zoology, Cambridge, Dr. S. B. Peck of Carleton University, Ottawa, or by the author. These specimens were stored in alcohol, later dried using a critical-point drier, and then mounted. Specimens were also borrowed from the following institutions: Biosystematics Research Institute, Ottawa, Canada (BRI); American Museum of Natural History (AMNH); University of California at Berkeley (BERK); California Academy of Sciences, San Francisco (CAS); Field Museum of Natural History, Chicago (FLD); Florida State Collection of Arthropods, Gainesville (FSC); Museum of Comparative Zoology, Cambridge (MCZ); Frost Entomological Museum, Pennsylvania State University (PSU); National Museum of Natural History, Washington (USNM); Naturhistorisches Museum Wien, Austria (NMW); and the University Zoological Museum, Helsinki, Finland (ZMH). Unless otherwise noted, specimens are retained in the University of Guelph Collection or, in the case of long paratype series, distributed to other museums with large sphaerocerid collections such as the Silesian Museum, Opava, Czechoslovakia (JRO).

In order to examine male and female terminalia, the abdomens of many specimens were removed and macerated in hot 10% KOH. Abdominal preparations were examined in glycerin or glycerin gel, then stored in plastic microvials pinned under the specimen.

Minilimosina Roháček 1983:27
Type Species *Limosina fungicola* Haliday 1836

Generic diagnosis. Length 0.9-2.1 mm. Colour brown to shining black. Interfrontal bristles small, equal or subequal, in 2-5 pairs. Eye 1-3 times as high as gena, anterior genal bristle short to medium length. Katepisternum with a large dorsal bristle and a small anterodorsal setula. Mid tibia of both sexes with only weak ventral setulae at middle, males sometimes with a row of distal ventral spinules; apicoventral bristle well developed. Mid tibia with a dorsal bristle in distal 1/4, an anterodorsal bristle in proximal 1/3, and smaller anterodorsal and posterodorsal bristles just above distal 1/4 (referred to as distal anterodorsal and distal posterodorsal bristles) (Figs. 1-5). Acrostichal bristles in 4-8 rows, dorsocentral bristles in 1 or 2 pairs, the anterior pair short. Wings always well developed, costa extended beyond apex of R₄₊₅ (except in *contrasta* n.sp.), outer angle of cell dm usually weakly appendiculate. Sternite 5 of male usually with a comb-like structure posteromedially. Sternite 6 simple or with posterior lobes. Epandrium with uniformly short bristles. Cercus weakly developed, with at least 1 long bristle. Surstylus and internal genitalia variable; distiphallus simple in structure. Female postabdomen long and retractile; tergite 8 long, often divided into 2 or 3 pigmented areas; sternite 8 often reduced; hypoproct large and well developed; cercus very long, with long sinuate hairs.

KEY TO THE NEARCTIC AND NEOTROPICAL SUBGENERA AND SPECIES OF *MINILIMOSINA* ROHÁČEK

- 1. Upper of 2 costagial bristles long, usually subequal in length to posterior dorsocentral bristle. (Costagial bristles often broken on pinned specimens.) Sternite 5 of male concave and deflexed posteromedially, deflexed part often long and projected posteriorly through concavity (Figs. 43-47). Left paramere well developed, right paramere vestigial. Distiphallus reduced to a small, sclerotized lobe; epiphallus well developed (Fig. 112). Sternite 8 of female reduced, often split into small pieces *Amputella* new subgenus 2
- Costagial bristles subequal in length. Sternite 5 of male usually with a posteromedial comb or short deflexed process, never with a concave margin. Parameres equally developed. Distiphallus usually largely membranous; epiphallus absent. Sternite 8 of female consisting of a single sclerite 7

- 2. Second costal sector 0.7-0.8 times as long as third. Tergite 8 of female complete, at most slightly depigmented medially (Fig. 160) 3
- Second costal sector subequal to third. Tergite 8 of female apparently split medially or with a window-like area posteriorly (Fig. 154) 4
- 3. Surstylus with 3 (rarely 4) stout bristles forming a compact comb (Fig. 113). Sternite 8 of female reduced to 2 small sclerites (Fig. 162) *ternaria* n.sp. North America.
- Surstylus with stout bristles spread out along posterior margin (Fig. 110). Sternite 8 of female forming a single, ring-shaped sclerite (Fig. 153) *digitata* n.sp. Mexico.
- 4. Posteromedial lobe of male sternite 5 very large, over half as long as sternite (Fig. 43). Division between anterior and posterior lobes of surstylus shallow (Fig. 98). Tergite 8 of female darkly pigmented medially; sternite 8 made up of a central and 2 lateral sclerites *priapismus* n.sp. Mexico.
- Posteromedial lobe of male sternite 5 shorter (Figs. 45, 47). Division between anterior and posterior lobes of surstylus deep (Figs. 101, 104, 107). Tergite 8 of female depigmented medially; sternite 8 made up of 4 pieces or reduced to a single piece 5
- 5. Tergite 8 of female with a posterior, desclerotized, window-like area (Fig. 154). Sternite 8 of female simple, pale (Fig. 156). Apex of posterior process of male sternite 5 bent ventrally (Fig. 45) *erecta* n.sp. Mexico.
- Tergite 8 of female dark, shining; with a straight medial suture line dividing it into 2 halves (Fig. 148). Sternite 8 of female divided into 4 dark pieces (Fig. 147). Process male of sternite 5 straight (Fig. 47). 6
- 6. Anterolateral process of surstylus long, whip-like, curving posteriorly (Fig. 108). Lateral pieces of female sternite 8 elongate, much longer than central piece (Fig. 150) *curvistylus* n.sp. Panama.
- Anterolateral process of surstylus short, projected ventrally (Fig. 104). Lateral pieces of female sternite 8 short (Fig. 147) *bistylus* n.sp. Mexico, Panama.
- 7. Two pairs of dorsocentral bristles. Body often shining black subgenus *Svarciella* Roháček 24
- One pair of dorsocentral bristles. Body never shining black 8
- 8. Cell dm very short, anterior outer corner obtuse-angled and posterior outer corner acute-angled. Second costal sector no more than 0.7 times as long as third (Fig. 203). Surstylus without posteroventral spur. Hypandrium short subgenus *Allolimosina* Roháček 9
- Cell dm longer, with anterior outer angle acute-angled to rectangular, or rarely slightly obtuse-angled; posterior outer corner never acute-angled. Second costal sector usually over 0.7 times as long as third. Surstylus with a posteroventral spur. Hypandrium long subgenus *Minilimosina* Roháček 10
- 9. Sternite 5 of male with 2 comb-plates in front of posteromedial region (Fig. 25). Surstylus long, dark, and almost bare (Figs. 79, 187). Tergites 6 of 7 of female greatly reduced *M. (Allolimosina) rotundipennis* (Malloch) Florida, Arizona, Puerto Rico, Brazil.
- Sternite 5 of male with a single posteromedial comb row. Surstylus pale, broad, many-lobed, and setose. Tergites 6 and 7 of female simply sclerotized

- *M. (Allolimosina) albinervis* (Duda)
Eastern North America.
- 10. Apical scutellar bristles 0.5-1.4X length of scutellum 11
— Apical scutellar bristles over 1.5X length of scutellum 14
- 11. Apical scutellar bristles slightly longer than scutellum. Sternite 5 of male with the solid, dark apex of posteromedial comb longer than length or width of its base which is evenly curved with scale-like bristles (Fig. 21) *intermedia* n.sp.
Quebec.
— Apical scutellar bristles shorter than or equal to scutellar length. Dark apical part of male sternite 5, if present, shorter 12
- 12. Second costal sector at least 0.8x length of third. Sternite 5 of male with a blunt, hairy posteromedial lobe (Fig. 18). Hypoproct entirely setulose (Fig. 132)
..... *fungicola* (Haliday)
Holarctic.
— Second costal sector usually less than 0.8x length of third. Posteromedial comb of male sternite 5 with a solid apical process (Figs. 19-21). Hypoproct usually with a bare anterior lobe (Fig. 135) 13
- 13. Middle of katepisternum with a shining spot. Basal part of posteromedial comb on male sternite 5 with a bare central area (Fig. 20). Spermathecae short, cup-shaped (Fig. 116) *longisternum* n.sp.
Mexico.
— Middle of katepisternum polliose, only anterior corner of katepisternum shining. Basal part of posteromedial comb covered with scale-like bristles. Spermathecae wrinkled-cylindrical (Fig. 134) *gemella* Roháček
Holarctic.
- 14. Outer half of R₄₊₅ strongly curved towards costa (Fig. 201). Paramere strongly setose (Fig. 50). Anterior margin of hypoproct deeply concave *sclerophallus* n.sp.
Venezuela, Ecuador.
— R₄₊₅ more gently curved up to costa. Paramere with at most a few minute setulae. Anterior margin of hypoproct straight or lobate 15
- 15. Greatest eye height at least twice as high as gena 16
— Greatest eye height less than 1.8x genal height 19
- 16. Mid tibia with distal anterodorsal and posterodorsal bristles small, subequal, much smaller than distal dorsal. Posteromedial comb of male sternite 5 made up of 2 short rows of flat bristles, the outer row strongly convex (Fig. 12). Female sternite 8 Y-shaped, with 3 lobes (Fig. 123) *parva* (Malloch)
Widespread in North America.
— Mid tibia with distal posterodorsal bristle larger than distal anterodorsal bristle. Posteromedial comb concave or with a single dark lobe. Female sternite 8 not Y-shaped 17
- 17. Sternite 5 of male with posteromedial comb bearing a solid, pointed lobe (Fig. 16). Female sternite 8 much larger than hypoproct, deeply concave on anterior margin (Fig. 120) *nasuta* (Spuler)
Western North America.
— Sternite 5 of male with a concave or split posteromedial comb. Female sternite 8 usually smaller and lobate rather than concave anteriorly 18
- 18. Frons with 2 inclinate inner orbital setulae between interfrontal and orbital bristles. Posteromedial comb of male sternite 5 deeply concave, apparently divided into 2 tufts of flat setae (Fig. 11). Sternite 8 of female trilobate anteriorly (Fig. 141)

- *zed*a n.sp.
 Alberta.
- Frons bare between orbits and interfrontal strips. Posteromedial comb gently concave (Fig. 9). Sternite 8 of female T-shaped *parvula* (Stenhammar) Holarctic.
19. Sternite 5 of male with a long, pointed posteromedial process which is longer than the bristled row at its base (Fig. 15). Surstylus with a subquadrate anteroventral lobe (Fig. 68) *trogeri* Roháček Ontario, Quebec, Wyoming, Austria, Finland.
 - Sternite 5 of male never with a long, pointed posteromedial process. Anterior part of surstylus rounded, pointed, or club-shaped 20
 20. Sternite 5 of male with a posteromedial lobe ending in a serrate-tipped plate resembling a butterfly scale (Fig. 17). Parameres bifid at apex (Fig. 75) *lepida* n.sp. Saskatchewan, Ontario.
 - Sternite 5 never with a solid posteromedial plate. Parameres simple or curved at apex 21
 21. Surstylus with a large anteroventral club (Fig. 58). Posteromedial lobe of male sternite 5 with a small, dark process distally (Fig. 13) *baculum* n.sp. Ontario, British Columbia, Finland.
 - Surstylus never with a large ventral club. Posteromedial lobe of sternite 5 with uniformly small setulae 22
 22. Sternite 5 of male with 6 large bristles projected over posteromedial lobe (Fig. 10). Parameres short, thick (Fig. 78) *accinta* n.sp. Utah.
 - Sternite 5 never with large bristles projected over posteromedial lobe. Parameres long and slender 23
 23. Apex of posteromedial lobe on male sternite 5 sinuate (Fig. 14). Length about 1.0 mm *pulpa* n.sp. Wyoming.
 - Apex of posteromedial lobe on male sternite 5 straight (Fig. 23). Length closer to 1.5 mm *tuberculum* n.sp. Wyoming.
 24. Sternite 8 of female reduced, narrow, no wider than hypoproct (Fig. 165). Sternite 5 of male with a simple posteromedial, setulose lobe (Fig. 40) *bipara* n.sp. Panama, Venezuela.
 - Sternite 8 of female larger than hypoproct. Sternite 5 of male concave or with a comb of stout bristles 25
 25. All abdominal tergites heavily sclerotized, dark. Distiphallus narrow, simple. Each spermatheca cylindrical, with an apical invagination 26
 - Tergites 1-5 pale, contrasting with the darkly, sclerotized terminalia. Distiphallus usually large, mostly membranous, with a long ventral flagellum (Fig. 93). Each spermatheca of known females short, usually with an apical evagination (Fig. 185) 28
 26. Mid tibia of male with only simple setulae along ventral surface. Sternite 5 of male with a very large convex bulge in front of posteromedial comb (Figs. 38, 39). Surstylus large, cup-shaped, without stout bristles (Fig. 38). Sternite 8 of female longer than wide, bare except for area surrounding a posterior concavity (Fig. 174) *dissimilicosta* Spuler Europe, western North America.
 - Mid tibia of male with a double row of ventral spines. Sternite 5 of male flat, with a posteromedial comb of stout, flat bristles (Fig. 30). Surstylus with 3 stout bristles on

- posterior lobe (Fig. 31). Hypoproct wider than long, mostly setulose (Fig. 171) 27
27. Antennae and anterior part of frons yellowish brown or orange. Epimeron with large shining spots. Surstylus with a small external lobe (Fig. 31) *intercepta* n.sp.
Eastern North America.
— Antennae and frons brown. Epimeron with very small shining spots. Surstylus with a large external lobe (Fig. 35) *vixa* n.sp.
Northeastern North America.
28. Antennae orange or yellow-brown. Second costal sector less than or equal to half as long as third 29
— Antennae brown. Second costal sector 0.7-0.8x as long as third 31
29. Antennae, gena, lower frons and face orange or yellow-brown. Second costal sector 0.4 times as long as third (Fig. 206). Hind tibia with a dorsal, preapical tibial bristle. First 2 tarsomeres of hind leg subequal in length and width *masoni* n.sp.
Mexico.
— Antennae sharply contrasting in colour with the dark frons, gena and face. Second costal sector 0.5 times as long as third. Hind tibia with only small dorsal setulae. Second tarsomere of hind leg longer and thinner than first tarsomere 30
30. Scutum and scutellum strongly convex. Sternite 5 of male with a simple posterior margin. Spermathecal ducts very long (Fig. 179) *niveipennis* (Malloch)
Costa Rica.
— Scutum and scutellum flat. Sternite 5 with a dark, deflexed posteromedial lobe (Fig. 28). Spermathecal ducts short (Fig. 176) *contrastata* n.sp.
Ontario, Quebec, Maryland.
31. Frons, ocellar triangle, lunule, face, facial cavity and gena silvery white to silvery blue dusted, only the frontal triangle bare and shining. Tergites 3-5 greatly reduced, sclerotization indistinct. Deflexed posteromedial process of male sternite 5 broadly Y-shaped (Fig. 29) *vitripennis* (Zetterstedt)
Holarctic.
— Head without silvery white areas, frontal triangle lightly pollinose, middle of interfrontal area bare. Tergites 3-5 pale but distinctly sclerotized. Deflexed posteromedial process of sternite 5 with a large comb of flat bristles and 2 lateral apically setose lobes (Fig. 26) *archboldi* n.sp.
Florida.

Descriptions (or diagnoses of taxa recently described by Roháček) follow in alphabetical order within each subgenus. The subgenera are dealt with the following order: *Minilimosina*, *Allolimosina*, *Svarciella*, and *Amputella*.

Subgenus *Minilimosina* Roháček 1983:37
Type Species *Limosina fungicola* Haliday 1836

Subgeneric diagnosis. Small, 1.0-1.9 mm; usually dull in colour. Orbits, ocellar triangle and interfrontal strips silvery to pollinose; middle of interfrontal plate shining brown to silvery black, intervening areas forming a dull, black M-shape. Postocellar bristle minute or absent; face protrudent between antennae (Fig. 189), strongly concave and carinate below. Mid femur with 2-5 long ventral bristles near base, mid tibia of male with at least some weak spinules forming a distal ventral row. Costa always extended clearly beyond tip of R_{4+5} , cell dm rounded or obtuse angled and indistinctly or not appendiculate at outer posterior corner. Dorsocentral bristles in a single prescutellar pair or anterior pair difficult to distinguish from acrostichal setulae. Sternite 5 of male with a narrow posteromedial lobe covered with comb-like bristles. Basiphallus and distiphallus simple; distiphallus with

sclerotized dorsal and ventral processes and relatively little exposed membrane. Tergites 6 and 7 of female often reduced, sternite 8 often greatly reduced.

Minilimosina (Minilimosina) accinta new species

Figs. 10, 76, 77, 78, 191

Description, male (female unknown). Length 1.1 mm. Interfrontal plate broad, slightly tapering, bordered by 3 equal interfrontal bristles, subequal in width and height. Eye 1.3 times as high as gena. Mid tibia with a row of very weak distal bristles and an apical bristle ventrally. Distal posterodorsal bristle of mid tibia twice as long as adjacent anterodorsal bristle, half as long as distal dorsal bristle. Scutum with 4-5 rows of acrostichal setulae between dorsocentral lines, dorsocentral bristles in 1 prescutellar pair 0.7 times as long as scutellum. Prescutellar acrostichal bristles in a single pair, 3 times as long as acrostichal setulae. Scutellum 0.7 times as long as wide, apical bristles as long as scutellar width. Mesopleuron pollinose except shining anterior part of episternum. Halter uniformly light brown. Wing with costagial bristles subequal, small; second costal sector slightly greater than half as long as third; veins uniformly light in colour (Fig. 191).

Abdomen. Syntergite 1+2 1.5 times as long as tergite 3. Sternite 5 with 6 long bristles posteromedially, projecting over a lobe bearing rows of small scale-like setae (Fig. 10). Surstylus with a long, lobate are anteriorly, a stout posterior bristle and several smaller bristles (Figs. 76, 77). Paramere broad, blunt; distiphallus broad, distally bilobed (Fig. 78).

Types. *Holotype* (♂, BRI): U.S.A. **Utah.** Duchesne Co., Uinta Mts., Rocky Sea Pass, 11200', 30.vii-12.viii.1979, carrion, rocky tundra, S.&J. Peck. *Paratype:* **Utah.** Duchesne Co., Mirror Creek, 10300', 30.vii-12.viii.1979, meadow, malaise trap, S.&J. Peck (1♂).

Etymology. The specific name is from the Latin for "well armed", and refers to the armature of sternite 5.

Comments. Although known from only 2 specimens, the strong constriction of the anterior surstylar lobe and the conspicuous chaetotaxy of the male sternite 5 make this an easily identifiable species. Its probable closest relative is another rare, western species, *M. pulpa*. Both species are known only from high alpine sites, and were collected on carrion. Their closest relative is the European species *M. tenera*, known only from a peat bog in Czechoslovakia.

Minilimosina (Minilimosina) baculum new species

Figs. 13, 58, 59, 192

Description, male (female unknown). Length 1.5 mm. Interfrontal plate broad, width at top almost equal to height; slightly tapered, bordered by 4 long, almost cruciate interfrontal bristles. Eye 1.5 times as high as gena. Mid tibia of male ventrally with a distal row of weak spinules and an apical bristle. Distal anterodorsal bristle slightly shorter than posterodorsal bristle, much shorter than distal dorsal bristle. Scutum with 4-5 rows of long acrostichal setulae between dorsocentral lines, dorsocentral bristles in a single prescutellar pair subequal in length to scutellum. Prescutellar acrostichal bristles in a single pair slightly longer than acrostichal setulae. Scutellum twice as wide as long, apical bristles as long as scutellar width. Halter dark brown with lighter stem. Wing with costagial bristles subequal, short; second costal sector 0.7 times as long as third (Fig. 192).

Abdomen. Syntergite 1+2 1.8 times as long as tergite 3. Sternite 5 of male with posteromedial lobe bearing rows of small, scale-like bristles and a small posterior spur-like process (Fig. 13). Surstylus with a distinctive anteroventral clubbed lobe (Figs. 58, 59). Parameres curved anteriorly at tip.

Types. *Holotype* (♂, BRI) and 2 *paratypes:* CANADA. **Ontario.** Ottawa, viii.1980., in lawn clippings, A. Telka. *Other paratypes:* **British Columbia.** Telegraph Creek, 2.vii.1960, 1100', in *Carex* and *Equisetum* beside lake, R. Pilfrey (1♂, BRI). **Finland.** Kilpisjarvi, R. Frey, "742" (1♂, ZMH).

Biology. This northern, Holarctic species is probably phytosaprophagous. Most of the type series was collected in piles of decaying grass.

Comments. *M. baculum* is a distinctive species that does not appear to be closely related to any other known species. Dr. J. Roháček was kind enough to send me the specimen from Finland, which he recognized as a new species I had described in an early manuscript version of this paper.

Etymology. The specific epithet is from the Latin for "club", and refers to the club-like anterior lobe of the surstylus.

***Minilimosina (Minilimosina) fungicola* (Haliday)**

Figs. 18, 130, 131, 132, 133, 195

Limosina fungicola Haliday, 1836:330.

Minilimosia (Minilimosina) fungicola: Roháček, 1983:39, synonymy and description.

Diagnosis. Length 1.2-1.5 mm. Eye 1.8 times as high as gena. Posterior scutellar bristles subequal in length to scutellum. Distal anterodorsal bristle of mid tibia much larger than adjacent posterodorsal. Second costal sector subequal to third (ratio 0.8-1.0) (Fig. 195).

Male abdomen. Sternite 5 with medial spinose patch covered with hairs, not showing distinct bristles (Fig. 18). Surstylus with only setulae ventrally but with the usual stout postervertebral bristle.

Female abdomen. Tergites 6 and 7 of female completely sclerotized, tergite 8 with tripartite pigmentation (Fig. 130). Sternite 8 long, rectangular, and weakly sclerotized; hypoproct subquadrate, setulose on entire surface (Fig. 132). Each spermatheca round-oval, surface reticulate, oval swelling of duct very small (Fig. 131).

Material examined. CANADA. **British Columbia:** Woodbury Creek, near Ainsworth, 5.viii.1980, dung vacuum, S.A. Marshall (1 ♀); Vancouver, U.B.C. campus, conifer duff, dung, 23&28.vii.1980, S.A. Marshall (4 ♂, 2 ♀). **New Brunswick:** St. Andrews, 15.viii.1979, dead seagull, S.A. Marshall (5 ♂, 1 ♀). **Ontario:** Lanark, 11.viii.1979, dead fish, S.A. Marshall (1 ♀); Iron Bridge, 5.viii.1981, S.A. Marshall (1 ♂); Thunder Bay, 24.v.1980, M. Kaulbars (1 ♀); Honey Harbour, 25.iv.1959, J.G. Chillcott (1 ♂, BRI). **Quebec:** Gt. Whale R., 18.viii.1949, "host *Agaricus*", J.R. Vockeroth (2 ♀, BRI). **Northwest Territories:** Reindeer Depot, Mackenzie Delta, 16.viii.1948, J.R. Vockeroth (2 ♀, BRI). U.S.A. **Colorado:** Roatte Co., 5miNE Clark Hinman Cpgrd., 7600', 23-25.vi.1972, dung trap (1 ♂). **Michigan:** Gogebic Co., Crooked Lake Bog, 11.viii.1977, Berlese sample, mammal dung, H.S. Dybas (1 ♂, 3 ♀, FLD). **North Carolina:** Gt. Smoky Mt. Nat. Pk., Clingman's Dome, 6300', on bear dung, 3.vi.1952, J.R. Vockeroth (1 ♀, BRI). **Washington:** 23.2miS South Bend, 9.x.1968, Malaise trap, D.D. Munroe (1 ♀, BRI); Sequim Bay, 3.ix.1934, A.L. Melander (1 ♂, USNM). This species is also known throughout Europe (Roháček 1983).

Biology. This species is common and synanthropic throughout at least the northern Holarctic Region, and has been collected from a wide variety of substrates. In spite of the specific name, it is rarely associated with fungi. Roháček (1983) suggested that *M. fungicola* is primarily phytosaprophagous.

***Minilimosina (Minilimosina) gemella* Roháček**

Figs. 19, 133, 134, 135, 196

Minilimosina (Minilimosina) gemella Roháček, 1983:40, male only.

Diagnosis. Length 1.0-1.3 mm. Eye 2.5 times as high as gena. Scutellum twice as wide as long, marginal bristles short, apical scutellar bristles less than or equal to scutellar length. Distal anterodorsal bristle of mid tibia much longer than adjacent posterodorsal bristle. Wing with second costal sector 0.7-0.9 times as long as third (Fig. 196). Sternite 5 of male with posteromedial lobe basally covered with small, bifurcate scale-like setae, with a solid projection distally (Fig. 19). Surstylus with a stout posterior bristle and 1 or 2 smaller robust blunt bristles ventrally.

Description, new female. Tergites 6 and 7 small but complete and sclerotized dorsally, with tripartate pigmentation (Fig. 133). Epiproct setulose on posterior half, with 2 bristles. Sternite 8 large, lightly pigmented anteriorly; hypoproct with a bare anterior lobe (Fig. 135). Each spermatheca longer than wide, duct with 2 swellings (Fig. 134).

Material examined. CANADA. **New Brunswick:** St. Andrews, 11-15.viii.1978, pitfall traps, S.A. Marshall (5 ♂). **Ontario:** Algonquin Park, S. of Shirley Lake, 26.v-16.vi.1984, mushroom traps in deciduous forest, K. Pendreigh (2 ♂, 2 ♀); Algonquin Park, S. of Shirley Lake, 18-26.v.1984, moose dung baited traps in deciduous forest, K. Pendreigh (2 ♂, 6 ♀); Lanark, l.ix.1979, mushroom, S.A. Marshall (1 ♂). **Quebec:** Lac Roddick, 23.iv.1984, L. Masner (1 ♂). **Saskatchewan:** Cypress Hills, 26.v.1955, J.R. Vockeroth (1 ♂, BRI). U.S.A. **Michigan:** Gogebic Co., Crooked L. Bog, 11&15.viii.1977, Berlese-mammal dung, H.S. Dybas, and 23.vi.1978, Berlese-Otter dung and root-mat substrate, J. Wagner (11 ♂, 5 ♀, FLD). **West Virginia:** Pendleton Co., Spruce Knob, 4600', 27.vi-9.vii, carrion trap among conifers, A. Newton (2 ♂, MCZ). Otherwise this species is known only from the two type males, collected in Austria.

Biology. The type material (2 ♂, JRO) was collected using a photoeclector in a manured alpine meadow in Austria, suggesting an association with dung-enriched substrates and boreal-alpine habitats. This association is substantiated by the longest series cited above, which was taken from dung-enriched vegetation in a bog.

Comments. Of the several species with a similar male sternite 5, *M. gemella* is most closely related to *M. fungicola* and *M. longisternum*, both of which also have very short scutellar bristles.

Minilimosina (Minilimosina) intermedia new species

Figs. 21, 65, 66, 67, 136, 137, 138, 197

Description. Length 1.3-1.5 mm. Interfrontal plate bordered by 4 small, equal interfrontal bristles, width at top 0.8 times height. Eye 2.0 times as high as gena. Mid tibia of male ventrally with a distal row of about 7 short spinules and a distinct apical bristle. Distal anterodorsal bristle of mid tibia slightly shorter than distal posterodorsal bristle. Scutum with 4-6 rows of acrostichal setulae between dorsocentral lines, dorsocentral bristles in a single prescutellar pair 0.5 times as long as scutellum. Prescutellar acrostichal bristles in a single minute pair, no longer than other acrostichal setulae. Scutellum 0.7 times as long as wide, apical scutellar bristles 1.1 times as long as scutellum. Mesopleuron pollinose except for shining anterior part of episternum. Halter uniformly light brown. Wing with costagial bristles small, upper 0.7 times as long as lower; second costal sector 0.8-1.0 times as long as third (Fig. 197).

Abdomen. Syntergite 1+2 1.4 times as long as tergite 3.

Male abdomen. Sternite 5 with a long posteromedial lobe bearing overlapping rows of scale-like bristles and a long, solid pointed process posteromedially (Fig. 21). Surstylus with a blunt, ventrally setulose anterior lobe, a single stout posteroventral bristle, and 2 small, blunt posteroventral bristles (Figs. 65, 66). Parameres narrow, slightly curved apically. Distiphallus simple, mostly sclerotized (Fig. 67).

Female abdomen. Tergites 6-8 complete but lightly pigmented medially; epiproct setulose on posterior quarter only (Fig. 136). Sternite 8 elongate, quadrate and darkly sclerotized on posterior half; medial bristles forming a transverse row (Fig. 138). Hypoproct entirely setulose, with an even anterior margin. Each spermatheca somewhat peanut-shaped, with a reticulate surface and short ducts (Fig. 137).

Types. *Holotype* (♂, BRI): CANADA. **Quebec:** Mt. Albert, Gaspé Prov. Pk., 5.vi-24.vii.1980, Dondale and Redner. *Paratypes:* **Quebec:** CampLeRelais, Laurentide Pk., 3000', 29.viii.1956, H.S. Dybas (4 ♂, 1 ♀, FLD, GUELPH) **Nova Scotia:** Cape Breton Highland Nt. Pk., North Mt., 400m, 5.viii.1983, "PG766864", fen pan trap, J. Vockeroth (1 ♂, BRI).

Comments. *M. intermedia* is closely related to *M. gemella* and *M. longisternum*, each of

which also have short scutellar bristles and a solid, dark, posteromedial lobe on the male fifth abdominal sternite.

Etymology. Prior to the discovery of *M. intermedia*, the species of this genus could be neatly separated into those with apical scutellar bristles no longer than the scutellum (*gemella*, *fungicola*, *longisternum*) and those with very long scutellar bristles (all other species). The name *intermedia* was chosen to reflect the intermediate length of the apical scutellar bristles in this new species.

***Minilimosina (Minilimosina) lepida* new species**

Figs. 17, 74, 75

Description. Length 1.2-1.3 mm. Interfrontal plate subequal in height and width, slightly tapered; bordered by 4 equal interfrontal bristles. Eye 1.7 times as high as gena. Mid tibia of male ventrally with distal row of weak spinules and a strong apicoventral bristle. Distal anterodorsal and posterodorsal bristles of mid tibia small, subequal. Scutum with 4-5 rows of acrostichal setulae between dorsocentral lines, dorsocentral bristles in a single prescutellar pair half as long as scutellum. Prescutellar acrostichal bristles in a single pair twice as long as acrostichal setulae. Scutellum half as long as wide, apical scutellar bristles longer than scutellar width. Mesopleuron pollinose except for anterodorsal corner of katepisternum. Halter brown with lighter stem. Wing with costagial bristles short; second costal sector dark and slightly shorter than third, other veins light brown; distance between crossvein dm-cu and crossvein r-m 5 times as long as dm-cu, cell dm faintly appendiculate.

Abdomen. Syntergite 1+2 1.4 times as long as tergite 3.

Male Abdomen. Posteromedial lobe of sternite 5 basally with rows of short, scale-like setae, with a crenulate-tipped solid projection posteriorly (Fig. 17). Surstylus (Fig. 74) with a stout posteroventral bristle, paramere bifurcate apically (Fig. 75). Distiphallus broad, short.

Female Abdomen. Tergites 6 and 7 sclerotized laterally but membraneous dorsally as in *M. nasuta* (Fig. 118), tergite 8 with tripartate pigmentation. Epiproct bare except for 2 small bristles. Sternite 8 large and darkly sclerotized, similar to *M. nasuta* (Fig. 120) except with a large, rounded lobe in anterior concave part of sclerite. Hypoproct setulose on posterior 1/3, anterior portion bare, much darker than posterior part; anterior margin with a deep median cleft. Spermathecae spherical, similar to *M. nasuta* (Fig. 119).

Types. *Holotype* (♂, *BRI*): CANADA. Saskatchewan: Cypress Hills, 15-17. vii.1980, wet spruce, intercept trap, R.A. Anderson. *Paratypes*: Ontario: Algonquin Park, S. of Shirley Lake, pitfall traps baited with moose dung, deciduous forest, 18-26.v.1984, K. Pendreigh (2♂, 1♀).

Comments. In spite of the distinctive and autapomorphic sternite 5, *M. lepida* can be seen to be closely related to *M. nasuta*. The very similar anteriorly narrowed surstyli, bifid parameres, split female tergites, and huge female sternite 8 are shared characters supporting this relationship. The Ontario paratypes differ from the holotype (Fig. 17) in having a greater number of crenulations on the posteromedial lobe of male sternite 5.

Etymology. The specific epithet *lepida* is from the Latin for "pleasant", but also refers to the close similarity between the posteromedial lobe of the fifth sternite and a lepidopteran scale.

***Minilimosina (Minilimosina) longisternum* new species**

Figs. 20, 62, 63, 64, 115, 116, 117, 194

Description. Length 1.5-1.7 mm. Interfrontal plate bordered by 4 small, subequal interfrontal bristles, width at top 0.7 times height. Eye 1.5 times as high as gena. Mid tibia of male ventrally with a distal row of short spinules and a distinct apical bristle. Distal anterodorsal bristle of mid tibia equal in length to distal posterodorsal bristle. Scutum with

6-7 rows of acrostichal setulae between dorsocentral lines. Dorsocentral bristles in 2 pairs; anterior pair indistinct, twice as large as acrostichal setulae; prescutellar pair 0.5 times as long as scutellum. Prescutellar acrostichal setulae in a single pair twice as long as acrostichal setulae. Scutellum 0.8 times as wide as long, apical scutellar bristles shorter than scutellum. Mesopleuron pollinose except shining anterior part of episternum and separate large shining area below katepisternal bristle. Halter dark brown with yellow stem. Wing with costagial bristles small, upper twice as long as lower. Second costal sector 0.8 times as long as third (Fig. 194).

Abdomen. Syntergite 1+2 1.6 times as long as tergite 3.

Male abdomen. Sternite 5 with a long posteromedial lobe, central basal part of lobe bare, basal part of lobe otherwise bearing scale-like setae, distal part of lobe forming a long, darkly sclerotized process (Fig. 20). Surstylus with a very narrow anterior lobe, a single strong ventral bristle posteriorly, and 2 short blunt ventral bristles (Figs. 62, 63). Parameres weakly clubbed at apex, with 3 small anterior setulae (Fig. 64). Distiphallus simple, largely sclerotized with a narrow distal dorsal process (Fig. 64).

Female abdomen. Tergites 6 and 7 entire but shortened medially, tergite 8 much longer, with tripartate pigmentation (Fig. 115). Epiproct longer than cerci, bare except for the usual 2 bristles. Sternite 8 very elongate, with sinuate lateral margins and trilobed anterior margin (Fig. 117). Hypoproct entirely setulose. Each spermatheca small, dark, subspherical, flattened and invaginated apically, duct short (Fig. 116).

Types. *Holotype* (♂, MCZ) and 11 *paratypes* (10 ♂, 1 ♀, BRI, GUELPH): MEXICO. **Oaxaca:** 1.4mi E jct. Mex. 175 and Yuvila Rd., 9300' 9-19.viii.1973, mesic oak forest. A. Newton. *Other paratypes:* MEXICO. **Oaxaca:** 3.3mi E jct. Mex. 175 and Yuvila Rd., 8100', 9-19.viii.1973, oak-pine, dung. A. Newton (2 ♂, MCZ).

Etymology. The Latin name *longisternum* refers to the very long sternite 8 of the female.

***Minilimosina (Minilimosina) nasuta* (Spuler) new combination**

Figs. 16, 71, 72, 73, 118, 119, 120, 198

Leptocera (Scotophilella) nasuta Spuler, 1925:84.

Description. Length 1.2-1.5 mm. Interfrontal plate bordered by 4 equal interfrontal bristles, width at top 0.7 times height. Eye 1.6 times as high as gena. Mid tibia of male ventrally with a distal row of 7 short spinules and a distinct apical bristle. Distal anterodorsal bristle of mid tibia shorter than long distal posterodorsal and longer distal dorsal bristle. Scutum with 4-6 rows of acrostichal setulae between dorsocentral lines, dorsocentral bristles in 1 prescutellar pair subequal in length to scutellum. Prescutellar acrostichal bristles in a single pair twice as long as acrostichal setulae. Scutellum 0.7 times as long as wide, apical scutellar bristles twice as long as scutellum. Mesopleuron pollinose except for shining anterior part of episternum. Halter uniformly light brown. Wing with costagial bristles small, upper 0.7 times as long as lower. Second costal sector 0.7-0.8 times as long as third (Fig. 198).

Abdomen. Syntergite 1+2 2.0 times as long as tergite 3.

Male abdomen. Sternite 5 with a long posteromedial lobe with rows of scale-like setae on basal half and a solid, pointed process distally (Fig. 16). Surstylus with a long anterior lobe and a broader posterior lobe bearing the usual small spur (Figs. 71, 72). Parameres broad, apically bifid (Fig. 73). Distiphallus narrow, simple.

Female abdomen. Tergites 6 and 7 sclerotized laterally but membranous dorsally; tergite 8 with tripartate pigmentation (Fig. 118). Epiproct small bare except for 2 central bristles. Sternite 8 large and darkly sclerotized, deeply emarginate anteriorly, larger than hypoproct (Fig. 120). Hypoproct largely setulose, with a bare anteromedial lobe. Each spermatheca spherical, with several small papillae at base, stem with a single short swelling (Fig. 119).

Types. *Holotype* (♂, no abdomen): U.S.A. **Washington:** Pullman, May 19, 1912, A.L.

Melander (USNM). *Paratype* (♀, dissected): **Washington:** Almota (no collector or date, A.L. Melander collection, USNM). All other paratype material not conspecific with holotype, see *M. parva*.

Other material examined: CANADA. **British Columbia:** Terrace, 3.vii.1960, swept off carcass, J.G. Chillcott (1♂, BRI). U.S.A. **Arizona:** Apache Co., Alpine, Luna Lake, 7900', 9-14.vii.1979, alpine meadows, S.&J. Peck (31♂, 5♀, BRI, GUELPH); Coconino Co., Flagstaff, 7100', 18-25.vii.1979, pond-pine-meadow, S.&J. Peck (1♀); 10miNW Flagstaff, San Francisco Mtns, 9500', 18-24.vii.1979, spruce-fir-aspen, meadow malaise, S.&J. Peck (3♂, 1♀); Oak Creek Canyon, 5900', 17-25.vii.1979, riparian woods, S.&J. Peck (8♂, 4♀); Cochise Co., Huachuca Mts., 6000', Miller Canyon, ix.1970, dung trap in oak woodland, A.F. Newton (1♂, MCZ). **New Mexico:** Catron Co., 5miW Luna, 7400', 9-14.vii.1979, pond-pine-meadows, San Francisco River, S.&J. Peck (10♂, 5♀); Lincoln Co., Gallinas Pk. 8600', 10miW Corona, 17-22.viii.1975, carrion trap in bog w. pond, fir, pine, S. Peck (1♀); Socorro Co., 20miW Socorro, Water Canyon, 7000', 2.vi-7.1979, mixed mesic forest, S.&J. Peck (2♂, 1♀); Sandoval Co., Rabbit Mtn., 25.v.1959, W.W. Wirth (1♂, USNM).

Biology. Although most of the specimens examined lacked habitat information, two of the records suggest an association with carrion. This western species has been collected over a wide range of elevations throughout the summer months, but has been most frequently collected at higher elevations in the southwest.

Minilimosina (Minilimosina) parva (Malloch) new combination

Figs. 12, 51, 52, 53, 121, 122, 123, 199

Limosina parva Malloch, 1913:371.

Leptocera (Scotophilella) parva: Spuler, 1925b:82.

Description. Length 1.1-1.3 mm. Interfrontal plate narrow and tapered, width at top 0.7 times height; bordered by 3-4 small equal interfrontal bristles. Eye 3.0 times as high as gena. Mid tibia of male with a distal row of several small ventral spinules and a weak apicoventral bristle. Mid tibia of both sexes with a strong distal dorsal bristle, a slightly shorter distal posterodorsal bristle and a much shorter distal anterodorsal bristle. Acrostichal setulae in 6-7 rows between dorsocentral lines, prescutellar acrostichal bristles 2-3 times as long as others. Scutellum twice as wide as long, apical bristles twice as long as scutellum. Mesopleuron entirely pollinose. Halter uniformly light brown. Wing with costagial bristles small, subequal. Second costal sector 0.5-0.8 times as long as third (Fig. 199).

Abdomen. Syntergite 1+2 1.7 times as long as tergite 3.

Male abdomen. Sternite 5 with 2 rows of flat spines posteromedially, forming a lobe which is widest distally and convex at apex (Fig. 12). Surstylus with stout posterior and ventral spurs (Figs. 52, 53). Paramere thin, slightly curved at apex. Distiphallus simple, scoop-shaped, mostly sclerotized (Fig. 51).

Female abdomen. Tergites 6 and 7 entire; tergite 8 with tripartate pigmentation, pigmentation of dorsal part irregular. Epiproct bare except for 2 small bristles, anterior margin incised (Fig. 21). Sternite 8 Y-shaped, with some bristles but general surface bare (Fig. 123). Hypoproct subquadrate, entire surface setulose. Each spermatheca subspherical, apical invagination shallow (Fig. 122).

Type. *Holotype* (♂, USNM): "Nat. Mus. on windows Ap. 1912 Malloch"

Other material examined. CANADA. **British Columbia:** 10miW Hope, wet forest, 8-28.vii.1908, S.A. Marshall (1♀); **Manitoba:** Erickson, 1-5.viii.1983, Pengelly and Barber, mushroom traps (2♂, 3♀); **New Brunswick:** Kouchibouguac N.P., 23.v.1977, Hanley and Cooper, code 5113Q (1♂, BRI); St. Andrews, vii & viii.1978, S.A. Marshall (7♂, 8♀). **Nova Scotia:** Cape Breton Highlands Nt. Pk., North Mt., 400m, 29.vii.1983, fen and for., D. Bright (4♀); Antigonish Co., 1kmN Antigonish, 2.vii-5.viii.1984, L. MacMillan, flight intercept trap (3♂, 4♀, BRI). **Ontario:** Alfred, Alfred Bog, 25.ix.1983, sifted from moss under fungi and moose dung, S. Peck (1♂); Algonquin Park, S. of Shirley Lake, 26.v-21.vii.1984, mushroom traps in deciduous forest, K. Pendreigh (7♂, 10♀); Algonquin Park, S. of Shirley Lake, 18-26.v.1984, moose dung baited traps in deciduous

forest, K. Pendreigh (4 ♂); Guelph, 10.vi-8.vii.1983, mushroom bait, B. Brown (11 ♂, 7 ♀); Guelph, 19.vii.1983, vacuumed from mushroom, B. Brown (1 ♂); Guelph, 9-11.vi.1984 (1 ♀), 9-12.vii.1984 (1 ♀), 12-14.vii.1984 (2 ♂, 1 ♀), 1.viii.1984 (2 ♂, 1 ♀), 7-12.ix.1984 (1 ♂), mushroom traps in coniferous forest, B. Brown & S. Marshall; Guelph, 21-24.vii.1984, mushroom trap in field (1 ♂); Guelph, 17-27.v.1984 (1 ♀), 25-30.vii.1984 (2 ♀), 1.viii.1984 (1 ♂, 1 ♀), 5.viii.1984 (1 ♂, 4 ♀), 26.ix-3.x.1984 (1 ♀), mushroom traps in deciduous forest, B. Brown and S. Marshall. Constance Bay, 26.viii.1980, on mushroom, S.A. Marshall (1 ♀); Lanark, 1.ix.1979, decaying mushrooms, S.A. Marshall (5 ♂, 4 ♀); Lanark, 12.viii.1979, bear feces, emerged 20.viii, S.A. Marshall (1 ♀); Deux Rivieres, 2-3.ix.1979, mixed forest, carrion, S.B. Peck (1 ♂); Iron Bridge, 5.viii.1981, on fungus, S.A. Marshall (3 ♂); Heckston, 24.vi-21.vii.1984, M. Kaulbars, flight intercept trap (1 ♂, 1 ♀); Thunder Bay, 13.vii.1980, M. Kaulbars (3 ♂, 1 ♀); Bells Corners, 4.vi.1952, swept from bare rock, J.F. McAlpine (1 ♀, BRI); Port Severn, 18.vi.1959, Black Spruce bog, J.G. Chillcott (1 ♂, BRI); Normandale, 30.v.1956, J.R. Vockeroth (1 ♀, BRI); Ottawa, 10.vii.1956, J.R. Vockeroth (1 ♀, BRI); Mer Bleue, 25.vi.1964, J.R. Vockeroth (1 ♀, BRI); Chaffey's Locks, Queen's University Biological Stn., mushroom in forest, S.A. Marshall (1 ♂); Strathroy, v.1953 (1 ♂, BRI); Chalk River, 14.ix.1984, vacuumed from fungi, S. Marshall (4 ♂). **Quebec:** Gatineau Park, Blue Sea Lake, 10.ix.1978, assoc. with mushroom, R. Sexton (3 ♀, BRI); Gatineau Park, 8.iv.1981, car net, Masner and Goulet (3 ♂, BRI); Old Chelsea, 10.x.1961, 21.vi.1959, 9.x.1955, 13.viii.1958, 1.x.1963, 30.viii.1961, J.R. Vockeroth (4 ♂, 5 ♀, BRI); Beechgrove, 29.vi.1962, J.R. Vockeroth (1 ♀, BRI); CampLeRais, Laurentian Pk., 3000', 29.viii.1956, berl. ex. rabbit hutch debris, H.S. Dybas (1 ♂, FLD); Great Whale River, 18.viii.1949, Host. *Agaricus*, J.R. Vockeroth (1 ♂, BRI). U.S.A. **Alaska:** Matanuska, 28.iv.1944, rotary trap, J.C. Chamberlain (1 ♂, USNM). **Arizona:** Flagstaff, Oak Ck. Canyon, 5900', 17-25.vii.1979, S.B. Peck (1 ♀). **Arkansas:** Garland Co. 1.2miN Crystal Springs, Hwy.270, 6-8.iii.1977, Woodruff and Wiley, pig dung traps (1 ♂). **District of Columbia:** Washington, "9238 on cabbage" (1 ♂, USNM); **Georgia:** Dade Co., Cloudland Canyon St. Pk., 16-23.v.1972, Rhododendron thicket dung trap, S.B. Peck (2 ♂, 1 ♀); Rabun Co., Chatahoochee St. For., 5-25.vi.1984, mushroom trap, S.A. Marshall (30 ♂, 10 ♀); Telfair Co., Little Ocmulgee St. Pk., 6-25.vi.1984, on mushroom and in mushroom trap, S.A. Marshall (2 ♂); Wilkinson Co., Big Sandy Creek, 8miS Irwinton on US441, 5-25.vi.1984, intercept trap in mixed forest, S.A. Marshall (16 ♂, 17 ♀). **Illinois:** Champaign Co., Mahomet Hart Woods, 20-26.v.1979, oak woods intercept, S.B. Peck (♂); Knox Co., Green Oaks, 22.ix.1980, sublitter under decaying mushrooms, H.S. Dybas (2 ♀, FLD). **Indiana:** Burns Hbr., 7-10.vi.1983, sand-oak mushroom traps, S.A. Marshall (3 ♂, 2 ♀); Gary, 7-10.vi.1983, sand-oak mushroom traps, S.A. Marshall (1 ♂, 2 ♀). **Kentucky:** Laurel Co., 15miW London, 4-30.vi.1984, intercept trap in oak forest, S. Marshall (5 ♀); Whitley Co., Cumberland Falls State Pk., 29-30.vi.1984, mushroom trap, S.A. Marshall (10); Daniel Boone Nat. For., 4-30.vi.1984, *Rhododendron* thicket, flight intercept trap, S. Marshall (7 ♂, 6 ♀); Rowan Co., 24kmSW Moorehead Cave, 14.v-20.viii.1983, *Fagus* for. flight intercept trap, S. Peck (1 ♀). **Louisiana:** Alexandria, 11miSW, 21.iii.1960, J.G. Chillcott (1 ♀, BRI), Grant Parish, 18kmN Alexandria, 19.v-17.viii.1983, forest intercept trap, S.B. Peck (1 ♂, 2 ♀). **Maryland:** Plummers Id., 25.vi.1914, ex fungus, R.C. Shannon (1 ♀, USNM); Montgomery Co., Bethesda, 5.v.1969, G. Steyskal (1 ♂, USNM). **Massachusetts:** Middlesex Co., Bedford, mixed for., vi.1969, carrion, A.F. Newton (1 ♂, 2 ♀). **Michigan:** Gogebic Co., Crooked L. Bog, 9.viii.1977, Leg. J. Wagner (1 ♂, 4 ♀, FLD). **Mississippi:** Scott Co., Beinville Nat. For., 10-14.iv.1972, dung, A.F. Newton (1 ♂). **Missouri:** Pontotoc Co., 17.v-19.vii.1983, oak forest intercept trap, S. Peck (1 ♂, 1 ♀). **New Hampshire:** Mt. Washington, Lakes of the Clouds, 5000', 9.viii.1954, W. Mason (1 ♂, BRI). **New Jersey:** Burlington Co., 4miWNW Mt. Misery, 17-24.vii, dung, A.F. Newton (1 ♂). **New York:** Lake Placid, 30.viii.1979, mushroom, S.A. Marshall (1 ♂); Cairo, 1.vii.1980, S.A. Marshall (2 ♂); Rochester, 5.viii.1983, vacuumed from dead *Pleurotus*, S.A. Marshall (2 ♂); Speculator, 5.viii.1983, vacuumed from mushroom, S.A. Marshall (1 ♂). **North Carolina:** Sampson Co., Falcon., 28.ix-4.x.1983, pig dung, R. Woodruff; Jackson Co., Blue Ridge Pkwy., Grassy Ridge Mine Overlook and Bear Paw Gap, 5-25.vi.1984, 42000-5250', mushroom traps, S.A. Marshall (17 ♂, 6 ♀); Haywood Gap and Bear Paw Gap, intercept traps, 5-27.vi.1984, S.A. Marshall (4 ♂, 5 ♀); Cullowhee, 2200', 6-12.vi.1984, pan under malaise trap, S.A. Marshall (9 ♂, 10 ♀); Swain Co., NE Mt. Collins, 5900', 17-22.v, carrion, A.F. Newton (1 ♂); Chapel Hill, 31.vii.1980, snail carrion, K. Kneidel. **Pennsylvania:** Center Co., State College, 22.iv.1982, soil trap, A. Norrbom (4 ♂, 6 ♀, PSU); State College, 15.v.1982, housefly medium, A. Norrbom (1 ♂, 2 ♀, PSU); Pine Grove Mills, 11.iv.1972, D.D. Wilder, (1 ♀, CAS). **Tennessee:** Cumberland Co., 2miE Ozone, mixed hardwood forest, 17.vi-14.vii, A.F. Newton (14 ♂, 5 ♀); Sevier Co., 2.5miN Gatlinburg, 5-28.vi.1984, rotting mushroom trap, S.A. Marshall (5 ♂, 5 ♀). **Texas:** San Jacinto Co., 5kmS Coldspring, 2.v-16.viii.1983, forest intercept trap, S.&J. Peck (2 ♀). **Washington:** Mt. Rainier, Ohanapecosh, 11.viii.1940, A.L. Melander (1 ♂, USNM). **Virginia:** Bath Co., 9.6kmN Clifton Forge, 13.v-21.viii.1983, *Tsuga-Fagus* forest, flight intercept trap, S. Peck (2 ♂, 1 ♀); Smyth Co., 6mi.Marion on Va.16, 2800', mixed hwd., 17.vi-14.vii.1972, dung, A.F. Newton (1 ♀). **West Virginia:** Fayette Co., Clifftop, Babcock St. Pk., 14.v-21.viii.1983, flight intercept trap, S. Peck (1 ♂, 2 ♀); Pendleton Co., Spruce Knob, 4600',

conifers, carrion, 27.vii-9.viii, A.F. Newton (6 ♂, 2 ♀); Randolph Co., Bickle Knob, 6.5miE Elkina, 4000', mixed decid. for., 27.vii-9.viii.1969, A.F. Newton (1 ♂, 1 ♀, dung trap; 1 ♂, carrion trap).

Biology. Although this common species has been collected in a wide range of habitats and has been reared from bear feces and snail carrion, it is primarily fungivorous. *M. parva* is one of the most common flies associated with decaying mushrooms in southern Ontario and has been found on mushrooms in Manitoba, Quebec, Illinois, Indiana, Maryland and New York.

Comments. *Limosina meszarosi*, *Limosina parafungicola*, and *Limosina similissima*, all described by Papp (1974) from central Asia, appear to be closely related to *M. parva*, however the descriptions are very superficial. He mentioned sternite 8 of the female of only one of these species, *parafungicola*, and described it as inverse Y-shaped. This suggests that *M. parafungicola* is very closely related to, and perhaps a junior synonym of, *M. parva*. *M. parva* is closely related to *M. parvula*, a Holarctic species which is easily distinguished by its concave male sternite 5 and T-shaped female sternite 8. These 2 species are often sympatric in North America. *M. tubercula*, known only from Wyoming, also appears to be related to *M. parva*.

***Minilimosina (Minilimosina) parvula* (Stenhammar)**

Figs. 7, 9, 200

Limosina parvula Stenhammar, 1854:422

Minilimosina (Minilimosina) parvula: Roháček, 1983:42, synonymy and description.

Diagnosis. Length 1.1-1.3 mm. Scutellum twice as wide as long, apical marginal bristles twice as long as scutellum (Fig. 7). Distal posterodorsal bristle of mid tibia subequal to distal anterodorsal. Wing with second costal sector 0.8-0.9 times as long as third (Fig. 200).

Male abdomen. Posteromedial comb of male sternite 5 made up of blunt spines, posterior margin of comb concave (Fig. 9). Outer lobe of surstylus large, densely haired along ventral margin, internal lobe small. Parameres thin, curved at apex.

Female abdomen: Tergites 6 and 7 complete but weakly sclerotized dorsally, broad and dark laterally. Tergite 8 with tripartate pigmentation. Epiproct setulose in posterior 2/3 and with 2 dorsal bristles. Cercus with preapical dorsal bristle shorter and much thicker than apical bristle. Sternite 8 forming a T-shaped sclerite, the head of the T (posterior) complete. Hypoproct large, entire surface setulose. Each spermatheca spherical.

Material examined. CANADA. **Alberta:** Edmonton, iv.5.1924, Owen Bryant (1 ♂, CAS). **Manitoba:** Fort Churchill, 20.vi.1952, ecological data f-2-15, J.G. Chillcott (1 ♂, BRI). **New Brunswick:** St. Andrews, 25.vii.1978, pitfall traps, S.A. Marshall (4 ♂). **Nova Scotia:** Antigonish, 2.vii-5.viii.1984, flight intercept trap, L. MacMillan (2 ♂, BRI); Lockeport, 4.vii.1958, J.R. Vockeroth (1 ♂, BRI); Cape Breton Highland Nt. Pk., Paquets L. Rd., 260m, 7.vii.1983, pan trap (2 ♂, 4 ♀). **Ontario:** Algonquin Pk., 14-21.vii.1984, deciduous forest mushroom traps, K. Pendreigh (1 ♂); Algonquin Park, deciduous forest moose dung traps, 18-26.v.1984, K. Pendreigh (3 ♂); Deux Rivieres, 2-30.ix.1979, carrion in mixed forest, S.&J. Peck (1 ♂); Lanark, 1.ix.1979, mushroom, S.A. Marshall (1 ♀); Mer Bleue, Ottawa, 21.viii.1968, O. Peck (1 ♂, BRI). **Quebec:** Old Chelsea, 21.vi.1959, Summit King Mtn., J.R. Vockeroth (5 ♀, BRI); Old Chelsea, 10.x.1961, J.R. Vockeroth (1 ♂, BRI); Mt. Albert, Gaspé Park, vi-vii.1980, C. Dondale (1 ♂). U.S.A. **Alaska:** Matanuska, 27.v.1942 and 10.v.1944, J.C. Chamberlin, Rotary trap (1 ♂, 1 ♀, USNM). **Massachusetts:** Middlesex Co., Bedford, carrion in pines, 7.vii.1969, A.F. Newton (2 ♂, MCZ). **New York:** Lake Placid, 30.viii.1979, dung, S.A. Marshall (1 ♂); Piseco Lake, wet area mushroom trap, 1-5.vii.1983, S.A. Marshall (3 ♂, 1 ♀); Speculator, Snowy Mtn. Trail, mushroom bait, 1-4.viii.1983, S.A. Marshall (1 ♂). **Michigan:** Gogebic Co., Crooked Lake Bog, 15.viii.1977, J. Wagner (3 ♂, 4 ♀, FLD). **New Hampshire:** Passaconaway, Lily Pond, 2050', 4-6.vii, dung, A. Newton (1 ♂, MCZ). **North Carolina:** Jackson Co., Cullowhee, Cane Creek Rd., 5-25.vi.1984, dung trap along creek, S.A. Marshall (1 ♂). **Oregon:** Grant Co., 5000', E. Prairie City, Dixie Pass, Blue Mtn., 1.vi.1957, Berlese garbage and forest subliter (1 ♂, FLD). **Pennsylvania:** Center Co., State College, 6.v.1982, soil trap, A. Norrbom, (2 ♀, PSU). **Tennessee:** Sevier Co., Greenbriar Cove, Ramsey Cascade Trail, 2700', 3100', 17-23.v.1972, carrion, A.F. Newton (20 ♂, 15 ♀); Henderson Co., Natchez Trace St. Pk.,

1000', 18.vi-13.vii.1972, dung, A.F. Newton (1 ♂). **Virginia:** Smyth Co., Marion, 2800', 14.vi.1972, carrion in mixed hardwood, A.F. Newton (2 ♂). **West Virginia:** Pendleton Co., Spruce Knob, 4600', carrion in conifers, 27.vii-9.viii, A.F. Newton (4 ♂, 2 ♀); Randolph Co., Bickle Knob, 6.5miE Elkins, 4000', 27.vii-9.viii, carrion, A. Newton (3 ♂, 5 ♀). Also known from throughout Europe.

Biology. Although occasionally found on mushrooms or dung, Nearctic collection records suggest that this is primarily a necrophagous species. Roháček (1983) stated that it is most commonly collected on decaying fungi in Europe, however extensive collecting of fungivorous sphaerocerids in eastern North America has failed to yield a significant number of *M. parvula*. Where it is found on fungi, it is almost always outnumbered by the closely related *M. parva*.

***Minilimosina (Minilimosina) pulpa* new species**

Figs. 14, 56, 57

Description, male (female unknown). Length 1.0 mm. Interfrontal plate tapered, bordered by 3-4 equal interfrontal bristles, width at top 2/3 of height. Eye 1.4 times as high as gena. Mid tibia of male ventrally with a distal row of 7 short spinules and a long apical bristle; distal posterodorsal bristle subequal to distal anterodorsal bristle. Scutum with acrostichal setulae in 4-5 rows between dorsocentral areas, dorsocentral bristles in 1 prescutellar pair 0.5 times as long as scutellum. Prescutellar acrostichal bristles in a single pair twice as long as acrostichal setulae. Scutellum 0.7 times as long as wide, marginal bristles long, apical pair 3 times as long as scutellum. Mesopleuron pollinose except anterior part of episternum. Halter uniformly light brown. Wing with costagial bristles subequal, small; second costal sector 0.7 times as long as third, cell dm narrow, not appendiculate, crossvein dm-cu 0.2 times as long as distance between dm-cu and r-m; veins uniformly light brown.

Male abdomen. Sternite 5 with a darkly pigmented, bare patch immediately anterior to the posteromedial comb; comb sinuate (Fig. 14). Outer lobe of surstylus sharply pointed anteriorly and with a thin, bifurcate process laterally. Inner portion of surstylus with a subquadrate process anteriorly (Figs. 56, 57). Paramere short, thick, truncate at apex. Distiphallus smoothly concave dorsally.

Type. *Holotype* (♂, BRI): U.S.A. WYOMING: Sublette Co., 7miN Pinedale, 16-24.viii.1979, pine meadow, 9000', malaise-carrion, S.&J. Peck.

Comments. The remarkable trilobed anterior part of the surstylus makes this a distinctive species, but the formation of sternite 5 suggests a close relationship to another rare western species, *M. accinta*.

Etymology. The specific name *accinta* is from the Latin for flesh, and refers to the type habitat.

***Minilimosina (Minilimosina) sclerophallus* new species**

Figs. 3, 4, 22, 48, 49, 50, 124, 125, 126, 201

Description. Length 1.7-1.9 mm. Interfrontal plate broad and slightly tapered, width at top equal to height, bordered by 3 small, equal interfrontal bristles. Eye 3.0 times as high as gena. Mid tibia of male with a distal row of short ventral bristles and a short apical ventral bristle; mid tibia of female with a long apical ventral bristle only (Fig. 4); mid tibia of both sexes with a long distal dorsal bristle and weaker, subequal distal anterodorsal and distal posterodorsal bristles (Fig. 3). Scutum with 6-8 rows of acrostichal setulae between dorsocentral lines, dorsocentral bristles in 2 pairs but anterior pair barely larger than acrostichal setulae, prescutellar pair subequal to scutellar length. Prescutellar acrostichal bristles in a single pair 2-3 times as large as acrostichal setulae. Scutellum 0.7 times as long as wide, apical bristles twice as long as scutellum. Mesopleuron pollinose except for 2 separate shining areas on anterior part of episternum, shining area on anepisternum very large. Halter dark brown, stem yellow. Wing with small, subequal costagial bristles. Second costal sector 0.7-0.8 times as long as third (Fig. 201). Cell dm broad, outer angle obtuse.

Abdomen. Syntergite 1+2 equal in length to tergite 3.

Male abdomen. Sternite 5 with a posermial process bearing 12-14 long flat bristles (Fig. 22). Surstylus simple, with a broad anterior lobe and a much smaller posterior one; ventral surface with several long bristles and posterior surface with shorter bristles (Figs. 48, 49). Paramere with a dense patch of anterior bristles distally (Fig. 50). Distiphallus massive, forming a completely sclerotized hood-like structure (Fig. 50).

Female abdomen. Tergite 8 complete but lightly pigmented medially. Epiproct small, bare except for 2 bristles (Fig. 124). Sternite 8 elongate, with posterior part tri-lobed (Fig. 126). Hypoproct entirely setulose, deeply emarginate anteriorly. Each spermatheca wrinkled-funnel shaped, with a small apical invagination (Fig. 125).

Types. *Holotype* (♂, BRI) and 16 *paratypes* (5 ♂, 11 ♀, BRI, GUELPH): VENEZUELA. Tachira, 4.5kmNE San Cristobal, 9000', 20-22.v.1974, dung trap, S. Peck. *Other paratypes*: ECUADOR. **Pichincha**: 9300', 35kmE Tandapi, 24-29.vi.1975, S. Peck, Bamboo (3 ♂, 14 ♀): Napo, 27kmNW Baeza, 2-6.iii.1976, 2700m, dung trap, S. Peck (1 ♂, 13 ♀). COLUMBIA. **Santander**: Above Pamplona, 9000', 9-13.v.1984, dung trap, S. Peck (1 ♀); 30kmS Chinacota, 8000', 10-14.v.1974, dung trap, S. Peck (2 ♀).

Comments. *M. sclerophallus* is the most anomalous member of the subgenus *Minilimosina*. The single comb row of male sternite 5 is similar to that of *Allolimosina* species, but no other feature suggests an affinity to *Allolimosina*, and the massive distiphallus is in marked contrast to the reduced distiphallus characteristic of that subgenus. The surstylus of *M. sclerophallus* is of the general form of *Minilimosina* but is unique in this subgenus in lacking a posteroventral bristle. Another striking autapomorphy of this species is its setose paramere.

Etymology. The name *sclerophallus* is descriptive of the unusual, large, sclerotized distiphallus.

Minilimosina (Minilimosina) trogeri Roháček

Figs. 15, 68, 69, 70, 127, 128, 129, 193

Minilimosina (Minilimosina) trogeri Roháček, 1983:41.

Diagnosis. Length 1.0-1.3 mm. Eye 1.5 times as high as gena. Mid tibia of male ventrally with a distal row of 6-8 weak spinules and a distinct apicoventral bristle. Distal anterodorsal and posterodorsal bristles of mid tibia subequal. Scutellum 0.6 times as long as wide, apical bristle over twice as long as scutellum. Mesopleuron pollinose except shining anterior part of episternum. Halter uniformly light brown. Wing with lower costagial bristle twice as long as upper, half as long as dorsocentral bristle. Second costal sector 0.5-0.8 times as long as third (Fig. 193).

Male abdomen. Sternite 5 with 2 rows of short bristles posteromedially, behind which a solid, dark, long lobe projects (Fig. 15). Surstylus setulose on anterior surfaces (Figs. 68, 69). Parameres thin, simple (Fig. 70).

Female abdomen. Tergites 6 and 7 lightly pigmented dorsally, each appearing as 2 separate lateral sclerites; tergite 8 with tripartate pigmentation (Fig. 127). Sternite 8 largely membranous, rectangular in posterior sclerotized area, pattern of pigmentation giving sclerite an apparent irregular outline (Fig. 129). Hypoproct bare on anterior half, lobate anteromedially. Each spermatheca irregular in shape, roughly short-cylindrical (Fig. 128).

Material examined. CANADA. **Ontario**: Ottawa, grass piles, vii.1979, A. Telka (3 ♂, 1 ♀); Ottawa, 19.iv.1959, J.G. Chillcott (1 ♂, BRI); Ottawa, 16.viii.1952, J.R. Vockeroth (1 ♂, BRI); Bells Corners, 21.ix.1951, on toadstool, J.F. McAlpine (5 ♀, BRI); Mer Bleue, 27.v-3.vi.1982, L. Dumouchel, intercept trap (1 ♂, BRI); Stouffville, 5-13.v.1983, B.V. Brown, Malaise-pan (1 ♂). **Quebec**: King Mountain, near Old Chelsea, 1.ix.1980, K. Barber (1 ♀). U.S.A. **Massachusetts**: Middlesex Co., Medford, Pine forest, 11-17.viii, carrion trap, A. Newton (1 ♂, MCZ). **Wyoming**: Wind River Mountains, 20miNE Pinedale, nr. Nelson Lake, 10400-11000', carrion, tundra, 15-25.viii.1979, S. Peck (1 ♂).

Biology. Some of the type specimens were collected using a photoeclector in a manured alpine meadow, and Roháček (1983) suggests that this is a boreal-alpine species. All type specimens were either from the central high alps of Austria or from Finland. The Holarctic distribution reported here, with the Nearctic records primarily alpine or northern, fits well with Roháček's suggestion. The longest series of *M. trogeri* have been collected on decaying vegetation and on fungi. The series collected from fungi is an isolated record, and is not repeated in the hundreds of fungus-baited trap samples examined by the author. Phytosaprophagous communities are less well studied, and probably include *M. trogeri* as well as other rarely collected *Minilimosina* species.

Comments. *M. trogeri* is closely related to *M. nasuta* and *M. lepida*. *M. nasuta* bears the greatest superficial similarity because of its long scutellar bristles and similar male sternite 5, but the narrow surstylus and very distinctive female sternite 8 of *M. nasuta* make these species easy to separate. Slight differences can be noted between the Nearctic material illustrated here and the Palearctic material illustrated by Roháček (1983), for example the pigmentation of female sternite 8. These small differences are interpreted as intraspecific variation.

***Minilimosina*, (*Minilimosina*) *tuberculum* new species**

Figs. 23, 60, 61

Description, male (female unknown). Length 1.5 mm. Interfrontal plate 0.7 times as wide as high, slightly tapered, bordered by 3 pairs of long, almost cruciate interfrontal bristles. Face more strongly tuberculate between antennae than in congeners; lower half of face smoothly concave. Eye slightly higher than gena. Mid tibia of male with ventral setulae of distal half slightly enlarged, only apicoventral bristle distinct. Distal dorsal bristle of mid tibia large, reaching tip of tibia; distal anterodorsal and posterodorsal bristles very small. Scutum with 5-6 rows of acrostichal setulae between dorsocentral lines, dorsocentral bristles in 1 prescutellar pair 0.7 times as long as scutellum. Prescutellar acrostichal bristles in 1 pair slightly longer than other acrostichal setulae. Scutellum 0.7 times as long as wide, apical scutellar bristles as long as scutellar width. Mesopleuron entirely pollinose. Halter dark brown with pale knob. Wing with costagial bristles small and subequal; second costal sector subequal in length to third. Costa surpassing R_{4+5} by length of dm-cu, dm-cu half as long as distance from dm-cu to r-m.

Male abdomen. (Preabdominal sternites of type destroyed) Sternite 5 with a subquadrate lobe bearing 3 rows of short flat setae (Fig. 23). Surstylus broad, with several posterior and medial short bristles (Figs. 60, 61). Paramere narrow, with a small pointed anteroventral process at apex.

Type. *Holotype* (♂, BRI, abdomen severely damaged); U.S.A. **Wyoming:** Uinta Co., 8miSE Evanston, 10.vii-11.vii.1979, sage-grass-riparian, 7100', carrion, S.&J. Peck.

Comments. Although I was hesitant to name this species on the basis of a single, damaged specimen, there are enough distinctive features to ensure its separation from any other known species. The small eyes, relatively long interfrontal bristles, and strongly tuberculate face give it a distinctive habitus, and the rows of posteromedial lamellae on sternite 5 are clearly diagnostic. The most similar species is *M. parva*, from which it can be distinguished by the above features and very different wing venation.

Etymology. Although the presence of a strongly projecting upper face is characteristic of the entire subgenus, the upper face is especially swollen and tubercle-like in this species, thus giving rise to the specific name *tuberculum*.

***Minilimosina* (*Minilimosina*) *zeda* new species**

Figs. 11, 54, 55, 139, 140, 141, 202

Description. Length 1.5-1.6mm. Interfrontal plate bordered by 4 interfrontal bristles, upper 3 barely cruciate; width 0.5 times height. Three inner orbital bristles, uppermost

bristle largest, present between orbital and interfrontal bristles (inner orbitals are not found elsewhere in the genus). Eye 2.0 times as high as gena. Mid tibia of male ventrally with a row of about 10 short, stout bristles on distal half or more; apical ventral bristle short but distinct. Distal anterodorsal bristle of mid tibia 0.6 times as long as distal posterodorsal bristle. Scutum with 6-8 rows of acrostichal setulae between dorsocentral lines, dorsocentral bristles in a single, prescutellar pair 0.7 times as long as scutellum. Prescutellar acrostichal setulae in a single pair slightly longer than other acrostichal setulae. Scutellum 0.9 times as wide as long, apical scutellar bristles twice as long as scutellum. Mesopleuron pollinose except for a small area along anterior margin of episternum (the entire type series is light brown, probably teneral, making it difficult to ascertain with certainty the extent of pollinosity). Halter uniformly light brown. Wing with costagial bristles short, equal. Second costal sector 0.9 times as long as third (Fig. 202).

Abdomen. Syntergite 1+2 2.7 times as long as tergite 3.

Male abdomen. Sternite 5 setose, posteromedial area with a distally concave group of rows of short, dark bristles; rows of bristles strong laterally and very weak medially (Fig. 11). Surstylus with a broad, setulose anterior lobe and a single large posteroventral bristle (Figs. 54, 55). Paramere weakly clubbed and truncate apically. Distiphallus angulate, pointed distally.

Female abdomen. Tergites 6 and 7 complete, simple; tergite 8 large, with tripartate pigmentation. Epiproct large, bare except for the usual 2 bristles (Fig. 139). Sternite 8 deeply tri-lobed anteriorly, flat posteriorly (Fig. 141). Hypoproct entirely setulose. Each spermatheca wrinkled-oval, ducts short (Fig. 140).

Types. *Holotype* (♂, BRI), and 5 *paratypes* (3 ♂, 2 ♀, JRO, GUELPH): CANADA. **Alberta:** Hinton, 12.viii.1980, on an old, dried up mammal carcass, S.A. Marshall. Other *paratypes*: **Alaska:** Alaska Hwy, 12 mi N Tok, carrion trap, 14-20.vii.1985, S.A. Marshall (1 ♂, 1 ♀, BRI); Sawmill Creek, White Spruce bog, 18 mi S Delta Jctn., carrion FIT, 15.vii.1985, S.A. Marshall (1 ♂, GUELPH).

Comments. The very unusual head chaetotaxy gives this species a superficial similarity to *Halidayina* species, and the distinctive male sternite 5 reinforces the impression that this is an unusual *Minilimosina*. Other features, the typical surstyli in particular, provide ample evidence that *zeda* does belong in the subgenus *Minilimosina*.

Etymology. Since this species has resided in my collection since 1980 as "unplaced species Z", the coined word *zeda* was chosen as a permanent, easily remembered specific epithet.

Subgenus *Allolimosina* Roháček, 1983:43

Type Species *Limosina (Scotophilella) albinervis* Duda, 1918

Subgeneric diagnosis. Size small, 0.9-1.2 mm. Colour brown, mostly pollinose. Postocellar bristles present. Face protruding between antennae, strongly concave and carinate below. Dorsocentral bristles in a single, prescutellar pair. Mid tibia of male ventrally with only minute setulae or a row of distal spinules; mid femur with 1-3 stout basal bristles. Costa distinctly overpassing R_{4+5} , second costal sector less than 0.7 times length of third; discal cell very short, with anterior outer corner always obtuse-angled, posterior outer corner acute angled. Sternite 5 of male with a posteromedial comb of blunt spines. Sternite 8 of female reduced or weakened. Distiphallus simple and sclerotized.

Minilimosina (Allolimosina) albinervis (Duda)

Figs. 24, 82, 83, 84, 142, 143, 144

Limosina (Scotophilella) albinervis Duda, 1918: 131.

Minilimosina albinervis: Roháček, 1983:44, synonymy and description.

Diagnosis. Length 1.1-1.2 mm. Mid tibia of male with a long apicoventral bristle and no other ventral bristles; distal posterodorsal bristle and distal anterodorsal bristles short, subequal. Scutum with 5 rows of acrostichal setulae between dorsocentral lines, dorsocentral bristles in 1 prescutellar pair 0.8 times as long as scutellum. Apical scutellar bristles 1.6

times as long as scutellum. Wing with second costal sector 0.5-0.6 times as long as third, veins others than costa very light, membrane milky-white.

Male abdomen. Sternite 5 with a single posteromedial row of about 20 flat bristles (Fig. 24). Surstylus large, flat, setulose on medial and ventral surfaces; posterior lobe with a single, unbranched lobe with an apical bristle which is branched in some specimens (Figs. 82, 83). Paramere broad (Fig. 84).

Female abdomen. Tergite 8 complete but depigmented medially. Epiproct emarginate anteriorly, bare except for the usual 2 bristles (Fig. 142). Sternite 8 reduced to a minute setulose patch immediately behind sternite 7; hypoproct small, bare, anteriorly emarginate (Fig. 144). Spermatheca short-cylindrical, with a deep apical invagination (Fig. 143).

Material examined. CANADA: **Ontario:** Marmora, 3.vi.1952, J.R. Vockeroth (1 ♀, BRI). U.S.A. **District of Columbia:** Washington, 7.xi.1912, R.C. Shannon (1 ♀, ANSP). **Illinois:** Cook Co., Homewood, 11.x.1952, Berlese of decaying vegetation, H.S. Dybas (1 ♂, FLD). **Minnesota:** Ramsey Co., Luth. Sem. Grounds, 29.v.1965, on dead Grackle, B. Cutler (2 ♂, 1 ♀, PSU). **Virginia:** Fairfax Co., Dead Run, ex debris in wild bee hive, 14.xi.1914, issued 30.i.1915, R.C. Shannon (1 ♂, USNM).

This species is also known from Spain, England, Germany, Czechoslovakia, Hungary, Israel, and Afghanistan.

Biology. Roháček (1983) recorded this as a rare species, most often associated with decaying vegetation. Some of the above records, especially the rearing record from bee hive debris, further suggest that this is a phytosaprophagous species; however, three of the specimens examined were collected on a dead bird.

Comments. Slight differences can be noted between the Nearctic specimens illustrated here and the Palaearctic material illustrated by Roháček (1983), especially in the details of the posteroventral surstylar process. I feel that these differences represent intraspecific variation, and that the Nearctic populations should not be considered a distinct species. The Holarctic species *M. albinervis* is most distinctive for its complex surstylus, short second costal sector, and reduced, tab-like female sternite 8. Its closest relatives are the Palaearctic *M. alloneura* and *M. secundaria*.

Minilimosina (Allolimosina) rotundipennis (Malloch)

Figs. 25, 79, 80, 81, 187, 203

Limosina rotundipennis Malloch, 1913:370.

Limosina curvitaris Duda, 1925:167, New Synonymy.

Description. Length 0.9-1.2 mm. Interfrontal plate narrow, width at top 0.7 times height, tapering to 0.5 times height below; bordered by 4 equal interfrontal bristles. Lunule rounded, face projecting knob-like between antennae, concave below. Eye 2.1 times as high as gena. Mid tibia of male ventrally with a distal row of 5-6 weak short spines and a stout anteroventral bristle, femur with 3 stout bristles basally. Distal posterodorsal bristle of mid tibia slightly shorter than distal anterodorsal and much shorter than distal dorsal. Scutum with 4-5 rows of acrostichal setulae between dorsocentral lines, dorsocentral bristle in 1 prescutellar pair subequal to length of scutellum. Prescutellar acrostichal bristles in a single pair twice as long as acrostichal setulae. Scutellum 1.5 times as broad as long, apical scutellar bristles 1.7 times scutellar length. Halter uniformly light brown. Wing with 2 equal costal bristles, second costal sector less than half as long as third (Fig. 203).

Abdomen. Syntergite 1+2 1.5 times as long as tergite 3, tergites 3-5 wide and fully sclerotized.

Male abdomen. Synsternite 1+2 dark, deeply emarginate posteriorly (Fig. 25). Sternite 3 convex and membranous at middle. Sternite 5 with posterolateral corners heavily sclerotized, posteromedial comb split into oblique angled combs (Fig. 25). Surstylus with a long, thin outer lobe (Figs. 79, 80, 187). Distiphallus minute (Fig. 81).

Female abdomen. Tergite 6 greatly reduced, distinctly sclerotized only at setal bases.

Tergite 7 divided into 2 small lateral sclerites with anteromedial lobes. Tergite 8 divided into 2 sclerites, almost contiguous anteromedially. Epiproct greatly reduced, membranous. Sternites 6 and 7 small and very lightly pigmented, sternite 8 lightly pigmented but larger than the darker, setulose hypoproct. Each spermatheca subspherical, apical invagination small, stem with a single bulbous swelling.

Types. *Holotype* (♀, USNM): PUERTO RICO. Culebral, Feb, 1899, Aug. Busck (specimen also bears a label "perparva Williston").

Type of Limosina curvitaris Duda: BRAZIL. Blumenau, Loth.Hetschke (1♂, NMW, labelled and described by Duda as ♀).

Other material examined. U.S.A. (5♂, BRI): **Arizona:** Pima. Co., Santa Catalina Mountains, Mt. Lemmon Highway, 4900', dung, ix.1970, A.Newton (4♂, BRI); Cochise Co., Huachuca Mts., 6000', Miller Canyon, dung, oak woodland, ix.1970, A.Newton (1♂); Portal, Southwestern Research Stn., Chiricahua Mts., 18-23.viii.1984, mushroom trap, B.V. Brown (2♀); Stewart Campground, 16-19.viii.1984, dung trap, B.V.Brown (1♀); Santa Cruz Co., 8miWNW Nogales, Walker Canyon, 3900', oak woodland, ix.1970, dung, A.Newton (1♂, 4♀); Patagonia Lk. St. Pk., 9-11.viii.1984, flight intercept trap, B.V.Brown (1♀). **Florida.** Hendry Co., LaBelle, Capt. Hendry Rd., iv.1971, pine, hardwood near river, human dung, A.Newton (1♂); Volusia Co., Tomoka St. Pk., 20.4i.1984, S. Marshall (1♂); Sarasota Co., Myakka River St. Pk., 21.v.1982, pig dung trap, R.E. Woodruff (5♂, 1♀, FSC); Orange Co., E. Orlando, 2-3.vii.1982, pig dung trap, R.E. Woodruff (1♀).

Comments. The abdominal characters of this species are highly modified, and it is difficult to compare them to any other group within *Minilimosina*. The long, dark surstyli, the small, anterolaterally deflexed parameres, the incomplete subanal plate, and the minute, membranous distiphallus are unique. *M. rotundipennis* is included in the subgenus *Allolimosina* because it keys there on the basis of wing venation and resembles other *Allolimosina* species in a few superficial features such as the presence of postocellar bristles. There is no convincing evidence for a close phylogenetic relationship between *M. rotundipennis* and other *Allolimosina* species.

Subgenus *Svarciella* Roháček 1983:30

Type Species *Limosina (Scotophilella) splendens* Duda, 1982

Subgeneric diagnosis. Size 0.9-1.9, body at least partly shining black. Postocellar bristle absent. Face weakly concave, usually weakly or not at all projecting between antennae (Fig. 188). Dorsocentral bristles in 2 pairs, anterior pair small; acrostichal bristles in 4-6 rows. Mid tibia of male with only minute setulae ventrally or with a row of spinules on distal 2/3. Mid femur with only a single basal ventral bristle or with long ventral hairs over most of its length. Costa usually weakly surpassing tip of R_{4+5} , cell dm obtuse angled and sometimes appendiculate on outer posterior corner. Sternite 5 of male variable, usually with a large posteromedial comb or process. Sternite 8 of female large, not reduced. Distiphallus sometimes with a long ventral flagellum (*vitripennis* group).

Comments. The subgenus *Svarciella* contains two distinctive species groups. *M. albifrons*, *M. contrasta*, *M. niveipennis*, *M. archboldi*, *M. vitripennis* and probably *M. masoni* (known only from females) form an apparently monophyletic group of species sharing several unique characters, such as a very unusual long flagellum on the distiphallus. *M. dissimilicosta*, *M. vixa*, *M. intercepta* and the related European *M. splendens*, *M. ismayi*, and *M. v-atrum* form a distinctive, but probably paraphyletic, group sharing such characters as the very uniform and distinctive type of male fifth sternite (Figs. 30, 34) and a slender distiphallus quite different from the found in the *vitripennis* group. The one remaining species of *Svarciella*, *M. bipara*, does not fit well into either group.

Most of the features listed in the subgeneric diagnosis are probably plesiomorphic, and the apparent transformation series from the type of male sternite 5 found in *v-atrum* to that found in *vitripennis* is the strongest evidence for the monophyly of *Svarciella*. *M. dissimilicosta*, *M. splendens*, and *M. archboldi* provide the intermediate states required to support the suggestion that the phenotypically dissimilar species groups of *Svarciella* make up a single monophyletic group.

Minilimosina (Svarciella) archboldi new species

Figs. 26, 89, 90

Description. (Male only). Length 1.5 mm. Colour brown, pollinose. Orbits, ocellar triangle and narrow interfrontal strips pollinose, middle of interfrontal plate shining brown, intervening areas forming a black M-shape. Interfrontal plate broad and slightly tapered, width at top equal to height, bordered by 4 short, equal interfrontal bristles. Eye 4.0 times as high as gena. Mid tibia with a very short apicoventral bristle and no other ventral bristles; distal anterodorsal bristle longer than distal posterodorsal bristle. Scutum with 5-6 rows of acrostichal setulae between dorsocentral lines, dorsocentral bristles in 2 pairs, anterior pair twice as long as acrostichal setulae, posterior pair as long as scutellum. Prescutellar acrostichal bristles in a single pair twice as long as other acrostichal setulae. Scutellum flat, 0.9 times as long as wide, apical bristles twice as long as scutellum. Mesopleuron pollinose except for shining, bare anterior half of katepisternum, anteroventral corner of anepisternum, and middle of anepimeron. Halter very dark brown, stem yellow. Costagial bristles much shorter than dorsocentrals. Second costal sector 0.75 times as long as third. Cell dm broad, outer angle obtuse.

Abdomen. Syntergite 1+2 2.5 times as long as tergite 3, tergites 1-5 lightly pigmented but fully sclerotized.

Male abdomen. Sternite 5 with a posteromedial comb of 12 dark, blunt bristles flanked by a setose tubercle on each side; a shelf-like 4-bristled projection anterior to posteromedial comb (Fig. 26). Surstylus broad with a small, digitate, setose, anterior lobe and a larger posteromedial lobe bearing a long, stout bristle (Figs. 89, 90). Distiphallus with a long dorsal flagellum (Fig. 89). Parameres thin, apically curved.

Female. Unknown.

Types. *Holotype* (σ , BRI): **Florida:** Archbold Biological Station, Highlands Co., 23.iv.1967, B.V. Peterson. *Paratype:* **Florida:** De Land Co., nr. Barberville, Hwy.40, 18-20.vi.1984, mushroom baited pitfall trap, S.Marshall (1 σ).

Biology. Beyond the fact that one of two known specimens was collected in a mushroom trap, nothing is known of the biology of this species.

Comments. *M. archboldi* is clearly related to the *vitripennis* species group, as evinced by the strongly deflexed posteromedial portion of sternite 5, the whip-like ventral portion of the distiphallus, and the *vitripennis*-like surstyli. It also shows some significant similarities to the *Svarciella v-atrum* species group, such as the membranous lobes to each side of the posteromedial comb of male sternite 5, detail of the posteromedial comb, and the plesiomorphic retention of well developed preabdominal tergites. *M. archboldi* is thus treated as a plesiomorphic member of the *vitripennis*-group, and forms a sort of operational "missing link" uniting the *vitripennis* and *v-atrum* groups into *Svarciella*.

Minilimosina (Svarciella) bipara new species

Figs. 40, 94, 95, 96, 163, 164, 165, 209

Description. Length 1.5-1.7 mm. Colour brown, pollinose. Middle part of interfrontal plate, interfrontal strips and orbits silvery, lower frons reddish, upper part of interfrontal plate and areas flanking ocellar triangle shining black, frons otherwise dull black. Interfrontal plate narrow, almost parallel-sided, twice as high as wide, bordered by 4 very fine equal interfrontal bristles. Lunule projecting as a carinate knob between antennae, face concave-carinate below. Eye 3.5 times as high as gena. Mid tibia of male ventrally with a distal row of 9 spinules and a long apicoventral bristle. Anterodorsal bristle in distal 1/4 of mid tibia shorter than distal posterodorsal bristle; distal dorsal bristle slightly displaced anteriorly; and additional small dorsal bristle present between distal anterodorsal and posterodorsal bristles. Scutum with 4-6 rows of acrostichal setulae between dorsocentral lines; dorsocentral bristles in 2 pairs, anterior pair 3 times as long as acrostichal setulae, posterior pair subequal to scutellar length. Prescutellar acrostichal bristles in a single pair

twice as long as acrostichal setulae. Scutellum flat, 0.7 times as long as wide, apical bristles twice scutellar length. Mesopleuron pollinose except central and anterior parts of katepisternum; anepisternum bulging out in type specimen. Halter uniformly dark brown. Wing with upper costagial bristle 2.5 times as long as lower costagial. Second costal sector 0.75 times as long as third, all veins pale in colour (Fig. 209).

Abdomen. Syntergite 1+2 1.8 times as long as tergite 3, other tergites lighter in pigmentation than syntergite 1+2 but fully sclerotized.

Male abdomen. Sternite 5 with a setulose posteromedial swelling (Fig. 40), sternite 6 simple. Surstylus flat, almost triangular with an elongate anteroventral point and a blunt posteroventral angle with a short bristle (Figs. 94, 95). Paramere S-shaped, strongly curved near apex (Fig. 96). Distiphalus very narrow, sclerotized, rod-like (Fig. 96).

Female abdomen. Tergite 8 long, complete but weakly pigmented medially; epiproct small, bare except for 2 bristles (Fig. 163). Sternite 8 broadest posteriorly, bare except for 8 small bristles; hypoproct setulose except for anterolateral lobes (Fig. 165). Each spermathecae spherical, with deep apical invagination (Fig. 164).

Types. *Holotype* (σ , BRI) and 9 *paratypes* (4 σ , 5 ♀ , BRI, GUELPH): PANAMA. **Chiriqui:** 2kmE Cerro Punta, 2200m., 1-4.vi.1977, forest carrion trap, S.B. Peck. *Other paratypes:* MEXICO. **Oaxaca:** 5miE jct. Hwy.175 & Yuvila Rd., 7600', 9-19.viii.1973, oak-pine dung, A.Newton (1 σ , MCZ); Oaxaca, 15.5miS Ixtlan de Juarez, 7600', 10-18.viii.1973, oak woods, dung, A.Newton (1 ♀ , MCZ); **Hidalgo:** 3.2miN Tlanchinol, 5100', 6-11.vii.1973, cloud forest dung, A.Newton (1 ♀ , MCZ). PANAMA. **Chiriqui:** 2200m., 2kmE Cerro Punta, 28.v-8.vi.1977, oak, dung, S.Peck (3 σ , 3 ♀). VENEZUELA. **Tachira:** 45kmNE SanCristobal, 9000', 20-22.v.1974, dung trap, S.Peck (1 σ); Tachira, 38kmNE SanCristobal, 7000', 18-20.vi.1974, carrion, S.Peck (1 σ , 1 ♀).

Biology. Beyond the fact that the type material was taken in both dung and carrion traps over a wide range of elevations, nothing is known of the biology of this species.

Comments. *M. bipara* does not fit well with either of the main species groups of *Svarciella*, and in fact bears a greater general similarity to species of *Amputella* than to any other group. As it lacks the defining characters of *Amputella* (reduction of right paramere and female sternite 8) but exhibits the diagnostic characters of *Svarciella* (2 pairs of dorsocentral bristles, relatively large female sternite 8), *M. bipara* is included in the latter subgenus.

Etymology. The name chosen reflects the fact that, unlike similar and sympatric species in the subgenus *Amputella*, this species has 2 complete parameres. The name *bipara* is a coined word formed from the Latin *bi* plus the first part of the word 'paramere'.

Minilimosina (Svarciella) contrasta new species

Figs. 28, 91, 92, 93, 175, 176, 177

Description. Length 1.0-1.2 mm. Colour shining dark brown except yellow-orange antennae. Interfrontal plate small, bordered by 2 minute interfrontal bristles; frons pollinose except for a large, wider than long, rounded, shining frontal triangle; face shining and weakly carinate. Eye 3 times as high as gena. Mid tibia with only an apical bristle ventrally; distal anterodorsal bristle and distal posterodorsal bristle minute. Acrostichal setulae sparse, in 4 rows between dorsocentral lines. Dorsocentral bristles in 2 pairs, anterior pair short, prescutellar pair 0.7 times as long as scutellum. Prescutellar acrostichal setulae in a single pair equal in length to other acrostichal setulae. Scutellum flat, 0.6 times as long as wide, apical scutellar bristles as long as scutellar width. Halter dark brown with yellow stem. Wing with costagial bristles small and subequal; veins yellow, second costal sector half as long as third; crossvein dm-cu 1/3 as long as distance between dm-cu and r-m; costa ending at or just beyond tip of R_{4+5} .

Abdomen. Syntergite 1+2 2.0 times as long as tergite 3, lightly pigmented but distinctly sclerotized. Tergites 3-5 very lightly pigmented, sclerotization indistinct, preabdomen appearing largely membranous.

Male abdomen. Sternite 5 with a small, dark, deflexed T-shaped posteromedial process; apex of process with a row of 5 bristles and sometimes concave (Fig. 28). Surstylus broad, with several stout posteroventral bristles and a large inner basal lobe bearing a strong bristle (Figs. 91, 92). Parameres thin, somewhat S-shaped. Distiphallus similar to *M. vitripennis*, but ventral flagellum weaker (Fig. 93).

Female abdomen. Tergite 8 longitudinally divided into a dorsal and 2 lateral dark areas. Epiproct large, setulose on posterior half, with 2 long bristles. Sternite 8 large, as broad as long, lightly pigmented anteriorly (Fig. 175); hypoproct setulose except along anterior margin (Fig. 177). Each spermatheca spherical, with a large apical evagination which is longer than spermathecal body, duct short, sclerotized part very short (Fig. 176).

Types. *Holotype* (♂, BRI): CANADA. **Ontario:** Ottawa, 18.ix.1956, on ground under prostrate *Picea*, J.R. Vockeroth. *Paratypes:* CANADA. **Ontario:** Mer Bleue Bog, Ottawa, 19.vii.1963, J.R. Vockeroth (1 ♂, BRI). **Quebec:** Old Chelsea, Summit King Mtn., 1150', 25.vi.1962, J.R. Vockeroth (1 ♀, BRI). U.S.A. **Florida:** Marion Co., Zay Prairie, Ocala Nat.For., 14-18.vi.1984, human dung, S.A. Marshall (1 ♂). **Maryland:** Plummer's I. 19.iv.1903, E.A. Schwarz (1 ♀, USNM), **Virginia:** Prince William Co., 8 air kmNW Haymarket, 25.vi.1966, P.H. Arnaud, Jr. (1 ♂, 5 ♀, CAS).

Comments. *M. contrasta* has previously been misidentified as *M. varicosta* (itself a junior synonym of *M. niveipennis*), from which it differs in having a flat scutellum, a deflexed process on male sternite 5, and different male and female genitalia. *M. contrasta* forms part of a complex of species including the Holarctic *M. vitripennis*, the Nearctic *M. archboldi*, the Neotropical *M. niveipennis*, and the Neotropical *M. masoni*. *M. furcalisterna*, (Deeming, 1969) from Nepal also appears to belong to this complex, and resembles *M. contrasta* in having yellow or orange antennae.

Etymology. The specific name is a coined word referring to the contrast in colour between the head and antennae.

Minilimosina (Svarciella) dissimilicosta (Spuler) new combination

Figs. 38, 39, 172, 173, 174, 204

Leptocera Scotophilella dissimilicosta Spuler, 1925:148.

Limosina hackmani Roháček, 1977:115, New Synonymy

Minilimosina (Svarciella) hackmani, Roháček, 1983: 34, male only

Description. Length 1.6-1.9 mm. Colour shining black. Frons pollinose except for large, longer than wide, shining frontal triangle surrounding the pollinose ocellar triangle. Interfrontal plate 0.8 times as wide as high, 0.3 times as wide as frons. Face concave, subshining, lunule yellowish brown, small and almost flat. Eye 3.0 times as high as gena, gena dull black. Mid tibia in both sexes with only an apical bristle ventrally; distal anterodorsal larger than distal posterodorsal bristle. Acrostichal setulae long, in 5 or 6 rows between anterior dorsocentral bristles. Dorsocentral bristles in 2 pairs, anterior pair twice as long as acrostichal setulae; prescutellar dorsocentral bristles slightly shorter than scutellum; prescutellar acrostichals in a single pair twice as long as other acrostichals. Scutellum flat, 0.8 times as long as wide, apical scutellar bristles twice as long as scutellum. Mesopleuron almost completely pollinose or katapisternum with a small anterodorsal bare area. Halter black, with contrasting yellow stem. Second costal sector dark, 0.9 times as long as third, other veins pale. Costa slightly surpassing tip of R_{4+5} ; cell dm with outer corner acute, weakly appendiculate.

Abdomen. Syntergite 1+2 1.9 times as long as tergite 3, all abdominal sclerites dark.

Male abdomen. Sternite 5 with a large convex bulge preceding a posteromedial comb of flat setae (Figs. 38, 39). Surstylus very large, almost spoon-shaped (Fig. 38). Parameres simple, blunt-tipped. Distiphallus simple, with thin dorsal and ventral processes.

Female abdomen. Tergite 8 longitudinally divided into a dorsal and 2 lateral dark

areas. Epiproct elongate, bare except for 2 bristles (Fig. 172). Sternite 8 large, slightly longer than wide, setulose on posterior half, notched posteromedially, darkly pigmented on anterior half. Hypoproct setulose on posterior third, bare and tri-lobed anteriorly (Fig. 174). Each spermathecae large, peanut-shaped, duct very short with no exposed sclerotized part (Fig. 173).

Types. *Holotype*: (♀, USNM): U.S.A. **Washington**: Olga, 17.v.10, Melander Collection. *Paratypes*: **Washington**: Dewatto, 15.viii.1910 (1♂, dissected, USNM); Mt. Constitution, 17.v.1910 (1♀, dissected, USNM); Ilwaco, 25.v.1917, Melander (1♂, USNM).

Other Material Examined. CANADA. **Alberta**: Elk Island Nat. Pk., Trail 6, 13.v.1982, sifting moose dung, R.A. Anderson (1♂); Coleman, 24-26.vii.1980, S.A. Marshall (2♀). **British Columbia**: King Salmon L., 3.viii.1960, 1750', W.W. Moss (1♀, BRI); Hot Springs, 5miS Lake Ise, 8.vii.1960, C.H. Mann (1♂, BRI); Summit Lake, mi392 Alaska Hwy., 7,8,16.vii.1959, 4500-4700', R.E. Leech (1♂, 2♀, BRI). U.S.A. **Alaska**: Iditarod, 12.vi.1918, Alice Twitchell (1♂, USNM); Matanuska, 5.15.1944, rotary trap, J.C. Chamberlin (2♂, 5♀, USNM). **Colorado**: Rio Grande Co., 10,000', Beaver Creek, 21.vi.1972, W.W. Wirth, Malaise Trap (1♂, USNM). **New Mexico**: Socorro Co., S. Baldy Pk., 10,400', 20miW Socorro, 28.vi-7.vii.1979, alpine meadow, S.&J. Peck (1♂); Taos Co., 1.7miSE Tres Ritos, 8500', 3-5.vii.1972, dung, A.F. Newton (1♂, MCZ). **Utah**: Little Brush Creek, 25miW Vernal, 8.vii.1961, 8000', J.G. Chillcott (2♂, BRI). Also known from Finland (holotype of *hackmani* Roháček).

Biology. Of all the known specimens of this species, including the one from Finland, the only specimen with biological information was collected from moose dung in Elk Island National Park, Alberta.

Comments. *M. dissimilicosta* is a highly distinctive species due to the conically highly bulging male sternite 5 and the very large surstyli. The posteromedial comb of sternite 5, often deflexed and obscured by the conical bulge, is similar to that found in *M. vixa* and *M. intercepta* but also shows important similarity to that found in *M. archboldi* and the related European *M. splendens*.

Minilimosina (Svarciella) intercepta new species

Figs. 30, 31, 32, 33, 166, 167, 168, 188, 205

Description. Length 1.6-1.8 mm. Colour black except antenna, stem of halter, trochanters, and tips of tibia and femur, which are orange or yellowish brown. Frons pollinose except for large, longer than wide, shining frontal triangle surrounding the pollinose ocellar triangle (Fig. 188). Interfrontal plate as wide as high, bordered by 3 or 4 interfrontal bristles. Lunule subquadrate, weakly projecting between antennae, face weakly concave, carinate, subshining. Antennae bright orange in contrast to black face and frons. Eye 3.5 times as high as gena, gena lightly pollinose except bare, shining spot below eye. Mid tibia of male curved, with a double row of distinct ventral spinules and an anteroventral bristle. Acrostichal setulae in 6-8 rows between the small anterior dorsocentral bristles; dorsocentral bristles in 2 pairs, anterior pair small, prescutellar pair subequal to length of scutellum; prescutellar acrostichals in a single pair slightly longer than other acrostichals. Scutellum flat, 0.7 times as long as wide, apical scutellar bristles slightly longer than scutellar width. Mesopleuron with 2 large bare, shining areas on anterior half, the lower spot twice as large as the upper. Halter black with orange stem. Second costal sector dark, 0.7-0.8 times as long as third; other veins lighter in colour; costa slightly surpassing R_{4+5} ; outer angle of cell dm not appendiculate (Fig. 205).

Abdomen. Syntergite 1+2 1.5 times as long as tergite 3. All abdominal sclerites large, dark, heavily sclerotized and weakly punctate.

Male abdomen. Sternite 5 with a long posteromedial comb of short stout bristles, comb flanked by longer bristles on each side (Fig. 30); sternite 6 with 2 small, dark lobes at middle (Fig. 33). Surstylus bilobed, inner lobe longer, with 3 large spurs (Figs. 31). Parameres weakly bent anteriorly at tip (Fig. 32). Distiphallus slender, simple, mostly sclerotized (Fig. 32).

Female abdomen. Tergite 8 with tripartate pigmentation, epiproct broad, bare except for 2 bristles (Fig. 166). Sternite 8 shield-shaped, almost entirely setulose (Fig. 168). Hypoproct large, entirely setulose. Cercus long, with long bristles. Each spermatheca cylindrical with a reticulate surface (Fig. 167).

Types. *Holotype* (♂, BRI) and 13 *paratypes* (8 ♂, 5 ♀, GUELPH, JRO): U.S.A. **Illinois:** Champaign Co., Mahomet Hardwoods, 20-26.v.1979, Peck, Malaise intercept trap in oak woods. *Other paratypes* (BRI, GUELPH): CANADA. **Ontario:** Foxmead, 25.v.1959, dense maple woodland, J.G. Chillcott, (1 ♀, BRI); Heckston, 20kmSE Kemptville, 15.v-24.vi.1984, flight intercept trap, M. Kaulbars (1 ♀); Pt. Pelee N.P. Leamington, 14.vi.1984, K.N. Barber (1 ♂). U.S.A. **Arkansas:** Scott Co. 7miE Y City, Jct. Hwy270&Rt.71 on 270, 6-8.iii.1977, pig dung trap, Woodruff & Wiley (1 ♀, FSC). Montgomery Co., 5.4miE IdaHwy270, 6-8.iii.1977, pig dung trap, Woodruff & Wiley (1 ♀, FSC). **Georgia:** Chatahoochee St. For., US441 N of Turnerville, 5-25.vi.1984, mushroom trap, S.A. Marshall (1 ♂); Rabun Co., Pine Mtn., 1400', 4.v.1957, J.R. Vöckeröth (1 ♂); Wilkinson Co., Big Sandy Ck., 8miS Irwinton, US441, 5-25.vi.1984, intercept trap near dung, S.A. Marshall (1 ♂). **Illinois:** Savanna, Miss. Palisades Pk., 13-17.v.1979, oak woods intercept trap, Peck (1 ♂, 2 ♀). **Kentucky:** Rowan Co., 24kmSW Borehead Cave, 14-20.vii.1983, *Fagus* forest intercept trap, Peck (1 ♀). **Louisiana:** 3miS Oak Grove, 31.iii.1960, J.G. Chillcott (2 ♂). **North Carolina:** Jackson Co., Cullowhee, 5-28.vi.1984, intercept trap and 6-17.vi, pan trap, S.A. Marshall (2 ♂, 2 ♀). **Oklahoma:** Latimer Co., 5miW Red Oak, 9.iii.1977, pig dung trap, K. Stephen (1 ♀, FSC). **Tennessee:** Sevier Co., 2900', Greenbrier Cove, Ramsey Cascade Cove Forest, 18.v-23.v.1972, carrion trap, A. Newton (2 ♂, MCZ); 2.5miN Gatlinburg, 5-28.vi.1984, riparian, rotting mushroom trap, S.A. Marshall (1 ♀). **Texas:** San Jacinto Co., 5kmS Coldspring, Double Lk. Camp, 22.v-16.viii.1983, forest flight intercept trap, Peck (2 ♂, 1 ♀). **Virginia:** Shenandoa Co., 16km Strasburg, 12.v-22.viii.1983, flight intercept trap in forest, Peck (2 ♂).

Biology. The majority of the known specimens were collected in hardwood forests using intercept traps, although 4 specimens were collected on dung, and one on carrion. The related European *M. ismayi* Roháček is known only from the holotype, collected in Spain and with no associated biological information.

Comments. *M. intercepta* is very similar to the European *M. ismayi* Roháček, both of which have light antennae contrasting with a dark body, and both of which have very similar male genitalia. Unfortunately, the female of *M. ismayi* is not known. Dr. Roháček, describer of *M. ismayi*, was kind enough to compare specimens of *M. intercepta* with the holotype of *M. ismayi*. He agreed that *ismayi* and *intercepta* are different species. Although they are extremely similar, in *M. intercepta* the projections of sternite 6 are smaller and more widely separated, the posteromedial comb of sternite 5 is longer, and there are small differences in the surstylus. In addition to these differences, *M. intercepta* has a shining spot below the eye which is lacking or indistinct in *M. ismayi*, and has a much larger mesopleural shining area. The Nearctic species most closely related to *M. intercepta* is *M. vixa*.

Etymology. The specific name refers to the type of trap in which most of the type series was collected.

Minilimosina (Svarciella) masoni new species

Figs. 181, 182, 183, 206

Description. (Female only). Length 0.9 mm. Colour shining black except tarsomeres, tips of tibiae, lower frons, face antennae, and anterior part of gena which are contrasting orange. Interfrontal plate small, twice as high as wide, bordered by 4 very small interfrontal bristles. Frons pollinose except for a large, equilateral, shining frontal triangle; ocellar triangle in a square pollinose patch. Face carinate between antennae, concave and weakly carinate below. Eye 4.0 times as high as gena. Mid tibia with only an apical bristle ventrally,

dorsally with an anterodorsal bristle just above middle, a posterodorsal bristle just below middle, and a posterodorsal bristle just before apex in addition to the usual proximal anterodorsal, distal anterodorsal and dorsal bristles shown in Fig. 1 Hind tibia with a long, thin, preapical dorsal bristle (absent in all congeners); first 2 tarsomeres of hind leg subequal in length and width (tarsomere 2 longer and thinner in congeners). Acrostichal setulae long, sparse, in 4 rows between dorsocentral areas. Dorsocentral bristles in 2 pairs, anterior pair barely longer than acrostichal setulae, prescutellar pair subequal to scutellar length. Prescutellar acrostichal setulae in a single pair, slightly longer than acrostichal setulae. Scutellum strongly convex, 0.5 times as long as wide, apical scutellar bristles as long as scutellum. Halter shining black with yellow stem. Wing with upper costagial bristle 1.5 times as long as lower costagial; second costal sector very short, 0.4 times as long as third sector, R_{4+5} diverging from R_{2+3} at a large angle (Fig. 206).

Abdomen. Syntergite 1+2 2.0 times as wide, 2.0 times as long, and much darker than tergite 3; tergites 3, 4 and 5 greatly reduced, almost membranous; tergite 7 darkly pigmented (Fig. 181); tergite 8 darkly pigmented, setulose along posterior margin only; epiproct bare except for 2 bristles. Sternites 1-6 lightly pigmented, sternite 7 normal; sternite 8 large, setulose; hypoproct entirely setulose (Fig. 183). Each spermatheca spherical, with a shallow, lateral depression; sclerotized part of duct short (Fig. 182).

Types. *Holotype* (♀, BRI) and 7 *paratypes* (7 ♀, BRI): MEXICO. **Sinaloa:** 20miE Concordia, 3000', 4.viii.1964, W.R.M. Mason.

Comments. *M. masoni* differs markedly from other *Minilimosina* species in the colouration of the face and frons, the rich mid tibial chaetotaxy, the sharply up-turned R_{2+3} , and the preapical dorsal bristle of the hind tibia. The sharply up-turned R_{2+3} is similar to that found in (and diagnostic for) the distantly related genus *Pterogramma*, and the dorsal hind tibial bristle is a diagnostic character of the closely related genus *Xenolimosina*. Since there is good evidence that *M. masoni* is a derived member of the *M. vitripennis* species complex, these characters appear to have developed independently in this species. Characters suggesting the placement of *M. masoni* in the *vitripennis* group include the greatly reduced sclerites of abdominal segments 3-5, the large sternite 8, the large, sparse acrostichals, head chaetotaxy, and general habitus. Within the *vitripennis* group, the very short second costal sector and convex scutellum are considered derived characters. It is predicted that when the male is discovered, it will have a large, membranous distiphallus with a long dorsal flagellum similar to that found in *M. niveipennis*.

Etymology. This species is named after the collector of the type series, Dr. W.R.M. Mason of the Biosystematics Research Institute, Canada Agriculture, Ottawa.

***Minilimosina (Svarciella) niveipennis* (Malloch) new combination**

Figs. 27, 85, 86, 178, 179, 180

Limosina niveipennis Malloch, 1913:370.

Limosina varicosta Malloch, 1914:14, New synonymy.

Limosina mollis Richards, 1963:243, New synonymy.

Description. Length 0.9-1.1 mm. Colour black except contrasting orange antennae, yellow tarsomeres, and brown tibiae. Orbits and ocellar triangle pollinose; interfrontal plate shining brown; relatively narrow strip between interfrontal plate and orbits black. Interfrontal plate broad and slightly tapered, width at top equal to height, bordered by 3 very fine, equal interfrontal bristles. Lunule small, flat and shining, face shining except pollinose carina. Eye 2.5 times genal height. Mid tibia of both sexes with a short apicoventral bristle and no other ventral bristles; distal anterodorsal bristle long, distal posterodorsal bristle minute or absent. Scutum and scutellum strongly convex, shining; with 4 rows of acrostichal setulae between anterior dorsocentral bristles. Dorsocentral bristles in 2 pairs, both short, twice as long as acrostichal setulae. Prescutellar acrostichal setulae in a single, small pair. Scutellum strongly convex, short, 2.1 times as wide as long, apical bristles 1.4

times as long as scutellum. Mesopleuron pollinose on posterior half, episternum shining. Halter light brown. Costagial bristles short; second costal sector half as long as third, costa only slightly surpassing R_{4+5} . Cell dm narrow, outer angle obtuse. Veins brown, second costal sector thickened and dark.

Abdomen. Syntergite 1+2 sclerotized; tergites 3-5 greatly reduced and difficult to distinguish from membrane.

Male abdomen. Sternite 5 simple, without posteromedial ornamentation. Surstylus broad, with strongly setose posterodorsal and posteroventral angles and a posteromedial lobe bearing a strong bristle (Figs. 85, 86). Distiphallus with a long, split dorsal flagellum and a lateral cluster of spines in membrane near base (Fig. 85). Parameres thin, simple.

Female abdomen. Tergite 8 darkly pigmented laterally, very lightly pigmented medially (Fig. 178). Epiproct small, entirely setulose, with 2 long bristles. Sternite 8 large, broader than long; lightly pigmented, especially anteriorly. Hypoproct large, setulose over entire surface (Fig. 180). Each spermatheca almost spherical, with a large apical invagination; duct very long, including sclerotized part (Fig. 179).

Types. *Holotype* (σ , USNM): "Porto Rico, Mayaguez, Jan. 1899". A. Busck. USNM #14953. **Type series of *L. varicosta*** (all ANSP): COSTA RICA: Alajuela, 15.ix.1909, 3100', sweepings, P.P. Calvert (holotype σ and 7 paratypes, 1 σ and 1 φ dissected); Bonnefil Farm, Rio Surubres, 20.x.1909, 800', sweepings, P.P. Calvert; Peralta Stn., 10.viii.1909, 3100', sweepings, P.P. Calvert; La Carpintera, Cartago, 4.xii.1909, sweepings, P.P. Calvert; Cartago, 27.x.09, 800', sweepings, P.P. Calvert. **Type series of *L. mollis*** (holotype σ , 5 σ and 28 φ paratypes, CAS): HONDURAS. Bras Lagoon, 25.iv.1947, C.W. Cook.

Other material examined. COSTA RICA: San Mateo, Higuito, Pablo Schild Coll. (1 φ , USNM). JAMAICA: "Bath St Thos" Sta. 433 (1 φ , USNM); Battersea, ii.1910, R. Thaxter (1 σ , 1 φ , labelled *L. varicosta* det. Spuler, USNM).

Comments. This neotropical species is closely related to *M. vitripennis*, *M. archboldia* and *M. contrasta*. Nearctic records of this species have been based on misidentifications of *M. contrasta*.

Minilimosina (Svarciella) vitripennis (Zetterstedt)

Figs. 8, 29, 87, 88, 184, 185, 186, 208

Limosina vitripennis Zetterstedt, 1847:2505

Leptocera (Scotophilella) albifrons Spuler, 1925b:147, New synonymy.

Minilimosina (Svarciella) vitripennis: Roháček 1983:31, description and synonymy.

Diagnosis. Length 1.2-1.4 mm. Colour shining brown except whitish pollinose gena and face. Frons pollinose except large, wider than long, shining frontal triangle surrounding pollinose ocellar triangle. Interfrontal plate small, 1/4 as wide as frons, bordered by 2-3 almost cruciate interfrontal bristles. Face pollinose, weakly concave-carinate; lunule small and weakly projecting between antennae. Eye 3.0 times as high as gena, gena pollinose, often whitish. Mid tibia of both sexes with only an apical bristle ventrally; distal posterodorsal bristle minute. Acrostichal setulae sparse, 4 rows between anterior dorsocentral bristles (Fig. 8). Dorsocentral bristles in 2 pairs, anterior pair twice as long as acrostichal setulae; prescutellar dorsocentral bristles equal in length to scutellum; prescutellar acrostichal bristles no larger than other acrostichal setulae. Scutellum flat, 0.8 times as long as wide, apical scutellar bristles equal in length to scutellum. Mesopleuron pollinose except shining anterodorsal half of katapisternum. Halter uniformly light brown. Wing with costagial bristles small, subequal; second costal sector glossy black, 0.8 times as long as third; other veins lighter in colour. Cell dm with posterior outer corner weakly appendiculate (Fig. 208).

Abdomen. Syntergite 1+2 2.5 times as long as tergite 3; tergites 1-5, especially 3-5, pale-pigmented, reduced.

Male abdomen. Sternite 5 with a dark Y-shaped process posteromedially (Fig. 29)

which is often deflexed giving sternite 5 a misleading similarity to that of *M. ternaria* (Fig. 42). Surstylus broad, with several posteroventral bristles, and a posteromedial lobe bearing a strong bristle (Figs. 87, 88). Parameres thin, simple. Distiphallus with a long, split ventral flagellum (Fig. 87).

Female abdomen. Tergite 8 longitudinally divided into a dorsal and 2 lateral dark areas. Epiproct large, setulose on posterior half, with 2 long bristles (Fig. 184). Sternite 8 large, broader than long, lightly pigmented anteriorly (Fig. 186). Hypoproct setulose over entire surface. Each spermatheca flattened basally, with a large apical evagination which is shorter than spermathecal body; duct short, sclerotized part relatively long (Fig. 185).

Type. *Holotype* of *Scotophilella albifrons* Spuler: **Idaho:** Kendrick, 7.vi.1917, A.L. Melander (♂, USNM).

Other Material examined: CANADA. **Alberta:** Lethbridge, 5.vii.1956, O. Peck (1♂, BRI); 28.v.1929, J.H. Pepper (1♂, BRI); McMurray, 30.v.1953, G.E. Ball (1♀, BRI). **British Columbia:** Aiyansh, Nass R., 500', 25.vi.1960, J.G. Chillcott (1♀, 2♂, BRI); Hatzic, 30.vii.1953, W.R.M. Mason (1♂, BRI); Terrace, 3.vii.1960, swept from carcass, J.G. Chillcott (3♂, 1♀, BRI), 1.vi.1960, W.R. Mason (1♂, BRI). **Manitoba:** Churchill 13.vii.1952, J.G. Chillcott (1♂, 1♀, BRI); Ninette, 15.vii.1958, J.G. Chillcott, *Betula glandulosa*-*Populus balsamifera* Associes (2♂, 1♀, BRI); Trees-bank, "vii-20-15" (1♂, USNM). **New Brunswick:** Kouchibouguac N.Pk., 19.v.1977, code5087Q, W.P. Hanley (1♀, BRI). **Newfoundland:** Hebron, 19.vii.1954, J.F. McAlpine (2♂, BRI). **North West Territories;** Aklavik, 8.vi.1931, Bryant (1♀); Chesterfield, 6.vii.1950, J.R. Vockeroth (2♂, BRI); Reindeer Depot, Mackenzie Delta, 29.vi.1948, J.R. Vockeroth. **Nova Scotia:** West end Sable Is., 5, 11, 13.vii.1967, D.M. Wood (8♂, 1♀, BRI). **Ontario:** Ancaster, 1.iv.1967, J.E.H. Martin (1♀, BRI); Arkell, 20.vi.1956, D.H. Pengelly (1♀); Constance Bay, 1.x.1953, J.F. McAlpine (2♂, BRI); Guelph, 14-16.vii, K.N. Barber, pan trap (1♀), 14.v.1978, J.M. Cumming, pan trap (1♀); Marmora, 1.ix.1952, C. Boyle (1♂, BRI); Midland, 30.vii.1956, J.G. Chillcott (1♂, BRI); Norval, 16.v.1980, on carrion, S.A. Marshall (4♂, 2♀); Ottawa, 22.iv.1957, on ground among *Carex* roots, J.R. Vockeroth (2♀, BRI), 24.iv.1957, C.D. Miller (1♀, BRI), 15.v.1963, H. Rutz (2♀, BRI), 5.v.1952, J.G. Chillcott (1♂, BRI), 26.vii.1951, J.F. McAlpine (1♂, BRI), 26.vii.1955, J.G. Chillcott (1♂, BRI); MerBleue, 12.x.1960, J.R. Vockeroth (1♂, BRI); Penetang, 2.v.1959, J.G. Chillcott (1♂, BRI); Port Severn, 18.v.1959, black spruce bog, J.G. Chillcott (1♂, BRI). **Quebec:** Indian House Lake, 29.vii.1954, W.R. Richards (1♂, BRI); Lac Roddick, 23.iv.1984, L. Masner (1♀, BRI). **Yukon:** La Force, 3300', 7.vii.1960, J.E.H. Martin (1♂, BRI); Rampart House, 5.vi.1951, J.E.H. Martin (1♂, BRI); Ross River, 3000', 21.vi.1960, J.E.H. Martin (1♀, BRI). **U.S.A. Alaska:** Anchorage, 27.vi.1951, R.S. Bigelow (1♀, USNM); Matanuska, 15.v.1944, rotary trap, J.C. Chamberlin (1♂, 1♀, USNM). **Arizona:** Flagstaff, Oak Ck. Cany. 5900', 17-25.vii.1979, S.&J. Peck (1♂); **Colorado:** Nederland, 8300', 5.vii.1961, J.G. Chillcott (1♀, BRI); Nederland, Caribou, 10,000', 10.vi.1961, C. Mann (1♀, BRI); Boulder, 10.vi.1961, C.H. Mann (1♂, BRI). **California:** Siskiyou Co., McBride Springs, 5200', 10-14.vi.1974, J. Doyen (1♂, BERK); Yosemite Valley, 22.v.1908, E.T. Cresson (1♂, paratype of *albifrons* Spuler, ANSP). **Idaho:** Franklin Co., Cub River Canyon, 26.vi.1971, G.F. Knowlton, (1♂, USNM). **New Hampshire:** Mt. Washington, Lakes of the Clouds, 5000', 9.viii.1954, W. Mason, (1♂, BRI). **North Carolina:** Franklin, 2000', 8.v.1957, J.R. Vockeroth (1♀, BRI). **Oregon:** Tumalo State Pk., 5.iv.1970, Oman (1♀, USNM). **Pennsylvania:** Center Co., Pine Grove Mills, 24.v.1981, P.A. Adler, sticky trap over slab cabin run (1♂, 1♀, PSU). **Utah:** Summit Co., Bear R.Cp., Wasatch For., 30.vii-11.viii.1979, malaise, streamside, 8400', (1♀). **Washington:** Mt. Vernon, 5.vii.1925, A.L. Melander (1♀, USNM); Seattle, 28.vi.1917, H.G. Dyar (1♂, 1♀, USNM).

This species is also known from Europe, Afghanistan, and Mongolia (Roháček, 1983).

Biology. As indicated by the above data, this species is commonly collected in northern North America, and appears to be the most frequently encountered sphaerocerid at very high latitudes. Roháček (1983) pointed out a similar distributional pattern in Europe, where it is common in the north and primarily restricted to high elevations in South Europe. A most unusual feature of the North American collection records is the relative frequency with which *M. vitripennis* has been taken by general collectors, and the conspicuous absence of this species from baited pitfall trap samples. This suggests that, in contrast to other sphaerocerid species, *M. vitripennis* frequents exposed situations. It seems to be collected most often in wet areas and has been swept off carrion, collected in mammal runs, and collected among decaying vegetation.

Comments. This species is closely related to *M. contrasta*, *M. archboldi*, *M. niveipennis*, and *M. masoni*, as evinced by the many synapomorphies of male and female terminalia, the reduced preabdominal sclerites, wing venation, and other external characters. Previous North American authors, including Marshall (1982), have treated this species under the name *albifrons* Spuler, now considered as a junior synonym.

***Minilimosina (Svarciella) vixa* new species**

Figs. 34, 35, 36, 37, 169, 170, 171, 207

Description. Length 1.5-1.9 mm. Colour black except stem of halter, tarsomeres and tips of tibiae and femora, which are orange or yellowish brown. Frons black, shining except for silvery pollinose orbits and narrow interfrontal strips and brown pruinose ocellar triangle. Interfrontal plate 0.8 times as wide as high, bordered by 3-4 small, subequal interfrontal bristles. Lunule small, flat; face weakly concave, distinctly carinate. Eye 3.0 times as high as gena. Mid tibia of male ventrally with a distal double row of short, stout bristles and a weak apical bristle. Distal anterodorsal bristle of mid tibia slightly longer than the weak distal posterodorsal bristle. Scutum with 6 rows of acrostichal setulae between dorsocentral areas, dorsocentral bristles in 2 pairs, anterior pair 0.5 times as long as posterior pair. Prescutellar acrostichal bristles in a single pair twice as long as acrostichal setulae. Scutellum flat, 0.7 times as long as wide, apical bristles 1.3 times scutellar length. Mesopleuron pollinose except anterior part of katepisternum, anterior part of anepisternum, and an isolated shining area on mid dorsal part of katepisternum. Halter shining black with a yellow stem. Wing with costagial bristles equal, second costal sector 0.7 times as long as third, dark black; other veins yellow to brown (Fig. 207).

Abdomen. Syntengite 1+2 1.7 times as long as tergite 3. All abdominal sclerites large, heavily sclerotized, weakly punctate.

Male abdomen. Sternite 5 with a posteromedial comb of flat bristles flanked by long bristles on each side (Fig. 34). Sternite 6 with 2 dark posteromedial processes sometimes visible behind sternite 5 (Fig. 37). Surstylus with a narrow posterior lobe bearing 3 large, stout spurs (Fig. 35). Paramere narrow, with 2 or 3 anterior setulae. Distiphallus narrow, with a short ventral piece and a longer dorsal piece (Fig. 36).

Female abdomen. Tergite 8 short, with tripartate pigmentation. Epiproct large, bare except for two bristles (Fig. 169). Sternite 8 subquadrate, setulose. Hypoproct entirely setulose (Fig. 171). Each spermatheca cylindrical, surface strongly tuberculate, apex with a deep invagination (Fig. 170).

Types. *Holotype* (♂, BRI): CANADA. **Nova Scotia:** Cape Breton Highland N.Pk., North Mt., 400m, 10.viii.1983 "PG766864", Fen pan trap, J. Martin. *Paratypes:* CANADA. **New Brunswick:** Kouchibouguac N.Pk., 19,20,22,24.v and 17,24,30.vi.1977, B. Cooper, G.A. Calderwood, J.R. Vockeroth (5 ♂, 4 ♀, BRI, codes 5117u, 5085o, 51110, 5314j, 5097a, 5453s, 5366j, 5043y). **Nova Scotia:** Cape Breton Highland N.Pk., North Mt., 400m, vii.1983, "pg766864", bog pan trap, J. Vockeroth (1 ♀, BRI), North Mt., 400m, 24.viii.1983, "pg766864", fen pan trap, M. Sharkey (1 ♂, BRI), Mackenzie Mt., 300m., 29.viii.1983, "pg64851" *Picea-Betula* Malaise Tp. (2 ♀, BRI), South Harbour, 12.vii.1983, "pg929935" mixed forest Malaise trap, J.R. Vockeroth (1 ♀, BRI); Mount Uniacke, 5.viii.1958, J.R. Vockeroth (1 ♂, BRI). **Ontario:** Algonquin Park, S. of Shirley Lake, deciduous forest, moose dung trap, 18-26.v.1984, K. Pendreigh (2 ♂); Algonquin Park, Pen Lake, 29-31.v.1984, forest intercept trap, B.V. Brown (1 ♂, 4 ♀). U.S.A. **Maine:** Penob Co., 2miSW Orono, 28.v.1982, Malaise trap, D.S. Chandler (1 ♀, UNH).

Biology. *M. vixa* seems to be associated with wet deciduous forests or boggy areas of the northeast. Nothing further is known of its biology. The closely related *M. v-atrum* is a rare species of bogs and wet forests in north central Europe.

Comments. This species is close to *M. v-atrum* (Villeneuve) and was treated provisionally under that name by Marshall (1982). Since then, Dr. Roháček has compared North American and European specimens and has pointed out that the Nearctic material differs in having a smaller anal fissure and possessing ornamentation of sternite 6 (a doubled projection) not found in *M. v-atrum*, and that the North American populations therefore should be considered as a different species. In addition to these features, *M. vixa* differs from *M. v-atrum* in having strongly tuberculate spermathecae, larger shining spots on the mesopleuron, and equivocal differences in some trivial indices such as relative eye height. *M. v-atrum* and *M. vixa* are very closely related to *M. ismayi* (Palearctic) and *M. intercepta* (Nearctic), both of which differ in having yellow or orange antennae.

Etymology. The name *vixa* is a coined word (noun in apposition), reminiscent of the Latin adverb *vix* meaning 'hardly, scarcely or with difficulty', and reflects the difficulty of deciding whether or not this species should indeed be considered separate from *v-atrum*.

Amputella new subgenus

Type Species *Minilimosina (Amputella) ternaria* new species

Subgeneric description. Length 1.0-2.1 mm, usually dull brown in colour. Postocellar bristles minute or absent, face narrowly tuberculate to carinate between antennae, concave-carinate below. Mid tibia of male with at least some weak spinules forming a distal ventral row; mid femur with a corresponding basal ventral row of bristles (Fig. 6). Upper costial bristle long, subequal in length to basal scutellar bristle. Costa always extending clearly beyond tip of R_{4+5} , cell dm obtuse angled and usually weakly appendiculate on posterior outer corner. Dorsocentral bristles in 2 pairs, anterior pair small and often hard to distinguish from acrostichal setulae, prescutellar pair *ca.* as long as scutellum. Sternite 5 of male concave posteromedially (Figs. 41-47), never with a posteromedial comb, but deflexed posteromedial part often with a median lobe or process (Figs. 43-47). Surstylus with one or more anterior lobes and a large posterior lobe bearing 3 or 4 stout bristles. Basiphallus elongate, with an epiphallus (Fig. 100). Ejaculatory apodeme well developed. Left paramere large, often sinuate. Right paramere atrophied to an inconspicuous, terminally membranous lobe. Distiphallus simple, greatly reduced, more or less cylindrical. Female sternite 8 greatly reduced, often made up of 2 or more small plates. Hypoproct large, deeply concave anteriorly, setulose posteriorly. Female tergite 8 and often tergite 7 split or depigmented medially. Epiproct long, bare at least on anterior half. Each spermatheca short, with a deep, usually lateral, invagination.

Etymology. The name *Amputella* is descriptive of the most striking autapomorphy of the subgenus, which is the presence of one normal paramere and a greatly shortened one.

Discussion. This subgenus is characterized by a number of outstanding apomorphic characters. The atrophied right paramere and reduced, tubular distiphallus, for example, are unique in the Limosiniinae. Other characters, such as the long epiphallus and long costial bristle, as apomorphic within the framework of *Minilimosina* and related genera but occur as homoplasies elsewhere in the Limosiniinae. *Amputella* shares some characters with *Svarciella*, such as having two dorsocentrals, reduced postocellars and a low number of acrostichals. The dorsocentral and postocellar characters are plesiomorphic, being found in closely related genera, and acrostichal number is a very weak character on which to base any suggestion of relationship. Similarities between the sexual characters of *Amputella* and *Svarciella* are difficult to interpret. The possession of 3 surstylar bristles could be interpreted as synapomorphic with the *v-atrum* group of *Svarciella*, and the deflexed sternite 5 could be interpreted as synapomorphic with the *vitripennis* group. The shape of the spermathecae and the reduction of female sternite 8, on the other hand, suggest an affinity to *Allolimosina*. For these reasons, *Amputella* is placed on Fig. 216 as a highly autapomorphic group of uncertain affinity.

***Minilimosina (Amputella) bistylus* new species**
Figs. 5, 6, 46, 47, 103, 104, 105, 145, 146, 147, 210

Description. Length 1.4-1.8 mm. Interfrontal plate narrow and tapered, width at top 0.7 times height, bordered by 3-4 short, subequal, interfrontal bristles. Frontal triangle shining brown and extended almost to frontal suture (similar to Fig. 188), orbits and thin interfrontal strips brown, rest of frons dull black. Eye 2.7-3.0 times as high as gena. Mid tibia with distal anterodorsal bristle shorter than distal posterodorsal bristle; distal dorsal bristle displaced anteriorly, almost in line with small, distal anterodorsal (Fig. 5). Scutum with 4-5 rows of long acrostichal setulae between anterior dorsocentral bristles, prescutellar dorsocentral bristles subequal to scutellar length. Prescutellar acrostichal bristles in a single pair twice as long as acrostichal setulae. Scutellum 2/3 as long as wide, marginal bristles long, apical marginals twice as long as scutellum. Mesopleuron pollinose except shining anterodorsal corner of katepisternum. Halter uniformly light brown. Second costal sector 0.9-1.0 times as long as third (Fig. 210).

Male abdomen. Sternite 5 concave, darkly pigmented and long-setose posteromedially (Fig. 47). Posteromedial deflexed part of sternite 5 projecting posteriorly as a blade-like structure originating on a black, quadrate base (Figs. 46, 47). Surstylus with a curved, anterior lobe, apex serrate and with a thin, sinuate bristle; posterior lobe broad, with 3 short, stout bristles; anteromedial, membranous lobe also present but difficult to see in cleared material (Figs. 104, 105). Paramere narrow, constricted near apex. Basiphallus with a long epiphallus. Distiphallus short, simple, sclerotized (Fig. 103).

Female Abdomen. Tergites 6 and 7 complete but tergite 7 lightly pigmented medially; tergite 8 large, darkly pigmented. Epiproct setulose on posterior 1/4 (Fig. 145). Sternite 8 reduced to 4 sclerites; lateral ones short, posterior one setose. Hypoproct setulose, with 2 dark, bare anterior lobes (Fig. 147). Each spermatheca spherical, with a lateral, spherical invagination (Fig. 146).

Types. *Holotype* (♂, MCZ) and 12 *paratypes* (3♂, 9♀, MCZ): MEXICO. **Hidalgo:** 3.2 & 3.5miN Tlanchinol, 5100', 6-11.vii.1973, cloud forest, dung, A. Newton. *Other Paratypes:* MEXICO. **Chiapas:** Lagunas de Montebello Parque Nacional, Aqua Tinta, 4900', 21-24.viii.1971, oak-pine, human dung, A. Newton (2♀). **Hidalgo:** 2.5miN Tlanchinol, 5200', 6-11.vii.1973, cloud forest, dung, A. Newton (6♀). **Oaxaca:** 12miS Valle Nacional, 3200', 23-31.vii.1971, tropical montane forest, carrion (shrimp), A. Newton (6♂, 1♀). **Puebla:** 4.5miE Teziutlan, 5000', 10-14.vii.1971, cloud forest, human dung, A. Newton (4♀). **Veracruz:** 10miSW Teocelo, 4400', 1-16.vii.1971, oak, wet, human dung, A. Newton (2♀). PANAMA. **Chiriqui:** 15kmNW Hartman Finca, 1200m, 20-31.v.1977, carrion trap, S. Peck (1♀); 27kmW Cerro Punta, 1260m, 2.vi.1977, S. Peck (25♂, 21♀); 15kmNW Volcan Hartmann Finca, 1500m, 20-31.v.1977, carrion, S. Peck (6♂, 2♀); 27kmW Cerro Punta, 1700m, 5.v.1977, carrion, S. Peck (75♂, 40♀, BRI, GUELPH); 2kmW Cerro Punta, Baldwin Forest, 1750m, 30.v-2.vi.1977, carrion and dung traps, S. Peck (9♂, 15♀, from carrion; 9♂, 14♀ from dung).

Biology. As detailed above, this species has been taken in large numbers in dung and carrion traps in Panama and Mexico. Unlike related *Amputella* species, which are known from higher elevations, *M. bistylus* is associated with cloud forest or tropical montane forest.

Comments. *M. bistylus* is very closely related to *M. priapismus*, *M. erecta*, and *M. curvistylus*. It is most closely related to the latter species, from which it differs most obviously in having a relatively short anterior surstylar lobe and in having sternite 8 of the female with short lateral pieces.

Etymology. The name *bistylus* refers to the deeply cleft surstylus which, in lateral view, appears to be divided into anterior and posterior pieces.

Minilimosina (Amputella) curvistylus new species

Figs. 106, 107, 108, 148, 149, 150, 211

Description. Length 1.7-1.9 mm. Interfrontal plate strongly tapered, width at top subequal to height, bordered by 4 short, subequal interfrontal bristles. Frontal triangle silvery-brown and extended to frontal suture, orbits and thin interfrontal strips also brown, rest of frons dull black and forming an M-shape. Eye 2.5-3.0 times as high as gena. Distal anterodorsal and distal posterodorsal bristles of mid tibia large, posterodorsal bristle longer than anterodorsal, slightly shorter than distal dorsal bristle. Scutum with 6 rows of acrostichal setulae between anterior dorsocentral bristles; anterior dorsocentral bristles *ca.* 3 times as long as acrostichal setulae; posterior dorsocentrals slightly longer than scutellum. Prescutellar acrostichal bristles in a single pair twice as long as other acrostichals. Scutellum 0.8 times as long as wide, marginal bristles long, apical marginals 2.2 times as long as scutellum. Mesopleuron pollinose except for shining areas anterodorsally on katepisternum and anteriorly on anepisternum. Halter uniformly brown. Second costal sector equal in length to third (Fig. 211).

Male abdomen. Sternite 5 concave, darkly pigmented and long-setose posteromedially; deflexed part projecting posteriorly as a blade-like structure originating on a small, black, quadrate base. Surstylus very distinctive; posterior lobe large, with 3 large, closely placed bristles; anterior lobe long, thin, curving posteriorly, with long apical bristles; medial surfaces setose; anteromedial lobe also present, but largely membranous and difficult to see (Figs. 107, 108). Paramere simple, almost straight. Basiphallus with a long epiphallus, distiphallus small, simple, sclerotized, convex dorsally (Fig. 106).

Female abdomen. Tergites 6 and 7 complete but lightly pigmented medially; epiproct setulose in posterior 1/4 (Fig. 148). Sternite 8 divided into 2 long lateral pieces, a short dark anterior piece, and a small setulose posterior piece (Fig. 150); hypoproct setulose on posterior half, anterior half consisting of 2 broad lobes. Each spermatheca spherical, duct of medium length, inserted almost at right angles to deep apical invagination (Fig. 149).

Types. *Holotype* (♂, BRI) and 4 *paratypes* (3 ♂, 1 ♀, BRI): PANAMA. **Chiriqui:** 4.5kmE Cerro Punta, 2500m, 23-28.v.1977, carrion trap, S. Peck. *Other paratypes:* PANAMA. **Chiriqui:** 2kmE Cerro Punta, 2200m., 1-4.vi.1977, forest carrion trap, S. Peck (9 ♂, 7 ♀).

Biology. All known specimens were collected in Panama, using carrion traps set at 2200-2500m.

Comments. Despite the strongly modified surstylus, this species is clearly related to *M. priapismus*, *M. erecta*, and *M. bistylus*. Both *M. bistylus* and *M. curvistylus* have female sternite 8 divided into 4 parts, although the lateral parts are strikingly long in *M. curvistylus*.

Etymology. The name *curvistylus* refers to the long, thin, and curved anterolateral process of the surstylus (Fig. 108).

Minilimosina (Amputella) digitata new species

Figs. 41, 109, 110, 111, 151, 152, 153, 212

Description. Length 1.6 mm. Interfrontal plate, narrow interfrontal strips and orbits silvery brown, intervening areas dull black; lower frons red. Interfrontal plate narrow and tapered, width at top 0.75 times height; bordered by 4 short, subequal interfrontal bristles. Eye 2.4 times as high as gena. Mid tibia with distal anterodorsal bristle slightly shorter than distal posterodorsal; long distal dorsal bristle displace anteriorly; an additional small dorsal bristle present between distal anterodorsal and posterodorsal. Scutum with 4-5 rows of long acrostichal setulae between dorsocentral areas, anterior dorsocentral areas damaged on type material but posterior dorsocentral bristles present, *ca.* 0.7 times as long as scutellum. Prescutellar acrostichal bristles in a single pair 2-3 times as long as other

acrostichal setulae. Scutellum 0.7 times as long as wide, apical marginal bristles 2.0 times as long as scutellum. Mesopleuron pollinose except shining anterodorsal part of katepisternum and anterior part of anepimeron. Halter brown, stem yellow. Second costal sector 0.7 times as long as third.

Male abdomen. Sternite 5 with concave posteromedial area flanked by 2 tubercles (Fig. 41), deflexed area membranous. Surstylus elongate, with 4 stout bristles evenly spaced along posteroventral margin (Figs. 110, 111). Left paramere long, curved, swollen preapically and apically narrowed to a finger-like projection (Fig. 109). Basiphallus elongate-triangular, distiphallus small, cylindrical (Fig. 109).

Female abdomen. Tergites 6 and 7 complete but tergite 7 lightly pigmented medially; tergite 8 large, darkly pigmented. Epiproct subequal in length and width to cerci together, setulose and darkened on posterior 1/4, swollen laterally (Fig. 151). Sternite 8 ring-like, desclerotized centrally (Fig. 153). Hypoproct slightly larger than sternite 8, anteriorly with 2 bare, lateral lobes; posteriorly setulose (Fig. 153). Each spermatheca wrinkled, expanded apically, with a deep apical invagination, sclerotized parts of ducts short (Fig. 152).

Types. *Holotype* (♂, MCZ) and 1 *paratype* (♀, BRI): MEXICO. **Veracruz:** 4miN Huatusco, 4100', 11-16.vii.1971, cloud forest, dung, A. Newton. *Other Paratypes:* MEXICO. **Oaxaca:** 3.3miE jct. Yuvilla Rd. & Mex.175, 9-19.viii.1973, Oak, pine, dung, A. Newton (1 ♂, BRI).

Biology. The short type series was taken on dung.

Comments. Several synapomorphies suggest that *M. digitata* is the sister species to *M. ternaria*. The surstylus, with a small inner lobe and broad outer lobe bearing 3-4 large bristles, and the paramere with a finger-like apex, are the two most striking synapomorphies shared by these species.

Etymology. The name *digitata* refers to the long, digit-like bristles of the outer surstylar lobe.

Minilimosina (Amputella) erecta new species

Figs. 44, 45, 100, 101, 102, 154, 155, 156, 213

Description. Length 1.5-2.1 mm. Interfrontal plate, interfrontal strips, and orbits dull brown, intervening areas black; interfrontal plate narrow and tapered, width at top 0.75 times height, bordered by 3-4 small interfrontal bristles, pair below top pair largest. Eye 2.5 times as high as gena. Mid tibia of male ventrally with a distal row of 8-9 short spinules and a long apical ventral bristle. Anterodorsal bristle in distal 1/4 of mid tibia much shorter than distal posterodorsal bristle; an additional small bristle present above distal dorsal bristle. Scutum with 4-6 rows of long acrostichal setulae between dorsocentral areas; dorsocentral bristles in 2 pairs, anterior pair barely longer than acrostichal setulae, posterior pair subequal to scutellar length. Prescutellar acrostichal bristles in a single pair 2-3 times as long as acrostichal setulae. Scutellum 2/3 as long as wide, marginal bristles long, apical marginals twice as long as scutellum. Mesopleuron pollinose, except shining anterodorsal part of katepisternum and contiguous anterior part of anepisternum. Halter brown, stem yellow. Second costal sector 0.9-1.0 times length of third (Fig. 213).

Male abdomen. Sternite 5 concave posteromedially, with several long, thin bristles but no other adornment (Fig. 45); deflexed part projecting posteroventrally as a beak-like structure (Fig. 44). Surstylus with 3 stout bristles on posterior surface; anterior lobe small, with a cluster of ventral bristles; membranous anteromedial lobe also present but difficult to see, weakly tuberculate (Figs. 101, 102). Left paramere long, curved, swollen preapically and apically narrowed to a finger-like projection; basiphallus elongate, with epiphallus; distiphallus simple, sclerotized (Fig. 100).

Female abdomen. Tergites 6 and 7 complete but lightly pigmented medially; tergite 8 with a triangular, lightly pigmented area posteromedially (Fig. 154). Sternite 8 greatly reduced, broadest and setulose posteriorly; hypoproct setulose, with narrow, bare, antero-

lateral processes (Fig. 156). Each spermatheca cup-shaped, duct short and inserted at right angles to deep invagination (Fig. 155).

Types. *Holotype* (♂, MCZ) and 20 *paratypes* (13 ♂, 7 ♀, MCZ): MEXICO. **Oaxaca:** 1.7miW jct. Mex. 175 and Yuvilla Rd., 9400', 9-19.viii.1973, mesic oak, carrion (fish) trap, A. Newton. *Other paratypes:* MEXICO. **Morelos:** 7miW Tres Cumbres, 9600', 29.viii-4.ix.1971, oak, pine, fir, dung, A. Newton (1 ♂, 1 ♀). **Oaxaca:** 29.7miS Valle Nacional, 6800', cloud forest, carrion, 11-17.viii.1973, A. Newton (6 ♂, 5 ♀, BRI); 35miS Valle Nacional, 8000', 10-12.viii.1970, Oak, dense thicket, human dung, A. Newton (1 ♂, 4 ♀); 25miN Ixtlan, 9100', 23-29.vii.1971, oak, pine, dung, A. Newton (6 ♂, 11 ♀); 10miN Ixtlan de Juarez, 10-16.viii.1973, oak, pine carrion (fish) trap, A. Newton (11 ♂, 3 ♀); 1.4miW jct. Mex 175 & Yuvila Rd., 9-19.viii.1973, 9300', mesic oak for., dung, A. Newton (12 ♂, 9 ♀); 2miW jct. Mex. 175 & Yuvilla Rd., 9500', 8-19.viii.1973, oak, pine, dung, A. Newton (1 ♂, 4 ♀).

Biology. This species is known only from dung and carrion baited traps set at high elevations in southern Mexico.

Comments. *M. erecta* is closely related to *M. curvistylus*, *M. priapismus*, and *M. bistylus*. The median lobe of male sternite 6, which is a synapomorphy shared by these 4 species, is bent apically in *M. erecta* unlike the other 3 species. *M. erecta* is also alone in this species group in having a simple female sternite 8.

Etymology. This species was named *erecta* because, when examining the male abdomen in ventral view, the apex of the posteromedial process of sternite 5 stands erect and above the plane of the rest of the sternite.

Minilimosina (Amputella) priapismus new species

Figs. 43, 97, 98, 99, 157, 158, 159, 214

Description. Length 2.0 mm. Interfrontal plate, narrow interfrontal strips, and orbits dull brown, intervening areas dull black; lower frons reddish. Interfrontal plate narrow and tapered, width at top 0.7 times height, bordered by 2-3 interfrontal bristles, upper two almost cruciate. Eye 3.0 times as high as gena. Mid tibia of male ventrally with a distal row of 5-6 short spinules and a long apical ventral bristle. Anterodorsal bristle in distal 1/4 of mid tibia shorter than distal posterodorsal bristle; an additional small bristle present above large distal dorsal bristle. Scutum with 4-6 rows of long acrostichal setulae between dorsocentral areas, dorsocentral bristles in 2 pairs, anterior pair small, posterior pair longer than scutellum. Prescutellar acrostichal bristles in a single pair, twice as long as acrostichal setulae. Scutellum 0.8 times as long as wide, apical marginal bristles 2.5 times as long as scutellum. Mesopleuron pollinose except shining anterodorsal part of katepisternum and anterior part of anepisternum. Halter brown, stem yellow. Second costal sector 0.8 times as long as third. Discal cell broad, outer angle obtuse (Fig. 214).

Male abdomen. Sternite 5 with posteromedial area dark, concave, flanked by setose areas; deflexed part projecting as a large, dark, sinuate lobe flanked by 2 basal, setose lobes (Fig. 43). Surstylus broad, large posteroventral bristles clustered in a group of 3 on posterior margin; anterior lobe barely separated from posterior lobe, with a tuft of bristles ventrally; a membranous anteromedial lobe also present but difficult to see on cleared specimens (Figs. 98, 99). Left paramere long, curved, swollen preapically and apically narrowed. Basiphallus long, curved, with epiphallus; distiphallus thin, simple, weakly serrate dorsally (Fig. 97).

Female abdomen. Tergites 6 and 7 complete but tergite 7 lightly pigmented medially; tergite 8 large, darkly pigmented, setulose on posterior half; epiproct setulose on posterior 3/4 (Fig. 157). Sternite 8 complex, with a dark anterior piece and small lateral pieces (Fig. 159); hypoproct setulose, with 2 bare, anterior arms. Each spermatheca bent-cylindrical, with reticulate surface and small apical invagination (Fig. 158).

Types. *Holotype* (♂, MCZ) and 3 *paratypes* (2 ♀, MCZ, 1 GUELPH): MEXICO. **Chiapas:** 10miSE San Cristobal de las Casas, 8000', 30.vii.-1.ix.1973, fungus trap, A. Newton.

Biology. The type series was taken in a fungus baited trap, suggesting that this species might be fungivorous.

Comments. *M. priapismus* belongs to the species group including *M. (Amputella) bistylus*, *M. erecta*, and *M. curvistylus*.

Etymology. The name *priapismus* refers to the large dark process of the male sternite 5.

Minilimosina (Amputella) ternaria new species

Figs. 42, 112, 113, 114, 190, 215

Description. Length 1.0-1.8 mm. Interfrontal plate narrow and tapered, width at top 0.7 times height, bordered by 3-4 small subequal interfrontal bristles. Eye 2.0-2.5 times as high as gena. Mid tibia with distal anterodorsal bristle shorter than distal posterodorsal. Scutum with 4-5 rows of long acrostichal setulae between anterior dorsocentral bristles; anterior dorsocentral bristles barely larger than acrostichal setulae, prescutellar dorsocentral bristles subequal in length to scutellum. Prescutellar acrostichal bristles in a single pair twice as long as acrostichal setulae. Scutellum 0.7 times as long as wide, marginal bristles long, apical marginals twice as long as scutellum. Mesopleuron pollinose except shining anterodorsal part of katepisternum and contiguous anterior part of anepisternum. Halter uniformly light brown. Second costal sector 0.6-0.8 times as long as third (Fig. 215).

Male abdomen. Sternite 5 concave posteromedially, with several long, thin bristles but no other adornment (Fig. 42); deflexed part simple, membranous. Surstylus with a broad posteromedial lobe bearing 3 dark spurs (Figs. 113, 114, 190). Left paramere long, curved, narrowed abruptly to a finger-like tip (Fig. 112). Basiphallus with a relatively short, blunt epiphallus; distiphallus a short, simple lobe (Fig. 112).

Female abdomen. Tergites 6 and 7 complete; tergite 8 divided into 2 lateral sclerites. Epiproct oval, subequal in length and width to cerci together, setulose on posterior 1/3, with 2 bristles (Fig. 160). Sternite 8 greatly reduced, sclerotized only at setal bases; hypoproct large, with 2 anterolateral lobes, setulose on posterior 1/2 (Fig. 162). Each spermatheca with rugose surface, invagination very large (Fig. 161).

