

A review of the tachinid parasitoids (Diptera: Tachinidae) of Nearctic *Choristoneura* species (Lepidoptera: Tortricidae), with keys to adults and puparia

JAMES E. O'HARA

*Invertebrate Biodiversity, Agriculture and Agri-Food Canada, 960 Carling Avenue, Ottawa, Ontario, Canada,
K1A 0C6. E-mail: oharaj@agr.gc.ca.*

Table of Contents

Abstract	2
Introduction	2
Materials and Methods	4
Key to adults of tachinid parasitoids of Nearctic <i>Choristoneura</i> species	5
Key to puparia of tachinid parasitoids of Nearctic <i>Choristoneura</i> species	9
Reproductive strategies of tachinid parasitoids of <i>Choristoneura</i> species	15
<i>Actia diffidens</i> Curran	15
<i>Actia interrupta</i> Curran	17
<i>Ceromasia auricaudata</i> Townsend	19
<i>Compsilura concinnata</i> (Meigen)	20
<i>Cyzenis incrassata</i> (Smith)	21
<i>Eumea caesar</i> (Aldrich)	22
<i>Hemisturmia parva</i> (Bigot)	24
<i>Hyphantrophaga blanda</i> (Osten Sacken)	25
<i>Hyphantrophaga virilis</i> (Aldrich and Webber)	26
<i>Lypha fumipennis</i> Brooks	26
<i>Madremyia saundersii</i> (Williston)	28
<i>Nemorilla pyste</i> (Walker)	30
<i>Nilea erecta</i> (Coquillett)	31
<i>Phryxe pecosensis</i> (Townsend)	34
<i>Smidtia fumiferanae</i> (Tothill)	36
Excluded species	38
Acknowledgements	39
References	39

Abstract

The genus *Choristoneura* (Lepidoptera: Tortricidae) comprises about 16 species in the Nearctic Region and includes several destructive pests of importance to forestry and agriculture. The following 15 species of Tachinidae (Diptera) are recognized as occasional or common parasitoids of *Choristoneura* species in this region: *Actia diffidens* Curran, *Actia interrupta* Curran, *Ceromasia auricaudata* Townsend, *Compsilura concinnata* (Meigen), *Cyzenis incrassata* (Smith), *Eumea caesar* (Aldrich), *Hemisturmia parva* (Bigot), *Hyphantrophaga blanda* (Osten Sacken), *Hyphantrophaga virilis* (Aldrich and Webber), *Lypha fumipennis* Brooks, *Madremyia saundersii* (Williston), *Nemorilla pyste* (Walker), *Nilea erecta* (Coquillett), *Phryxe pecosensis* (Townsend), and *Smidtia fumiferanae* (Tothill). Keys to the adults and puparia of these tachinid species are provided. The known distribution, biology, and rates of parasitism are reviewed for each species and published host records from *Choristoneura* species are listed. Colour habitus images of adults, illustrations of all puparia, and illustrations of features mentioned in the adult key are included. Thirteen other species of Tachinidae recorded from *Choristoneura* species but excluded from the main text as highly dubious, rare, or accidental records are briefly discussed.

Key words: Tachinidae, *Choristoneura*, Nearctic, keys

Introduction

The genus *Choristoneura* (Lepidoptera: Tortricidae) comprises about 16 species of defoliators in the Nearctic Region (Dang 1992). These species include such destructive forestry pests as the spruce budworm (*C. fumiferana* (Clemens)), western spruce budworm (*C. occidentalis* Freeman), two-year cycle spruce budworm (*C. biennis* Freeman), jack pine budworm (*C. pinus* Freeman) and large aspen tortrix (*C. conflictana* (Walker)), as well as the agriculturally important obliquebanded leafroller (*C. rosaceana* (Harris)). Conifer-feeding *Choristoneura* species periodically attain outbreak status in the forests of Canada and the United States, causing considerable economic losses to the forestry industry and attracting great research interest in their biology and control. The developing resistance of the obliquebanded leafroller to certain chemical insecticides in apple orchards and other agricultural crops (Pree *et al.* 2001) has heightened research interest in this species. The destructiveness of these species has made *Choristoneura* one of the most studied genera in the Lepidoptera (Otvos 1991; Sanders 1991).

There have been many studies on the natural control factors that help to keep populations of *Choristoneura* species in check. Among the most important control factors are endoparasitoids, which attack all life stages of *Choristoneura* species. The best studied species, *C. fumiferana*, has a primary parasitoid complement of more than 90 species (Huber *et al.* 1996). Most endoparasitoids of *Choristoneura* species are Hymenoptera in the families Braconidae and Ichneumonidae or Diptera in the family Tachinidae.

This paper focuses on the tachinid parasitoids of Nearctic *Choristoneura* species. Fifteen species are recognized as occasional or common parasitoids of nine Nearctic *Choris-*

toneura species (Table 1). These species all attack their *Choristoneura* hosts in the larval stage, though some species emerge from the host pupae. Most species attack late larvae, and within this age group the tachinids are among the most significant parasitoids. Mortality during the late larval stage due to hymenopterous and dipterous parasitoids and various predators can be considerable and can significantly affect generation survival (Carolin & Coulter 1959; Allen *et al.* 1969; Royama 1984; Nealis 1991).

TABLE 1. Rearing records of Tachinidae from Nearctic species of *Choristoneura*, as compiled from published records and examination of reared specimens in the Canadian National Collection (Ottawa) and several other Canadian collections. Several columns in the table contain two or three *Choristoneura* species because the published records upon which they are based did not distinguish between the species listed.

Tachinid species/ Tortricid species	<i>C. conflictana</i>	<i>C. fractivittana</i>	<i>C. fumiferana</i>	<i>C. fumiferana</i> and/or <i>C. occidentalis</i>	<i>C. fumiferana</i> , <i>C. occidentalis</i> and/or <i>C. pinus</i>	<i>C. lambertiana</i>	<i>C. occidentalis</i>	<i>C. occidentalis</i> and/or <i>C. retiniana</i>	<i>C. parallela</i>	<i>C. pinus</i>	<i>C. rosaceana</i>	<i>C. rosaceana</i> and/or <i>Pandemis limitata</i>
<i>Actia diffidens</i>	•										•	
<i>Actia interrupta</i>	•		•	•	•	•	•	•		•	•	
<i>Ceromasia auricaudata</i>			•		•		•	•				
<i>Compsilura concinnata</i>			•								•	•
<i>Cyzenis incrassata</i>							•	•				
<i>Eumea caesar</i>	•	•	•	•	•		•	•	•	•	•	
<i>Hemisturmia parva</i>			•	•	•		•	•		•	•	•
<i>Hyphantrophaga blanda</i>											•	
<i>Hyphantrophaga virilis</i>							•					
<i>Lypha fumipennis</i>	•		•	•	•		•	•		•	•	
<i>Madremyia saundersii</i>	•		•	•	•		•	•	•	•		
<i>Nemorilla pyste</i>			•	•	•		•		•	•	•	•
<i>Nilea erecta</i>			•	•	•		•			•	•	•
<i>Phryxe pecosensis</i>	•		•	•	•		•			•	•	
<i>Smidtia fumiferanae</i>	•		•	•	•		•			•		

Parasitism by Tachinidae is generally low in endemic populations of *Choristoneura* species, but may be high periodically and locally and is sometimes associated with a budworm outbreak or the declining phase of an outbreak. Examples of high parasitism are cited below for individual species to provide some indication of the relative importance of each as a *Choristoneura* parasitoid. Because these rates were obtained by researchers using a variety of collecting protocols and methods of analysis, they may not be directly comparable among the studies.

Most of the Nearctic *Choristoneura* species in Table 1 have one generation per year, with the notable exception of *C. rosaceana*, which has two generations per year over most of its range. In contrast, the tachinids in Table 1 have two or more generations per year, except for a single generation in *Lypha fumipennis* and usually *Smidtia fumiferanae*. For this reason, most tachinids attacking *Choristoneura* species require alternate hosts to complete their second and later generations, and their ability to respond to *Choristoneura* outbreaks is limited not only by their intrinsic abilities to reproduce but by the availability of alternate hosts.

This paper provides keys to the puparia and adults of the 15 occasional or common tachinid parasitoids of Nearctic *Choristoneura* species (Table 1). These keys and their associated illustrations supersede the puparial key by Ross (1952) and adult key by Coppel (1960). Additionally, the life history of each species is reviewed and *Choristoneura* host records are listed as completely as possible at the beginning of each species. Thirteen species of Tachinidae recorded from *Choristoneura* species but excluded from the main text as highly dubious, rare, or accidental records are briefly discussed.

Materials and Methods

This study was based on a review of the literature, examination of reared material, taxonomic study of problematic species (*Ceromasia auricaudata*, see O'Hara & Wood 2004; *Lypha fumipennis*, see O'Hara 2002), and consultation with ecologists studying the parasitoids of Nearctic *Choristoneura*. The keys were based on puparia and adults housed in the Canadian National Collection of Insects in Ottawa. Morphological terms follow McAlpine (1981).

The names of *Choristoneura* species have been corrected to conform with modern usage as much as possible (Dang 1992). Some published rearings may have included more than one species, so multiple names are shown in some columns of Table 1 and in the lists of host records at the beginning of each species in the text. Tachinid names are those recognized by O'Hara & Wood (2004).

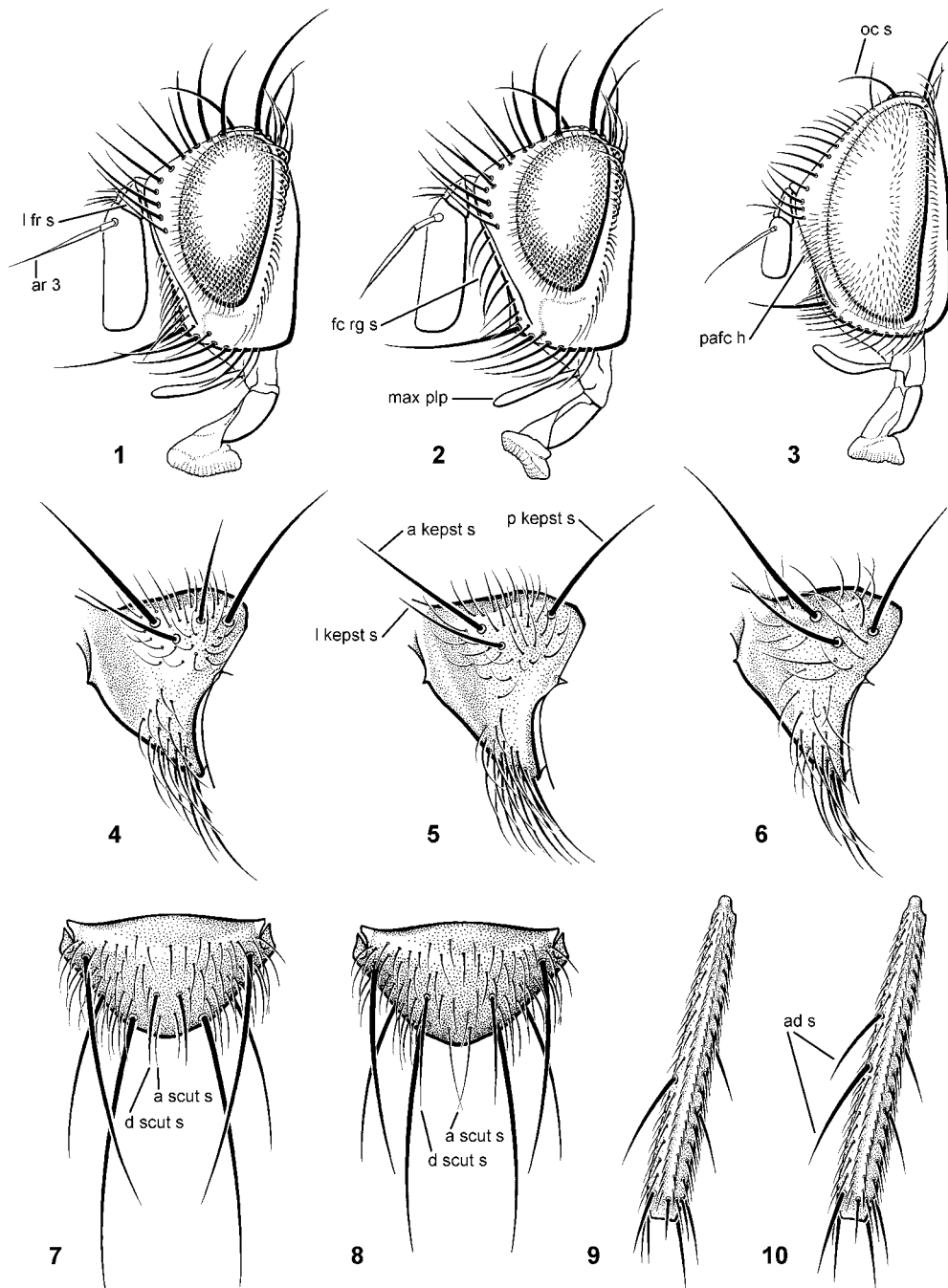
A dagger symbol (†) is used in the lists of host records to denote a record that was based on previously published information. For example, the host-parasite catalogue of Arnaud (1978) was based entirely on previously published records and is therefore always cited with a dagger in the lists of host records. In papers combining new and published records (e.g., O'Hara 1991), a dagger is placed next to previously published state or province records.

Colour habitus images (Figs. 37–50) were taken with a Leaf Microlumina digital camera mounted on a Wild M8 stereoscopic microscope. To create images with greater depth of field, several digital images of each specimen were taken at different focal planes and manually blended into montage images using Adobe Photoshop 6.01. Insect pins passing through specimens were digitally removed. Images of puparia (Figs. 22–36, b & c) were

taken with a Nikon Coolpix 995 digital camera mounted on a Nikon SMZ-U stereoscopic microscope. Multiple images were blended into a single image for each puparial view using Syncrosopy AutoMontage 4.0. Line drawings (Figs. 1–13) were modified from existing images in Wood (1987) and O'Hara (1991) using Adobe Photoshop CS (= Photoshop version 8). Images in Figs. 14–21 were taken in digital format with a scanning electron microscope. Adobe Photoshop CS was used for all final manipulation of images and preparation of plates.

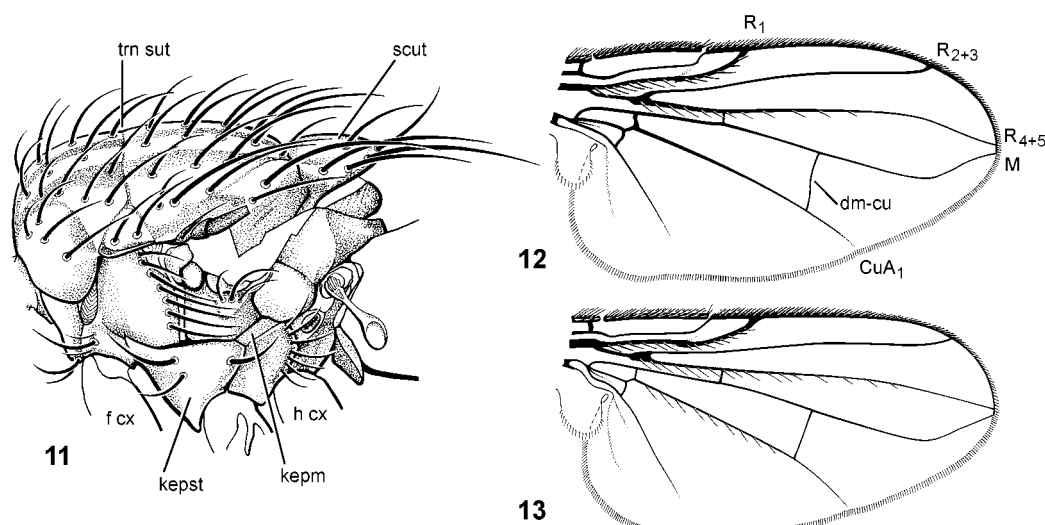
Key to adults of tachinid parasitoids of Nearctic *Choristoneura* species

