

Current status of invasive alien birch-leafmining sawflies (Hymenoptera: Tenthredinidae) in Canada, with keys to species

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Abstract—In the 20th century, five species of birch-leafmining sawflies were inadvertently introduced from Europe to North America: *Heterarthrus nemoratus* (Fallén), *Fenusa pumila* Leach, *Profenusa thomsoni* (Konow), *Fenusella nana* (Klug), and *Scolioneura vicina* Konow. All have been recorded at outbreak levels in North America, and three (*F. pumila*, *P. thomsoni*, and *H. nemoratus*) have been the targets of successful biological control programs. The most recently detected species, *F. nana* and *S. vicina*, are good candidates for future biological control in Canada. We review the biology of all five of these birch-leafmining sawflies in North America and present keys to adults, larvae, and mines to aid correct identification.

Résumé—Au cours du dernier siècle, cinq espèces de tenthrèdes mineuses du bouleau ont été introduites involontairement d'Europe en Amérique du Nord: *Heterarthrus nemoratus* (Fallén), *Fenusa pumila* Leach, *Profenusa thomsoni* (Konow), *Fenusella nana* (Klug) et *Scolioneura vicina* Konow. Elles ont toutes été rapportées à des niveaux épidémiques en Amérique du Nord et trois de ces espèces (*F. pumila*, *P. thomsoni* et *H. nemoratus*) ont fait l'objet de programmes de contrôle biologique réussis. Les deux espèces détectées plus récemment, *F. nana* et *S. vicina*, constituent de bonnes candidates pour un éventuel contrôle biologique au Canada. Nous révisons la biologie de cinq espèces de tenthrèdes mineuses du bouleau en Amérique du Nord et présentons des clés pour faciliter l'identification des adultes, des larves et des mines.

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Introduction

Exotic leafmining sawflies (Hymenoptera: Tenthredinidae) on birches, *Betula* L. (Betulaceae), have become widely distributed in Canada since their introduction to eastern North America in the 20th century (Digweed *et al.* 1997). The amber-marked birch leafminer, *Profenusa thomsoni* (Konow), the birch leafminer, *Fenusa pumila* Leach, and the late birch leaf edgeminer, *Heterarthrus nemoratus* (Fallén), all occur across Canada, whereas the early birch leaf edgeminer, *Fenusella nana* (Klug), and *Scolioneura vicina* Konow have been previously reported only from eastern Canada (Lindquist and Thomson 1970; Nystrom and Evans 1989; Digweed *et al.* 1997). When these sawflies are abundant, feeding damage on birch leaves is unsightly and decreases the aesthetic value of urban birch trees, which leads to public concern. Repeated severe defoliation reduces birch growth (Peirson and Brower 1936) and contributes to the decline of ornamental birch trees in the urban landscape (Hoch *et al.* 2000). Application of pesticides to control these insects is expensive and can have undesirable side effects in the urban forest.

At present, information about the identification and biology of these sawflies is fragmented among numerous publications and some has never been published. As a result, North American outbreaks of insects called birch leafminers have sometimes been attributed to incorrect species. For example, *P. thomsoni* was, for several years, confused (and briefly synonymized) with a co-occurring leafminer on oak, *Profenusa alumna* (MacGillivray) (Lindquist 1959; Watson 1959; Smith 1971). Similarly, extensive leafmining damage on birch in Anchorage, Alaska (AK), United States of America (USA), was attributed to *F. pumila* (Matthews *et al.* 1997) until more detailed study during 2002 revealed that the most damaging species was *P. thomsoni* (Wittwer *et al.* 2003).

Little is known about the current distributions of these sawflies in Canada. The most recent information is from Alberta (AB) (Digweed *et al.* 1997), Northwest Territories (NT), and Yukon Territory (YT) (Digweed and Langor 2004). Published distributions for eastern Canada date from the 1970s and 1980s (Lindquist and Thomson 1970; Quednau 1984; Nystrom and Evans 1989). Determination of current distributions is a prerequisite for assessing future needs for management of these species.

Fenusa pumila and *P. thomsoni* have been the subjects of life-table studies in Europe

(*e.g.*, Eichorn and Pschorn-Walcher 1973) and North America (*e.g.*, Cheng and LeRoux 1965, 1969; Digweed *et al.* 1997; Digweed 1998). These species, along with the less studied *H. nemoratus*, have been the targets of successful biological control programs in North America (Dowden 1941; Fuester *et al.* 1984; Quednau 1984; van Driesche *et al.* 1997; Langor *et al.* 2002). *Fenusella nana* and *S. vicina* are more recent introductions, are less well known in both Europe and North America, and have not yet been subjected to biological control efforts.

In this article we review information about the biology, natural enemies, hosts, and Canadian distributions of birch-leafmining sawflies and provide keys to adults, larvae, and mines. We then summarize the current literature for each species.

General biology

Leafmining sawflies on birches have similar life histories. They overwinter either as a prepupa in a translucent brown, soil-encrusted underground cocoon or as a pupa in a lens-shaped hibernaculum within the mine. The following summer, adults emerge and mate (although in North America, males occur only in *F. pumila* and *S. vicina*), and the females use their sawlike ovipositor to lay eggs within birch leaves. Oviposition behaviour is diagnostic for some species: *F. nana*, *H. nemoratus*, and *S. vicina* lay their eggs at the leaf margin and *F. pumila* oviposits only in young leaves on new long shoots. The larvae are prognathous and bear diagnostic melanized sclerites. They feed on leaf tissue between the epidermal layers, forming blotch mines that coalesce under crowded conditions. There are five or six larval instars, the last of which is hypognathous, nonfeeding, and free of melanized sclerites. In the tribe Fenusini (which includes the genera *Fenusa* Leach, *Fenusella* Enslin, *Profenusa* MacGillivray, and *Scolioneura* Konow), final-instar larvae pierce the mine wall and drop to the ground, where they burrow into the soil and construct soil cocoons. In the tribe Heterarthrini (which includes the genus *Heterarthrus* Stephens), final-instar larvae do not exit the leaf but instead construct a cocoon within the mine. Most species are univoltine, but *F. pumila* has up to four generations per year (Friend 1933; Cheng and LeRoux 1965; Eichorn and Pschorn-Walcher 1973; Digweed *et al.* 1997), and *S. vicina* appears to be the spring-feeding member of a species complex that

includes the later occurring *Scolioneura betuleti* (Klug) (Altenhofer and Taeger 1998; but see MacQuarrie *et al.* 2007).

Host plants

Twenty-four species of *Betula* and 6 species in five other genera (*Alnus* Mill. (Betulaceae), *Corylus* L. and *Ostrya* Scop. (Corylaceae), *Ame-lanchier* Medik. (Rosaceae), and *Populus* L. (Salicaceae)) have been recorded as hosts of birch-leafmining sawflies (Table 1). Some species of Palearctic birches have been introduced to North America as ornamentals (*e.g.*, *B. pendula* Roth), and for these species we include host records from both the Palearctic and Nearctic Regions. In the Nearctic Region, 10 of the 13 native species of *Betula* have been recorded as hosts.

Natural enemies

Sixty-three parasitoid species have been recorded attacking birch-leafmining sawflies in Europe and North America (Table 2). Each species in the Fenusini and Heterarthrini has a characteristic Hymenoptera parasitoid fauna that consists of one to three species of host-taxon-specific koinobiont ichneumonoids and a suite of idiobionts that attack various hosts in leaf mines or at a particular life stage (Pschorn-Walcher and Altenhofer 1989). The host-taxon-specific ichneumonoids attacking Fenusini are endoparasitoids from the genus *Lathrolestes* Förster (Ichneumonidae: Ctenopelmatinae), ectoparasitoids from the genus *Grypocentrus* Ruthe (Ichneumonidae: Tryphoninae), and the endoparasitic species *Pseudichneutes levis* (Wesmael) (Braconidae: Ichneutinae) (Table 2). Host-taxon-specific parasitoids of the Heterarthrini are species of *Dolophron* Förster or *Olesicampe* Förster (Ichneumonidae: Campopleginae), although *H. nemoratus* is also attacked by *Mesoleius phyllotomae* Cushman (Ichneumonidae: Ctenopelmatinae) (Table 2) (Dowden 1941; Pschorn-Walcher and Altenhofer 1989).

The idiobiont parasitoid complex is shared among the Fenusini and Heterarthrini, and comprises species from the Eulophidae (Chalcidoidea), Hormiinae (Ichneumonoidea: Braconidae), and Pimplinae (Ichneumonidae) (Table 2). These parasitoids attack insects from a variety of orders on a variety of host plants, specializing on those with a leafmining habit (Eulophidae and Hormiinae) or on a particular host life stage (Pimplinae) (Pschorn-Walcher and Altenhofer 1989).

Materials and methods

Distribution maps were drawn using occurrence records from field surveys and data on museum specimen labels. National surveys were conducted during the period 2003–2006, but earlier data from Alberta (for 1992–1994) and Quebec (QC) (1984–2004) are also included. Leafminer species were distinguished in the field by examining characteristics of mine shape or markings on larvae or their cast skins. When species could not be identified in the field, mines were collected and later examined microscopically. Most surveys were conducted in late summer, when larval development was complete and mines were well developed. Surveys encompassed native birch species in natural settings as well as cultivars of native and introduced birches in urban settings. Voucher specimens of larvae of all species are deposited in the arthropod museum at the Northern Forestry Centre, Edmonton AB, Canada (NFRC).

Museum specimens were examined to improve the resolution of species distributions in eastern Canada where less surveying was done (*i.e.*, Ontario (ON), New Brunswick (NB), Nova Scotia (NS), Prince Edward Island (PE), QC, and Newfoundland and Labrador (NL)). All specimens except those from the Canadian National Collection of Insects, Arachnids, and Nematodes were examined by S.C.D. to confirm identity. Museum specimens were collected during the period 1913–1996, with more than half of all collection events (141 of 222) occurring between 1950 and 1989. Specimens from the following Canadian collections were examined:

- ACNS Atlantic Food and Horticulture Research Centre, Agriculture and Agri-Food Canada, Kentville, Nova Scotia
- CNC Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario
- DEBU University of Guelph Entomology Collection, Guelph, Ontario
- FRLC Atlantic Forestry Centre, Canadian Forest Service, Fredericton, New Brunswick
- LEMQ Lyman Entomological Museum, McGill University, Montréal, Quebec
- MUNC Memorial University of Newfoundland, St. John's, Newfoundland and Labrador
- NSMC Nova Scotia Museum of Natural History, Halifax, Nova Scotia

The complete survey and museum specimen database is available from C.J.K.M.

Keys to species of leafmining sawflies and their damage on birch

Adults

Nearctic Heterarthrinae can be identified to genus using the keys of Goulet (1992) and to species (excluding *Scolioneura* spp.) using the keys of Smith (1971). *Heterarthrus betulae* Togashi and *S. betuleti*, the only birch-leafmining sawflies not known to occur in North America, are included in our key to assist their early detection should they be introduced. The key also includes *Fenusa dohrnii* (Tischbein) because it attacks alders, *Alnus* spp., which often co-occur with birches, and adult *F. dohrnii* are thus sometimes collected while sampling for birch-leafmining sawflies. We have not included other leafmining sawflies that are occasionally confused with those attacking birches, especially *Fenusa ulmi* Sundevall, which attacks elms, *Ulmus* L. (Ulmaceae), and *P. alumna*, which attacks oaks, *Quercus* L. (Fagaceae); the keys of Smith (1971) distinguish these. Our terminology follows Goulet (1992).

Before this key is used, the keys of Goulet (1992) should be consulted to ensure that the specimen is a tenthredinid sawfly in the subfamily Heterarthrinae.

- 1 Forewing with veins 2A and 3A complete (Fig. 1a); face and body with pale markings (Figs. 1b, 1c); body up to 8 mm in length; females only (males unknown) 2
- 1' Forewing with veins 2A and 3A usually incomplete (Fig. 2a); face and body uniformly brown or black; body <6 mm in length; males known for some species 3
- 2(1) Pronotum pale yellow laterally (Fig. 1c) *Heterarthrus nemoratus* (Fallén)
- 2' Pronotum entirely black; not yet recorded from North America (Japan only)
. *Heterarthrus betulae* Togashi
- 3(1') Occipital carina present (Fig. 3a); sixth antennal flagellomere 3 times longer than wide (Fig. 3b) 4
- 3' Occipital carina absent (Fig. 2b); sixth antennal flagellomere at most 1–2 times longer than wide (Fig. 2e) 5
- 4(3) Flying in spring and early summer (May or June) *Scolioneura vicina* Konow
- 4' Flying in late summer and autumn (July or August); not yet recorded from North America
. *Scolioneura betuleti* (Klug)
- 5(3') Hind wing with cell R1 closed or nearly so, anal cell closed and with vein at apex (Fig. 3d); tegula white; females black; males mostly yellow and very rare, known only from United Kingdom
. *Fenusella nana* (Klug)
- 5' Hind wing with cell R1 open, anal cell open (Fig. 4b) or closed and with vein at apex; tegula black; females and males (if known) black. 6
- 6(5') First metasomal tergum with curved posterior margin, wide submedially (Fig. 4d); forewing with vein 3A not connecting to vein 1A (Fig. 4a); median lobe of mesoscutum with lateral hairs (Fig. 4c); females only; ovipositor lancet robust and wide, dark orange, with obvious arches connecting teeth (Fig. 4e) *Profenusa thomsoni* (Konow)
- 6' First metasomal tergum with nearly straight posterior margin, narrow submedially (Fig. 2c); forewing with vein 3A connecting to vein 1A to form a closed or nearly closed cell (Fig. 2a); median lobe of mesoscutum hairless or nearly so (Fig. 2d); males known (for some species); ovipositor lancet relatively smaller and finer, pale orange to yellow, without arches connecting teeth (Fig. 2f). 7
- 7(6') Antennae longer than mesosoma, with first flagellomere 1.5 times as long as second, and second and third flagellomeres at least 2 times as long as broad (Fig. 3c); hind tibia dark brown or black; females only; larvae on *Alnus* *Fenusa dohrnii* (Tischbein)
- 7' Antennae shorter than mesosoma, with first flagellomere 2 times as long as second, and second and third flagellomeres less than 2 times as long as broad (Fig. 2e); hind tibia light brown, yellow, or white; males and females; larvae on *Betula* *Fenusa pumila* Leach

Larvae

Keys to North American genera and species of larvae in the Fenusini (except those of *Scolioneura* spp.) and Heterarthrini were published by Smith (1971). A key to larvae of leafmining sawflies on birches provided by Lindquist (1959) was later supplemented to include *F. nana* and *S. vicina* (Lindquist and Thomson 1970;

Nystrom and Evans 1989). Larvae of *H. betulae* are not included in our key (below) because they have not been described (Togashi 1992). Our key can be used to identify larvae other than those in the first instar and the last (nonfeeding) instar. It can also be used with cast larval skins recovered from empty mines.

The key does not distinguish larvae of birch-leafmining sawflies from those of native leafminers from other insect orders (*e.g.*, Lepidoptera). If necessary, an appropriate general key should be consulted (*e.g.*, Chu and Cutkomp 1992; Rose and Lindquist 1997).