Types. *Holotype* (♂, BRI) and 21 *paratypes* (14 ♂, 7 ♀, BRI, GUELPH): U.S.A. **Arizona:** Coconino Co., Flagstaff, Oak Creek Canyon, 5900', 17-25.vii.1979, riparian woods, S.&J. Peck. *Other paratypes:* CANADA. **Manitoba:** Erickson, 1-5.viii.1983, mushroom pitfalls, D.H. Pengelly and K.N. Barber (1 ♂, 1 ♀). **Ontario:** Heckston, 20kmSE Kemptville, 15-24.vi.1984, intercept trap, M. Kaulbars (1 ♂). **Quebec:** Old Chelsea, summit King Mountain, 1150', 24.vi.1964 and 1.ix.1963, J.R. Vockeroth, (2 ♂, BRI). U.S.A. **Arizona:** Apache Co., 25miW Springerville, Green's Peak, 10100', 10-13.vii.1979, forest-meadow malaise trap, S.&J. Peck (1 ♂, 1 ♀); Apache Co., Alpine, Luna Lake, 9-14.vii.1979, pine-meadows, 7900', S.&J. Peck (6 ♂, 2 ♀); Cochise Co., Chiricahua Mts., Rustler Park, 8250', ix.1970, dung trap, A. Newton (5 ♂, 1 ♀); Huachuca Mts., 6000', Miller Canyon, dung trap, ix.1970, oak woodland, A. Newton (2 ♂); Chiricahua Mts., E. Tunkey Ck., 6500', 15-21.vii.1978, dung traps, O. Kukal (5 ♂, 3 ♀); Coconino Co., 20miN Flagstaff, Bonito Park, 5-8.viii.1984, 7000', mushroom trap, Ponderosa Pine-meadow, B.V. Brown (2 ♂); Navajo Co., 15miS Holbrook, 14-16.vii.1975, 5300', grassland carrion, S.&J. Peck (1 ♂); Pima Co., Santa Catalina Mts., Mt. Lemmon, 9000', A. Newton (1 ♀); Santa Cruz Co., Santa Rita Mts., Madera Canyon, 5500', stream-dung trap, ix.1972, A. Newton (1 ♂). **Arkansas:** Wash Co., 3miS Devil's Den State Park, 28-31.v.1979, oak, hickory, S.&J. Peck (2 ♂). **Florida:** Marion Co., Ocala Nat. For., Rd.65, 1.5miW St. Rd. 19, 15-16.iii.1984, dung trap, R. Woodruff (1 ♂, FSC). **Massachusetts:** Middlesex Co., Medford, pine forest, carrion, A. Newton (1 ♂). **New Mexico:** Lincoln Co., 10miW Corona, 8600', 17-22.viii.1975, carrion, S.&J. Peck (4 ♂, 7 ♀); 7miW

Angus, 7700', 6-8.vii.1972, dung trap, A. Newton (6 ♂, 3 ♀); Catron Co., 5miW Luna, 7400', 9-14.vii.1979, San Francisco River, pond, pine, meadows, S.&J. Peck (4 ♂, 2 ♀); Socorro Co., 20miW Socorro, Water Canyon, 7000', 28.vi-7.vii.1979, mixed mesic forest, S.&J. Peck (2 ♂). **North Carolina:** Jackson Co., Cullowhee, 5-28.v.1984, intercept trap, S.A. Marshall (1 ♂). **Texas:** Brewster Co., Big Bend National Park, 30.vii-4.viii.1975, S. Peck (3 ♂, 8 ♀, BRI). **MEXICO. Oaxaca:** 5miE jct. Yuquilla Rd. & Mex. 175, 7600', 9-19.viii.1973, dung, pine-oak, A. Newton (9 ♂, 12 ♀); 3.3miE jct. Yuquilla Rd. & Mex. 175, 8100', 9-19.viii.1973, pine-oak, dung, A.F. Newton (1 ♂, 3 ♀).

Biology. Most of the collection records of this species are from dung at high elevations.

Etymology. The specific name is from the Latin "consisting of 3", referring to the triple comb of large spurs on the surstylus.

Comments. *M. ternaria* appears to be common, probably coprophagous, species at high elevations in Mexico and southwestern U.S.A. The existence of a few specimens collected in the northeast presents a puzzle. The fact that *M. ternaria* is the northernmost representative of an otherwise strictly Neotropical subgenus makes this apparent disjunction all the more anomalous. Only further collecting will show if this is a real disjunction, or a case of a common southern species being rare in the north, but present continuously from Mexico to Quebec.

Phylogeny

Figure 216 is a summary of the perceived phylogenetic relationships within *Minilimosina*, and of the putative synapomorphies proposed as evidence for these relationships. The confidence with which characters are accepted as synapomorphic varies widely with the complexity of the characters and the pattern of their occurrence or non-occurrence elsewhere in the Sphaeroceridae. For example, some characters are unique in the family and are treated as strong evidence for unique common ancestry. Characters of this type are coded (+++) on Fig. 216. The development of a long ventral flagellum on the distiphallus, reduction of tergites 3-5, and the loss of a single paramere are examples of such heavily weighted characters. Other characters seen as strong evidence for common ancestry, but more open to misinterpretation than (+++) characters, are coded (++). These are characters which occur elsewhere in the Limosininae or Copromyzinae and therefore of equivocal polarity or homology at the level used. In the absence of a clear sister group to *Minilimosina*, all possible sister groups (the rest of the Limosininae) plus the Copromyzinae (probable sister group to the Limosininae) were considered in out-group analysis. Characters uniform in the Copromyzinae, such as the retractile female abdomen, were considered plesiomorphic and therefore are ignored, even though rare in the Limosininae. Characters not found in the Copromyzinae and rare in the Limosininae were usually considered apomorphic and coded (++). Characters which occur or could occur commonly within the outgroups, such as ratios or minor chaetotaxy differences, are especially subject to non-homology within the groups considered, and determination of the polarity of these characters is subject to great uncertainty. Such characters are coded (+). Autapomorphies are not listed for terminal taxa unless they are losses of a previously considered apomorphy, in which case they are coded (-) and given the same number as the apomorphy. Although this paper has dealt primarily with New World species, Roháček (1983) has provided enough information on European species for their inclusion on Fig. 216. These are indicated by an (E).

Discussion

The picture that emerges from this analysis is one of a heterogeneous genus of questionable monophyly, made up of 3 or 4 distinct clades. One of these clades, subgenus *Amputella*, is strictly New World, primarily Neotropical. It is a distinctive and highly autapomorphic group sharing no unequivocal synapomorphy with other *Minilimosina*.

Another distinctive clade, the subgenus *Svarciella*, is similarly included in *Minilimosina* primarily on the basis of weak characters but is itself divided into distinctive subgroups. Each subgroup of *Svarciella* includes Nearctic and Palaeartic species, and the *vitripennis* group includes Holarctic and Neotropical species. The subgenera *Allolimosina* and *Minilimosina* together form the largest defensible monophyletic group in the genus. *Allolimosina* includes 2 Palaeartic, 1 Holarctic, and one New World species, but the New World species is of questionable affinity. The large subgenus *Minilimosina* also includes a Neotropical species of questionable affinity, but the rest of the subgenus consists of Nearctic, Holarctic, and Palaeartic species. Each of the well-defined subgroups of *Minilimosina* includes both Nearctic and either Holarctic or Palaeartic species.

Several important problems remain to be solved in this genus. As more of the New World genera of Limosiniinae are studied and become available for comparison, it will be necessary to reconsider the affinities of the subgenera *Svarciella* and *Amputella*. Cladistic analysis will eventually refute or support the inclusion of these taxa in *Minilimosina*. Another problem area is the question of eastern Palaeartic affinities. Almost nothing is known of eastern Palaeartic *Minilimosina*, a gap in our knowledge which prevents full understanding of *Minilimosina* phylogeny and zoogeography. Similarly, almost nothing is known of the biology of *Minilimosina* or most other Limosiniinae. It is hoped that this and similar basic taxonomic works will stimulate study of the diverse saprophagous communities dominated by Limosiniinae.

Acknowledgements

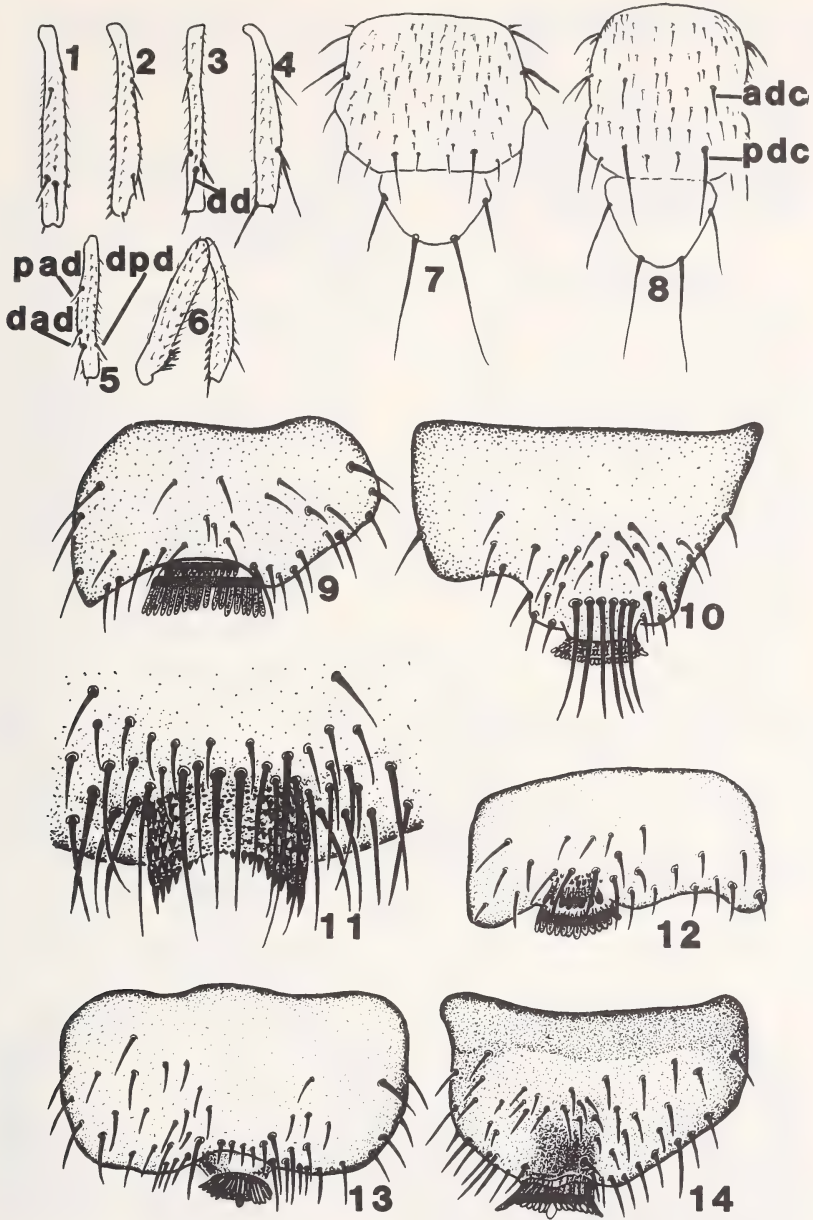
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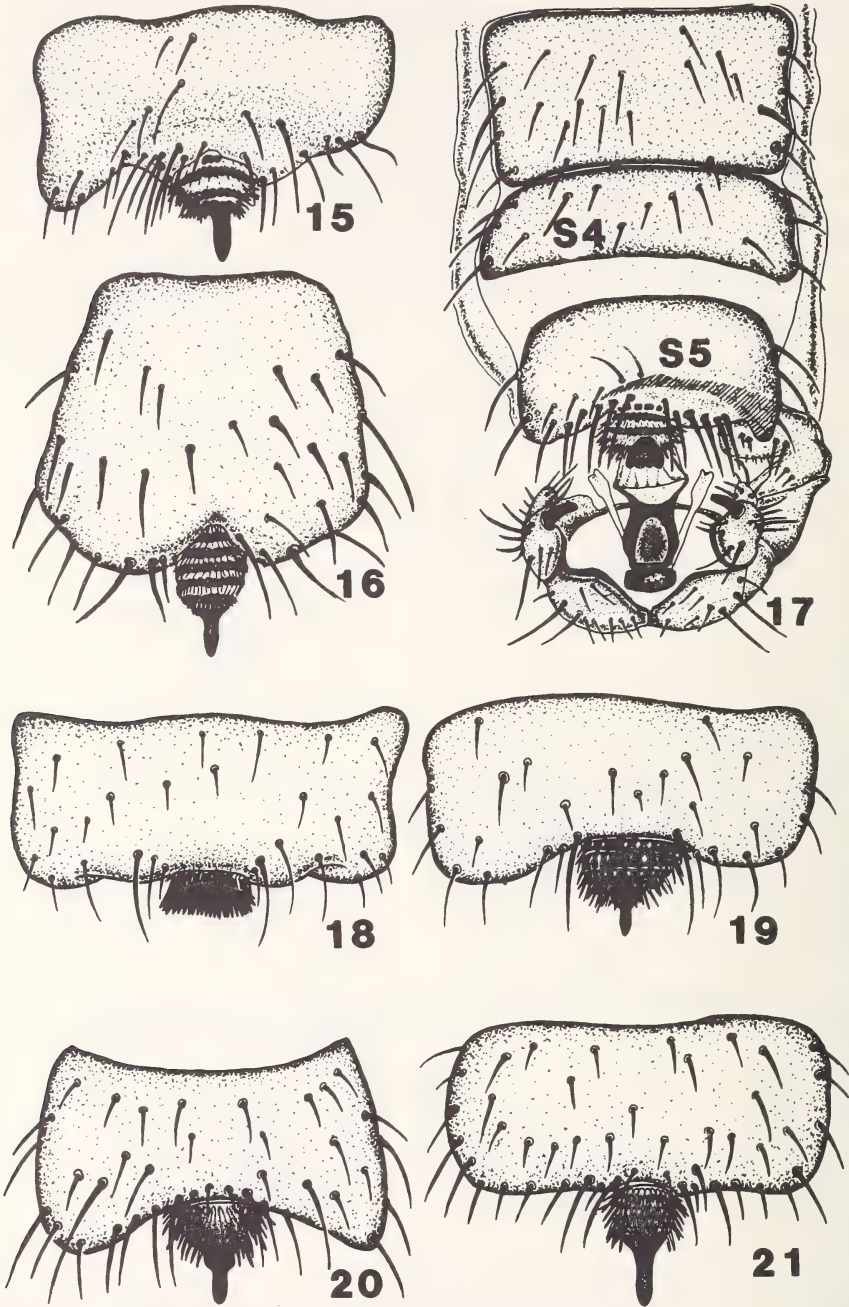
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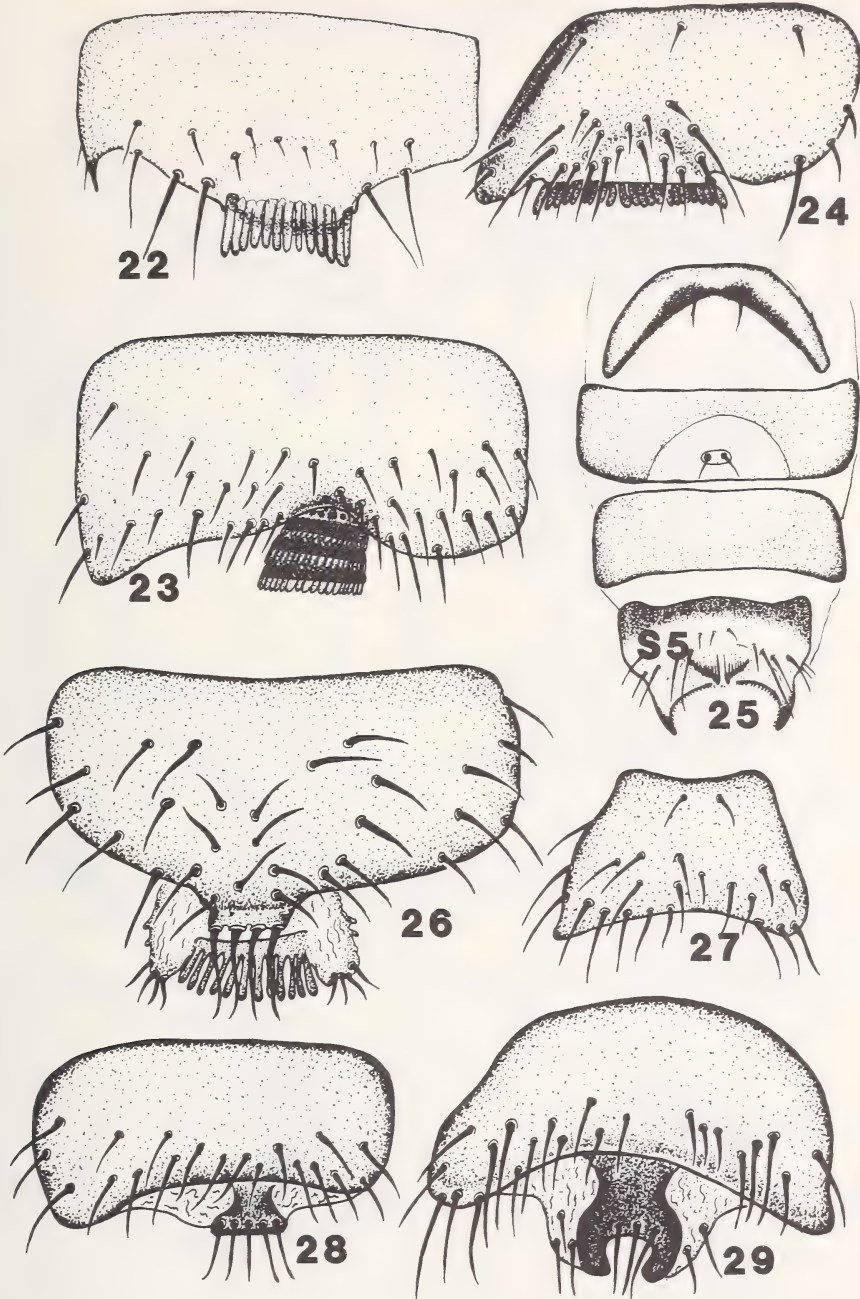
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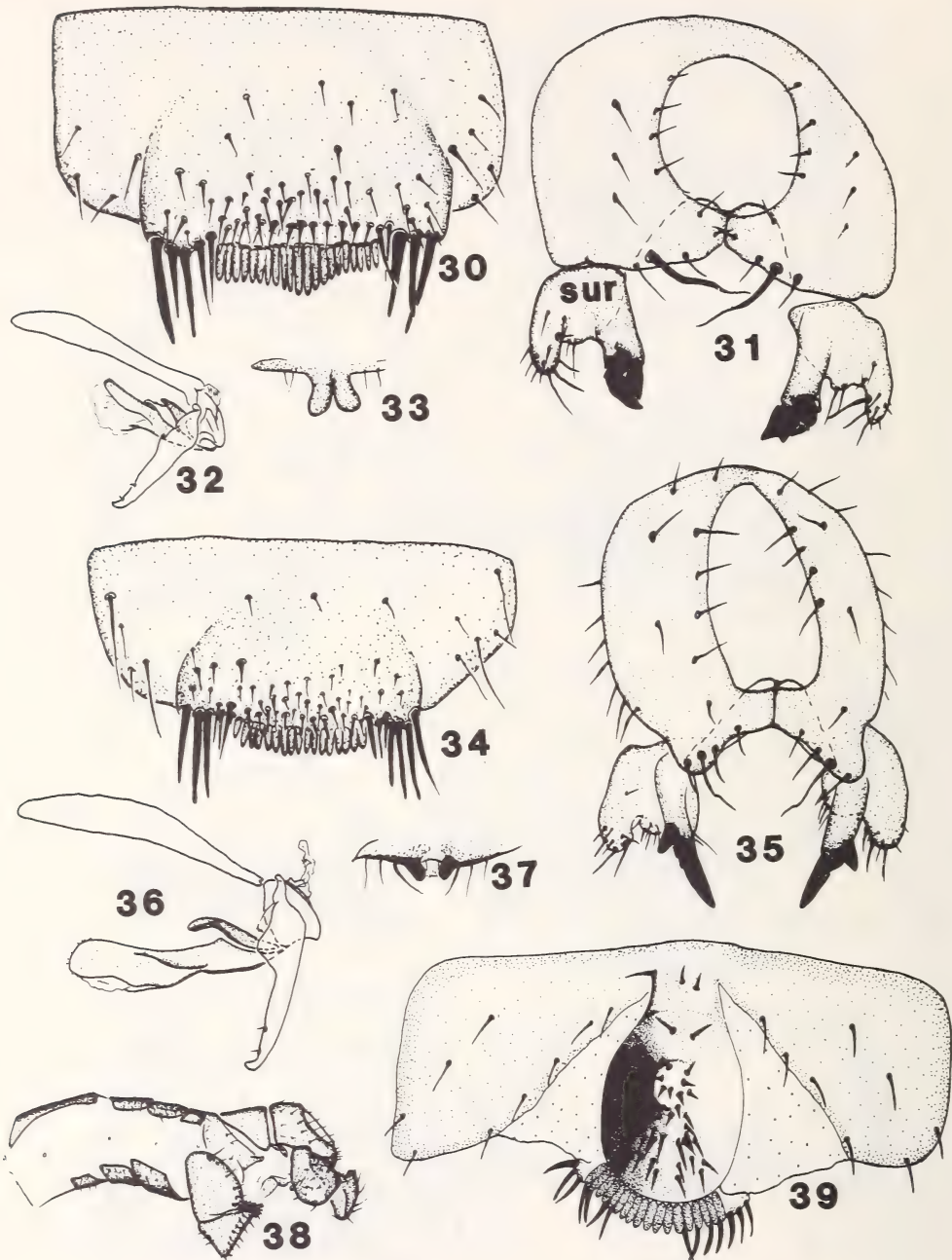
FIGS. 1-14. *Minilimosina* spp. 1-5, mid tibia of males: 1, *M. intercepta*, dorsal; 2, *M. intercepta*, anterior; 3, *M. sclerophallus*, dorsal; 4, *M. sclerophallus*, anterior; 5, *M. bistylus*, dorsal. 6, *M. bistylus*, anterior, mid femur and tibia of male. 7, *M. parvula*, mesonotum. 8, *M. vitripennis*, mesonotum. 9-14, *Minilimosina* (*Minilimosina*) spp. male sternite 5: 9, *M. parvula*; 10, *M. accinta*; 11, *M. zeda*; 12, *M. parva*; 13, *M. baculum*; 14, *M. pulpa*. Abbreviations: pad - proximal anterodorsal; dad - distal anterodorsal; dpd - distal posterodorsal; dd - distal dorsal; adc - anterior dorsocentral; pdc - posterior dorsocentral.



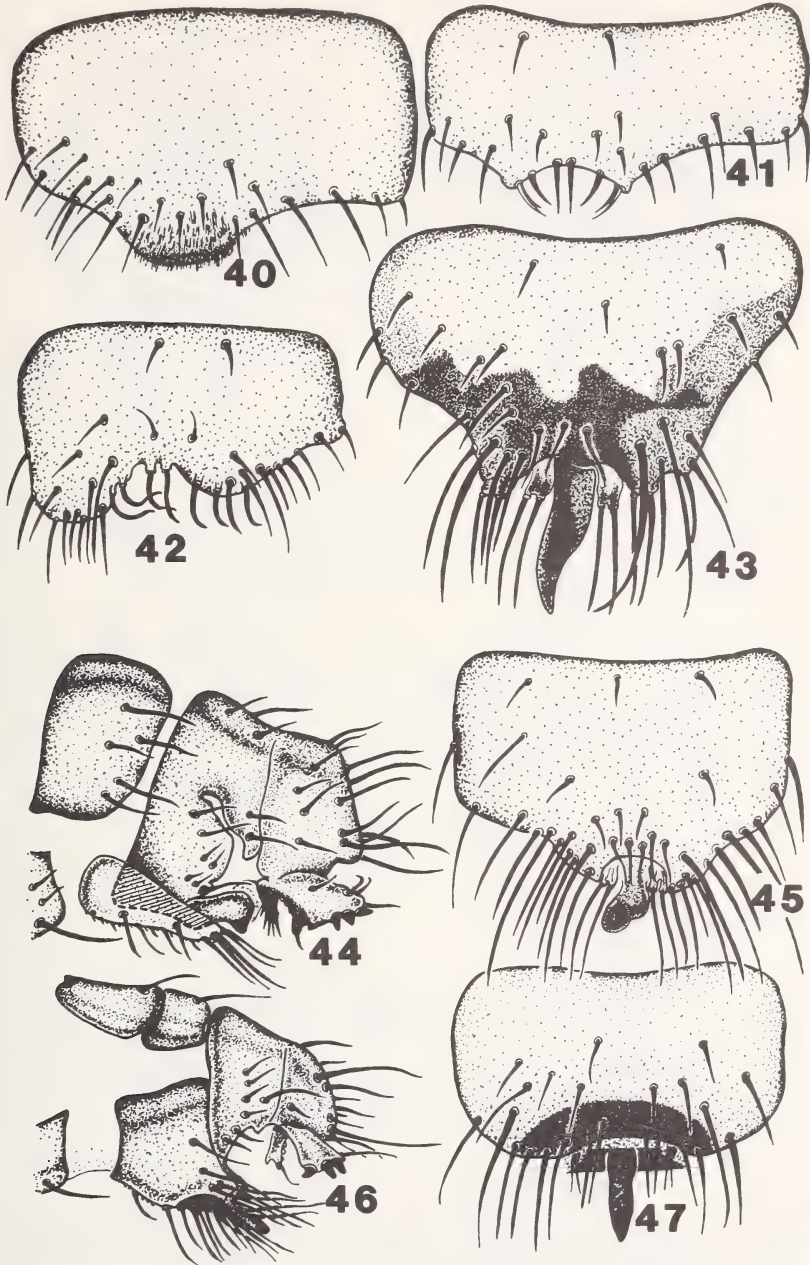
FIGS.15-21. *Minilimosina (Minilimosina)* spp. male sternite 5 (17 includes terminalia and sternites 3 & 4). 15, *M. trogeri*; 16, *M. nasuta*; 17, *M. lepida*; 18, *M. fungicola*; 19, *M. gemella*; 20, *M. longisternum*; 21, *M. intermedia*. Abbreviations: S4 - sternite 4; S5 - sternite 5.



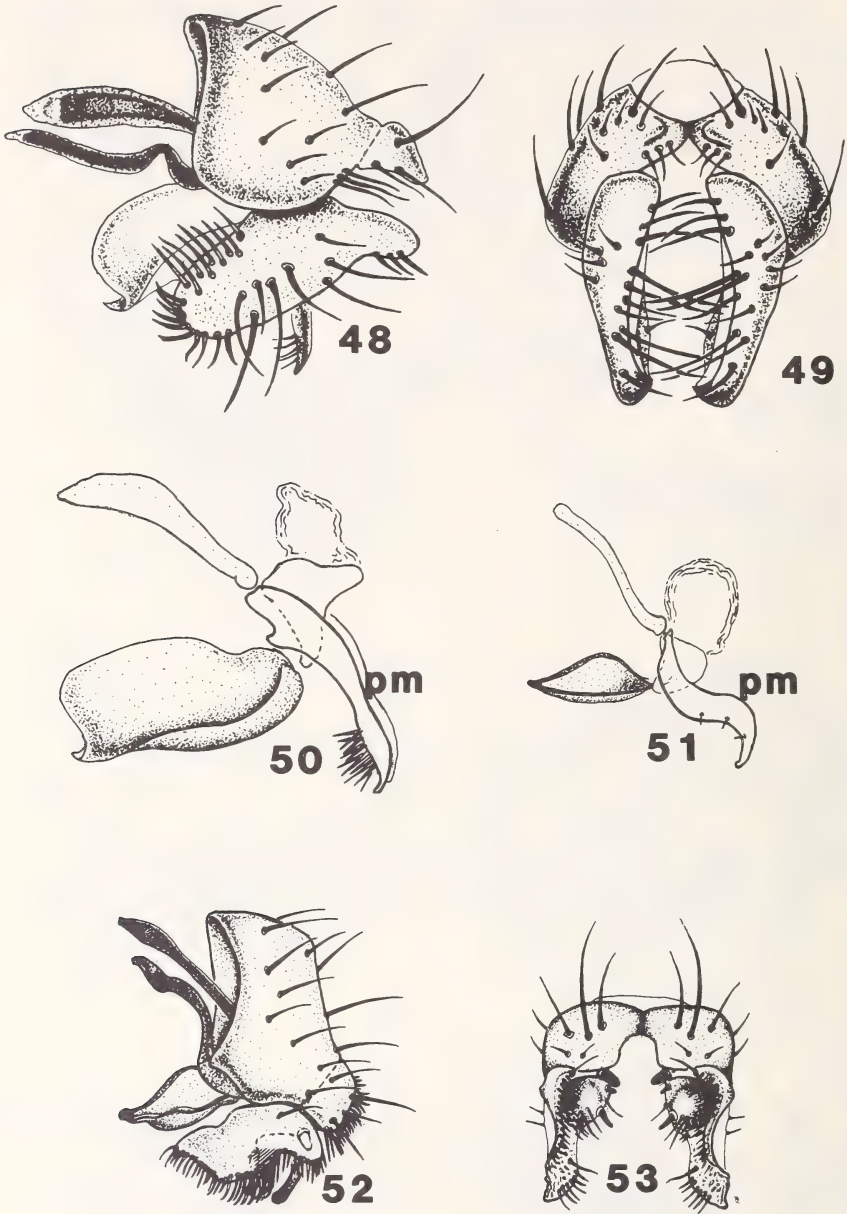
FIGS. 22-29. *Minilimosina* spp. male sternite 5 (25 is sternites 1-5). 22, *M. sclerophallus*; 23, *M. tuberculum*; 24, *M. neoalbinervis*; 25, *M. rotundipennis*; 26, *M. archboldi*; 27, *M. niveipennis*; 28, *M. contrasta*; 29, *M. vitripennis*. Abbreviations: S5 - sternite 5.



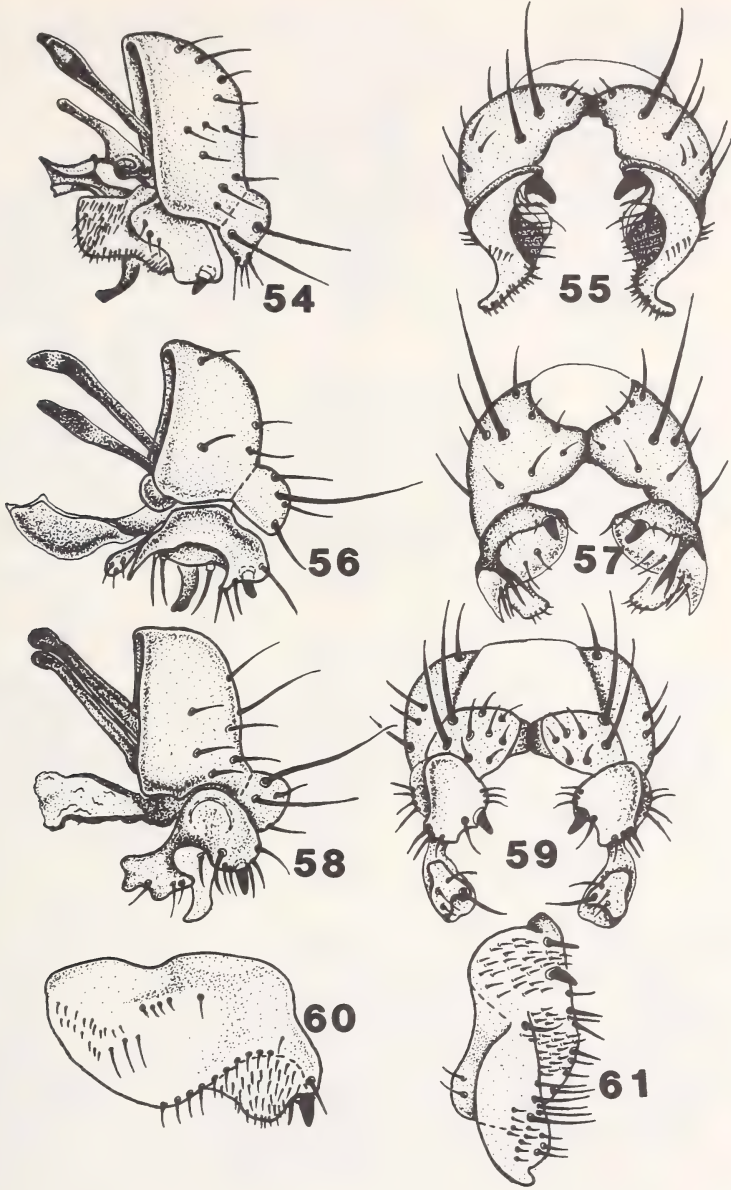
FIGS. 30-39. *Minilimosina* (*Svarciella*) spp. males. 30-33, *M. intercepta*: 30, sternite 5; 31, terminalia, posterior; 32, aedeagal complex, left lateral; 33, posteromedial margin of sternite 6. 34-37, *M. vixa*: 34, sternite 5; 35, terminalia, posterior; 36, aedeagal complex, left lateral; 37, posteromedial margin of sternite 6. 38-39, *M. dissimilicosta*: 38, abdomen, left lateral; 39, sternite 5.



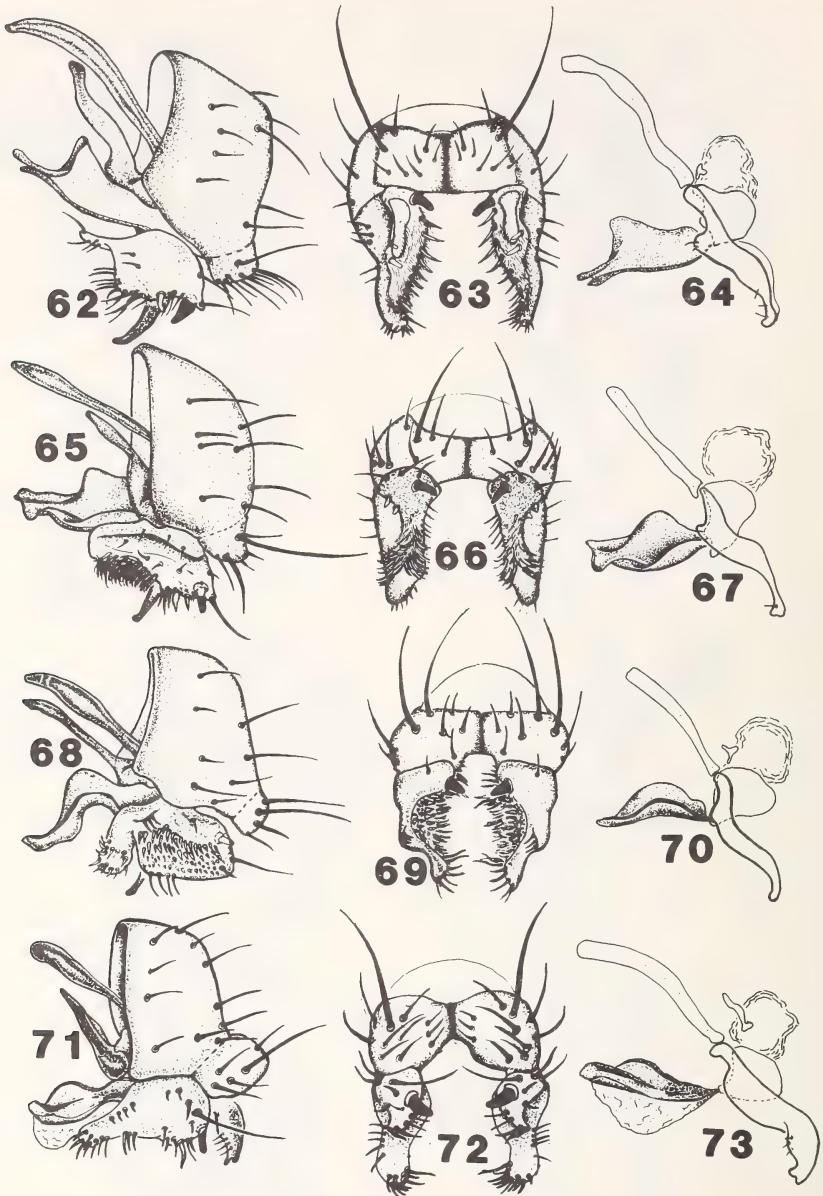
FIGS. 40-47. *Minilimosina* spp. males. 40, *M. bipara*, sternite 5; 41, *M. digitata*, sternite 5; 42, *M. ternaria*, sternite 5; 43, *M. priapismus*, sternites 5 and 6; 44, *M. erecta*, left lateral view to show terminalia and sternites 5 and 6; 45, *M. erecta*, sternites 5 and 6; 46, *M. bistylus*, left lateral view to show terminalia and sternites 5 and 6; 47, *M. bistylus*, sternites 5 and 6.



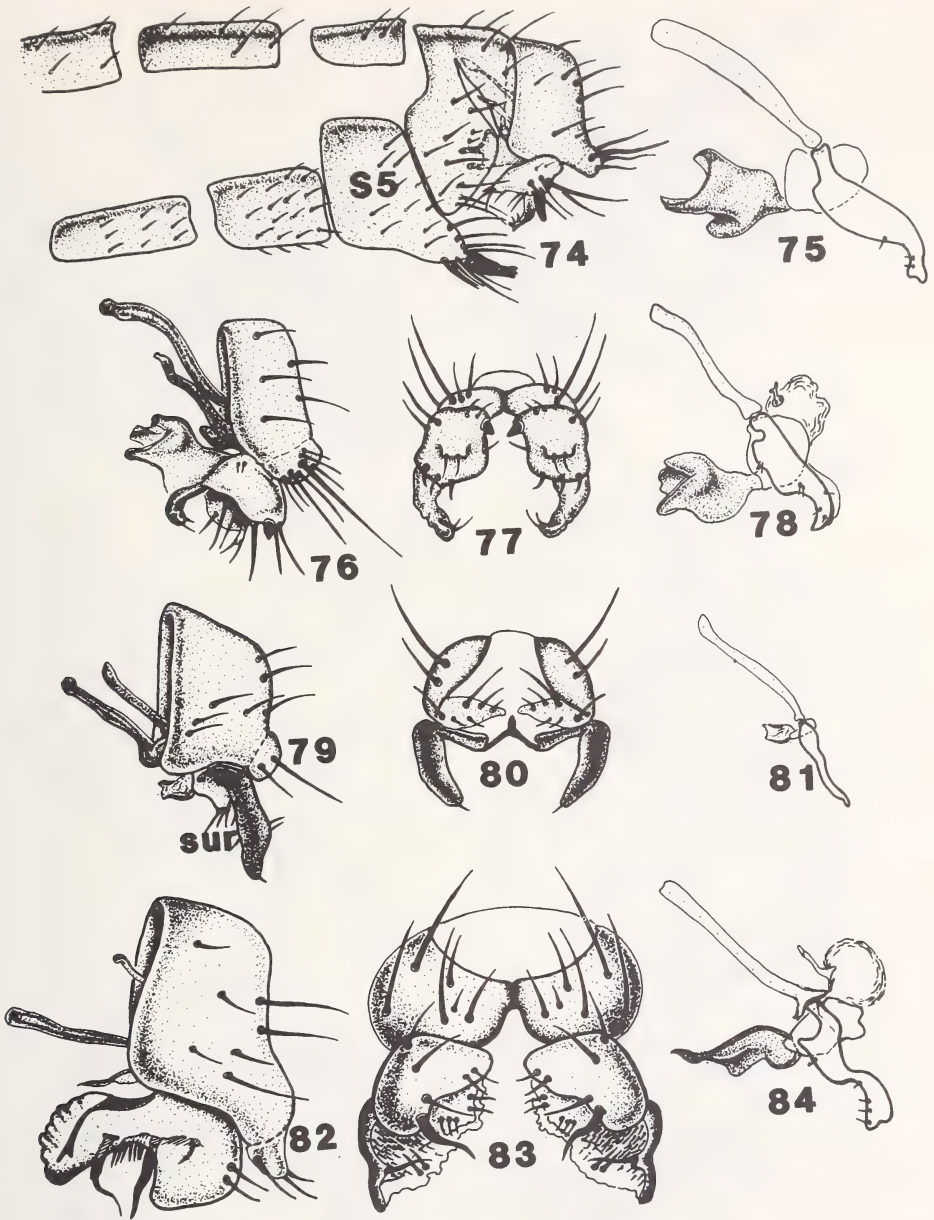
FIGS. 48-53. *Minilimosina* (*Minilimosina*) spp. male terminalia. 48-50, *M. sclerophallus*: 48, left lateral; 49, posteroventral; 50, aedeagal complex (left lateral). 51-53, *M. parva*: 51, aedeagal complex (left lateral) 1; 52, left lateral; 53, posteroventral. Abbreviations: pm - paramere.



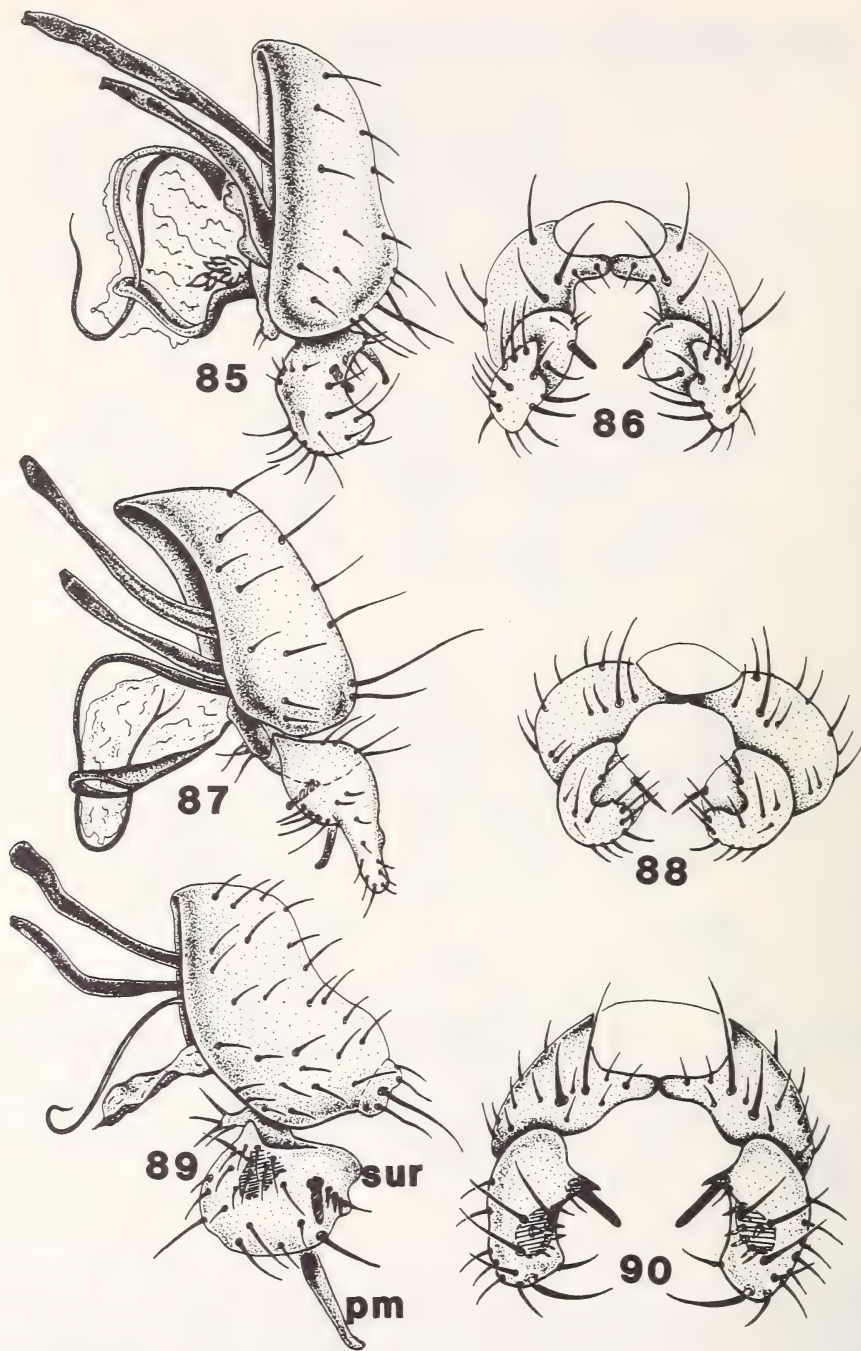
FIGS. 54-61. *Minilimosina (Minilimosina)* spp. male terminalia. 54-55, *M. zeda*: 54, left lateral; 55, posteroventral (external only). 56-57, *M. pulpa*. 56, left lateral; 57, posteroventral (external only). 58-59, *M. baculum*: 58, left lateral; 59, posteroventral (external only). 60-61, *M. tuberculum*, surstylus: 60, left lateral; 61, ventral.



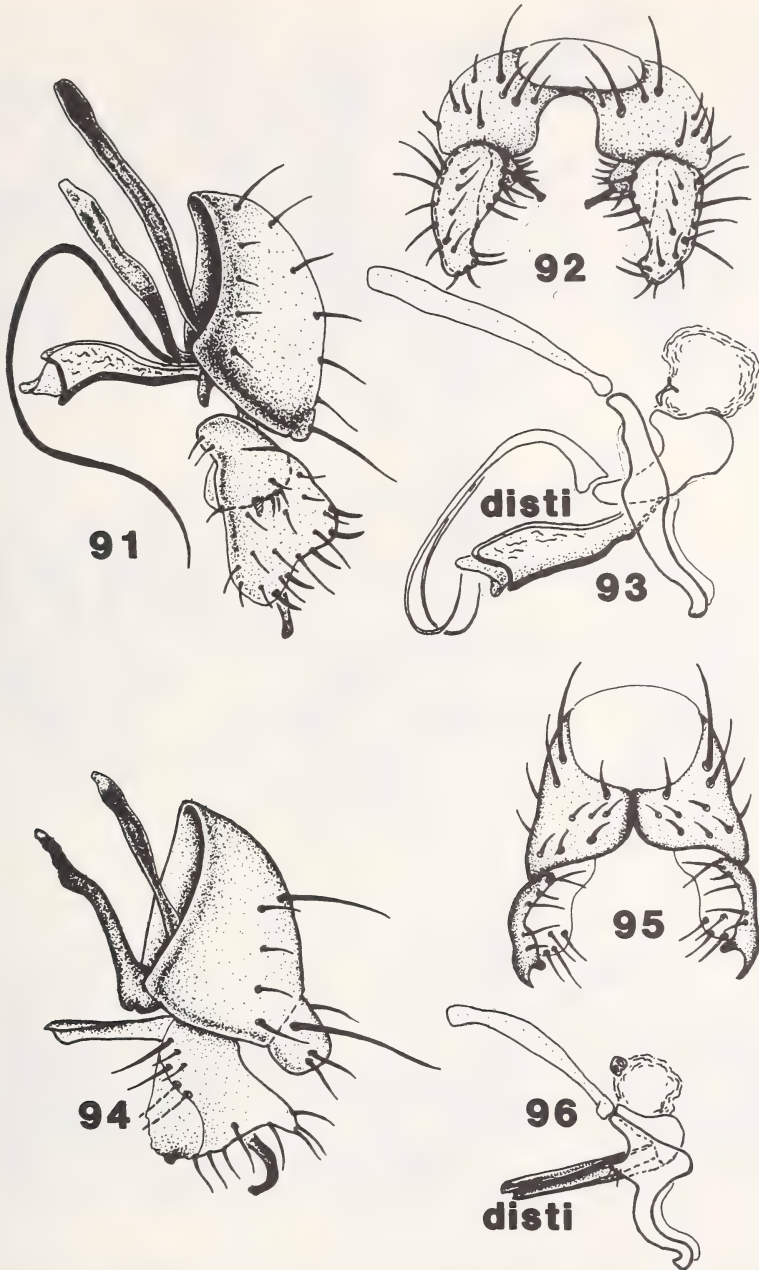
FIGS. 62-73. *Minilimosina (Minilimosina)* spp. male terminalia. 62-64, *M. longisternum*. 62, left lateral; 63, posteroventral (external only); 64, aedeagal complex, left lateral. 65-67, *M. intermedia*: 65, left lateral; 66, posteroventral (external only); 67, aedeagal complex, left lateral. 68-70, *M. trogeri*: 68, left lateral. 69, posteroventral (external only); 70, aedeagal complex, left lateral; 71-73, *M. nasuta*: 71, left lateral; 72, posteroventral (external only); 73, aedeagal complex, left lateral.



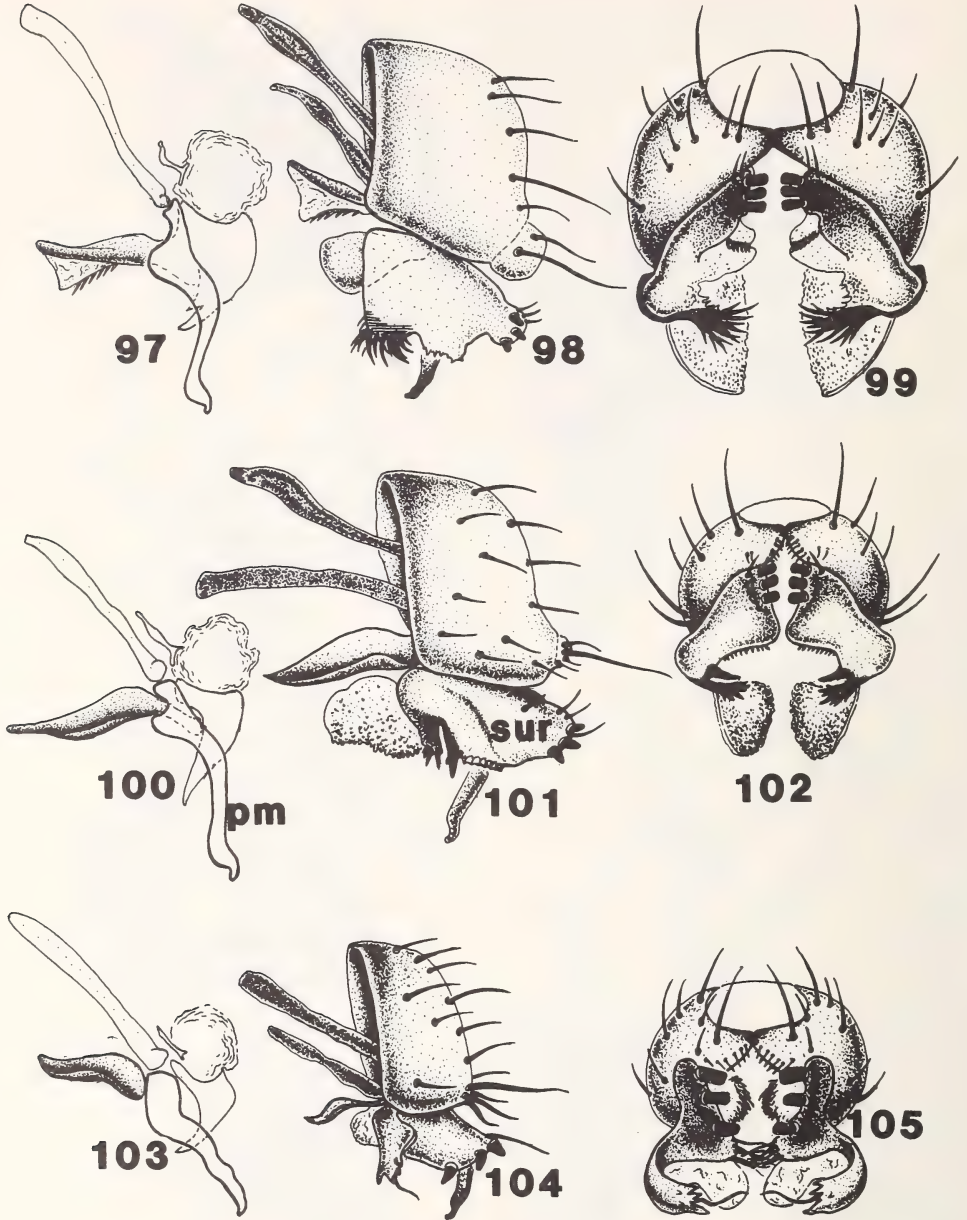
FIGS. 74-84. *Minilimosina* spp. males 74-75, *M. lepida*: 74, abdomen, left lateral; 75, terminalia, aedeagal complex, left lateral. 76-78, *M. accinta*: 76, terminalia, left lateral; 77, terminalia, ventral; 78, aedeagal complex, left lateral. 79-81, *M. rotundipennis*: 79, terminalia, left lateral; 80, terminalia, posteroventral (external only); 81, aedeagal complex, left lateral. 82-84, *M. albinervis*: 82, terminalia, left lateral; 83, terminalia, posteroventral (external only); 84, aedeagal complex, left lateral. Abbreviations: S5 - sternite 5; sur - surstylus.



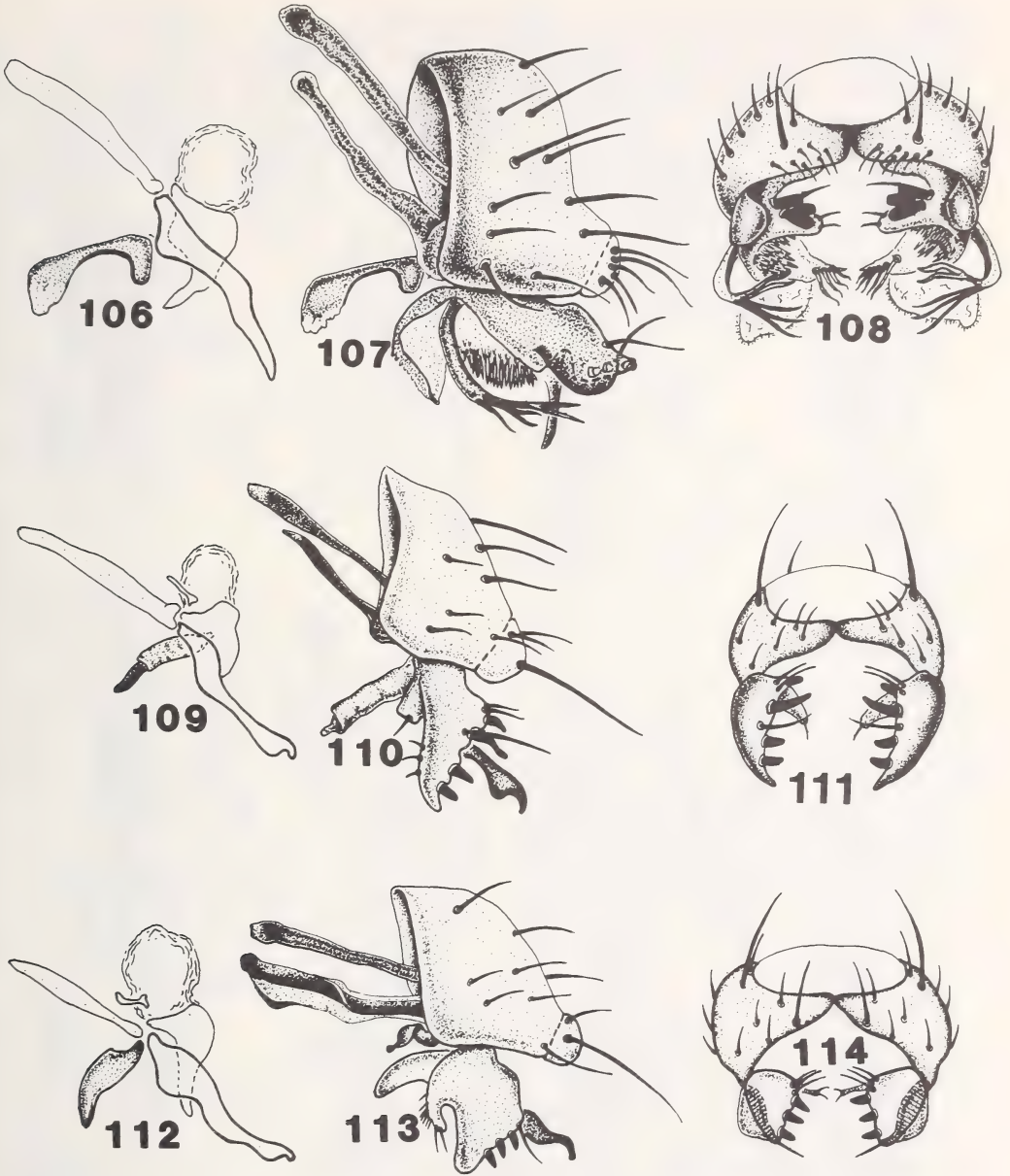
FIGS. 85-90. *Minilimosina* (*Svarciella*) *vitripennis* species group male terminalia. 85-86, *M. niveipennis*: 85, left lateral; 86, posteroventral (external only). 87-88, *M. vitripennis*: 87, left lateral; 88, posteroventral (external only). 89-90, *M. archboldi*: 89, left lateral; 90, posteroventral (external only). Abbreviations: sur - surstylus; pm - paramere.



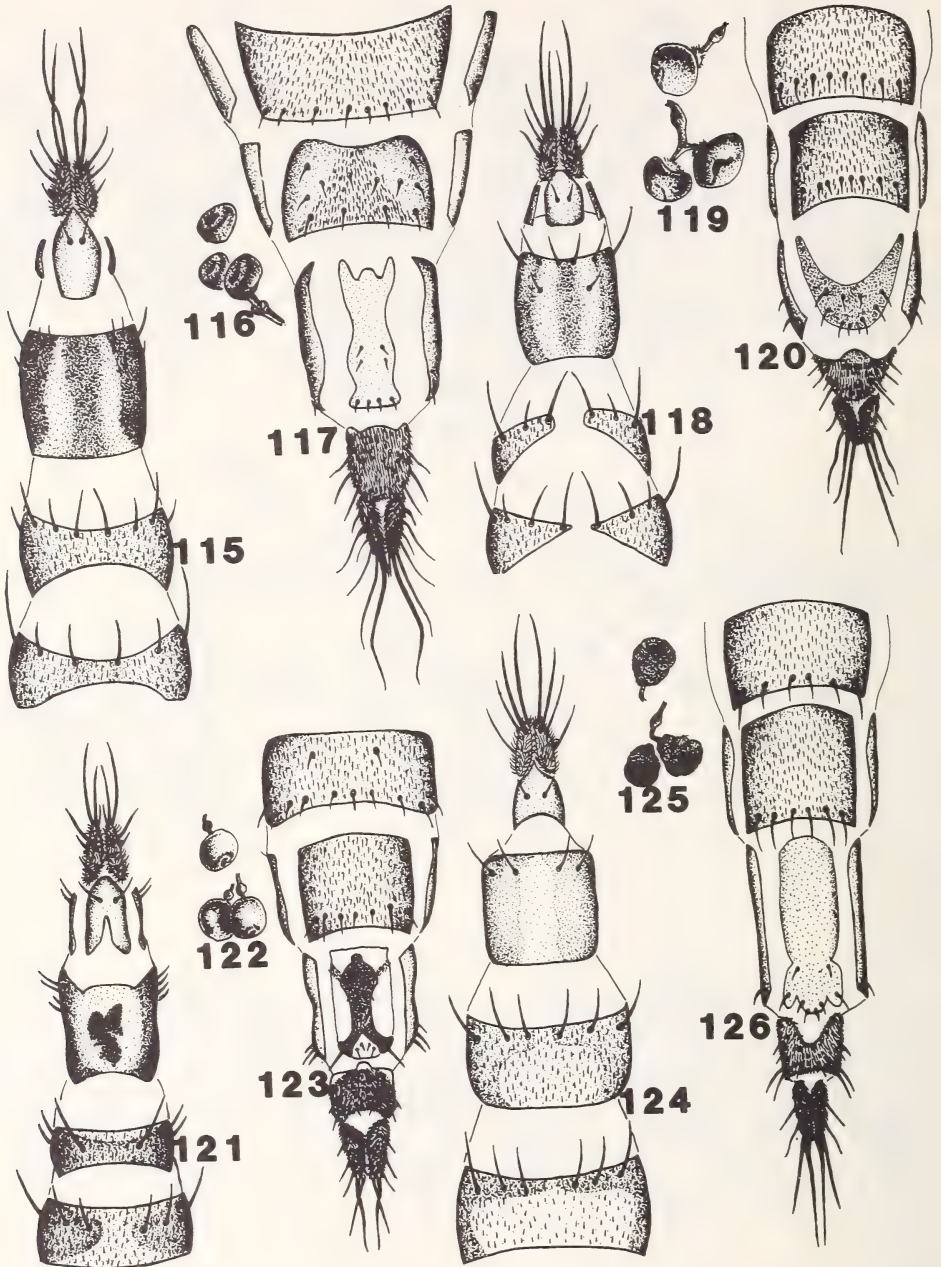
FIGS. 91-96. *Minilimosina* (*Svarciella*) spp. male terminalia. 91-93, *M. contrasta*: 91, left lateral; 92, posteroventral (external only); 93, aedeagal complex, left lateral. 94-96, *M. bipara*: 94, lateral; 95, posteroventral (external only); 96, aedeagal complex, left lateral. Abbreviations: disti - distiphallus.



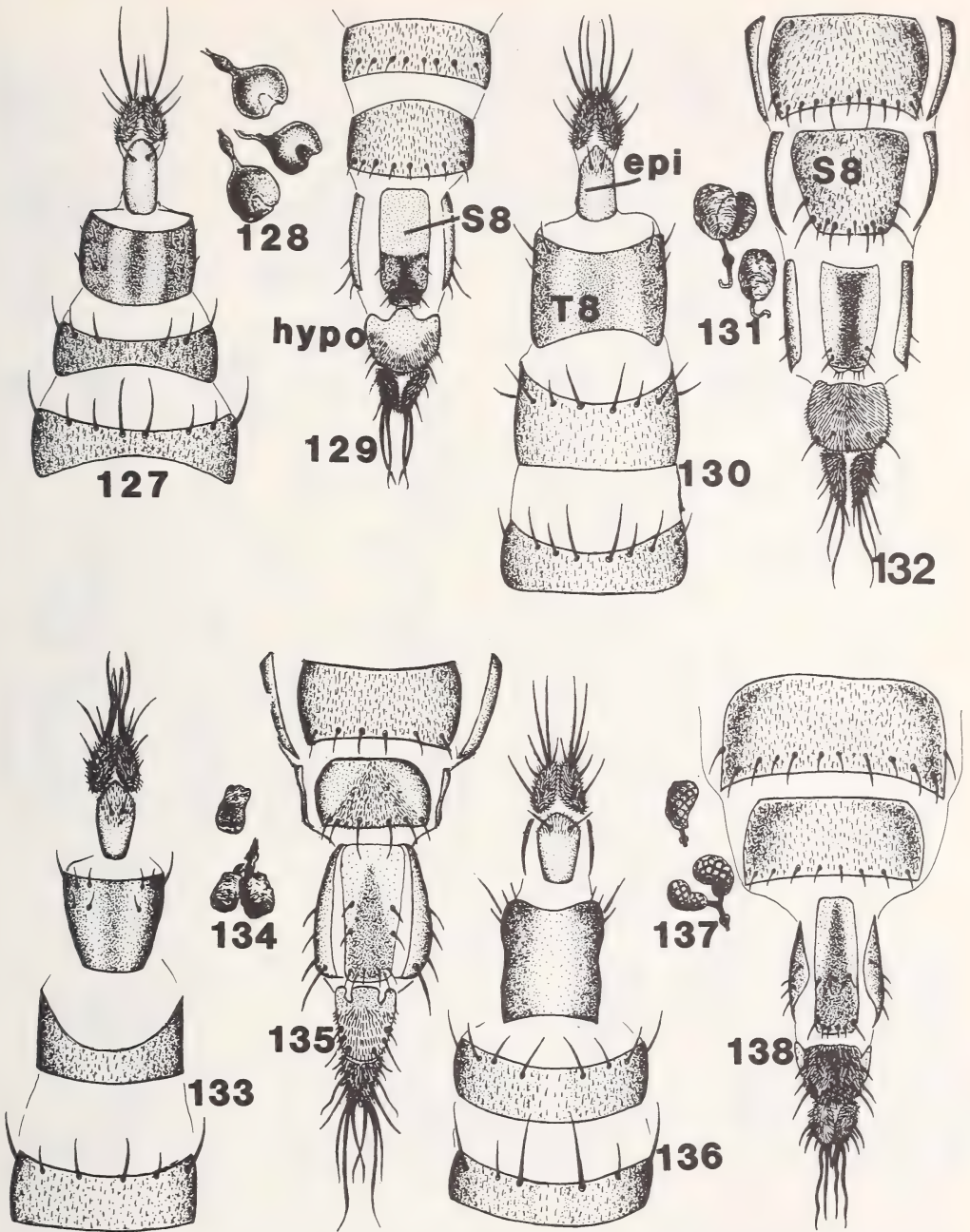
FIGS. 97-105. *Minilimosina (Amputella)* spp. male terminalia. 97-99, *M. priapismus*: 97, aedeagal complex, left lateral; 98, left lateral; 99, posteroventral (external only). 100-102, *M. erecta*: 100, aedeagal complex, left lateral; 101, left lateral; 102, posteroventral (external only). 103-105, *M. bistylus*: 103, aedeagal complex, left lateral; 104, left lateral; 105, posteroventral (external only). Abbreviations: sur - surstylus.



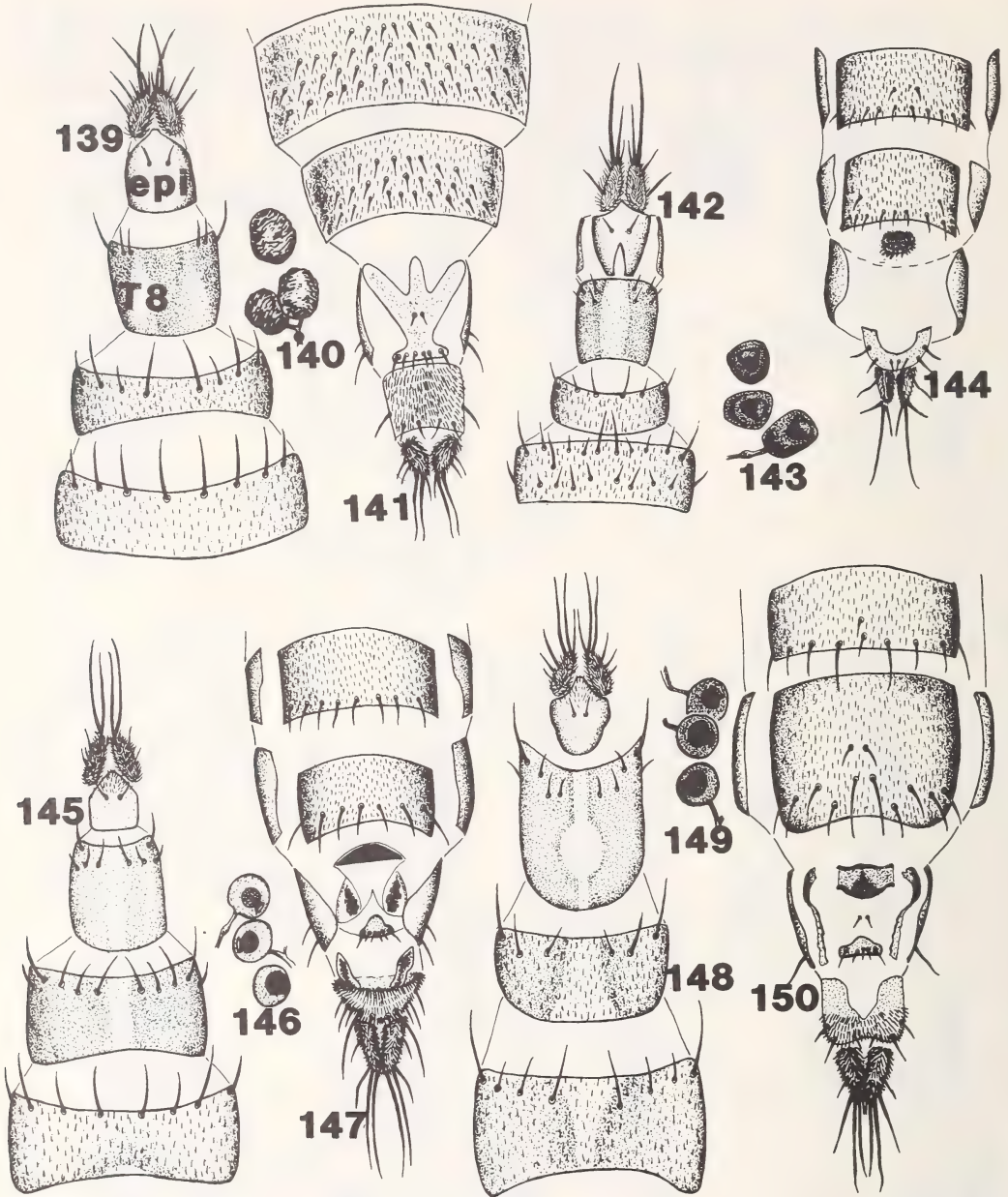
FIGS. 106-114. *Minilimosina (Amputella)* spp. male terminalia. 106-108, *M. curvistylus*: 106, aedeagal complex, left lateral; 107, left lateral; 108, posteroventral (external only). 109-111, *M. digitata*: 109, aedeagal complex, left lateral; 110, left lateral; 111, posteroventral (external only). 112-114, *M. ternaria*: 112, aedeagal complex, left lateral; 113, left lateral; 114, posteroventral (external only).



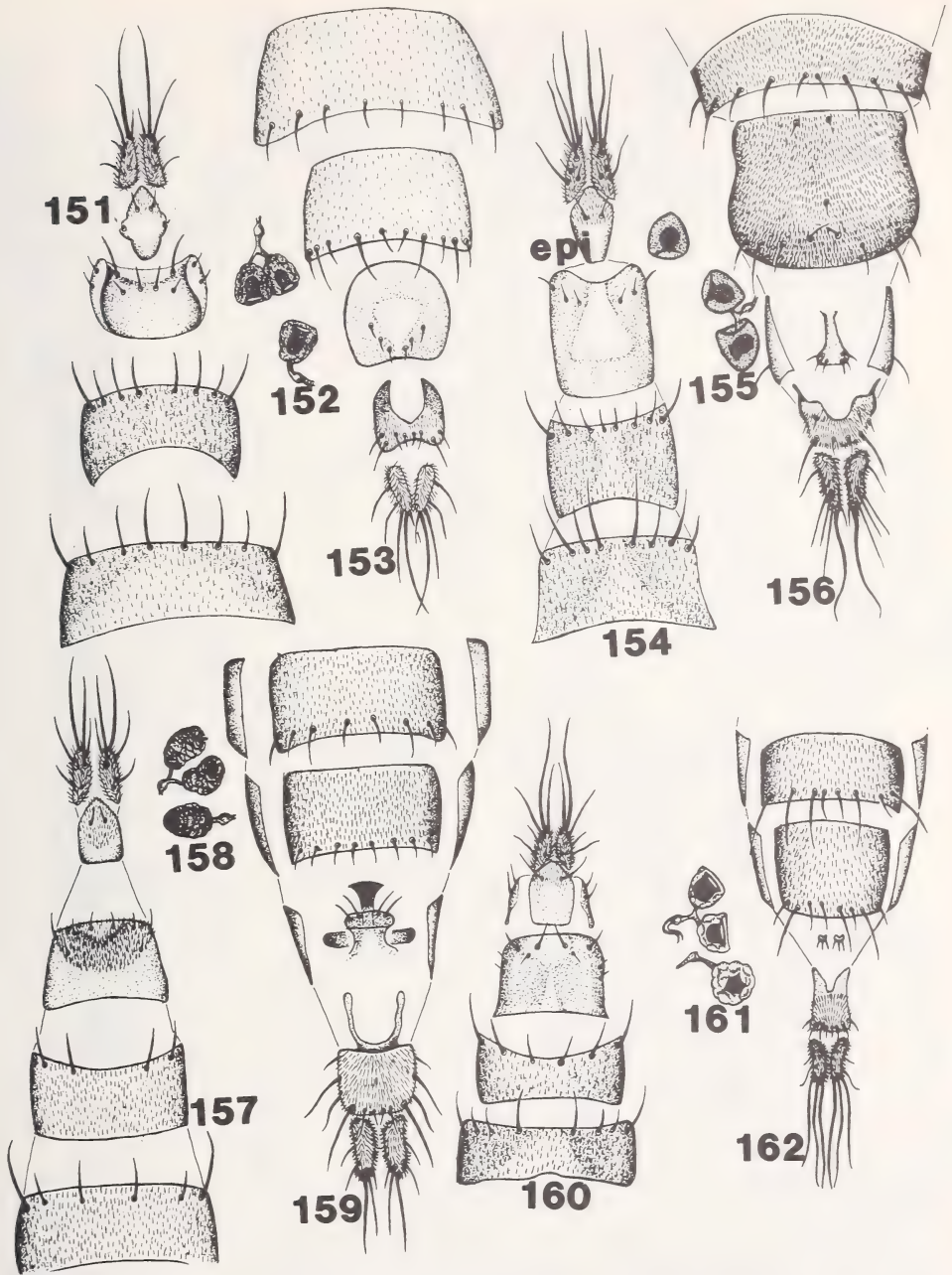
FIGS. 115-126. *Minilimosina* (*Minilimosina*) spp. female terminalia and spermathecae. 115-117, *M. longisternum*: 115, dorsal; 116, spermathecae; 117, ventral. 118-120, *M. nasuta*: 118, dorsal; 119, spermathecae; 120, ventral. 121-123, *M. parva*: 121, dorsal; 122, spermathecae; 123, ventral. 124-126, *M. sclerophallus*: 124, dorsal; 125, spermathecae; 126, ventral.



FIGS. 127-138. *Minilimosina (Minilimosina)* spp. female terminalia and spermathecae. 127-129, *M. trogeri*: 127, dorsal; 128, spermathecae; 129, ventral. 130-132, *M. fungicola*: 130, dorsal; 131, spermathecae; 132, ventral. 133-135, *M. gemella*: 133, dorsal; 134, spermathecae; 135, ventral. 136-138, *M. intermedia*: 136, dorsal; 137, spermathecae; 138, ventral. Abbreviations: S8 - sternite 8; hypo - hypoproct; epi - epiproct; T8 - tergite 8.



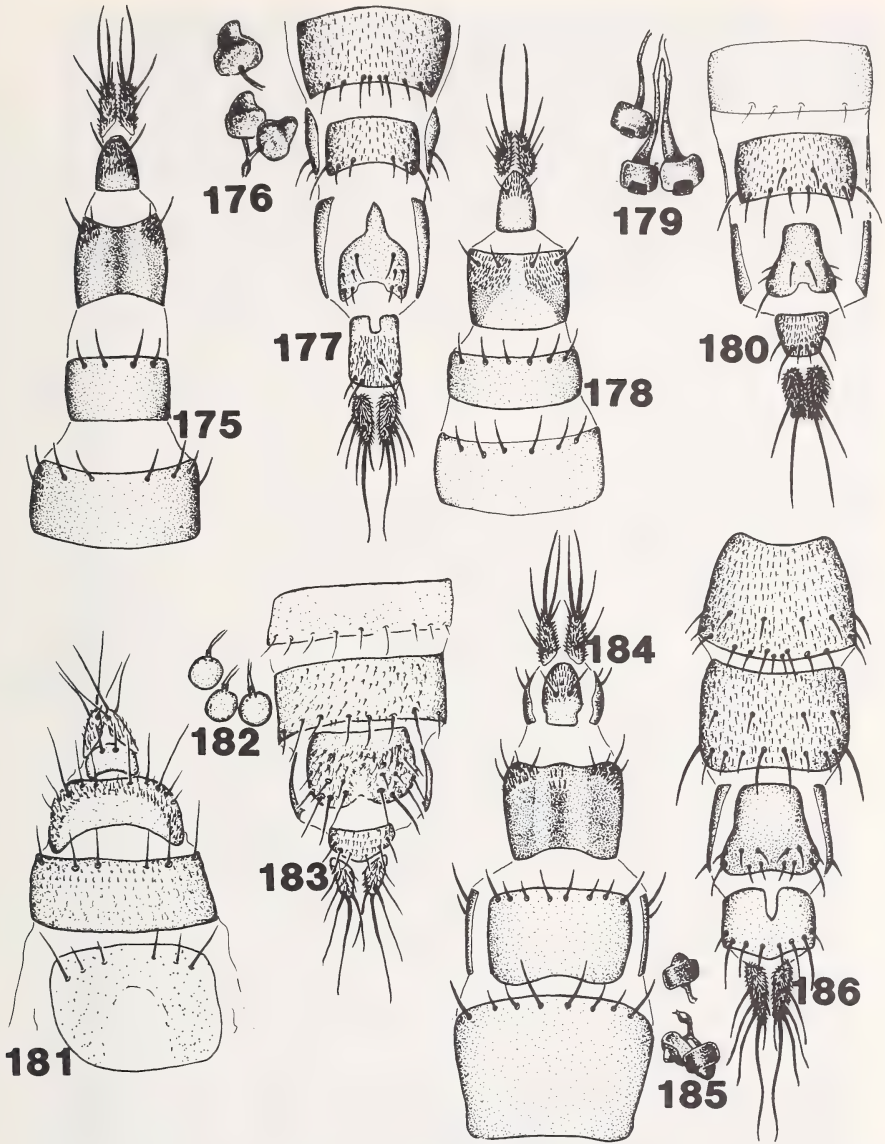
FIGS. 139-150. *Minilimosina* spp. female terminalia and spermathecae. 139-141, *M. zeda*: 139, dorsal; 140, spermathecae; 141, ventral. 142-144, *M. albinervis*: 142, dorsal; 143, spermathecae; 144, ventral. 145-147, *M. bistylus*: 145, dorsal; 146, spermathecae; 147, ventral. 148-150, *M. curvistylus*: 148, dorsal; 149, spermathecae; 150, ventral. Abbreviations: epi - epiproct; T8 - tergite 8.



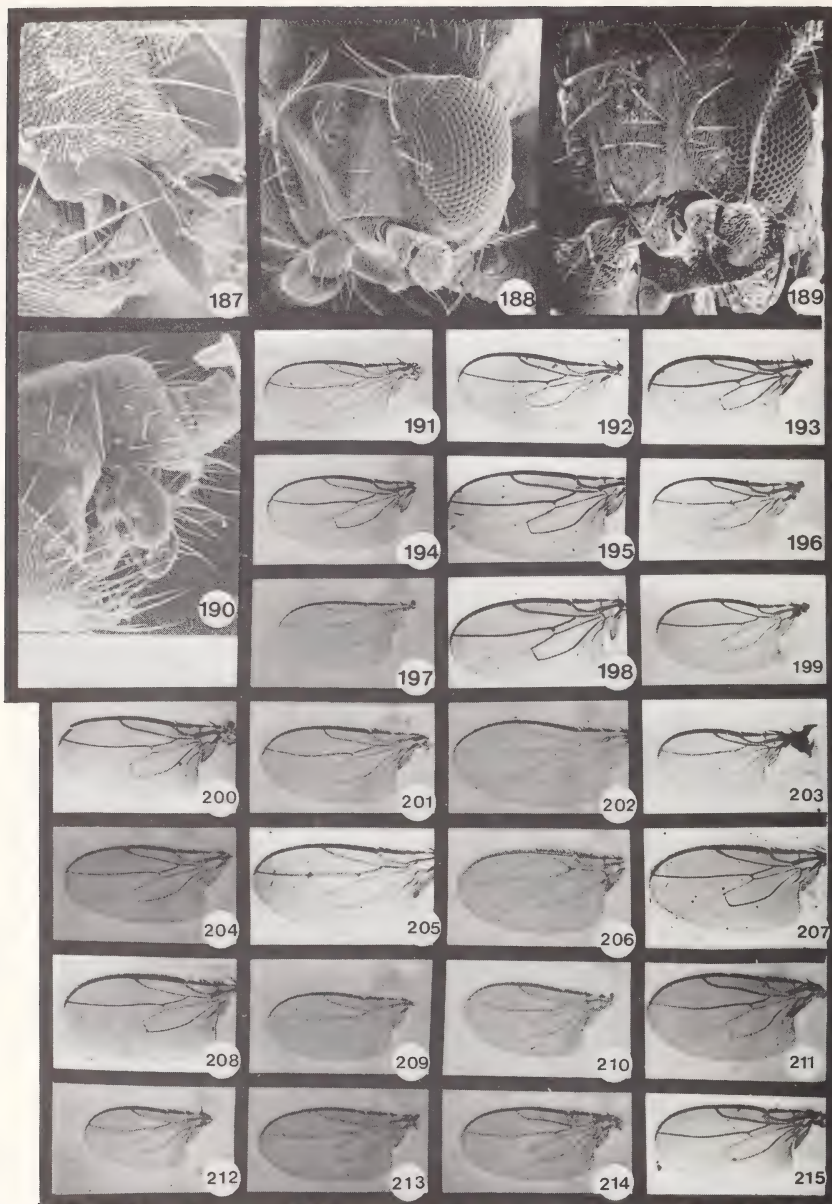
FIGS. 151-153. *Minilimosina (Amputella)* spp. female terminalia and spermathecae. 151-153, *M. digitata*: 151, dorsal; 152, spermathecae; 153, ventral. 154-156, *M. erecta*: 157-159, *M. priapismus*: 157, dorsal; 158, spermathecae; 159, ventral. 160-162, *M. ternaria*: 160, dorsal; 161, spermathecae; 162, ventral. Abbreviations: epi - epiproct.



FIGS. 163-174, *Minilimosina (Svarciella)* spp. female terminalia and spermathecae. 163-165, *M. bipara*: 163, dorsal; 164, spermathecae; 165, ventral. 166-168, *M. intercepta*: 166, dorsal; 167, spermathecae; 168, ventral. 169-171, *M. vixa*: 169, dorsal; 170, spermathecae; 171, ventral. 172-173, *M. dissimilicosta*: 172, dorsal; 173, spermathecae; 174, ventral.



FIGS. 175-186. *Minilimosina (Svarciella)* spp. female terminalia and spermathecae. 175-177, *M. contrasta*: 175, dorsal; 176, spermathecae; 177, ventral. 178-180, *M. niveipennis*: 178, dorsal; 179, spermathecae; 180, ventral. 181-183, *M. masoni*: 181, dorsal; 182, spermathecae; 183, ventral. 184-186, *M. viiripennis*: 184, dorsal; 185, spermathecae; 186, ventral.



FIGS. 187-215. 187, *M. rotundipennis*, male terminalia, posterolateral. 188, *M. intercepta*, head, anterodorsal. 189, *M. nasuta*, head, dorsolateral. 190, *M. ternaria*, male terminalia, left lateral. 191-215, left wings of *Minilimosina* species: 191, *M. accinta*; 192, *M. baculum*; 193, *M. trogeri*; 194, *M. longisternum*; 195, *M. fungicola*; 196, *M. gemella*; 197, *M. intermedia*; 198, *M. nasuta*; 199, *M. parva*; 200, *M. parvula*; 201, *M. sclerophallus*; 202, *M. zeda*; 203, *M. rotundipennis*; 204, *M. dissimilicosta*; 205, *M. intercepta*; 205, *M. masoni*; 207, *M. vixa*; 208, *M. vitripennis*; 209, *M. bipara*; 210, *M. bistylus*; 211, *M. curvistylus*; 212, *M. digitata*; 213, *M. erecta*; 214, *M. priapismus*; 215, *M. ternaria*.

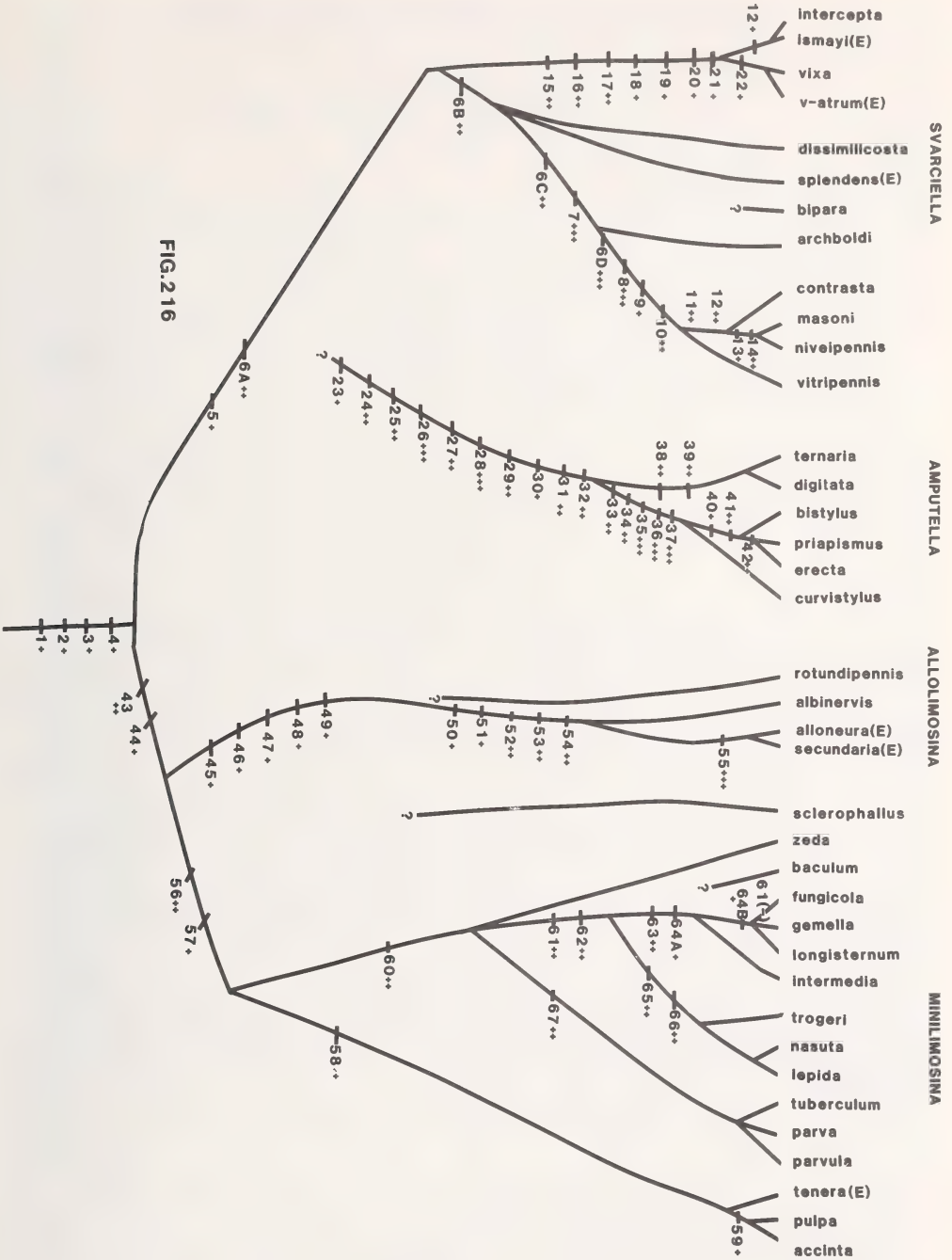


FIG. 216. A phylogenetic hypothesis for the genus *Minilimosina*. Character weighting is indicated by (+), (++) or (+++), as discussed in text; (-) indicates a reversal. Numbers on the figure refer to the following synapomorphic characters: 1, wing venation with second costal sector less than or equal to third and costa extending beyond tip of R_{4+5} . 2, alula narrow. 3, posteromedial area of male sternite 5 with a row of flat bristles. 4, mid tibia without a midventral bristle. 5, acrostichal bristles sparse, in 4 rows. 6A, male sternite 5 with a single posteromedial comb row flanked by setose areas. 6B, sternite 5 with posteromedial comb and flanking setose lobes slightly deflexed. 6C, sternite 5 with posteromedial comb and flanking setose lobes strongly deflexed and differentiated from sternite. 6D, posteromedial area of sternite 5 totally deflexed, no longer comb-like. 7, ventral process of distiphallus forming a long, whip-like flagellum. 8, preabdominal sclerites greatly reduced. 9, spermathecae short. 10, apex of spermatheca evaginated. 11, interfrontal bristles greatly reduced. 12, antennae orange. 13, Neotropical. 14, scutellum convex. 15, mid tibia of male with a double row of small ventral spines distally. 16, sternite 8 large, shield-shaped. 17, sternite 6 with a double posterior process. 18, abdominal sclerites enlarged. 19, body black, heavily sclerotized and weakly punctate. 20, spermathecae elongate and wrinkled. 21, katapisternum with separate shining areas. 22, one of three posterior surstylar bristles greatly enlarged. 23, spermathecae round, with deep, narrow-necked invaginations. 24, one long costagial bristle. 25, developed epiphallus. 26, right paramere vestigial. 27, female sternite 8 greatly reduced. 28, distiphallus greatly reduced. 29, surstylus with 3-4 short, stout posterior bristles. 30, distal dorsal bristle of mid tibia shifted anterodorsally. 31, apex of paramere constricted. 32, loss of posteromedial comb on male sternite 5. 33, female sternite 8 divided into 4 pieces. 34, spermathecal invagination lateral. 35, surstylus strongly divided into anterior and posterior parts. 36, posteromedial process of male sternite 5 greatly enlarged and projecting beyond sternite. 37, surstylus with a large, membranous posteromedial lobe. 38, male sternite 5 simple, posteromedial process lost. 39, female sternite 8 reduced to 1 or 2 minute pieces. 40, lateral parts of female sternite 8 short. 41, hypoproct with strongly differentiated, bare anterior arms. 42, surstylus with a linear midventral comb of small bristles. 43, face strongly tuberculate between antennae. 44, anterior dorsocentral bristles reduced. 45, distiphallus reduced. 46, postvertical bristles enlarged. 47, discal cell short. 48, second costal sector short. 49, surstylus without posteroventral bristle. 50, sternite 5 of male with a single, short row of flat bristles. 51, paramere apically swollen. 52, sternite 8 of female greatly reduced. 53, surstylus with a complex, split anterior lobe. 54, hypandrium short. 55, sternite 8 of female absent. 56, male sternite 5 with a narrow posteromedial lobe made up of rows of flat bristles. 57, female sternite 8 narrow and partly desclerotized. 58, surstylus narrow anteriorly, posterior lobe with ventral processes. 59, posteromedial comb of male sternite 5 sinuate. 60, surstylus flattened, inner surface setulose. 61, posteromedial comb of male sternite 5 including a heavily sclerotized median piece. 62, basal part of posteromedial comb covered with short, scale-like bristles. 63, surstylus with a second slightly enlarged bristle anterior to the large posteroventral bristle. 64A, apical scutellar bristles short. 64B, apical scutellar bristles very short. 65, apex of paramere bifid. 66, anterior lobe of surstylus evenly tapered. 67, comb row of male sternite 5 made up of large, flat bristles overlapping dark lamellae.

A REVISION OF THE NEARCTIC EUCHARITINAE (HYMENOPTERA: CHALCIDOIDEA: EUCHARITIDAE)

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Abstract

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The species of the subfamily Eucharitinae (Eucharitidae) are revised and keys provided for the five genera and 16 described species of the Nearctic region. The taxonomic history of the Eucharitidae is briefly reviewed and the defining characters of the subfamilies Oraseminae and Eucharitinae are given. Five new species of *Pseudometagea* Ashmead are described: *barberi* (from Ontario), *hirsuta* (from California), *nefrens* (from lower Boreal), *occipitalis* (from central North America), and *rugosa* (from Mexico). The species *Stilbula montana* Ashmead is newly combined in *Pseudometagea*. The species within *Pseudometagea* are referred to three species groups. Redescriptions of species and keys are provided for the Nearctic species of *Kapala* Cameron and *Lophyrocera* Cameron. A key to the Nearctic species of *Pseudochalcura* Ashmead is included. A new genus, *Obeza*, is proposed for the New World species which were previously included in the Old World genus *Stilbula* Spinola and includes the following species which are all new combinations: *floridana* (Ashmead), *grenadensis* (Howard), *maculata* (Westwood), *meridionalis* (Kirby), *nigromaculata* (Cameron), *semifunipennis* (Girault) and *septentrionalis* (Brues). Phylogenetic relationships among genera and species are discussed briefly.

Introduction

The Eucharitidae is a morphologically diverse family within the Chalcidoidea. There are 44 genera presently recognized and more than 332 species distributed in every zoogeographic region of the world with the only notable exceptions being New Zealand, the polar regions and a few of the more isolated oceanic islands. The only available keys to genera are those provided by Ashmead (1904) and Schmiedeknecht (1909) which deal with only 25 and 26 genera, respectively. In the nearctic region, there are six genera and over 33 species distributed throughout, with at least one species extending as far as the northern tree limit in Canada and Alaska.

The Eucharitidae are treated in this paper as a separate family which is distinct from the Pteromalidae and closely related to the Perilampidae (Graham 1969, Bouček 1978). The Eucharitidae have been separated into two subfamilies (Burks 1979), the Oraseminae which is represented in the New World by the single widespread genus *Orasema* Cameron, and the Eucharitinae which is represented in the nearctic by five genera: *Pseudometagea* Ashmead, *Kapala* Cameron, *Obeza* n. gen., *Lophyrocera* Cameron and *Pseudochalcura* Ashmead.

Almost all of the World genera Eucharitidae are endemic. A few species of the genus *Orasema* are distributed in the Ethiopian, Oriental and Australasian regions, and one species of *Kapala* is found in the Ethiopian. Three species of *Eucharomorpha* Girault have been described from the Neotropics, with the genus being more commonly reported from Australia. I have not seen any representatives of this genus in the collections of Neotropical material to verify the records. There are no taxa at the generic level or below shared with the Palaearctic. The New World genera appear to be closely related to the genera of Australasia.

Published information on the Nearctic Eucharitidae is limited mostly to sporadic distributional data and rearing records, and the only workable key to genera is by Ashmead (1904). The species of *Orasema* were dealt with by Gahan (1940), although this must be considered as only an initial treatment of a very diverse and widespread genus. The only revision of a New World genus of Eucharitinae was of *Pseudometagea* by Burks (1961).

Biology

As far as is known, the Eucharitidae include only genera which are specialized ant parasites (Wheeler and Wheeler 1937, Clausen 1941). Adult females oviposit away from the host into plant tissue, with eggs being either scattered on the leaf surface, laid into incisions on the leaf, or into developing flower buds (Clausen 1940). The number of eggs laid in a single oviposition ranges from one or two by *Orasema* to as many as ten thousand by females of *Stilbula manipurensis* Clausen (Clausen 1928, 1940). The range of plant hosts is fairly restricted and in one case, eggs were observed to be laid in association with the eggs of *Solenothrips rubrocinctus* (Giard) (Thripidae) (Clausen 1940). The eggs may remain stationary or can be dispersed on falling bud scales or even attached to the sides of wind-dispersed achenes (Clausen 1940).

Development may be immediate or the eggs may overwinter (Clausen 1940). The active first instar of the eucharitid, termed a planidium, moves by crawling or jumping and, if successful, is able to attach itself to an adult ant. It is then transported into the brood chamber of the ant nest where it relocates on an ant larva (Clausen 1940, 1941). The planidium remains attached to the ant larva as a quiescent first instar until the host pupates at which time the eucharitid consumes the host (Wheeler 1907, Clausen 1941). Eucharitids pupate and emerge within the ant nest.

Nomenclature

The nomenclature of the Eucharitidae is relatively stable for a group with 332 described species. The relatively few nomenclatural problems compared to other groups is probably due to the small number of workers who have studied the group, and the diverse and bizarre morphology which allows relatively easy separation of taxa. Most of the genera and species were described near the turn of the century by F. Walker, J.O. Westwood, W.H. Ashmead and A.A. Girault. Except for sporadic regional works, the family has been largely untouched over the past 80 years.

Eucharis Latreille (1802) was the first proposed generic name and was based on a Palaearctic species previously referred to as *Cynips adscendens* Fabricius (1787). Several genera were described after *Eucharis* and eventually combined to form the subfamily Eucharinae within the larger family Chalcididae (Ashmead 1897). Walker (1862) first recognized the group as a family and proposed the name Eucharidae. Foerster was the second author to recognize the group as a family level taxon in 1856 under the name Eucharoidae (Ashmead 1897). The family level status was not generally accepted until a more formal designation was made by Ashmead (1897) as the Eucharidae. In Dalla Torre's (1898) catalogue of species, the subfamily name Eucharidinae was used. The first usage of the name Eucharitinae appears to be by Girault (1928). Until the first catalogue of North American Hymenoptera established the family name Eucharitidae (Muesebeck *et al.* 1951), the name of the group used most often was Eucharidae or Eucharididae at either the family or subfamily level. *Eucharis* is a Greek noun for "pleasing" or "charming". The stem of the third declension noun is *Eucharito-* and is used to form the family name, Eucharitidae. The preferred name over the past thirty years has been Eucharitidae.

The first key available to the genera of Eucharitidae was Ashmead (1897) which dealt with 23 of the 42 genera now recognized. Ashmead's (1904) revised key included the genera *Pseudochalcura* and *Philomides* Haliday (= *Destefania* Dalla Torre in key). Five years later, a key was produced, in German, by Schmiedeknecht (1909) which was identical to that of Ashmead (1904) with the addition of one genus, *Stilbulaspis* Cameron. Since these world keys were produced, only a few regional keys have been provided (Ruschka 1924, Gemignani 1933, Gahan 1940, Bouček 1956, Hedqvist 1978).

I have adopted the more traditional treatment of the eucharitids as a distinct family (Graham 1969, Bouček 1978) and not as a subfamily within the Pteromalidae (Riek 1970). The exact morphological limits which define the family have not been fully resolved. However, the Eucharitidae can be generally defined by the reduced pronotum not visible

from above and not overlapping the mesoscutum medially, the falcate mandibles, the malar groove obliterated and the first tergite almost always covering the following segments. Another character, which is shared with the Chrysolampinae (Pteromalidae) and the Perilampidae, is the presence of a digitate labrum (Darling 1983). The above characters would exclude the Philomidinae which was included as a subfamily of Eucharitidae by Bouček (1978).

The Oraseminae (on a world basis) would be comprised of *Orasema* Cameron, *Losbanus* Ishii, *Psilogastrellus* Ghesquière (in part) and probably *Parasemora* Gemignani, whereas the Eucharitinae include all of the remaining genera. These subfamily concepts within the Eucharitidae are straight-forward within the Nearctic region but need to be reviewed on a world-wide basis. The Oraseminae are recognized by having a free prepectus not fused anteriorly to the pronotum, the male and female antennal flagellomeres cylindrical with an indistinct basal anellus, and the ovipositor expanded subapically and strongly ridged. The New World species of *Orasema* were revised and a key to 19 species provided by Gahan (1940). They are distributed throughout the United States and Mexico, with rare, northern records from Alberta, Manitoba, and Ontario. The ant hosts of *Orasema* have been reported as *Solenopsis* Westwood and *Pheidole* Westwood (Wheeler 1907, Wheeler and Wheeler 1937). Females of this genus oviposit into incisions made by their ovipositors in the leaf surface (Clausen 1940).

The Eucharitinae are a much more diverse group than the Oraseminae. Members of the Eucharitinae have the following characters in common: the prepectus fused anteriorly to the pronotum, the shape of the male and female antennal flagellomeres variable (cylindrical, serrate or ramose) and without a basal anellus, and the ovipositor usually long and acicular (may be laterally flattened and sword-shaped in some African genera such as *Mateucharis* Bouček and Watsam or thickened along the entire length and strongly ridged in some *Schizaspidia* Westwood). The ant hosts are known for only three of the Nearctic Eucharitinae: *Pseudometagea schwarzii* (Ashmead) from *Lasius* (Ayre 1962), *Pseudochalcura gibbosa* (Prov.) from *Camponotus* Mayr, and *Kapala floridana* (Ashmead) from *Pogonomyrmex* Mayr (Wheeler 1907). All of the known plant associations for Nearctic eucharitines are based on records of oviposition into the fruiting bodies of grasses, composites or other plants, but never into incisions in the leaf surface. The range of oviposition methods are much broader in eucharitines from other regions and the method of oviposition into leaf surface has been recorded in *Kapala terminalis* Ashmead (Clausen 1941) and *Schizaspidia foveatella* (Girault) (Ishii 1932).

The genera of Nearctic Eucharitinae can be divided into three distinct monophyletic groups. *Pseudometagea* forms one group endemic to North America with no apparent relationships to any Neotropical genera. The few species of *Kapala* which are found in the Gulf States are part of a large and diverse Neotropical element. Species of *Obeza*, *Lophyrocera* and *Pseudochalcura* are northern extensions of more diverse Neotropical genera, which form a monophyletic grouping, with *Obeza* the sister group of the other two. There are no genera shared with the Palearctic region and the closest relationships of the three groups appear to be with genera of the Australasian region.

Materials and Methods

Specimens of Eucharitidae were obtained from over 90 museums in North and South America, Europe, Japan, and Australia. The large amount of material accumulated allowed for an effective, although by no means complete, examination of the world genera of Eucharitidae and, in particular, the Neotropical species. Due to their generally large size and bizarre morphology, eucharitids tend to be accumulated in many collections where more "typical" chalcidoids would usually be ignored. This provided a fairly complete survey of the Nearctic Eucharitidae based on the holdings of both large and small collections.

Material referred to in the text was borrowed from the following institutions (curators' names appear last in parentheses): American Museum of Natural History, New York,

NY (AMNH) (M. Favreau); Academy of Natural Sciences of Philadelphia, Philadelphia, PA (ANSP) (D. Otte); University of Arizona, Tucson, AZ (ARZ) (F.G. Werner); British Museum of Natural History, London, England (BMNH) (J. Noyes); Biosystematics Research Institute, Ottawa, Ont. (BRI) (C. Yoshimoto); California Academy of Sciences, San Francisco, CA (CAS) (W. Pulawski); Carnegie Museum of Natural History, Pittsburgh PA (CMNH) (G.E. Wallace); Colorado State University, Fort Collins, CO (COR) (H.E. Evans); Cornell University, Ithaca, NY (COR) (L.L. Pechuman); Florida State Collection of Arthropods, Gainesville, FL (FLA) (H.V. Weems, Jr.); University of Georgia, Athens, GA (GEO) (C.L. Smith); University of Guelph, Guelph, Ont. (GUE) (S.A. Marshall); University of Idaho, Moscow, ID (IDA) (W.F. Barr); Iowa State University, Ames, IA (IOW) (R.E. Lewis); University of Kansas, Lawrence, KA (KAN) (G.W. Byers); Los Angeles County Museum of Natural History, Los Angeles, CA (LACM) (R.R. Snelling); Lyman Collection, McGill University, Montreal, Que. (LYM) (V.R. Vickery); Museum of Comparative Zoology, Cambridge, MA (MCZ) (A. Newton); Mississippi Entomological Museum, Mississippi State, MS (MISS) (R.L. Brown); Montana State University, Bozeman, MT (MON) (S. Rose); University of Michigan, Ann Arbor, MI (MMZ); Rutgers University, New Brunswick, NJ (RUT) (G.W. Wolfe); South West Research Station of the American Museum of Natural History, Portal, AZ (SWRS) (V. Roth); University of California, Berkeley, CA (UCB) (L.E. Caltagirone); University of California, Davis, CA (UCD) (R.O. Schuster); University of Michigan, Ann Arbor, MI (UMI) (T.E. Moore); University of Minnesota, St. Paul, MN (UMS) (P.J. Clausen); United States National Museum of Natural History, Washington, DC (USNM) (E.E. Grissell).

A detailed description of the methods of analysis, special terms and applications of the terms, and a review of the variation found in characters of the adults is given in Heraty (in press). The following methods supply only information which is of direct relevance to this paper.

Detailed measurements of various structures were based, where possible, on a representative sample of 10 males and 10 females over the geographic ranges of each species. Maximum and minimum values of each measurement are reported in an attempt to include most of the range of variation that would be encountered.

The descriptions are based on the total number of specimens examined for both previously described and newly described species. All type material was examined for all of the species dealt with unless otherwise stated. Deviations in the type material or from the material examined are discussed in the remarks section accompanying each description.

Terms used to describe adult morphology are based largely on Graham (1969) with some deviation to follow terms used by Snodgrass (1911), Bucher (1948) and Masner (1980). Mesosoma is used instead of thorax to include the propodeum or first abdominal segment as a part of the thorax (Masner 1980). The metasoma is composed of a petiole and gaster. Disc of the propodeum defines the central area of the propodeum bounded laterally by the spiracles. Postspiracular furrow refers to the longitudinal depression running from the spiracle to the coxal base between the propodeal disc and callus (or metapleuron). Genal bridge is a term used to describe the fusion or almost complete fusion of the genae (=postgenae) behind the mandibles (Figs. 69, 70). Some of the most commonly used terms are illustrated in Figures 1-5, and 12. Descriptive terms for sculptures follow Harris (1978) as closely as possible.

The symbol [?] refers to label information which could not be accurately read and [!] refers to a misspelling of a name in the literature.

Synopsis of Nearctic Eucharitinae

Pseudometagea
schwarzii group

barberi n.sp.
schwarzii (Ashmead)
bakeri Burks
hirsuta n.sp.

<i>occipitalis</i> group	<i>occipitalis</i> n.sp. <i>rugosa</i> n.sp.
<i>montana</i> group	<i>montana</i> (Ashmead) n. comb. <i>nefrens</i> n.sp.
<i>Kapala</i>	<i>floridana</i> (Ashmead) 3 spp. [unplaced]
<i>Obeza</i>	<i>floridana</i> (Ashmead) n. comb. <i>septentrionalis</i> (Brues) n. comb.
<i>Lophyrocera</i>	<i>apicalis</i> Ashmead
<i>Pseudochalcura</i>	<i>americana</i> (Howard) <i>gibbosa</i> (Prov.) <i>liburna</i> Heraty <i>sculpturata</i> Heraty

KEY TO THE GENERA OF EUCHARITIDAE OF NORTH AMERICA

1. Prepectus completely separated from pronotum and reaching tegula (Fig. 47); antenna with basal anellus (Fig. 47); body metallic; ovipositor scimitar-shaped (Fig. 48); first gastral sternite constricted basally by transverse crenulate furrow (Fig. 48) *Orasema* Cameron
- Prepectus fused with pronotum (Fig. 1); antenna without basal anellus (Fig. 5); body yellow to black, sometimes with metallic colouration on head and mesosoma; ovipositor acicular (Fig. 3); first gastral sternite smooth or striate, without median transverse furrow 2
2. Prepectus reaching tegula, sometimes distinguished from pronotum by shallow furrow (Figs. 1, 50, 52); occiput broadly concave; metepisternum distinct from propodeum (Figs. 51, 65); mesepimeron strongly, and almost completely, transversely striate (Fig. 50); axillae constricted medially (Fig. 4); male and female flagellomeres cylindrical *Pseudometagea* Ashmead
- Prepectus not reaching tegula (Figs. 24, 53) and without separating furrow; occiput flat; metepisternum indistinct; mesepimeron variously sculptured, at most weakly transverse-striate around femoral groove; axillae transverse, not constricted medially (Figs. 57, 58); male flagellum usually ramose (Figs. 26, 43) (cylindrical in *Obeza*) 3
3. Frenum produced posteriorly into two long apical spines as long as mesosoma (Fig. 24), and frenal groove absent dorsally (Fig. 57); genae widely separated behind mandibles; mesosoma greatly elevated above dorsal margin of head; spiracle recessed into dorsal margin of pronotum but not enclosed dorsally *Kapala* Cameron
- Frenum without processes or with pair of short blunt processes, frenal groove distinct (Fig. 38, 58); genae meeting behind mandibles (Figs. 69, 70), encircling reduced mouthparts; mesosoma globose; spiracle recessed into dorsal margin of pronotum and enclosed by the pronotum dorsally 4
4. Frenum rounded; propodeum without expanded processes between disc and spiracle; genae fused behind mandibles; female flagellum serrate to slightly lobate basally and male flagellum ramose basally *Pseudochalcura* Ashmead
- Frenum produced apically as two short blunt processes; propodeum with expanded processes between disc and spiracles (Fig. 38, prp); genae not completely fused behind mandibles (Figs. 69, 70); female flagellomeres lobate, and male flagellum cylindrical or with a ramus present on all flagellomeres 5
5. Body testaceous with brown to black patterns, head black or dark cyaneous (Fig. 30); male and female flagellomeres cylindrical; angle of genal bridge greater than 110° (Fig. 69) *Obeza* n. gen.

— Body and head black; female flagellomeres lobate (Fig. 37); male flagellum with a long flat ramus on each segment (Fig 43); angle of genal bridge sharp, about 90° (Fig. 70)
 *Lophyrocera* Ashmead

***Pseudometagea* Ashmead**

Pseudometagea Ashmead, 1897: 239 (in key, no species); Ashmead 1904: 267, 386; Burks 1961: 253-257 (key to species).

Type-species. *Metagea schwarzii* Ashmead, 1892: 356 [by subsequent designation].

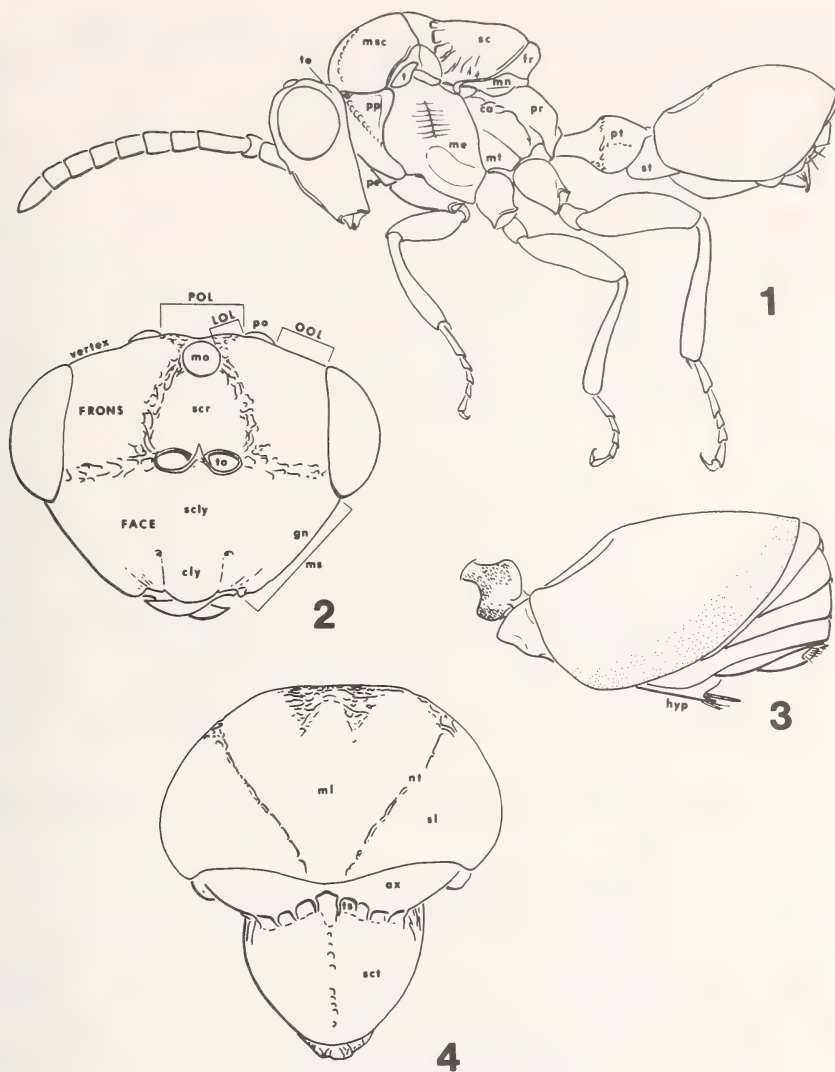
The genus *Pseudometagea* was originally described by Ashmead (1897) with *Metagea schwarzii* Ashmead being designated as the type-species (by monotypy) in Ashmead (1904). The two defining characters of the genus were the dorsally smooth mesosoma and the abruptly enlarged petiole. A second species, *Pseudometagea hillmedia* was described by Girault (1916) and later reduced to a synonym of *P. schwarzii* by Burks (1961). Burks (1961) described the genus in detail based on two species, *P. schwarzii* and *P. bakeri*. *Pseudometagea bakeri* has a rugulose mesoscutum and carinate scutellum which left only the enlarged petiole to define the genus. Burks (1961) supplied two further apomorphic characters: the depressed interocellar area and the (apparently) single metatibial spur.

The generic limits of the genus *Pseudometagea* are redefined and broadened to include two new species groups which are closely related but lack most or all of the above characters which were used to define this genus. Four species form the *schwarzii* group (*Pseudometagea*, *sensu* Ashmead and Burks) based largely on the interocellar depression (Fig. 75: 14), enlarged first sternite (:15) and expanded petiole (:17). From the Nearctic material gathered in this study, the known distributions of the previously described species are extended and two new species added based only on two isolated captures, *P. hirsuta* from California and *P. barberi* from Ontario. The *occipitalis* group is comprised of two new species, *P. rugosa* and *P. occipitalis*, which share only a few apomorphic characters (Fig. 75). The *montana* group includes *Pseudometagea montana* (Ashmead) n. comb., and a new species, *Pseudometagea nefrens*. The *montana* group is well defined on the basis of five apomorphies (Fig. 75).

There are several characters shared among the three groups, supporting their monophyly (Fig. 75). The complex is morphologically distinct from other New World genera and its closest relationships may be with some Australian genera such as *Tricoryna* Kirby or *Prometagea* Girault. It must suffice for the moment to say that *Pseudometagea* is monophyletic and does not share any close relationship with other New World genera.

The lack of a close sister group makes it difficult to determine the polarity of character states. The plesiomorphic character states shared by all of the *Pseudometagea* species groups (synapomorphies of the genus, characters 1-5) were recognized by comparing shared character states between *P. barberi* of the *schwarzii*-group, the *occipitalis*-group and the *montana*-group. I have interpreted *P. schwarzii*, *P. bakeri* and *P. hirsuta* to be the most apomorphic species within the genus since they possess the expanded petiole (18) and expanded first sternite (16), the median depression of the interocellar area (15), the bare eye (21) and a reduced number of flagellomeres in males (19). Two character states, the sculptured proepisternum (4b) and the absence of eye setae (5b), are considered as reversals within the genus and are found only in the most apotypic species of the *schwarzii*-group. The plesiomorphic state (4a, 5a) is apotypic for the genus in relation to other genera of Eucharitinae. The outer metatibial spur is greatly reduced but not absent, giving the appearance of a single metatibial spur and is a character state shared by the *schwarzii*- and *montana*-groups and *P. occipitalis*. A reduction in a character state is not considered as strong enough evidence of relationship between groups to aid in resolution of the proposed trichotomy and the character was not presented in the cladogram (Fig. 75).

Synapomorphies were not found which would determine evolutionary relationships between the three groups. Each species group could be recognized as a separate genus. This classification would be valid but yields two bitypic genera; an unnecessary splitting of taxa



FIGS. 1-4. *Pseudometagea schwarzii*: 1, habitus, ♂ ; 2, head, ♀ ; 3, metasoma (petiole + gaster), ♀ ; 4, dorsum of mesosoma, ♀ .

- | | | | | | |
|-----|------------------------|-----|--------------------------------|-----|----------------------|
| ax | - axilla | ms | - malar space | pt | - petiole |
| ca | - callus | msc | - mesoscutum | scl | - supra-clypeal area |
| cly | - clypeus | mt | - metepisternum | scr | - scrobe |
| fr | - frenum | nt | - notaulix | sct | - scutellum |
| gn | - gena | OOL | - ocular ocellar line | sl | - side-lobe |
| hyp | - hypopygium | pe | - propodeum | st | - first sternite |
| LOL | - lateral ocellar line | po | - posterior or lateral ocellus | t | - tegula |
| me | - mesepimeron | POL | - posterior ocellar line | te | - temple |
| ml | - mid-lobe | pp | - prepectus | to | - torulus |
| mn | - metanotum | pr | - propodeum | ts | - transcutal furrow |
| mo | - median ocellus | | | | |

for a small monophyletic group. To recognize the *schwarzii*-group as one genus, and the *occipitalis*-and *montana*-groups as a separate genus, based on shared plesiomorphic characters, could lead to a paraphyletic taxon if either group is more closely related to the *schwarzii*-group. The expansion of the generic limits of *Pseudometagea* to include the two new species groups appears to be the most prudent, since it recognizes the three groups appears to be the most prudent, since it recognizes the three groups as being monophyletic and leaves a workable number of species in the genus.

Generic Diagnosis. Head as broad as mesosoma, subtriangular in frontal view, 1.3 times broader than high (Fig. 2). Median ocellus anterior to lateral ocelli. Vertex rounded, without well defined occipital carina, occiput broadly rounded. Clypeus as long as wide and shorter than supraclypeal area. Mandible small, falcate; right mandible with three teeth, left mandible with two teeth (Fig. 20), apical tooth only slightly longer than width of oral fossa. Mouthparts well developed. Malar depression, if present, less than one-eighth malar space. Labrum usually 3 to 5-digitate, digits long (Fig. 20). Gena not produced posterior to mandible. Antenna without basal anellus, flagellomeres cylindrical in both sexes.

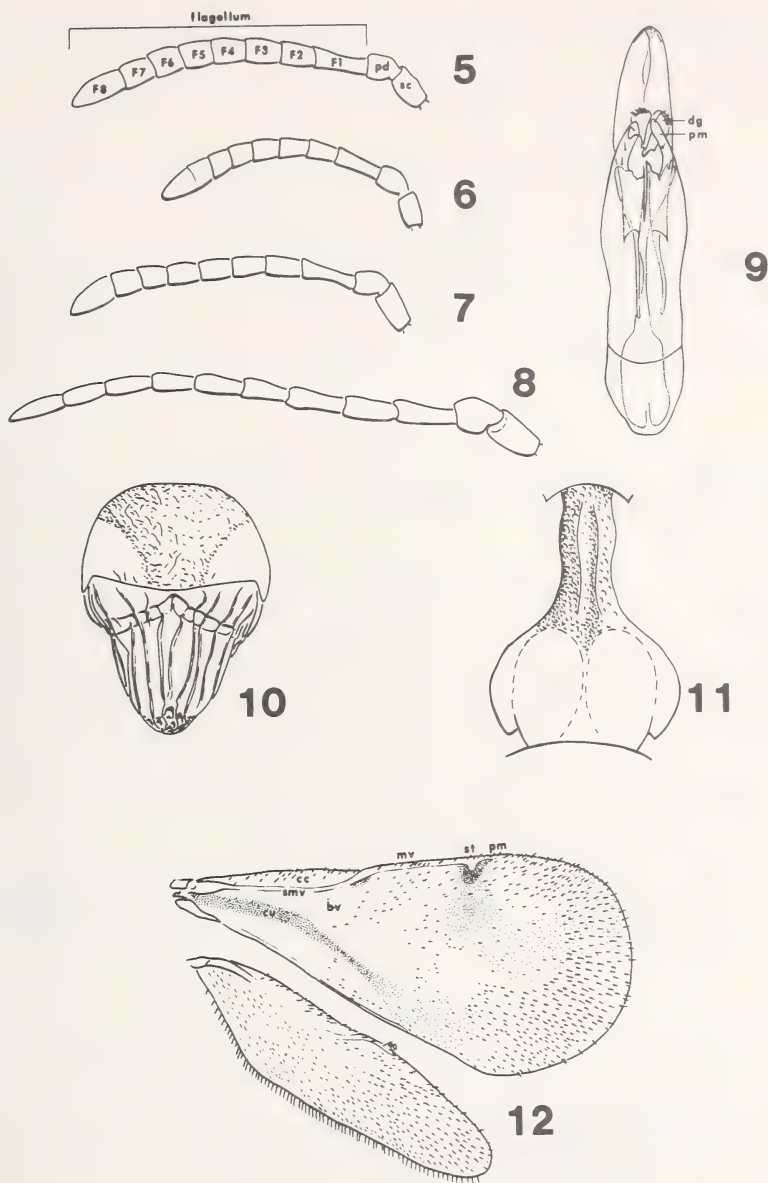
Mesosoma slightly longer than and as high as broad (Fig. 1), notaulices present or absent. Axillae fused and constricted medially, not transverse; joined to scutellum by crenulate transcubital furrow. Scutellum usually half as wide as mesoscutum; frenum produced beyond apex of scutellum, truncate or emarginate. Propodeum rounded; metepisternum distinct, usually separated from rest of propodeum by shallow furrow dorsally and posteriorly. Mesepimeron longitudinally strigate, femoral groove central, shallow (Figs. 50, 52, 65, 66). Prepectus fused to pronotum, reaching tegula, posterior and dorsal edge glabrous; spiracle inset into dorsal margin, not enclosed dorsally. Coxae large and globose; mesocoxa without lateral carina. Legs stout; metatibia with two apical spurs, outer spur shorter, sometimes reduced and indistinguishable from apical setae. Costal cell 0.4 times length of forewing; wing veins usually distinct. Hindwing broadly rounded apically (Figs. 12, 21).

Petiole elongate (Fig. 49) or globose (Figs. 50, 51). Female gaster elongate, twice as long as high, hypopygium strongly produced (Figs. 3, 49). Male gaster rounded or elongate (Fig. 1). Ovipositor acicular.

Distribution. Nearctic. Figs. 71, 72.

KEY TO THE SPECIES OF *PSEUDOMETAGEA* ASHMEAD

1. Petiole strongly expanded apically, first gastral sternite constricted medially and strongly expanded basally (Figs. 1, 3, 50, 51); callus striate, usually forming a distinct ridge posteriorly (Fig. 65) *schwarzii* group 2
- Petiole only slightly expanded medially, first gastral sternite at most with slight basal constriction (Fig. 49); callus areolate-rugose, not strongly produced or forming a ridge posteriorly (Fig. 66) 5
2. Eyes setose; male antenna 12-segmented (Fig. 8) *P. barberi* n.sp.
- Eyes bare; male antenna 10-11-segmented 3
3. Scutellum smooth (Figs. 4, 54); proepisternum glabrous ... *P. schwarzii* (Ashmead)
- Scutellum longitudinally strigate (Fig. 55); proepisternum rugulose 4
4. Dense, erect hairs over dorsum of mesosoma; femora and tibiae with dense long setae *P. hirsuta* n.sp.
- Fine, short decumbent setae on mesosoma dorsally; femora and tibiae with sparse short setae *P. bakeri* Burks
5. Dorsum of mesosoma sparsely setose; metacoxa smooth; anterior margin of hindwing bare; one or two metatibial spurs clearly visible *occipitalis* group 6
- Dorsum of mesosoma densely setose; metacoxa granulate to rugulose; fringe of setae



FIGS. 5-12. *Pseudometagea*. 5-8, antenna: 5, *P. schwarzii*, ♀, larger size scale than others; 6, *P. bakeri*, ♀; 7, *P. hirsuta*, ♀; 8, *P. barberi*, ♂. 9, *P. schwarzii*, genitalia in ventral view, ♂. 10-11, *P. barberi*, ♂: 10, dorsum of mesosoma; 11, petiole, dorsal view. 12, *P. schwarzii*, fore and hind wings, ♀.

- | | | |
|--------------------------|------------------------|------------------------|
| bv - basal vein | mv - marginal vein | sc - scape |
| cc - costal cell | pd - pedicel | smv - submarginal vein |
| cu - cubital vein | pm - postmarginal vein | st - stigmal vein |
| F1-8 - flagellomeres 1-8 | | |

- around entire margin of hindwing; one metatibial spur apparent
 *montana* group7
- 6. Midlobe of mesoscutum mostly smooth; head and eye with sparse, long setae, dorsum of mesosoma with longer erect setae; forewing with short setae dorsally
 *P. occipitalis* n.sp.
- Midlobe of mesoscutum completely rugulose; head and mesosoma dorsum with short, appressed setae, eye with short, erect setae; forewing with microtrichia dorsally
 *P. rugosa* n.sp.
- 7. Scape long, reaching median ocellus; frenum emarginate at apex (Fig. 56); mandible well developed (Fig. 20); mouthparts not unusually developed; dense setae extensive over body and head (Figs. 49, 56) *P. montana* (Ashmead)
- Scape shorter, not reaching median ocellus; frenum truncate; mandible short, peg-like; mouthparts expanded (Fig. 19); dense setae restricted to dorsum of mesosoma
 *P. nefrens* n.sp.

P. schwarzii group

Group Diagnosis. Forewing hyaline; brown-infusate below stigma and along cubital vein, faintly infusate along basal vein and around apex of wing; wing rarely completely hyaline or completely infusate.

Interocellar space with prominent longitudinal depression from median ocellus to occiput; temple posterior to eye bulging (Figs. 1, 50); postoccipital carina present or absent; postgenal carina present. Lateral margin of clypeus poorly defined. Antennal scrobe narrow, as deep as width of scape, smooth. Scape short, only slightly longer than broad, only reaching halfway to median ocellus; antenna scabridulous.

Notaulices present, sometimes reduced posteriorly. Axilla variously sculptured, usually longitudinally striate along posterior margin only. Scutellum rounded, frenum rounded or truncate. Disc of propodeum areolate-rugose; callus longitudinally striate, interstices narrow, carinae joining posteriorly to form a sharp ridge usually extending to metacoxal base; metepisternum distinct, raised, usually not separated from propodeum by broad furrow. Proepisternum variously sculptured. Coxae sculptured. Metatibia with two apical spurs, outer spur indistinguishable from apical setae.

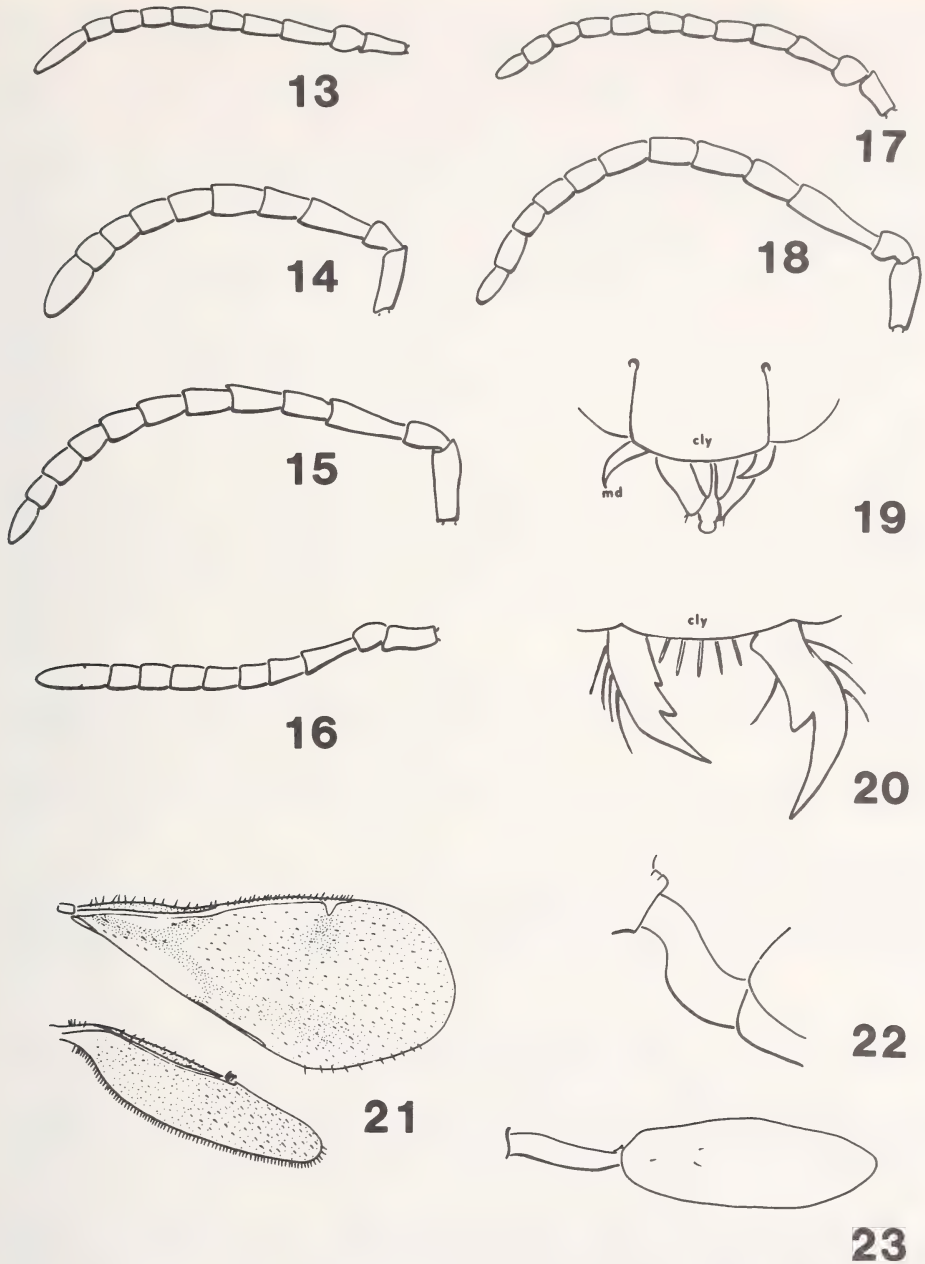
Petiole globose, appearing two-segmented, second segment formed by anterior projection of first gastral sternite (Fig. 51); petiole shorter than or equal to metacoxa in female, longer than or equal to metacoxa in male. Hypopygium of female with 6-10 long apical setae. Gaster rounded in male (Fig. 1).

Pseudometagea barberi new species

Figs. 8, 10, 11, 71

Male. Length 2.2 mm. Black; tegula, tibiae, tarsi and apices of femora dark testaceous.

Head slightly narrower than mesosoma, gena straight, temple slightly produced posterior to eye. POL 1.6 times LOL, POL 1.9 times OOL (see Fig. 2 for characters). Face not broadly rounded, slightly concave lateral to supraclypeal area, no transverse line of punctation from torulus to margin of eye; frons including scrobe, vertex, and gena laterally rugulose; weak occipital carina lateral to median depression, extending just past the lateral ocellus; occiput weakly transverse-striate; postoccipital carina absent; head including occiput dorsally covered by short erect setae; clypeus, supraclypeal area and eye with long, erect setae. Eyes separated by 1.8 times their height. Malar space equal to height of eye. Clypeus marked laterally and basally by weak lateral grooves. Mandible small. Labrum appearing 3-digitate. Antenna 12-segmented, tapered apically (Fig. 5); scape short, slightly longer than broad, reaching just over halfway to median ocellus; length of flagellum 1.6 times width of head, not thickening distally, first flagellomere 3.0 times as long as apical



FIGS. 13-23. *Pseudometagea*. 13-18, antenna: 13, *P. occipitalis*, ♀ ; 14, *P. rugosa*, ♀ ; 15, *P. montana*, ♀ ; 16, *P. nefrens*, ♀ ; 17, *P. occipitalis*, ♂ ; 18, *P. montana*, ♂ . 19-20, lower face in frontal view: 19, *P. nefrens*, ♀ ; 20, *P. montana*. 21, *P. occipitalis*, wings, ♀ . 22, *P. nefrens*, petiole in lateral view, ♀ . 23, *P. occipitalis*, male metasoma, lateral view. cly - clypeus, md -mandible.

width, following flagellomeres twice as long as broad; sensilla comprised of long and erect setae on scape, pedicel and basal flagellomere, decumbent on remaining.

Mesosoma dorsally with covering of fine erect setae; entire mid-lobe of mesoscutum rugulose, side-lobes smooth. Mesoscutum 2.4 times broader than long dorsally, notaulices indistinct (Fig. 10). Axilla shining, longitudinally striate, ridges continuing onto scutellum. Scutellum slightly longer than wide, rounded posteriorly, longitudinally striate, interstices wide, median depression lacking; frenum produced slightly beyond edge of scutellum, rounded, rugose. Disc of propodeum confused-areolate, interstices large, postspiracular furrow deep; callus with setae dorsally, not extending along ridge ventrally. Prepectus rugulose with shallow separating furrow, weakly carinate along posterior edge of furrow. Proepisternum weakly areolate. Coxae globose, finely alveolate, pro- and mesocoxae setose ventrally. Legs stout, with long inclinate setae; femora finely alveolate, tibiae and tarsi finely sculptured. Forewing twice as long as broad; both surfaces of costal cell with many long setae, dorsal and ventral surfaces of forewing disc covered by short setae, basal area with scattered setae dorsally; sparse fringe of setae around margin of wing except basal half of posterior margin; wing veins distinct; stigma large, almost twice as long as broad. Hindwing 4.0 times as long as broad, sparse fringe of hairs around entire wing margin.

Petiole 1.2 times as long as broad, more than 1.5 times longer than metacoxa, dorsal angle obtuse; anterior half narrow, cylindrical, and weakly sculptured dorsally, with dorsal longitudinal carinate groove, posterior half greatly expanded, flattened, bilobed dorsally, smooth and shining, expanded lateroventrally as lobes which extend out over the first gastral sternite (Fig. 11), broadly V-shaped ventrally to receive first gastral sternite. Gaster glabrous, as long as mesosoma.

Female. Unknown.

Type Material Examined. *Holotype* ♂, Pinery Pk., Grand Bend, Ont. [ONTARIO], 14 VII 1980, K.N. Barber. Deposited in BRI. Antennae broken at pedicel and mounted on point (by author).

Remarks. Although represented only by a single specimen, species status is justified by the possession of several unique features which place it well outside the variation encountered in the other species of *Pseudometagea*.

Distribution. Ontario. Fig. 71.

Etymology. This species is named in honour of K.N. Barber, Dept. of Environmental Biology, University of Guelph for his help in supplying me continually with both eucharitids and excellent collecting locations and also for being the first collector of this species.

***Pseudometagea schwarzii* (Ashmead)**

Figs. 1-5, 9, 12, 50, 51, 54, 59, 62, 65, 71

Metagea schwarzii Ashmead, 1892: 356.

Pseudometagea schwarzii; Ashmead 1900: 555; Ashmead 1904: 267, 386; Wheeler 1907: 12 (biology); Burks 1961: 255 (revision); Ayre 1962: 157-164 (biology).

Pseudometagea hillmedia Girault, 1916: 113.

Female. Length 2.0-2.3 mm. Brown to black; tibiae, tarsi and apices of femora testaceous. Gaster darker ventrally, occasionally all black.

Head subtriangular, gena broadly rounded (Figs. 2, 59, 62). POL 1.9-2.3 times LOL, POL 1.4-1.6 times OOL. Occiput with or without vague occipital carina lateral to median depression; face broadly rounded, transverse line of punctation from torulus to margin of eye extending dorsally around margin of scrobal cavity to anterior ocellus, rugosity sometimes more widespread; face and lateral areas of frons always smooth, dispersed-punctate with very short fine setae; posterior margin of gena rugose; occiput weakly areolate, postoccipital carina distinct (Fig. 62); eye bare. Eyes separated by 2.1-2.5 times

their height. Malar space 1.1-1.4 times height of eye. Labrum 4-digitate. Antenna 9 to 10-segmented, apical two flagellomeres sometimes fused (Fig. 5); scape short, only slightly longer than wide, weakly sculptured; flagellum slightly shorter than width of head, slightly thickened distally, first flagellomere 2.2 times as long as apical width, remaining flagellomeres subquadrate; sensilla comprised of dense, erect setae.

Dorsum of mesosoma smooth and shining, dispersed-micropunctate, completely bare (Fig. 59); rugosity of anterior vertical face of mesoscutum extending less than one third distance of mesoscutum. Mesoscutum 2.0-2.4 times broader than long dorsally, notaulices distinct, almost always complete (Figs. 4, 54). Axilla smooth, lacking carinae. Scutellum smooth, slightly longer than wide, rounded, with shallow median depression; frenum produced slightly beyond edge of scutellum, rounded, weakly crenulate dorsally, rugose laterally. Disc of propodeum areolate-rugose, interstices narrow (Fig. 65); postspiracular furrow pronounced, callus with setae dorsally, not extending ventrally along ridge; metepisternum longitudinally reticulate or foveate. Prepectus demarked from pronotum by oblique, areolate furrow with raised margins (Fig. 50), rugose to shallow-areolate. Proepisternum smooth. Coxae globose, finely alveolate to scabriculous, bare. Legs stout; femora scabriculous basally with sparse, appressed setae; metatibia and tarsi smooth, densely setose ventrally, sparse dorsally. Forewing 2.1-2.4 times as long as broad; costal cell with irregular row of long setae dorsally and ventrally; basal area bare, disc of wing covered dorsally and ventrally with dense setae or microtrichia, longer setae apically on dorsal surface; scattered setae around anterior margin of wing and restricted to apical third of posterior margin, may be present or absent; postmarginal vein 0.2 times length of marginal, stigma usually large, as long as broad, rarely long and narrow (Fig. 12). Hindwing 4.2 times as long as broad; scattered fringe of short setae along anterior margin, dense long setae along posterior margin.

Petiole 1.0-1.3 times as long as broad, 0.8-1.0 times as long as metacoaxa; globose, dorsal angle acute, bilobed dorsally; anterior half rugulose-areolate, with shallow longitudinal depression dorsally, posterior half glabrous, flattened dorsally and laterally (Fig. 51), not concave ventrally. Gaster glabrous (Fig. 3).

Male. Length 1.6-2.2 mm. Colour pattern as in female but usually darker and gaster always uniform in colour. Malar space 1.0-1.3 times height of eye. Antenna 10 to 11-segmented (Fig. 1); flagellum longer than in female, length 1.2 times head width. Petiole 1.3-1.6 times as long as wide, 1.3-1.7 times as long as metacoaxa; anterior narrow half cylindrical, longer than in female (Figs. 1, 50), equal in length to posterior expanded half, with vaguely margined dorsal longitudinal groove (as in Fig. 11); dorsal angle usually acute. Gaster short and rounded, bare; 0.7 times as long as mesosoma (Fig. 1). Genitalia large, digitus with 3-5 sensilla, paramere with 2-5 long setae (Fig. 9).

Type Material Examined. *Lectotype* of *Metagea schwarzii* Ashmead (♀) designated by Burks (1961) is "type 2140" (USNM) labelled "Washington, D.C., 30.6, *Metagea schwarzii*, ♀ Type". *Paratypes*: ♀, ♂ [?] Washington [DISTRICT OF COLUMBIA], (no. 2140 USNM); 2 ♀♀ Oakland [Maryland], June 10, 12 (no. 2140 USNM).

Holotype of *Pseudometagea hillmedia* Girault (♀) is "type 20319" labelled "♀". Collection data is "Glendale, Maryland, June 16 1916" taken from the original description. *Paratypes* are 2 specimens taken two weeks later [not seen].

Other Material Examined. 145 ♀♀ 256 ♂♂. **Alberta:** ♀ Medicine Hat, August [?] 14 1927, F.S. Carr (BRI); ♂ Scandia, July [?] 26 1956, O. Peck, swept from grass range (BRI); ♂ Oldman River, Lethbridge, June 22 1956, O. Peck (BRI). **Colorado:** ♂ Weld Co., Owl Creek, 12 mi NE Nunn, August 1977, H.E. Evans, Malaise (COL). **Delaware:** ♀ Milford, June 16 1964 (USNM); ♂ Milford, June 29 1964, swept beans (USNM). **Georgia:** 4 ♂♂ Pine Mt., 1 mi N., July 12 1957, W.R. Richards (BRI); ♂ Hiawassee, August 19 1957, L.A. Kelton (BRI). **Illinois:** ♀ Chicago, July 25, O. Bryant (MCZ). **Indiana:** ♀ Angola, June 7 1966, R. Lalonde & W. Boyle. **Iowa:** ♂ Sioux City, C.N. Ainslie (UMS); ♂ Sioux City, September 19 1919, C.N. Ainslie (USNM); ♂ South Ravine, Sioux City, August 6 1929 C.N. Ainslie, swept mixed veg (USNM); ♂ Sioux City, C.N. Ainslie, swept from alfalfa (USNM); ♀ 1 mi S Amana, June 23 1928, G.O. Hindrickson (IOW); ♀ 3 ♂♂ Ames, July

28 1950, D.L. Goleman, swept red clover (IOW); ♂ Ute, June 15 1960, W.S. Craig (USNM). **Maryland:** 2 ♀♀ 4 ♂♂ Patuxent Res. Refuge, August 31 1953, H. Owens (USNM); ♂ Howard Co., August 9 1961 (USNM); ♂ Prince George's County, Patuxent Research St., June 25 1982, M. Schauff (USNM); 13 ♀♀ 24 ♂♂ Prince George's Co., Bowie Wasteground, August 5 1978, E.E. Grissell (USNM); ♂ Fredktnw (paratype no. 2140) [not mentioned in original description]; ♀ Morgan Co., June 16 1952, red clover (USNM); ♂ Dorchester Co., nr. Lloyd's, July 10 1907, H.S. Barber (USNM). **Massachusetts:** ♂ N. Brookfield, August 18 1952, Nadel, clover (USNM); 2 ♀♀ Provincetown, June 28 1891, A.P. Morse (MCZ, USNM); 4 ♀♀ Lexington, June 23 1966, H.E. Evans (MCZ); 2 ♀♀ ♂ Holliston, August 7, 9, 13, N. Banks (MCZ); 2 ♀♀ Bedford, July 1-15 1968, H.E. Evans, Malaise (MCZ). **Michigan:** ♀ Wexford Co., June 14 1952, R.R. Dreisback (USNM); ♀ Midland Co., June 28 1958, R.&K. Dreisback (USNM); ♀ Wexford Co., June 15 1965, J.H. Shaddy, pit trap in scotch pine (MISS); ♀ Holland, August 4 1954, R.L. Fischer (MISS); ♂ Gladwin Co., June 10-16 1951, R.R. Dreisback (MISS); ♂ Gd. Ledge, June 29 1964, G.B. Noland (MISS); 3 ♂♂ Detroit, June 6 1937, G. Steyskal (MISS); ♀ 8 ♂♂ Bay Co., Consumers Power Co., Quanicassae Plant Site, 9 July 1973, R. L. Fischer (IDA, MISS); 4 ♀♀ 6 ♂♂ Midland Co., June/August, R.R. Dreisback (USNM); ♂ Tuscola Co., July 9 1950, R.R. Dreisback (USNM); ♂ Montcalm Co., June 20 1941, R.R. Dreisback (USNM); ♂ Crawford Co., June 21 1953, R.R. Dreisback (USNM); ♂ Saginaw Co., June 23 1952, R.R. Dreisback (USNM); ♂ Washtenaw Co., Ann Arbor, June 21 1936, G. Steyskal (USNM); ♂ Oakland Co., Milford, June 29 1923, T.H. Hubbell (USNM); ♂ Ag. Coll., C.F. Baker (USNM); ♂ Midland Co., June 14 1952, R.R. Dreisback (USNM); ♂ Rose Lake Wildf. Expt. Stn., Shiawassee Co., July 29 1972, D.K. Young (IDA). **Minnesota:** 7 ♀♀ 3 ♂♂ Pope Co., Glacial Lakes State Park, July 31, August 7, 14 1974, Malaise trap (MISS); ♀ Ft. Snelling, High Prairie, July 29 1925, C.E. Wickel (UMS). **Missouri:** ♀ Columbia, Boone Co., July 31 1967, F.D. Parker, Malaise (USNM). **Nebraska:** ♂ Broken Bow, August 1 1953, R.R. Dreisback (MISS); ♂ Thomas Co., Nebr. Nat'l Forest, 25 mi W Halsey, July 17 1967, H.B. Leech (CAS); 2 ♂♂ "Neb." (USNM). **New Brunswick:** ♂ Shediac, July 12 1940[?], G.S. Walley (BRI); ♂ Kouchibouguac N.P., S.J. Miller (BRI). **New Hampshire:** ♂ Franconia, A.T. Slosson (AMNH). **New Jersey:** ♂ Ocean Grove, July 19 1893 (USNM). **New York:** ♀ 3 ♂♂ Ithaca, July 5 1947, W. Mason (BRI); ♀ ♂ Campus, Ithaca, June 15 1937, P.P. Babiy (ZST); ♂ Auburn, July 1969, F.E. Kurczewski, wasp prey (USNM); ♂ Cayuga Co., Auburn, July 27 1970, R.C. Miller, prey from *Lindenius errans*[?] (Fox) (USNM); 8 ♀♀ Ulster Co., Cherrytown, 4 mi NNW Kerhonkson, June 15-39 1971, P.B. Wygodzinsky (AMNH). **North Carolina:** ♂ Smokemount, Swain Co., July 17 1941 (MCZ); ♂ Franklin, May 24 1957, W.R.M. Mason (BRI); ♂ Transylvania Co., Cedar Mtn., May 29 1978, J.B. Whitfield (UCB); 2 ♂♂ Cherokee, June 4 1979, M. Sharkey (LYM). **Ohio:** ♂ Lyons, July 7 1966, R. Lalonde & W. Boyle (LYM); ♂ Shaker Heights, June 17 1939, E.D. McDonald (USNM); ♂ Summit Co., August 4 1936, L.J. Lipovsky (KAN); ♂ Marietta, June 16 1957, W.A. Drew (MISS). **Ontario:** 6 ♀♀ 20 ♂♂ Mer Bleue, Ottawa, June 23, 26 1971 (BRI); 5 ♀♀ 3 ♂♂ Ottawa, June 20, 29 1955, O. Peck, swept from *Lotus corniculatus* (BRI); ♀ Ottawa, June 10 1951, O. Peck, swept from *Dactylis glomerata* (BRI); ♀ Ottawa, July 6 1947, O. Peck (BRI); ♀ Ottawa, July 15 1957, J.E.H. Martin (BRI); ♀ 3 ♂♂ Belleville, June 7, 21, July 25, August 3 1971, C.D. Rollo (GUE); ♀ 2 ♂♂ Belleville July 3, 15 1950, J.C. Martin (BRI); 2 ♂♂ Chatterton, July 24 1956, J.C. Martin (BRI); ♂ Chatterton, 13 mi N Belleville, June 20 1967, C.D. Dondale, meadow (BRI); ♀ ♂ Constance Bay, July 24 1973, L. Masner (BRI); ♀ 2 ♂♂ Bancroft, July 2 1954, J.C. Martin (BRI); 4 ♀♀ ♂ Braeside, July 2 1956, J.C. Martin (BRI); ♂ Brighton, July 4 1954, J.C. Martin (BRI); ♂ Crystal Beach, Madoc, July 27 1950, J.C. Martin (BRI); ♀ Maynooth, June 28 1955, J.C. Martin (BRI); 2 ♂♂ Actinolite, June 24 1950, J.C. Martin (BRI); ♂ Paris, June 24 1955, D.H. Pengelly (GUE); ♀ Grimsby, June 14 1977, W.A. Attwater (GUE); ♂ Pinery Pk., Grand Bend, July 14 1982, K.N. Barber (GUE); 2 ♂♂ Walpole Isl., July 13 1980, K.N. Barber (GUE); ♀ 2 ♂♂ Windsor, June 17 1980, K.N. Barber (GUE); 4 ♀♀ 12 ♂♂ Ojibway Prairie Res., June 17, 19 1980, Cashaback/Harvey/Beierl (GUE); 3 ♀♀ 4 ♂♂ Ojibway Pk., Windsor, June 10, July 11 1980, K.N. Barber (GUE); 2 ♂♂ Rondeau Pk., August 15 1980, K.N. Barber (GUE); 2 ♂♂ Pt. Pelee, July 7, 10 1980, K.N. Barber (GUE); ♀ ♂ Pt. Pelee, July 20, 22 1979, J.M. Heraty (GUE); 4 ♂♂ Ipperwash, July 14 1980, K.N. Barber (GUE); 36 ♀♀ 59 ♂♂ Ojibway Prairie Reserve, Windsor, June 11 1981, J.M. Heraty (GUE); ♀ Bells Corners, July 20 1958, S.M. Clark (BRI); ♀ Gananoque, August 14 1977, J.M. Cumming (GUE); ♂ Whitby, July 6 1974, G.J. Umphrey (GUE); ♀ ♂ Orangeville, June 30 1976, M.J. Sharkey (GUE); ♀ Belwood, July 16 1972, D.H. Pengelly (GUE); 2 ♂♂ Belwood, July 2 1965, C.J. Edwards (GUE); ♀ ♂ Arkell, June 23 1959, D.H. Pengelly (GUE); 2 ♂♂ Campbellville, June 10 1977, W.A. Attwater (GUE); ♀ Hills, July 11 1978, M. Lichtenberg (GUE); ♀ Port Rowley, July 3 1977, D. Levin (GUE); 4 ♀♀ 9 ♂♂ Priceville, June 26 1955, July 17 1956, July 7 1960, D.H. Pengelly (GUE); 2 ♂♂ Goderich, June 22 1977, K.N. Barber (GUE); ♀ Guelph, June 28 1979, J.E. Corrigan (GUE). **Pennsylvania:** 2 ♂♂ Wilawana, July 15 1937, R.H. Crandall (ARZ); 2 ♀♀ Pymatuning I., Crawford Co., June 27 1967, G.E. Wallace (CMNH); 4 ♀♀ 3 ♂♂ Pittsburg, June 16, 22 1940, G.E. Wallace (CMNH); ♂ Pittsburg, July (CMNH); ♀

Rochester, July 12 1952, G.E. Wallace (CMNH). **Quebec:** ♀ ♂ Lac Brule, August 7, 9 1945, O. Peck (BR1); ♀ Kazubazua, July 10 1947, O. Peck (BR1); ♀ Hodgens, July 23 1958, L.A. Kelton (BR1). **Tennessee:** 2 ♀♀ 3 ♂♂ Townsend, June 2 1979, M. Sharkey (LYM). **West Virginia:** ♀ "W. Va.", July 20 1891, A.D. Hopkins (USNM); ♂ Monongalia Co., June 11 1938, G.E. Wallace (CMNH).