1. Eye bare or very sparsely haired 2
 - Eye densely haired (Figs. 1–3) 4
2. Wing vein R_1 bare dorsally *Ceromasia auricaudata*
 - Wing vein R_1 haired dorsally along most of its length (Figs. 12–13) 3
3. Wing vein CuA_1 usually bare dorsally (very rarely with 1–3 hairs) and distal portion of CuA_1 0.27–0.38 length of proximal portion (Fig. 12); male with flagellomere 1 not enlarged (Fig. 37) *Actia diffidens*
 - Wing vein CuA_1 usually haired dorsally most of distance to crossvein *dm-cu* (very rarely with as few as 4 hairs) and distal portion of CuA_1 0.37–0.51 length of proximal portion (Fig. 13); male with flagellomere 1 enlarged (Fig. 38) *Actia interrupta*
4. Prosternum bare *Lypha fumipennis*
 - Prosternum haired (Fig. 14) 5
5. Katepisternum with four setae (Fig. 4) *Nilea erecta*
 - Katepisternum with two or three setae (Figs. 5–6, 11) 6
6. Facial ridge haired on 1/2 or more of distance between vibrissa and lower margin of scape (Figs. 1–2) 7
 - Facial ridge haired on 1/3 or less of distance between vibrissa and lower margin of scape (Fig. 3) 11
7. Eye very large, distance between eye and lower margin of head in lateral view not wider than basal width of maxillary palpus (Fig. 43); two katepisternal setae; katepimeron haired along most of length *Hemisturmia parva*
 - Eye smaller, distance between eye and lower margin of head in lateral view several times wider than basal width of maxillary palpus (Figs. 1–2); three katepisternal setae (Figs. 5–6); katepimeron bare or with one to several hairs anteriorly (Fig. 11) 8
8. Maxillary palpus (Fig. 2) dark coloured; katepisternum with lowermost seta nearly equidistant between outer two setae (Fig. 6) 9
 - Maxillary palpus yellow; katepisternum with lowermost katepisternal seta closer to anterior than posterior seta (as in Fig. 5) 10



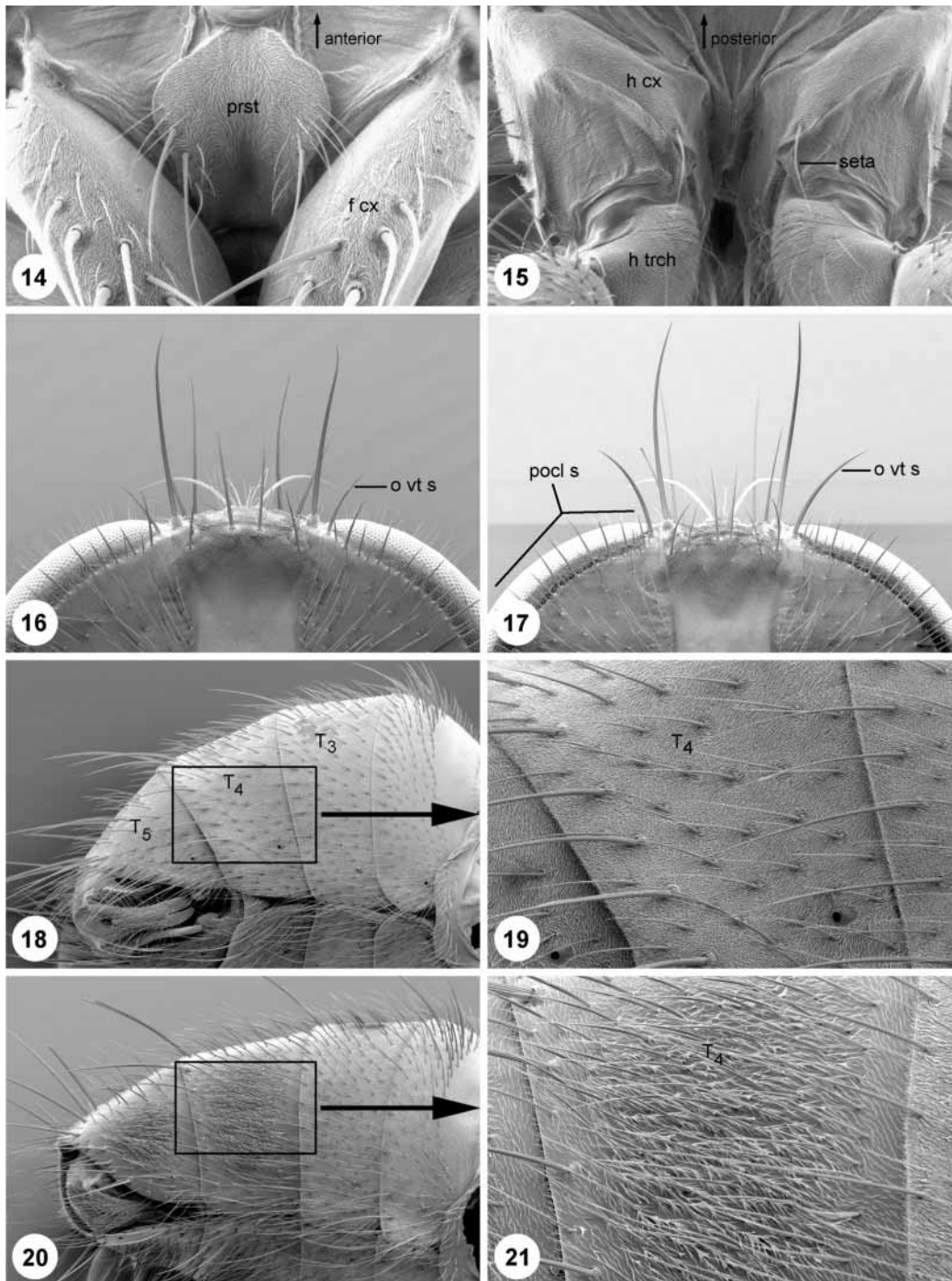
FIGURES 1–10. 1. *Phryxe pecosensis*, male head. 2. *Madremyia saundersii*, male head. 3. *Smidtia fumiferanae*, male head. 4. *Nilea erecta*, katepisternum. 5. *Eumea caesar*, katepisternum. 6. *Phryxe pecosensis*, katepisternum. 7. *Cyzenis incrassata*, scutellum. 8. *Compsilura concinnata*, scutellum. 9. *Hyphantrophaga blanda*, dorsal view of mid leg. 10. *Eumea caesar*, dorsal view of mid leg.

Abbreviations: ad s, anterodorsal setae; a kepst s, anterior katepisternal seta; ar 3, aristomere 3; a scut s, apical scutellar seta; d scut s, discal scutellar seta; fc rd s, facial ridge setae; l fr s, lowermost frontal seta; l kepst s, lowermost katepisternal seta; max plp, maxillary palpus; oc s, ocellar seta; pafc h, parafacial hairs; p kepst s, posterior katepisternal seta.



FIGURES 11–13. 11. Lateral view of tachinid thorax. 12. *Actia diffidens*, right wing. 13. *Actia interrupta*, right wing.
 Abbreviations (not including veins and crossveins): f cx, fore coxa; h cx, hind coxa; kepm, katepimeron; kepst, katepisternum; trn sut, transverse suture.

- 9. Facial ridge with hairs decreasing to tiny size on upper portion of haired area (Fig. 1); aristomere 3 evenly tapered to tip (Fig. 1) *Phryxe pecosensis*, in part
- Facial ridge with strong setae only (Fig. 2); aristomere 3 thickened along most of length and tapered near tip (Fig. 2) *Madremyia saundersii*
- 10. Scutellum (Fig. 11) with posterior half orange; discal scutellar setae narrowly separated, distance between them not greater than distance between apical scutellar setae (Fig. 7); female with tiny non-piercing ovipositor; ocellar setae well developed (as in Fig. 3)
- Scutellum mostly gray; discal scutellar setae more widely spaced, distance between them twice the distance between apical scutellar setae (Fig. 8); female with long piercing ovipositor (Fig. 40); ocellar setae usually absent or very weak
- *Compsilura concinnata*
- 11. Parafacial with fine hairs on middle portion (Fig. 3) *Smidtia fumiferanae*
- Parafacial bare (Figs. 1–2) or with a few hairs directly below lowermost frontal seta... .. 12
- 12. Mid tibia with one anterodorsal seta (Fig. 9) 13
- Mid tibia with two or more anterodorsal setae (Fig. 10) 15
- 13. Hind coxa bare on posteroapical margin; dorsal surface of thorax anterior to transverse suture (Fig. 11) with three black stripes when viewed from behind, centre stripe along midline *Nemorilla pyste*



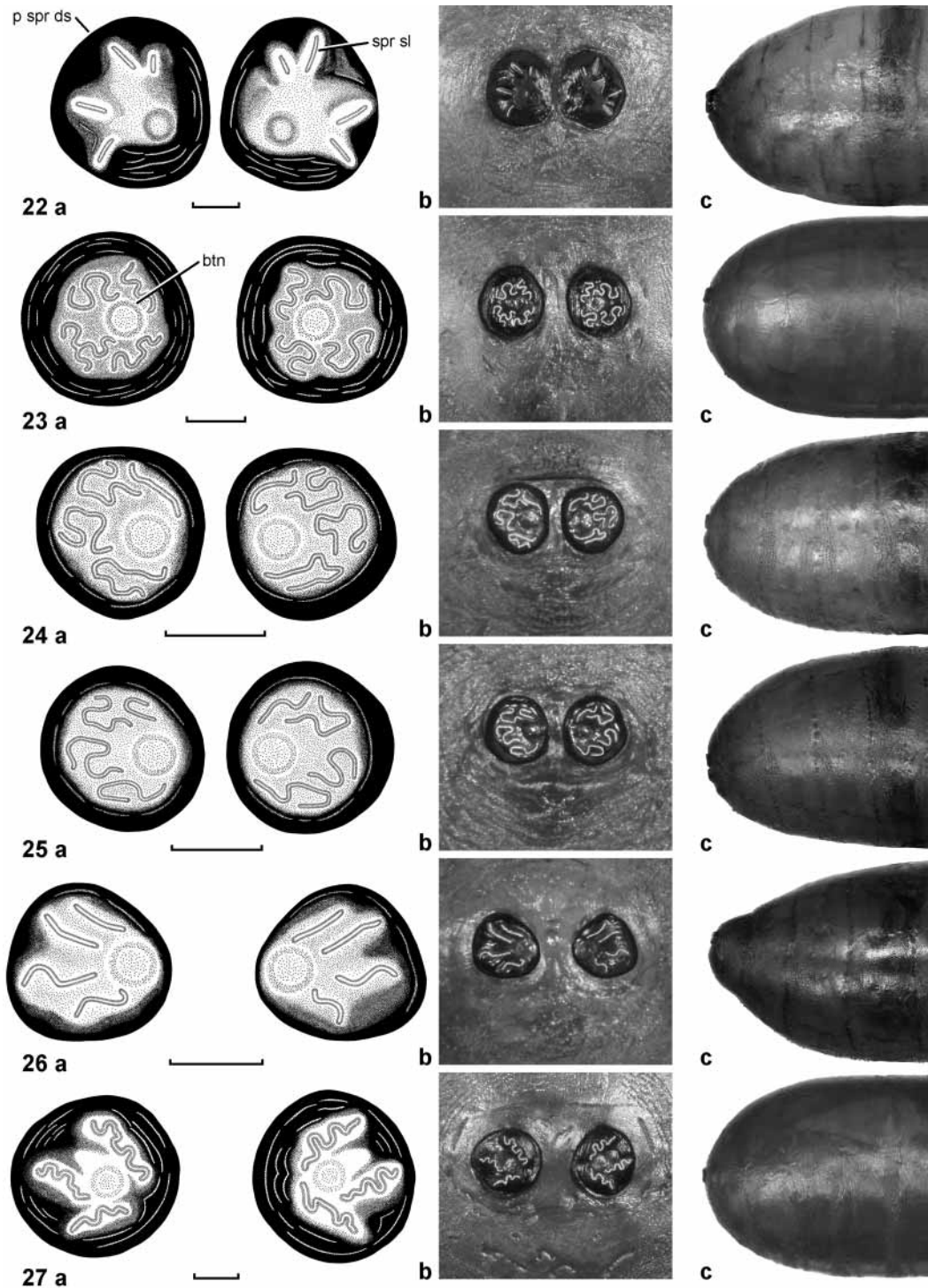
FIGURES 14–21. 14. Ventral view of prosternum of *Hyphantrophaga virilis*. 15. Posteroventral view of hind coxae of *Hyphantrophaga blanda*. 16. Posterior view of head of *Hyphantrophaga blanda*, female. 17. Posterior view of head of *Hyphantrophaga virilis*, female. 18. Ventral view of abdomen of *Hyphantrophaga blanda*, male. 19. Magnified view of area shown in Fig. 18. 20. Ventral view of abdomen of *Hyphantrophaga virilis*, male. 21. Magnified view of area shown in Fig. 20.

Abbreviations: f cx, fore coxa; h cx, hind coxa; h trch, hind trochanter; o vt s, outer vertical seta; pocl s, row of postocular setae; prst, prosternum; T3, T4, T5, abdominal tergites 3, 4, 5.

- Hind coxa with one or more setae on posteroapical margin (Fig. 15); dorsal surface of thorax anterior to transverse suture with four black stripes when viewed from behind, inner two stripes to either side of midline 14
- 14. Male with underside of abdominal tergites 4 and 5 silver pruinose and with regular black hairs only (Figs. 18–19); female with outer vertical seta only slightly stronger than setae of postocular row (Fig. 16) *Hyphantrophaga blanda*
- Male with underside of abdominal tergites 4 and 5 dark coloured and with a mat of tiny fine hairs in addition to regular (and much longer) black hairs (Figs. 20–21); female with outer vertical seta much stronger than setae of postocular row (Fig. 17) ..
..... *Hyphantrophaga virilis*
- 15. Parafacial with a few hairs below lowermost frontal seta; scutellum (Fig. 11) dark coloured; katapisternum with lowermost seta closer to anterior than posterior seta (Fig. 5) *Eumea caesar*
- Parafacial bare below lowermost frontal seta (Fig. 1); scutellum with posterior half orange; katapisternum with lowermost seta nearly equidistant between outer two setae (Fig. 6) *Phryxe pecosensis*, in part

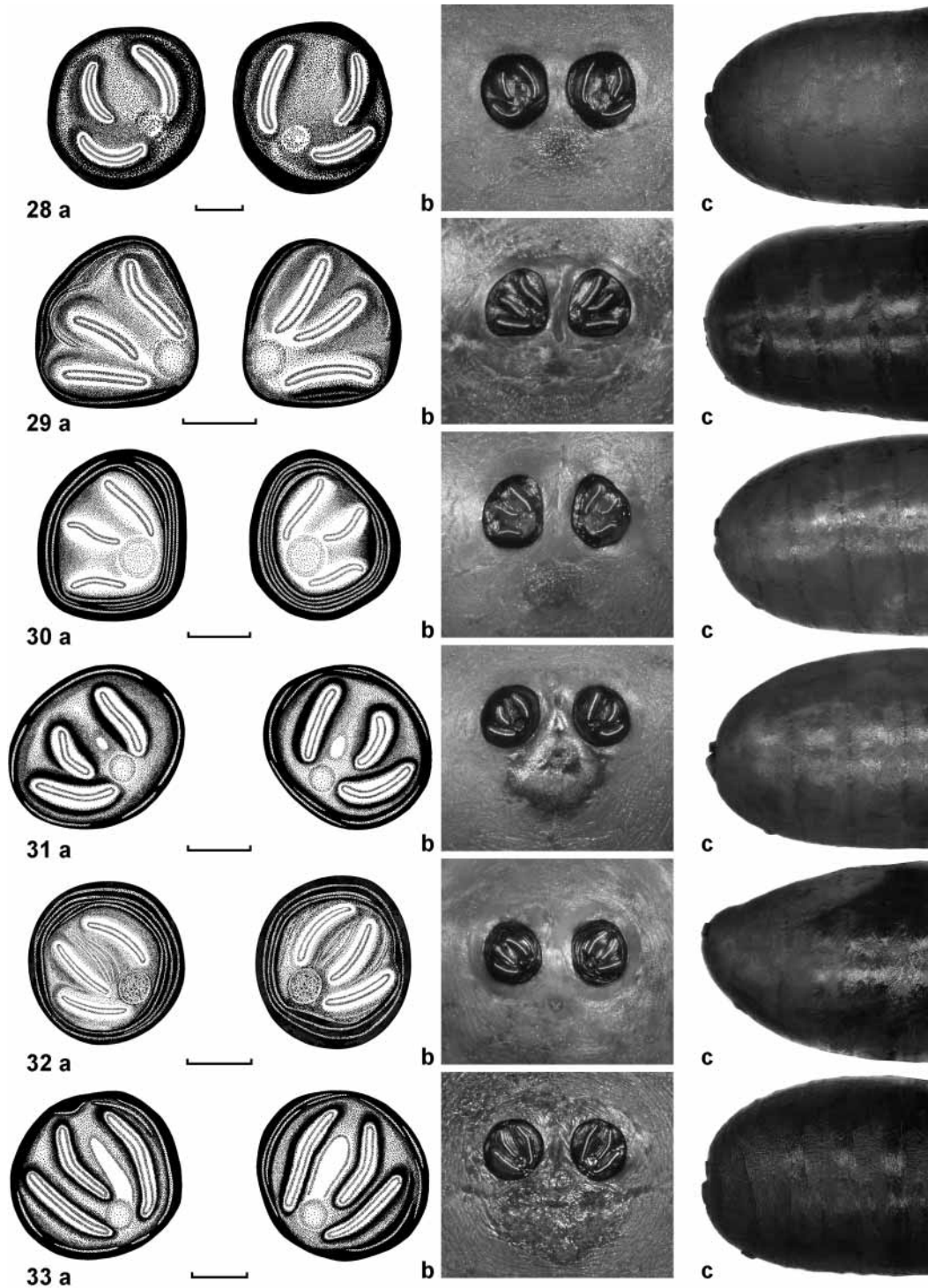
Key to puparia of tachinid parasitoids of Nearctic *Choristoneura* species