- 1 Thoracic legs clearly multisegmented, segments often sclerotized and pigmented, giving legs a striped appearance (Fig. 5c); a pair of C-shaped dark sclerites present on each abdominal sternum (Fig. 5c) . . . 2
- 1' Thoracic legs short, peg-like or cone-like, not well sclerotized or pigmented (Figs. 6d, 6e); abdominal sterna without paired dark sclerites (Fig. 6b) . . . 4
- 2(1) Small dark lateral spots on each abdominal segment (Figs. 5b, 5c); pale goblet-shaped pattern dorsally on head (Fig. 5a) . . . 3
- 2' Lateral spots absent from abdominal segments (except spiracles) (Figs. 5e, 5f); no goblet-shaped pattern dorsally on head (Fig. 5d) . . . *Fenusella nana* (Klug)
- 3(2) Feeding in spring and early summer (June or July); found on *Betula* only. . . *Scolioneura vicina* Konow
- 3' Feeding in late summer and autumn (August through October); found on *Betula* and some *Alnus*; not yet recorded from North America. . . *Scolioneura betuleti* (Klug)
- 4(1) In ventral view, thorax and first abdominal segment with darkly pigmented median stripe (Fig. 6b); thoracic legs with claws (Fig. 6f) . . . *Fenusa pumila* Leach
- 4' In ventral view, prothorax with a pigmented sclerite; meso- and meta-thorax each with a small central dark spot (Figs. 6d, 6e); thoracic legs without claws . . . 5
- 5(4') Larval body obviously broadened at thorax in ventral view (Fig. 6a); ventral prothoracic sclerite distinctly hourglass-shaped with semicircular invaginations around each prothoracic leg (Fig. 6e); meso- and meta-thoracic ventral dark spots usually faint (Fig. 6e) . . . *Heterarthrus nemoratus* (Fallén)
- 5' Larval body not broadened at thorax (Fig. 6c); ventral prothoracic sclerite with subquadrate invaginations with spurs extending laterally (Fig. 6d); meso- and meta-thoracic ventral dark spots usually more prominent (Fig. 6d) . . . *Profenusa thomsoni* (Konow)

Mines

This key is provided as a guide and should be used with caution because several species of native leafmining Lepidoptera on birches construct mines similar to those of birch-leafmining sawflies (*e.g.*, Rose and Lindquist 1997, p. 85). With experience, blotch mines of lepidopterous leafminers can be distinguished from those of birch-leafmining sawflies, using characteristics of the frass (generally fine or threadlike in lepidopterous mines) and mine wall (*e.g.*, thicker with a central dark spot or very thin, papery, and translucent in lepidopterous mines).

Ours is the first published key to mines of birch-leafmining sawflies, but several authors have described differences among them (*e.g.*, Nystrom and Evans 1989). We use these and our own observations of mines in *Betula papyrifera* Marsh. in the key. Note that some qualities such as thickness of the mine wall may vary among birch species.

- 1 Mine originating at leaf edge (location of egg not always obvious, but mine appears to begin at leaf edge and progress inward) . . . 2
- 1' Mine originating on leaf lamina, often along or near a major lateral vein; location of egg often obvious after hatching (as a darker puckered spot on mine wall or a small translucent egg-shaped blister) (Figs. 7c, 7d) . . . 5
- 2(1) Mine reddish brown, darker centrally at leaf edge and lightening as mine grows (Fig. 7a); mine wall relatively thick and not easily torn; mine often large when mature, covering most of leaf and containing a large larva or a round, lens-shaped larval hibernaculum (Fig. 7b) . . . *Heterarthrus nemoratus* (Fallén)
- 2' Mine not obviously reddish brown, usually uniform in colour throughout; mine wall not obviously thick and therefore more easily pierced; mine not usually so large, and not containing a larval hibernaculum . . . 3
- 3(2') Mine origin a short serpentine tunnel expanding medially on leaf into a blotch mine (Fig. 7e) . . . *Fenusella nana* (Klug)
- 3' Short serpentine tunnel absent; mine origin on leaf edge expands directly into a blotch mine (Fig. 7f) . . . 4

- 4(3') Mine occupied during spring and early summer (June or July); found on *Betula* spp. only *Scolioneura vicina* Konow
- 4' Mine occupied during late summer and autumn (August through October); found on *Betula* and *Alnus*; not yet recorded from North America *Scolioneura betuleti* (Klug)
- 5(1') Mines on new, expanding, long-shoot leaves at top or periphery of crown; old mined leaves often curled and dried; location of egg in the developing blotch mine evident as a darkened area along a major lateral vein (Fig. 7c). *Fenusia pumila* Leach
- 5' Mines not restricted to new long-shoot leaves; more typically on mature leaves on long or short shoots, often more numerous in lower, shaded portion of crown; old mined leaves rarely curled; location of egg in developing blotch mine evident as a small, deflated blister on upper leaf surface, often near a major lateral vein (Fig. 7d) *Profenusia thomsoni* (Konow)

***Heterarthrus nemoratus* (Fallén): late birch leaf edgeminer**

Taxonomy

Of the 20 valid species in the genus *Heterarthrus*, only *H. nemoratus* has been recorded from North America (Smith 1971; Taeger and Blank 2006). The only other birch-leafmining *Heterarthrus* species, *H. betulae*, is known only from Japan (Togashi 1992).

Introduction, distribution, and abundance

Heterarthrus nemoratus is native throughout much of the Palearctic Region from Europe to Siberia (Viramo 1969; Zhelokhovtsev 1994). It has not been recorded at outbreak levels in its native range. In North America this species was first recorded from NS: Dowden (1941) reported a 1905 record ("in Nova Scotia"), Smith (1971) reported a 1908 record from Pictou NS, and there is a specimen in CNC from Bridgetown NS collected 8 July 1913. From 1926 to 1933, *H. nemoratus* caused severe browning of birch in Maine (ME) and other parts of the northeastern USA (Dowden 1941). Museum specimens show that it was present in NB and QC by the late 1920s and throughout ON by the 1950s. Drouin and Wong (1984) found it abundantly in Edmonton AB in the 1970s, and in 2003, Digweed and Langor (2004) found it in Yellowknife and Hay River NT and Snyder *et al.* (2007) reported it from Anchorage AK.

Our surveys, combined with museum-specimen data, show that *H. nemoratus* occurs across Canada (Fig. 8). It is usually rare (*e.g.*, Digweed *et al.* 1997) but occasionally it is the most abundant birch-leafmining sawfly locally (*e.g.*, Deschambeault Lake SK and Avola BC during 2005). We observed a localized outbreak of *H. nemoratus* in Swan Hills AB in 2006 in which more than 90% of leaves on some urban birches bore *H. nemoratus* mines.

Life cycle and biology

Heterarthrus nemoratus overwinters in a parchment-like hibernaculum within the mined leaf (Fig. 7b). Peirson (1929) suggested that pupation occurs from May through July, with adults emerging 9 days later (Dowden 1941). In AB, however, pupation occurs in the autumn (C.J.K.M., personal observation). Emergence from hibernacula peaks during early June in Anchorage AK (Snyder *et al.* 2007), late June in ME (Dowden 1941) and Prince George BC, and early July in Yellowknife and Hay River NT (S.C.D., personal observation). All adults are parthenogenetic females that lay their eggs at the leaf margin between the upper and lower leaf surfaces. Larvae develop slowly, taking 5–10 weeks in ME (Dowden 1941) and probably longer farther north (we found many mines in AB and AK in early September that contained feeding larvae in all developmental stages). This species exhibits a behaviour unique among the birch-leafmining sawflies: it makes a small slit in the edge of the leaf through which it ejects frass and shed larval skins from the mine (Peirson 1929).

The biology of *H. nemoratus* has been little studied beyond basic life history, which was investigated in eastern North America by Peirson (1929). Phenological information was reported from AB by Drouin and Wong (1984) and from AK by Snyder *et al.* (2007).

Mortality, natural enemies, and biological control

In Europe, *H. nemoratus* hosts a typical Heterarthrini parasitoid assemblage consisting of the species-specific endoparasites *Dolophron nemorati* Horstmann and *M. phyllotomae*, as well as several generalist leafminer parasitoids. The generalists include species not recorded from the Fenusini, such as *Monodontomerus indiscretus* Gahan (Hymenoptera: Torymidae), *Agrothereutes abbreviatus* (F.), and *Mastrus laplantei*

Table 1. Recorded hosts of birch-leafmining sawflies.

Host ^a	<i>Fenusella nana</i>	<i>Fenusa pumila</i>	<i>Heterarthrus nemoratus</i>	<i>Profenusa thomsoni</i>	<i>Scolioneura vicina</i> ^b
Nearctic birches (Betulaceae)					
<i>Betula</i> × <i>caerulea</i> Blanch. ^c		●	●		
<i>B. alleghaniensis</i> Britton		▲	●	●	
<i>B. glandulosa</i> Michx.		●	●	●	
<i>B. lenta</i> L.		▲	●		
<i>B. nana</i> L. ^d		●		●	
<i>B. neoalaskana</i> Sarg.		●		●	● ^e
<i>B. nigra</i> L.		●	●		
<i>B. occidentalis</i> Hook.		●	●	●	
<i>B. papyrifera</i> Marsh.	●	●	●	●	● ^e
<i>B. papyrifera</i> Marsh. var. <i>cordifolia</i> (Regel) Regel			●		
<i>B. populifolia</i> Marsh.		●	●	●	
<i>B. pumila</i> L.		●	● ^f		
Palaearctic birches					
<i>B. costata</i> Trautv.		▲			
<i>B. dahurica</i> Pall. ^g	●	●	●	●	●
<i>B. ermanii</i> Cham.		●			
<i>B. grossa</i> Siebold and Zucc.		▲			
<i>B. maximowicziana</i> Regel		●			
<i>B. pendula</i> Roth ^h	●	●	●	●	●
<i>B. pendula</i> Roth var. <i>pendula</i>		●			●
<i>B. pendula</i> Roth var. <i>oycowiensis</i> (Besser) Dippel	●	●	●	●	●
<i>B. platyphylla</i> Sukaczew		▲			
<i>B. platyphylla</i> subsp. <i>mandshurica</i> (Regel) Kitag	●	●	●	●	●
<i>B. pubescens</i> Ehrh.	●	●	●	●	●
<i>B. pubescens</i> Ehrh. var. <i>pubescens</i>		●	●		
<i>B. pubescens</i> Ehrh. var. <i>pumila</i> (L.) Govaerts	●	●			●
<i>B. schmidtii</i> Regel		▲			
<i>B. szechuanica</i> (C.K. Schneid.) C.-A. Jansson		▲			
<i>B. turkestanica</i> Litv.	●	●	●	●	●
<i>B. utilis</i> var. <i>jacquemontii</i> (Spach) H.J.P. Winkl.		▲			
Other hosts					
<i>Alnus viridis</i> Chaix DC. subsp. <i>crispa</i> (Aiton) Turrill (Betulaceae)			●		
<i>Alnus viridis</i> Chaix DC. subsp. <i>fruticosa</i> (Rupr.) Nyman		●			●
<i>Amelanchier</i> Medik. (Rosaceae)			▲ ^f		
<i>Corylus cornuta</i> Marsh. subsp. <i>cornuta</i> (Corylaceae)			▲ ^f		
<i>Ostrya virginiana</i> (P. Mill.) K. Koch (Corylaceae)			▲ ^f		

Table 1 (concluded).

Host ^a	<i>Fenusella</i> <i>nana</i>	<i>Fenusa</i> <i>pumila</i>	<i>Heterarthrus</i> <i>nemoratus</i>	<i>Profenusa</i> <i>thomsoni</i>	<i>Scolioneura</i> <i>vicina</i> ^b
<i>Populus grandidentata</i> Michx. (Salicaceae)			▲ ^f		
<i>P. tremuloides</i> Michx.			▲ ^f		

Note: ▲, sawflies observed to oviposit on the host; ●, sawflies observed to oviposit and complete larval development on the host. References are as follows: Peirson and Brower (1936); Martin (1960); Cheng and LeRoux (1965); Koponen (1973); Smith (1981); Tuomi *et al.* (1981); Drouin and Wong (1984); DeClerck and Shorthouse (1985); Fiori and Craig (1987); Nystrom and Evans (1989); Pschorn-Walker and Altenhofer (1989); Schönrogge and Altenhofer (1992); Pieronek and Soltik (1993); Kenis and Carl (1996); Digweed *et al.* (1997); Altenhofer and Taeger (1998); Hoch *et al.* (2000).

^aSpecies names conform to current nomenclature (*i.e.*, Govaerts and Bopp 1998; Integrated Taxonomic Information System 2008).

^bPooled host records for *S. betuleti*, *S. betulae*, and *S. vicina*. Host records from the Palearctic Region are known only for *S. betuleti* and *S. betulae*.

^cHybrid of *B. papyrifera* var. *cordifolia* and *B. populifolia* Marsh.

^dHolarctic species but only recorded as a host in the Palearctic Region.

^eUnpublished record from rearings of *S. vicina* in Alberta by the authors.

^fRecorded as a host only from a cage study (Peirson and Brower 1936).

^gIncludes references to *B. davurica* (Hoch *et al.* 2000) and *B. daurica* (Pieronek and Soltik 1993), which are likely misspellings of “*dahurica*”, as neither is recorded as a synonym of any *Betula* species listed in Govaerts and Bopp (1998) or Integrated Taxonomic Information System (2008).

^hCommon in North America as an ornamental.

Mason (Hymenoptera: Ichneumonidae: Cryptinae) (Table 2).

Dowden (1941) released five species of European parasitoids of *H. nemoratus* in ME during 1931–1935: an unidentified species of *Chrysocharis* Förster and *C. nitetis* (Walker) (Hymenoptera: Eulophidae), *Shawiana phyllotomae* (Muesebeck) (Hymenoptera: Braconidae), *Scambus foliae* (Cushman) (Hymenoptera: Ichneumonidae), and *D. nemorati*. Only *C. nitetis* and *S. phyllotomae* were subsequently confirmed as established. Unknown to Dowden, *C. nitetis* was apparently a Holarctic species (Hansson 1987) and did not need to be introduced. In Europe, *C. nitetis* is the most effective parasitoid of *H. nemoratus* (Dowden 1941) and this may also be true for endemic populations in Canada (Digweed 1998).

Late-instar *H. nemoratus* suffer heavily (20%–50% of larvae consumed) from bird predation in Austria, and ants were important predators where their nests were near infested birches (Dowden 1941).

***Fenusa (Fenusa) pumila* Leach: birch leafminer**

Taxonomy

During the 20th century this species was known as either *F. pumila* (Klug) or *F. pusilla* (Lepeletier). Taeger and Blank (1996, 2006) recently designated *Fenusa (Fenusa) pumila* Leach as the valid name. They also divided the

genus *Fenusa* Leach into two subgenera: *Fenusa (Kaliofenusa)* Viereck, which includes the five species attacking elm, and *Fenusa (Fenusa)* Leach, for two species on birch and alder.

Introduction, distribution, and abundance

Fenusa pumila is native throughout the Palearctic Region from Ireland through Siberia, China, and Japan (Friend 1933; Viramo 1969; Eichorn and Pschorn-Walcher 1973; Smith 1981; Zhelokhovtsev 1994). When first recorded in North America in 1923 it was already widespread, occurring in Connecticut (CT), Rhode Island, Massachusetts, eastern New York (NY), and Vermont, USA (Britton 1924, 1926).