Remarks. This species is unique within the genus because of the sculpture-free head and mesosoma (dorsally). The scutellum does not have the longitudinal carinae found in the other species.

Variation. Variability is extreme in the general colour, sculpturing and shape of the abdominal petiole, fusion of the apical flagellomeres, surface sculpture of the mesosoma and body size. Variation ranges from black specimens in New Brunswick to a mixture of light brown to black in Ontario and Michigan to black with metallic reflections in the western states. This variation is not limited to different geographical localities but can be found to some degree within almost every series.

The length of the wing disc setae, marginal fringe and stigmal spot are associated and show clinal variation from east to west, although only a few western specimens are available for verification. The Alberta and Colorado specimens almost completely lack a marginal fringe, the stigmal spot is very faint and the wing disc setae are very short (microtrichia). All of the eastern specimens have a prominent stigmal spot, long wing disc setae and almost always a complete marginal fringe of long setae (except posterior proximal margin). In Minnesota and Nebraska, the wing disc setae are slightly longer than the far-western specimens but shorter than the setae of the eastern material, the marginal fringe is complete except for the wing apex and the stigmal spot is distinct. More western material is needed to demonstrate this variation clearly.

Distribution. Generally northeastern and sparsely across the central prairies. Fig. 71.

Host and Biology. A summary of the biology and a description of the first-instar larva are found in Ayre (1962) and Heraty and Darling (1984). The adults prefer to oviposit into the buds and flower heads of various Compositae. The ant host is recorded as *Lasius neoniger* Emery (Ayre 1962) and *Lasius* sp. (Heraty and Darling 1984).

Pseudometagea bakeri Burks

Figs. 6, 55, 60, 71.

Pseudometagea bakeri Burks, 1961: 256.

Female. Length 2.0-2.4 mm. Brown to black; head and mesosoma with or without green metallic reflections; tibiae, tarsi and apices of femora light testaceous. Gaster darker ventrally, rarely all black.

Head slightly narrower than mesosoma, with gena slightly rounded ventrally (Fig. 55), temple slightly or strongly produced posterior to eye. POL 1.7-2.2 times LOL, POL 1.5-2.0 times OOL. Face broadly rounded; shallow transverse line of punctation from torulus to margin of eye; frons, vertex and gena rugulose; scrobe and face glabrous; occipital carina lacking, postoccipital carina present, occiput irregularly transverse-striate; face with short appressed setae, rarely without setae; eye bare. Eyes separated by 2.1-2.8 times their height. Malar space 1.3-1.6 times height of eye. Clypeus weakly margined. Labrum 4-digitate. Antenna 9 to 10-segmented; apical 2 flagellomeres usually fused (Fig. 6); scape short, slightly longer than broad, weakly sculptured; length of flagellum equal to width of head, stout, slightly thickening distally; first flagellomere narrow, twice longer than apical width, following flagellomeres longer than broad; sensilla comprised of dense, short setae.

Mesosoma with covering of very fine short appressed setae dorsally, mid-lobe of mesoscutum finely punctate, anterior vertical aspect rugulose, side-lobes weakly rugulose anteriorly and smooth posteriorly. Mesoscutum 2.1-2.6 times broader than long; notaulices poorly defined, vaguely reaching posterior margin (Fig. 55). Axilla scattered micro-

punctate, lacking carinae. Scutellum slightly longer than wide, rounded, with or without median depression, longitudinally striate, interstices narrow; frenum produced beyond edge of scutellum, truncate posteriorly, crenulate dorsally, areolate on vertical sides. Disc of propodeum areolate-rugose, interstices wide, postspiracular furrow shallow and narrow; callus ridge indistinct ventrally, with short setae dorsally, not extending ventrally along ridge; metepisternum longitudinally reticulate or alveolate, produced dorsally as a ridge separated by a deep furrow from propodeum. Prepectus without oblique furrow; reticulate to finely alveolate. Proepisternum finely alveolate. Coxae globose, finely alveolate, bare. Legs stout, femora scabriculous with sparse appressed setae; tibiae with setae sparse dorsally, dense ventrally. Forewing 2.1-2.6 times as long as broad; costal cell with irregular row of sparse short setae on dorsal and ventral surfaces; basal area bare, disc of wing covered dorsally and ventrally with microtrichia, longer apically; sparse marginal fringe of setae restricted to apical third of posterior margin; wing veins poorly defined, postmarginal vein absent, stigma small, rounded. Hindwing 3.8-4.3 times as long as broad; marginal fringe of long setae restricted to posterior margin.

Petiole 1.0-1.1 times as long as wide, 0.8-1.0 times as long as metacoxa; globose, not distinctly bilobed dorsally; anterior half areolate-rugose, strongly tapering, with shallow depression dorsally, posterior half glabrous, strongly tapered, flattened dorsally and laterally. Gaster glabrous.

Male. Length 1.9-2.2 mm. Colour as in female but usually darker, gaster always uniform in colour. Malar space 1.1-2.1 times height of eye. Antenna 11-segmented; flagellum longer than in females, 1.2 times width of head. Postspiracular furrow usually more pronounced than female. Petiole 1.4-1.8 times as long as broad; anterior half narrow, equal in length to posterior half, cylindrical, with or without longitudinal margined groove dorsally, dorsal angle usually acute. Gaster short, rounded, 0.9 times as long as mesosoma, with sparse microtrichia dorsally. Genitalia large (as in Fig. 9).

Type Material Examined. *Holotype* of *Pseudometagea bakeri* Burks (♀) is "type 65750" (USNM) labelled "Colo 1563, Coll. C.F. Baker" [=Ft. Collins, Colorado, sweeping, June 13 1895, C.F. Baker; data taken from original description] *Paratypes*: 11 ♀♀ 37 ♂♂ with information reported in the original description: collected from June 20 - August 4 1895 at Ft. Collins, Colorado; Camptons, Colorado; and in July 1920 at Centennial, Wyoming, 4 ♂♂ swept from *Carex*.

Other Material Examined. 29 ♀♀ 99 ♂♂. **Alberta:** 9 ♀♀ 18 ♂♂ Scandia, June 26, July 9, 10 1956, O. Peck, swept from grass range (BRI); 4 ♀♀ 8 ♂♂ Medicine Hat, July 16 1956, O. Peck, swept from *Agropyron cristatum* (BRI); ♂ Oldman River, Lethbridge, June 22 1956, O. Peck (BRI); 2 ♂♂ Lethbridge area, 1924-26, H.L. Semans[?] (BRI); 6 ♂♂ Stevieville, August 21 1957, A.R. & J.E. Brooks (BRI); ♀ Gilchrist Ranch, Aden, June 28 1956, O. Peck, swept from crested wheatgrass (BRI); ♀ Turin, June 28 1938, R.W. Salt, host alfalfa (BRI). **Colorado:** ♀ (1582) Chamber's Lake, July 18 1895, C.F. Baker, misc. sweeping (USNM); ♀ 12 ♂♂ (2142) Ft. Collins, June 29 1896, C.F. Baker, general collecting - mostly *Carex* (USNM); 4 ♀♀ 10 ♂♂ (2191) Ft. Collins, June 11 1896, C.F. Baker, in meadow - mostly *Carex* (USNM); ♂ Fort Collins, Baker (USNM); ♂ Colo. Spr. 6000'-7000', June 15-30 1896, H.F. Wickham (BRI); ♀ Lodore, June 23 1946, M.T. James (COL); 2 ♂♂ Lindon, June 21 1937, C.L. Johnston (KAN); ♂ Pagosa Springs 7200', June 22-24 1919 (AMNH); ♂ Mishawauka, July 11 1937, C.L. Johnston (KAN). **Iowa:** ♂ July 1893[?] (USNM). **Minnesota:** ♂ Pope Co., Glacial Lakes St. Pk., July 4 1973, Malaise (UMS). **Montana:** 3 ♀♀ 4 ♂♂ 1.5 mi S, 5 mi W Winnett, Petroleum Co., June 16 1969, May [?] 28 1970, A.G. Hamilton (USNM); ♂ Glendive, Dawson Co., June 21 1956, R.C. Froeschner (MON). **New Mexico:** ♂ Ruidoso, June 26 1940, D.E. Hardy (KAN); 3 ♀♀ 23 ♂♂ Springer, July 28 1909, C.N. Ainslie (USNM). **North Dakota:** ♂ New England, July 1918, C.N. Ainslie, swept from *Agropyron* (USNM). **Saskatchewan:** ♂ Willow Bunch, July 24 1955, C.D. Miller (BRI). **South Dakota:** ♀ 1967, sweeping wheat (USNM). **Utah:** ♂ (1650) "S.W. Utah", 1895, C. Palm (USNM); ♀ 2 ♂♂ Utah Co., G.E. Wallace (CMNH).

Remarks. This species appears to be restricted to the prairie grasslands and is the only widespread member of the *schwarzii* group which is characterized by longitudinal carinae on the scutellum. Collections have been made from two species of *Agropyron* (Gramineae) and in this preferred oviposition site it resembles the habits of *P. montana*. *Pseudometagea*

bakeri is most closely related to the Californian species *P. hirsuta* and differs largely in the length of the setae on the dorsum of the mesosoma.

Variation. There is large variation in the degree of metallic colouration on the head and mesosoma (zero to complete), body colour, sculpture, and general body size. There is also variation in the elevation of the scutellum compared to the mesoscutum. In the type series, most of the specimens from Colorado and a series of 7 males from Steveville, Alberta, the scutellum and mesoscutum are on the same longitudinal plane. As well, the specimens from Steveville are the only specimens which are metallic over the entire mesosoma. The remaining specimens, including two long series from Medicine Hat, Alberta and Scandia, Alberta, have the scutellum on a lower plane. There are specimens belonging to single series of both groups which have the features of the other. *Pseudometagea schwarzii* also has series with differences in the plane of the scutellum and mesoscutum. It is hard to say if the transcutal furrow is flexible in the adult or whether it is a result of differential development in the pupal stages.

Distribution. Central plains. Fig. 71.

Biology. Two large series of *P. bakeri* from Alberta were taken from a grass range and from crested wheatgrass, *Agropyron cristatum* (L.) (Gramineae). The type series was collected from *Carex* (Cyperaceae) in Colorado. Only a single specimen from Turin, Alberta was collected from a legume, alfalfa (*Medicago sativa* L., Fabaceae). The ant host is unknown.

Pseudometagea hirsuta new species

Figs. 7, 71.

Female. Length 2.0 mm. Light brown; tibiae and tarsi dark testaceous. Gaster darker ventrally. Strongly infusate along basal vein of forewing.

Head large, slightly broader than mesosoma, gena only slightly rounded, temple broadly and strongly produced. POL 1.7-2.1 times LOL, POL 1.6-1.8 times OOL. Face broadly rounded; weak transverse line of punctation from torulus to margin of eye; frons, vertex and gena finely rugulose, face and scrobe ventrally smooth; occipital carina lacking; postgenal carina vague; occiput weakly areolate; head covered by short appressed setae, these longer on face below toruli; eye bare. Eyes separated by 2.4 times their height. Malar space 1.3 times height of eye. Clypeal margins weakly impressed. Labrum appearing 4-digitate. Antenna 10-segmented, apical 2 flagellomeres fused, conical apically (Fig. 7); scape short, twice longer than broad, weakly sculptured; length of flagellum slightly greater than width of head, slightly thickening distally, first flagellomere 2.7 times as long as apical width, following flagellomeres longer than broad to subquadrate apically; sensilla comprised of dense, long setae.

Mesosoma with dense covering of fine inclinate setae dorsally, mesoscutum scattered-micropunctate, lightly rugose on anterior vertical face tapering to narrow faint median depression extending to posterior edge. Mesoscutum 2.1 times broader than long dorsally, notaulices distinct and reaching posterior margin. Axilla smooth and shining, lacking carinae. Scutellum as long as wide, broadly rounded, longitudinally striate, interstices narrow; frenum produced beyond edge of scutellum, truncate posteriorly, confused-crenulate dorsally, rugose laterally and ventrally. Disc of propodeum areolate, interstices large; postspiracular furrow shallow; callus ridge weak ventrally, setae of callus continuing along ridge to base of metacoxa; metepisternum finely alveolate. Prepectus with shallow oblique furrow, rugulose to areolate. Proepisternum finely alveolate. Coxae globose, scabriculous, pro- and metacoxa setose ventrally. Legs stout, femora scabriculous with long appressed setae; tibiae and tarsi with weak sculpturing and long inclinate setae. Forewing 2.2-2.3 times as long as broad; costal cell with sparse long setae on dorsal and ventral surfaces, basal area bare except scattered setae dorsally along cubital vein; disc of wing covered dorsally and ventrally by dense setae, sparse fringe of short setae around margin of wing except basal half of posterior margin; wing veins distinct, postmarginal

vein short, less than width of stigma; stigma large, as broad as long. Hindwing 4.0 times as long as broad; marginal fringe of short setae restricted to posterior margin.

Petiole 0.9-1.0 times as long as broad, 0.9-1.0 times as long as metacoxa, globose, not distinctly bilobed dorsally; anterior half areolate-rugose, tapering; posterior half glabrous, strongly tapered, flattened dorsally and laterally. Gaster elongate, 1.7 times as long as high, glabrous.

Male. Length 2.3 mm. Colour pattern as in female but darker, gaster uniform in colour. Head as broad as mesosoma; narrow glabrous furrow along OOL, rugulose sculpture more extensive around face, postgenal carina distinct. Malar space 1.2 times height of eye. Antenna 11-segmented; flagellum longer than in female, 1.5 times head width. Petiole 1.5 times as long as metacoxa; anterior half narrow, cylindrical, lacking dorsal carinae, shorter than expanded posterior half; dorsal angle of posterior half not acute, glabrous, side-lobes slightly expanded. Gaster short, rounded, 0.9 times as long as mesosoma, sparse appressed microtrichia dorsally.

Type Material Examined. *Holotype* ♀, *Allotype* ♂, *Paratype* ♀, Oroville, Cal. [CALIFORNIA], VII.23.1926, H.H. Kiefer Collector. Deposited in CAS.

Remarks. Represented by a single series from California, this species is closely related to *P. bakeri* and is separated most easily by the presence of dense, erect hairs over the dorsum, and dense long setae covering the femora and tibiae.

Distribution. California. Fig. 71.

P. occipitalis group

Group Diagnosis. Forewing infuscate except basal and costal cell, and below marginal vein, darker along cubital and medial veins. Interocellar space without depression; temple small, hardly produced past posterior margin of eye; postoccipital carina lacking, postgenal carina present (Fig. 66), eye setose. Lateral margin of clypeus deeply impressed (Fig. 61). Antennal scrobe shallow, sculpture continuous with frons. Scape more than twice as long as broad, reaching just over halfway to median ocellus. Antenna scabriculous, scape weakly sculptured.

Notaulices of mesosoma reaching posterior margin. Axilla smooth, longitudinally striate (Fig. 66). Scutellum rounded, frenum truncate. Disc of propodeum areolate; callus areolate, not forming a distinct ridge posteriorly; metepisternum distinct, separated from propodeum by broad furrow. Proepisternum glabrous. Coxae smooth and shining with sparse lateral setae. Outer metatibial spur either distinct and half as long as inner, or reduced and indistinguishable from apical setae.

Petiole 2-3 times as long as broad, only slightly expanded medially, 2.0-3.0 times longer than hind coxa in female, flattened dorsally with erect setae laterally. First sternite of gaster not constricted basally. Hypopygium of female with 6-10 long apical setae. Male gaster elongate (Fig. 23).

Pseudometagea occipitalis new species

Figs. 13, 17, 21, 23, 61, 66, 72.

Female. Length 1.8-2.2 mm. Dark brown to black; head and scutellum with weak blue-green metallic reflections; antenna, coxae and femora brown; tibiae, tarsi and apices of femora testaceous. Gaster darker ventrally.

Head subtriangular, gena not broadly rounded (Fig. 61). POL 2.1-2.2 times LOL, POL 1.4-1.5 times OOL. Frons, scrobe, vertex and occiput rugulose; gena weak or strong-rugulose; face including clypeal region smooth; face and eye covered by sparse, long, erect setae. Eyes separated by twice their height. Malar space 0.9-1.0 times height of eye, malar depression less than one-eighth of malar space or absent. Mandibles as in Fig. 20. Labrum 3 to 4-digitate. Antenna 10 to 11-segmented, apical two flagellomeres partially or completely fused, conical apically (Fig. 13); scape twice as long as broad, flagellum

slightly longer than width of head, stout, not thickening distad, first flagellomere 2.6 times as long as apical width, following flagellomeres slightly longer than broad to quadrate distally; sensilla comprised of sparse, long, decumbent setae.

Mesosoma with covering of erect setae dorsally. Mesoscutum 1.8-2.1 times broader than long, smooth and shining, anterior vertical aspect weakly areolate-rugose, notaulices distinct and weakly reaching posterior margin. Scutellum slightly longer than wide, with weak median depression, rounded posteriorly, longitudinally strigate, interstices narrow; frenum slightly produced beyond edge of scutellum, rugose. Disc of propodeum rounded, areolate-rugose; postspiracular furrow indistinct (Fig. 66); callus with several long erect hairs; metepisternum weakly alveolate, demarked dorsally by sharp, deep furrow. Proepisternum glabrous. Prepectus rugulose. Legs slender, femora smooth and shining with sparse, long, semi-erect setae; tibiae and tarsi with dense, long, decumbent setae. Forewing 2.1-2.3 times as long as broad; both surfaces of costal cell with sparse fine setae, basal area below submarginal vein with scattered setae on both sides, disc of wing covered dorsally by short setae and ventrally by microtrichia, sparse marginal fringe of setae restricted to basal two-thirds of anterior margin and apical third of posterior margin; wing veins distinct, postmarginal vein vague, 0.2 times length of marginal; stigma large, rounded (Fig. 21). Hindwing 3.8-4.3 times as long as broad; except for few short setae, marginal fringe restricted to posterior margin.

Petiole 2.5-2.8 times as long as broad, 1.3-1.5 times as long as metacoxa, slightly expanded medially, with few fine longitudinal carinae laterally, glabrous. Gaster glabrous.

Male. Length 1.9-2.3 mm. Darker brown than female with blue metallic reflections more extensive on head and dorsum of mesosoma. Antenna 12-segmented (Fig. 17); flagellum longer than in females, 1.4 times width of head. Median depression of scutellum and postspiracular furrow more prominent than in female. Petiole 3.2-3.6 times as long as broad, 2.6-2.8 times as long as metacoxa, cylindrical, glabrous, without lateral carinae, two parallel basal carinae dorsally. Gaster elongate, 2.6-2.8 times as long as wide with few dorsal microtrichia (Fig. 23).

Type Material Examined. *Holotype* ♀, 11 mi. e Libby, Lincoln Co., Mont. [MONTANA], July 20, 1955, R.C. Froeschner. Deposited in USNM. *Paratypes*: 7 ♀♀ 3 ♂♂ **Alberta**: ♂ Elkwater Lake, July 19 1956, O. Peck (BRI). **Arizona**: ♂ Eagar, Ranger Station, June 25 1957, G. Butler & F. Werner (ARZ). **British Columbia**: ♀ Elko, E. Kootenay, July 9 1949, H.B. Leech (CAS). **Colorado**: ♂ Dolores Co., Cottonwood Spring, 21 mi NE Dolores, Montezuma Co., 7800', July 23 1976, N.L. Hernan (AMNH). **Montana**: 6 ♀♀, same data as holotype (4 ♀♀ MON, 2 ♂♂ USNM).

Remarks. This species differs from *P. rugosa* in the restricted sculpture on the mesoscutum, large erect setae on the dorsum and head, and only faint metallic reflections dorsally.

Included in this species is a single specimen from Arizona (♀ S.W.R.S., Cochise Co. 5400', 5 mi W Portal, June 30 1970 (SWRS) [lacks petiole and abdomen]) although it may represent a different species. The lack of a metasoma yields the specimen unsuitable for accurate placement. Many characters are shared with the type material of which the most notable are the long erect setae on the eye, reduced metatibial spur and restricted metallic colouration. The differences from the type material (which have little morphological variation over the range) are as follows: setae of face short and appressed; first flagellomere 3.0 times as long as apical width, not enlarged from base to apex; dorsum of mesosoma with short appressed setae, weakly rugulose over entire mid-lobe of mesoscutum; scutellum faintly longitudinally striate, more reticulate in sculpture; metepisternum with broad shallow furrow; basal cell of forewing with sparse short setae, costal cell setae short.

Distribution. Central North America. Fig. 72.

Pseudometagea rugosa new species

Figs. 14, 72.

Female. Length 2.5-2.9 mm. Head and mesosoma with dark metallic green reflections; antenna, coxae and femora dark brown; tibiae, tarsi and apices of femora light testaceous. Gaster dark brown, with or without faint green tinge above.

Head slightly transverse, 1.5 times wider than long, gena not broadly rounded. POL 2.2-2.9 times LOL, POL 1.5-1.6 times OOL. Frons, scrobe, vertex and face lateral to clypeal area weakly rugulose; clypeus and supra-clypeal area smooth and shining; occiput with fine, transverse striae; face covered by sparse, very short appressed setae, frons essentially bare, eye with sparse, short, erect setae. Eyes separated by 2.1-2.2 times their height. Malar space 1.0-1.2 times height of eye, malar depression shallow but broadly impressed. Mandibles large, basal teeth of right mandible well developed. Labrum 4-digitate. Antenna 11-segmented, rounded apically (Fig. 14); scape 3.0 times as long as broad; flagellum 1.1 times as long as width of head, stout, slightly thickening apically, first flagellomere 2.7 times as long as apical width, following flagellomeres longer than broad; sensilla comprised of dense, short setae.

Mesosoma with covering of short appressed setae dorsally, dense on mesoscutum, sparse over scutellum. Mesoscutum 2.0-2.1 times broader than long, mid-lobe of mesoscutum weakly rugulose over entire surface, side-lobe smooth and shining, notaulices faint but reaching posterior margin. Scutellum as long as wide, rounded posteriorly, with shallow median depression, weakly rugulose; frenum produced slightly beyond apical edge of scutellum, rugulose. Disc of propodeum rounded, areolate; postspiracular furrow broad and shallow; callus with dense setae continuing as a row to base of metacoxa; metepisternum rugose, demarked dorsally by strong furrow. Proepisternum glabrous. Prepectus rugulose. Legs slender, femora and tibiae smooth and shining with erect setae, tarsi dense setose. Forewing 2.2-2.4 times as long as broad; costal cell with sparse microtrichia dorsally and ventrally; basal area with very few setae, disc of wing covered by microtrichia ventrally, bare dorsally, posterior margin with fringe of sparse setae apically; wing veins distinct; postmarginal vein present, 0.3 times marginal; stigma small, elongate. Hindwing 3.9-4.3 times as long as broad, marginal fringe restricted to posterior margin.

Petiole 3.0 times as long as broad, 1.5-1.8 times as long as metacoxa, slightly expanded medially and ventrally, with fine longitudinal carinae, long erect setae basolaterally and dense basoventrally. Gaster smooth, few microtrichia basally on first tergite.

Male. Length 2.8 mm. Colour as in female but darker. Rugulose sculpture more extensive than in female. Antenna 12-segmented, flagellum longer than in female, twice width of head. Petiole 5.3 times as long as broad, 2.4 times as long as metacoxa, cylindrical, and dorsally flattened with pair of fine dorsolateral longitudinal carinae. Gaster elongate, 3.0 times as long as high, 1.1 times as long as mesosoma, with sparse appressed setae dorsally.

Type Material Examined. *Holotype* ♀, *Allotype* ♂, *Paratype* ♀, MEX. [MEXICO], Dgo. [Durango], 9000', El Salto, 10 mi. W., 7 June 1964, W.R.M. Mason. Deposited in BRI.

Remarks. This is a more robust species than *P. occipitalis*, which has extensive metallic colouration over the entire body and a completely rugulose mesoscutum.

Distribution. Mexico. Fig. 72.

P. montana group

Group Diagnosis. Forewing hyaline or infusate, with faint darker infuscation along cubital vein.

Interocellar space with weak median depression, postgenal carina absent, eye setose. Lateral margins of clypeus faintly impressed. Antennal scrobe shallow, smooth and shining. Scape longer than broad, reaching median ocellus or almost so. Antenna scabricu-

lous, scape weakly sculptured.

Notaulices of mesosoma weak. Axilla weakly sculptured, lacking carinae. Scutellum elongate, frenum emarginate or rounded. Disc of propodeum areolate; callus striate to rugulose, not forming a distinct ridge posteriorly; metepisternum distinct, separated from propodeum by deep or shallow furrow. Proepisternum glabrous. Coxae weakly sculptured. Outer metatibial super indistinct from apical setae. Stigma of forewing vague or absent.

Petiole 2-3 times as long as broad, only slightly expanded medially and slightly flattened dorsoventrally, 1.2-1.4 times longer than metacoxa in both sexes. First sternite of gaster with or without weak basal constriction (Fig. 46). Hypopygium of female with 15-20 long apical setae. Male gaster rounded.

***Pseudometagea montana* (Ashmead) new combination**

Figs. 15, 18, 20, 49, 52, 56, 72.

Stibula [?] *montana* Ashmead, 1890: 24.

Stilbula montana; Ashmead 1892: 356.

Female. Length 2.0-2.6 mm. Brown to black; tibiae, tarsi and apices of femora testaceous. Gaster brown ventrally in lighter specimens. Wings infusate, darker along cubital vein.

Head subtriangular, gena rounded, slightly bulging lateral to mandibles. POL 1.9-2.5 times LOL, POL 1.5-1.8 times OOL. Frons and vertex granulate, face and scrobe smooth and shining, occiput transversely aciculate; head covered by dense appressed setae except in scrobe, occiput and a narrow line along the OOL; eye densely setose. Eyes separated by 1.9-2.1 times their height. Malar space 0.9-1.2 times height of eye, malar depression absent. Supraclypeal area only slightly raised above level of face. Mandibles as in Fig. 20. Labrum 4 to 5-digitate. Antenna 11 to 12-segmented (Fig. 15), apical flagellomeres separated or partially fused; scape 4.0 times as long as broad, reaching median ocellus; flagellum longer than width of head, stout, not thickening distally, first flagellomere 3.0 times as long as apical width, equal in length to scape, as long as two following flagellomeres combined, following flagellomeres longer than wide and becoming quadrate apically; sensilla comprised of dense long setae.

Mesosoma with covering of dense appressed setae (Figs. 52, 56), except vertical face of mesoscutum, pronotum, proepisternum and propodeal disc bare; sculpture granulate. Mesoscutum 1.7-2.0 times broader than long, notaulices absent. Axilla smooth to lightly granulate, transcutal furrow narrow. Scutellum longer than wide, tapering apically, with median longitudinal depression, finely and longitudinally strigate (Fig. 56); frenum produced beyond edge of scutellum, strongly emarginate apically, scabriculous. Disc of propodeum areolate-rugose; postspiracular furrow shallow; callus lightly longitudinally strigate, with dense erect setae; metepisternum longitudinally reticulate or alveolate, separated dorsally by shallow furrow. Prepectus scabriculous. Coxae large, subglobose, sculpture granulate, densely pubescent. Legs stout, sculpture granulate, densely appressed-setose. Forewing 2.3-2.5 times as long as broad; entire wing surface covered by dense setae dorsally and ventrally, fringe of long setae along anterior wing margin, around apex and posterior apical third; wing veins poorly defined, postmarginal vein present, 0.3 times as long as marginal, stigma oblong or absent. Hindwing 4.2-5.0 times as long as broad, fringe of hairs around entire wing margin.

Petiole 2.3-2.8 times as long as broad, with shallow dorsal depression, cylindrical, smooth and shining with sparse lateral fringe of short setae. Gaster elongate, 1.6 times as long as high (Fig. 49), smooth and shining; covered by appressed setae, tergites bare apically; first gastral sternite slightly constricted basally, basal constricted area glabrous.

Male. Length 2.1-2.5 mm. Colour as in female, gaster darker, uniform in colour. Antenna 12-segmented (Fig. 18). Mesosoma slightly more elongate than in female. Petiole and gaster as in female [no dimorphism].

Type Material Examined. *Lectotype* of *Stilbula montana* Ashmead (♀) is "type 2131" (USNM) labelled "West Cliff, Col., Type". *Paralectotype* ♀ with the same data.

Other Material Examined. 117 ♀♀ 4 ♂♂. **Alberta:** 7 ♀ Calgary, July 1980, R.B. Madge (BMNH, GUE); 8 ♀♀ Red Deer, June 25 1957, Brookes & MacNay (BRI); 2 ♀♀ Devon, July 11 1978, R. Roughley (GUE). **Arizona:** 8 ♀♀ Marshall Gulch Sta., Catalina Mts., August 1959, F. Werner, ovip. in green seeds of *Koeleria cristata* (USNM); ♀ Pima Co., Ben Wallow, Santa Catalina Mts., 8200', July 25, 1965, R & J Matthews (MISS); 6 ♀♀ Sta. Rita Mts., Madera Canyon For., August 11 1977, L. Masner (BRI); 23 ♀♀ Box Canyon, 7000', ca. 2-3 mi W Ramsay Cyn bird sanctuary, Huachuca Mtns, August 14 1984, J.M. Heraty, ovipositing in *Panicum hallii* Vasey and *Dactylis glomerata* L. (Gramineae) (GUE). **Colorado:** ♀ Teller Co., Florissant, Petrified Forest Area, 2530m, August 11 1973, P.H. Arnaud, Jr (CAS); ♀ Summit Col., Ouray, July 11 1919 (AMNH); ♀ Saguache, July 4 1938, M.T. James & U. Lanhem (COL); ♀ Mt. Vernon Cn., nr. Golden 7200', July 31 1961, W.R.M. Mason (BRI), 2 ♀♀ S base Blue Mtn., 8426', nr. Florissant, Teller Co., August 1 1966, T. Emmel & M. Fosdick (LACM); 3 ♀♀ Cimarron Canyon, 10-12 mi below Eagle's Nest, August 4 1950 (WAS). **Michigan:** ♀ Menominee Co., July 31 1937, R.R. Dreisback (MISS); 2 ♀♀ Christmas, Alger Co., July 25 1971, D.D. Wilder (MISS). **Minnesota:** ? Olmstead Co., July 18 1906, C.N. Ainslie, from timothy (USNM); ♀ Aitkin Co., August 7 1973, D.F. Raw (UMS); ♀ Lincoln Co., August 14 1936, H.R. Dodge (UMS); 5 ♀♀ Itasca Park, July 12, August 5 1938, K.G. Kobes / H.E. Milliron (UMS); ♀ Lake Itasca, June [?] 1911 (UMS). **Montana:** ♀ nr. Missouri River, Richland Co., July 15 1957, R.C. Froeschner (MON). **New Brunswick:** ♀ St. Andrews, August 9 1957, G.E. Shewell (BRI); 13 ♀♀ ♂ Kouchibouguac N.P. August 3-5, 15, 20 1977, S.J. Miller (BRI). **New Mexico:** ♀ Ruidoso, Lincoln Co., July 2 1961, G.C. Eickwort (MISS); 16 ♀♀ ♂ Karr Cyn., 8000', Lincoln Nat. For., July 30 1977, L. Masner (BRI). **North Dakota:** ♂ Drayton, July 9 1935, D.G. Denning (UMS). **Nova Scotia:** 13 ♀♀ ♂ Lockport, July 20, 21, 31, August 1, 1958, J.R. Vockeroth (BRI); ♀ Truro, July 31 1913 (USNM); ♀ Pleasant Bay, August 10 1961, G.S. Walley (BRI); ♀ Lawrencetown, Halifax Co., July 19-20 1967, D.M. Wood (BRI). **Ontario:** ♀ Ottawa, July 7 1943, O. Peck (BRI); ♀ Prescott, July 20 1977, K.N. Barber (GUE); ♀ Ottawa, September 19 1970, A. Sauve, swept from brome grass (BRI); ♀ Ottawa, July 7 1943, O. Peck (BRI); ♀ Ottawa, August 25 1960, O. Peck (BRI); ♀ Rainy River, July 14 1960, S.M. Clark (BRI); ♀ Elora, August 16 1976, E.A. Innes (GUE); 12 ♀♀ Johnstown, August 3-4 1980, K.N. Barber (GUE); 78 ♀♀ Johnstown, July 24 1982, J.M. Heraty (GUE). **Oregon:** ♀ Sand Lake, Tillamook Co., July 7 1962, G.C. Eickwort (MISS). **Prince Edward Island:** 2 ♀♀ Red Point, August 10, 1963, R.L. Randall (LYM); 2 ♀♀ Dalvay House, Can. Nat. Park, August 17 1940, G.S. Walley (BRI). **Quebec:** ♀ Cascapedia, August 3 1954, J.E.H. Martin (BRI); ♀ Montreal, August 19 1925, L. Daviault (BRI). **Saskatchewan:** 4 ♀♀ 50 mi E Regina, June 11 1980, S.A. Marshall (GUE); 3 ♀♀ 2 mi E Gull Lake, July 12 1980, S.A. Marshall (GUE); ♀ Wood Mountain, August 5 1955, C.D. Miller (BRI). **Wyoming:** ♀ Tie Siding, August 9 1950, R.R. Dreisback (USNM); ♀ Summit, Albany Co., 8500', August 10 1950, R.R. Dreisback (USNM).

Remarks: This species is distinguished from *P. nefrens* by the presence of developed mandibles and extensive pubescence over the entire body. *Pseudometagea montana* and *P. nefrens* share the dorsal pubescence, rugulose metacoxa and reduction of tibial spurs.

Distribution. Lower Boreal and extending along the foothills of the central states. Fig. 72.

Biology. Details of the egg-laying habits on *Poa pratensis* (Gramineae) and *Agropyron repens* (Gramineae) are given in Heraty and Darling (1984). A further oviposition record was made on the green seeds of *Koeleria cristata* (Gramineae) and collection associations have been made with timothy and brome grass, both Gramineae. Adult females collected in the Huachuca Mountains (Ramsay Canyon), Arizona, were observed ovipositing into the seed heads of *Panicum hallii* and *Dactylis glomerata*, both Gramineae, in a forest clearing at an elevation of 2000m. Dissections of some seed heads revealed similar egg clusters and locations to those previously described in Ontario (Heraty and Darling 1984). Observations at Johnstown, Ontario, showed the females to be highly selective of oviposition sites and restricted to a small area where the two previously mentioned species of *Poa* and *Agropyron* were found, even though other species of Gramineae were abundant in the area. Females would not oviposit on a bouquet of various Compositae in the lab. An unverifiable exception to this was discovered in a photographic slide [in the author's collection] provided by an amateur photographer. This slide, taken in Manitoba, shows a female of *P. montana* ovipositing into a composite flower head.

Males of *P. montana* are rare. At Johnstown, Ontario, numerous females were collected but no males were ever recovered; either mating takes place at a location away from the oviposition sites or this could be a thelytokous species.

Pseudometagea nefrens new species

Figs. 16, 19, 22, 72.

Female. Length 1.9-2.1 mm. Dark brown to black; head and mesosoma with faint blue metallic colouration; femora and apical flagellomeres of antenna brown; tibiae, tarsi and apex of femora testaceous. Gaster darker ventrally and apically. Forewing hyaline, sometimes infuscate along base of cubital vein.

Head subtriangular, gena not broadly rounded. POL 1.9-2.4 times LOL, POL 1.4-1.8 times OOL. Frons, vertex, and occiput rugulose; face and scrobe smooth; head except occiput covered by short appressed setae; eye with erect setae. Eyes separated by 2.1-2.7 times their height. Malar space 1.2-1.6 times height of eye, malar depression absent. Supraclypeal area bulging. Mandible small, peg like, acutely pointed at tip, each a single tooth (Fig. 19). Mouthparts enlarged. Labrum not visible, possibly absent or greatly reduced. Antenna 11-segmented (Fig. 16); scape 2.5 times as long as broad, almost reaching median ocellus; flagellum 1.5 times as long as width of head, stout, only slightly narrower at base than pedicel, not thickening distad, first flagellomere 2.8 times as long as apical width, as long as two following flagellomeres, following flagellomeres only slightly longer than broad to quadrate distally; sensilla comprised of dense short setae.

Dorsum of mesosoma and prepectus with silvery covering of fine appressed setae, frenum and callus with short erect setae, mesosoma otherwise bare. Mesoscutum 1.9-2.2 times broader than long dorsally, mid-lobe of mesoscutum shining and weakly granulate, anterior vertical aspect finely rugulose, notaulices visible only as weak depressions. Axilla smooth or weakly sculptured, transcutal furrow narrow. Scutellum slightly longer than wide, rounded posteriorly, without median depression, strongly granulate with barely visible fine longitudinal striae; frenum produced beyond edge of scutellum, rounded posteriorly, scabriculous, not emarginate. Disc of propodeum rounded, areolate; postspiracular furrow shallow; callus striate to rugulose, with several erect hairs; metepisternum obliquely reticulate, separated dorsally by deep furrow. Prepectus sculpture granulate. Coxae globose, granulate to rugulose basally, setae dense ventrally. Legs stout, sculpture granulate, with dense appressed setae. Forewing 2.3-2.6 times as long as broad; both surfaces of costal cell with sparse long setae; basal area bare dorsally, completely bare below cubital vein; disc of wing with dense short setae dorsally and ventrally, dense fringe of short setae around entire wing margin except basal third of posterior margin; wing veins faint, stigma absent. Hindwing 4.2-5.3 times as long as broad, fringe of hairs around entire wing margin.

Petiole 2.6-2.9 times as long as broad, with shallow longitudinal depression dorsally, curved ventrally in lateral view (Fig. 22), smooth and shining with sparse lateral fringe of short setae. Gaster elongate, twice as long as high, few scattered microtrichia dorsally, first gastral sternite not constricted basally, first sternite bare.

Male. Length 1.8-2.0 mm. Colour as in female but usually darker, metallic colouration widespread. Antenna 12-segmented. Petiole 3.4-3.8 times as long as broad, 1.4-1.5 times longer than metacoxa, cylindrical. Gaster short, rounded.

Type Material Examined. *Holotype* ♀, Medicine Hat, 14-VII-56, Alta. [ALBERTA], O. Peck Deposited in BRI. *Paratypes*: 8 ♀♀ 2 ♂♂. **Alberta**: ♀ Gilchrist Ranch, Aden, June 28 1956, O. Peck (BRI). **Idaho**: ♀ Butte Co., 6 mi S Howe, June 29 1982, M. Stafford (IDA); ♀ 6 mi S. Howe, Butte Co., July 7 1981, M. Stafford (IDA). **Michigan**: ♀ Clare Co., July 8 1950, R.R. Dreisback (USNM). **Minnesota**: ♀ Marshall Co., June 18 1936, D.G. Denning (UMS); ♂ Lancaster, June 25 1937, D.G. Denning (UMS). **Montana**: 2 ♀♀ 3 mi NW Winnett, Petroleum Co., July 16 1969, A.G. Hamilton (USNM). **Pennsylvania**: ♀ ? ♂ (Pr 2045, C.F. Baker) Philadelphia, July 27 1896, C. Liebeck

(USNM) [This is the only record of an eastern specimen with the locality taken from Baker's notes and based on the numbered specimen label. The locality is not considered as valid until more material can verify the information].

Remarks. This species is easily recognized by the reduced mandibles and enlarged mouthparts. Its distribution is generally sympatric with, but less extensive than *P. montana*, although they have not been collected together.

Distribution. Lower Boreal from the Great Lakes to Rockies. Fig. 72.

Kapala Cameron

Kapala Cameron, 1884: 102.

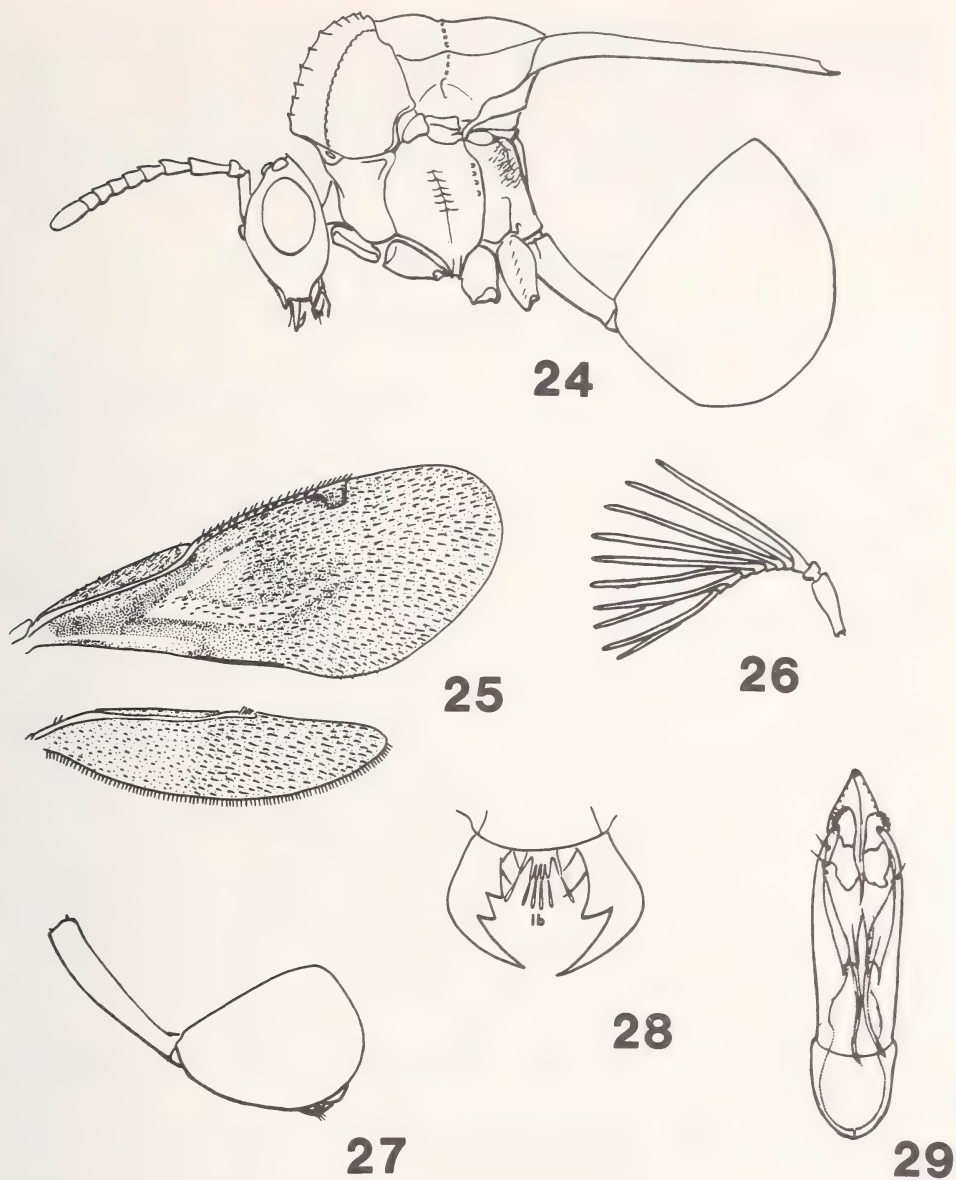
Type-species. *Eucharis furcata* Fabricius, 1804: 158 [type by original designation].

The taxonomic status of the species in this genus is uncertain. None of the types have been adequately described and at present there is no way of distinguishing species other than a few of the more distinctive forms. Previously, the *Kapala* from Texas have been referred to as *Kapala furcata* (Fabr.). I have examined the type of *K. furcata* and have found it to be a species which has been rarely collected and probably is restricted to Brazil. In North America, three "apparent" species other than *K. floridana* are found in Arizona (BRI), Texas (AMNH, KAN, TEX, USNM) and the southern tip of Florida (FLA), respectively. The availability and distinctiveness of the *K. floridana* type make it the only Nearctic species which can be identified with any certainty. A revision of the entire genus will be needed before the unidentified species can be correctly placed.

Generic Diagnosis. Head subtriangular, as broad as mesosoma. Median ocellus only slightly anterior to posterior ocelli; occipital carina strong medially, temple behind eye narrow; occiput vertical, flat. Antennal scrobe narrow, as deep as width of scape, broadly rounded laterally. Genae only slightly extended behind base of mandibles, not encircling mouthparts. Clypeus as long as wide, slightly shorter than supraclayal area; base of clypeus without distinct groove, laterally with fine groove. Mandible large, falcate, apical tooth longer than width of clypeus. Mouthparts well developed. Scape about 5.0 times longer than broad, not reaching median ocellus; antenna without basal anellus; apical two flagellomeres fused, rounded apically; flagellomeres cylindrical to weakly serrate in female, each with a long slender ramus in male.

Mesosoma robust, usually greatly elevated above dorsal margin of head; sculpture transversely carinate on mesoscutum, strongest on mid-lobe, weakening ventrolaterally on side-lobe; longitudinally carinate on axillae, scutellum and frenal spines; notaulices reaching posterior margin, widely separated apically. Axillae broadly fused medially, joined posteriorly to scutellum across broadly impressed furrow, each carina with nodule along transcutal suture. Scutellum truncate apically, only slightly narrower than mesoscutum; frenum not separated from scutellum by distinct suture, sometimes replaced by carina, frenum produced posteriorly into two long spines about equal to mesosoma in length. Disc of propodeum usually flat, vertical, callus rounded, with dense fine setae; metepisternum not distinct. Femoral groove shallow, sharply impressed dorsally. Prepectus fused to pronotum, without distinct furrow or suture, not reaching tegula; spiracle set into emargination of pronotum, not closed off dorsally. Two metatibial spurs. Marginal vein of hindwing absent. Petiole stout, cylindrical, slightly longer than metacoxa in female, much longer in male. Gaster globose, semicircular, first tergite covering following segments; first sternite smooth. Ovipositor acicular.

Distribution. Neotropics; extending into Arizona, Texas and Florida. One species recorded from northern Africa.



FIGS. 24-29. *Kapala floridana*: 24, habitus, ♀ ; 25, wings, ♀ ; 26, male antenna; 27, male metasoma, lateral view; 28, lower face in frontal view, ♀ ; 29, male genitalia, ventral view.

KEY TO THE NORTH AMERICAN SPECIES OF *KAPALA* CAMERON

- 1. Scutellum gently sloped at apex to base of scutellar spines (Figs. 24, 53); propodeum including callus completely colliculate (Fig. 67); female gaster orange-brown *Kapala floridana* (Ashmead)
- Scutellum angled abruptly at apex to base of scutellar spines, forming a distinct arch in posterior view; propodeum weakly colliculate with glabrous areas laterally; female gaster dark brown to black *Kapala* spp.

***Kapala floridana* (Ashmead)**
 Figs. 24-29, 53, 57, 63, 67, 73.

Thoracantha floridana Ashmead, 1885a: 96; Ashmead 1885b: 11-12.
Kapala floridana; Ashmead 1892: 357.

Female. Length 2.6-3.7 mm. Black; antenna and femora brown; tibiae, tarsi and apices of femora lighter. Gastral tergites orange-brown. Wings infusate, venation dark brown, sometimes darker along cubital and medial veins.

Head 1.4-1.5 times broader than high (Fig. 63). POL 2.2-2.6 times LOL, POL 2.4-3.0 times OOL. Frons and face finely and weakly striate, scrobe variously sculptured laterally, usually smooth centrally. Clypeus and supraclypeal area smooth, with sparse curved setae. Eyes separated by 2.0-2.2 times their height. Malar space 0.9-1.0 times height of eye, malar depression absent. Labrum 6 to 8-digitate, digits long (Fig. 28). Antenna 10-segmented, weakly serrate basally, first flagellomere equal to or slightly longer than second; apical segment twice longer than broad, stout; sensilla comprised of dense setae.

Mesosoma robust with strong dorsal striae (Fig. 57); prepectus, callus and dorsum with finely reclinate setae; notaulices complete dorsally. Mesoscutum 2.1-2.6 times broader than long dorsally, 1.3-1.8 times higher than long. Apex of scutellum gently sloping to level of frenal spines, not elevated between spines (Fig. 24); frenal spines stout, strongly striate; apex of spines bluntly bifurcate, 1.7-1.9 times as long as axillae and scutellum; ventral surface of frenum colliculate, usually with complete median carina (Fig. 67). Propodeum colliculate, laterally without strong sculpture, disc flat, bordered by carinae (Fig. 67). Mesepimeron weakly to strongly striate dorsally, mostly smooth (Fig. 53); femoral groove sharply defined, elongate, smooth and shining, sparsely setose. Metacoxa 1.6-2.1 times as long as wide. Legs slender, with sparse erect setae on femora and tibiae; outer metatibial spur about twice length of inner. Forewing 2.4-2.7 times as long as broad (Fig. 25); costal cell 0.3-0.4 times length of wing; ventral surface densely setose; marginal vein with few dorsal setae; basal area bare, rest of wing with dense long setae on both surfaces; postmarginal vein short, less than half length of stigma; stigma large, twice longer than broad. Hindwing 3.7-4.3 times as long as broad.

Petiole 3.1-4.1 times as long as broad, 1.4-1.6 times length of metacoxa, shagreened with irregular weak carinae. Gaster globose, semicircular, only slightly longer than high; smooth and shining.

Male. Length 3.0-3.7 mm. Colour as in female but darker, sometimes with faint cupreous reflections dorsally; gaster dark brown. Antenna 12-segmented, rami long, slender (Fig. 26); scape expanded in apical half. Dorsal median longitudinal depression of mesosoma pronounced, mesosoma dorsally striate or rugose; patches of long setae dorsally on scutellum next to inner margin of bases of frenal spines. Propodeal disc smaller than in female, with few irregular carinae, callus rugose. Petiole 6.6-8.1 times as long as wide (Fig. 27); two parallel carinae dorsally, often lacking at least in apical half. Genitalia as in Fig. 29.

Type Material Examined. *Holotype* of *Thoracantha floridana* Ashmead (♂) is "type 2827" (USNM) labelled "E. Fla., Ashmead, *Thoracantha floridana* ♂ type".

Other Material Examined. 274 ♀♀ 630 ♂♂. **Alabama:** 2 ♂♂ Cowarts, August 1-3 1916 (AMNH). **Florida:** 13 ♀♀ 12 ♂♂ Alachua Co., Gainesville, March 28 1976, E.E. Grissell,

deciduous forest (FLA): 3 ♂♂ Alachua Co., November 11 1956, R.A. Morse, sweeping weeds (FLA, USNM); 5 ♂♂ Alachua Co., August 27,28 1955, R.A. Morse, sweeping weeds (FLA, LACM); ♂ Alachua Co., Waldo Road, November 11 1927, H.E. Bratley (FLA); ♂ Gainesville, September 26- October 2 1914 (AMNH); 4 ♀♀ 5 ♂♂ Gainesville, October 24 1919, L.H. Weld (USNM); ♀ Gainesville, May 5 1967, F.W. Meads, moist oak-pine flat-woods, *Vacc. myrcinites* grass [?](USNM); 2 ♂♂ Branford, July 31 1930, R.H. Beamer (KAN); 2 ♂♂ Cocoa, July 22 1939, R.H. Beamer (KAN); ♀ ♂ Cedar Keys, June 4 (ANSP); ♀ Levy Co., Cedar Keys, August 28 1976, E.E. Grissell (FLA); ♂ Cedar Keys, July 12 1939, P.B. Lawson (KAN); 5 ♂♂ Columbia & Baker Co., Osceola Nat. For. nr. Rt. 90, May 16 - June 2, June 2-24 1977, J. Wiley, Malaise (FLA); ♀ Duval Co., Jacksonville, September 2 1957, P.H. Thompson (USNM); 2 ♀♀ ♂ Duval Co. (ANSP); 3 ♀♀ 3 ♂♂ Elfers, July 14 1939, P.B. Lawson (KAN); 2 ♂♂ Ft. George (USNM); 2 ♂♂ Ft. George, August 27 1882 (USNM); ♀♂ "Fla", July 16 1883 (USNM); ♂ Gold Head Branch St. Pk., Clay Co., May- June 1954, L.H. Krombein (USNM); ♀ 2 ♂♂ Haw Creek [?], July 1883, Schwarz (USNM); ♀ ♂ Hernando Co., Weeki Wachee Spr. August 16 1968, G.F. Hevel (USNM); ♀ Haw Creek (USNM); 4 ♂♂ Highlands Hammock nr. Sebring, May 4 1961, H.E. Evans (MCZ); ♀ ♂ Hilliard, August 19 1930, J. Nottingham (USNM); ♂ Hilliard, October 5 1938, Oman (USNM); 3 ♀♀ 13 ♂♂ Hilliard, August 19 1930, Oman/ Tuthill/ Beamer/ Nottingham (KAN); 2 ♂♂ Hillsboro, May 2-3 (USNM); ♀ Hillsborough Co., 4 mi NE Thonotosassa, August 18 1938, Hubbell-Friauf (MMZ); 2 ♂♂ Indian River (USNM); 2 ♀♀ ♂ Jacksonville, November 3 1911 (AMNH); ♀ LaBelle, July 16 1939, P.B. Lawson (KAN); ♀ 2 ♂♂ LaBelle, April 1919, J.M. Knull (USNM); 3 ♂♂ Liberty Co., Torreya State Pk., June 13,15 July 22 1974, H.V. Weems Jr. (FLA); ♂ Loughnan, August 2 1930, L.D. Tuthill (KAN); 5 ♀♀ 9 ♂♂ Marion Co., 9 mi SW Ocala, Kingland Country Est., August 27- September 4 1975, J. Wiley (FLA); 4 ♀♀ ♂ same data, September 4-10 1975, Malaise in turkey oak (FLA); 14 ♀♀ 45 ♂♂ same data, September 19- October 2 1975 (FLA); 4 ♀♀ 5 ♂♂ same data, October 2-8 1975 (FLA); 4 ♂♂ same data, October 8-13 1975 (FLA); 16 ♀♀ 42 ♂♂ same data, October 13- November 5 1975 (FLA); 38 ♀♀ 79 ♂♂ Marion Co., Lake Eaton, August 27-September 10 1975, J. Wiley, Malaise trap (FLA); 63 ♀♀ 111 ♂♂ same data, September 10- October 2 1975 (FLA); 24 ♀♀ 51 ♂♂ same data, October 2-9 1975 (FLA); 16 ♀♀ 47 ♂♂ same data, October 8-13 1975 (FLA); 42 ♀♀ 100 ♂♂ same data, October 13- November 5 1975 (FLA); 2 ♂♂ Monticello, October 4-8 1914 (AMNH); ♂ Orange Co., May 11 (USNM); ♂ 8 mi N Perry, July 12 1953, E.S. Ross (CAS); ♀ Plant City, July 14 1939, P.B. Lawson (KAN); ♀ 2 ♂♂ Putnam Co., Welaka, November 10 1939, J.J. Friauf (MMZ); 10 ♂♂ Putnam Co., 2 mi NW Orange Spr., August 2-27 1975, Drummond & Wiley, Malaise (FLA); 5 ♂♂ same data, September 10- October 2 1975, J. Wiley (FLA); ♀ 6 ♂♂ same data, October 13- November 5 (FLA); ♂ Sanford, October 3 1925, W.H. White (USNM); ♂ Sanford, April 6 1926, E.D. Ball (USNM); ♀ Sanford, May 7 1908, Van Duzee (MCZ); 5 ♂♂ Sanford, August 8 1939, R.H. Beamer (KAN); ♀ St. John's Bluff, Duval Co., August 30 1976, E.E. Grissell (FLA); ♂ St. Petersburg, April 28 1904, Van Duzee (CAS); 3 ♂♂ Tampa, May 2 1908, Van Duzee (CAS); 2 ♂♂ Tampa, April 26 (USNM); ♀♂ Taylor Co., Blue Spring Lake, June 4 1972, R. Duffield, black light (GEO); ♀ 7 ♂♂ same data, June 5 1974, C.L. Smith, black light (GEO); 1 ♂ Taylor Co., Tidewater Swamp, 10 mi W Stein Latchee, June 5 1972, C.L. Smith (GEO); ♂ Titusville, November 8 1911 (MCZ); Waldo, August 18 1930, R.H. Beamer (KAN); ♀ Wakullah, July 11 1939, P.B. Lawson (KAN); 2 ♂♂ Yankeetown, July 31 1930, L.D. Tuthill (KAN); ♀ 4 ♂♂ Zolfo Spr., July 15 1939, R.H. Beamer (KAN). **Georgia:** 23 ♀♀ 57 ♂♂ Billy Island, Okefenokee Swamp, June 1912 (COR); ♂ Billy Island, Okefenokee Sw., September 1-5 1913 (COR); ♀ 9 ♂♂ Okefenokee Swamp, August 3 1934, July 25,27, August 11 1939, Beamer/Hardy (KAN, USNM); 5 ♂♂ Waycross, October 5 1938, Oman (USNM); ♂ Beachton Chubb Place, August 7 1924, C.O. Handley (USNM); ♂ Thomasville, June 10-15, W.D. Pierce, on cotton (USNM); ♂ Tifton (USNM); ♀ 3 ♂♂ Savannah, August 10 1930, Barber (RUT); ♂ 8 mi S of Waycross, July 16 1953, E.S. Ross (CAS); ♂ Chaser's Isl., June 14 1922 (COR). **Louisiana:** ♂ Orleans Canal nr. Spanish Fort, August 5-7 1915, R & H (ANSP).

Remarks. Distinguished from other *Kapala* by the sloped scutellum, and from its closest relative, *Kapala terminalis* Ashmead by having the propodeum including the callus completely colliculate, scutellum not strongly arched medially, male petiole with parallel carinae dorsally and male rami shorter.

Distribution. Southern Georgia to southern Florida, not found south of Lake Okechobee (localities for Alabama and Louisiana could not be found). Fig. 73.

Obeza new genus

Type-species. *Lophyrocera floridana*, Ashmead 1888: 187.

The genus *Obeza* is erected to encompass the New World species which have been previously referred to *Stilbula*. *Obeza* differs from Old World *Stilbula* largely in the possession of the lateral propodeal processes (Figs. 30, 32, 68), and the posterior extension of the genae, which enclose the mouthparts, behind the mandibles. The propodeal processes of *Obeza* differ from any closely related structures in *Stilbula* by occurring laterally on the propodeal disc, but within the bounds of the postspiracular furrow (never outside). Character states shared with the Australasian *Stilbula* are the prepectus not reaching the tegula, transverse head, cylindrical antenna, lateral mesocoxal carina, frenal processes, and a similarly patterned colouration of the mesosoma. The frenal processes are similar apically in the bifurcated spines but the basal unbranched portion of the spines is much shorter in all of the New World species.

Obeza shares several character states with *Lophyrocera* including the frenal and propodeal processes, the genae strongly produced behind the mandibles but not fused, and a lateral mesocoxal carina. *Obeza* retains the plesiomorphic features of cylindrical antenna and two metatibial spurs. *Obeza* is more distantly related to *Pseudochalcura* as evidenced by the transverse shape of the head, globose mesosoma, gena produced behind the mandibles and lateral mesocoxal carina. These three genera form a monophyletic group unique to the New World which are sister to *Stilbula*.

Generic Diagnosis. Head transverse, narrower than mesosoma. Median ocellus only slightly anterior to posterior ocelli; occipital carina strong; temple behind eye narrow; occiput vertical, flat. Antennal scrobe narrow, as deep as width of scape, sharply margined laterally. Genae not completely fused behind mandibles, not strongly angulated, angle between ventral and posterior faces more than 110° , with circular opening for mouthparts (Fig. 69). Clypeus as long as wide, shorter than supraclypeal area; base of clypeus without distinct groove, laterally with fine groove. Mandible large, falcate, apical tooth longer than width of clypeus. Mouthparts reduced, visible externally. Scape short, only slightly longer than broad, not reaching median ocellus; antenna without basal anellus, stout, cylindrical in both sexes, longer than width of head.

Mesosoma globose, colour pattern as in Fig. 30, notaulices broadly impressed, joining at posterior margin. Axillae broadly fused medially, joined posteriorly to scutellum across deep, broad, crenulate furrow. Scutellum broadly rounded, narrower than mesoscutum, usually produced apically into blunt process; frenum produced into two narrow apical processes. Disc of propodeum broadly concave, produced as blunt propodeal processes dorsolaterally between propodeal disc and spiracle, with numerous long setae; callus rounded, with several long setae; metepisternum not distinct. Femoral groove shallowly and broadly impressed. Prepectus fused to pronotum, without distinct groove or furrow, not reaching tegula; spiracle recessed into dorsal margin of pronotum and enclosed dorsally; distance between spiracle and dorsal margin narrow. Anterior margin of metasternum sharply produced between metacoxae. Procoxa elongate, meso and metacoxae globose; mesocoxa with lateral carina. Two metatibial spurs. Marginal veins of forewing distinct, not discernible in hindwing.

Petiole stout, more than twice length of metacoxa. Gaster globose, first tergite covering following segments. Ovipositor acicular.

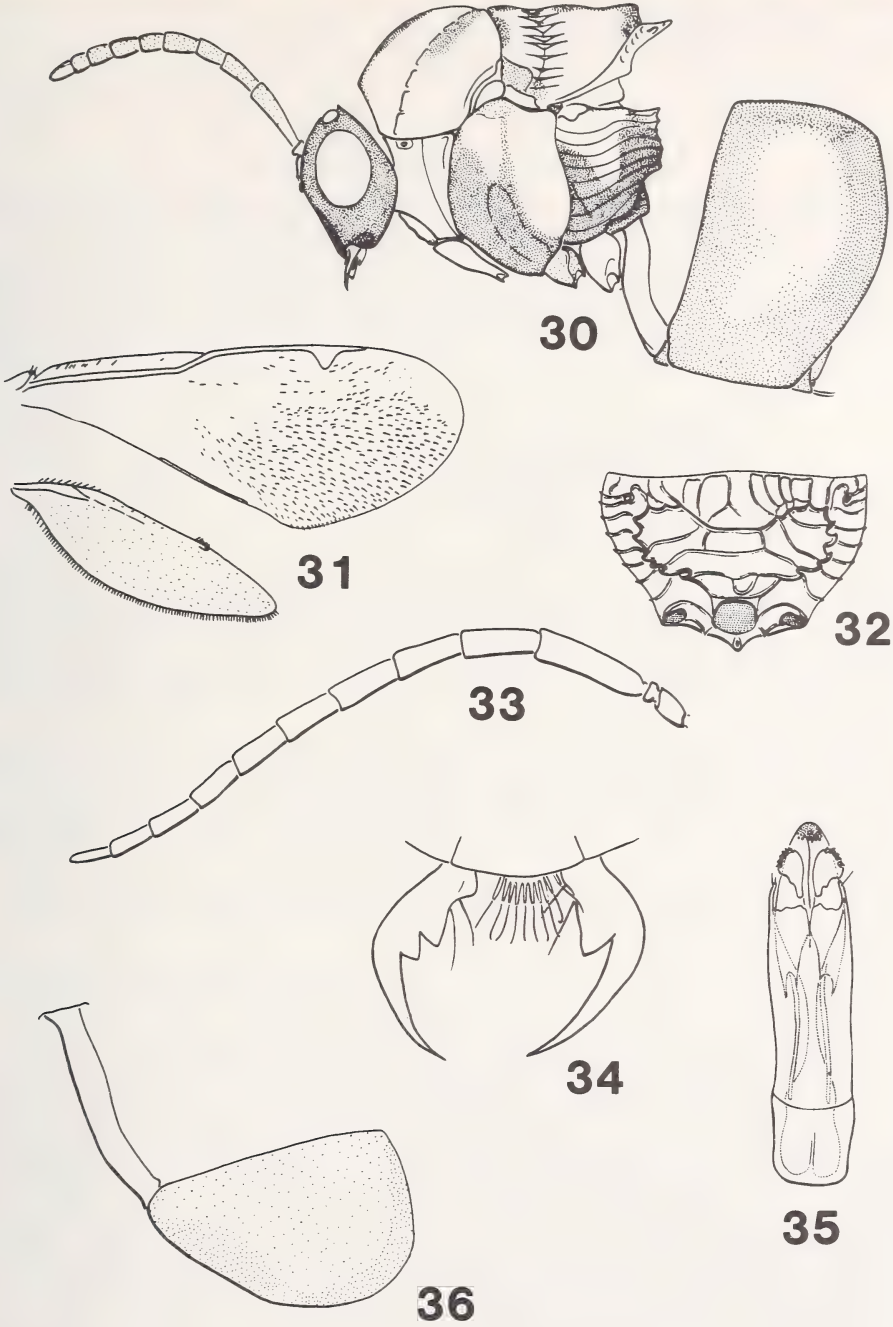
Distribution. Neotropical, and Nearctic in southwestern U.S.A. and Florida.

Remarks. The following Neotropical species are included in the genus *Obeza*:

grenadensis (Howard 1896: 133, *Stilbula*); **n. comb.**, Grenada, W.I. [type examined].

maculata (Westwood 1874: 153, *Schizaspidia*); *maculata* (Westwood), Kirby 1886: 29, *Orasema*; **n. comb.**, Brazil [from original description and figure].

meridionalis (Kirby 1889: 144, *Tetramelia*); **n. comb.**, Brazil [pers. comm. Z. Bouček (BMNH)].



FIGS. 30-36. *Obeza floridana*: 30, habitus (areolate sculpture of mesosoma not figured), ♀ ; 31, wings, ♀ ; 32, propodeum in posterior view, ♀ ; 33, male antenna; 34, lower face in frontal view; 35, male genitalia in ventral view; 36, male metasoma in lateral view.

nigromaculata (Cameron 1884: 104, *Lophyrocera*); **n. comb.**, Nicaragua [from original description and figure].

semifumipennis (Girault 1911: 392, *Stilbula*); **n. comb.**, Paraguay [from original description].

KEY TO THE NORTH AMERICAN SPECIES OF *OBEZA* N. GEN.

1. Female antenna 11-segmented, male antenna 12-segmented; head black; ventral setae of forewing long; overall orange-red colouration in both females and males
 *Obeza floridana* (Ashmead)
- Female antenna 12-segmented, male antenna 12-segmented; head cyaneous or black; ventral surface of wing with microtrichia; testaceous colouration with either restricted or extensive black patterning in female; almost completely black mesosoma in male
 *Obeza septentrionalis* (Brues)

Obeza floridana (Ashmead) new combination

Figs. 30-36, 58, 64, 68, 69, 74.

Lophyrocera floridana Ashmead, 1888: 187; Ashmead 1892: 357.

Stilbula floridana; Gahan 1940: 435-6.

Female. Length 3.4-4.8 mm. Head black; mesosoma light testaceous to darker orange-brown, dark brown to black patterned markings dorsally and laterally (Fig. 30); antenna dark brown, scape and pedicel testaceous; apex of antenna light brown. First gastral tergite orange-testaceous to dark brown, testaceous laterally, following segments testaceous and dark brown posteriorly. Coxae range from partially to wholly testaceous. Petiole and legs testaceous. Wings infuscate to hyaline.

Head 1.5-1.6 times broader than high. POL 2.6-3.4 times LOL, POL 1.4-1.8 times OOL. Face with prominent striae (Fig. 64), continuous across clypeus and supraclypeal area, carina between posterior and anterior ocellus continued laterally onto frons, crenulate between posterior ocelli; occipital carina extending to eye margin; malar depression and scrobe smooth. Eyes separated by 1.8-2.1 times their height. Malar space 0.7-0.9 times height of eye; malar depression deeply impressed, equal to half malar space. Labrum 10 to 11-digitate (Fig. 34). Antenna 11-segmented (Fig. 30); first flagellomere 4.0 times as long as apical width, following flagellomeres 2.0 times longer than broad, becoming quadrate apically; sensilla comprised of fine and thick setae.

Mesosoma robust; mesoscutum, prepectus and mesepimeron areolate-rugose; axilla and scutellum areolate-rugose (Fig. 58) to longitudinally carinate; sparse short setae on mid-lobe of mesoscutum and apex of scutellum; dense, long setae on callus and propodeal process. Mesoscutum 1.9-2.1 times broader than long dorsally. Scutellum wider than long, with only a slight median depression; frenal spines 0.2 times length of scutellum. Disc of propodeum vertical; few transverse carinae across disc, longitudinally carinate laterally; lateral processes strongly carinate apically. Femoral groove poorly defined. Proepisternum areolate-rugose. Coxae smooth, metacoxa globose. Legs slender, femora glabrous except dorsal row of short setae; tibiae with sparse erect long setae, tarsi dense setose. Forewing 2.5-3.0 times as long as broad; costal cell 0.3-0.4 times as long as wing, single row of ventral setae; submarginal vein dorsally with few erect setae; basal area of wing and area below marginal vein bare; rest of wing disc with dense long ventral setae, bare dorsally; veins distinct, stigma prominent, twice as long as broad; postmarginal vein slightly longer than stigma. Hindwing 3.2-3.8 times as long as broad.

Petiole 2.9-3.8 times as long as broad, 2.1-3.0 times longer than metacoxa, flattened dorsally, bare with weak irregular longitudinal carinae laterally and ventrally. Gaster 1.1-1.5 times longer than high, smooth.

Male. Length 3.4-5.3 mm. Slightly darker than female. Antenna 12-segmented,

longer than female (Fig. 33); first flagellomere 4.0 times as long as broad, following flagellomeres more than 3.0 times as long as broad. Propodeal processes prominent, rounded apically (Fig. 68). Petiole 4.5-6.5 times as long as broad, glabrous, cylindrical.

Type Material Examined. *Holotype* of *Lophyrocera floridana* Ashmead (♂) is "type 41192" (USNM) labelled "Jacksonville, Fla, Type *Lophyrocera floridana* Ashmead" [captured in April, from original description].

Other Material Examined. 14 ♀♀ 33 ♂♂. **Florida:** ♀ Clearwater, April 30, 1908, Van Duzee (MCZ); ♀ Orlando, April 29, D.M. DeLong (USNM); ♀ Suwanee Co., July 26 1954, F.W. Mead (FLA); ♀ Alachua Co., Pierces Homestead, May 8 1974, W.H. Pierce, Malaise (FLA); 2 ♀♀ Tampa, May 2 1908 Van Duzee (CAS); ♀ Monroe Co., Big Pine Key, April 4 1972, J.B. Hepner, blacklight (FLA); ♀ Key West, April 1 1903, E.A. Schwarz (USNM); ♀ Torreya State Park, Liberty Co., May 9-17 1968, H.V. Weems, Jr., Malaise (BRI); 2 ♀♀ Ross & Castello Hamm., Dade Co., April 6 1963, H.V. Weems (FLA); ♀ Dade Co., Fuch's Hammock, nr. Homestead, May 23-24 1939, T.S. Dicke & H.V. Weems, Malaise (FLA); ♀ Royal Palm Hammock, Everglades Nat. Pk., December 19 1940, G.S. Walley (BRI); ♀ Cape Sable, February 14 1950, J.S. Caldwell (USNM); ♂ Key Largo, March 26 1954, K.V. Krombein (USNM); 3 ♂♂ Waldo, August 18 1930, R.H. Beamer (USNM); ♂ N of Picnic, September 8 1938, Onan (USNM); ♂ Paradise Key, April 5, J.N. Knull (USNM); ♀ Ft. George, Type[?], [not mentioned in original description] (USNM); ♂ Indian River (USNM); ♂ Alachua Co., August 27 1955, R.A. Morse, sweeping weeds (FLA); 2 ♂♂ Munroe Co., Big Pine Key, December 1970, W.H. Pierce, sweeping grass (LACM); ♂ Dade Co., Miami Plant Intro. Lab., May 1 1974, W.H. Pierce, Malaise (FLA); ♂ Sanford, August 8 1939, R.H. Beamer (KAN); 5 ♂♂ Hudson, July 13 1939, R.H. Beamer (USNM, KAN); ♂ Hilliard, August 19 1930, R.H. Beamer (KAN); ♂ Clearwater, May 1 1908, Van Duzee (MCZ); 2 ♂♂ Archbold Bio. St., Lk. Placid, May 6 1961, H.E. & M.A. Evans (MCZ); ♂ Hudson, July 13 1939, Oman (USNM); ♂ Tampa, April 29 (USNM); 2 ♂♂ Tampa, May 2 1908, Van Duzee (CAS); ♂ Tampa, April 13[?]; ♂ Sanford, April 30 1908, Van Duzee (MCZ); ♂ Levy Co., Cedar Key, May 18 1970, D.L. Bailey, Malaise (USNM); ♂ Stock Island, Monroe Co., October 15 1963, H.V. Weems, Jr. (FLA); ♂ Brevard Co., Eau Gallie Beach 101, August 8 1938, Hubbell-Friauf (MMZ); ♂ Budnell, August 19 1942 (USNM). **Georgia:** ♂ Seminole Co., Lake Seminole, Henry Cummings Landing, August 23 1975, C.L. Smith (GEO).

Remarks. Easily distinguished from *O. septentrionalis* by its generally smaller size, 11-segmented antenna in females, black head, long ventral setae on forewings and overall orange-red colouration in both females and males.

Distribution. Florida and southern Georgia. Fig. 74.

Obeza septentrionalis (Brues) new combination

Fig. 74.

Schizaspidia septentrionalis Brues, 1907: 104.

Stilbula septentrionalis; Gahan 1940: 435-6.

Female. Length 4.5-6.4 mm. Head black with faint to strong metallic green reflections; mesosoma testaceous with dark brown to black patterned markings dorsally and laterally; antenna dark brown; scape and pedicel testaceous, apical flagellomeres and rarely base of first flagellomere light brown. First gastral tergite dark brown, testaceous laterally, following segments testaceous, dark brown posteriorly and dorsally. Coxae range from partially to wholly testaceous. Petiole and legs testaceous. Wings infusate or hyaline.

Head 1.6-1.7 times broader than high. POL 2.9-3.8 times LOL, POL 1.3-1.7 times OOL. Face with prominent striae, continuous across clypeus and supraclypeal area, without definite carina between posterior and anterior ocellus, crenulate between posterior ocelli; occipital carina extending weakly past posterior ocelli; scrobe and malar depression smooth. Eyes separated by 1.8-2.0 times their height. Malar space 0.7-0.9 times height of eye; malar depression deeply impressed, equal to half malar space. Labrum 9 to 15-digitate. Antenna 12-segmented; first flagellomere 5.0 times as long as apical width, following flagellomeres 3.0 times as long as broad, becoming subquadrate apically; sensilla comprised of dense, fine and thick setae.

Mesosoma robust; prepectus, mesepimeron and dorsum areolate, sparsely covered

with short setae; callus and propodeal processes with dense, long setae. Mesoscutum 1.8-2.1 times broader than long dorsally. Scutellum wider than long, with shallow median longitudinal depression; frenal spines 0.1-0.2 times length of scutellum. Disc of propodeum vertical, deep-rugose, few transverse carinae across disc; longitudinally reticulate laterally, lateral processes rounded. Femoral groove poorly defined. Proepisternum areolate-rugose. Coxae smooth, metacoxa subglobose, about 1.5 times as long as broad. Legs slender, femora glabrous except dorsal row of short setae; tibiae with sparse erect long setae, tarsi densely setose. Forewing 2.7-4.0 times as long as broad; costal cell 0.4 times as long as wing, with scattered ventral setae; submarginal vein dorsally with few erect setae; basal area of wing and area below marginal vein bare; rest of wing disc with dense microtrichia ventrally, bare dorsally; veins distinct, stigma prominent, twice as long as broad; postmarginal vein longer than stigma. Hindwing 3.5-4.3 times as long as broad.

Petiole 1.8-4.2 times as long as broad, 1.4-3.0 times as long as metacoxa, stout, flattened dorsally, bare with weak (or robust) carinae laterally and ventrally. Gaster 1.2-1.5 times as long as high, smooth.

Male. Length 6.3 mm. Head cyaneous; mesosoma patterned with dark brown and black, no testaceous areas; antenna, legs, petiole light testaceous; gaster dark brown to black. Antenna 12-segmented, longer than in female, first flagellomere 6.0 times as long as wide, apical segment 4.3 times as long as wide. Propodeal processes prominent, broadly rounded. Petiole 7.2 times as long as broad, 7.6 times as long as metacoxa; cylindrical, with few weak carinae. Gaster smaller than female.

Type Material Examined. *Holotype* of *Schizaspidia septentrionalis* Brues (♀) is "type 42707" (USNM) labelled "Huach Mts, VI, Ariz, TYPE, Catal. No. 357, Collection Brooklyn Museum".

Other Material Examined. 20 ♀♀ 1 ♂. **Arizona:** 3 ♀♀ Post Creek Cn., Pinaleno Mtns., Fort Grant, July 15-18 1917 (MCZ); ♀ Huachuca Mtns., June 9 1935, J.N. Knull (USNM); ♀ "Ariz.", [Ashmead determination as] *Lophyrocera nigromaculata* Cameron (ANSP); ♀ 5 mi W Portal, Cochise Co., June 17 1959, L.A. Stange (DAV); ♀ S.W. Res. Stn., Portal, June 19 1956, H. & A. Howden (BRI); ♀ Garcia, August, N. Banes (USNM); ♀ Garcia (USNM); ♀ Santa Rita Mts., 4500', June 27 1968, A.A. Nichol (USNM); ♂ Prescott, June 8 1941, D.J. & J.N. Knull (USNM). **New Mexico:** ♀ Otero Co., 4 mi NE La Luz, June 25 1964, D.R. Smith & C.W. Baker (USNM); ♀ Cloudcroft, June 27 1940, R.H. Beamer (KAN). **Texas:** 5 ♀♀ Limpia Canyon, Davis Mts., June 17-20 1961, R.L. Westcott (LACM); ♀ Davis Mtns., July 2 1940, D.J. & J.N. Knull (USNM). **MEXICO:** **Chiapas** ♀ Santa Clara, Namiquipa Dist., 6500', July 3 1947, D. Rockefeller (AMNH).

Remarks. Distinguished from *O. floridana* by 12-segmented antenna present in females (apical flagellomeres may be fused but suture evident), usually cyaneous colouration of the head, microtrichia on ventral surface of wing, testaceous colouration of females and almost black mesosoma of males.

Variation. The colour of the body varies from restricted patterns to almost wholly black, and of the head from a strong metallic colouration to black. There is no correlation between the two.

Distribution. Arizona, New Mexico, Texas and Mexico. Fig. 74.

Lophyrocera Cameron

Lophyrocera Cameron, 1884: 103.

Type-species. *Lophyrocera stramineipes* Cameron, 1884: 103 [type by original designation].

The almost total fusion of the genae posterior to the mandibles, reduction of mouthparts, mesocoxal carina and single metatibial spur provide evidence of a close sister group relationship between *Lophyrocera* and *Pseudochalcura*. The generic diagnosis does not distinguish *Lophyrocera* from *Tetramelia*, a genus restricted to the Neotropical region. There is a lack of good characters which can be used to separate the two genera. The

previous character used for separation was the direction of the propodeal processes (downward or horizontal) which does not hold true for all of the species. The males of *Tetramelia* have a more elongate and angulated gaster but this is not a valuable character for defining generic limits. The species within these two genera are morphologically diverse but, unfortunately, poorly collected. A proper treatment of a potential synonymy of these two genera will require a more comprehensive review of the Neotropical species. From the Neotropical material examined, there are several undescribed species in this genus additional to the two species now recognized.

Generic Diagnosis. Head transverse, as broad as mesosoma. Median ocellus only slightly anterior to posterior ocelli; occipital carina present; temple behind eye narrow; occiput vertical behind eye, flat. Antennal scrobe narrow, as deep as width of scape. Genae not completely fused behind mandibles, forming a sharply angulated ridge, angle between ventral and posterior faces about 90° (Fig. 70). Clypeus slightly wider than long, shorter than supraclypeal area, base of clypeus without groove, deeply impressed laterally. Mandibles falcate, apical tooth wider than width of clypeus. Mouthparts reduced, usually visible externally. Scape long, not reaching median ocellus; antenna stout, without basal anellus, flagellomeres lobate in female, rarely serrate, flagellum shorter than width of head; each flagellomere of male with long flattened ramus, only slightly decreasing in length apically.

Mesosoma globose; notaulices joining at posterior margin. Axillae broadly fused medially, on same plane as mesoscutum dorsally, joined posteriorly to scutellum across crenulate to punctuate furrow. Scutellum broadly rounded, narrower than mesoscutum, usually produced apically into blunt process; frenum produced into two narrow apical processes. Disc of propodeum flattened; propodeal processes blunt or pointed; callus slightly bulging, with several short erect setae; metepisternum not distinct. Femoral groove broadly impressed. Prepectus fused to pronotum, without distinct suture or furrow, not reaching tegula; spiracle recessed into pronotum dorsally and broadly enclosed dorsally. Anterior margin of metasternum slightly produced between mesocoxae. Procoxa elongate, meso- and metacoxae globose, mesocoxa usually with lateral carina. One metatibial spur. Marginal vein of forewing distinct, vaguely discernible in hindwing.

Petiole stout, at least twice length of metacoxa. Gaster globose, first tergite covering following segments. Ovipositor acicular.

Distribution. Neotropical and Nearctic (western states).

Lophyrocera apicalis Ashmead

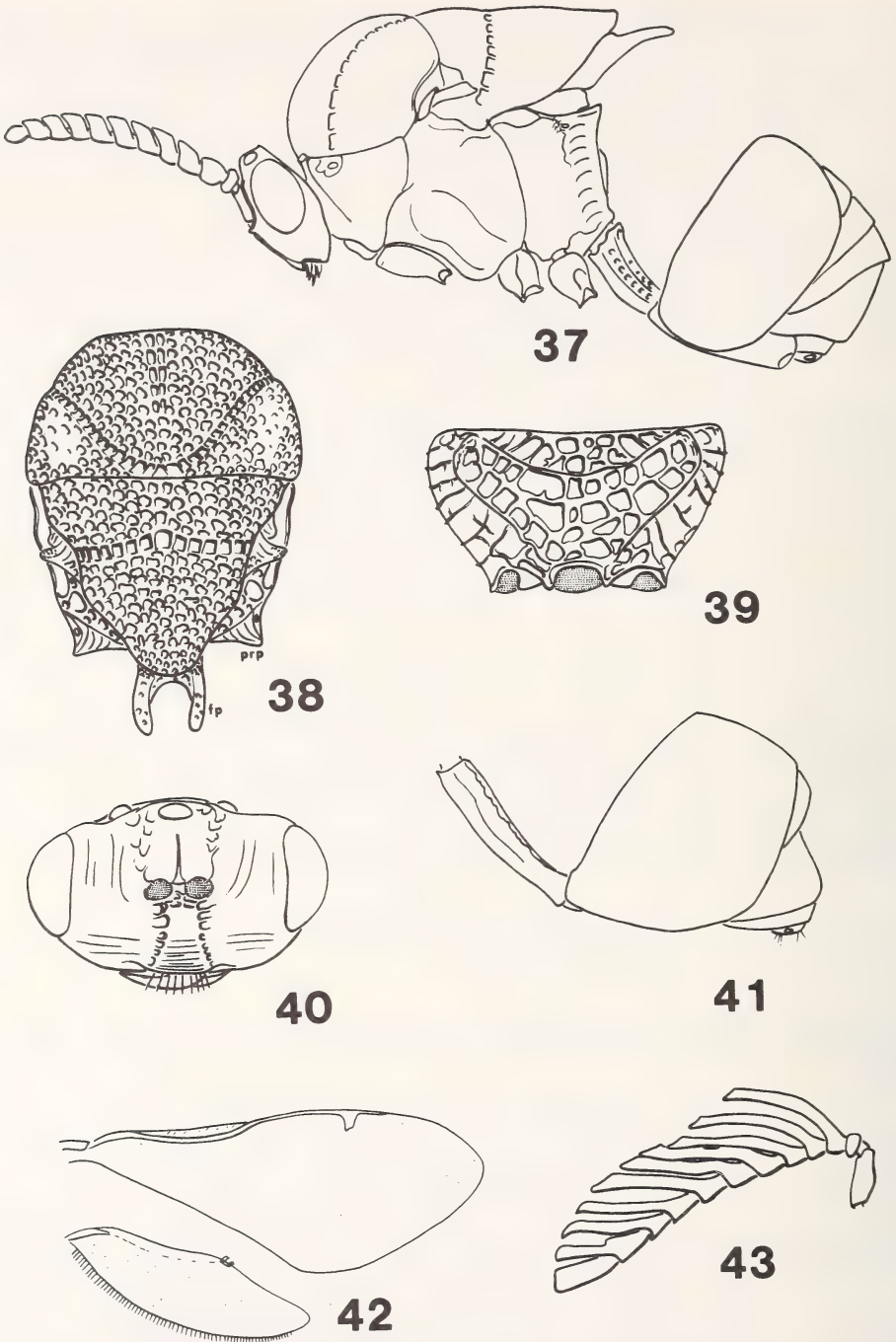
Figs. 37-43, 74.

Lophyrocera apicalis Ashmead, 1892: 357.

Female. Length 4.3-5.0 mm. Black; scape, pedicel, coxae, gaster and basal half of femora brown; apical two flagellomeres of antenna and rest of legs testaceous. Wings hyaline.

Head 1.7-1.8 times broader than high (Fig. 40). POL 2.7-3.2 times LOL, POL 1.6-2.0 times OOL. Frons and face with weak striae, scrobe rugose, finely striate across clypeus, supraclypeal area bare; carina between posterior and anterior ocelli continued laterally on frons, occipital carinae present. Eyes separated by 2.1-2.2 times their height. Malar space 0.8-0.9 times height of eye; malar depression shallow, less than half malar space. Labrum 7 to 9-digitate. Antenna 12-segmented (Fig. 37), flagellomeres equal in length, apical two flagellomeres sometimes fused; sensilla comprised of short dense appressed setae.

Mesosoma robust, areolate-rugose to coarsely punctate, side-lobes bare, sometimes smooth dorsally. Mesoscutum 1.7-2.3 times broader than long dorsally. Axilla and scutellum with shallow median longitudinal depression; frenal spines 0.3 times length of scutellum. Disc of propodeum vertical, propodeal processes sharp (Figs. 37, 38). Proepisternum areolate-rugose. Coxae smooth. Legs slender; femora smooth, with scattered short setae; dense appressed setae on tibiae and tarsi. Forewing 2.1-2.5 times as long as broad



FIGS. 37-43. *Lophyrocera apicalis*: 37, habitus, ♀ ; 38, mesosoma in dorsal view, ♀ ; 39, propodeum in posterior view, ♀ ; 40, head in frontal view, ♀ ; 41, male metasoma, lateral view; 42, wings, ♀ ; 43, male antenna. fp - frenal process, prp - propodeal process.

(Fig. 42); costal cell 0.3-0.4 times length of wing, scattered short ventral setae; submarginal vein dorsally with few short setae; basal area bare, rest of wing disc with very short microtrichia ventrally, bare dorsally; stigma twice longer than broad; postmarginal vein longer than stigma. Hindwing 3.0-3.6 times as long as broad.

Petiole 1.6-3.2 times as long as broad, 1.2-2.3 times longer than metacoxa (Fig. 37); flattened dorsally, areolate dorsally and dorsolaterally, with irregular carinae along dorsal edge; ventrally with fine longitudinal striae. Gaster 1.2-1.7 times as long as high, smooth; apical tergites scattered-micropunctate, with scattered short setae dorsally, first sternite smooth.

Male. Length 4.6-5.0 mm. Slightly darker colour than female. Antenna 12-segmented, flagellomeres dorsoventrally flattened, each dorsally with long, flat, gently curved ramus (Fig. 43). Propodeal processes longer than in female, extending as far as apex of frenal spines, with several short setae along dorsal edge. Disc of propodeum gently curved between processes. Petiole 8.0-9.0 times longer than broad, 2.7-3.0 times as long as metacoxa, sculpture as in female (Fig. 41).

Type Material Examined. *Holotype* of *Lophyrocera apicalis* Ashmead (♀) is "type 2141" (USNM) labelled "Santa Cruz Mts., Cal".

Other Material Examined. 9 ♀♀ 2 ♂♂. **Arizona:** ♂ Williams, July 13 1929, E.D. Ball (USNM). **California:** ♀ Cajon Ps., June 26 1941, D.J. & J.N. Knull (USNM); ♀ ♂ San Antonio Valley, Mount Hamilton, June 26 1975, J.B. Johnson (IDA); ♀ Kelseyville, Lake Co., June 20 1959, S.M. Fidel (DAV); ♀ Camp Baldy, Los Angeles Co., June 26 1950, J.C. Hall (DAV); ♀ Burney, Shasta Co., July 8 1946, P.D. Hurd & R.F. Smith, *Eriogonum* (BER). **Colorado:** ♀ Poudre Canyon, June 9 1934, K. Maehler (COL). **South Dakota:** ♀ 2 mi S Blue Bell Custer St. Pk., June 10 1961, H. & A. Howden (BRI). **Texas:** ♀ Brewster Co., Big Bend Nat'l Park, 12.5 mi SE Panther Jct., 2500', June 23-26 1982, G. Gibson (GUE). **Washington:** ♀ ♂ 22 mi N Goldendale, Klickitat Co., June 26 1969, R.L. Westcott (IDA).

Variation. The single male from Arizona differs from the rest of the specimens in having a 12-digitate labrum with the digits small and close together. All of the other specimens have a 6 to 8-digitate labrum with long, widely spaced digits. No other characters distinguish the male and since the latter type of labrum surrounds the Arizona location (Texas and California), it is interpreted as an aberration.

Distribution. Western United States of America. Fig. 74.

***Pseudochalcura* Ashmead**
Figs. 44-46.

Type-species. *Eucharis gibbosa* Provancher, 1881: 292 [type by original designation].

Revision. Heraty (in press).

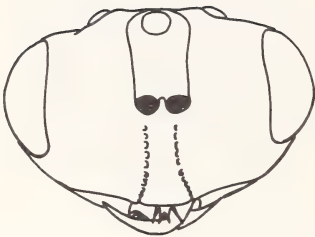
Remarks. *Pseudochalcura* can be distinguished from all other eucharitids by the genal bridge being completely fused behind the mandibles. Relationships are discussed in Heraty (in press) and suggest close relationships with *Obeza* and *Lophyrocera*, with *Pseudochalcura* being the more apomorphic of the three. Four species are found in North America: *P. gibbosa* is widespread in the north throughout Canada and Alaska, west in the Sierra-Cascades and Rocky Mountains, and occurs sporadically in the southwestern states; *P. americana*, *P. liburna* and *P. sculpturata* are restricted to southern Florida.

KEY TO THE NORTH AMERICAN SPECIES OF
PSEUDOCHALCURA ASHMEAD

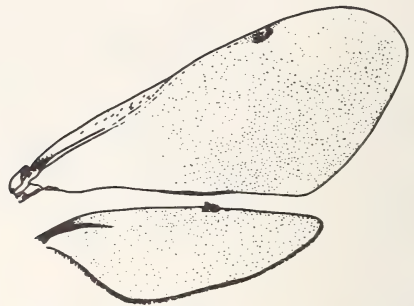
- 1. Dorsal setae on submarginal vein absent, setae of forewing disc extremely short (microtrichia), barely visible; lateral carina of mesocoxa reduced or absent; first gastral sternite of female longitudinally striate 2
- Dorsal setae on submarginal vein present, setae of forewing disc short or long; lateral carina of mesocoxa present; first gastral sternite of female smooth 3



44



45



46

FIGS. 44-46. *Pseudochalcura gibbosa*, ♀ : 44, habitus; 45, head in frontal view; 46, wings.

- 2. Metatibial spur present; antenna of female lobate or serrate, antenna of male with 4 basal rami; petiole of female pinched ventroapically; mesosoma completely dark brown or black in female *P. gibbosa* (Prov.)
- Metatibial spur absent; antenna of female strongly lobate or ramose basally, antenna of male with 7 basal rami; petiole of female not pinched ventroapically; mesosoma patterned black or brown and testaceous in female *P. sculpturata* Heraty
- 3. Disc of propodeum with fairly dense, long setae; forewing disc with long setae; usually with infuscate spot below stigma; metafemur bare laterally *P. americana* (Howard)
- Disc of propodeum bare or with few isolated setae; forewing disc with microtrichia in female, longer in male; forewing hyaline; metafemur with long erect setae laterally *P. liburna* Heraty

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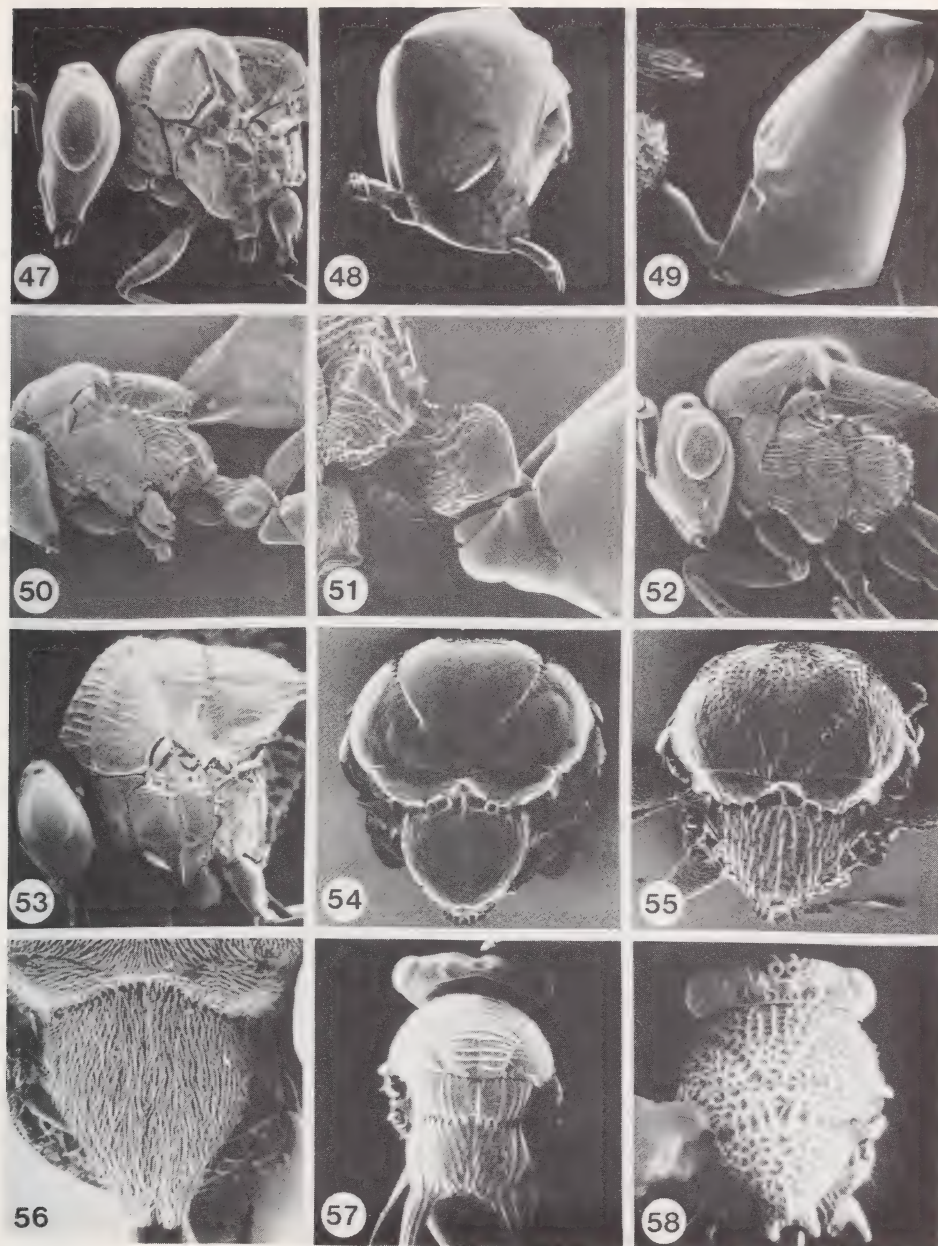
Government, allowed me to carry out extensive collecting at Ojibway Prairie Reserve, Windsor, Ontario and Pinery Provincial Park near Grand Bend, Ontario. Dr. S.A. Marshall and Mr. K.N. Barber and Dr. Z. Bouček (Commonwealth Institute of Entomology, London) have made well appreciated comments on this manuscript. Finally, I would like to extend my thanks to Dr. "D.H." Pengelly for helping to provide the initial enthusiasm which has carried on throughout the course of this study.

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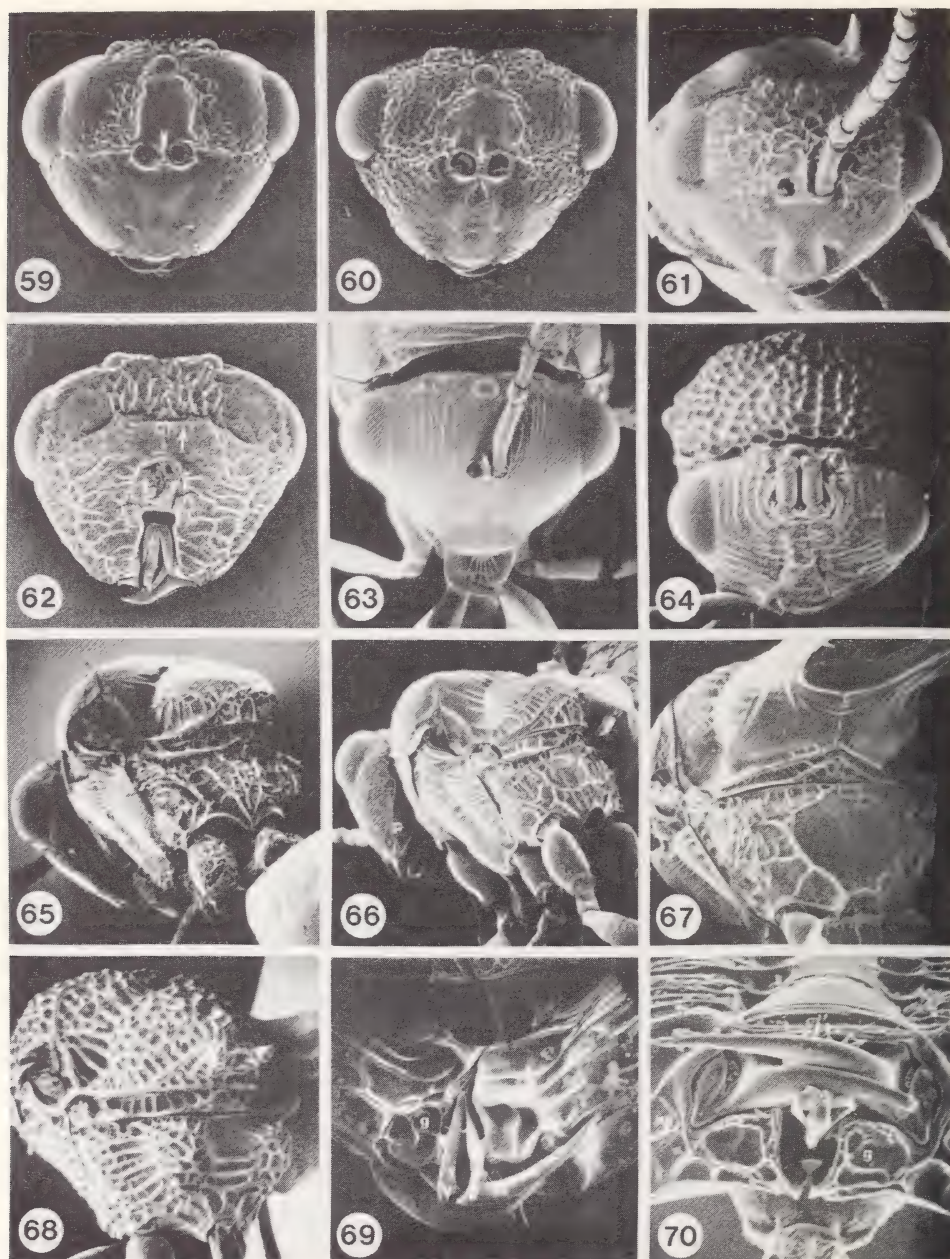
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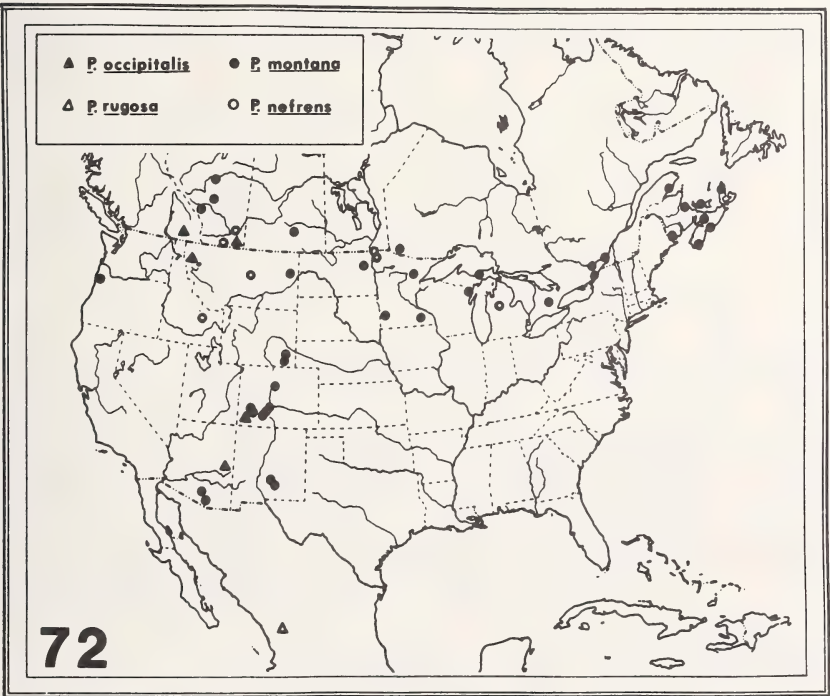
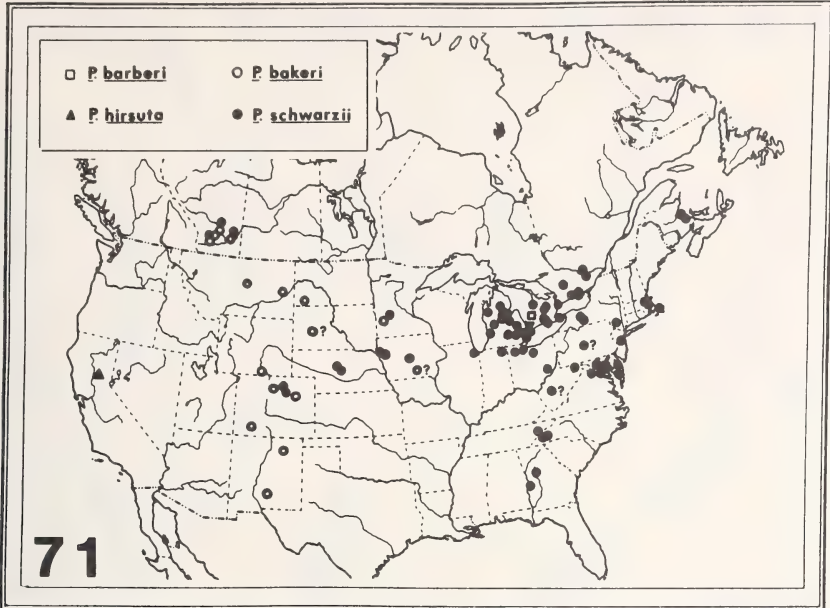
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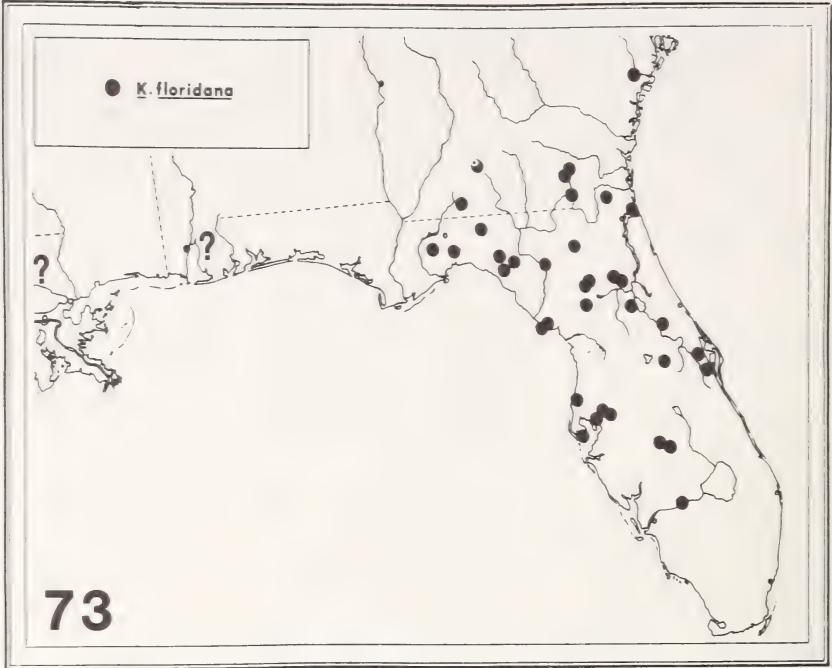
FIGS. 47-58. 47-48, *Orasema* sp. nr. *cockerelli* Gahan, ♀ : 47, mesosoma, arrow points to anellus; 48, metasoma. 49, *Pseudometagea montana*, metasoma, ♀ . 50-51, *Pseudometagea schwarzii*: 50, mesosoma, ♂ ; 51, petiole in lateral view, ♀ . 52, *Pseudometagea montana*, mesosoma, ♀ . 53, *Kapala floridana*, mesosoma, ♀ . 54, *Pseudometagea schwarzii*, mesosoma, ♀ . 55, *Pseudometagea bakeri*, mesosoma, ♀ . 56, *Pseudometagea montana*, scutellum, ♀ . 57, *Kapala floridana*, mesosoma, ♀ . 58, *Obeza floridana*, mesosoma, ♂ .



FIGS. 59-70. 59-61, heads in frontal view: 59, *Pseudometagea schwarzii*, ♀ ; 60, *Pseudometagea bakeri*, ♀ ; 61, *Pseudometagea occipitalis*, ♀ . 62, *Pseudometagea schwarzii*, posterior view of head, arrow points to the postoccipital carina, ♀ . 63-64, heads in frontal view: 63, *Kapala floridana*, ♀ ; 64, *Obeza floridana*, ♂ . 65-68, postero-lateral view of mesosoma: 65, *Pseudometagea schwarzii*, ♀ ; 66, *Pseudometagea occipitalis*, ♀ ; 67, *Kapala floridana*, ♀ ; 68, *Obeza floridana*, ♂ . 69, *Obeza floridana*, posterior view of genal bridge and reduced mouthparts. 70, *Lophyrocera* sp., ventral view of genal bridge enclosing reduced mouthparts. g - genal bridge, p - postgenal carina.



FIGS. 71-72. Distribution maps: 71, species of the *schwarzii*-group of *Pseudometagea*; 72, species of the *occipitalis*- and *montana*-groups of *Pseudometagea*. ? = state record, locality not verified.



FIGS. 73-74. Distribution maps: 73. *Kapala floridana*; 74, species of *Obeza* and *Lophyrocera*. ? = state record, locality not verified.

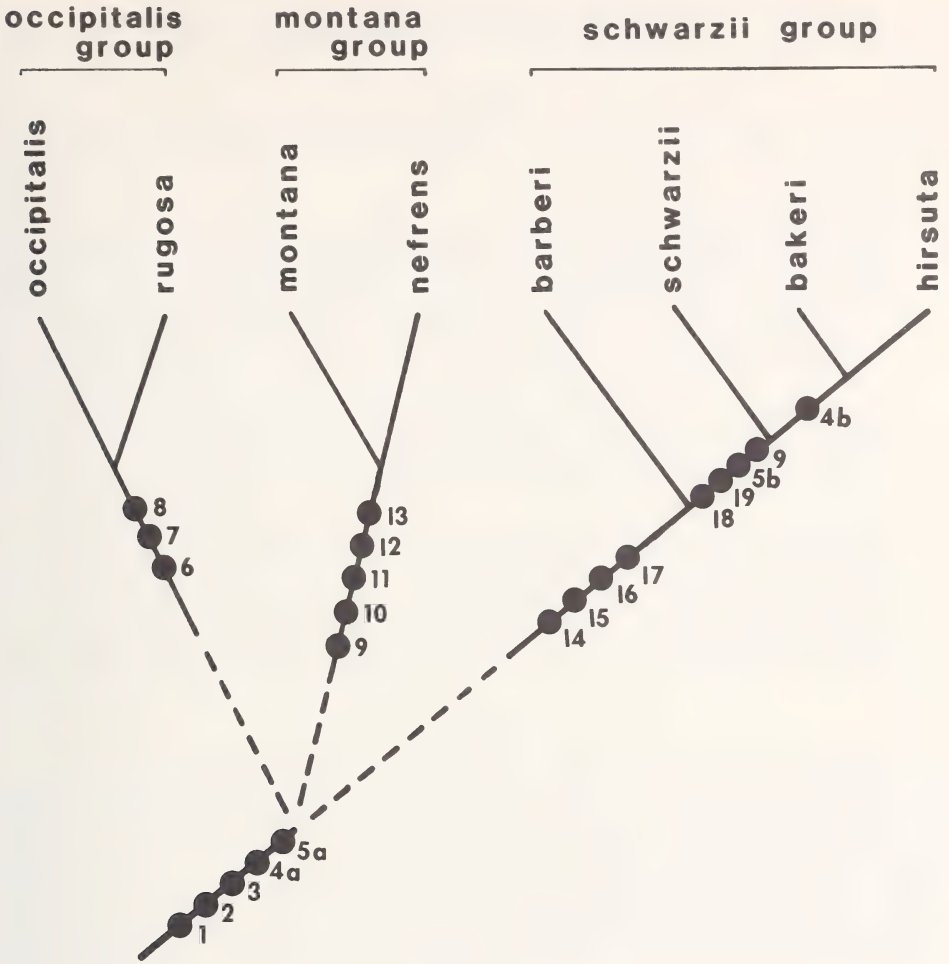


FIG. 75. Cladogram showing proposed relationships among species of *Pseudometagea*.

Apomorphic character states:

1 - hindwing broadly rounded apically; 2 - mandibles small; 3 - mesepimeron strigate; 4a - proepisternum glabrous; 4b - proepisternum sculptured; 5a - eye setose; 5b - eye bare; 6 - scrobe rugulose; 7 - male gaster elongate; 8 - medial vein infuscate; 9 - axilla lacking carinae; 10 - postgenal carina lacking; 11 - dorsum pubescent; 12 - coxal sculpture granulate; 13 - hindwing completely fringed; 14 - interocellar area depressed; 15 - first sternite strongly produced; 16 - coxa scabriculous or rugulose; 17 - petiole strongly expanded; 18 - male flagellomeres fewer; 19 - callus ridged.

A REVISION OF THE GENUS *PSEUDODINIA* COQUILLET (DIPTERA: CHAMAEMYIIDAE)

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Abstract

Proc. ent. Soc. Ont. 116:105-167 (1985)

The genus *Pseudodinia* Coquillett is revised. Two species groups are recognized, containing 17 species including 10 new species and one new name. The *P. polita* group contains *P. tuberculata* new species, *P. polita* Malloch, and *P. meridionalis* Hennig. The *P. varipes* group contains *P. cinerea* new species, *P. nigrirarsis* new species, *P. slussi* new species, *P. varipes* Coquillett, *P. latiphallis* new species, *P. melanitida* new name (for *P. nitida* Melander), *P. occidentalis* new species, *P. pruinosa* Melander, *P. hamata* new species, *P. angustata* new species, *P. nitens* (Melander and Spuler), *P. angelica* new species, *P. obscura* new species, and *P. antennalis* Malloch.

Illustrations are provided of male genitalia for the 16 species for which males are known, and of other salient features of both sexes of adults and of the larvae. Scanning electron micrographs of features of adult and immature stages are included. Distribution maps are provided for all species. A phylogenetic analysis of 19 characters of the adults is presented.

All immature stages are described for *P. pruinosa* in southern Ontario where this species is associated with *Schyzachyrium scoparium* (Michaux) Nees (Gramineae: Andropogonaceae). The larvae feed on the mealybug *Trionymus winnemucuae* McKenzie (Homoptera: Pseudococcidae) which lives within the leafsheaths of this grass. Another sympatric species of grass, *Andropogon gerardi* Vitman, supports populations of *P. antennalis* and *P. varipes* and another *Trionymus* species that infests that species of grass. *Pseudodinia melanitida*, which also occurs in southern Ontario, is not associated with either of these grasses.

Introduction

The family Chamaemyiidae is comprised of rather small flies often referred to as aphid-killing flies or silver flies. These descriptive names refer to the larval feeding habits and to the silvery grey vestiture of the adults, respectively. The number of described species in the family, on a worldwide basis, is only several hundred. These are divided among about 20 genera and subgenera, and representatives occur in every zoogeographic region. The vast majority of the species of the family belong to the genus *Leucopis* Meigen and its various subgenera. The genus *Pseudodinia* Coquillett, which is the subject of this study, is relatively small (17 species), and is restricted to the New World from Canada south to Costa Rica.

McAlpine (1963) redefined the family and classified it into two subfamilies, the Cremifaniinae containing only the genus *Cremifania* Czerny, and the Chamaemyiinae containing all the remaining genera [McAlpine 1960 (but see Steyskal 1971 and Griffiths 1972)]. The Chamaemyiinae is comprised of the two tribes, Chamaemyiini and Leucopini. The genus *Pseudodinia* belongs to the Chamaemyiini. Members of the Chamaemyiini are distinguished from those of the Leucopini by a relatively small, bare lunule, and more complete head chaetotaxy. As well, in the male there are two pairs of sternal and tergal elements between the fifth and ninth segments, compared to only one pair of sclerites in the same position in the members of the Leucopini.

Pseudodinia is unique among New World Chamaemyiidae in the frequent reduction of body pruinosity, leaving the frons and abdominal apex shiny black. Also, it is the only genus in the New World in which a solitary, well developed anepisternal seta is present. Dark, paired fasciae or spots on the abdominal tergites, which commonly occur elsewhere in the family, are absent in all species of *Pseudodinia*.

The literature dealing with *Pseudodinia* is restricted to the descriptive works listed by McAlpine (1965), the description of *P. meridionalis* Hennig (1941), and the lectotype designation for *P. polita* Malloch (Frison 1927). To date, there has been no definitive study

made on adults of the genus *Pseudodinia*, and no key to all the described species has yet been published. No life history or larval host associations have been previously documented for any of the species but Barber (1984) discusses some relationships and associations observed in Ontario. Sluss (1977) dealt with morphometric and electrophoretic characterization of some *Pseudodinia* populations in the southwestern United States. He implicated a *Muhlenbergia* species of grass as an associate of *Pseudodinia*.

Materials and Methods

Collections were made primarily in Ontario during the seasons of 1980-1984. The ethanol-preserved Malaise trap residues of several collectors also provided valuable specimens and information. Immature stages of *Pseudodinia* and pseudococcid hosts were obtained in Ontario, primarily through an artificial rearing system described by Barber (1984).

A total of about 3500 adult specimens of *Pseudodinia* were examined, the majority of which were obtained through loans from the institutions and curators listed below. Abbreviations, as indicated in brackets, are used in the text to show specimen deposition. American Museum of Natural History, New York, NY (AMNH), Dr. P. Wygodzinsky; Academy of Natural Sciences of Philadelphia, Philadelphia, PA (ANSP), Dr. D. Azuma; Biosystematics Research Institute, Ottawa, Ontario (BRI), Dr. J.F. McAlpine; Connecticut Agricultural Experiment Station, New Haven, CT (CTAS), K.A. Welch; California Academy of Sciences, San Francisco, CA (CAS), Dr. P.H. Arnaud, Jr.; Cornell University, Ithaca, NY (CUI), Dr. L.L. Pechuman; Institut für Pflanzenschutzforschung, Akademie der Landwirtschaftswissenschaften, Eberswalde, D.D.R. (DDRE), Dr. G. Morge; Field Museum of Natural History, Chicago, IL (FMNH), Dr. J.S. Ashe; University of Guelph, Guelph, Ontario (GUE), Dr. S.A. Marshall; Illinois Natural History Survey, Urbana, IL (INHS), Dr. D.W. Webb; Iowa State University, Ames, IA (ISU), Dr. R.E. Lewis; Natural History Museum of Los Angeles County, Los Angeles, CA (LACM), Dr. C.L. Hogue; Museum of Comparative Zoology, Harvard University, Cambridge, MA (MCZ), Dr. M.K. Thayer and Dr. N.E. Woodley; North Dakota State University, Fargo, ND (NDSU), Dr. E.U. Balsbaugh, Jr.; Kent State University, Kent, OH (OKSU), Dr. B.A. Foote; Oregon State University, Corvallis, OR (OSU), Dr. J.D. Lattin and J.D. Oswald; Frost Entomological Museum, Pennsylvania State University, University Park, PA (PSU), Dr. K.C. Kim and A.L. Norrbom; Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands (RNHL), Dr. P.J. van Helsdingen; University of Arizona, Tucson, AZ (UAT), Dr. F.G. Werner; University of California, Berkeley, CA (UCB), G.W. Ulrich; R.M. Bohart Museum of Entomology, University of California, Davis, CA (UCD), Dr. R.O. Schuster; University of California, Riverside, CA (UCR), Dr. S.I. Frommer; University of Idaho, Moscow, ID (UIM), F. Merickel; Snow Entomological Museum, University of Kansas, Lawrence, KS (UKL), Dr. G.W. Byers; Museum of Zoology, University of Michigan, Ann Arbor, MI (UMIC), M. O'Brien; University of Minnesota, St. Paul, MN (UMIN), Dr. P.J. Clausen; University of New Hampshire, Durham, NH (UNHD), Dr. D.S. Chandler; University of Nebraska State Museum, Lincoln, NE (UNL), Dr. B.C. Ratcliffe; United States National Museum, Washington, DC (USNM), Dr. B.V. Peterson and Dr. W.W. Wirth; Utah State University, Logan, UT (USU), Dr. W.J. Hanson; University of Wyoming, University Station, Laramie, WY (UWY), Dr. R.J. Lavigne; James Entomological Collection, Washington State University, Pullman, WA (WSUP), Dr. R.S. Zack.

Adult specimens preserved in 70% ethanol were processed by serial dehydration to 95% ethanol and then by critical point drying.

The terminology reference systems followed are those of McAlpine (1981) for adults, and Teskey (1981) for larvae, both in the recent Manual of the Nearctic Diptera [McAlpine *et al.* 1981 (but see Griffiths 1972)]. The majority of morphological terms used in the

following sections are illustrated in Figs. 1-65. One departure from McAlpine's terminology is that the setae anteroventral to the genal-occipital furrows and anterodorsal to the postgenal setae are referred to as genal setae. The term subvibrissal setae is not used.

Square brackets — “[]” — are used to insert additional data, or interpretations of existing data on specimen labels.

Measurements of bilateral structures were generally taken from one side only, usually the left side. The origins of the orbital setae were measured on both sides and averaged for each individual. A minimum of ten specimens of each sex were measured for each species where possible. Measurements are reported as ranges where possible but are not to be considered absolute. Several measurements require clarification. Height and length of the compound eye were measured from the anterolateral aspect in nearly a $\frac{3}{4}$ view to provide maximum planar exposure of each dimension. Genal width was measured as the minimum perpendicular distance from the subcranial margin to the compound eye when viewed from slightly below to maximize the planar exposure of this area. Length of flagellomere 1 was measured as the maximum distance from the base of the arista to the apex of flagellomere 1. Widths of wing cells r_1 and r_{2+3} were measured at the level of crossvein dm-cu, perpendicular to vein R_{2+3} . Width of cell r_1 included the entire width of the costal vein while midpoints of veins R_{2+3} and R_{4+5} were used.

Adult Morphology and Taxonomic Characters

Morphological conservatism predominates in *Pseudodinia*. Colour and details of the male terminalia are the characters of most taxonomic value, and are discussed below. For a detailed discussion of the morphology of *Pseudodinia*, see Barber (1984).

Colour. This is the most obviously variable character when comparing species of *Pseudodinia* but it is difficult to use exclusively. The predominant ground colour of the cuticle is black (excluding the wing, calypteres, and halter), with yellow sometimes occurring on the antenna and palp, and always on the fleshy parts of the proboscis and on parts of the legs. Any grey appearance is the product of reclinate microtrichia or pruinosity with the density and angle of view determining the intensity of grey colouration. There are no notal vittae and no abdominal fasciae or spots in species of *Pseudodinia*.

The principal areas where pruinosity is taxonomically significant are the frons, abdominal tergites, gena, parafacial, and notum.

Male terminalia. Tergite 6 is divided medially (Fig. 10) except in members of the *polita* group (Fig. 8; male of *P. tuberculata* new species not known), and *P. cinerea* new species (Fig. 9) and *P. nigratarsis* new species of the *varipes* group. One specimen each of *P. varipes* Coquillett and *P. occidentalis* new species, have a complete and partially divided tergite 6, respectively, suggesting that unless these specimens are misidentified, tergite 6 can vary intraspecifically.

The lengths of the tergite 6 and syntergosternite 7+8, relative to tergite 5, are useful only in the extremes where, for example, syntergosternite 7+8 is 0.2-0.3 times the length of tergite 5 in members of the *polita* group, 0.3 times in *P. angelica* new species and *P. nigratarsis*, and 0.4 times or 0.4-0.5 times in all other species of the *varipes* group.

Sternites 6 and 7 provide some useful differences in the degree to which a strap-like sclerite is present on the left side. This is best developed in the *polita* group where it runs from the left sensory setula of sternite 6 to the left sensory setula of sternite 7, encircles spiracle 7, and continues completely across the dorsum as a narrow sclerotized rim on the basal margin of syntergosternite 7+8 (Fig. 8). This sclerite is variably developed in the *varipes* group but never extends beyond spiracle 7 (Fig. 9). The predominant condition has two separate sclerotized patches, one on the anterolateral margin of each of sternites 6 and 7 (Fig. 10).

The lateral profile of the epandrium, paramere, and aedeagus are extremely important. That of the gonopod is somewhat more variable and must be considered in combination with other characters. The relative lengths of the gonopod and paramere are useful in distinguishing *P. polita* (Fig. 13) from *P. meridionalis* (Fig. 14) and for recognizing *P.*

nigritarsis (Fig. 16), all three species having an elongate gonopod. The gonopod usually bears two or three setae (rarely one) in all species except the holotype of *P. nigritarsis* which has three or four. The pattern of setulae on the parameres is useful only in defining the two species groups. The shape of sternite 10 is useful in defining the *polita* group and *P. cinerea*. For details, reference to the descriptions of the species groups should be made.

Taxonomically, the aedeagus is perhaps the most important genitalic structure. Its relative length, curvature, and ventral outline have proved useful in recognizing some otherwise cryptic species such as *P. pruinosa* Melander and *P. latiphallis* new species. The curvature of the aedeagus and the degree to which a pair of preapical ventral keels is developed are useful in distinguishing sympatric populations of *P. varipes* (Fig. 21) and *P. pruinosa* (Fig. 26) in Ontario.

Female terminalia. Very little discriminatory information is provided by the female terminalia. The greatest morphological divergence exists between the two species groups and yet the female terminalia are very similar (Figs. 11-12). Tergite 6 is divided medially in the *varipes* group (Fig. 12) but is complete in the *polita* group (Fig. 11). The segments posterior to this are predominantly weakly sclerotized and their limits are not readily defined.

Pseudodinia Coquillett

Pseudodinia Coquillett, 1902: 187. Type-species *Pseudodinia varipes* Coquillett 1902: 187 (original designation).

Pseudodinia; Melander 1913: 295; Malloch 1915: 151; Malloch 1921: 347; Frison 1927: 196; Curran 1934: 365; Malloch 1940: 268; Hennig 1941: 63; McAlpine 1960: 53; McAlpine 1965: 708.

Diagnosis. [for a detailed description see Barber (1984)]. Chamaemyiini with the following characteristics. Small flies of about 2-4 mm. in length. Colour ranging from sparsely pruinose or shining black, to densely pruinose or dull grey; apical abdominal tergites usually bare especially in females. No mesonotal vittae and no contrasting black spots or fasciae on abdomen. Usually some yellow on tarsi, tibiae, and knees, and occasionally on palp and antenna. Calypteres and halter white to yellow. Wing hyaline to lightly infusate. Flagellomere 1 subovate, rarely with an anterodorsal angle. Two reclinate orbital setae, 0+2 dorsocentral setae, and one anepisternal seta present. Paramere with medially bevelled apex bearing one outstanding preapical setula on medioventral surface.

KEY TO THE SPECIES OF *PSEUDODINIA*

(Species descriptions are arranged in the order in which they appear in the key.)

1. Lower orbital seta arising at or behind 0.4 (usually 0.2 or less) of frontal length (Figs. 1-2, 42). Orbits with a complete series of erect to reclinate setulae; these often longer anteriorly, especially in males. Erect setulae sparsely scattered over most of frons; these weaker than ocellar setulae. Anepisternal seta arising at or above 0.6 of anepisternal height (Fig. 4b). Cell r_{2+3} 1.2-1.5X width of cell r_1 at level of crossvein dm-cu (Fig. 6). Tibiae entirely yellow *polita* group 2
- Lower orbital seta arising at or anterior to 0.4 (usually 0.5-0.6) of frontal length (Fig. 3, 44). Orbits with only short proclinate and a few reclinate setulae in anterior half. About 25-30 proclinate setulae on anterior half of frons; these subequal to ocellar setulae. Anepisternal seta arising at 0.5 of anepisternal height (Fig. 5b). Cell r_{2+3} 0.8-1.1X width of cell r_1 at level of crossvein dm-cu (Fig. 7). Tibiae with at least basal third darkened *varipes* group 4
2. Lower orbital seta arising at about 0.4 of frontal length (Fig. 1). Median tuberculate prominence present on lower margin of face. Southern Mexico *tuberculata* new species
- Lower orbital seta arising at or behind 0.2 of frontal length (Figs. 2, 42). Facial

- prominence not developed 3
3. Orbital setae usually reduced (Figs. 2, 42); upper orbital seta 0.3-0.7X length of inner vertical seta, subequal to or shorter than postocellar seta; lower orbital seta even shorter, often barely distinguishable from adjacent setulae. Male genitalia as in Figs. 13, 43; epandrium relatively elongate distal to condyle; paramere at least 3.0X length of gonopod; tip of aedeagus gradually tapering in ventral view, with low median carina on swollen ventral surface. Eastern North America w. to Nebraska *polita* Malloch
- Orbital setae usually longer; upper orbital seta 0.5-0.6X length of inner vertical seta, distinctly longer than postocellar seta; lower orbital seta slightly shorter than, or subequal to, upper orbital seta. Male genitalia as in Fig. 14; epandrium more quadrate; paramere shorter, at most 2.5X length of gonopod; aedeagus abruptly narrowed preapically in ventral view, terminating in a truncate tip, apicoventral surface swollen but lacking median carina. Southern Mexico; Costa Rica ... *meridionalis* Hennig
4. Frons entirely pruinose grey 5
- Frons bare, shiny black on at least anterior 0.5 10
5. Antenna and palp entirely dark brown to black 6
- Antenna with at least scape, pedicel, and basal 0.3 of flagellomere 1 paler, usually yellow (rarely brown in *P. antennalis*). Palp entirely yellow 8
6. Densely pruinose grey species. Abdomen entirely pruinose in both sexes. Tergite 6 of male complete (Fig. 9), not divided medially. Male genitalia as in Fig. 15; epandrium broadly triangular; paramere broadened apically; sternite 10 linear; aedeagus relatively narrow in ventral view. Colorado; central Mexico *cinerea* new species
- Less densely pruinose species. Abdomen of male completely pruinose; of female with successively larger sublateral bare areas on tergites 3-5, leaving tergite 5 almost completely bare. Tergite 6 of male divided medially (Fig. 10). Male genitalia as in Figs. 31-32; epandrium strongly narrowed apically; paramere not broadened apically; sternite 10 quadrate to trapezoidal; aedeagus variable 7
7. Male genitalia as in Fig. 30; apex of aedeagus recurved dorsally forming an acute point, and with no preapical ventral raised area or keels. Tarsomeres 3-5 usually only slightly darkened to brown. Arizona; Colorado; New Mexico *hamata* new species
- Male genitalia as in Fig. 31; apex of aedeagus truncate, and with ventral preapical median area slightly raised with keels poorly defined. Tarsomeres 2-5 or 3-5 usually darkened to brown or black. Arizona; New Mexico; central Mexico *angustata* new species
8. Tarsomeres 2-5 gradually darkening to dark brown or black apically. Male genitalia as in Fig. 33; aedeagus nearly parallel-sided on apical half, with apical emargination well developed, and with preapical keels poorly defined, but median trough well developed. California *angelica* new species
- Tarsi entirely yellow. Male genitalia as in Figs. 34-37; aedeagus more bulbous on apical half, apical emargination lacking or poorly developed, and with preapical ventral keels poorly developed and median trough variable 9
9. Wing membrane distinctly infuscated in male (female not known). Male genitalia as in Fig. 37; epandrium relatively long and narrow; aedeagus widely truncate apically, and with median trough very well developed. Southern Mexico .. *obscura* new species
- Wing membrane hyaline. Male genitalia as in Figs. 34-36; epandrium relatively short and broad; aedeagus more rounded apically, and with median trough very poorly developed. Eastern North America to Manitoba; Arizona; New Mexico; central Mexico *antennalis* Malloch

10. Tarsi entirely black; legs black except narrowly yellow on knee of foreleg, and on apical 0.4 of all tibiae. Male genitalia as in Fig. 16; gonopod narrow and elongate; preapical ventral surface of aedeagus with median trough poorly defined, and with keels poorly developed, but noticeably higher basally. Santa Cruz Island, California
 *nigritarsis* new species
 — At least tarsomere 1 yellow; legs black to pruinose grey with variable extent of yellow on knees and tibiae. Male genitalia as in Figs. 17-29, 32, 45; gonopod shorter; preapical ventral surface of aedeagus variable 11
11. Abdomen of male with pruinosity extending broadly across full length of tergites 1-4; sublateral bare areas sometimes present on tergite 4 and with tergite 5 dorsally bare, or entire abdomen lightly pruinose. Abdomen of female with sublateral bare areas present on tergites 3 and 4 and with tergite 5 bare dorsally; pruinosity on tergite 4 extending full length at least as a narrow median strip of scattered microtrichia. Vertex and ocellar triangle distinctly pruinose. Male genitalia as in Fig. 32; epandrium strongly narrowed, apices nearly parallel-sided, in lateral view; apex of aedeagus truncate, in ventral view, and with preapical area slightly raised with slight median depression. Washington; Wisconsin; Wyoming to Arizona and New Mexico
 *nitens* (Melander and Spuler)
 — Abdomen of male with pruinosity extending broadly across tergites 1-3 and narrowly across tergite 4; tergite 5 entirely bare; tergites 2-4 with successively larger sublateral bare areas, leaving tergite 4 predominantly bare. Abdomen of female with pruinosity on tergite 4 somewhat less extensive than in male; if median strip reaches apex of tergite 4, then vertex and ocellar triangle bare. Male genitalia as in Figs. 17-29, 45; epandrium broader, more gradually tapered or abruptly narrowed preapically (Fig. 18); apex of aedeagus variable 12
12. Ocellar seta usually reduced, 0.6-0.7X length of upper orbital seta. Male genitalia as in Fig. 22; epandrium broad, in lateral view, with apices curved posteriorly; aedeagus heavily sclerotized, usually gradually curved in lateral view, apex broadly rounded in ventral view, and with preapical keels well developed. Arizona; central Mexico ...
 *latiphallis* new species
 — Ocellar seta usually longer, 0.7-1.1X length of upper orbital seta. Male genitalia as in Figs. 17-18, 20-29, 45; epandrium more elongate, in lateral view, apices not curved posteriorly; aedeagus less sclerotized, with curvature, apex, and keels variable 13
13. Strap-like sclerite on left side of sternites 6 and 7 of male, a single uninterrupted piece, bearing both left sensory setulae and encircling spiracle 7 (as in Fig. 9). Male genitalia as in Fig. 17; paramere nearly straight on medial surface, in ventral view; apex of aedeagus with ventral area raised, but with only an indistinct median depression. Arizona; New Mexico *slussi* new species
 — Strap-like sclerite represented at most by two discrete, often indistinctly sclerotized, anterolateral areas on left side of sternites 6 and 7 (Fig. 10); that of sternite 7 often continuing to encircle spiracle 7. Male genitalia as in Figs. 18, 20-29, 45; paramere sinuate on medial surface, in ventral view; apicoventral surface of aedeagus usually with moderately to well developed median trough and preapical keels 14
14. Male genitalia as in Fig. 18; epandrium abruptly narrowed preapically, medially curved; aedeagus with preapical keels and median trough, well developed, and with rounded apex, in ventral view. Thorax usually only lightly pruinose to shiny. Eastern Quebec to Yukon, s. to Indiana and Colorado *melanitida* new name
 — Male genitalia as in Figs. 20-29, 45; epandrium with apices broader, or if acute, then gradually narrowed, not medially curved; aedeagus variable. Thorax often more densely pruinose 15
15. Male genitalia as in Figs. 19-21; aedeagus gradually curved in lateral view with apex

- rounded in ventral view, and with preapical keels usually well developed. Western specimens usually with short paramere, elongate gonopod, and anterodorsally angular flagellomere 1 (Fig. 20). British Columbia s. to California, Nevada, and New Mexico; Ontario *varipes* Coquillett
- Male genitalia as in Figs. 23-29, 45; aedeagus with more abrupt angulation at about basal 0.3, with apex usually more truncate in ventral view, and with preapical keels variably developed 16
16. Male genitalia as in Figs. 23-24; aedeagus usually with widely truncate apex and deep median trough. Vertex and ocellar triangle bare. Thorax shiny; anterior acrostichal setulae usually extending anterior to level of postpronotal seta and subequal in strength to following acrostichals. British Columbia s. to California and New Mexico *occidentalis* new species
- Male genitalia as in Figs. 25-29, 45; aedeagus usually with narrower apex, but if as widely truncate, then median trough not as deep and ocellar triangle and thorax very pruinose. If ocellar triangle and vertex completely bare and thorax lightly pruinose, then anterior acrostichal setulae usually not extending anterior to level of postpronotal seta, but if so, then weaker than following acrostichals. Widespread; Ontario to British Columbia, s. to Tennessee and southern Mexico *pruinosa* Melander

The *Pseudodinia polita* Group

This group contains three species, *P. tuberculata*, *P. polita*, and *P. meridionalis*. They form a cluster of closely related species which together constitute the sister group of the remainder of the genus which is treated as the *varipes* group (Fig. 72).

Description (see key for diagnosis). Body length 1.8-3.1 mm. Predominantly shiny black with reduced pruinosity. Frons bare, shiny black, rarely with thin pruinosity (occasional specimens of *P. polita*). Antenna brown to black, often basally paler. Trochanters, tibiae, tarsi, and tips of femora yellow. Wing distinctly infuscated. Abdomen with dorsal wedge of pruinosity extending broadly across basal half of tergite 2 to basal third of tergite 3 leaving sublateral bare areas; remainder shiny black to apex of tergite 5.

Head (Figs. 1-2). Height of compound eye 1.1-1.2X length, 6.4-10.0X genal width. Genal width 0.4-0.7X height of flagellomere 1. Lower margin of face projecting abruptly, rarely produced into median swelling. Frontal width 0.8-1.2X length. Upper orbital seta arising from slightly posterior to level of median ocellus to about 0.1 of frontal length. Lower orbital seta usually arising at 0.1-0.2 (0.4 in *P. tuberculata*) of frontal length. Orbits also with complete series of erect to reclinate setulae; setulae often longer anteriorly, especially in males. Frons with weaker, erect to reclinate setulae sparsely scattered over most of surface; setulae weaker than ocellar setulae. Ocellar setulae in two or three pairs. Length of flagellomere 1 0.8-1.0X height; anterodorsally rounded.

Thorax (Fig. 4). Acrostichal setulae denser than in *varipes* group. Anepisternal seta arising at 0.6-0.8 of anepisternal height. Wing cell r_{2+3} 1.2-1.5X width of cell r_1 at level of crossvein dm-cu (Fig. 6).

Abdomen. Tergal and sternal setae more dense (Fig. 8) than in *varipes* group.

Male terminalia (Fig. 8; male of *P. tuberculata* not known). Tergite 6 complete, not divided medially, length 0.2-0.3X tergite 5; syntergosternite 7+8 0.2-0.3X length of tergite 5. Strap-like sclerite on left side extending posterodorsally from left sensory setula of sternite 6 to include sensory setula of sternite 7, encircling spiracle 7 and continuing completely across dorsum as narrow sclerotized band fused to anterior margin of syntergosternite 7+8. Genitalia as in Figs. 13-14, 43. Epandrium broadly oval, in lateral view, without strong anteroventral emargination; condyle developed into hook. Paramere and gonopod elongate; paramere 2.2-3.0X gonopod length. Paramere with scattered setulae, and with a cluster of setulae extending short distance basoventrally from level of outstanding preapical setula. Gonopod bearing two or three setae. Aedeagus elongate, basally curved through much more than 90°; preapical ventral area swollen, lacking median

trough (medially carinate in *P. polita*). Sternite 10 quadrate, slightly emarginate basally; condyles relatively long.

Female terminalia (Fig. 11). Tergite 6 complete, not divided medially, about 0.6X length of tergite 5.

***Pseudodinia tuberculata* new species**

Figs. 1, 66.

Description. Holotype female (male not known). Body length 2.6 mm. Colour as in *P. polita* except as follows. Antenna and palp entirely black. No evidence of frontal pruinosity. Abdomen with dorsal wedge of pruinosity extending broadly onto basal third of tergite 3.

Head (Fig. 1). Height 1.3X length; width 1.8X length. Height of compound eye 1.1X length, 6.4X genal width. Frontal width 1.0X length. Orbital setae strong; upper orbital seta 0.8X length of inner vertical seta, arising slightly anterior to level of median ocellus; lower orbital seta 0.8X length of upper orbital seta, arising at about 0.4 of frontal length. Ocellar seta 0.6X length of upper orbital seta. Two pairs of ocellar setulae present. Gena with five or six setae. Length of flagellomere 1 0.8X height. Lower margin of face with a protruding medial prominence (Fig. 1).

Thorax. Anepisternal seta arising at 0.6 of anepisternal height. Katepisternum with one setula anterior to posterodorsal seta. Anterior acrostichal setulae extending anterior to level of postpronotal seta, but weaker than following acrostichals.

Type material examined. *Holotype* ♀. MEXICO. Chiapas: San Cristobal [de las Casas], 7000', 22.v.1969, H.J. Teskey (BRI).

Remarks. This species can be separated from the other two members of this species group by the more anteriorly placed orbital setae and the obviously bulbous swelling on the lower medial margin of the face.

Tergite 6 of the intact female holotype can be seen to be complete, not divided medially. This is consistent with other external characters of the *polita* group, and the unknown male is expected to have similarly consistent external and internal characters.

Distribution (Fig. 66). *Pseudodinia tuberculata* is known only from the type locality in Chiapas, Mexico.

Biology. The holotype was taken in the same locality, but not on the same day, as three specimens of *P. meridionalis*. No specific data are known.

Etymology. From the Latin *tuber* meaning "swelling", the specific epithet *tuberculata* refers to the median swelling on the lower margin of the face.

***Pseudodinia polita* Malloch**

Figs. 2, 4, 6, 8, 11, 13, 42-43, 66.

Pseudodinia polita Malloch, 1915: 152.

Pseudodinia polita; Malloch 1921: 347; Frison 1927: 196 (lectotype designation); Curran 1934: 365; Malloch 1940: 268; Hennig 1941: 64; McAlpine 1965: 708.

Description. Body length 1.8-3.1 mm. Body generally with reduced pruinosity, appearing shiny black. Surface of frons bare, shiny black, rarely with obscure pruinose appearance anteriorly. Parafacial, gena, and face pruinose; face shinier medioventrally. Antenna usually brown, rarely black; scape, pedicel, and arista usually paler than flagellomere 1. Palp brown to black. Thoracic pruinosity light, heaviest along notopleural suture. Legs as for species group. Wing usually infusate, rarely hyaline. Abdomen of male with dorsal wedge of pruinosity usually extending across basal 0.5-0.8 of tergite 2; at most, pruinosity extending to posterior margin of tergite 2 with basomedial patch on tergite 3, leaving tergite 2 with extensive sublateral bare areas, and tergites 3-5 predominantly to entirely bare. Of female, with pruinosity slightly less extensive.

Head (Figs. 2, 42). Height 1.2-1.5X length; width 1.7-2.0X length. Height of compound eye 1.1-1.2X length, 6.6-10.0X genal width. Frontal width 0.8-1.2X length. Orbital setae reduced, arising on posterior 0.2 of frons; upper orbital seta 0.3-0.7X length of inner vertical seta, arising from slightly posterior to slightly anterior to level of median ocellus in male, in female arising to about 0.1 of frontal length; lower orbital seta even shorter, often difficult to distinguish from adjacent orbital setulae, arising at 0.1-0.2 of frontal length. Orbital setulae usually increasing in length anteriorly, particularly in male. Ocellar seta 1.0-1.5X length of upper orbital seta. Ocellar setulae in two or three pairs. Gena with 5-10 setae. Length of flagellomere 1 0.8-1.0X height.

Thorax (Figs. 4, 6). Anepisternal seta arising at 0.7-0.8 of anepisternal height. Katepisternum with 1-3 setulae anterior to posterodorsal seta. Anterior acrostichal setulae often extending anterior to level of postpronotal seta but weaker than following acrostichals.

Male terminalia (Fig. 8). Tergite 6 0.2-0.3X length of tergite 5; syntergosternite 7+8 0.2-0.3X length of tergite 5. Genitalia as in Figs. 13, 43. Epandrium relatively elongate-oval, somewhat tapered apical to the condyle. Paramere about 3.0X length of gonopod. Apex of aedeagus gradually tapering in ventral view; preapical ventral area broadly swollen, with a median carina.

Type material examined. *Lectotype* ♀ and *allolectotype* ♂ (neither dissected). U.S.A. **Illinois:** Centerville[?] (White Heath), 16.viii.1914, Sangamon River, (C.A. Hart and J.R. Malloch) (INHS). The lectotype is badly damaged, possibly by dermestids, and has apparently been remounted on the original point. It lacks the head and several legs. *Paralectotypes* (3 ♂, 3 ♀). U.S.A. **Illinois:** same data as lectotype, 1 ♀ (INHS), 1 ♂ (AMNH), 2 ♂ (USNM), 1 ♀ (BRI); Urbana, 30.viii.1914, dredge ditch [J.R. Malloch], 1 ♀ (INHS). Frison (1927) corrected the collection dates for the type material which were apparently reported incorrectly by Malloch (1915). All the type material has been seen and these corrections are confirmed above. However, the type locality of Centerville was apparently doubted by Frison since the Sangamon River is not nearby, and he inserted "White Heath", as well as the names of the collectors. All paralectotypes bear "paratype" labels.