1. Posterior spiracular discs borne on a cylindrical projection that is about as long as wide (Fig. 36) *Actia interrupta*
- Posterior end of puparium without such a projection (Figs. 22–35) 2
2. Slits of posterior spiracular discs broadened considerably (Fig. 35) *Actia diffidens*
- Slits narrow (Figs. 22–34) 3
3. Each posterior spiracular disc with three slits (Figs. 27–34) 4
- Each posterior spiracular disc with four slits (Figs. 22–26) 12
4. Prominent bulge present below posterior spiracular discs, much broader and higher than a single disc (Figs. 31, 33) 5
- Bulge below posterior spiracular discs absent or small, not higher or broader than a single disc (Figs. 28–30, 32) 7
5. Posterior spiracular discs scarcely raised above surface of puparium, with shallow grooves between spiracular slits; bulge below spiracular discs rarely extended dorsally to region between discs (Fig. 33) *Smidtia fumiferanae*
- Posterior spiracular discs protruding above surface of puparium, with deep grooves between spiracular slits; bulge below spiracular discs varied along dorsal edge (Figs. 28, 31) 6
6. Bulge below spiracular discs very prominent, raised off surface of puparium to at least height of posterior spiracular discs and upper portion between discs (Fig. 31)
..... *Hemisturmia parva*



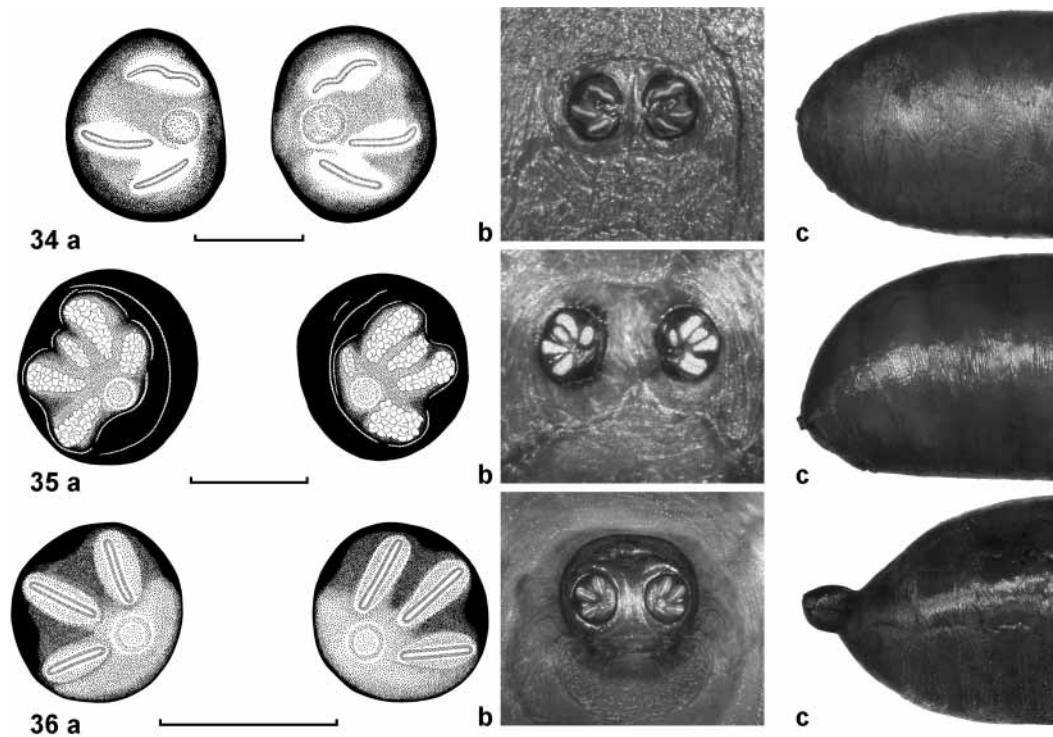
FIGURES 22–27. Tachinid puparia. **a**, posterior view of posterior spiracular discs (scale bar = 0.1 mm); **b**, posterior view of posterior spiracular discs and surrounding region; **c**, lateral view of posterior half of puparium. **22.** *Cyzenis incrassata*. **23.** *Hyphantrophaga blanda*. **24.** *Madremyia saundersii*. **25.** *Phryxe pecosensis*. **26.** *Nilea erecta*. **27.** *Hyphantrophaga virilis*. Abbreviations: btn, button; p spr ds, posterior spiracular disc; spr sl, spiracular slit.

- Bulge below spiracular discs smaller, rarely raised off surface of puparium to height of posterior spiracular discs and rarely developed between discs (bulge scarcely developed in some specimens, see couplet 10 and Fig. 28) .. *Ceromasia auricaudata*, in part
- 7. Slits of posterior spiracular discs sinuous (Fig. 27) *Hyphantrophaga virilis*
- Slits of posterior spiracular discs straight or gently curved (Figs. 28–30, 32, 34) 8
- 8. Puparium posteriorly with dorsal surface depressed slightly or flat anterior to spiracular discs and ventral surface broadly rounded; spiracular discs situated high above midline of puparium in lateral view and often slightly upturned; spiracular discs small, round, and raised above surface of puparium (Fig. 32) *Nemorilla pyste*
- Puparium posteriorly more or less evenly rounded on upper and lower surfaces; spiracular discs near midline of puparium and not upturned; spiracular discs varied in size, shape, and height (Figs. 28–30, 34) 9
- 9. Surface of puparium posteriorly very wrinkled; spiracular discs small, more or less round in shape; no trace of a bulge medially below spiracular discs (Fig. 34)
..... *Lypha fumipennis*
- Surface of puparium posteriorly mostly smooth, only rarely with conspicuous and close-set wrinkles; spiracular discs larger, more or less round to subtriangular in shape; slight bulge present or absent medially below spiracular discs, bulge generally darker in colour than surrounding area (Figs. 28–30) 10
- 10. Posterior spiracular discs raised above surface of puparium, with deep grooves between spiracular slits (Fig. 28) *Ceromasia auricaudata*, in part
- Posterior spiracular discs scarcely raised above surface of puparium, with shallow grooves between spiracular slits (Figs. 29–30) 11
- 11. Outer ring of posterior spiracular disc black, contrasting with mostly reddish orange surface of disc between spiracular slits; black outer ring not noticeably thinned next to button (Fig. 30) *Eumea caesar*
- Entire posterior spiracular disc mostly black, with reddish orange restricted to small areas between spiracular slits; black region much thinned next to button (Fig. 29)
..... *Compsilura concinnata*
- 12. Slits of posterior spiracular discs straight or gently curved (Figs. 22, 26) 13
- Slits of posterior spiracular discs more sinuous, forming convoluted patterns (Figs. 23–25) 14
- 13. Posterior spiracular discs raised above surface of puparium; discs entirely black and shiny except for light-coloured spiracular slits; spiracular slits short and straight; spiracular discs close together; posterior end of puparium rounded or very slightly pointed (Fig. 22) *Cyzenis incrassata*
- Posterior spiracular discs almost flat against surface of puparium; button and spiracular slits reddish orange, some specimens with rest of disc between slits also reddish orange; spiracular slits longer and straight or gently curved; spiracular discs usually separated by at least 1/3 the width of a disc; posterior end of puparium usually slightly protuberant (Fig. 26) *Nilea erecta*



FIGURES 28–33. Tachinid puparia. **a**, posterior view of posterior spiracular discs (scale bar = 0.1 mm); **b**, posterior view of posterior spiracular discs and surrounding region; **c**, lateral view of posterior half of puparium. **28.** *Ceromasia auricaudata*. **29.** *Compsilura concinnata*. **30.** *Eumea caesar*. **31.** *Hemisturmia parva*. **32.** *Nemorilla pyste*. **33.** *Smidtia fumiferanae*.

- 14. Posterior spiracular discs positioned above midline of puparium in lateral view; button close to centre of disc; surface of puparium surrounding discs relatively smooth except for tiny spinules (Fig. 23) *Hyphantrophaga blanda*
 - Posterior spiracular discs positioned at or below midline of puparium in lateral view; button close to edge of disc; surface of puparium more rugose posteriorly, especially below discs (Figs. 24–25) 15
 - 15. Cuticle slightly bulged above posterior spiracular discs, forming a fine edge of cuticle across the top of the discs (bulge rarely faint or lacking) (Fig. 24) *Madremyia saundersii*
 - Cuticle flat above posterior spiracular discs (Fig. 25) *Phryxe pecosensis*
- Note:** Ross (1952) noted that the central portion of the posterior spiracular disc is lighter in *M. saundersii* than in *P. pecosensis*, i.e., more reddish orange than black. Though this difference seems to hold true for most specimens, there are nevertheless some exceptions. *Madremyia* and *Phryxe* are closely related genera and their puparia are quite similar.



FIGURES 34–36. Tachinid puparia. **a**, posterior view of posterior spiracular discs (scale bar = 0.1 mm); **b**, posterior view of posterior spiracular discs and surrounding region; **c**, lateral view of posterior half of puparium. **34.** *Lypha fumipennis*. **35.** *Actia diffidens*. **36.** *Actia interrupta*.

TABLE 2. Reproductive strategies used by tachinid parasitoids of Nearctic *Choristoneura* species.

Species and their systematic placement	Egg type and mode of attack	Approximate no. of eggs produced
Exoristinae		
Blondeliini		
<i>Compsilura concinnata</i>	incubated egg injected into host with a piercing ovipositor ²	50–200 ³
Eryciini		
<i>Madremyia saundersii</i>	incubated egg laid on host ⁴	ca. 100 ⁴
<i>Nilea erecta</i>	incubated egg laid on host ¹	ca. 100 ¹
<i>Phryxe pecosensis</i>	incubated egg laid on host ⁵	<100 ⁵
Goniini		
<i>Ceromasia auricaudata</i>	incubated microtype egg ingested by host ⁶	>1000 ⁶
<i>Cyzenis incrassata</i>	incubated microtype egg ingested by host ⁷	ca. 1000 ⁷
<i>Eumea caesar</i>	incubated microtype egg ingested by host ⁸	ca. 1000 ⁸
<i>Hyphantrophaga blanda</i>	incubated microtype egg ingested by host ⁹	ca. 1000 ⁹
<i>Hyphantrophaga virilis</i>	incubated microtype egg ingested by host ¹	ca. 1000 ¹
Winthemiini		
<i>Hemisturmia parva</i>	unincubated egg laid on host ¹	<100 ¹
<i>Nemorilla pyste</i>	unincubated egg laid on host ¹	<100 ¹
<i>Smidtia fumiferanae</i>	unincubated egg laid on host ¹⁰	80–180 ¹⁰
Tachininae		
Polideini		
<i>Lypha fumipennis</i>	incubated egg laid near host ¹¹	<150 ¹¹
Siphonini		
<i>Actia diffidens</i>	incubated egg laid near host ¹	ca. 100 ¹
<i>Actia interrupta</i>	incubated egg laid near host ¹	ca. 100 ¹

¹ Inferred from systematic placement of genus and known habits of related taxa.² Culver (1919).³ Inferred from number of ovarioles reported in females, which varied according to female size (Bourchier 1991).⁴ Coppel and Maw (1954b).⁵ Maw and Coppel (1953).⁶ Coppel and Maw (1954a).⁷ Coppel (1958).⁸ Wishart (1945).⁹ Thompson (1953).¹⁰ Hébert et al. (1989).¹¹ Inferred from biology of European *L. dubia* (Schröder 1969).

Reproductive strategies of tachinid parasitoids of *Choristoneura* species

One of the reasons why the Tachinidae are so successful is their varied repertoire of reproductive strategies (O'Hara 1985). These strategies, which encompass both behavioral and morphological traits, are an outcome of the phylogenetic history of the Tachinidae and hence are reflected in the more recent classifications of the family (Herting 1984; Wood 1987; O'Hara & Wood 2004). Species that are phylogenetically close tend to have similar reproductive strategies and be classified together in the same genus or tribe. By grouping the 15 tachinid species treated here according to their tribe and subfamily (Table 2), certain commonalities in reproductive type become more evident.

Members of the Winthemiini are presumably among the more primitive tachinids, lacking the ability to develop ("incubate") their eggs internally. The eggs of winthemiines must be laid directly on a host and generally require a few days for the first instar to develop before hatching can occur.

The rest of the tachinids treated here belong to lineages in which fertilized eggs are retained and incubated within the female reproductive system. The eggs are ready to hatch immediately after oviposition. Eggs may be laid on or near a host, laid on foliage and consumed by a host, or injected into a host. *Compsilura concinnata*, a member of the Blondeliini, employs the last method; the female possesses a piercing ovipositor which is used to inject eggs singly into a host. Most other blondeliines lay their incubated eggs on or near a host, as do eryciines. The eggs of these taxa hatch after deposition and the motile first instar actively finds and parasitizes a host.

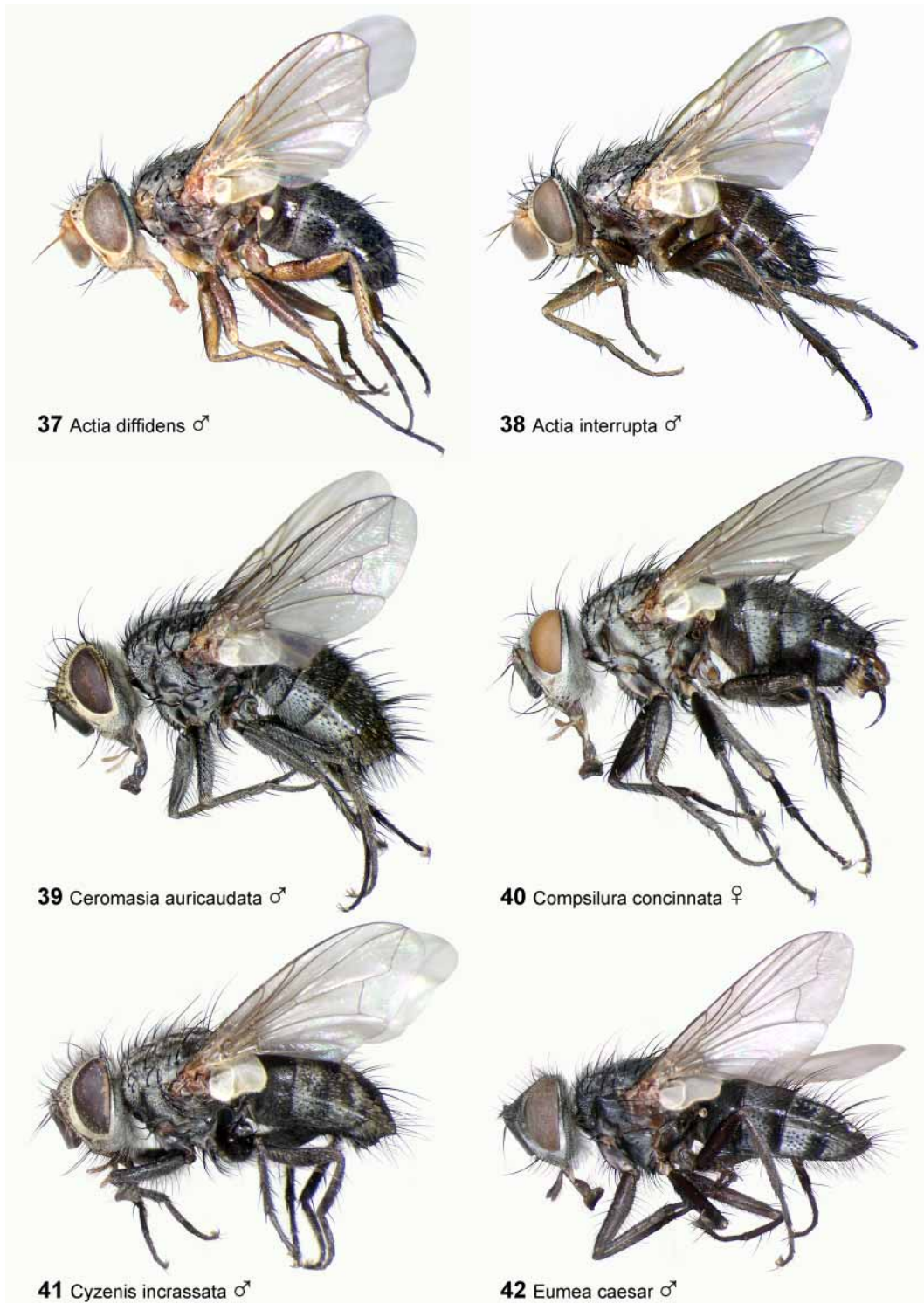
Goniines have the curious adaptation of producing tiny ("microtype") eggs that are laid on foliage and do not hatch until ingested by a potential host. The likelihood of a successful parasitization per egg is extremely low but this reproductive strategy is countered by a ten-fold increase in the number of eggs produced compared to tachinids with more typical strategies. One-third of the tachinids that parasitize *Choristoneura* belong to the Goniini. These species have the reproductive potential to respond quickly to an outbreak but may be limited by the availability of alternate hosts.