The earliest record from Canada is 8 June 1922 from Vineland ON (CNC specimen accession No. CNC Hymen #05–320). *Fenusa pumila* was collected regularly in QC from the late 1920s (Davialt 1937; specimens in CNC), had spread throughout ON, NS, NB, and NL by the 1950s (Lindquist 1959; Jones and Raske 1976; specimens in NSMC and FRLC), and had arrived in AB by the 1960s (Drouin and Wong 1984). *Fenusa pumila* was present in patches across Canada by the 1980s (Quednau 1984), was continuing to spread northward in AB during the 1990s (Digweed *et al.* 1997), and in 2003 was recorded in NT (Digweed and Langor 2004) and AK (Snyder *et al.* 2007) (Fig. 9).

This species was the first of the Fenusini to become pestiferous on birch in North America

Table 2. Parasitoids (Hymenoptera) recorded attacking birch-leafmining sawflies in Europe and North America (useful synonyms for valid parasitoid names are presented in the footnotes).

	Type ^a	<i>Fenusella nana</i>		<i>Fenusa pumila</i>		<i>Heterarthrus nemoratus</i>		<i>Profenusa thomsoni</i>		<i>Scolioneura vicina</i> ^b	
		North		North		North		North		North	
		Europe	America	Europe	America	Europe	America	Europe	America	Europe	America
Ceraphronoidea											
Ceraphronidae											
<i>Aphanogmus</i> sp.	id, ec, hy				✓						
Chalcidoidea											
Eulophidae											
Entedoninae											
<i>Chrysocharis eurynota</i> Graham	id/ko, en							✓			
<i>C. nephereus</i> (Walker)	id, en, hy	✓		✓		✓		✓		✓	
<i>C. nitetis</i> (Walker) ^c	id, en, hy	✓		✓	✓	✓	✓	✓		✓	✓
<i>C. purpurea</i> Bukovskii	id, en, hy			✓		✓		✓			
<i>Chrysonotomyia</i> sp.	id, ec				✓				✓		
<i>Closterocerus cinctipennis</i> Ashmead	id, en, hy				✓						
<i>C. diastatae</i> (Howard) ^d	id, en	na		na	✓	na		na		na	
<i>C. donna</i> (Girault) ^e	id, en	na		na	✓	na		na		na	
<i>C. formosus</i> Westwood ^f	id, en				✓						
<i>C. trifasciatus</i> Westwood ^g	id, en, hy	✓		✓	✓	✓				✓	
<i>C. utahensis</i> Crawford	id, en	na		na	✓	na		na		na	
<i>Closterocerus</i> sp.	id, en, hy		✓ ^h							✓	
Eulophinae											
<i>Cirrospilus cinctithorax</i> (Girault)	id, ec	na		na	✓	na	✓	na		na	
<i>C. flavicinctus</i> Riley	id, ec	na		na		na	✓	na		na	
<i>C. pictus</i> (Nees)	id, ec, hy			✓	✓	✓	✓			✓	
<i>C. vittatus</i> Walker ⁱ	id, ec, hy			✓	✓	✓				✓	
<i>Cirrospilus</i> sp.	id, ec		✓		✓						
<i>Elachertus fenestratus</i> Nees ^j	id, ec			✓	✓						
<i>Hemiptarsenus fulvicollis</i> Westwood	id, ec		na		na	✓	na	na		na	
<i>H. ornatus</i> (Nees) ^k	id, ec		na		na	✓	na	na		na	
<i>Pnigalio agraulis</i> (Walker)	id, ec, hy		na	✓	na	✓	na	na		✓	na
<i>P. cruciatus</i> (Ratzeburg) ^l	id, ec		na		na	✓	na	na		✓	na

Table 2 (continued).

	Type ^a	<i>Fenusella nana</i>		<i>Fenusa pumila</i>		<i>Heterarthrus nemoratus</i>		<i>Profenusa thomsoni</i>		<i>Scolioneura vicina</i> ^b	
		North		North		North		North		North	
		Europe	America	Europe	America	Europe	America	Europe	America	Europe	America
<i>P. longulus</i> (Zetterstedt)	id, ec	✓		✓		✓				✓	
<i>P. maculipes</i> (Crawford)	id, ec	na		na	✓ ^m	na	✓	na		na	✓ ⁿ
<i>P. minio</i> (Walker) ^o	id, ec	na		na	✓	na	✓	na		na	✓ ⁿ
<i>P. pallipes</i> (Provancher)	id, ec	na		na	✓ ^p	na		na		na	
<i>P. pectinicornis</i> (L.)	id, ec, hy		na	✓	na	✓	na		na	✓	na
<i>P. soemius</i> (Walker)	id, ec		na	✓	na		na		na	✓	na
<i>P. uroplatae</i> (Howard)	id, ec	na	✓ ^q	na		na		na		na	
<i>Pnigalio</i> sp.	id, ec				✓				✓		
<i>Sympiesis marylandensis</i> Girault	id, ec	na		na		na	✓	na		na	
<i>S. sericeicornis</i> (Nees)	id, ec					✓ ^r					
<i>Sympiesis</i> sp.	id, ec, hy					✓			✓	✓	
<i>Zagrammosoma multilineatum</i> (Ashmead)	id, ec	na		na	✓	na		na		na	✓
<i>Zagrammosoma</i> sp.	id, ec								✓		
Tetrastichinae											
<i>Minotetrastichus frontalis</i> (Nees) ^s	id, ec, hy			✓	✓	✓	✓			✓	✓ ⁿ
<i>Minotetrastichus</i> sp. ^t	id, ec				✓				✓		
<i>Peckelachertus</i> sp.	id, ec				✓						
Torymidae											
<i>Monodontomerus indiscretus</i> Gahan	id, ec	na		na		na	✓	na		na	
Trichogrammatidae											
<i>Trichogramma aurosum</i> Sugonj. and Sorok.	id, egg								✓		
<i>T. minutum</i> Riley	id, egg				✓		✓				
Ichneumonoidea											
Braconidae											
Hormiinae^u											
<i>Shawiana catenator</i> (Haliday)	id, ec	✓	na	✓ ^v	na		na		na		na
<i>S. laevis</i> (Thomson)	id, ec		na		na		na		na	✓ ^w	na
<i>S. phyllotomae</i> (Muesebeck) ^x	id, ec			✓ ^y		✓	✓				
<i>Xenarcha abnormis</i> (Wesmael)	id, ec	✓		✓ ^z							
<i>X. lustrator</i> (Haliday)	id, ec			✓ ^A							

Table 2 (concluded).

	Type ^a	<i>Fenusella nana</i>		<i>Fenusa pumila</i>		<i>Heterarthrus nemoratus</i>		<i>Profenusa thomsoni</i>		<i>Scolioneura vicina</i> ^b	
		North		North		North		North		North	
		Europe	America	Europe	America	Europe	America	Europe	America	Europe	America
Ichneutinae											
<i>Pseudichneutes levis</i> (Wesmael)	ko, en		na		na		na		na	✓ ^B	na
Ichneumonidae											
Campopleginae											
<i>Dolophron nemorati</i> Horstmann ^C	ko, en					✓	✓				
Cryptinae											
<i>Agrothereutes abbreviatus</i> (F.) ^D	id, ec					✓	✓				
<i>Gelis obscurus</i> (Cresson)	id, ec	na		na		na	✓	na		na	
<i>Gelis</i> sp. ^E	id, ec				✓						
<i>Mastrus laplantei</i> Mason	id, ec	na		na		na	✓	na		na	
Ctenopelmatinae											
<i>Lathrolestes nigricollis</i> (Thomson)	ko, en			✓	✓						
<i>L. luteolator</i> (Gravenhorst) ^F	ko, en							✓			
<i>Lathrolestes</i> sp. near <i>macropygus</i> (Holmgren)	ko, en		na		na		na	na		✓	na
<i>Lathrolestes</i> sp. 2514 ^G	ko, en	✓	na		na		na	na			na
<i>Mesoleius phyllotomae</i> Cushman	ko, en		na		na	✓	na	na			na
Pimplinae											
<i>Alophosternum foliicola</i> Cushman	id, ec	na		na	✓	na	✓ ^H	na		na	✓ ⁿ
<i>Scambus (Scambus) foliae</i> (Cushman)	id, ec					✓	✓ ^I				
<i>S. (S.) hispae</i> (Harris)	id, ec	na		na		na	✓	na		na	
<i>Scambus (Scambus)</i> sp.	id, ec				✓	✓ ^J					✓ ⁿ
Tryphoninae											
<i>Grypocentrus albipes</i> Ruthe ^K	ko, ec			✓	✓						

Note: “na” indicates that the parasitoid has not been recorded in the specified region. References are as follows: Dowden (1941); Bouček and Askew (1968); Cheng and LeRoux (1969); Miller (1970); Eichorn and Pschorn-Walcher (1973); Krombein *et al.* (1979); Shaw (1983); van Achterberg (1983); Yoshimoto (1983); Hansson (1985, 1987, 1994, 1995); Schauff (1985); Nystrom and Evans (1989); Pschorn-Walcher and Altenhofer (1989); Shaw and Huddleston (1991); Barron (1994); Grissell (1995); Wharton *et al.* (1997); Digweed (1998); Entomological Information Services (1998); Pinto (1998); Evans (1999); Wahl (1999); Noyes (2003); Fauna Europaea Web Service (2005).

^aid, idiobiont; ko, koinobiont; ec, ectoparasitoid; en, endoparasitoid; egg, egg parasitoid; hy, facultative hyperparasitoid.

^bPooled parasitoids recorded from *Scolioneura betuleti* (Klug), *S. betulae* (Zaddach), and *S. vicina* Konow (as resurrected by Altenhofer and Taeger 1998).

^cIncludes records of *C. laricinellae* (Ratzeburg) in Dowden (1941), *C. pentheus* (Walker) in Yoshimoto (1973), and *C. pallipes* (Gahan) in Cheng and LeRoux (1969). For synonyms see Hansson (1985, 1987).

^dAlthough not recorded from Europe, this species occurs in China and Greenland (Noyes 2003). It is sometimes recorded as a species of *Neochrysocharis* (e.g., Hansson 1995, who also noted that the type is now lost), but Gumovsky (2001) synonymized *Neochrysocharis* with *Closterocerus*. Fisher and LaSalle (2005) resurrected *Neochrysocharis*, but did not convincingly support their opinion; hence, current lists (e.g., Noyes 2003) uphold Gumovsky (2001).

^eIncludes records of *Achrysocharis donna* Girault. This genus was synonymized with *Closterocerus* by Hansson (1994), but *C. donna* was later moved to *Neochrysocharis* by Hansson (1995) (who thought that the type was lost, but it exists on a slide at the United States National Museum (type No. 13664); Noyes 2003). However, *Neochrysocharis* was synonymized with *Closterocerus* by Gumovsky (2001). Fisher and LaSalle (2005) resurrected *Neochrysocharis*, but did not convincingly support their opinion; hence, current lists (e.g., Noyes 2003) uphold Gumovsky (2001).

^fIncludes records of *Derostenus fullowayi* Crawford, synonymized under *Closterocerus formosus* Westwood by Yoshimoto (1978). This species is sometimes recorded as a species of *Neochrysocharis* (e.g., Hansson 1990, 1995), but Gumovsky (2001) synonymized *Neochrysocharis* with *Closterocerus*. Fisher and LaSalle (2005) resurrected *Neochrysocharis*, but did not convincingly support their opinion; hence, current lists (e.g., Noyes 2003) uphold Gumovsky (2001).

^gIncludes records of *Closterocerus tricinctus* (Ashmead), synonymized by Hansson (1994), and *Closterocerus sesquifasciatus*, synonymized by Bouček (1968).

^hIncludes records of *Achrysocharis* sp., synonymized under *Closterocerus* by Hansson (1994).

ⁱIncludes records of *Zagrammosoma nigrolineatum* Crawford, synonymized by Bouček (1988).

^jIncludes records of *Elachertus argissa* (Walker), synonymized by Graham (1988).

^kIncludes records of *Hemiptarsenus dropion* (Walker), synonymized by Graham (1993).

^lRecorded from *H. nemoratus* and *S. betuleti* by Bouček and Askew (1968) but not Pschorn-Walcher and Altenhofer (1989).

^mRecorded attacking *F. pumila* by Cheng and LeRoux (1969) but not Yoshimoto (1983).

ⁿReared from *S. vicina* in Alberta by the authors.

^oIncludes records of *Pnigalio flavipes* (Ashmead), synonymized by Evans (1999).

^pRecorded as *Pnigalio metacomet* (Crawford) by Digweed (1998), synonymized by Yoshimoto (1983).

^qThe list of material examined by Yoshimoto (1983) for *P. uroplatae* suggests that this may be the species recorded as *Pnigalio* sp. by Lindquist and Thomson (1970).

^rRecorded from *H. nemoratus* by Bouček and Askew (1968) but not Pschorn-Walcher and Altenhofer (1989).

^sIncludes records of *Minotetrastichus ecus* (Walker) and *Tetrastichus xanthops* (Ratzeburg), synonymized by Graham and LaSalle (1991).

^tRecorded as "*Minotetrastichus* nr. *treron*" by Digweed (1998).

^uTerminology follows Wharton *et al.* (1997). Subfamily names used by other authors include Rogadinae and Doryctinae.

^vConfusion surrounds these records from *F. pumila*. This entry includes records of *S. catenator* from *F. pumila* by Pschorn-Walcher and Altenhofer (1989), which probably includes *Phanomeris dimidiatus* (Nees) reared from *F. pumila* by Eichorn and Pschorn-Walcher (1973). Shenefelt (1975) erroneously synonymized these taxa, but van Achterberg (1983) clarified the situation and synonymized *P. dimidiatus* with *Xenarcha lustrator* (Haliday). However, Fuester *et al.* (1984) suggested that the *Shawiana* sp. attacking *F. pumila* in Europe is distinct, reporting it as "near *catenator*"; this view is supported by Shaw (1983), who found that *S. catenator* would not attack *F. pumila* or *S. betuleti* when offered these species. *Shawiana* sp. near *catenator* was released in North America (Fuester *et al.* 1984), but apparently did not become established.

^wRecorded from *S. betuleti* by Pschorn-Walcher and Altenhofer (1989), but not by Shaw (1983) or van Achterberg (1983).

^xIncludes records of *Phanomeris phyllotomae* Muesebeck, which was moved to *Shawiana* by van Achterberg (1983).

^yRecorded by Krombein *et al.* (1979), but it is not clear whether this was a European or North American record. We assume that it refers to the record from Austria reported by Thompson (1944), but none of Eichorn and Pschorn-Walcher (1973), van Achterberg (1983), or Pschorn-Walcher and Altenhofer (1989) records *S. phyllotomae* as attacking *F. pumila* in Europe.

^zThis is the *Xenarcha* sp. recorded from *F. pumila* by Shaw (1983) and probably also by Pschorn-Walcher and Altenhofer (1989).