Other material examined. (36 ♂, 28 ♀). CANADA. **Ontario:** Windsor, 11.viii.1976, S.A. Marshall, 1 ♂ (GUE). U.S.A. **District of Columbia:** [no locality], 11.vi.1926, J.M. Aldrich, 1 ♀ (USNM); Washington, [no date], A.L. Melander Collection, 1 ♂ (USNM). **Florida:** Torreya State Park, 28.iv.1952, O. Peck, 1 ♂ (BRI). **Georgia:** Tennessee River, 13.vii.1957, C.J. Durden, 1 ♂ (BRI); Rabun Co., Addie Branch, E. Fork Chattooga River, 2400', 1.viii.1957, J.G. Chillcott, 1 ♂ (BRI); Rabun Co., Rabun Bald, 3000', 14.viii.1957, J.G. Chillcott, 1 ♀ (BRI); Fanning Co., Margaret [Margaret], 22.vii.1957, J.G. Chillcott, 1 ♀ (BRI). **Illinois:** Urbana, Brownfield Woods, 20.vi.1919, [no collector] 1 ♂ (INHS); Urbana, 9.viii.1920, J.R. Malloch, 1 ♀ (INHS); White Heath, 30.v.1915, [J.R. Malloch] 1 ♂ (INHS); DuPage Co., Argonne Nat. Lab., 1.vii.1972, leg. D. Pearson, 1 ♂ (FMNH); Springfield, 24.ix.1939, Mohr and Burks, 1 ♀ (INHS); Carbondale, 15.v.1910, [J.R. Malloch] 1 ♀ (INHS); Du Bois, 24.v.1917, [J.R. Malloch], 1 ♀, 10.v.1918, J.R. Malloch, 1 ♀ (INHS); Augerville, 6.vi.1915, [J.R. Malloch], 1 ♀ (INHS). **Indiana:** LaFayette, J.M. Aldrich, 14.vii.1915, 1 ♂, 9.vi.1916, 1 ♂, 4.vii.1916, 1 ♀, 5.viii.1917, 1 ♂, 21.vii.1917, A.L. Melander Collection, 1 ♂ (USNM); Parke Co., 4mi W Rockville, Hajji Hollow, 12.vi.1975, leg. H.S. Dybas, Malaise trap, 1 ♀ (FMNH). **Kentucky:** Pineville, 28.viii.1940, B.D. Burks, 1 ♀ (INHS). **Maryland:** Montgomery Co., Rockville, G. Steyskal, 13.vi.1965, 1 ♀, 30.v.1969, 1 ♂ (USNM); Beltsville, 21.v.1922, J.R. Malloch, 1 ♂ (USNM); Jacksons Is., 30.vi.1914, R.C. Shannon, 1 ♀ (USNM); Hyattsville, 2.viii.1908, F. Knab, 1 ♀ (USNM); Plummers Is., R.C. Shannon, 14.v.1915, 1 ♂, 26.vi.1915, 2 ♂, 3.viii.1915, at light, 1 ♂ (USNM); Plummers Is., K.V. Krombein, 8.ix.1963, 1 ♂, 21.vii.1971, 1 ♂ (USNM); Glen Echo, J.R. Malloch, 23.vii.1921, 1 ♂, 8.viii.1921, 1 ♀, 18.vi.1922, 1 ♂, 25.vi.1922, 1 ♂, 10.vi.1923, 1 ♂, 1.vii.1923, 1 ♀ (USNM). **Michigan:** Midland Co., 21.vii.1952, R.R. Dreisbach, 1 ♂ (USNM); Ingham Co., 11.vii.1949, R. Namba, 1 ♂ (USNM). **Mississippi:** Lafayette Co., [?].vi.1934, F.M. Hull, 1 ♀ (BRI). **Missouri:** Boone Co., Columbia, F.D. Parker, Malaise trap, 17-31.viii.1968, 1 ♂, 4.ix.1968, 1 ♀, 20.v.1970, 1 ♀ (USNM); Lincoln Co., Cuiivre River State Park, 26.viii.1961, J.L. Laffoon, 1 ♂ (ISU). **Nebraska:** Crete, 3.vii.1960, W.F. Rapp, 1 ♂ (UNL). **New Jersey:** Riverton, 6.vii.1917, C.W. Johnson, 1 ♀ (MCZ). **New York:** Rochester, 8.vii.1933, R.L. Post, 1 ♂ (USNM). **North Carolina:** Looking Glass Rock nr. Pisgah Forest, 2500', 19.vii.1957, J.G.

Chillcott, 3 ♂ (BRI); Macon Co., Wayah Gap, 4100', 29.vii.1957, J.G. Chillcott, 1 ♂ (BRI); Pisgah Forest, 12.viii.1957, W.R. Richards, 1 ♀ (BRI); Highlands, Whiteside Mt., 21.viii.1957, C.J. Durden, 1 ♀ (BRI). **Virginia:** Fairfax Co., Dead Run, 29.viii.1915, R.C. Shannon, 1 ♂ (USNM); Glencarlyn, J.R. Malloch, 2.vi.1925, 1 ♀, 11.vii.1925, 1 ♂ (USNM); Great Falls, [?].vi.1922, J.M. Aldrich Collection, 1 ♀ (USNM); Falls Church, 20.vi.[?], N. Banks Collection, 1 ♀ (MCZ); Bon Air, 16.viii.1936, [no collector], 1 ♀ (USNM). One additional male with only the following data: W.H., 11.viii.[?], A.H. Sturtevant Collection (USNM).

Remarks. This species can be distinguished from the two other members of this small species group by the relatively reduced orbital setae, paler antenna, details of the male genitalia (male of *P. tuberculata* not known), and its more northerly distribution.

Malloch (1915) described the frons of *P. polita* as "about twice as long as broad". This observation is misleading since measurements of four paralectotypes yielded a range of frontal length 1.0-1.1X width compared to measurements of 16 other specimens which gave a range of frontal length 0.8-1.2X width at the level of the median ocellus. He later illustrated the head of *P. polita* (Malloch 1921, P1.XLVI, Fig. 7), and in his key (p. 268) he referred to the frons as distinctly longer than wide. Measurements of his figure give a length near 1.2X the width. The possibility that he was including the vertex in his measurements may account for this discrepancy.

Curran (1934) remarked that one female paralectotype of *P. polita* "lacks the two strong frontals [orbital setae] and I would place it in *Paraleucopsis* but it lacks the setulae on the underside of the costa". This remark was necessitated by his use of the presence or absence of "distinct" orbital setae to distinguish four genera of Chamaemyiini from *Leucopsis* and *Paraleucopsis*. The reduction of the orbital setae is best shown by *P. polita* and, to a lesser extent, by *P. meridionalis* and is also associated with a posterior placement on the orbital plates.

Variation. The broken female from Margaret, Georgia, might represent a new species but is provisionally treated under this name. The frons is obviously pruinose though somewhat dirty. The variation in the frontal vestiture of the males suggests that this could be only an extreme variant.

One female paralectotype has the anepisternal seta duplicated on the left side.

Distribution (Fig. 66). *Pseudodinia polita* is widely distributed in eastern North America. It is allopatric with respect to the other two species in this species group. The doubtful Centerville "type locality" (see above) is not included.

Biology. No specific biological information is available, but several of the collection labels above suggest riparian habitats. The complete tergite 6 of the female, a characteristic of this species group, suggests adaptation to oviposition in sites where the lateral compression of the terminalia is not required to the same degree as those of the *varipes* group, in which tergite 6 is divided in females of all members. Specimens of *Plunomia elegans* Curran have been collected from sedges growing in wetlands in Ontario and Manitoba and females of *Plunomia* species have a similarly complete female tergite 6. There is a possibility that this characteristic has arisen convergently in *Plunomia* and the *polita* group of *Pseudodinia*.

Some specimens of *P. antennalis* bear the same collection data as some specimens of *P. polita*, indicating that perhaps these two species can share a similar generalized habitat.

Pseudodinia meridionalis Hennig

Figs. 14, 66.

Pseudodinia meridionalis Hennig, 1947: 63.

Description. Body length 2.1-2.9 mm. Colour as in *P. polita* except antenna and palp usually black, sometimes narrowly brown basally.

Head. Height 1.3-1.5X length; width 1.8-2.0X length. Height of compound eye 1.1-1.2X length, 6.7-9.3X genal width. Frontal width 1.0-1.2X length. Upper orbital seta 0.5-0.6X length of inner vertical seta, arising at or slightly anterior to level of median

ocellus; lower orbital seta 0.7-1.0X length of upper orbital seta, arising at 0.2 of frontal length. Ocellar seta 0.9-1.2X length of upper orbital seta. Ocellar setulae in two or three pairs, the anterior pair sometimes nearly subequal to ocellar seta. Gena with 4-6 setae. Length of flagellomere 1 0.8-0.9X height.

Thorax. Anepisternal seta arising at 0.6-0.7 of anepisternal height. Katepisternum with one or two setulae anterior to posterodorsal seta. Anterior acrostichal setulae sometimes extending anterior to level of postpronotal seta, but weaker than following acrostichals.

Male terminalia. Tergite 6 0.2-0.3X length of tergite 5; syntergosternite 7+8 0.2-0.3X length of tergite 5. Genitalia as in Fig. 14. Epandrium less tapered than in *P. polita*. Paramere about 2.2X gonopod length. Aedeagus narrowing preapically in ventral view, apex rather truncate; preapical ventral area broadly raised but no median carina evident.

Type material examined. *Holotype* ♂ (dissected). COSTA RICA. San José: La Caja, 8km W San José, [??], 1930, leg. H. Schmidt (DDRE). Dr. Morge (at DDRE) has indicated that the microscope slide mount of the dissected abdomen is apparently lost. Two paratype males were dissected and examined. *Paratypes* (6 ♂, 2 ♀, and 1 lacking head and abdomen). Same data as holotype (DDRE). Hennig (1947) listed only 6 male and 1 female paratypes.

Other material examined (1♂, 2♀). MEXICO. Chiapas: San Cristobal de las Casas, 7087', 28.vi.1969, B.V. Peterson, 1♂, 7000', 20.v.1969, H.J. Teskey, 1♀, 7200', 27.v.1969, W.R. Mason, 1♀ (BRI).

Remarks. This species can be distinguished from *P. polita* by the usually longer orbitals and darker antenna, by details of the male genitalia, and by its more southerly distribution. The sympatric *P. tuberculata* has the orbitals displaced anteriorly, and the median margin of the face has a distinctive swelling.

Hennig (1947) described this species without having seen any other representative of the genus, working only from published descriptions. There are no published figures of the male genitalia of any *Pseudodinia* species except for that in his description of this species. Hennig's use of the "long frons" of *P. polita* (see "Remarks" under *P. polita*) to differentiate between these two species is confusing. *Pseudodinia meridionalis* specimens exhibit frontal dimensions wider than those of many *P. polita* specimens, but there is considerable overlap in these dimensions in the two species.

Variation. One paratype male has a low facial projection medially on the lower margin, similar to that of *P. tuberculata*, but much smaller. Other specific characters of the head, thorax, and genitalia hold true for this specimen.

The type material is dirty and abraded. Some of the relative lengths of the head setae might be underestimated since some of the setal sockets are large, and some of the setal stumps are thick.

Distribution (Fig. 66). *Pseudodinia meridionalis* is known from only one locality in Costa Rica and one locality in Mexico. This species is known to be sympatric with *P. tuberculata* and *P. obscura* but allopatric to its proposed sister species, *P. polita*.

The *Pseudodinia varipes* Group

This group contains all species of *Pseudodinia* that are not referable to the *polita* group, a total of 14 species. Several of the included species may represent complexes of incipient or sibling species. These are discussed after the respective descriptions.

Description (see key for diagnosis). Body length 1.8-3.5 mm. Predominantly shiny black to densely grey pruinose. Antenna and palp usually black, sometimes basally pale, rarely nearly entirely yellow. Frons entirely pruinose or bare from anterior margin to at least level of upper orbital. Trochanters, femora (except knees), and at least basal third of tibiae, grey to black, matching general body colouration. Knees and apical 0.2-0.3 (sometimes 0.4-0.7)

of tibiae usually yellow. Tarsi yellow or darkened to brown or black, especially tarsomeres 3-5. Wing usually hyaline to slightly infuscate, rarely distinctly so (*P. obscura*). Abdomen of male with tergites 1-5 entirely pruinose or with successively larger sublateral bare areas on tergites 2-5, 3-5, or 4-5, narrowing the dorsal pruinosity in the form of a wedge and often leaving tergites 4-5 predominantly to entirely bare. Of female, with tergites 1-5 completely pruinose in *P. cinerea* only, otherwise with sublateral bare areas on tergites 2-5 or 3-5 leaving tergites 4 and 5 predominantly bare.

Head (Figs. 3, 44, 46). Height 1.0-1.5X length; width 1.5-2.1X height. Height of compound eye 0.8-1.1X length, 3.5-6.8X genal width. Genal width 0.6-1.0X height of flagellomere 1. Lower margin of face receding, not projecting abruptly. Frontal width 1.1-1.7X length. Upper orbital seta arising at 0.1-0.3 of frontal length. Lower orbital seta arising at 0.4-0.7 (usually 0.5-0.6) of frontal length. Orbits lacking complete series of reclinate setulae. Frons (including orbits) with transverse band of about 25-30 proclinate setulae extending from anterior margin to, or slightly posterior to, level of lower orbital seta; only a few of these setulae reclinate and restricted to level of lower orbital seta; setulae subequal in strength to ocellar setulae. Ocellar setulae in 1-3 pairs. Length of flagellomere 1 usually 0.8-1.0X height (Figs. 19c, 21c), often 1.1X in *P. varipes* (Fig. 20c); anterodorsal margin rounded, sometimes with variably developed angle (Fig. 20c).

Thorax (Fig. 5). Acrostichal setulae less dense than in *polita* group. Anepisternal seta arising at 0.5 of anepisternal height. Wing cell r_{2+3} 0.8-1.1X width of cell r_1 at level of crossvein dm-cu (Fig. 7).

Abdomen (Figs. 9-10). Tergal and sternal setae less dense than in *polita* group.

Male terminalia. Tergite 6 usually divided medially (Fig. 10), except in *P. cinerea* (Fig. 9), *P. nigritarsis*, and one occurrence in each of *P. occidentalis* and *P. varipes*, 0.2-0.4X length of tergite 5; sytergosternite 7+8 0.3-0.5X length of tergite 5. Strap-like sclerite on left side of sternites 6 and 7 variably developed (Figs. 9-10), not extending beyond spiracle 7, never fusing with the posterior margin of sytergosternite 7+8; sometimes absent. Genitalia as in Figs. 15-37, 45. Epandrium never broadly oval, at most broadly triangular (*P. cinerea*, Fig. 15); usually anteroventrally emarginate producing tapered apices; condyle acute but never hooked. Paramere variable, usually considerably more than 4.0X gonopod length; with only scattered setulae, lacking distinct apical cluster of setulae of *polita* group. Gonopod usually poorly to moderately differentiated [exceptionally well developed in *P. nigritarsis* (Fig. 16) where paramere is only 2.8X gonopod]. Aedeagus relatively shorter and less angular basally than in *polita* group; preapical ventral area variable, usually with median depression or trough bordered by two keels. Sternite 10 usually quadrate to trapezoidal (linear in *P. cinerea*), variably emarginate basally; condyles relatively short.

Female terminalia (Fig. 12). Tergite 6 divided medially, 0.4-0.5X length of tergite 5.

Pseudodinia cinerea new species

Figs. 9, 15, 67.

Description. Body length 2.2-3.0 mm. Body entirely and densely grey pruinose except as follows. Antenna and palp black. Knees, tarsomere 1, and apical 0.0-0.3 of tibiae, yellow. Tarsomeres 2-5 gradually darkening to brown or black. Wing hyaline. Abdominal tergites 1-6 entirely pruinose in both sexes.

Head. Height 1.2-1.4X length; width 1.7-2.1X length. Height of compound eye 0.9-1.1X length, 3.5-4.1X genal width. Frontal width 1.4-1.7X length. Upper orbital seta 0.7-0.9X length of inner vertical seta, arising at 0.2-0.3 of frontal length in male, in female arising at 0.2-0.4 of frontal length. Lower orbital seta 0.6-0.7X length of upper orbital seta, arising at 0.6-0.7 of frontal length. Ocellar seta 0.8-1.0X length of upper orbital seta. Ocellar setulae in one or two pairs. Gena with 4-6 setae. Length of flagellomere 1 0.8-0.9X height, usually anterodorsally rounded, sometimes with slight angle preapically.

Thorax. Katepisternum with one or two setulae anterior to posterodorsal seta. Anterior acrostichal setulae sometimes extending anterior to level of postpronotal seta, but weaker than following acrostichals.

Male terminalia (Fig. 9). Tergite 6 complete, not divided medially, length 0.3-0.4X tergite 5; syntergosternite 7+8 0.4-0.5X length of tergite 5. Strap-like sclerite running uninterruptedly from left sensory setula of sternite 6 to that of sternite 7, and continuing posteriorly to encircle spiracle 7. Genitalia as in Fig. 15. Epandrium broadly triangular in profile, gradually tapering to a broad, blunt apex. Paramere with broad apex and sharp apical bevel. Gonopod evident only as low angulation, bearing two or three setae. Aedeagus narrow, apically emarginate in ventral view; preapical ventral keels well developed. Sternite 10 unusually wide and short. Vestige of tergite 10 relatively elongate, associated with reduced inner margin of epandrial apex.

Type material examined. *Holotype* ♂ (not dissected). MEXICO. **Durango:** 30miW Durango, 8000', 6.v.1961, Howden and Martin (BRI). *Paratypes* (17♂, 21♀). U.S.A. **Colorado:** Teller Co., Florissant Fossil Beds, 8.viii.1973, D. Wilder and D. Shetlar, 2♂, 2♀ (GUE), 4♂, 4♀ (CAS), 2♂, 1♀ (PSU). MEXICO. **Durango:** same data as holotype, 6♂, 9♀ (BRI); 30miW Durango, 8000', 6.vi.1964, J.F.McAlpine, 1♀ (BRI); 3miE El Salto, 8400', 21.vi.1964, J.F.McAlpine, 2♂, 1♀ (BRI); 10miW El Salto, 9000', 10.vi.1964, J.F.McAlpine, 1♀ (BRI); Navios, 26miE El Salto, 8000', 27.vii.1964, J.F.McAlpine, 1♀ (BRI). **Mexico:** Atlacomulco, 8500', 18.viii.1954, J.G.Chillcott, 1♂, 1♀ (BRI).

Remarks. This is a very distinctive, entirely and densely pruinose grey species. The males can be distinguished from those of all other species by a combination of their pruinose frons, dark antenna, and complete tergite 6. This is the only species where tergites 1-6 of the female abdomen are entirely pruinose. Additional characters of the male genitalia are diagnostic.

Distribution (Fig. 67). *Pseudodinia cinerea* is known from several localities in Mexico and one locality in Colorado. It is surprising that there still exists a large geographical gap between the records from Durango and Colorado when the extensive collections from Arizona and the distinctiveness of this species are considered.

Biology. This species has been collected with specimens of *P. pruinosa* and *P. nitens* in Colorado, and *P. latiphallis*, *P. angustata*, and *P. pruinosa* in Mexico. No specific biological data are known.

Etymology. From the Latin *cinereus* meaning "ash-coloured or grey", the specific epithet *cinerea* refers to the extreme density and extent of grey pruinosity of this species.

Pseudodinia hamata new species

Figs. 30, 70.

Description. Body length 2.1-2.8 mm. Predominantly grey pruinose though not as intensely as *P. cinerea*. Antenna and palp entirely dark brown to black, scape and pedicel sometimes slightly paler. Thorax and legs dark grey pruinose except knees, tarsomere 1, and apical 0.2-0.03 of tibiae yellow; tarsomeres 2-5 gradually darkening to dark brown at least dorsally. Wing hyaline. Abdomen of male with tergites 1-5 entirely pruinose. Of female, with dorsal wedge of pruinosity extending narrowly to broadly across tergite 4, and sometimes as a narrow medial strip onto basal half of tergite 5, rarely extending its full length; sublateral bare areas on tergites 3-5 leaving tergite 4 predominantly, and tergite 5 almost entirely, bare.

Head. Height 1.2-1.5X length; width 1.7-2.0X length. Height of compound eye 1.0-1.1X length, 4.1-6.3X genal width. Frontal width 1.3-1.6X length. Upper orbital seta 0.8-1.0X length of inner vertical seta, arising at 0.1-0.2 of frontal length. Lower orbital seta 0.6-0.8X length of upper orbital seta, arising at 0.5-0.6 of frontal length. Ocellar setulae in 1-3 pairs. Gena with 4-7 setae. Length of flagellomere 1 0.8-0.9X height, anterodorsally rounded.

Thorax. Katepisternum with one or two setulae anterior to posterodorsal seta. Anterior acrostichal setulae sometimes extending anterior to level of postpronotal seta but

weaker than following acrostichals.

Male terminalia. Tergite 6 divided medially, length 0.3-0.4X tergite 5; syntergosternite 7+8 0.4-0.5X length of tergite 5. Sternites 6 and 7 with no trace of strap-like sclerite on left side. Genitalia as in Fig. 30. Epandrium narrow in apical half, often swollen posteriorly opposite ventral apex of cercus. Paramere of moderate length. Gonopod short, bearing two or three setae. Aedeagus abruptly narrowed into dorsally recurved, apical hook; no preapical ventral keels evident.

Type material examined. *Holotype* ♂ (not dissected). U.S.A. **New Mexico:** Catron Co., 8miSE Luna, 7500', 9-14.vii.1979, S&J. Peck, pond. pine at stream [Malaise trap] (BRI). *Paratypes* (18♂, 13♀). U.S.A. **Arizona:** Apache Co., 16miS Big Lake, 4.ix.1973, T.P.Sluss, 3♂ (UAT), 3♂ (USNM), 1♂ (BRI); Apache Co., Alpine, Luna Lake, 7900', 9-14.vii.1979, S&J. Peck, pine meadows [Malaise trap], 2♀ (GUE); Cochise Co., Chiricahua Mts., Barfoot Lookout, 8.vii.1973, T.P.Sluss, 2♂ (UAT); Graham Co., Pinaleno Mts., Helio-graph Park, 15.vii.1972, T.P.Sluss, 1♂ (UAT), 1♂ (BRI); Graham Co., Pinaleno Mts., Hospital Flat, 15.vii.1972, T.P.Sluss, 1♂ (UAT); Graham Co., Pinaleno Mts., Goudy Creek, 9200', 7.vii.1973, T.P.Sluss, 1♀ (UAT). **Colorado:** Saguache Co., Valley View Springs, about 7miE of Mineral Hot Springs, on W. foot of Sangre de Cristo range, about 8500', 14.viii.1965, H.B.Leech, 1♂ (CAS). **New Mexico:** same data as holotype, 4♂, 6♀ (GUE); Socorro Co., S. Baldy Park, 10400', 20miW Socorro, 28.vi-7.vii.1979, S&J. Peck, alpine meadow [Malaise trap], 1♀ (USNM); Cloudcroft, 16.vi.1902, [no collector], 1♂, 3♀ (ANSP).

Remarks. *Pseudodinia hamata* can be distinguished from all other species except *P. angustata* by the combination of its pruinose frons, dark antenna, divided tergite 6 of the male, and shiny apical tergites of the female abdomen. Details of the male genitalia, particularly the aedeagus, are required to confidently separate males of these two species.

The colouration of the tarsi (see key couplet 7) and the abdominal pruinosity of the females can assist in distinguishing these two species. The dorsal pruinosity of the female abdomen extends onto tergite 5 in *P. angustata* but rarely so in *P. hamata* where the sublateral bare areas on tergites 3-5 are larger. Some specimens of *P. hamata* have the scape and pedicel paler, but the pale area on flagellomere 1 is restricted to the basal 0.2, unlike *P. angelica*, *P. antennalis*, and *P. obscura*, where at least the basal 0.3 is yellow.

Distribution (Fig. 70). *Pseudodinia hamata* is known from several montane localities in the southwestern United States.

Biology. No specific data are known, although pine and pine meadow habitats are implicated by some collection data.

Etymology. From the Latin *hamatus* meaning "hooked", the specific epithet *hamata* refers to the distinctive apical hook on the aedeagus.

Pseudodinia angustata new species

Figs. 31, 70.

Description. Body length 2.1-2.9 mm. Colour as in *P. hamata* except as follows. Antenna never basally paler. Abdomen of female with dorsal wedge of pruinosity extending broadly across tergite 4 and narrowly to broadly across tergite 5, usually even onto tergite 6; sublateral bare areas present on tergites 3-5 leaving tergite 5 predominantly bare.

Head. Height 1.2-1.5X length; width 1.7-2.1X length. Height of compound eye 0.9-1.1X length, 4.0-4.9X genal width. Frontal width 1.3-1.6X length. Upper orbital seta 0.8-1.0X length of inner vertical seta, arising at 0.1-0.3 of frontal length. Lower orbital seta 0.5-0.7X length of upper orbital seta, arising at 0.5-0.6 of frontal length. Ocellar seta 0.8-1.1X length of upper orbital seta. Ocellar setulae in two or three pairs. Gena with 4-6 setae. Length of flagellomere 1 0.8-0.9X height, anterodorsally rounded.

Thorax. Katepisternum with one or two setulae anterior to posterodorsal seta.

Anterior acrostichal setulae sometimes extending anterior to level of postpronotal seta but weaker than following acrostichals.

Male terminalia. Tergite 6 divided medially, length 0.3-0.4X tergite 5; syntergosternite 7+8 0.4X length of tergite 5. Sternites 6 and 7 with no trace of strap-like sclerite on left side. Genitalia as in Fig. 31. Epandrium very narrow in apical half. Paramere of moderate length. Gonopod poorly developed, bearing two or three setae. Aedeagus with preapical ventral area raised with median depression poorly developed or lacking, and keels indistinct.

Type material examined. *Holotype* ♂ (not dissected). U.S.A. **Arizona:** Apache Co., 25miW Springerville, Greens Peak, 10100', 10-13.vii.1979, S&J. Peck, forest-meadow Malaise trap (BRI). *Paratypes* (22 ♂, 7 ♀), U.S.A. **Arizona:** same data as holotype, 8 ♂, 2 ♀ (BRI), 4 ♂, 2 ♀ (GUE), 4 ♂, 1 ♀ (USNM), 2 ♂ (UAT). **New Mexico:** Lincoln Co., Sierra Blanca, 9700' 10-26.vi.1979, S&JPeck, Malaise trap, spruce-fir along stream, 1 ♂, 1 ♀ (BRI). **MEXICO. Durango:** 30miW Durango, 6.v.1961, Howden & Martin, 2 ♂, 1 ♀ (BRI); 30miW Durango, 6.vi.1964, J.F.McAlpine, 1 ♂ (BRI).

Remarks. *Pseudodinia angustata* is externally similar only to *P. hamata*. Distinguishing characters of these two species are discussed in "Remarks" under *P. hamata*. *Pseudodinia angustata* is also very similar to *P. nitens* in details of the male genitalia, including the very narrow epandrium and the preapical ventral area of the aedeagus. The glabrous condition of the frons and more extensive bare areas on the apex of the abdomen of *P. nitens* allow for ready recognition.

Distribution (Fig. 70). *Pseudodinia angustata* is known from only four collections in montane areas of the southwestern United States and central Mexico.

Biology. The Durango specimens of Howden & Martin were taken with *P. cinerea*, *P. latiphallis*, and *P. pruinosa*. This is an example of the possibility of several species of *Pseudodinia* co-occurring, in a relatively small area. No specific data are known.

Etymology. From the Latin *angustus* meaning "narrow", the specific epithet *angustata* refers to the very narrow epandrial apices, a character shared only with *P. hamata* and *P. nitens*.

***Pseudodinia angelica* new species**

Figs. 33, 71.

Description. Body length 3.2-3.5 mm. Predominantly grey pruinose except scape, pedicel, palp, knees, tarsomere 1, basal 0.3-0.5 of flagellomere 1, and apical 0.2-0.3 of tibiae yellow. Apical 0.5-0.7 of flagellomere 1 and tarsomeres 2-5 gradually darkening to brown or black. Wing hyaline. Abdomen of male with dorsal wedge of pruinosity extending completely across tergites 1-3 and broadly onto tergite 4, continuing across distal half of tergite 4 as a narrow medial strip; sublateral bare areas on tergites 2-4; tergite 5 completely bare dorsally. Of female, with pruinosity extending broadly across tergites 1-3 and sometimes narrowly onto basal half of tergite 4; sublateral bare areas larger, leaving tergite 4 predominantly and tergite 5 entirely bare.

Head. Height 1.0-1.2X length; width 1.8-2.0X length. Height of compound eye 0.8-0.9X length, 3.8-4.0X genal width. Frontal width 1.2-1.5X length. Upper orbital seta 0.9-1.0X length of inner vertical seta, arising at 0.1-0.2 of frontal length. Lower orbital seta 0.7-1.0X length of upper orbital seta, arising at 0.5-0.6 of frontal length. Ocellar seta 0.8-1.0X length of upper orbital seta. Ocellar setulae in one or two pairs. Gena with six or seven setae. Length of flagellomere 1 0.9-1.0X height, anterodorsally rounded.

Thorax. Katapisternum with two setulae anterior to posterodorsal seta. Anterior acrostichal setulae extending anterior to the level of postpronotal seta, subequal in strength to following acrostichals.

Male terminalia. Tergite 6 divided medially, length 0.2X tergite 5; syntergosternite 7+8

0.3X length of tergite 5. Strap-like sclerite represented by small sclerotized area on left side of sternite 7 only, running from left sensory setula to encircle spiracle 7. Genitalia as in Fig. 33. Epandrium relatively elongate with broadly rounded apices. Paramere moderately developed. Gonopod moderately developed, bearing three setae. Aedeagus gradually tapering in ventral view, with an emarginate truncate apex, shallow median trough, and moderately developed preapical keels.

Type material examined. *Holotype* ♂ (dissected). U.S.A. **California:** Los Angeles Co., Beverly Glen, 520616X [16.vi.1952?] [no collector] (USNM; courtesy of LACM). This specimen was poorly mounted on a minuten pin and the wings were fractured. After softening and removal of the abdomen, the specimen was reglued to the minuten and the apical half of one wing removed and glued to the base of the minuten. *Paratypes* (3♀). U.S.A. **California:** Los Angeles Co., Mandeville Cn., Sta. Monica Mts., 1.v.1952, [no collector], 1♀ (USNM); Mts. nr. Claremont, [no date], Baker, 1♀ (ANSP); Sta. Barbara Co., Sta. Cruz Is., Coches Prietos, 17.vi.1967, R.L.Brumley, 1♀ (BRI).

Remarks. *Pseudodinia angelica* can be distinguished from all other species by the combination of its pruinose frons, basally yellow flagellomere 1, and darkened tarsomeres 2-5.

Variation. Syntergosternite 7+8 of the holotype male has the setae arranged in two discrete dorsolateral patches with the medial third lacking setae. The significance of this condition is not clear. In virtually all other dissections in all species, there is a continuous band of setae present along the posterior half or more. In some series of *P. pruinosa*, there is a range from a complete to a medially narrowed band of setae.

The holotype also has the lower orbital seta duplicated on the left side and a supernumerary seta near the lateral base of the right paramere (Fig. 33b). The latter condition has been observed in some *P. antennalis* and *P. occidentalis*.

Distribution (Fig. 71). *Pseudodinia angelica* is known only from the mountains surrounding Los Angeles and from Santa Cruz Island.

Biology. This species may be sympatric with *P. occidentalis* on the continent, and with *P. nigritarsis* on Santa Cruz Island. No specific data are known.

Etymology. *Pseudodinia angelica* is named for its apparently restricted distribution surrounding Los Angeles. The Latin *angelus* meaning "angel", is also appropriate. The request for a loan of material from LACM was made in an effort to acquire more specimens of this species of which there were only three females. The arrival of the male, the only specimen of *Pseudodinia* at LACM, was a godsend.

Pseudodinia obscura new species

Figs. 37, 71.

Description (male only, female unknown). Body length 3.0-3.1 mm. Predominantly pruinose grey except scape, pedicel, knees, tarsi, basal half of flagellomere 1, apex of palp, and apical 0.3-0.4 of tibiae yellow. Apical half of flagellomere 1, and base of palp brown. Wing distinctly infusate. Abdominal tergites entirely pruinose grey.

Head. Height 1.3X length; width 1.9X length. Height of compound eye 1.0X length, 4.5-4.7X genal width. Frontal width 1.4X length. Upper orbital seta 0.8-0.9X length of inner vertical seta, arising at 0.2 of frontal length. Lower orbital seta 0.7X length of upper orbital seta, arising at 0.5-0.6 of frontal length. Ocellar seta 0.9-1.0X length of upper orbital seta. Ocellar setulae in two or three pairs. Gena with 6-9 setae. Length of flagellomere 1 0.8-0.9X height, anterodorsally rounded.

Thorax. Katepisternum with two setulae anterior to posterodorsal seta. Anterior acrostichal setulae extending anterior to level of postpronotal seta but weaker than following acrostichals.

Male terminalia. Tergite 6 divided medially, length 0.3X tergite 5; syntergosternite 7+8

0.4X length of tergite 5. Strap-like sclerite represented by a separate sclerotized area on left anterolateral corner of each of sternites 6 and 7, bearing the left sensory setula; that of sternite 7 running posteriorly to encircle spiracle 7. Genitalia as in Fig. 37. Epandrium relatively elongate, gradually tapering. Paramere relatively broad apically, with ventral margin of bevel sharp. Gonopod moderately developed, bearing two or three setae. Aedeagus ventrally with very broad, emarginate apex; preapical keels moderately developed but median trough deep, providing most of the definition of median margin of keels.

Type material examined. *Holotype* ♂ (not dissected). MEXICO. **Chiapas:** 10miNE San Cristobal [de las Casas], 5.v.1969, 7500', H.J.Teskey (BRI). *Paratype* (1 ♂, dissected). Same data as holotype (BRI).

Remarks. *Pseudodinia obscura* can be distinguished from all other species except *P. antennalis* and *P. angelica* by the combination of its pruinose frons and basally yellow flagellomere 1. It can be distinguished from the latter two species by a distinctive infuscation of the wing and characters of the male genitalia. The deep trough of the aedeagus is matched only by some specimens of *P. occidentalis*. The infuscation of the wing, when viewed comparatively, is very distinctive. It is the relative nature of this character that determined its subordination to the tarsal colouration of *P. angelica* in the sequence of the key couplets. Both characters are known to vary intraspecifically in other species but at present, not in *P. angelica*, *P. antennalis*, and *P. obscura*. Since they are not known to be sympatric, distribution should be considered when keying specimens of these three species. It is expected that the females of *P. obscura* will have infuscated wings and that the abdomen will be sublaterally bare on tergites 2-5 or 3-5.

Distribution (Fig. 71). *Pseudodinia obscura* is known only from the type locality in Chiapas, Mexico. This is the most southerly record for any member of the *varipes* group.

Biology. *Pseudodinia tuberculata* and *P. meridionalis* have been collected near this locality but at 300-500 feet lower altitude. No specific data are known.

Etymology. From the Latin *obscurus* meaning "dark, indistinct", the specific epithet *obscura* refers to the infuscation of the wing.

Pseudodinia antennalis Malloch

Figs. 34-36, 71.

Pseudodinia antennalis Malloch, 1940: 269.

Pseudodinia antennalis; McAlpine 1965: 708.

Description. Body length 2.0-2.8 mm. Predominantly pruinose grey, of varying intensity, except scape, pedicel, and at least basal third of flagellomere 1 yellow to sometimes brown; flagellomere 1 apically yellow to brown. Palp, knees, tarsi, and apical 0.3 or more (rarely nearly entire) of tibiae yellow. Wing hyaline. Abdomen of male ranging from entirely pruinose to broadly pruinose across tergites 1-3 leaving tergites 4-5 essentially bare or with narrowing median pruinose strip on tergite 4 and sometimes also on tergite 5, and sublateral bare areas present on tergites 2-5. Of female, with sublateral bare areas on tergites 2-5 (only 3-5 on most southwestern specimens) slightly larger, tergites 4-5 usually entirely bare; tergite 4 sometimes with basal strip of pruinosity widened medially, but not with median strip as in some males.

Head. Height 1.2-1.4X length; width 1.7-2.0X length. Height of compound eye 1.0-1.2X length, 4.9-6.8X genal width. Frontal width 1.1-1.5X length. Upper orbital seta 0.8-1.0X length of inner vertical seta, arising at 0.1-0.3 of frontal length. Lower orbital seta 0.6-0.7X length of upper orbital seta, arising at 0.5-0.7 of frontal length. Ocellar seta 0.8-1.0X length of upper orbital seta. Ocellar setulae in 1-3 pairs. Gena with 6-9 setae. Length of flagellomere 1 0.8-1.0X height, anterodorsally rounded, rarely with slight preapical angle.

Thorax. Katepisternum with two or three setulae anterior to posterodorsal seta.

Anterior acrostichal setulae sometimes extending anterior to level of postpronotal seta, but weaker than following acrostichals.

Male terminalia. Tergite 6 divided medially, length 0.3X tergite 5; syntergosternite 7+8 0.4-0.5X length of tergite 5. Strap-like sclerite represented by a separate sclerotized area on left anterolateral corner of each of sternites 6 and 7, bearing the left sensory setula; that of sternite 7 not extending to spiracle 7. Genitalia as in Figs. 34-36. Epandrium usually broadly rounded apically, although sometimes more acute in profile (Fig. 34a). Paramere of variable profile shape, due mostly to differential torsion. Gonopod weakly differentiated (Fig. 34) to broadly truncate (Fig. 36), bearing two or three setae. Apex of aedeagus, in ventral view, rounded with preapical keels poorly developed; keels relatively approximate with slight median depression between them.

Type material examined. *Holotype* ♂ (dissected). U.S.A. **Virginia:** Chain Bridge, 10.ix.1922, J.R. Malloch (USNM). *Paratypes* (3 ♂, 4 ♀, and 2 others lacking abdomen, all at USNM). CANADA. **Manitoba:** Aweme, 7.viii.1916, N.Criddle, 1 ♂ and 1 other paratype lacking both head and abdomen; Treesbank, 27.viii.1915, N. Criddle, 1 ♂. U.S.A. **Arizona:** Tucson, 17.vi.1917, J.M. Aldrich, 1 ♂. **Maryland:** Chesapeake Beach, 18.viii.1922, J.R. Malloch, 1 ♀; Glen Echo, 6.viii.1922, J.R. Malloch, 1? (abdomen missing, possibly slide mounted at USNM). **Tennessee:** Knoxville, 28.viii.1916, J.M. Aldrich, 1 ♀. **Virginia:** same data as holotype, 2 ♀ (1 abdomen slide mounted in euparal).

Two other paratypes listed by Malloch (1940), the male from Tennessee: Knoxville, 28.viii.1916, J.M. Aldrich, and the female from Utah: Salt Lake City, 18-20.vii.1917, J.M. Aldrich, are referred to *P. pruinosa* (Southern variant). These specimens lack the completely pruinose frons of *P. antennalis* with only the vertex and the frons pruinose to the level of the upper orbital seta. The scape, pedicel, and palp are yellow but flagellomere 1 is only very narrowly pale basally. The male from Knoxville was dissected and is readily assigned to *P. pruinosa* based primarily on the shape of the aedeagus as discussed under that species.

Only the paratypes from Manitoba, Arizona, Utah (*P. pruinosa*), and Tennessee (one male, *P. pruinosa*) bear USNM Paratype No. 51613 labels, but it is clear that the above specimens account for all the material that Malloch listed in his description.

Other material examined (235 ♂, 154 ♀). CANADA. **Manitoba:** 2miW Stockton, J.G. Chillcott, spruce sand community, 16.vii.1958, 1 ♂, 28.vii.1958, 1 ♂ (BRI); Bald Head Hills, 12kmN Glenboro [Spruce Woods Forest Reserve], swept from *Andropogon gerardi* Vit., 1.viii.1983, K.N. Barber & W.E. Ralley, 6 ♂, 4 ♀, 4.viii.1983, K.N. Barber, 2 ♂, 2 ♀ (GUE). **Ontario:** Grand Bend, 20.vii.1939, G.E. Shewell, 1 ♂ (BRI); Grand Bend, Pinery Prov. Park, K.N. Barber, swept from *Andropogon gerardi* Vit., 15.viii.1982, 3 ♂, 25.viii.1983, 4 ♂, 5 ♀, 19.viii.1984, 34 ♂, 12 ♀ (GUE), 10 ♂, 10 ♀ (BRI), 5 ♂, 5 ♀ (USNM), 5 ♂, 5 ♀ (UAT), 5 ♂, 2 ♀ (CAS), 2 ♂, 2 ♀ (USU), 2 ♂, 2 ♀ (LACM); Grand Bend, Pinery Prov. Park, K.N. Barber, reared from a third-instar larva ex. *Andropogon gerardi* Vit., 25.viii.1983, 1 ♂ (GUE); Sauble Beach, K.N. Barber, swept from *Andropogon gerardi* Vit., 9.viii.1983, 2 ♀, 10.viii.1983, 3 ♀ (GUE); Ipperwash Prov. Park, 14.vii.1980, K.N. Barber, swept from *Andropogon gerardi* Vit., 1 ♂ (GUE); Windsor, Ojibway Prairie Reserve, K.N. Barber, swept from *Andropogon gerardi* Vit., 21.vii.1981, 1 ♀, 18.viii.1983, 1 ♀ (GUE). U.S.A. **Arizona:** Tucson, Upper Sabino Canyon, B.A. Foote, 10.v.1971, 1 ♂, 1 ♀ (BRI), 12.v.1971, 1 ♀ (OKSU); Pima Co., Quinlan Mts., Kitt Peak, 6875', 4.viii.1977, T.P. Sluss, 10 ♂, 20 ♀ (UAT), 5 ♂, 5 ♀ (USNM), 3 ♂, 5 ♀ (GUE), 3 ♂, 4 ♀ (BRI); Pima Co., Mt. Lemmon, 16.v.1975, T.P. Sluss, 1 ♀ (UAT); Pima Co., Santa Catalina Mts., Bear Can., Mi. 10 Hitchcock Hwy., 3.vii.1961, L.B. Koenig, 1 ♀ (UCB); Santa Rita Mts., Madera Canyon, K.N. Barber, 25.iv.1979, 1 ♂, 2 ♀, 26.iv.1979, 2 ♂, 1 ♀ (GUE); Huachuca Mts., Miller Canyon, 5500', 7.vi.1969, S.L. Wood, 7 ♂, 9 ♀ (OSU); Miller Canyon, 30.iv.1948, A.L. Melander, 1 ♀ (USNM); W. side Huachuca Mts., Ramsey Canyon, 22.vi.1974, T.P. Sluss, 3 ♂, 3 ♀ (UAT); Cochise Co., W. side Huachuca Mts., Sunnyside Canyon, 6000', 4.viii.1952, H.B. Leech & J.W. Green, 2 ♂ (CAS); Scotia Canyon, nr. Sunnyside, 14.v.1971, B.A. Foote, 1 ♀ (OKSU); Cochise Co., Chiricahua Mts., ImiS Rustler Pk., 27.v.1975, T.P. Sluss, 1 ♂, 1 ♀ (UAT); Cochise Co., Rustler Park, 22.v.1974, T.P. Sluss, 1 ♂ (UAT); Cochise Co., Chiricahua Mts., Barfoot Lookout, T.P. Sluss, 6.ix.1970, 1 ♂ (BRI), 17.ix.1972, 1 ♀, 8.vii.1973, 1 ♀ (UAT); Cochise Co., Chiricahua Mts., Onion Saddle, 26.viii.1973, T.P. Sluss, swept from *Muhlenbergia* sp., 1 ♀ (UAT), 1 ♂ [lacking plant record] (BRI); Cochise Co., S.W.R.S., 5miW Portal, 5400', 24.ix.1966, P.H. Arnaud, Jr., 1 ♀ (CAS); Cochise Co., S.W.R.S., 7.vi.1957, J.W. Green, 1 ♂ (CAS); Cochise Co., S.W.R.S., 9.ix.1970,

T.P. Sluss, 1 ♂, 2 ♀ (BRI), 1 ♀ (UAT); Cochise Co., S.W.R.S., 8.v.1967, D.M. Wood, 1 ♂ (BRI); Chiricahua Mts., 4000', 15.[Je or JI].1952, A.H. Sturtevant Collection, 2 ♂ (USNM). **Connecticut:** Hartford, 6.vii.1946, L.C. Rosene, sweeping in swamp, 1 ♀ (CTAS). **Georgia:** Rabun Co., Rabun Bald, 3000', 14.vii.1957, J.G. Chillcott, 1 ♂, 1 ♀ (BRI); Brasstown Bald, 4800', 19.viii.1957, J.G. Chillcott, 2 ♂ (BRI). **Maryland:** Suitland Bog, 14.vi.1951, W.W. Wirth, 1 ♂ (USNM); Cupids Bower Is., 4.vii.1915, R.C. Shannon, 1 ♂ (USNM). **Massachusetts:** Truro, Cape Cod, 3.viii.1964, J.R. Vockerroth, 1 ♂ (BRI); Vineyard Haven, 17.viii.1954, A.H. Sturtevant, 3 ♀ (USNM); Middleboro, A.H. Sturtevant Collection, 4.viii.1924, 1 ♀, 28.vii.1922, 1 ♂, 2 ♀ (USNM); Holliston, N. Banks, 17.vii.[?], 1 ♂, 7.viii.[?], 1 ♀, 11.viii.[?], 1 ♂, 1 ♀ (MCZ). **Michigan:** Berrien Co., Warren Dunes St. Park, 22.viii.1981, M&A.O'Brien, 1 ♂ (UMIC). **Minnesota:** Taylors Falls, 2.viii.1925, S. Kepperley, 1 ♂, 1 ♀ (UMIN). **Missouri:** Carter Co., 4.5miSW Van Buren, Ridge Road at Road C, 4.viii.1967, H. Leech, at light, dry pine-oak woods area, 1 ♂, 1 ♀ (CAS). **New Jersey:** Seaside Park, 20.viii.[?], Weiss & West, 2 ♀ (MCZ). **New Mexico:** Pinos Altos, Cherry Ck., 22.vi.1953, W.W. Wirth, 1 ♀ (USNM); Alomogordo, 30.iv.1902, [no collector], 1 ♀ (ANSP); Catron Co., 5miW Luna, 7400', 9-14.vii.1979, S&J. Peck, San Francisco River, pond, pine-meadow [Malaise trap], 1 ♂ (GUE). **New York:** Long Island, Huntington, Kalbfleisch Res. Station, 28.vii.1962, P.H. Arnaud, Malaise trap, 1 ♂ (AMNH). **North Carolina:** Highlands, 3800', J.G. Chillcott, 15.vii.1957, 1 ♀, 17.viii.1957, 1 ♂ (BRI); Highlands, Whitesides Mt., 4900', J.G. Chillcott, 20.vii.1957, 2 ♂, 2 ♀, 21.viii.1957, 1 ♀ (BRI); Highlands, Whiteside Cave, 2800', 11.viii.1957, J.G. Chillcott, 1 ♀ (BRI); Highlands, Whiteside Mt., 21.viii.1957, C.J. Durden, 1 ♂ (BRI); Highlands, Little Bear Pen Mt., 5.viii.1957, W.R. Richards, 1 ♂ (BRI); Looking Glass Rock, nr. Pisgah Forest, 2500', 19.vii.1957, J.G. Chillcott, 1 ♀ (BRI); Lake Toxaway, 12.vii.1957, J.G. Chillcott, 1 ♂ (BRI); Black Mt. City, Black Mts., 12.viii.1930, Banks, 1 ♂ (MCZ); Pettigrew St. Park, 1.ix.1963, B.S. Heming, 1 ♂ (GUE); Gates Co., 3.ix.1963, B.S. Heming, 1 ♂ (GUE); Cumberland Co., Fort Bragg, J.D. Birchim, 14.v.1967, 3 ♂, 1 ♀, 15.v.1967, 11 ♂ (CAS), 16.v.1967, 35 ♂, 5 ♀ (CAS), 5 ♂, 2 ♀ (GUE), 28.v.-3.vi.1967 [some apparently mistakenly printed 1968], 27 ♂, 1 ♀, 6-13.vi.1967, 1 ♂ (CAS). **Tennessee:** Townsend, 2.vi.1979, M.J. Sharkey, 1 ♀ (GUE); Gatlinburg, GSMNP, R.H. Whittaker, sweeper, 17.vii.1947, pine-oak forest, 1500', 1 ♂, 19.vii.1947, pine heath, 3500', 1 ♂ (ISU). **MEXICO. Zacatecas:** Laguna Balderama, 25miW Fresnillo, 7900', 23.vi.1954, R.H. Brewer, 1 ♀ (CAS). One additional female with the following data: W.H., "8.10.1913", A.H. Sturtevant Collection (USNM).

Remarks. *Pseudodinia antennalis* can be distinguished from all other species by the combination of its pruinose frons, basally yellow flagellomere 1, yellow tarsi, and hyaline wing. The extent of abdominal pruinosity of the male varies more than in any other species, from predominantly bare on tergites 4 and 5 to completely pruinose. The distinctive form of the male aedeagus is virtually diagnostic on its own. Until further data become available, the name *P. antennalis* is applied to all the forms discussed below.

Variation. This is a widespread but infrequently collected species. Over half the specimens examined are from only three series. There is considerable variation in this species and comparison of the extremes only would suggest that they represent distinct species.

The pruinosity is generally reduced and tergites 4 and 5 of the male are predominantly bare in the Canadian specimens. This condition is apparent in some specimens from Maryland, Massachusetts, North Carolina, and Georgia. A completely pruinose abdomen occurs in male specimens from Massachusetts, North Carolina, and Georgia. The long series from Fort Bragg includes many males with entirely though lightly pruinose abdomens, and a minority with sublateral bare areas on tergites 3-5. The holotype, previously dissected, can be seen to bear microtrichia (pruinosity) over the entire abdomen except for a small dorsolateral area on the left side of tergite 4, possibly due to abrasion.

All western males (except the series from Kitt Peak, Arizona) have the abdomen completely pruinose and densely so, the density comparable to some eastern males. The series from Kitt Peak contains one male with this characteristic western-type pruinosity extending over the entire abdomen. All other males in the series have tergites 4 and 5 predominantly bare with only a fairly narrow medial strip of pruinosity running a variable length along tergite 4. The broadly truncate gonopod (Fig. 36) is a fairly consistent character within this series but is very closely approximated by at least one other male from the west and the east, as well as by the completely pruinose co-series male. There are no consistent differences between this series and the other western specimens and it is considered a conspecific variant at this time. Further collections in the west might provide intergrades.

There are two regional genitalic variations noted. Eastern specimens tend to have the aedeagus relatively thick at the apex in lateral view (Fig. 35a). In western specimens, the aedeagus is thinner at the apex in lateral view (Fig. 36a). This, however, is not an entirely consistent difference (Fig. 34a).

Some western specimens have the epandrium somewhat acute apically. This is roughly correlated with the antenna and tibiae being more extensively yellow, flagellomere 1 entirely so, and the tibiae with only an indistinct darkening in the basal third. This variation also is apparently not discrete and is best exemplified by the series from Miller Canyon (S.L. Wood) which includes the full range of variation.

There are three dissections that have a supernumerary seta present at the lateral base of the right paramere. This has also been noted in the holotype of *P. angelica* (Fig. 33b) and one specimen of *P. occidentalis*. One specimen in the series from Fort Bragg has the anepisternal seta duplicated. Both conditions are considered anomalous.

Distribution (Fig. 71). *Pseudodinia antennalis* is widely distributed, occurring in eastern North America, southern Arizona, New Mexico, and central Mexico, but it is noticeably absent from the midwest corridor from North Dakota to Texas. This is a poorly collected area for this genus as similarly sparse records of the widespread *P. pruinosa* demonstrate (Fig. 69). More extensive collecting in this area might provide additional records.

Biology. This species has been associated with the grass *Andropogon gerardi* (Gramineae: Andropogonaceae) in Ontario and Manitoba (Barber 1984). It probably feeds on a species of mealybug, *Trionymus* sp., found in the leafsheaths of this grass in Ontario. *Pseudodinia antennalis* is known to co-occur with *P. pruinosa*, *P. varipes*, and *P. melanitida* in Windsor, Ontario.

The only other plant with which *P. antennalis* has been associated is the grass *Muhlenbergia* sp., from which T.P. Sluss also collected *P. pruinosa*, *P. latiphallis*, and *Chamaemyia herbarum* (Robineau-Desvoidy).

Pseudodinia nigratarsis new species

Figs. 16, 67.

Description. Body length 3.1-3.4 mm. Predominantly dark grey pruinose. Head pruinose except for frons, which is bare and shiny from level of upper orbital seta anteriorly; bare area extending onto parafacial to level of antennal base. Antenna nearly unicolorous dark brown or black in female; with scape, pedicel, and flagellomere 1 to base of arista yellowish brown in male. Thorax entirely covered with dark grey pruinosity though appearing shiny black in some angles. Legs mostly black except knee of foreleg, and apical 0.3-0.4 of all tibiae yellow. Tarsomeres 1-5 entirely black. Wing hyaline. Abdomen of male with dorsal wedge of pruinosity extending broadly across tergites 1-4, with successively larger sublateral bare areas on tergites 3-5 leaving tergite 5 with narrow medial strip of pruinosity in basal half. Abdomen of female with dorsal pruinosity extending broadly across tergites 1-3 with sublateral bare areas on tergites 2-3; tergites 4 and 5 entirely bare.

Head. Height 1.2X length; width 2.0X length. Height of compound eye 0.8-0.9X length, 3.6-3.8X genal width. Frontal width 1.4-1.5X length. Upper orbital seta 0.8-0.9X length of inner vertical seta, arising at 0.2 of frontal length. Lower orbital seta 0.9-1.0X length of upper orbital seta, arising at 0.5-0.6 of frontal length. Ocellar seta 1.1X length of upper orbital seta. Ocellar setulae in two pairs. Gena with nine or ten setae. Length of flagellomere 1 0.9X height, with slight preapical angulation anterodorsally.

Thorax. Katepisternum with three setulae anterior to posterodorsal seta. Anterior acrostichal setulae barely extending to level of postpronotal seta, slightly weaker than following acrostichals.

Male terminalia. Tergite 6 complete, not medially divided, length 0.2X tergite 5; syntergosternite 7+8 0.3X length of tergite 5. Sternites 6 and 7 very weakly sclerotized transversely near anterior margin; strap-like sclerite well developed, running uninterruptedly from left sensory setula of sternite 6 to that of sternite 7 and continuing posteriorly to

encircle spiracle 7. Genitalia as in Fig. 16. Epandrium moderately tapered. Paramere with well defined, sharply bevelled edge. Gonopod long for this species group, about 0.4X paramere, bearing three or four setae. Aedeagus roundly tapered, in ventral view, with shallow apical emargination and preapical keels poorly developed but noticeably higher in basal half.

Type material examined. *Holotype* ♂ (dissected). U.S.A. **California:** Sta. Cruz. Is., Cal. Beach at Water Cyn., 2.v.1969, R.O.Schuster (UCD). *Paratype* (1 ♀). Same data as holotype (UCD). Both of the type specimens lack one complete flagellum and flagellomeres 3-4 of the opposite antenna.

Remarks. *Pseudodinia nigratarsis* is the only species in which tarsomere 1 is black along with tarsomeres 2-5. In other species of *Pseudodinia*, there is considerable intraspecific variation in the darkening of tarsomeres 2-5.

The undivided condition of tergite 6 in the male requires further verification. This is a specific character for *P. cinerea* but one specimen each of *P. varipes* and *P. occidentalis* have an undivided and a partially divided tergite 6, respectively.

Distribution (Fig. 67). *Pseudodinia nigratarsis* is known only from Santa Cruz Island, California.

Biology. No specific data are known. *Pseudodinia angelica* is the only other species of *Pseudodinia* known to occur on Santa Cruz Island.

Etymology. From the Latin *niger* meaning "black", the specific epithet *nigratarsis* refers to the entirely black tarsi which are unique.

Pseudodinia nitens (Melander and Spuler)

Figs. 32, 70.

Piophila nitida Wulp, 1867: 160 (preoccupied by *Piophila nitida* Brullé 1832).

Piophila nitens Melander and Spuler, 1917: 70 (new name for *Piophila nitida* Wulp).

Pseudodinia nitida (Wulp), McAlpine 1965: 708; not *Pseudodinia nitida* Melander 1913: 295, McAlpine 1965: 708, notwithstanding.

Pseudodinia nitens; McAlpine 1965: 708, holotype only.

Description. Body length 2.2-3.0 mm. Predominantly dark grey pruinose except knees, tarsomere 1, and apical 0.2-0.3 of tibiae yellow; tarsomeres 2-5 gradually darkening to brown. Antenna dark brown to black, scape and pedicel sometimes paler. Palp brown to black, sometimes basally paler. Pruinosity present on ocellar triangle, on vertex to level of posterior ocelli, and on orbits usually to level of median ocellus. Frons bare, shiny black, bare area extending medially onto parafacial to level of antennal base or below. Head otherwise pruinose. Wing lightly infusate. Abdomen of male with dorsal wedge of pruinosity extending broadly across tergites 1-4; tergite 5 with at least a narrow medial strip of pruinosity running entire length, sometimes nearly entirely pruinose; successively larger sublateral bare areas present on tergites 3-5 or 4-5. Of female, with pruinosity extending narrowly to apex of tergite 4, at least as a few scattered microtrichia, and sometimes slightly onto medial base of tergite 5; with successively larger sublateral bare areas on tergites 2-5.

Head. Height 1.3-1.5X length; width 1.8-2.0X length. Height of compound eye 1.0-1.1X length, 4.1-6.0X genal width. Frontal width 1.3-1.6X length. Upper orbital seta 0.8-0.9X length of inner vertical seta, arising at 0.1-0.3 of frontal length. Lower orbital seta 0.6-0.9X length of upper orbital seta, arising at 0.5-0.6 of frontal length. Ocellar seta 0.9-1.1X length of upper orbital seta. Ocellar setulae in 1-3 pairs. Gena with 4-7 setae. Length of flagellomere 1 0.8-1.0X height, anterodorsally rounded.

Thorax. Katepisternum with two setulae anterior to posterodorsal seta. Anterior acrostichal setulae rarely extending anterior to level of postpronotal seta, if so then weaker than following acrostichals.

Male terminalia. Tergite 6 divided medially, length 0.3-0.4X tergite 5; syntergosternite 7+8 0.4X length of tergite 5. Strap-like sclerite represented by an indistinct sclerotization on left anterolateral corner of each of sternites 6 and 7, bearing left sensory setula; that of sternite 7 not extending to encircle spiracle 7. Genitalia as in Fig. 32. Epandrium strongly narrowed, almost parallel-sided on apical half when viewed laterally. Paramere moderately developed. Gonopod weakly differentiated, bearing two or three setae. Aedeagus, in lateral view, tapering to a narrow tip; in ventral view, apex somewhat rounded to slightly emarginate; preapical ventral keels weakly differentiated, at most a median raised area with slight median depression.

Type material examined. *Holotype* ♀ . U.S.A. **Wisconsin:** Kumlien [no other data] (RNHL). Both flagella are missing and there is some green corrosion on the pin. Otherwise, the holotype is in good condition.

Other material examined (23 ♂ , 16 ♀). U.S.A. **Arizona:** Apache Co., Alpine, Luna Lake, 7900', 9-14.vii.1979, S&J. Peck, pine meadows [Malaise trap], 1 ♂ (BRI); Flagstaff, Oak Creek Canyon at Sterling Canyon, 5900', 17-25.vii.1979, S&J. Peck, riparian woods, Malaise trap, 1 ♂ (BRI); Graham Co., Pinaleno Mts., Heliograph Park, 15.vii.1972, T.P. Sluss, 1 ♂ (UAT); Cochise Co., Chiricahua Mts., Barfoot Lookout, 23.v.1974, T.P. Sluss, 1 ♂ (UAT); Grand Canyon Nat. Park, No. Rim, 15.vii.1954, W.L. Downes, 5 ♀ (ISU). **Colorado:** Saguache Co., Valley View Springs about 7miE of Mineral Hot Springs on W. foot of Sangre de Cristo range, 8500', 13.viii.1965, H.B. Leech, 1 ♂ , 1 ♀ (CAS); Fairplay, 3.viii.1938, M. James & U. Lanhan, 1 ♀ (GUE); Teller Co., Florissant Fossil Beds, 8.viii.1973, D. Wilder & D. Shetlar, 1 ♀ (CAS); Estes Park, 14.vii.1934, A.L. Melander, 1 ♀ (USNM). **New Mexico:** Catron Co., 8miSE Luna, 7500', 9-14.viii.1979, S&J. Peck, pond, pine at stream [Malaise trap], 2 ♂ , 1 ♀ (BRI), 3 ♂ (GUE). **Utah:** Garfield Co., Bryce Canyon, 19.vii.1954, W.L. Downes, 1 ♂ , 3 ♀ (ISU); Summit Co., Henrys Fork Park, 1-10.viii.1979, 9000', S&J. Peck, meadow w/willow, Malaise trap, 5 ♂ , 1 ♀ (BRI), 5 ♂ , 1 ♀ (GUE). **Washington:** Mt. Adams, 24.vii.1921, A.L. Melander, 1 ♂ (USNM). **Wyoming:** Yellowstone Park, Upper Geysers Basin, 7.viii.1918, A.L. Melander, 1 ♂ , 1 ♀ (USNM).

Remarks. *Pseudodinia nitens* can be distinguished from all other species of the *varipes* group by a combination of its predominantly shiny frons, yellow tarsomere 1, and the extensively pruinose abdomen. The abdominal pruinosity of *P. nitens* extends the full length of tergite 4 in the female and across tergite 5 in the male, similar to the conditions found in *P. hamata* and, to a lesser extent, *P. angustata*. The male genitalia are very similar to those of *P. angustata* in the possession of narrow epandrial apices and the relatively flat, preapical ventral area of the aedeagus.

The holotype female is readily referable to this species with its extensively pruinose abdomen, vertex, and ocellar triangle. This rather pruinose condition is in direct opposition to previous literature and keys which actually refer to the very shiny *P. nitida* Melander (= *P. melanitida* new name). The somewhat difficult nomenclatural history of *P. nitens* requires some explanation.

The deposition of the holotype in RNHL, The Netherlands, restricted access to it by North American dipterists. Melander and Spuler (1917), when reviewing the Nearctic Piophilidae, drew attention to the description of *Piophila nitida* Wulp (1867), which suggested the genus *Pseudodinia*, a genus in which the senior author had previously described *Pseudodinia nitida* Melander (1913). They also uncovered the senior primary homonym of Brullé (1932) and renamed *Piophila nitida* Wulp as *Piophila nitens* Melander and Spuler.

When McAlpine (1965) catalogued the Nearctic Chamaemyiidae, C.W. Sabrosky, USNM, who had examined the holotype of *Piophila nitida* Wulp, confirmed its proper placement in the genus *Pseudodinia*. McAlpine (1965) used this information and formally transferred *Piophila nitida* Wulp and *Piophila nitens* Melander and Spuler to the genus *Pseudodinia*. This action created a junior secondary homonym of *Pseudodinia nitida* Melander which then had to be rejected [ICZN Article 57(b)], but it was wrongly treated by McAlpine as a junior synonym of *Pseudodinia nitens* Melander and Spuler. The senior homonym, *Pseudodinia nitida* (Wulp), could not be used since it had already been permanently rejected as a junior primary homonym in *Piophila* by Melander and Spuler.

according to ICZN Article 57(a).

Since that time, there has been a reliance on Melander's (1913) description of *Pseudodinia nitida* and application of the senior synonym, *Pseudodinia nitens*, to this description and to any shiny specimen of *Pseudodinia*. This has led to the misconception of *P. nitens* as being a very shiny species.

Variation. The holotype has perhaps the most darkly infuscated wing of any of the specimens studied. Despite being an isolated eastern record for this otherwise western montane species, this wing character along with the abdominal pruinosity, readily places this holotype female in this species.

Distribution (Fig. 70). *Pseudodinia nitens* has a primarily western montane distribution, with the type locality in Wisconsin, an apparently disjunct record. The latter record is represented by a nonspecific symbol in the centre of the state in Fig. 70.

Biology. This species has been taken with *P. hamata* and *P. pruinosa* at Luna Lake, Arizona, and each of these two species at two other localities in Arizona. Collection data suggest riparian woods and pine meadows as possible habitats.

Pseudodinia latiphallis new species

Figs. 20, 67.

Description. Body length 2.0-2.8 mm. Predominantly dark grey pruinose except knees narrowly brown, and tarsi and apical 0.2-0.3 of tibiae yellow. Antenna and palp black. Ocellar triangle, vertex, and orbits posterior to level of median ocellus pruinose, sometimes forming a nearly complete transverse band to level of median ocellus; frons otherwise bare, shiny black. Parafacial and gena predominantly bare with narrow lateral band of pruinosity immediately next to eye and along lower margin of gena. Wing hyaline to very lightly infuscate. Abdomen of male with dorsal wedge of pruinosity extending broadly across tergites 1-3, at most, continuing as a narrow medial strip to apex of tergite 4; successively larger sublateral bare areas on tergites 2-4 leaving tergite 4 predominantly and tergite 5 entirely bare. Of female, with pruinosity not extending onto tergite 4; sublateral bare areas on tergites 2 and 3 somewhat larger.

Head. Height 1.1-1.3X length; width 1.7-1.8X length. Height of compound eye 0.9-1.0X length. 4.8-6.1X genal width. Frontal width 1.0-1.1X length. Upper orbital seta 0.9-1.0X length of inner vertical seta, arising at 0.2-0.3 of frontal length. Lower orbital seta 0.6-0.7X length of upper orbital seta, arising at 0.5-0.6 of frontal length. Ocellar seta 0.6-0.7X length of upper orbital seta. Ocellar setulae in one or two pairs. Gena with 4-7 setae. Length of flagellomere 1 0.8-1.0X height, anterodorsally rounded.

Thorax. Katepisternum with two setulae anterior to posterodorsal seta. Anterior acrostichal setulae sometimes extending anterior to level of postpronotal seta, but weaker than following acrostichals.

Male terminalia. Tergite 6 divided medially, length 0.2-0.3X tergite 5; syntergosternite 7+8 0.4-0.5X length of tergite 5. Strap-like sclerite represented by a separate sclerotized area on left anterolateral corner of each of sternites 6 and 7, bearing left sensory setula; that of sternite 7 not extending to spiracle 7, sometimes absent. Genitalia as in Fig. 20. Epandrium relatively broad in lateral profile with apices slightly deflected posteriorly. Paramere relatively broad. Gonopod moderately developed, bearing two or three setae. Aedeagus relatively heavily sclerotized, usually evenly curved in lateral profile; in ventral view, very wide with very well developed preapical keels which continue basally as low ridges bordering the median concavity.

Type material examined. *Holotype* ♂ (not dissected). MEXICO. Durango: 30miW Durango, 8000', 6.v.1961, Howden & Martin (BRI). *Paratypes* (10 ♂, 13 ♀). U.S.A. Arizona: Pima Co., Mt. Lemmon, 16.v.1975, T.P.Sluss, 2 ♂, 2 ♀ (USNM), 3 ♂, 6 ♀ (UAT); Cochise Co., Chiricahua Mts., Barfoot Lookout, 17.v.1972, T.P.Sluss, swept from *Muhlenbergia* sp., 1 ♂ (UAT); Madera Canyon, Santa Rita Mts., 26.iv.1979, K.N.Barber,

1 ♂ (GUE). MEXICO. **Durango**: same data as holotype, 3 ♂, 5 ♀ (BRI).

Remarks. *Pseudodinia latiphallis* can be confused with *P. pruinosa* with its anteriorly bare frons, very grey thorax, and extensively (variably in *P. pruinosa*) bare parafacial and gena. All specimens of *P. latiphallis* have been taken with *P. pruinosa* and most can be recognized by their relatively short ocellar seta. *Pseudodinia slussi* might also be confused with *P. latiphallis* but the specimens from Arizona are considerably less pruinose than those of *P. latiphallis*. Specimens of the similar *P. varipes* often have an anterodorsal angulation on flagellomere 1. Confident identification of these four species can only be made by examining the male genitalia. Specimens of *P. occidentalis* from Arizona have strong genal setae which are subequal to the postgenal setae.

Most male specimens share with *P. varipes* a gradually curved aedeagus in profile with very well developed preapical keels, and a slightly anteroventrally emarginate epandrium. These two species appear to be parapatric or narrowly sympatric.

Variation. The Durango specimens have the epandrial apices most strongly curved posteriorly.

Distribution (Fig. 67). *Pseudodinia latiphallis* is known from only four collections in montane areas of Arizona and Durango, Mexico.

Biology. As mentioned above, all specimens have been taken with *P. pruinosa*. In addition, the series from Durango was taken with *P. cinerea* and *P. angustata*, and the specimens from Madera Canyon and Mt. Lemmon were taken with *P. antennalis*.

The one plant record of *Muhlenbergia* sp. provides little information since *P. antennalis* and two variants of *P. pruinosa* have also been taken on this plant.

Etymology. From the Latin *latus* and Greek *phallos* meaning "wide" and "penis", respectively, the specific epithet *latiphallis* refers to the distinctively, preapically widened aedeagus.

Pseudodinia slussi new species

Figs. 17, 67.

Description. Body length 2.3-2.8 mm. Shiny black to lightly grey pruinose except knees, tarsi, and apical 0.2-0.3 of tibiae yellow. Antenna black, except scape and pedicel sometimes dark brown. Ocellar triangle sometimes lightly pruinose. Vertex, orbits, and frons entirely bare. Parafacial and gena bare, shiny black except oral margin narrowly pruinose. Face lightly pruinose, rather shiny medioventrally, becoming more heavily pruinose toward the densely pruinose lunule. Head otherwise grey pruinose. Thorax entirely lightly pruinose, pruinosity heavier along notopleural suture and upper anepisternum; notum appearing shiny. Abdomen of both sexes with dorsal wedge of pruinosity extending to posterior margin of tergite 3, at most tergite 4 with a slight medial widening of basal strip; tergites 2-5 with successively larger sublateral bare areas leaving tergites 4 and 5 essentially bare.

Head. Height 1.2-1.3X length; width 1.7-2.0X length. Height of compound eye 1.0-1.1X length, 4.3-5.9X genal width. Frontal width 1.2-1.4X length. Upper orbital seta 0.8-1.0X length of inner vertical seta, arising at 0.1-0.3 of frontal length. Lower orbital seta 0.5-0.7X length of upper orbital seta, arising at 0.5-0.6 of frontal length. Ocellar seta 0.8-1.0X length of upper orbital seta. Ocellar setulae in one or two pairs. Gena with 5-7 setae. Length of flagellomere 1 0.8-0.9X height, anterodorsally rounded.

Thorax. Katepisternum with one or two setulae anterior to posterodorsal seta. Anterior acrostichal setulae extending anterior to level of postpronotal seta, weaker or subequal in strength to following acrostichals.

Male terminalia. Tergite 6 divided medially, length 0.2-0.3X tergite 5; syntergosternite 7+8 0.4-0.5X length of tergite 5. A single, uninterrupted strap-like sclerite bearing left sensory setulae of sternites 6 and 7, and extending posteriorly to encircle left spiracle 7.

Genitalia as in Fig. 17. Epandrium with relatively broadly rounded apices. Paramere relatively elongate and straight, particularly on medial surface when viewed ventrally. Gonopod relatively well developed as a short but quite narrow projection bearing two or three setae. Apex of aedeagus, in ventral view, truncate to slightly emarginate; preapical median area raised with an indistinct median depression; distinct keels not evident.

Type material examined. *Holotype* ♂ (dissected). U.S.A. **Arizona:** Pima Co., Kitt Peak, Quinlan Mts., 6875', 4.viii.1977, T.P.Sluss (USNM; courtesy of UAT). *Paratypes* (5 ♂, 3 ♀). U.S.A. **Arizona:** same data as holotype, 2 ♂, 1 ♀ (UAT), 1 ♂, 1 ♀ (BRI), 1 ♀ (USNM); Sulphur Draw, s. Portal, 29.v.1967, C.W.Sabrosky, 1 ♂ (USNM). **New Mexico:** Torrance Co., Town of Gran Quivira 6500', 20.viii.1967, H.B.Leech, 1 ♂ (CAS).

Remarks. *Pseudodinia slussi* can be confused with *P. pruinosa*, *P. varipes*, and, to a lesser extent, *P. latiphallis*. The populations of *P. occidentalis* from Arizona have distinctively enlarged genal setae, while *P. melanitida* is apparently allopatric. The variable density of thoracic pruinosity necessitates examination of the male genitalia for confident identification. The complete, uninterrupted strap-like sclerite on the left side of sternites 6 and 7 of the male, which also encircles spiracle 7, is a condition otherwise found only in the distinctive *P. nigritarsis* and *P. cinerea*.

The Kitt Peak specimens were taken with a larger number of *P. occidentalis* which have enlarged genal setae and strong anterior acrostichal setulae. This allowed the recognition and designation of the three female paratypes listed above. Dr. Sluss misidentified the series from Kitt Peak as *P. nitens* [of authors, = *P. melanitida*] and the Gran Quivira specimen as *P. varipes* [of authors, = *P. pruinosa*].

Variation. The Gran Quivira specimen has the epandrial apices considerably wider than those of the five other male specimens listed above.

Distribution (Fig. 67). *Pseudodinia slussi* is known from only three montane localities in Arizona and New Mexico.

Etymology. This species is named after Dr. T.P. Sluss, Fort Lewis College, Durango, Colorado, whose diligent collecting in the southwestern United States provided a large proportion of the specimens studied here.

Pseudodinia melanitida new name

Figs. 18, 68.

Pseudodinia nitida Melander, 1913: 295 (preoccupied by *Pseudodinia nitida* (Wulp) 1867: 160, McAlpine 1965: 708); not *Pseudodinia nitens* (Melander and Spuler) 1917: 70, McAlpine 1965: 708.

Pseudodinia nitida; Malloch 1915: 152; Malloch 1921: 347; Malloch 1940: 269 (in part); Hennig 1941: 64.

Description. Body length 1.8-2.7 mm. Density of pruinosity reduced, usually appearing shiny black. Tarsi, knees usually, and apical 0.2-0.3 of tibiae yellow. Frons and vertex entirely bare, rarely with sparse pruinosity within ocellar triangle. Parafacial bare; gena bare to lightly pruinose; face lightly pruinose medioventrally, increasing in density laterally and dorsally toward heavily pruinose lunule. Occiput and oral margin pruinose. Antenna usually entirely black, scape and pedicel sometimes brown. Palp black. Thorax lightly pruinose, heaviest laterally especially along notopleural suture; notum usually very shiny. Wing hyaline to slightly infuscate. Abdomen of male with dorsal wedge of pruinosity extending broadly across tergites 1-3, and at least halfway across tergite 4 as a narrow strip; more often extending broadly to apex of tergite 4; tergite 5 entirely bare, sometimes with basal pruinosity slightly widened medially; successively larger sublateral bare areas on tergites 2-5. Of female, tergite 4 almost entirely bare with basal pruinosity slightly widened medially, rarely with narrow median strip continuing to apex; tergite 5 bare.

Head. Height 1.2-1.4X length; width 1.7-2.0X length. Height of compound eye

1.0-1.1X length, 4.2-6.2X genal width. Frontal width 1.1-1.3X length. Upper orbital seta 0.8-1.0X length of inner vertical seta, arising at 0.1-0.3 of frontal length. Lower orbital seta 0.6-0.8X length of upper orbital seta, arising at 0.5-0.6 of frontal length. Ocellar seta 0.7-1.0X length of upper orbital seta. Ocellar setulae in 1-3 pairs. Gena with 4-7 setae. Length of flagellomere 1 0.8-1.0X height, anterodorsally rounded.

Thorax. Katepisternum with one or two setulae anterior to posterodorsal seta. Anterior acrostichal setulae variable, often extending anterior to level of postpronotal seta, usually as strong as following acrostichals.

Male terminalia. Tergite 6 divided medially, length 0.2-0.3X tergite 5; syntergosternite 7+8 0.4-0.5X length of tergite 5. Strap-like sclerite represented by a separate sclerotized area on left anterolateral corner of each of sternites 6 and 7, bearing left sensory setula; that of sternite 7 not extending to spiracle 7. Genitalia as in Fig. 18. Epandrium abruptly narrowing preapically to an acute point, usually medially curved. Paramere and gonopod moderately developed; gonopod bearing two or three setae. Apex of aedeagus, in ventral view, gently rounded, with slight medial emargination; preapical keels well developed.

Type material examined. *Holotype* ♀ (abdomen slide mounted in euparal). U.S.A. **Idaho:** Avon, 26.vii.1912, [Melander?] (USNM).

Other material examined (67♂, 58♀). **CANADA. Alberta:** McMurray, 30.vii.1953, G.E. Ball, 1♂ (BRI); Eisenhower Jct., Banff Nat. Park, 15.vii.1962, K.C. Herrmann, 1♀ (BRI). **Manitoba:** Aweme, N. Criddle, 18.vii.1916, 1♀ (BRI), 25.vii.1916, 3♂ (USNM), 15.viii.1916, 2♀ (USNM), 19.vii.1917, 1♀ (BRI); Treeshbank, N. Criddle, 23.vii.1915, 1♂ (USNM), 6.viii.1915, 2♀ (BRI), 1♀ (USNM); Ninette, 15.vii.1958, J.G. Chillcott, *ex. Betula glandulosa*, 1♂ (BRI); Spruce Woods Forest Reserve, 15miN Glenboro, 24.vii.1958, J.G. Chillcott, 1♂ (BRI). **Northwest Territories:** Norman Wells, G.E. Shewell, 2.vii.1969, 1♂, 8.vii.1969, 1♂ (BRI); Yellowknife, 18.viii.1949, R.R. Hall, 1♂ (BRI). **Ontario:** Hamilton, M. Sanborne, Malaise trap, 15-20.vi.1980, 2♂, 2♀ (UAT), 28.vi.1980, 2♂, 10-13.vii.1980, 2♂ (GUE), 13-19.vii.1980, 2♂, 2♀ (CAS), 2♂ (GUE), 31.vii.1980, 1♂, 1.viii.1980, 2♂ (GUE); Windsor, Ojibway Prairie Reserve, 18.vi.1980, S. Beierl, 3♂, 2♀, 11.vi.1981, K.N. Barber, 1♂ (GUE); Windsor [edge of Ojibway Prairie Reserve], S.A. Marshall, Malaise trap, 3-7.vi.1982, 1♂, 8-14.vi.1983, 2♂, 14-21.vi.1982, 1♂ (GUE); Georgian Bay Island 421, 15.viii.1963, J.P. Bogart, 1♂ (GUE); Coniston, 26.vii.1915, Parish, 1♂, 2♀ (USNM); Ogoki, 8.vii.1952, J.B. Wallis, 1♂, 1♀ (BRI); Osgoode, 22.v.1964, J.R. Vockerth, 1♀ (BRI); Guelph, 1.viii.1976, P.R. Heels, 1♀ (GUE); 60miW Hearst, 5.vii.1954, A.H. Sturtevant, 1♂ (USNM); Waubamick, 15.vii.1915, J.M. Aldrich, 1♀ (USNM). **Quebec:** LaVerendrye Prov. Park, 29.vi.1965, D.M. Wood, 1♀ (BRI); Bonaventure Is., 25.vii.1954, G.P. Holland, gull nest, 1♀ (BRI); Old Chelsea, Summit King Mt., 1150', J.R. Vockerth, 25.v.1960, 1♂, 2♀, 13.vi.1961, 1♀, 16.vi.1961, 1♂, 25.v.1964, 3♂, 1♀, 26.v.1964, 1♂, 1♀, 4.vi.1964, 1♂, 8.vi.1964, 2♂, 7.vi.1965, 2♂, 16.vi.1971, 2♂, 1♀, 16.vi.1961, 1♀ [with J.G. Chillcott's label] (BRI); Summit King Mt., 13.vi.1980, K.N. Barber, 2♂ (GUE). **Saskatchewan:** Attons Lake, 21.viii.1940, A.R. Brooks, 1♂ (BRI); Indian Head, K. Stewart, 7.viii.1929, 1♂, 1♀, 27.vii.1929, 1♀ (BRI); Big River, 5.vii.1959, A&J. Brooks, 1♀ (BRI). **Yukon Territory:** Dawson, W.W. Judd, 1.vii.1949, 1♂, 1♀, 17.vii.1949, 1♀ (BRI). U.S.A. **Colorado:** Clear Cr. Co., West Chicago Cr., 9800', 11.viii.1961, S.M. Clark, 1♂ (BRI); 5miSW Idaho Springs, 27.vii.1961, 8600', C.H. Mann, 1♂, 1♀ (BRI). **Illinois:** Urbana, 3.ix.1916, [no collector], 1♂ (INHS); Urbana, 30.viii.1914, dredge ditch, [J.R. Malloch], 1♀ (INHS); White Heath, 11.vii.1915, [no collector], 1♀ (INHS); Chicago, [no date], A.L. Melander Collection, 1♀ (USNM). **Indiana:** LaFayette, J.M. Aldrich, 10.v.1915, swept from grass, 4♂, 12.v.1915, 1♀, 2.vii.1915, 1♂, 16.vii.1915, 1♂, 1♀, 12.vii.[1915?], 1♀, 18.viii.1916, 1♀, 7.v.1918, 1♂ (USNM). **Iowa:** ImiS Amana, 13.viii.1927, G.O. Hendrickson, 1♂ (ISU); Boone Co., Ledges St. Park, 19.v.1954, Wartens & Malcom, 1♀ (UMIN). **Massachusetts:** Woods Hole, "[5 or S].5.50", A.H. Sturtevant Collection, 1♂ (USNM). **Minnesota:** Carlton, 10.vi.1934, D. Denning, 1♀ (UMIN). **Montana:** Lake McDonald, Glacier Park, 14.viii.1916, A.L. Melander, 1♂, 1♀ (USNM). **New Hampshire:** Rockingham Co., Rye, 31.vii.1979, J.F. Burger, 3♀ (UNHD). **New York:** Franklin Co., Paul Smiths, 20.vii.1962, J.R. Vockerth, 1♂ (BRI); Lake Placid, 2000', 19.vii.1962, J.R. Vockerth, 1♀ (BRI); Lake George, 26.vii.1929, A.L. Melander, 1♀ (USNM). **South Dakota:** Waubay, 6.vi.1918, J.M. Aldrich, 1♂, 1♀ (USNM); Aberdeen, 29.v.1916, J.M. Aldrich, 1♀ (USNM). **Vermont:** St. Albans, 21.vi.[?], C.W. Johnson, 1♂ (MCZ). **Wyoming:** Park Co., Pahaska Teepee, 6800', 24.viii.1979, riverside meadow and pine forest, S&J. Peck [Malaise trap], 2♂, 2♀ (GUE).

Remarks. *Pseudodinia melanitida* can be distinguished from all other species in the east and midwest by its predominantly shiny black appearance. At its western distributional

limits, *P. melanitida* usually can be separated from shiny forms of *P. varipes* by its more extensively bare gena and parafacial, and by its uniformly dark flagellomere 1 which lacks any indication of an anterodorsal angle. *Pseudodinia occidentalis* differs by often having more extensive yellow on the tibiae but examination of the male genitalia is required for positive identification. Shiny forms of *P. pruinosa* require examination of the male genitalia as well, to confirm that the aedeagus and epandrial apices are not as described above for *P. melanitida*. *Pseudodinia slussi* is apparently allopatric with *P. melanitida* while *P. latiphallis* is both allopatric and more extensively pruinose.

The holotype female has been placed here mainly because it is not as similar to other shiny western species, despite being somewhat beyond the known distributional range of the more confidently identified males. The slide mounted abdomen has the dorsal pruinosity extending medially onto the basal third of tergite 4. The acrostichal and postpronotal setulae are not strongly developed so this specimen is less likely referable to *P. occidentalis* in which these are usually strong. Because the antenna does not have an anterodorsal angle and is unicolourous, the holotype is not likely a shiny form of *P. varipes*.

Pseudodinia melanitida is not readily confused with the very pruinose *P. nitens*, especially when considering details of the male genitalia (Figs. 18, 30). Specimens of *P. melanitida*, and in fact shiny specimens of several species, have in the past been called *P. nitens* (see "Remarks" under that species). Malloch (1940) listed two additional specimens from Idaho and Alberta under the name *P. nitida* Melander, but these are referred to *P. occidentalis* and *P. pruinosa*, respectively.

Variation. There are a few eastern specimens with one or two protpronotal setulae that are strengthened to about half the length of the postpronotal seta. This condition has also been observed in three specimens of *P. pruinosa* from Arizona. Otherwise, the anterior acrostichal and postpronotal setulae are often of similar strength to the more posterior acrostichals, as in *P. occidentalis*.

Distribution (Fig. 68). *Pseudodinia melanitida* is widely distributed from eastern Quebec to the Yukon Territory, south to Indiana and Colorado. It is absent from the southeastern and extreme western and southwestern United States. This is the most northerly recorded species (although one female from Alaska may belong to *P. pruinosa*).

Biology. Ecological observations in Ontario suggest that *P. melanitida* is ecologically distinct from sympatric populations of *P. antennalis*, *P. pruinosa*, and *P. varipes*. No specific grass or mealybug associations were discovered (Barber 1984). The reference to a gull nest on the label below the specimen from Bonaventure Island, Quebec, likely represents only a fortuitous collection, although gulls are known to line their nests with grasses (Godfrey 1976).

Etymology. From the Latin *melan-* and *nitidus* meaning "black" and "shining", respectively, the specific epithet *melanitida* refers to the general appearance of this species. This name is also a combination of Melander and his preoccupied name, *nitida*.

Pseudodinia varipes Coquillett

Figs. 19-21, 67.

Pseudodinia varipes Coquillett, 1902: 187; not *Pseudodinia pruinosa* Melander 1913: 295, Malloch 1940: 269 and McAlpine 1965: 708, notwithstanding.

Pseudodinia varipes; (type material only) Melander 1913: 295; Malloch 1921: 347; Malloch 1940: 269; McAlpine 1960: 53; McAlpine 1965: 708.

Description. Body length 1.8-2.7 mm. Colour varying from predominantly shiny black to grey pruinose. Palp and antenna brown to black; scape and pedicel sometimes paler. Knees, tarsi, and apical 0.2-0.3 of tibiae yellow; tarsomeres 2-5 sometimes gradually darkened apically. Ocellar triangle and lateral extremities of vertex often pruinose. Frons entirely bare with anterior extension of bare area onto parafacial, usually to half height of

face, rarely with parafacial entirely bare. Gena predominantly pruinose; sometimes anteromedially bare, rarely almost entirely bare. Head otherwise lightly pruinose. Thorax and dark parts of legs pruinose, often lightly so, appearing shiny. Wing hyaline. Abdomen of male with dorsal wedge of pruinosity extending broadly across tergites 1-3 and sometimes basally on tergite 4, continuing as a narrow, medial strip a variable distance across tergite 4; tergite 5 occasionally with basal strip slightly widened medially. Sublateral bare areas present on tergites 2-5 or 3-5 leaving tergite 4 largely, and tergite 5 almost entirely, bare. Of female, with sublateral bare areas somewhat larger, leaving wedge of pruinosity extending no more than about 0.7 of tergite 4.

Head. Height 1.2-1.4X length; width 1.6-2.0X length. Height of compound eye 0.9-1.0X length, 3.8-5.9X genal width. Frontal width 1.1-1.3X length. Upper orbital seta 0.7-1.0X inner vertical seta, arising at 0.1-0.3 of frontal length. Lower orbital seta 0.6-0.9X length of upper orbital seta, arising at 0.5-0.6 of frontal length. Ocellar seta 0.7-1.0X length of upper orbital seta. Ocellar setulae in one or two pairs. Gena with 4-8 setae. Length of flagellomere 1 often 1.0-1.1X height, usually with an anterodorsal angulation (Fig. 20c, most western specimens); can be 0.8-1.0X height and apically rounded (Figs. 19c, 21c, generalized condition for genus).

Thorax. Katepisternum with two setulae anterior to posterodorsal seta. Anterior acrostichal setulae variable, if extending anterior to level of postpronotal seta, then usually weaker than following acrostichals.

Male terminalia. Tergite 6 divided medially (except specimen from Creston, B.C.), length 0.2-0.3X tergite 5; syntergosternite 7+8 0.4X length of tergite 5. Strap-like sclerite represented by a separate sclerotized area on left anterolateral corner of each of sternites 6 and 7, usually bearing the left sensory setula; that of sternite 7 sometimes extending posteriorly to encircle spiracle 7. Genitalia as in Figs. 19-21. Epandrium with anteroventral margin nearly straight to moderately concave when viewed laterally. Usually with paramere relatively short and gonopod relatively elongate (Fig. 20), bearing two or three setae, but sometimes with paramere moderately long and gonopod variable (Figs. 19, 21). Aedeagus, in lateral view, gradually curved; in ventral view, variably narrowing preapically giving a rounded (not truncate) apex with slight emargination; preapical keels well developed and median trough moderately so.

Type material examined. *Holotype* ♂ (dissected). U.S.A. **New Mexico:** Las Vegas Hot Springs, 3.viii.[1901], H.S. Barber, Type No. 6651 (USNM). *Paratypes* (2 ♀, USNM). Same data as holotype except for the following dates: 8.viii.[1901], and 15.viii.1901 (abdomen missing, not seen, presumed to be slide mounted at USNM). See discussion under "Variation" regarding association of the type material.

Other material examined (71 ♂, 53 ♀). **CANADA. British Columbia:** 10miE Creston, 31.vii.1980, G. Gibson, sweeps, 1 ♂ (BRI); Robson, H.R. Foxlee, 22.vi.1947, 1 ♂, 3.vii.1947, 1 ♀, 13.vii.1947, 1 ♀ (BRI); Kaslo, "16.7", A.N. Caudell, 1 ♀ (USNM); 10miE Osoyoos, 30.vii.1980, G. Gibson, sweeping *Pinus ponderosa* forest meadow, 2 ♂ (BRI). **Ontario:** Windsor, Ojibway Prairie Reserve, K.N. Barber, swept from *Andropogon gerardi* Vit., 11.vii.1980, 1 ♀, 18.viii.1980, 1 ♂ (GUE), 21.vii.1981, 23 ♂, 15 ♀ (GUE), 10 ♂, 10 ♀ (BRI), 5 ♂, 5 ♀ (USNM), 3 ♂, 2 ♀ (UAT), 2 ♂, 2 ♀ (CAS), 12.vii.1982, 6 ♂, 7 ♀, 18.viii.1983, 2 ♂ (GUE); Ojibway Prairie Reserve, K.N. Barber, reared from eggs of females collected 21.vii.1981, fed on *Trionymus winnenucae* McKenzie, 2 ♀ (GUE); Windsor [edge of Ojibway Prairie Res.], 9-16.viii.1982, S.A. Marshall, Malaise trap, 1 ♂ (GUE). **U.S.A. California:** Shasta Springs, [?].vii.1915, A.L. Melander, 1 ♂ (USNM). **Idaho:** Oneida Co., Black Pine Canyon, 5800', 12-25.vi.1974, [no collector] Malaise trap, 1 ♂, 3 ♀ (USU); Oneida Co., Rock Creek, 17.vii.1972, G.F. Knowlton, 1 ♂ (USU); Elmore Co., 11miS Pine, 22.vi.1977, W.F. Barr, 1 ♂ (UIM). **Montana:** Ravalli Co., 6miSE Hamilton, 3950', 13.vii.1973, C. Musgrave, 1 (OSU). **Nevada:** Harrison Pass, 25.vi.1953, A.B. Gurney, 1 ♂ (USNM); Angel Lake, 12miSW Wells, 8400', 11.vii.1961, B.H. Poole, 1 ♂ (BRI). **Oregon:** Crook Co., 8miSE Prineville, 19.vi.1970, Oman, 1 ♂ (OSU). **Utah:** Cache Co., Rock Creek, 22.vii.1976, W.J. Hanson, 1 ♂ (USU); Cache Co., Logan Canyon, China Row, 10.viii.1979, G.F. Knowlton, 1 ♂ (USU); Cache Co., Green Canyon, W.J. Hanson, 2-10.viii.1973, 1 ♀, 25-31.vii.1968, Malaise trap, 1 ♂, 2 ♀ (USU). **Washington:** Kamiac Butte, 25.viii.1914, A.L. Melander Collection, 1 ♂ (USNM); Colton, C.C. Shelton, virgin prairie population study project, 9.vii.1948, plot #9, 1 ♀, 24.vii.1948, plot #8, 1 ♂ (WSUP).

Remarks. The use of the name *P. varipes* is restricted to a relatively rare but widely distributed species or species complex (see "Variation" below). All specimens share a gradually curved aedeagus when viewed laterally (Figs. 19a-21a), similar to that of *P. latiphallis* (Fig. 22a).

The keys provided by Melander (1913) and Malloch (1921) use frontal dimensions and diverging apices of "third and fourth veins" to distinguish *P. varipes* from *P. melanitida* (as *P. nitida* Melander) and *P. pruinosa*. This is both misleading and inaccurate since the type material, the only specimens available at the time, does not differ substantially from most other species in these characteristics.

Pseudodina varipes is often difficult to recognize on the external characters alone due to the variable density of pruinosity. Those specimens with a much reduced pruinosity usually have the anterodorsal corner of flagellomere 1 angular and the scape and pedicel paler in colour. The shortened paramere and elongate gonopod assist in recognizing these specimens. The gradually curved aedeagus, in lateral view, is a character shared only by *P. latiphallis* which has a considerably wider aedeagus and the epandrial apices deflected posteriorly. The more heavily pruinose, disjunct population from Ontario can be separated from the sympatric populations of *P. pruinosa* by the usually predominantly pruinose gena and parafacial in *P. varipes*, and the aedeagal characters as above.

Variation. This is a fairly variable species as illustrated by the three variants of male genitalia (Figs. 19-21), and might, in fact, be a complex of several sibling species. Most of the western male specimens have genitalia similar to those of the specimen from Creston, B.C., (Fig. 20), with a relatively short paramere and a well developed gonopod. The aedeagal width, in ventral view, varies considerably, with some as narrow as that of the holotype (Fig. 19b), and others nearly as wide as that in Fig. 21b (disjunct Ontario population). As well, these typical western specimens are usually quite shiny and have the length of flagellomere 1 1.0-1.1X the height, with the anterodorsal aspect usually quite angular (Fig. 20c). The shorter flagellomere 1 is nearly rounded anterodorsally and the scape and pedicel are usually pale brown to yellow in these shiny western specimens.

The holotype, and the specimens from Harrison Pass, Nevada, and Ontario, exhibit the generalized conditions (for the genus) of flagellomere 1, i.e. length 0.8-1.0X height and anterodorsally rounded (Figs. 19c, 21c). They have a relatively elongate paramere and poorly developed gonopod (Figs. 19, 21). In addition, the holotype and the specimen from Harrison Pass have the parafacial and gena more extensively bare and the thorax slightly more pruinose than most other western specimens. The specimens from Ontario have the most pruinose thoraces and the widest aedeagi, although the narrowest among them are comparable to some western specimens.

One of the specimens from Robson, B.C., possesses an elongate gonopod, and a long, angular flagellomere 1, but an elongate paramere. The other specimen is easily placed here, having the more prevalent western condition of all three structures. The two specimens from Osoyoos possess a long paramere, a short gonopod, and an elongate but rounded flagellomere 1.

It has been determined that the pruinose population of *P. varipes* in Ontario is ecologically distinct from the sympatric population of *P. pruinosa* (Barber 1984). The genitalia are quite distinct (Figs. 21, 26) and specimens of *P. pruinosa* in Ontario have entirely bare parafacials and genae while these areas are predominantly pruinose in the sympatric *P. varipes* specimens. It is quite unlikely that these are conspecific variants (see "Biology" below).

Until more biological information is gathered for the western populations and more sampling is conducted in the wide geographic area separating these populations from that in Ontario, all are considered variants of *P. varipes*. This is in spite of the fact that the holotype is at the extreme of the range of variation of males in the extent of the bare areas on the gena and parafacial, and the gena is the widest measured in proportion to the eye height (eye/gena=3.8). The female paratypes are somewhat shinier than the holotype and their genae and parafacials are entirely bare. Although these are associated with the male,

it is not entirely certain that they are properly associated.

The specimen from Harrison Pass has the lower orbital setae distinctly proclinate. This is the only known occurrence of proclinate orbitals within the family Chamaemyiidae. The specimen from Creston has tergite 6 undivided medially, a specific character for *P. nigratarsis* and *P. cinerea*. A single specimen of *P. occidentalis* has this tergite only slightly emarginate anteromedially. These conditions are considered anomalous in *P. varipes* and *P. occidentalis*.

Distribution (Fig. 67). Principally a western species, *P. varipes* is known from southern British Columbia south to northern California, Nevada, and New Mexico, with an apparently disjunct population in Ontario.

Biology. Specimens of the population in Ontario are associated with the grass *Andropogon gerardi* Vitman. A mealybug, *Trionymus* sp., is known to infest this grass at another locality in Ontario (Barber 1984). This disjunct population is sympatric with *P. antennalis*, *P. melanitida*, and *P. pruinosa*, but it is evidently ecologically distinct from the latter two species by its plant association. This is not so with *P. antennalis* which is also associated with *A. gerardi*. Several western specimens of *P. varipes* were also taken with *P. pruinosa*, but their host associations are unknown.

Laboratory rearings of two adult females from eggs obtained from field-collected females, suggest a physiological difference between *P. varipes* and *P. pruinosa* (Barber 1984). Larvae of both species were fed specimens of the same mealybug species, *T. winnemucae* McKenzie, the natural host of *P. pruinosa* in Ontario, but the developmental time was considerably longer in *P. varipes*. This biological information supports the morphological evidence that these are two distinct species.

Pseudodinia occidentalis new species

Figs. 23-24, 68.

Pseudodinia nitida; Malloch 1940: 269, in part; not *Pseudodinia nitida* Melander 1913: 295.

Description. Body length 2.0-3.2 mm. Pruinosity reduced, colour ranging from shiny black to lightly grey. Palp and antenna brown to black; scape, pedicel, and base of flagellomere 1 sometimes lighter. Knees, tarsomere 1, and apical 0.2-0.5 of tibiae yellow; tarsomeres 2-5 yellow or gradually darkening apically. Vertex, ocellar triangle, and frons entirely bare. Parafacial and gena bare to lightly pruinose. Head otherwise lightly pruinose. Thorax and dark parts of legs very lightly to moderately pruinose, usually appearing shiny. Wing hyaline to lightly infuscate. Abdomen of male with dorsal wedge of pruinosity extending broadly across tergites 1-3, and a narrow median strip variably extending across tergite 4, at most the full length; successively larger sublateral bare areas present on tergites 2-5 or 3-5, leaving tergite 4 mostly, and tergite 5 essentially bare. Of female, with sublateral bare areas sometimes slightly more extensive.

Head. Height 1.1-1.3X length; width 1.5-2.0X length. Height of compound eye 0.9-1.1X length, 4.2-6.2X genal width. Frontal width 1.1-1.4X length. Upper orbital seta 0.8-1.0X length of inner vertical seta, arising at 0.1-0.2 of frontal length. Lower orbital seta 0.6-1.0X length of upper orbital seta, arising at 0.5-0.6 of frontal length. Ocellar seta 0.8-1.1X length of upper orbital seta. Ocellar setulae in one or two pairs. Gena with 5-10 genal setae. Length of flagellomere 1 0.8-1.0X height, anterodorsally rounded.

Thorax. Katepisternum with two setulae anterior to posterodorsal seta. Anterior acrostichal setulae usually extending anterior to level of postpronotal seta, usually subequal in strength to following acrostichals.

Male terminalia. Tergite 6 divided medially (except specimen from Wyoming in which it is incompletely divided), length 0.2-0.3X tergite 5; syntergosternite 7+8 0.4-0.5X length of tergite 5. Strap-like sclerite represented by a separate, indistinctly sclerotized area on left, anterolateral corner of each of sternites 6 and 7, usually bearing the left sensory setula; that

of sternite 7 sometimes extending posteriorly to encircle spiracle 7. Genitalia as in Figs. 23-24. Epandrial apices relatively broadly rounded. Paramere moderately long. Gonopod short to moderately developed, bearing two or three setae. Aedeagus, in lateral view, relatively thick throughout its length; in ventral view, apex usually widely truncate with shallow emargination, well defined median trough, and low, preapical keels.

Type material examined. *Holotype* ♂ (not dissected). U.S.A. **Arizona:** Pima Co., Quinlan Mts., Kitt Peak, 6875', 17.v.1975, T.P.Sluss (USNM); courtesy of UAT). *Paratypes* (147 ♂, 108 ♀). CANADA. **British Columbia:** Penticton, 3.viii.1967, J.R.Vockeroth, 7 ♂, 3 ♀ (BRI); Terrace, 31.v.1960, R.J. Pilfrey, 1 ♂, 8.vi.1960, J.G.Chillcott, along railroad, 1 ♀ (BRI); 32miSW Terrace, 9.vii.1960, C.H.Mann, 1 ♂ (BRI). U.S.A. **Arizona:** same data as holotype, 5 ♂, 9 ♀ (UAT), 5 ♂, 5 ♀ (BRI), 5 ♂, 5 ♀ (USNM); same data as holotype but with the following dates, 4.viii.1977, 5 ♂, 2 ♀, 12.viii.1977, 4 ♂, 4 ♀ (UAT); Cochise Co., Chiricahua Mts., S.W.R.S., 8.ix.1970, T.P.Sluss, 5 ♂, 3 ♀ (UAT); S.W.R.S., 5400', 30.iv.1979, K.N.Barber, 3 ♂, 3 ♀ (GUE); S.W.R.S., 5miW Portal, 5400', 5.viii.1971, P.O.Ritcher, 2 ♀ (OSU); S.W.R.S., P.H.Arnaud, Jr., 24.ix.1966, 1 ♂, 1 ♀, 25.ix.1966, 1 ♂ (CAS); S.W.R.S., 5.vii.1963, J.G.Rozen, D.K.Oliver, A.R.Moldenke, J.A.Woods, 1 ♂ (AMNH); S.W.R.S., 3.viii.1966, D.R.Miller, 1 ♀ (UCD); Apache Co., Alpine Divide Camp, 4miN Alpine, 8500', 15.vii.1965, F.P&M.Rindge, 1 ♂ (AMNH). **California:** Mt. San Jacinto, 10.v.1935, A.L.Melander, 30 ♂, 12 ♀ (USNM); Victorville, 16.v.1955, W.R.M.Mason, 6 ♂, 14 ♀ (BRI); Pacific Grove, A.H.Sturtevant Collection, 21.v.1920, 2 ♂, 13-30.vi.1920, 1 ♂, 2 ♀, 8-23.viii.1920, 1 ♂, 20.viii.1920, 1 ♂ (USNM); Valyermo, 13.v.1944, A.L.Melander, 1 ♂, 2 ♀ (USNM); Mt. Home Can., 13.v.1947, A.L.Melander, 1 ♂, 2 ♀ (USNM); Nevada Co., Truckee River, 4.5miE Truckee, Hwy. 40, 5600', 27.viii.1965, H.B.Leech, 1 ♂ (CAS); Kern Co., Onyx, 25.iv.1950, E.I.Schlinger, 2 ♂ (UCD); Onyx, 23.vii.1940, R.H.Beamer, 1 ♂ (UKL); Inyo Co., S. edge Lone Pine, 17.vi.1962, J. Tomlinson, roadside weeds and grasses, 1 ♀ (CAS); Inyo Co., Lone Pine, 9.vi.1929, R.L.Usinger, 1 ♂ (CAS); Plumas Co., Mt. Ingalls, 11.vii.1964, [no collector], 1 ♀ (UCD); Plumas Co., Clio, 9.vii.1916, H.G.Dyar, 2 ♂ (USNM); Camp Angelus, 2.vi.1947, A.L.Melander, "Wh Ceanothus", 1 ♂ (USNM); Crestline, 13.vii.1944, A.L.Melander, 1 ♂ (USNM); Contra Costa Co., Antioch, 18.x.1936, R.C.Dickson, 1 ♂ (UCR); Antioch, 25.vi.1947, A.L.Melander, 1 ♂ (USNM); Felton, St. Cruz Mts., 20-25.v.1907, 300-500', Bradley, 1 ♂ (CUI), 1 ♀ (PSU); Napa Co., 2miS Spanish Flat, 29.vi.1961, R.O.Schuster, 1 ♀ (UCD); Napa Co., St. Helena, 3.vi.1909, C.Fuchs, 1 ♂ (ANSP); Alameda Co., Berkeley Hills, 20.iv.1908, [no collector], 1 ♂ (ANSP); Alameda Co., Tesla, 21.ix.1951, W.C.Bentinck, 3 ♂, 1 ♀ (UCB); Solano Co., Solano Lake, 24.iv.1970, B.L.Villegas, 1 ♂, 1 ♀ (UCD); Palo Alto, 10.vi.1921, A.H.Sturtevant Collection, 1 ♀ (USNM); Pasadena, [?].v.1952, A.H.Sturtevant Collection, 1 ♀ (USNM); Pescadero [Pescadero], 16.viii.1951, A.H.Sturtevant Collection, 1 ♀ (USNM); Barton Flat, So. Fork Camp, 2.ix.1944, A.L.Melander, 1 ♀ (USNM); Helendale, 18.v.1953, W.R.Richards, 1 ♀ (BRI); S. Fks. Sta. Ana [River], A.L.Melander, 2.viii.1942, 1 ♀, 17.vi.1945, 1 ♀, 18.vi.1945, 2 ♀ (USNM); Up Sta. Ana R., 11.viii.1948, A.L.Melander, 1 ♀ (USNM); Nevada Co., Sagehen Ck., 23.vii.1968, D.S.Horning, Jr., 1 ♀ (UCD); Yolo Co., Davis, 20.vi.1966, C.R.Kovacic, 2 ♀ (UCD); El Dorado Co., Freds Place, 10.vii.1967, R.O.Schuster, 1 ♀ (UCD); San Diego Co., Mt. Palomar, 28.vi.1963, C.H.Frady, 1 ♀ (OSU); Siskiyou Co., road to Taylor Lake, 5750', S. of Sawyers Bar-Etna road, 28.vii.1968, H.B.Leech, 1 ♂ (CAS); Riverside, 5.v.1935, A.L.Melander, 1 ♂, 2 ♀ (USNM); Riverside, 7-21.vi.1983, D.Yu, Malaise trap, 1 ♂ (GUE). **Colorado:** 6miSW Idaho Spring, 27.vii.1961, J.G.Chillcott, 1 ♂ (BRI); Clear Cr. Co., Chicago Cr., 8800', 5.viii.1961, B.H.Poole, 2 ♂, 1 ♀ (BRI); Jackson Co., Rabbit Ears Pass, 7.vii.1961, J.G.Chillcott, 1 ♂ (BRI). **Idaho:** Lake Waha, 9.vi.1918, A.L.Melander, 1 ♂ (USNM); Chatcolet, [?].viii.1915, A.L.Melander, 1 ♂, 2 ♀ (USNM); Moscow Mt., 4.vii.1911, A.L.Melander Collection, 1 ♂ (USNM); Priest Lake, 1.viii.1916, A.L.Melander, 1 ♂ (USNM); Viola, 26.vi.1912, J.M.Aldrich, 1 ♂, 1 ♀ [reported as *P. nitida* Melander by Malloch 1940] (USNM). **Nevada:** Washoe Co., Verdi, 25.vi.1961, F.D.Parker, 1 ♂ (UCD); Washoe Co., Patrick, 30.vi.1964,

J.A.Froebe, 1 ♂ (UCD); Angel Lake, 12miSW Wells, 8400', 11.vii.1961, J.G.Chillcott, 2 ♂ (BRI). **New Mexico:** Catron Co., 8miSE Luna, 7500', 9-14.vii.1979, S&J. Peck, pond. pine at stream, 1 ♂ (GUE); 5miW Luna, 7400', 9-14.vii.1979, S&J. Peck, San Francisco River, pond. pine meadows, 1 ♂ (GUE). **Utah:** Summit Co., Bear River R.S., 3miSE, 5-12.viii.1971, Hanson & Knowlton, Malaise trap, 4 ♂, 2 ♀ (USU); Summit Co., Henrys Fork Camp, 1-10.viii.1979, 9600', S&J. Peck, pine aspen at stream, carrion Malaise trap, 1 ♂ (GUE); Grand Co., 10miSE Moab, 30.v.1974, Knowlton & Hanson, 1 ♂ (USU); San Juan Co., Pack Ck. C.G., La Sal Mts., 3.vi.1977, Hanson & Knowlton, 1 ♀ (USU); Cache Co., Blacksmith Fork Can., 3.vii.1971, G.F.Knowlton, 1 ♂ (OSU); Cache Co., Green Canyon, 2-10.viii.1973, W.J.Hanson, Malaise trap, 2 ♂, 5 ♀ (USU); Cache Co., Tony Grove Canyon, 7800', 1-7.viii.1975, Knowlton & Hanson, Malaise trap, 1 ♂ (USU); Cache Co., Mendon Cold Spg., 20.vi-4.vii.1977, 11-17.viii.1977, [no collector], Malaise trap, 2 ♂ (USU); Cache Jct., 20.vi.1913, H.R.Hagan, 1 ♂ (AMNH); Franklin Basin, 21.vii.1967, G.F.Knowlton, 1 ♂ (USU). **Washington:** Mica, 14.vii.1918, A.L.Melander, 1 ♂, 2 ♀ (USNM); Copalis, 26.viii.1951, A.H.Sturtevant Collection, 1 ♂ (USNM); Valleyford, 19.vi.1919, A.L.Melander, 1 ♂ (USNM); Seattle, 2.viii.1908, A.L.Melander Collection, 1 ♂ (USNM); Lowden, 22.vi.1921, A.L.Melander, 1 ♂ (USNM); Holland, 5.vii.1919, A.L.Melander, 2 ♂ (USNM). **Wyoming:** North Fork Sibylee Cr. nr. Wheatland, 16.viii.1940, H.E.Milliron, 1 ♂ (UMIN).

Remarks. The male genitalia of the typical populations from Arizona and California are virtually indistinguishable and this similarity has led to the inclusion of these forms in one rather bimodally variable species (see "Variation" below). Figures 23-24 show extremes in epandrial and aedeagal proportions and should not be considered specific to the respective populations. The holotype was selected from the population in Arizona since it is more readily distinguished from all other species and is known to be sympatric with several species, including the highly variable *P. pruinosa*.

Pseudodinia occidentalis is sometimes difficult to distinguish from some other species with a bare frons. All Arizona specimens (and four others, see "Variation" below) have the genal setae relatively thickened. Most specimens have the anterior acrostichals extending anterior to the level of the postpronotal seta and are of subequal strength to the following acrostichals. This latter character, combined with the usually wide aedeagal apex and reduced notal pruinosity, serves to distinguish this species from *P. pruinosa* as indicated in the key. *Pseudodinia occidentalis* can be distinguished from *P. melanitida* by its wider epandrial apices and the usually wider aedeagus.

The characters given above should be used to supplement those given in the key. In addition, the extensively yellow tibiae (apical 0.3-0.5), especially on the foreleg, assist in recognizing this species. Malloch (1940) determined the male specimen from Viola, Idaho, as *P. nitida* Melander.

Variation. Specimens from the rather singular populations from Arizona have thickened genal setae, which are subequal in strength to the postgenals. These specimens also have the parafacial and gena more extensively bare and the wings are hyaline.

The specimens outside of Arizona (except the four specimens from Catron Co., New Mexico, Moab, Utah, and Pack Creek, Utah) have unmodified genal setae and the wing is lightly infuscate in the specimens from the west coast states and British Columbia. The more easterly specimens are variable in the expression of wing infuscation.

As mentioned previously, the specimen from Wyoming has tergite 6 only basally emarginate, not entirely divided. One other dissection has a supernumerary seta near the lateral base of the right paramere (see Fig. 33b). Both conditions are considered anomalous in this species.

Distribution (Fig. 68). *Pseudodinia occidentalis* ranges widely in western North America, from British Columbia to California and New Mexico.

Biology. Few data are available. Melander's specimen from Camp Angelus, California,

bears a collection label referring to *Ceanothus* (Rhamnaceae), but probably only suggests the type of habitat as rocky hills [as per *C. sanguineus* Pursh in Gleason and Cronquist (1963)] and not an association with this shrub. One of the specimens from Lone Pine, California, was taken in roadside weeds and grasses, which is very similar to the type of habitat where other *Pseudodinia* species have been found.

Etymology. From the Latin *occidens* meaning "west", the specific epithet *occidentalis* refers to the western distribution of this species.

***Pseudodinia pruinosa* Melander**

Figs. 3, 5, 7, 10, 12, 25-29, 38-41, 44-65, 69. Table I.

Pseudodinia pruinosa Melander, 1913: 295.

Pseudodinia pruinosa; Malloch 1921: 347.

Pseudodinia nitida; Malloch 1940: 269, in part; not *Pseudodinia nitida* Melander 1913: 295.

Pseudodinia antennalis; in part, Malloch 1940: 269 (two paratypes).

Pseudodinia varipes; in part, Malloch 1940: 269, McAlpine 1965: 708; not Coquillett 1902: 187.

Description. Body length 1.9-3.1 mm. Pruinosity variable, colour ranging from relatively shiny black to densely grey. Antenna and palp usually brown to black, rarely with scape, pedicel, and palp paler brown to yellow. Knees black to yellow, tarsomere 1, and apical 0.2-0.4 of tibiae (sometimes entirely black dorsally) yellow; tarsomeres 2-5 sometimes darkened to brown or black. Frons, vertex, and ocellar triangle ranging from entirely bare to transversely pruinose in a solid band to level of upper orbital seta. Parafacial and gena bare to pruinose. Head otherwise lightly pruinose. Thorax and dark parts of legs lightly to moderately pruinose. Wing hyaline. Abdomen of male with dorsal wedge of pruinosity extending broadly across tergites 1-3, and often more narrowly across a variable or entire length of tergite 4; successively larger sublateral bare areas (Fig. 47) present on tergites 2-5 or 3-5 (Fig. 47) leaving tergite 4 largely, and tergite 5 entirely, bare. Of female, with sublateral bare areas slightly larger and dorsal pruinosity extending narrowly to no more than basal third of tergite 4 leaving tergite 4 largely to entirely, and tergite 5 entirely bare.

Head (Figs. 3, 44, 46). Height 1.1-1.4X length; width 1.6-2.0X length. Height of compound eye 0.8-1.1X length, 4.0-6.1X genal width. Frontal width 1.0-1.3X length. Upper orbital seta 0.7-1.1X length of inner vertical seta, arising at 0.1-0.3 of frontal length. Lower orbital seta 0.4-0.7X length of upper orbital seta, arising at 0.4-0.6 of frontal length. Ocellar seta 0.7-1.0X length of upper orbital seta. Ocellar setulae in one or two pairs. Gena with 3-7 setae. Length of flagellomere 1 0.8-1.0X height; usually anterodorsally rounded, rarely with very slight preapical angulation.

Thorax (Figs. 5, 7). Katepisternum with 1-4 setulae anterior to posterodorsal seta. Anterior acrostichal setulae variable, usually not extending anterior to level of postpronotal seta, but if so, then weaker than following acrostichals.

Male terminalia (Figs. 10, 47). Tergite 6 divided medially, length 0.2-0.3X tergite 5; syntergosternite 7+8 0.3-0.5X length of tergite 5. Strap-like sclerite represented by a separate, lightly sclerotized area on left, anterolateral corner of each of sternites 6 and 7, each usually bearing the left sensory setula; that of sternite 7 sometimes extending posteriorly to encircle spiracle 7. Genitalia as in Figs. 25-29, 45. Epandrium varying from nearly triangular to more elongate. Paramere of moderate length to relatively elongate. Gonopod of variable development, bearing two or three setae. Aedeagus, in lateral view, relatively short to elongate with apex narrow to thick; in ventral view, apex bluntly rounded to truncate, sometimes with slight emargination; preapical keels variably developed; median trough shallow to moderately deep.

Egg (Figs. 48-51). Length 0.7-0.8 mm., greatest width 0.2 mm. White, cylindrical, ends slightly tapering, slightly flattened ventrally (Fig. 48). Surface of chorion with 30-34

parallel, longitudinal, anastomosing ridges which are weaker ventrally. Cross ridges predominantly weakly developed, but strongly developed near ends, especially near eclosion cap where they form irregular, rectangular cells. Microsculpture of sides of longitudinal ridges appearing raspberry-like except at carinate apex (Fig. 49). Bottom of inter-ridge trough relatively smooth with small, irregularly arranged aeropyle pores. Micropyle consisting of 12-14 pores (Fig. 50); eclosion cap with 14-17 smaller pores (Fig. 51).

First-instar larva (Figs. 38, 54-59). As in third instar except as follows. Length 0.7-1.7 mm., greatest width 0.2-0.3 mm. Recently hatched specimens with contrasting yellow internal tissue in abdominal segments 5-7. Integument not shagreened in region of creeping welts (Figs. 55, 57).

Head (Fig. 54). Antenna more slender. Maxillary plate with only two marginal sensilla. Cephalopharyngeal skeleton (Fig. 38) about 0.15 mm. long, dark brown; hypopharyngeal sclerite more slender; mandible less pigmented at apex than at base; base not as broadly rounded.

Thorax (Figs. 55-56). Dorsal and ventral creeping welts bearing fewer and shorter ridges; two or three pairs of sensilla dorsolaterally on segments 2-3 in lateral extremities of creeping welts. Metapneustic, anterior spiracles absent.

Abdomen (Figs. 57, 59). Dorsal creeping welts of segment 1 with some short ridges but by segment 3, all welts bearing discrete spinules; segments 1-7 with three or four pairs of lateral sensilla as in thorax; segment 7 lacking ridges or spinules, with four pairs of lateral sensilla only; segment 8 with one pair of lateral sensilla only. Ventral creeping welts consisting of discrete spinules on segments 1-8, integument apparently not shagreened. Segment 8 with perianal pad also bearing spinules (Fig. 59); two pairs of elongate, peg-like sensilla posterolateral to perianal pad. Posterior spiracular tubes not sclerotized; internal trachea bifurcate, opening as two spiracular slits; spiracular plate also bearing four strong, simple interstigmatal hairs (Fig. 58).

Second-instar larva (Figs. 39, 52). As in third instar except as follows. Length 1.1-2.7 mm., greatest width 0.3-0.4 mm.

Head. Cephalopharyngeal skeleton (Fig. 39) about 0.24 mm. long, dark brown; hypopharyngeal sclerite slightly more slender; mandible less pigmented at apex; base more irregular in outline, not as broadly rounded.

Thorax. Anterior spiracle with four or five papillae.

Abdomen. Only apical half of spiracular tubes sclerotized; spiracular slits and ecdysial scar more prominent (Fig. 52).

Third-instar larva (Figs. 40-41, 53, 60-65). Length 3.6-5.0 mm., greatest width 0.6-0.8 mm., somewhat dorsoventrally flattened, gradually tapering through thorax to head. Abdominal segment 8 slightly narrower than segment 7, posteriorly rounded, bearing a pair of elongate, sclerotized, spiracular tubes dorsolaterally at apex. Thoracic and abdominal segments separated by conspicuous primary integumentary folds isolating intersegmental elliptical areas laterally (Fig. 53); each segment with two, often obscured, secondary integumentary folds. Colour pinkish brown with abundant creamy white fat bodies visible; scattered dark spots laterally; dorsal tracheal trunks conspicuous. Integument transparent, often bearing a dusty white coating in life, readily removed in fluid (presumably of mealybug host origin); predominantly smooth with no spines, papillae, or tubercles, but with scattered plate-like sensilla; ventral and dorsal creeping welts shagreened on areas surrounding patches of ridges on thoracic and abdominal segments (more weakly so dorsally, especially on thoracic segments).

Head. Each antennomaxillary lobe with a two-segmented, papilla-like antenna, dorsolaterally, and a maxillary palp (Figs. 41, 62) consisting of a discrete plate bearing two sensilla, surrounded by four marginal sensilla, two additional sensilla dorsolaterally (a third is indistinct), and an indistinct plate ventrally, bearing one sensillum. Two pairs of sensilla in longitudinal lines, dorsomedial to the maxillary palps. Preoral margin bounded

anterolaterally by papillate sensillum (Fig. 41); laterally produced into spine-like emarginations with lateral sensillum. Labial lobe an elongate tab-like structure. Area posterior to labial lobe bearing posteriorly oriented spines, entire area often retracted with head (Fig. 62). Cephalopharyngeal skeleton (Fig. 40) about 0.31 mm. long, black; tentoropharyngeal sclerite fused anteriorly with hypopharyngeal sclerite, dorsal and ventral cornua tapering apically, lacking windows; lateral rami of hypopharyngeal sclerite broadly fused ventrally at about midlength (Fig. 40b); mandible lightly sclerotized dorsobasally, expanded ventrally to form rounded base.

Thorax. Series of sharp, transverse ridges on creeping welts completely encircling segment 1 (Figs. 60, 63), but only a small number of lateral ridges connecting dorsal and ventral patches on segments 2 and 3. Anterior-most ridges can be broken into spinule-like sections especially dorsally on segment 1. Anterior spiracles (Fig. 61) on posterolateral surface of segment 1 not sclerotized; usually bearing four or five papillae but rarely three or six. Ventral surface of segments 1-3 each with pair of three closely grouped, needle-like sensilla situated submedially, posterior to ridges (Fig. 63); a transverse row of six sensilla dorsal to this, and two (segments 2-3) or three (segment 1) larger sensilla more laterally. Dorsal surface of segment 1 with transverse, sinuous row of ten sensilla, the most lateral pair larger, and with two pairs of sensilla posterior to these. Segments 2 and 3 dorsally with row of eight sensilla, the outer pair larger (inner six each appearing to consist of a cluster of 1-3 sensilla using light microscopy but as poorly defined pits using scanning electron microscopy).

Abdomen. Segments 1-8 with discrete dorsal and ventral creeping welts, the ventral welts more extensive on each segment and the dorsal welts lacking on segments 7-8; segments 1-3 or 1-4 with progressively smaller patches of nearly discrete spinule bands (broken ridges) anterior to the ventral creeping welt ridges (similar to thoracic segment 1 dorsally). Ventral surface of segments 1-7 bearing transverse row of six sensilla; a median pair of sensilla immediately posterior to the creeping welts but anterior to the row of six. Segments 1-7 dorsally bearing a transverse row of six sensilla "clusters" and two pairs of posterolateral sensilla "clusters". Segment 8 ventrally with a transverse row of six sensilla anterior to the perianal pad and two pairs of sensilla posterolateral to the perianal pad below the posterior spiracles; dorsally with only the lateral two pairs of sensilla "clusters". Perianal pad broad, oval, and conspicuous, with median, longitudinal anal slit; no associated spinules or sensilla (Fig. 64). Posterior spiracular disc undifferentiated, without marginal lobes; bearing two cylindrical, sclerotized spiracular tubes about twice as long as basal diameter (Fig. 64), with internal trachea trifurcate, opening on spiracular plate as three radially arranged slits (Fig. 65); spiracular plate also bearing an ecdysial scar and four bifurcate, often broken, interstigmatal hairs bordering the slits.

Puparium. Length 2.8-3.8 mm., greatest width 0.7-1.0 mm.; subcylindrical, flattened ventrally, convex dorsally; tapering in anterior fifth and slightly so to abdominal segment 8 which is rounded posteriorly. Integument brown, heavily sclerotized, lateral spots inconspicuous; finely wrinkled, more densely so on thoracic segments and abdominal segments 1 and 8. Integumentary folds of thoracic segments 2-3, and abdominal segments conspicuous. Apex (thoracic segment 1 since head retracted) truncate in dorsal view with sclerotized anterior spiracles projecting from anterolateral aspects above ecdysial suture. Posterior spiracles diverging though bases more approximated than in larva. Perianal pad slightly invaginated. Other fine details as in third-instar larva.

Type material examined. *Holotype* ♂ (dissected). U.S.A. Texas: "5.11.0", A.L.Melander Collection (USNM). The holotype is near one extreme in its extensive pruinosity and is discussed further under "Variation".

Other material examined (1179 ♂, 1142 ♀, ?? = sex undetermined). CANADA. Alberta: One-four, 3.vi.1956, E.E.Sterns, 1 ♂, 1.vi.1956, O.Peck, swept from *Agropyron cristatum*, 1 ♀ (BRI); One-four, 2.viii.1980, G.Gibson, sweeping, 27 ♂, 28 ♀ (GUE); 5miW Writing-on-Stone Prov. Pk., Milk River Valley, 15.vii.1980, G.Gibson, sweeping, 19 ♂, 18 ♀ (GUE); 0.5miE Writing-on-Stone Prov.

Pk., Milk River Valley, 1.viii.1980, G.Gibson, sweeping, 8 ♂, 11 ♀ (GUE); Medicine Hat, [?].x.1911, J.R.Malloch, 1 ♀ [reported as *P. nitida* Melander by Malloch 1940] (USNM); Medicine Hat, 16.vii.1956, O.Peck, swept from *Agropyron cristatum*, 4 ♂, 5 ♀ (BRI); Oyen, 22.vi.1979, D.H.Pengelly, 1 ♂ (GUE); Oldman River, Lethbridge, 22.vi.1956, O.Peck, [some] swept from *Bromus inermis*, 11 ♂, 8 ♀ (BRI); Lethbridge, 5.vii.1956, O.Peck, 3 ♀ (BRI); Elkwater Lake, 21.vii.1956, O. Peck, 2 ♂, 2 ♀ (BRI); Scandia, 9.vii.1956, O.Peck, 1 ♀ (BRI); Gilchrist Ranch, Aden, 28.vi.1956, O.Peck, swept from grass range, 1 ♂, swept from alfalfa and crested wheatgrass, 1 ♀ (BRI). **British Columbia:** Robson, H.R.Foxlee, 13.vii.1947, 2 ♂, 1 ♀, 22.vi.1947, 1 ♂ (BRI); 10miE Osoyoos, 30.vii.1980, G.Gibson, sweeping *Pinus ponderosa* forest meadow, 2 ♂, 2 ♀ (GUE); Okanogan Valley nr. Osoyoos, 10.vii.1980, sage, S.A.Marshall, 1 ♀ (GUE); 5miNW Canal Flats, 17.vii.1970, Oman, 1 ♀ (OSU). **Manitoba:** Treesbank, N.Criddle, 20.vii.1915, 3 ♂, 1 ♀ (USNM), 23.vii.1915, 1 ♂ (INHS), 1 ♀ (USNM), 28.vii.1915, 1 ♀ (INHS), 1 ♂, 3 ♀ (USNM), 6.viii.1915, 3 ♂, 1 ♀ (BRI), 1 ♂ (USNM); Aweme, N. Criddle, 25.vii.1916, 1 ♂, 2 ♀, 1.viii.1916, 1 ♂ (USNM); 2miW Stockton, J.G.Chillcott, 6.viii.1958, 1 ♂, 1 ♀, spruce sand community, 16.vii.1958, 2 ♂, 28.vii.1958, 3 ♂, 2 ♀ (BRI); Bald Head Hills, 13miN Glenboro, 12.vii.1958, J.G.Chillcott, 2 ♂, 6 ♀ (BRI); Bald Head Hills, [Spruce Woods Forest Reserve], 12kmN Glenboro, K.N.Barber, swept from *Schizachyrium scoparium*, 1.viii.1983, 3 ♂, 1 ♀, 4.viii.1983, 1 ♂ (GUE); 5miSW Shilo, 22.vii.1958, J.G.Chillcott, at margin of grain field, 1 ♂ (BRI). **Ontario:** Rondeau Prov. Pk., Rondeau Park, 15.viii.1980, K.N.Barber, swept from *Schizachyrium scoparium*, 25 ♂, 44 ♀ (GUE); Rondeau Prov. Pk., 17.vi.1983, R.Gadawsky, 2 ♂, 4 ♀ (GUE); Rondeau, 2.vii.1960, D.H.Pengelly, 1 ♂, 1 ♀ (GUE); Pt. Pelee Natl. Pk., Leamington, K.N.Barber, swept from *Schizachyrium scoparium*, 7.vii.1980, 2 ♂, 4 ♀, 9.vii.1980, 2 ♂, 2 ♀, 17-18.viii.1980, 48 ♂, 57 ♀, 1?, 22.vii.1981, 31 ♂, 24 ♀, 1?, 11.vii.1982, 20 ♂, 8 ♀ (GUE); Pt. Pelee, W.Ralley, reared by K.N.Barber from egg of female collected 5.vii.1981, fed on *Trionymus winnemucuae*, 1 ♀ (GUE); Pt. Pelee, 19-21.vi.1981, W.Ralley, 3 ♂, 8 ♀ (GUE); Pt. Pelee, 13.vi.1971, D.Krailo, 1 ♀ (GUE); Ojibway Prairie Reserve, Windsor, 21.vii.1981, K.N.Barber, swept from *Schizachyrium scoparium*, 2 ♂ (GUE); Ipperwash Prov. Pk., 14.vii.1980, K.N.Barber, swept from *Schizachyrium scoparium*, 1 ♂, 7 ♀ (GUE); Pinery Prov. Pk., Grand Bend, K.N.Barber, swept from *Schizachyrium scoparium*, 14-15.vii.1980, 21 ♂, 12 ♀, 19.viii.1980, 41 ♂, 33 ♀ (GUE), 11.vii.1981, 112 ♂, 124 ♀ (GUE), 10 ♂, 10 ♀ (UAT), 10 ♂, 10 ♀ (BRI), 10 ♂, 10 ♀ (USNM), 5 ♂, 5 ♀ (LACM), 12.ix.1981, 8 ♂, 4 ♀, 13.vi.1982, 15 ♂, 11 ♀, 15.viii.1982, 47 ♂, 47 ♀, 6.vii.1983, 25 ♂, 8 ♀, 25.viii.1983, 4 ♂, 6 ♀ (GUE), swept from *Andropogon gerardi*, 25.viii.1983, 2 ♀, 19.viii.1984, 1 ♂, 1 ♀ (GUE); Pinery Prov. Pk., K.N.Barber, reared from eggs of females collected 11.vii.1981, fed on *Trionymus winnemucuae*, 18 ♂, 17 ♀ (GUE); Pinery Prov. Pk., 13.vii.1979, W.A.Attwater, 1 ♂ (GUE); Pinery Prov. Pk., 6.vii.1983, B.V.Brown, 2 ♂, 1 ♀ (GUE); Sauble Beach, 10.viii.1983, K.N.Barber, swept from *Schizachyrium scoparium*, 1 ♂, 3 ♀ (GUE); Wagersville [Wagarville], 14.vii.1967, H.J.Teskey, 1 ♂ (BRI). **Saskatchewan:** Elbow, A.R.Brooks, 3.vi.1960, 3 ♂, 5 ♀, 17.vi.1960, 6 ♂, 1 ♀, 26.vi.1960, 3 ♂, 3 ♀, 12.vii.1960, 2 ♂, 3 ♀ (BRI); Indian Head, K.Stewart, 9.vii.1929, 2 ♂, 27.vii.1929, 4 ♂, 2 ♀ (BRI); Saskatoon, K.Stewart, 24.vii.1937, 1 ♀, 10.viii.1938, 2 ♀, 30.vi.1940, 1 ♀ (BRI); Bestville, 5.vii.1923, K.M.King, 2 ♂, 1 ♀ (BRI); St. Victor, 5.viii.1931, G.F.Manson, 1 ♂ (BRI). **U.S.A. Arizona:** Cochise Co., Dos Cabezas Mts., Mineral Park, 6500', 11.viii.1976, D.S.Chandler, sweeping low vegetation, 2 ♀ (UAT); Cochise Co., Willcox, 19.ix.1956, E.Orday, 1 ♀ (AMNH); Cochise Co., Round Valley Ref., 3miNW Portal, 26.viii.1976, D.S.Chandler, sweeping low vegetation, 1 ♂, 1 ♀ (UAT); Portal, 4800', 17.v.1973, C.W.Sabrosky, 1 ♂ (USNM); Cochise Co., Rustler Pk., 22.v.1974, T.P.Sluss, 5 ♂, 6 ♀ (UAT) [Arizona I, Typical variants]; Cochise Co., Chiricahua Mts., 1miS Rustler, 27.v.1972, T.P.Sluss, 55 ♂, 35 ♀ (UAT), 10 ♂, 10 ♀ (USNM), 5 ♂, 5 ♀ (GUE), 5 ♂, 5 ♀ (BRI) [Arizona I, Arizona II, Apache-Catron variants]; Cochise Co., Chiricahua Mts., Onion Saddle, T.P.Sluss, 17.ix.1972, 1 ♂, 2 ♀ (BRI), 3 ♀ (UAT) [Apache-Catron variant], 26.viii.1973, 1 ♂, 4 ♀ (UAT) [Arizona I, Arizona II variants]; S.W.R.S., 5400', 24.ix.1966, P.H.Arnaud, Jr., 2 ♂ (CAS) [Arizona I or Typical variant]; S.W.R.S., 5400', 23.v-5.vi.1967, C.W.Sabrosky, eye gnat, 1 ♂ (USNM) [Arizona II variant]; 9mi[?] S.W.R.S., T.P.Sluss, 22.v.1974, 1 ♂, 3 ♀, 27.v.1975, 2 ♂, 2 ♀ (UAT) [Arizona I variant]; S.W.R.S., T.P.Sluss, 6.ix.1970, 6 ♂, 6 ♀, 8.ix.1970, 1 ♂, 9.ix.1970, 2 ♂, 2 ♀, 10.ix.1970, 5 ♂, 3 ♀ (UAT) [Arizona I, Arizona II, Apache-Catron? variants]; S.W.R.S., 7.vi.1957, J.W.Green, 1 ♀ (CAS) [Arizona I? variant]; Chiricahua Mts., A.H.Sturtevant Collection, 13.vii.1952, 8500', 1 ♀, 15.vii.1952, 4000', 1 ♂ (USNM) [Arizona II or Typical variants]; Cochise Co., Chiricahua Mts., Barfoot Lookout, T.P.Sluss, 26.viii.1971, 5 ♂, 7 ♀ (UAT), 8 ♂, 4 ♀ (BRI), 7.v.1972, [most] swept from *Muhlenbergia* sp., 34 ♂, 14 ♀ (UAT), 8 ♂, 4 ♀ (BRI), 5 ♂, 2 ♀ (GUE), 17.vi.1973, 5 ♂, 2 ♀ (UAT), 8.vii.1973, 14 ♂, 15 ♀ (UAT), 5 ♂, 3 ♀ (BRI), 22.v.1974, 11 ♂, 5 ♀ (UAT), 23.v.1974, 5 ♂, 3 ♀ (UAT), 28.vii.1975, 17 ♂, 14 ♀ (UAT), 4 ♂, 4 ♀ (BRI) [Arizona I, Arizona II variants]; Cochise Co., Chiricahua Mts., Bartoot Park, 6.ix.1970, T.P.Sluss, 3 ♂, 4 ♀ (UAT), 1 ♂ (BRI) [Arizona I variant]; Cochise Co., Chiricahua Mts., road to Herb Martyr, 6000', 17.viii.1984, B.V.Brown, live oak grass, sweeps, 1 ♀ (GUE); Grand Canyon N.P., No. Rim, 15.vii.1954, W.L.Downes, 3 ♂, 4 ♀ (ISU) [Apache-Catron, Arizona II?, Typical? variants]; Apache Co., Alpine, Luna Lake, 7900', 9-14.vii.1979, S&J.Peck, pine meadows, 2 ♂, 3 ♀ (GUE) [Apache-Catron variant]; Apache Co.,

16miS Big Lake, 4.ix.1973, T.P.Sluss, 8♂, 9♀ (UAT), 3♂, 3♀ (BRI), 3♂, 3♀ (USNM) [Apache-Catron variant]; Graham Co., Pinaleno Mts., Goudy Creek, 9200', 7.vii.1973, T.P.Sluss, 6♂, 2♀ (UAT) [Arizona I variant]; Sedona, Oak Creek Canyon, 29.vi.1953, W.W.Wirth, 1♂, 1♀ (USNM) [Southern variant]; Coconino Co., Flagstaff, 7100', 18-25.vii.1979, S&J.Peck, pond pine meadow Malaise trap, 2♂, 1♀ (GUE); Coconino Co., 20miN Flagstaff, Bonito Park, 7000', ponderosa pine/ meadow, 5-8.viii.1984, B.V.Brown, sweeps, 3♂, 4♀, Malaise trap head, 3♂, 6♀, L.B.Carlson, sweeps, 1♂, 1♀, Malaise trap head, 1♀ (GUE); Huachuca Mts., Miller Canyon, A.L.Melander, 30.iv.1948, 1♀, 1.v.1948, 1♀, 2.v.1948, 2♂, 2♀, 3.v.1948, 1♀ (USNM) [Arizona II variant]; Pima Co., Mt. Lemmon, T.P.Sluss, 27.vi.1972, 8000', 2♀ (UAT), 29.vi.1972, 8500', swept from *Muhlenbergia* sp., 3♂, 4♀ (UAT), 21.vii.1972, 8200', 8♂, 7♀ (UAT), 2♂, 3♀ (BRI), 6.ix.1973, 8300', 3♂, 4♀ (UAT), 16.v.1975, 24♂, 31♀ (UAT), 5♂, 5♀ (BRI), 23.ix.1975, 8300', 5♂ (UAT) [Arizona I, Arizona II variants]; Pima Co., Quinlan Mts., Kitt Peak, 6875', 4.viii.1977, T.P.Sluss, 1♂, 1♀ (UAT) [Arizona II variant]; Tucson, 17.vi.1917, J.M.Aldrich, 1♂, 1♀ (USNM). **California:** Sierra Co., Sattley, 9.vii.1975, B.Villegas, 1♂ (UCD); Siskiyou Co., Salmon Trinity Alps Wilderness Area, Big Flat Cpgd., 5000', 2.viii.1968, H.B.Leech, 1♂ (CAS); Trinity Co., Mtn. Mdw. Rch., head Coffee Cr., 5100', 8-10.vii.1969, W.G.Goodman, 3♂ (UCD); Shasta Co., Platina, 1/2miE Jct. SR36 & A16, 16.vi.1974, Oman, 1♀ (OSU); Inyo Co., Deep Springs, 16.vii.1953, E.I.Schlinger, 1♀ (UCD); Inyo Co., Deep Springs, 11.vii.1953, J.W. MacSwain, 1♀ (UCB); Mint Canyon, Solemint, 28.iv.1955, W.R.Richards, 1♀ (BRI); Palmdale, Leona Valley, 6.v.1949, A.L.Melander, 2♀ (USNM); Victorville, 30.v.1944, A.L.Melander, 1♂, 1♀ (USNM); Marin Co., Mill Valley, 9.vii.1950, H.B.Leech, cheesecloth trap, 1♂ (CAS). **Colorado:** Jefferson Co., Evergreen, 8200', 19.vii.1974, T.P.Sluss, 4♂, 2♀ (UAT); El Paso Co., Garden of the Gods Pk., Colorado Springs, 7500', 15.vii.1974, T.P.Sluss, 4♀ (UAT); El Paso Co., Rampart Range Mts., 11miN Colorado Springs, 9000', 15.vii.1974, T.P.Sluss, 1♂, 6♀, 1♀ (UAT); Teller Co., Florissant Fossil Beds, 8.viii.1973, D.Shetlar & D.Wilder, 5♂ (CAS) [Typical, Apache-Catron? variants]; La Plata Co., Durango, 10.vi.1977, Hanson & Knowlton, 1♂, 1♀ (USU); Boulder, 5miS, 5800', W.R.M. Mason, 19.vi.1961, 4♂, 1♀, C.H.Mann, 9.vi.1961, 1♂, 12.vi.1961, 1♂, 16.vi.1961, 3♂, 1♀ (BRI); Boulder, 4.5 miN, 5500', C.H.Mann, alkali slough prairie grass, 10.vi.1961, 4♀, 13.vi.1961, 5♂, 6♀, 20.vi.1961, 1♀ (BRI); Boulder, Flagstaff Canyon, 5800', 10.vi.1961, C.H.Mann, on side of stream, 14♂, 6♀ (BRI); Boulder, 6000', 4.vi.1961, B.H.Poole, 6♂, 1♀ (BRI); Boulder, 5500', B.H.Poole, 1.vi.1961, 1♂, 9.vi.1961, 1♂, 10.vi.1961, 2♂, 1♀ (BRI); Boulder, Valmont Butte, 5300', 7.vi.1961, C.H.Mann, 6♂, 3♀ (BRI); Boulder, Boulder Resvr., 5000', 30.v.1961, B.H.Poole, in marsh, 1♂ (BRI); State Bridge nr. Bond, 7000', 24-25.vi.1961, C.H.Mann, dry river bed and bank, 1♂ (BRI); 5 miE Nederland, 7500', 2.vii.1961, J.G.Chillcott, 1♂ (BRI); Estes Park, 7500', 20.vii.1961, C.H.Mann, 1♂, 5♀ (BRI) [Typical?, Apache-Catron? variants]; Grand Jct., 14.vi.1927, J.M.Aldrich, 1♂ (USNM); Holly, 19.ix.1951, A.H.Sturtevant Collection, 1♀ (USNM). **Idaho:** Cassia Co., 9miE Malta, R.P.Wight, [swept from *Agropyron cristatum*], 28.v.1981, 3♂, 1♀, 29.v.1981, 4♂, 1♀, 1.vi.1981, 2♂, 1.vii.1981, 1♂, 15.vii.1981, 1♂, 5♀, 16.vii.1981, 1♂, 28.vii.1981, 2♀, 31.vii.1981, 1♂, 1♀, 10.viii.1981, 3♂, 6♀, 12, 11.viii.1981, 26♂, 38♀, 12.viii.1981, 2♂, 10♀, 13.viii.1981, 2♂, 3♀ (UIM); Cassia Co., 5miW Raft River, 4.vi.1981, R.P.Wight, 1♂ (UIM); Oneida Co., Holbrook Summit, G.F.Knowlton, 22.vii.1969, 1♂, 8.vii.1969, 1♀ (USU); Oneida Co., Holbrook, 1.ix.1971, G.F.Knowlton, on *Gutierrezia sarothrae*, 1♀ (USU); 5miS Holbrook, 17.vii.1972, G.F.Knowlton & G.E.Bohart, sand dunes, 1♀ (USU); 5miNW Holbrook, 6.vii.1972, W.J.Hanson, Malaise trap, 1♂ (USU); Oneida Co., Rock Creek, 28.viii.1974, G.F.Knowlton, 1♂, 17.vii.1972, Knowlton & Bohart, 1♂, 3♀ (USU); Oneida Co., Twin Springs, 28.viii.1974, G.F.Knowlton, 1♂, 1♀ (UCD); Oneida Co., Salyer Cow Camp, 23.vii.1971, W.J.Hanson, 1♂, 2♀ (USU); Salyer Cow Camp, 11.viii.1972, G.F.Knowlton, 1♂ (UMIN); Oneida Co., S. of Roy, 13.vii.1972, G.F.Knowlton, 3♂, 2♀ (UMIN); Curlew Nat. Grasslands, 3miS Roy Summit, 6.vii.1972, G.F.Knowlton, 1♂ (UMIN); Oneida Co., Curlew V. Res., 22.vii.1969, G.F.Knowlton, 1♂ (USU); Oneida Co., Meadow Brook Cr., 29.vii.1972, G.F.Knowlton, 1♀ (UMIN); Blaine Co., Galena Summit, 15.vii.1961, 8600', J.G.Chillcott, dry hillside, 2♂ (BRI); Butte Co., 6miS Howe, M.Stafford, 7.vii.1981, Malaise trap, 7♂, 5♀, 27.vii.1981, *Elymus cinereus*, 1♀ (UIM); Owyhee Co., 17miW Silver City, 8.viii.1963, A.R.Gittins, 1♀ (UIM); Hollister, 27.viii.1928, D.E.Fox, *Artemisia*, 1♀ (USNM); Castleford, 28.vi.1928, [no collector], "*S. sophia*" [?= *Descurainia sophia* (L.) Webb], 1♀ (USNM); Moscow, 8.vii.1916, J.M.Aldrich, 1♀ (USNM). **Kansas:** Atwood, 23.vii.1954, W.L.Downes, 2♂ (ISU); Nat. Hist. Res., Lawrence, 28.iv.1956, J.G.Chillcott, 1♂ (BRI); Stafford Co., 29.iv.1934, C.W.Sabrosky, 1♀ (PSU). **Michigan:** Warren Dunes St. Pk., 11.vi.1983, K.N.Barber, swept from *Schizachyrium scoparium*, 27♂, 37♀, 1♀ (GUE), 5♂, 5♀ (BRI); Warren Dunes, 13.ix.1952, A.H.Sturtevant Collection, 1♂, 2♀ (USNM). **Montana:** Geraldine, [no date], F.T.Cowan, 1♂, 3♀ (USNM); Gardiner, 17.viii.1918, A.L.Melander, 1♂ (USNM); 6miNW Browning, 18.vii.1969, B.A.Foote, 1♀ (UAT); Prairie Co., Barriall, [?].v.1953, R.B.Knapp, reared from slender wheatgrass clump, 1♂ (USNM); Liberty Co., "Spring", 1953, H.W.Somsen, reared from grass clump, 1♂ (USNM); Daniels Co., Butler, 8.vi.1953, R.B.Knapp, reared from slender wheatgrass clump, 1♀ (USNM). **Nebraska:**

Crete, 3.vii.1960, W.F.Rapp, 1 ♀ (UNL) [Southern variant]. **New Mexico:** Taos Co., San Cristobal, 7400', 13.vii.1974, T.P.Sluss, 3 ♂, 6 ♀ (UAT); Taos Co., Cabresto Lake, Sangre de Cristo Mts., 9000', 13.vii.1974, T.P.Sluss, 4 ♂, 1 ♀ (UAT) [Apache-Catron, Typical variants]; Bernalillo Co., Isleta, 4900', 16.vi.1979, S&J.Peck, cottonwood-tamarisk forest along canal, 2 ♀ (GUE); McKinley Co., 19miN Gallup, 14.viii.1972, J.G.Rozen & R.McGinley, 1 ♂ (AMNH); Hidalgo Co., 7.5miESE Portal, Arizona, 31.vii.1975, S.Frommer, 1 ♂ (UCR); Lincoln Co., Nogal Lake, 3miSE Nogal, 8.viii.1965, H.B.Leech, 1 ♀ (CAS); White Sands Nat. Mon., 5.viii.1966, D.R.Miller & R.L.Brunley, 2 ♀ (UCD); Las Cruces, 16.vi.1917, J.M.Aldrich, 1 ♂ (USNM); High Rolls, 4.vi.1902, [no collector], 1 ♀ (ANSP); Albuquerque, "viii", M.Bates, 1 ♀ (MCZ); San Ysidro, 3.vi.1961, W.J.Hanson, 1 ♀ (USU); Cloudfroft, 26.v.1964, J.F.McAlpine, 1 ♂ (BRI) [Apache-Catron variant]; Valencia Co., El Morro, 7200', 9.ix.1935, T&G.Hubbell, 1 ♂ (UMIC) [Apache-Catron variant]; Catron Co., 8miSE Luna, 7500', 9-14.vii.1979, S&J. Peck, pond, pine at stream, [Malaise trap], 4 ♂, 3 ♀ (GUE), 3 ♂, 3 ♀ (BRI), 2 ♂, 2 ♀ (USNM) [Apache-Catron variant]; 5miW Luna, 7400', 9-14.vii.1979, S&J. Peck, San Francisco River, pond, pine meadows, [Malaise trap], 3 ♂, 6 ♀ (GUE) [Apache-Catron variant]; San Miguel Co., ½miNE Montezuma, 26.vi.1973, W.N. Mathis, 1 ♂ (OSU) [Apache-Catron variant]. **North Dakota:** Golden Valley Co., Beach, [?].v.1953, R.B. Knapp, reared from slender wheatgrass clump, 4 ♂, 2 ♀, 1 ♀ (USNM); Golden Valley Co., 18.v.1953, C. Benton, reared from slender wheatgrass clump, 1 ♂, 1 ♀ (USNM); Burke Co., 18.v.1953, C. Benton, reared from slender wheatgrass clump, 1 ♂, 1 ♀ (USNM); Burke Co., Powers Lake, [?].v.1953, C. Benton, reared from slender wheatgrass clump, 2 ♀ (USNM); Sioux Co., Solen, [?].v.1953, R.B. Knapp, reared from wild rye grass clump, 1 ♂ (USNM); Williams Co., Ray, [?].v.1953, C. Benton, reared from slender wheat grass clump, 1 ♂ (USNM); Divide Co., Ambrose, [?].v.1953, C. Benton, reared from western wheatgrass clump, 1 ♀ (USNM); Morton Co., 19.viii.1958, R.L. Post, 2 (NDSU); Minot, 13.vii.1953, C. Benton, reared from slender wheatgrass clump, 1 ♂ (USNM). **Oklahoma:** Murray Co., Sulphur, Chickasaw Rec. Area, 4.vi.1979, S&J. Peck, prairie vegetation, 1 ♂ (BRI) [Southern variant]. **Tennessee:** Knoxville, 28.viii.1916, J.M. Aldrich Collection, 1 ♂ (*P. antennalis* paratype, USNM) [Southern variant]. **Texas:** Big Bend N.P., Green Gulch 5000', 14.v.1959, L. Bottimer, 6 ♂, 6 ♀ (BRI); Big Bend N.P., Panther Jct., 3500', 13.v.1959, J.F. McAlpine, 1 ♂ (BRI); Big Bend N.P., Chisos Mts., Basin, 6000', 15.v.1959, J.F. McAlpine, 1 ♂ (BRI); Big Bend N.P., Pulliam Canyon, 55-6500', 12.v.1959, J.F. McAlpine, 1 ♂ (BRI); Big Bend N.P., Spring Oak, 19.v.1959, J.F. McAlpine, 1 ♀ (BRI); 10miW Ft. Davis, nr. Pt. of Rocks, 5000', 30.v.1959, J.F. McAlpine, 1 ♂ (BRI); 14miW Ft. Davis, Hwy. 166, 9.v.1980, A. Konecny, dry grass pine & juniper, 3 ♂, 1 ♀ (GUE); Terrell Co., 7miN Sanderson, 28.viii.1974, G. Bohart & W. Hanson, 1 ♀ (USU); Real Co., Rio Frio, 2.iv.1955, W.W. Wirth, 1 ♂, 2 ♀ (USNM); Llano Co., Enchanted Rock, 15.vi.1953, W.W. Wirth, 1 ♂ (USNM); Jeff Davis Co., Toyahvale, 22.iii.1967, D.M. Wood, 1 ♂ (BRI); Kerrville, Henkes Pond, [?].iv.1955, W.W. Wirth, 1 ♀ (USNM); one additional male from Loew Collection, label illegible (USNM). **Utah:** Uintah Co., Bonanza, G.E. Bohart, 30.viii.1975, 1 ♂, 1 ♀, 4.ix.1975, 1 ♀, 17.vii.1974, on *Melilotus alba*, 1 ♂, 8.viii.1974, wet meadow, 1 ♂ (USU); Box Elder Co., Locomotive Springs, 22.vii.1969, G.F. Knowlton, 1 ♂, 5 ♀, 25.vii.1969, Knowlton & Hanson, 1 ♂ (USU); Box Elder Co., Snowville, 17miSW, [no collector], 9.vi.1969, 1 ♂, 29.v.1974, *Sitanion hystrix*, 3 ♂, 2 ♀, 24.vii.1975, *Agropyron cristatum*, 1 ♀ (USU); Box Elder Co., Cedar Creek Jct., 6.vi.1969, G.F. Knowlton, 1 ♂, 1 ♀ (USU); Box Elder Co., Kelton Pass, 9.vi.1969, G.F. Knowlton & J.Waldron, 1 ♀ (USU); Grand Co., Castleton, 20.vii.1968, [no collector], Malaise trap, 2 ♀ (USU); Grand Co., Moab, 23.v.1969, G.F. Knowlton, 1 ♂ (USU); Utah Co., Colton, 14.vii.1960, G.F. Knowlton, 1 ♂ (UCD); Garfield Co., Bryce Canyon, 19.vii.1954, W.L. Downes, 1 ♀ (ISU); Washington Co., Red Cliff Rec. Area, 14.vi.1978, Hanson & Knowlton, 1 ♀ (USU) [Southern variant]; Zion Nat. Pk., Birch Creek, 28.vii.1965, W.J. Hanson & D.W. Davis, Malaise trap, 1 ♀ (USU); 10miSE Vernon, Wasatch Nat. For., 8.vii.1972, R.M. Miller, 1 ♀ (ISU); Mantua, 30.vi.1953, Knowlton & Hanson, 1 ♂ (USU); Vernal, 22.vii.1954, W.L. Downes, 1 ♂ (ISU) [Southern variant]; Salt Lake, [?].1912, C.N. Ainslie, reared from *Hordeum*, 1 ♂ (USNM) [Southern variant]; Salt Lake City, 18-20.vii.1917, J.M. Aldrich, 1 ♀ (*P. antennalis* paratype, USNM) [Southern variant]; Hooper, 28.vi.1937, D.E. Hardy, 1 ♀ (USU) [Southern variant]; Rainbow Bridge, [?].vii.1962, A.H. Sturtevant Collection, 1 ♀ (USNM) [Southern variant]. **Washington:** Colton, C.C. Shelton, virgin prairie population study, 18.vi.1948, 1 ♀, 6.vii.1948, 1 ♂, 1 ♀, 15.vii.1948, 5 ♂ (WSUP); Pullman, [no other data], A.L. Melander Collection, 1 ♂ (USNM); Pullman, 9.vii.[?], J.M. Aldrich, 1 ♀ (USNM); Pullman, 11.v.1922, A.L. Melander, 1 ♀ (USNM); Wawawai, 22.vi.[?], A.L. Melander Collection, 1 ♀ (USNM); Wenatchee, 4.v.1919, A.L. Melander, 1 ♂ (USNM). **Wyoming:** Manville, 25.vii.1951, R.E. Pfadt, 2 ♂, 2 ♀ (UWY); Torrington, 24.viii.1955, R.E. Pfadt, 1 ♂ (UWY); Centennial, 12.vii.1960, R.J. Lavigne, 1 ♀ (UWY); Gillette, Wyodok Plant Station 18, 6.vii.1977, D. Molnar, 1 ♀ (UWY); Glendo, R.E. Pfadt, 23.vii.1959, 20.vi.1963, 2 ♂ (UWY); Guernsey, 26.vii.1951, [no collector], 1 ♂ (UWY); Yellowstone Pk., Madison R., 4.viii.1918, A.L. Melander, 1 ♀ (USNM); Fremont Co., 52miSE Lander, 4.viii.1973, J. Sawbridge, 1 ♂ (OSU); Lincoln Co., 8miSE Smoot, 7.viii.1974, W.J. Hanson, 1 ♀ (USU); Lincoln Co., 1miN Alpine, 10.vii.1973, 5900',

Oman & Musgrave, 1 ♀ (OSU); Laramie Co., 4miW Granite Canyon, 6.vii.1972, W.B. Stoltzfus & R.M. Miller, 2 ♂, 2 ♀ (ISU) [Typical, Apache-Catron? variants]; Laramie, Herrick's Lane, 26.vii.1960, R.J. Lavigne, 1 ♂ (UWY), MEXICO. **Durango:** 30miW Durango, 8000', 6.v.1961, Howden & Martin, 4 ♂, 2 ♀, 6.vi.1964, J.F. McAlpine, 1 ♀ (BRI) [Arizona I or Southern variant]; 25miW Durango, 7500', 6.v.1961, Howden & Martin, 1 ♀ (BRI) [Arizona I or Southern variant]. **Morelos:** 6miN Cuernavaca, 7500', 15.viii.1954, J.G. Chillcott, 1 ♂, 1 ♀ (BRI) [Arizona I or Southern variant].