Two species belong to the Siphonini and one to the Polideini, both in the Tachinae. Members of this subfamily deposit eggs that are ready to hatch. In some taxa the eggs are laid near a host and the first instar searches for it, whereas in other taxa the first instar stays rooted to the remains of the egg and waits for a host to pass by. It is likely that the three polideine and siphonine species treated here lay eggs in the vicinity of a host and the first instar actively seeks out its prey.

Actia diffidens Curran, 1933, Fig. 37

Host records ex. *Choristoneura conflictana*: Prentice 1955 (SK, MB); O'Hara 1991 (†SK, MB); †Arnaud 1978 (SK, MB); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura rosaceana*: O'Hara 1991 (ON); †Huber *et al.* 1996 (America north of Mexico).



FIGURES 37–42. Habitus images. 37. *Actia diffidens*. 38. *Actia interrupta*. 39. *Ceromasia auricaudata*. 40. *Compsilura concinnata*. 41. *Cyzenis incrassata*. 42. *Eumea caesar*.

This species is an uncommonly recorded parasitoid of *Choristoneura* species. It is similar in size and appearance to *A. interrupta* except that wing vein CuA_1 is almost always bare dorsally (only rarely with one to several hairs; veins R_1 and R_{4+5} haired as in *A. interrupta*; cf. Figs. 12 and 13). *Actia diffidens* is common and widespread throughout Canada and the northern and eastern United States, with scattered records throughout the rest of the United States and Mexico (O'Hara 1991). The first instar of *A. diffidens* was figured by O'Hara (1988) and the adult was redescribed by O'Hara (1991) in his revision of the Nearctic species of *Actia*. The three larval instars, pupa, and puparium were described and illustrated by Prebble (1935).

Prebble (1935) studied parasitism of the tortricid *Acleris variana* (Fernald) (as *Pero-nea variana*) by *A. diffidens* in Nova Scotia. He found that adult *A. diffidens* appeared in June, parasitism of third to fifth instar *A. variana* occurred from late June to mid July, and fully developed maggots emerged from their hosts and formed puparia from mid July to mid August. Known hosts of *A. diffidens* are mostly Tortricidae but include a few species of Geometridae, Gracillariidae, Noctuidae, and Pyralidae (Arnaud 1978; O'Hara 1991).

Actia interrupta Curran, 1933, Fig. 38

Host records ex. *Choristoneura conflictana*: Prentice 1955 (SK, MB); O'Hara 1991 (†MB, SK); †Arnaud 1978 (SK, MB); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura fumiferana*: Daviault 1946, ex. *Archips fumiferana* (QC); Reeks *et al.* 1948 (Maritime provinces and NF); Daviault 1950 (QC); Dowden *et al.* 1951, ex. *Archips fumiferana* (NY); Miller 1955, as *Gymnophthalma interrupta* (NB); McGugan & Blais 1959 (ON); Blais 1960 (QC); MacDonald & Webb 1963 (NB); †Miller 1963 (NB); Blais 1965 (QC); †Tilles & Woodley 1984 (ME); Huber *et al.* 1996 (NB); Cappuccino *et al.* 1998 (QC); Cappuccino *et al.* 1999 (QC); Schoenmaker *et al.* 2001 (QC); †Smith *et al.* 2002 (eastern Canada); Cusson *et al.* 2002 (QC).

Host records ex. *Choristoneura fumiferana* and/or *Choristoneura occidentalis*: Brown 1941 ex. *Cacoecia fumiferana* (Canada); Dowden *et al.* 1948, ex. *Archips fumiferana* (North America); †Zwolfer 1961, ex. *C. fumiferana* (North America); †Arnaud 1978, ex. *C. fumiferana* (BC, OR, ON, QC, NB, NF, NY); O'Hara 1991, ex. *C. fumiferana* (BC, ID, †OR, CO, AB, MB, ON, QC, NB, NF, NY, VT).

Host records ex. *Choristoneura fumiferana*, *Choristoneura occidentalis* and/or *Choristoneura pinus*: †Ross 1952, ex. spruce and/or jack pine budworm (Canada).

Host records ex. *Choristoneura lambertiana*: O'Hara 1991 (MT); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura occidentalis*: McKnight 1974 (CO); Harris & Dawson 1979 (BC); O'Hara 1991 (BC, ID, MT); †Huber *et al.* 1996 (America north of Mexico).

Host records probably ex. *Choristoneura occidentalis*: Bedard 1938, as *Actia pilipennis* ex. *Cacoecia fumiferana* on Douglas fir ("northern Rocky Mountain region"); Wilkes *et al.* 1949, as *Gymnophthalma interrupta* ex. *C. fumiferana* (BC); Carolin & Coulter 1959, ex. *C. fumiferana* (OR); †Coppel 1960, as *Gymnophthalma interrupta* ex. *C. fumiferana* (BC).

Host records ex. *Choristoneura occidentalis* and/or *Choristoneura retiniana*: Schaupp *et al.* 1991 (OR).

Host records ex. *Choristoneura pinus*: Benjamin & Drooz 1954 (MI); Dixon & Benjamin 1963 (WI); Allen *et al.* 1969 (MI); †Arnaud 1978 (WI, MI); O'Hara 1991 (MB, ON, †WI, MI); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura rosaceana*: Schuh & Mote 1948, ex. *Archips rosaceana* (OR); Neunzig & Gyrisco 1955 (NY); †Arnaud 1978 (OR, NY); Hagley & Barber 1991 (ON); O'Hara 1991 (†OR, ON, NS, NY); †Huber *et al.* 1996 (America north of Mexico); Wilkinson *et al.* 2004 (MI).

Actia interrupta is a very small tachinid, generally 4–5mm long, that is easily recognized among the species treated here by the dorsally haired wing veins R_1 , R_{4+5} and CuA_1 (Fig. 13). It is a common and widespread species found mostly in wooded areas from Alaska and British Columbia to Newfoundland, and south to California in the West and Virginia and Tennessee in the East (O'Hara 1991). *Actia interrupta* was included in a key to the puparia of dipterous parasitoids of *Choristoneura* species by Ross (1952) and in a key to the adults of dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia by Coppel (1960, as *Gymnophthalma interrupta*). Tilles and Woodley (1984) included *A. interrupta* among the five tachinids treated in their manual of spruce budworm parasitoids in Maine. O'Hara (1991) redescribed *A. interrupta* and figured portions of its puparium in his revision of the Nearctic species of *Actia*.

Eggs laid by *Actia* females contain fully developed first instars that hatch soon after oviposition. It is likely that the eggs are laid in the vicinity of a host and the first instar actively searches for the host.

Actia interrupta attacks conifer-feeding *Choristoneura* species as late instar larvae, usually attacking the fifth or sixth instar but occasionally the fourth, and emerges from the sixth instar (Dowden *et al.* 1948; Miller 1955; Carolin & Coulter 1959; Cusson *et al.* 2002). *Choristoneura rosaceana* is apparently attacked earlier, from the third instar onwards, with emergence from the third to sixth instar (Bostanian, pers. comm.; Westbrook, pers. comm.). There are two or more generations per year (Schaffner 1959, Westbrook, pers. comm.), with a variety of alternate hosts. Fully developed maggots pupariate away from the host and the species overwinters in the pupal stage (Tilles & Woodley 1984).

Actia interrupta is frequently recorded from *Choristoneura* species, but parasitism rates are generally low. However, Blais (1965) recorded up to 32% parasitism in a residual *C. fumiferana* outbreak in Québec, and Schaupp *et al.* (1991) reported 40% parasitism in an endemic population of *Choristoneura* sp. in southern Oregon. Schaupp *et al.* (1991) noted that *A. interrupta* is usually rare in epidemic populations of conifer-feeding *Choristoneura* species. The relatively low fecundity of *A. interrupta* (probably not more than a hundred or so eggs, compared to thousands in goniine tachinids that produce microtype eggs) may limit its ability to respond quickly to outbreaks.

Hosts of *A. interrupta* include about 25 species of Tortricidae and a species each of Geometridae and Notodontidae (Arnaud 1978; O'Hara 1991).

***Ceromasia auricaudata* Townsend, 1908, Fig. 39**

Host records ex. *Choristoneura fumiferana*: †Dowden *et al.* 1948, as *Masicera rutila* ex. *Archips fumiferana* (eastern North America); Blais 1960 (QC); Huber *et al.* 1996, as *Ceromasia aurifrons* (NB) and *C. auricaudata* (†America north of Mexico).

Host records ex. *Choristoneura fumiferana*, *Choristoneura occidentalis* and/or *Choristoneura pinus*: †Ross 1952, as *Ceromasia aurifrons* and *C. auricaudata* ex. spruce and/or jack pine budworm (Canada); †Arnaud 1978, as *Ceromasia aurifrons* (Canada) and *C. auricaudata* (BC, OR, CO, ON, QC) ex. *C. fumiferana*.

Host records ex. *Choristoneura occidentalis*: McKnight 1974 (CO); Harris & Dawson 1979 (BC); Schmid 1981 (NM); Torgersen *et al.*, 1984 (WA, OR, ID, MT); †Harris & Dawson 1985 (BC); †Torgersen 1985 (WA, OR, ID, MT).

Host records probably ex. *Choristoneura occidentalis*: Tothill 1913, as *Masicera rutila* ex. *Tortrix fumiferana* (BC); Wilkes 1946, ex. *Archips fumiferana* (BC); Coppel 1947, ex. *Archips fumiferana* (BC); Dowden *et al.* 1948, ex. *Archips fumiferana* (western North America); †Wilkes 1949, ex. *Archips fumiferana* (BC); Wilkes *et al.* 1949, ex. *C. fumiferana* (BC); Coppel 1953, ex. *C. fumiferana* (BC); Carolin & Coulter 1959, ex. *C. fumiferana* (OR); †Coppel 1960, ex. *C. fumiferana* (BC); †Zwolfer 1961, ex. *C. fumiferana* (BC); †Graham & Jones 1962, ex. *C. fumiferana* (BC); †McGugan & Coppel 1962, ex. *C. fumiferana* (BC); †Clausen 1978, ex. *C. fumiferana* (BC).

Host records ex. *Choristoneura occidentalis* and/or *Choristoneura retiniana*: Schaupp *et al.* 1991 (OR).

Ceromasia aurifrons and *C. auricaudata* were considered to be distinct species until recently, with the former having an eastern distribution and the latter a western distribution (e.g., Sabrosky & Arnaud 1965). O'Hara and Wood (2004) synonymized *C. aurifrons* with *C. auricaudata* and gave the known distribution of this species as transcontinental in Canada and ranging southward to California, New Mexico, Kansas, and Massachusetts. Adults are typically 7–9mm long, rather robust, and mostly gray with a mottled abdomen. The head and tip of the abdomen are usually golden, though less so in eastern specimens. The egg, three larval instars, and puparium of *C. auricaudata* were described and illustrated by Coppel and Maw (1954a). *Ceromasia auricaudata* was included in a key to the puparia of dipterous parasitoids of *Choristoneura* species by Ross (1952, as separate species *C. aurifrons* and *C. auricaudata*) and in a key to the adults of dipterous parasitoids of *Choristoneura occidentalis* (as *C. fumiferana*) in British Columbia by Coppel (1960).

Ceromasia auricaudata belongs to the Goniini and produces microtype eggs that are ingested by the host. Further information on general goniine biology is given below under *Cyzenis incrassata*. *Ceromasia auricaudata* attacks late instar larvae of *Choristoneura* species and the mature maggot emerges from the host pupa and pupariates in the soil (Dowden *et al.* 1948; Coppel & Maw 1954a; Carolin & Coulter 1959). In a study of *C. occidentalis* parasitism in British Columbia by Harris and Dawson (1979), emergence from sixth instar hosts as well as from host pupae was reported. Adult flies emerge from their puparia in about 9–11 days (Coppel & Maw 1954a).

Adults of the second generation of *C. auricaudata* overwinter in alternate hosts including pupae of the fall webworm, *Hyphantria cunea* (Drury) (Coppel 1947). The few other

known hosts of *C. auricaudata* include two tortricids, a species each of Geometridae and Noctuidae, and three species of Pieridae and Pyralidae that served as hosts under laboratory conditions (Arnaud 1978, including records from “*C. aurifrons*”).

The rate of parasitism of *C. auricaudata* in conifer-feeding *Choristoneura* is negligible in the East but significant in the West, with parasitism of up to 13% reported by Wilkes *et al.* (1949) and up to 16% reported by Harris & Dawson (1979) in British Columbia, and up to 13% reported by Schaupp *et al.* (1991) in Oregon. Wilkes *et al.* (1949) ranked *C. auricaudata* as the fourth most important parasitoid, and second most important dipterous parasitoid, of *C. occidentalis* (as *C. fumiferana*) in British Columbia.

Efforts were made during the 1940s and 1950s to establish several western species of budworm parasitoids in eastern Canada to help control outbreaks of *Choristoneura fumiferana*. Among these was *C. auricaudata*, which was reared in huge numbers in Belleville, Ontario, from budworms collected mostly from the Lillooet area of British Columbia (Wilkes 1946; Coppel 1947). About 21,000 *C. auricaudata* were released in eastern Canada between 1944 and 1953, with an additional 2363 specimens released in Maine and 6317 specimens released in New York during this period (McGugan & Coppel 1962; Clausen 1978). There is no evidence that any western *C. auricaudata* became established in the East. Blais (1960) recorded a single *C. auricaudata* from Québec, but that specimen could well have represented parasitism from the endemic population of the species. The only other published report of *C. auricaudata* parasitizing *Choristoneura fumiferana* in the East is that of Huber *et al.* (1996, as *C. aurifrons*) based on a rearing record from New Brunswick.

***Compsilura concinnata* (Meigen, 1824), Fig. 40**

Laboratory experiment ex. *Choristoneura fumiferana*: Dowden *et al.* 1948, ex. *Archips fumiferana* (lab. experiment in northeastern United States); †Arnaud 1978; †Huber *et al.* 1996.

Host records ex. *Choristoneura rosaceana*: Wilkinson *et al.* 2004 (MI); four specimens from QC (examined), from unpublished data of N. Bostanian (Agriculture and Agri-Food Canada, St. Jean-sur-Richelieu).

Host records ex. *Choristoneura rosaceana* and/or *Pandemis limitata*: Cossentine *et al.* 2004 (BC).

Compsilura concinnata is a mostly gray tachinid with four conspicuous, black, longitudinal stripes on the thorax and a black-and-gray banded abdomen. Adults are typically 7–8mm long but some individuals are as small as 4mm. *Compsilura concinnata* was introduced repeatedly into North America from Europe throughout the 1900s for control of a number of lepidopterous pests, most notably the gypsy moth (*Lymantria dispar* (L.)) and browntail moth (*Euproctis chrysorrhoea* (L.)). It became established and is presently recorded from most of southern Canada and the northeastern and western United States (O’Hara & Wood 2004). Because *C. concinnata* is continuing to expand its range, it may well be more widely distributed than current records suggest.

Compsilura concinnata is an extremely polyphagous parasitoid that has been reared from nearly 200 species of Lepidoptera, Hymenoptera (Symphyta), and Coleoptera in North America (Arnaud 1978; Boettner *et al.* 2000). Females have a long piercing ovipositor that is used to inject thin-shelled eggs into the body of a host. The eggs hatch immediately and the first instars migrate to the midgut, where they develop within the narrow space between the peritrophic membrane and midgut wall (Ichiki & Shima 2003). The species has two or more generations per year, often alternating hosts throughout the season, and can develop gregariously in larger hosts (Culver 1919; Webber & Schaffner 1926; Schaffner & Griswold 1934). The maggot overwinters within the host prepupa or pupa and emerges in the spring to pupariate nearby (Culver 1919; Webber & Schaffner 1926).

Compsilura concinnata has been recorded only recently from *C. rosaceana* (see host records above) but readily parasitizes *C. fumiferana* in the laboratory (Dowden *et al.* 1948) and hence has the potential to be a significant budworm parasitoid. It is the most polyphagous tachinid known and its parasitism of *Choristoneura* species will likely occur whenever suitable opportunities arise. Parasitism of *Choristoneura* larvae can occur only during a summer generation of *C. concinnata*.