^AVan Achterberg (1983) did not record *X. lustrator* from *F. pumila*, but Eichorn and Pschorn-Walcher (1973) recorded *Phanomeris dimidiatus* (Nees), synonymized under *X. lustrator* by van Achterberg (1983), from *F. pumila*. See the footnote referring to *S. catenator*.

^BRecorded from *S. betulae* by Pschorn-Walcher and Altenhofer (1989, as *Ichneutes levis* Wesmael) but not by Belokobylskij (1996).

^CIncludes records of *Dolophron pedellum* (Holmgren) and *Tranosema pedella* (Holmgren), which is monophagous on *Heterarthrus vagans* Fallén. These records almost certainly refer to *D. nemorati*, which is monophagous on *H. nemoratus* (Horstmann 1977; Pschorn-Walcher and Altenhofer 1989).

^DIncludes records of *Agrothereutes abbreviator iridescens* (Cresson) from North America and *Agrothereutes pygoleucus* (Gravenhorst) from Europe.

^fRecorded as *Alegina* sp. by Cheng and LeRoux (1969).

^gThe *Lathrolestes* species attacking *P. thomsoni* in Alberta (Digweed 1998) was determined by Barron (1994) as *L. luteolator*, but in our recent examination of *L. luteolator* from *Callitroa cerasi* (L.) in Europe, we have determined that the parasitoid is not *L. luteolator* and is likely undescribed (see the text).

^hThe species number is from a reference system in the collection of Mr. Rolf Hinz, Einbeck, Germany (cited in Pschorn-Walcher and Altenhofer 1989).

ⁱRecorded from *H. nemoratus* by Townes (1969) and Zwakhals (1987) but not Dowden (1941) or Krombein *et al.* (1979).

^jThis species was released in North America (Dowden 1941) but may not have established (Krombein *et al.* 1979).

^kReported by Dowden (1941) as the indistinguishable species *Epiurus* [= *Scambus* (*Scambus*) *brevicornis* (Gravenhorst) and *Epiurus* (= *Scambus* (*Scambus*) ?*buoliana*e (Hartig). Both are Holarctic species.

^lAlso referred to as *Grypocentrus* sp. C1 near *albipes* Ruthe by Pschorn-Walcher and Altenhofer (1989).

(Friend 1931, 1933) and has occurred in high numbers in eastern North America (van Driesche *et al.* 1997) and on young nursery stock in AB (Digweed 1995). However, our recent surveys suggest that *F. pumila* is currently not abundant across Canada; at most locations visited, it was rare or absent.

Life cycle and biology

Fenusa pumila prepupae overwinter in soil cocoons averaging 3.80 mm long and 2.14 mm wide (Cheng and LeRoux 1965). Pupation and adult eclosion occur in spring, coinciding with flushing of long-shoot leaves on which female *F. pumila* oviposit almost exclusively (DeClerck and Shorthouse 1985). This preference reduces potential direct competition for leaf resources with other birch-leafmining sawflies such as *F. nana* (DeClerck and Shorthouse 1985) and *P. thomsoni* (Digweed *et al.* 1997; Digweed 2006). Long-shoot leaves are abundant on young trees and sucker growth, where *F. pumila* can cause extensive leaf browning (Friend 1933). However, long-shoot growth occurs only on the top and periphery of mature trees (Digweed 1995), and *F. pumila* mining causes little visible damage on such trees.

Females live for up to 5 days, laying eggs between major lateral leaf veins and along the leaf midrib (DeClerck and Shorthouse 1985). Each female lays, on average, 80 eggs, which hatch within 4–13 days (Cheng and LeRoux 1965). Larvae proceed through four feeding instars in 8–12 days and a complete summer generation takes 5–6 weeks (Friend 1933; Cheng and LeRoux 1965). Early-instar larvae feed mostly on palisade parenchyma and will not mine through vascular tissue; however, during the final feeding stage all types of leaf cell are consumed, leaving only the cuticle (Cheng and LeRoux 1965; DeClerck and Shorthouse 1985). The fifth, nonfeeding instar makes a hole in the top of the mine, drops to the ground, and burrows for a few centimetres before constructing a cocoon (Friend 1933; Cheng and LeRoux 1965). Friend (1933) published head-capsule widths for all instars and Cheng and LeRoux (1965) published body lengths and widths.

The number of generations per year depends on summer weather, with more generations occurring in years with higher day-degree accumulations (Digweed *et al.* 1997). Development–day-degree relationships for eggs and larvae in Edmonton AB were developed by Digweed (1995). Adults were first active in spring as leaves flushed (around mid-

Fig. 1. Diagnostic structures of adult *Heterarthrus nemoratus*: *a*, forewing, showing the second anal vein (2A) and third anal vein (3A); *b*, head, frontal view; *c*, whole body, lateral view. Scale bars = 0.5 mm.

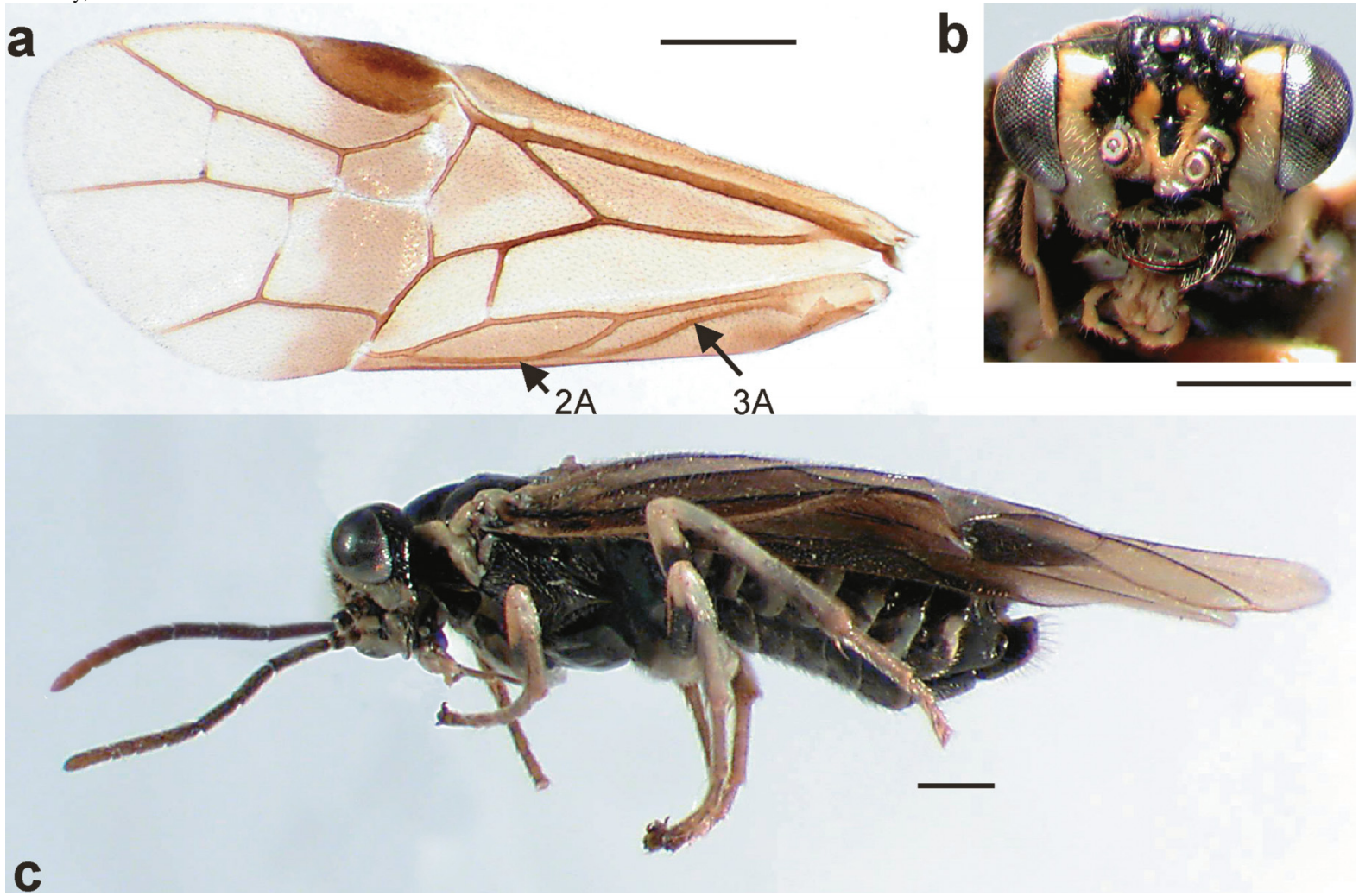


Fig. 2. Diagnostic structures of adult *Fenusa pumila*: *a*, forewing, showing the first anal vein (1A), second anal vein (2A), and third anal vein (3A); *b*, head, posterolateral view; *c*, anterior portion of the metasoma, dorsal view (the double-headed arrow indicates the narrowness of the first metasomal tergum, T1); *d*, mesosoma, dorsal view (the arrow indicates the hairless median lobe of the mesoscutum); *e*, antenna; *f*, ovipositor (the image is digitally enhanced to emphasize the structure of the lancet). Scale bars = 0.5 mm.

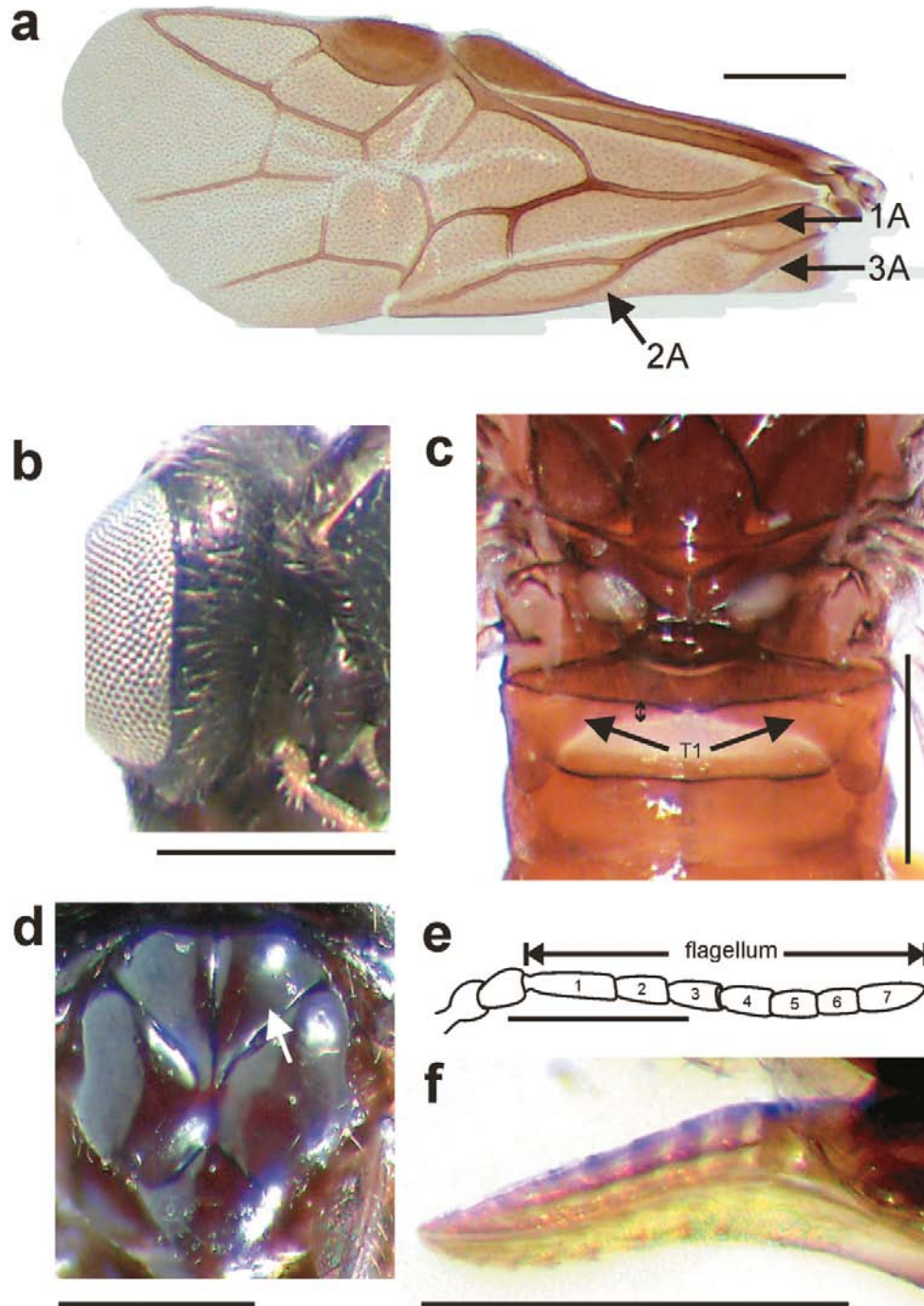
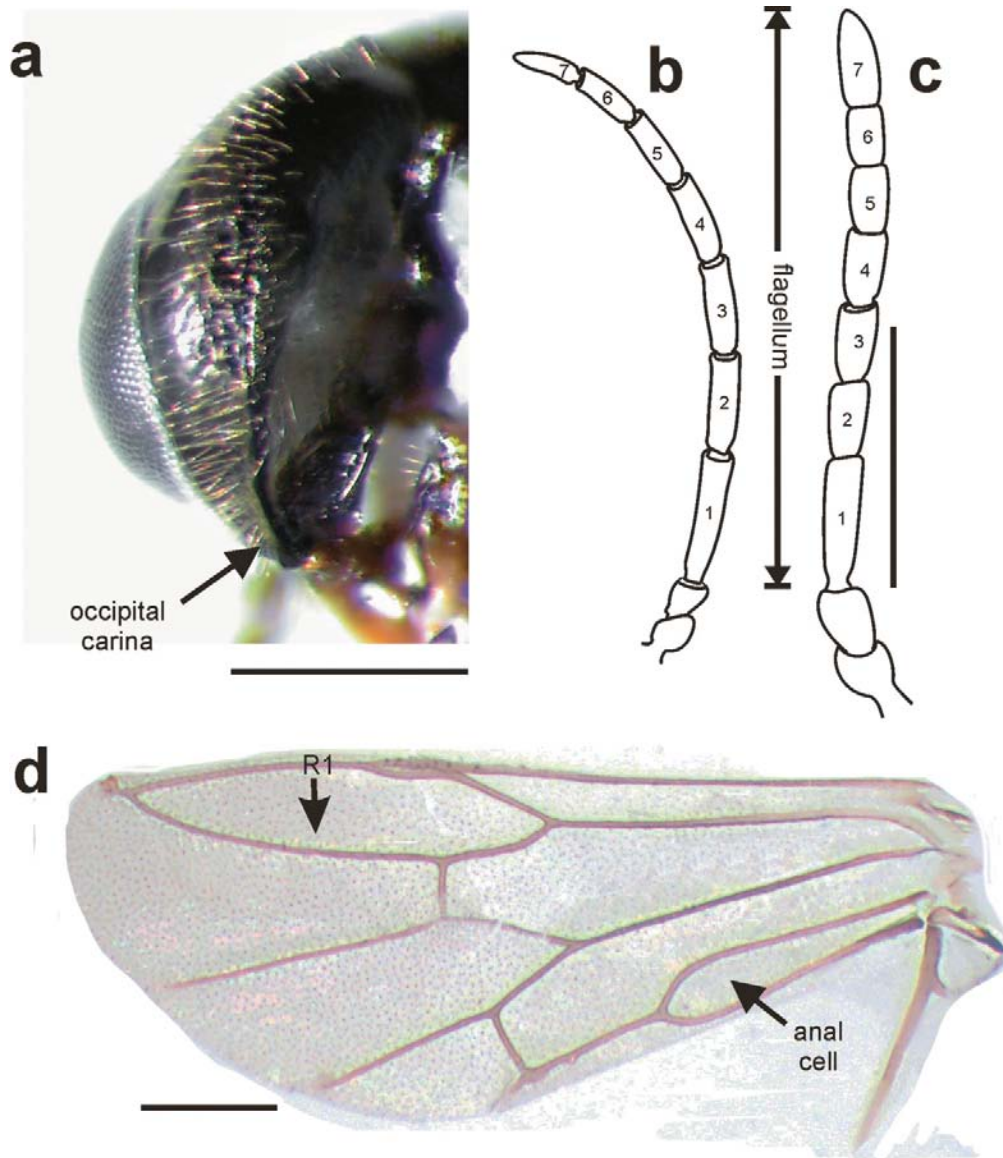


Fig. 3. Diagnostic structures of adult leafmining sawflies: *a*, head of *Scolioneura vicina*, posterolateral view, showing the occipital carina; *b*, antenna of *S. vicina*; *c*, antenna of *Fenusa dohrnii*; *d*, hind wing of *Fenusella nana*, showing R1 and anal cells. Scale bars = 0.5 mm.