Remarks. The name *P. pruinosa* is here applied to perhaps the widest ranging and the most commonly collected species of the genus. It is highly variable and might involve a complex of several sibling species as discussed below under "Variation". The combination of the predominantly bare frons, the yellow tarsomere 1, and the presence of lateral bare areas on tergites 3-5 of the male place it with five other species. *Pseudodinia pruinosa* is most readily defined by the absence of the key characters used to recognize these other five species and thus identification usually requires dissection of the male genitalia, particularly with specimens from the western parts of its known range. The greatest difficulty lies in separating *P. pruinosa* from *P. occidentalis* and this is discussed in the "Remarks" under the latter species.

Malloch (1940) wrongly synonymized *P. pruinosa* with *P. varipes*, and since then all references to *P. varipes*, except for the type material of Coquillett, have in reality been to *P. pruinosa*. Malloch (1940) also listed a specimen from Medicine Hat, Alberta, under the name *P. nitida* Melander which is included in the list of material above.

Variation. Considerable variation occurs within this species, and five somewhat distinct variants, i.e., Typical, Apache-Catron, Southern, Arizona I, Arizona II, have been recognized. These variants are listed in Table I along with their respective geographical distributions and a summary of several ranges of salient character conditions. Most of the specimens in the previous list of "Other material examined" belong to the Typical variant; specimens that belong to each of the remaining four variants are indicated in square brackets.

The most prevalent of **Typical** variant is widely distributed from Ontario to British Columbia, south to California, Arizona, and Texas. It is characterized by having the vertex, frons, parafacial, and gena predominantly bare with only the ocellar triangle usually pruinose. In addition, the eye is usually longer than high (Fig. 3). In most genitalic characters, this variant could be described as average (Fig. 26). It is notable that the long series from Warren Dunes, Michigan, includes males with the widest aedeagi seen in this species, equivalent in width to the prevalent condition in *P. occidentalis*.

The **Apache-Catron** variant is named for the counties in which the largest series referred here were collected. This variant is recorded from the southwest with only occasional northern occurrences. It is very similar to the Typical variant but has a somewhat less pruinose thorax, the ocellar triangle is usually bare, and the hind tibia is entirely darkened dorsally in about half of the specimens. The genitalia (Fig. 27) usually exhibit a more elongate aedeagus and paramere, and the aedeagus usually has a well developed median trough.

The **Southern** variant corresponds to the appearance of the holotype. It ranges from Tennessee through Texas and Oklahoma to Arizona, Utah, and possibly central Mexico. This variant is characterized by the extensively pruinose vertex and upper frons usually forming a nearly complete transverse band to the level of the upper orbital seta. The parafacial is mostly, and the gena is entirely pruinose. The scape, pedicel, flagellomere 1 basal to the base of the arista, and the palp are paler, even yellow in several specimens, especially the two *P. antennalis* paratypes. These are only slightly but noticeably paler in the holotype male. The genitalia of the holotype (Fig. 25) are most similar to those of the Apache-Catron variant (Fig. 27) although the variation observed among the five other males blends into all others. The Southern and Apache-Catron variants are at opposite extremes in the density and extent of their pruinosity. Only 12 specimens, in addition to the holotype, are referred here.

Table I. Summary of variation and distribution of five nominal variants of *Pseudodinia pruinosa* Melander.

Variant	n	Measurements and Proportions									
		Body length mm.	Head h:l	w:l	Eye h:l	Eye:Gena h:w	Frons w:l	Orbital origin upper	lower	tergites (n/2) T6:T5 TS7+8:T5	
Typical	54	1.9-2.9	1.1-1.4	1.6-2.0	0.8-1.0	4.0-5.6	1.1-1.3	0.1-0.3	0.4-0.6	0.2-0.3	0.4-0.5
Apache-Catron	10	2.1-2.5	1.2-1.4	1.7-2.0	1.0-1.1	4.1-5.4	1.2-1.3	0.2-0.3	0.5	0.2-0.3	0.4-0.5
Southern	11	2.5-2.6	1.1-1.3	1.8-2.0	0.9-1.1	4.4-6.1	1.0-1.3	0.2-0.3	0.5-0.6	0.2-0.3	0.4-0.5
Arizona I	10	2.0-3.0	1.2-1.3	1.8-2.0	1.0	4.7-5.5	1.1-1.4	0.2-0.3	0.5-0.6	0.2-0.3	0.4
Arizona II	10	2.4-3.1	1.3-1.4	1.8-2.0	1.0-1.1	4.5-5.7	1.2-1.3	0.2	0.5-0.6	0.2-0.3	0.4

Variant	Pruinosity ^a						Ground colour ^b	
	Ocellar triangle	Orbital plate	Parafacial	Gena	Notum	Abdomen (bp:1) ^c	Antenna & palp	Hind tibia ay: length
Typical	+,+	-	-	-	++,+++	0.0-1.0xT4 0.0-0.3xT4	bl,br	0.2-0.3
Apache-Catron	-,+	-	-	-	+,++	0.0-1.0xT4 0.7-1.0xT3	bl,br	0.0-0.3
Southern	++ ^d	+	+,+	++	++,+++	0.7-1.0xT4 0.0-0.5xT4	bl,br,by	0.3-0.4
Arizona I	++ ^d	+	+,+	++	++,+++	0.0-0.7xT4 0.7-1.0xT3	bl	0.2-0.3
Arizona II	+	-	-,+,	-,+	++,+++	0.0-1.0xT4 0.7-1.0xT3	bl	0.2-0.3

Variant	Relative Measures of Male Genitalia ^e					Distribution
	Epandrium length	Paramere length	Aedeagus length	apex (thick)	keels	
Typical	1,2	1,2,3	1,2	1,2	1,2	BC to ONT south to AZ
Apache-Catron	2	3	3	2	1,2	AZ,NM,CO,WY
Southern	2	2,3	2,3	2	1,2	AZ,NE,OK,TN,UT,(MEX?)
Arizona I	1	1,2	1,2	1	2,3	AZ,(MEX?)
Arizona II	2	2	2,3	1	1	AZ

a +, ++, +++ = progressively, relatively denser pruinosity; - = pruinosity absent; + = variable or difficult to interpret.

b ay = apically yellow; bl = black; br = brown; by = basally yellow.

c bp:1 = pruinosity extends dorsomedially from base to as far as a basal proportion of indicated tergite.

d ocellar and orbital pruinosity often continuous, forming a transverse band.

e 1,2,3 = progressively larger relative measures.

The remaining two variants are restricted to Arizona, except possibly for the Mexican specimens, and are generally collected together, even from the same plant as T.P. Sluss's collections from *Muhlenbergia* indicate.

The **Arizona I** variant, is externally very similar to the Southern variant in its extensive head pruinosity. It is more variable in the degree to which the transverse band of vertical pruinosity is developed, varying from discrete patches on the ocellar triangle and upper orbits to a nearly complete band, especially so in the Mexican specimens. No specimens have basally pale antennae or palps and the aedeagus is often relatively short with usually well defined preapical keels, and the epandrial apices are often slightly bent forward (Fig. 28). The Mexican series is somewhat intermediate between this variant and the Southern variant in characters of the genitalia.

The **Arizona II** variant has less extensive head pruinosity with the ocellar triangle usually lightly pruinose but the orbits and the intervening frontal area bare. The parafacial is predominantly, and the gena usually entirely bare. The aedeagus is usually rather

flattened apically with poorly developed keels, appearing thin in lateral view (Fig. 29).

Some series from Arizona show quite a discrete dimorphic separation of the last two variants but others do not. These latter series are difficult to align one way or the other. The other three variants each show considerable intravariant variation as well, often obscuring their definitions. The Southern and Apache-Catron variants, which represent extremes in pruinosity, are perhaps the most similar in details of the genitalia. The narrow lateral profile of the aedeagus in the Arizona II variant is matched by at least one series (Valmont Butte, Colorado) of the Typical variant. Despite the relatively regionalized distribution of these five variants, intermediate forms in genitalic characters can be found to satisfy virtually any combination of all of them. The relative restriction of three of these variants to Arizona testifies considerably to the importance of this region in providing relatively isolated pockets of suitable habitat for *Chamaemyiini* (Sluss 1977). In the interest of taxonomic conservatism, all five variants are treated under one name, *P. pruinosa*. Further resolution of this problem will require ecological investigations of possible resource partitioning.

Distribution (Fig. 69). *Pseudodinia pruinosa* is widely distributed across southern Canada and central to western United States, south to southern Mexico, but noticeably absent from the eastern United States and rare in the west coast states. One undetermined female from Olmes Alaska (USNM), may be *P. pruinosa* but has not been included in the above list or in Figure 69, because of doubts concerning its identity.

Biology. Adult *P. pruinosa* have been associated with the grass *Schizachyrium scoparium* (Michaux) Nees (Gramineae: Andropogonaceae) in Ontario, Manitoba, and Michigan (Barber 1984). The mealybug *Trionymus winnemucuae* has been implicated as the prey species found in the leafsheaths of this grass and was used in successful egg to adult laboratory rearings of 36 individuals. These populations are referable to the Typical variant discussed above.

No other records of mealybugs are available nor do any other label data implicate *S. scoparium* as a plant associate. However, adult *P. pruinosa* referable to the Typical variant have been swept from the following plants: *Agropyron cristatum* (L.) Gaertner (crested wheatgrass) in Alberta, Idaho, and Utah; *Bromus inermis* Leyss (smooth brome) in Alberta; *Sitanion hystrix* (Nuttall) J.G. Smith (squirreltail) in Utah; alkali slough prairie grass in Colorado; *Artemisia* sp. (sage) in Idaho; and *Descurainia sophia* (L.) Webb (herb-Sophia) in Idaho.

In addition, label data using the word "reared" suggest an even stronger association with the following grasses: *Agropyron trachycaulum* (Link) Malte (slender wheatgrass) in Montana and North Dakota; *Agropyron smithii* Rydberg (western wheatgrass) in North Dakota; and *Elymus* sp. (wild rye) in North Dakota. These specimens are also referable to the Typical variant.

One female referred to the Southern variant was "reared" from *Hordeum* sp. (barley) in Utah and many specimens of the Arizona I & II variants were swept from *Muhlenbergia* sp. (Muhly) in Arizona.

Among the above plant associates for the Typical variant, it is likely that only the grass species are significant. Certainly this variant is not restricted to one plant species and this would then account for its occurrence on the west coast where *S. scoparium* is not recorded (Hitchcock 1971). The significance of the plant records of the other variants cannot be assessed.

The type material of *T. winnemucuae* was likely collected from a species of *Agropyron* in northwestern California (McKenzie 1967) but the status of a specific predator-prey relationship is not known (Barber 1984).

Phylogeny

Figure 72 summarizes the hypothesized phylogenetic relationships within *Pseudodinia*, and the putative synaptotypes proposed as evidence for these relationships. Suffices A,

B, and C represent different character states in linear transformation series. Autapotypic character states of terminal taxa are shown only if they are similar to character states in other lineages.

There is considerable difficulty in attempting a phylogenetic analysis (*sensu* Hennig 1966) of the species of *Pseudodinia* for two primary reasons. One is the lack of a clear sister-group relationship between *Pseudodinia* and any other member of the Chamaemyiini. Knowledge of a sister group would help to determine the polarity or direction of change between homologous character states. *Parochthiphila* Czerny [including *Euestelia* Enderlein (Tanasijtshuk 1968)] was selected as the sister group of *Pseudodinia* since the former contains members which have a discrete, well developed anepisternal seta similar to that found in *Pseudodinia*; a character that is possibly a synapotypy indicating a sister-group relationship. This allowed determination of the ground-plan state of several characters for the genus *Pseudodinia* as a whole and recognition of two monophyletic species groups within *Pseudodinia*. In order to determine the polarity of homologous character states within a species group, the other species group served as the out-group.

A second problem with applying a phylogenetic analysis to this genus is the morphological conservatism of *Pseudodinia* species, which limits the number of unambiguous character states available for analysis. A combination of these two restrictions has left two unresolved trichotomies, a polychotomy, a questionable placement of *P. cinerea*, and necessitated the acceptance of a number of homoplasies (Fig. 72). The latter is partly due to the utilization of pruinosity characters which could readily be subject to homoplasy.

A survey was made of representatives of the other genera of the Chamaemyiini in order to help assess character states. One of these, *Melanochthiphila*, was originally erected by Frey (1958) as a subgenus of *Parochthiphila* to contain the single species *P. (Melanochthiphila) nigroaenea* Frey. Since then, McAlpine (1960) and Cogan (1980) have treated these as separate genera. It is highly probable that *Melanochthiphila* should be considered a junior synonym of *Parochthiphila* and will be treated as such here.

A representative of *Chaetoleucopsis* Malloch has not been dissected but is considered very distantly related to *Pseudodinia*. Examinations were made of the male genitalia of at least one species of *Acrometopia* Schiner, *Toropamecia* Cogan, *Parapamecia* Cogan, *Pseudoleucopsis* Malloch, *Plunomia* Curran, *Chamaemyia* Meigen, and *Parochthiphila* Czerny (including *Euestelia* Enderlein). Drawings of the male genitalia of *Parochthiphila nigroaenea* (provided by Dr. J.F. McAlpine), and the revisionary works of Cogan (1978), and Tanasijtshuk (1968, 1970) were also consulted. Character states occurring outside of *Pseudodinia* + *Parochthiphila*, which are similar to character states within *Pseudodinia*, are discussed under each apotypy defined below. Use of the term "out-group" below, refers to the Chamaemyiini including *Parochthiphila*.

Apotypic Character State Definitions

1 - apex of paramere bevelled with one outstanding setula near anteroventral aspect (Figs. 13-37, 45).

This condition is apparently unique to species of *Pseudodinia* (*Chaetoleucopsis* not seen). The plesiotypic character state has not been clearly resolved but is probably an unmodified tubular structure with no apical modifications and with scattered setulae of equal strength.

2 - tibiae entirely yellow.

Basally darkened tibiae predominate in the out-group though entirely yellow tibiae occur in some species in several genera.

3A - lower orbital seta arising at 0.4 of frontal length (Fig. 1).

3B - lower orbital arising at 0.1-0.2 of frontal length (Figs. 2, 42).

The members of the out-group have the lower orbital arising in the lower half of the frons (0.5-1.0 of frontal length). This is considered the plesiotypic state and is shared by members of the *varipes* group (Figs. 3, 44). This allows recognition of an apparent transformation series in the *polita* group where this seta arises at sequentially higher levels

on the frons (3A to 3B). Only rarely do specimens of the *varipes* group have the lower orbital approaching the 0.4 level (0.4-0.7), but in these specimens, the seta is still arising slightly more anterior than in *P. tuberculata* (3A).

4 - full series of well developed orbital setulae (Figs. 1-2, 42).

The out-group condition is similar to that of the *varipes* group (Figs. 3, 44), with only scattered orbital setulae in the lower half at the lateral extremities of the anterior band of frontal setulae (see 10 below). A full series of well developed orbital setulae is found in the *polita* group, but not elsewhere in the Chamaemyiidae.

5 - lower margin of face projecting in lateral view (Figs. 1-2).

The out-group condition is a receding facial margin when viewed laterally, as in the *varipes* group (Fig. 3).

6 - anepisternal seta arising at 0.6-0.8 of anepisternal height (Fig. 4).

Within the out-group, only some *Parochthiphila* species bear a single, well developed anepisternal seta, arising at 0.5 of the anepisternal height, as in the *varipes* group (Fig. 5). A somewhat ambiguous transformation series exists within the *polita* group (0.6 in *P. tuberculata*, 0.6-0.7 in *P. meridionalis*, 0.7-0.8 in *P. polita*) but this has not been utilized.

7 - width of wing cell r_{2+3} 1.2-1.5X width of cell r_1 (Fig. 6).

The condition in the out-group is a relatively narrow cell r_{2+3} , subequal to cell r_1 as in the *varipes* group (Fig. 7; 0.8-1.1X r_1).

8 - female tergite 6 complete, not divided medially (Fig. 11).

The predominant out-group condition of this tergite is to be medially divided as in the *varipes* group (Fig. 12).

Plunomia species and *Chamaemyia paludosa* Collin also have this tergite complete, although in most species of *Chamaemyia* it is divided. Cogan (1978) indicates that the female tergite is complete in species of *Toropamecia* but examinations of *T. caribbea* Cogan, *T. jujuyensis* Cogan, and *T. veenota* Cogan have revealed a median division. A female specimen of *Chaetoleucopsis* was not available.

9 - ratio of height of compound eye to genal width relatively high at 6.4-10.0 (Figs. 1-2).

The out-group condition is a relatively wide gena similar to that of the *varipes* group (Fig. 3). There is a slight overlap in the proportions between the *polita* group (6.4-10.0) and the *varipes* group (3.5-6.8) and each varies to an equivalent extent intraspecifically.

10 - frons with relatively weak, erect to slightly reclinate setulae sparsely scattered over most of its surface (Figs. 1-2, 42).

The predominant condition in the out-group is the relatively narrow band of proclinate setulae on the anterior half of the frons as in the *varipes* group (Figs. 3, 44). In the out-group, the only occurrence of relatively weak, erect to reclinate setulae scattered over most of the frons, is found in an Australian species (only one female seen) of *Pseudoleucopsis*. The setulae are more dense than in the *polita* group and they are strongly reclinate. These two conditions are of doubtful homology and likely convergent in origin.

11 - epandrial condyle reduced, not hook-like (Figs. 15-37).

The development of the epandrial condyle varies considerably in the out-group. The elongate, hook-like condyle of the *polita* group (Figs. 13-14) is found in species of *Chamaemyia* and *Parochthiphila*, and is associated with epandrial shape (see 12 below).

12A - epandrium broadly triangular, apices only slightly tapered (Fig. 15).

12B - epandrial apices moderately tapered (Figs. 16-29, 33-37, 45, 47).

12C - epandrial apices strongly tapered, nearly parallel-sided (Figs. 30-32).

The predominant epandrial shape in the out-group most closely resembles that of the *polita* group (Figs. 13-14; associated with 11 above). A transformation series runs through the three consecutive stages of tapering defined above. The autapotypic, preapically

narrowed and medially curved condition found in *P. melanitida* (Fig. 18), is not indicated (Fig. 72).

The conditions found in *Plunomia*, *Pseudoleucopis*, and *Acrometopia reicherti* (Enderlein) approach that of the *varipes* group but are interpreted to be convergent in origin.

13A - strap-like sclerite of male not extending dorsally, but running uninterruptedly from the left sensory setula of sternite 6, to that of sternite 7, and continuing posteriorly to encircle spiracle 7 (Fig. 9).

13B - strap-like sclerite interrupted, reduced, sometimes absent; at most consisting of a separate sclerite on each of sternites 6 and 7 near the left sensory setula (Fig. 10).

The predominant condition in the out-group is similar to that of the *polita* group (Fig. 8) where this sclerite bears the left sensory setulae of sternites 6 and 7, encircles spiracle 7, and continues dorsally to fuse with the basal margin of tergite 7. A transformation series is recognized as running to the two successively reduced conditions above.

This sclerite is apparently completely lacking in *Plunomia* (similar to 13B) and the condition exhibited by *Chamaemyia* approaches that of 13A. Both examples are considered convergent in origin with similar conditions in *Pseudodinia*.

14 - male tergite 6 divided medially (Fig. 10).

The predominant out-group condition is a complete tergite 6 similar to the condition seen in the *polita* group (Fig. 8) and some members of the *varipes* group (Fig. 9). The divided condition is considered apotypic for some members of the *varipes* group, and yet the intraspecific considered apotypic for some members of the *varipes* group, and yet the intraspecific variation recognized in *P. varipes* and *P. occidentalis* suggests a rare plasticity of this character state.

Acrometopia wahlbergi (Zetterstedt) has a medially divided male tergite 6 and, as well, one specimen of a *Chamaemyia* species has been found to have an apparent median division.

15 - aedeagus strongly but gradually curved, in lateral view (Figs. 19-22).

The condition in the *varipes* group is an aedeagus which is basally less angular (Figs. 15-18, 23-37) relative to that of the *polita* group (Figs. 13-14). Within the *varipes* group, this basal shape is retained in all species except *P. varipes* (Figs. 19-21) and *P. latiphallis* (Fig. 22) in which the aedeagus has a strong, gradual curvature.

16A - frons entirely pruinose.

16B - frons bare on at least anterior half (reversal to plesiotypic state; as in Fig. 44).

The occurrence of a shiny frons in all members of the *polita* group (Fig. 42), and some members of the *varipes* group, indicates that the probable ground-plan state for *Pseudodinia* is a shiny frons. The pruinose frons (16A) is hypothesized to have arisen on two separate occasions. A reversal to the ground-plan state (16B) is interpreted as autapotypic in *P. nitens*.

A shiny frons is only rarely [*Parochthiphila nigroaenea* and *Acrometopia carbonaria* (Loew)] found outside of *Pseudodinia*.

17 - sublateral bare areas usually reduced on male tergites, often leaving tergites entirely pruinose.

The plesiotypic or ground-plan state for *Pseudodinia* is deduced to be that shared by all members of the *polita* group plus seven members of the *varipes* group, in which tergites 2-5 or 3-5 have successively larger sublateral bare areas (Fig. 47). The other seven species in the *varipes* group usually have a more extensively, often entirely, pruinose abdomen. Of these, two species, *P. nitens* and particularly *P. antennalis*, are known to be polymorphic with variably developed bare areas often present. As well, the only male specimen of *P. angelica* has relatively extensive sublateral bare areas. The relatively rare *P. hamata*, *P. angustata*, and *P. obscura*, have entirely pruinose abdomens. These latter four species may yet be determined to be similarly polymorphic for this character.

In all but one species of *Pseudodinia*, the female abdomen is never entirely pruinose, suggesting that the entirely pruinose abdomen is a male sex-linked character. However, the abdomen is entirely pruinose in both sexes of *P. cinerea* which suggests that there could be a different genetic basis for abdominal pruinosity in this species. Apotypic state 17 is interpreted to have arisen independently in *P. cinerea* and this relatively rare species is not expected to be found to be polymorphic for abdominal pruinosity.

The shiny bare tergites of *Parochthiphila nigroaenea* and *Acrometopia carbonaria* are likely convergent in origin (see 16 above).

18 - length of male tergite 6 0.3-0.4X tergite 5.

The predominant condition in the out-group is 0.2-0.3 (although that of *Plunomia* is about 0.6); the condition found in the two species of the *polita* group for which males are known, and in some members of the *varipes* group. The 0.3-0.4 condition is interpreted to be synapotypic in *P. hamata*, *P. angustata*, and *P. nitens* and convergently acquired in *P. cinerea*. The measurements for *P. obscura* and *P. antennalis* are ambiguous since each was consistently 0.3.

19 - flagellomere 1 basally yellow to at least base of arista.

The plesiotypic state is unicolourous or only very narrowly pale basally, as found in all *polita* group members and most *varipes* group members.

Discussion of Relationships

Examination of the genitalia of species of the out-group suggests that, as in *Pseudodinia*, the genera are recognizable and discrete phenetic entities. Thus, these generic concepts, which were originally based on combinations of external characters, are supported by internal comparisons. Exceptions are the three genera (*Acrometopia*, *Toropamecia*, and *Parapamecia*) which were studied by Cogan (1978). Cogan gave the synapotypic possession of "bifoliate processes" as evidence of their monophyly, but these structures are here considered to be of questionable homology. These three genera likely form a monophyletic group as suggested by Cogan (1978) but their interrelationships remain unclear. For convenience, these three genera will be referred to below, as the *Acrometopia* group.

The potential sister groups for *Pseudodinia* can be reduced to six in the following order of likelihood: *Parochthiphila* (including *Euestelia* and *Melanochthiphila*), *Chamaemyia*, *Plunomia*, *Pseudoleucopis*, the *Acrometopia* group, and *Chaetoleucopis*. More extensive study will be required before a precise sister group of *Pseudodinia* is identified with any degree of confidence.

The only readily demonstrable synapotypy for all species of *Pseudodinia* is the unique structure of the apex of the paramere (1). Its interpretation as a synapotypy is supported by the unique combination of thoracic chaetotaxy of 0+2 dorsocentral setae and one anepisternal seta, the absence of pruinosity on the frons and abdomen (which occurs only in *Parochthiphila nigroaenea* and the distantly related *Acrometopia carbonaria*), and the geographical restriction of all *Pseudodinia* species to North America.

The monophyly of the *polita* group is supported by 9 synapotypies (2, 3A, 4-10). This is not a complete list since the unknown male of *P. tuberculata* precludes the use of the preapical cluster of setulae on the paramere (the plesiotypic conditions of male genitalic characters 11-13 were assumed). There could also be a difference in habitat selection between the two species groups whereby the *polita* group may be associated with riparian habitats and less restricted ovipositional sites.

The *varipes* group is less distinctive and its monophyly is supported by three putative synapotypies (11, 12A, 13A). Similar character states elsewhere in the Chamaemyiini are interpreted as convergent in origin. A significant character is the strap-like sclerite of the male and its reduction (13A) relative to that of the *polita* group. A further reduction in this sclerite (13B) unites the majority of the *varipes* group as a monophyletic group distinct from *P. cinerea*, *P. nigratarsis*, and *P. slussi*.

The alignment of *P. cinerea* as the sister group of the rest of the *varipes* group (12B

above), requires a convergent acquisition in *P. cinerea*, of a pruinose frons (16A) and a more extensively or entirely pruinose male abdomen (17) with the *P. hamata* + *P. angustata* + *P. nitens* + *P. angelica* + *P. obscura* + *P. antennalis* lineage, and a relatively elongate male tergite 6 (18) with the *P. hamata* + *P. angustata* + *P. nitens* lineage. These convergences may be overcome by placing *P. cinerea* as sister species of the latter three species. This arrangement however, would create two reversals in two structural characters [a complete male tergite 6 (character 14) and an undivided, well developed strap-like sclerite in the male (13A)] in *P. cinerea*, or a minimum of four convergent acquisitions of the apotypic states (13B, 14) in other lineages of the *varipes* group. Due to the plasticity of vestiture or pruinosity characters (16B, 17), the latter arrangement involving homoplasies in two structural characters would appear less parsimonious than the former involving homoplasies in two pruinosity characters and only one structural character. *Pseudodinia cinerea* is a very distinctive species (female abdomen entirely pruinose, paramere expanded apically, sternite 10 linear, vestige of tergite 10 relatively elongate), most readily interpreted as highly autapotypic despite retaining the relatively plesiotypic states of characters 13 and 14. The convergent acquisition of character states 16A, 17, and 18 are therefore interpreted to be autapotypic in *P. cinerea*.

The six species clustered around *P. varipes* and *P. pruinosa* comprise a weakly characterized group. There is a possibility that all but *P. slussi* could prove to be a monophyletic group. Presently, this complex is defined on symplesiotypies with one sister species pair, *P. latiphallis* + *P. varipes*, supported by the synapotypic condition of the aedeagus (15). This sister-group relationship is also suggested by a tendency for the epandrium to be more triangular than most other species of the *varipes* group, though not to the same extent as *P. cinerea*. This is quite variable and no attempt was made to use this in the analysis.

The extensive pruinosity of the frons (16A) and male abdomen (17), both convergently acquired by *P. cinerea*, supports the monophyly of six species. Within this grouping, the monophyly of the *P. hamata* + *P. angustata* + *P. nitens* lineage is relatively well supported (12C, 18), despite the convergent acquisition of a relatively elongate male tergite 6 (18) in *P. cinerea*. The almost identical male genitalia of *P. angustata* and *P. nitens* suggest a close relationship but this has not been confirmed with a recognized synapotypy. The reversal to a bare frons (16B) in *P. nitens* indicates the questionable value of this character at other levels in Figure 72. The grouping of *P. angelica* + *P. obscura* + *P. antennalis* is supported only by the yellow base of flagellomere 1 (19).

Summary

The genus *Pseudodinia* fits well within the Chamaemyiini in morphological and ecological attributes of the larva and adult. The larva lacks the abundant cuticular processes of the Leucopini and feeds on mealybugs found on grasses. The adult has a narrow lunule lacking setulae, the male has two pairs of sternal and tergal elements between segment 5 and the genital segment, and the adults are found closely associated with the larval habitat.

Pseudodinia has been well diagnosed but the monophyly of the genus has been supported by only one synapotypy. Further work within the Chamaemyiini is needed to clearly identify a sister group to *Pseudodinia*. The two species groups recognized here, the *polita* group and the *varipes* group, are quite distinct, while the exact relationship of *P. cinerea* within the *varipes* group remains questionable.

Morphological conservatism predominates within each species group. Decisions on specific limits have been similarly conservative, with a preference to accept several phenetically variable species concepts (*P. pruinosa*, *P. antennalis*, *P. varipes*, and *P. occidentalis*). These decisions have been strongly influenced by ecological observations made in Ontario (Barber 1984) which have correlated resource partitioning with morphological divergence. Although resource partitioning is clearly evident among some sympatric species associated with different plants in Ontario (*P. pruinosa* on *S. scoparium*, *P. antennalis* on *A. gerardi*,

and *P. nitens* on neither), it is presumed to be considerably more subtle among others (*P. antennalis* and *P. varipes* on *A. gerardi*). The possibility of several species co-occurring on the same plant cannot be discounted (*P. pruinosa*, *P. antennalis*, and *P. latiphallis* on *Muhlenbergia* in Arizona).

Future work should be directed toward morphological and ecological investigations in the southwestern United States, particularly on the variants of *P. pruinosa* and *P. antennalis*, and how they relate to other species. Arizona appears to be the best study area since all variants of *P. pruinosa*, and seven of the remaining 13 species of the *varipes* group, occur in that state. As well, the collection at the University of Arizona (UAT) has one of the most extensive holdings of *Pseudodinia* species.

Acknowledgements

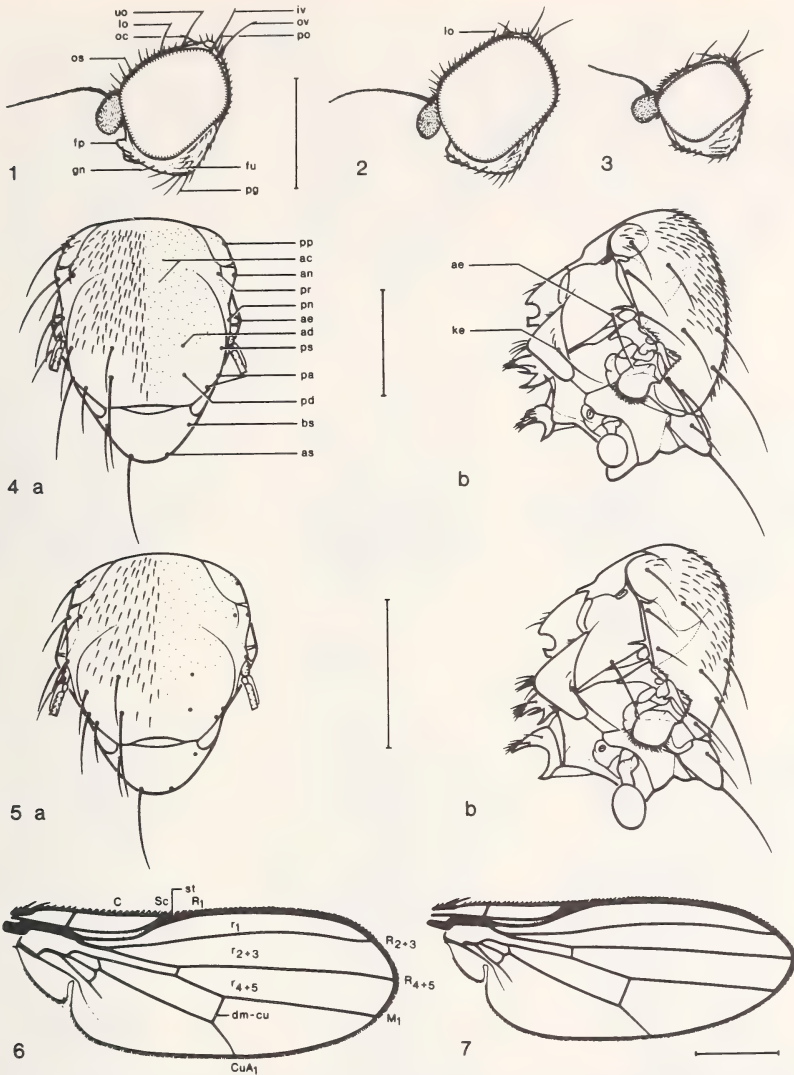
Dr. D.H. Pengelly was the person who introduced me to the Insecta. His constant encouragement has carried on into his retirement near Erickson, Manitoba, where he and Fran provide an oasis for travelling insect collectors. My M.Sc. committee members, Drs. S.A. Marshall, J.F. McAlpine (Biosystematics Research Institute), and J.E. Laing, provided valuable input, encouragement, and critical review, while financial support from NSERC Grant No. 852-36 to SAM was received. Drs. S.B. Peck, M. Sanborne (Carleton University), and G.A.P. Gibson (University of Alberta) provided valuable alcohol-preserved trap residues. Dr. D.R. Miller (Systematic Entomology Laboratory, Beltsville) identified the pseudococcid specimens. Cooperation from Parks Canada and Ontario Ministry of Natural Resources personnel provided access to parks in Ontario. D.J. Hamilton and A.K. Smith provided technical assistance and advice in preparing the figures and electron micrographs, respectively. B.V. Brown, J.M. Heraty, and Dr. H.J. Teskey (BRI) have reviewed and offered valuable criticisms of previous drafts.

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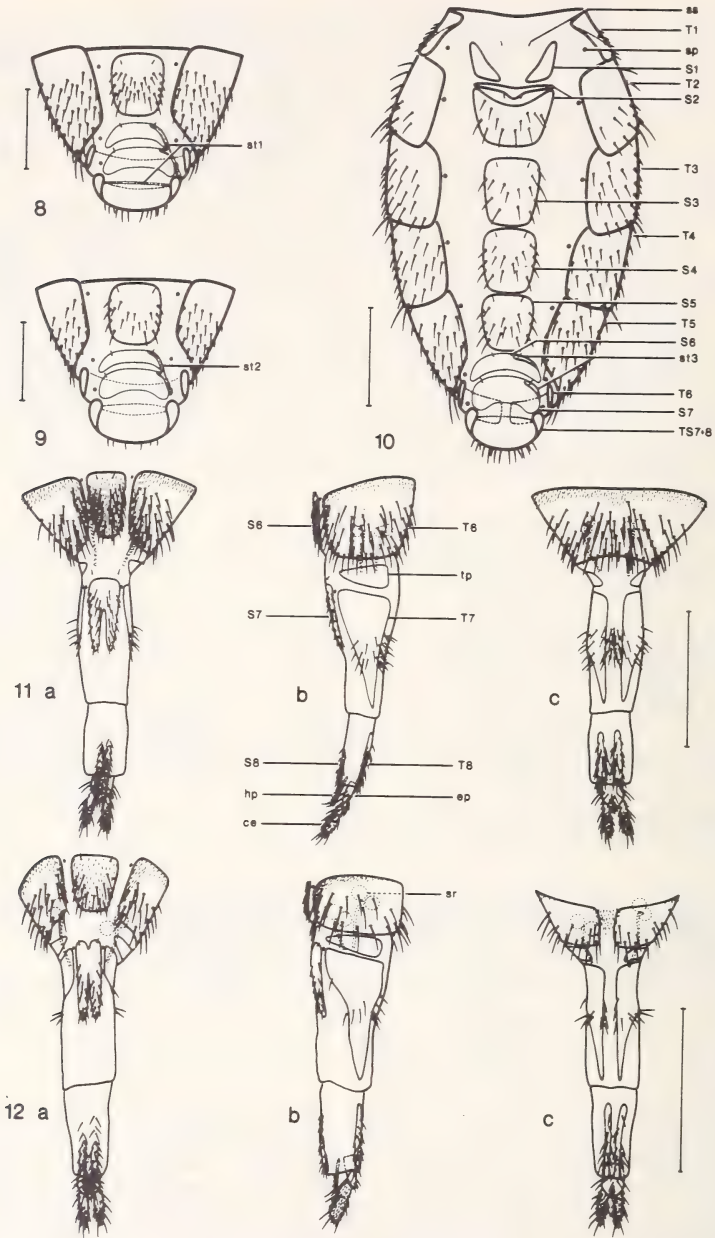
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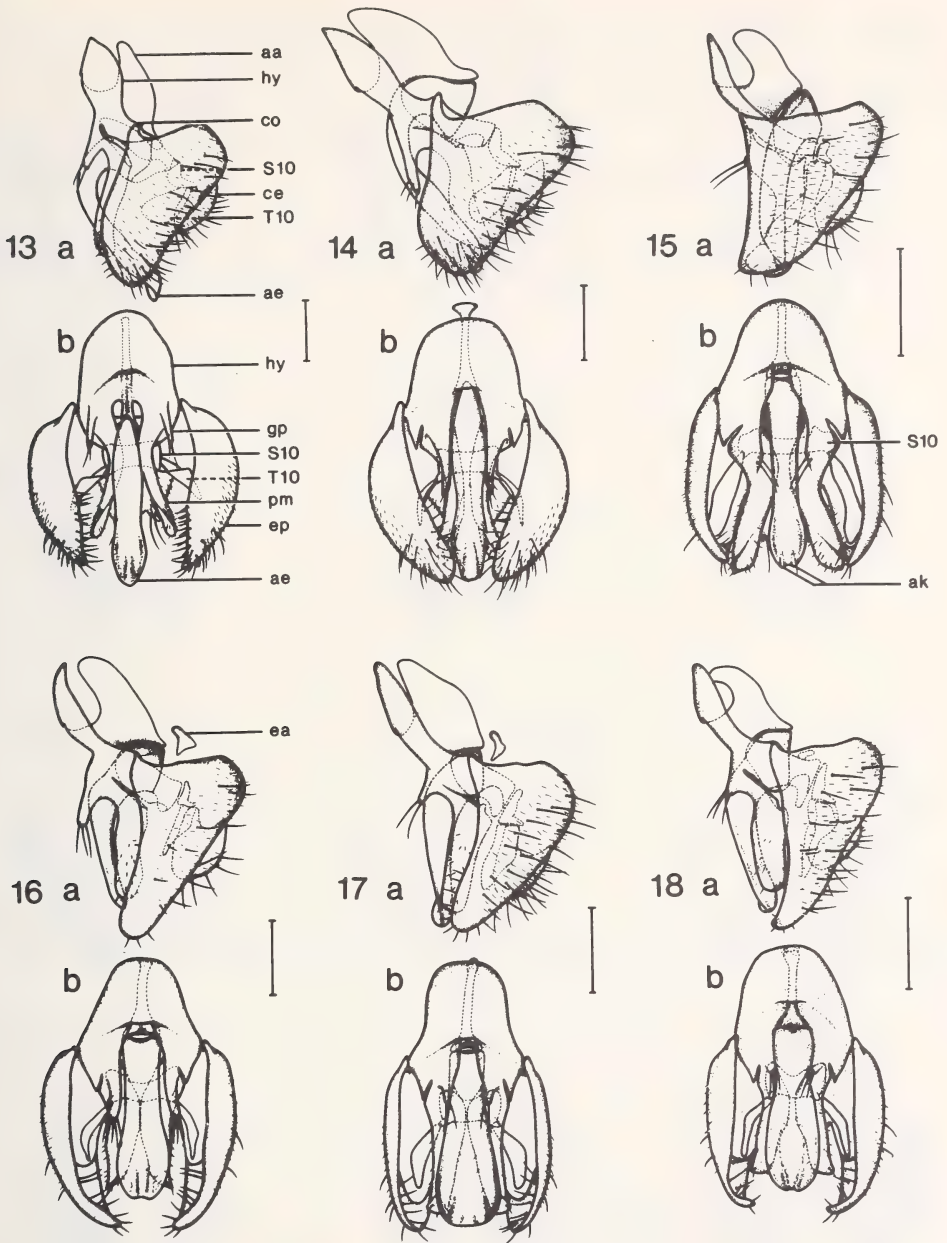
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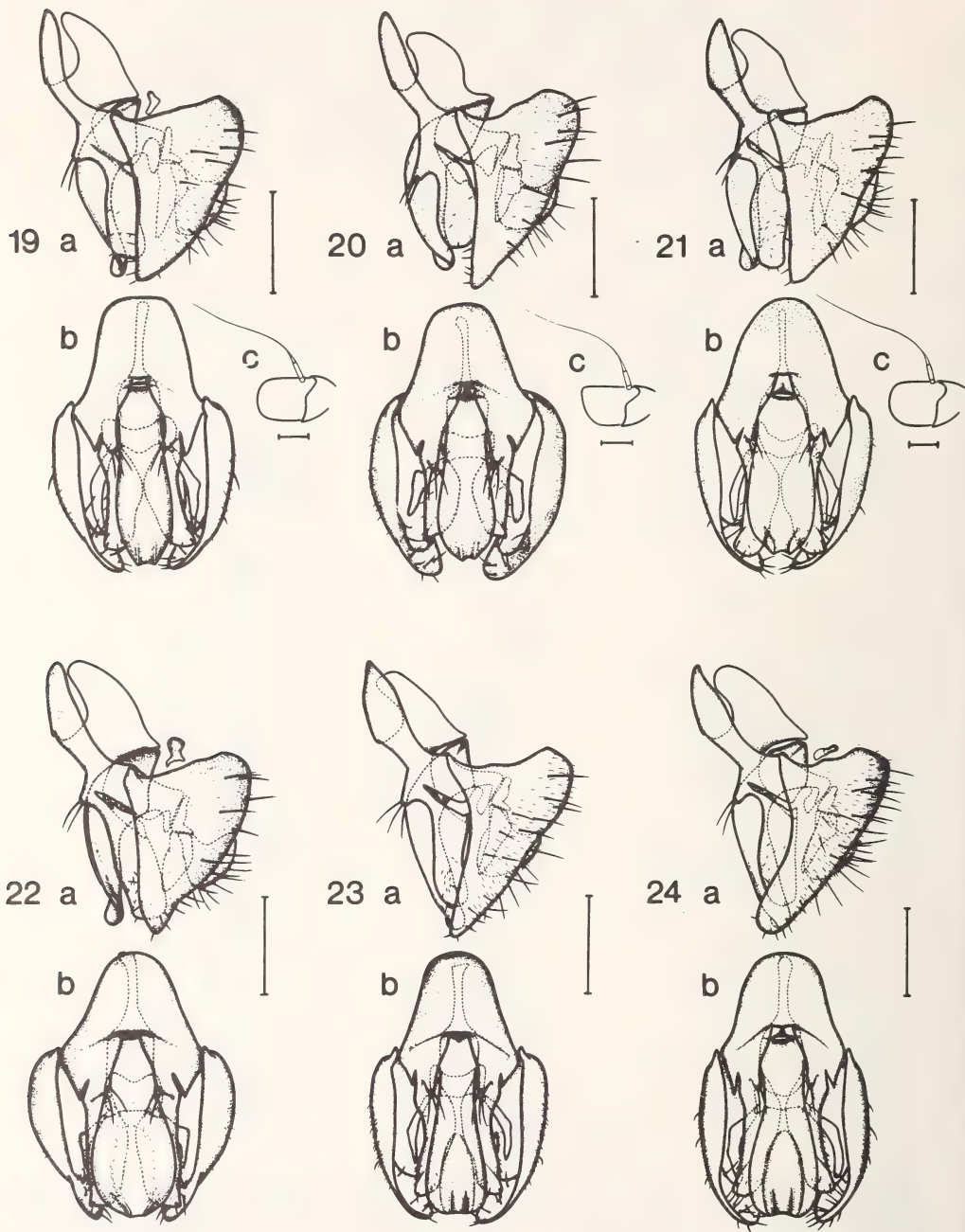
FIGS. 1-7. Heads, thoraces, and wings (bars = 0.5 mm.). 1-3, heads, female, left lateral: 1, *P. tuberculata*, holotype, Chiapas; 2, *P. polita*, paratype, Illinois; 3, *P. pruinosa*, Ontario. 4-5, thoraces, female (wings and pruinosity not included), a, dorsal (setae included on left side only), b, left lateral: 4, *P. polita*, paratype, Illinois; 5, *P. pruinosa*, Ontario. 6-7, left wings, male, ventral: 6, *P. polita*, Ontario; 7, *P. pruinosa*, Ontario. Abbreviations: ac - acrostichal setulae; ad - anterior dorsocentral seta; ae - anepisternal seta; an - anterior notopleural seta; as - apical scutellar seta; bs - basal scutellar seta; C - costa; CuA₁ - anterior branch of cubitus; dm-cu - discal medial-cubital crossvein; fp - facial prominence; fu - genal-occipital furrow; gn - genal seta; iv - inner vertical seta; ke - katepisternal seta; lo - lower orbital seta; M₁ - media; oc - ocellar seta; os - orbital setula; ov - outer vertical seta; pa - postalar setae; pd - posterior dorsocentral seta; pg - postgenal seta; pn - posterior notopleural seta; po - postocellar seta; pp - postpronotal seta; pr - presutural supra-alar seta; ps - postsutural supra-alar seta; R₁ - anterior branch of radius; R₂₊₃, R₄₊₅ - posterior branches of radius; r₁, r₂₊₃, r₄₊₅ - radial cells; st - stigma of subcostal cell; Sc - subcosta; uo - upper orbital seta.



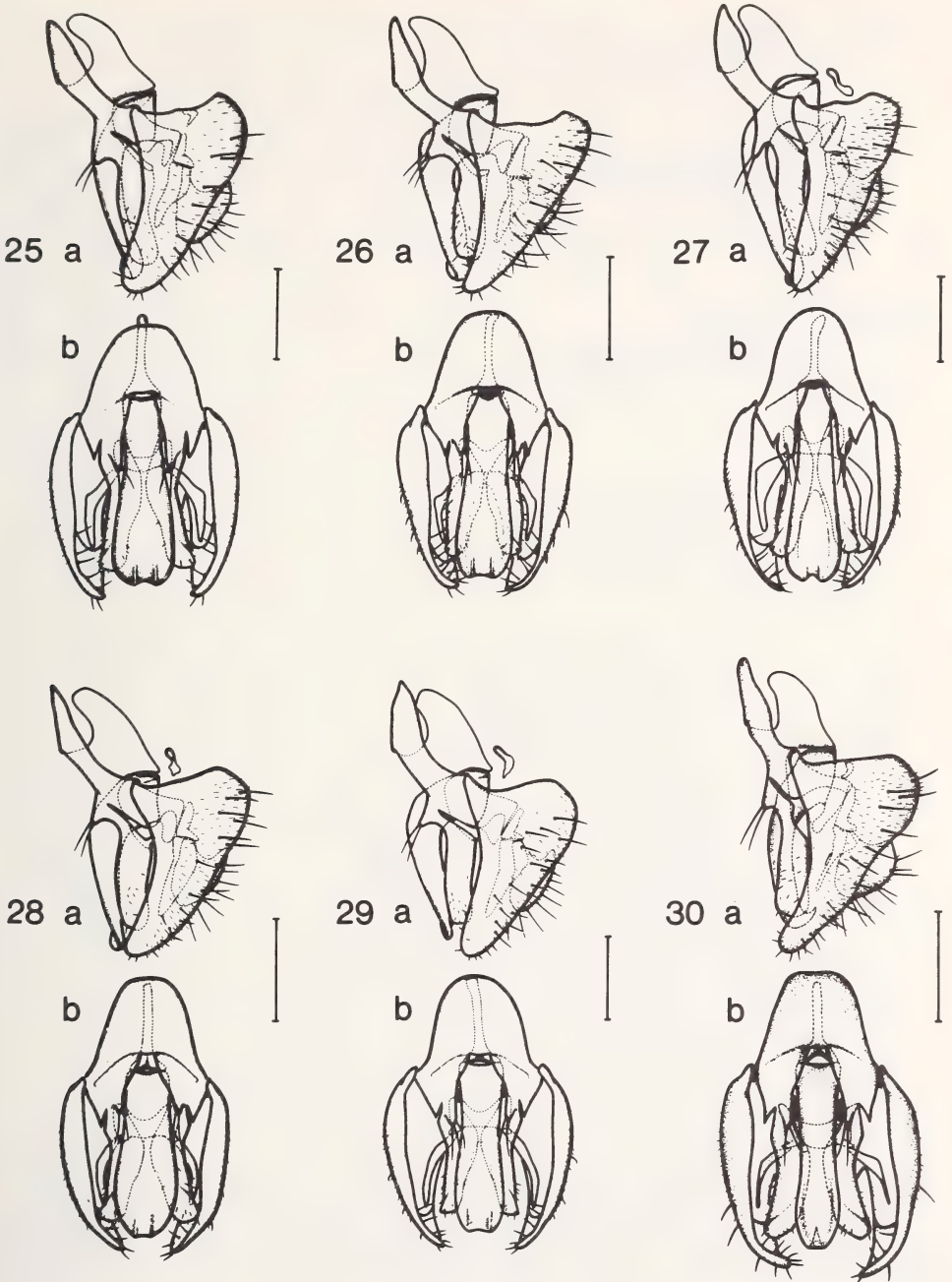
FIGS. 8-12. Abdomens. 8-10, male, genitalia removed, ventral (pruinosity not included, bars = 0.25 mm.): 8, *P. polita*, Nebraska, segments 5-7; 9, *P. cinerea*, paratype, Durango, segments 5-7; 10, *P. pruinosa*, Ontario, segments 1-7. 11-12, female, segment 6 to proctiger (bars = 0.5 mm.), a, ventral, b, lateral, c, dorsal: 11, *P. polita*, paratype, Illinois; 12, *P. pruinosa*, Ontario. Abbreviations: ce - cercus; ep - epiproct; hp - hypoproct; S1-8 - sternites; sp - spiracle; sr - spermatheca; ss - sensory setula; st1-3 - successively reduced conditions of strap-like sclerite; T1-8 - tergites; tp - triangular piece; TS7+8 - syntergosternite 7+8.



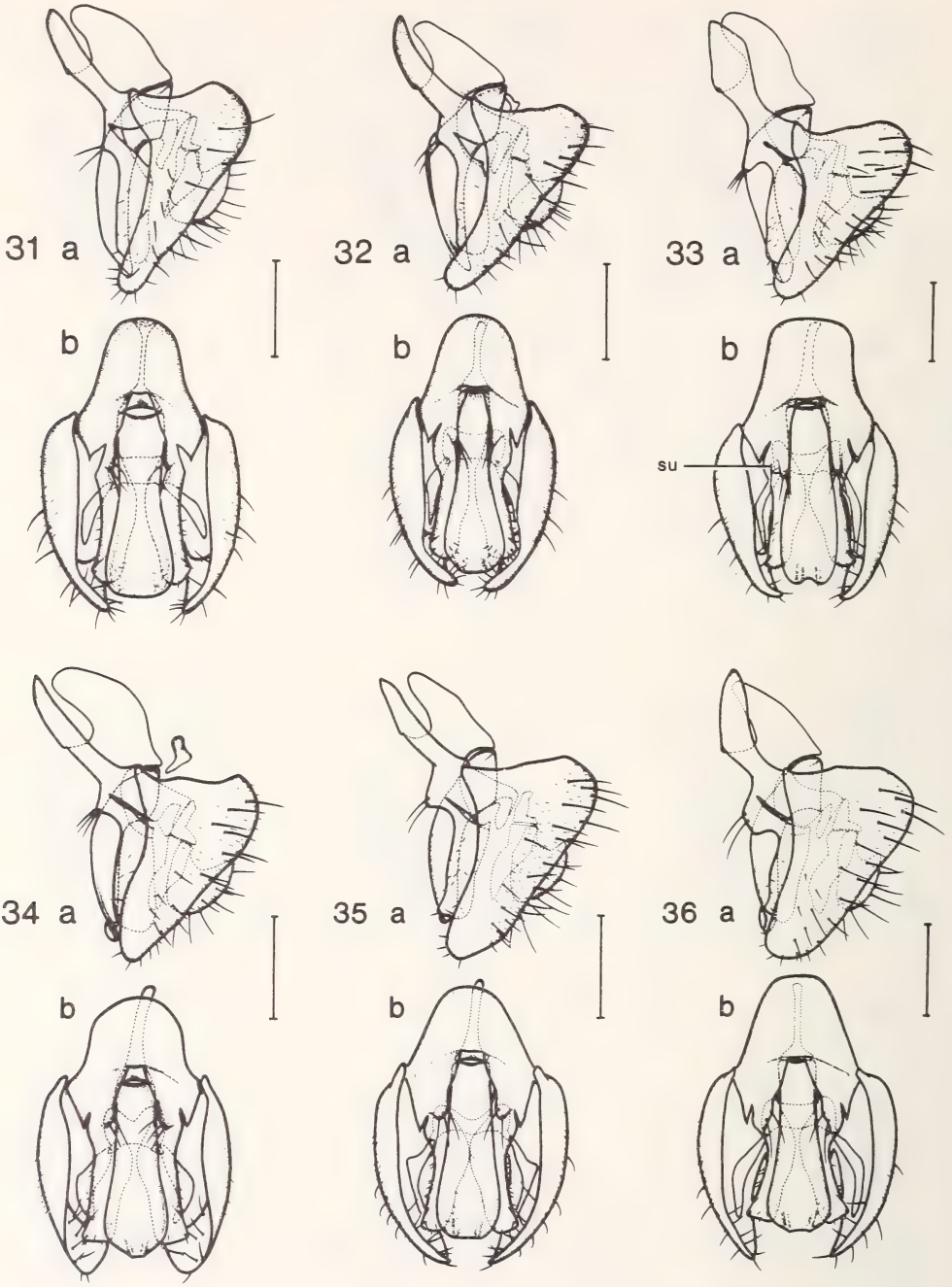
FIGS. 13-18. Male genitalia (bars = 0.1 mm.), a, left lateral, b, ventral. 13, *P. polita*, paratype, Illinois. 14, *P. meridionalis*, paratype, Costa Rica. 15, *P. cinerea*, paratype, Durango. 16, *P. nigritarsis*, holotype, California. 17, *P. slussi*, holotype, Arizona. 18, *P. melanitida*, Manitoba. Abbreviations: aa - aedeagal apodeme; ae - aedeagus; ak - aedeagal keels; ce - cercus; co - epandrial condyle; ea - ejaculatory apodeme; ep - epandrium; gp - gonopod; hy - hypandrium; pm - paramere; S10 - sternite 10; T10 - vestiges of tergite 10 and epiproct.



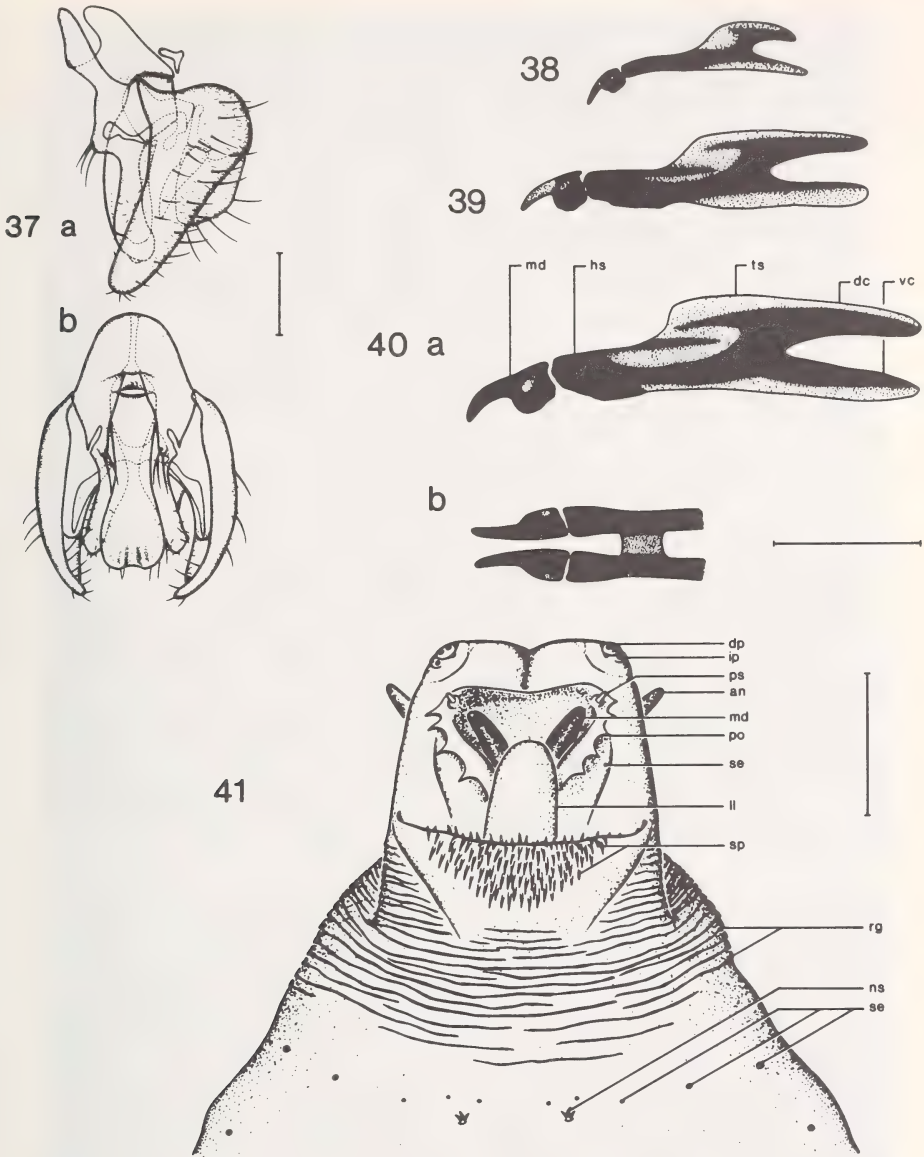
FIGS. 19-24. Male genitalia and antennae (bars = 0.1 mm.), a, genitalia, left lateral, b, genitalia, ventral, c, left antenna, lateral. 19-21, *P. varipes*: 19, holotype, New Mexico; 20, Creston, British Columbia; 21, Ontario. 22, *P. latiphallis*, paratype, Durango. 23-24, *P. occidentalis*, paratypes: 23, Arizona; 24, California.



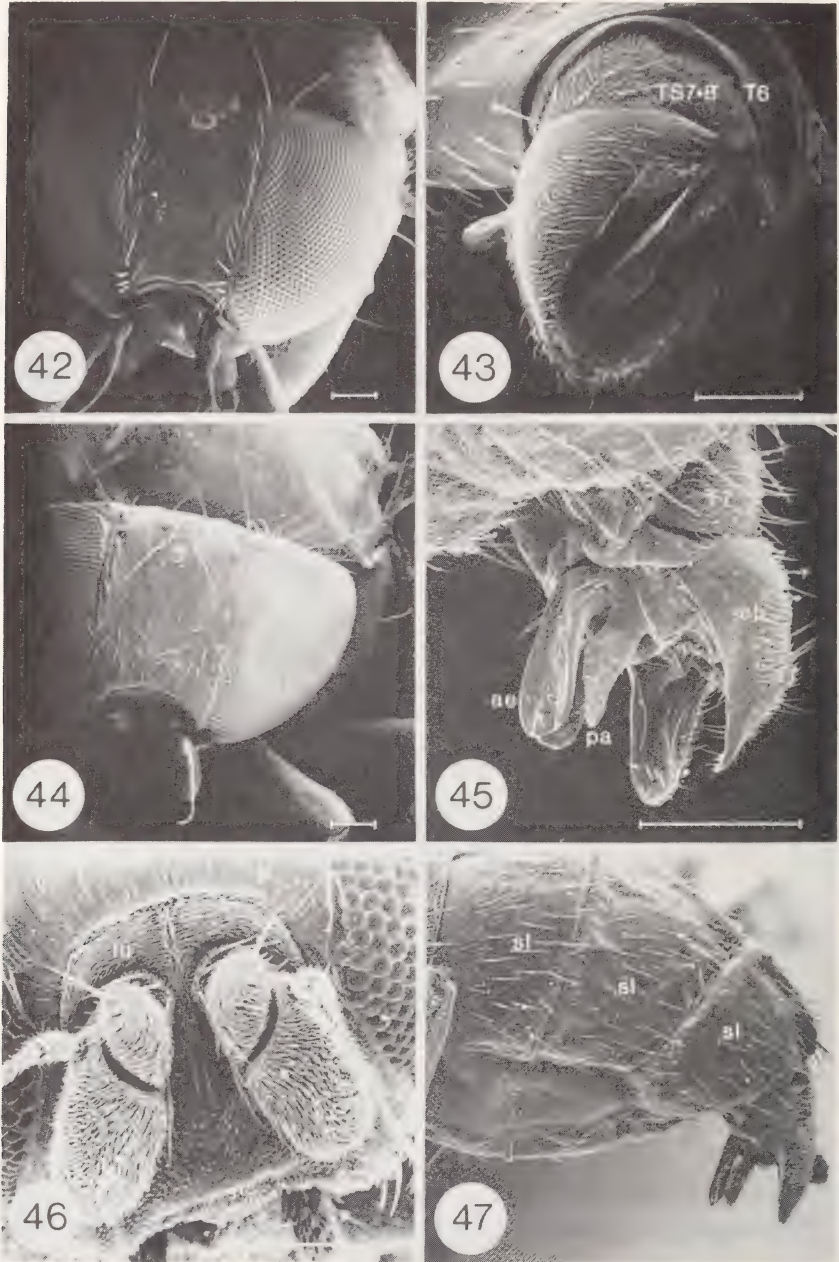
FIGS. 25-30. Male genitalia (bars = 0.1 mm.), a, left lateral, b, ventral. 25-29, *P. pruinosa*: 25, holotype, Texas; 26, Ontario, Typical variant; 27, New Mexico, Apache-Catron variant; 28, Arizona, AZ I variant; 29, Arizona, AZ II variant. 30, *P. hamata*, paratype, Arizona.



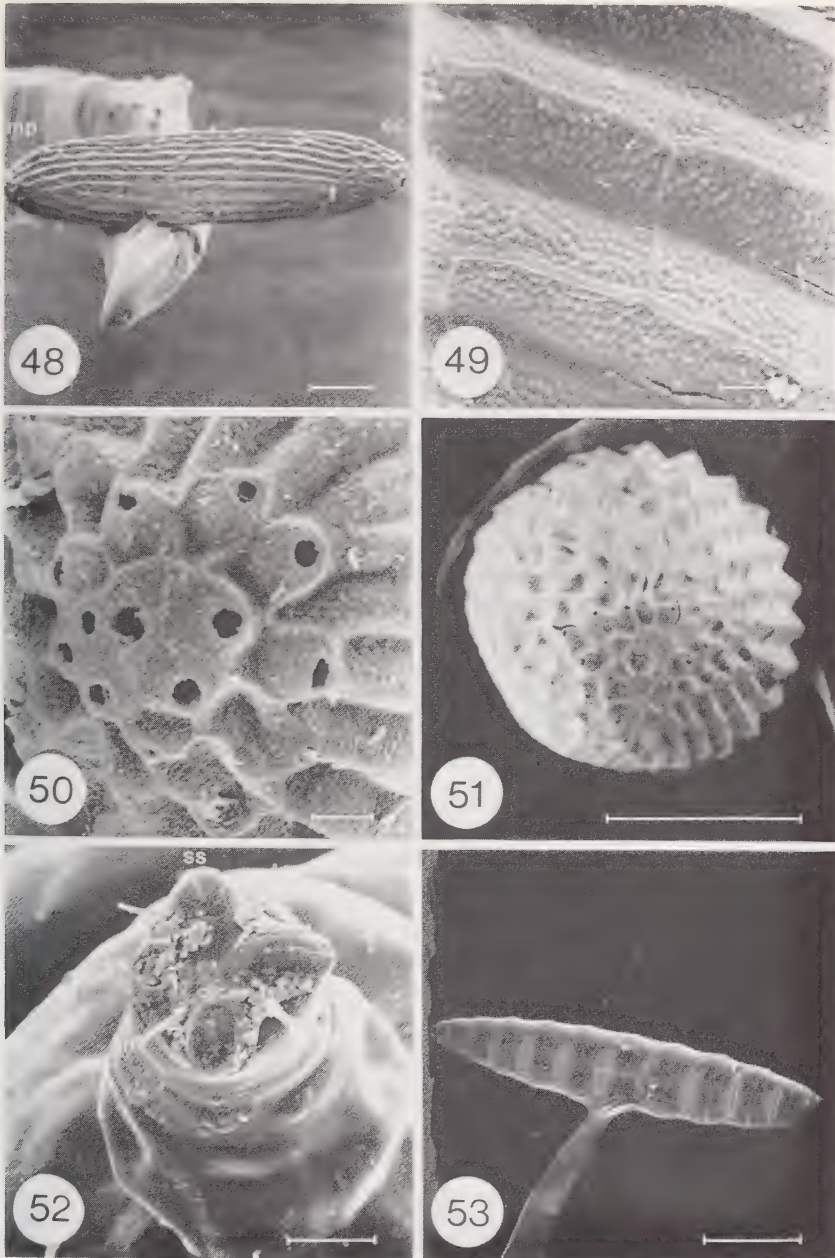
FIGS. 31-36. Male genitalia (bars = 0.1 mm.), a, left lateral, b, ventral. 31, *P. angustata*, paratype, Arizona. 32, *P. nitens*, New Mexico. 33, *P. angelica*, holotype, California. 34-36, *P. antennalis*: 34, holotype, Virginia; 35, Ontario; 36, Kitt Peak, Arizona. Abbreviation: su - supernumerary seta.



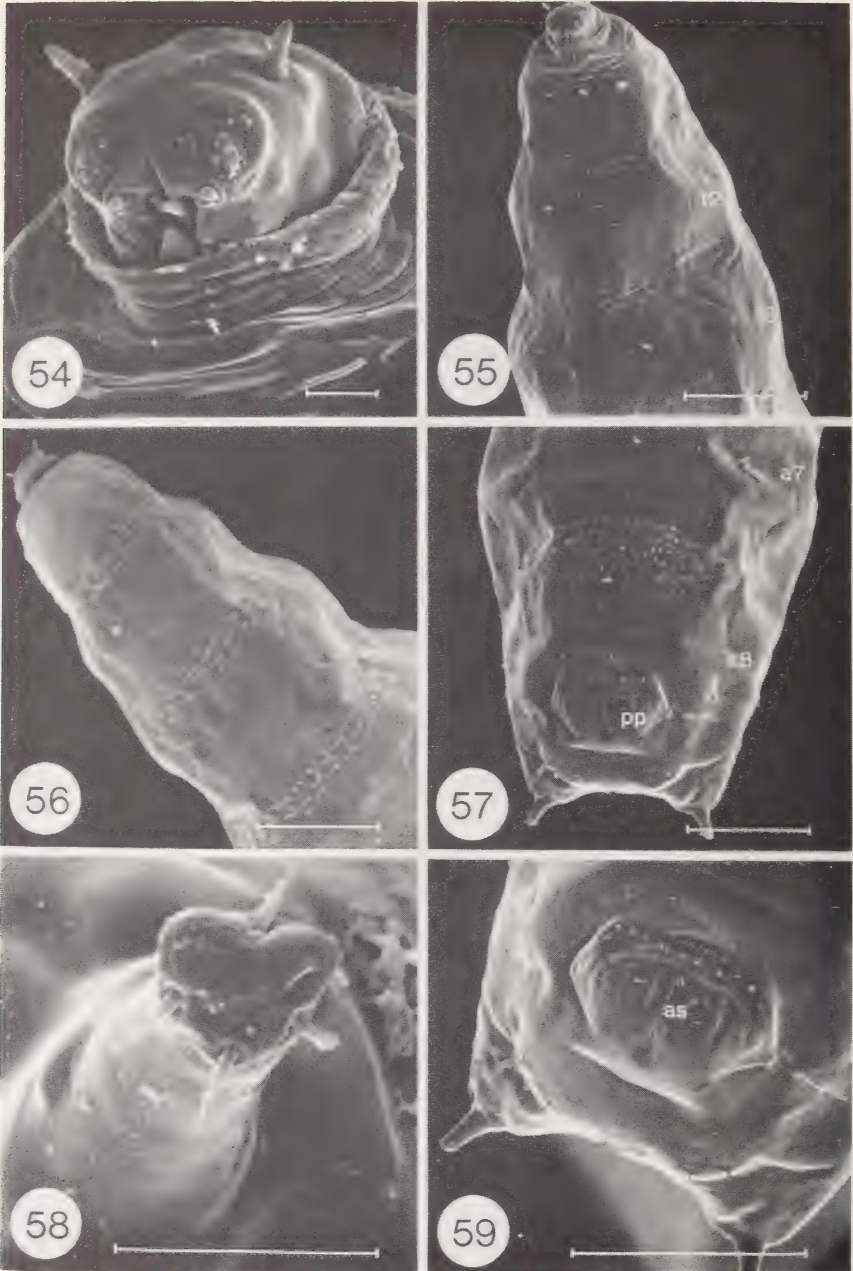
FIGS. 37-40. Male genitalia, cephalopharyngeal skeletons, and larval head (bars = 0.1 mm.). 37, male genitalia, *P. obscura*, paratype, Chiapas, a, left lateral, b, ventral. 38-40, cephalopharyngeal skeletons of larval *P. pruinoso*, Ontario: 38, first instar, left lateral; 39, second instar, left lateral; 40, third instar, a, left lateral, b, dorsal (tentoropharyngeal sclerite not included). 41, head of third-instar larva of *P. pruinoso*, Ontario, ventral. Abbreviations: an - antenna; dc - dorsal cornu of tentoropharyngeal sclerite; dp - discrete plate of maxillary palp; hs - hypopharyngeal sclerite; ip - indistinct plate of maxillary palp; ll - labial lobe; md - mandible; ns - needle-like sensillum; po - preoral margin; ps - papillate sensillum; rg - ridges of thoracic segment I; se - sensilla; sp - spines; ts - tentoropharyngeal sclerite; vc - ventral cornu of tentoropharyngeal sclerite.



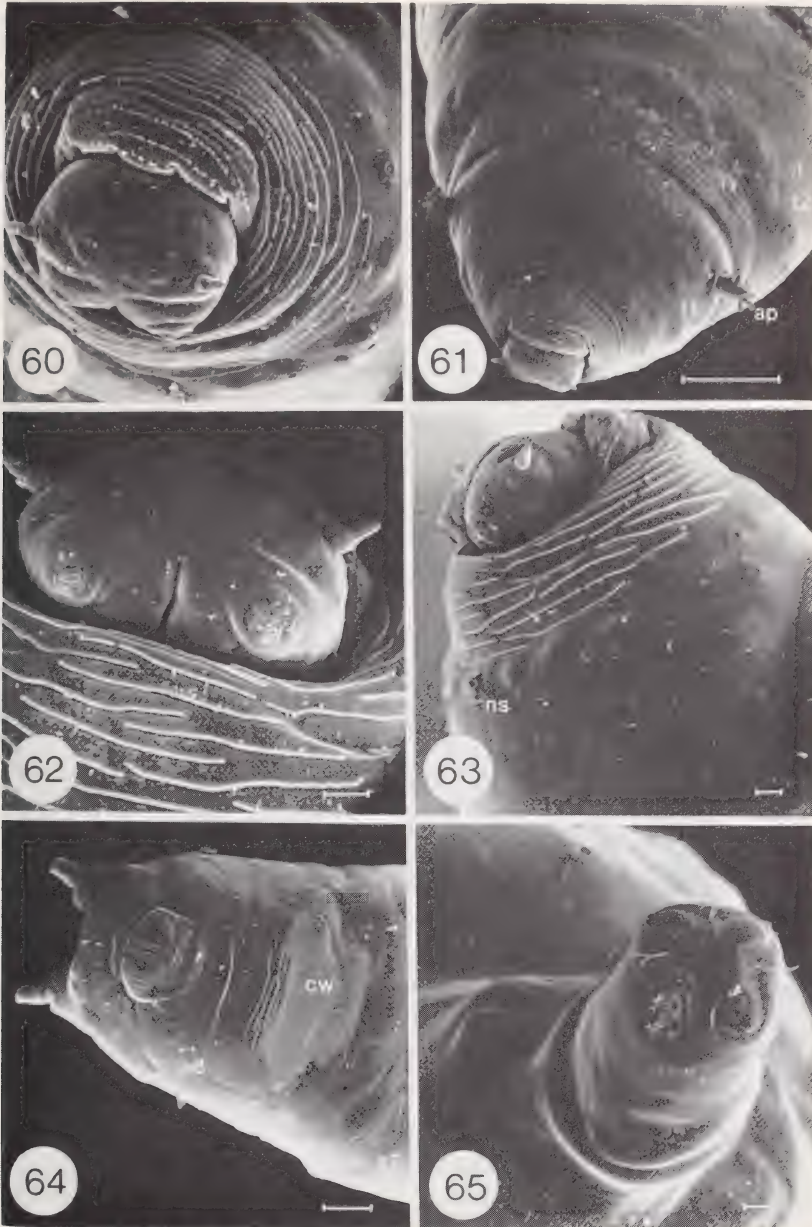
FIGS. 42-47. Adult male *Pseudodinia* (bars = 0.1 mm.). 42-43, *P. polita*, Maryland: 42, head, frontal; 43, genitalia, posterior, aedeagus everted. 44-47, *P. pruinosa*, Ontario: 44, head, frontal; 45, genitalia, anterolateral; 46, face and antennae, frontal; 47, abdomen, segment 3 to apex, lateral. Abbreviations: ae - aedeagus; ep - epandrium, lu - lunule; pm - paramere; sl - sublateral bare areas on tergites 3-5; T6 - tergite 6; TS7+8 - syntergosternite 7+8.



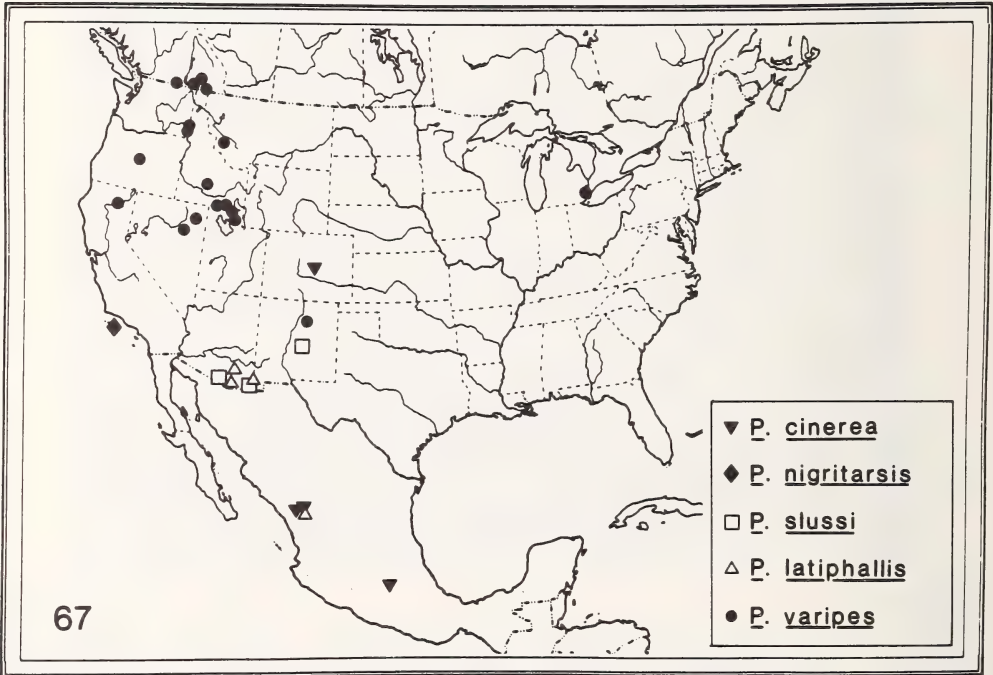
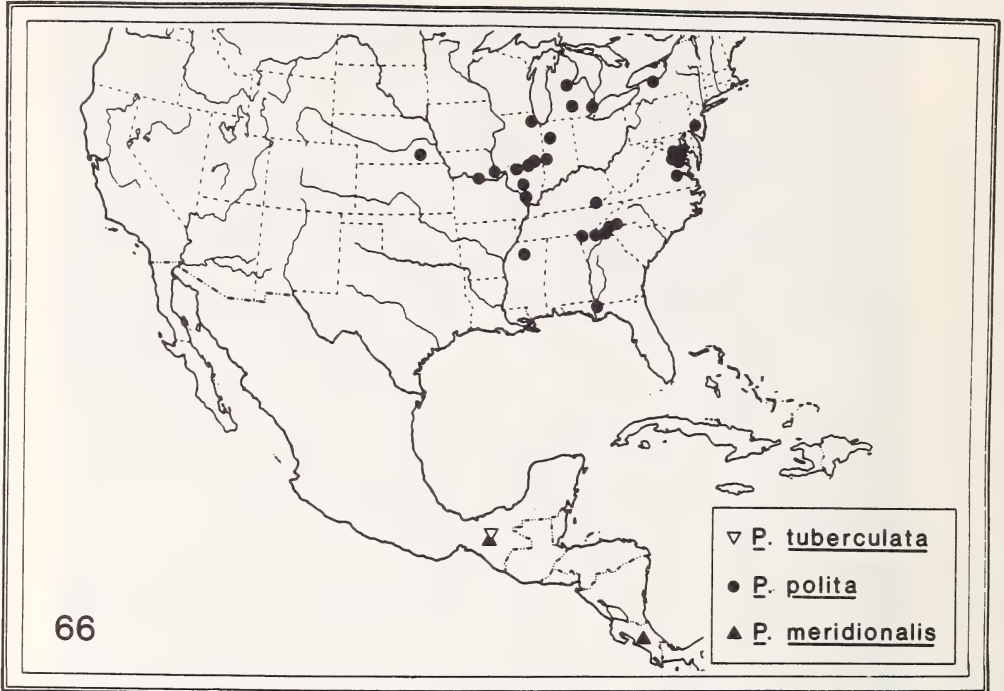
FIGS. 48-53. Eggs and larvae of *P. pruinosa*, Ontario. 48-51, eggs: 48, lateral (bar = 0.1 mm.); 49, microsculpture of chorion (bar * 0.01 mm.); 50, micropyle (bar = 0.01 mm.); 51, eclosion cap (bar = 0.1 mm.). 52-53, larvae: 52, second instar, posterior spiracle, apical (bar = 0.01 mm.); 53, third instar, habitus, ventral (bar * 1.0 mm.). Abbreviations: ec - eclosion cap end; es - ecdysial scar; ih - interstigmatal hair; mp - micropylar end; ss - spiracular slit.



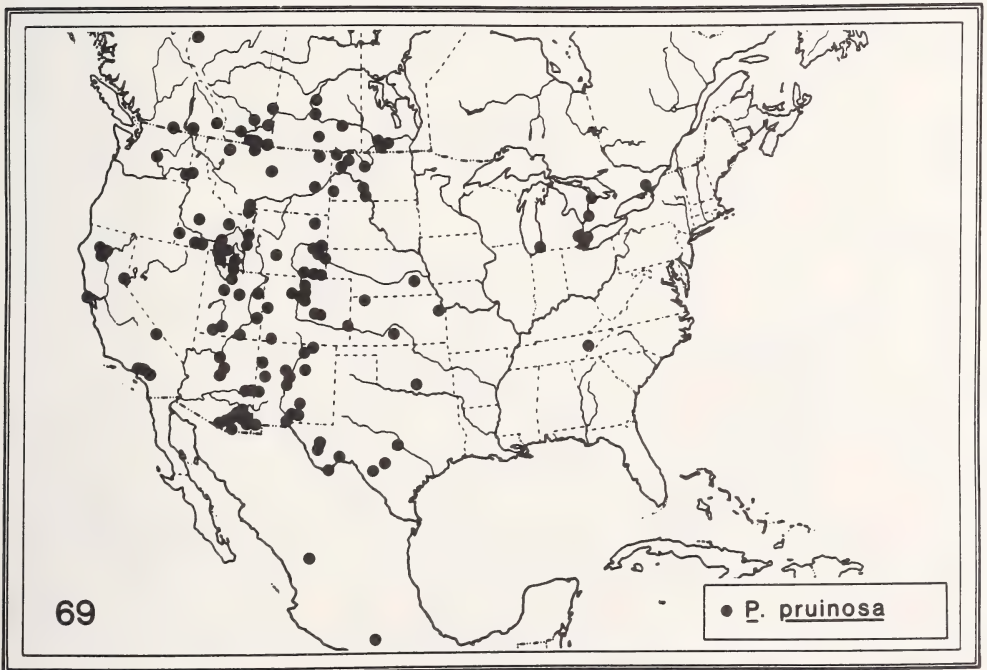
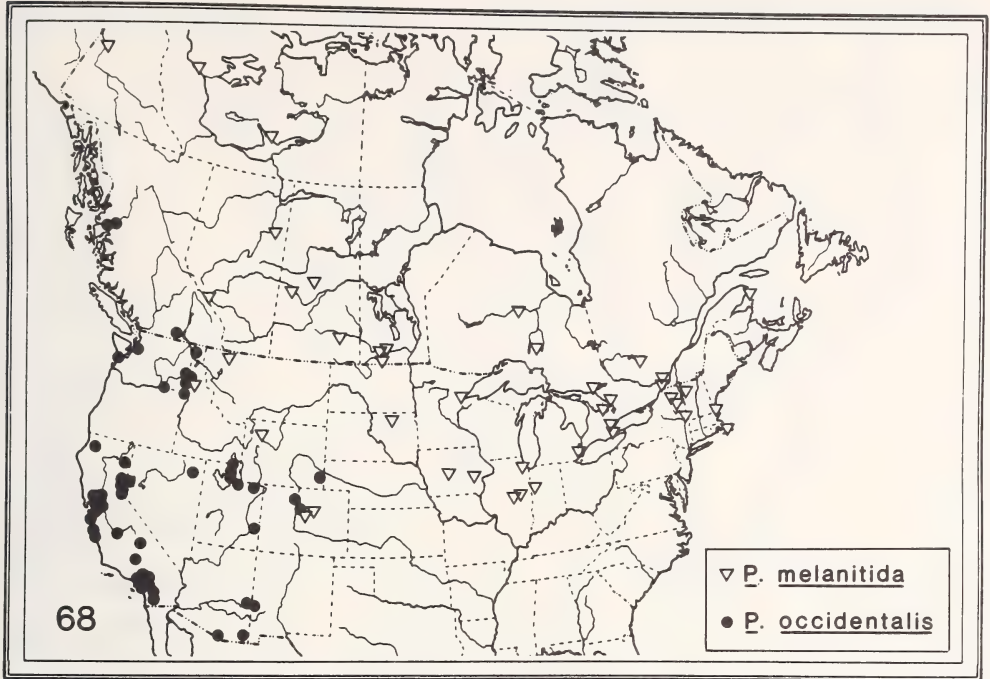
FIGS. 54-59. First-instar larva of *P. pruinosa*, Ontario. 54, head, ventral (bar = 0.01 mm.). 55, head and thorax, ventral (bar = 0.1 mm.). 56, head and thorax, dorsal (bar = 0.1 mm.). 57, abdominal segment 8 and apical portion of segment 7, ventral (bar = 0.1 mm.). 58, posterior spiracle, apical (bar = 0.01 mm.). 59, apical portion of abdominal segment 8, ventral (bar = 0.1 mm.). Abbreviations: as - anal slit; a7-8 - abdominal segments; pp - perianal pad; ps - papillate sensillum; t1-3 - thoracic segments.



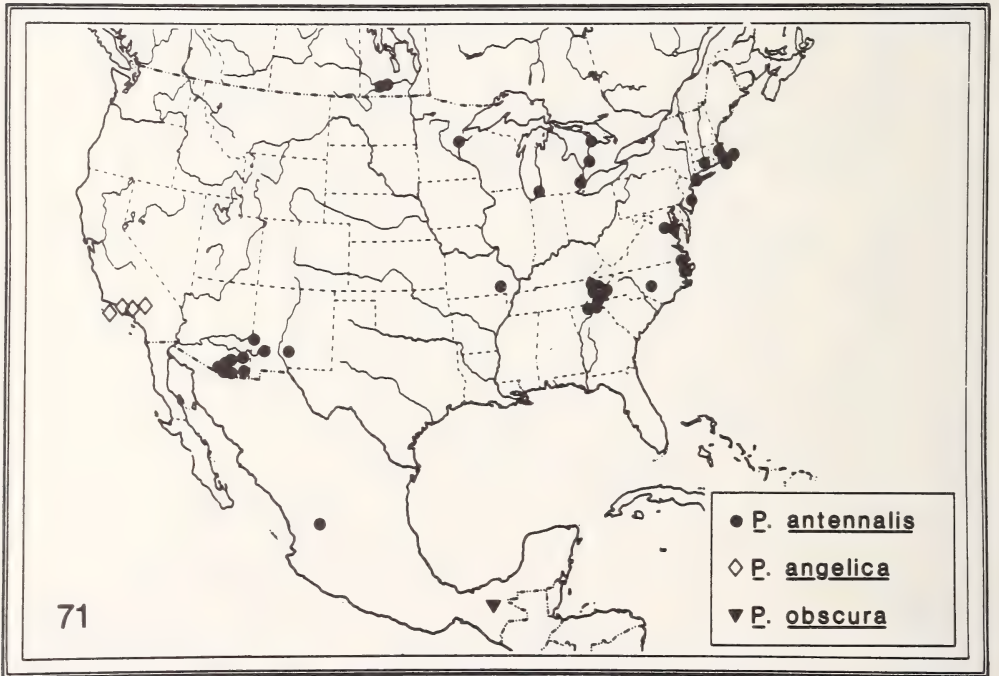
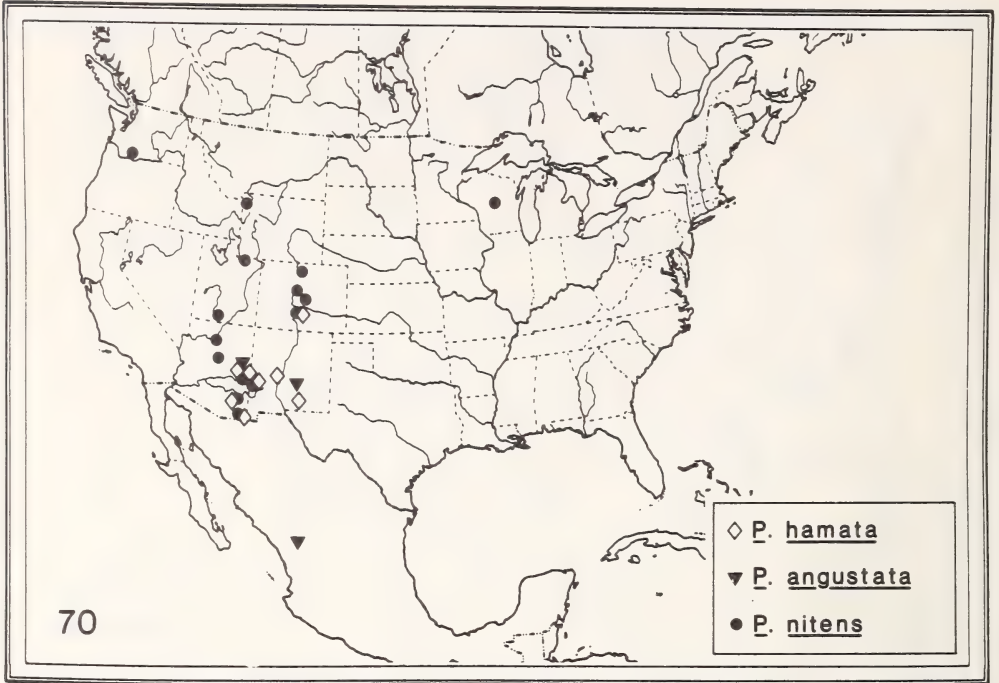
FIGS. 60-65. Third-instar larva of *P. pruinosa*, Ontario. 60, head and anterior portion of thoracic segment 1, anterior (bar = 0.01 mm.). 61, head and thoracic segments 1-2, anterodorsal (bar = 0.1 mm.). 62, head and anterior portion of thoracic segment 1, ventral (bar = 0.01 mm.). 63, head and thoracic segment 1, lateral (bar = 0.01 mm.). 64, abdominal segment 8, ventral (bar = 0.1 mm.). 65, posterior spiracle, apical (bar = 0.01 mm.). Abbreviations: ap - anterior spiracle; a7-8 - abdominal segments; cw - shagreened creeping welt; ns - needle-like sensilla; tl-2 - thoracic segments.



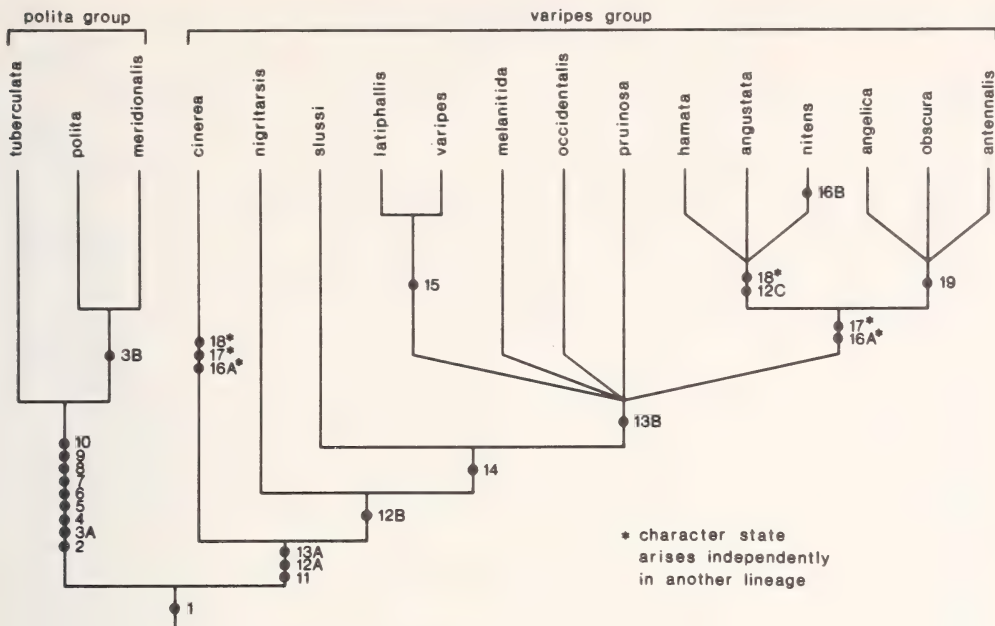
FIGS. 66-67. Geographical distributions. 66, *P. tuberculata*, *P. polita*, and *P. meridionalis*. 67, *P. cinerea*, *P. nigritarsis*, *P. slussi*, *P. latiphallis*, and *P. varipes*.



FIGS. 68-69. Geographical distributions. 68, *P. melanitida*, and *P. occidentalis*. 69, *P. pruinosa*.



FIGS. 70-71. Geographical distributions. 70, *P. hamata*, *P. angustata*, and *P. nitens*. 71, *P. antennalis*, *P. angelica*, and *P. obscura*.



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FIGS. 72. Hypothesis of phylogenetic relationships among species of *Pseudodinia*. Apotypies. 1 - apex of paramere bevelled with one outstanding setula near anteroventral aspect (Figs. 13-17, 45). 2 - tibiae entirely yellow. 3A - lower orbital seta arising at 0.4 of frontal length (Fig. 1). 3B - lower orbital seta arising at 0.1-0.2 of frontal length (Figs. 2, 42). 4 - full series of well developed orbital setulae (Figs. 1-2, 42). 5 - lower margin of face projecting in lateral view (Figs. 1-2). 6 - anepisternal seta arising at 0.6-0.8 of anepisternal height (Fig. 4). 7 - width of wing cell r_{2+3} 1.2-1.5X width of cell r_1 (Fig. 6). 8 - female tergite 6 complete, not divided medially (Fig. 11). 9 - ratio of height of compound eye to genal width relatively high at 6.4-10.0 (Figs. 1-2). 10 - frons with relatively weak, erect to slightly reclinate setulae sparsely scattered over most of its surface (Figs. 1-2, 42). 11 - epandrial condyle reduced, not hook-like (Figs. 15-37). 12A - epandrium broadly triangular, apices only slightly tapered (Fig. 15). 12B - epandrial apices moderately tapered (Figs. 16-29, 33-37, 45, 47). 12C - epandrial apices strongly tapered, nearly parallel-sided (Figs. 30-32). 13A - strap-like sclerite of male not extending dorsally, but running uninterruptedly from the left sensory setula of sternite 6, to that of sternite 7, and continuing posteriorly to encircle spiracle 7 (Fig. 9). 13B - strap-like sclerite interrupted, reduced, sometimes absent, at most consisting of a separate sclerite on each of sternites 6 and 7 near the left sensory setula (Fig. 10). 14 - male tergite 6 divided medially (Fig. 10). 15 - aedeagus strongly but gradually curved, in lateral view (Figs. 19-22). 16A - frons entirely pruinose. 16B - frons bare on at least anterior half (reversal to plesiotypic state; as in Fig. 44). 17 - sublateral bare areas usually reduced on male tergites, often leaving tergites entirely pruinose. 18 - length of male tergite 6 0.3-0.4X tergite 5. 19 - flagellomere 1 basally yellow to at least base of arista.

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ROLE OF THE INQUILINE, *DASINEURA BALSAMICOLA* (DIPTERA: CECIDOMYIIDAE), IN THE BALSAM FIR NEEDLE GALLJ.D. SHORTHOUSE and R.J. WEST¹

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Abstract*Proc. ent. Soc. Ont.* 117:1-7 (1986)

The cecidomyiid, *Dasineura balsamicola* Lintner, is an inquiline commonly found within the balsam fir needle gall induced by another cecidomyiid, *Paradiplosis tumifex* Gagné. Larvae of *D. balsamicola* enter galls soon after gall initiation and feed, alongside the larvae of *P. tumifex*, on nutritive cells induced by *P. tumifex*. *D. balsamicola* does not alter the structure of host galls. Third-instar larvae of *D. balsamicola* kill the larvae of *P. tumifex* before they reach the third instar. It is suggested that death results from abrasion by the thick spinous integument of *D. balsamicola* against the thin integument of *P. tumifex*.

Introduction

The gall midge, *Paradiplosis tumifex* Gagné, induces a globular, single-chambered, pro-soplasmic gall on the needles of balsam fir, *Abies balsamea* (L.) Miller. The gall has been known since 1888, but recently has received attention because its damage affects the Christmas tree industry of southeastern Canada and northeastern U.S.A. (MacGowan and Osgood 1972, Bergdahl and Mazzola 1985). The gall is frequently inhabited by the inquiline midge, *Dasineura balsamicola* Lintner, but only recently did Osgood and Gagné (1978) establish that *P. tumifex* was the inducer and *D. balsamicola* was the inquiline.

The term inquiline has been used broadly to identify phytophagous gall inhabitants that are incapable of initiating the galls in which they feed. Askew (1971) regarded inquilinism as a type of commensalism in which the inquiline lives in a close spatial relationship with the gall inducer, and the lives of the inquilines are closely associated with the galls of other species. Skuhravá and Skuhravý (1973) defined inquiline gall midges as gall inhabitants that feed on gall tissues without causing direct harm to the gall inducer.

The roles of inquilines in galls of cecidomyiids are poorly understood compared to the roles of cynipid inquilines in cynipid galls. The adult females of some cynipid inquilines, for example, kill the larvae of the gall inducer at oviposition and then their larvae modify the inhabited gall (Shorthouse 1980). Several authors have reported finding inquiline midges in mature cecidomyiid galls without the gall inducer being alive (Parnell 1964, Sylvén 1975, Skuhravá *et al.* 1984); however, it was not determined how the inducer was killed. The members of most cecidomyiid genera are typical gall-inducers, with only a few species of some genera being inquilines. For example, only 15 of the 250 Palearctic species of *Dasineura* are inquilines; the rest are gall inducers (Skuhravá *et al.* 1984).

While studying the gall of *P. tumifex* in central Ontario (West and Shorthouse 1982), we found numerous galls inhabited by larvae of both *P. tumifex* and *D. balsamicola* or by a mature larva of *D. balsamicola* along with a dead *P. tumifex*. We fixed about 60 galls with larvae at all stages of development and recently sectioned and stained the material. The purpose of this paper is to report on our findings and suggest how *D. balsamicola* kills the larvae of *P. tumifex*.

Materials and Methods

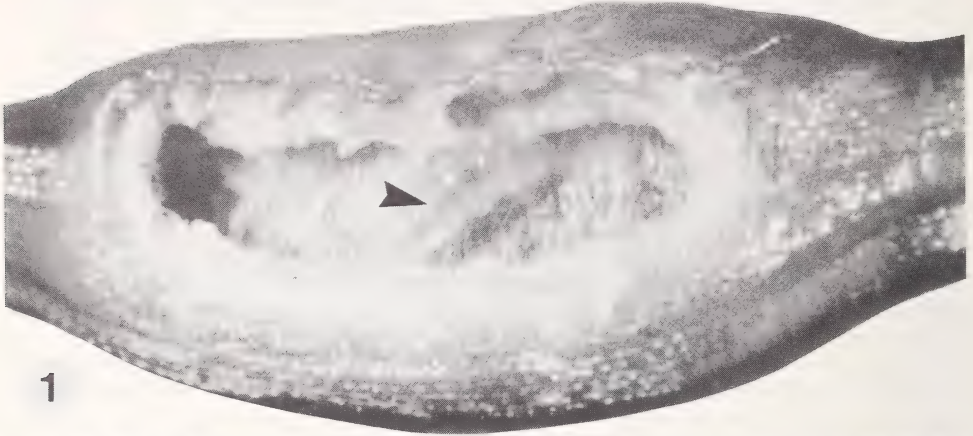
Galls were collected periodically throughout the summers of 1978, 1979 and 1981 near Burwash, Chalk River and Grundy Provincial Park, Ontario. Galls were returned to the laboratory, their contents determined and the galls fixed in formalin-acetic acid-alcohol (FAA). Gall tissues were then dehydrated in a tertiary butyl alcohol series and embedded

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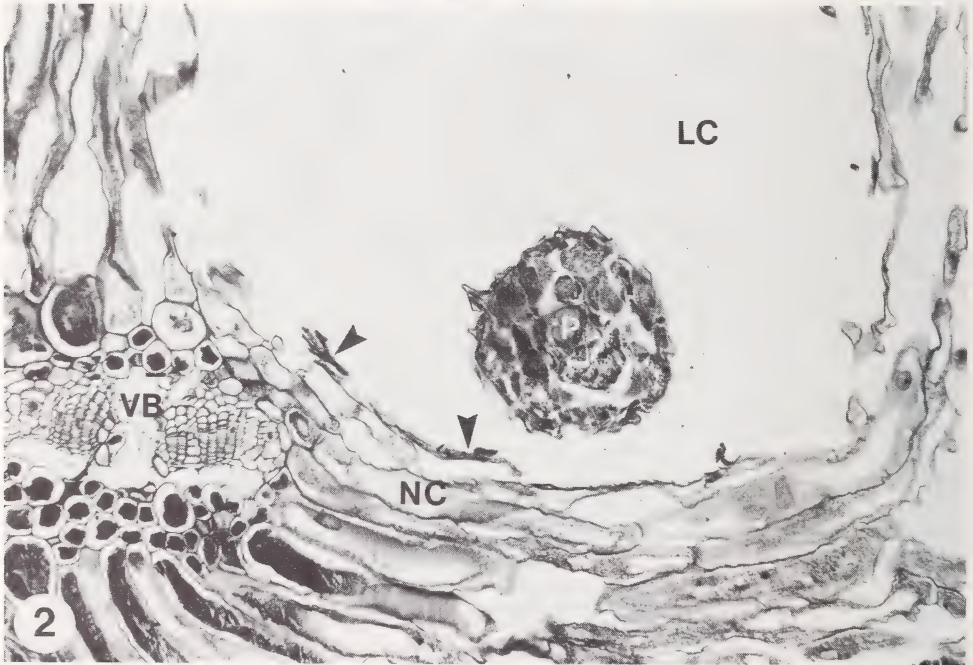
in paraffin (Jensen 1962). All tissues were sectioned at 8 μ with a rotary microtome and stained with safranin-fast green (Johansen 1940).

Results and Discussion

Adults of *P. tumifex* emerge from the leaf litter in early May in Ontario, mate and oviposit in the tips of flushing buds of balsam fir. The eggs hatch in 2-3 days and the individual larvae are enclosed by proliferating cells within the first week of feeding, except for



1



2

FIGURE 1. Gall occupied by second-instar larva of *Paradiplosis tumifex* (arrow) collected in mid-July. Mag. X27.

FIGURE 2. Section of gall near base of larval chamber (LC) occupied by second-instar larva of *P. tumifex* (P), collected in mid-July. Note the thin-walled nutritive cells (NC) and a few collapsed cells (arrows) due to larval feeding. VB, vascular bundle. Mag. X100.

the ostiolar opening which is present throughout gall development (West and Shorthouse 1982). The second instar larvae appear in early July and the third instar larvae appear in late August. Second-instar larvae occupy only a small portion of the larval chamber (Fig. 1). The larvae feed throughout the period of gall growth by sucking the contents of unmodified nutritive cells along the base of the larval chambers, and as with other gall midges (Rohfritsch 1971, Redfern 1975), only rarely are the cells damaged. Nutritive cells fed upon by *P. tumifex* are small and vacuolate, whereas in other cecidomyiid galls nutritive cells are characterized by increased cytoplasm and an enlarged nucleus and nucleolus (Bronner 1977).

Growing and mature galls are composed almost entirely of enlarged, vacuolate mesophyll cells and thin-walled nutritive cells along the base of the larval chamber (Fig. 2). Gall mesophyll cells contain more starch granules than do corresponding mesophyll cells in non-galled needles. As the gall matures a gradient of starch develops from the nutritive tissue to the mesophyll cells near the resin ducts and the base of the gall with the latter having the greatest concentrations and largest granules (West and Shorthouse 1982). The gall can be considered mature by mid-July. Third instar larvae begin to exit the galls via the ostiole by mid-September, and all have left by mid-October. Both larvae and empty galls fall to the leaf litter where the larvae spin a cocoon to overwinter.

The life cycle of *D. balsamicola* is similar to that of *P. tumifex*. *D. balsamicola* adults emerge at the same time as *P. tumifex* adults (Osgood and Gagné 1978) and lay their eggs within flushing buds. The first galls with larvae of both species were found on May 19 in Maine, U.S.A. (Osgood and Gagné 1978) and on May 31, 1979 near Burwash. It is assumed that eggs of *D. balsamicola* are laid near those of *P. tumifex* and are enveloped by gall tissues along with the larva of *P. tumifex* or that first instar *D. balsamicola* crawl to immature galls and enter through the ostiole. Galls at this early stage of development were barely discernible as slight swellings (1.0 mm in length and width and 0.8 mm in thickness) on the adaxial surface of needles (West and Shorthouse 1982). Larvae of both species in the same gall were situated apart and were apparently feeding on nutritive cells at the base of the larval chambers.

The two larvae are readily distinguishable throughout gall growth (Osgood and Gagné 1978). Larvae of *D. balsamicola* have spinules and setae on the abdominal segments whereas the integument of *P. tumifex* is smooth. Larvae of *D. balsamicola* are darker orange than those of *P. tumifex*. The sternal spatula is present in second instar larvae of *P. tumifex*, but absent in second-instar larvae of *D. balsamicola*. The two larvae remain about the same size until mid-July when both are in their second instar (Fig. 3). Throughout this period the two larvae are found apart and do not appear to interfere with one another. However, when *D. balsamicola* is present, the larvae of *P. tumifex* never moult from the second instar.

Larvae of *D. balsamicola* begin moulting to the third instar by the end of August and continue to grow, whereas the second instar larvae of *P. tumifex* stop growing and become lethargic. The larvae are always found close to one another (Fig. 4) by mid-August. Mature third-instar larvae of *D. balsamicola* nearly fill the larval chamber. The integrity of the gall remains throughout the period when both larvae are feeding (Fig. 4), when *P. tumifex* is dying and after *P. tumifex* has died.

Death of larvae of *P. tumifex* in galls inhabited by *D. balsamicola* begins in mid-August. Larvae of *P. tumifex* in galls without *D. balsamicola* normally reach the third instar about two weeks before *D. balsamicola* and leave their galls before *D. balsamicola* leave their adopted galls. Bergdahl and Mazzola (1985) found larvae of *P. tumifex* beginning to exit from their galls by September 13 and all had departed by October 18, in contrast to *D. balsamicola* which begins to exit in mid-October with the last leaving in early December. Needle abscission caused by infestation by either *P. tumifex* or *D. balsamicola* generally does not occur until after the third-instar larvae have left their galls.

Death of larvae of *P. tumifex* in galls inhabited by *D. balsamicola* begins in mid-August and by the middle of September all larvae of *P. tumifex* are dead. Bergdahl and Mazzola (1985) reported that in Vermont, some mortality associated with *D. balsamicola* occurred as

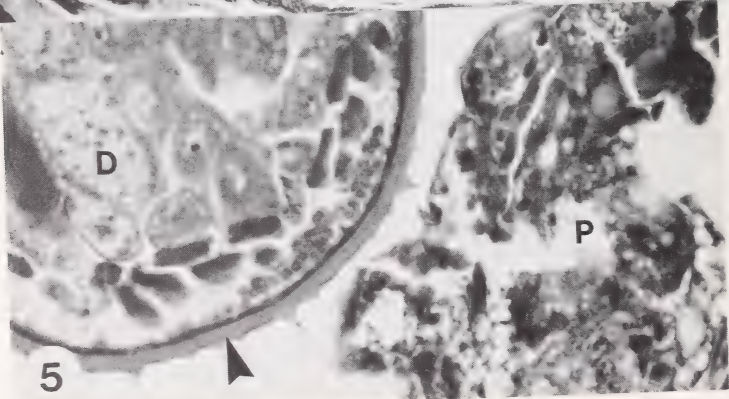
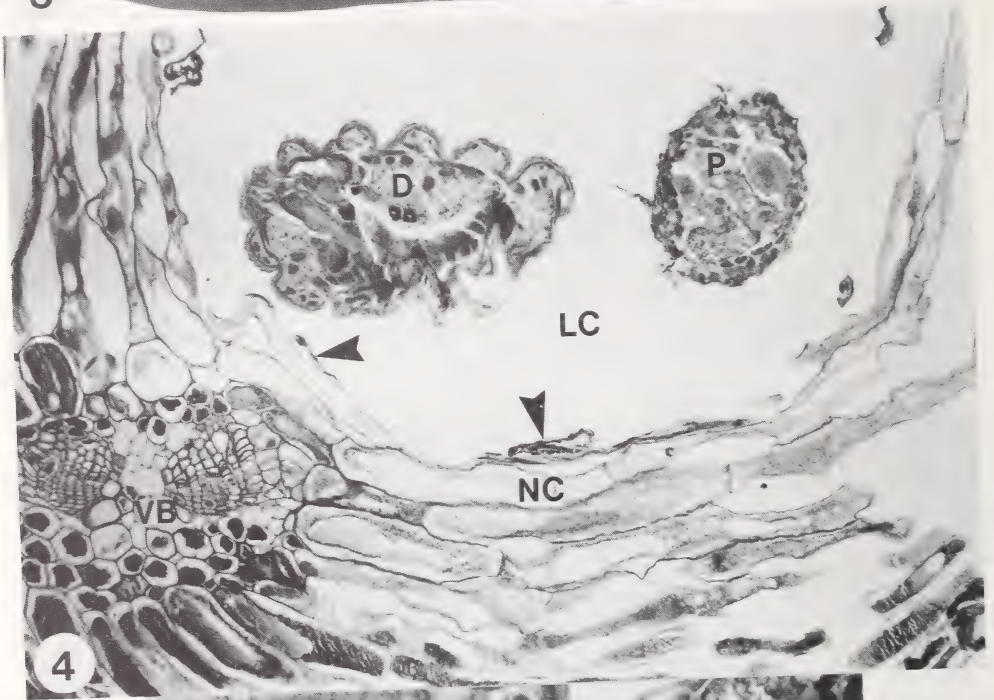
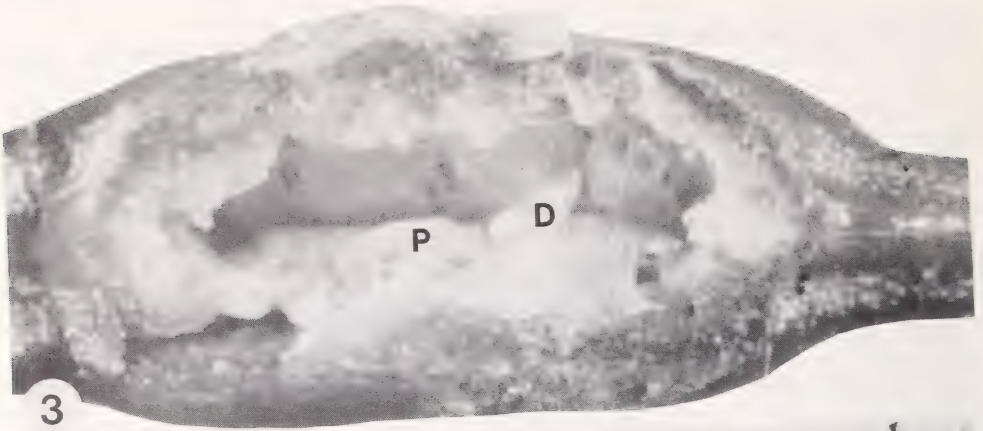


FIGURE 3. Gall occupied by second-instar larva of *Paradiplosis tumifex* (P) and *Dasineura balsamicola* (D), collected in mid-July. Mag. X27.

FIGURE 4. Section of gall near base of larval chamber (LC) occupied by second-instar larvae of *D. balsamicola* (D) and *P. tumifex* (P), collected in late July. Note the thin-walled nutritive cells (NC) and collapsed cells (arrows) caused by larval feeding. VB, vascular bundle. Mag. X100.

FIGURE 5. Section of third-instar larva, *in situ*, of *D. balsamicola* (D) along side second-instar larva of *P. tumifex* (P). Note the thick integument (arrow) and spinules of the larvae of *D. balsamicola*. Mag. X210.

early as July 14 with a sharp increase in mid-September. When the two larvae are viewed in cross section, the integument of the third-instar larva of *D. balsamicola* is clearly much thicker than that of *P. tumifex* (Fig. 5) and the spinules are evident. The thin and smooth-skinned *P. tumifex* is probably killed by the much larger *D. balsamicola* through abrasion by the latter's spines. The much thinner integument of *P. tumifex* (Fig. 5) would be punctured easily by the spines of *D. balsamicola* and by the middle of September all that remains of the *P. tumifex* larva is a black pellet (Fig. 6). We suggest that the larvae of *P. tumifex* die because there is not enough room within the larval chamber to fully mature and avoid contact with *D. balsamicola*.

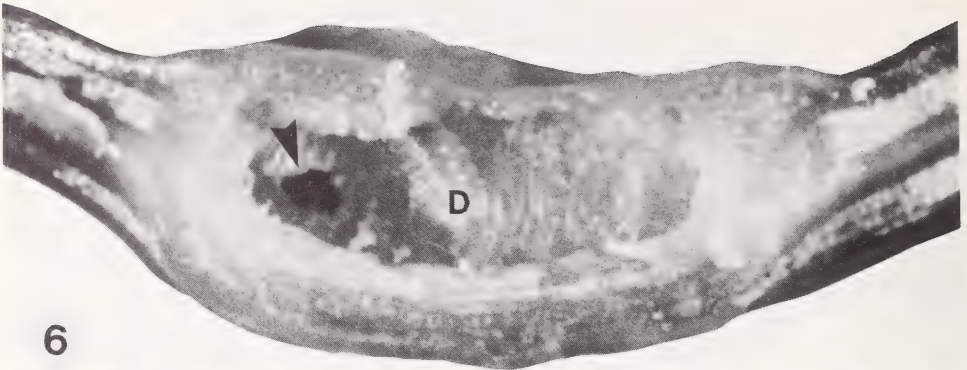
Larvae of *D. balsamicola* appear to have no effect on the development or structures of galls they inhabit (Figs. 4 and 7); however, galls with an active larva of *D. balsamicola* and a dead one of *P. tumifex* do not exhibit the starch gradient as seen in galls with only a larva of *P. tumifex*, implying that a live larva of *P. tumifex* must be present for this gradient to occur. The nutritive cells in galls with only a live larva of *D. balsamicola* (Fig. 7) appear similar to the nutritive cells in galls of similar age with a healthy larva of *P. tumifex*. (Fig. 2). We assume that larvae of *D. balsamicola* feed on *P. tumifex*-induced nutritive cells throughout their development.

Since immature larvae of *D. balsamicola* were always found within galls with a live first- or second-instar larva of *P. tumifex*, it appears certain that larvae of *D. balsamicola* are unable to induce galls of their own and are restricted to an inquiline habit within galls of *P. tumifex*. Larvae of *D. balsamicola* feed along side first- and second-instar larvae of *P. tumifex* and do not harm the inducer while it is immature. Only when the larva of *D. balsamicola* reaches the third instar does it kill the larva of the gall inducer.

Several workers have shown that development of immature and maturing galls ceases with the death of the gall-inducing larvae (Rohfritsch 1971; Bronner 1977) and we suggest that the gall of *P. tumifex* would cease growing and die if the gall inducer was killed at an early stage of gall morphogenesis. Thus, it is significant that the death of larvae of *P. tumifex* does not occur until the gall is mature and the gall inducer has reached the latter part of its second instar.

Thirty-eight percent of all the galls collected in 1978, 49% in 1979 and 50% in 1981 contained larvae of *D. balsamicola*. Clearly, this inquiline represents a major mortality factor and should be considered for release in any plantation where *P. tumifex* is the sole occupant of balsam fir needle galls. Introductions would not prevent gall formation in the year of release, but if established, might contribute to a drop in population levels of *P. tumifex* in later years.

The findings reported in this paper provide evidence, at the level of plant anatomy, of the intricacy of the relationships that exist between gall-inducing and inquiline midges. As Askew (1971) suggested for other inquilines, the life cycle of *D. balsamicola* is intimately associated with the life cycle of the gall inducer. Similar relationships undoubtedly exist between other gall inducers and inquilines and it will be fascinating to examine the tissues of their galls to determine whether or not the affects on gall structures are the same as *D. balsamicola* in galls of *P. tumifex* or are similar to the affects of cynipid inquilines.



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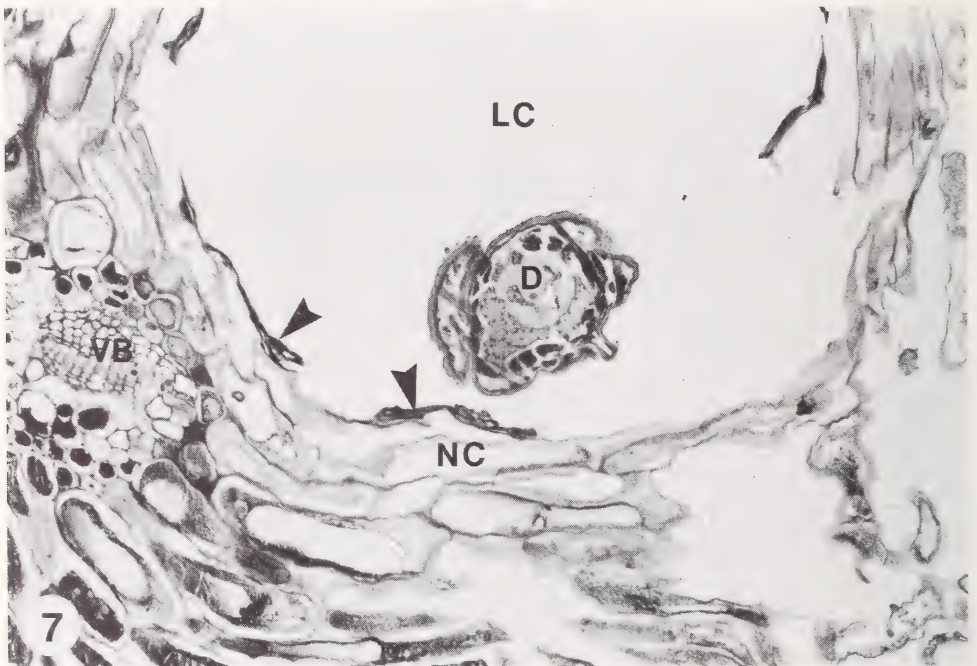


FIGURE 6. Gall occupied by an early third-instar larva of *Dasineura balsamicola* (D) and a dead larva of *Paradiplosis tumifex* (arrow), collected in early August. Mag. X26.

FIGURE 7. Section of gall near base of larval chamber (LC) occupied by a live third-instar larva of *D. balsamicola* (D) and dead larva of *P. tumifex*, collected in early September. Note the thin-walled nutritive cells (NC) and a few collapsed cells (arrows). VB, vascular bundle. Mag. X105.

Acknowledgments

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THE MADICOLOUS FAUNA IN SOUTHERN ONTARIO

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Abstract

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Madiculous habitats, created by thin sheets of water trickling over various substrates, support a characteristic fauna. More than 70 species of arthropods are recorded from madicolous sites in southern Ontario. Thirteen of these species are restricted to the madicolous habitat. One new Canadian record, *Ochrotrichia confusa* (Morton) (Hydroptilidae) and one new Ontario record, *Tipula (Pterelachisus) perparvula* Alexander (Tipulidae) are reported. The habitat and substrate preference of some species are discussed.

Introduction

The fauna living on rocks covered by a thin layer of water was termed *fauna hygropetrica* by Thienemann (1909). He listed approximately 24 characteristic insect species (euhygropetric), typical of localities in central Europe. Sampling a larger geographical area, Bertrand (1948) compiled a more extensive list of flora and insect fauna present in the hygropetric habitat.

Vaillant (1955) found that many species of insects were restricted to films of water on substrates other than rocks and thus considered Thienemann's definition to be too restrictive. Consequently, Vaillant (1955:4) designated the term madicolous (the Latin verb *madero*: to ooze, trickle) for fauna living in thin films of water 2 mm or less in thickness, flowing over various substrates (e.g., rock, mud, moss). He collected over 400 species in 74 madicolous sites, of which only 83 species were restricted to the madicolous habitat (eumadiculous).

The madicolous fauna of North America, especially of Chironomidae, has received little attention. Investigations have been restricted to taxonomic papers dealing with single species (e.g., Aldrich (1893): *Liancalus hydrophilus*, Needham (1908): *Limonia simulans*, Vaillant (1984): *Ochrotrichia confusa*, Huynh and Wallace (1984): *Madeophylax altus*), and there are no comprehensive ecological studies. Madicolous habitats are formed by roadcut seeps, spray zones of waterfalls and emergent rocks along edges of small streams and springs. The former two habitats are frequently encountered along the Niagara Escarpment in southern Ontario and support a rich, uniform, yet poorly known madicolous fauna. This paper is a first description of the fauna associated with madicolous habitats in southern Ontario.

Materials and Methods

A general survey of 40 madicolous sites in southern Ontario was conducted during the summer of 1985. Five of these sites, all in limestone regions, were sampled at three-week intervals from April 1985 to April 1986. Four sites were located along the Niagara Escarpment, and included a uniform temperature madicolous spring (9°C), a roadcut seep and two madicolous springs with fluctuating daily temperatures. The other limestone site, located at Kingston was a roadcut spring seepage with intermittent flow during the summer months.

The fauna was sampled by flushing organisms off the substrate with water, picking the larvae directly from the substrate by using forceps, or by sorting through filamentous algae and other debris from the madicolous face. To facilitate positive associations of larvae with adults and species determinations, live material was removed and transported in cool, moist petri dishes. The material was then reared using two methods in the laboratory. The first rearing system comprised a recirculating pump which trickled water over natural substrates (limestone). In the second method, each larva was placed into a separate

petri dish containing a thin layer of water, filamentous algae and leaves. Both systems were maintained at 10°C using a 16:8 L:D photoperiod.

The species in Table I were categorized into four groups according to the system of Vaillant (1955) for the European madicolous fauna, based on published habitat data, observations at the five sites studied in detail and comparisons with non-madiculous habitats (e.g., rheocrene springs and saturated mats of moss). Voucher specimens are housed in the Canadian National (C.N.C.) and University of Guelph collections.

All specimens were collected and preserved in 70% ethanol. Adult flies were dried in a critical point drier and mounted on points with water soluble glue. All three life stages of Chironomidae were mounted on slides following the methods of Oliver and Roussel (1983).

Results and Discussion

The madicolous fauna listed in Table I, was divided into the following four categories defined by Vaillant (1955:46). Eumadiculous organisms are restricted to the madicolous habitat and not found in any other biotope (Group A). The madicolous habitat is the only environment that the immature stages of a particular species can utilize. Tychomadiculous organisms are found in other habitats in addition to madicolous habitats and can be further divided into three groups. Species in Group B are most common in the madicolous habitat, but are able to survive in thicker films of water. Species in Group C spend only part of their life cycle (larval or pupal stage) in the madicolous habitat. They are infrequently collected in the madicolous habitat and are more commonly found in first or second order streams, among moss growing in brooks and in the psammon habitat. Species in Group D are visitors, or accidental occurrences and do not breed in madicolous habitats.

In Ontario, 13 eumadiculous species in 10 genera were found. These comprise mostly Diptera, but also includes a single hydroptilid species and the red water mite *Trichothyas musciola* which parasitizes *Limonia humidicola* (Tipulidae) (Mitchell 1953). The generic composition of Ontario and eastern North American sites is similar to that of the European madicolous fauna, however there is much lower diversity in North American localities. Vaillant (1955:82) found 83 eumadiculous species in 18 genera with many species of *Thaumalea* (Thaumaleidae), *Pericoma* (Psychodidae) and *Oxycera* (Stratiomyidae).

The most widespread and often collected eumadiculous species in southern Ontario include *Euparyphus* spp. (Stratiomyidae), *Limonia humidicola*, *L. simulans* (Tipulidae) and *Orthocladius* (*Eudactylocladius*) sp. (Chironomidae). Generally eumadicoules are direct air-breathers with their spiracles located dorsally on a dorsoventrally flattened body, and have reduced prehensile organs (Thienemann 1909; Bertrand 1948).

The microcrustaceans were not studied, however Vaillant (1955:49) found them to be largely stream associated species.

Some madicolous habitats; for example, roadcut and natural rock cliff seeps, in Ontario experience intermittent flow during the summer months. The typical fauna of these intermittent madicolous habitats include *Dactylocladius* spp. (Tipulidae), *Pseudokiefferiella* sp. and *Orthocladius* (*Eudactylocladius*) sp. (Chironomidae). They are cold-adapted organisms and are able to complete their development prior to summer drought (Hynes 1970). They probably survive until October as drought resistant eggs or as very small larvae remaining deep in cracks and under algae mats.

Some of the more common madicolous species are discussed below, with specific data for Ontario collections listed for new species records. Unless otherwise noted, collections listed below were made by the senior author.

Ochrotrichia confusa (Morton) (Trichoptera: Hydroptilidae): Ross (1944) reported this species to be present in Tennessee and New York. It is now believed to be common in the Appalachian Mountains (Vaillant 1984). *Ochrotrichia confusa* is a new Canadian record, restricted to a cool, wet dripping rock substrate.

Material examined: CANADA. **Ontario:** Ancaster/Tiffany Falls, madicolous spring beside

TABLE I. The madicolous fauna in southern Ontario. (Group A: Eumadicolous; Group B: Tychomadicolous 'madicoles preferentielles'; Group C: Tychomadicolous 'madicoles occasionnelles'; Group D: Tychomadicolous 'madicoles hotes' (Vaillant 1955)).

Species	Group	Species	Group
Turbellaria		Thaumaleidae	
Planarians	C	<i>Thaumalea americana</i> Bezzi	A
Hirudinea		Ceratopogonidae	
<i>Dina parva</i> Moore	D	<i>Atrichopogon</i> sp.	A
Malacostraca		<i>Dasyhelea</i> sp. Thomsen	B
<i>Gammarus pseudolimnaeus</i> Bousfield	C	Chironomidae	
Collembola		<i>Parochlus kiefferi</i> (Garrett)	C
<i>Tomocerus minor</i> (Lubbock)	D	<i>Diamesa nivoriunda</i> (Fitch)	C
Plecoptera		<i>Pseudokiefferiella</i> sp.	B
<i>Soyedina vallicularia</i> (Wu)	C	<i>Orthocladius</i> (<i>Eudactylocladius</i>) sp.	B
<i>Nemoura trispinosa</i> Claassen	C	<i>Metriocnemus</i> sp.	B
Hemiptera		<i>Parametrioctenemus lundbecki</i> (Johannsen)	C
<i>Microvelia americana</i> (Uhler)	C	<i>Paratrachocladus nitedellus</i> (Malloch)	C
<i>Saldula pallipes</i> (Fabricius)	C	<i>Eukiefferiella claripennis</i> (Lundbeck)	C
<i>S. saltatoria</i> (Linnaeus)	C	<i>Chaetocladus stamfordi</i> (Johannsen)	C
Trichoptera		<i>Limnophyes fumosus</i> (Johannsen)	C
<i>Ochrotrichia confusa</i> (Morton)	A	<i>Thienemanniella</i> sp.	C
<i>Lepidostoma sommermanae</i> Ross	C	<i>Tokunagaia</i> sp.	C
<i>Rhyacophila</i> sp. (<i>invaria</i> group)	C	<i>Hudsonimyia</i> sp.	B
<i>Neophylax aniqua</i> Ross	C	<i>Microspectra nigripila</i> (Johannsen)	C
<i>Pseudostenophylax sparsus</i> (Banks)	C	Stratiomyidae	
Coleoptera		<i>Euparyphus</i> (s.s.) <i>stigmatalis</i> Loew	A
Carabidae		<i>E. (Aochletus) brevicornis</i> Loew	A
<i>Bembidion</i> spp.	D	<i>Caloparyphus greylockensis</i> (Johnson)	B
<i>Agonum</i> sp.	D	<i>C. tetraspilus</i> (Loew)	C
Dytiscidae		<i>Odontomyia (Odontomyiina)</i> sp.	C
<i>Hydroporus pseudovilis</i> Young	C	Empididae	
Hydraenidae		<i>Clinocera lineata</i> Loew	B
<i>Hydraena angulicollis</i> Notman	C	<i>C. fuscipennis</i> Loew	B
<i>Ochthebius kaszabi</i> Janssens	C	<i>C. maculata</i> Loew	C
Hydrophilidae		<i>Clinocera</i> sp.	B
<i>Cymbiodyta blanchardi</i> Horn	B	Dolichopodidae	
<i>Laccobius spangleri</i> Malcolm	B	<i>Liancalus genualis</i> Loew	A
<i>Anacaena limbata</i> (Fabricius)	C	Muscidae	
Staphylinidae	D	<i>Lispoides aequifrons</i> (Stein)	C
Diptera		<i>Spilogona torreyae</i> (Johannsen)	C
Tipulidae		Tachinidae	
<i>Tipula (Pterelachisus) perparvula</i> Alex.	B	<i>Chaetostigmoptera angulicornis</i> (Curran)	parasitoid
<i>Limonia simulans</i> (Walker)	A	Ephydriidae <i>Scatella</i> sp.	C
<i>L. (Dicranomyia) humidicola</i> (O.S.)	A	Hymenoptera	
<i>L. (Dicranomyia) stulta</i> (O.S.)	B	Ichneumonidae	
<i>L. (Geranomyia) diversa</i> (O.S.)	B	<i>Phygadeuon</i> sp.	parasitoid
<i>L. (Geranomyia) canadensis</i> (Westw.)	B	Araneae	
<i>Dactylolabis hudsonica</i> Alex.	A	<i>Erigone atra</i> Blackwell	D
<i>D. montana</i> (O.S.)	A	<i>Eperigone tridentata</i> (Emerton)	D
<i>Pedicia</i> (s.s.) <i>albivitta</i> Walker	C	<i>Pirata</i> sp.	D
<i>Dicranota (Rhaphidolabis)</i> sp.	C	Acari	
Psychodidae		<i>Trichothyas (Lundbladia) musciola</i> (Mitchell)	A
<i>Pericoma slossonae</i> (Williston)	A	<i>Tyrrellia circularis</i> Koenike	B
<i>P. kincaidi</i> Quate	C	<i>Panisopsis (Marshallothyas) aspos</i> (Cook)	C
<i>Threticus bicolor</i> (Banks)	A	<i>Pergamasus septentrionalis</i> (Oudemans)	D
Dixidae		<i>Calyptostoma</i> sp.	D
<i>Dixa similis</i> Johannsen	B	Gastropoda	
		<i>Limnaea (Fossaria) obrussa</i> Say	C

falls, 1.viii.1985 (5 larvae); Dundas/Borer's Falls, madicolous spring behind falls, 1.viii.1985 (7 larvae); Dundas/Webster's Falls, madicolous spring next to falls, 17.vii., 13,17.viii., 30.ix and 12,31.x.1985 (4♀ collected on 13.viii.1985); Fergus/Templin Gardens, seepage, 28.ix., 6.x.1986, S.A. Marshall (20 larvae); Picton, Lake on the Mountain Prov. Pk., madicolous spring seepage, 7.x.1985 (17 larvae).

Cymbiodyta blanchardi Horn (Coleoptera: Hydrophilidae): Adults and larvae were most commonly found in the madicolous zone of springs, roadcut seeps, small streams and were often found on bare wet rocks or beneath mats of algae and moss. *Cymbiodyta blanchardi* was the most common hydrophilid beetle collected in southern Ontario madicolous sites.

Tipula (Pterelachisus) perparvula Alex. (Diptera: Tipulidae): This species was previously known only from Manitoba and its larval habitat was unknown (Alexander 1926). During this study, the larvae were collected from algal mats and thin layers of mud and debris at the edge of cascading springs and roadcut seeps.

Material examined: CANADA. **Ontario:** Ancaster-Hwy 403, roadcut seep, 29.v.1985 (larvae); Dundas/Rock Chapel Sanctuary, madicolous spring, 15,29.v.1985 (larvae), 12.v., 12.vi., 29.vii.1985, 7,29.vi.1986 (4♂,2♀); Hamilton/Jolly Cut, roadcut seepage, in moss, 14.vi.1985 (reared 1♀); Kingston-Hwy 401, roadcut seep, 3.v.1985 (larvae); Orangeville (Hockley Valley), limestone seep, 19.vi.1985 (larvae); Owen Sound/Inglis Falls Conc. A., roadcut seep, 18.vi.1986 (larvae); Warton-Hwy 6, roadcut seep, 6.v., 20.vii.1986 (larvae, pupae exuvia).

Dactylolabis hudsonica Alex. and *Dactylolabis montana* (O.S.) (Diptera: Tipulidae): The larvae of these species were collected on exposed wet rocks or in thin layers of mud in the madicolous zone of natural rock bluff and roadcut seepages. These two species were commonly found in localities with intermittent flow during the summer months.

Pericoma slossonae (Williston) (Diptera: Psychodidae): The larval habitat of this species was previously unknown. *Pericoma slossonae* was the most common psychodid found and the larvae preferred thin layers of mud and algae in the madicolous zone of 67 springs, small streams and roadcut seeps.

Pericoma kincaidi Quate (Diptera: Psychodidae): This is a first record of the larval habitat. The larvae of this species were found in mats of filamentous algae of cool springs and wet moss at the edge of waterfalls.

Threticus bicolor (Banks) (Diptera: Psychodidae): The larval habitat of *T. bicolor* was previously unknown. The larvae were infrequently collected in thin layers of mud and debris in madicolous springs.

Thaumalea americana Bezzi (Diptera: Thaumaleidae): In Ontario this species was found only along the Niagara Escarpment corridor, including outlying localities at Elora and Rockwood. Larvae of *T. americana* were found to be restricted to smooth bare, wet rocks of uniform temperature madicolous springs (9°C) and in seeps where summer daytime temperatures reach a high of 18 to 20°C and during the winter drops to 2 to 4°C. This relatively wide thermal tolerance has probably enabled this species to disperse widely even though the adults were found to be generally weak fliers. In contrast, European thaumaleids have narrower temperature tolerances and this strict requirement prevents dispersal across lowlands where cool, rocky springs are not present (Vaillant 1977). Their restriction to mountain springs and streams has resulted in many endemic species (Vaillant 1977).

Chironomidae (Diptera): *Metriocnemus* sp., *Orthocladius (Eudactylocladius)* sp., *Pseudokiefferiella* sp. and *Hudsonimyia* sp. are the characteristic chironomids of the madicolous habitat. The former three species appear to be cold-adapted and were infrequently collected during the summer at warm madicolous localities. The other chironomids listed in Table I are widespread, often occurring in first or second order streams.

Euparyphus (Euparyphus) stigmatalis Loew (Diptera: Stratiomyidae): This is the first record of the larval habitat of this species. The larvae were found to be widespread in Ontario and a common element of the madicolous habitat. They are found on bare wet rocks and in filamentous algae (Chlorophyta: *Cladophora*).

Euparyphus (Aochletus) brevicornis Loew (Diptera: Stratiomyidae): This species was found to be very common and widespread in Ontario madicolous habitats, especially roadcut seeps. An ichneumonid parasitoid, *Phygadeuon* sp. was reared from a pupa of *E. brevicornis*. Adults of *Phygadeuon* can be found in large numbers crawling on the madicolous surface where these stratiomyid larvae are common. Bertrand (1948) reared an unidentified species of *Phygadeuon* from the pupae of two species of *Oxycera*, a genus of European stratiomyid eumadicoles closely related to *Euparyphus*.

Caloparyphus greyllockensis (Johnson) (Diptera: Stratiomyidae): Larvae of this species were collected with *Euparyphus* spp. in the madicolous zone of cascading spring streams and spring seeps near waterfalls and in rocky ravines. Larvae of *C. greyllockensis* have also been reported 'in the water in overhanging vegetation growing on the margin of a brook' (Johannsen 1922). Although preferring the madicolous habitat, larvae were also collected in mats of saturated moss, a non-madicolous habitat and therefore *C. greyllockensis* was classified as a tychomadicole-Group B.

Clinocera spp. (Diptera: Empididae): Adults of *Clinocera* spp. were collected throughout the year. During the winter months adult flies were found in association with larvae of *Thaumalea americana* and nymphs of *Soyedina vallicularia*, on the underside of wet rocks. One adult of *Clinocera* was observed feeding on a larva of a thumaleid.

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THE TERRESTRIAL, SAPROPHAGOUS DIPTERA OF AN ONTARIO BOG, WITH SPECIAL REFERENCE TO SMALL DUNG FLIES (SPHAEROCERIDAE)

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Abstract

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Fungivorous and coprophagous Diptera were sampled using baited (mushroom and moose dung) pitfall traps in a Sphagnum bog in Algonquin Provincial Park during the summer of 1984. The specimens collected are enumerated, discussed and compared with specimens collected during concurrent sampling in adjacent deciduous forest. Sphaeroceridae were the most diverse and abundant saprophagous Brachycera in the bog. Eleven species of sphaerocerids were collected including four apparently bog-restricted species – *Pullimosina dahl* (Duda), *Pullimosina geminata* Marshall, *Spelobia acadensis* Marshall and *Spelobia pappi* Roháček.

Introduction

Detailed vegetational, ornithological and even mammalian species lists have been compiled for bogs (Larsen 1982). However, few studies have involved the insect inhabitants of bogs, which is surprising considering that peatlands cover at least 12 to 14% of Canada (Zoltai and Pollet 1983). A notable few have included those involving pselaphid (Reichle 1966) and carabid beetles (Lindroth 1969). Insect studies by Judd (1958, 1960) in Byron Bog in southwestern Ontario most closely approximate this study; however, Judd's work was rather general and failed to identify a characteristic bog insect community.

The purpose of this study was to accumulate baseline information on the terrestrial, saprophagous dipteran fauna of an Ontario bog and to make comparisons with the fauna of similar substrates in nearby deciduous forest. We selected this faunal group because it can be efficiently sampled throughout the season using baited pitfall traps. Within this fauna, Sphaeroceridae comprise the most diverse and abundant element in the bog, and our analysis is primarily restricted to this group of flies.

The Habitats

The bog. The bog which we studied (hereafter referred to as Billy Lake Bog) is situated in Ontario's Algonquin Provincial Park, 0.5 km south of Billy Lake. The bog lies approximately at 45° 37' N, 78° 8' W. This small (400 m x 90 m) bog is based on a thick layer of Sphagnum. The remaining vegetation consists primarily of a dense covering of Leatherleaf (*Chamaedaphne calyculata* [L.] Moench), several widely separated Black Spruce trees (*Picea mariana* [Mill]), and clumps of Labrador Tea (*Ledum groenlandicum* Oeder) and similar shrubs 1/2 to 1 m high. According to the classification systems of Stanek (1973) and Larsen (1982), the bog is ombrotrophic, i.e., water near its surface most of the season, nutrient-poor and highly acidic (pH 3.2 to 3.7).

The forest. The deciduous forest site selected for this study lies approximately at co-ordinate points 45° 40' N, 78° 8' W. This mixed-hardwood forest is typical of the deciduous forest found near Billy Lake Bog and is dominated by White Birch (*Betula papyrifera* Marsh), Poplar (*Populus* spp.), and Sugar Maple (*Acer saccharum* Marsh).

Materials and Methods

Four pitfall traps baited with moose dung were set continuously in Billy Lake bog from May until August 1984. Three pitfall traps baited with mushrooms were also set in the bog from June until August 1984. Equal numbers of similar pitfall traps, using the same baits, were set concurrently in the nearby deciduous forest. The pitfall traps consisted of 9 cm

wide x 11 cm deep white plastic tubs sunk into the Sphagnum (bog) or soil (forest). Mushroom stems (*Agaricus bisporus* [Lange]) or moose dung were wrapped in cheesecloth and suspended over the traps as bait. These baits were changed periodically throughout the season. Salt, water and soap made up the trap fluid. The traps were emptied weekly. Insects were collected into alcohol and later sorted to order. All flies were dried using a critical point drier. The Sphaeroceridae were identified to species; other flies to family or genus. All specimens were retained in the University of Guelph collection with the exception of one individual of an undescribed *Campsicnemus* sp. (Dolichopodidae) and one individual of *Leptomorphus nebulosus* (Walker) (Mycetophilidae), which are retained in the Biosystematics Research Institute, Ottawa, Canada.

Results and Discussion

Sphaeroceridae. A summary of the results from the collection of sphaerocerids made during this study is provided in Table I. Of the eleven species collected in the bog, seven are known from various habitats (published and unpublished records in the junior author's collection). Most of these species were collected during this study in deciduous forest or both habitats (see Table I). *Opalimosina mirabilis* (Collin), despite its abundance in our bog samples, is a common synanthropic species and not a bog-restricted species (Roháček 1983, and numerous unpublished records). The remaining four species were identified as bog-restricted sphaerocerids (see Table II).

TABLE I: Numbers of Sphaeroceridae collected during 1984 in Billy Lake Bog and a nearby deciduous forest using baited (moose dung and mushroom) pitfall traps

Species	Bog		Forest		Totals	
	Moose Dung	Mushroom	Moose Dung	Mushroom	Bog	Forest
<i>Apteromyia claviventris</i> (Strobl)	0	0	0	1	0	1
<i>Coproica</i> spp.	1	6	0	1	7	1
<i>Halidayina spinipennis</i> (Haliday)	0	0	2	0	0	2
<i>Ischiolepta</i> sp.	1	0	0	0	1	0
<i>Leptocera</i> spp.	2	6	0	4	8	4
<i>Minilimosina gemella</i> Roháček	0	0	8	0	0	8
<i>M. lepida</i> Marshall	0	0	3	0	0	3
<i>M. parva</i> (Malloch)	0	0	5	0	0	5
<i>M. parvula</i> (Stenhammer)	0	0	3	1	0	4
<i>M. vixa</i> Marshall	0	0	2	0	0	2
<i>Nearcticorpus canadense</i> Roháček and Marshall	0	0	0	1	0	1
<i>Opalimosina mirabilis</i> (Collin)	2	7	0	0	9	0
<i>Pullimosina dahli</i> (Duda)	3	16	0	0	19	0
<i>P. geminata</i> Marshall	0	1	0	0	1	0
<i>P. longicosta</i> (Spuler)	1	0	2	0	1	2
<i>Spelobia acadensis</i> Marshall	3	1	0	0	4	0
<i>S. brevipteryx</i> Marshall	0	0	1	2	0	3
<i>S. clunipes</i> (Meigen)	0	0	4	1	0	5
<i>S. luteilabris</i> (Rondani)	0	0	2	6	0	8
<i>S. maculipennis</i> (Spuler)	2	0	0	0	2	0
<i>S. pappi</i> Roháček	3	0	0	0	3	0
<i>S. quinata</i> Marshall	0	0	0	1	0	1
<i>Trachyopella nuda</i> Roháček and Marshall	1	0	0	0	1	0

TABLE II: Bog-restricted Sphaeroceridae collected during 1984 in Billy Lake Bog using baited (moose dung and mushroom) pitfall traps

Species	Number/Bait	Biology and Distribution	Reference
<i>Pullimosina dahli</i> (Duda)	3 - moose dung 16 - mushroom	Found in Czechoslovakian alpine bogs; Found in several bogs in Ontario and Nova Scotia, and throughout Yukon and Alaska.	Roháček 1983 Marshall 1986
<i>Pullimosina geminata</i> Marshall	1 - mushroom	To date, found only in Ontario: Billy Lake Bog in Algonquin Provincial Park.	Marshall 1986
<i>Spelobia acadensis</i> Marshall	3 - moose dung 1 - mushroom	Rare, found only in Canadian bogs. New Brunswick: Gibson Lake boggy area. Ontario: Alfred, Alfred Bog; Billy Lake Bog, Algonquin Provincial Park.	Marshall 1985
<i>Spelobia pappi</i> Roháček	3 - moose dung	Rare, Holarctic, bogs only, found in European peat-bogs (Czechoslovakia and Germany) and in Ontario: Mer Bleue Bog, Ottawa; Billy Lake bog, Algonquin Provincial Park.	Marshall 1985

Other Diptera. The number of flies (Brachycera only) collected, per family, is shown for both habitats in Table III. The relatively high numbers of individuals and species collected in the forest probably reflects the relative nutrient richness of the forest when compared to the nutrient-poor bog (436 flies collected in the forest versus 138 in the bog). The previously discussed sphaerocerids were the most abundant family of flies in the bog, whereas phorids (almost solely of the genus *Megaselia*) dominated the forest collections.