Cyzenis incrassata (Smith, 1912), Fig. 41

Host records ex. *Choristoneura occidentalis*: Torgersen, *et al.* 1984, as *Phorocera incrassata* (WA, OR, ID, MT); †Torgersen 1985, as *P. incrassata* (WA, OR, ID, MT); O'Hara & Cooper 1992 (BC, OR, NM); †Huber *et al.* 1996 (America north of Mexico).

Host records probably ex. *Choristoneura occidentalis*: Wilkes 1946, as *Phorocera incrassata* ex. *Archips fumiferana* (BC); Coppel 1947, as *P. incrassata* ex. *A. fumiferana* (BC); †Dowden *et al.* 1948, as *P. incrassata* ex. *A. fumiferana* (western North America); †Wilkes 1949, as *P. incrassata* ex. *A. fumiferana* (BC); Wilkes *et al.* 1949, as *P. incrassata* ex. *C. fumiferana* (BC); †Ross 1952, as *P. incrassata* ex. spruce and/or jack pine budworm (Canada); Coppel 1958, as *P. incrassata* ex. *C. fumiferana* (BC); Carolin & Coulter 1959, as *P. incrassata* ex. *C. fumiferana* (OR); †Coppel 1960, as *P. incrassata* ex. *C. fumiferana* (BC); †Zwolfer 1961, as *Clemelis incrassata* ex. *C. fumiferana* (BC); †Graham & Jones 1962, as *P. incrassata* ex. *C. fumiferana* (BC); †McGugan & Coppel 1962, as *P. incrassata* ex. *C. fumiferana* (BC); †Arnaud 1978, as *P. incrassata* ex. *C. fumiferana* (BC, OR); †Clausen 1978, as *P. incrassata* ex. *C. fumiferana* (BC); †Huber *et al.* 1996, ex. *C. fumiferana* (America north of Mexico).

Host records ex. *Choristoneura occidentalis* and/or *C. retiniana*: Schaupp *et al.* 1991, as *Phorocera incrassata* (OR); †O'Hara & Cooper 1992 (OR).

Cyzenis incrassata is a grayish black tachinid about 5–7.5mm long with a known range comprising British Columbia, Washington, Idaho, Oregon, and New Mexico (O'Hara & Cooper 1992; O'Hara & Wood 2004). Attempts to establish *C. incrassata* in eastern Canada were unsuccessful (McGugan & Coppel 1962; O'Hara & Cooper 1992). The Nearctic species of *Cyzenis* were revised, and *C. incrassata* redescribed, by O'Hara and Cooper (1992). *Cyzenis incrassata* (as *Phorocera incrassata*) was included in a key to the puparia of dipterous parasitoids of *Choristoneura* species by Ross (1952) and in a key to the adults

of dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia by Coppel (1960). The egg, larval instars, and puparium of *Cyzenis incrassata* were described and illustrated by Coppel (1958). Records of *Cyzenis incrassata* parasitizing *C. fumiferana* in western North America are likely erroneous and based on misidentifications of *C. occidentalis*.

Cyzenis belongs to the Goniini (Exoristinae), a tribe characterized by the production of huge numbers of microtype eggs in the female reproductive system (Herting 1984; Wood 1987). These eggs are deposited on foliage, sometimes in response to feeding damage (Roland *et al.* 1989), and contain fully developed first instars. The eggs are ingested by a feeding host and pass unharmed into the gut, where they soon hatch under the influence of digestive enzymes and perhaps physical trauma (Mellini 1990). First instars burrow through the gut wall and move to specific locations within the host (Mellini 1990). In the case of *Cyzenis incrassata*, the first instar delays development until the host begins to pupate, then rapidly completes larval development and forms a puparium within the host's pupal case (Coppel 1958). Adults emerge from their puparia after 12–14 days (Coppel 1958).

Adults of *Cyzenis incrassata* appear in June in British Columbia and attack maturing *C. occidentalis* larvae (Coppel 1958). Adults of the next generation appear in July and early August when *C. occidentalis* larvae are unavailable. *Cyzenis incrassata* must therefore overwinter in an alternate host, but its identity has not been determined (Coppel 1958). *Choristoneura* species remain almost exclusively the only known hosts of this species (Arnaud 1978; O'Hara & Cooper 1992).

Wilkes *et al.* (1949) ranked *Cyzenis incrassata* (as *Phorocera incrassata*) as the eighth most important parasitoid, and fifth most important dipterous parasitoid, of *C. occidentalis* (as *C. fumiferana*) in British Columbia, with an average parasitism rate of 1.1% during 1943–1947. Other studies have reported similarly low levels of parasitism, e.g., 0.008–0.500% in British Columbia (Coppel 1958) and 0.0–2.5% in Oregon (Schaupp *et al.* 1991, with higher rates found in epidemic than endemic populations).

***Eumea caesar* (Aldrich, 1916), Fig. 42**

Host records ex. *Choristoneura conflictana*: Prentice 1955 (SK, MB); †Arnaud 1978, as *Aplomya caesar* (SK, MB); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura fractivittana*: †Wishart 1945, as *Aplomya caesar* ex. *Archips "practivittana"* (North America); †Arnaud 1978, as *Aplomya caesar* (North America); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura fumiferana*: Wilkes & Anderson 1947, as *Zenillia caesar* ex. *Archips fumiferana* (ON, QC); Daviault 1950, as *Aplomyia caesar* (QC); Dowden *et al.* 1951, as *Aplomya caesar* ex. *Archips fumiferana* (NY); Jaynes & Drooz 1952, as *Aplomya caesar* (NY, ME); Raizenne 1952, as *Epimasicera caesar* (ON); Dowden *et al.* 1953, as *Aplomya caesar* (ME); Miller 1955, as *Aplomya caesar* (NB); McGugan & Blais 1959 (ON); Blais 1960 (QC); MacDonald & Webb 1963, as *Aplomya caesar* (NB); †Miller 1963 (NB); Blais 1965

(QC); †Tilles & Woodley 1984, as *Aplomya caesar* (ME); Hébert *et al.* 1989 (QC); Huber *et al.* 1996 (NB).

Host records ex. *Choristoneura fumiferana* and/or *Choristoneura occidentalis*: Tothill 1913, as *Exorista nigripalpis* ex. *Tortrix fumiferana* (BC, QC); Brown 1941, as *Zenillia caesar* ex. *Cacoecia fumiferana* (Canada); Sellers 1943, as *Aplomya caesar* ex. *Archips fumiferana* (North America); †Wishart 1945, as *Aplomya caesar* ex. *Archips fumiferana* (North America); Dowden *et al.* 1948, as *Aplomya caesar* ex. *Archips fumiferana* (North America); †Zwolfer 1961, ex. *C. fumiferana* (North America); †Arnaud 1978, as *Aplomya caesar* ex. *C. fumiferana* (BC, OR, ON, QC, NB, NF, NY, ME).

Host records ex. *Choristoneura fumiferana*, *Choristoneura occidentalis* and/or *Choristoneura pinus*: †Ross 1952, as *Aplomya caesar* ex. spruce and/or jack pine budworm (Canada).

Host records ex. *Choristoneura occidentalis*: McKnight 1974, as *Aplomya caesar* (CO); Harris & Dawson 1979, as *Aplomya caesar* (BC).

Host records probably ex. *Choristoneura occidentalis*: Wilkes *et al.* 1949, as *Aplomya caesar* ex. *C. fumiferana* (BC); Coppel 1953, as *Zenillia caesar* ex. *C. fumiferana* (BC); Carolin & Coulter 1959, as *Aplomya caesar* ex. *C. fumiferana* (OR); †Coppel 1960, ex. *C. fumiferana* (BC).

Host records ex. *Choristoneura occidentalis* and/or *Choristoneura retiniana*: Schaupp *et al.* 1991, as *Aplomya caesar* (OR).

Host records ex. *Choristoneura parallela*: Sellers 1943, as *Aplomya caesar* ex. *Archips parallela* (North America); †Wishart 1945, as *Aplomya caesar* ex. *Archips parallela* (North America); †Arnaud 1978, as *Aplomya caesar* (North America); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura pinus*: Drooz & Benjamin 1956, as *Aplomya caesar* (Michigan); Kulman & Hodson 1961, as *Aplomya caesar* (Minnesota); Dixon & Benjamin 1963, as *Aplomya caesar* (Wisconsin); Allen *et al.* 1969, as *Aplomya caesar* (Michigan); †Arnaud 1978, as *Aplomya caesar* (Minnesota, Wisconsin, Michigan); Nealis 1991 (ON); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura rosaceana*: †Wishart 1945, as *Aplomya caesar* ex. *Archips rosaceana* (North America); Raizenne 1952, as *Epimasicera caesar* ex. *Archips rosaceana* (ON); †Arnaud 1978, as *Aplomya caesar* (ON); †Huber *et al.* 1996 (America north of Mexico).

Eumea caesar is a common tachinid found throughout temperate and boreal Canada, and south to California and Texas in the West and Virginia in the East (O'Hara & Wood 2004). Adults are generally 7–8mm long and mostly black with a black-and-gray banded abdomen. It was included in a key to the puparia of dipterous parasitoids of *Choristoneura* species by Ross (1952, as *Aplomya caesar*) and in a key to the adults of dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia by Coppel (1960). Wishart (1945) described and illustrated the immature stages of *E. caesar* (as *Aplomya caesar*) and provided a detailed account of larval development in the European corn borer (*Ostrinia nubilalis* (Hübner)). Tilles and Woodley (1984) included *E. caesar* (as *Aplomya caesar*) among the five tachinids treated in their manual of spruce budworm parasitoids in Maine.

Eumea caesar belongs to the Goniini, and like other members of that tribe produces microtype eggs that are laid on foliage and ingested by the host (see *Cyzenis incrassata* above for further information on goniine biology). It parasitizes fifth or sixth instar budworms, and the fully developed maggot emerges from the sixth instar or pupa and pupariates away from the host (Dowden *et al.* 1951; Carolin & Coulter 1959; Allen *et al.* 1969;

Hébert *et al.* 1989). *Eumea caesar* has more than one generation per year and occasionally two maggots emerge from a single *Choristoneura* host (Dowden *et al.* 1951). Dowden *et al.* (1951) reported that *E. caesar* overwinters in an alternate host, whereas Tilles and Woodley (1984) stated that it overwinters as a pupa in the soil.

Eumea caesar is recorded from a number of Tortricidae and six other families of Microlepidoptera (Arnaud 1978, as *Aplomya caesar*). Parasitism of *Choristoneura* species in western North America is reportedly low (Carolin & Coulter 1959; McKnight 1974; Harris & Dawson 1979; Schaupp *et al.* 1991) and *E. caesar* (as *Aplomya caesar*) was not included by Wilkes *et al.* (1949) in the top 15 hymenopterous and dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia. Parasitism of budworms in the East is also usually low but there are several reports of rates in excess of 25% (Dowden *et al.* 1948; Jaynes & Drooz 1952; Blais 1965). Parasitism of *C. pinus* was reported as low by Drooz and Benjamin (1956) in Michigan, by Dixon and Benjamin (1963) in Wisconsin, and by Nealis (1991) in Ontario, but as high as 13% in a study by Allen *et al.* (1969) in Michigan.

***Hemisturmia parva* (Bigot, 1889), Fig. 43**

Host records ex. *Choristoneura fumiferana*: Dowden *et al.* 1951, as *Phorocera tortricis* ex. *Archips fumiferana* (NY); Huber *et al.* 1996, as *Hemisturmia tortricis* (NB).

Host records ex. *Choristoneura fumiferana* and/or *Choristoneura occidentalis*: †Arnaud 1978, as *Hemisturmia tortricis* ex. *C. fumiferana* (BC, NY).

Host records ex. *Choristoneura fumiferana*, *Choristoneura occidentalis* and/or *Choristoneura pinus*: †Ross 1952, as *Phorocera tortricis* ex. spruce and/or jack pine budworm (Canada).

Host records ex. *Choristoneura occidentalis*: Harris & Dawson 1979, as *Hemisturmia tortricis* (BC).

Host records probably ex. *Choristoneura occidentalis*: Wilkes *et al.* 1949, as *Phorocera tortricis* ex. *C. fumiferana* (BC); †Coppel 1960, as *Ceratochaeta tortricis* ex. *C. fumiferana* (BC).

Host records ex. *Choristoneura occidentalis* and/or *Choristoneura retiniana*: Schaupp *et al.* 1991, as *Hemisturmia tortricis* (OR).

Host records ex. *Choristoneura pinus*: Dixon & Benjamin 1963, as *Phorocera tortricis* (WI); †Arnaud 1978, as *Hemisturmia tortricis* (WI); †Huber *et al.* 1996, as *Hemisturmia tortricis* (America north of Mexico).

Host records ex. *Choristoneura rosaceana*: Schuh & Mote 1948, as *Phorocera tortricis* ex. *Archips rosaceana* (OR); †Arnaud 1978, as *Hemisturmia tortricis* (OR); †Huber *et al.* 1996, as *Hemisturmia tortricis* (America north of Mexico); Li *et al.* 1999, as *Hemisturmia tortricis* (BC); †Li *et al.* 2002, as *Hemisturmia tortricis* (BC); Wilkinson *et al.* 2004 (MI).

Host records ex. *Choristoneura rosaceana* and/or *Pandemis limitata*: Vakenti *et al.* 2001, as *Hemisturmia tortricis* (BC); Cossentine *et al.* 2004 (BC).

Hemisturmia parva is found throughout most of the forested regions of North America (O'Hara & Wood 2004). Adults are generally 5–7.5mm long, rather dark coloured, with an exceptionally large eye, a striped or black thorax, mostly orange scutellum, and banded or mottled abdomen. *Hemisturmia parva* was included in a key to the puparia of dipterous

parasitoids of *Choristoneura* species by Ross (1952, as *Phorocera tortricis*) and in a key to the adults of dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia by Coppel (1960, as *Ceratochaeta tortricis*).

Hemisturmia belongs to the Winthemiini, a tribe in which the females oviposit unincubated eggs directly on a host (Wood 1987). The first instar probably develops within the egg for several days, then exits the egg and burrows into the host. *Hemisturmia parva* attacks late instar larvae of *Choristoneura* and emerges from the larva or, more commonly, the pupa (Schuh & Mote 1948; Harris & Dawson 1979; Li *et al.* 1999). It has at least two generations per year and its method of overwintering is not known (Schaffner 1959). Parasitism rates are rarely above 1% in *Choristoneura* species (Dixon & Benjamin 1963; Harris & Dawson 1979; Schaupp *et al.* 1991; Li *et al.* 1999). Wilkes *et al.* (1949) did not include *H. parva* (as *Phorocera tortricis*) among the 15 dominant hymenopterous and dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia, and Tilles and Woodley (1984) excluded it from their manual of spruce budworm parasitoids in Maine.

Hemisturmia parva is recorded from more than ten species of Tortricidae and a species each in the families Glyphipterygidae, Nymphalidae, Pterophoridae, and Pyralidae (Arnaud 1978, as *H. tortricis*; Fitzpatrick *et al.* 1994, as *H. tortricis*).

***Hyphantrophaga blanda* (Osten Sacken, 1887)**

Host records ex. *Choristoneura rosaceana*: Wilkinson *et al.* 2004 (MI).

Hyphantrophaga blanda and *H. virilis* are, at best, uncommon parasitoids of *Choristoneura* species. They are included here rather than classed as accidental parasitoids of *Choristoneura* because a record each of *H. blanda* and *H. virilis* parasitizing different species of *Choristoneura* suggests that such parasitization is more opportunistic than accidental, and probably occurs occasionally. Both species are small to medium-sized tachinids (5–8mm long), mostly gray with four black stripes on the thorax and a lightly banded abdomen. They are widely distributed throughout North America (O'Hara & Wood 2004).

Sellers (1930) examined reared specimens of *H. blanda* and *H. virilis* (both as species of *Zenillia* Robineau-Desvoidy) and described differences between the species in the puparium and both sexes of the adult. Thompson (1953) described and illustrated the egg, larval instars, and puparium of *H. blanda*.

Hyphantrophaga is a member of the Goniini, producing microtype eggs that are laid on foliage and consumed by a host (see *Cyzenis incrassata* above; also Thompson 1953). Records from a number of hosts indicate that the mature maggot of both *H. blanda* and *H. virilis* generally emerges from the host pupa but sometimes forms a puparium within the host (Sellers 1930). Similarly, Ciesla (1964) reported that *H. blanda* (as *Eusisyropa blanda*) emerges from the pupa of *Ennomos subsignaria* (Hübner) (Geometridae). How-

ever, Burgess and Crossman (1927) reported the emergence of *H. blanda* (as *Zenillia blanda*) from the larva of *Leucoma salicis* (L.) (as *Stilpnotia salicis*; Lymantriidae), and Evans (1962) reported the emergence of *H. virilis* (as *Eusisyropa virilis*) from the larva of *Melanolophia imitata* (Walker) (Geometridae). Sellers (1930) found that both *H. blanda* and *H. virilis* overwinter as larvae in the host pupa, and noted that “if parasitic on hosts producing adults in the same season, both parasites completed their development that season; but if parasitic on hosts that pass the winter in the pupal stage and emerge the following spring or summer, the flies likewise did not emerge until the following spring” (p. 574). There are usually two generations per year and multiparasitism can occur in larger hosts (Schaffner & Griswold 1934; Schaffner 1959).