May in Edmonton, about 280 day-degrees above 5 °C) and persisted until mid-June (Digweed *et al.* 1997). Second-generation adults were active in the last half of July and those of a third generation in the last half of August (Digweed *et al.* 1997). Phenology is similar in eastern North America, with adults of three or sometimes four generations active from May until mid-September (Friend 1933; Cheng and LeRoux 1965). The ratio of male to female *F. pumila* is approximately 1:1 (Friend

1933; Cheng and LeRoux 1965; Digweed *et al.* 1997).

Fenusa pumila attacks all birch species in North America and Europe (Table 1), but certain species and cultivars suffer less damage or exhibit resistance. Friend (1933) and Cheng and LeRoux (1965) reported *Betula populifolia* Marsh., common introduced ornamentals (e.g., *B. pendula*), and native birches (e.g., *B. papyrifera*) as prime hosts in North America. Both

Fig. 4. Diagnostic structures of adult *Profenus thomsoni*: *a*, forewing, showing the first anal vein (1A) and third anal vein (3A); *b*, hind wing, showing R1 and anal cells; *c*, mesosoma, dorsal view (the arrow indicates the hairy median lobe of the mesoscutum); *d*, anterior portion of the metasoma, dorsal view (the double-headed arrow indicates the width of the first metasomal tergum, T1); *e*, ovipositor (the image is digitally enhanced to emphasize the structure of the lancet). Scale bars = 0.5 mm.

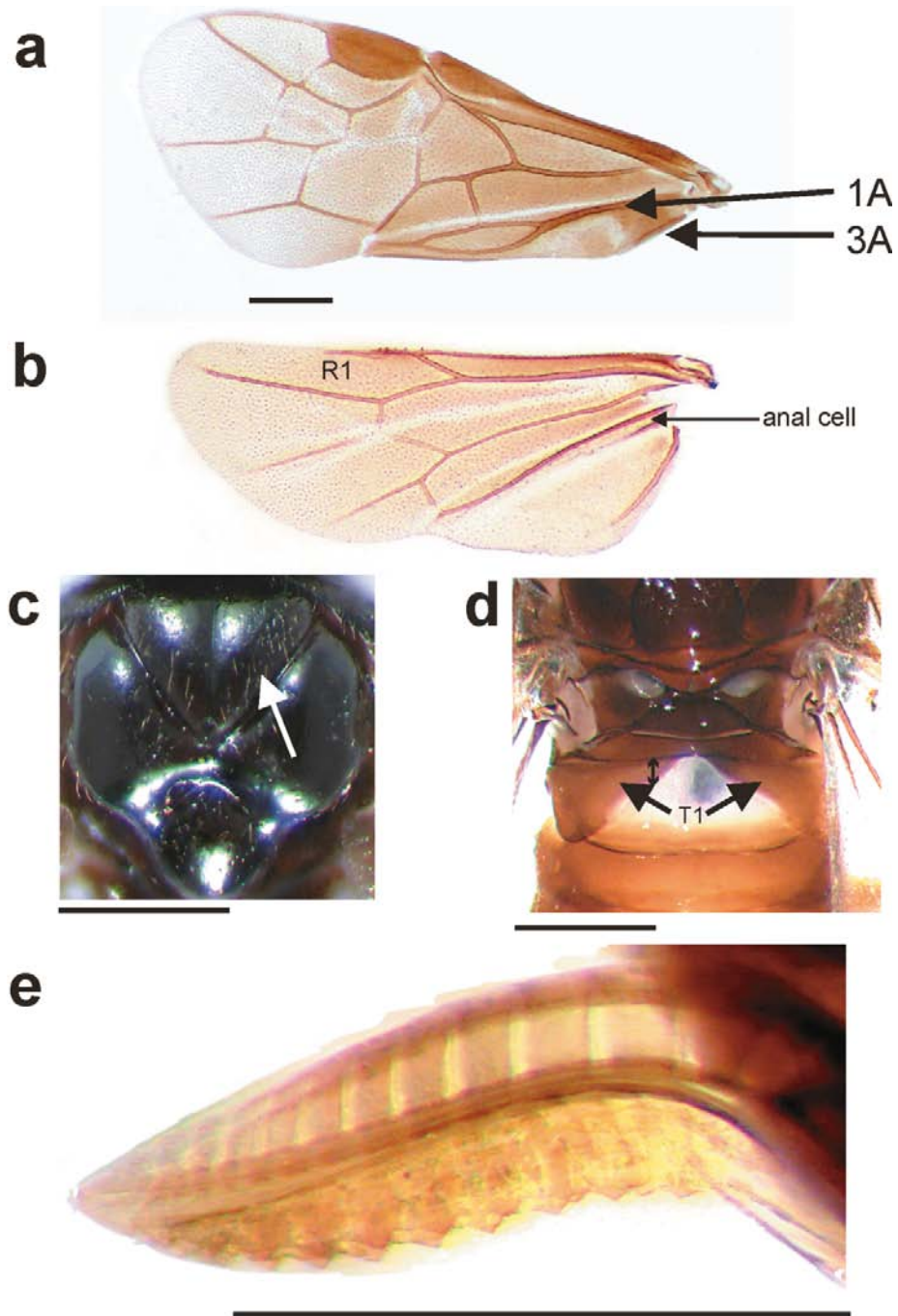
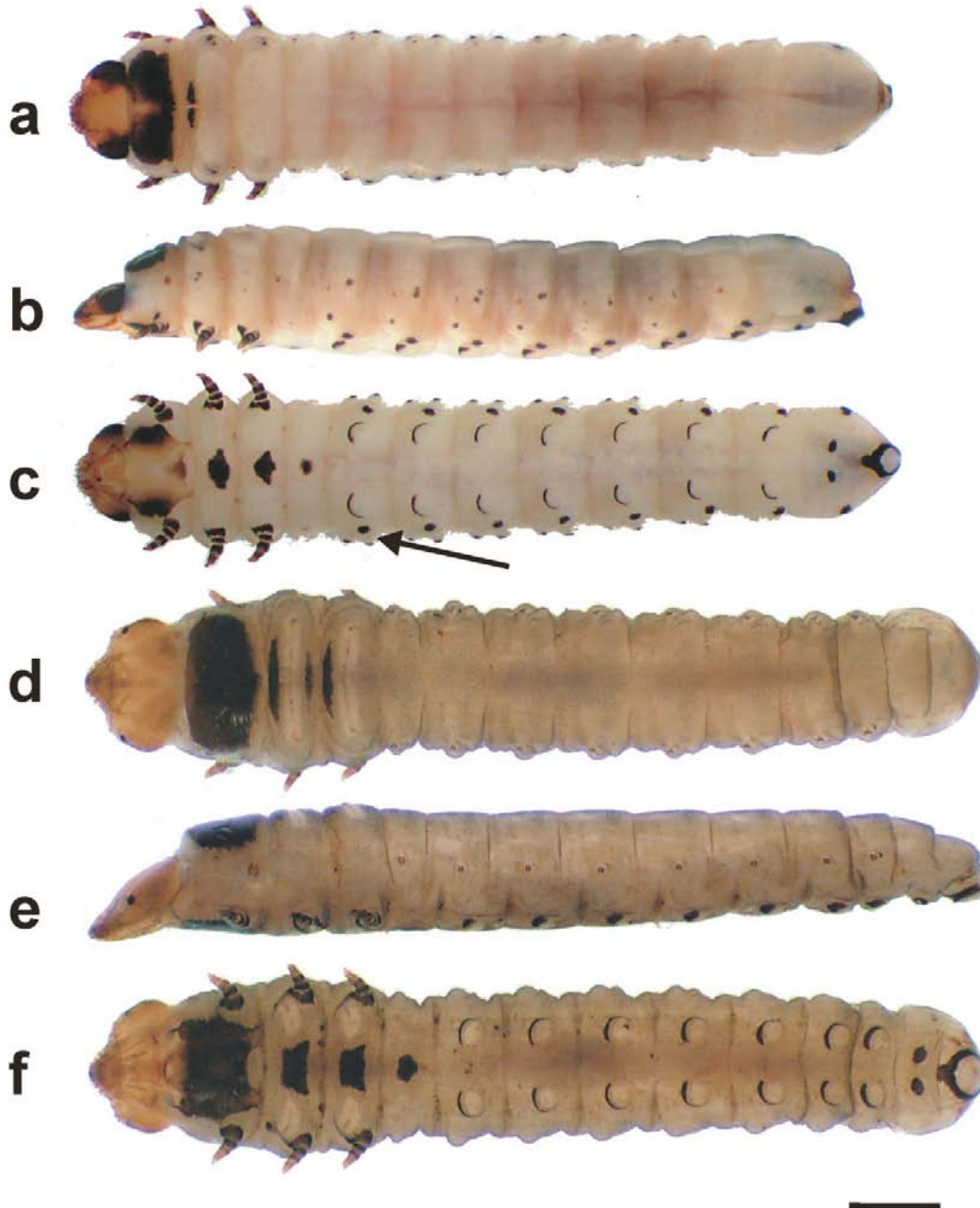


Fig. 5. Dorsal, lateral, and ventral views of larvae of *Scolioneura vicina* (*a*, *b*, and *c*, respectively) and *Fenusella nana* (*d*, *e*, and *f*, respectively). The arrow in *c* indicates the position of the lateral spot on an abdominal segment of *S. vicina*. Scale bar = 0.5 mm.



also reported limited attack on *Betula alleghaniensis* Britton. Hoch *et al.* (2000) reported that no larvae survived to maturity in leaves of *B. alleghaniensis*, *Betula grossa* Siebold and Zucc., and *Betula lenta* L. used in their experiments. In no-choice tests, a gradient of oviposition preferences has been observed across

birch species, with *B. alleghaniensis*, *B. grossa*, *B. lenta*, *Betula costata* Trautv., and *Betula dahurica* Pall. the least appealing to *F. pumila* (Fiori and Dolan 1984; Fiori and Craig 1987; Hoch *et al.* 2000; see also the footnote to Table 1). It has been observed that in eastern Canada, *B. populifolia* is more sensitive to attack

Fig. 6. Diagnostic structures of larval birch-leafmining sawflies: *a*, *Heterarthrus nemoratus*, ventral view; *b*, *Fenusa pumila*, ventral view; *c*, *Profenusa thomsoni*, ventral view; *d*, thorax of *P. thomsoni*, ventral view; *e*, thorax of *H. nemoratus*, ventral view (the image is digitally enhanced to emphasize the central dark spots); *f*, leg of *F. pumila*. Scale bars = 0.5 mm unless otherwise indicated.