Of the Nematocera collected, Chironomidae were the most abundant in the bog; Mycetophilidae and Sciaridae were the most numerous in the forest.

Summary

Although less diverse than in nearby woodland habitats, the terrestrial, saprophagous, dipteran community of an Algonquin Provincial Park bog contains a distinctive assemblage of species. With the possible exception of the Chironomidae, which were not studied below the family level, the Sphaeroceridae are the most diverse and abundant members of this community. Three of the eleven sphaerocerid species collected in the bog are known from other bogs but from no other habitat, and one *Pullimosina* species is known only from the Billy Lake bog.

We conclude that Canadian bogs do contain a unique, very poorly known, terrestrial insect fauna which certainly merits further study.

Acknowledgements

We thank Kevin Barber for his unlimited support and assistance; Dr. J.R. Vockeroth for the identification of some species; and Terri Myhr for her help collecting specimens.

TABLE III: Numbers of higher Diptera (Brachycera) collected during May to August, 1984, in baited (moose dung and mushroom) pitfall traps

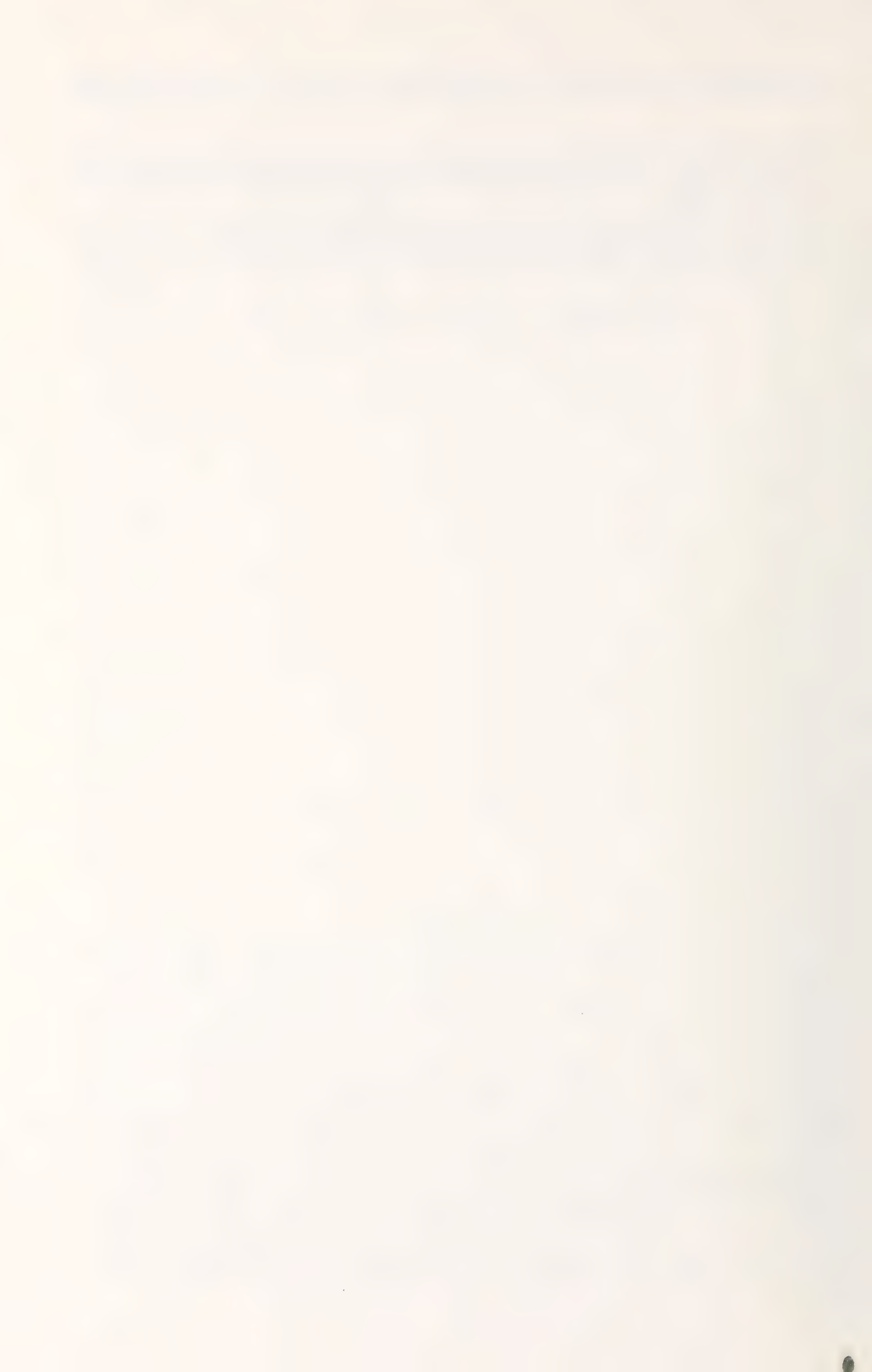
Taxon	Bog			Forest		
	moose dung	mushroom	total	moose dung	mushroom	total
Bombyliidae	1	0	1	0	0	0
Empididae	3	0	3	2	1	3
Dolichopodidae	1	0	1	2	0	2
Phoridae	16	2	18	175	41	216
Syrphidae	0	0	0	1	0	1
Psilidae	0	0	0	1	0	1
Lonchaeidae	0	0	0	1	1	2
Acartophthalmidae	1	0	1	2	1	3
Carnidae	1	3	4	0	0	0
Sciomyzidae	0	0	0	1	0	1
Sepsidae	2	5	7	0	0	0
Lauxaniidae	0	0	0	4	7	11
Heleomyzidae	0	0	0	1	6	7
Sphaeroceridae	19	37	56	32	18	50
Drosophilidae	2	8	10	19	38	57
Diastatidae	14	1	15	0	0	0
Ephydriidae	1	1	2	0	0	0
Chloropidae	3	0	3	7	6	13
Scathophagidae	0	1	1	1	2	3
Anthomyiidae	2	0	2	5	8	13
Muscidae	1	1	2	14	29	43
Calliphoridae	0	1	1	1	0	1
Sarcophagidae	0	7	7	2	0	2
Tachinidae	2	2	4	1	6	7
TOTALS	69	69	138	272	164	436

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PARASITES OF THE ALFALFA BLOTCH LEAFMINER, *AGROMYZA FRONTELLA* (DIPTERA: AGROMYZIDAE), NEAR GUELPH, ONTARIO

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Abstract*Proc. ent. Soc. Ont.* 117:21-27 (1986)

Five species of parasites, *Diglyphus begini* (Ashmead), *D. intermedius* (Girault), *D. isaea* (Walker), *D. pulchripes* (Crawford), and *Pnigatio maculipes* (Crawford), were reared from maggots of the alfalfa blotch leafminer (ABL), *Agromyza frontella* (Rondani). Two additional parasitic species, *Cyrtogaster vulgaris* Walker and *Chrysocharis giraulti* Yoshimoto, were reared from puparia of the ABL. Two of the seven species, *D. isaea* and *C. vulgaris*, are exotic and constitute a new distribution and new host and distribution records, respectively. During a two-year study (ie. 6 generations of the ABL) this complex parasitized an average of only 3.4% of the ABL, caused, in part, by poor synchrony between the parasites and the host. Parasites emerged later than the ABL in the spring and, as a result, only the second and third generations were parasitized. *D. intermedius* was the most abundant larval parasite and *Diglyphus* spp. accounted for >75% of the parasites reared from ABL maggots. All but one specimen of the pupal parasites were *C. vulgaris* which parasitized less than 1% of the puparia with a maximum rate of parasitism (3.3%) in the third generation.

Introduction

The alfalfa blotch leafminer (ABL), *Agromyza frontella* (Rondani) (Diptera: Agromyzidae), is a pest of European origin which was first recorded in the United States in 1968 (Miller and Jensen 1970) and in Canada in 1972 (Harcourt 1973). Twenty species of indigenous parasites (Hymenoptera: Chalcidoidea) have been reared from the ABL in the northeastern U.S.A. (Hendrickson and Barth 1979a; Plummer and Byers 1981), four in Prince Edward Island (Thompson 1981) and four in eastern Ontario and Quebec (Harcourt and Guppy 1977; Guppy *et al.* 1984). Indigenous species parasitized an average of 36% of the ABL in the U.S.A. (Hendrickson and Barth 1979a) and up to 13% in eastern Ontario (Harcourt and Guppy 1977). Because parasitism by these indigenous species did not provide adequate control of the ABL in North America (Hendrickson and Barth 1979a; Guppy *et al.* 1984), importation of European parasites was begun in 1974 (Hendrickson and Barth 1979b). By 1978 three parasites, *Dacnusa dryas* (Nixon) (Hymenoptera: Braconidae), *Chrysocharis punctifacies* Delucchi (Hymenoptera: Eulophidae), and *Miscogaster hortensis* Walker (Hymenoptera: Pteromalidae), were established in Delaware (Hendrickson and Plummer 1983), and *D. dryas* is now established in eastern Ontario, Quebec and the Maritime provinces (Guppy *et al.* 1984). In areas where these exotic parasites are established, populations of the ABL have been reduced below suggested economic thresholds (Hendrickson and Plummer 1983).

The ABL has been spreading southwestward in Ontario, and in 1981 most counties producing alfalfa in southwestern Ontario were infested (Bereza 1981). Nevertheless, because of its more recent date of establishment, biological control of this pest has not been studied west of Belleville, Ontario. The level of parasitism of the ABL by parasites already found in southwestern Ontario should be evaluated before exotic species are released in order to assess the added impact of exotic species at a later date. This paper reports the percent parasitism of maggots and puparia of the ABL by parasites near Guelph (43°35'N, 80°20'W), Ontario.

Materials and Methods*Study Area*

The ABL and its parasites were sampled from three alfalfa fields near Guelph in 1983 and 1984. The square study area in each field was divided into four 324 m² plots. Sampling

for each generation of the ABL was completed before the plots were harvested (after sampling for puparia in 2 fields and after sampling for maggots in one field); after harvesting, plots were re-established on regrowth elsewhere in the field.

Parasite Populations

Two methods were used to determine parasitism of ABL maggots: 1) parasites were reared from individual maggots; 2) parasites were dissected from ABL mines. All the mined leaflets from five alfalfa stems collected randomly from each plot two or three times per generation of the ABL beginning the second week of June were used to rear parasites from individual maggots. Stems were cut below the lowest leaflets, placed in plastic bags, and transported to the laboratory in coolers. Samples were kept at 6°C for a maximum of 5 h after which leaflets were then placed in rearing chambers similar to those of Quiring and McNeil (1984).

ABL mines from three alfalfa stems collected randomly from each plot two or three times per generation of the ABL were dissected to estimate parasitism. A maximum of five maggots of each of the three instars was removed from each of the three stems in the four plots (maximum 180). Because 60 maggots of each instar were never present, the actual sample size ranged from 72 to 161 maggots. The mines were opened with insect pins under a stereomicroscope and numbers of eggs, larvae, and pupae of parasites found on the maggot or in the mine were recorded.

Parasitism of the puparia was estimated from puparia which were collected once per generation from four or six, 16 by 16 by 5 cm deep soil samples taken randomly in each of the four plots in 1983, and from two to four samples per plot in 1984. The soil was washed through U.S. Standard Nos. 10 and 40 mesh sieves and the residue was rinsed to collect floating puparia. Whole and apparently undamaged puparia were transferred to plastic petri dishes containing moist filter paper and were kept at $22.2 \pm 0.9^\circ\text{C}$, $74.8 \pm 7.6\%$ RH, and 14L:10D photoperiod to observe the numbers of parasites that emerged.

Two methods were used to identify adults of parasites that could potentially parasitize the ABL: 1) parasites were reared from maggots on whole stems of alfalfa; 2) parasites were collected in sweep nets. Twelve alfalfa stems that had maggot-infested leaflets were taken randomly from each plot one or two times per generation of the ABL and were placed in a 11 by 13 cm plastic container with 6 cm of moist vermiculite. These containers were then placed in a 47 by 43 by 32 cm wooden cage covered with fine Decosheer® and were kept at $22.2 \pm 0.9^\circ\text{C}$, $74.8 \pm 7.6\%$ RH, and 14L:10D photoperiod until parasites emerged. From this technique we could not determine the host of the parasite therefore we used known host associations to determine if the ABL was a potential host. Although no substrate was provided to facilitate pupation of the maggots, maggots pupated in the bottom of the cage; thus it was possible to rear both larval and larval/pupal parasites.

In the second method to identify potential parasites of the ABL, adult parasites were also obtained from 50 sweeps taken once per week adjacent to each plot beginning the first week of May. Only Eulophidae and Pteromalidae (Hymenoptera: Chalcidoidea) were identified from these samples because all previously reported indigenous parasites of the ABL belong to these groups (Harcourt and Guppy 1977; Hendrickson and Barth 1979a). All parasites were identified by the senior author and identifications of representative specimens were confirmed by Dr. C.M. Yoshimoto, Biosystematics Research Institute, Agriculture Canada, Ottawa, Ontario.

ABL Populations

Adults of the ABL were collected in the same sweeps as the parasites so that synchrony of the parasites with the host could be determined. The adults of the ABL were counted in the laboratory or estimated volumetrically when there were more than 1000 flies per sample.

Results and Discussion

Twenty-four species of Eulophidae and Pteromalidae were identified from the various

Table I. Species and numbers of parasites (Hymenoptera: Chalcidoidea) reared from maggots and puparia of *A. frontella*, reared from maggots on whole stems of alfalfa, and collected in sweep nets near Guelph, Ontario, 1983 and 1984.

Species	Numbers of Parasites		
	From 7972 maggots and 7851 puparia	From 528 alfalfa stems	From 1700 sweeps in alfalfa
EULOPHIDAE			
<i>Aprostocetus cincinnatus</i> (Girault)	0	0	1
<i>Chrysocharis giraulti</i> Yoshimoto ^a	1	0	0
<i>Closterocerus cinctipennis</i> Ashmead	0	0	3
<i>Closterocerus tricinctus</i> (Ashmead)	0	3	1
<i>Diaulinopsis albiscapus</i> (Girault)	0	0	1
<i>Diaulinopsis callichroma</i> Crawford	0	1	21
<i>Diglyphus begini</i> (Ashmead) ^b	0	0	6
<i>Diglyphus intermedius</i> (Girault) ^a	8	85	78
<i>Diglyphus isaea</i> (Walker) ^b	0	1	0
<i>Diglyphus pulchripes</i> (Crawford) ^a	1	13	21
<i>Necremnus</i> sp.	0	0	1
<i>Notanisomorpha ainsliei</i> Crawford	0	1	0
<i>Pnigalio maculipes</i> (Crawford) ^a	3	8	0
<i>Pnigalio uroplatae</i> (Howard)	0	0	1
<i>Sympiesis ancylae</i> Girault	0	0	1
<i>Sympiesis conica</i> (Provancher)	0	2	0
<i>Sympiesis enargiae</i> Miller	0	0	1
<i>Sympiesis viridula</i> (Thomson)	0	0	1
<i>Sympiesis</i> sp.	0	0	1
<i>Tetrastichus centricolae</i> (Ashmead)	0	0	1
<i>Tetrastichus</i> poss. n. sp.	0	0	10
TOTALS	13	114	149
PTEROMALIDAE			
<i>Asaphes vulgaris</i> Walker	0	1	1
<i>Cyrtogaster vulgaris</i> Walker ^a	27	0	109
<i>Eunotus</i> sp.	0	0	1
TOTALS	27	1	111

^a Species were reared from maggots or puparia of *A. frontella*.

^b Species were not reared from field-collected maggots but were found to be contaminant species while establishing a colony of *D. intermedius* in the laboratory.

sampling methods (Table I). Of these, five species, *Chrysocharis giraulti* Yoshimoto, *Diglyphus intermedius* (Girault), *D. pulchripes* (Crawford), *Pnigalio maculipes* (Crawford), and *Cyrtogaster vulgaris* Walker, were reared from field-collected maggots or puparia of the ABL. Two additional species, *D. begini* (Ashmead) and *D. isaea* (Walker), were not reared from field collected maggots but were found to be contaminant species while establishing a colony of *D. intermedius* in the laboratory (for rearing methods, see Coote and Ellis 1986).

Among the species collected from sweep net samples or reared from maggots on whole stems of alfalfa, were 10 previously recorded parasites of the ABL, including six of the seven species listed above, as well as *Closterocerus cinctipennis* Ashmead, *C. tricinctus* (Ashmead), *Diaulimopsis callichroma* Crawford and *Notanisomorpha ainsliei* Crawford. The complex of seven species reared from the ABL in this study was less than half that found by Hendrickson and Barth (1979a) but included four species not reported by them.

Two of the seven species, *D. isaea* and *C. vulgaris*, are exotic species. *D. isaea* was released into the northeastern U.S.A. in 1975 and 1976 to control the ABL but releases were terminated when the species was found to interbreed with the indigenous parasite, *D. intermedius* (Hendrickson and Barth 1979b). This collection of *D. isaea* in Ontario constitutes a new distribution record. The second exotic species, *C. vulgaris*, was released in British Columbia in the 1930s to control the holly leafminer, *Phytomyza ilicis* Curt. (Cameron 1939). Rearing of *C. vulgaris* from the ABL in Ontario constitutes a new host and a new distribution record.

The average percentage of leaflets infested by maggots of the ABL over the three generations in 1984 was 17.2% (range 4.5 to 31.6%, n = 20,274) in one field and 15.4% (range 1.4 to 30.2%, n = 20,952) in another (Fig. 1). Because of high mortality of maggots reared in leaflets, the seasonal percent parasitism was based on dissection of mines and was 4.8% (range 0 to 21.3%, n = 898 mines) in one field and 3.9% (range 0 to 20.6%, n = 582 mines) in the other. In comparison, the complex in the northeastern U.S.A. parasitized an average of 36% of the ABL from 1975 to 1977 (Hendrickson and Barth 1979a). The probable reason for this difference is that the indigenous parasites in the northeastern U.S.A. had more time to adapt to the ABL at the time of the study by Hendrickson and Barth (1979a) than did the parasites near Guelph. Seasonal levels of parasitism in Ontario will probably not reach levels found in the U.S.A. because the 1st generation is not parasitized in Ontario (Fig. 1) and there are three generations in Ontario as compared to five in most of the eastern U.S.A.

Diglyphus spp., primarily *D. intermedius*, accounted for >75% of the parasites reared from maggots of the ABL (including *D. begini* and *D. isaea*) and 88% of the parasites reared from maggots on infested stems. Adults of *Diglyphus* spp. were present at Guelph in low numbers or were undetected (Fig. 2B) until after the 2nd generation of the ABL had begun (Fig. 2A). Hendrickson (1979) showed that the complex of indigenous parasites attacking the ABL was derived from the parasites attacking the indigenous serpentine leafminer, *Liriomyza trifoliarum* Spencer, and Hendrickson and Barth (1979a) reported that indigenous parasites of the ABL in the northeastern U.S.A. emerged two to three weeks too late to control the 1st generation of the ABL. Low numbers of *L. trifoliarum* (n = 19 mines) and poor synchronization between *Diglyphus* spp. and the ABL could possibly explain low parasitism of ABL maggots near Guelph.

Less than 1% of the puparia (28 of 7851) of the ABL were parasitized in 1983 and 1984 by *Cyrtogaster vulgaris* and only one specimen was parasitized by *Chrysocharis giraulti*. There were too few *C. vulgaris* in June (<5 per 50 sweeps) to be effective against the 1st generation of the ABL (Fig. 2C) even though maximums of 56 and 33 adults of *C. vulgaris* were collected per 50 sweeps, in fields 1 and 2, respectively, late in the 2nd generation of the ABL (Fig. 2C), suggesting that parasitism should be higher in the 2nd and 3rd generations than was observed. However, because *C. vulgaris* is strictly a pupal parasite (Cameron 1939; Simmonds 1952) and the ABL usually pupates in the soil, only the few puparia formed on leaves and on the soil surface were potential hosts, which could explain why overall parasitism was low.

Rates of parasitism by parasites near Guelph are not likely to maintain the ABL below economic levels, therefore exotic parasites now established in the U.S.A. and parts of eastern Canada should be released in areas of Ontario where the pest is found. *Dacnusa dryas* is a good candidate because it is well established in eastern Ontario and is an endoparasite of the maggots and emerges from the puparia (Hendrickson and Barth 1979b), a "niche" that is currently underutilized.

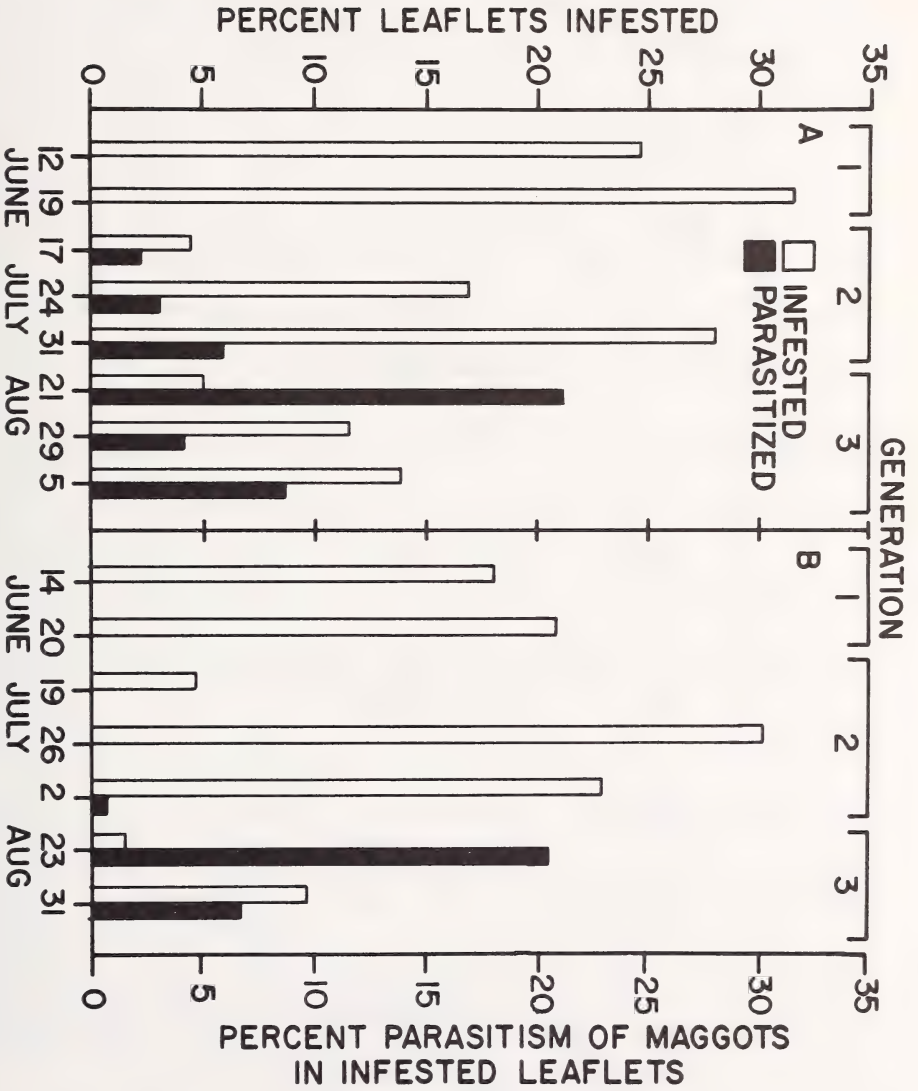


FIGURE 1. Percent alfalfa leaflets infested with maggots of *Agromyza frontella* and percent parasitism of these maggots near Guelph, Ontario, 1984; A, field 1; B, field 2.

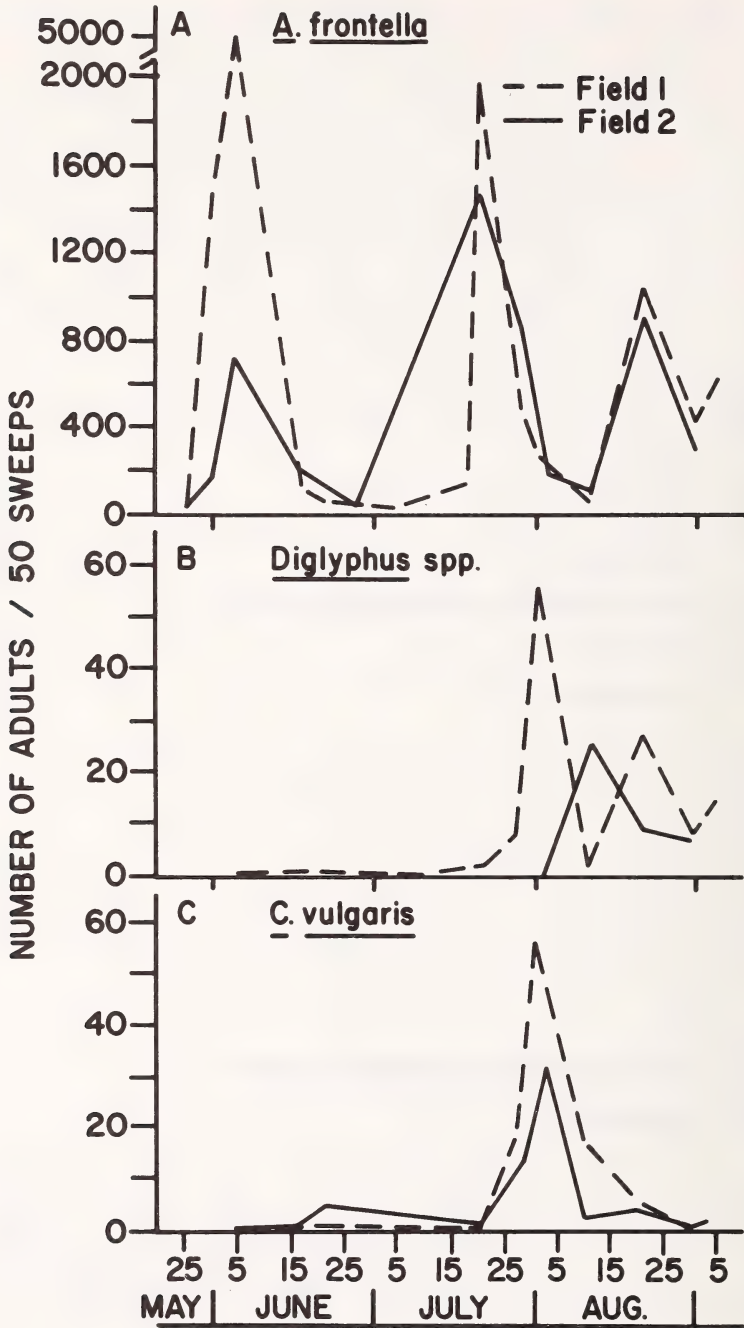


FIGURE 2. Numbers of adults collected in alfalfa fields near Guelph, Ontario, 1984; A, *Agromyza frontella*; B, *Diglyphus* spp.; C, *Cyrtogaster vulgaris*.

Acknowledgments

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**ESTABLISHMENT AND SPREAD OF *DACNUSA DRYAS*
(HYMENOPTERA: BRACONIDAE), AN EXOTIC PARASITE OF THE
ALFALFA BLOTCH LEAFMINER IN ONTARIO¹**

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Abstract

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Dacnusa dryas (Nixon), a European larval-pupal endoparasite of the alfalfa blotch leafminer, *Agromyza frontella* (Rond.), has become established in most counties of southern Ontario. A detailed survey in 1985 showed that it was well established throughout the eastern region of the province and, in the southwestern region, was spreading north and west from the Niagara area. Rates of attack in several counties where it was first released varied from 65 to 95%, averaging 84%. Dispersal in Ontario has been the result of recolonization from nursery plots and natural spread from release sites.

Introduction

Since its invasion of eastern Ontario in the mid 1970s, populations of the alfalfa blotch leafminer (ABL), *Agromyza frontella* (Rond.), have undergone two distinct phases of population behaviour. During its colonization phase, populations of the pest in the Ottawa Valley increased rapidly for three or four years and then declined gradually to near tolerable levels because of mortality from intraspecific competition and the attack of indigenous non-specific predators (Harcourt *et al.* 1987). This pattern of events was later repeated in the Bay of Quinte area, and beyond, as populations spread westward across the province in a succession of wave-like oscillations (Harcourt and Guppy 1982, 1983). A gradation to still lower levels began in 1982. This coincided with the successful colonization of the parasite *Dacnusa dryas* (Nixon) (Hymenoptera: Braconidae) throughout eastern Ontario. First released at Ottawa in 1979, this agent of European origin has quickly become a key mortality factor of the ABL and has played an important role in reducing populations to below economic levels (Harcourt and Guppy 1985). A noticeable decline in host survival was recorded throughout the Ottawa Valley in 1982 and in the Bay of Quinte area, two years later.

Dacnusa dryas has three generations a year and is well synchronized with its host (Meloche and Guppy personal communication). Spring emergence of the parasite occurs about a week after that of the ABL, and the females deposit their eggs singly in late first-, second-, or early third-instar miners. The parasite develops through its first instar in the feeding larva and through its second and third in the fully-fed host following its evacuation of the mine. It passes the winter as a mature larva within the puparium of the cadaver. *Dacnusa dryas* was initially recovered in the year of release at Ottawa (Guppy *et al.* 1984). Following propagation in nursery plots at the Central Experimental Farm, Agriculture Canada, Ottawa, specimens were released, or shipped to cooperators for release, in 1981 and 1982 at one or more sites in the southern Ontario counties of Grenville, Dundas, Hastings, Renfrew, Norfolk, and Haldimand. In the same two years, it was also collected

¹ Contribution from the Ottawa Research Station (No. 823) and the University of Guelph.

from nursery plots in central New York and redistributed at single sites in Elgin, Lincoln, York and Halton counties (Williamson 1984, 1985). However, prior to 1985, it had not been recovered west of Hastings county in the Bay of Quinte area. For this reason, a survey was carried out in 1985 to determine the extent of its current distribution in Ontario.

Materials and Methods

During the spring of 1985, sweep-net samples were taken from leafminer-infested fields of alfalfa in each county of southern Ontario. Keyed to adult flight of the first generation of *D. dryas*, samples in all areas were timed between 375 and 425 DD >5°C. Sampling began in southwestern Ontario on 21 May and was completed progressively later across the province. The parasites were collected with a standard 38-cm sweep-net, and 100 sweeps were taken at each of 96 locations in 41 counties. Usually two sites were sampled per county; however, as many as five were sampled at the leading edge of the distribution. All samples were sorted in the laboratory and categorized according to numbers of parasites collected.

To obtain data on rates of parasitism in populations of the host, bouquets of alfalfa foliage containing ABL larvae were randomly collected in mid July from 10 of the 96 locations. In nine of the 10 sites selected, populations of the adult parasite were high in the initial survey and in one site they were at trace levels. The samples were taken just prior to prepupal drop of the second generation of the host. The bouquets were bagged, brought to the laboratory, and held at 22°C until the maggots evacuated the mines. A subsample of 100 prepupae were dissected from each site and the incidence of parasitism was recorded.

Results and Discussion

The parasite was found in 28 of the 41 counties and at 56 of the 96 sampling sites (Fig. 1, Table I). For the most part, numbers of parasites were high throughout eastern Ontario,

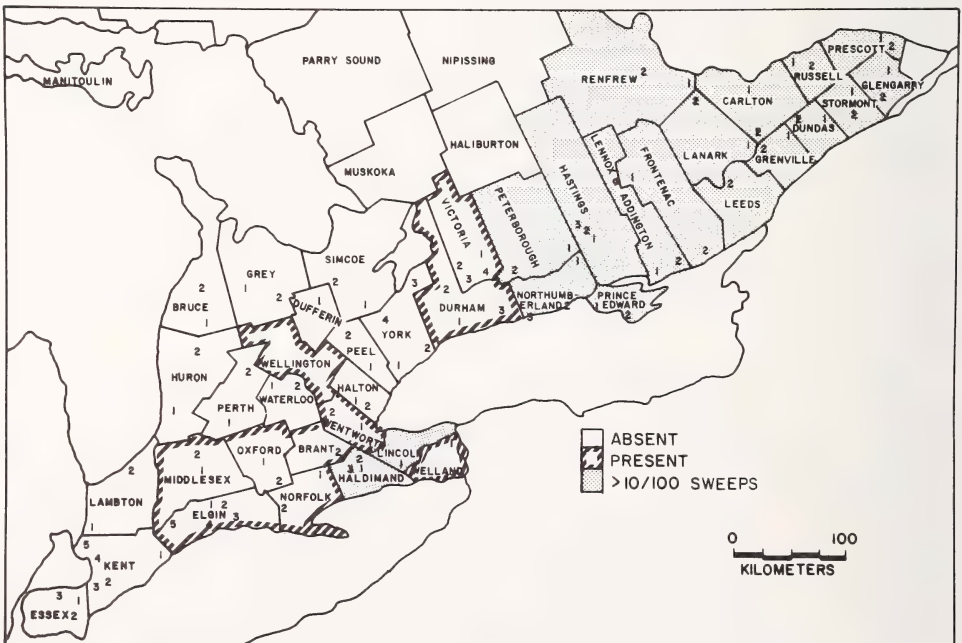


FIGURE 1. Sampling sites for *Dacnusa dryas* in southern Ontario, 1985; integers 1-5 refer to sampling locations.

Table I. Incidence of *Dacnusa dryas* adults in sweep-net samples of alfalfa in southern Ontario, 1985

County	Site	Rating ¹	County	Site	Rating ¹
Brant	1	+	Leeds	1	+++
	2	+		2	+++
Bruce	1	0	Lennox & Addington	1	++
	2	0		2	+++
Carleton	1	+++	Lincoln	1	+++
	2	+++	Middlesex	1	+
Dufferin	1	0	Norfolk	2	0
	2	0		1	+
Dundas	1	+++	Northumberland	2	0
	2	+++		1	+++
Durham	1	+++	Oxford	2	+++
	2	++		3	+++
	3	++		1	0
Elgin	1	+++	Peel	2	+++
	2	+		1	0
	3	+	2	0	
	4	0	Perth	1	0
	5	0		2	0
Essex	1	0	Peterborough	1	+++0
	2	0	Prescott	2	+++
	3	0		1	++
Frontenac	1	++	Prince Edward	2	+++
	2	+++		1	+++
Grey	1	0	Renfrew	2	+++
	2	0		1	+++
Glengarry	1	++	Russell	2	+++
	2	+++		1	++
Grenville	1	+++	Simcoe	2	+++
	2	+++		1	0
Haldimand	1	+++	Stormont	2	0
	2	0		1	++
	3	+++		2	++
Halton	1	0	Victoria	1	+
	2	0		2	++
Hastings	1	+++	Waterloo	3	++
	2	+++		4	++
	3	+++		1	0
Huron	1	0	Welland	2	0
	2	0		1	+
Kent	1	0	Wellington	1	0
	2	0		2	+
	3	0	Wentworth	3	0
	4	0		1	+++
	5	0		2	+
Lambton	1	0	York	1	0
	2	0		2	0
Lanark	1	+++		3	0
	2	+++		4	0

¹ Numbers per 100 sweeps: 0, absent; +, 1-3; ++, 4-12; +++, 13 or more.

averaging 10 or more per 100 sweeps. Numbers were also high in the Niagara area (Lincoln, Haldimand counties) but declined to the north and west as the limits of its distribution were approached. Based on the prepupal dissections, the incidence of parasitism where parasites were numerous in the sweep-net samples varied from 65 to 95% with an average of 84% (Table II). By contrast, the incidence of parasitism at the leading edge of the distribution (e.g., Wellington county) was only 3%.

Table II. Parasitism of the alfalfa blotch leafminer in Ontario by the second generation of *D. dryas*, 1985

County	Site	% Parasitism	County	Site	% Parasitism
Hastings	1	86	Carleton	1	88
	2	79	Lanark	1	75
	3	91	Lincoln	1	90
Haldimand	1	65	Renfrew	2	95
	3	90	Wellington	2	3

The pattern of parasite recovery from both eastern and southwestern Ontario has been consistent with the release program followed since 1979. Apparently natural spread from the release sites in both regions was a factor in extending the distribution across Ontario. From our data, it appears that the parasite has increased its range at the rate of *ca.* 60 km/year, somewhat faster than that observed by Hendrickson and Plummer (1983) in Delaware. However, it is less mobile than its host whose rate of spread has been estimated at 80 km/year (Helgeson 1976).

Life table data from four sites in eastern Ontario indicate that once established, *D. dryas* takes less than three years to reduce populations of the ABL to below economic levels (Harcourt and Guppy 1985). However, it is too early to conclude that the parasite has the capacity to maintain itself as an effective biological control agent at low host densities. The fact that host populations have remained subeconomic and rates of parasitism have not yet declined in the Ottawa Valley is a positive sign.

Acknowledgements

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REPRODUCTION IN NON-AESTIVATING SUMMER ALFALFA WEEVILS, *HYPERA POSTICA* (COLEOPTERA: CURCULIONIDAE), IN EASTERN ONTARIO

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Abstract

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In populations of non-aestivating summer adults (first generation) of the alfalfa weevil, *Hypera postica* (Gyll.), in eastern Ontario in 1984 and 1985, the first sexually mature females appeared in about mid-July of both years. Sperm was detected in male testes beginning in late July, 1984 and the second week of August, 1985. Mated females appeared about mid-July, 1984 and early August, 1985 but, because they were sexually mature before the males, most females had not mated before the first week of August in both years. As a result, few fertilized eggs are laid soon enough to develop into second generation adults before freeze-up.

Introduction

In northeastern North America, first generation adults of the alfalfa weevil, *Hypera postica* (Gyll.) develop in early summer, and after a short feeding period disperse and aestivate until the fall (Blickenstaff *et al.* 1972; Mailloux and Pilon 1975; Manglitz 1958; Manglitz and App 1957; Miller and Guppy 1972). However, in eastern Ontario (latitude 44°24'N), Loan *et al.* (1984) found that a small portion of first generation adults, termed summer weevils (SW) remain active in alfalfa, develop sexually without aestivation and produce a complete second generation. Similar, uninterrupted development in the field has not been documented elsewhere. Barnes (1967) concluded that summer larvae in New Jersey are offspring of late maturing overwintered females, whereas, in Illinois, White *et al.* (1969) based their evidence of a second generation on progeny of SW females caged with overwintered males. In Ontario, following the establishment of the euphorine *Microctonus aethiopooides* Loan (Abu and Ellis 1974; 1976; Harcourt *et al.* 1979), more than 90% of the overwintered adults are parasitized and killed each year in late May (Loan, unpublished). Therefore, adult SW form a relatively discrete population.

Earlier work on alfalfa weevil reproduction (Guerra and Bishop 1962; Huggans and Blickenstaff 1964; Le Cato 1970; Snow 1928; Tombes 1964) was based on laboratory observations using reared weevils or field-collected SW which had aestivated. Loan *et al.* (1984) reported preliminary observations on ovarian development in field-collected, non-aestivating SW in eastern Ontario, and the present paper gives details on the sequence of events during sexual maturation and reproduction.

Materials and Methods

From early July, at peak emergence of new SW weevils, to early September, adults were net-collected at intervals of 2 to 13 days in eastern Ontario near Moira in 1984 and near Kemptville in 1985. The samples were held in the laboratory at 3°C until the insects were dissected. Occasionally, overwintered adults occurred in the collections. Because they had a characteristic, brittle, dark grey integument and rubbed elytra, they were easily separated from the light brown, heavily-scaled SW. The females were examined for the presence of mature eggs in the ovaries (gravid females) and males for sperm in the testes.

Male testes, and the spermatheca were removed in 0.9% saline and examined at 100x magnification for sperm. The quantity of sperm in the spermatheca was categorized as follows: absent (spermatheca transparent, insect presumed to be virgin); small (spermatheca still transparent, containing a few sperm); large (spermatheca opaque, sperm dense and filling most of the spermatheca).

The number of mature eggs in ovaries of the non-aestivating SW examined in 1984 was compared with that in overwintered adults collected during May in 1984.

The data were analysed by ANOVA, Duncan's multiple range test, and chi-square analysis by 2x2 contingency tables.

Results and Discussion

The first gravid females were found by 16 July in both 1984 and 1985 but most were not gravid before the beginning of August, 1984, and the second week of August, 1985 (Fig. 1). In 1984, the percentage of gravid and mated females increased gradually from mid-July until early September, whereas, in 1985, the percentage in these categories increased sharply beginning 6 August.

In 1984, there were 8 mated females in the sample of 16-19 July (Fig. 1), however, males with sperm were not observed until late July. Most of the males on 8 August, 1984, and 12-14 August, 1985, contained sperm. The increase in percentage of mated females generally was coincident with sexual maturation of males; chi-square analysis showed that the proportion of males with sperm in the testes was not significantly different from that of mated females for each of the collection periods of 16-19 July, 23-26 July and 2 August, 1984, and 6-11 August, 1985 ($P > 0.05$, χ^2 values 0.004-2.69). The analysis indicates that the number of sexually mature males was sufficient in the SW population to account for the small number of inseminated females observed before 2 August, 1984, and early August, 1985, even if it is assumed that males mate only once.

The percentage of gravid females was significantly greater than of males with sperm for each of the collection periods 23-26 July and 2 August, 1984, and 6-11 August, 1985 ($P < 0.05$, χ^2 values 5.17-36.36). This suggests that most of the females were sexually mature before the males and remained unmated until after the first week in August in both years.

There were significantly fewer mature eggs in virgin females than in mated females containing large quantities of sperm $P < 0.05$, $F = 21.40$) (Table I). This agrees with LeCato's (1970) finding that virgin female weevils laid 65 to 77% fewer eggs than did mated ones; he suggested that "sperm or a sperm factor" stimulates oviposition. Engelmann (1970) cites a number of examples of other insect species for which mated females developed and laid more eggs than did virgin females. Because the smaller numbers of mature eggs observed in virgin females during the present study correspond to the lower oviposition rate of LeCato's virgin females, "sperm or a sperm factor" may stimulate the rate of egg maturation, and not oviposition directly. Our data (Fig. 1, Table I) agree with those of LeCato (1970) who reported that egg maturation initially is not dependent on the presence of sperm.

The mean numbers of mature eggs in virgin females and in females with small quantities of sperm in the spermatheca were similar (Table I). Therefore, it seems that the females with small quantities of sperm in our study did not receive sufficient sperm to stimulate egg maturation appreciably.

In 1984, the number of mature eggs in gravid summer females generally increased from mid-July to mid-August. After mid-August, when most of them had mated, the numbers were similar to those found in overwintered females in May (Table II). It is not known whether the gravid SW oviposited prior to their being collected; collection sites were not sampled for eggs and the history of oviposition cannot be detected by examination of ovaries. However, Loan *et al.* (1984) observed eggs of SW in alfalfa fields in the last half of July and in August of 1981 and 1982, and LeCato (1970) found that oviposition of laboratory-reared females increased progressively after mating. These observations suggest that

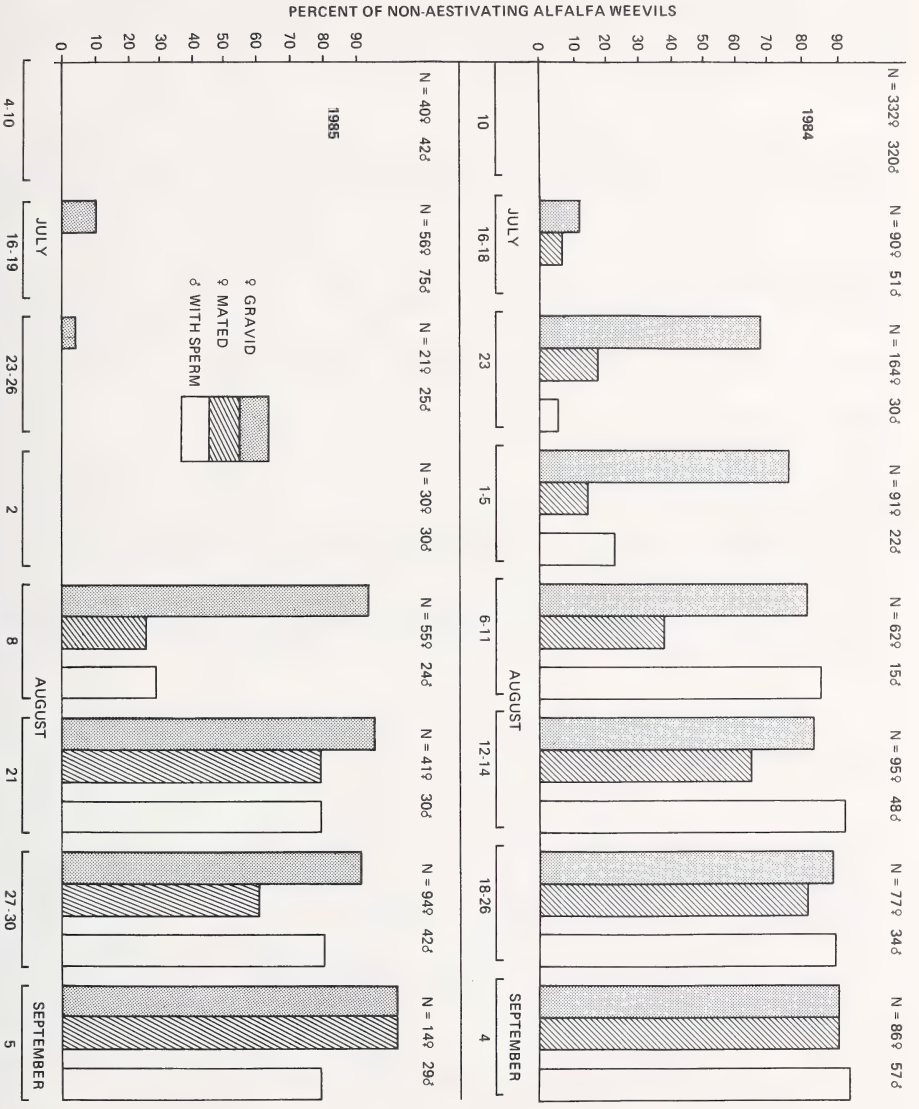


FIGURE 1. Percent gravid females, percent mated females, and percent males with sperm in the testes in non-aestivating summer weevils of the alfalfa weevil from 16 July - 5 September 1984 and 1985.

the gradual increase in the number of mature eggs in ovaries of SW in July and August (Table II) coincided with an increase in the rate of oviposition in the field.

In eastern Ontario, the alfalfa weevil overwinters only in the adult stage. Therefore, survival of a second generation is dependent upon the accumulation of sufficient heat units for development through a complete life cycle. Loan *et al.* (1984) found that eggs laid in late July and early August, gave rise to adults before the end of September. Although the present study showed that gravid summer females were always present after mid-July, males matured later than females; this suggests that few fertilized eggs are laid early enough for development of a large number of second generation adults in most years in eastern Ontario.

Table I. Total number of eggs observed and mean number of mature eggs/female in non-aestivating, gravid summer females of the alfalfa weevil with different amounts of sperm in the spermatheca in eastern Ontario from 16 July - 5 September 1984 and 1985.

Amount of sperm in spermatheca	Years	No. of gravid females	Total no. of eggs	Average no. eggs/female*
	1984			
Large		241	5924	24.58 ^a
Small		20	228	11.40 ^b
Absent		164	1486	9.06 ^b
	1985			
Large		46	897	19.50 ^a
Small		21	236	11.24 ^b
Absent		61	570	9.34 ^b

* Means followed by the same letter are not significantly different at the 5% level.

Table II. Mean number ± SE of mature eggs per female in gravid, overwintered females and gravid, non-aestivating summer females of the alfalfa weevil in eastern Ontario in May and in July-September, 1984.

Overwintered females			Summer females		
Eggs/female			Eggs/female		
Date	N	Mean ± SE	Date	N	Mean ± SE
May 3	27	19.41 ± 1.30	July 19	8	4.50 ± 0.82
May 7	6	20.83 ± 4.46	July 23	22	9.96 ± 1.39
May 10	22	20.18 ± 2.37	July 26	84	8.50 ± 1.04
May 22	28	29.57 ± 1.80	Aug. 2	68	12.69 ± 1.63
			Aug. 8	50	13.78 ± 1.84
			Aug. 21	75	20.20 ± 1.63
			Aug. 27	30	26.70 ± 1.93
			Aug. 30	41	28.00 ± 1.47
			Sept. 5	79	31.13 ± 1.39

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**INFLUENCE OF POSTTREATMENT TEMPERATURE ON THE CONTACT
TOXICITY OF TEN ORGANOPHOSPHORUS AND PYRETHROID
INSECTICIDES TO ONION MAGGOT ADULTS
(DIPTERA: ANTHOMYIIDAE)**

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Abstract

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Posttreatment temperature effects on the contact toxicity of five organophosphorus and five pyrethroid insecticides to 24 to 48 h-old adult onion maggots, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae) were determined. Chlorpyrifos, diazinon, malathion, and parathion toxicities were positively correlated with temperature, with the insecticides being from 1.2x to 2.0x more toxic at 32° than at 15°C. Temperature had little effect on naled toxicity. Fenvalerate, deltamethrin, PP993 (2,3,5,6-tetrafluoro-4-methylbenzyl *cis*-3-(*Z*-2-chloro-3,3,3-trifluoroprop-1-enyl)-2,2-dimethylcyclopropanecarboxylate), permethrin, and cypermethrin toxicities were negatively correlated with temperature. These effects were least pronounced with fenvalerate and most obvious with cypermethrin, which was 6.9x more toxic at 15° than at 32°C.

Introduction

The onion maggot, *Delia antiqua* (Meigen) (Diptera: Anthomyiidae) is a serious pest of onions grown in Canada and the northern United States. Average yield losses in Ontario in the absence of control measures range from 39-45% (McEwen 1978; Tolman *et al.* 1986). Control measures for onion maggot typically involve an insecticide application to seed furrows to suppress first and, to a lesser extent, second generation larvae. That treatment, combined with sprays, aims to reduce the adult population. Current measures to control adult onion maggots rely on organophosphorus (OP) insecticides. Recent reports (Harris and Svec 1976; Harris *et al.* 1982; Carroll *et al.* 1983) indicate that the onion maggot is developing OP resistance. Carroll *et al.* (1983) found that some pyrethroid insecticides were highly toxic to OP-susceptible and -resistant onion maggots and suggested that they might have potential as onion maggot adulticides. Since then, cypermethrin has been registered for onion maggot control in Ontario.

Sprays to reduce populations of adult onion maggots may be applied at various times during the growing season depending on the size of the adult population, onion variety being grown, and environmental conditions. The latter, particularly temperature, can influence insecticide toxicity. Toxicity of OP insecticides is generally thought to be positively correlated with temperature. However, a number of recent studies indicate that, like DDT, the toxicity of pyrethroid insecticide is negatively correlated with temperature, with the extent of the effect varying with both the insecticide and the insect being tested. Studies on the negative correlation of the toxicity of pyrethroids with temperature implicate physiological processes (e.g. the rate of metabolism, excretion and redistribution as well as reactivity at the site of action) are involved, but the exact mechanisms are unknown (Scott and Georghiou 1984). The literature has been reviewed extensively elsewhere (Harris and Kinoshita 1977; Sparks *et al.* 1982; Riskallah 1984; Ewen *et al.* 1984; Hinks 1985). In view of the fact that sprays against onion maggot adults may be applied under varying temperature conditions during the growing season, we felt it would be useful to compare the effect of temperature on the contact toxicity of OP insecticides currently used for adult onion maggot control with that of potentially useful pyrethroids.

Materials and Methods

A strain of insecticide-susceptible onion maggots was obtained originally from southwestern Ontario in 1961 (Harris *et al.* 1962). This strain was maintained and reared as described by Tolman *et al.* (1985). Emerging adults of the onion maggot were held at $27 \pm 1^\circ\text{C}$ and $65 \pm 5\%$ RH. Solutions of technical or analytical grade standards ($>93\%$ purity) of five OP (chlorpyrifos, diazinon, malathion, naled, parathion) and five pyrethroid (cypermethrin, deltamethrin, fenvalerate, permethrin, PP993) insecticides were prepared in 19:1 acetone:olive oil and were applied to 24 to 48 h-old adults with a Potter spray tower (Harris 1972). Two groups of 10 flies (5♀, 5♂), anaesthetized with diethyl ether, were tested at each dosage, using six to ten insecticide concentrations that caused mortalities ranging from 5-95%. Controls (solvent only) were included with all tests. Treated flies were placed in waxed-paper cups, each containing a dental roll saturated with water for a moisture source. The cups were covered with 9 cm glass petri dishes and were held at

Table I. Direct contact toxicity of five organophosphorus and five pyrethroid insecticides to adults of the onion maggot, *Delia antiqua*, at 15° and 32°C .

Insecticide	Temp. (°C)	Equation of regression line	SE ^{a)} of slope	LC ₅₀ (95% F.I.) ^{b)} % sol. ($\times 10^{-3}$)	LC ₅₀ ratio 32:15 ^{c)}
Parathion	32	$Y = 29.4 + 9.43 X$	0.75	2.6 (2.5-2.7)	+2.0
	15	$Y = 18.4 + 5.90 X$	0.47	5.3 (5.0-5.6)	
Malathion	32	$Y = 24.3 + 8.35 X$	0.85	4.9 (4.7-5.1)	+1.7
	15	$Y = 22.9 + 8.58 X$	0.75	8.3 (8.0-8.6)	
Diazinon	32	$Y = 34.8 + 10.5 X$	0.91	1.4 (1.4-1.5)	+1.4
	15	$Y = 35.0 + 11.2 X$	0.93	2.0 (1.9-2.0)	
Chlorpyrifos	32	$Y = 30.0 + 8.92 X$	0.74	1.6 (1.5-1.6)	+1.2
	15	$Y = 46.9 + 15.4 X$	1.18	1.9 (1.8-1.9)	
Naled	32	$Y = 37.5 + 10.4 X$	0.96	0.77 (0.74-0.79)	-1.1
	15	$Y = 26.8 + 6.89 X$	0.49	0.68 (0.66-0.71)	
Fenvalerate	32	$Y = 15.0 + 3.78 X$	0.27	2.3 (2.1-2.4)	-2.1
	15	$Y = 16.8 + 4.02 X$	0.32	1.1 (1.0-1.2)	
Deltamethrin	32	$Y = 20.4 + 3.96 X$	0.29	0.13 (0.12-0.13)	-2.7
	15	$Y = 27.5 + 5.22 X$	0.35	0.049 (0.046-0.051)	
PP993 ^{d)}	32	$Y = 20.9 + 5.45 X$	0.43	1.2 (1.0-1.3)	-5.5
	15	$Y = 28.8 + 6.51 X$	0.49	0.22 (0.21-0.23)	
Permethrin	32	$Y = 19.2 + 5.92 X$	0.40	4.0 (3.8-4.2)	-6.3
	15	$Y = 31.7 + 8.34 X$	0.64	0.63 (0.61-0.66)	
Cypermethrin	32	$Y = 17.9 + 4.23 X$	0.32	0.90 (0.84-0.96)	-6.9
	15	$Y = 19.2 + 3.63 X$	0.32	0.13 (0.12-0.14)	

^{a)} Standard Error

^{b)} Fiducial Interval

^{c)} +, positive temperature coefficient; -, negative temperature coefficient.

^{d)} 2,3,5,6-tetrafluoro-4-methylbenzyl *cis*-3-(Z-2-chloro-3,3,3-trifluoroprop-1-enyl)-2,2-dimethylcyclopropanecarboxylate.

either $15^{\circ}\pm 1^{\circ}$ or $32^{\circ}\pm 1^{\circ}$ C under continuous light. Mortality was assessed after 18 h. Each bioassay was repeated three times, results were pooled and were analyzed by probit analysis (Finney 1971). Temperature coefficients of toxicity were determined by comparison of LC_{50} values obtained at the two temperatures.

Results and Discussion

Knockdown of the onion maggot adults occurred very quickly with all of the insecticides and no recovery was noted after 18 h. This has also been reported for some other species of insects (Sparks *et al.* 1982; Ewen *et al.* 1984) and adults of Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (unpublished data).

OP insecticides tested were ranked by LC_{50} to onion maggot as follows: naled > chlorpyrifos = diazinon > parathion > malathion (Table I). With the exception of naled, which had a very slight negative temperature coefficient of toxicity, the other OP insecticides showed positive temperature coefficients. The effect was most pronounced with parathion which was twice as toxic at 32° C than at 15° C.

Permethrin, fenvalerate, and PP993 showed contact toxicities to adults of onion maggot similar to those of the OP insecticides (Table I). Cypermethrin and deltamethrin were markedly more toxic at the LC_{50} level, e.g., deltamethrin was 38x and 169x more toxic than malathion and 6x and 14x more toxic than naled at 32° and 15° C, respectively. All the pyrethroids exhibited negative temperature coefficients of toxicity with the effect being least obvious with fenvalerate and deltamethrin and most apparent with cypermethrin. Given the proposed rate of application of cypermethrin at 70 g/ha, the results suggest that reduced efficacy of the pyrethroid caused by higher temperatures would be offset by the actual rate of application in the field. As more pyrethroid insecticides are recommended for control of adult onion maggots, temperature conditions at application time will be an important factor in selecting an appropriate insecticide or application rate.

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**EFFECTIVENESS OF SUPERIOR OIL APPLIED
TO APPLE FOR CONTROL OF THE SAN JOSE SCALE,
QUADRASPIDIOTUS PERNICIOSUS, AND THE EUROPEAN FRUIT SCALE,
QUADRASPIDIOTUS OSTREAIFORMIS (HOMOPTERA: DIASPIDIDAE)**

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Abstract

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Annual applications of superior oil reduced populations of the San Jose scale, *Quadraspidiotus perniciosus* (Comstock), and the European fruit scale, *Q. ostreaiformis* (Curtis), on apple trees and reduced fruit infestation in the last two years of a three-year study. However, the proportion of fruit infested with scales was not substantially reduced after three successive years of oil applications. More fruit from the top portions of treated trees were infested with scales than fruit from the lower portions, this indicated that spray application was not evenly distributed or that motile stages of scales selectively moved to upper portions of trees.

Introduction

Scale insects were recognized as pests of tree fruits in Ontario prior to 1900 (Lochhead 1899). Two of the more troublesome species are the San Jose scale (SJS), *Quadraspidiotus perniciosus* (Comstock) and the European fruit scale (EFS), *Quadraspidiotus ostreaiformis* (Curtis) (Homoptera: Diaspididae). Infestations of these scales on the fruit may lower quality or exclude fruit from world markets (Anonymous 1970) and infestations on the tree bark have reduced the vigour of the tree and caused mortality (Howard and Marlatt 1896, Caesar 1914, Quaintance 1919). Although these insects occasionally cause damage to apple in localized areas of Ontario, because of their generally low density in orchards, they have received little attention in recent years.

With the implementation of an insect pest management program for apples in which application of insecticides was reduced, the impact of scale insects has received renewed interest (McKay *et al.* 1983). In Ontario, the recommended control tactic for scale insects is the application of superior oil (60-70 vis.) prior to the green-tip stage of tree development (Anonymous 1985). This control measure is recommended if more than 5% of the fruit harvested in the previous year were infested by scale insects (McKay *et al.* 1981). The objective of this study was to evaluate the ability of our application of superior oil to reduce fruit infestation by SJS and EFS.

Materials and Methods

Studies were carried out in six commercial apple orchards, located near London, Ontario, during the period from spring 1982 to fall 1984. Each orchard was *ca.* 1 ha and contained trees of several cultivars, but only 'McIntosh' were used in this study. All trees were 18 years old in 1982, grafted on seedling rootstock, and planted at a spacing of 10 m x 10 m (100 trees per hectare). Three of the orchards received an application of superior oil (vis. 70) at a rate of 65 L/ha in volumes ranging from 3500 to 4000 L/ha applied by commercial airblast sprayers. Prior to treatment, the sprayers were calibrated following guidelines outlined by Fisher *et al.* (1976). Fan speed was adjusted to 160 km/hr and nozzle pressure was, on average, 1,725 kPa. Application dates were April 17 and 18 in 1982, April 14 and 15 in 1983, and April 21 and 22, 1984 when trees were in a fully dormant state. The remaining three orchards served as nontreated controls. All orchards received the same number of insecticide and fungicide applications applied at similar rates each year, with the exception of a miticide application in one control orchard. Differences in survival and infestation of scales between the two groups of orchards was, therefore, a function of the applications of dormant oil.

In 1982 and 1983, estimates of the density of live scales were obtained from the same

two trees from each of the six orchards. Scale populations were concentrated on the lower scaffold branches and trunk of the trees (Ker 1984). The trees were examined before treatment, five to six days after treatment, and again at four weeks after treatment. Samples consisted of four circular pieces of bark, 1.9 cm in diameter, excised from the scaffold limbs or trunk of each tree. Each piece was examined under 40x magnification and all scale exuvia were counted, removed and the species recorded.

Species were identified using morphological features described by Morgan and Arrand (1971). These features included the location of the nipple on the exuvia, presence or absence of grooves around the nipple and coloration of the central area of the underside of the exuvia. Only first- and second-instar nymphs were present at time of treatment. Live scales, after removal of the exuvia, were turgid and pale orange in colour but dead scales were flaccid and translucent. The mean numbers of survivors were compared by analysis of variance and when the F-statistic was significant ($P < 0.05$), the means were separated by Duncan's New Multiple Range Test (Duncan 1955).

Infestations of scales on fruit were recorded at harvest each year. All apples from the two trees in each orchard were removed from the top (> 2.0 m above the ground) and the bottom (< 2.0 m above the ground) of the trees. Infestation levels were classified according to grading guidelines of the Ontario Farm Grades and scales Act in which fruit is considered out-of-grade when three or more scales are found on the fruit (Anonymous 1970, McKay *et al.* 1982).

Results and Discussion

Significant mortality of scales on the bark was recorded one week after application of superior oil at recommended rates (Table I) in both 1982 and 1983. Oil sprays reduced scale populations by 40 to 50% compared with the proportion of live scales on the control trees. No further decrease in survival was apparent more than one month after application: results similar to those obtained by Pree *et al.* (1984). The population of scales

Table I. Mean number of scales of *Quatraspidiotus perniciosus* and *Q. ostreaeformis* per 10 cm² of bark on scaffold limbs or trunks of apple trees treated with superior oil (vis. 70)¹ near London, Ontario.

Year	Date	Treatment	Scales/ 10 cm ² (\pm S.E.) ²	Live Scales 10 cm ² (\pm S.E.) ²	% Live scales ³
1982	April 16	Check	98.8 (15.6)	33.3 (8.7)	33.7a
		Oil	77.1 (3.8)	26.3 (2.9)	34.1a
	April 22	Check	85.0 (3.0)	29.4 (1.9)	34.5a
		Oil	82.1 (5.2)	16.7 (0.8)	20.4 b
	May 26	Check	88.6 (3.5)	29.2 (1.1)	32.9a
		Oil	78.3 (6.2)	13.0 (3.5)	16.7 b
1983	April 13	Check	81.3 (4.2)	27.8 (3.3)	34.2a
		Oil	80.0 (7.2)	26.7 (2.7)	33.4a
	April 20	Check	82.8 (4.2)	27.3 (3.3)	32.6a
		Oil	89.5 (11.4)	14.0 (2.1)	15.6 b
	May 17	Check	86.5 (0.9)	26.4 (0.5)	30.5a
		Oil	85.4 (1.2)	12.8 (2.1)	15.1 b

¹ Oil was applied to trees in three orchards on April 17 and 18, 1982 and April 14 and 15, 1983. No oil was applied to trees in control orchards.

² Means estimated from four circular (1.90 cm diameter) pieces of bark from the scaffold limbs or trunks of six trees.

³ Percentages followed by same letter NSD according to Duncan's Multiple Range Test (1955) ($P \leq 0.05$; data transformed by arcsine \sqrt{x} before analysis).

on nontreated trees remained constant throughout the test period in each year. European fruit scale outnumbered SJS by a ratio of 4:3 on the scaffold limbs of the trees that were sampled (Ker 1984).

In 1982, there was no significant decrease in infestation of fruit at harvest in those orchards treated earlier that year with oil (Table II). In 1983 and 1984, fruit from trees treated with oil had fewer scales than in 1982. Despite oil treatments in 1982 and 1983, damage to samples of fruits with both SJS and EFS equalled or exceeded the 5% limit for damage by all pests (McKay *et al.* 1982). However, by 1984, the percentage of fruit infested by scales had declined below the 5% limit.

In each year, more infested fruit was found in the top than in the bottom of the trees (Table II). Although populations of scales were in about equal density on scaffold limbs, SJS was more common on fruit than was EFS in each year, regardless of treatment or location (Table III). That may reflect a tendency for less dispersal by EFS or a preference by this species for more mature areas of bark on the trees. Of all fruit examined, none were infested by both SJS and EFS. This observation may indicate an important behaviour by crawlers, i.e., interspecific avoidance which has not been recorded previously.

Table II. Proportion of apples at harvest infested by *Quadraspidiotus perniciosus* (SJS) and *Q. ostreaeformis* (EFS) after treatment with superior oil (vis. 70) at green tip, near London, Ontario.¹

Year	Treatment	Mean % of Fruit Infested ²			Total ³
		Location in tree		Total ³	
		top	bottom		
1982	Check	5.9a	3.9b	9.8A	
	Oil	4.2ab	2.1 c	6.4AB	
1983	Check	7.2a	3.6b	10.8A	
	Oil	3.7 b	1.3 c	5.0 B	
1984	Check	8.8a	3.9b	12.7A	
	Oil	3.2 b	1.1 c	4.2 B	

¹ Fruit at harvest with three or more scales were considered infested. The number of fruit examined each year ranged from 8,300 to 9,000 for each treatment.

² Means within each year followed by a different lower case letter are significantly different (Duncan's New Multiple Range Test [1955], $P < 0.05$). Means transformed by arcsine \sqrt{x} before analysis.

³ Column means followed by a different upper case letter are significantly different (Duncan's New Multiple range test [1955], $P < 0.05$). Means transformed by arcsine \sqrt{x} before analysis.

Table III. Proportion of harvested apples infested by *Quadraspidiotus perniciosus* (SJS) and *Q. ostreaeformis* (EFS) from top or bottom of trees sprayed with superior oil (vis. 70) and from trees not treated with oil near London, Ontario.

Treatment	Mean % ¹ of Fruit Infested ² by			
	SJS		EFS	
	Top	Bottom	Top	Bottom
Check	5.5a	2.8b	1.6bc	1.2c
Oil	3.2a	1.1b	0.6 c	0.5c

¹ Means within each treatment followed by a different letter are significantly different (Duncan's New Multiple Range Test [1955], $P < 0.05$). Data transformed by arcsine \sqrt{x} before analysis.

² Percentage of fruit with three or more scales present; data were pooled for 1982-1984.

Although populations of scales in oil-sprayed orchards were reduced and mortality of scales located on the lower scaffold limbs of the trees was demonstrated, sufficient numbers of scales remained to colonize the lower limbs and to contaminate fruit each season. Scales of both species were a greater problem on fruit in the upper portion of the trees than on the lower, and this could reflect a lack of adequate spray coverage on the upper parts of the tree or the tendency for crawlers to move to the upper parts of the tree from dense concentrations on the scaffold limbs. Obviously, considerable redistribution of the scale populations occur each year when the crawlers hatch. Further information on the distribution of SJS and EFS populations in apple trees and the effect of repeated oil applications on populations in all areas of the trees must be obtained before improvements can be made to the control recommendations currently available.

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CHEMICAL ATTRACTANTS FOR MONITORING FOR ADULT NORTHERN AND WESTERN CORN ROOTWORMS (COLEOPTERA: CHRYSOMELIDAE) IN ONTARIO

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Abstract

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The numbers of adult northern and western corn rootworms, *Diabrotica barberi* Smith and Lawrence and *D. virgifera virgifera* LeConte, collected in either white or yellow sticky traps baited with either the 2*R*,8*R* enantiomer or the racemic mixture of the sex pheromone of the western corn rootworm (8-methyl-2-decyl propanoate) were recorded in cornfields in Wellington county, Ontario. White traps baited with pheromone attracted 5.5 times (1984) and 5.8 times (1985) more western corn rootworms than did yellow pheromone traps but only 1.7 times (1984) and 1.2 times more northern corn rootworms. The numbers of both species of beetles on whole corn plants correlated poorly with the numbers caught in white, sticky traps baited with the racemic mixture of the pheromone. The attraction of adults to various extracts of squash blossoms was also tested. Female corn rootworms were attracted to an extract of squash blossoms in 10% ether/hexane. Monitoring for corn rootworms using sticky traps baited with attractants requires further study due to a poor correlation between numbers of adults caught in pheromone traps and counted on whole corn plants.

Introduction

Northern (NCR) and western (WCR) corn rootworms, *Diabrotica barberi* Smith and Lawrence and *D. virgifera virgifera* LeConte, respectively, are the major insect pests of field corn in Ontario. A pest management program for corn requires biologically and statistically valid methods of monitoring adult populations. Such methods should estimate the females because the economic importance of the population is dependent on the ovipositing females (Godfrey and Turpin 1983), and because the proportion of females can vary significantly between fields. The abundance of the two species must also be determined because larvae of the WCR cause more damage than those of the NCR (Fisher 1985).

The sex pheromone of the WCR has potential as a bait in traps to monitor populations of both species. Guss *et al.* (1982) identified the pheromone of the WCR as 8-methyl-2-decyl propanoate, an optically active compound with four enantiomers. The 2*R*,8*R* enantiomer is attractive to males of both species. However, the 2*S*,8*R* enantiomer is inhibitory to NCR males, and the other isomers had no effect on either species (Guss *et al.* 1984, 1985). The pheromone can be synthesized as the racemic mixture or as single enantiomers. Therefore in the future, lure components could be manipulated to preferentially attract one species over the other. Johnson *et al.* (1985) examined the response of corn rootworms in the field to traps baited with the racemic mixture of the WCR sex pheromone, however, no one has evaluated the economics and usefulness of an extensive monitoring program in southern Ontario.

Adult corn rootworms are attracted to yellow surfaces (Tollefson and Owens 1975; Ball 1982) which have been used alone (Hein and Tollefson 1984, 1985; Matin *et al.* 1984; Johnson *et al.* 1985), and in conjunction with chemical attractants (Ladd 1984; Ladd *et al.* 1983, 1984, 1985) to monitor populations. Ball (1982) suggested that yellow traps baited

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with the racemic sex pheromone would be more efficient than unbaited yellow traps but no one has tested this hypothesis.

There is a close association between beetles in the genus *Diabrotica* and plants in the genus *Cucurbita* (Chambliss and Jones 1966). Howe *et al.* (1976) hypothesized that the aggregation of adult corn rootworms on the foliage of cucurbits was facilitated by volatile host-produced attractants. However, Johnson *et al.* (1985) found that corn rootworms were not attracted to extracts of leaves and stems of a bitter *Cucurbita* species. The isolation and identification of any attractant would be useful for monitoring corn rootworms because females are more attracted to squash, *Cucurbita maxima* Duchesne, than are males (Fisher *et al.* 1984).

The objective of this research was to determine the usefulness of sticky traps baited with certain chemical attractants for monitoring corn rootworms. The attraction of corn rootworms to yellow or white traps baited with the sex pheromone of the WCR and to white traps baited with extracts of squash blossoms was studied.

Materials and Methods

Trapping with sex pheromone. In all experiments, pheromone was dispensed from red rubber septa (A.H. Thomas No. 8753-D22). The septa were Soxhlet-extracted for 24 h in methylene chloride, and air-dried prior to formulation. Septa were loaded with 100 μ L of hexane (Fisher, HPLC grade) containing either 1 μ g of the racemic mixture or 1 μ g of the 2*R*,8*R* enantiomer of the WCR sex pheromone, and were air-dried for 24 h prior to placement in Pherocon 1C[®] (Zoecon Corp., Palo Alto, CA) pheromone traps. Traps were attached 1-m high to wooden stakes that were placed between the rows of corn in fields in Wellington county, Ontario.

Two types of traps were used to monitor corn rootworms in a cornfield during August and September 1984. Yellow cylinders (Lily-Tulip Nestrith[®], 1-L volume), coated externally with Tangle Trap[®] (The Tanglefoot Company, Grand Rapids, Michigan), were used as unbaited standards to which captures of beetles in pheromone traps were compared by regression analysis. Six of these traps, separated by 10 m, were placed near the centre of the experimental plot over the ends of corn plants that had been truncated at ear height. The second type of trap was the Pherocon 1C[®] trap baited with a racemic mixture of the WCR sex pheromone and coated internally with Tangle Trap[®]. Six pairs of Pherocon[®] traps, one white and one painted yellow on their exterior surfaces (Pratt and Lambert #5602 enamel paint), were arranged in a randomized complete block design near the centre of the field with 4 m between traps and 15 m between pairs of traps.

All beetles were removed from pheromone traps and cylinders, and Tangle Trap[®] was reapplied twice a week from 5 to 29 August, and then once a week until 12 September for a total of 10 sample dates. A random sample of 5 WCR and 5 NCR was taken from each trap (total = 60 beetles per type of trap), and placed in petroleum ether to dissolve the Tangle Trap[®]. Species and sex ratios were determined in the laboratory. Numbers of NCR and WCR caught in yellow and white traps on each of the 10 sampling dates were compared by paired, two-tailed *t* tests. Numbers of beetles caught in pheromone traps were compared by regression analysis, with numbers caught on sticky cylinders. The percentages of WCR on sticky traps and in the two types of pheromone trap were compared by two-tailed *t* tests.

The effect of trap colour and the purity of pheromone on attraction of males was investigated in August 1985 in two cornfields. The experiment was designed as a 2 X 3 factorial, replicated 6 times, with two colours (white and yellow), and three levels of pheromone purity: 2*R*,8*R* enantiomer (purity of Guss *et al.* 1984), racemic mixture, and a hexane check (blank control). Thirty-six traps were each separated by 15 m in a 75 X 75-m plot in each field. The traps were left in field 1 for 3 days (25-27 August), and in field 2 for 2 days (28-29 August), after which time the trapped beetles were sorted to species and sex. The percentage of WCR present in the fields was determined by counting beetles on 40 plants during the experiment, and ratios of beetles captured in pheromone traps was com-

pared to this standard. Data were normalized by the square root transformation, an analysis of variance was performed for each field, and means were separated by Duncan's (1955) multiple range test (DMRT).

Monitoring was conducted in 20 cornfields in Wellington county using traps baited with the racemic mixture of the WCR sex pheromone. Five traps were left in each field for four, 2-day intervals in August 1985. Beetles were counted on 60 whole plants once during the same 2-day intervals for comparison. Average numbers of beetles per pheromone trap were compared by regression analysis with average numbers of beetles per plant in each field. The time to monitor with five traps in each field (i.e. construction, installation and counting of beetles), and the time to count beetles on 60 plants were recorded.

Chemical attractants from squash blossoms. The attractiveness of 'Blue Hubbard' (*Curcurbita maxima* Duchesne) squash blossoms and of extracts of blossoms to corn rootworms was evaluated in August 1985 in one cornfield. All experimental material was placed in sticky, Pherocon 1C[®] pheromone traps that were attached 1-m high to wooden stakes placed between the rows of corn. Three experiments were completely randomized with either 7 or 10 replicates. After 2 days, the traps were brought into the laboratory and the beetles were sorted to species and sex. Significant differences between treatment and control means were determined by one-tailed *t* tests.

Attraction to whole blossoms was tested by comparing numbers of beetles in unbaited traps with numbers in traps baited with two squash blossoms suspended in small, plastic-screen bags. Traps were separated by 10 m along one row of corn. Extracts were obtained by soaking blossoms in either methanol (Fisher, HPLC) or 10% ether (Fisher, anhydrous reagent)/hexane (Fisher, HPLC) for 24 h at -9°C . The extract in methanol was concentrated under reduced pressure to one blossom-equivalent per 10 mL. One blossom-equivalent of the extract or 10 mL of methanol was placed in a 15-mL glass vial in each of the traps that were separated by 10 m along one row of corn. The extract in 10% ether/hexane was separated from the water that had exuded from the thawing blossoms, and was dried over anhydrous magnesium sulfate. The extract was concentrated under reduced pressure to one blossom-equivalent per 2.5 mL. Two blossom-equivalents of the extract or 5 mL of ether/hexane were placed in a 7-mL glass watchglass in each of the traps that were separated by 15 m in a 45 X 60-m plot.

Results

Trapping with sex pheromone. In 1984, more WCR were caught in white pheromone traps than in yellow ones on 10 of 10 dates, and more NCR were recorded in white traps than in yellow ones on 5 of 10 dates ($P = 0.05$; paired *t* test; $df = 5$) (Table I). The percentage of WCR caught in white and yellow pheromone traps and on sticky cylinders was not different in 19 of 20 comparisons ($P = 0.05$; two-tailed *t* test); for the remaining comparison (12 August 1984) a higher percentage of WCR was present in white pheromone traps than on sticky cylinders. Correlations between numbers of beetles in pheromone traps and numbers on sticky cylinders were significant for NCR in yellow pheromone traps and WCR in white traps (Table I).

Pheromone and the combination of pheromone and trap colour significantly affected the number of beetles captured in both fields in August 1985 for both NCR and WCR beetles (ANOVA; $P = 0.05$). Colour had a significant effect on the number of WCR caught (ANOVA; $P = 0.001$) (i.e. yellow traps caught fewer beetles), but not on the number of NCR caught (ANOVA; field 1 $P = 0.059$, and field 2 $P = 0.863$). Traps baited with the racemic mixture of the pheromone and traps baited with the 2*R*,8*R* enantiomer caught significantly more NCR and WCR beetles than did control traps (Table II). Traps baited with the 2*R*,8*R* enantiomer were more attractive to NCR than were traps baited with the racemic pheromone in both fields, whereas traps baited with the 2*R*,8*R* enantiomer were more attractive to WCR in field 2 only (Table II).

Values of r^2 for regression equations of numbers of corn rootworms caught in the extensive monitoring trial in pheromone traps (*Y*) compared to numbers counted on

Table I. Average numbers of northern (NCR) and western (WCR) corn rootworms caught per day in traps baited with the racemic WCR sex pheromone in a cornfield near Guelph, Ontario during August and September 1984

Trap type	Species			
	NCR		WCR	
	No./trap/day ± SE	r ²	No./trap/day ± SE	r ²
Pherocon 1C (yellow) + a pheromone	13.9 ± 0.8	0.46	7.4 ± 0.7	0.00 NS
Pherocon 1C (white) + pheromone	24.0 ± 1.0	0.06 NS	41.0 ± 2.0	0.54
Cylinder (yellow) unbaited	31.7 ± 3.3		30.2 ± 2.7	

r² values obtained from linear regression of numbers of NCR and WCR caught in pheromone traps (Y) as a function of numbers caught on sticky cylinders (X). NS, not significantly different from 0 (P = 0.05; df = 8; N = 10).

Table II. Average numbers of northern (NCR) and western (WCR) corn rootworms caught in Pherocon 1C® traps with various combinations of colour and sex pheromone in two cornfields near Guelph, Ontario during August 1985

Treatment	No. per trap per day ± SE		
	NCR	WCR	% WCR
Field 1 (23% WCR)			
Hexane			
-white trap	4.0 ± 2.0 a	0.3 ± 0.1 a	7
-yellow trap	4.4 ± 0.8 a	0.7 ± 0.1 a	14
Racemic mixture			
-white trap	18.0 ± 2.0 b	43.0 ± 5.0 c	71
-yellow trap	17.0 ± 3.0 b	5.0 ± 1.0 b	23
2R,8R enantiomer			
-white trap	122.0 ± 14.0 d	39.0 ± 5.0 c	24
-yellow trap	86.0 ± 11.0 c	3.3 ± 0.9 b	4
Field 2 (71% WCR)			
Hexane			
-white trap	1.8 ± 0.9 a	1.3 ± 0.5 a	42
-yellow trap	2.4 ± 0.8 a	0.8 ± 0.4 a	24
Racemic mixture			
-white trap	8.0 ± 1.0 b	15.0 ± 3.0 c	64
-yellow trap	12.0 ± 1.0 b	8.0 ± 1.0 b	40
2R,8R enantiomer			
-white trap	84.0 ± 4.0 d	33.0 ± 5.0 d	28
-yellow trap	71.0 ± 7.0 c	6.0 ± 1.0 b	7

Means of six replicates. Means in a column within a field and followed by the same letter were not significantly different (DMRT; P = 0.05).

Table III. Linear regressions of numbers of northern (NCR) and western (WCR) corn rootworms captured per pheromone trap (Y) as a function of numbers of beetles counted per whole plant (X) using data obtained from 20 cornfields in Wellington county, Ontario during August 1985

Sampling date	Regression equations			
	NCR	r ²	WCR	r ²
August				
5-9	Y = 5.00 + 24.50X	0.45	Y = 29.10 + 21.50X	0.39
12-15	Y = 3.23 + 9.79X	0.30	Y = 26.50 + 15.20X	0.26
19-22	Y = 1.97 + 3.22X	0.52	Y = 6.98 + 5.85X	0.07 NS
26-30	Y = 1.81 + 2.49X	0.26	Y = 1.21 + 4.14X	0.32

NS, r² values were not significantly different from 0 (P = 0.05; df = 18).

whole plants (X) were different from 0 (P = 0.05) except for WCR in the third week of August 1985 (Table III). Numbers of corn rootworms on plants increased throughout August while numbers caught in pheromone traps decreased (Fig. 1). Seventy-four percent of the beetles caught in pheromone traps during August were WCR whereas 63% of the beetles on whole plants were WCR.

Because sampling time is important when monitoring as part of a pest management program, the sampling time was calculated. Both the time to monitor five pheromone traps and the time to count beetles on 60 plants was approximately 40 minutes.

Chemical attractants from squash blossoms. Neither NCR nor WCR were attracted to traps baited with methanol extracts of squash blossoms at a concentration of one blossom per trap (P = 0.05; one-tailed t test; df = 12) (Table IV). Both sexes of the NCR and female WCR were attracted to traps baited with two intact blossoms (P = 0.05; one-tailed t test; df = 12) (Table IV). Twice as many WCR males were caught in baited traps than in control traps, but the difference was not significant because of the low numbers trapped. Females of both species were attracted to the 10% ether/hexane extract of squash blossoms whereas males were not (P = 0.05; one-tailed t test; df = 18) (Table IV).

Table IV. Average numbers of northern (NCR) and western (WCR) corn rootworms caught in sticky traps baited with methanol extracts of squash blossoms, whole squash blossoms, and ether/hexane (Et/Hex) extracts of squash blossoms in a cornfield near Guelph, Ontario in August 1985

Date	Treatment	n	Average no. per trap/2 days ± SE				% female	% WCR
			NCR		WCR			
			Males	Females	Males	Females		
19-21 Aug.								
	Methanol extract	7	3.3±0.9a	0.4±0.3a	0.4±0.2a	0.3±0.2a	16	16
	Control	7	4.0±1.0a	0.9±0.4a	0.3±0.2a	0a	17	6
21-22 Aug.								
	Whole blossoms	7	14.3±2.3a	2.4±1.1a	0.7±0.4a	2.0±1.0a	23	14
	Control	7	2.6±0.4b	0.3±0.2b	0.4±0.3a	0b	9	13
26-27 Aug.								
	Et/Hex extract	10	5.3±0.9a	4.5±0.8a	2.0±0.6a	2.3±0.6a	48	30
	Control	10	4.1±0.6a	1.3±0.5b	3.7±0.4a	0.3±0.2b	17	42

Means in a column within a sampling period and followed by the same letter were not significantly different (one-tailed t test; P = 0.05).

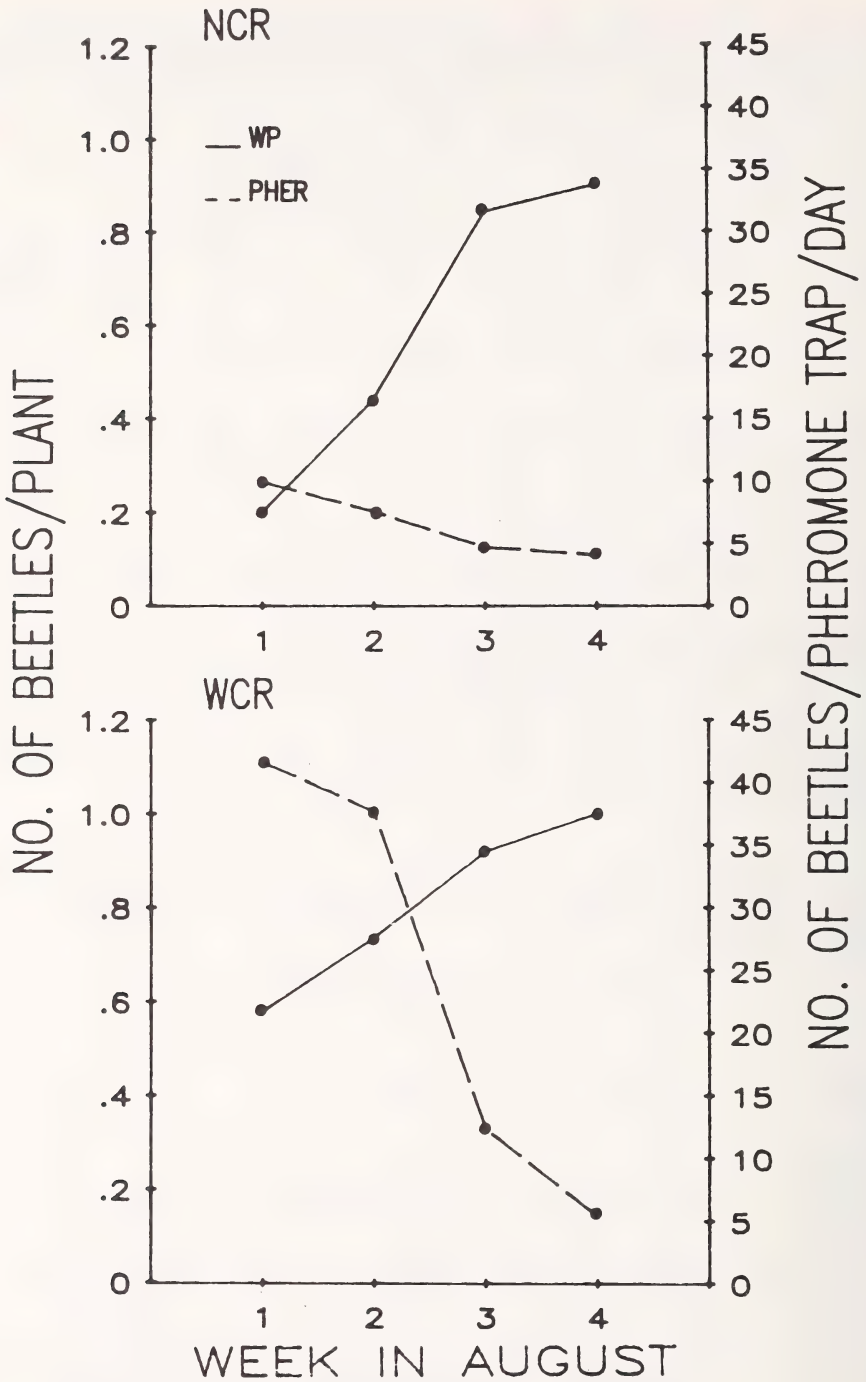


FIGURE 1. Average numbers of northern (NCR) and western (WCR) corn rootworms counted on 60 whole plants (WP) and in 5 pheromone traps (PHER) in each of 20 cornfields in Wellington county, Ontario in August 1985.

Discussion

Our results showed that the colour yellow did not enhance attraction to pheromone traps as Ball (1982) suggested (Tables I and II). Ladd *et al.* (1985) did not find enhanced attraction from the combination of eugonal (a food lure for the NCR) and the sex attractant. Because the wavelengths of light reflected from yellow surfaces and green leaves (i.e. food) are similar our similar results were expected. Yellow, however, has been observed to increase capture on traps baited with eugenol alone (Ladd *et al.* 1984).

More NCR were attracted to traps baited with the 2*R*,8*R* enantiomer than to traps baited with the racemic mixture of the pheromone (Table II). This difference was expected due to the presence of the inhibitory 2*S*,8*R* enantiomer in the racemic mixture (Dobson 1985). The unexpected result was the significantly greater attraction of WCR in one field to the traps baited with the single enantiomer. Further experiments could determine if this observed greater attraction of WCR was an artifact caused by too small a sample size.

White traps baited with the racemic mixture of the pheromone were the best choice for extensive monitoring of both species for the following reasons: 1) the most abundant corn rootworm in southern Ontario is the WCR and in field 2 (i.e. predominantly WCR) these traps caught the two species in approximately the same ratio as was indicated by counting beetles on whole plants, and 2) the racemic mixture of the pheromone is considerably less expensive and easier to synthesize than is the pure 2*R*,8*R* stereoisomer. The percentage of WCR that was caught in pheromone traps (74%) and the percentage counted on whole plants in 20 fields in Wellington county (63%) did not differ greatly. However, the opposite trends in abundance over time indicated by the two methods of monitoring (Fig. 1) present a major problem to the use of pheromone traps for monitoring. A second problem is that, although monitoring 5 pheromone traps takes the same amount of time as counting beetles on 60 plants, the additional cost of the pheromone and the traps reduces the usefulness of traps for monitoring.

The reduction in attraction to pheromone traps during August 1985 was probably not the result of the release of inadequate amounts of pheromone because 6-week-old lures still caught beetles in large numbers in August 1984 (McAuslane 1986). Nor was the reduction in attraction due to maturation of the population because males emerge throughout August in Ontario. The reduction in numbers caught in 1985 was more likely caused by low temperatures associated with rain and hail in the last 2 weeks of the month. VanWoerkom *et al.* (1980) found that the activity of WCR beetles decreased with decreasing temperatures. They suggested that using temperature in an equation to predict relative activity would increase the accuracy of assessments of field populations. Such an equation has yet to be developed, but is necessary in view of the poor relationship between numbers of corn rootworms counted on whole plants and numbers captured in pheromone traps.

Because pheromone traps declined in effectiveness over the period of trapping, a monitoring system based on traps might be more effective if other baits were used. A baited trap that caught higher proportions of females would have obvious advantages for pest management. Our research showed that ether/hexane extracts of 'Blue Hubbard' squash blossoms were attractive to female corn rootworms. Females were not caught in the high proportions found by Fisher *et al.* (1984) but did increase from 17% in the control traps to 48% in traps baited with extracts in ether/hexane (Table IV). Andersen and Metcalf (1986) identified indole as a volatile attractant in the blossoms of *C. maxima*, but suggested that the attraction in the field has many components. The isolation and identification of these attractive chemicals should be pursued.

In conclusion, future studies should be conducted on combinations of attractants (sex pheromones and host-plant attractants) in traps for monitoring corn rootworms. Traps baited with both types of attractants should monitor both male and female populations. If sex pheromone is to be used to bait sticky traps to monitor both species, lures should be loaded with less than 1 µg of the racemic mixture to prevent inhibition of the response of

NCR (Dobson 1985). Further studies should examine meteorological factors that may influence the numbers of beetles caught in traps baited with attractants.

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EVALUATION OF A NEW FUTURA® FORMULATION OF *BACILLUS THURINGIENSIS* ON POPULATIONS OF JACK PINE BUDWORM, *CHORISTONEURA PINUS PINUS* (LEPIDOPTERA: TORTRICIDAE)

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Abstract

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Futura®, a new concentrated formulation of *Bacillus thuringiensis* Berliner var. *kurstaki* was field tested in 1985 to determine its effectiveness against the jack pine budworm *Choristoneura pinus pinus* Freeman. Two concentrations, 20×10^9 and 30×10^9 international units per hectare (20 and 30 BIU/ha), were applied undiluted with a Cessna Ag-truck aircraft fitted with rotary atomizers. The 30 BIU/ha dosage satisfactorily suppressed *C. pinus pinus* populations (71% corrected larval mortality) and prevented serious defoliation of the host trees (64% foliage protection). The 20 BIU/ha treatment was only marginally effective in controlling jack pine budworm (44% corrected mortality) and was ineffective in preventing extensive defoliation (28% foliage protection).

Introduction

The jack pine budworm (JPBW), *Choristoneura pinus pinus* Freeman, is probably the most important insect pest of jack pine, *Pinus banksiana* Lambert in central Canada and the Lake States region of the United States (DeBoo and Hildahl 1967). Outbreaks of JPBW occur periodically and normally last from one to four years (DeBoo and Hildahl 1967), and can kill up to a third of the merchantable volume in jack pine (Clancy *et al.* 1980). Even when trees are not killed, many are deformed because the most severe feeding by the insect, in relation to the volume of available foliage, usually starts at the top of the trees causing top-kill and crooked or multiple leaders (Rose and Lindquist 1984).

In 1985, for the second consecutive year, infestations of JPBW increased dramatically in Ontario (M. Applejohn and G. Howse, unpublished Canadian Forestry Service 1985 Survey Bulletin) and Manitoba (K. Knowles, personal communication). These infestations threatened the wood supply of some sectors of the pulp and paper industry which depend almost exclusively on jack pine. Fenitrothion technical insecticide was the only insecticide registered in Canada at this time for aerial application against JPBW; therefore it was considered necessary to determine the efficacy of other insecticides prior to registering them for use against this species.

The toxicity of a number of chemical insecticides to JPBW had been determined in the laboratory (Nigam 1969-70, 1970; Robertson *et al.* 1978; B.V. Helson 1985, personal communication). Only preliminary bioassays have been conducted with the biological agent, *Bacillus thuringiensis* Berliner (*B.t.*), against JPBW (P. Fast, unpublished data), and not many field trials, conducted to control JPBW, are published (Benjamin *et al.* 1961; Benjamin and Renlund 1969, 1976; DeBoo and Hildahl 1967, 1971).

This paper presents results of a field trial which was conducted in the summer of 1985. The objective of the study was to evaluate the effectiveness of a new *B. thuringiensis* var. *kurstaki* formulation, Futura® XLV, in reducing populations of JPBW and protecting jack pine foliage.

Materials and Methods

The research was conducted ca 25 km southeast of Gogama in north-central Ontario. Three 50-ha (1.0 x 0.5 km) blocks, two for treatments and one as a control, were selected in

25 to 35 year old jack pine stands. Three 10- to 15-ha plots transected each block. Between 24 and 30 trees of uniform size (*ca* 10-m tall) were selected at random in each treatment plot as sample trees.

Spray Application. A new concentrated extra low viscosity *B.t.* formulation, Futura XLV (potency = 14.4×10^9 international units/L; density = 1.067 g/mL at 5°C; viscosity = 230 centipoises at 5°C) was applied undiluted. Blocks 1 and 2, the two treated blocks, received single applications at 20×10^9 international units per hectare (20 BIU/ha) and 30×10^9 international units per hectare (30 BIU/ha), respectively (Table 1).

Table 1. Spray deposit characteristics of Futura XLV

Plot	Number of samples (n)	Treatment*		Spray deposit					
		BIU/ha	L/ha	Drops/cm (X ± SD)	L/ha (X ± SD)	VMD µm	NMD µm	D _{max} µm	
1A	24	20	1.39	3.6 ± 5.1a	0.35 ± .21a				
1B	30	20	1.39	3.9 ± 5.9a	0.32 ± .17a				
1C	30	20	1.39	8.3 ± 5.9a	0.36 ± .19a				
Pooled	84	20	1.39	5.4 ± 6.4ab	0.34 ± .19a	57	12	220	
2A	30	30	2.08	6.9 ± 3.9abc	0.24 ± .11a				
2B	30	30	2.08	11.7 ± 7.3c	0.28 ± .15a				
2C	30	30	2.08	6.6 ± 7.0abc	0.28 ± .34a				
Pooled	90	30	2.08	8.4 ± 6.6bc	0.27 ± .22a	62	16	143	

Means in the same column followed by different letters are statistically different at Bonferroni P value < 0.003. [t-test adjusted for multiple pairwise comparisons at the P = 0.05 level.]

*20 and 30 BIU applied on 23 and 25 June respectively.

Erioacid red dye (Keystone Aniline and Chemical Co., Chicago, USA) was added as a tracer to the insecticide in 0.2% weight/volume proportions to facilitate droplet assessment. A Cessna 188-B Ag-truck aircraft fitted with four Micronair AU3000 rotary atomizers was used to apply the treatments. The aircraft flew *ca* 10 m above the forest canopy at 160 km/h. The sprays were applied under 'stable-inversion' weather conditions. Winds were on average 8.0 and 12.0 km/h and the R.H. 97 and 92% during the 20 and 30 BIU treatments, respectively. Sprays were applied when the jack pine needles were beginning to escape their fascicle sheaths and most budworm were fourth instar larvae.

Deposit Sampling. To monitor the spray deposit, clearings were made around each sample tree (Cadogan *et al.* 1984) and a deposit sample unit (Randall 1980) was placed in each clearing 1 h before the spray. Approximately 1 h after the spray, the sample units were retrieved and their Kromekote cards and glass slides were wrapped in aluminum foil and stored in a freezer at -4°C. The droplet stains on the cards were counted and their diameters measured using a card reader (Zylstra 1980) at the Canadian Forestry Service Laboratory in Sault Ste. Marie. Diameters of actual aerodynamic droplets were derived by applying spread factors (Rayner and Haliburton 1955). In our study the spread factor was determined to be $x = (y/1.0185)^{0.9191}$, where x is the droplet diameter and y the stain diameter. Each glass slide was washed with 1.5 mL of 0.1% NaOH solution to remove the *B.t.* deposit. The eluates were analyzed colorimetrically for dye content using a Pye Unicam PU8600 spectrophotometer. This facilitated volumetric estimates of spray deposits at ground level.

Sampling Jack Pine Budworm. One prespray and three postspray samples were taken at *ca* 5- to 7-day intervals to monitor populations of budworm larvae in the treated and control plots. Two 60-cm midcrown branch tips were taken with polepruners from each

sample tree, at each sampling. The branches were assessed visually (Cadogan *et al.* 1984) and with the branch-beating technique (Martineau and Benoit 1973). Reductions of larval populations were calculated and those in the treatment blocks were corrected for natural mortality occurring in the control block by using Abbott's (1925) method adapted to accommodate asynchronous dates (Cadogan *et al.* 1984). Pupae were collected and taken to the laboratory to monitor and evaluate adult emergence as a measure of the treatments' effects on pupal viability.

Defoliation. In October 1985, the sample trees were examined for defoliation. Two 60-cm midcrown branches were taken from each sample tree and assessed using Fettes' (1950) method with 6 defoliation classes instead of 10. The assessment was modified (unpublished data) to accommodate jack pine/JPBW relationships which differ substantially from the balsam fir/spruce budworm (*Abies balsamea* (L.) Mill./*C. fumiferana* [Clemens]) association for which Fettes designed his method.

Although the prespray populations were shown to be statistically not significantly different from each other (Table 2), we postulated that, in terms of defoliation, the observed differences might yet be of biological significance. Thus, sample trees in the control block with prespray populations of JPBW very similar to those in the treated plots were grouped together and their mean defoliation was matched against that *observed* in the treated plots. The defoliation in the grouped control trees represents the *expected* defoliation of the relevant treated plot. Using these observed and expected amounts of defoliation, we calculated the magnitudes of foliage protection attributed to the treatments (PAT): % PAT = $100(\% \text{ expected defoliation} - \% \text{ observed defoliation})/\% \text{ expected defoliation}$.

Statistical Analysis. The data relating to JPBW populations, jack pine defoliation and spray deposit were analyzed on a VAX/VMS computer system using BMDP statistical software (Dixon 1983). We primarily used the P7D (t-tests with and without the Bonferroni procedure; using, where relevant, either separate or pooled statistics) component of the software. Hypotheses are tested at $\alpha = 0.05$.

Results and Discussion

Spray Assessment. Table 1 presents deposit data that provide insight into the quality and, ultimately, the effectiveness of the applications. The volume and number median diameters (VMD and NMD) that resulted from the two treatments indicate that the droplet size compositions of the two sprays were basically similar. However, the sizes of the largest drops (D_{\max}) found in the two sprays indicate there were differences. Eleven to 13.5% and 23 to 26% of the 30 and 20 BIU/ha spray volumes, respectively, were collected at ground levels. The larger volumes deposited from the 20 BIU/ha treatment (Table 1) probably because of a few large drops as the D_{\max} suggests.

The 30 BIU/ha application had, on average, a higher density of droplets (drops/cm²) than the 20 BIU/ha application, this being caused by the larger emitted volume of the former. On the basis of these ground deposits on artificial media, we postulated that the trees were exposed to sprays, from both the 20 and 30 BIU/ha treatments, which were capable of providing sufficient deposit on foliage to control JPBW. The foliage that was examined showed that old needles had >3.0 drops/contaminated needle and the new growth <1.0 drop/contaminated needle. In general, more drops per needle were observed on the foliage treated with Futura at 30 BIU/ha than on that treated at 20 BIU/ha.

It has been postulated that both the potency of the drop i.e., the concentration of *B.t.* crystal and/or spores in the drop, and a drop frequency of 1.0 drop/needle are the primary determinants of an efficacious *B.t.* spray (P. Fast, unpublished Forest Pest Management Institute. File Report No. 67). Our results indicate that both Futura XLV sprays had the potential to be efficacious against JPBW.

Population Reduction. Reductions in larval populations in the treated and untreated plots are presented in Table II. Statistical analysis indicates that the prespray means were not significantly different from each other ($\alpha = 0.05$). Nevertheless large variances in population densities were observed between the samples. These variances were evidently

Table II. Jack pine budworm population reductions and host tree defoliation in Futura XLV-treated and untreated plots.

Block	Plot	Sample trees (n)	Treatment	Larvae/60 cm branch ($\bar{X} \pm SD$)		Final postspray*	Percent population reduction**	Percent defoliation ($\bar{X} \pm SD$)		% Protection attributed to treatment
				Prespray	Observed			Expected		
1	A	24	20 BIU/ha	16.6 ± 15.2a	7.8 ± 4.6acdhi	53	74 ± 19	60 ± 23adeg	19	
	B	30		14.9 ± 13.6a	7.9 ± 4.8ahi	47	82 ± 23	60 ± 21aghi	27	
	C	30		13.9 ± 8.2a	7.3 ± 5.1acdhi	47	78 ± 26	50 ± 22a	36	
2	Pooled	84		15.0 ± 12.4a	7.6 ± 4.1ahi	49(44)	78 ± 23	56 ± 22a	28	
	A	30	30 BIU/ha	7.3 ± 8.7a	2.0 ± 2.2efg	73	79 ± 22	27 ± 28c	66	
	B	30		15.6 ± 26.5a	3.5 ± 2.6acfj	78	79 ± 25	27 ± 22c	66	
Check	Pooled	90		7.4 ± 16.8a	2.2 ± 2.8dfj	70	59 ± 27	24 ± 17c	54	
	A	30	untreated	10.8 ± 18.9a	2.6 ± 2.6begj	74(71)	72 ± 26	26 ± 23c	64	
	B	18		12.8 ± 13.5a	11.9 ± 9.1hno	7	—	68 ± 25abefh	—	
Pooled	C	12		17.1 ± 21.3a	16.4 ± 14.4lop	4	—	85 ± 20bf	—	
	C	12		20.5 ± 22.3a	13.4 ± 7.4imoq	35	—	86 ± 18bdf	—	
	Pooled	60		15.6 ± 17.9a	13.5 ± 10.7knpq	13	—	77 ± 24efi	—	

Means in the same column followed by different letters are statistically different at Bonferroni *P* value <0.05 level [t-test adjusted for multiple pairwise comparisons of means using the Bonferroni test (Dixon 1983). Significance at the 0.05 level required a Bonferroni *P* value 0.001.

*Sampled 19-20 days after the spray.

**Reductions in parentheses were corrected for natural mortality (Abbott 1925).

caused by some of the sample trees having much more staminate buds than others. It has been reported that jack pine trees with staminate flowers have higher numbers of surviving budworm than those without (Graham 1935; LeJeune and Black 1950, Dixon and Benjamin 1962; Kulman *et al.* 1963).

Futura at 30 BIU/ha reduced larval populations from *ca* 10 insects/branch to between 2.0 and 3.5 per branch. These numbers of survivors were shown to be significantly less than in the other blocks and might be construed as satisfactory JPBW suppression by a microbial insecticide. Plots treated with 20 BIU/ha had surviving larval populations ranging from 7.3 to 7.9 insects/branch. These numbers suggest that the dosage was only marginally effective in suppressing moderate populations of JPBW.

When the population reductions in the treated blocks were corrected to reflect natural mortality, it was shown that 44 and 71% corrected reductions were recorded in the 20 and 30 BIU/ha blocks, respectively. These percentage reductions support our earlier contention (see above) that only the 30 BIU/ha dosage could be considered as satisfactory in controlling JPBW.

In the laboratory, adult moths emerged from 32% of the pupae collected from the 20 BIU/ha plots ($n = 32$) and 41% of the pupae from the control plots produced moths ($n = 220$). Only 10 pupae were collected from the 30 BIU plots. This number was considered too low to make an acceptable assessment of that treatment's effect on adult emergence. Four adults emerged from them. The emergence data suggest that Futura XLV at either of the applied doses did not seem to impair the viability of pupae of *C. pinus pinus*.

Defoliation. Defoliation which occurred in the treated and untreated plots are shown in Table II. An average of 26% defoliation was found in the plots treated with 30 BIU/ha. The 20 BIU/ha and control plots had, on average, 56 and 77%, respectively. Adjustments to determine the % PAT showed that Futura XLV at 20 BIU/ha protected 28% of the foliage whereas 64% foliage protection could be attributed to the 30 BIU/ha dosage. These figures support the data on population reduction which indicated that only the 30 BIU/ha treatment satisfactorily controlled JPBW.

To our knowledge, this is the first time *Bacillus thuringiensis* has been applied in Canada to control *C. pinus pinus*. On the basis of our findings, we believe that Futura XLV applied undiluted at 30 BIU/ha provided satisfactory JPBW population reduction and foliage protection. Although laboratory bioassays showed that a similarly concentrated formulation of *B.t.* at 20 BIU/ha was toxic to JPBW (P. Fast unpublished data) our 20 BIU/ha treatment was only marginally effective in suppressing JPBW populations and preventing defoliation of the host tree. It is evident that the lower dosage needs further testing to elucidate its inadequacies under field conditions.

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A REVIEW OF AERIAL SPRAY TRIALS WITH LECONTVIRUS FOR CONTROL OF REDHEADED PINE SAWFLY, *NEODIPRION LECONTEI* (HYMENOPTERA: DIPRIONIDAE), IN ONTARIO

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Abstract

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Redheaded pine sawfly nuclear polyhedrosis virus (Lecontvirus) was found to be a highly effective pathogen against redheaded pine sawfly, *Neodiprion lecontei* (Fitch), when applied as an aerial spray. This method of treatment is recommended. Between 1976 and 1980, 14 plantations with a total area of 175.5 ha were sprayed experimentally in Ontario and such factors as dosage, emitted volume, application equipment and tank mix adjuvants were evaluated. A preparation of lyophilized, virus-infected larvae ground to a fine powder and suspended in water was used. That preparation was applied on first-, second- or third-instar redheaded pine sawfly larvae in the field. A dosage of 5×10^9 polyhedral inclusion bodies per ha in emitted volumes ranging from 2.4 to 9.4 L/ha gave excellent control. The best assessment method was found to be examination of 100 trees each with one sawfly colony from which the following were recorded; the length of time from spray application until first virus-induced mortality; and the length of time until the entire colony was dead. None of the plantations required re-treatment following application of the virus.

Introduction

The redheaded pine sawfly, *Neodiprion lecontei* (Fitch), is one of the most damaging insects attacking young hard pine (*Pinus* spp.) plantations in Ontario, Quebec and New Brunswick. This insect also occurs in the eastern United States and is found as far south as Florida. Severe defoliation by redheaded pine sawfly can cause reduced growth in height, branch mortality, tree deformity if the leader is killed, and tree mortality. Trees continue to be susceptible to attack until they reach the size when crown closure occurs, at which time sawfly colonies are only found around the perimeter of a plantation. Although red pine, *Pinus resinosa* (Ait.), is the principal host, jack pine, *P. banksiana* Lamb., and Scots pine, *P. sylvestris* L., can also be attacked (Benjamin 1955; MacAloney and Wilson 1964).

Neodiprion lecontei has one generation per year in Canada. From mid-June to early July adult sawflies emerge from overwintered cocoons in the duff layer of the soil. Females lay 80 to 140 eggs and the typical incubation period in southern Ontario and Quebec is three to four weeks. The sawfly larvae are gregarious and feed on foliage of all ages although they show preference for the previous year's foliage. Larvae are fully grown 25 to 30 days after eclosion. Sawfly larvae pass through five feeding instars and one non-feeding instar before spinning their cocoons (Middleton 1921; Benjamin 1955; Griffiths 1960). Red-headed pine sawfly is the most serious insect pest of red pine (Rose and Linquist 1973) and large areas in Ontario and Quebec have been planted with this species in the last 20 years. Until recently, most attempts to control redheaded pine sawfly have used chemical insecticides applied from the ground; malathion has been the usual choice. In many instances, sufficient larvae survived to reinfest the areas, which required re-treatment the following year (personal observations).

In 1950, a nuclear polyhedrosis virus (NPV) disease of the redheaded pine sawfly was found in Ontario (Bird 1961). Such viruses are classified as *Baculoviridae*, sub-group A (Matthews 1979) and have been found to infect only invertebrate animals. In a series of laboratory and ground spray trials, Bird demonstrated that the virus was highly virulent,

effectively controlled sawfly populations and was transmitted from one insect generation to the next (Bird 1961; 1971; Anonymous 1970). In 1975, a research project was initiated at the Forest Pest Management Institute to develop redheaded pine sawfly NPV as an operational biocontrol agent. Aerial spray trials were conducted between 1976 and 1980 to study such factors as dosage, application volume, application equipment and tank mix so that recommendations could be made on its effective use. These trials are reported in detail by Kaupp and Cunningham (1977), Kaupp *et al.* (1978), de Groot *et al.* (1979) and de Groot and Cunningham (1983). In this report, results obtained over the 5-year period are summarized and the implications of the entire project are discussed.

Materials and Methods

Virus Production

To propagate the redheaded pine sawfly NPV, a plantation with a high density of sawfly colonies was selected. When larvae reached the fourth instar, the plantation was sprayed, using mistblowers to deliver about 20 L/ha, with a suspension of 10^6 polyhedral inclusion bodies (PIB)/mL. Usually every third or fourth row of trees was treated. After about seven days, when colonies started to die, diseased and moribund colonies were clipped from the trees and taken to a laboratory where the larvae were removed. Collections were made daily until all larvae had either died or pupated. Diseased larvae were frozen, lyophilized and ground to a fine powder. The virus representing the active ingredient (A.I.) was only about 0.05% of the preparation, the rest being milled insect parts. This virus-containing larval powder produced by Forest Pest Management Institute staff has been named *Lecontivirus*.

Standardization of Virus Preparations

Virus preparations were standardized using a Petroff-Hausser bacteria counter under phase contrast microscopy at 250x magnification. A weighed sample of lyophilized virus-infected larval powder was suspended in a known volume of water, ground in a tissue grinder and left to stand in a refrigerator at 2°C for about 30 days to allow breakdown of insect tissue and release of PIBs. These PIBs are very small in comparison with PIBs from NPV-infected Lepidoptera and have a mean diameter of 0.72 μm , ranging from 1.44 μm to 0.29 μm . Batches were standardized to 2×10^9 to 10^{10} PIB/g lyophilized powder.

Experimental Plots

A description of the 14 treatment plots and the 7 untreated control plots located in central and southeastern Ontario is given in Table I. All plantations contained only red pine except 1977 plot 3, which also contained jack pine and 1977 untreated control plot 1, which contained only jack pine. The total area treated over the 5-year period was 175.5 ha.

Spray Applications

Fixed-wing aircraft fitted with either boom and nozzle equipment or four Micronair® AU 3000 units were used for all applications. Applications were done in the early morning when relative humidity was high and wind velocity low. The various tank mixes used are given in Table I. Additives used were a sunscreen called IMC 90-001®, later renamed Sandoz Shade®, and animal feed-grade molasses. The sunscreen made spray droplets visible on Kromekote® cards and facilitated measurement of spray coverage. Rhodamine B, at a concentration of 0.04%, was added to the tank mixes to monitor the deposit on spray cards when purified PIBs or lyophilized, virus-infected larvae were applied in water only.

In 1976, three dosages were tested and, in 1977 and 1978, these results were verified at the same time as the application efficiency of boom and nozzle and Micronair equipment was compared. In 1979, virus in water alone was compared to virus formulated in molasses plus the sunscreen. Between 1976 and 1979, the emitted volume on all plantations was 9.4 L/ha. In 1980, emitted volumes of 2.4, 4.7 and 9.4 L/ha were compared and purified virus was compared to the lyophilized, virus-infected larval preparation. Details of insect development at the time of application, dosages, emitted volumes, tank mixes and spray equipment are also listed in Table I.

Table I. Summary of experimental site characteristics, insect population density and stage of larval development, and application rates, dosages, formulations equipment and spray coverage for plantations used to assess the efficacy of Lecontevirus to control redheaded pine sawfly in Ontario between 1976 and 1980

Year treated	Plot No.	Location (Nearest Settlement)	Area (ha)	Mean height of trees (m)	No. of colonies/ 100 trees, pre-sprayed	Predominant instar at application date	Emitted volume (L/ha)	Dosage (PIB/ha x 10 ⁹)	Tank no.*	Spray equip-ment**	Droplets /cm ² (Krome-kote cards)
1976	1	Lakefield	16.0	0.8	118	2	9.4	1.3	3	B&N	33
	2	Lakefield	8.0	1.8	176	2	9.4	3.8	3	B&N	45
	3	Lakefield	19.2	1.4	346	2	9.4	6.3	3	B&N	28
1977	Control			Lakefield	4.0	2.0	138	2			
	1	Renfrew	13.2	2.2	163	2/3	9.4	5.5	5	B&N	10
	2	Renfrew	30.8	1.2	81	2/3	9.4	5.5	5	B&N	11
1978	3	Richmond	8.0	2.0	132	4	9.4	5.5	5	M	60
	Control 1			Richmond	0.5	1.8	248	2/3			
	Control 2			Renfrew	4.0	2.6	217	4			
1979	1	Dalhousie Lake	12.6	2.5	255	2	9.4	5.0	4	M	62
	2	Crow Lake	13.6	2.1	174	2	9.4	5.0	4	M	103
	Control 1			Claredon Stn.	0.8	1.2	202	2			
1980	Control 2			Crow Lake	1.8	1.6	204	2			
	1	Golden Lake	4.9	2.0	77	1/2	9.4	5.0	2	M	132
	2	Cobden	16.2	2.1	5	2	9.4	5.0	5	M	93
1980	Control			Petawawa	1.0	1.6	95	1/2			
	1	Minden	7.0	2.9	52	1	2.4	5.0	2	M	64
	2	Minden	18.0	1.4	173	1	4.7	5.0	2	M	91
	3	Gelert	4.0	2.4	225	1	9.4	5.0	2	M	35
1980	4	Carravon	4.0	1.1	25	1	9.4	5.0	1	M	115
	Control			Minden	25.0	7.0	56	1			

* Key to tank mixes: 1. Purified PIB in water alone

2. Lyophilized virus-infected larvae (LVIL) in water alone

3. LVIL + 60 g/L sunscreen (IMC 90-001 or Sandoz Shade)

4. LVIL + 13.5% molasses + 32 g/L sunscreen

5. LVIL + 25% molasses + 60 g/L sunscreen.

**B&N = Boom and nozzle; M = Micronair AU 3000 atomizers.

Effect of Treatments on the Sawfly Populations

Between 1976 and 1980 the impact of the virus applications was recorded visually by three methods: 1) by death or total disappearance of colonies (1976 and 1977), 2) by the appearance of virus-infected larvae in colonies (1978), and 3) by rating colonies either as healthy, virus-infected or dead (1979 and 1980). Initially, larvae were examined microscopically for NPV infection, but in later years, this was found to be unnecessary because virus-killed larvae were so distinctive.

In 1976, a line of 50 trees across the plots, at right angles to the flight lines of the spray aircraft, was selected without consideration as to whether the trees harboured sawfly colonies. The same procedure was used in 1977 and 1978, but with more tagged trees, either 100 or 150 per plot. Untreated plots were evaluated in the same manner. In 1976 and 1977, sawfly colonies were recorded either as dead or missing and, in 1978, they were scored as containing diseased larvae. In 1976, observations were recorded 12, 18 and 22 days post-spray, in 1977, 5, 11, 13, 20 and 26 days post-spray and in 1978, 9, 10, 11, 12, 15, 16, 18, and 23 days post-spray.

In 1979, based on our experience in the previous three years, we radically changed the procedure and 100 trees with only one colony/tree were selected in the treated and untreated control plots. If necessary, colonies were removed from some trees so that only one remained. Observations were made daily, commencing five days post-spray, and each colony was scored as healthy, virus-infected or dead. This method was found to be satisfactory and was used again in 1980.

Surveys in the Years Following Virus Application

The treated plantations were examined annually for at least two years following the virus application when redheaded pine sawfly larvae were in the fourth-instar or larger, and easy to detect. Depending on the amount of time and manpower available, these surveys were based on the examination of 200, 300 or 400 trees per plot. Some of the untreated control plots were also examined, but later these were abandoned because; a) they had been treated with malathion, b) the trees had been killed by the sawflies, c) the sawfly population had been decimated by egg parasites, or d) the trees had grown so that crown closure had occurred and they were no longer susceptible.

In 1982, four of the treated plots were left out of the survey. Two of them, 1976 plot 1 and 1976 plot 3, had been heavily damaged by web-spinning sawflies, *Cephalcia* spp., and a further two, 1977 plot 1 and 1978 plot 1, had developed closed crowns.

Results

Deposit Analysis

The number of droplets/cm² on Kromekote cards placed on the ground ranged from 10 to 135 (Table I). Usually a larger number of smaller droplets was obtained with Micro-nair than with boom and nozzle equipment.

Redheaded Pine Sawfly Mortality

In 1976 there was little difference in the impact of the three dosages tested (Table II). The lower mortality figure from the intermediate dosage is misleading because insect development was slower than that in the other two plots and 27% of the egg clusters had not hatched at the time of spray application. Microscopic examination of 50 larvae per plot revealed infection of 92, 96 and 98% in plots 1, 2 and 3 respectively at 17 days post-spray.

Neither a change in application equipment nor an approximately 50% reduction in the amount of molasses and sunscreen affected the efficacy of the virus application in 1977 and 1978. In both years 100%, or nearly 100% sawfly mortality was obtained. A comparison of the virus in water alone with the virus formulated with 25% molasses and 60 g/L Sandoz Shade at a dosage of 5×10^9 PIB/ha (1979 test) showed that both gave complete control of the sawfly. There was no difference in the effect when the same dosage of virus was applied in 2.4, 4.7 or 9.4 L/ha or between lyophilized, virus-infected larval material and purified PIBs at the dosage used in the 1980 test.

A sudden decline in the number of sawfly colonies in 1977 on plot 3 prompted an

Table II. Percent mortality* of redheaded pine sawfly colonies due to viral infection following aerial application of Ieconvirus in Ontario

Year treated	Plot no.	DAYS POST-SPRAY																									
		5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26				
1976	1	---	---	---	---	---	---	---	---	---	24	---	---	---	---	---	---	---	---	---	---	---	---	---	---		
	2	---	---	---	---	---	---	---	---	---	16	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
	3	---	---	---	---	---	---	---	---	---	37	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
1977	Control 0	---	---	---	---	---	---	---	---	---	---	3	---	---	---	---	---	---	---	---	---	---	---	---	---	---	
	1	6	---	---	---	---	---	---	---	45	---	43	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
	2	2	---	---	---	---	---	---	---	41	---	40	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
1979	3***	64	---	---	---	---	---	---	---	64	---	69	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
	Control 1	0	---	---	---	---	---	---	---	---	0	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
	Control 2	0	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
1980	1	---	---	---	---	---	---	---	---	4	43	55	---	---	56	---	---	---	---	---	---	---	---	---	---	---	---
	2	---	---	---	---	---	---	---	---	12	47	52	---	---	53	---	---	---	---	---	---	---	---	---	---	---	---
	Control 1	---	---	---	---	---	---	---	---	0	0	0	---	---	0	---	---	---	---	---	---	---	---	---	---	---	---
1979	Control 2	---	---	---	---	---	---	---	---	0	0	0	---	---	0	---	---	---	---	---	---	---	---	---	---	---	---
	1	4	8	21	28	41	55	72	88	91	95	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
	2	5	9	19	32	44	62	72	82	87	91	93	99	100	---	---	---	---	---	---	---	---	---	---	---	---	---
1980	Control	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	1	0	0	3	5	13	26	45	57	70	82	92	98	99	100	---	---	---	---	---	---	---	---	---	---	---	---
	2	0	0	0	3	8	20	36	51	56	75	88	96	98	100	---	---	---	---	---	---	---	---	---	---	---	---
1977	3	3	7	14	19	22	46	63	73	79	84	95	99	99	99	99	99	99	99	99	99	99	99	99	99	99	100
	4	0	0	1	9	15	40	58	69	75	82	93	100	---	---	---	---	---	---	---	---	---	---	---	---	---	---
	Control	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

* In 1976 and 1977 mortality was recorded as complete disappearance of colonies, in 1978 it was recorded as the appearance of virus-infected colonies and in 1979 and 1980 both occurrences were recorded although only the appearance of virus-infected colonies is recorded in this table.
 ** Indicates no observation made on that date.
 *** Tank mix was contaminated with 522 µg/ml of the insecticide phosphamidon.
 **** Onset of pupation confounded estimate of percent mortality.

analysis of the tank mix. It was found to contain 522 µg/mL of the insecticide phosphamidon (K.M.S. Sundaram, personal communication). This material had been used in the aircraft for a previous spray application and, although the Sorrensen® belly tank on the aircraft had been flushed out, sufficient traces remained to kill sawfly larvae. Some species of sawfly larvae are highly susceptible to phosphamidon (Randall and Nigam 1966).

During the 5-year period, no naturally occurring virus was found in any of the 7 untreated control plots. The slight decline in number of colonies in 1976 and 1977 (Table II) probably resulted from colonies coalescing when there was more than one colony per tree. This possible problem was eliminated in 1979 and 1980 when sample trees with only one sawfly colony per tree were selected.

Surveys in the Years Following the Year of Application

Of the 14 treated plots surveyed all but two, 1978 plots 1 and 2, were completely free from sawflies the year after treatment (Table III). Only in 1978 plot 2, did the infestation continue and increase until it reached 20.7 colonies/100 trees 5 years after treatment. This figure appears to be high and may be misleading because most of the colonies were restricted to a few trees with high numbers of colonies per tree. None of the plantations required re-treatment following application of NPV.

Table III. Survey of plantations treated with redheaded pine sawfly NPV in years following the year of application.

Year treated	Plot	Number of colonies/100 trees					
		1977	1978	1979	1980	1981	1982
1976	1	0	0	0	0	0	—*
	2	0	0	0	0	0.75	1.0
	3	0	0	0	0	0	—*
1977	1	—	0	0	0	0.75	—**
	2	—	0	0	1.75	0	0
	3	—	0	0	0	0.5	3.7
1978	1	—	—	2.5	1.25	2.0	20.7
1979	1	—	—	—	0	0.25	0
	2	—	—	—	0	0	0
1980	1	—	—	—	—	0	0
	2	—	—	—	—	0	0
	3	—	—	—	—	0	0
	4	—	—	—	—	0	0

* Survey discontinued because of heavy damage to the plantations by *Cephalcia* spp.

** Survey discontinued because crown closure had occurred and the plantations were no longer at risk.

Discussion

Redheaded pine sawfly NPV is a highly effective biocontrol agent and, in many respects, is preferable to chemical pesticides. It is highly specific and affects only redheaded pine sawfly larvae. Also, when it is correctly applied, plantations do not require re-treatment in subsequent years. Compared to chemicals, however, the virus is slow-acting; high insect mortality is usually noted about 15 days post-spray, although often 24 to 31 days elapse before complete mortality occurs. The length of time required for larvae to die varies because of variation in such factors as spray deposit, stage of development of the insects at the time of application and temperature.

From our tests, we conclude that a dosage of 5×10^9 PIB/ha can consistently provide effective control when the sawfly larvae are in the first, second, or third instar. Unfortunately, no dosage/response trials were conducted to determine the minimum effective dosage. In comparison to dosages of NPV used to control lepidopterous pests in forests, the dosage for redheaded pine sawfly NPV is about one-fiftieth lower and is the same as recommended for European pine sawfly (Cunningham 1982). Fifty virus-infected red-headed pine sawfly larvae can produce enough virus to make dosage of 5×10^9 PIB/ha and, in 1985 on a cost only basis, this has been estimated to be about \$2.50/ha.

Regardless of the changes made in tank mixes, application volumes, types of virus material used and spray equipment, excellent results were obtained at all dosages used when the NPV was applied on first-, second- and third-instar larvae. Because additives in the tank mix did not increase efficacy, the use of virus in water alone is recommended. Lyophilized, virus-infected larval preparations are as effective as purified PIBs and, as considerable expense is involved in purification, use of the former preparation is advised. Emitted volumes of 9.4, 4.7 or 2.4 L/ha all gave effective control. Because the application rate of 9.4 L/ha gave consistently good results over the 5-year period and our experience with lower application rates is limited, we suggest an application rate of 9.4 L/ha until the efficacy of lower rates is further verified. Further studies should be directed at determining the lowest effective application rate of Lecontivirus.

The evaluation methods were greatly improved during the project. Selecting 100 trees, each with one sawfly colony, avoided problems in counting colonies which may coalesce and divide. Scoring colonies as healthy, diseased and totally dead gave a reliable record of the progress of the epizootic.

Lecontivirus received temporary registration in 1983 under the Pest Control Products Act (Canada), and has been used every year by the Ontario Ministry of Natural Resources personnel who have treated about 353 plantations with ground spray equipment.

Acknowledgements

We wish to thank Dr. J.R. Carrow, head of the Ontario Ministry of Natural Resources (OMNR) Forest Protection Branch at the time of this project, for his enthusiasm and encouragement. OMNR staff was helpful in identifying experimental sites in Lindsay, Pembroke, Minden, Ramsayville, Tweed and Lanark districts.

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A COMPUTER-BASED MANAGEMENT SYSTEM FOR ALFALFA PESTS IN ONTARIO¹

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Abstract

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A pilot system of on-line pest management has been developed at the Ottawa Research Station for use by extension personnel in southern Ontario. The system is based on an interactive software program, SIMWEEVIL/SIMABL, that monitors seasonal development of the alfalfa weevil, *Hypera postica* (Gyll.), and the alfalfa blotch leafminer, *Agromyza frontella* (Rond.), together with their host crop, and automatically prints advisories that describe actions to be taken by field scouts and/or farmers. SIMWEEVIL/SIMABL is complemented by a computer-mapping package that provides supervisors of pest management teams with a graphical display of pest and crop development as they occur across the province. An additional software routine enables users to interface crop/pest phenologies. SIMWEEVIL/SIMABL is available on-line to all agencies with terminal access to the Agriculture Canada mainframe computer.

Introduction

During the past decade, management of agricultural pests has been greatly facilitated by the rapid development of computer technology. The essential components, both hardware and software, have proliferated almost exponentially, and recent market trends have brought these elements within the budget of many farm organizations. This has greatly increased the prospects for implementing on-line integrated pest management (IPM). Such an IPM system should accommodate the following information: 1. Biological data on pest population and crop status provided by IPM scouts, extension agents, and farmers. 2. Environmental data which determine the rate of growth and development in pest and crop models. 3. Decision aids such as damage thresholds, phenology data, and sequential decision plans. 4. Reference files which contain a menu of pest life cycles, descriptions of damage, and specific control measures. It should also provide for transmission of messages and reports between terminals (electronic mail).

Many of these features are embodied in a pilot program recently developed at the Ottawa Research Station (ORS) for pest management on alfalfa.

Central System

The ORS pest management system is primarily based on an interactive software program that goes by the acronym SIMWEEVIL/SIMABL – SIMulated WEEVIL and SIMulated Alfalfa Blotch Leafminer program (Yee and Harcourt 1983). First deployed in 1981, SIMWEEVIL/SIMABL consists of a set of files and procedures that were designed to monitor seasonal development of the alfalfa weevil, *Hypera postica* (Gyll.), and the alfalfa blotch leafminer, *Agromyza frontella* (Rond.), together with their host crop, *Medicago sativa* L. Written in Fortran, the program is housed in the Agriculture Canada VAX 8600 computer (the mainframe) and may be accessed by a series of simple commands on typewriter terminals such as DECWRITER III (Digital Equipment Corp.).

¹ Contribution from the Ottawa Research Station (NO. 823 A). From an address given by the senior author entitled "The concept and development of on-line pest management." National Work Planning Meeting on Pest Management, Mont St. Marie, Quebec, May 6-8, 1985.

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SIMWEEVIL/SIMABL was constructed on the basis of current research on crop and pest phenology, trend forecasting, and a detailed knowledge of the pests' demographic histories gained from life table studies. The computer models (algorithms) are temperature driven and use equations that mimic the developmental durations of the three biological components of the system. These equations interpolate a daily temperature curve from maximum and minimum temperatures and have been validated in the field over a period of years (Harcourt and Yee 1982, Harcourt *et al.* 1983). Weather data are obtained on-line from the Agrometeorology Section (AGMET) of the Land Resource Research Institute at Ottawa which provides daily temperatures from a network of 18 weather stations in southern Ontario. Thus, rapid updates are possible, enabling dynamic simulations of insect and crop development as they occur across the province.

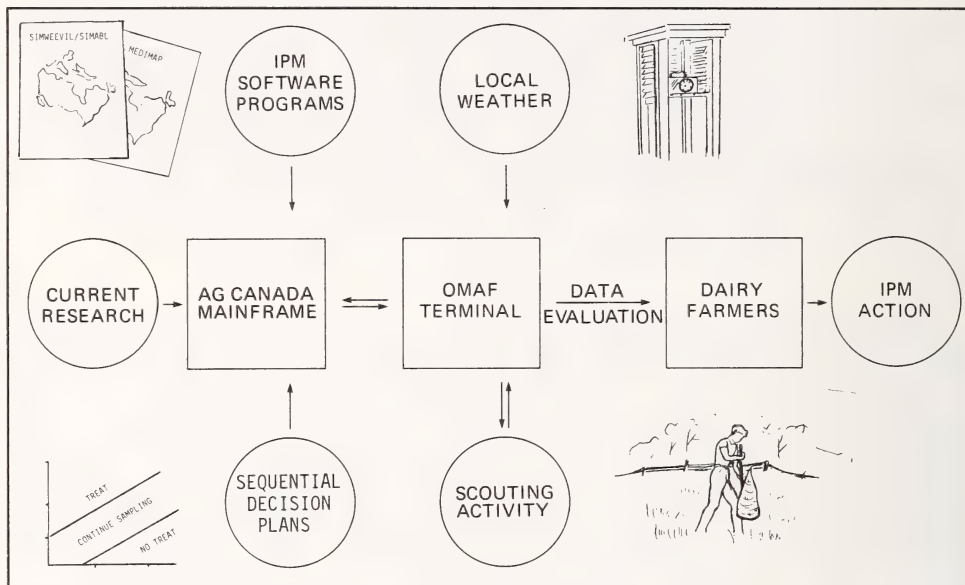


FIGURE 1. Flow chart for Ottawa Research Station pest management system.

At the operational level, the objective of the program is to produce scouting and pest management advisories for extension agents and farmers. Figure 1 outlines the steps involved and the activities required. To access the system, the client (OMAF³ scout in this example) utilizes a remote terminal linked interactively to the mainframe. To obtain the daily scouting advisory, the scout simply inserts local temperature minima and maxima for the previous 24 h period. The printout consists of reports on current stage of development of the pests and the crop, together with a projection of the number of days to the next stage or the occurrence of critical events such as peak flight or larval hatch. An additional message describes actions to be taken by the crop manager (Fig. 2).

Temperatures may be entered daily or periodically throughout the season beginning on 1 April. In addition, data from five-day forecasts may be used for predictive purposes and then overwritten by actual values. To enable scouts to assess the economic status of the target pests, sequential decision plans (Harcourt and Guppy 1976, Harcourt 1983) are included in the scouting kit. However, a directory of sequential plans is also housed in the mainframe computer; for the alfalfa weevil these are indexed to reflect geographic variation in the proportion of eggs laid in the ground litter.

LOCATION : SMITHFIELD
 STATUS AS OF OO:OH 29-MAY-84

ALFALFA CROP STAGE : EARLY BUD
 MID BUD EXPECTED WITHIN 4 DAYS.
 MAXIMUM PROTEIN LEVELS HAVE BEEN REACHED.

ALFALFA WEEVIL STAGE : LARVAL INSTAR 1 : DEVELOPMENT 2%
 LARVAL INSTAR 2 PEAK EXPECTED WITHIN 4 DAYS.
 CHECK FOR LARVAL FEEDING DAMAGE IN FOLIAGE. IF 25% OF STEMS
 SHOW FEEDING DAMAGE IN THE TIPS, HARVEST OR SPRAY
 IMMEDIATELY.

ALFALFA B. L. STAGE : ADULT G1
 EGG G1 PEAK EXPECTED WITHIN 3 DAYS.
 PINHOLING WILL BE EVIDENT IN AREAS OF HIGH INFESTATION.
 STARTING IN 1 DAY
 USE EARLY WARNING SYSTEM TO ARRIVE AT A TREAT/NO TREAT DECISION.
 IF NO TREATMENT INDICATED, RESAMPLE IN 3 OR 4 DAYS. IF
 TREATMENT INDICATED, HARVEST IMMEDIATELY IF CROP HAS REACHED
 BUD STAGE AND THERE IS SUFFICIENT BULK. OTHERWISE SPRAY
 WITH A PESTICIDE.

FIGURE 2. A typical advisory message generated by SIMWEEVIL/SIMABL.



FIGURE 3. A typical computer map generated by the MEDIMAP program.

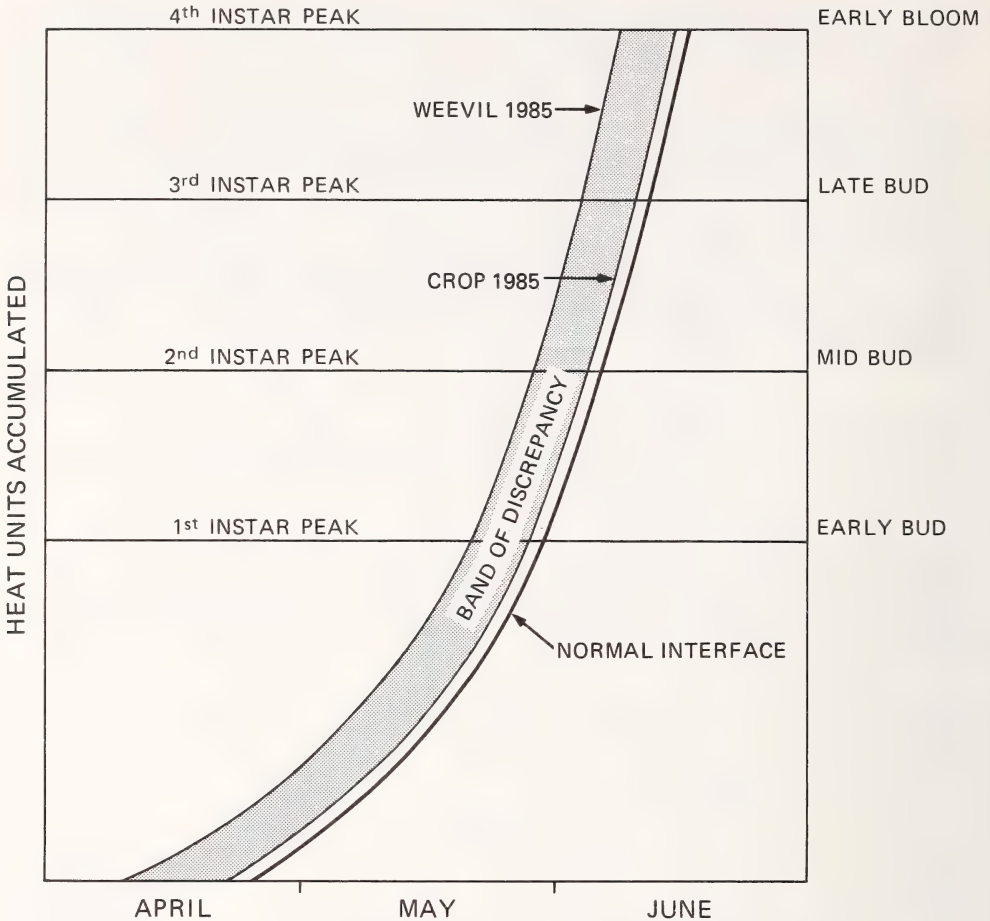


FIGURE 4. Weevil and crop phenology in the Bay of Quinte area. Note that peak attack normally coincides with the late bud stage of the first crop.

Complementary Software

There are two complementary software programs. A management package, MEDIMAP (an acronym for MEDICago MAPPING system) has been developed to provide an overview of current pest and crop development on a geographical basis (Yee and Harcourt 1984). This program enables the IPM supervisor to generate lineprinter style maps to coordinate scouting activities. It uses AGMET temperatures from selected sites to produce a graphical display of insect and crop development as they occur throughout southern Ontario. Figure 3 illustrates a typical computer map for the alfalfa weevil.

A second complementary package is entitled SUMHEAT (a SUMmation of HEAT units). This program tracks the phenology of the two pests and their host plant from 1 April to enable users to follow synchrony of development. The routine uses degree-day accumulations above base values of 9°C for the weevil and 5°C for the leafminer and alfalfa crop (Harcourt 1981, 1984; Harcourt *et al.* 1983). The weather inputs are maximum and minimum daily temperatures which are transmitted from the 18 network stations and a

number of farm sites. This program enabled us to detect the alarming discrepancy between weevil and crop development in 1985. Figure 4 shows the average dates of occurrence for the larval instars in relation to crop development (normal interface) in the Bay of Quinte area based on records for the past 14 years. However, in 1985, plots of the data early in the season showed that the weevil was a full stage ahead of the expected schedule, whereas the crop was just two days early. This greatly increased the potential for damage and occurred at a time when data from the life tables signalled a population increase. This information enabled us to issue a media alert for south-central Ontario in early May. The alert was also transmitted to scouts, by electronic mail.

Availability of System

SIMWEEVIL/SIMABL is available on-line to all agencies in Ontario and Quebec with terminals that can access the VAX computer. During the past 5 years, field scouts based at Ottawa and Simcoe have used the system to inspect a total of 10,000 acres of forage alfalfa across Ontario, with scouting circuits in the Grenville-Dundas, Haldimand-Norfolk, and Bay of Quinte areas. To extend this coverage and provide greater access to the program, we are currently developing microcomputer software (in the form of diskettes) for distribution to extension offices in the major alfalfa growing regions of central Canada.

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OCCURRENCE OF *TRICHOGRAMMA* SPP. (HYMENOPTERA: TRICHOGRAMMATIDAE) IN APPLE ORCHARDS IN SOUTHERN ONTARIO

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Trichogramma spp. have been released for the biological control of the codling moth, *Cydia pomonella* (L.) by several workers (see Dolphin *et al.* 1972; Dysart 1972; Nagy 1973). In Ontario, Yu *et al.* (1984) showed that, after inundative release, both *T. pretiosum* Riley and *T. minutum* Riley dispersed in apple orchards and parasitized eggs of *C. pomonella* on cards placed within the tree canopy. To assess the importance of these species as parasites of *C. pomonella*, as well as to better understand their population trends in apple orchards, the occurrence of *Trichogramma* spp. was monitored in 27 unsprayed (no insecticides) and seven sprayed apple orchards in six counties in southern Ontario from 1982 to 1984.

Parasites were monitored using egg cards containing 40, 24 to 48 h old eggs of *C. pomonella* or the oriental fruit moth (*Grapholitha molesta* [Busck.]). Cards were prepared by cutting sections from waxed paper oviposition cages (George and Howard 1965) and sticking them onto 7.5 x 12.5 cm white index cards. Four egg cards were then stapled to individual apple trees, one in each quadrant, just within the edge of the canopy and about 2 m above ground level. Cards were set out, at irregular time intervals, on three to five trees per orchard from early May to late August except at Louth and Jordan Station (Lincoln county) where weekly placements on three or four trees were made. The cards were collected after five days and placed in 20-cm diam. petri dishes in the laboratory at 20 to 24°C to allow development of the host and parasite. When the eggs turned black, indicating parasitism, they were placed in small glass vials and parasite emergence subsequently checked.

In 1982 and 1983, *T. pretiosum* was the only species recovered in the 27 unsprayed apple orchards. In the orchards sampled at weekly intervals at Louth and at Jordan Station, parasitism was generally greatest in July and August (Fig. 1).

The availability of eggs of *C. pomonella* for *Trichogramma* spp. and the levels of parasitism in sprayed and unsprayed orchards were determined from randomly selected foliage samples. Twenty-five to 50 leaves were taken periodically from five to ten trees in each orchard during the season. Eggs of *C. pomonella* were present in *ca.* 89% (n = 14) and 93% (n = 23) of the unsprayed orchards sampled in 1982 and 1983, respectively. In 1982, parasitism of eggs of *C. pomonella* was observed in 64.3% of the orchards sampled, but in only 14% of the orchards was parasitism 20% or more. However, in August during the second generation of *C. pomonella*, 68.8% and 44.0% parasitism was observed in an orchard at Bowmanville (Durham county) and at Louth, respectively. In the former orchard, the density of eggs of *C. pomonella* was 4.9/100 leaves and in the latter 3.7/100 leaves. In 1983, parasitism was observed in 19 of the 34 orchards sampled but in only two was the level of parasitism 20% or greater. The highest level of parasitism (60%) was recorded on 18 August in an orchard at Trenton (Northumberland county) where the natural density of eggs of *C. pomonella* was 13/100 leaves.

Trichogramma spp. were also recovered on egg cards in some commercial apple orchards in which several pesticides were applied during the growing season. In 1982, no parasitism was recorded in two orchards surveyed on 16 and 27 July. In 1983, egg cards were placed in five orchards sprayed with pesticides. *Trichogramma pretiosum* was recorded in one orchard on 21 July, in two on 23 August and in one on 25 August, and the level of parasitism ranged between 2.2% and 11.9%. Leaf samples were taken in three of these

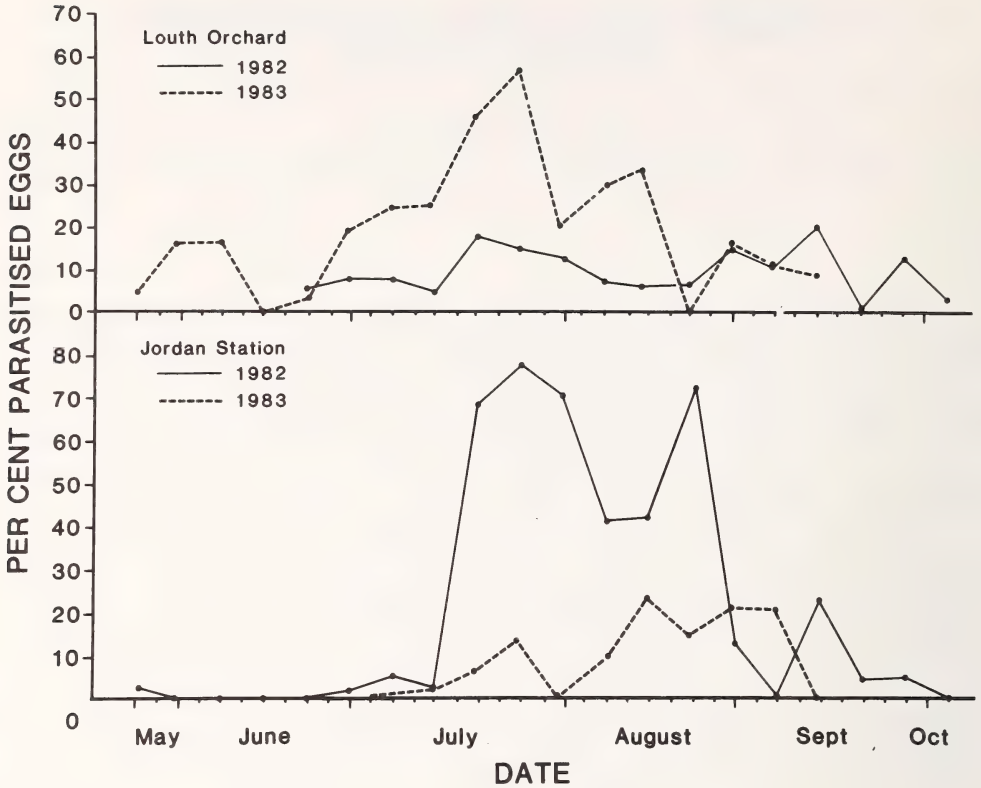


FIGURE 1. Occurrence of *Trichogramma pretiosum* in unsprayed (no insecticides) apple orchards at Louth and Jordan Station, Lincoln county, Ontario, in 1982 and 1983. In 1982, 10,120 and 9,440 eggs and in 1983, 8,720 and 6,400 eggs were exposed at Louth and at Jordan Station, respectively.

orchards to determine the occurrence of eggs of *C. pomonella*. Eggs were not recovered in one orchard sampled on 16 July, 1982, and in either orchard sampled on 11 and 18 August in 1983.