Sellers (1930) examined the host records for *H. blanda* and *H. virilis* and found that only about one-third of the hosts known for these two species are shared. They are parasitoids of a wide variety of Lepidoptera, attacking hosts belonging to about 15 families. *Hyphantrophaga blanda* is a well known parasitoid of several tortricids, especially *Archips* species (Sellers 1930; Arnaud 1978, as *Eusisyropa blanda*).

***Hyphantrophaga virilis* (Aldrich and Webber, 1924), Fig. 44**

Unpublished host record ex. *Choristoneura occidentalis*: one specimen from BC (examined), from collection of Pacific Forestry Centre, Victoria.

This species is discussed under *Hyphantrophaga blanda*.

***Lypha fumipennis* Brooks, 1945, Fig. 45**

Host records ex. *Choristoneura conflictana*: Prentice 1955, as *Lypha setifacies* (SK, MB); †Arnaud 1978, as *Lypha setifacies* ex. *C. fumiferana* (SK, MB); †Huber *et al.* 1996, as *Lypha setifacies* (America north of Mexico); O’Hara 2002 (AB, †SK, MB).

Host records ex. *Choristoneura fumiferana*: Brooks 1945, as *Lypha setifacies* ex. *Archips fumiferana* (ON, QC); Wilkes & Anderson 1947, as *Lypha setifacies* ex. *Archips fumiferana* (ON); Dowden *et al.* 1951, as *Lypha setifacies* ex. *Archips fumiferana* (NY); Jaynes & Drooz 1952, as *Lypha setifacies* (NY, ME); Miller 1955, as *Lypha setifacies* (NB); Dowden *et al.* 1953, as *Lypha setifacies* (ME); McGugan & Blais 1959, as *Lypha setifacies* (ON); Blais 1960, as *Lypha setifacies* (QC); MacDonald & Webb 1963, as *Lypha setifacies* (NB); †Miller 1963, as *Lypha setifacies* (NB); Blais 1965, as *Lypha setifacies* (QC); †Tilles & Woodley 1984, as *Lypha setifacies* (ME); Hébert *et al.* 1989, as *Lypha setifacies* (QC); Huber *et al.* 1996, as *Lypha setifacies* (NB); Bouchier & Smith 1998, as *Lypha setifacies* (ON); Cappuccino *et al.* 1999, as *Lypha setifacies* (QC); †Smith *et al.* 2002, as *Lypha setifacies* (eastern Canada); O’Hara 2002 (ON, †NB, †QC, †NY, ME).

Host records ex. *Choristoneura fumiferana* and/or *Choristoneura occidentalis*: Brown 1941, as *Lypha dubia* ex. *Cacoecia fumiferana* (Canada); †Dowden *et al.* 1948, as *Lypha setifacies* ex. *Archips fumiferana* (North America); †Zwolfer 1961, as *Lypha setifacies* ex. *C. fumiferana* (North America); †Arnaud 1978, as *Lypha setifacies* ex. *C. fumiferana* (BC, ON, QC, NB, ME, NY).

Host records ex. *Choristoneura fumiferana*, *Choristoneura occidentalis* and/or *Choristoneura pinus*: †Ross 1952, as *Lypha setifacies* ex. spruce and/or jack pine budworm (Canada).

Host records ex. *Choristoneura occidentalis*: O'Hara 2002 (BC, †OR).

Host records probably ex. *Choristoneura occidentalis*: Coppel 1947, as *Lypha setifacies* ex. *Archips fumiferana* (BC); Wilkes *et al.* 1949, as *Lypha setifacies* ex. *C. fumiferana* (BC); Coppel 1953, as *Lypha setifacies* ex. *C. fumiferana* (BC); Carolin & Coulter 1959, as *Lypha setifacies* ex. *C. fumiferana* (OR); †Coppel 1960, as *Lypha setifacies* ex. *C. fumiferana* (BC).

Host records ex. *Choristoneura occidentalis* and/or *Choristoneura retiniana*: Schaupp *et al.* 1991, as *Lypha setifacies* (OR).

Host records ex. *Choristoneura pinus*: Benjamin & Drooz 1954, as *Lypha setifacies* (MI); Dixon & Benjamin 1963, as *Lypha setifacies* (WI); Allen *et al.* 1969, as *Lypha setifacies* (MI); †Arnaud 1978, as *Lypha setifacies* (WI, MI); Nealis 1991, as *Lypha setifacies* (ON); †Huber *et al.* 1996, as *Lypha setifacies* (America north of Mexico); †Frankenhuyzen 2002, as *Lypha setifacies* (ON, prairie provinces); O'Hara 2002 (ON, †WI, †MI).

Host records ex. *Choristoneura rosaceana*: Brooks 1945, as *Lypha setifacies* ex. *Archips rosaceana* (QC); †Arnaud 1978, as *Lypha setifacies* (QC); †Huber *et al.* 1996, as *Lypha setifacies* (America north of Mexico); †O'Hara 2002 (QC).

Lypha fumipennis is a dark coloured tachinid, 5–7.5mm long, that occurs throughout southern Canada and the northern United States and is also recorded from Georgia (O'Hara 2002). It was redescribed by O'Hara (2002) in his revision of the Polideini of America north of Mexico. *Lypha fumipennis* (as *L. setifacies*) was included in a key to the puparia of dipterous parasitoids of *Choristoneura* species by Ross (1952) and in a key to the adults of dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia by Coppel (1960). Tilles and Woodley (1984) included *L. fumipennis* (as *L. setifacies*) among the five tachinid species treated in their manual of spruce budworm parasitoids in Maine.

Almost all the North American species of *Lypha* were combined under the name *L. dubia* (Fallén), a Palearctic species, until Brooks (1945) revised the Canadian species of the genus. Brooks did not examine the type series of *L. setifacies* (West), however, and O'Hara (2002) showed that Brooks misapplied this name. O'Hara (2002) discovered that the species described by Brooks as *L. intermedia* is in fact *L. setifacies*, and that the *L. setifacies* of Brooks is conspecific with the species Brooks (1945) described from British Columbia as *L. fumipennis*. Hence, the valid name for this *Choristoneura* parasitoid is *L. fumipennis*. Unfortunately, the name used by Brooks (i.e., *L. setifacies*) became entrenched in the literature on *Choristoneura* parasitoids because this species has long been known as a parasitoid of the spruce budworm.

Host attack by *L. fumipennis* has not been described but is probably similar to that of its Palearctic relative, *Lypha dubia* (Fallén). *Lypha dubia* deposits fully incubated eggs in the vicinity of a host, the eggs hatch soon afterwards, and the first instars search for and parasitize the host (Schröder 1969). *Lypha fumipennis* parasitizes fifth and sixth instar larvae of *Choristoneura* and the fully mature maggot emerges from the sixth instar of its host, or more rarely from the pupa (Benjamin & Drooz 1954; Carolin & Coulter 1959; Allen *et al.* 1969; Hébert *et al.* 1989). The maggot enters the ground, overwinters in the puparium,

and emerges as an adult in spring (Brooks 1945; Coppel 1947). Adults are only seen during spring and early summer (O'Hara 2002), so there is probably only one generation per year. Females of *L. dubia* in Europe live for 30–50 days, have a preoviposition period of approximately a month, and develop about 150 eggs (Schröder 1969).

Lypha fumipennis is one of the most significant tachinid parasitoids of late instar *Choristoneura* larvae. Most studies of budworm parasitism have reported its presence (as *L. setifacies*) and parasitism rates are sometimes high. Benjamin and Drooz (1954) and Allen *et al.* (1969) reported parasitism of up to 16% and 9% respectively in *C. pinus* in Michigan, Dowden *et al.* (1951) reported up to 18% parasitism of *C. fumiferana* in New York, Jaynes and Drooz (1952) reported up to 17% parasitism of *C. fumiferana* in Maine, Nealis (1991) found greater than 20% parasitism of *C. fumiferana* in northwest Ontario, and Wilkes *et al.* (1949) reported up to 10% parasitism of *C. occidentalis* (as *C. fumiferana*) in British Columbia. In several studies *L. fumipennis* was the most dominant, or one of the most dominant, parasitoids of late instar budworms (Benjamin & Drooz 1954; Tilles & Woodley 1984; Nealis 1991). *Lypha fumipennis* (as *L. setifacies*) was ranked by Wilkes *et al.* (1949) as the fifth most important parasitoid, and third most important dipterous parasitoid, of *C. occidentalis* (as *C. fumiferana*) in British Columbia. Jaynes and Drooz (1952), Nealis (1991), and Bouchier and Smith (1998) reported increased rates of spruce budworm parasitism prior to the collapse of an outbreak, suggesting that *L. fumipennis* may have played a role in budworm decline.

Lypha fumipennis is almost exclusively a parasitoid of *Choristoneura* species (O'Hara 2002). The other known hosts are a tortricid, *Pseudosciaphila duplex* (Walsingham), and a pyralid, *Dioryctria reniculelloides* (Mutuura & Munroe) (O'Hara 2002).

***Madremyia saundersii* (Williston, 1889), Fig. 46**

Host records ex. *Choristoneura conflictana*: Prentice 1955 (SK, MB); †Arnaud 1978 (SK, MB); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura fumiferana*: Dowden *et al.* 1951, ex. *Archips fumiferana* (NY); Miller 1955 (NB); Blais 1960 (QC); †Miller 1963 (NB); Blais 1965 (QC); Huber *et al.* 1996 (NB).

Host records ex. *Choristoneura fumiferana* and/or *Choristoneura occidentalis*: Dowden *et al.* 1948, ex. *Archips fumiferana* (North America); †Arnaud 1978, ex. *C. fumiferana* (BC, OR, QC, NB, NY); †Zwölfer 1961, as *Phryxe saundersii* ex. *C. fumiferana* (North America)

Host records ex. *Choristoneura fumiferana*, *Choristoneura occidentalis* and/or *Choristoneura pinus*: †Ross 1952, ex. spruce and/or jack pine budworm (Canada).

Host records ex. *Choristoneura occidentalis*: McKnight 1974 (CO); Harris & Dawson 1979 (BC); Schmid 1981 (NM); Torgersen *et al.*, 1984 (WA, OR, ID, MT); †Torgersen 1985 (WA, OR, ID, MT).

Host records probably ex. *Choristoneura occidentalis*: Bedard 1938, ex. *Cacoecia fumiferana* on Douglas fir (“northern Rocky Mountain region”); Wilkes *et al.* 1949, ex. *C. fumiferana* (BC); Coppel 1953, ex. *C. fumiferana* (BC); Carolin & Coulter 1959, ex. *C. fumiferana* (OR); †Coppel 1960, ex. *C. fumiferana* (BC).

Host records ex. *Choristoneura occidentalis* and/or *Choristoneura retiniana*: Schaupp *et al.* 1991 (OR).

Host records ex. *Choristoneura parallela*: Johnson 1925, ex. *Cacoecia parallela* (MA); Franklin 1950, ex. *Archips parallela* (MA); †Arnaud 1978 (MA); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura pinus*: Kulman & Hodson 1961 (MN); Dixon & Benjamin 1963 (WI); Allen *et al.* 1969 (MI); †Arnaud 1978 (MN, WI, MI); †Huber *et al.* 1996 (America north of Mexico).

Madremyia saundersii is a common and widespread species ranging from the Yukon and British Columbia to Newfoundland, and south to Mexico in the West and Virginia in the East (O'Hara & Wood 2004). Adults are generally 4.0–7.5mm long and mostly dark coloured with faint silvery bands on the abdomen. *Madremyia saundersii* was included in a key to the puparia of dipterous parasitoids of *Choristoneura* species by Ross (1952) and in a key to the adults of dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia by Coppel (1960). The egg, larval instars, and puparium were described by Coppel and Maw (1954b).

Madremyia belongs to the tribe Eryciini (in the Exoristinae) and is closely related to *Phryxe*, a species of which is treated below. The biology of *M. saundersii* was studied by Coppel and Maw (1954b). They observed that females deposit fully incubated eggs directly on the integument of a host. Soon after oviposition, the first instar exits from the end of the egg through the underside of the chorion and burrows into the host. Females generally lay 75–100 eggs during a lifetime of 20–60 days. Usually only one parasitoid emerges per host but multiparasitism also occurs. *Madremyia saundersii* attacks late instar larvae of *Choristoneura* species and emerges from the sixth instar or pupa (Dowden *et al.* 1948; Coppel & Maw 1954b; Carolin & Coulter 1959; Allen *et al.* 1969). The fully mature maggot falls to the ground and pupariates in the soil (Coppel & Maw 1954b). A second generation is passed in an alternate host, and perhaps a third generation as well (Schaffner & Griswold 1934; Coppel & Maw 1954b). Coppel and Maw (1954b) speculated that *M. saundersii* passes the winter as a first or second instar in an alternate host.

Parasitism of conifer-feeding *Choristoneura* species by *M. saundersii* has been reported as higher in western than eastern North America. Dowden *et al.* (1948) recorded emergence of *M. saundersii* from up to 6% of larvae and up to 14% of pupae in Colorado. Coppel and Maw (1954b) reported up to 7.5% parasitism in British Columbia. In Oregon, Carolin and Coulter (1959) reported parasitism approaching 10% and Schaupp *et al.* (1991) recorded parasitism as high as 13%; in both these studies there was an increase in parasitism as budworm outbreaks progressed. Wilkes *et al.* (1949) ranked *M. saundersii* as the twelfth most important parasitoid, and sixth most important dipterous parasitoid, of *C. occidentalis* (as *C. fumiferana*) in British Columbia. Dowden *et al.* (1951) and Blais (1960) reported very low parasitism of *C. fumiferana* in New York and Québec, respectively. In northwestern Ontario, McGugan and Blais (1959) did not rear *M. saundersii* from *C. fumiferana* and Nealis (1991) did not rear it from *C. pinus*. Tilles and Woodley

(1984) excluded *M. saundersii* from their treatment of spruce budworm parasitoids in Maine, presumably because of its rarity as a parasitoid of *C. fumiferana* in that state.

Madremyia saundersii has a broad host range of over 30 known species, including members of the Danaidae, Geometridae, Lasiocampidae, Lymantriidae, Noctuidae, Nymphalidae, Pieridae, Pyralidae, and Tortricidae (Arnaud 1978).

***Nemorilla pyste* (Walker, 1849), Fig. 47**

Host records ex. *Choristoneura fumiferana*: Tothill 1913, as *Exorista pyste* ex. *Tortrix fumiferana* (QC); Richmond 1941b, as *Nemorilla* [= *N. maculosa*] ex. *Cacoecia fumiferana* on spruce (SK, MB, ON); Daviault 1946, as *Nemorilla maculosa* ex. *Archips fumiferana* (QC); Dowden *et al.* 1951, as *Nemorilla floralis* ex. *Archips fumiferana* (NY); Raizenne 1952 (ON); McGugan & Blais 1959 (ON); Schaffner 1959, as *Nemorilla floralis* (northeastern United States); Blais 1960 (QC); Blais 1965 (QC); Huber *et al.* 1996 (NB).

Host records ex. *Choristoneura fumiferana* and/or *Choristoneura occidentalis*: Brown 1941, as *Nemorilla maculosa* ex. *Cacoecia fumiferana* (Canada); †Dowden *et al.* 1948, as *Nemorilla floralis* ex. *Archips fumiferana* (North America); †Zwolfer 1961, as *Nemorilla maculosa* ex. *C. fumiferana* (North America); †Arnaud 1978, ex. *C. fumiferana* (BC, OR, SK, MB, ON, QC, NY).

Host records ex. *Choristoneura fumiferana*, *Choristoneura occidentalis* and/or *Choristoneura pinus*: †Ross 1952, ex. spruce and/or jack pine budworm (Canada).

Host records ex. *Choristoneura occidentalis*: McKnight 1974 (CO).

Host records probably ex. *Choristoneura occidentalis*: Bedard 1938, as *Nemorilla floralis* ex. *Cacoecia fumiferana* on Douglas fir (“northern Rocky Mountain region”); Wilkes *et al.* 1949, ex. *C. fumiferana* (BC); Carolin & Coulter 1959, as *Nemorilla floralis* ex. *C. fumiferana* (OR); †Coppel 1960, ex. *C. fumiferana* (BC).