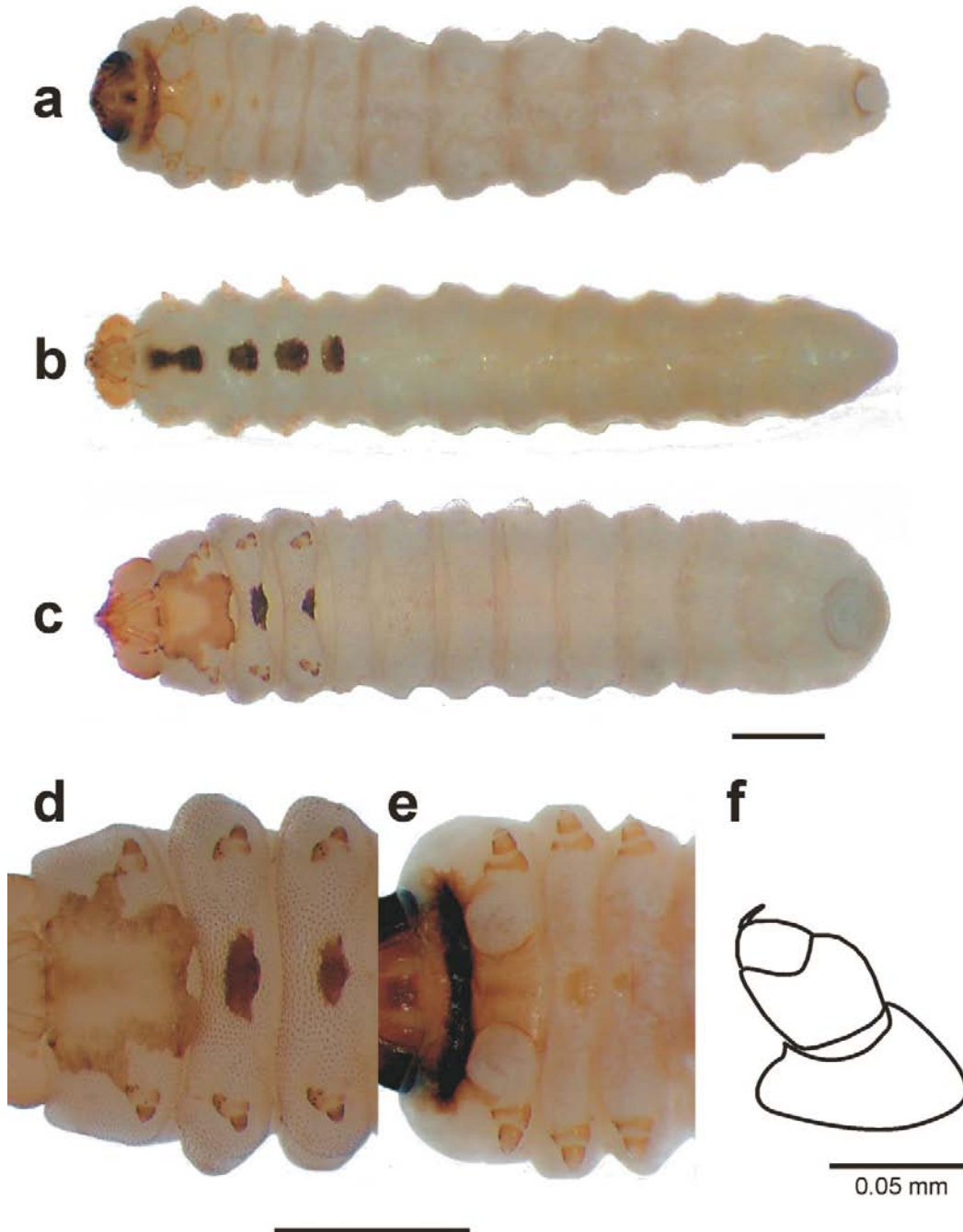
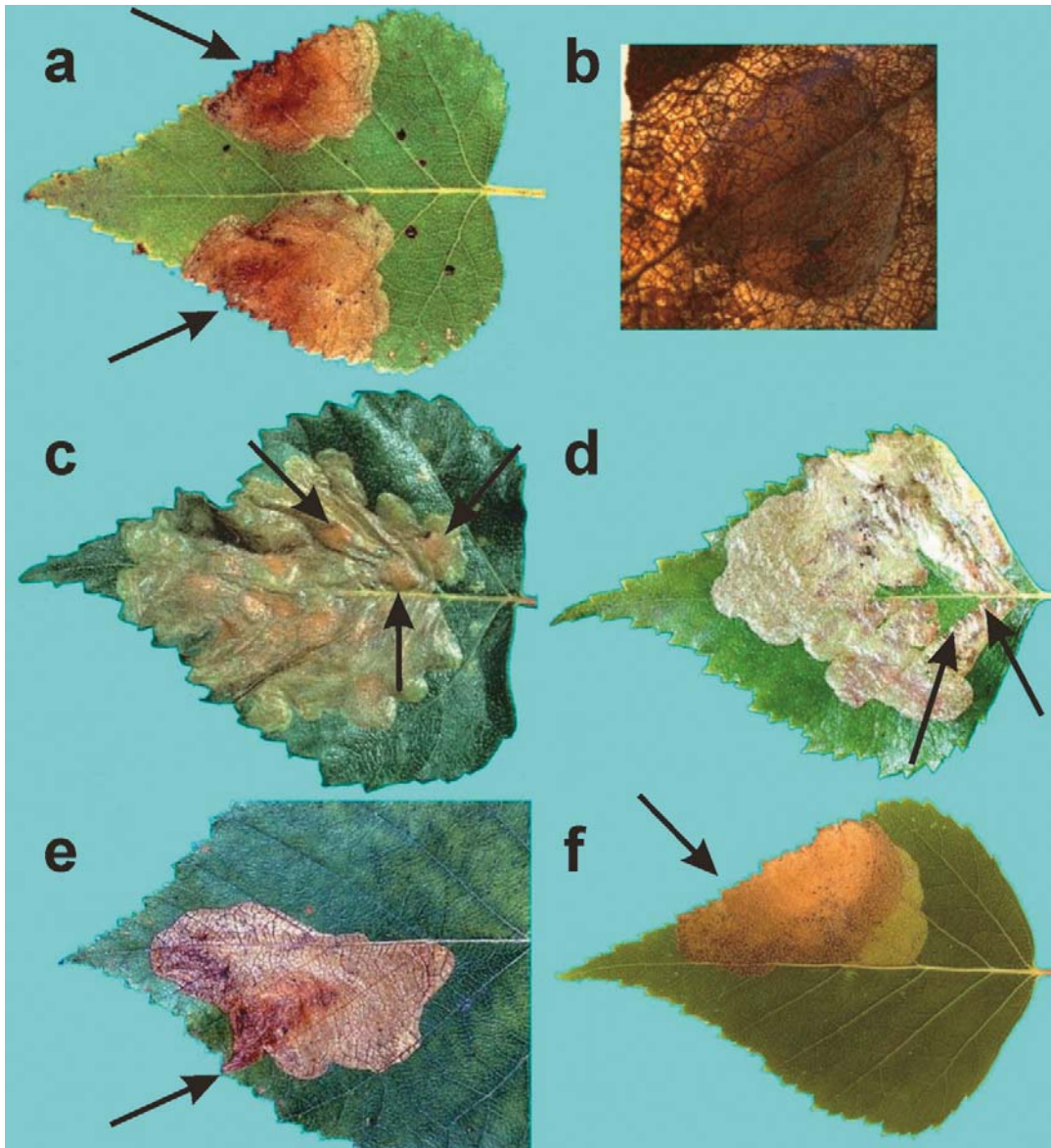


Fig. 7. Mines of birch-leafmining sawflies: *a*, *Heterarthrus nemoratus*; *b*, hibernaculum of *H. nemoratus* within a mine; *c*, *Fenusella pumila*; *d*, *Profenus thomsoni*; *e*, *Fenusella nana*; *f*, *Scolioneura vicina*. The arrows indicate the approximate locations of egg scars.



than *B. papyrifera*, except where leaf litter is removed (*e.g.*, in urban settings or on floodplains) (H. Goulet, personal communication). In Europe, *F. pumila* also attacks *Alnus viridis* (Chaix) DC. subsp. *fruticosa* (Rupr.) Nyman (Altenhofer 1980b; Altenhofer and Taeger 1998).

Mortality, natural enemies, and biological control

The ability of predators and parasitoids to regulate outbreaking *F. pumila* populations in

North America has been investigated. Life tables were constructed for *F. pumila* in QC (Cheng and LeRoux 1966, 1970) and AB (Digweed 1998). In both studies, significant egg mortality occurred because of desiccation, consumption by conspecifics, predators, or parasitoids, and other, unknown causes. Generalist avian and insect predators kill many larvae, especially the vulnerable final-instar larvae when they drop to the ground (Friend 1933; Cheng and LeRoux 1966; Pezolesi and Hager

Fig. 8. Canadian distribution of *Heterarthrus nemoratus*, based on recent surveys and museum specimens.

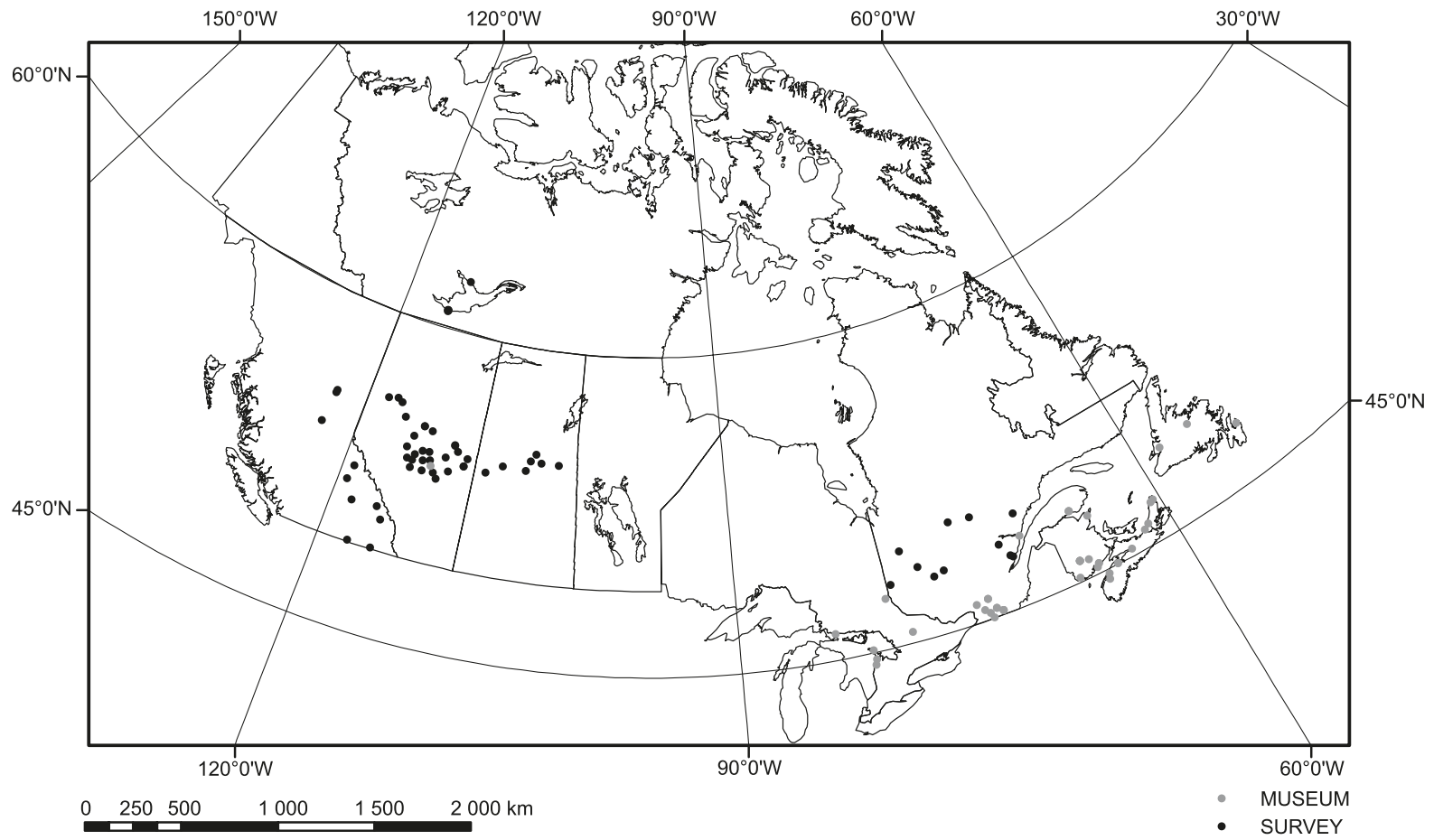
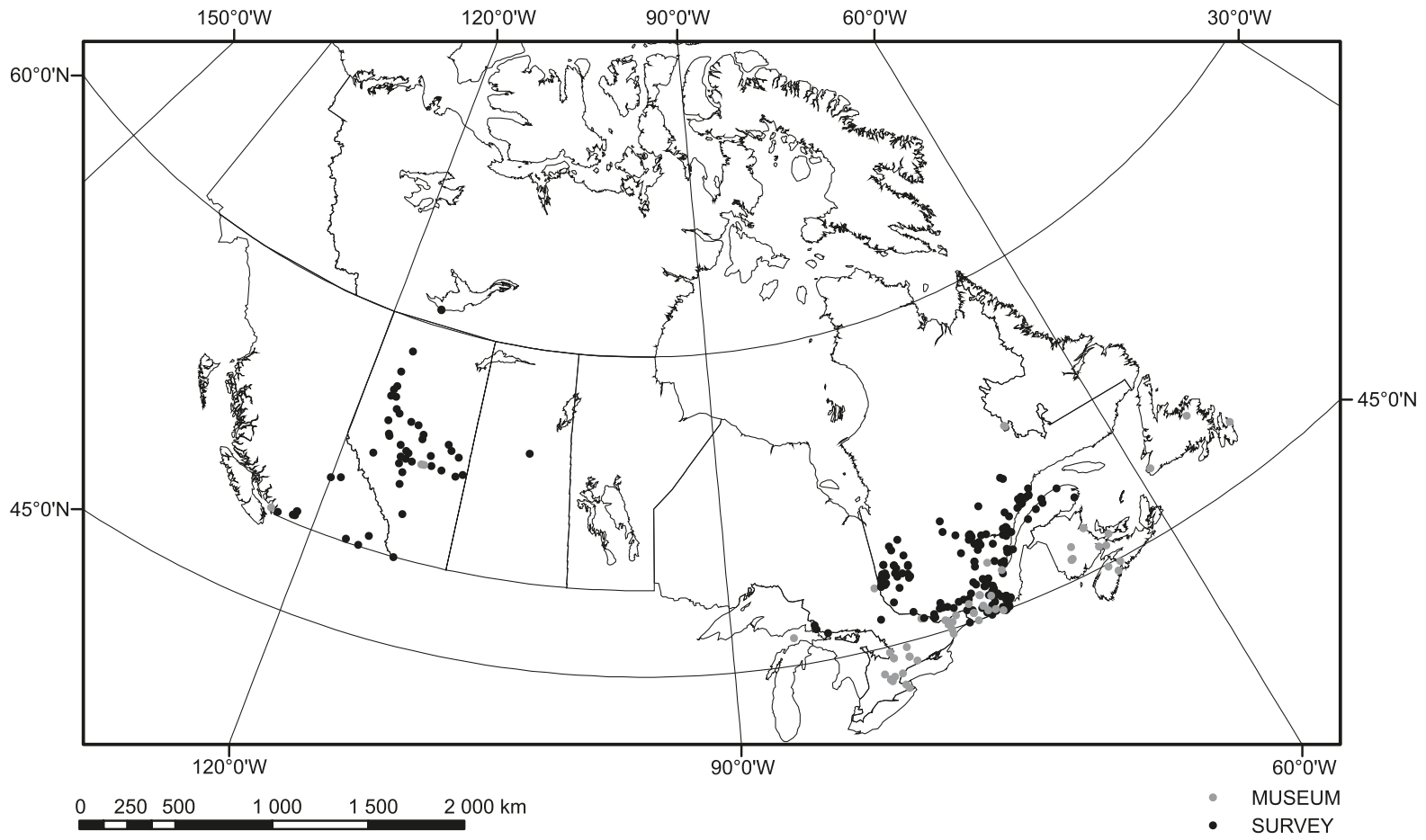


Fig. 9. Canadian distribution of *Fenusa pumila*, based on recent surveys and museum specimens.



1994; McQueen 1996; Digweed 1998). Several foliar chemical sprays and systemic insecticides are effective against *F. pumila* larvae (Friend 1931, 1933; Matthyse and Naegele 1952; Schread 1958, 1959, 1960, 1961, 1962, 1964, 1966, 1968; Cheng and LeRoux 1968; Drouin and Wong 1984).

Generalist parasitoids that attack *F. pumila* are diverse (Table 2) but cause minimal larval mortality (Cheng and LeRoux 1966; Digweed 1998). No effective host-specific native North American parasitoids were detected during life-table studies, which prompted attempts to introduce parasitoids from Europe into North America. Detailed study of the European parasitoid complex of *F. pumila* identified *Lathrolestes nigricollis* (Thomson) and *Grypocentrus albipes* Ruthe as the best candidates for mass release in North America (Eichorn and Pschorn-Walcher 1973) (Table 2). These two species were released in NL in 1972–1973 (Raske and Jones 1975), QC in 1974–1978 (Guèvremont and Quednau 1977; Quednau 1984), the eastern USA in 1976–1982 (Fuester *et al.* 1984; van Driesche *et al.* 1997), and AB in 1994–1996 (Langor *et al.* 2000). *Lathrolestes nigricollis* was also translocated within the eastern USA in 1989–1990 (van Driesche *et al.* 1997). *Lathrolestes nigricollis* established at all locations, but establishment of *G. albipes* has been confirmed only in QC (Quednau 1984) and AB (Langor *et al.* 2002). By 2003, *L. nigricollis* had spread from Edmonton AB 280 km west to Hinton AB and most *F. pumila* larvae found in Edmonton during 2003–2006 contained melanized *L. nigricollis* eggs (S.C.D., personal observation).