Although only *T. pretiosum* was recovered in 1982 and 1983, *T. minutum* emerged from apple leaves raked from the floor of one commercial orchard at Simcoe (Norfolk Co.) in January, 1983 (the leaf collection had been made to obtain pupae of the spotted tentiform leafminer, *Phyllonorycter blancardella* [Fabr.]). The host eggs, from which these parasites emerged, could not be identified. Garlick (1955) reported levels of parasitism of 10.2 to 17.1% of eggs of *C. pomonella* by *T. minutum* in an orchard at Vineland, and Yu *et al.* (1984) collected this species in an unsprayed orchard in the same locality in 1979. Although Garlick (1955) reported the highest levels of parasitism in August and September, *T. minutum* was not recovered in the orchards monitored during these months in 1982 and 1983. Nevertheless, in view of the reported (Peterson 1930) recovery of *T. minutum* on 12 May in 1927, and on 16 May in 1928 from eggs of *G. molesta*, egg cards were set out on 10 and 17 May in four, and on 6 June in two, unsprayed orchards in 1984. *Trichogramma minutum* was the only species recovered from the six orchards and levels of parasitism ranged between 0.9 and 40.4%.

Peterson (1930), van Steenburgh (1934) and Garlick (1955) reported considerable variation in the occurrence of *T. minutum* in fruit orchards in different years. Those authors suggested that the parasite did not overwinter in eggs of *C. pomonella* and *G. molesta* but migrated into the orchards in spring after emergence from the eggs of alternative hosts. This likely occurred in the orchards monitored in the present study as both *T. minutum* and *T. pretiosum* were recovered on egg cards before eggs of either pest species were present. Peterson (1930) also suggested that *T. minutum* had as many as 13 generations per year in New Jersey. However, from the results from cage rearings of this insect by van Steenburgh (1934) and the studies of Yu *et al.* (1984), it appears that *T. minutum* passes through six to eight generations per year in Ontario apple orchards. *Trichogramma pretiosum* probably also passes through several generations in these orchards between May and September, as suggested by the biological data of Orphanides and Gonzalez (1971) and Pak and Oatman (1982).

In summary, *T. pretiosum* was the predominant *Trichogramma* sp. recovered in unsprayed (no insecticides) and sprayed apple orchards in southern Ontario in 1982-83. The greatest amount of parasitism on egg cards and of eggs of *C. pomonella* on foliage occurred in July and August in both years. In 1984, *T. minutum* was the only species recovered in six unsprayed orchards sampled early in May and June. The data indicate that *Trichogramma* spp. migrated into apple orchards from alternative hosts and occurred in low numbers early in the season. The late build-up in numbers of *Trichogramma* spp. and the low levels of parasitism generally observed in the apple orchards sampled, suggest that augmentation and management of parasite populations might improve their effectiveness against *C. pomonella*.

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**DIGLYPHUS INTERMEDIUS (HYMENOPTERA: EULOPHIDAE),
AN INDIGENOUS PARASITE OF THE ALFALFA BLOTCH LEAFMINER,
AGROMYZA FRONTELLA (DIPTERA: AGROMYZIDAE)**

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Diglyphus intermedius (Girault) is an important indigenous parasite of the imported, alfalfa blotch leafminer (ABL), *Agromyza frontella* (Rondani), in the northeastern U.S.A. and in southwestern Ontario, accounting for 57% (Hendrickson and Barth 1978), 29% (Plummer and Byers 1981), and 19% (Coote and Ellis 1986) of all parasites reared in these studies. Differences in the biology of populations of *D. intermedius* between the U.S.A. and Ontario may influence the effectiveness of the parasite in biological control of the ABL in Ontario. Therefore, we investigated the biology of *D. intermedius* as a parasite of the ABL, both in the field and on ABL maintained on greenhouse alfalfa, *Medicago sativa* L., at Guelph (43°35'N, 80°20'W), Ontario.

In the northeastern U.S.A., aspects of the biology of *D. intermedius* were determined in the laboratory by Hendrickson and Barth (1978) and by Patel and Schuster (1983). Hendrickson and Barth (1978) reared the parasite on maggots of *Liriomyza trifoliarum* Spencer maintained on snap or lima beans and Patel and Schuster (1983) reared the parasite on maggots of *L. sativae* Blanchard from tomato leaves. The former study used populations from Newark (39°42'N, 75°45'W), Delaware and the latter from Bradenton (27°30'N, 32°20'W), Florida.

In the present study, the parasite colony was maintained for 10 generations over a 9-month period in the laboratory at 22.3 ± 0.8°C, 80% RH and a natural photoperiod, using rearing chambers similar to those of Quiring and McNeil (1984). Adult parasites were held individually (except for mating when 3 males were enclosed with 1 female for 24 h) in 40-dram plastic vials. These vials had one end covered with fine Decosheer® and the other with Parafilm® stretched under a snap lid. A continuous supply of liquid honey was provided as a source of food and water. Each female was confined with one 3rd-instar maggot for 1 to 4.75 h twice daily to determine fecundity, and to obtain additional parasites to determine developmental time, and sex ratio of the parasites. Longevity was determined as follows for both mated and unmated adults: individuals were either given no alfalfa leaves or were provided daily with a fresh trifoliolate leaf, containing neither pinholes nor maggots of the ABL, until the parasite died. In addition, longevity of females ovipositing daily was also determined. The logarithmic transformation was used on longevity data followed by analysis of variance (general linear model procedure). The instar of the host which was attacked, the number of eggs laid per host, and sex ratio of the parasites were determined from field-collected maggots (for collection methods, see Coote and Ellis 1986).

D. intermedius females laid a single egg on 51% of the 3rd-instar larvae (n = 160) parasitized in the laboratory, with a maximum of four parasites maturing per maggot. Twenty-nine percent of the parasitized maggots received 2 eggs, 11% received 3, and 8% received 4. On four separate occasions, 5, 6, 7 and 10 eggs were laid per maggot by different females. However, the exposure time to *D. intermedius* in the laboratory (1 to 4.75 h) did not affect the number of eggs laid per maggot ($r^2=0$; $P > 0.05$; $n=372$ parasitized maggots). Indeed, 5 eggs were laid within 1 hour, 7 and 10 eggs within 2 hours and 6 eggs within 2.5 hours, but most females laid only 1 egg per maggot even after 4 hours. These results show that the parasite usually exhibited restraint and preferred to lay 1 or 2 eggs per maggot. Hendrickson and Barth (1978) found similar results. The parasite was "usually" solitary on 3rd-instar larvae of *L. trifoliarum* in the laboratory but "commonly oviposited" 2 eggs per maggot and on one occasion oviposited 3 eggs. However, parasites at Guelph laid more eggs per maggot and were gregarious on a greater percentage of mag-

gots than in their study. This was probably because of the larger size of ABL maggots (viz., *D. intermedius* only survived on 3rd instars of *L. trifoliarum* in the laboratory because 2nd instars were too small).

Field data at Guelph indicated that over 88% of the ABL maggots ($n = 64$) parasitized by *Diglyphus* spp. were in their 3rd instar with the remainder being in the 2nd instar, and that over 95% received only 1 egg (a maximum of 3 eggs per maggot was found). These data are similar to those of Hendrickson and Barth (1978).

D. intermedius had an average realized fecundity in the laboratory of 41.8 eggs per female (range 26 to 82; $n = 6$). This value is probably an underestimate because females were allowed to oviposit on only 2 maggots per day and likely could have oviposited more (viz., no significant difference in the number of eggs laid on a maggot in 1 h versus 4.75 h). This hypothesis is supported by Hendrickson and Barth (1978) who found an average of 40.2 progeny per female ($n = 6$) when the females were supplied daily with fresh plants containing maggots of *L. trifoliarum*. Allowing for egg mortality, their females must have produced an average of more than 40 eggs per female.

The average developmental time of *D. intermedius* from egg to adult ($n = 699$) was 16.2 ± 0.08 (SE) days. Patel and Schuster (1983) calculated the following equation to predict developmental time of *D. intermedius*: $Y = -0.2028 + 0.0214X - 0.0004X^2$ ($r^2 = 0.96$ at $P = 0.001$), where Y = developmental rate (reciprocal of days) and X = temperature ($^{\circ}\text{C}$). Using our temperature of 22.3°C , developmental time as predicted by their equation would be 13.2 days. Assuming that the variance in their 13.2 days was similar to that of our results, the difference between the developmental times of the two populations was minor.

D. intermedius is arrhenotokous, whereby unfertilized females ($n = 42$) produced only males. Based on the progeny ($n = 264$) from mated females used to maintain the colony, the sex ratio was 1:1, whereas the sex ratio of adults reared from field-collected maggots ($n = 41$) was $1\text{♀}:1.7\text{♂}$. Sexual dimorphism in *D. intermedius* suggests that smaller males may be produced from smaller (i.e., 2nd-instar) hosts, a common phenomenon in parasitic Hymenoptera (Charnov *et al.* 1981). The sex ratio from the field was biased towards males possibly because 22% of the hosts were 2nd-instar larvae but only 3rd instars were used in the laboratory. Furthermore, the sex ratio from field-collected samples included males produced from unmated females. Werren (1983) showed that increased population density (i.e., increased numbers of ovipositing females) resulted in increased numbers of males. That may further explain the male-biased sex ratio from the field which was probably more indicative of the "true" sex ratio. Hendrickson and Barth (1978) found that the parasite had a sex ratio of $1\text{♀}:2.2\text{♂}$ ($n = 204$) when reared from *L. trifoliarum* on snap beans and 1:1 ($n = 117$) on lima beans. Their sex ratio was more biased towards males than that at Guelph possibly because of the smaller hosts; parasites could only develop on 3rd instars of *L. trifoliarum* and maggots reared from beans were smaller than those reared from alfalfa (Drea and Hendrickson 1986). Furthermore, their maggots were obtained by caging adult parasites with plants (compared to 1 female per vial in the present study) which possibly led to crowded conditions. Hamilton (1967) stated that crowded conditions in laboratory cultures may lead to the production of more males. Hendrickson and Barth (1978) offered no explanation for the difference in sex ratio of *D. intermedius* when reared on the two species of beans.

Sex of the parasites and presence or absence of maggots did not significantly affect longevity ($P \geq 0.32$); only virginity and presence or absence of alfalfa had an effect. Because these factors interacted, the four means were examined. There was no significant difference in average longevity among unmated parasites without alfalfa, unmated parasites with alfalfa, and mated parasites without alfalfa ($t < 1$), therefore these data were pooled. The average longevity of mated parasites with alfalfa (37.8 days; range 24 to 55; $n = 8$) was significantly shorter than the average of the other three combinations (49.9 days; range 22 to 85; $n = 100$; $t = 2.35$; $0.01 < P < 0.025$; $df = 104$). The 95% C.I. (1.3 ± 1.2 days) of the difference between these average longevity values indicates that mated parasites with alfalfa lived not less than 4% and not more than 68% fewer days than

the other three combinations. The longevity of 3 to 4 weeks estimated by Hendrickson and Barth (1978) was considerably shorter than our estimates. Their females were held at conditions similar to ours (i.e., $25.5 \pm 1.1^\circ\text{C}$, $60 \pm 5\%$ RH, and a 16-h photoperiod) but were continuously exposed to whole plants containing maggots of *L. trifoliarum*, versus exposure to single leaves. Searching for hosts possibly accounted for the shorter longevity in their study.

Our data suggest only minor differences in the biology of *D. intermedius* in Guelph compared to those described in earlier studies from the U.S.A., and that these differences are not likely to affect the performance of *D. intermedius* in the biological control of the ABL in Ontario.

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**A NEW DISCOVERY OF THE ALFALFA SNOUT BEETLE,
OTIORHYNCHUS LIGUSTICI (COLEOPTERA: CURCULIONIDAE),
IN EASTERN ONTARIO**

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The alfalfa snout beetle (ASB), *Otiorhynchus ligustici* (L.), is a Palearctic weevil which is widely distributed in Europe and found primarily on alfalfa (Warner and Negley 1976). In North America, it was first detected in New York State during the early 1930's (Herrick 1933). Over the past 50 years it has spread very slowly in the northern part of that state where it has been confined to 5 counties that border Lake Ontario (K. Severson, personal communication). The initial area of infestation has increased from 129 to 1423 km² (York *et al.* 1971). In 1986, it was found in an additional county, that of St. Lawrence, near Morristown (G. Cooke, personal communication). In Canada, it was found on Wolfe Island near Kingston, Ontario in 1967 by D.G. Nielsen (G.G. Gyrisco, personal communication). This distribution record was published by Warner and Negley (1976) and Becker (1977).

In the spring of 1986, large numbers of adults were discovered in Grenville county near Prescott, approximately 85 km east of Wolfe Island. This is the first record of the ASB on mainland Ontario.

Like other otiorhynchines, all of the adults are female and reproduction is parthenogenetic (Warner and Negley 1976). The adult is flightless, dark grey and 11.93 ± 0.16 mm long (mean and SE, N=20) (Fig. 1). Although adult feeding is not economically important, it is distinctive and provides a clue to egg-laying activity (Fig. 2). The ASB has a



5.0mm

1

FIGURE 1. Dorsal view of the adult of *Otiorhynchus ligustici*.



FIGURE 2. Feeding damage caused by adult *Otiorhynchus ligustici* to alfalfa.

2-year life cycle. The eggs are laid in the soil in late spring and summer. Larvae hatch in early summer, feed on alfalfa roots, and most are nearly mature by fall. In the second year, they feed for a short period before pupation. The adults eclose in mid summer but remain inactive in soil until the spring of the third year when they emerge from the soil and disperse in search of suitable sites for oviposition (Willson *et al.* 1976).

The first sighting of the ASB was made on 30 April, 1986, at a private residence on the Blue Church Road in Augusta township, *ca.* 1 km north of the St. Lawrence River (Fig. 3). Large numbers of adults had aggregated on the exterior walls of the house. Others were found on the road in front of the house and in catch-basins on the approach to the overpass of Highway 401, 175 m from the house. On 5 May, about 1500 live adults were counted on one side of the road between the house and the overpass. Small numbers were also observed within a few metres of the north side of the overpass. Although Highway 401 was a potential barrier to the migration, live weevils escaped traffic and were found on the service road to the north on 12 May. Numbers of dispersing weevils decreased after 12 May.

Similar migrations of large numbers of ASB were described in New York by Lincoln and Palm (1941), Palm (1935), Palm *et al.* (1941) and Nielsen and Edwards (1969).

Dissection of adults collected 2 May showed that about 20% were gravid. This suggests that the migration had begun well before 30 April.

The apparent source of the population was a 5-year-old, 4-ha stand of alfalfa 350 m west of the house. Many of the migrants also infested a nearby field that contained 2-year old alfalfa. From that field, at the peak of the dispersal, 50-60 adults/100 sweeps were collected in a standard sweepnet.

Following the migration, a total of 32 alfalfa fields within 15 km of the site of initial discovery were net-sampled for adults. Three gravel pits were examined for adults and larvae because there is evidence that weevils may be transported in pit gravel (Willson *et al.* 1976). Adults were collected in 12 fields within a radius of 3 km of the migration site (Fig. 3). Numbers per 100 sweeps ranged from 2 to 26. Most of the alfalfa was less than 3 years old,

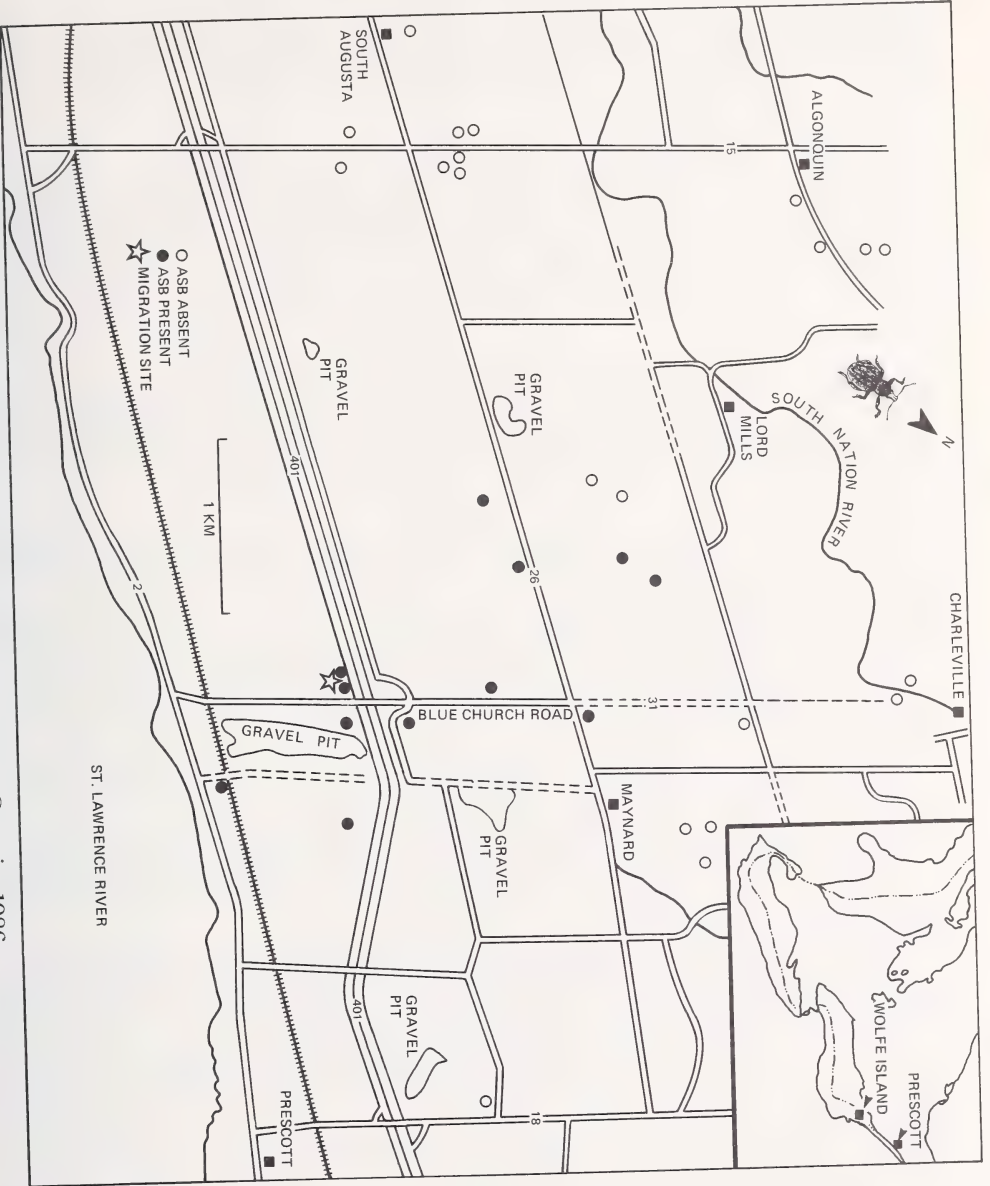


FIGURE 3. Distribution of *Otioryndus ligustici* near Prescott in eastern Ontario, 1986.

and the absence of ASB in samples before mid-May suggests that the adults were migrants. No ASB were found in gravel pits.

This survey shows that dispersal by walking from the breeding site was important in the colonization of the new fields. Various authors note that 100-200 metres is the maximum walking distance, whereas the spread of ASB over longer distances is attributed to transport of adults on farm machinery, with pit gravel, and dispersal by water. Nielsen and Edwards (1969) note that 6 islands (including Wolfe Island) were colonized in the St. Lawrence River during the 1960's presumably by passive drifting of adults in water currents from an infested area.

Eradication of ASB populations was not attempted on Wolfe Island in 1967, nor at Prescott in 1986. Though the Wolfe Island population has remained small (K. Bereza, personal communication), the weevils may find the environment in Prescott more suitable for population increase. In Europe, the weevil is most abundant in cool regions (Lincoln and Palm 1941). Such an adaptation could favor its northward movement from the St. Lawrence River. Therefore, the establishment of ASB at Prescott represents a potential threat to alfalfa production and the dairy industry of eastern Ontario.

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**THE EFFECTS OF *VAIRIMORPHA NECATRIX* (MICROSPORIDA) ON
THE SPRUCE BUDWORM, *CHORISTONEURA FUMIFERANA*
(LEPIDOPTERA: TORTRICIDAE)**

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The microsporidium, *Vairimorpha necatrix* was first reported from the army worm, *Pseudaletia unipunctata*, and was originally considered to be a mixed infection of *Nosema* and *Thelohania*. However, it is now known to be a single dimorphic species of microsporidia with two distinctly different spore forms (Pilley 1976; Maddox and Sprenkel 1978). *V. necatrix* has a wide host range and has been isolated from numerous species of field-collected lepidopterous larvae (Maddox et al. 1981). To my knowledge it has not been reported as occurring naturally in the eastern spruce budworm, *Choristoneura fumiferana* (Clem.), but because of its potential as a microbial control agent (Fuxa and Brooks 1979; Chu and Jacques 1981; Lewis et al. 1982; Wilson 1984) this microsporidium was tested against this forest pest. Maintenance of the insects and construction of the bioassay capsule were the same as those used for determining the dose response of spruce budworm to the microsporidium, *Nosema fumiferanae* (Thom.) (Wilson 1983). Spores of *V. necatrix* were originally obtained from Dr. J.V. Maddox (Illinois State Natural History Survey, Champaign, Il. USA) and have been cultured in our laboratory since 1981 using the forest tent caterpillar, *Malacosoma disstria* Hbn. as the host. Spores of the microsporidium were stored in water at 5°C for up to six weeks before use. Spores were counted in suspension using a hemacytometer and dilutions were made to give the desired concentrations. Individual needles of balsam fir, *Abies balsamea* (L.) Mill. were treated with 5µL of spore suspensions of *V. necatrix* to provide a deposit of 5×10^2 , 5×10^3 and 5×10^4 spores/needle. The suspensions also contained 0.5% (v/v) of the spreader-sticker Nu-Film® (Miller Chemical and Fertilizer Corp., Hanover, Pennsylvania). Fir needles for the control test were treated with distilled water containing Nu-Film. Microsporidia-free fourth (12 days out of hibernacula) and sixth (20 days out of hibernacula) instar budworm were used in all experiments. One larva was allowed to feed on one needle for 72 h, and those that consumed the entire treated area were returned to cups (individually) that contained artificial diet. Tests were performed with these larvae under a regime of 16:8 L:D, $23 \pm 1^\circ\text{C}$ and 60-80% R.H. Experiments were replicated twice, with mortality and days to mortality recorded for each dose.

V. necatrix caused high mortality of spruce budworm; a dose of 5×10^4 spores resulted in 100% insect death. Mortality was dose-dependent (Table 1) as noted for other insects treated with *V. necatrix* (Lewis et al. 1982; Fuxa 1981). Two types of mortality caused by *V. necatrix* have been reported (Fuxa and Brooks 1979; Fuxa 1981). Large doses of spores produce rapid death caused by gut damage and bacterial septicemia; low doses cause death by microsporidiosis, usually just before pupation. Similar results were found for the spruce budworm, although some larvae that lived after the treatments for up to 20 or more days before dying did not contain spores of the pathogen (Table II). However, examination of stained smears indicated that meronts may be present in the older larvae without spores. This phenomenon was also noted in spruce budworm treated with *Vairimorpha* sp.. 696 (Bauer, University of Kentucky, personal communication). In that study, although no spores were present and mortality was high, dissection revealed vegetative stages extensively infecting salivary glands.

There appears to be a relationship between larval age, spore dose and percentage of dead insects with *V. necatrix* spores. Treatment of fourth-instar larvae with the lowest dose resulted in the highest number of dead insects containing spores. The opposite is true for

sixth-instar larvae, i.e. the highest dose resulted in the most dead insects that contained spores.

Days to 50% larval mortality did not vary greatly with the dose of spores tested (Table II), whether insects contained spores or not. However, as indicated by the range, first mortality occurred earlier with the highest dose. Pupal and adult longevity and pupal weights of those insects that survived were not adversely affected by this microsporidium.

Table I. Mortality of spruce budworm when fed various doses of *Vairimorpha necatrix* (V.n.) as IV and VI instar and successful spore production.

	Treatment (dose)	Number larvae	Number pupae	Total larval mortality %	Total pupal mortality %	% dead larvae with V.n.	% dead pupae with V.n.
IV instar	Control	61	53	13	0	0	0
	5 x 10 ²	62	29	53.2	8.0	34.4	20.6
	5 x 10 ³	66	18	72.7	50.0	22.7	22.2
	5 x 10 ⁴	64	0	100	0	18.7	0
VI instar	Control	39	39	0	0	0	0
	5 x 10 ²	80	65	18.7	27.6	5.0	16.9
	5 x 10 ³	78	45	42.3	62.2	16.6	46.6
	5 x 10 ⁴	81	26	67.9	100.0	20.9	88.4

Table II. Days to larval mortality for spruce budworm treated as IV and VI instar with various doses of *Vairimorpha necatrix*.

	Treatment (dose)	Days to 50% larval mortality	
		with spores	without spores*
IV instar	5 x 10 ²	18 (18-37)	20 (10-37)
	5 x 10 ³	24 (15-38)	24 (12-31)
	5 x 10 ⁴	23 (9-38)	17 (4-32)
VI instar	5 x 10 ²	20 (10-31)	18 (10-25)
	5 x 10 ³	23 (9-25)	17 (11-36)
	5 x 10 ⁴	24 (9-31)	17 (9-24)

* Larvae treated with *V.necatrix*, but spores were not present in cadavers. Numbers in parenthesis indicate range in days for larval mortality.

The physiological mechanisms which cause the dimorphism in this genus are not clearly understood. Whatever these mechanisms are, they may have a bearing on the fact that spores were not always produced in the spruce budworm. A time/temperature function for this mechanism is discussed by Maddox and Sprenkel (1978). They suggest that the switch from a schizogonic to a sporogonic cycle results from a humoral signal and the titer of this signal could be a function of time or temperature. Further studies will be needed to determine how and why many spruce budworm larvae that die and do not contain spores, have a vegetative infection.

Although this microsporidium caused high mortality in the spruce budworm, further

laboratory investigations are needed before considering this pathogen as a biological control agent against the budworm in this field.

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REDUCING SEED LOSSES TO INSECTS BY TREATING WHITE SPRUCE CONELETS WITH CONIDIOSPORES OF *BEAUVERIA BASSIANA*W.H. FOGAL, G.S. THURSTON¹, and G.D. CHANT²Petawawa National Forestry Institute, Canadian Forestry Service
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Several insects feed on cones of white spruce, *Picea glauca* (Moench) Voss and cause substantial seed losses (Tripp and Hedlin 1956). They can be controlled with systemic insecticides applied by means of foliar sprays (Hedlin 1973; Fogal and Lopushanski 1985) or stem injections (Fogal and Lopushanski 1983), but such treatments may cause phytotoxic stress to trees, and are potentially hazardous to humans and wildlife. This prompted us to consider biological control using entomopathogenic fungi. Tyul'panova *et al.* (1975) demonstrated that *Paecilomyces farinosus* Brown and Smith, and *Beauveria bassiana* (Bals.) Vuill, can control the larch fly, *Chortophila larvicicola* Karl, and the larch coneworm, *Dioryctria abietella* Schiff, on Siberian larch, *Larix sibirica* L. As well, several insects that feed on cones and seeds of white spruce are susceptible to infection by *B. bassiana* and *Metarrhizium anisopliae* (Metch.) Sor. (Timonin *et al.* 1980). Susceptible insects include the spruce cone maggot, *Lasiomma anthracina* (Czerny), and the spruce seed moth, *Cydia youngana* (Kearfott), two of the most damaging insects of white spruce cones (Tripp and Hedlin 1956). One of several possibilities for delivering conidiospores to these insects is to spray or dust conelets shortly after pollination (Fogal *et al.* 1986) when adults are ovipositing between cone scales (Tripp 1954; Tripp and Hedlin 1956). Larvae and, perhaps, eggs of insects can be infected by fungi (Rodriguez-Rueda and Fargues 1980), so treatment of conelets with conidiospores during or before oviposition might prevent losses of seed to the cone maggot and seed moth. The following experiment, using *B. bassiana* as the potential control agent, was designed to test this hypothesis.

Three flower-bearing branches were randomly selected in early May, 1982, on each of 19 trees in a 20-year-old white spruce plantation located 5.2 km northeast of the Ottawa International Airport on National Capital Commission property (UTM grid reference 452502). The plantation is managed by the Carleton Place District Office of the Ontario Ministry of Natural Resources. The mean number of flowers on selected branches for all the trees was 13.4 ± 1.1 (mean \pm SE). On 18 May, when flowers on 18 of the trees had closed to become conelets, those on one branch were treated with a conidiospore preparation of *B. bassiana*. Conelets on the second branch were treated on 21 May, when they were firmly closed on all trees, and conelets on the third branch served as untreated controls. The conidiospore preparation, containing 7.3×10^7 viable spores per mg of infectious spore powder, was produced with the isolate and method described elsewhere (Timonin *et al.* 1980; Fogal *et al.* 1986). Each conelet was thoroughly covered with unformulated spore powder by dusting with a camel-hair brush loaded with the conidiospore preparation (*ca.* 13 mg).

Cones and any aborted conelets were collected on 19 July. Cones were sliced longitudinally to expose damage caused by cone maggot and seed moth (Fogal and Lopushanski 1985) and to count sound seeds on the cut face of one of the halves. Data from all trees were used to analyze recovery of sound and aborted conelets as a percentage of original conelets. Four trees with less than five sound cones on any one of the three treatment branches were excluded from analysis of cone damage and seed counts. Percentage data were transformed to arc sine square roots to equalize variance among treatments;

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numbers of sound seed were not transformed. Treatments and untreated controls were compared by analysis of variance followed by Duncan's new multiple range test (Steel and Torrie 1980).

Daily radiation records were obtained from a recording station at the National Research Council of Canada, Ottawa (Atmospheric Environment Service 1982a) and precipitation from a station at the Ottawa International Airport (Atmospheric Environment Service 1982b).

Average recovery of cones ranged from 82 to 88% of original conelets on treated and untreated branches (Table I). Some were lost, perhaps to foraging squirrels or to abortion; however, very few of the recovered strobili were aborted. Treatments had no significant influence on percentages of cones or aborted conelets recovered. Average cone maggot damage ranged from 27 to 37% and seed moth damage ranged from 19 to 20% for treated and untreated branches. Treatments did not significantly reduce evidence of damage. Nonetheless, a significant increase in numbers of sound seed per 10 cone slices was evident in cones treated on 21 May. Apparently, larvae were able to emerge and cause detectable feeding damage before being killed by the fungus. Deferred mortality such as this is common for fungal control agents (Roberts and Yendol 1971; Rodriguez-Rueda and Fargues 1980) and similar delays have been observed where residual insecticides were at a low enough level to allow larvae of these insects to leave identifiable signs of feeding yet high enough to kill them and prevent seed losses (Fogal and Lopushanski 1983). The increase in sound seed resulting from treatments on 21 May amounted to 55% over controls. This compares favorably with yield increases of up to 43% following chemical sprays of dimethoate (Miller and Hutcheson 1981) and 80% with stem injections of dicrotophos and oxydemetonmethyl (Fogal and Lopushanski 1983).

Table I. Effect of dusting conelets of white spruce with conidiospores of *Beauveria bassiana*

	Untreated cones	Cones treated with conidiospores		ANOVA F-value
		18 May	21 May	
1. Recovery (%)				
Cones	88±5 ^a	82±5 ^a	83±6 ^a	0.23 NS
Aborted conelets	1±1 ^a	1±1 ^a	2±1 ^a	0.08 NS
2. Cones damaged (%)				
Seedmoth	23±5 ^a	19±4 ^a	28±8 ^a	0.25 NS
Cone maggot	37±5 ^a	28±4 ^a	27±6 ^a	1.59 NS
3. Number of sound seed per 10 cone slices	42±5 ^b	54±5 ^{ab}	65±5 ^a	5.58**

Means bearing the same letter in each row are not significantly different from each other at the 95% level of probability as judged by Duncan's multiple range test. ANOVA F-value significant at the 99% (* *) level of probability; not significant at the 95% level of probability (NS).

The data suggest that time of treatments in relation to time of insect oviposition and duration of conidiospores viability may be critical factors influencing the success of fungal treatments. Since adults of cone maggot and seed moth oviposit between cone scales after pollination has taken place (Tripp 1954; Tripp and Hedlin 1956), it is highly likely that a large number of eggs were oviposited after conidiospores were applied to the surface of conelets. The chances of eggs or larvae encountering conidiospores should have been high, especially with the earlier treatment. However, the conidiospores may have been washed off by rainfall after application or perhaps inactivated by sunlight or contact with rainwater (Roberts and Yendol 1971; Roberts and Campbell 1977). Skies were mostly

sunny on both treatment days and total radiation was 22.3 and 29.4 MJ/m² for 18 and 21 May, respectively. Rainfall amounting to 6.4 mm was recorded the day following the early treatments whereas significant rainfall did not occur for two days following the later treatments. Perhaps, with the earlier treatment, conidiospores were inactivated or washed off strobili before the peak of insect oviposition. Treatment at the later time may have been closer to the peak of oviposition, allowing less time for possible inactivation by sunlight and more time for contact with insects before the next rainfall.

Anderson and Roberts (1983) suggested that entomopathogenic fungi might be used to enhance the efficacy of chemical insecticides. Perhaps *B. bassiana* can be used as a supplement, in mixed formulations of insecticides or as a separate application, to reduce seed losses to insects in white spruce seed trees and lessen potential environmental hazards and possible phytotoxic stress associated with the use of chemicals. However, before we can take advantage of this approach we need more knowledge about the oviposition behavior of the insects in relation to flower and cone development, about the infection process, and about climatic factors that are likely to influence the above factors and the viability of conidiospores.

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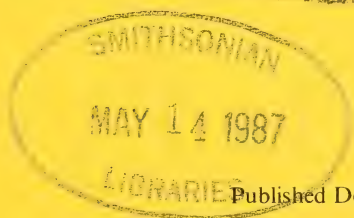
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*Supplement to Volume
One Hundred and Sixteen
1985*

White Pine Symposium



Published December, 1985

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WHITE PINE SYMPOSIUM
Petawawa National Forestry Institute
14 September 1984

Sponsored by
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WHITE PINE SYMPOSIUM

FOREWORD

White pine! A foundation for the early economic growth of eastern Canada. It provided shelter, furniture, industries and jobs; created transportation networks, led to exploration and attracted foreign capital. Throughout the nineteenth century the sale of white pine cutting rights made up the single largest source of revenue for the provincial treasury of the province of Ontario. The majestic pine forests are gone now, victims to take-all logging, pioneer fires, and agricultural clearance. But, to recognize the importance of white pine in the cultural and economic development of the province, Ontario, by Act of Parliament, decreed eastern white pine (*Pinus strobus*) as its official arboreal emblem in 1984.

White pine has not been a favored species for regeneration because it does not compete well with faster-growing vegetation and because of depredations of the white pine weevil and blister rust. However, these problems can be overcome by proper management. There is a growing body of information on management of white pine, and many aspects of its management were dealt with in a symposium on white and red pine management sponsored by the Ontario Ministry of Natural Resources and the Canadian Forestry Service in 1978 at Petawawa National Forestry Institute, known then as the Petawawa Forest Experiment Station. That symposium failed to fully address the problems of insect and disease pests. To redress that shortcoming the Algonquin Section of the Canadian Institute of Forestry and the Entomological Society of Ontario sponsored a second symposium at Petawawa in 1984. It was intended to be a supplement to the earlier symposium with particular emphasis on insects and diseases of white pine.

Petawawa National Forestry Institute was a fitting location for the symposium on two counts. First, the Institute is located in the heart of the Ottawa Valley which was designated Forestry Capital of Canada for 1984 by the Canadian Forestry Association. Forestry plays a dominant role in the socio-economic makeup of the Valley and in the nineteenth century white pine provided a prosperous sawtimber export business to Britain and the United States. Second, the Institute is the oldest continuous national forest research establishment in Canada. Research on white pine has been an integral part of programs of the Canadian Forestry Service in Ontario, with much of the work carried out at the Institute. Studies on white pine weevil biology, ribes eradication, white pine physiology, have been undertaken over the years, and silvicultural prescriptions for control of weevil damage have been developed.

The organizing committee gratefully acknowledges the support of numerous individuals and organizations for contributing to the success of the symposium. We gratefully acknowledge financial contributions from the following: The Algonquin Forestry Authority, Huntsville, Ontario; Consolidated Bathurst Inc., Portage-du-Fort, Quebec; Mrs. Rosamond Gillies, Braeside, Ontario; G.W. Martin Lumber Ltd., Harcourt, Ontario; McRae Lumber Co. Ltd., Whitney, Ontario; Murray Bros. Lumber Co. Ltd., Barry's Bay, Ontario. These funds were collected and administered by Mr. J.O. Smith, Braeside, Ontario and Mr. J.D. Coats, Executive Vice President, The Ontario Forestry Association, Willowdale, Ontario. Ontario Ministry of Natural Resources, Toronto, and Petawawa National Forestry Institute, Chalk River, Ontario provided additional funding. Finally, we are grateful to the contributors for presenting and publishing their papers.



Mature white pine, Petawawa National Forestry Institute, Chalk River, Ontario. Height, 37.5 m and diameter (DBH), 118 cm in 1984.

OPENING ADDRESS

P.J. YAKABUSKI¹

Parliamentary Assistant to the Ontario Minister of Natural Resources, (1975-1985)
Whitney Block, Queen's Park, Toronto, Ontario M7A 1W3

Thank you for inviting me to deliver the opening address of this symposium devoted to white pine (*Pinus strobus* L.). It was people such as yourselves who were brought together last year in an *ad hoc* committee, called the Ontario Tree Council, to choose a tree that Ontario could call its own. That committee was made up of 32 representatives from industry, government and various organizations. They chose the white pine, and this year the white pine was adopted as Ontario's official arboreal emblem.

I think it was a perfect choice—but what else can I say, coming from Renfrew County, the heart of the Ottawa Valley. Around here, the 19th-century boom in white pine logging was deafening. White pine was king here. Our communities got their start, our roads were built and our schools and local government were financed by white pine. It provided our bread and butter. One hundred years ago, people around here began and ended life surrounded by white pine—from white pine cradle to white pine casket. And white pine is still important in the Ottawa Valley, particularly in Renfrew where many of my constituents are employed in the forest industry. So in Renfrew, we are happy with the choice made by people such as yourselves.

But I must tell you an inside story. The vote for white pine by members of the Ontario Tree Council was not unanimous. There were two holdouts from the north who stuck faithfully by black spruce (*Picea mariana* [Mill.] B.S.P.)—one of the world's great paper trees—right to the end. That unswerving loyalty, I think, illustrates how strongly some Ontarians feel about the economic importance of forestry. You can understand their loyalty to spruce. I only wish all Ontarians felt that strongly about trees and were that tuned-in to the economic importance of our forests.

I am sure many people, especially in major southern Ontario centres, believe that manufacturing and tourism are the big money-makers. Forestry probably never crosses their minds. They might be surprised to find out that forestry and tourism are economically neck-and-neck. Some 160,000 jobs throughout Ontario depend on the forest industry, either directly or indirectly. Ontario exports wood and paper products worth about \$6.6 billion a year. In northwestern Ontario, three-quarters of the people earn their living directly from the forest.

As forestry people, you all know how hard it is to get that message across. Those figures, even if highly publicized, will not make a lasting impression. There are no constant daily reminders to rival what southern commuters see in the office and on the way home—growing numbers of computers and word processors and acres of light and heavy industry. Unlike people in other parts of the province, they are not constantly exposed to pulp mills and logging trucks. That is one reason Ontario's Natural Resources Minister, Alan Pope, believed it was important to finish the job begun by the late James Auld, the Resources Minister who preceded him. That job was giving Ontarians an official provincial tree. Having an official tree is a constant reminder of the importance of forestry. This year, the official proclamation was followed by a special bicentennial year arbor day on 25 May 1984. Five thousand white pine seedlings were distributed for planting by school children across the province. We hope that this special day becomes a traditional event every year and a time when Ontarians reflect on their forests.

In recent years, Ontario has embarked upon a new era of forest management. Let me describe briefly what is being done. First, we have substantially strengthened our forest

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management program. The Ministry's total forest management budget in 1984-85 is \$162.6 million—a substantial increase over the \$99 million allotted in 1981-82. We are spending these additional funds on a whole range of innovative forest management programs to ensure a healthy future for our forests.

Ontario's forest sector is an excellent example of how natural resources can be managed through cooperation and sharing of responsibility—of how private industry and government can both profit by working together, and of how government can achieve long-term resource management goals through negotiation and partnership. For instance, we have signed contracts with 21 private nurseries throughout northern Ontario to produce 64 million container-tree seedlings for planting this year alone. Next year, private greenhouses will produce 80 million trees, accounting for more than half of the provincial seedling production.

Private contracts are just one more illustration of the progress we are making in creating a new forest in Ontario. The private nurseries are a direct result of our single most important forestry initiative: the program of Forest Management Agreements, or FMAs, that we began back in 1980. Many people are calling FMAs the most important development in forestry in Ontario in decades. Under these agreements, we have made rapid and impressive strides toward achieving the objectives we have set for ourselves. One thing we have achieved under FMAs is unparalleled cooperation with the industry. Forest companies are starting to assume responsibility for preparing sites, for planting trees, and for tending the new forest. This in itself is a revolution of sorts. Today, forest managers know that the forest is a highly complex, natural ecosystem.

My ministry, with cooperation from industry and assistance from the Canadian Forestry Service, is developing new forest site classification systems in selected areas of the province to help us make decisions concerning regeneration. Forest managers know that the process of cutting mature timber and the process of growing new trees are two closely related activities within that system. And they know that it makes a lot of sense to integrate the two and to work at both activities together, planning them carefully. In summary, the second major accomplishment of FMAs is better forest management.

We have come to realize that we need balanced forest management. We must prepare sites properly for seedlings. We must tend young trees to ensure their survival. We must trim, thin and clean up plantations to reduce disease, and to allow quality timber to mature. We must protect forests against insects and fire. We need this balanced management in all our forests.

In many parts of the province, including Renfrew County, we are taking greater care to ensure that cutting in white pine areas is not done at the expense of the forest canopy. White pine is still the most valuable softwood in eastern Canada. Its future must be protected. And the best way to ensure that is to leave enough mature trees so that there is the right amount of light to support natural regeneration, yet enough shelter to protect the young trees. Another benefit, of course, is that a shelterwood system protects the young trees from white pine weevil. And any cutting must also be followed up by a sequence of treatments: brush control, tending, and cutting in careful stages to maintain that all-important overstory. The final precaution, of course, is minimizing the damage caused by small-scale logging operations.

The change to this system cannot be accomplished overnight. There is a strong tradition among operators in many white pine areas *not* to do things this way, because the profit margins are not as wide. I can tell you, from long experience, that those are factors that cannot be overlooked when you are practising forestry on the local level. Nevertheless, for the good of local economies and the generations of future residents, this sequential treatment of white pine is the direction in which we have to move. We have to do it slowly and we have to explain carefully why we are doing it.

At the same time, foresters have to support and publicize the need for local woods industries to move more aggressively into secondary processing of this fine wood we are producing. Most of the small wooden matches Ontarians use now to light their pipes, or

whatever, are being manufactured in England or the Far East. Yet the wood comes from here. Opportunity is knocking. I think it is sad that most of the knocking is being done on doors made of western red cedar (*Thuja occidentalis* L.) and not on doors of Ontario white pine made right here in Renfrew County, or in another provincial forestry town. Every day, new machinery is being developed that is revolutionizing the way wood products are being made. Not all these machines are multi-million-dollar monstrosities either. Many operators who run small yards can afford them.

Forest management in Ontario has really come of age over the last few years. The days of confrontation and competition for Ontario's natural resources, I believe, are over. We are building cooperation between the industry and government, between government and resource user groups. Naturalists and foresters from private industry are sitting down together to work out their problems. So are foresters and mineral explorers. So are developers and environmentalists.

In return for the honor of being asked to open this symposium, I would like to leave you with a thought. The cooperation, the ideas, the improvements rest on something people like you provide; new information, new knowledge. Without this we have no alternative courses of action so that we can make choices, debate, and cooperate.

WHITE PINE: A HISTORICAL PERSPECTIVE

J.W. McNUTT

William Milne & Sons Limited, Box 237, North Bay, Ontario P1B 8H2

Abstract

This review deals broadly with the impact of eastern white pine (*Pinus strobus* L.) on the economic well-being and development of Ontario and Canada. It touches on the transition from the 'cut out and get out' philosophy to a more constructive view based on the long-term availability of white pine. It tells of Ontario's misguided early land-use policy, with its negative effect on agricultural development and on lands better suited to forestry.

The fur trade waned toward the late 1700s, and for the next century or more eastern white pine was the most important single factor in the newly developing Canadian economy. It figured in the construction of canals and railroads and in a rapidly accelerating international trade.

Whereas forestry activity and funds have been channeled more aggressively into the reforestation and tending of pulp species since the burgeoning of the pulp and paper industry in the early 20th century, there are encouraging signs that the Ontario government is at last recognizing the uniqueness and the trade value of eastern white pine and the need to focus on its perpetuation.

Introduction

My purpose in this paper is to take a broad look at eastern white pine (*Pinus strobus* L.) and to make some observations about the changes that have taken place since this species first began to play a significant role in the history of Canada and Ontario. It may also be helpful to take an even broader perspective and comment on the changes that have taken place in forestry in Canada generally, and in attitudes toward that profession, during the last half-century or so. For the attitudes of the public and of the government are of key importance in establishing the future of white pine in Ontario.

In 1932 in the Montmorency River region of the province of Quebec, it was inadvisable, in my experience, to let it be known that anyone directly involved in forest operations had a university degree. Great emphasis was placed upon the wisdom of what was then described as the "practical man". Against this background the introduction of new practices or new attitudes was especially difficult. Others who were involved in forest operations in Ontario at that early stage apparently encountered the same skepticism about the value of university training in resolving the practical problems encountered in the woods.

Today a dramatic change of view has taken place. It now seems evident that the decision makers in government forestry services, at both the federal and the provincial level, have been impressed with the need to apply extensively the skills and knowledge of graduates in many disciplines to the resolution of forestry problems. Certainly today, in light of the extreme difficulty experienced in re-establishing the white pine forest in Ontario, the application of the best and most highly trained minds to the resolution of the problem is not an over-reaction. We have not, over a period of many decades, resolved the white pine replacement problem *without* educated people in the forest; perhaps we can do it *with* them.

Assurance of a Continuing Supply

The primary objective of this symposium should be to promote the regeneration of high-quality white pine in sufficient quantities to meet anticipated future needs. There continue to be grave doubts, however, as to how far we have really come in realizing this objective, and how quickly we are moving. How much better is our assurance of a

continuing supply than it was a half century ago, or for that matter, at the conclusion of the 1977 White and Red Pine Symposium (Cameron 1978) held in this same place, under similar auspices?

Let me assure Mr. Wray of the Ontario Ministry of Natural Resources (OMNR) that I am not about to usurp the territory that he has staked out for this afternoon in his paper "The Future of White Pine in Ontario". But it is, of course, impossible to look at years gone by without reaching some opinion, perhaps even some conclusion, as to what the future may hold for us, even while focusing primarily on the past.

White pine's historic economic contribution: Let us for the moment review briefly what white pine has meant for Canada, and for Ontario in particular. Most people at this symposium will have probably been over this historical ground before, perhaps as recently as the aforementioned symposium of 1977, but the importance of our subject may justify running the risk of boredom by repetition.

To begin with, I suggest that not one Canadian in a thousand is aware that white pine was for about a century or more (from the time of the Treaty of Paris in 1763) so important economically that it was described as "the keystone in Canada's economic arch". During that period the dominant factors in Canadian economic life were agriculture, the trade in pine masts and square timber with England, and beginning about 1827, the trade in deals and boards with the United States.

Forest and farm—the conflict: It has long been recognized that in the early days of settlement in Canada the forest was viewed as an obstacle to, and even an enemy of, the much more pressing and important undertaking of agriculture. Forest removal required an immense output of labor, usually not compensated for by the value of the timber removed. Indeed, the record seems to show that much of the herculean effort of clearing non-agricultural lands for agricultural purposes was almost fruitless.

It seems no exaggeration to say that our early Canadian pattern of land use has not been very different from the 'shifting agriculture' found throughout so much of the developing world today—cut and burn the forest growth, farm for 2 or 3 years until the soil nutrients have become exhausted, then move on to another forest location and repeat the process. The principal difference between pioneer Canada (including Ontario) and Zambia or Zaire is the much higher cost, in terms of both labor and materials, of the structure we erected on our ill-chosen farmland. To this extent the Ontario farmer, struggling to make ends meet, had a firmer commitment to the land than his African counterpart. He was stuck with it. When he finally discovered that forest land is not always the same as agricultural land, 2 or 3 generations would often have sweated it out as subsistence farmers, before tossing in the sponge. Generally speaking, neither agriculture nor forestry appears to have benefited much from the experience.

Alexander Sherriff, in a report dated 1831, describes glowingly the 'agricultural possibilities' of the Ottawa-Huron region, which includes, for example, Algonquin Park! Only after another half century or more, and many thousands of back-breaking hours of land clearing, did the enormity of his misconception come to be known (Lower 1938).

Stimulus to Canada-United States trade: About the same time (early 19th century), white pine was recognized as so valuable in trade with the United States that it proved to be the primary impetus underlying the intensive canal building program that took place between 1822 and 1835 to facilitate its delivery to the American market (Lower 1938).

These canals linked the St. Lawrence River basin with New York City via the Richelieu and Hudson Rivers, and placed the great Ottawa Valley pineries within easy economic reach of New York by way of the Rideau, Erie and Oswego canals. Although the Rideau Canal was viewed as having strategic military importance for the movement of troops and material between the Ottawa and St. Lawrence rivers, its most significant contribution to the nation was in the movement of many thousands of barge loads of white pine to the American market.

But the enterprising people of the United States and Canada had scarcely come to

appreciate fully the value of the new canals in international trade when the aggressive construction of railroads, spurred by the Industrial Revolution, was undertaken on both sides of the border. Beyond question the demand for pine lumber was the major factor underlying the construction of the New York Central Railroad from New York to Buffalo in 1853. As well, 2 railroads were built from Boston to transport Ottawa Valley lumber, one to Ogdensburg, New York, which later became the Grand Trunk, and the other the wholly Canadian Bytown-Prescott Railway.

Resignation to liquidation: I clearly recall, with some anguish—but coupled with optimism because of today's changed attitudes—that during the 1950s the acknowledged policy of the Ontario Department of Lands and Forests (the predecessor of OMNR) was liquidation of white pine.

With respect to the white pine forest in the Temagami region, it was held that the pine forest was non-renewable because of geographic remoteness and the long rotation, of 100 years or more, which was anticipated. The average taxpayer could not be expected to support the long-term forestry expenditures necessary to assure replacement of the white pine forest being harvested.

I believe it is accurate to say that this is not the policy of OMNR today. In support of the view that there is a future for white pine, Morse (1984) states: "The white pine has also taught us that even plentiful natural resources have to be managed. The great pine forests that challenged and rewarded our first settlers are gone. But the white pine will never die out." It is important to ensure that such a comforting statement is not taken to mean that all's well with our white pine supplies, because we all know that it is not.

Early lumbermen: The loggers and sawmill operators of the 19th century have been accused, in what sometimes seems a rising crescendo in recent years, of being voracious, irresponsible rapists, bent on the destruction of the forest, and without regard for the rights or interests of future generations. One of the most frequently quoted passages that recalls the depredations of those 'cut-out-and-get-out' conscienceless, forest operators of the 19th century is the following: "The ravenous sawmills in this pine wilderness are not unlike the huge dragons that used in popular legend to lay waste the country; and like dragons, they die when their prey, the lordly pines, are all devoured." (Withrow 1899, cited in Lower 1938).

But some of our ancestors did display an early awareness of, and concern for, our white pine heritage which, in the relaxed atmosphere of the times, seems surprisingly prescient. It was 113 years ago that a man whose voice was often listened to with respect in those days, a man who exerted a measurable influence on Parliament Hill, sounded one of the earliest warnings. In a letter dated 22 June 1871, Sir John A. MacDonald, writing to Premier John Sandfield Macdonald of Ontario, made a statement which, because of its prophetic nature, may be well known to most of this audience, and is therefore repeated here only in part: "My dear Sandfield: The sight of the immense masses of timber passing my windows every morning constantly brings to my mind the absolute necessity there is for looking at the future of this great trade. We are recklessly destroying the timber of Canada and there is scarcely the possibility of replacing it."

In 1871, just as in today's federal-provincial relationship in forestry, from a position of limited authority but considerable moral clout, Sir John was urging our province to take the action only a province has the authority to take. While we can perhaps not accord him full credit for initiating white pine management in Ontario, we must award him top marks for foresight.

Despite Sir John's timely warning, for at least another 75 years a varied assortment of journalists, politicians, and even professional foresters continued to talk in glowing terms about our vast, inexhaustible, interminable, limitless forest resources. Stranger still, I am sure that many of them believed it!

The realization that our resources are finite: Only during the last decade or so have we come to the realization that we are in danger of running out of white and red pine. True,

there continue to be seemingly 'limitless, inexhaustible' volumes of the species that we did not want in the past, and cannot now utilize in the volumes available—species like poplar and white birch. But those fabulous pine species, on which this country's economy rested so firmly for more than a century, are certainly not being replaced in volumes sufficient to meet the demands of a rising world market, which is predicted to double between 1970 and the year 2000.

In view of the history of trade preferences for certain species in various industrial processes it is safe to say that if it is in demand now, it will be in still greater demand 10, 20, or 30 years from now. We can feel confident that, while white pine is a traditional, perhaps even an 'old-fashioned' species, it will continue to be in great demand for years to come.

For those who may not have been privileged to know and to work with eastern white pine, there is a passage in a recent publication issued by the Ontario Ministry of Natural Resources that almost induces salivation. ". . . they spot it: those creamy-white, long, seemingly grainless boards. They run a hand over that waxy, soft wood . . . Ahh! That's white pine, the real thing, the wood of pioneer trestle tables, river drives, history, a true North wood. Imagine working that wood, turning it into furniture that becomes honey-coloured through time. . . . Do-it-yourselfers know about white pine, but so do others. That's why it's in demand, commands the highest price of all softwoods. It's easy to love." (Mutton 1984).

This passionate, worldwide fondness for the species helps to explain, in this technological age of plastics, how the real thing continues to exert its fascination on those who know it well. But white pine, standing in the forest, contributes to the enjoyment of a host of 'non-consumptive' users of the forest as well—the canoeists, bird-watchers, cross-country skiers and recreationists generally.

Ontario's official arboreal emblem: Those 32 representatives of provincial tree and forest organizations who met in Toronto on 9 September 1983 and selected white pine as the official arboreal emblem of Ontario chose exceedingly well. But we must do much more than select an arboreal emblem and worship thereafter at its feet. We have been through many collective motions attesting to our appreciation of white pine. There has been more written about white pine than about any other tree species in North America.

True, there have been especially difficult problems to overcome in reestablishing the species after harvest or destruction by wildfire, insects or disease. But an acknowledged preference for the pulp species in Ontario, so as to permit the pulp and paper industry to retain or recover its competitive position in world trade, has no doubt had a still greater influence in diverting attention, and funding, from white pine.

Areas and volumes under white pine forest: Reference has been made earlier in this paper to the numbers by which we may measure what has happened to the eastern white pine forest. Ontario's total area is 1,054,000 km². Of this, 98,412 km², or slightly less than 10%, was reported under white and red pine forest in 1895. In 1874 when the first reasonably reliable estimate was made, the total volume of white pine in Ontario was reported to be 45.5 billion fbm. In 1895 estimates placed this figure at 19.5 billion fbm. It is important, however, to remember that few people placed confidence in these early volume estimates (Lower 1938). By 1949, just 54 years later than those 1895 area estimates, only 18,129 km², or 18%, of the area reported in 1895 was still under white pine forest.

Timber and sawnwood production: Ewan Caldwell advised delegates to the White and Red Pine Symposium in 1977 that in the 77 years from 1900 to 1977 Ontario's white and red pine production averaged 5,838,000 m³ per year for the entire 77-year period. For the 5-year period from 1980 to 1984 the average annual production of white and red pine was 774,870 m³ of round timber, or about 13% of the annual volume between 1900 and 1977 (E. Markus, Ontario Ministry of Natural Resources, pers. comm.). The figures for both periods are for Crown lands only. No separation of white and red pine volumes is provided, since there appear to be no reliable figures available for each species until more recent years.

The most cursory examination of the available data on total area under white (and red) pine forests in Ontario and evidence of the sharp decline in volumes harvested make it clear that if we are to obtain our share of the rapidly growing world market for high-quality softwood lumber, we have a great deal of catching up to do.

The other side of white pine: No historical review of the place of white pine in Ontario can be complete without some reference to its impact upon those aspects of our lives that lie outside the sphere of economics and industrial development. For white pine has provided color—some have even called it “glamor”—to a way of life that for many would have been almost unbearably tedious. These intangible values stand out in the memories of those who have spent a lifetime in the forest industry, and are an essential ingredient of whatever it was that kept them there, in the bush, often under conditions of great privation.

One industry is often compared with another, by means of a varied assortment of yardsticks. The techniques of steel making can be compared with techniques used in the forest industry, but steel making is not a very attractive or colorful business. Lumbering, on the other hand, is close to nature, providing its workers with a life in many ways comparable with that of the cowboy or sailor, calling for a response to nature's moods and becoming something much more than merely an occupation. Rather, it becomes a way of life that has attracted the interest of not only the social and economic analyst, but the poet and novelist as well. The extensive writings of Stewart Edward White and Joseph Conrad are two good examples of those that left us with a legacy embodying much of the color of the early days in the pine woods. Their contribution has been immeasurable.

Summary

What credit, or blame, is due to those individuals, be they politicians, civil servants, academics, or just plain lumbermen, who are collectively responsible for what has happened to our once great white pine forests?

As a member of one of those groups, I cannot be completely objective, but I shall try.

The ‘rape’, which seems to be such a popular term these days, of the forest has, over a number of decades, been deplored by many, often with deep emotion. People just do not like to see those ‘lordly pines’, to use W.H. Withrow’s phrase, devoured as if by ‘fire-eating dragons’, nor to see the ‘dragon’ move on when its prey, the ‘lordly pines’, are all devoured. It is bad for sawmill communities, and for the community at large.

The early lumbermen, as well as those of more recent times, are seen as rapacious, greedy, and completely unconcerned for the future of the forest or the interests of others. What would have happened to those ‘lordly pines’ had they not been harvested—wastefully or otherwise? We have seen it happen in the shoreline reserve areas around Lake Temagami, north of North Bay. Even ‘lordly pines’ grow old, are attacked by fungi or insects, and die!

As dead ‘chicots’ they have long stood on the ridge-tops, many of them sooner or later becoming targets for lightning strikes, which cause 70 to 80% of the fires in that region.

Concerned people have deplored the ‘waste’ of the early square timber days. Lumbermen then took only the almost defect-free square timber and left behind the outer portions, which today would contain most of the more valuable clear grades of lumber. They left it behind in the woods because no one, at the time, wanted to buy it.

The forest industry will always be that way unless it becomes government subsidized. Forest operators will harvest and process what they can sell. It may not be ideal, but it’s the real world of supply and demand.

Let us look just briefly at some of the positive effects of what we have done collectively since the first shipment of white pine was exported to the French West Indies in 1670.

The exploitation of a species that brought in its wake the construction of canals and railways, that has consistently made such an enormous contribution to our balance of international payments, and that led one man, J.R. Booth, single-handedly and without government funds, to complete the 400-km Canada Atlantic Railway, from Ottawa to Parry Sound, cannot be all bad!

WHITE PINE SYMPOSIUM

The story of the opening up and development of this province, and the part that white pine has played in it, is too long to be recited here. Many mistakes were made in the process. We continue to make them. As the years pass, they will be even more clearly visible to us, with all the benefits of hindsight. Nevertheless, as we begin to acknowledge that there can be white pine, in commercial volumes, in perpetuity, let us not, because of new information, new values and new markets (for what once was 'waste'), shed too many tears over what has gone before.

Forestry must look ahead.

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WHITE PINE: THE RESOURCE AND ITS UTILIZATION

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Abstract

The Forest Resource Inventory in Ontario is described briefly. On the basis of this system there are approximately 610,000 ha of the white pine (*Pinus strobus* L.) working group containing approximately 110 million m³ of gross total volume. Actual volume of white pine cut and scaled from crown land averages 500,000 m³ per year.

Introduction

Inventory and utilization statistics for white pine (*Pinus strobus* L.) are presented here in a way that will be useful for assessing losses attributable to pests. Described here as a basis for this assessment are the types of data collected in Ontario's Forest Resource Inventory (FRI)¹ and the ways in which these data are summarized.

Forest Resources Inventory

In Ontario the FRI is done on a 20-year cycle. This means that for any given part of the province the FRI data may be 1-20 years out of date. Anyone using local FRI data should be aware of this fact.

The FRI has several components (Table I). The more important items such as working group, site class, age classes and species composition will be defined below. Under ownership, the data will be summarized for crown land as distinct from patent (private) land. The ultimate recording unit in the FRI is a stand—an area in which the forest composition is more homogenous than in adjoining areas. Each stand is identified uniquely and fully described in Ontario's FRI. Several of the attributes used in the stand description, e.g., working group, species composition, age, stocking, and site class, are useful when one is considering potential susceptibility to pests and/or the impact of damage.

Table I. Categories of area used in the Forest Resources Inventory of Ontario

WATER

NON—FORESTED

developed agricultural land
grass and meadows
unclassified

FORESTED NON—PRODUCTIVE

muskeg
treed muskeg
brush and alder
rock

FORESTED PRODUCTIVE

Protection
working groups
site class 4 (poor)
islands (less than 40 ha)
forest reserve

Production — allowable cut
working groups
site classes (X,1,2,3)

Note: All components are identified by ownership: 1 = crown land, 3 = patent, 5 = provincial parks, 6 = Indian reserve, 9 = federal.

¹ A complete description of the methodology of the FRI in Ontario is given in Anon. (1978).

WHITE PINE SYMPOSIUM

Inventory Values

FRI data are aggregated in several ways. Stand data are summarized geographically for a map sheet (township) and then combined for each forest management unit. Similarly, management unit data are aggregated by the Ontario Ministry of Natural Resources (OMNR) districts and regions. The eight regions are shown in Fig. 1.

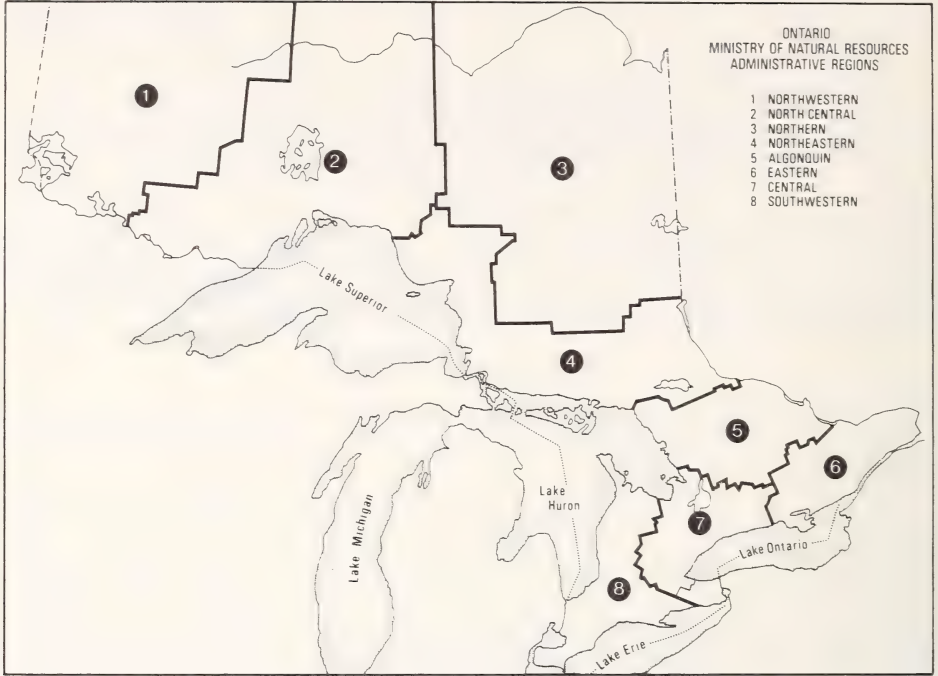


FIG. 1. Ontario Ministry of Natural Resources administrative regions.

Within the components of Table I, production forest is the most economically important. As the name suggests, this is an area in which commercial forest management is the major objective. Most production forest in Ontario is on crown land (Table II). However, the contribution of patent land in the utilization of white pine is important.

Table II. Distribution of production forest in Ontario (area and gross total volume) by major type and ownership

Owner	Working group					
	Area ('000 ha)			Gross total volume ('000,000 m ³)		
	Softwood	Hardwood	All	Softwood	Hardwood	All
Crown ^a	21,390	8,753	30,143	2,581	1,365	3,946
Patent	1,510	3,084	4,594	151	334	485
Total for province ^b	22,900	11,837	34,737	2,732	1,699	4,431

^a Crown land unencumbered (unalienated) except for inclusion of Algonquin Park and Lake Superior Provincial Park.

^b As covered by the FRI.

The white pine working group (W.G.) is made up of stands that are predominantly, but not necessarily exclusively, white pine. Many other species may be mixed in these white pine W.G. stands. Similarly, white pine occurs in many other working groups.

The white pine W.G. on crown land occupies 1.6% of the total production forest area and contains only 2.3% of the total growing stock volume of the production forest. The values for patent land are slightly higher at 2.7% and 3.7%, respectively. Table III shows the basic production for crown land and patent land by administrative region. The area and growing stock volume of the white pine W.G., all softwood W.G.s and all W.G.s are given. The percentage of area and volume represented by white pine in each region is also shown. Obviously white pine is of greater significance in some parts of the province, e.g., the Northeastern and Algonquin regions.

Table III. Distribution of the white pine working group in Ontario's production forest by administrative region on a) crown land, and b) patent land (area and gross total volume)

TYPE Region	Working group							
	Area			Volume				
	White pine		All softwood (ha)	Total ha	White pine		All softwood '000 m ³	Total '000 m ³
ha	% of area	% of vol.						
CROWN LAND								
Northwestern	18,669	0.2	6,866,938	8,045,695	3,632	0.4	760,007	949,010
North Central	8,143	0.1	5,400,456	7,293,657	1,968	0.2	696,229	1,001,700
Northern	19,570	0.2	6,708,835	8,815,646	3,139	0.3	785,374	1,122,676
Northeastern ^a	212,402	4.8	1,981,151	4,408,455	39,780	6.3	277,189	626,145
Algonquin ^b	191,757	15.3	345,981	1,253,635	35,376	17.4	49,123	203,663
Eastern	27,404	13.1	46,224	209,707	6,614	21.8	8,932	30,280
Central	4,871	4.3	38,934	114,176	818	6.4	4,000	12,697
Southwestern	499	28.1	1,013	1,775	82	28.0	190	1,122,293
Province	483,315	1.6	21,389,532	30,142,746	91,409	2.3	2,581,044	3,946,464
PATENT LAND								
Northwestern	690	0.3	76,565	227,222	140	0.6	6,304	21,553
North Central	275	0.1	152,711	293,563	62	0.1	18,455	38,877
Northern	150	0.0	258,820	483,329	15	0.0	20,270	47,122
Northeastern	13,830	1.3	324,800	1,030,209	1,973	2.1	35,553	94,282
Algonquin	50,984	4.6	307,363	1,104,342	7,574	5.6	32,541	135,851
Eastern	37,655	4.2	268,492	899,125	5,909	6.9	24,965	85,876
Central	16,322	4.4	102,454	368,114	1,575	3.5	10,847	45,284
Southwestern	6,746	3.6	19,058	188,307	936	5.9	1,715	15,855
Province	126,652	2.7	1,510,263	4,594,211	18,184	3.7	150,650	484,700

^a Northeastern Region includes Lake Superior Provincial Park.

^b Algonquin Region includes Algonquin Park.

WHITE PINE SYMPOSIUM

If we focus for a moment on the white pine W.G., the Northeastern and Algonquin regions, for example, are fairly different. Fig. 2 (data in Table IV) is an age-class distribution of the areas or volumes for crown land. Over all, the stands in the Algonquin Region are younger than those in the Northeastern Region. Further south in the Central Region there are even younger stands. Table V and Fig. 2 show the age-class distribution on patent land by region.

Table IV. White pine working group age-class distribution by region on crown land

Region		Age class								Total
		B & S ^a	1-20	21-40	41-60	61-80	81-100	101-120	121+	
Northwestern	ha	566	14	8	1,366	4,983	3,171	2,682	5,879	18,669
	'000 m ³	-	-	-	226	904	663	622	1,215	3,632
North Central	ha	371	-	92	704	770	1,392	1,791	3,023	8,143
	'000 m ³	-	-	11	108	152	347	468	883	1,968
Northern	ha	1,283	131	118	103	4,056	562	1,590	11,727	19,570
	'000 m ³	-	-	6	10	64	95	322	2,641	3,319
Northeastern ^b	ha	14,829	6,555	1,877	3,808	22,078	73,010	24,810	65,435	212,402
	'000 m ³	-	17	106	540	3,731	14,605	5,308	15,472	39,780
Algonquin ^b	ha	8,133	593	2,240	15,330	66,036	80,597	13,243	5,585	191,757
	'000 m ³	-	5	230	2,368	12,611	16,313	2,794	1,054	35,376
Eastern ^c	ha	1,196	182	1,779	6,059	15,039	2,907	229	13	27,404
	'000 m ³	-	-	248	1,181	4,150	947	82	6	6,614
Central	ha	896	244	507	600	1,888	625	77	34	4,871
	'000 m ³	-	5	54	117	444	170	19	9	818
Southwestern ^d	ha	9	135	127	92	136	-	-	-	499
	'000 m ³	-	2	17	26	37	-	-	-	82
Province	ha	27,283	7,854	6,748	28,062	114,986	162,264	44,422	91,696	483,315
	'000 m ³	-	29	672	4,576	22,093	33,140	9,615	21,280	91,409

^a B & S (barren and scattered) is the area in which there are too few trees to estimate age accurately. Technically the stocking is less than 30%.

^b Northeastern Region includes Lake Superior Provincial Park; Algonquin Region includes Algonquin Park.

^c Eastern Region does not have Carleton Place Management Unit data (N/A).

^d Southwestern Region does not have Owen Sound Management Unit data (N/A).

Table V. White pine working group age-class distribution by region on patent land

Region		Age class								Total
		B & S ^a	1-20	21-40	41-60	61-80	81-100	101-120	121+	
Northwestern	ha	35	11	21	60	131	37	251	144	690
	'000 m ³	-	-	2	8	33	6	56	35	140
North Central	ha	3	1	3	36	26	132	50	24	275
	'000 m ³	-	-	-	10	6	27	12	6	62
Northern	ha	52	-	-	-	25	-	1	72	150
	'000 m ³	-	-	-	-	4	-	-	11	15
Northeastern	ha	3,058	123	168	532	1,648	4,494	2,402	1,405	13,830
	'000 m ³	-	2	41	210	330	813	409	167	1,973
Algonquin	ha	11,526	74	423	2,466	13,844	18,493	2,924	1,234	50,984
	'000 m ³	-	-	44	386	2,646	3,721	596	181	7,574
Eastern ^b	ha	6,509	872	5,718	12,076	10,246	1,875	275	84	37,655
	'000 m ³	-	13	667	2,177	2,453	504	69	27	5,909
Central	ha	6,119	2,055	2,404	2,215	2,176	1,085	169	99	16,322
	'000 m ³	-	20	277	443	493	266	51	27	1,575
Southwestern ^c	ha	1,428	1,197	1,115	1,461	1,118	344	83	-	6,746
	'000 m ³	-	12	153	327	308	112	23	-	936
Province	ha	28,730	4,333	9,852	18,846	29,214	26,460	6,155	3,062	126,652
	'000 m ³	-	47	1,185	3,562	6,273	5,448	1,216	454	18,184

^a B & S (barren and scattered) is the area in which there are too few trees to estimate age accurately. Technically the stocking is less than 30%.

^b Eastern Region does not have Carleton Place Management Unit data (N/A).

^c Southwestern Region does not have Owen Sound Management Unit data (N/A).

WHITE PINE SYMPOSIUM

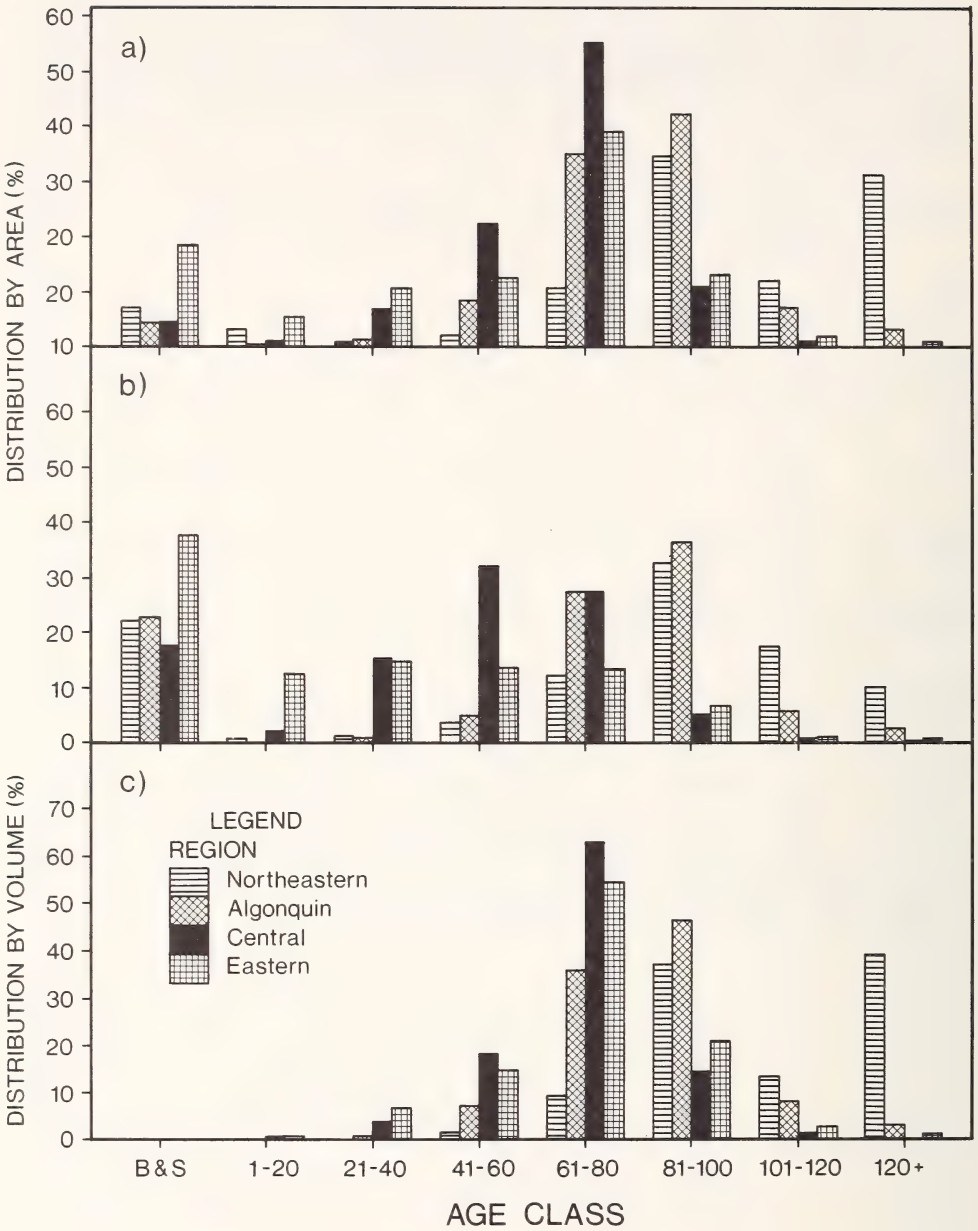


FIG. 2. White pine working group age-class distribution in years for four regions of Ontario on:

- a) crown land by proportional area,
- b) patent land by proportional area,
- c) crown land by proportional gross total volume.

Note: B&S = barren and scattered (see Table IV for definition)

The site-class distributions are important for some aspects of management. Site class in Ontario's FRI production forest ranges from X (excellent) to III (poor) (Table VI). It is based on a stand-height and stand-age relationship. The younger stands on crown land in the Central Region are on better sites than the older, natural stands in the Northeastern and Algonquin regions.

Table VI. White pine site-class distribution^a

Crown Land by Area				
Region	Site class			
	X	I	II	III
	% of total production area			
Northeastern	3.6	12.0	75.6	8.8
Algonquin	0.3	20.1	69.6	10.0
Eastern	8.2	56.4	34.7	0.7
Central	43.1	36.6	20.0	0.3

Crown Land by Volume				
Region	Site class			
	X	I	II	III
	% of gross total volume on production area			
Northeastern	0.4	2.7	95.6	1.3
Algonquin	0.2	24.4	69.1	6.3
Eastern	4.3	64.8	30.5	0.4
Central	28.3	50.0	21.4	0.3

^a Based on sample management units in each region.

Table VII provides inventory data on white pine based on a sample of the crown land of four management units in the Algonquin Region. These data are not necessarily representative of the older and ecologically different stands of the Northeastern or Northwestern regions, nor of the younger white pine in the southern regions, which is sometimes growing in plantations. Just as white pine W.G. volume is not pure white pine, other W.G.s may, and often do, contain white pine. This fact can be important in many managerial considerations of silviculture, harvesting and pest control.

Utilization

Data on the wood cut and scaled (net merchantable volume) from crown land are readily available, but data from private land are not. Data for white pine, softwoods and all species on crown land over the last 10 years are given in Table VIII. White pine cutting has averaged approximately 500,000 m³ yearly (net merchantable volume). The cutting of white pine has been remarkably stable over the 10-year period even though there have been noticeable differences in total harvest (Fig. 3).

WHITE PINE SYMPOSIUM

Table VII. The distribution of white pine volume as a percentage of the working group volume in four management units in the Algonquin Region

Working group	Management Unit				
	Bancroft	Minden Working Circle	Minden Working Circle	Parry Sound	All four units
	% of white pine volume in working group volume				
White pine	44	51	51	51	50
Red pine (<i>Pinus resinosa</i> Ait.)	30	23	20	20	23
Jack pine (<i>Pinus banksiana</i> Lamb.)	7	0	0	11	7
Spruce all (<i>Picea</i> spp.)	0	5	3	1	1
Balsam fir (<i>Abies balsamea</i> [L.] Mill.)	1	3	2	2	2
Hemlock (<i>Tsuga</i> [Endl.] Carr. spp.)	6	4	10	8	6
Other conifers	1	3	1	1	2
Maple all (<i>Acer</i> spp.)	1	0	0	3	1
Yellow birch (<i>Betula alleghaniensis</i> Britt.)	1	0	0	8	1
Other hardwoods	2	3	1	7	5
Poplar all (<i>Populus</i> spp.)	5	5	5	9	6
White birch (<i>Betula papyrifera</i> Marsh.)	3	3	3	9	4
All working groups	2	8	9	13	5

Data on tree-size classes are not readily available from scaling returns. It is known, however, that cutting is taking place in younger stands and that trees of smaller diameter are being utilized. It is apparent from comparing Table III with Table VIII that white pine utilization at 3.4% of the total cut is not the same as white pine W.G. volume at 2.3% of the total provincial growing stock on crown land. Such a comparison is not entirely valid. The data in Table VII indicate that 5% of the total volume of growing stock on this sample area is white pine.

Table VIII. Net merchantable volume of white pine, all softwoods and total wood harvested from crown land in Ontario from 1974 to 1983 inclusive, with proportional values of white pine

Year	Cut ('000 m ³ net merch.)			White pine as % of softwood cut	White pine as % of total cut
	White pine	Softwood	Total		
1974	544	12,531	14,319	4.34	3.80
1975	472	12,609	14,520	3.74	3.25
1976	447	8,032	9,261	5.56	4.82
1977	493	11,535	13,125	4.27	3.75
1978	587	13,892	15,858	4.22	3.70
1979	493	13,947	16,372	3.53	3.01
1980	561	15,401	17,914	3.64	3.13
1981	457	15,074	17,298	3.04	2.64
1982	529	14,617	17,513	3.62	3.02
1983	563	12,257	14,787	4.59	3.81
Total	5,146	129,894	150,967		
Average				3.96	3.41

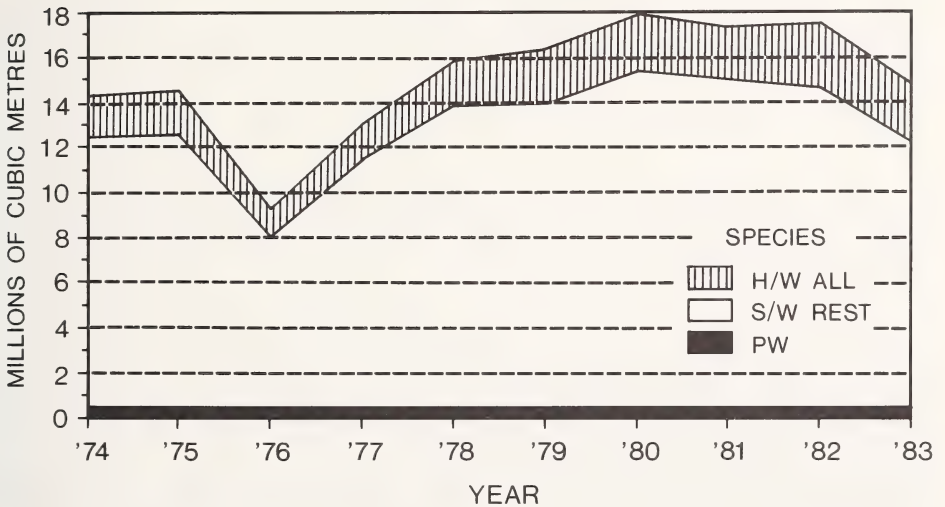


FIG. 3. Net merchantable volumes of white pine, softwood and all wood harvested from crown land in Ontario from 1974 to 1983, inclusive. H/W = all hardwoods; S/W = softwoods comprising the rest of the annual cut except white pine, PW.

WHITE PINE SYMPOSIUM

Summary

FRI data can indicate the volume and characteristics of white pine in a variety of ways. There are approximately 610,000 ha of production forest in the white pine W.G. supporting approximately 110 m³ of gross total volume. This area is not evenly distributed over the province.

The volume of white pine cut and scaled annually from crown land averages approximately 500,000 m³. This is close to 3.5% of the total volume of wood cut and scaled from crown land.

References

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EASTERN WHITE PINE IN ONTARIO: ITS ENTOMOLOGICAL, PATHOLOGICAL, PHYSIOLOGICAL AND OTHER PROBLEMS

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Abstract

The pest organisms and detrimental factors affecting eastern white pine (*Pinus strobus* L.) are reviewed. From a total of 277 insects and 110 disease organisms that are known to inhabit white pine, 56 organisms are mentioned, although only 16 insects and 7 diseases cause serious injury or mortality. An outline of their life history or mode of action and their effect on the tree form or health is presented. Insects and diseases are discussed in groups as they affect various portions of the tree and a summary of two sets of surveys of pests of pine plantations and of pine seeds and cones is given. It is concluded that eastern white pine in Ontario is in a healthy state.

Introduction

In Canada, the eastern white pine (*Pinus strobus* L.) ranges from the Atlantic coast to the southeastern corner of Manitoba. In Ontario it is a characteristic tree of the Great Lakes-St. Lawrence Forest Region, extending southward throughout the Deciduous Forest Region and northward into the southern portions of the Boreal Forest Region (Rowe 1972). Because it occupies a wide variety of soils from dry rocky ridges to soggy sphagnum bogs, is seen throughout the most heavily populated portions of the province, and is the tallest and most stately of all conifers in eastern Canada (Harlow and Harrar 1958), eastern white pine is an excellent choice for the provincial tree.

Eastern white pine commonly reaches a height of 30 m, and on favorable sites it may attain a height of 53 m and a diameter of 1.5 m (Petrides 1958). The tallest extant specimen in Ontario is 43 m tall and 1.35 m in diameter (Anon. 1975). The white pine frequently takes a most attractive form, from tall and conical to flat-topped or windswept, and it is probably the subject matter of thousands of amateur photographers, not to mention artists over the years, from Cornelius Kreighoff and the Group of Seven to modern artists of many styles. And it was, of course, the major economic species during the early development of this country.

The tree species that has been so important in the history and development of this province (MacDonald 1966) and has recently acquired status as the provincial tree, is not without its problems. Briefly discussed here are the more important pest species, an outline of their life history or mode of action and their effect on the form or health of trees. Included are brief summaries of 2 sets of surveys of the pests affecting white pine plantations, and seed and cone production.

Problems. Examination of the records of the Forest Insect and Disease Survey (FIDS) Unit of the Great Lakes Forestry Centre (GLFC), and of selected other references (Hepting 1971; Baker 1972; Wilson 1977), reveals that there are at least 277 insect species or groups and 110 disease organisms that are known to attack, or at least inhabit, white pine in natural stands or plantations in Ontario. Furthermore, there are numerous physiological or environmental problems that affect white pine (Hepting 1971; Wilson 1977; Linzon 1958, 1971; Rose and Lindquist 1984).

Despite the large number of organisms attacking eastern white pine, only 16 insects and 7 diseases cause sufficient injury or mortality to this species to be of concern to managers (Lindquist and Syme 1981). The remainder are considered to be of minor importance, although all have been recorded as causing some injury.

This compilation of insects and diseases is developed primarily from the data base accumulated since 1936 in Ontario by FIDS, an operational unit of the Canadian Forestry

Service. Much of the information in the handbook "Insects of Eastern Pines" by Rose and Lindquist (1973, revised 1984), and the corresponding handbooks on spruce, fir and hemlock; larch, cedar and juniper; and eastern hardwoods, was generated from the records and experience of the FIDS staff. The former handbook served as a major reference in the preparation of this paper.

The insects and diseases mentioned in this paper have all been found on eastern white pine in Ontario, although white pine is not always the primary host. These organisms have been known to cause some form of damage to white pine in natural or man-made stands. Eastern white pine in natural stands is not as susceptible to the ravages of insects or diseases as that grown in plantations (Wilson 1977; Rose and Lindquist 1984; Hepting 1971), and comments on the relative susceptibility of these 2 classes of trees will be made throughout the text as appropriate. The factors affecting eastern white pine (mostly insects and diseases) are discussed in groups as they affect various portions of the tree, and within these groups they are discussed in order of importance.

Bud or Shoot Pests

Insects. Throughout the range of eastern white pine in eastern North America, probably no insect is a more prevalent pest of conifers than the white pine weevil (*Pissodes strobi* [Peck]). By attacking and killing the leader of its coniferous hosts, the weevil seriously affects tree form and, consequently, the commercial and aesthetic potential of the tree. In poorly stocked plantations, repeated attack of trees 1 to 10 m in height can produce a commercially worthless stand.

The adult weevils hibernate in the litter under infested trees and usually emerge in April. Feeding in the spring is indicated by the copious flow of resin from the punctures made with their snouts. Mating occurs during this period, and eggs are laid in the feeding punctures. These hatch in about 2 weeks and the larvae tunnel downward in the inner bark. This tunnelling effectively girdles the leader, which withers and assumes the characteristic shepherd's crook shape. Damage is usually apparent in mid July. The mature larvae then tunnel into the wood and pupate in chambers plugged with chips. Adult weevils emerge in August and September and, after some feeding, seek hibernation sites. Further details of the biology of this most important pest are given by Wallace and Sullivan (1985) elsewhere in these Proceedings.

The eastern pine shoot borer (*Eucosma gloriola* Heinrich) has long been a moderately injurious pest of pines throughout the natural range of eastern white pine in Ontario. It has not been a serious problem in natural stands, and prefers new shoots of saplings, but it will attack shoots of trees up to 30 years old. It is often abundant on trees in thinly stocked, open-grown plantations, with heaviest attacks usually occurring in the upper part of the tree. All species of pine are attacked.

The larva of this insect attacks the new growth on laterals and terminals of its host in May and June, before the shoot has fully elongated. It hollows out most of the pith near the base of the shoot and then cuts an exit hole, drops to the ground and pupates in a cocoon in the soil. Injured shoots wilt and break easily at the last point of feeding. Crooks and forks develop when the terminal shoot is killed.

Six species of adelgids of the genus *Pineus* occur on several pine species at some stage of their complex life cycle. Spruce is usually the primary host on which a gall is found. Eastern white pine is a secondary host of 5 of the species. *Pineus pinifoliae* (Fitch) is most commonly found on western white pine, causing frequent injury. On this host, the adelgids settle on the new needles in early summer, characteristically facing towards the needle bases, and become covered with a woolly wax. Excessive feeding causes flagging of the twigs. Eggs are laid in clusters on the needles and are sheltered by the body of the dead female which remains attached, frequently into the winter months. The eggs hatch in July and the young move to new shoots where they feed on the sap through their fine tubular mouthparts. One winter is passed on the pine and a winged form is produced in the spring. This form flies to the spruce host where its progeny produce galls. The winged forms that

are produced in the galls return to the pine. This species is one of the most serious pests of eastern white pine where it grows adjacent to red spruce (*Picea rubens* Sarg.) or black spruce (*P. mariana* [Mill.] B.S.P.) in the northeastern United States and eastern Canada, but it has not been a serious problem in Ontario.

The white pine aphids (*Cinara strobi* [Fitch]) are small sucking insects, frequently grouped in loose colonies along branches and the upper trunk. They have a characteristically complex life history. Winged forms are almost 6 mm long and dark colored with a conspicuous pattern of white wax secretions. They produce a honeydew that becomes infested with a black sooty mold. The black shiny eggs, laid in rows along the needles, are a trait of this genus, and are useful as a diagnostic feature. The feeding by these insects can cause serious flagging and even mortality of young trees.

Plantation shoot tiers are a group of closely related caterpillars, *Aphelia pallorana* (Rob.), *A. alleniana* (Fern.), *Choristoneura rosaceana* (Harr.) and *Sparganothis sulfureana* Clem., that have caused serious injury to trees growing in young plantations on weedy, former agricultural land. The larvae are normally found on the herbaceous ground cover, but move to small trees, less than 1.5 m high, to feed on the new shoots, which they tie together with silk in May and June.

Other pests. Pine Grosbeaks (*Pinicola enucleator* [L.]) feed heavily on the buds, seeds and fruits of trees. They have, on occasion, caused the complete loss of buds to plantations of Scots pine (*Pinus sylvestris* L.) and are therefore of great concern to Christmas tree growers, but they can damage eastern white pine as well. Most or all of the living portion of the bud is removed by the sharp, hooked bill, with only the dried outer scales being left. Loss of the lead bud results in multiple leaders and, in severe cases, total bud loss can cause witch's brooms.

Foliage Pests

Insects. The family Diprionidae of the order Hymenoptera includes some of the most serious defoliators of conifers, and the genus *Neodiprion* contains 8 species of sawflies found on eastern white pine in Ontario. However, few of these are found commonly on this host. Sawflies, of course, get their name from the saw-like ovipositor at the tip of the female's abdomen with which she cuts slits in the needles to lay eggs. Upon hatching, the young larvae usually feed in colonies and eventually spin tough, oval, paper-like cocoons either in the foliage or in the duff below the tree (Wallace 1961).

The major sawfly feeding on white pine is the introduced pine sawfly (*Diprion similis* [Hartig]). This handsomely spotted species was first recorded in Canada in 1931, near Oakville, Ontario (Twinn 1934), but was not found elsewhere for years. During the 1970s it was found on mature eastern white pine near Fort Frances and at Sault Ste. Marie. It currently occurs throughout southern Ontario between London and Belleville and north to the base of the Bruce Peninsula, just north of Lake Simcoe, and at scattered locations from Cornwall to Lake of the Woods. Although all pines of all sizes are attacked, eastern white pine and Scots pine appear to be the preferred hosts, and ornamental, nursery and plantation trees are most frequently injured. Although 235 records on eastern white pine have been made over the years, this probably reflects, in part, the intensive monitoring of this introduced species.

Larvae are found as early as June, but may be more abundant in the usual second generation in late August and September. They feed gregariously at first but soon separate. Defoliation is therefore diffuse and is confined to the older needles during the first generation, but it involves both old and new foliage during the second generation. Populations of this sawfly appear to be maintained at relatively low levels by natural control factors (Baker 1972).

The white pine sawfly (*Neodiprion pinetum* [Nort.]) has been recorded 83 times to date in FIDS records, but is not known to have caused serious widespread damage to its preferred host. It can, however, be destructive locally. It feeds in colonies on both new and

old foliage, and therefore has the potential for killing trees by complete defoliation. It is present on the needles from mid June to late July and between mid August and late September.

Of the insect defoliators, the pine false webworm (*Acantholyda erythrocephala* [L.]) is becoming one of the most serious defoliators of pines grown in plantations or as ornamentals in southern Ontario. It occurs throughout most of southern Ontario and in the Lake of the Woods area of northwestern Ontario, and so has the potential for spreading throughout the range of eastern white pine (Syme 1981).

This insect creates silken tubes among the needles, incorporating bits of excreta. The larvae feed within these tubes between early May and late June. After feeding, the fully grown larvae drop to the ground and form earthen cells 5 to 8 cm below the surface. The prepupal stage lasts until March or early April. Eggs are laid by the female in slits cut on the flattened surface of pine needles of the previous year's growth.

Eastern white pine is readily attacked by the jack pine budworm (*Choristoneura pinus* P. Freeman) if growing under or near infested jack pine stands. Outbreaks occur frequently. The newly hatched larvae overwinter in silken shelters or hibernaculae without feeding, and mine fascicles of new needles or male flowers in the spring. Later, the larvae feed under loose silken webbing, spun about the flowers or new shoots. When mature, they are about 21 mm long and resemble spruce budworm larvae. They pupate on the shoot, and moths emerge in July or early August. Following mating, eggs are laid in clusters on the needles. Since the heaviest feeding usually occurs near the tops of trees, top kill, causing crooked or multiple leaders, frequently occurs. Tree mortality may occur in heavy infestations.

Ornamental trees are often heavily attacked by the pine needle scale (*Chionaspis pinifoliae* [Fitch]). Eastern white pine is particularly susceptible and attack causes needle discoloration and premature drop. Heavy attacks will kill twigs, branches and trees. The adult scales appear as elongate white flecks on the needles. Deep red eggs are produced by mid August under the female shell and these hatch in the spring. The crawlers then move to new sites. Lady beetles frequently prey upon the scale insects, and this probably keeps their numbers down in the forest. From the forestry point of view, this insect causes little harm to eastern white pine.

Another insect that can cause injury disproportionate to its size is the midge (*Cecidomyia pinifoliae* Felt). The larva of this fly feeds within the needle fascicle and causes the needles of eastern white pine to drop before they are fully grown and while the sheath is still present. Larvae apparently overwinter in the soil.

Mites also attack eastern white pine: *Trisetacus alborum* (Keifer) prevents needle development (usually in a single cluster), and causes a yellow discoloration of the shoot around the cluster. Small, shaded trees are most susceptible, and after heavy attack, all needles are discolored and the buds are dead.

Diseases. Of the defoliating diseases, leaf casts such as *Lophodermium nitens* Darker, *Hypoderma* sp., and *Cytospora* sp., especially *C. pini* Desm., have all been collected frequently on eastern white pine by FIDS staff. These fungi and others cause leaf-yellowing and, at times, premature defoliation and even death of eastern white pine, primarily in nurseries and forest plantings.

Pests Affecting Twigs or Branches

Insects. The pine spittlebug (*Aphrophora parallela* [Say]) is often abundant on eastern white pine and other pines in Ontario. The young nymphs hatch in the spring from eggs laid the previous fall at the branch tips. They pierce the bark to feed on the sap and soon cover themselves with a frothy mass, probably for protection. From May to July they feed progressively closer to the main stem, where they congregate in large masses of spittle. The adults continue to feed in a similar manner during July and August, but without producing spittle. They do, however, eject undigested sap in the form of a fine mist that may descend

like light rain from heavily infested trees. Trees may die from heavy infestations, and twig or branch mortality is common when these insects are present.

Other pests. By removing cones, the Red Squirrel (*Tamiasciurus hudsonicus* Er.) commonly causes the shoots above the cone site to flag; the damage resembles that caused by shoot-boring insects. Although the damage is done in the early fall, the dying twig turns red in the following spring.

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Stem or Log Injury

Insects. Wood-boring beetles, primarily of the genera *Monochamus* and *Chrysobothris*, probably cause more loss of productive pine than any other group of insects. They are secondary, though, in that they attack only trees that are weakened, dying, or recently dead from other causes. Therefore, losses occur in damaged or decadent stands, or in wood that has been cut and left in the forest. Populations build up locally when a large amount of brood material has been produced by a fire or another catastrophe.

The life cycle of some of these borers takes up to 2 years to complete (Gardiner 1961). The first feeding by the newly hatched larvae is just under the bark, and later feeding occurs deeper in the wood. This lowers the value of the timber if the tree is milled too late to remove the larvae in the slab wood. Borers are of little consequence to vigorous, healthy trees. They are, in fact, beneficial to healthy trees since their work on recently dead or dying trees hastens the decomposition process and the production of humus from wood.

Two families of borers are commonly encountered in pines, the roundheaded and the flatheaded borers. The northeastern sawyer (*Monochamus notatus* [Dru.]) is an example of the roundheaded group and *Chrysobothris* spp. are typical flatheaded types. The latter, as adult beetles, are known as metallic wood borers because of their coloring. They make an elliptical exit hole when the adult emerges from the log. The former are known as longhorned beetles because of their extraordinarily long antennae. They make a circular exit hole, so perfect that it appears to be drilled.

Another group of secondary beetles that attack pines in general, at least in central and eastern Canada, consists of the bark beetles of the family Scolytidae (Mitton and Sturgeon 1982). Two of these in particular are frequently found on eastern white pine. *Pityogenes hopkinsi* Sw. has been recorded 99 times and *Ips pini* (Say) 34 times. The latter, the pine engraver, normally attacks dying trees, dead branches and slash, but will attack and kill trees weakened from drought or other agents. Eastern white pine is apparently preferred, although the insect will attack most other pines and spruces. The adult engraver overwinters in the duff and emerges in the spring, when the male cuts a hole through the bark to the wood and creates a nuptial chamber. Two to five egg galleries are made, radiating out from this, depending upon the number of females that join the male. The tiny, legless larvae mine at right angles to the grain and construct a pupal cell at the end of the mine. Adults exit through tiny, round holes in the bark, and this behavior is characteristic of the group. A generation requires 4 to 5 weeks, and 2 may be produced in a season. If the beetles cannot find enough dead or dying material when they emerge, they may attack and kill living trees, particularly those in plantations (Thomas 1961).

The pine bark adelgid, (*Pineus strobi* [Hartig]), on the other hand, conspicuously attacks eastern white pine from the outside of the stem, and can kill young trees. It is a serious pest of nursery, ornamental and planted white pines. Infestations are heaviest on large pines, especially in well shaded areas. The insects are purplish to yellow, soft-bodied and less than 1 mm long. They feed under the woolly flocculence they produce, which is very conspicuous on the stems of heavily infested trees.

A serious pest in the northeastern United States, but less so in eastern Canada, the Zimmerman pine moth (*Dioryctria zimmermani* [Grt.]) severely damages saplings of several pine species and occasionally injures pole-size pines. It prefers Scots pine, but has been recorded 20 times on eastern white pine in the FIDS records. This insect bores under the bark in the spring, and masses of pitch and excreta accumulate on the stem. The larvae are fully grown by July, and adults emerge from the tunnels in later summer. Extensively tunnelled stems break easily in windstorms.

Mound ants of the genus *Formica* can destroy seedling and sapling conifers. Pine trees up to about 6 m from the nest are commonly killed by the ants injecting formic acid into the bark. A small gall-like lesion develops and the tree eventually dies. These ants, especially in more southerly climes, build large earthen mounds that may be up to 60 cm high and 2 to 2.5 m in diameter.

Apparently trees and other vegetation are killed to keep them from shading the mound. The mounds are most often found in openings of the natural forest or along stand edges, and the damage caused by these ants can be particularly severe in forest plantations (Baker 1972).

Diseases. Of all the diseases that attack eastern white pine, the white pine blister rust, caused by *Cronartium ribicola* J.C. Fisch., is the most serious disease in white pine forests and in ornamentals (Gross 1985). The fungus attacks the living bark and cambium of eastern white pine, first breaking out in blisters that exude a sweetish secretion, and later forming larger, bright, orange-colored pustules. These are filled with spores that transmit the disease to its alternate host, *Ribes* spp., where it develops during the summer to a red rust stage, and later, a winter stage. Spores from this host in turn infect healthy pines. The fungus spreads slowly, laterally and longitudinally, through the bark, killing the branches by girdling and the main trunk if it, too, becomes infected.

In contrast with white pine blister rust, stem decays are not so readily apparent, but can cause a major diminution of merchantable timber where they occur (Basham and Morawski 1964). Losses occur principally in trees older than 120 years and are caused by a variety of fungi. The most important of these is red ring rot (*Phellinus pini* [Brot.: Fr.] A. Ames), accounting for up to 90% of the total loss through decay in several instances (White 1953; Basham and Morawski 1964).

Corticium fuscostratum Burt and *Sytinostroma galactinum* (Fr.) Burt are 2 other rot-causing fungi that play a significant role in the loss through decay of merchantable eastern white pine in Ontario (White 1951, 1953).

Another stem disease is Scleroderris canker, caused by *Gremmeniella abietina* (Lagerb.) Morelet. Although red pine (*Pinus resinosa* Ait.) is the prime host, there are 19 FIDS records of the disease on eastern white pine in Ontario. There are 2 races, but the North American race is the only one present in Ontario. In red pine, mortality arises either from complete shoot dieback when trees are small, or from stem girdling by cankers when the fungus grows into the main stem from branch infections. This occasionally happens in eastern white pine. The disease is spread by conidiospores, shed in midsummer and produced in small pycnidia that form at the bases of dead needles or on small twigs. Ascospores form in May and June in cup-shaped apothecia that appear on the bark after the underlying tissue dies. Moist weather conditions favor sporulation of both types, and the infection and colonization of host tissue.

Eastern white pine trees in weakened condition, especially those in natural forests rather than in plantations, are subject to a large number of stem cankers. One of these is caused by *Cytospora pini* Desm., which hastens the death of younger stock. It could be

considered a secondary agent, as are bark beetles, in most cases, with something else predisposing the tree to attack. Other species of *Cytospora*, especially *C. kunzei* Sacc., cause various cankers of the stem and branches of white pine, but none of these is considered serious.

Sap-rotting fungi attack recently killed trees, and usually advance through the wood until almost all of the tree is infected. Studies of the several species of such fungi implicated in the deterioration of eastern white pine killed by fire in the 1948 Mississagi burn were made by Basham (1957, 1958).

A serious nursery stem dieback disease is caused by *Sphaeropsis sapinea* (Fr.) Dyko and B. Sutton, (= *Diplodia pinea* Kickx). In seedlings 3-5 years of age, it causes a rot that extends from below the soil line upward from the root collar zone. It causes a deep red stain on the bark and black streaks in the wood. Eastern white pine is particularly susceptible to this stain. A dieback of branches on older trees is also caused by this fungus. New growth is reduced, the needles turn brown and the buds exude excessive resin. Black pycnidia are formed at the bases of diseased needles and branchlet mortality may occur. The branch dieback form of the disease is not serious on eastern white pine, and the more serious stem dieback is not commonly detected by FIDS in Ontario.

Other pests. At least 2 species of hares or rabbits, the eastern cottontail (*Sylvilagus floridanus mearnsii* [J. Hallen]) and the snowshoe rabbit (*Lepus americanus virginianus* Harlan) injure pine during the winter months when they feed principally on bark and buds of young trees. They are especially destructive of young plantations and natural vegetation, and damage usually occurs low on the stem, although snow depth can influence this. Damage is usually noticed from mid- to late summer when girdled trees turn red. Damage frequently follows the population fluctuations of the rabbit, which are on a 10- to 11-year cycle (Hamilton 1939).

The Porcupine (*Erethizon dorsatum* L.) feeds on the bark of many tree species, including eastern white pine, during the winter months when herbaceous food is unavailable. Feeding usually occurs high in the tree and girdling causes dead tops. Damage is usually sporadic, but is concentrated around the dens of these colonial animals.

Birds, too, have their impact on eastern white pine stems. The yellow-bellied sapsucker (*Sphyrapicus v. varius* L.), in its attempts to gain access to sap, will sometimes attack pine trees. The preferred trees, birch (*Betula* sp.) and eastern hemlock (*Tsuga canadensis* [L.] Carr.), are frequently severely injured or killed. At the least, damage by sapsuckers exposes the tree to other pests.

The piliated woodpecker (*Dryocopus piliatus* [L.]) occasionally creates impressive holes in its endeavors to obtain insects that are within the tree. Since the insects, mainly carpenter ants or wood borers (Audubon 1946), are usually secondary and present only because of a previous rot or other degenerative condition, this bird is not generally a primary cause of destruction.

Root Collar or Root Pests

Insects. If any trees, including eastern white pine, are planted in soil with a heavy grass or weed cover, the fine roots are often destroyed by white grubs, mainly of the genus *Phyllophaga* (Rose and Lindquist 1984). Death or retarded growth is a frequent result of this damage. Severe injury of this type has occurred from time to time to eastern white pine in this province. The various species of white grubs take 2 to 5 years to complete their development, depending on location and species. The adults are the ubiquitous and well known June beetles.

The pine root collar weevil (*Hyllobius radialis* Buch.) and its associate, Warren's collar weevil (*H. warreni* Wood) are capable of killing younger pines, especially in plantations, but are not a particular problem with eastern white pine in Ontario. In fact the white pine is practically immune to attack by these pests unless it is interplanted with preferred hosts, such as jack pine, red pine or Scots pine. The legless larvae tunnel under the bark at the root collar and effectively girdle the tree.

Diseases. The shoestring or honey mushroom (*Armillaria mellea* [Fr.] Kummer) causes a very serious root rot of many tree species (Patton and Bravo 1967), including eastern white pine (Hepting 1971). It has been implicated 113 times in the FIDS records of this host. The disease spreads from old stumps by means of the black shoestring-like rhizomorphs. White fans of mycelium develop under the dead bark and the fruiting body is the familiar free-standing honey mushroom (Boyce 1961).

Fomes root rot, caused by *Heterobasidium annosum* (Fr.) Bref., though not found as extensively on eastern white pine as on red pine, is a serious disease capable of causing significant mortality in pine plantations on old field sites of sandy loam or loamy sand soil types. The fungus first infects from windborne basidiospores on freshly cut surfaces of stumps, and after the stump is colonized, infection spreads mainly by root contact, at a rate of about 84 cm per year from the margins of infection centers. Basidiospores are most prevalent in the fall and consequently infection occurs more readily then (Anon. 1978). Stump treatment with borax is recommended for control (Anon. 1978; Punter 1968).

Another serious root rot problem with eastern white pine is the black root stain caused by *Verticicladiella* sp. It has been detected by FIDS 19 times and goes by the name of white pine root decline. It is a potentially destructive disease of trees planted on wet sites. Delayed budbreak and reduced candle elongation are symptomatic. Rapid death of 3- to 15-year-old eastern white pine frequently results, with a uniform browning of the needles.

Other pests. Probably more important as a root collar pest than the root collar weevils are the complex of field mice or voles that can cause serious injury to young trees. As with rabbits, scarcity of food in winter forces the mice to feed on young transplants of many species (Hamilton 1939). Young plantations growing in grassy or weedy areas are particularly susceptible to girdling damage by mice, especially when rodent populations are high.

Flower or Cone Pests

Insects. The familiar jack pine budworm, alluded to earlier in this paper, is frequently found in the male flowers of pines, although eastern white pine is not the most heavily attacked species. More important to eastern white pine seed production is the fir cone-worm (*Dioryctria abietivorella* [Grote]), which feeds on the cones of pines and other conifers on a variety of sites. It has an overlap of generations and larvae may be found in pine cones all season. It has been recorded 70 times on eastern white pine in the FIDS records. The white pine cone beetle (*Conophthorus coniperda* [Schwarz]) is also an important pest throughout the range of white pine. It may do serious damage to the seed crop in years when only light-to-moderate seed set occurs. Many shoot tips are also killed when infestations are severe. The adult beetles overwinter in cones on the ground, and in spring the females bore into the bases of second-year cones to lay their eggs. The hatched larvae feed within the cones, doing extensive damage, and eventually pupate there. Adults develop by late July and remain in the cone, which is weakened by the boring near the petiole. These usually drop to the ground, where the adult overwinters.

The white pine cone borer (*Eucosma tocullionana* Heinrich) attacks the cones of eastern white pine in southern Ontario and eastward. The larvae burrow in the green second-year cones in June and July, drop to the ground and pupate in the soil. They do extensive damage to the inside of the cone.

In response to concerns expressed by foresters about seed production and its associated problems, special rotating surveys of various coniferous tree species have been conducted by the FIDS Unit in Ontario since 1980. In 1980 and 1983, surveys were made of eastern white pine cones in southern Ontario to determine the extent and cause of damage. Collections of 100 cones were made in a prescribed manner in each of 7 locations each year. Green, succulent cones, close to full size in the second year of development, were obtained. Where possible, collections came from seed production areas or tree seed orchards. The proportion of damaged cones varied widely from plot to plot and by year, but ranged as high as 74% in 1980. An average value for all plots in both years was in the order of 25%

damaged cones. Seed losses within the damaged cones, compared with undamaged cones, ranged from 0 to 55% and averaged 26% over all. The major causes of seed loss and cone damage in these surveys were the white pine cone beetle, the white pine cone borer, the fir coneworm, and other species of *Dioryctria*. Significant damage was also done by undetermined species of Lepidoptera which were probably among the species mentioned above. Locations in the southern and southwestern regions suffered virtually no loss of seed in 1983.

General Factors

In addition to the insects and diseases that attack eastern white pine, the species is susceptible to a multitude of environmental influences, both natural and human in origin. Such things as soil compaction, pollution, or change in water table in urban areas frequently cause sudden browning and death. Secondary insects quickly invade these trees and are often wrongly blamed for their demise. Air pollutants and noxious gases from manufacturing plants are often the cause of foliar damage and discoloration throughout the crowns of trees over large areas (Gordon and Gorham 1963). Eastern white pine is particularly susceptible to ozone damage. Careless use of herbicides will affect only that portion of the foliage contacted and damage from such abuse will be confined there. Salt spray injury occurs along highways where salt is used for ice control. Symptoms of needle browning are seen in the spring, but only those portions of the trees unprotected by snow are affected.

Tree mortality does not necessarily follow such abuses, unless they are repeated, and recovery of individual trees is the norm. However, physiological winter browning is prevalent on exposed trees subject to wide temperature extremes and strong winds during the winter months. This causes desiccation of the needles and, although only that portion of the tree above the snowline is affected, whole-tree mortality occurs when all foliage is affected. This is one of the more important, common and widespread problems of eastern white pine in Ontario.

Special Surveys

In another effort to obtain baseline data on various insect and disease pests affecting plantations or natural stands of the major tree species under regeneration in Ontario, the FIDS field program, in recent years, has included special surveys of these hosts on a rotating basis. Eastern white pine plantations throughout southern Ontario were examined in 1980 and 1983; 40 and 42 plantations, respectively, were examined each year.

The white pine weevil was most prevalent in trees 2-6 m high, and affected 55% of the stands. However, only 7% of the trees were affected. Pine bark adelgids affected a similar number of stands of all height classes, and 12 and 5% of the trees, respectively, in 1980 and 1983. Pine spittlebug affected 20 and 50% of stands, but only 7 and 4% of trees, and the pine false webworm affected only 5% of stands and attacked only 0.4 and 3% of trees in 1980 and 1983, respectively. It was most prevalent in the Central Region of Ontario. The eastern pine shoot borer was found mainly on trees less than 2 m high and although it affected more than 4 times as many stands in 1983 as in 1980, it attacked less than 1% of the trees.

White pine blister rust was the most damaging disease detected in both years. The damage level was low in most plantations with an average of 1.6% of trees affected, and about half of those had stem cankers in 1983. The most common form of foliar damage to eastern white pine over the years has been semimature tissue needle burn caused by air pollutants. Two stands in the Algonquin Region suffered moderate foliar damage from needle burn. Elsewhere, most stands were unaffected, but very low damage was noted occasionally. Disease-caused foliar damage was negligible.

Basal stem cankers were present in 10% of the stands sampled, but overall the percentage of trees affected was less than 1%. However, 2 stands in the Algonquin Region

had 7% of the trees affected. In view of the fact that basal cankers are usually fatal, these statistics represent a serious situation. The survey was designed to detect the presence of *Verticicladiella* root disease (*Verticicladiella procera* W.B. Kendr.) but this problem was not identified.

Most of the mortality encountered in these surveys was the result of white pine blister rust or *Armillaria* root infection. One stand had 15% mortality, but in that instance, the trees were small and drought was considered to be a contributing factor. Mortality in all other stands did not exceed 3% and usually was less than 1%.

Summary

Although white pine blister rust, white pine weevil and *Armillaria* root rot were relatively uncommon in the special surveys of eastern white pine conducted in recent years by the FIDS Unit, they are the 3 most important potential threats to eastern white pine growth and management in Ontario. In fact, this tree species was singularly avoided for many years in planting programs throughout the province because of the threats of white pine blister rust and the white pine weevil.

The remaining factors affecting tree growth, though numerous, remain generally minor in importance in terms of the overall success and management of eastern white pine in Ontario. However, other factors are capable of causing sporadic or localized injury or death, or can cause aesthetic deterioration of individual or small groups of ornamental or shade trees.

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IMPACT OF PESTS ON THE WHITE PINE RESOURCE OF ONTARIO

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Abstract

The importance of intensive management, including adequate pest control, is emphasized as vital to growing satisfactory white pine. The important pests of white pine in Ontario are white pine weevil (*Pissodes strobi* [Peck]), white pine blister rust (*Cronartium ribicola* J.C. Fisch.) and stem decay, caused primarily by *Phellinus pini*. Annual losses caused by decay are ca. 221,000 m³ in gross merchantable volume. Although decay in natural stands under 100 years of age is negligible, sites of injuries caused by weevils are favorable for infection by decay fungi, and adequate weevil control is necessary to keep decay levels low in plantations. Growth loss caused by weevils is ca. 8,000 m³, and annual volume loss ca. 15,400 m³, while an additional 15,600 m³ of timber suffers a 25% loss in value caused by degrade associated with injuries caused by weevils. Growth loss estimated at 8,000 m³, in the form of poorly stocked or totally devastated plantations, is caused by blister rust disease.

Introduction

White pine culture has appeal mostly because the white pine (*Pinus strobus* L.) was a majestic monarch in the forests encountered by the first settlers in eastern Canada. Abundance and high quality of products made white pine a valuable prize to these settlers. The recent publication "White pine, Ontario celebrates its history" (Morse 1984) illustrates the splendor once possessed by this species. Today, white pine retains much of its early popularity, as is evidenced by its selection in 1984 as the arboreal emblem of Ontario. Furthermore, cultivation of white pine has increased to the extent that it now exceeds red pine (*Pinus resinosa* Ait.) in nursery seedling production (Anon. 1983).

Attempts to reforest sites with pure cultures of white pine were thwarted by forest pests, mainly white pine weevil (*Pissodes strobi* [Peck]) and white pine blister rust (*Cronartium ribicola* J.C. Fisch.). These and a variety of other pests affect white pine (Syme 1985). Extensive damage in many plantings was largely responsible for a decline in the popularity of white pine for several decades. Its resurgence is due in large measure to pest management strategies that have resulted in greater plantation success.

The white pine resources of Ontario have remained fairly constant in recent years. Total gross standing volume is about 110,000,000 m³, and the annual harvest is about 500,000 m³ net merchantable volume (Osborn 1985). Dixon (1963) reported approximately the same standing volume and estimated the annual allowable cut at 1,300,000 m³. Impact estimates for this report are based on this allowable cut, which is equated with mean annual increment. The percentage of this increment that accrues in plantations was assumed to be 10% of the total, and for some estimates a mean annual increment per ha of m³ gross total volume for plantations was considered appropriate.

White pine requires intensive management. Pest control can complement good silviculture. For example, pruning of low branches reduces losses caused by blister rust. If branches are removed when trees are young, pruning wounds heal quickly because they are small. Hence, rust control reduces the hazard of infection by stem decay fungi and improves wood quality. Clipping leaders damaged by weevils also reduces this hazard and improves quality.

In many respects the impact of pests that is observed today is a result of lack of pest control in the past. Control strategies are available and should be integrated into white pine management. The feasibility of white pine culture today needs to be judged on the basis of cost and effectiveness of current cultural and pest control programs. Losses caused by pests over the years prove that control strategies are necessary.

WHITE PINE SYMPOSIUM

Insects

White pine weevil is the most important pest of white pine. Brace (1971) and Marty and Mott (1964) describe the damage it causes, and report on lumber recovery and volume losses associated with that damage. Two or more years of terminal growth are killed as a result of larval feeding. The new terminal, which grows from a lateral branch below the injury, consistently has a crook that persists over 2 or more years of new growth. The old dead leader remains attached, and the crook and stem stubs provide evidence of attack by weevils long after the injury has occurred.

Weevils do not usually kill trees, but in some instances virtually all of the trees in a plantation are badly distorted, and the plantation is rendered useless for producing timber because the trees never achieve commercial size. In plantation surveys conducted by the Forest Insect and Disease Survey (FIDS) of the Canadian Forestry Service in Ontario (Table I) this situation was not encountered, and the percentage of totally worthless stands is probably less than 1 or 2%, or ca. 2,000 ha. However, growth is lost each year because these sites are not productive, and at 4 m³ per ha such growth loss amounts to about 8,000 m³ annually.

When only a portion of the trees is rendered valueless, impact becomes a function of the percentage of crop trees that remain unaffected. The percentage is predictable, and Waters (1962) and Marty and Mott (1964) presented useful management guides based on this relationship. Brace (1971) developed an excellent method for predicting volume recovery on the basis of the amount of weevil damage. Depending on log size and the number of weevil injuries, sawlog volumes were reduced by 20-60%. Other studies report an average volume loss of 40% (Waters *et al.* 1955). The FIDS surveys (Table I) were based on counts of trees with current terminals damaged by weevils. If one assumes that such

Table I. Incidence of white pine weevil in southern Ontario stands of white pine

Location	Stands affected (%)	Trees with current terminal affected (%)		
		Trees under 2 m high	Trees 2.1 to 6.0 m high	Trees over 6.0 m high
1980				
Region				
Northeastern	60	7	20	17
Algonquin	75	1	22	9
Central	40	0	6	7
Eastern	0	0	0	0
Southwestern	57	6	0	5
Average	53	3	10	8
Current terminals affected on all trees = 8.0%				
1983				
Region				
Northeastern	58	14	28	0
Algonquin	60	6	15	1
Central	57	9	12	1
Eastern	83	1	1	1
Southwestern	43	1	3	0
Average	60	6	14	0.5
Current terminals affected on all trees = 6.8%				

damage (Table I) reflects only a portion, say 30%, of the trees that have been damaged by weevils, then a total of 20% affected seems plausible. With 20% of trees affected, and a volume loss of 40% per tree, weevils had an impact of about 8% on the growing stock in plantations, or an annual volume loss (cull) of about 10,400 m³. Injury caused by weevils also has an impact in natural stands; although background data for damage estimates in such stands are not as good as data for plantations, a much greater volume of timber is affected. A loss of about 5,000 m³ (cull) annually is a conservative estimate for natural stands. Brace (1971) also calculated a 25% reduction in value of lumber as a result of injuries caused by weevils, and this accounts for another 15,600 m³ in reduced value. While both the growth loss and volume loss (cull) estimates required certain interpretations of the available data, it is apparent that the weevil has had a tremendous impact on white pine.

Four other insects were featured as part of the FIDS surveys of white pine plantations. Eastern pine shoot borer (*Eucosma gloriola* Heinr.) kills shoot tips, but damage is usually less extensive than that caused by weevils. Damage encountered in both 1980 and 1982 was low, with overall averages of 0.05 and 0.60%, respectively, of terminals affected. Pine spittlebug (*Aphrophora parallela* [Say]) was detected in 8 plantations in 1980 and in 21 in 1983. Spittle masses were common on the pines, but spittlebug does not seem to cause as much damage or loss of vigor in white pine as in red pine; hence, impact was negligible. Pine bark adelgid (*Pineus strobi* [Htg.]) was the most common pest encountered in the 1980 FIDS survey, and was second in abundance to weevil in 1983. The insect is easily detected as it produces a white, waxy, flocculent substance. Pine bark adelgid was present in 58% of the plantations in 1980 and 50% in 1983. In instances in which this pest has affected the vigor of small trees, large populations were required to cause noticeable damage (Baker 1972). In the FIDS surveys, density conditions capable of affecting vigor were not encountered. Pine false webworm (*Acantholyda erythrocephala* [L.]) was detected causing defoliation in 12% of the plantations surveyed in 1980 and in 10% in 1983. One of the plantations surveyed in 1983 experienced moderate defoliation, but otherwise defoliation levels were light. Impact is currently considered negligible, but this exotic pest could become important in the future.

Gypsy moth (*Lymantria dispar* [L.]), another exotic pest, will probably be an important defoliator of white pines growing in mixtures with broadleaved species. White pine is listed as a host by Mosher (1915), but he noted that first-instar larvae cannot establish themselves on white pine. Hence, plantations and pure stands are probably resistant.

Diseases

White pine blister rust causes stem and branch cankers that eventually girdle and kill the affected stem or branch. Stem cankers usually kill the tree. Cafley (1958) found that about 8.8% of all the trees in plantations had cankers. This included 4.0% that had been killed by blister rust. FIDS plantation surveys in 1980 and 1983, respectively (Table II), revealed lower overall averages of 3.0 and 1.5% affected, but only trees that died in the current year were tallied. The fact that about half of the cankered trees had stem cankers indicates an annual mortality rate of about 1%. However, in some plantations as many as 9% of the trees had stem cankers.

Impact seems to be concentrated in zones of severe or high infection hazard, and Gross (1985), elsewhere in these proceedings, discusses hazard zones and blister rust control strategies. Severe and high hazard zones cover much of the Algonquin and Northeastern administrative regions in Ontario, and in these regions about 30% of the stands had stem cankers on 3% or more of the trees. This level of cankering will probably result in poorly stocked plantations containing trees with dense crowns and poor form. The total plantation area devastated is probably about 2,000 ha; an area that, if properly stocked, would provide about 8,000 m³ growth at 4 m³ per ha. However, blister rust and weevils have had a devastating effect in these areas, and many sites have been converted to alternative species. The impact of planting a less desirable species is difficult to measure. However, since white pine produces valuable wood, is the most tolerant of the native pine

WHITE PINE SYMPOSIUM

 Table II. White pine blister rust damage caused by *Cronartium ribicola* in northeastern and southern Ontario plantations

Location	Stands sampled (n)	Stands affected (%)	Trees affected		Stem cankers	
			(%)	(Range)	(%)	(Range)
1980 Survey						
Region						
Northeastern	10	30	1.0	0-5	0.6	0-2
Algonquin	12	75	6.5	0-27	1.5	0-7
Central	4	75	3.6	0-8	3.3	0-7
Eastern	6	83	1.5	0-6	1.5	0-3
Southwestern	8	50	1.9	0-11	1.6	0-9
Total/ Average	40	60	3.0	0-27	1.3	0-9
1983 Survey						
Region						
Northeastern	12	75	2.8	0-7	1.6	0-5
Algonquin	10	20	2.1	0-15	1.0	0-7
Central	8	88	0.7	0-3	0.4	0-2
Eastern	6	17	0.2	0-1	0.0	n.a.
Southwestern	6	33	0.4	0-2	0.3	0-1
Total/ Average	42	40	1.5	0-15	0.8	0-7

species, and competes well with sod and other forms of ground cover, this loss in value is significant. The impact in natural stands is also difficult to estimate because trees of alternative species often take up the space vacated when white pines die. Even in the low hazard zone, certain sites can have a high hazard of infection. In general, however, the impact of blister rust disease in the low hazard zone is negligible.

Basham and Morawski (1964) presented stem decay data for natural stands of white pine. Stands under 100 years of age had 3.3% decay. The amount of decay rose rapidly to stand age class 141-160, which had 21.3% decay. Most of the decay was caused by the white pocket rot, *Phellinus pini* (Brot. ex Fr.) Ames (= *Fomes pini* [Thore ex Pers.] Lloyd), which some authors called red rot or red ring rot. On the basis of an overall average of 17.0% defect (Basham and Morawski 1964), and on the assumption that the magnitude of decay in plantations was the same as that in natural stands, it is estimated that 221,000 m³ of white pine are lost to decay in Ontario each year.

When stands are managed on rotation ages under 100 years, as seems appropriate, this loss to decay will be considerably reduced. Pruning low branches when they are small will also reduce the hazard of infection by stem decay fungi. Stem stubs resulting from injuries caused by weevils are primary infection courts for decay fungi. Ostrander and Foster (1957) noted that 80% of the red rot encountered in white pine was associated with injury caused by weevils. Brace (1971) found a similar situation in Ontario, and noted that there was very little heartwood or rot until 30 years after injury caused by weevils, but that after that time the percentage of rot increased rapidly. Hence, the stubs created by weevils seem to remain susceptible to infection, or harbor the decay agent in a latent state, until heartwood forms. A possible explanation for the susceptibility of these stubs could be the lower content of phenolics in the stubs than in branches that die normally (de Groot 1966). The message is clear: control of stem decay will require weevil control if future losses to decay in plantations are to be acceptably low.

Armillaria root rot (*Armillaria mellea* (Vahl: Fr.) Kummer) was detected in 10% of the stands in the 1980 survey and in 5% of the stands in 1983. Usually only a few trees were

killed by *Armillaria*, and the impact on stand density was negligible. Current research indicates that certain strains of *A. mellea* are virulent, whereas others act as facultative saprophytes and usually kill only trees weakened by other causes. The latter situation seems to prevail in white pine plantations in Ontario, as is evidenced by the small percentage of killed trees detected in FIDS surveys.

White pine is affected by a variety of foliar problems, including air pollutants such as ozone and sulphur dioxide. These pollutants kill that portion of the current year's needle that is exposed at the time of injury. The condition is sometimes called tipburn, as the portion of the needle that grows later has the normal green color. Widespread damage occurs about once in 5 years. Pine needle rust (*Coleosporium asterum* [Diet.] Syd.) and needle cast (*Lopohodermium* spp.) are foliar diseases that were detected in the FIDS surveys, although usually less than 5% of the foliage was affected. Needle cast has caused damage to seedlings growing in nurseries, and both foliar diseases occasionally cause considerable foliar loss in young trees, especially when these trees are growing in the understory of a stand.

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THE WHITE PINE WEEVIL, *PISSODES STROBI* (COLEOPTERA: CURCULIONIDAE): A REVIEW EMPHASIZING BEHAVIOR AND DEVELOPMENT IN RELATION TO PHYSICAL FACTORS

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Abstract

The development and behavior of the white pine weevil (*Pissodes strobi* [Peck]) are reviewed in detail. Particular attention is paid to those features of biology that may be exploited in devising management schemes, especially the less favorable nature of shaded (cool) environments for adult activity and brood development.

Introduction

Professor W.D. Peck, in describing "the insect which destroys . . . the leading shoot of the Weymouth pine" in 1817, went on to speak of the natural control of the pest by an insect parasitoid. He said: "But the Ichneumon cannot destory the species, nor can man himself; the most effectual remedy then in our power is, to cut off the leading shoot in August, or as soon as it is perceived to be dead, an inch or two below the dead part, and commit it to the fire." Practising foresters for the last century would have gladly committed *Pissodes strobi* (Peck) to a hotter and more eternal fire than Peck (1817) had in mind. The reference to heat is appropriate in another sense, because temperature is one of the critical elements of stand climate affecting white pine weevil behavior and development, and will enter into the discussion repeatedly in later sections.

The purpose of this paper is to provide a background of general biological information and a more detailed description of the behavior of the white pine weevil, particularly in relation to the physical environment. The information provided is introduced to assist in the search for methods of managing the replenishment of the eastern white pine (*Pinus strobus* L.) resource with acceptable or minimal damage by the white pine weevil.

Identification and Related Species

In order to deal with any problem caused by a biological agent, one must be able to identify the causal organism. The white pine weevil belongs to the family Curculionidae (the snout beetles or weevils), which purportedly has more species than any other group of animals. Fortunately, the array of species of interest here is restricted to a small number in the genus *Pissodes* Germar, 1824, commonly called bark weevils. Hopkins (1911) recognized 30 species from North America to which Hopping (1920) added 1 species and Van Dyke (1927) 2. S.G. Smith and his associates have made the only major systematic revisions of the group, using cytogenetics, host association, and breeding site as the main criteria for delineating and identifying species. These findings for 21 of the 33 nomenclatorial entities are summarized in Smith and Sugden (1969) in 2 tables, which are reproduced here with some changes (Tables I and II). Smith and MacDonald (1972) later described *P. fiskei* Hopkins from spruce slash, and further notes on the identification of this species have been published by Stewart and Bright (1982).

Of the 11 described species of *Pissodes* not dealt with by Smith and Sugden or Smith and MacDonald, only 2 are from eastern North America, *P. puncticollis* Hopkins from "dying bark on felled and standing trees" and *P. deodarae* Hopkins. The latter is often a serious pest of deodar cedar (*Cedrus deodara* [Roxb.] Loud.), and the exotics Atlas cedar (*Cedrus atlantica* Manetti) and cedar of Lebanon (*C. libani* Loud.). It is often treated as synonymous with *P. nemorensis* Germar (Dietrich 1931) which attacks several species of pine as well. There is some problem in the separation of the white pine weevil, *P. strobi*, and the so-called deodar weevil, *P. nemorensis*, in the southeastern United States, especially

Table 1. Host trees of 12 North American species of *Pissodes* (after Smith and Sugden 1969)

<i>Pissodes</i> ^a	<i>Abies</i> ^b	<i>Larix</i> ^c	<i>Picea</i> ^d	<i>Pinus</i> ^e	<i>Pseudotsuga</i> ^f	<i>Tsuga</i> ^g	<i>Cedrus</i> ^h
<i>similis</i> Hopkins	1,2						
(= <i>utahensis</i> Hopkins)	3		7,8,9,10,12	14,23,25,26,28,29			
<i>strobi</i> (Peck)			11	15			
(= <i>sitchensis</i> Hopkins)			6,7,8,9	14,16,23,25,26,28,29,30,31			
(= <i>engelmannii</i> Hopkins)			7,8,9,12	14,15			
<i>approximatus</i> Hopkins				16,17,21,27,30,31			34,35,36
(= <i>canadensis</i> Hopkins)				14,15			
<i>nemorensis</i> Germar				13,15,18,20,22			
<i>terminalis</i> Hopping		5	6,7,8,9	19,22			
<i>schwarzi</i> Hopkins				24,29			
(= <i>yosemitae</i> Hopkins)					32		
<i>radiatae</i> Hopkins				14,28			
<i>fasciatus</i> LeConte			7,10				
<i>rotundatus</i> LeConte			8				
(= <i>nigrae</i> Hopkins)			6,7,8	15,20		33	
(= <i>ataskensis</i> Hopkins)							
<i>dubius</i> Randall 1							
(= <i>fraseri</i> Hopkins) 2				14,15,28,29			
(= <i>piperi</i> Hopkins) 3,4				15,20			
<i>affinis</i> Randall							
(= <i>currei</i> Hopkins)							
<i>fiskei</i> Hopkins			8				

^a Synonyms are indented and placed within parentheses.

^b *Abies*: 1, *balsamea*; 2, *fraseri*; 3, *lasiocarpa*; 4, *concolor*.

^c *Larix occidentalis*.

^d *Picea*: 6, *engelmannii*; 7, *glauca*; 8, *mariana*; 9, *pungens*; 10, *rubens*; 11, *sitchensis*; 12, *excelsa*.

^e *Pinus*: 13, *albicaulis*; 14, *banksiana*; 15, *contorta*; 16, *echinata*; 17, *elliottii*; 18, *flexilis*; 19, *lambertiana*; 20, *monticola*; 21, *palustris*; 22, *ponderosa*; 23, *pungens*; 24, *radiata*; 25, *resinosa*; 26, *rigida*; 7, *scrotinga*; 28, *strobus*; 29, *sylvestris*; 30, *taeda*; 31, *virginiana*.

^f *Pseudotsuga*: 32, *menziesii*.

^g *Tsuga*: 33, *heterophylla*.

^h *Cedrus*: 34, *atlantica*; 35, *deodara*; 36, *libani*.

Table II. The breeding sites of 12 North American *Pissodes* species (after Smith and Sugden 1969)

	<i>Abies</i>	<i>Larix</i>	<i>Picea</i>	<i>Pinus</i>	<i>Pseudotsuga</i>	<i>Tsuga</i>	<i>Cedrus</i>
Witches brooms ^a	<i>similis</i>						
Leaders				<i>terminalis</i>			
Year-old growth			<i>strobi</i>	<i>strobi</i> <i>radiatae</i> <i>nemorensis?</i>			<i>nemorensis?</i>
Boles	<i>dubius</i>	<i>schwarzi</i>	<i>rotundatus</i> <i>fiskei</i>	<i>radiatae</i> <i>rotundatus</i> <i>schwarzi</i> <i>approximatus</i> <i>nemorensis</i> <i>affinis</i>	<i>fasciatus</i>	<i>rotundatus</i>	<i>nemorensis</i>
Root collars		<i>schwarzi</i>		<i>approximatus</i> <i>schwarzi</i> <i>affinis</i>	<i>fasciatus</i>		

^a Those on *A. lasiocarpa* were caused by *Melampsorella caryophyllacearum* Schroet.

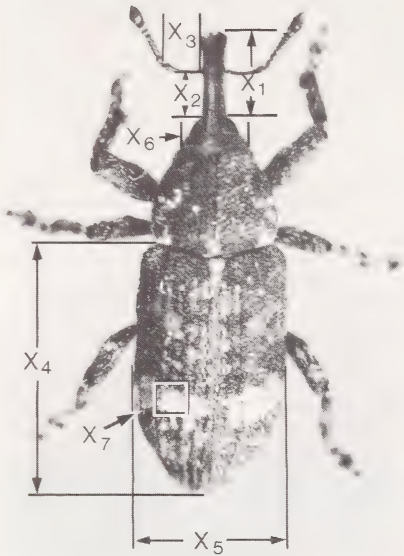
where white pine has been planted outside its natural range. Godwin *et al.* (1982) devised morphometric discriminant functions for the identification of *P. strobi*, *P. approximatus* Hopkins, and *P. nemorensis* adults with a reasonable error rate of 6-15%, depending on the species involved (Fig. 1). They also state that where *P. nemorensis* was verified cytologically, it shared no host with *P. strobi*. Finnegan (1958) published a detailed biology of *P. approximatus* in southern Ontario which may be useful for comparison with that of *P. strobi*. Differences in the mature larvae of the 2 species were described by Böving (1929). Harman and Harman (1972) described the stridulatory mechanism in *P. strobi*, but Harman and Kranzler (1969) could not differentiate *P. strobi* and *P. approximatus* on the basis of sound production. Booth and Lanier (1974) questioned the assumption of breeding isolation between *P. strobi* and *P. approximatus*. Phillips and Lanier (1983), however, showed that *P. strobi* is distinct in its breeding site and habits, although adult weevils may be hard to identify.

From the northwestern limit of the natural range of the eastern white pine near the Manitoba border and westward there is a potential for confusing *P. strobi* with *P. terminalis* Hopping, the lodgepole terminal weevil. Both may attack jack pine (*Pinus banksiana* Lamb.) across Manitoba, Saskatchewan and Alberta, and although there is no record of *P. terminalis* attacking eastern white pine, a careful watch should be kept. *Pissodes strobi* and *P. terminalis* cause the same sort of superficial damage; killing of the terminal growth of the pine. The first symptoms of attack in both cases are wilting and discoloration of the new growth in early summer. However, the behavior of the 2 species (Table III) is very different (Drouin *et al.* 1963). Further west *P. terminalis* attacks lodgepole pine (*Pinus contorta* Dougl.) in British Columbia, the Yukon and the western United States (Stark and Wood 1964; Stevens and Knopf 1974).

In central and northeastern North America, *P. strobi* attacks many species of native and exotic pines (Table IV) and also several species of spruce (VanderSar *et al.* 1977). Following Hopkins (1911), the leader-killing weevils on Sitka spruce (*Picea sitchensis* [Bong.] Carr.), and Engelmann spruce (*Picea engelmannii* Parry) in western North

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VARIABLES



- X_1 = snout length (mm)
 - X_2 = snout length from the insertion of the antenna to the eye (mm)
 - X_3 = \log_e of the scape length (mm)
 - X_4 = elytra length (mm)
 - X_5 = elytra width (mm)
 - X_6 = head width (mm)
 - X_7 = number of colored scales intermixed with the white scales of the apical elytral spot between the second and third elevated striae
 - $X_8 = \sqrt{X_7/X_5}$
 - $X_9 = X_2/X_5$
 - $X_{10} = \text{scape length (mm)}/X_5$
 - $X_{11} = X_2/\text{scape length (mm)}$
- All measurements taken to 0.1 mm.

FUNCTIONS

$$\begin{aligned}
 Y_S &= -364.3904 + 46.6634X_4 + 0.7537X_8 + 1276.626X_{10} + 170.1559X_{11} - 7.5894X_4^2 - 0.6617X_4X_8 + 14.1662X_4X_{10} \\
 &\quad + 6.1827X_4X_{11} - 0.6172X_8^2 + 9.0886X_8X_{10} + 1.9078X_8X_{11} - 1691.363X_{10}^2 - 339.2178X_{10}X_{11} - 40.6209X_{11}^2 \\
 Y_A &= -207.7803 + 33.2907X_4 - 11.7528X_8 + 643.5059X_{10} + 72.4990X_{11} - 4.9048X_4^2 - 0.4357X_4X_8 + 26.2193X_4X_{10} \\
 &\quad + 2.1466X_4X_{11} - 1.4374X_8^2 + 36.9605X_8X_{10} + 3.3095X_8X_{11} - 1041.270X_{10}^2 - 123.9905X_{10}X_{11} - 17.4299X_{11}^2 \\
 Y_N &= -180.8647 + 14.7729X_4 + 11.4995X_8 + 543.2856X_{10} + 83.3837X_{11} - 2.7397X_4^2 - 0.2382X_4X_8 + 22.8461X_4X_{10} \\
 &\quad + 1.3217X_4X_{11} - 2.5423X_8^2 - 4.8385X_8X_{10} - 2.4766X_8X_{11} - 703.9675X_{10}^2 - 114.9241X_{10}X_{11} - 17.7632X_{11}^2 \\
 Y_{SA} &= 40.5159 - 12.0030X_1 - 2.9720X_4 + 3.5560X_8 - 47.6006X_{10}
 \end{aligned}$$

DETERMINATION

- $Y_S \geq Y_A$ and $Y_S \geq Y_N$ = *Pissodes strobi*
- $Y_A > Y_S$ and $Y_A > Y_N$ = *Pissodes approximatus*
- $Y_N > Y_S$ and $Y_A > Y_A$ = *Pissodes nemorensis*

If only *P. strobi* and *P. approximatus* occur in the area, then $Y_{SA} \geq 0$ for *P. strobi*, otherwise *P. approximatus*.

FIG. 1. Discriminant functions for the identification of *P. strobi* and 2 associated species of *Pissodes* (after Godwin *et al.* 1982).

Table III. Diagnostic features of attacks by *Pissodes strobi* (Peck) and *P. terminalis* Hopk. on *Pinus banksiana* Lamb. (From Drouin *et al.* 1963)

Characteristic	Species	
	<i>P. strobi</i>	<i>P. terminalis</i>
Adult feeding sites	On <i>preceding</i> year's growth starting just <i>below</i> node.	On <i>current</i> year's elongating shoot starting just <i>above</i> node.
Oviposition sites	On <i>preceding</i> year's growth starting just <i>below</i> node.	On <i>current</i> year's elongating shoot starting just <i>above</i> node.
Adult feeding and oviposition	Progresses downward	Progresses upward
Larvae feed	Downward in groups ("Feeding ring")	Upward, individually, irregularly
Pupal chambers	In pith (mainly) of stem below current growth (1 or 2 years back)	In pith (mainly of killed current year's shoot)

Table IV. Native and exotic host species commonly reported for the 3 populations of *P. strobi* (after VanderSar *et al.* 1977)

Host species	<i>P. strobi</i> ecotype		
	<i>strobi</i>	<i>engelmannii</i>	<i>sitchensis</i>
<i>Pinus strobus</i> L.	x ^a		
<i>P. sylvestris</i> L. ^b	x		
<i>P. banksiana</i> Lamb.	x		
<i>P. resinosa</i> Ait.	x		
<i>P. rigida</i> Mill.	x		
<i>P. pungens</i> Michx.	x		
<i>P. contorta</i> Dougl.		x	
<i>Picea abies</i> (L.) Karst. ^b	x	x	x
<i>P. glauca</i> (Moench) Voss	x	x	x
<i>P. mariana</i> (Mill.) B.S.P.	x	x	x
<i>P. pungens</i> Engelm.	x	x	x
<i>P. rubens</i> Sarg.	x		
<i>P.itchensis</i> (Bong.) Carr			x ^a
<i>P. engelmannii</i> Parry		x ^a	x
<i>P. glauca</i> (Moench) Voss var <i>albertiana</i> (S. Brown) Sarg. ^c		x	
<i>Picea x lutzii</i> Little ^d			x

^a Preferred natural host species.

^b Exotic species.

^c Natural hybrid between *P. engelmannii* and *P. glauca*.

^d Natural hybrid between *P.itchensis* and *P. glauca*.

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America were considered separate species, *Pissodes sitchensis* Hopkins and *Pissodes engelmannii* Hopkins, respectively. However, Manna and Smith (1959) and Smith (1962) were not able to separate these 2 populations from the eastern *P. strobi* on the basis of morphology and cytogenetics. Because of this, Smith and Sugden (1969) treated the complex as a single species with 3 ecotypes. VanderSar *et al.* (1977) supported this interpretation after forced feeding bioassays of host preferences. They concluded that the *strobus* ecotype was ancestral to the 2 western types, but that because the preferred natural hosts do not overlap in distribution (Fig. 2), valid species based on behavioral differences may be recognized. Other studies and observations clearly indicate complex relationships



FIG. 2 Distribution of three principal hosts of the white pine weevil. *Pinus strobus* L., horizontal hatching; *Picea engelmannii* Parry, solid black; *Picea sitchensis* (Bong.) Carr., diagonal hatching (after Little 1971).

that show a considerable degree of host specificity, and perhaps breeding isolation of the 3 populations. Western white pine (*Pinus monticola* Dougl.) has been shown to be an acceptable host for the *Pinus strobus* ecotype of the weevil (Plank and Gerhold 1965; Soles *et al.* 1970), and it is attacked in plantations in eastern North America to some extent, although less than eastern white pine. VanderSar (1978) found that weevil females from Engelmann spruce would feed on western white pine, but would not oviposit, the latter agreeing with the absence of attack in nature (Stevenson 1967). Weevil adults from Sitka spruce were shown by Alfaro and Borden (1982) to feed preferentially on Sitka spruce over both western and eastern white pines, the latter contrary to VanderSar's earlier results from a somewhat different bioassay. Alfaro and Borden also report that various provenances of eastern white pine planted at the University of British Columbia Research Forest side by side with a Sitka spruce plantation have not been attacked, while up to 80% of the spruce have been weevilled. White spruce (*Picea glauca* [Moench] Voss) may be the linking host between east and west, with perhaps a contribution from jack pine/lodgepole pine, although not much is known about the latter cases. Phillips and Lanier (1983b) found that *P. glauca* is not a good host for brood production.

Nine of the 11 *Pissodes* species described by Hopkins (1911) and Van Dyke (1927) that were not studied by Smith and his colleagues, or others, are from the western United States; all are poorly known. Most, if not all, seem to be associated with thick bark on the lower trunks of several species of pine, spruce and fir and therefore are unlikely to be confused with or have connections with the *P. strobi* complex. The Monterey pine weevil, *Pissodes radiatae* Hopkins, usually breeds in the boles and root collars of pines, but sometimes attacks leaders in the manner of *P. strobi* (Furniss and Carolin 1977). It was considered a valid species by Smith and Sugden.

Often there are weevils other than *Pissodes* species associated with and causing damage to pine plantations, including white pine on occasion (Baker 1972). Table V lists the commonest of these species with a reference to more detailed information when available. All of these weevils may be readily differentiated from *Pissodes* species by major anatomical characteristics, life history and damage.

Table V. Weevils commonly associated with pine plantations

Species	Reference
<i>Hyllobius aliradicis</i> Warner	Ebel and Merkel 1967
<i>H. congener</i> D.T., S. and M.	Martin 1964
<i>H. pales</i> (Herbst.)	Finnegan 1959
<i>H. pinicola</i> (Cooper)	Ebel and Merkel 1967
<i>H. radialis</i> Buch.	Finnegan 1962
<i>H. rhizophagus</i> M., B. and W.	Millers <i>et al.</i> 1963
<i>H. warreni</i> Wood	Warren 1960
<i>Pachyllobius picivorus</i> (Germ.)	Franklin and Taylor 1970
<i>Thylacites incanus</i> (L.)	-----
<i>Brachyrhinus ovatus</i> (L.)	-----
<i>Cimberis</i> spp.	-----
<i>Diodyrhynchus</i> spp.	-----
<i>Magdalis austera</i> Fall.	Plumb 1950
<i>M. hispoides</i> LeC.	Plumb 1950
<i>M. perforatus</i> Horn.	Plumb 1950

Although the eastern white pine has been planted extensively in Europe, where it is known as Weymouth pine, the white pine weevil has not been introduced. There are 15 described species of *Pissodes* in Eurasia, 8 in Europe alone. Some of these attack the white pine, but none occupies the same ecological niche as *P. strobi* in North America. The closest is *P. notatus* Fabricius, which feeds under the bark of young pines. One European species, *P. validirostris* Gyllenhal, is a serious pest of pine cones and seeds (Kudela 1974). To date no Eurasian species has been introduced into North America.

A great deal is known about the systematic relationships of the white pine weevil, but there is an opportunity for collecting, field observation and biosystematic experimentation in the southeastern and western United States. In particular, a comprehensive study of host tree selection by the three *P. strobi* ecotypes might yield a more unified framework for understanding the evolution of this complex.

Generalized Life History

The life history of the white pine weevil in eastern North America was first described by Hopkins in 1907 (Belyea and Sullivan 1956). Hopkins' findings have been corroborated and elaborated by many other workers. Studies of the 2 western ecotypes, *P. sitchensis* on Sitka spruce and *P. engelmannii* on Engelmann spruce, such as those by Silver (1968) and Stevenson (1967), respectively, have demonstrated that the general developmental scheme is consistent across the continent. Briefly, the progression of events is as follows.

The weevil is univoltine, with the adults hibernating in the duff or on the trees. Emergence of the adults from hibernation varies with the season and location, but generally occurs during April when the adults move up the trees to the highest parts of the crown. Under favorable weather conditions, feeding, copulation, flight, and oviposition take place. Over a period of about 6 weeks, each female may deposit up to 200 eggs in 1-year-old leader internodes. The eggs hatch in about 2 weeks, and the larvae feed downward, consuming the inner bark. There are 4 or 5 larval feeding stages. Normally about 5 or 6 weeks are required to complete larval development, and pupae are formed within the pith or wood of the dead leader. The pupal stage lasts about 2 weeks and the callow adults may remain in the pupal chamber for an additional 2 weeks (MacAloney 1930). Adult emergence takes place in August or September and on into the fall. The new adults do not move far from the brood trees as they feed. Finally, as the season cools, they go into hibernation. Fig. 3 shows the life cycle in diagrammatic form and provides a base for the detailed descriptions of behavior in the next sections.