Host records ex. *Choristoneura parallela*: Franklin 1943, as *Nemorilla floralis* ex. *Cacoecia parallela* (MA); †Arnaud 1978 (MA); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura pinus*: Richmond 1938, as “*Hemorilla*” *maculosa* ex. spruce budworm, *Cacoecia fumiferana*, on jack pine (MB, ON); Richmond 1940, as *Nemorilla maculosa* ex. jack pine budworm, *Cacoecia fumiferana*, on jack pine (SK, MB, ON); Richmond 1941a, as *Nemorilla maculosa* ex. jack pine budworm, *Archips fumiferana*, on jack pine (SK); Dixon & Benjamin 1963, as *Nemorilla floralis* (WI); †Arnaud 1978 (WI); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura rosaceana*: Davis 1912, as *Exorista pyste* ex. *Archips rosaceana* (IL); Schaffner 1959, as *Nemorilla floralis* ex. *Archips rosaceana* (northeastern United States); †Arnaud 1978 (IL, northeastern United States); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura rosaceana* and/or *Pandemis limitata*: Pfannenstiel & Unruh 2003 (WA); Cossentine *et al.* 2004 (BC).

Nemorilla pyste is a common species that is widespread throughout Canada, the United States, and Mexico (O’Hara & Wood 2004). It is a dark coloured tachinid, generally 4.0–7.5mm long, with three black stripes on the thorax (median stripe quite broad) and a mottled abdomen. It was included in a key to the puparia of dipterous parasitoids of *Choristoneura* species by Ross (1952) and in a key to the adults of dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia by Coppel (1960).

The mode of oviposition has not been described for *Nemorilla pyste*, but is probably similar to that in other members of the tribe Winthemiini (including *Hemisturmia parva* and *Smidtia fumiferanae* of the species treated here). The female uses a telescopic ovipositor to attach eggs to the body of a host. The eggs hatch after several days and the first instar immediately burrows into the host. *Nemorilla pyste* attacks late instar larvae of *Choristoneura* species and emerges from the pupa (Davis 1912; Dowden *et al.* 1948; Carolin & Coulter 1959; McKnight 1974). It is likely, based on specimens of *N. pyste* in the Canadian National Collection of Insects reared from various hosts, that the tachinid either pupariates in the host pupa or emerges as a mature maggot and pupariates elsewhere. The parasitoid has two or more generations per year and overwinters as a larva in various hosts (Schaffner 1959).

Nemorilla pyste has been reported frequently as a parasitoid of *Choristoneura* species, but the level of parasitism was generally very low (Dixon & Benjamin 1963; Dowden *et al.* 1951; Carolin & Coulter 1959; McGugan & Blais 1959; Blais 1960; McKnight 1974). It was not ranked among the top 15 hymenopterous and dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia in a study by Wilkes *et al.* (1949), nor included among the parasitoids of spruce budworm in Maine by Tilles and Woodley (1984). However, during outbreaks of *C. pinus* in Saskatchewan in 1939 and 1940, *N. pyste* (as *N. maculosa*) was considered one of the most important parasitoids of the budworm (Richmond 1940; Richmond 1941a).

Nemorilla pyste has a broad host range. It is recorded from about 30 species in each of the Pyralidae and Tortricidae and has one to several hosts in each of the Gelechiidae, Glyphipterygidae, HesperIIDae, Lycaenidae, Lymantriidae, Noctuidae, Oecophoridae, and Yponomeutidae (Arnaud 1978).

Nilea erecta (Coquillett, 1902), Fig. 48

Host records ex. *Choristoneura fumiferana*: McGugan & Blais 1959, as *Pseudoperichaeta erecta* (ON); Blais 1960, as *Pseudoperichaeta erecta* (QC); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura fumiferana* and/or *Choristoneura occidentalis*: Dowden *et al.* 1948, as *Phorocera erecta* ex. *Archips fumiferana* (North America); †Zwolfer 1961, as *Pseudoperichaeta erecta* ex. *C. fumiferana* (North America); †Arnaud 1978, as *Pseudoperichaeta erecta* ex. *C. fumiferana* (BC, OR, ON, QC).

Host records ex. *Choristoneura fumiferana*, *Choristoneura occidentalis* and/or *Choristoneura pinus*: †Ross 1952, as *Phorocera erecta* ex. spruce and/or jack pine budworm (Canada).

Host records ex. *Choristoneura occidentalis*: Harris & Dawson 1979, as *Pseudoperichaeta erecta* (BC).

Host records probably ex. *Choristoneura occidentalis*: Wilkes *et al.* 1949, as *Phorocera erecta* ex. *C. fumiferana* (BC); Carolin & Coulter 1959, as *Phorocera erecta* ex. *C. fumiferana* (OR); †Coppel 1960, as *Pseudoperichaeta erecta* ex. *C. fumiferana* (BC).

Host records ex. *Choristoneura pinus*: Dixon & Benjamin 1963, as *Phorocera erecta* (WI); †Arnaud 1978, as *Pseudoperichaeta erecta* (WI); †Huber *et al.* 1996 (America north of Mex-

ico).

Host records ex. *Choristoneura rosaceana*: Knowlton & Allen 1937, as *Phorocera erecta* ex. *Cacoecia rosaceana* (UT); Knowlton & Hansen 1938, as *Phorocera erecta* ex. *Cacoecia rosaceana* (UT); Zeller & Schuh 1944, as *Phorocera erecta* ex. *Archips rosaceana* (OR); Schuh & Mote 1948, as *Pseudoperichaeta erecta* ex. *Archips rosaceana* (OR); Raizenne 1952, as *Pseudoperichaeta erecta* ex. *Archips rosaceana* (ON); Schaffner 1959, as *Phorocera erecta* ex. *Archips rosaceana* (northeastern United States); †Arnaud 1978, as *Pseudoperichaeta erecta* (OR, UT, ON, northeastern United States); †Huber *et al.* 1996 (America north of Mexico); Wilkinson *et al.* 2004 (MI).

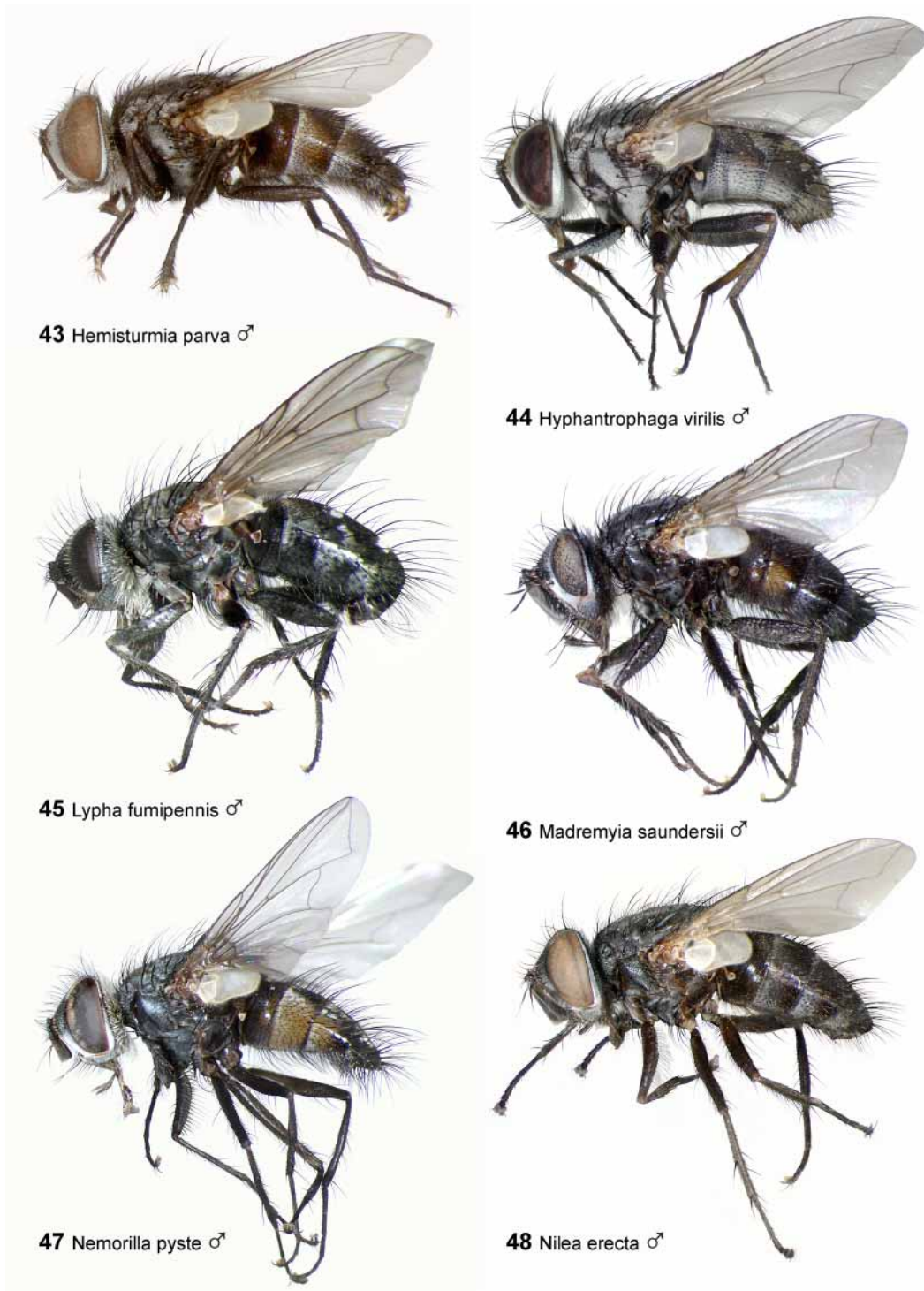
Host records ex. *Choristoneura rosaceana* and/or *Pandemis limitata*: Vakenti *et al.* 2001 (BC); Pfannenstiel & Unruh 2003 (WA); Cossentine *et al.* 2004 (BC).

Nilea erecta is a small (generally 4.0–6.5 mm long), grayish black tachinid with a somewhat mottled or banded abdomen. It differs from other tachinids treated here in possessing four katepisternal setae (Fig. 4) instead of two or three. It is a widespread species found throughout America north of Mexico (O'Hara & Wood 2004). *Nilea erecta* was included in a key to the puparia of dipterous parasitoids of *Choristoneura* species by Ross (1952, as *Phorocera erecta*) and in a key to the adults of dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia by Coppel (1960, as *Pseudoperichaeta erecta*).

The egg-laying habits of *N. erecta* have not been described but are likely similar to those of the other eryciines treated here, *Madremyia saundersii* and *Phryxe pecosensis* (Table 2). If this is the case, then a fully incubated egg is deposited on a host and the first instar emerges almost immediately and burrows into the host's body. *Nilea erecta* attacks late instar larvae of *Choristoneura* species and emerges from the sixth instar or pupa (Knowlton & Allen 1937; Dowden *et al.* 1948; Schuh & Mote 1948; Carolin & Coulter 1959; Harris & Dawson 1979). There is usually only one *N. erecta* per host, there are at least two generations per year, and the winter is passed in the puparium (Schaffner 1959).

Nilea erecta has been frequently reported as a parasitoid of *Choristoneura* species but levels of parasitism are generally low (Carolin & Coulter 1959; McGugan & Blais 1959; Blais 1960; Dixon & Benjamin 1963). However, Zeller and Schuh (1944) cited *N. erecta* (as *Phorocera erecta*) and a braconid wasp as the two most important parasitoids of *C. rosaceana* (as *Archips rosaceana*) in an Oregon study. Wilkes *et al.* (1949) placed *N. erecta* (as *Phorocera erecta*) low on their list of the 15 dominant parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia, ranking it thirteenth among all parasitoids and sixth among the Diptera. It was not included in a treatment of spruce budworm parasitoids in Maine (Tilles & Woodley 1984).

Nilea erecta is chiefly a parasitoid of the Tortricidae (15 host species) and Pyralidae (nine host species), with a single host species reported from each of the Noctuidae and Notodontidae (Arnaud, 1978).



FIGURES 43–48. 43. Habitus images. *Hemisturmia parva*. 44. *Hyphantrophaga virilis*. 45. *Lypha fumipennis*. 46. *Madremyia saundersii*. 47. *Nemorilla pyste*. 48. *Nilea erecta*.

49 *Phryxe pecosensis* ♂50 *Smidtia fumiferanae* ♂

FIGURES 49–50. 49. Habitus images. *Phryxe pecosensis*. 50. *Smidtia fumiferanae*.

***Phryxe pecosensis* (Townsend, 1926), Fig. 49**

Host records ex. *Choristoneura conflictana*: Prentice 1955 (SK, MB); Schaffner 1959, ex. *Archips conflictana* (northeastern United States); †Arnaud 1978 (SK, MB, ME); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura fumiferana*: Johannsen 1913, as *Exorista vulgaris* ex. *Tortrix fumiferana* (ME); Tothill 1913, as *Exorista vulgaris* ex. *Tortrix fumiferana* (QC); †Winn & Beaulieu 1915, as *Exorista vulgaris* ex. *Tortrix fumiferana* (QC); Wilkes & Anderson 1947, ex. *Archips fumiferana* (ON, QC); Daviault 1950 (QC); Dowden *et al.* 1951, ex. *Archips fumiferana* (NY); Jaynes & Drooz 1952 (NY, ME); Raizenne 1952 (ON); Dowden *et al.* 1953 (ME); Miller 1955 (NB); McGugan & Blais 1959 (ON); Schaffner 1959, as *Phryxe vulgaris* (northeastern United States); Blais 1960 (QC); MacDonald & Webb 1963 (NB); †Miller 1963 (NB); Blais 1965 (QC); †Arnaud 1978, as *Phryxe vulgaris* (MA, QC, ME); †Tilles & Woodley 1984 (ME); Hébert *et al.* 1989 (QC); Huber *et al.* 1996 (NB); †Huber *et al.* 1996, as *Phryxe vulgaris* (America north of Mexico); Cappuccino *et al.* 1999 (QC).

Host records ex. *Choristoneura fumiferana* and/or *Choristoneura occidentalis*: Brown 1941, as *Zenillia vulgaris* ex. *Cacoecia fumiferana* (Canada); Sellers 1943, ex. *Archips fumiferana* (North America); Dowden *et al.* 1948, ex. *Archips fumiferana* (North America); †Zwolfer 1961, ex. *C. fumiferana* (North America); †Arnaud 1978, ex. *C. fumiferana* (BC, OR, ON, QC, NB, NF, ME, NY).

Host records ex. *Choristoneura fumiferana*, *Choristoneura occidentalis* and/or *Choristoneura pinus*: †Ross 1952, ex. spruce and/or jack pine budworm (Canada).

Host records ex. *Choristoneura occidentalis*: McKnight 1974 (CO); Harris & Dawson 1979 (BC).

Host records probably ex. *Choristoneura occidentalis*: Wilkes *et al.* 1949, ex. *C. fumiferana* (BC); Carolin & Coulter 1959, ex. *C. fumiferana* (OR); †Coppel 1960, ex. *C. fumiferana* (BC).

Host records ex. *Choristoneura pinus*: Benjamin & Drooz 1954 (MI); Drooz & Benjamin 1956 (MI); Kulman & Hodson 1961 (MN); Dixon & Benjamin 1963 (WI); Allen *et al.* 1969 (MI); †Arnaud 1978 (MN, WI, MI); †Huber *et al.* 1996 (America north of Mexico).

Host records ex. *Choristoneura rosaceana*: Raizenne 1952, ex. *Archips rosaceana* (ON); †Arnaud 1978 (ON); †Huber *et al.* 1996 (America north of Mexico).

Phryxe pecosensis ranges from Alaska to Newfoundland, and south to California and New Mexico in the West and Virginia in the East. It is a dark coloured species about 4.0–7.5mm long. The adult and puparium resemble those of the related *Madremyia saundersii*, and the puparia of the two species (Figs. 24–25) are not always easily distinguished. *Phryxe pecosensis* was included in a key to the puparia of dipterous parasitoids of *Choristoneura* species by Ross (1952) and in a key to the adults of dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia by Coppel (1960). The egg, larval instars and puparium were described by Maw and Coppel (1953).

Phryxe vulgaris (Fallén) is a widely distributed Holarctic species that is very similar in appearance to *P. pecosensis*. This similarity has resulted in frequent misidentifications of *P. pecosensis* as *P. vulgaris* in the literature. Sellers (1943) provided useful characters by which to separate the species, but the differences between the species are so subtle that misidentifications continue to occur. Sellers (1943) considered host records of *P. vulgaris* from *C. fumiferana* (as *Archips fumiferana*) to be based on misidentifications of *P. pecosensis*, and I agree with his assessment.