Fuester *et al.* (1984) introduced two other promising parasitoids for use against *F. pumila* in the eastern USA during 1979–1981. *Chrysocharis nitetis* was introduced before it was known to be Holarctic (Hansson 1985, 1987). *Shawiana* near *catenator* (Haliday) (Hymenoptera: Braconidae; previously placed in *Phanomeris* Förster) was also introduced, but apparently did not become established.

***Profenusa thomsoni* (Konow): ambermarked birch leafminer**

Taxonomy

Originally described as *Fenusa thomsoni* Konow, this species was transferred to *Profenusa* by Benson (1941), then listed as a junior synonym of *P. alumna*, the oak-leafmining sawfly (Benson

1959), and subsequently resurrected as a valid taxon (Smith 1971). Studies referring to *P. alumna* on birch (*e.g.*, Lindquist 1959; Watson 1959) all actually refer to *P. thomsoni*. Thirteen species of *Profenusa* are recognized worldwide, with 5 recorded from North America, but only *P. thomsoni* has been recorded from birch (Smith 1971; Taeger and Blank 2006).

Introduction, distribution, and abundance

Profenusa thomsoni is native throughout the Palearctic Region and has been recorded from Great Britain, central Europe, Turkey, the Caucasus, Siberia, China, and Japan (Benson 1959, 1968; Viramo 1969; Shaw 1981; Smith 1981; Togashi 1981; Zhelokhovtsev 1994). It was first collected in CT, USA, in the 1920s (Smith 1971), ON, QC, and Manitoba (MB) in the late 1940s (Martin 1960; specimens in CNC), and AB in the late 1960s (Drouin and Wong 1984). The range of *P. thomsoni* is still expanding in northern AB, NT, YT, and AK (Digweed *et al.* 1997; Digweed and Langor 2004; Snyder *et al.* 2007).

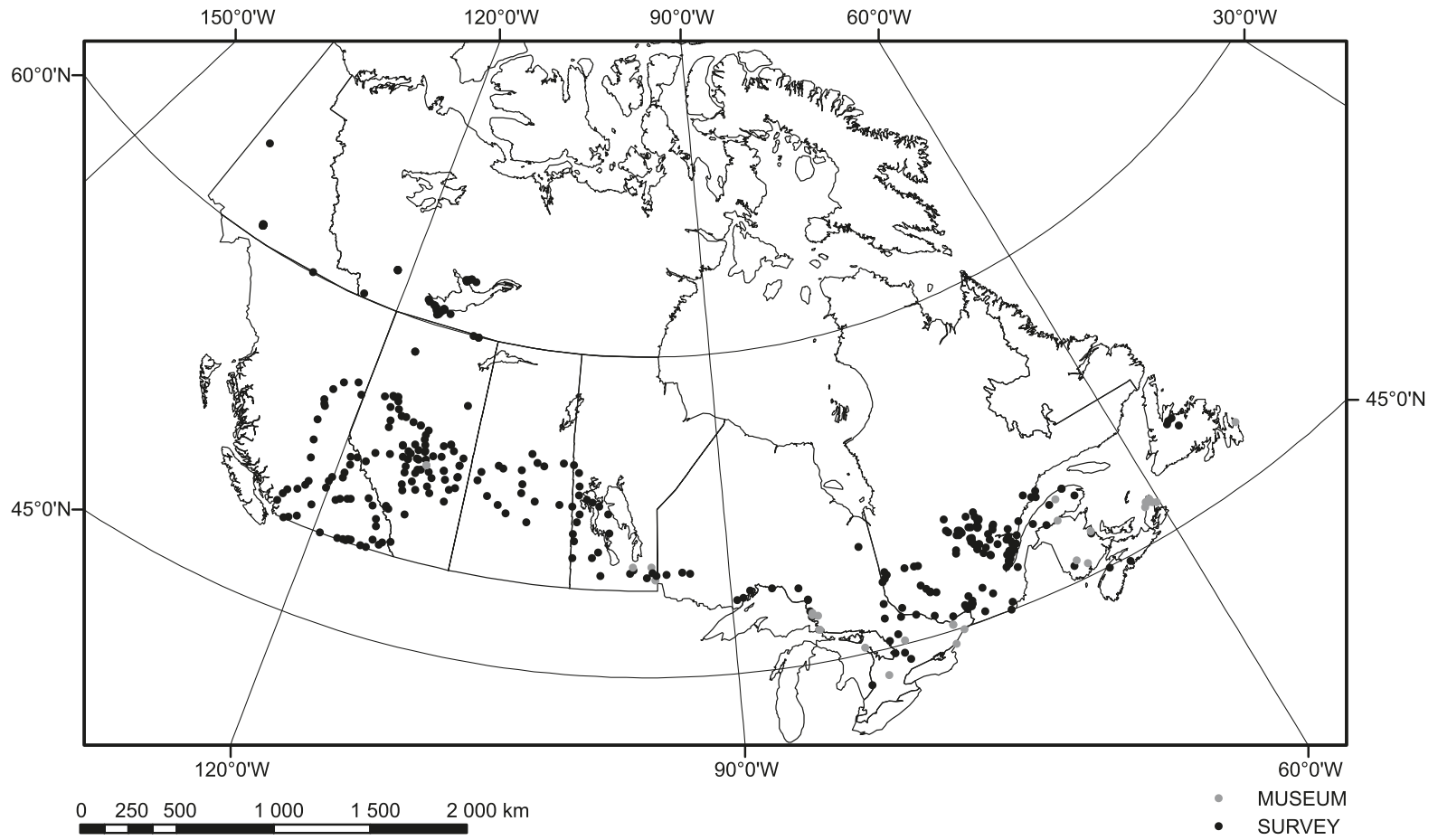
Profenusa thomsoni is currently the most prevalent leafmining sawfly on birch in Canada (Fig. 10). Its populations often reach epidemic levels (Benson 1959; Martin 1960) that can be sustained for decades (Drouin and Wong 1984; Digweed *et al.* 1997, 2003).

Life cycle and biology

Profenusa thomsoni pupates in soil cocoons for about 8 days in summer (Martin 1960) and adult emergence begins in late June or early July at between 400 and 550 day-degrees above 5 °C (Schönrogge and Altenhofer 1992; Digweed *et al.* 1997). All adults are parthenogenetic females and are active until August, ovipositing on mature leaves throughout the tree crown. Ovipositing females do not select leaves to maximize larval fitness during outbreaks; rather, they aggregate eggs on leaves already bearing the eggs of others and larval survival is reduced as a result (Martin 1960; Digweed 2006).

Eggs hatch within 12 days. Complete larval development takes about 24 days in ON (Martin 1960) and 40 days in Austria (Schönrogge and Altenhofer 1992), but can be much shorter in leaves exposed to warmer conditions (S.C.D., personal observation). The long adult-emergence period results in a protracted larval presence in leaves, with most completing their development

Fig. 10. Canadian distribution of *Profenusa thomsoni*, based on recent surveys and museum specimens.



between mid-August and mid-October in ON (Martin 1960) and mid-July to mid-September in AB, NT, and AK (by about 1200 day-degrees above 5 °C) (Digweed 1995; Digweed *et al.* 1997; MacQuarrie 2008).

Female *P. thomsoni* apparently do not prefer particular birch species for oviposition, although Martin (1960) noticed a preference for leaves on sucker growth in partially shaded, protected locations. In AB, *P. thomsoni* attacks all native and ornamental birch cultivars examined, including the tiny-leafed shrub *Betula glandulosa* Michx. (Digweed *et al.* 1997) (Table 1).

Mortality, natural enemies, and biological control

Life tables for *P. thomsoni* in AB showed significant mortality of eggs (caused by mechanical damage) and of larvae in crowded leaves (caused by competition and resource exhaustion) (Digweed 1998, 2006). An average-sized birch leaf can support 6–10 larvae (Martin 1960; Digweed 2006), but an increase in density reduces survival, especially for the larvae that develop last (Digweed 2006). Martin (1960) observed significant egg mortality from undermining (*i.e.*, larvae consuming the leaf tissue below eggs) and high larval mortality due to resource exhaustion. No larval cannibalism has been reported.

Predators kill many larvae feeding in leaves (Digweed 1998; but see MacQuarrie 2008), and ground-dwelling arthropods kill final-instar larvae and newly emerged adults (Martin 1960; McQueen 1996). Larvae are parasitized at low levels by generalist eulophid leafminer parasitoids and eggs are parasitized by *Trichogramma aurosum* Sugonjaev and Sorokina (Hymenoptera: Trichogrammatidae) (Martin 1960; Digweed 1998) (Table 2). Significant parasitism by *Lathrolestes luteolator* (Gravenhorst) on *P. thomsoni* has been recorded in western Canada (Barron 1994; Digweed 1998; Digweed *et al.* 2003). This parasitoid was previously recorded attacking *P. alumna* as well as species of *Caliroa* Costa (Hymenoptera: Tenthredinidae), which are externally feeding defoliators of *Quercus* spp. and *Nyssa sylvatica* Marsh. (Cornaceae) (Barron 1994). It has recently been determined that the *Lathrolestes* species reared from *P. thomsoni* is not *L. luteolator* but is likely an undescribed species (A. Bennett, personal observation). Nevertheless, this *Lathrolestes* sp. appears to regulate *P. thomsoni* populations effectively (Langor *et al.* 2002; Digweed *et al.* 2003) and has been

translocated as a biological control agent for epidemic *P. thomsoni* populations in Yellowknife NT and Anchorage AK (MacQuarrie 2008).

Little is known of the parasitoids of *P. thomsoni* in Europe, where it is rare (Liston 1981; Schönrogge and Altenhofer 1992). It is unique among birch-leafmining sawflies in that no specialist parasitoids have been recorded attacking it in Europe (Pschorner-Walcher and Altenhofer 1989). Various species of *Chrysocharis* have been reared from *P. thomsoni* there (Table 2), with *Chrysocharis purpurea* Bukovskii (Hymenoptera: Eulophidae) the most abundant (Schönrogge and Altenhofer 1992).

***Fenusella nana* (Klug): early birch leaf edgeminer**

Taxonomy

This species was originally described as *Tenthredo* (*Allantus*) *nana* Klug, but is best known as *Messa nana* (Klug) (Benson 1952; Smith 1971). However, Taeger and Blank (1996) deemed the genus *Messa* Leach uninterpretable and transferred all species to *Fenusella*. There are currently 10 species of *Fenusella* worldwide, with 6 of them found in North America. *Fenusella nana* is the only species that attacks birch (Smith 1971; Taeger and Blank 2006).

Introduction, distribution, and abundance

Fenusella nana is native throughout the Palearctic Region and has been recorded from Great Britain, central Europe, Siberia, Mongolia, and Japan (Benson 1952; Viramo 1969; Smith 1981; Zhelokhovtsev 1994; Csóka 2003). It was first collected in ME and NY, USA, in 1966 and in southern ON in 1967 (Lindquist and Thomson 1970; Smith 1971). It had reached Sudbury ON by 1982 (DeClerck and Shorthouse 1985). Our surveys showed that *F. nana* has since spread throughout eastern Canada, southwestern BC (Fig. 11), and Washington State (WA), USA (not shown). Where found, it was often the most abundant birch-leafmining sawfly species, sometimes causing severe defoliation.

Life cycle and biology

Overwintered *F. nana* pupate in spring and adults are active in ON from mid-May until early June (Lindquist and Thomson 1970; DeClerck and Shorthouse 1985). Eggs are laid into leaf edges near the ends of the main lateral veins (DeClerck and Shorthouse 1985). Most

Fig. 11. Canadian distribution of *Fenusella nana*, based on recent surveys and museum specimens.