Overwintering Stages

The principal overwintering stage in all 3 ecotypes of the white pine weevil is the adult (Harris 1862), which in most cases has emerged from an infested shoot in late summer. It has been shown, however, that some larvae and pupae from late oviposition or in situations where development is slow may not develop to adults the same summer and may enter the winter period. In eastern North America, Blackman and Ellis (1916) and MacAloney (1930) found that some of these late stage immatures may survive the winter and complete their development the following season. Other authors, e.g. Dixon and Houseweart (1982) working in Maine, do not indicate overwinter survival of immatures. More observations on this aspect of the life history have been made with the *P. sitchensis* and *P. engelmannii* ecotypes in British Columbia and the western United States. Stevenson (1967) working with *P. engelmannii* and Silver (1968) with *P. sitchensis* did not find survival over the winter, but VanderSar (1977) in another study of *P. sitchensis* found that 11% of the total adult population emergent from a sample of infested leaders had successfully overwintered either as late larvae, pupae or callow adults in the breeding site. Carlson (1971) also confirmed that overwintering as immatures occurs in *P. sitchensis*. This developmental sequence is well known in several European *Pissodes* species (Kudela 1974). It is likely that survival depends on the mildness of the winter, and therefore it is safe

to conclude that overwintering of immatures probably is more common in the western coastal populations and in southeastern areas where mild winters are prevalent. The importance of this component to dynamics of the population is unknown.

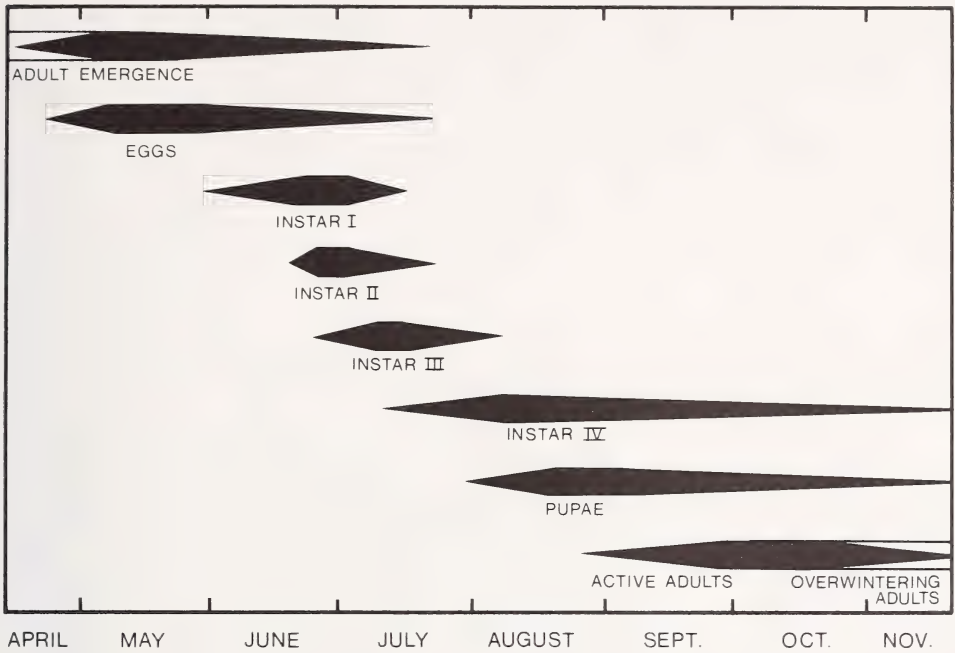


FIG. 3. Diagrammatic illustration of the life cycle of *Pissodes strobi*.

Adult Longevity

The newly emerged autumn adults do not gain full reproductive maturity immediately, and therefore to be successful in engendering a new generation, they must survive at least 1 winter in hibernation. Hopkins (1907) concluded that the adults may live 2 or 3 years and that the females will oviposit each year, but did not publish direct evidence for this statement. Harman and Kulman (1967) also claimed that adult weevils of the *P. strobi* ecotype can live 2 or more years, but again data were not presented. Working with the *P. sitchensis* race on Vancouver Island, McMullen and Condrashoff (1973) showed conclusively that adults can survive for at least 4 years and reproduce each season. No studies have been done to produce quantitative survival data, and it is clear that long life spans must be very dependent on local site and weather conditions. The contribution of adults that have overwintered more than once to maintaining a population is therefore unknown, but the potential for adults to survive several years must be taken into account in any suppression action.

Prehibernation Adult Activity

When the adult weevils emerge from their pupal cells in the leaders of the host trees in late summer, they usually drop to the ground or lower parts of the trees. Sullivan (1959) showed that, at temperatures below 26°C, these adults, especially ones if they have not fed (i.e., if they are starved), react positively to point light sources, and this causes them to move upward into the higher parts of the crowns. The normal activity at this time is feeding, which takes place more or less throughout the whole upper crown and not just on

the most recent terminal growth (Sullivan 1959; Dixon *et al.* 1979). These findings are in agreement with those of Gara *et al.* (1971) and McMullen and Condrashoff (1973) for western *P. strobi* on *Picea sitchensis*. The feeding sites are recognized as small, uncapped pits in tender bark and buds.

Sullivan (1960) concluded that the intensity of fall feeding is influenced mainly by temperature. Activity increases up to about 26°C, which is approximately the reversal temperature (weevils become photonegative) of fed adults (Sullivan 1959). When the temperature of exposed feeding sites rises above 26°C the adults move into more shaded locations and continue feeding. Dixon *et al.* (1979) found that most adults spent the night on apical buds and moved onto the stems and first branch whorls as the day progressed. In their particular observations more weevils were found in the north and east quadrants than in the south and west quadrants. The periods of daily activity become progressively shorter and more infrequent in response to the fall temperature trend. MacAloney (1930) remarks that settled cold is required to induce hibernation, and feeding may take place even after heavy snow has fallen if the weather warms again. The importance of fall feeding in accumulating body reserves and its influence on overwinter survival has not been studied. Sullivan (1959) notes that active adults in the fall may live 6 days at 20°C without feeding. During this fall feeding period the adults are usually solitary (Dixon *et al.* 1979; Booth *et al.* 1983); consequently males of *P. strobi* do not produce the aggregation pheromone in the autumn.

Hopkins (1911) remarked on the "slow sexual maturity" of *Pissodes* weevils in general and illustrated the reproductive organs of a newly emerged female. Barnes (1928) further described the undeveloped state of the female reproductive organs in young adults of *P. strobi* and noted that the possibility of oviposition is precluded until the following spring. Unpublished work by T.M. O'Dell, P.A. Godwin and R.T. Zerillo of the United States Forest Service was quoted by Booth *et al.* (1983) as showing that *P. strobi* females enter a reproductive diapause in response to shortening daylengths. This diapause is fulfilled by exposure to cool fall temperatures by early November (in Virginia) and females can lay viable eggs if temperature is suitable for activity (Harman and Kulman 1967). In the same study of ovariole development and oviposition, Harman and Kulman corroborated the findings of several earlier investigators that copulation can occur in the fall, and viable sperm can be stored by the females for long periods of time. Hence, the males are sexually mature during the fall activity period although they do not produce an aggregation pheromone. In some instances apparently a high proportion of the newly emerged females may mate in the fall before hibernation. Old-generation females (overwintered one or more times) may oviposit near the base of trees or even on current new growth long after the principal (spring) egg-laying period has ended (Harman and Kulman 1967). This suggests that the reproductive diapause of the new-generation females may not be totally under environmental control, or at least not induced after adult emergence. Retnakaran (1974) was able to induce sexual maturity in new-generation females by topical applications of juvenile hormone analogues. Kudela (1974) records that the females of some *Pissodes* species in Europe may oviposit the same year they emerge, but in general are sexually immature.

Numerous reports have dealt with flight and dispersal of white pine weevil adults and conflicting opinions have been expressed about the extent of flight activity. The differences appear to be resolved by considering fall and spring (new-generation and old-generation) weevil populations separately. Stevenson (1967) found with the *P. engelmannii* ecotype that the large flight muscles were not well developed in newly emerged adults and that when tossed into the air they would not initiate flight. Most movement was by walking. He found that adults held at cool temperatures (2°C) for 48 days had well developed flight muscles and would initiate flight when tested in the same manner. The adults require warm temperatures (24-27°C) (Barnes 1928; MacAloney 1930) for flight, however, and therefore the best conditions for flight of new adults occur early in the new-generation period when the adults do not have fully developed flight muscles. As the season progresses and cooler

temperatures become prevalent, muscular development is presumed to take place, but the ambient temperatures will attain suitable levels for flight for only short periods at infrequent intervals. Studies by Godwin *et al.* (1957) showed that few weevils moved away from the release trees after marking and release on 2 September (south-central New York State). Out of almost 1,600 weevils released, 60-70% were active on the release trees about 5 weeks later and only 12 had moved away from the immediate area, travelling about 35 m. Experiments by Dirks (1964) in Maine also indicate little movement in the fall. McMullen and Condrashoff (1973) and Overhulser and Gara (1975) working in Sitka spruce found similar conditions. These studies of fall dispersal have been conducted in open conditions. Droska (1982) concluded that weevils emerging from brood trees growing under heavy shade would disperse from or avoid shaded habitats. He believed that the great reduction in ultraviolet light under a forest canopy plays a major part in the observed response. Later Droska *et al.* (1983) showed that weevil adults are more responsive to ultraviolet than to white light. The conclusion is as Graham observed (1926), that flight is possible, but fall is not the principal dispersal period of the weevil.

Hibernation

In eastern North America, the fall adults respond to the progressively cooler and shorter days. They tend to be less responsive to light and follow temperature gradients to the warmest locations at and near the bases of the trees at night (Sullivan 1959). Few periods are satisfactory for feeding. Other responses such as positive geotaxis may also bring the weevils into the hibernation area around the base of the tree (Dixon *et al.* 1979). Sullivan (1959) found that if the average air temperature (1.3 m above ground) remains below about 5°C for several days, the adults enter hibernation. Dixon *et al.* (1979) observed that the weevils left the trees at temperatures somewhat above 5°C but at 3°C were penetrating the pine litter in preparation for dormancy. The overwintering sites of most adults were at the interface plane between the dry and moist litter zones and were concentrated in the west and north quadrants. The average distance of the overwintering adults from the tree boles was about 20 cm, with less than 4% beyond 30 cm. No adults were found beyond 60 cm. Dixon *et al.* (1979) found little movement in the hibernation zone over the winter. Their finding agrees with that of Sullivan, who states that temperatures in the hibernation sites seldom attain activity levels until the following spring.

A very wide range of winter conditions occur in western North America, and the weevil adults, *P. sitchensis* and *P. engelmannii*, apparently respond in a manner similar to that of weevils in the east. The *P. engelmannii* type occurs mainly in areas where winters are severe, and therefore it overwinters in the duff as does eastern *P. strobi* (Stevenson 1967). In contrast, *P. sitchensis* does not enter the needle litter in locations where conditions are mild, but overwinters in the tree crowns or on the boles of trees down to the root collars, or in the duff in progressively harsher climates. The adults feed throughout the winter whenever it becomes warm enough (McMullen and Condrashoff 1972; Gara *et al.* 1971; Silver 1968), and Carlson (1971) concluded that feeding must occur for survival over the winter.

Post-hibernation (Spring) Adult Activity

Emergence. The reactivation of weevil adults that have survived the winter in ground hibernation sites is dependent upon the warming of the location. Sullivan (1959) observed that adults became active and emerged from hibernation when the microhabitat had warmed to 6°C or higher. Hence, the time of emergence varies in relation to the characteristics of the site. Adults in exposed areas are frequently activated well in advance of those that have overwintered in shaded sites. On Vancouver Island, British Columbia, Silver (1968) did not record spring adult activity on Sitka spruce until the daily maximum air temperature was regularly 16°C or higher. Dixon and Houseweart (1983) show the seasonal progression of numbers of weevil adults on host trees at Lamoine, Maine,

beginning in late April and rapidly increasing to a peak in mid May. The building of a numerical simulator/predictor for emergence in the spring is an area worthy of research.

The behavior of overwintered adults is determined by a complex interplay of host physical and chemical factors, pheromones and microclimate.

Leader selection. The adults are strongly photopositive and starvation intensifies the reaction until about 2 days before death when the reaction weakens and finally reverses for the last few hours of life (Sullivan 1959). During normal scotophase, however, Dixon and Houseweart (1983) have shown that the weevils exhibit negative phototaxis, and they conclude that both temperature and photoperiodism affect the weevil activity at the end of the daily scotophase and the beginning of the photophase. Adults also exhibit strong negative geotaxis (VanderSar and Borden 1977b), and therefore the photic and geotactic responses act in concert. Upon crawling from the duff the adults probably orient visually to the vertical silhouettes of nearby tree trunks (VanderSar and Borden 1977a). The combination of geotactic, phototactic, and photic pattern responses then leads them to the uppermost and most vertically oriented parts of the trees, the leaders, where they begin feeding on the previous year's growth just below the apical buds, or occasionally on the buds themselves. The stoutest, most vigorous leaders are selected. Sullivan (1961) found in eastern white pine that leaders 4 mm in diameter or smaller were not selected, and that the attack rate increased steadily to about 80% at 9 mm diameter. The stouter leaders had thicker bark, and this was important to selection (Kreibel 1954) as the weevil utilized a range of thicknesses from 0.8 to 2.5 mm, with the greatest preference for the 1.8- to 2.2-mm range. Sullivan suggested that the 0.8- x 0.5-mm egg size probably influences the lower limit of bark thickness. The photic responses described by VanderSar and Borden (1977a) for the *P. sitchensis* ecotype showed preference for 3-cm vertical silhouettes. They were unable to show a strong relationship between silhouette width and actual leader diameter, but the mean midpoint width, including needles, of attacked leaders was about 3 cm, and this corresponds well with the laboratory silhouette trials. Longer leaders were also chosen, other factors being equal. Other leader characteristics, such as depth of cortical resin ducts (Stroh and Gerhold 1965) which is correlated with leader stoutness and vigor, as well as chemical properties may influence selection within a leader population. Dixon and Houseweart (1983) showed that at the beginning of the spring activity period, there were as many weevils on small eastern pines that subsequently were not attacked (feeding or oviposition) as on trees heavily attacked in later weeks. This indicates a concentrating effect on the preferred leaders.

Overhulser *et al.* (1972) reported that Sitka spruce that was previously attacked by weevils were less frequently reattacked than those that were not. They speculate that a similar reaction leads to the greater immunity to attack of older eastern white pine observed in the east, since most trees in older stands have been heavily attacked. Harman and Brown (1974), however, point out that several workers report weevil attack and brood production on large eastern white pines. The behavioral bases for this phenomena have not been elucidated.

Feeding. The uncapped feeding pits may be found readily because they exude resin. During the early part of the season, feeding constitutes the main activity (Sullivan 1961), while later, oviposition increases in intensity. The adults return to the leader tip after each interruption, period of inactivity, or movement to a new tree before beginning to move downward in the search for suitable feeding and oviposition sites. As a result of the early preponderance of feeding versus oviposition and the just-described behavior sequence, there tends to be a higher proportion of feeding punctures apically, including the lateral branches of the first whorl (Dixon and Houseweart 1983), although the distribution of total punctures, feeding and oviposition, is fairly uniform throughout the attacked portion of the leader.

Aggregation. Males and females are reproductively mature during the spring activity period (Harman and Kulman 1967), and copulation takes place. While new-generation

adults in the fall generally remain solitary, aggregations of adults are formed in the spring. Overhulser and Gara (1975) reported that 5 to 8 adults were commonly found on a single Sitka spruce leader in early May, and up to 15 have been counted. Dixon and Houseweart (1983) observed an average of 5.3 (max. 19) adults per white pine terminal in Maine, and this was 2.3 times the number found overwintering in the litter beneath a tree (Dixon *et al.* 1979). Booth and Lanier (1974) first presented evidence that feeding males of *P. strobi* produce an aggregation pheromone. The principal components of this pheromone were isolated and identified as grandisol and grandisal (Booth *et al.* 1983). Their production is associated with the hindgut of the male weevils. Host volatiles released by feeding are required to maximize the response. Both sexes of weevils are attracted. The synthetic mixtures tested in the field were not as effective as natural pheromone sources, i.e., feeding males. This aggregation ensures the opportunity for copulation and for a concentrated attack upon the selected leaders.

Dispersal. As stated earlier the fall adults do not disperse far from their brood trees and instead overwinter very close to the brood sites. During the spring, however, flight is common. Barnes (1928) showed that temperatures above 21°C are necessary for flight initiation and that strong winds deter flight. MacAloney (1930) also suggested that the optimum temperature for flight is between 24 and 27°C, with a lower limit near 21°C and an upper limit of about 30°C. The weevils take off mostly with the prevailing wind (Harman and Kulman 1967) from high parts (dead leaders, tips of laterals, upper boles) in the trees (Overhulser and Gara 1975) and even from elevated points on the ground (Harman and Kulman 1967). Harman (1975) reported that the direction of movement is influenced by the row orientation in a plantation. In Sitka spruce the highest activity found by Overhulser and Gara (1975) was between 1000 and 1400 h, corresponding to the highest air temperatures. They also found that most adults flew slightly below the level of susceptible host leaders.

All recent studies indicate that the majority of individuals do not move far. Harman and Kulman (1967) and Harman (1975) considered that most weevil adults stayed within 10 to 55 m of a release point, with 65% remaining within about 12 m. Harman also found that the majority of adults that left his release point changed trees only once and none more than 4 times. Single, long-distance flights have not been documented, although early workers, e.g., MacAloney (1930), thought that flights of several kilometres are possible. Dispersal over considerable distances has been recorded, possibly as a result of several shorter flights. Dirks (1964) observed spring dispersal mostly within 25 m, but possibly as many as 10% of the released weevils travelled 100-150 m. Harman and Kulman (1967) found released adults throughout the study plot up to 100 m from the release point and at 200-300 m beyond a hardwood barrier. They also observed that the flight activity of the overwintered adults decreased as the summer progressed. Godwin *et al.* (1957), also working in eastern white pine, found dispersal of 90-125 m during the spring flight period. Again Harman and Kulman (1969) found that a large concentration of released weevils remained within 10 m of the release point, but that dispersal occurred out to about 100 m. In this same study, dispersal onto host trees growing in heavy shade was less than to those in intermediate shade. In Sitka spruce McMullen and Condrashoff (1973) located weevils up to 180 m away from a release made the preceding fall, but marked weevils from 2 separate tests eventually were found 1.2 km from the release location. From this same study they found that some weevils survived 4 years. In all of these tests using marked adults, a significant proportion of the released adults were never found and may have moved long distances outside the study area. The success of dispersal studies has been remarkable in view of the difficulties of searching areas of even modest size. There is no doubt that significant numbers of weevils can disperse long distances, especially in regions where adults may survive for several years. Some of the dispersing females may be already carrying viable sperm from fall copulation, and the aggregation pheromone of feeding males would also serve to ensure brood production by dispersing adults. Godwin *et al.* (1957) report that in south-central New York State large weevil populations numbering

5,000-7,000 adults per hectare may be available to disperse. No studies have been made on the effect of weevil density on the initiation of dispersal flights.

Oviposition. After about a week following emergence from hibernation, during which time feeding and copulation are the main activities, the female weevils begin to oviposit. They excavate small chambers at the bottoms of normal feeding punctures and deposit 1 or more eggs in each puncture. The number quoted for *Pinus strobus* is 1 to 3. Gara *et al.* (1971) found up to 5 in Sitka spruce with an average of 1.4 per puncture. The eggs are pushed well into the chambers by the females, which use their beaks, and the punctures are capped with blackish frass. As with feeding, oviposition on exposed trees starts on the leader just below the terminal bud and progresses basally as the acceptable sites are utilized at the upper levels. The majority of the oviposition is located on the 1-year-old internode, with a somewhat higher proportion of oviposition than of total punctures in more basal portions of the leader. Up to 200 eggs may be laid in a single leader.

On shaded trees the patterns of feeding and oviposition are very different. On shaded stems the attack is not confined to the 1-year-old internode but occurs over the past 4 or 5 years' growth (Sullivan 1961). In exposed leaders there are usually about equal numbers of feeding and oviposition punctures over all, and the distribution is fairly even. (Concentration of oviposition near the top of the leader has been recorded [Dixon and Houseweart 1982], a condition that probably arises from a short, intense oviposition period.) Neither of these conditions holds for shaded stems. The pattern is irregular and the proportion of punctures containing eggs is much lower.

Microclimatic Relationships of Spring Adult Activities

Once the insect is on the leader, the amount of feeding, copulation, flight, oviposition or inactivity observed during any given period is a function of the existing climate. Within reasonable limits, factors such as wind seem to have little effect on the amount of weevil activity. Heavy rain halts all activity, although a small proportion of the insects may remain active during light rain. The most important elements influencing the extent and type of activity are bark temperature of the leader, solar radiation and atmospheric moisture, with bark temperature being the most influential. It is the body temperature of the adult weevils that is causally related to the level of activity and the body temperature is a function of air temperature, substrate (bark) temperature, and solar radiation. Bark temperature of the leader is influenced by incoming solar radiation in a manner very similar to that in which weevil body temperature is influenced, and is a more readily measured variable. In general, adult body temperature is about 2° C higher than leader bark temperature (Sullivan 1960).

When the bark temperature of the leader does not rise above 25° C, the insects exhibit a more or less orderly progression of diurnal behavior. During early morning, they rest at the base of the trees and among the terminal buds (Sullivan 1959), although Dixon and Houseweart (1983) found that once in the upper parts of the tree, the weevil adults never returned to the tree base. As they are warmed and activated they move to the most exposed sector of the leader, which is on the east side early in the day. As the day progresses, they move around the leader, keeping within the more exposed sectors until late evening, when they take up positions in the west and north sectors.

On a clear day, bark temperatures on exposed leader sectors may be as much as 7° C higher than ambient air temperature and as much as 4° C above that of shaded sectors. Thin cirriform and broken cumulus clouds allow sufficient insolation to raise the bark temperature of an exposed white pine leader as much as 5.5° C above air temperature, to between 15° C and 28° C. This temperature difference drops to about 2° C under heavy overcast (Sullivan 1959).

During periods when the bark temperature ranges between 25 and 32° C, observations on groups of adults reveal apparently random movements that can be interpreted only if their reactions to light and temperature are known. Consequently, a single observa-

tion of a group of weevils on a leader may indicate insects feeding and ovipositing on exposed and shaded sectors, others moving up and down these sectors, and still others moving out to the ends of needles in preparation for flight, all depending on the current temperature and their previous temperature conditioning. At temperatures above 32°C, those insects that have not left the leader begin congregating in the shaded sectors. Many leave the leaders entirely. At bark temperatures near 38°C all adults have left the leader. At these higher temperatures the adults are very sensitive to disturbance and drop readily after slight prodding (Sullivan 1959).

Sudden changes in temperature associated with rapid air mass changes cause disruptions in these more or less orderly patterns of behavior.

Atmospheric moisture also affects the activity of spring adult populations, but to a lesser degree than temperature. In general, as humidity rises, feeding, copulation, and oviposition decrease, but under natural conditions it is difficult to separate the effects of the 2 elements since relative humidity is inversely related to temperature in most situations.

Sullivan (1960) has provided the most rigorous quantitative treatment of the effects of temperature and humidity on spring adults. The regressions for the percentages of individuals feeding, copulating and ovipositing against bark temperatures are shown in Figs. 4-6. Total activity versus relative humidity is shown in Fig. 7. The most critical requirement is for oviposition activity, which rises exponentially at temperatures between 10 and 29° and then decreases rapidly from 29 to 35°C. Also, little oviposition occurs below 20°C. McMullen (1976a) found that the maximum rate of oviposition of the *P. sitchensis* ecotype on Sitka and white spruce occurs between 20 and 26°C, in general corresponding to the rate reported by Sullivan (1960). Gara *et al.* (1971) found that oviposition in the same ecotype peaked at about 32°C and then dropped off rapidly. They found a lower threshold at about 18°C.

While the effect of temperature alone on adult weevil activity is most critical, unusual combinations of temperature and humidity must be taken into account. Sullivan (1961) produced isopleth diagrams for total activity and oviposition activity, respectively, which clearly delineate the most favorable levels of these elements for the 2 activities (Fig. 8a, b). The narrow zone for high-level oviposition activity is obvious.

Brood Development

Eggs closest to the top of the leader are usually the first laid and those more basally situated will be progressively younger. Therefore, other factors being equal, the eggs near the top of the leader will be the first to hatch. The young larvae begin to feed immediately, at first enlarging the egg chambers and then working downward singly or in small groups. Shortly thereafter, they come together to form a downward moving ring of larvae, the so-called "feeding ring", around the circumference of the leader. There are usually 4 or 5 feeding instars (Stevenson 1967; Silver 1968; Harman 1970), more commonly 4, and each instar has a definitive head width. Hence, there is an upper limit to the number of larvae of each instar that can fit in a ring within the bark of a leader of a given diameter. For a set leader diameter this number diminishes rapidly as the larvae molt to successively larger stages. In nature, however, the larvae are moving downward from the top of the 1-year-old leader, and the stem diameter increases, providing more head-capsule room around the bark circumference. Nevertheless, much lower numbers of late-stage larvae can be accommodated. These relationships are shown clearly by Dixon and Houseweart (1982). Further interrelationships of the dimensional aspects of weevil attack and pine leaders are given by Sullivan (1961). They are of major importance in understanding how brood development of the weevil is influenced by intraspecific competition among feeding larvae, and the way in which this is related to maximizing adult production in the face of hazardous host conditions.

Considering a hypothetical example of an attacked, exposed white pine leader allows us to demonstrate and discuss these factors. Suppose we have a leader that has a top diameter of 8 mm, and the attack by weevil adults as determined by the presence of feeding

WHITE PINE SYMPOSIUM

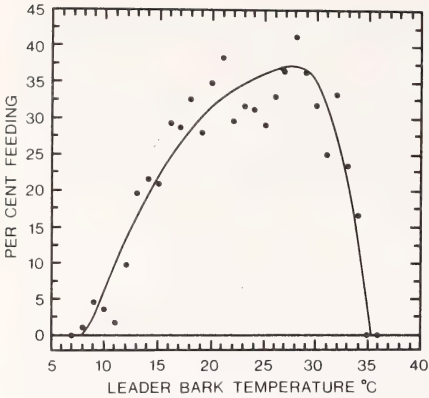


FIG. 4. The effect of white pine leader bark temperature on the frequency of feeding activity of the spring population of *P. strobi* adults (Sullivan 1960).

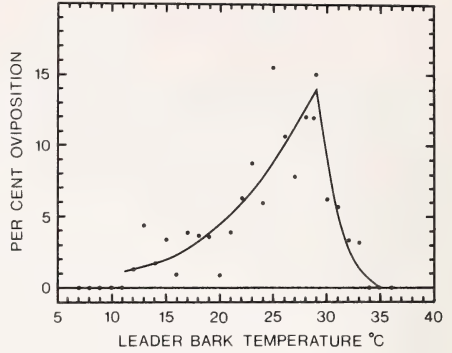


FIG. 6. The effect of white pine leader bark temperature on the frequency of oviposition of *P. strobi* (Sullivan 1960).

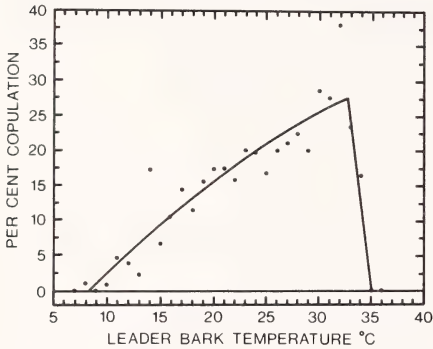


FIG. 5. The effect of white pine leader bark temperature on the frequency of copulation of *P. strobi* (Sullivan 1960).

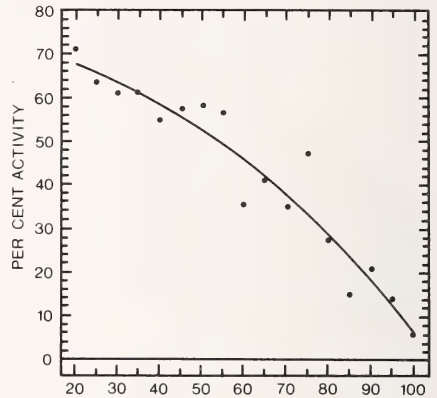


FIG. 7. The effect of relative humidity on the intensity of activity of the spring population of *P. strobi* adults (Sullivan 1960).

and oviposition punctures extends about 20 cm down the leader. Sullivan (1961) has shown that we can estimate the number of eggs from this amount of attack at about 155. Also, the bark thickness at the top can be estimated at 1.7 mm. The diameter inside the bark would be 4.6 mm, and at midbark about 6.3 mm. The circumference at this level would be 19.8 mm, and on the basis of Harman's (1970) mean head width of 0.3260 mm for first-instar larvae, about 60 larvae could line up in a single layer in the bark. (This could represent the complete hatch of eggs in as little as 10 cm of leader, or less, if the eggs are concentrated toward the top as shown by Dixon and Houseweart [1982]). At this first-instar stage the larval heads, the size of which largely determines the space needed for a feeding track, are not deep enough to occupy the total thickness of the bark. If we acknowledge that the heads are perhaps 1.25 times deeper than they are wide, the bark near the top of the shoot could support a feeding ring of first instars four layers deep, or perhaps a maximum of 240 larvae, almost 100 more than the total number of eggs laid. Not all the cross-sectional area of the leader is available for larval feeding, however. It has been noted that the attacked portion of the stem is marked by the flow of resin from feeding punctures, an indication that the adults have cut one or more cortical resin ducts, although Stroh and Gerhold (1965) have shown that the adults often stop the penetration of the leader in making a feeding puncture if they directly encounter an outside resin duct after

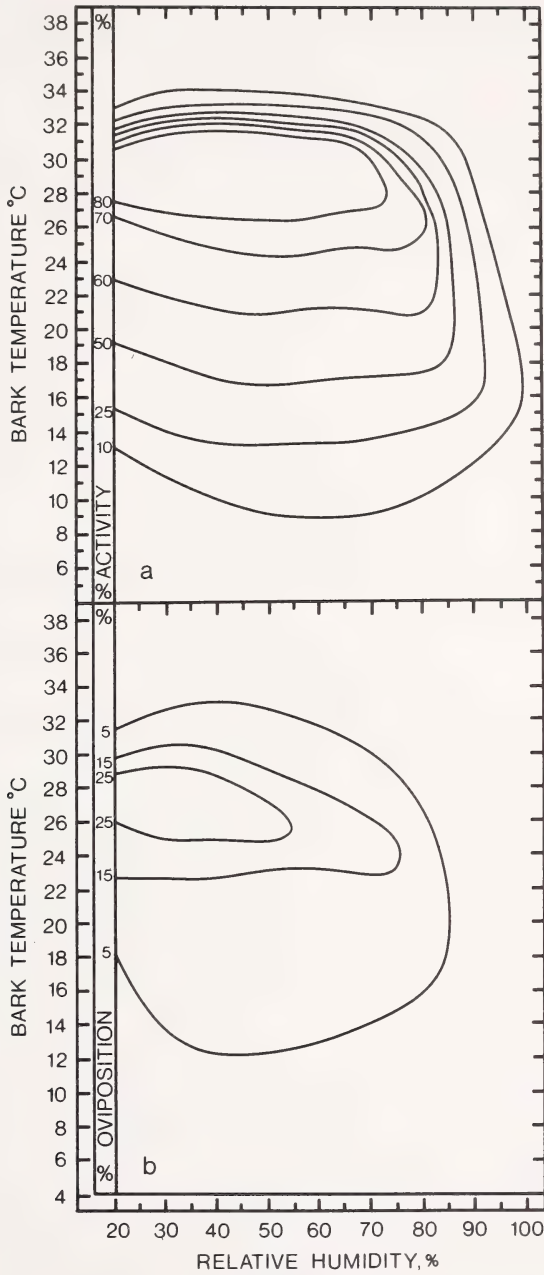


FIG. 8. Isopleth diagrams showing the combined effects of white pine leader bark temperature and relative humidity on a) the intensity of activity of *P. strobi* adults of the spring population and on b) the frequency of oviposition by *P. strobi* females (Sullivan 1960).

penetrating the periderm. Fully formed punctures go between the outer and inner resin ducts and do not-cut into the epithelial cells of the resin ducts. The same is presumed to be true for the oviposition punctures, since flooding of the egg chamber by cortical resin may result in the eggs being killed. Thus the space occupied by the resin ducts greatly restricts the cross-sectional area of shoot cortex that can be used for feeding. Clumps of young larvae are observed, and it seems probable that the feeding ring is composed of a varying number of layers that can accommodate a large proportion of the larvae from the total egg complement of an attacked shoot. Larvae hatching from eggs laid late may not find sufficient food to survive and larvae that feed singly and cut a resin duct are frequently killed by the cortical resin (Overhulser and Gara 1981b). Single larvae and eggs that are overtaken by an advancing feeding ring may be devoured.

We now consider what happens as the brood of larvae continue to feed and molt, following the observations of Sullivan (1961) and Dixon and Houseweart (1982). On the basis of the relationship between the extent of adult attack and the extent of attack by the brood, we calculate that feeding would extend downward about 36 cm where the leader diameter is approximately 11 mm and the bark is about 2.3 mm thick. The midbark circumference at the level where larval feeding ends is about 27 mm, and if we assume an equal mixture of fourth- and fifth-instar larvae, only 24 larvae can fit around inside the bark. The depth of the heads of these larvae might be 1.5 mm and only a single layer can be accommodated. Consequently, in our example, only about 15% of the eggs laid will develop to the late larval stage, and these represent perhaps 40% or less of the first instars in the initial feeding ring. The group feeding behavior in conjunction with the intense intraspecific competition (Dixon and Houseweart 1982) ensures the maximum production of mature larvae from the limited food resource and deals with the detrimental characteristics (resin canals) of the host.

There is some evidence of possible mechanisms through which the group of feeding larvae influence resin flow. Santamour (1965) observed that some factor present in the heads of weevil larvae can cause accelerated crystallization of the resin acids of cortical resin. This may protect the larvae from being drowned in the resin and masses of small larvae might be better able to regurgitate effective quantities of the substance(s). Several researchers have tried to use the lack of insect-induced cortical resin crystallization to screen white pines for resistance to the white pine weevil (Van Buijtenen and Santamour 1972; Santamour and Zinkel 1976; Bridgen *et al.* 1979; Wilkinson 1979). The results have been equivocal and suggest that the relationships are complex and warrant more detailed study. Furthermore, Overhulser and Gara (1981) have reported that when egg chambers of *Pissodes* in Sitka spruce, western white pine and lodgepole pine come in contact with cortical resin ducts, the contacted ducts became occluded with tylosoids involving the hypertrophy and proliferation of unligified duct epithelial cells. They suggest that the process could be associated with phellogen restoration after wounding (a purely plant reaction), or the host's reaction to secretions from the weevil.

At the end of feeding, the larvae form chip-cocoons in the pith or wood of the attacked shoot. In the developmental example we have been following, Sullivan's (1961) data would suggest that only 4 or 5 of the mature larvae (about 3% of the eggs laid in the spring) would complete development and emerge as adults. When very large numbers of eggs are laid in relation to the leader size, damage by the young larvae is so intense that the leader is killed prematurely and no brood survives.

Sullivan (1960) showed that the rate of feeding and consequently larval development is closely related to the leader temperature. He suggests that lower temperatures and therefore slower feeding by the younger larval stages allow more opportunity for being killed by resin flow. McMullen (1976a) studied the time-temperature relationship of brood development on Sitka and white spruce and showed that 7.2°C can be considered a lower threshold for development, and even at 15°C growth is very slow. At about 32°C early development was rapid but no individuals reached the pupal stage, mortality being complete. Brood development from egg to adult emergence took 888 and 785 degree-days

above 7.2°C on Sitka and white spruce, respectively. McMullen (1976b) applied this information to develop a hazard rating for weevil damage on Vancouver Island and concluded that field observations generally support the contention that accumulated heat is important in determining the potential for weevil damage.

Mortality Factors

Various factors that cause mortality of the white pine weevil have been referred to in earlier sections of this review. Many published reports also have indicated general levels of mortality that affect a white pine weevil population, but there have been few comprehensive quantitative studies. Recently, however, Dixon and Houseweart (1982) have published a life table of the weevil in central Maine. Their key factor analysis suggested that the major influences on population change were larval, pupal and overwintering mortalities. The principal causal factors of mortality in these age intervals were intraspecific competition of the larvae, natural enemies, and pitch drowning of larvae and pupae, and abiotic elements (physical environment factors) acting against overwintering adults. Among the biotic natural control agents, a dipteran predator, *Lonchaea corticis* (Lonchaeidae), and 2 hymenopteran parasites, *Eurytoma pissodis* (Eurytomidae) and *Dolichotomitus terebrans nubilipennis* (Ichneumonidae), were noted as having a positive intergenerational response. Moeck and Safranyik (1984) have published a report of predator and parasitoid control of bark beetles which may be relevant to the *Pissodes strobi* problem.

Dixon and Houseweart (1982) also pointed out the relatively slow rate of change in weevil population. They also suggest that potential control methods might include biological control, resistant trees, and destruction of overwintering weevils and weevil sites. Two other points of interest were the notably low mortality of eggs and the lack of information on the fate of fall adults before overwintering.

Stand-Weevil Interactions

The perception that the incidence and severity of attack by the white pine weevil are greatly influenced by the stand conditions in which the potential host trees are growing came early in the history of study of the pest. There may be a tendency to think of the weevil as a new problem, but this is certainly not true, as Peck himself recognized that mature trees which had suffered weevil attack in younger days were evident in the virgin forests of colonial America. The weevil became abundant in the widespread, nearly pure stands of young white pine that originated by seeding on abandoned farmland during the latter half of the 1800s. Such stands were generally poorly stocked, and the trees were repeatedly and severely attacked. Added to the area of these new stands were the numerous plantations established in the early 1900s which provided additional breeding sites. Observations made in the 1920s indicated that during the previous 50 years the incidence of weevil damage had increased greatly.

Graham (1918) recognized that in natural, open stands where the crowns were all free the trees were equally subject to attack, while in denser stands the percentage of trees suitable for the development of the weevil was lower, and in very dense stands injury was practically absent. In contrast to trees growing in full sunlight, trees growing in mixtures with hardwoods were relatively free from attack, injury decreasing with increasing shade.

Hence, while the concepts of a method for silvicultural management of the white pine weevil were known early this century, the scientific basis for understanding the behavioral and developmental mechanisms of the weevil which underlie the success of the weevil under certain stand conditions were developed mainly by Sullivan in the 1950s. In particular, Sullivan (1961) brings together much of the information on the weevil needed to develop sound management practices. Droska (1982) has added further details, particularly in relation to fall shading effects.

In the foregoing sections of this review, the characteristics of the weevil which adapt it to open, exposed trees have been dealt with in detail. Here we will highlight the factors that

make shaded habitats unfavorable. Shading considerably alters the microenvironment of weevil habitats, since the radiant heating of the sun is reduced in proportion to the amount of shade. Since the season of oviposition and feeding coincides with the period of overstory canopy development, the magnitude of the differences in habitat microenvironments between exposed and shaded stands continually varies throughout the active period of the adults. In terms of bark temperature of oviposition and brood sites, differences between exposed and shaded sites range from a minimum of about 3°C, at the time the shaded stems receive about 70% of insolation on clear days, to about 11°C at the time the canopy is fully developed and the leaders receive only about 20% of maximum insolation.

Weevil adults that hibernate within shaded stands suffer higher mortality when overwintering, and during the spring dispersal period there is likely to be less movement into heavily shaded stands (Harman and Kulman 1969; Droska 1982). Therefore, the adult weevil population on such sites is small and less suited to producing aggregations of weevils feeding and ovipositing. The weevil adults also exhibit a preference for larger-diameter, more vigorous leaders. White pines growing partially suppressed in understory situations tend to have leaders that are not satisfactory for weevil attack. Perhaps the physiological conditions of suppressed leaders are not as satisfactory either.

The weevil adults require certain conditions of temperature and humidity for feeding and oviposition, those for oviposition being particularly restricted. The lower temperature on shaded sites greatly restricts these activities. Furthermore, the adults do not confine their attack to the leader as on exposed trees, but may feed and oviposit on as many as 4 or 5 years' growth of the main stem. There is also no regularity to the distribution of the punctures, and the females fail to deposit a sufficient number of eggs in a localized area of the main stem to provide enough hatching larvae to aggregate into a feeding ring. Isolated individuals and small groups of larvae are usually drowned in pitch.

The lower temperature of shaded leaders retards larval development in instances in which the feeding ring is established. This prolonged development results in exposure of the larvae to natural biotic control agents for longer periods of time so that they are susceptible to higher mortality. Development may not be completed at all because of insufficient heat. Survival of late-stage immatures over the winter is generally low.

Thus shaded conditions are disadvantageous at all stages of weevil development and the practical problems of utilizing these relationships to grow white pine satisfactorily with a low level of weevil damage, and of producing the desired stocking of crop trees remain. In addition to providing a proper environment for the trees and also limiting the weevil, other major problems, such as the disease white pine blister rust, must be controlled. No one aspect can be treated in isolation.

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FACTORS DETERMINING THE FEEDING OF THE WHITE PINE WEEVIL (COLEOPTERA: CURCULIONIDAE) ON ITS COASTAL BRITISH COLUMBIA HOST, SITKA SPRUCE

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Abstract

The factors determining the acceptability to the white pine weevil (= Sitka spruce weevil, *Pissodes strobi* [Peck]), of its western host, Sitka spruce (*Picea sitchensis* [Bong] Carr.) were studied in laboratory experiments. A complex mixture of chemicals that triggered feeding in *P. strobi* was shown to be present in the bark and cuticle of Sitka spruce leaders. Feeding stimulants were also present in the xylem of leaders, but were absent from xylem elsewhere in the tree and from needles. Extensive testing of other species indicated that feeding stimulants were restricted to conifers and varied in quality and/or quantity among species. Only a few conifers, the western hosts included, elicited fall feeding activity. Chemicals with feeding deterrent or repellent activity were found. We conclude that final acceptance or rejection of a tree as a host by this weevil requires the presence of a complex profile of volatile and non-volatile chemicals that stimulate feeding, and an absence of feeding deterrents. This knowledge could be used in the development of weevil-resistant varieties or pest management strategies based on chemical feeding deterrents.

The white pine weevil (= Sitka spruce weevil) (*Pissodes strobi* [Peck]) is the most important pest of Sitka spruce (*Picea sitchensis* [Bong.] Carr.) in British Columbia (B.C.) (McMullen 1976). This weevil is also a pest of Engelmann spruce (*P. engelmannii* Parry ex Engelm.), white spruce (*P. glauca* [Moench] Voss), and Norway spruce (*P. abies* [L.] Karst.). Neither eastern white pine (*Pinus strobus* L.), the weevil's principal host in eastern North America, nor western white pine (*P. monticola* Dougl.) is affected in B.C.

On the basis of morphological and cytological characteristics, *P. strobi* populations from eastern and western North America are considered a single species (Manna and Smith 1959; Smith 1962; Smith and Sudgen 1969). However, apparently in the long period of isolation, eastern white pine and Sitka spruce populations have differentiated to the point at which *P. strobi* reared from Sitka spruce does not recognize eastern white pine as a host (VanderSar *et al.* 1977). All experiments reported herein were conducted with *P. strobi* populations from B.C. Sitka spruce.

The biology of *P. strobi* (MacAloney 1930; Belyea and Sullivan 1956; Silver 1968; McMullen and Condrashoff 1973) may be summarized as follows. The adult weevils overwinter in the duff or on the laterals of host trees, and resume activity in late April or early May. After mating, the females lay their eggs in small punctures chewed in the bark of the leader of a host tree, usually just below the terminal bud. The eggs hatch in 7 to 10 days. The small, white grubs soon form a feeding ring in the inner bark, and move downwards as a group, progressively girdling and killing the leader before pupating in the pith xylem. The newly formed adults emerge in August and feed on various parts of the tree until they go to their overwintering sites. The crook or fork deformations that result from the attack reduce tree growth and the value of the lumber. Repeatedly affected trees are unable to compete with surrounding vegetation and are often killed by suppression. In extreme situations, entire plantations may be rendered unmarketable (Alfaro 1982). To date, no practicable method of controlling the weevil has been developed.

One promising avenue of research for new pest control strategies is that of host

selection mechanisms in phytophagous insects. Methods involving the disruption of the host selection process with the use of repellents have been successful against biting insects. The insects' selection of the host plant for feeding or oviposition is a complex process involving physical and chemical cues emanating from the plant, coupled with the responses of the insects. The host finding and accepting process, as reviewed by Miller and Strickler (1984), involves the following behavioral sequence:

- a) finding: initiated by random movement not influenced by plant cues, progressing to oriented movement towards the plant in response to non-contact cues (visual, olfactory) and concluding in arrestment on plant (cessation of movement),
- b) examination of the plant by scanning with its sensory organs, including gustatory sensors (nibbling),
- c) consuming: sustained feeding or acceptance for oviposition.

The successful completion of each of the above stages is dependent upon the satisfaction of internal conditions in the insect, such as the existence of hunger, to initiate and maintain the process, or the completion of other prerequisite behavioral activities such as migration.

The host selection process in *P. strobi* begins in the spring when the weevils emerge from their overwintering sites and fly or crawl to their hosts. Searching *P. strobi* must precisely differentiate between host trees and several other sympatric conifer and non-conifer species. Vision apparently plays a role in long-range orientation; VanderSar and Borden (1977a) demonstrated that adult *P. strobi* are attracted to vertical or near-vertical black silhouettes that resemble the leaders of Sitka spruce. At close range, other responses such as positive phototaxis and negative geotaxis (VanderSar and Borden 1977b) allow the weevil to locate the terminal bud on an upright leader. Finally, chemical cues emanating from the host apparently determine its ultimate acceptance or rejection.

The summary that follows condenses several years of research on chemical ecology and host selection. The work was carried out in collaboration with Drs. H.D. Pierce, Jr. and A.C. Oehlschlager of the Department of Chemistry, Simon Fraser University. The specific objectives of the work were as follows:

- a) to investigate whether the feeding behavior of *P. strobi*, a component of the host selection behavior, is chemically mediated,
- b) to determine the distribution of feeding stimulatory chemicals within Sitka spruce trees and among various conifers,
- c) to determine if feeding behavior in this insect can be chemically manipulated.

Materials and Methods

Paired agar discs immersed in paraffin wax in petri dishes were used to bioassay candidate feeding stimulants and deterrents (Alfaro *et al.* 1979). Each disc was covered with lens paper through which the weevils made feeding punctures which were easily counted. The test material was applied to the lens paper surface of one disc while the other served as a control. Discs of pure agar were used in testing feeding stimulants. Deterrents were assayed on agar discs that contained 2% ground, dried Sitka spruce bark. This bioassay was used effectively to test for the presence of chemicals that determine whether a plant is accepted or rejected as food by the weevil.

Results and Discussion

The weevils exhibited a concentration-dependent response to the amount of Sitka spruce bark in the agar disc; the threshold for response was 0.02 and 0.003% bark for males and females, respectively. Through detailed chemical analysis of host bark extracts, a complex mixture of non-volatile chemicals that elicited a feeding response in the weevil was detected (Alfaro *et al.* 1980). However, the exact makeup of these chemicals has not been determined and therefore identification is not yet complete. A wax, present in the cuticle of the leader, and a mixture of resin acids were highly stimulatory.

Volatile chemicals from Sitka spruce bark and foliage, captured in Porapak-Q, did not attract walking *P. strobi* in 2 olfactometers, nor did they trigger a feeding response when tested on plain agar. However, the monoterpenes α -pinene, β -pinene, and β -myrcene acted as synergists to the non-volatile chemicals present in the bark; piperitone had a marked feeding deterrent effect, and (+)-camphor and limonene stimulated the feeding at low concentrations but inhibited feeding when the concentration rose above a particular threshold (Alfaro *et al.* 1980). Such deterrence may play a role in resistance to insect attack.

The distribution of chemical feeding stimulants within Sitka spruce trees corresponded with the preferred site for feeding by the weevils, i.e., the leader bark. The stimulants appeared to be present in largest quantities or in best blends in the bark of the tree's leader, stem and branches. Needles elicited little feeding, and contained chemicals with feeding-deterrent activity. Xylem tissue contained feeding stimulants only in the terminal leaders.

Extensive testing of conifer and non-conifer species was conducted to determine whether the chemical stimuli triggering feeding in *P. strobi* were widely or narrowly distributed among plant species (Alfaro and Borden 1982). No-choice feeding experiments (in which weevils either eat or starve) showed that the weevil fed readily only on conifer species of the genera *Pinus* and *Picea*. Feeding was reduced on species of *Abies*, *Pseudotsuga*, *Tsuga* and other conifers tested. Non-conifers failed to elicit feeding responses. These results suggested that the feeding stimuli were unique to conifers but that they varied in quantity and/or quality among the species tested. Choice experiments, in which Sitka spruce was presented alongside a non-host tree, indicated that the stimuli were optimal only on Sitka spruce and on a few other *Pinus* and *Picea* species. Coastal B.C. weevils preferred Sitka spruce to the eastern host, eastern white pine.

Our work also showed that western *P. strobi* is highly sensitive to chemicals that have a feeding deterrent action (Alfaro *et al.* 1981, 1984). Feeding deterrents were found in Sitka spruce needles, and in the bark of several non-host species, including western red cedar (*Thuja plicata* Donn.) and eastern and western white pine.

The final acceptance or rejection of a tree as a host by this weevil probably requires the presence of a complicated profile of volatile and non-volatile compounds. Susceptible trees would be those having an adequate diversity and quantity of feeding stimulants and an absence or a low concentration of feeding deterrents. Identification of the various chemicals involved, especially the key chemicals determining host specificity, may provide the basis for developing resistant varieties by selectively breeding out the key feeding stimulants, or by similarly altering the balance of stimulants and deterrents within them.

Introduction of feeding deterrents into susceptible varieties by inter-specific hybridization with resistant species like *Picea omorika* (Pancic) Purkyne., or perhaps selection for deterrents already present, may prove to be productive methods of developing resistance to the weevil. Currently, researchers at the University of British Columbia are conducting field tests of pine oil, a complex mixture of extractives, primarily monoterpenes, derived from the pulp industry, as a repellent for *P. strobi*.

P. strobi may also be sensitive to variation in ovipositional stimulants and in the nutritional quality of the host plant. Ovipositional resistance was postulated by VanderSar (1978) as a possible explanation for the failure of *P. strobi* to colonize western white pine in British Columbia. Removal of ovipositional stimulants or key nutrients from susceptible varieties of Sitka spruce may produce lines that do not support a healthy, fecund weevil population.

The process of host selection by *P. strobi* and of resistance by host and non-host plants is complex and involves physical and morphological factors identified by earlier workers (Stroh and Gerhold 1965; VanderSar and Borden 1977a; Kriebel 1983) and complex biochemical interactions between the plant and the insect. Elucidation of the nature of this interaction may prove to be a landmark in the understanding of host selection by conifer-infesting insects.

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CHEMICAL CONTROL OF INSECT PESTS OF WHITE PINE

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Abstract

Chemical control of insect pests is occasionally required to protect the merchantability of eastern white pine (*Pinus strobus* L.). A review of current methods of chemical control for the insect pests of major economic importance is presented, with a brief discussion of future prospects in chemical control.

Introduction

Eastern white pine (*Pinus strobus* L.) is host to a wide variety of insect species. Fortunately, only a few of these are of economic importance. Management for some of these pests is required from time to time as part of an overall silvicultural program to protect the merchantability of this commercially important tree species. Chemical insecticides are an important tool in the management of insect pests of white pine.

The purpose of this paper is to review briefly the current chemical control methods for these major insect pests. For the purposes of this paper, the publications of Rose and Lindquist (1984) and Johnson and Lyon (1976) provide the basis for identifying and determining the significance of these pests.

Chemical Control Methods

Injury by insects that feed on buds or shoots seldom results in tree mortality except in the case of seedlings. The principal concern with this group of insects is the damage caused to tree form, and consequently to the commercial value of the tree. Generally, bud and shoot insects are difficult to control with chemical insecticides.

Probably no other insect has frustrated foresters attempting to grow white pine as much as the white pine weevil (*Pissodes strobi* [Peck]). By girdling the leader, the weevil destroys the vertical shoot and consequently has an adverse effect on tree form and sawlog production. The first 20-30 years in the life of a white pine plantation are the most critical for the growth of straight stems for sawlogs because during this time the microenvironmental conditions within the stand are most conducive to the presence of white pine weevils.

Control of the white pine weevil with chemicals is difficult because the insect spends most of its early life inside the leader (MacAloney 1930; Sullivan 1957). Hence, only the adult stage of this insect is susceptible to control with contact insecticides. Chemical control measures can be undertaken either in the spring when adults are feeding or ovipositing on the leaders, or in the fall after the new generation of adult weevils emerges from the leaders. Early spring (late April-early May) applications of insecticides are favored in Ontario, although fall applications are gaining acceptance in the northeastern United States. Whichever time of year is chosen for adult control, treatment will be effective only if females are prevented from ovipositing in the spring.

Two factors critical to the success of a chemical control program for white pine weevil are timing of the application, and optimal coverage of the terminal buds and leader with the insecticide. Both are difficult to achieve.

In eastern Canada, adult feeding, mating, and oviposition in the white pine weevil may extend from late April to mid July. Accurate prediction of periods of peak adult activity and timing of chemical treatment for the prevention of oviposition are major problems with insecticides that have short residual activity (DeBoo and Campbell 1971).

Methoxychlor is at present the only chemical insecticide registered in Canada for white pine weevil control. Analyses of methoxychlor residues on leaders of white pine

(Sundaram 1973) showed that this insecticide had effective residual activity for approximately 5 days when applied by aircraft, and for 2 to 3 weeks when applied with ground spray equipment. The greatly reduced period of chemical activity when the insecticide was applied aerially increased the importance of timing to coincide with peak activity of the weevils (DeBoo and Campbell 1974).

Adequate insecticide coverage of the leader surface is as important as proper timing for effective control of the weevil (DeBoo and Campbell 1971). Good coverage of the leader increases the probability of contact with the insect, and as a result the females are killed prior to egg laying. Potts (1958) indicated that small droplets would be most effective and that 1000+ droplets per square inch (155+/cm²) would be required over the bark surface to provide adequate control. The best droplet size or range of sizes, and the optimal density of such droplets for impaction on the leader, have yet to be clearly determined for most effective control of the white pine weevil.

DeBoo and Campbell (1971, 1972a) used hydraulic sprayers to apply 2 doses of methoxychlor to white pine leaders, one on each side of the point of runoff. Although such applications ensure complete coverage of the leader, as much as 95% of the insecticide applied can be wasted as a result of this practice. Mistblowers can also be used to provide thorough coverage of the leaders (Connola 1961). Ground application equipment can be used to treat trees less than 3.6 m high, but taller trees require aerial application (DeBoo 1978). Aerial applications of methoxychlor generally have been less successful than ground applications in controlling the weevil, because single-direction, low-volume spraying with aircraft usually provides inadequate coverage, especially on the vertically oriented leader (DeBoo and Campbell 1971, 1972b).

Sippell *et al.* (1975) suggested that future studies in control of white pine weevil "... not only include studies of improved methoxychlor formulations, but also investigations to find new alternative chemicals for aerial applications, new formulations incorporating adjuvants to improve droplet quality and quantity, new emission equipment or modifications to equipment to obtain a very dense coverage required for control of this insect, and entomological studies especially designed to optimize the timing of spray operations." For the most part, research and development to address these needs have advanced slowly since 1975 although there are a few bright spots on the horizon.

Application technology to deliver large numbers of small droplets has continued to improve, with spray units such as the Micronair AU 3000 and 5000 becoming standard equipment. New insecticides or formulations continue to be evaluated both in the United States (Houseweart and Seymour 1984) and in Canada¹, with the synthetic pyrethroids holding the greatest promise. In addition to the evaluation of "conventional" insecticides, third-generation chemicals such as insect growth regulators are being tested (Retnakaran and Smith 1982).

Finally, as with any control program involving chemical insecticides, chemical methods for control of the white pine weevil must be based on sound biological, ecological and economic considerations. Marty and Mott (1964) have prepared an excellent document to aid in determining when control measures are necessary and if the control program will be cost effective.

Several species of moths occasionally cause serious damage to white pine shoots. Within this group, the eastern pine shoot borer (*Eucosma gloriola* Heinr.) is probably the most important. This shoot borer is often abundant in unmanaged or understocked plantations, but is rarely a problem in natural mixed stands (DeBoo *et al.* 1971). The insect is most injurious to conifers 1 to 3 m high, although trees up to 10 m high are attacked (DeBoo *et al.* 1971; Wilson 1972). The larvae bore directly into the pith of the new shoots, which wilt and eventually break off, causing the trees to become crooked, stunted or forked.

¹ Helson, B. Forest Pest Management Institute, Sault Ste. Marie, Ont. Pers. comm. 1984.

Control of shoot borer larvae with chemical insecticides is difficult and at present not practicable. Although systemic insecticides have been suggested, DeBoo (1966) found that only heavy applications of aldicarb at the time of shoot entry by larvae gave good protection. Systemic insecticides, in general, do not work well in conifers and massive amounts are often required. DeBoo *et al.* (1971) concluded that soil applications of systemic insecticides must provide a continuous supply of toxicant for a period of at least 6 weeks if they are to kill the larvae as they bore through xylem to the feeding site. Furthermore, phenological variation of the pest in spring, and the difficulty in detecting and measuring insect populations at this time of the year, are cited by DeBoo *et al.* (1971) as some of the reasons that control is difficult. Repetitive foliar sprays for the control of the adults was suggested by DeBoo *et al.* (1971) as a promising method for controlling the shoot borer with insecticides. This method, however, has not been tried.

Insects affecting the root or root collar of white pine seldom warrant chemical control in plantations. White grubs, mainly of the genus *Phyllophaga*, feed on the roots and can cause death or retardation of tree growth. They are most often pests in nurseries where they can be readily controlled with applications of chlordane to the soil. Grubs are often pests on land that has been under sod for 2 years or more (Hammond 1960). The best policy is to avoid planting in such areas until populations are below 20 grubs/m² unless chemical treatments are planned (Sutton and Stone 1974). If planting cannot be delayed, the roots can be treated with a stomach poison before planting (Sutton and Stone 1974), or chlordane can be incorporated into the soil (Smith *et al.* 1981).

Insects affecting cones and seeds are of great economic importance in stands of white pine grown for, or designated as areas of, seed production.

The white pine cone beetle (*Conophthorus coniperda* [Sz.]) is a serious pest (Peirson 1927) which destroys up to 98% of the cones and causes crop failures (Graber 1964). Past attempts to control the white pine cone beetle with insecticidal sprays have been generally unsuccessful, probably because the foliage obstructs deposition of the control agent on the petiole and base of the cone where the beetles initially enter (DeBarr *et al.* 1982). Soil applications of the systemic insecticide carbofuran in seed orchards in North Carolina, USA, however, were effective in controlling the cone beetle as well as the white pine cone borer (*Eucosma tocullionana* Heinr.) (DeBarr *et al.* 1982). Carbofuran was applied once a year at rates of 4.5, 9.0 or 13.5 g AI per cm tree diameter at breast height. Increasing the rate of carbofuran application per tree from 4.5 to 13.5 g AI did improve control, although the improvement was not statistically significant (DeBarr *et al.* 1982). Carbofuran can be incorporated into the soil either by hand raking or disking or by a modified John Deere Pow'r-Till seeder (Overgaard *et al.* 1983).

Future Prospects

Newer insecticides are being developed for controlling insect pests including those in forests. The trend toward the use of less persistent and more environmentally acceptable chemicals continues. Research and development of formulation additives such as spreaders, stickers, sunlight protectants and extenders to improve the efficacy of the insecticide are also advancing. Formulation becomes more important with the increased use of less persistent insecticides, and water as a spray diluent in aerial applications. Improvements in spray delivery systems will continue to focus on emitting a narrow range of very small droplets at reduced spray volume. Equipment used in forestry will probably continue to be that developed for the agricultural market.

The determination and evaluation of optimal meteorological conditions for the aerial applications of insecticides is an exciting field that has received considerable attention recently. Contrary to general opinion, unstable meteorological conditions probably minimize drift and favor the inertial impaction of small spray droplets in the target².

² Payne, N. Forest Pest Management Institute, Sault Ste. Marie, Ont. Pers. comm., 1984.

From a pest manager's standpoint, any control method that reduces the need for chemical insecticides is a step forward. Chemical control measures should be regarded as a last resort rather than a first line of defense, although the choices are limited in the case of insect pests of white pine. A judicious combination of white pine silviculture and new developments in pest control could pave the way for more environmentally acceptable and practicable control methods in the future.

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WHITE PINE BLISTER RUST: A DISCUSSION OF THE DISEASE AND HAZARD ZONES FOR ONTARIO

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Abstract

Infection hazard zones for the white pine blister rust disease caused by *Cronartium ribicola* J.C. Fisch. are presented for Ontario. Interpretation of climatological, topographic, and physiographic data is based on methods used previously in the Lake States to rate infection hazard. Survey data on intensity of infection in the various hazard zones indicate that the methods work for Ontario. Other aspects of blister rust control are discussed. Pruning of the highly susceptible branches on the lower part of the tree is promoted as a method for providing good control of the disease.

Introduction

The white pine blister rust disease, caused by the fungus *Cronartium ribicola* J.C. Fisch., was first noticed in North America in 1909. The disease spread rapidly through the range of the native species of white pine, and extensive research and control projects were established to cope with the destructive capacity of this fungus. Considerable information and experience have accumulated, and successful culture of eastern white pine (*Pinus strobus* L.) is now possible, provided that pests, mainly the blister rust disease and white pine weevil (*Pissodes strobi* [Peck]), are controlled, and that good site selection procedures are followed.

Early blister rust control concentrated on the eradication of the herbaceous hosts (*Ribes* spp.) on which the host-alternating fungus completes part of its life cycle. Currently in Ontario, eradication of *Ribes* spp. is practicable near tree nurseries. Local sources of rust spores for pine infection are effectively controlled by *Ribes* spp. eradication, but infection by spores transported long distances by mass air movement as described by Van Arsdel (1961) also causes considerable damage. Anderson (1973) noted that long-range transport of spores probably was a major reason that local eradication of *Ribes* spp. did not always give satisfactory control. Eradication of *Ribes* spp. near nurseries and seed orchards is essential because of the value of the crops; however, long-distance as well as local sources of inoculum need to be considered for an effective program.

Several chemical treatments for preventing or curing pine infection were attempted in the 1950s and 1960s. These are no longer considered operationally effective (Anderson 1973).

Current control methods are based on the biology of the rust fungus and its mode of infecting pine. The fungus has fairly specific temperature and moisture requirements for successful infection of pine (Van Arsdel *et al.* 1956, 1961). Climatological and physiographic characters that are correlated with infection hazard were examined in Wisconsin by Van Arsdel *et al.* (1961). Infection hazard zones and local topographic and vegetational influences were presented by Van Arsdel (1961) for the Lake States area in the United States. His work has since been used to define hazard zones for the northeastern United States (Charlton 1963) and Quebec (Lavallée 1974).

Pruning the highly susceptible lower branches from eastern white pine also reduces losses caused by the blister rust disease (Weber 1964). Guidelines for pruning white pine to control blister rust disease are available for the Lake States (Brown 1972).

Breeding and selection of eastern white pine for resistance to the blister rust fungus, and to weevil injury, hold promise for the future (Anderson 1973; Zsuffa 1981). At present, however, good pest control strategy is necessary for successful white pine culture; damage caused by white pine weevil and/or blister rust disease can be devastating.

This paper presents blister rust infection hazard zones for Ontario, discusses pruning and makes other recommendations for avoiding losses caused by the blister rust disease.

Discussion

Plantation surveys of eastern white pine conducted by the Forest Insect and Disease Survey (FIDS) of the Canadian Forestry Service to rate the importance of the blister rust disease were performed in 1975, 1980, and 1983. Other diseases and insect pests were included in the 1980 and 1983 surveys. The survey results (Gross 1985) indicated that the abundance of damage caused by white pine weevil and blister rust varied for the different administrative regions of the Ontario Ministry of Natural Resources. For example, both blister rust and weevil damage levels were low in the Eastern Region. The data suggest the possibility that hazard zones for infection with blister rust can be defined for Ontario.

Climatic data for the Great Lakes basin (Phillips and McCulloch 1972) and Ontario (Chapman and Thomas 1968; Brown *et al.* 1968) were examined for the criteria that Van Arsdel *et al.* (1961) used as a basis for delineating hazard zones for the Lake States. Slight modifications of the methods used by Van Arsdel *et al.* (1961) were necessary in order to utilize the climatic data available. The range in conditions used to identify hazard zones for Ontario are in Table I. The spores that infect pine are produced in July, August and September, after a buildup of infection on the herbaceous *Ribes* spp. hosts; hence, the emphasis on July climate.

Table I. Climatic data^a used to identify blister rust infection hazard in Ontario

Hazard zone	Mean minimum July temp (°C)	Mean daily July temp (°C)	Mean annual frost-free period (days)	Mean date of first frost
1. Low	> 14.4	> 21.1	140	10 Oct.
2. Intermediate	13.3 - 14.4	18.9 - 21.1	120	5 Oct.
3. High	12.2-13.2	17.8 - 18.8	120	30 Sept.
4. Severe	< 12.2	<17.8	< 120	before 30 Sept.

^aThe original data were whole numbers in degrees Fahrenheit. The decimals result from conversion to Celsius.

Landform and other physiographic characters influence climate as well as the hazard of infection by blister rust (Van Arsdel 1961). The site districts described by Hills (1959) include many landform and physiographic characters, and conformed reasonably well with the hazard zone boundaries that were based solely on climate (Table I). The boundaries of the zones of infection hazard that are presented for Ontario (Fig. 1) were adjusted to conform to the boundaries of site districts (Hills 1959). Since the isozones defined by each of the climatic variables in Table I did not match precisely, the slight shifts needed to make this adjustment merely added another variable to the decision process.

The significance of the hazard zones for infection with blister rust was tested by using the FIDS survey results (Fig. 2, Table II). Zone differences were significant in 1980 ($P = 0.05$) and 1983 ($P = 0.001$). Significant differences between zones were not investigated. The surveys were not designed to test zone relationships, and sample size was inadequate for some of these specific comparisons. However, the data in Table II provide evidence for trends in infection hazard by zone.

Local differences in microclimate within a hazard zone also influence infection hazard. Consequently, the hazard zones presented in Fig. 1 provide only a broad base for predicting blister rust infection. Anderson (1973) and Van Arsdel *et al.* (1961) described vegetational and topographical characters that were correlated with hazard of blister rust infection. Anyone attempting to apply the data on infection hazard zones contained herein (Fig. 1) should be familiar with guidelines presented by Anderson (1973) and Van Arsdel (1961). Briefly, conditions favorable to infection increase as topography favors the occurrence of clear, cool, windless nights that are conducive to dew formation and slow drying.

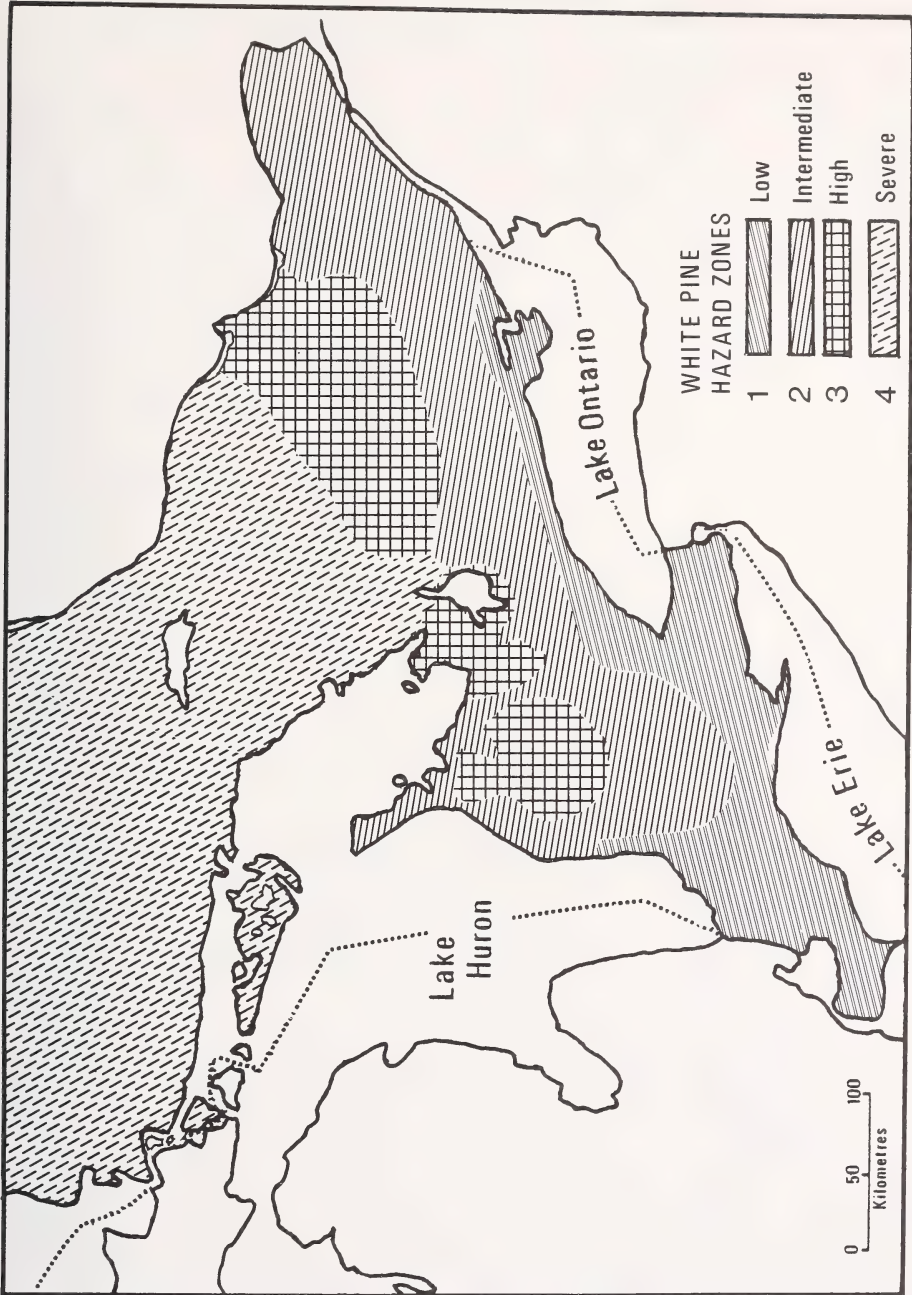


FIG. 1. Hazard zones for predicting the amount of infection expected in Ontario by the white pine blister rust fungus.

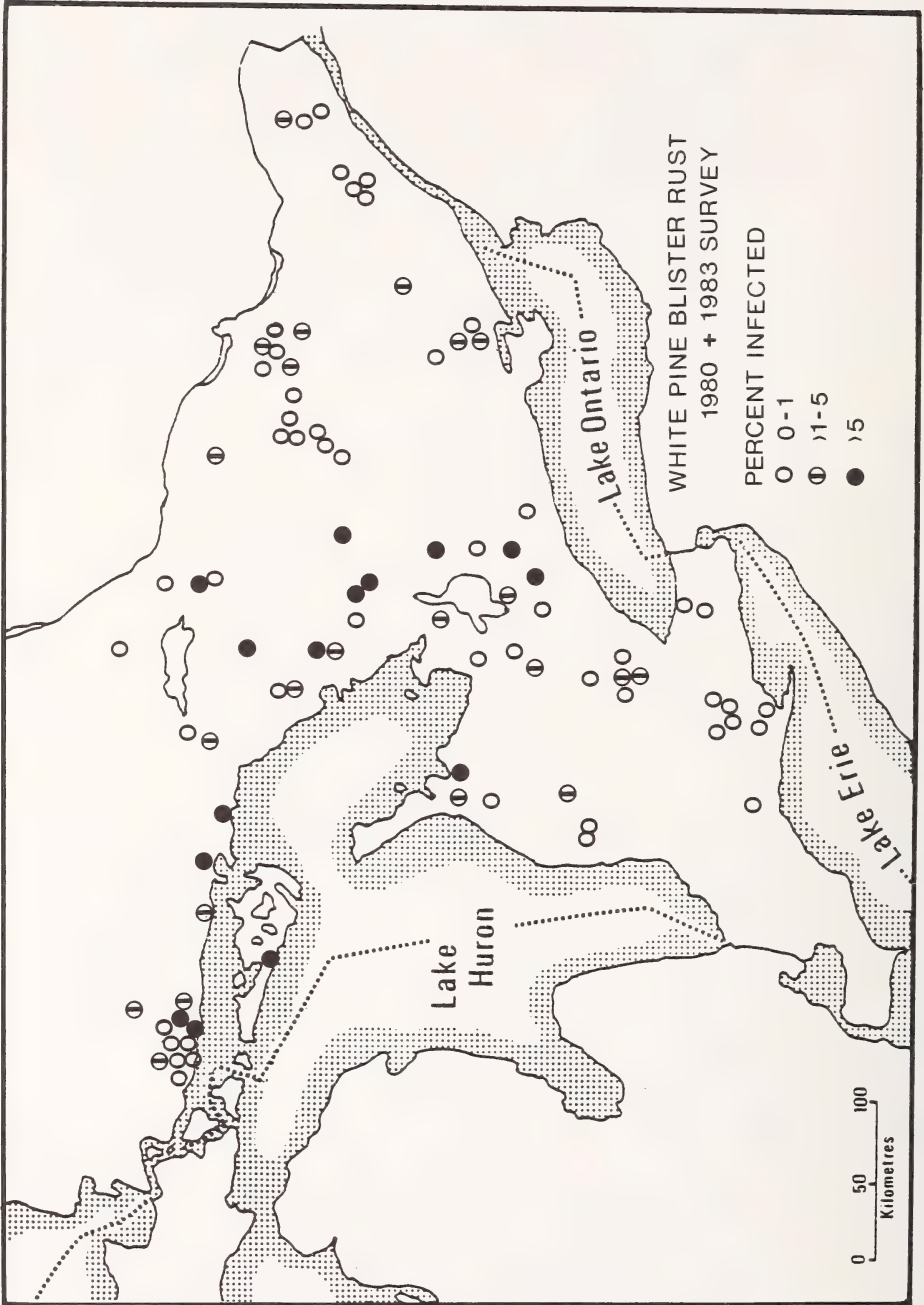


FIG. 2. The location and intensity of white pine blister rust infection in plantations sampled in the 1980 and 1983 pest surveys.

Table II. White pine blister rust data presented to show differences in the amount of rust infection detected in different zones of infection hazard

Hazard zone	Plantations sampled ^a n	Trees affected	
		%	Range
1975 Survey			
1. Low	3	0.4	0 - 1.3
2. Intermediate	15	6.0	0 - 17.3
3. High	12	11.5	0 - 53.0
4. Severe	1	6.0	n.a.
All zones	31	7.6	0 - 53.0
1980 Survey			
1. Low	7	0.5	0 - 2.0
2. Intermediate	8	1.9	0 - 4.0
3. High	7	2.8	0 - 11.0
4. Severe	12	7.0	0 - 27.0
All zones	34	3.6	0 - 27.0
1983 Survey			
1. Low	5	0.1	0 - 0.7
2. Intermediate	17	1.1	0 - 6.0
3. High	12	0.7	0 - 2.7
4. Severe	19	4.1	0 - 14.7
All zones	53	2.0	0 - 14.7

^a The number of plantations sampled does not match data in Gross (1985), as data were incomplete for 6 stands of the 1980 survey, and in 1983 an additional 11 stands were sampled to help test zone boundaries.

Depressions, valleys, lower slope positions and north facing slopes are examples of favorable topography. Dense ground vegetation also accumulates cool air and prolongs drying of wet surfaces.

The vegetational and topographic features that are correlated with infection hazard in the Lake States seem to apply in Ontario as well. As part of the 1983 FIDS survey, plantations were rated for topography, percent slope, aspect of slope, vegetational character, and distance to a wet area in accordance with the methods of Van Arsdel *et al.* (1961). In all hazard zones, plantations with negligible infections of blister rust were found, and in 2 stands in zone 2 (intermediate hazard), 6% of the trees were infected. Most of these situations reflected local conditions that explained much of the variance in the amount of infection in stands of a particular zone. If the 2 stands with 6% infection (Table II) were given a higher hazard rating, as seems appropriate, the data would reflect an even better correlation with the zones of infection hazard. Similarly, some of the stands with negligible infection in the high and severe hazard zones represent sites on which local conditions for infection were less favorable than elsewhere. These situations illustrate the importance of local microclimatic influences. Plantations with negligible infection were sampled in all zones in all surveys (Table II). This fact seems to indicate that white pine can be grown successfully in all of the hazard zones, but as hazard increases, the necessity for selecting sites resistant to blister rust disease and implementing pest control programs also increases.

The following is a composite of recommendations by Anderson (1973) and Van Arsdel (1961) for growing white pine in the various hazard zones for blister rust:

1. Low hazard zone. On most sites, blister rust does not cause serious losses and no control is necessary.
2. Intermediate hazard zone. Losses to blister rust can be reduced to acceptable levels. Sites characterized by a microclimate favorable to rust infection should be avoided. An overstory is recommended for juvenile stands. Pruning of low branches will reduce losses to blister rust.
3. High hazard zone. Most areas will experience unacceptable levels of mortality. Warm sites with light ground vegetation conducive to fast drying may support acceptable stands. Pruning of low branches is necessary to achieve acceptable survival levels, and an overstory will help protect juvenile stands.
4. Severe hazard zone. Losses probably cannot be reduced to acceptable levels at this time. Control recommendations for zone 3 will apply in any attempt to establish white pine in this zone.

With respect to recommendations for zones 3 and 4, plantations have been observed in the course of FIDS surveys (Fig. 2, Table II) in which the level of infection by blister rust was low. Such infection often occurs in understories or in plantations on warm, dry sites. Hence, there appear to be some sites in zones 3 and 4 on which white pine can be grown successfully. Over all, however, in zones 3 and 4 the number of satisfactory sites is low, and control programs for blister rust are essential.

Van Arsdel (1961) lists three aids to blister rust control: (1) maintaining a closed canopy to keep the air dry below the canopy and shade out susceptible side branches early; (2) pruning the lower branches of crop trees; (3) refraining from planting small openings as these tend to remain cool and wet. Marty (1966) presents economic guides for making blister rust control decisions. Prediction models are included for estimating the number of crop trees expected to survive both blister rust infection and weevil damage.

Pruning the susceptible low branches from crop trees seems to be a particularly good method of controlling the blister rust disease. Hunt (1983) discussed the feasibility of pruning to control blister rust on western white pine (*Pinus monticola* Dougl.) in British Columbia. As disease hazard increases, the height of infections on pines increases. More cankers are found higher on the trees (Anderson 1973); however, the bulk of infection still occurs on the lower branches. Infection occurs through needles, most frequently on the side branches. Van Arsdel (1961) noted that 99% of all blister rust cankers in the Lake States were located within 2 m (6 ft) of the ground. Brown (1972) reported several studies, all of which detected that over 90% of the infections occurred below 3 m (9 ft). For Ontario, Cafley (1958) reported that 84% of the infections occurred below 2 m (6 ft) of the ground, and 26% of these were still confined to branches. Since infection takes place through the needles (Patton and Johnson 1970) and the fungus progresses toward the main stem via branches, considerable infection can be eliminated by removing susceptible branches before the main stem is endangered.

To be effective, low pruning needs to be started early (Weber 1964; Brown 1972). An infection survey at stand age 4 or at an average tree height of 0.6 m (2 ft) to establish the necessity for blister rust control is recommended by Brown (1972). Naturally, stand treatment should also include removal of weevil-infested leaders. Weevil-injured crop trees can be trimmed to promote good tree form, or can be replaced by designating crop tree status for a new tree.

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PROTEINS, ISOZYMES AND RESISTANCE TO WHITE PINE BLISTER RUST

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Abstract

An attempt has been made to correlate protein and isozyme patterns with resistance to white pine blister rust. Leaves of resistant, susceptible and immune clones, varieties and species of white pine have been analyzed by polyacrylamide electrophoresis. No obvious difference in the protein pattern among leaves of resistant, susceptible and immune plants has been observed. Immune plants seem to show the lowest protein band intensity in August. While isozyme patterns of Peroxidase (PO), Esterases (EST) and Malate dehydrogenase (MDH) show differences between clones of *Pinus strobus* and *Pinus excelsa*, no difference between susceptible and resistant clones of *P. strobus* has been found. Further comparison among resistant and susceptible clones of *Pinus strobus* x *griffithii* indicates that only PO shows a difference in isozymes between the very resistant clone and the very susceptible clone.

Introduction

White pine blister rust, caused by the fungus *Cronartium ribicola* J.C. Fisch., threatens white pine (*Pinus strobus* L.) stands in North America, and for 80 years has hampered the cultivation of this species.

The fungus was introduced to North America about 1900, and spread very quickly into the areas covered by white pine stands. Great efforts have been made to control the disease by extensive *Ribes* eradication programs aimed at eliminating or reducing the primary host of the pathogen. However, these efforts were not successful, and other means of controlling this disease were sought. Breeding for resistance and applying epidemiological principles seemed to be more effective methods of control. None of the white pines is immune to the fungus, but differences in degree of susceptibility to the disease have been recorded (Bingham 1972). In addition, differences have been found in the mechanisms of resistance to white pine blister rust (Kinloch 1980). Hoff *et al.* (1980) identified and described the following 6 mechanisms of resistance: 1) prevention of needle lesions, 2) reduced frequency of lesions, 3) premature shedding of infected needles, 4) fungicidal reaction in short shoots, 5) reactions that eliminate established bark infections, and 6) the ability of a seedling to remain alive when infected.

The most common mechanism for resistance is reduced susceptibility to infections. According to Patton and Johnson (1970), infection of white pine by *C. ribicola* occurs generally by way of the stomata of primary and secondary leaves. The fungus produces abundant mycelia in the needle and grows down through the vascular tissue of the needle and short shoots into the bark of the branch or stem, where it produces cankers. Mortality occurs after cankers have girdled the branch or stem. Trees may not express any symptoms for a long time.

Not until 1940 was a research program developed that aimed at the production of western pines resistant to blister rust. In 1950 a program was instituted to develop genetic resistance to *C. ribicola* in *Pinus monticola* Dougl. Hoff *et al.* (1980) found that some of the mechanisms of resistance are inherited by single genes, others by many genes.

Variability in resistance within one species is well known (Hoff *et al.* 1980; Nelson 1980). This variability is being tested in infection experiments; however, such experiments are time consuming. Therefore, a method that demonstrates a relationship between specific biological markers and resistance of the host plant would greatly enhance the selection and breeding of varieties resistant to blister rust. Knowledge of the genetic composition of a tree would be useful as well. Analysis of genetic composition and its variation, expressed by the protein pattern of the tree or its isoenzyme profile, could also provide useful information (Gottlieb 1971; Conkle and Adams 1977; Feret and Bergmann 1976).

Variations in enzyme proteins can be related directly to changes in the gene structure of the codon sequence and always follow the Mendelian law of segregation. Proteins are not only widely distributed within the living cell but are also implicated in its metabolism. Therefore, they are ideal biological markers. Any defence mechanism of a plant, if genetically controlled, should be identifiable by its protein or enzyme pattern. On the basis of this assumption, demonstration of the entire complement of soluble proteins should reveal differences between resistant and susceptible clones of white pines. Once such a difference is identified, the appropriate isoenzymes could be identified and linked to the corresponding mechanism of resistance. This paper reports on our attempts to correlate protein and isoenzyme patterns with varieties or clones of white pine that are susceptible or resistant to blister rust.

Materials and Methods

Protein pattern. Current-year needles of *Pinus strobus* (susceptible and resistant to white pine blister rust) and *Pinus excelsa* (immune to blister rust) were collected from trees grown at the Maple Research Station, Ontario Ministry of Natural Resources, in July, August, September and November 1979. These trees had been tested previously by Dr. L. Zsuffa for their resistance to white pine blister rust.

To prepare the needle powder for protein extraction, frozen needles were cut into 0.5-cm pieces, and ground with a Brinkmann homogenizer (Polytron). During grinding the needles were kept in an acetone-petroleum ether mixture in a proportion of 4:1. Dry ice, added to the mixture, kept the plant material frozen. After homogenization, the ground needles were filtered and further washed with the cold acetone-petroleum mixture until the washing solution remained clear. The needle powder was stored in a deep freeze. One gram of the dry acetone needle powder was soaked overnight at 4°C in 10-ml 0.01M tris-phosphoric acid buffer solution consisting of 8M urea (pH 6.8). After soaking, the slurry was filtered through a Whatman filter paper No. 1, and the filtrate mixed with equal amounts of the sample buffer. The sample buffer (0.01M tris-phosphoric acid) contained 1% SDS, 5% 2-mercaptoethanol and 20% glycerol (Payne 1976). After it had been heated for 2 min at 100°C, 20 µl of the treated sample, as well as M.W. marker (ranging from 94,000 to 14,300 daltons), were loaded on the slab of 10% polyacrylamide gel (cross-linking 37.5:1), and electrophoresis was carried out for 4-5 h at approx. 18-20 V/cm in 0.01M tris-phosphoric acid buffer containing 0.1% SDS. After electrophoresis, the gel was removed and stained overnight in 0.025% Coomassie blue solution containing water (45%), acetic acid (10%) and methanol (45%). Destaining with 7% (v/v) acetic acid + 5% (v/v) methanol in water was done by diffusion until the solution became clear.

Isozyme pattern. A separate set of needle samples was collected in September 1980 for isozyme pattern analysis. In addition, needles of *Pinus strobus* x *griffithii* (susceptible and resistant to blister rust) were collected from the same location and analyzed to determine whether apparent differences are merely differences in chemotaxonomic characters between *P. strobus* and *P. excelsa* (Table I).

Needle powder was prepared as described earlier. Either urea (8M) or Triton X100 (1%) was added to the sample buffer solution (0.01M tris-phosphoric acid, pH 6.8) for protein extraction. Other enzymatic protective reagents (0.2% ascorbic acid and 0.1% L-cysteine) were added to the buffer solution to inactivate phenoloxidase enzymes and reduce oxidation of phenols during the extraction procedures (Feret and Bergmann 1976).

One gram of the dry acetone needle powder was soaked overnight at 4°C in 10 ml of buffer solution (0.01M tris-phosphoric acid solution), and the slurry was centrifuged at 5,000 rpm for 30 min. The supernates were collected and 20% of glycerol and a trace of bromophenol blue were added. Twenty microlitres of the sample were subjected to electrophoresis for 4-5 hours on slabs of 5% polyacrylamide gels at 200 volts.

The gels were then stained for different enzymes. Peroxidase (PO) was stained

according to the methods of Kieliszewska-Rokicka (1980). Since there are marked differences in activity with different substrates, 11 phenolic compounds were tested (Table II). Other enzymes (Table III) were analyzed according to the staining recipes of Shaw and Prasad (1970) and Siciliano and Shaw (1976).

Table I. White pine clones tested and their susceptibility to blister rust

Clones	Species	Susceptibility
5-450	<i>Pinus strobus</i>	resistant
5-459	<i>Pinus strobus</i>	resistant
5-468	<i>Pinus strobus</i>	resistant
5-2	<i>Pinus strobus</i>	susceptible
5-255	<i>Pinus strobus</i>	susceptible
5-546	<i>Pinus strobus</i>	susceptible
5-315	<i>Pinus excelsa</i>	immune
5-323	<i>Pinus excelsa</i>	immune
5-327	<i>Pinus excelsa</i>	immune
5-832	<i>Pinus strobus</i> x <i>griffithii</i>	susceptible
5-840	<i>Pinus strobus</i> x <i>griffithii</i>	susceptible
5-937	<i>Pinus strobus</i> x <i>griffithii</i>	susceptible
5-835	<i>Pinus strobus</i> x <i>griffithii</i>	resistant
5-916	<i>Pinus strobus</i> x <i>griffithii</i>	resistant
5-918	<i>Pinus strobus</i> x <i>griffithii</i>	resistant

Table II. Phenolic substrates used for peroxidase detection

Substrates	Type of phenol	Reactions
p-Coumaric acid	monophenol	(+)
p-Cresol	monophenol	weak
Guaicol	monophenol	(-)
Tyrosine	monophenol	weak
Caffeic acid	o-dihydroxyphenol	(+)
Catechol	o-dihydroxyphenol	(+)
L-Dopa	o-dihydroxyphenol	(+)
Hydroquinone	p-dihydroxyphenol	(+)
Resorcinol	m-dihydroxyphenol	weak
Gallic acid	triphenol	(+)
Pyrogallol	triphenol	(-)

WHITE PINE SYMPOSIUM

Table III. Enzymes tested

A. Hydrolases, lyases and transferases	Reactions ^a
Acid phosphatase (AP)	(+)
Alkaline phosphatase (AkP)	(+)
Esterase (EST)	(+)
Leucine aminopeptidase (LAP)	(+)
Phosphoglucomutase (PGM)	(+)
B. Dehydrogenases	
Alcohol dehydrogenase (ADH)	(-)
Glucose-6-phosphate dehydrogenase (G6PDH)	(-)
Glutamic dehydrogenase (GDH)	(-)
Isocitrate dehydrogenase (IDH)	(+)
Lactate dehydrogenase (LDH)	(-)
Malate dehydrogenase (MDH)	(+)
C. Others	
Glutamate oxaloacetate transaminase (GOT)	(+)
Malic enzyme (ME)	(+)

^a (+) indicates enzyme activity.
 (-) indicates no reaction.

Results

Protein pattern. The protein pattern did not show any obvious differences among resistant, susceptible and immune clones. In general, the band intensity and, therefore, the protein content decreased from July to August and then increased to the highest level in November (Fig. 1). However, the protein band intensity of immune clones was lowest in August.

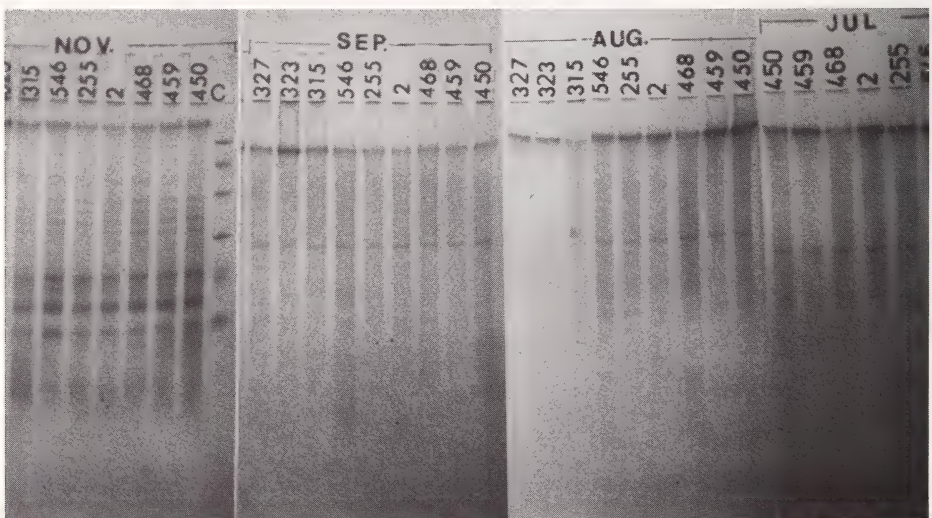


FIG. 1. Seasonal change in protein patterns of white pine clones identified in Table I.

Isozyme patterns. Protein patterns fluctuated seasonally from July to November. Since blister rust infection takes place in the fall, September needle samples were used as a standard against which to measure differences in isozyme patterns among the tested clones.

Peroxidase (PO). Of 11 phenolic substrates tested, only catechol showed differences in locus II between clones of *P. strobus* and those of *P. excelsa*. No differences could be found between the susceptible and resistant clones of *P. strobus* (Fig. 2). However, there were differences in the isozyme pattern of PO between the very resistant clone (916) and the very susceptible clone (832). Clone 916 had only one band in locus I whereas clone 832 had two. Clone 937, which was classified by the plant breeder as susceptible, gave uncertain results; the number of bands at locus I resembled that of the resistant clones.

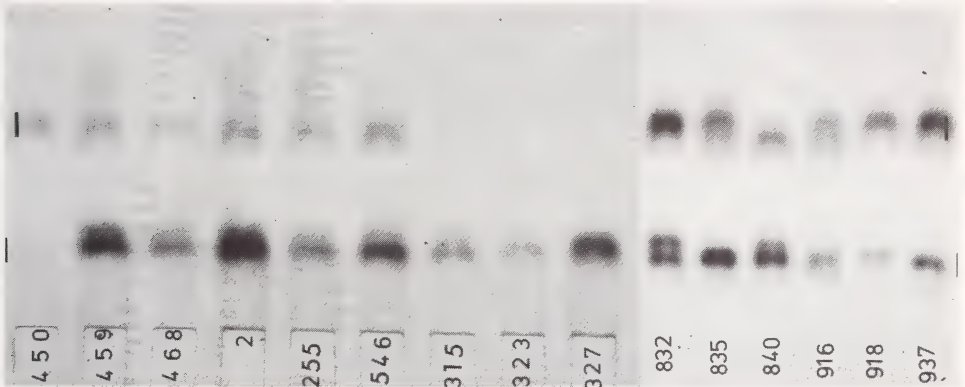


FIG. 2. Peroxidase (PO) isozymes shown with catechol as substrate. (Clone identity as in Table I).

Other enzymes. Tests were made for the presence of isozymes of 13 other enzymes classified according to their different catalytic characters as well as their functions in different pathways, i.e., Krebs cycle, Pentose phosphate pathway, etc. Only 9 enzymes could be detected in the samples investigated (Table III).

Only with EST and MDH were differences evident between clones of *P. strobus* and *P. excelsa*. No differences could be detected between the susceptible and resistant clones of *P. strobus* or of *P. strobus* x *griffithii* (Fig. 3 and 4).

Discussion

For the past 30 years, an extensive white pine selection and breeding program has been in operation in an attempt to control blister rust fungus (Kinloch 1980). The results of this program are only now becoming evident. The time required for white pine to grow and the lack of understanding of the phenotypic expression of resistance and of the genetic mechanisms that control it pose great difficulties for a breeding program. In addition, resistance to blister rust is expressed only after the host has reached a certain age (Patton 1961; Patton and Ricker 1966; Patton 1967; Bingham *et al.* 1967; Kinloch 1980). Furthermore, in spite of efficient methods of inoculation, disease escape, disease recovery and predisposing factors may obscure the expression of true resistance.

Therefore, a method is needed that detects at a very early stage of plant development whether the plant will be resistant or susceptible to white pine blister rust. Logically, such a method would detect and link the occurrence of certain compounds in the host with the expression of host resistance. The analysis of the protein pattern of the host seems most appropriate, because proteins, whether structural or functional, are primary gene products and resistance to blister rust is genetically controlled.

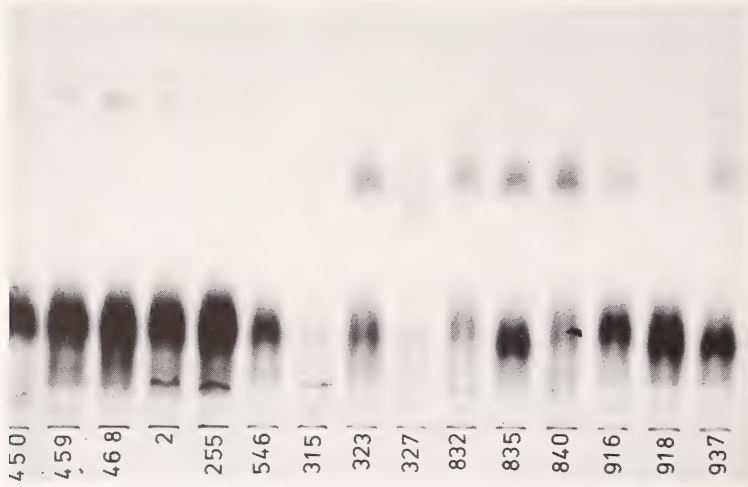


FIG. 3. Esterase (EST) isozymes in clones of *P. strobus* and *P. excelsa*. (Clone identity as in Table I).

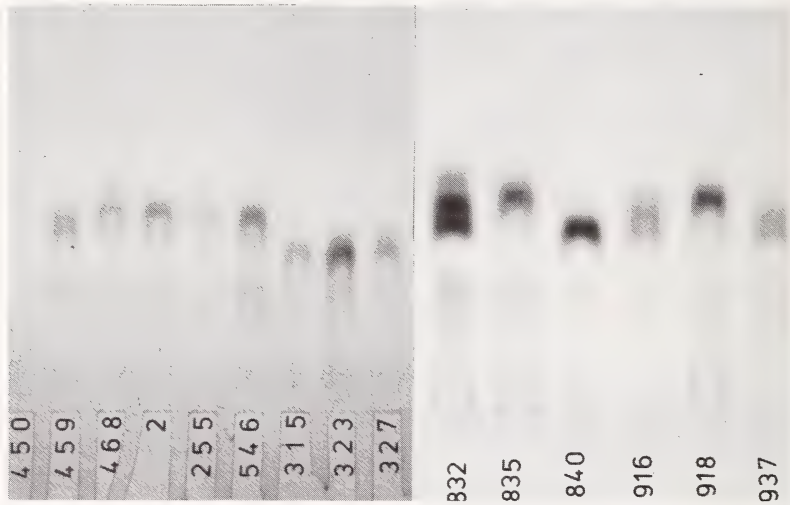


FIG. 4. Malate dehydrogenase (MDH) isozymes in clones of *P. strobus* and *P. excelsa*. (Clone identity as in Table I).

For this reason, we investigated the protein pattern in needles of resistant, susceptible and immune clones, since other metabolites such as phenols and auxins could not be directly related to disease resistance (Boyer 1964, 1966). Analysis of protein patterns has been reported by Hare (1972) for tissue resistant or susceptible to fusiform rust. Hare (1972) showed that similar tissues of all southern pines yielded remarkably similar protein patterns, but several bands differed between susceptible and resistant tissues.

A comparison of the protein patterns of resistant, susceptible and immune pine clones showed no striking differences. When the July, August and September samples were examined, however, a general trend became evident. The number of protein bands increased from July to November, with the samples from November being richest in protein patterns.

The immune clones of *P. excelsa* are low in proteins in August, when the fungus infects the needles. Analysis of the nutrient composition of jack pine (*Pinus banksiana* Lamb.) needles and white spruce (*Picea glauca* [Moench] Voss) seedlings also revealed that the highest accumulation of nitrogen occurred in September, October and November (Morrow and Timmer 1981; Armonson 1960)—a trend that is similar to that of the protein pattern in white pine needles. However, we do not know whether the mechanisms of resistance in the clones are located in the needles or in the stems, as indicated by Hoff *et al.* (1980). The selection of resistant clones analyzed during this work has been based on symptom expression of the bark and not on that of the needles. Possibly the crucial mechanisms of resistance are not located in the needles and therefore are not strikingly expressed in this tissue.

Since proteins represent structural and functional elements of the host cells, their relationship with defense mechanisms may not be readily identified; therefore, further attempts were made to differentiate isozyme patterns of clones in relation to disease resistance.

These experiments would show such differences only if factors of resistance were formed before infection and located in the needles of the host. Since we had no indication from the literature which isozymes might show the differences between resistance and susceptibility of the host, we investigated enzymes of each major metabolic pathway.

The isozyme patterns of PO, EST and MDH show differences between *P. strobus* and *P. excelsa*, but none between resistant and susceptible clones of *P. strobus*. On the basis of these results, one may assume that the differences between *P. strobus* and *P. excelsa* are taxonomic traits and are not necessarily correlated with resistance or susceptibility. To test this assumption, resistant and susceptible clones of *P. strobus* x *griffithii* were also analyzed. The results showed that resistant and susceptible clones of this cross may be separated by PO but further experiments are needed to prove this conclusively.

It is believed that PO may oxidize phenols for more fungitoxic quinones in the presence of organic peroxides (Fehrmann and Dimond 1967; Hare 1972) and consequently may play an important role in mechanisms of resistance. However, since resistance is polygenic, one would expect differences in several isozyme systems and would assume that resistance is expressed at the same site, i.e., on needles or bark. If resistance is expressed by different clones at different sites, then its mechanisms may be more difficult to correlate with isozyme patterns.

Another problem encountered is the method of enzyme extraction. There is agreement in the literature that the method of extraction is dictated by the chemical characteristics of the enzyme and the tissue from which it is to be isolated (Feret and Bergmann 1976). However, many substances such as organic acids and, in particular, phenols, that are liberated during the process of enzyme extraction, may combine with proteins and enzymes, causing precipitation and denaturation (Loomis and Battaile 1966). Tannins are the principal cause of plant enzyme instability in plant extracts (Harborne 1964; Loomis 1969).

Extensive efforts have been made to prevent inactivation and denaturation of enzymes in plant extracts. There is no general remedy for this; each system has to be tested. The general aim is to inactivate the polyphenol oxidases or to reduce the phenols as they are formed. To do this, some researchers have used sodium hydrosulfite (Gell *et al.* 1960), while others have used ascorbic acid (Macko *et al.* 1967), cysteine, PVP and other compounds or chromatographic techniques (Anderson 1968). For our purpose, ascorbic acid and L-cysteine were the most effective protectants.

To eliminate any doubts about the site of expression of resistance and whether resistance is manifested before or after infection, inoculation experiments should be carried out under controlled conditions. Such experiments could also clarify the differences that exist between field and greenhouse resistance.

In addition, the characterization and development of plant material resistant to blister rust should be an integral part of the white pine breeding program. It is a long-term project, but it shows great promise in the control of white pine blister rust.

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THE GENETIC IMPROVEMENT OF EASTERN WHITE PINE IN ONTARIO

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Abstract

Past research on the improvement of white pine concentrated on developing varieties resistant to blister rust (*Cronartium ribicola* J.C. Fisch.). The most significant result was the breeding of rust-resistant and vigorous eastern white pine (*Pinus strobus* L.) x Himalayan white pine (*P. griffithii* McClelland) hybrids. Current research concentrates on progeny testing of eastern white pine plus trees, on breeding and field testing of eastern white pine x Himalayan white pine hybrids and on developing and testing clonal varieties.

Introduction

The first European explorers of North America were awed by the great forests of white pine that covered vast areas of the land. Pioneers reported that trees 45 m tall were fairly common; some were 73 m tall and some 3.6 m in diameter (Wilson and McQuilkin 1963).

By the end of the 19th century Ontario had nearly exhausted its finest stands of eastern white pine, *Pinus strobus* L. Around 1900 reforestation of the waste lands in the older agricultural parts of southern Ontario was begun. To satisfy the demand for planting stock, considerable white pine was imported from Germany. These trees were an early source of infection by blister rust (*Cronartium ribicola* J.C. Fisch.). The white pine weevil (*Pissodes strobi* [Peck]) problem was also present during the entire reforestation era and indeed much before it. This insect poses the greatest threat to Ontario's white pine plantations. Planting of white pine in Ontario has been carried out on a rather small scale since the 1960s because of the threats posed by weevils and blister rust. However, in recent years examples of successful plantations have brought about renewed interest in white pine reforestation.

The genetic base. Eastern white pine varies in appearance in different parts of its range, a fact which suggests that as yet unidentified ecological or geographical races may exist (Heimburger and Holst 1955). The almost complete elimination of white pine stands by logging may have resulted in genetic drift in remaining small populations and in a reversion to relatively small populations of common parental types. Variation in certain characteristics, such as stratification requirements of seed, height and diameter growth, and response to day length, indicate this random fixation of genes and the possibility of improvement by seed source selection (Wright 1970).

Trees immune to white pine blister rust and white pine weevil occur. This suggests the feasibility of selection, propagation and breeding of resistant varieties (Wright 1970).

Eastern white pine crosses fairly easily with most of the other 5-needle pines in the series *Strobi*. This ability provides scope for introducing various desirable traits, including resistance to specific pests, through interspecific hybridization (Heimburger 1972).

White pine does not propagate vegetatively under natural conditions. However, scions from the crowns of mature trees can be grafted readily on young stock (Heimburger 1985). Small cuttings of the last-season's twigs from young trees can be rooted. This allows development of clones, providing genetically identical material for testing and, eventually, planting (Zsuffa 1972).

Ontario's White Pine Breeding Program

History. White pine breeding research in Ontario was initiated in 1946 and was conducted by C. Heimburger until his retirement in 1968. Throughout the 1950s and early 1960s it was the major breeding program.

The main goal was the development of varieties resistant to blister rust. It was hoped to achieve this goal by selecting and propagating eastern white pine trees free of disease symptoms, by crossing resistant trees and producing their progenies, and by producing hybrids with white pine species resistant to blister rust (such as Himalayan pine, *P. griffithii* McClelland). Rich arboreta of exotic white pine species were developed for this purpose at Maple research station and at St. Williams nursery (Turkey Point) of the Ontario Ministry of Natural Resources.

No real plus-tree selection was conducted, as blister rust resistance was the major objective. The absence of disease symptoms was the major selection criterion, and less attention was paid to other silviculturally important traits, such as growth rate and form. Also, the enrolled genetic base was incomplete. In 1960, 89 selected eastern white pine clones were on register. Half of these were from Point Platon, Quebec (trees originally imported from Germany) and Petawawa Forest Experiment Station (now the Petawawa National Forestry Institute) and many significant white pine regions were not represented at all. In addition, many of the selections proved susceptible to blister rust when they were inoculated artificially with the disease. By 1971 fewer than 30 clones, half of them from Point Platon, Quebec, remained free of blister rust. These trees were insufficient in number and the sources were poorly distributed; consequently, they were inadequate as a base for improved seed production.

The field tests indicated that progenies which succumbed to highly concentrated inoculum might be tolerant of the lower field levels of blister rust hazard. For areas with very high blister rust hazards, either cloning of resistant parent trees (Zsuffa 1973) or introduction of major genes for resistance from another white pine species (Heimburger 1972) by interspecific breeding may offer immediate solutions.

The breeding of interspecific white pine hybrids resistant to blister rust has been successful (Zsuffa 1981). In particular, hybrids between eastern white pine and Himalayan white pine grow vigorously and have a "practical level" of resistance to blister rust, with advanced generations seeming to maintain these characteristics (Heimburger 1972; Zsuffa 1976).

The breeding for weevil resistance also started early. Eastern white pine trees with narrow crowns and slender leaders were more immune to weevil attacks than were those with thick leaders. While the selection of the former type is possible, the thickness of the leader and the width of the crown may vary greatly with environment, especially with stand density and shading. The resistance to weevils is also influenced by resin flow. However, environmental factors, such as climate and day length, may change the intensity of resin flow and thus break down the resistance.

Some exotic white pine species, such as Balkan pine (*Pinus peuce* Griseb) and western pine (*P. monticola* Lamb.), have weevil resistance and could be considered for hybridization (Heimburger and Sullivan 1972a, 1972b). Unfortunately, the introduced western white pine sources and their hybrids are poorly adapted to Ontario's conditions. Balkan pine is of variable resistance, and in several hybrids with eastern white pine the resistance broke down.

Provenance testing of eastern white pine started in the early 1950s. The trials did not include a satisfactory representation of sources and were inconclusive. A range-wide study of eastern white pine, in cooperation with the United States Forest Service, was started in 1955. Only one Ontario source (Algoma) is represented and only two plantations have been established (Ganaraska and Turkey Point), each with 12 range-wide seed sources). The 7-year and 12-year results were reported (Fowler and Heimburger 1969; Zsuffa 1975a). The Pennsylvania, Nova Scotia and New York sources had better height and diameter growth in southern Ontario than did the Algoma source.

Present status. The main objective of the present work is to develop genetically improved seed sources to satisfy the needs of the expanding reforestation program. Therefore, stand and plus-tree selection have been intensified in all important white pine regions. The goal is to develop seed production areas and to secure parents for seed orchard establishment.

This program has been carried out in cooperation with Ontario's forest managers and has resulted during the last 10 years in over 500 plus-tree selections. The plus-trees were used for grafting to establish 8 seed orchards.

Progeny testing is in progress to establish the genetic quality of selected plus-trees and to identify the best combiner parents in seed orchards. The early (5-year) height growth of open pollinated plus-tree progenies varied greatly (Zsuffa 1978).

Haddow's (1969) surveys show that blister rust does not present a great threat to white pine plantations in all regions. In many areas the disease causes only inconsequential damage. For these areas, resistant strains of white pine are not essential.

In southern Ontario, eastern white pine x Himalayan white pine hybrids are promising because of their rust resistance and vigorous growth. In a replicated field trial, at 6 years of age the hybrid white pine outgrew the eastern white pine control by 61% (Zsuffa 1976). More experimental plantations of this type have been established across Ontario to gather information on site tolerance.

Cloning, by rooting of cuttings, offers a solution for the fast development of strains of eastern white pine resistant to blister rust. Methods for vegetative propagation of white pine by rooting cuttings have been developed and clones of reliable rooting ability have been established (Zsuffa 1972, 1973). Nursery stools, for mass propagation of cutting propagules, have been planted.

Cloning, by preserving and copying outstanding and desired genetic combinations, also provides a shortcut in breeding and can secure large, immediate genetic gains. A study of 8 clones belonging to a single progeny showed sufficient variation to indicate that potential genetic gains can be achieved with clonal propagation (Zsuffa 1975b).

The present program concentrates also on interspecific breeding. Most attention is being focussed on crosses with Himalayan pine. More complete gene pools of this species have been obtained through the International Union of Forestry Research Organizations (IUFRO) and trees are being grown in Ontario. Further crosses with Balkan pine and western white pine are being attempted as well, with the goal of producing fast-growing, weevil-resistant hybrids (Zsuffa 1970, 1971; Zsuffa 1975a).

Many years of work and large investments went into genetic improvement of eastern white pine in Ontario. The results of this work are already being used; however, only a continuous effort will secure the full benefit of the effort made.

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SILVICULTURE OF EASTERN WHITE PINE

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Abstract

The silviculture, growth characteristics, and physical properties affecting utilization are described for eastern white pine (*Pinus strobus* L.). Regeneration methods and tending procedures to exploit the attributes of pine and to accommodate its demands are outlined, with particular reference to problems caused by competing vegetation, the white pine weevil (*Pissodes strobi* (Peck)), and white pine blister rust (*Cronartium ribicola* J.C. Fisch.). The importance of selecting final crop trees at a young age and subsequently fostering and protecting them is stressed.

Introduction

Silviculture, by my own definition, is technique employed in manipulating forest vegetation for the establishment of a new stand of trees or for improving the growth or quality of an existing stand. The silvicultural procedures to be followed for a particular species are determined by physical properties of the species that affect its utilization, by its environmental requirements, and by its growth characteristics. Or, as stated by Daniel *et al.* (1979), "silvics is the basis of silviculture on the biological side". Effective silviculture, therefore, entails providing those conditions most favorable for developing the subject species, and at the same time actively limiting those agents that run counter to such development.

This paper deals chiefly with the attributes and demands of white pine that have a bearing on this matter, and with the silvicultural measures that must be taken to exploit and accommodate them.

Characteristics of White Pine

The natural range of white pine (*Pinus strobus* L.) in Canada extends from south-eastern Manitoba to Newfoundland. White pine occurs widely in the Great Lakes-St. Lawrence, the Acadian, and (formerly at least) the Deciduous forest regions described by Rowe (1972), and to a limited extent in the southern Boreal region (Horton and Bedell 1960). In the United States it ranges through the Lake States south to Iowa and Illinois, throughout much of the northeast, and south in the Appalachian Mountains to Georgia (Critchfield and Little 1966).

White pine is a long-lived species, and although it is not particularly fast-growing in its early years, its volume per hectare in pure stands exceeds that of every other eastern Canadian species on favorable sites by about age 70, and sustained growth ultimately provides by far the greatest yields (Plonski 1974). The exceptional "processing" quality of white pine wood produces the most valuable softwood lumber in the east (Hosie 1970; Mullins and McKnight 1981).

Mature trees have thick, fire-resistant bark. Root systems are wide-spreading, with numerous branching laterals, and are moderately deep. Crowns are irregular and tend to develop long horizontal branches in the open. Even in closed stands self-pruning is very gradual.

White pine is adapted to a range of site conditions, and is capable of growing, and even thriving, under a wide variety of soil textures and moisture regimes. The species is found most often on soils relatively high in sand content, particularly on finer sands or sandy loams; best growth can be achieved on heavier soils but only if hardwood competition is controlled. White pine prefers fresh to moist well-drained soils, although it is found from wet swamps to dry sand plains and rocky ridges. Soils of moderate to low fertility, with surface pH from 4.0 to 7.5, are adequate for satisfactory growth of natural stands of white pine in Canada (Horton and Bedell 1960).

White pine is capable of producing good cone crops by about age 50 years, and these occur at intervals of 3 to 10 years. The winged seeds are dispersed mostly in September and October. More open stands permit larger crowns and higher cone yields per tree. Natural, overwinter stratification on the forest floor breaks seed dormancy and allows germination in late spring. Favorable seedbeds are moist mineral soil, or polytrichum moss or short grass on exposed sites.

White pine seedlings can achieve maximum height growth in as little as 45% of full sunlight, and height growth at a reduced rate is possible under overhead shade admitting only 25% of full light; however, leader diameter and plant biomass increase markedly up to complete light exposure (Logan 1962, 1966).

Such a widely distributed, long-lived, site-tolerant tree as white pine can be expected to associate with a variety of other species on different habitats and at different stages in its life. The commonest and most persistent associate is red pine (*Pinus resinosa* Ait.) which continues as a component of pine stands for many decades. In the Great Lakes-St. Lawrence Region, 4 pine cover types, usually containing red and white pine, have been recognized (Horton and Brown 1960). The pine-tolerant hardwood type includes sugar maple (*Acer saccharum* Marsh.) with lesser amounts of American beech (*Fagus grandifolia* Ehrh.), yellow birch (*Betula alleghaniensis* Britt.), red oak (*Quercus rubra* L.), basswood (*Tilia americana* L.), and eastern hemlock (*Tsuga canadensis* [L.] Carr.); (red pine does not occur in this type). The pine-intolerant hardwood type contains trembling aspen (*Populus tremuloides* Michx.), largetooth aspen (*P. grandidentata* Michx.) and white birch (*Betula papyrifera* Marsh.). The pine-softwood type is represented mainly by balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Moench] Voss), black spruce (*P. mariana* [Mill.] B.S.P.) and, less frequently, by white cedar (*Thuja occidentalis* L.). Jack pine (*Pinus banksiana* Lamb.) is an associate of the pine type, in which the long-enduring white pine finally outlives both red pine and jack pine. In the United States a similar system recognizes white pine as a major component of 4 forest cover types: white pine, white pine-hemlock, white pine-northern red oak, and white pine-chestnut oak (*Quercus prinus* L.) (Eyre 1980). In all cases cited above, occurrence of these associations depends on both site conditions and history of disturbance.

Damaging Agents

Although numerous pests, some minor, others serious but transitory, pose threats to survival or optimum growth of white pine, the management of this species is constrained by 3 chronic, major sources of trouble: vegetative competition, the white pine weevil (*Pissodes strobi* [Peck]) and the white pine blister rust caused by *Cronartium ribicola* J.C. Fisch.

Vegetative competition, by denying light and/or soil moisture, is important far into the life of the stand but is most critical in the seedling phase. Daniel *et al.* (1979) rank white pine as intermediate in shade tolerance, i.e., less tolerant than balsam fir and the spruces, more so than red pine and jack pine. Site ratings, in terms of competing vegetation, for the capacity to regenerate white pine in the Great Lakes-St. Lawrence Region have been established by Logan and Brown (1956) as follows: easy (sparse heath, heath-grass and grass-herb types of lesser vegetation, usually on very dry and poor soil); moderately easy (dense heath or weak shrub-herb and herb types, usually on somewhat dry and poor soil); difficult (moderate shrub-herb and herb types, usually with fresh, rich soil); and very difficult (shrub-herb, shrub and herb types with strong development towards dense shrubs or hardwoods, usually with moist, rich soils).

The white pine weevil is the most serious insect pest of white pine. Larval feeding kills the leading shoot, resulting in crooked or multiple stems and associated losses in lumber volume and quality. Attacks are most damaging in young trees where the valuable first log is affected. The weevil prefers sunlight, and the thicker leaders that develop in that condition (Logan 1966; Sullivan 1961).

White pine blister rust is the most destructive disease of white pine. It is caused by a

fungus which infects the needles, and spreads to the twig, branch and finally the stem which it eventually girdles. Seedlings and saplings are killed rapidly, larger trees die more slowly. The disease is transmitted to the pine by spores from infected gooseberry and currant bushes (*Ribes* spp.) which are the alternate hosts necessary for completion of the pathogen's life cycle. The spores may be carried on air currents for at least a few kilometers (Anderson 1973). Blister rust, distributed throughout the range of white pine, has caused heavy losses, especially to regeneration, wherever *Ribes* spp. occur, e.g., particularly in hardwood stands. Canopy closure in plantations eventually suppresses the gooseberries and currants and infection rates decrease with stand age.

The foregoing synopsis has numerous implications for successful white pine silviculture that can now be described in broad terms. The preeminence of the species as a producer of quality lumber suggests the importance of growing a sufficient number of large, straight boles with clear wood as the ultimate crop. Besides growing the stand on a productive site, release from competition and thinning will promote best height and diameter growth. The main hindrance to straight stems is weevil damage which can be limited directly by chemical control of the insect or indirectly by growing the pine in the shade. (The latter, however, will result in some sacrifice of height growth — an example of compromise not uncommon in silviculture.) Clear wood cannot be produced in any reasonable rotation without artificial pruning. Maintaining a satisfactory stand density to ensure adequate numbers of crop trees for the final harvest (ca. 370/ha) will, in many situations, entail protection from blister rust through avoidance of high-hazard areas, pruning lower branches of crop trees, and removing infected individuals.

Such may be the desirable model for white pine silviculture, but application involves dealing with many complexities and exceptions that will be considered in some detail.

Site Implications

Performance of white pine on specific soils in Ontario, and the problems associated with establishing the species on them, have been noted by several authors (Scott 1958; Horton and Bedell 1960; Scott 1983). These accounts show clearly that increasing productivity of the site for pine tends to mean increasing productivity for other species as well, and consequently inducing a greater degree of competition. This trend reaches a maximum on richer, moister, heavier soils where excellent growth may occur if, through some successional accident such as an intense fire, the pine becomes established well ahead of the hardwoods that usually occupy such sites. However, these hardwoods soon become densely established as an understory, after which the cost of eventually regenerating the pine would be out of the question; these are the "very difficult" sites referred to earlier.

The manageable sites, in terms of other vegetation, range from deep, moist, wind-blown and ponded materials and till soils, on lower slopes, through dry and somewhat dry sand plains and terraces, to upper slopes and dry ridgetops representing shallow soils over bedrock. This range includes the "difficult" to "easy" sites. Another category, one that can be regenerated only by planting, comprises abandoned fields. These are generally fairly level and can be of almost any soil material. If they stand fallow for long they may be heavily invaded by brush and hardwoods, but often they support only a grass sod and meadow plants. A site-associated factor in old-field regeneration is the vulnerability of young white pine to attack by the weevil if there is any source of the insects in the vicinity. Since there is no possibility of protection by shade, the cost of direct control measures has to be considered.

An important aspect of site selection is the prevalence of blister rust infection, a matter influenced by local climate, the population of *Ribes* spp. and the structure of other vegetation. This is a complicated matter and appraisal by an experienced pathologist is recommended. If infection hazard is judged to be high, the sites in question are best avoided for growing white pine.

Regeneration

Crop establishment marks the start of the life cycle of the stand and is a good place to begin this account of silvicultural operations. Either the forester will rely on natural seedfall or he will plant. Occasionally he combines the two, but for convenience, discussion of naturally and artificially established stands are handled separately.

Site Preparation

Advance treatment of an area to facilitate stand establishment and growth may be necessary whether regeneration is to be achieved naturally or artificially. There are 2 main objectives, both of which may be accomplished by one operation to provide a suitable seedbed or plantable site and to limit vegetation that will compete with the young white pine.

In providing a suitable seedbed or plantable site, physical objects such as slash and brush must be cleaned away, and mineral soil must be exposed over at least 20% and preferably 40% or more of the area; on old field sites, furrows must be plowed. Numerous mechanical devices have been used successfully for white pine site preparation, and selection will depend on stand, slash, and soil conditions. This equipment, usually pulled or pushed by tractors or skidders, includes straight or V-blades, discs, scarifying teeth, tractor pads, spiked anchor chains, plows, rock rakes, finned barrels, and scalpers (Miller 1978; Scott 1983). Self-propelled equipment, e.g., flails and scarifiers, are less energy-intensive and new developments using this principle can be expected (Heikurinen 1975).

The role of seedbed preparation is mixing humus and soil, not creating deep disturbance that removes or buries the upper layers of mineral soil. Scraping of shallow soils over bedrock likewise defeats the purpose. If the site is to be planted it must be made negotiable and operable by the planters, whether they are using hand tools or machines.

Another technique for preparing sites, which is feasible in mature pine stands owing to thick, heat-resistant bark, is prescribed burning. This is effective in removing the duff layer. It also kills shrubs and small trees, but as they are not consumed they remain as obstacles. Burning should not be carried out after a partial cut, however, since the slash provides too hot a fire and crown scorch may cause excessive mortality in the residual pine (Van Wagner and Methven 1978). Slash burning on clearcuts, of course, is not so constrained.

Removing vegetation that will compete with the young white pine may be necessary even when its density is insufficient to impede planting operations. Removing competition before establishing the regeneration is easier, more economical and less damaging to the young pine than returning after several years and attempting to release it; necessary though that operation can be, on occasion, to deal with invading weed species.

Some of the aggressive, tolerant species found in the understory of white pine stands are balsam fir, red maple (*Acer rubrum* L.) and beaked hazel (*Corylus cornuta* Marsh.). In more open stands, clearcuts or burns, common competitors are cherries (*Prunus* spp.), aspen and white birch. Mechanical removal may be less permanent than other means, especially with suckering species (aspen, hazel) which proliferate rapidly after cutting or root disturbance. Such species may have to be treated with herbicides in a year or two; sometimes as a planned sequence (Miller 1978). Control with chemicals is especially valuable in its own right, since application can be made before the appearance of the pine seedlings that are vulnerable to them. Like fire, herbicides do not remove the vegetation they kill.

Prescribed burning effectively controls vegetation for several years. Balsam fir is killed by 1 fire; hardwood species require 2 fires in consecutive years for satisfactory results. In areas of heavy brush, burns should be carried out in spring before leaves flush, in a period of high hazard (Van Wagner and Methven 1978). Unpredictability of weather conditions suitable for burning is a drawback to reliance on fire. Suitable conditions may not occur for several years in a row.

Competition on old fields tends to be from meadow plants, grasses and sedges on a

sod base. Seedling establishment in regular rows is feasible and chemical treatment of the vegetation can be combined with the planting operation. Appropriate herbicides and specifications for their use in these situations are described by Campbell (1981) and Coons (1978). On drier sites, plowing furrows physically removes the competition and allows the seedlings to be planted in moister soil conditions (Staley 1970), although it provides future problems for machine access by wheeled vehicles.

Natural Regeneration

The application of traditional even-aged silvicultural systems to white pine, and their pros and cons, have been described in varying detail by a number of authors. Scott (1958), Horton and Bedell (1960), Smith (1962), Little *et al.* (1973), Lancaster and Leak (1978), Anon. (1981) and Scott (1983) are among the most recent, and the following descriptions have been taken from them. The merits of each system depend on both biological and economic factors, and hence no one system will be universally chosen. The following are most generally considered.

Shelterwood systems. These rely on the existing stand to provide both seed source and shelter for the regeneration. The overstory is removed in 2 or more cuts, starting fairly late in the rotation. This *preparatory cut*, if done, opens the stand to promote crown expansion and seed production; the subsequent *seed cut* provides space for seedling establishment; and, the *removal cut* harvests the remaining mature trees after the regeneration is well established. At least the last 2 cuts should be carried out in a good seed year. Site preparation includes the killing of understory species by fire or chemicals before the seed cut, or chemicals before the final removal cut. The logging operations should provide scarification of the forest floor, or mechanical site preparation may be used to produce a seedbed after the seed cut.

Variations of the shelterwood system include *uniform* as described above; *group*, in which patches are clearcut and subsequently enlarged as they become regenerated; and *strip* in which narrow parallel clearcuts are seeded by the residual stand, which also provides side shade. This last approach, using north-south strips in which the ratio of strip width to stand height is 0.66 to 1.00, has been found effective for control of the weevil to a height of 1 log-length, offers better control of light conditions than a partial canopy, and avoids problems of later overstory removal (Stiell and Berry 1985).

Shelterwood silviculture is well suited to white pine because this species tolerates shade and the trees are partly protected from the light-loving weevil. Shelterwood also inhibits competition by intolerants, gives a continuous seed supply, and diameter growth of the final crop trees is accelerated by the partial cuts. Amenity values are well preserved. Some disadvantages are higher logging costs, the potential for logging damage, and the need to sell the (usually smaller) material removed in the partial cuts. Nevertheless, most authorities consider shelterwood silviculture the preferred system for white pine, and it is employed in 50% of the districts in Ontario managing that species.

Clearcutting. This system relies on advance growth, planting, or seeding for regeneration. The second most commonly used system in Ontario, clearcutting usually implies a final harvest cut over a large area, or on wide strips, followed by artificial regeneration. It is used in overmature stands and other situations in which seed supply is insufficient or unreliable. Site preparation requires removal of heavy slash and treatment for sprouts and suckers if there were many hardwoods in the stand. Little if any marking is needed and logging costs are minimal. Dependence on young advance growth to establish the new stand is risky and exposure of seedlings to full sunlight subjects them to hazards of drying and weevil attack. Regeneration costs by artificial means are high, and amenity values depreciate. Clearcutting should be avoided in situations subject to erosion or likely to provide difficulties for regeneration.

Seed tree. With this method the harvest is removed in one cut, leaving 35 trees/ha or fewer

with good crowns, well distributed over the site, as seed bearers. This method is favored for extensive forestry practice. It approaches clearcutting, and offers similar advantages and disadvantages, while providing an adequate and continuing seed supply. There is a real risk of losing the entire seed source from fire or windthrow, however, and when regeneration is obtained some damage will be incurred if the seed trees are removed at a later date. Suitable conditions are shallow till soils and other dry sites. If the harvested stand was mixedwood, residual hardwoods may afford some protection against the weevil.

Artificial Regeneration

This procedure is necessary where a natural seed source is lacking, e.g., on large burns and clearcuts, in old fields, for regenerating overmature stands, and where stand conversion to white pine is desired. It is the only means of reproducing genetically improved material.

Seed source. Use of seed collected from stands adapted to local climatic conditions is important, and white pine shows such a pattern of broad adaptation (Yeatman 1976). In southern Ontario there may be some advantages to using seed from more easterly and southerly locations, e.g., in a 12-year-old trial, trees derived from sources in Pennsylvania, New York and Nova Scotia showed better growth than those from the local provenance (Zsuffa 1975). However, pending the results of such trials, it is safest to use seed from local sources, i.e., from within the same seed zones, such as have been delineated for Canadian provinces (Stiell 1976).

To facilitate seed supply from good quality stands, both Nova Scotia and Ontario have established white pine seed collection areas in which some trees are felled every good seed year and cones are collected from them. In addition, Ontario has identified a number of white pine seed production areas, "plus" stands that are upgraded by removal of the poorer individuals, and tended to promote seed production. Cones are collected by climbing and trees are not felled (Lamontagne 1979).

Direct seeding. Despite successful experiments and pilot trials of seeding white pine by different techniques (Graber and Thompson 1969; Horton and Wang 1969; Berry 1982), direct seeding of this species is not yet considered a reliable regeneration method, and does not appear to be used operationally by reforestation agencies. The erratic results obtained generally mean that the operation has to be repeated, and the cost advantage over planting is lost. Even if successful, seedling stocking is highly variable when broadcast methods are used. Since up to 10-15 seeds need to be sown for each anticipated seedling, seed supply is a constant problem.

Perhaps the underlying cause of seeding failure is the vulnerability of the seeds prior to germination and of the young seedlings during the first few years after germination, the very period when nursery conditions would be protecting and nurturing them (Stiell 1976). Conditions that seem to offer the best chance for successful white pine seeding include scarification to expose mineral soil over 20 to 50% of the site, using spot or furrow methods, covering the seed after sowing to a depth of about 65 mm, using seed treated with bird and small mammal repellents, and sowing in the fall to allow natural overwinter stratification (Horton and Wang 1969; Brown 1974).

Planting. The annual planting program for eastern white pine in Canada is currently ca 8.25 million trees, with 85% in Ontario, 12% in Quebec and 3% in the Maritimes (mostly in Nova Scotia).

Bare-root stock is most commonly planted in Ontario. Despite better survival and growth on all sites, white pine transplants (Mullin and Howard 1973) are now used mainly in more difficult situations in northern districts. Less expensive 3-0 seedlings are considered satisfactory for old field planting if they are well balanced and have a minimum height of 15 cm and root collar diameter at least 3.6 mm (Coons 1978).

Container stock requires good control of vegetation, and up to 700,000 white pine

seedlings grown in multipots are planted annually in Ontario, mainly on prepared spots where competition is removed.

Spring planting is generally preferred where logistics permit (Campbell 1977). Ten-year results of trials with both seedlings and transplants of white pine showed inferior survival of fall-planted stock (Mullin and Howard 1973). Attempts to extend the spring planting season into June for bare-root white pine have resulted in reduced survival and height growth (Mullin and Bunting 1977; Mullin 1978). Summer planting with container stock has been successful but should not extend beyond August, preferably July.

The spacing interval at which seedlings are planted markedly affects individual tree growth, rate of crown closure, timing of thinnings, and yield by type of product, and is a major factor in plantation establishment costs. Briefly, closer spacings give higher planting costs, and at a given age result in smaller crowns and DBH, and thinner branches, but greater volume per hectare.

A spacing of 1.8 x 1.8 m is common for white pine in Ontario, but at least 2.1 x 2.1 m would be desirable to promote diameter growth and allow removal of saleable products at the first thinning. Severe risk of weevil attack may indicate planting at 1.5 x 1.5 m or closer to allow sufficient trees to escape damage for at least 1 log-length. These trees must be released later, however.

Machine planting offers the advantages (over hand methods) of greater productivity and a solution to the shortage of suitable labor. Planting with tractor-drawn equipment that opens a continuous slit in the soil, closed by packing wheels after the seedlings have been inserted in it, works well on areas devoid of obstacles on or in the soil (slash, rocks and stumps) and are used on old-field sites. A furrow may precede the slit on dry sites to allow placing of roots in moister soil. Weed control with chemicals may be applied concurrently with planting, by means of spray equipment mounted on the machine. Up to 1,000 trees/hr can be machine-planted on old fields (Staley 1970; Coons 1978).

In forest conditions (cutovers and burns) other types of equipment are needed, but are limited to sites with slopes of 25% or less, a humus layer of less than 15 cm, and a soil depth greater than 90 cm (Cameron 1977). Machines are pulled by a bulldozer (75 to 100+ kW) with a front-mounted V-blade, crushing debris and clearing a narrow path for planting. Both continuous-slit and intermittent planting types are available, and are capable of planting rows not closer than 2.1 m apart. Maximum productivity is about 800 trees/hr (Erickson 1977).

Hand planting continues to be employed on the numerous sites that for various reasons are unsuitable for efficient operation of machines. Good crew training and organization are essential to an efficient planting operation, including delivery of stock to the site, field storage, supply to the planters and detailed plan of procedure.

Planting tools for old fields are shovels, used chiefly with wedge- or L-methods, or hoes or dibbles for small seedlings. Planting rates average 125 trees/hr. On forest sites L-planting with shovels is found efficient (Stevens 1970; Carlson 1977; LeClaire and Dunne 1977). A split-point, pedal-operated, hollow planting stick may be used for container stock.

Stand Tending

Release treatments. Site preparation often succeeds only in setting back competing vegetation and although this may be enough to give regeneration a sufficient head start, in other circumstances rapid hardwood regrowth requires later treatment to prevent excessive overtopping and whipping of the young pine. This cleaning treatment is complicated with white pine by the need to maintain a degree of shade that will discourage the weevil but not seriously inhibit height growth—perhaps 50 to 75% of full light would be satisfactory, and ensuring this may require a subsequent cleaning. In both old-field and forest-site plantations, hand tools and chemicals, including aerial application of the latter when competing vegetation provides a full leaf canopy over the susceptible pine, are used

to remove the heaviest competition from grass, brush and overtopping hardwood trees (Miller 1977; Struik 1978; Anon. 1981).

When the regeneration reaches a height of one log-length (about 5 m) the selection of final crop trees should be made on the basis of approximately 370 undamaged stems/ha. All efforts should thereafter be directed towards promoting growth of these individuals which at this time may be given almost full overhead release, and lateral release should be applied selectively to them to allow crown expansion.

Even at a much later stage, previously unmanaged stands can benefit greatly from improvement cutting. Pine mixedwoods, for example, comprising 80-year-old aspen and white birch with an understory of middle-aged pine, were treated by a commercial cut which removed the hardwoods. The pine responded with accelerated diameter increment and in 10 years produced up to 80% more growth in sawlog-sized material than that made in untreated stands (Stiell 1984). This type of operation, carried out with wheeled skidders, requires detailed planning and crew training and supervision to keep logging damage to the residual pine to a minimum.

Thinning. Thinning reduces the number of trees composing the main crop species. This is done to promote or maintain diameter growth of the remainder, and/or to provide a supply of wood.

Precommercial thinning. This treatment does not produce merchantable material, but is carried out in overstocked young stands to reduce mutual competition. This can be important in dense natural regeneration of white pine and close-spaced plantations experiencing sustained attack by the weevil. In these stands the trees that escape injury and deformation are mostly in the codominant or lower crown classes, and, unless released by thinning, will eventually succumb to intraspecific competition, leaving mostly larger, damaged trees (Stiell 1979).

Commercial thinnings. Commercial thinnings are made in merchantable stands to give an immediate financial return, forestall mortality and concentrate growth on the best remaining trees. The final crop trees should be selected and the large competing trees removed during the first cut. To reduce the stand density to the desired level, additional trees unlikely to survive to the next treatment, and poorly formed, damaged or diseased individuals should be removed as well.

Smithers (1954) proposed a regime of thinning natural red and white pine stands on medium quality sites at intervals from 5 years at age 30 to 15 years at age 85, for the purpose of increasing net basal area to about 43.5 m²/ha by the end of a 100-year rotation. Cuts should not reduce basal area below 70% of that of an untreated, fully stocked stand.

Regular thinning of plantations will accelerate diameter growth sufficiently to shorten the rotation significantly. For white pine plantations in Quebec, Castonguay (1979) developed thinning regimes based on site and spacing, from extrapolated yield data. He concluded that ideal spacings would vary between 2 x 2 m and 3 x 3 m, and optimum rotations would vary between 55 and 58 years for best financial returns. For these spacings he recommended 3 thinnings for Site Class I, 2 for Site Class II and 1 for Site Class III.

Pruning. Removal of branches by artificial means is necessary if clear wood is to be formed on the bole. Pruning should be applied to crop trees and will add greatly to the value of the lumber ultimately sawn from them. Meanwhile, this additional investment cost once again dictates the importance of maintaining the growth rate of those trees. Pruning is usually carried out to a height of 1 log-length and can be accomplished in 1 operation if the tree is at least 10 m tall, or it can be done in 2 stages, starting when the tree is smaller. A 3.7-m polesaw is efficient for pruning the whole log if the stand is not too dense.

Even natural stands of middle age or older offer excellent prospects for economic returns from pruning if the operation is coordinated with thinning to stimulate diameter growth (Calvert and Brace 1969). Pruning in these stands is feasible since fewer dead branches and stubs are present on the lower bole. In these circumstances late-winter pruning on snowshoes can simplify the job (Murray 1977).

Fertilization. Fertilization to promote growth of white pine is not practised except in nurseries. The relatively low nutrient requirements of the species, which permit it to perform well on sandy soils of moderate-to-low fertility, perhaps accounts for the lack of interest in the subject. In natural stands having a mixture of tree species and more ground vegetation, fertilization may stimulate the growth of the non-pine components. Crop trees cannot be stimulated individually by fertilizers as well as they can by above-ground release (Stiell 1970).

On the other hand, plantations established on poorer outwash sands, for example, would no doubt respond to perhaps 335 kg/ha of nitrogen. Application should be after the canopy has closed and shaded out understory species. More critical from a nutritional standpoint may be old-field sites if their fertility has been depleted by long periods of farming without fertilization. Such cases have been reported for white pine plantations in New York State where both potassium and magnesium deficiencies were corrected with applications of potassium chloride and magnesium sulphate, respectively (Heiberg and White 1951; Stone 1953). Similar conditions were identified, and similarly treated, in white pine planted on abandoned farmland in the St. Lawrence River lowlands of Quebec (Lafond 1958). In these instances obvious foliar symptoms and stunted growth gave clues to the problem. Determination of soil nutrient status *before* planting is obviously important. The character of the ground vegetation may be indicative, but if there is any doubt, soil scientists should be asked to make a chemical analysis.

A different use of fertilizers is for the purpose of promoting flower production. Ammonium nitrate applied at 59 kg/ha to young white pine significantly increased the number of female flowers in 1 trial (Stephens 1964), but the matter is not yet well understood and results may be unpredictable.

Pest Management.

The two most damaging insect and disease pests affecting white pine are dealt with here. These are the white pine weevil and white pine blister rust.

White pine weevil. Control efforts are worthwhile if one considers that weevil-caused losses in volume for sawlog sizes can range from 22 to 63%, and associated reductions in lumber values average 25%, owing to lowered grades (Brace 1972).

Indirect methods using side and overhead shade and close spacing have been discussed under "Shelterwood systems" and "Release treatments." Direct methods are more expensive, often involving repeated applications of insecticide. Trees up to 3.65 m tall can be sprayed with ground equipment, using methoxychlor, in spring, or the infested leaders can be removed with pole clippers and burnt each summer; all top-whorl laterals but one (to form the new leader) have to be clipped also. Taller trees require aerial spraying with methoxychlor until the trees reach the desired height. Aerial spraying cannot be guaranteed to protect every crop tree, owing to imperfect coverage of the leaders (DeBoo 1978), but improved technology for delivery of the spray mixture in small droplets holds promise (de Groot 1985). Another approach is to trap the adult weevils in spring before they lay eggs by using sections of pine bark soaked in turpentine and then to destroy them (Scott 1983).

White pine blister rust. Local climate, topography, vegetation and the presence of water bodies influence spore production and dispersal, resulting in areas of varying prevalence of infection, and such blister rust hazard zones have been mapped in the Lake States (Anderson 1973). Avoidance of high hazard areas for white pine management is a practical measure. This approach is being carried out in Quebec where 2 low-hazard zones suitable for growing white pine have been delineated (Lavallée 1974). In Ontario 4 hazard zones have been established (low, intermediate, high and severe), with little blister rust control required in the first 2 (Gross 1985).

Direct control methods include removing infected trees in the course of other stand-tending operations, endeavoring to maintain a sufficiently closed canopy to shade

out the alternate host plants (*Ribes* spp.), and pruning branches close to the ground where they are most vulnerable to infection, as well as removing all branches already infected when feasible on small trees (Hiratsuka and Powell 1976). Another method, formerly used on a wide scale, and still considered practical near tree nurseries (Gross 1985), is the wholesale removal of *Ribes* spp. in areas where they are abundant. Results often were disappointing, in part because of underestimates of the distance that wind-borne viable spores of the rust fungus could travel (Anderson 1973). Banning of 2,4,5-T has increased the cost of eradicating *Ribes* spp. (Scott 1983).

A promising approach, now being pursued in Ontario and Quebec, is the crossing of eastern white pine with Himalayan white pine (*P. griffithii* McClelland), which has produced vigorous hybrids with a considerable degree of rust resistance and hardiness, in southern and central Ontario at least; a clonal orchard of this material has been established at Midhurst, Ontario (Corriveau 1979; Zsuffa 1979).

Rotation Age

One criterion for rotation length is the age at which the mean annual increment of sawtimber volume culminates. For naturally established stands this was estimated by McCormack (1956) to be 80, 110, 120 and 130 years for his site groups I, II, III and IV, respectively.

Castonguay (1979), following an analysis based on site, spacing, extrapolated yield data, establishment costs and stumpage values, recommended rotations of 55 to 58 years for spacing varying from 2 x 2 m to 3 x 3 m for white pine plantations in Quebec.

Another definition of rotation age is the time taken to grow a pole or sawlog of specific dimensions (the technical rotation). This period is obviously longer in unmanaged stands than where diameter growth has been stimulated by intermediate cuts. Smithers (1954) assumed a minimum crop tree DBH of 30.5 cm for white pine, which in treated stands could be attained at age 100, or in unmanaged stands at age 120. Technical rotations adopted in Ontario range from 100 to 140 years, aiming at dimensions from a 12.2 m merchantable bole with a 15.2 cm top to a 14.6 m bole with a 25.4 cm top (Anon. 1981). Harvesting at much greater age is liable to be constrained by stem decay, which results in a pathological rotation for white pine in Ontario of 160 to 170 years (White 1953).

The shortest rotations are achieved in intensively treated plantations. The uniform spacing of these stands, coupled with the periodic release of crop trees, produces boles of a given size even sooner than in managed natural stands. Likewise, the merchantable yields attained are greater in these plantations.

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SECURING THE FUTURE OF WHITE PINE IN ONTARIO

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Abstract

The demand for white pine (*Pinus strobus* L.) lumber is expected to remain at the current level. Regeneration is not replacing white pine at the rate at which it is being depleted. Control of competing vegetation by prescribed fire or chemical means, and the rapid establishment of new stands of white pine, are the key factors in forest regeneration. A commitment to the continuation of white pine as a commercially valuable tree species and an increase in funding are necessary to ensure that a future supply is available to meet the anticipated demand.

The future of white pine as a commercially valuable tree species in Ontario is unclear. However, the demand for white pine in the past has been consistent with the harvested volume, averaging 500,000 m³ per year since the late 1960s.

White pine is an easily worked wood which is light, relatively strong and dimensionally stable. These characteristics, which have made it a popular tree for almost 200 years, continue to make white pine important commercially. The demand for white pine, therefore, should continue relatively unabated in the future.

The white pine that has been harvested to the present has come almost exclusively from natural stands. Most of the old-growth, overmature stands of white pine, which were once so abundant in Ontario, have disappeared. There are still significant remnants of these stands stretching from the Lake Temagami area through to the Lake Superior shoreline but they are greatly reduced from the huge pine forests that supplied, at peak production, more than 800 million board feet of white pine lumber between 1908 and 1911. The average annual production during those years equalled approximately 3 times our current average annual production and only the biggest and the best trees were used.

In recent years, second-growth stands have supplied most of the volume. These stands originated 80-100 years ago after harvesting of the old-growth stands. This harvesting was often followed by the fires that characterized the heyday of pine logging in Ontario.

Another source of current supply has been from mixed stands in which white pine is only a small component. Most of the highest-quality, largest-diameter logs have come from white pine trees growing in what are predominantly hardwood stands.

Most of our future supply can be expected to be provided by existing pine stands. In this regard, the basic concepts of white pine silviculture are provided by Horton and Bedell (1960) and, more recently, Scott (1983). Where pine is being managed on a shelterwood system, part of the existing stand is retained after harvest to provide seed and shelter. Eventually a crop of white pine seedlings will replace the current stand that is being removed incrementally. To date, the success of establishing regeneration in these stands has been far from complete. Seed must be deposited on a suitable seedbed before tall-shrub and shade-tolerant tree species become established. On dry sites, such as the deep, coarse-textured Petawawa sands, the establishment of competing vegetation is delayed and the degree of competition is fairly weak. White pine, which can germinate and develop under these low-moisture conditions, often becomes established.

On fresh-to-moist sites, however, the establishment and development of competing vegetation are much more rapid. Under these conditions pine regeneration from natural seeding seldom occurs. The pine forests that currently occupy fresh-to-moist sites are usually pioneer stages in the succession following fire. The fires eliminate much of the competition and delays reestablishment of competing species by temporarily desiccating the site, thus allowing the growth of white pine.

In order to have these fresh-to-moist sites produce a continuous supply of pine in the future, treatments must be applied which reduce competition, and delay its redevelop-

ment, on a much larger scale than is currently done. There are numerous examples of prescribed fire being used for this purpose on the grounds of the Petawawa National Forestry Institute. Chemical site preparation can accomplish the same results as fire in terms of reduction and control of competition.

Following the treatment of competing vegetation, pine must be established on the site quickly through natural seeding, direct seeding or planting.

Each year many areas are cut and planted, but the seedlings are lost through competition. Other areas are merely cut, and these revert directly to hardwood. The commitment and the required funding to carry out the necessary silvicultural treatments to ensure white pine regeneration are still inadequate.

To this point, the discussion has dealt with forest stands consisting primarily of white pine. However, white pine is often found in stands that are predominantly hardwood, usually either poplar or tolerant hardwoods such as maple or beech. In this situation the objective of management usually has been to perpetuate the pine component. This is often attempted by leaving residual seed trees and sometimes by supplementary site preparation. The expenditures to maintain pine under these conditions have been relatively low, but unfortunately the successes are proportionately low. The supply of pine in mixed stands is being removed much faster than it is being replaced, and it will be a less and less important portion of the harvest in the future.

Another source of future supplies of white pine is the plantations that are being established at an increasing rate. For many years white pine had fallen into disfavor with foresters as a species for plantation establishment. The 2 major pests, white pine weevil (*Pissodes strobi* (Peck)) and white pine blister rust (*Cronartium rubicola* J.C. Fisch.), have caused many to consider white pine an undesirable species for planting. Only recently more intensive silvicultural management has overcome these 2 problems to some degree.

In 1978, 2.4 million white pine seedlings were produced by Ontario nurseries. By 1983 this had increased to 7.6 million. This year, 1984, white pine bare-root seedling production will reach 8 million, one tenth of the total bare-root nursery stock production for the province. Container stock production of white pine is now under way as well, providing the forest manager with another option that may have advantages in particular situations.

The commercial value of white pine provides an incentive to managers to establish more white pine plantations. This will brighten the future supply picture. The increased availability of blister rust-resistant hybrids and the improvement of plantation management techniques to reduce the seriousness of weevil damage should provide further incentive.

These are some of my views of the future of white pine in Ontario. In plantation establishment we are gaining and will probably continue to gain. In hardwood stands with a pine component we are losing and will probably continue to lose. This brings us, finally, back to the existing pine forest. We are working at maintaining the productivity in these areas, winning some, losing others. With a commitment of effort and resources such as has been made to other commercially important species in the past, white pine will continue to contribute to the economy of the province of Ontario.

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