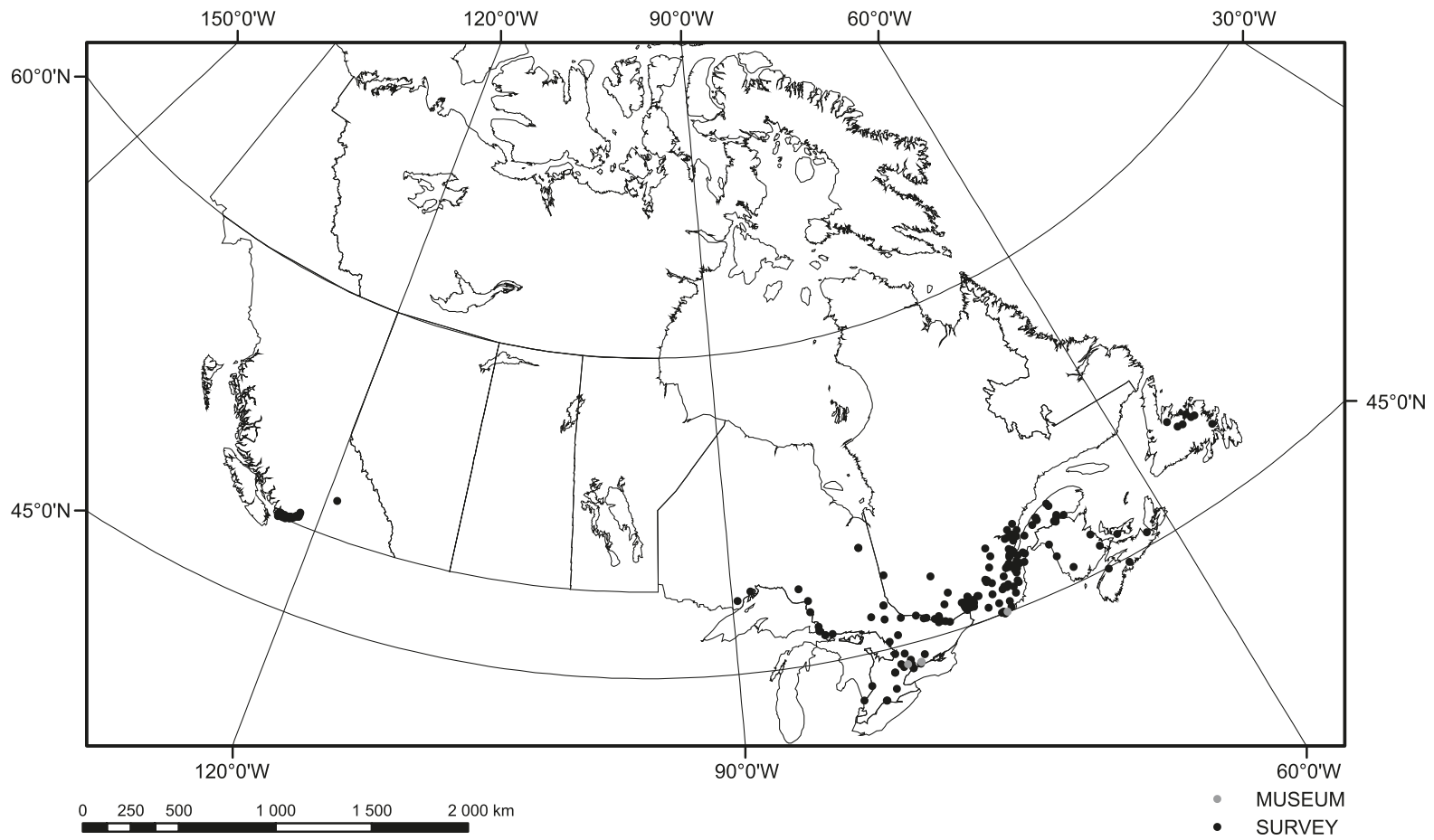
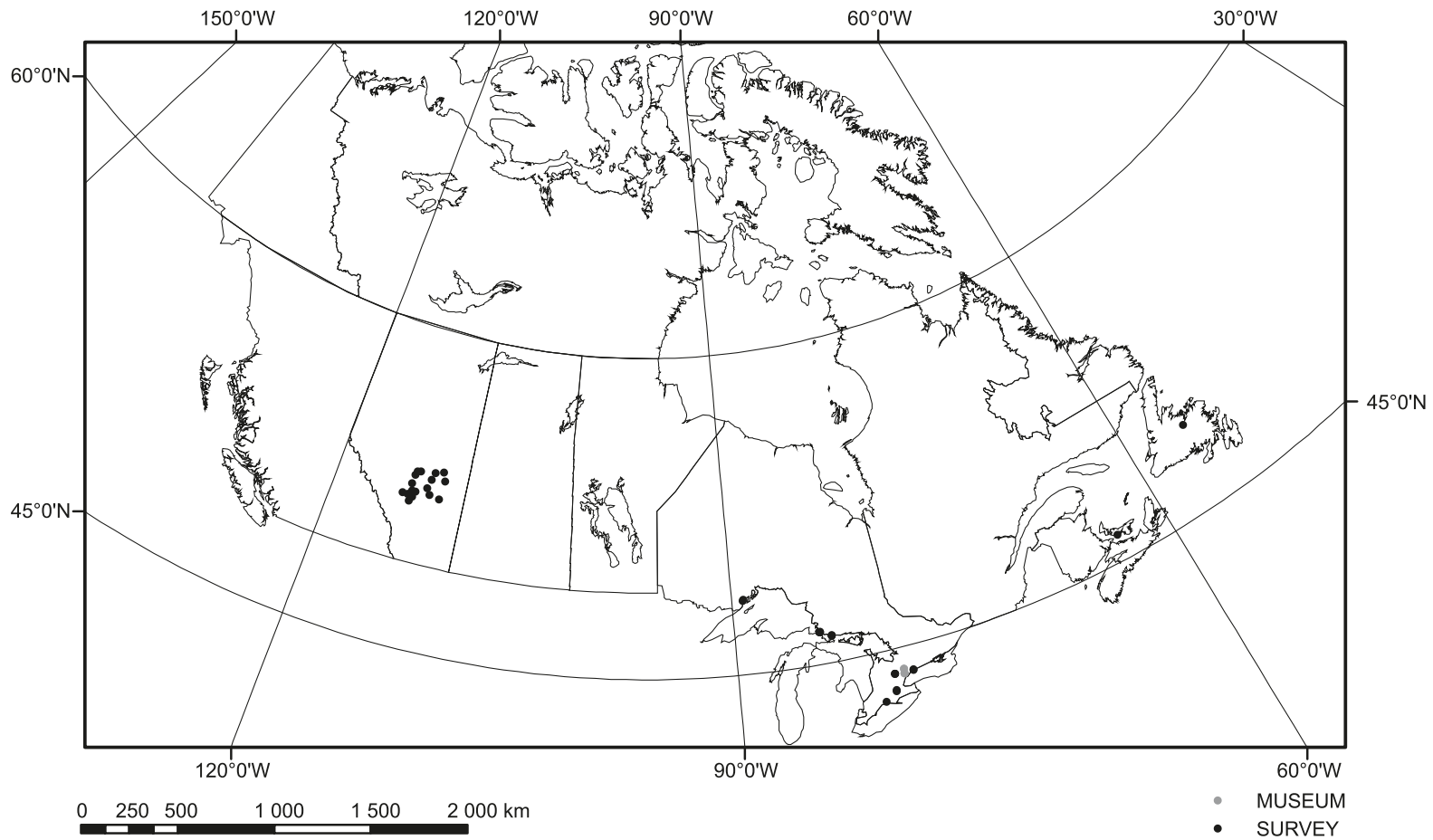


Fig. 12. Canadian distribution of *Scolioneura vicina*, based on recent surveys and museum specimens.



leaves bear no more than 3 eggs but up to 10 may occur on larger leaves (Lindquist and Thomson 1970). There are five or six larval instars and larvae feed almost exclusively on palisade mesenchymal cells, thus never forming a full-depth mine (DeClerck and Shorthouse 1985).

Fenusella nana has been recorded from multiple species of *Betula* in the USA (Smith 1971) and Europe (Benson 1952; Viramo 1969) but when discovered in Canada it was found only on *B. papyrifera* (Lindquist and Thomson 1970). During our surveys we observed it on *B. papyrifera* and ornamental cultivars (Table 1).

Mortality and natural enemies

Fenusella nana is attacked in North America and Europe by generalist eulophid leafminer parasitoids and in Europe by an undescribed species of *Lathrolestes* (Lindquist and Thomson 1970; Pschorn-Walcher and Altenhofer 1989) (Table 2). Nothing is known of mortality rates in Canada except that fewer than 3% of *F. nana* larvae were parasitized in ON when the species was first discovered there (Lindquist and Thomson 1970).

Scolioneura vicina Konow

Taxonomy

Specimens of *S. vicina* and its putative sibling species *S. betuleti* are behaviourally different but morphologically indistinguishable. This has resulted in a confused taxonomic history. For a time a single bivoltine species (*S. betuleti*) was recognized (Benson 1952). Subsequently, Altenhofer (1980a, 1980b, 1980c) and Altenhofer and Taeger (1998) recognized two univoltine non-overlapping cohorts: the early-season *S. vicina* (attacking *B. pendula* and *B. pubescens* Ehrh. in May and June) and the late-season *S. betuleti* (attacking *B. pendula* and *B. pubescens*, as well as *Alnus viridis* subsp. *crispa* (Aiton) Turill in July and August). Altenhofer and Taeger (1998) resurrected the name *S. vicina* for the early species, placed *Scolioneura* sp. B of Altenhofer (1980b) and *Scolioneura* sp. cf. *betulae* of Pschorn-Walcher and Altenhofer (1989) in *S. vicina*, and synonymized *S. betulae* (Zaddach) under *S. betuleti*. However, subsequent molecular work on *S. vicina* and *S. betuleti* supports the hypothesis that they constitute a single bivoltine species (MacQuarrie *et al.* 2007).

Potential taxonomic confusion must be borne in mind when consulting literature involving species of *Scolioneura* on birch. For example, the insect studied by Tuomi *et al.* (1981) was active in September and is indeed *S. betuleti*, whereas the "*S. betuleti*" studied by Nystrom and Evans (1989) was active in May and June and is now assumed to have been *S. vicina* (MacQuarrie *et al.* 2007).

Introduction, distribution, and abundance

Scolioneura vicina is native to the Palearctic Region and its distribution may be identical with that of *S. betuleti*, which has been recorded from Ireland, Great Britain, central Europe, Siberia, and Mongolia (Benson 1952; Viramo 1969; Zhelokhovtsev 1994; Csóka 2003). In North America, *S. vicina* was first collected in southern ON in 1983 (Evans *et al.* 1985; Nystrom and Evans 1989). Our sticky-trap sampling of birch-leafmining sawfly adults in 1994 at 20 locations across Canada detected *S. vicina* near Guelph ON only; this species was not detected in surveys in AB during the early 1990s (Digweed *et al.* 1997). However, our surveys during 2004–2006 detected *S. vicina* in NL, PE, northern ON, and AB (Fig. 12). At some locations in AB in 2006 (*e.g.*, Olds, Sylvan Lake, and Rimbey), *S. vicina* populations were at outbreak levels.

Life cycle and biology

Adult *S. vicina* are active in ON from early May until early June. Eggs are laid into the edges of mature, fully expanded leaves, either at the edge of a leaf tooth or along the smooth basal leaf edge. Most leaves bear no more than 2 eggs but up to 10 have been observed (Nystrom and Evans 1989). There are six larval instars (Nystrom and Evans 1989). Tuomi *et al.* (1981) found that larvae of *S. betuleti* had lower masses on leaves bearing more conspecifics and suggested that this late-feeding species produces more frass (because of the lower quality of later birch foliage) than earlier feeding leafminers on birch.

In Europe, *S. vicina* and *S. betuleti* attack a variety of birch species (Table 1). When first detected in Canada, *S. vicina* appeared to attack only European birch species (Nystrom and Evans 1989) but we subsequently observed it attacking native birch species in ON and AB.

Mortality and natural enemies

A typical suite of generalist eulophid leafminer parasitoids attacks *S. vicina* and *S. betuleti* in Europe and *S. vicina* in North America, and each hosts an undescribed species of *Lathrolestes* in Europe (Nystrom and Evans 1989; Pschorn-Walcher and Altenhofer 1989) (Table 2). Nystrom and Evans (1989) found 12% of larvae parasitized by native eulophids. We have reared similar eulophids, as well as pimpline ichneumonids, from *S. vicina* in AB (Table 2).

Discussion

We have attempted to describe the current state of knowledge about birch-leafmining sawflies in Canada. It should be apparent that although much is known about the basic life history and host preferences of these insects, there is still much to learn about the mechanisms driving population dynamics and other aspects of their ecology. We hope that this review will stimulate more detailed ecological research on these significant pests of Canadian urban landscapes.

Our synthesis suggests that birch-leafmining sawflies remain a significant threat to birches in Canada despite recent successful biological control programs against them. Without exception, birch leafminers in Canada have increased their ranges over the past 20 years and all are now found (at least patchily) across Canada. We predict that the ranges of these species will continue to expand in coming years, particularly in western and northern Canada. Past evidence suggests that populations of these leafminers will, at least initially (and potentially for many years after), reach outbreak levels as they spread into new regions.

The most effective controls of birch-leafmining sawflies have been natural enemies imported from Europe, which have become established and have succeeded in limiting populations of *H. nemoratus* and *F. pumila* in the Nearctic Region (Dowden 1941; Fuester *et al.* 1984; Langor *et al.* 2000). Similarly, *P. thomsoni* populations have been suppressed by an apparent specialist parasitoid, an undescribed species of *Lathrolestes* (Digweed *et al.* 2003). However, biological control of *F. nana* and *S. vicina* is a more distant prospect because of the poor state of the taxonomy of *Lathrolestes*, the most widely introduced and effective genus of specialist parasitoids of fensine sawflies. Doubt

surrounds the identity of some described *Lathrolestes* species (*e.g.*, the one that attacks *P. thomsoni*), and the host ranges of various species have not been formally tested. Further, many *Lathrolestes* species remain undescribed, including those that attack *F. nana*, *S. vicina*, and *S. betuleti*. Indeed, none of the potential biological control agents for *F. nana*, *S. vicina*, and *S. betuleti* in Europe (Table 2) have been evaluated as candidates for introduction to North America and nothing is known about the role that native natural enemies may play in suppressing these sawflies in North America. Much remains to be done if damage to Canadian birches by birch-leafmining sawflies is to be managed effectively.

All native and introduced birch species in Canada are suitable hosts for at least one birch-leafmining sawfly species (Table 1). Most non-*Betula* hosts were recorded only by Peirson and Brower (1936), who caged female *H. nemoratus* on branches in no-choice tests. Eggs hatched only on *A. v. crispa* and some larvae matured on this host. In Europe, *F. pumila* and *S. betuleti* have also been recorded from *Alnus* species (Table 1). This "straying" onto *Alnus* is not surprising, given its taxonomic closeness to *Betula* and the fact that species in these genera share habitat preferences and often co-occur (S.C.D., personal observation). These records from alternative hosts highlight the need for careful identification of leafminer and host species.

Records of host plants and parasitoids of birch-leafmining sawflies in the eastern Palearctic Region are incomplete, reflecting a dearth of research on these species in that region. Moreover, existing host-plant records for Asia and Siberia are mostly from studies of transplanted hosts in European and North American arboreta (*e.g.*, Fiori and Dolan 1984; Pieronek and Soltys 1993; Hoch *et al.* 2000). A reason for the paucity of information could be the rarity of birch-leafmining sawflies in the eastern Palearctic Region. Certainly, the lack of parasitoid records on *P. thomsoni* in Europe reflects its rarity there (Schönrogge and Altenhofer 1992). Data collected so far suggest that some Palearctic birch species are resistant to birch-leafmining sawflies (Fiori and Dolan 1984; Hoch *et al.* 2000) (Table 1). Additional study of the performance of leafmining sawflies on eastern Palearctic birches could prove fruitful for the development of birch cultivars resistant to attack by birch-leafmining sawflies.

Parasitological and ecological evidence suggests that leafmining evolved separately in the Fenusini and Heterarthrini and casts doubt on the current classification of these sawflies. The leafmining habit has evolved at least twice in tenthredinid sawflies: once in the Nematinae (tribe Pseudodineurini) and once or twice in the Heterarthrinae (tribes Fenusini and Heterarthrini) (Pschorn-Walcher and Altenhofer 1989). Goulet (1992) defined the subfamily Heterarthrinae according to shared wing-vein characters and included the two leafmining tribes, Fenusini and Heterarthrini, as well as the Caliroini, a tribe of free-feeding skeletonizers. This arrangement follows earlier classifications by Smith (1971) and Ross (1937) in suggesting that leafmining arose once within the Heterarthrinae (Phyllotominae of Ross 1937). However, Benson (1952) included only *Heterarthrus* within the Heterarthrinae, moving the Fenusini and Caliroini into Blenno-campinae. Benson's view is supported by the divergent nature of specialist parasitoid assemblages in the Fenusini and Heterarthrini (Pschorn-Walcher and Altenhofer 1989; Table 2) and by the differences in the mining biology of these leafminers on birch described above.

The complex of five species of invasive birch-leafmining sawflies described here constitutes a model system for examining questions of population and community ecology. For the Nearctic Region this system is now described well enough that more detailed and manipulative ecological study should be possible. Leafminers are attractive subjects for the study of generalized ecological concepts because their lifestyle is restricted (which makes them good subjects for ecological manipulation), they feed within discrete resource patches (which makes them sensitive to resource limitation), and they leave an interpretable record of their activities (the mined leaf and the cast larval skins it contains). Study of these species as they continue to spread across Canada and combine in new complexes at varying population densities should provide a unique opportunity to manipulate and study intra- and inter-specific interactions, preference-performance relationships, the evolution and dynamics of parasitoid communities, and the population dynamics of invasive species.

Recommendations

Biological control programs should be extended to minimize damage caused by birch-leafmining sawflies to ornamental birch trees across Canada. First, the species of *Lathrolestes*

attacking *F. nana*, *S. betuleti*, and *S. vicina* in Europe must be described, ideally within a taxonomic revision of *Lathrolestes* clarifying species relationships and host-range specificities. Concurrently, Canadian life-table studies of *F. nana* and *S. vicina* should be undertaken to characterize the diversity and effects of native parasitoids attacking these species in both eastern Canada, where they have been present for decades, and the west, where they have established more recently. Nationwide control of all birch-leafmining sawfly species is desirable because it can yield financial and environmental savings through reduced use of pesticides in urban settings (Digweed *et al.* 2003).

Acknowledgments

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