Phryxe pecosensis is an eryciine tachinid that develops mature eggs within the female reproductive system. In a study of the biology of this species, Maw and Coppel (1953) found that eggs are deposited directly on the host. The first instar usually emerges soon after egg deposition, exiting through the ventral surface of the egg and burrowing into the host. Maw and Coppel (1953) observed a maximum deposition of 32 eggs in the laboratory but found many more eggs in the reproductive systems of dissected females, so females probably deposit close to 100 eggs under natural conditions. Females have a pre-oviposition period of about 10 days and adults live up to about 50 days (Maw & Coppel 1953). *Phryxe pecosensis* attacks late instar larvae of *Choristoneura* species and emerges from the sixth instar or pupa (Dowden *et al.* 1948; Carolin & Coulter 1959; Allen *et al.* 1969; McKnight 1974). The fully mature maggot leaves the host to pupariate elsewhere (Sellers 1943; Maw & Coppel 1953). Adults are active from May to October, there are two or more generations per year, and the parasitoid overwinters as a larva in an alternate host (Schaffner & Griswold 1934; Schaffner 1959).

Phryxe pecosensis is a commonly recorded parasitoid of *Choristoneura* species that is generally responsible for low levels of parasitism but occasionally has been found at higher levels. Parasitism of *C. pinus* was reported as low (less than 3% parasitism of late larvae) in Michigan by Benjamin and Drooz (1954) and Allen *et al.* (1969) and in Wisconsin by Dixon and Benjamin (1963). In Quebec, Daviault (1950) reported spruce budworm parasitism as high as 7.4% in larvae and 1% in pupae, whereas Blais (1960) reported relative parasitism as high as 15%. In New York, Dowden *et al.* (1951) reported parasitism of spruce budworm larvae as high as 18% and of pupae as high as 6%. Jaynes and Drooz (1952) found up to 24% parasitism of mature larvae of spruce budworm in New York and

up to 12% parasitism of budworm larvae in Maine. Tilles and Woodley (1984) included *P. pecosensis* as one of five tachinids in their manual of spruce budworm parasitoids in Maine. Parasitism in the West has been reported as low. Wilkes *et al.* (1949) ranked *P. pecosensis* fifteen among the 15 dominant dipterous and hymenopterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia.

The hosts from which *P. pecosensis* has been reported are many and varied: a species of Tenthredinidae (Hymenoptera), a species each in Danaidae, Hesperidae, Pieridae, and Saturniidae, two species of Pyralidae, several species in each of Geometridae and Noctuidae, and about ten species of Tortricidae (Arnaud 1978).

Smidtia fumiferanae (Tothill, 1912), Fig. 50

Host records ex. *Choristoneura conflictana*: Prentice 1955, as *Omotoma fumiferanae* (SK, MB); †Arnaud 1978, as *Omotoma fumiferanae* (SK, MB); †Huber *et al.* 1996, as *Winthemia fumiferanae* (America north of Mexico).

Host records ex. *Choristoneura fumiferana*: Wilkes & Anderson 1947, as *Omotoma fumiferanae* ex. *Archips fumiferana* (ON, QC); Dowden *et al.* 1951, as *Omotoma fumiferanae* ex. *Archips fumiferana* (NY); Raizenne 1952, as *Omotoma fumiferanae* (ON); Miller 1955, as *Omotoma fumiferanae* (NB); McGugan & Blais 1959, as *Omotoma fumiferanae* (ON); Blais 1960, as *Omotoma fumiferanae* (QC); MacDonald & Webb 1963, as *Omotoma fumiferanae* (NB); †Miller 1963, as *Winthemia amoena* (NB); Blais 1965, as *Winthemia amoena* (QC); †Tilles & Woodley 1984, as *Omotoma fumiferanae* (ME); Hébert *et al.* 1989, as *Winthemia fumiferanae* (QC); Hébert & Cloutier 1990a, as *Winthemia fumiferanae* (QC); Hébert & Cloutier 1990b, as *Winthemia fumiferanae* (QC); Hébert *et al.* 1990, as *Winthemia fumiferanae* (QC); Huber *et al.* 1996, as *Winthemia fumiferanae* (NB); Bouchier & Smith 1998, as *Winthemia fumiferanae* (ON); †Smith *et al.* 2002, as *Winthemia fumiferanae* (eastern Canada).

Host records ex. *Choristoneura fumiferana* and/or *Choristoneura occidentalis*: Tothill 1912, as *Winthemia fumiferanae* ex. *Tortrix fumiferana* (BC, QC); Hewitt 1913, as *Winthemia fumiferanae* ex. *Tortrix fumiferana* (BC, QC); Tothill 1913, as *Winthemia fumiferanae* ex. *Tortrix fumiferana* (BC, QC); †Johannsen 1913, as *Winthemia fumiferanae* ex. *Tortrix fumiferana* (Canada); Tothill 1923, as *Winthemia* ex. spruce budworm (BC, NB); Brown 1941, as *Winthemia fumiferanae* ex. *Cacoecia fumiferana* (Canada); Dowden *et al.* 1948, as *Omotoma* (*Winthemia*) *fumiferanae* ex. *Archips fumiferana* (North America); †Zwölfer 1961, as *Winthemia amoena* ex. *C. fumiferana* (North America); †Arnaud 1978, as *Omotoma fumiferanae* ex. *C. fumiferana* (BC, OR, ON, QC, NB, NH, NY).

Host records ex. *Choristoneura fumiferana*, *Choristoneura occidentalis* and/or *Choristoneura pinus*: †Ross 1952, as *Omotoma fumiferanae* ex. spruce and/or jack pine budworm (Canada).

Host records ex. *Choristoneura occidentalis*: McKnight 1974, as *Omotoma fumiferanae* (CO); Doganlar & Beirne 1978, as *Winthemia fumiferanae* (BC); Harris & Dawson 1979, as *Winthemia fumiferanae* (BC); Schmid 1981, as *Timnavia* [= *Timavia*] *fumiferanae* (NM); Torgersen *et al.* 1984, as *Timavia fumiferanae* (WA, OR, ID, MT); †Harris & Dawson 1985, as *Winthemia fumiferanae* (BC); †Torgersen 1985, as *Timavia fumiferanae* (WA, OR, ID, MT).

Host records probably ex. *Choristoneura occidentalis*: Coppel 1947, as *Omotoma fumiferanae* ex. *Archips fumiferana* (BC); Wilkes *et al.* 1949, as *Omotoma fumiferanae* ex. *C. fumiferana* (BC); Coppel 1953, as *Omotoma fumiferanae* ex. *C. fumiferana* (BC); Carolin & Coulter 1959, as *Omotoma fumiferanae* ex. *C. fumiferana* (OR); †Coppel 1960, as *Omotoma fumiferanae* ex. *C. fumiferana* (BC).

Host records ex. *Choristoneura pinus*: Nealis 1991 (ON).

This distinctive and common species is found throughout most of America north of Mexico (O'Hara & Wood 2004). For many years it was variously assigned to *Omotoma* Lioy, *Winthemia* Robineau-Desvoidy, or *Timavia* Robineau-Desvoidy, but was recently moved to *Smidtia* Robineau-Desvoidy by Shima (1996), who also placed *Omotoma* and *Timavia* as generic synonyms of *Smidtia*. *Smidtia fumiferanae* can be distinguished from the other tachinids treated here by the presence of hairs on the mid portion of the parafacial (Fig.3); it differs from *Winthemia* species in having the hairs on the dorsum of the abdomen mostly erect (hairs recumbent in *Winthemia*). Adults are mostly 5–9mm long. The egg, larval instars, and puparium were described by Coppel and Smith (1957). *Smidtia fumiferanae* (as *Omotoma fumiferanae*) was included in a key to the puparia of dipterous parasitoids of *Choristoneura* species by Ross (1952) and in a key to the adults of dipterous parasitoids of *C. occidentalis* (as *C. fumiferana*) in British Columbia by Coppel (1960).

Females of *S. fumiferanae* lay unincubated eggs directly on their hosts, as is typical of members of the Winthemiini. Eggs are laid primarily on sixth instar budworms and the first instar maggot is capable of parasitizing its host after about three days of development (Coppel & Smith 1957; Hébert & Cloutier 1990a). However, the first instar maggot generally waits in the egg for the host to begin pupation before entering it (Coppel & Smith 1957; Hébert & Cloutier 1990a). Hence, parasitoid development usually takes place entirely within the host pupa. Less frequently, fourth or fifth instar hosts are attacked (Doganlar & Beirne 1978), and emergence from sixth instar hosts has been reported (Harris & Dawson 1979). Once the maggot has completed development, it leaves the host pupa and pupariates in the soil (Coppel & Smith 1957; Hébert *et al.* 1989). The parasitoid overwinters in the puparium and there is typically one generation per year (Schaffner & Griswold 1934; Coppel & Smith 1957; Hébert *et al.* 1989).

Smidtia fumiferanae is arguably the most important tachinid parasitoid of *Choristoneura* species in Canada. It was ranked by Wilkes *et al.* (1949, as *Omotoma fumiferanae*) as the third most important parasitoid, and single most important dipterous parasitoid, of *C. occidentalis* (as *C. fumiferana*) in British Columbia. Harris and Dawson (1979) reported parasitism of late instar *C. occidentalis* larvae by *S. fumiferanae* (as *Winthemia fumiferanae*) as high as 18% in British Columbia. *Smidtia fumiferanae* (as *Omotoma fumiferanae*) was considered a major parasitoid of budworms in Colorado by Dowden *et al.* (1948) and in Oregon by Carolin and Coulter (1959). In the East, budworm parasitism by *S. fumiferanae* has not matched the levels reported in the West, but the species is common and parasitism can be locally significant (Coppel and Smith 1957, Blais 1960; Hébert *et al.* 1989). The species was included among the five tachinids treated by Tilles and Woodley (1984) in their manual of spruce budworm parasitoids in Maine.

The hosts of *S. fumiferanae* include two species of Geometridae and a few species of Noctuidae (Arnaud 1978, as *Omotoma fumiferanae*), in addition to the *Choristoneura* species indicated in Table 1.

Excluded species

The following 13 species of Tachinidae were excluded from consideration as true *Choristoneura* parasitoids, either because the identifications are highly dubious, or because the records are erroneous, or represent rare or accidental parasitism of *Choristoneura* species.

Blondelia eufitchiae (Townsend) (as *Phrynolydella eufitchiae*).— Recorded by Graham (1965) from *C. rosaceana* (as *Archips rosaceana*) but based on Caesar (1915). Caesar (1915) reared *B. eufitchiae* (as *Masicera eufitchiae*) from a leafroller on apple, but *C. rosaceana* (as *Tortrix rosaceana*) was one of three tortricid species found on apple and *B. eufitchiae* could have emerged from any of them. *C. rosaceana* was the least common of the three tortricids studied (Caesar 1915).

Campylocheta sp. (as *Chaetophlepsis* sp.).— Unverified record (Prentice 1955).

Chaetogaedia townsendi Sabrosky and Arnaud.— A single verified record in the collection of the Northern Forestry Centre, Edmonton. The host was collected in Manitoba and identified as a “budworm.” A tortricid host is unusual for a *Chaetogaedia* species so possibly the host was misidentified.

Chetogena sp. (as *Euphorocera* sp.).— Unverified record (McKnight 1974).

Drino sp. (as *Sturmia* sp.).— Arnaud (1978) cited Gardiner (1946) as the source of this host record. However, Arnaud was in error because the original record in Gardiner (1946) was based on a rearing from the spruce sawfly, not spruce budworm.

Erynnia tortricis (Coquillett) (as *Tortriciophaga tortricis*).— Unverified record (Raizenne 1952).

Lespesia sp.— A single verified record in the collection of the Northern Forestry Centre, Edmonton. The host was collected in Saskatchewan and identified as *C. fumiferana*. There are many species of *Lespesia* and hundreds of host records in the literature, but no records from Tortricidae. Either the host was misidentified or the host record is aberrant.

Lypha setifacies (West).— A single verified record from Alberta ex. *C. conflictana* (O’Hara 2002).

Panzeria ampelus (Walker).— A single verified record in the collection of the Pacific Forestry Centre, Victoria. The host was collected in British Columbia and identified as *C. occidentalis*. If the host was correctly identified, then this rearing represents an unusual host record for *P. ampelus*.

Phryxe vulgaris (Fallén).— Cited frequently, particularly in older literature, but most likely based on misidentifications of *P. pecosensis*.

Prooppia crassiseta (Aldrich & Webber) (as *Aplomya crassiseta*).— Unverified record (Prentice 1955).

Tachinomyia nigricans Webber.— Unverified record (Ross 1952).

Xanthophyto sp.— Unverified record (Dowden *et al.* 1948).

Acknowledgments

First and foremost I thank *Choristoneura* researchers who have generously assisted with this project, either by providing me with reared tachinid specimens or information about tachinid parasitism. They are, in alphabetical order, N. Bostanian (Horticultural Research and Development Centre, Agriculture and Agri-Food Canada [AAFC], St. Jean-sur-Richelieu, Quebec), J.E. Cossentine (Pacific Agri-Food Research Centre, AAFC, Summerland, British Columbia), E. Eveleigh (Atlantic Forestry Centre, Natural Resources Canada [NRCan], Fredericton, New Brunswick), V. Nealis (Pacific Forestry Centre, NRCan, Victoria), I.S. Otvos (Pacific Forestry Centre, NRCan, Victoria), M. Sarvary (graduate student, Department of Entomology, Cornell University, Ithaca, New York), C.J. Westbrook (graduate student, Department of Entomology, Cornell University, Ithaca, New York), and T.K. Wilkinson (graduate student, Department of Entomology, Michigan State University, East Lansing, Michigan). D.M. Wood (Research Associate, AAFC, Ottawa) gave freely of his time and expertise in Tachinidae, helping to resolve several taxonomic problems encountered during this study. J.T. Huber (Canadian Forest Service, NRCan, Ottawa) and I.S. Otvos (Canadian Forest Service, NRCan, Victoria) kindly reviewed the manuscript. My colleagues J.M. Cumming, D.J. Lafontaine, and J.H. Skevington (all AAFC, Ottawa) provided advice on various matters. I am especially grateful to my technician, B.E. Cooper (AAFC, Ottawa), for preparing the colour images, taking the original scanning electron microscope images and assisting with the preparation of the puparial images. D.N. Moorhouse skillfully prepared the puparial drawings of posterior spiracular discs. I thank D. Kritsch (AAFC, Ottawa) for his assistance with various technical aspects of this work. Specimens useful to this study were provided by L. Humble (Pacific Forestry Centre, NRCan, Victoria) and D.J. Williams (Northern Forestry Centre, NRCan, Edmonton, Alberta). Our summer student in the Diptera Unit (AAFC, Ottawa), J. King, carefully checked the References and proofread the manuscript. Financial support for this study from the Canadian Forest Service of NRCan, as provided by J.T. Huber (NRCan, Ottawa) and I.S. Otvos (NRCan, Victoria), is gratefully acknowledged.

References

- Aldrich, J.M. (1916) Two new Canadian Diptera. *Canadian Entomologist*, 48, 20–22.
- Aldrich, J.M. & Webber, R.T. (1924) The North American species of parasitic two-winged flies belonging to the genus *Phorocera* and related genera. *Proceedings of the United States National Museum*, 63 (Art. 17) [= No. 2486], 1–90.
- Allen, D.C., Knight, F.B., Foltz, J.L. & Mattson, W.J. (1969) Influence of parasites on two populations of *Choristoneura pinus* (Lepidoptera: Tortricidae) in Michigan. *Annals of the Entomological Society of America*, 62, 1469–1475.
- Arnaud, P.H., Jr. (1978) A host-parasite catalog of North American Tachinidae (Diptera). *United States Department of Agriculture, Miscellaneous Publication*, 1319, 860 pp.
- Bedard, W.D. (1938) An annotated list of the insect fauna of Douglas fir (*Pseudotsuga mucronata*

- rafinesque*) in the northern Rocky Mountain region. *Canadian Entomologist*, 70, 188–197.
- Benjamin, D.M. & Drooz, A.T. (1954) Parasites affecting the jack-pine budworm in Michigan. *Journal of Economic Entomology*, 47, 588–591.
- Bigot, J.-M.-F. (1889) Diptères nouveaux ou peu connus. 34^e partie. XLII. Diagnoses de nouvelles espèces. *Annales de la Société Entomologique de France, Série 6*, 8, 253–270.
- Blais, J.R. (1960) Spruce budworm parasite investigations in the Lower St. Lawrence and Gaspé regions of Quebec. *Canadian Entomologist*, 92, 384–396.
- Blais, J.R. (1965) Parasite studies in two residual spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks in Quebec. *Canadian Entomologist*, 97, 129–136.
- Boettner, G.H., Elkinton, J.S. & Boettner, C.J. (2000) Effects of a biological control introduction on three nontarget native species of saturniid moths. *Conservation Biology*, 14, 1798–1806.
- Bourchier, R.S. (1991) Growth and development of *Compsilura concinnata* (Meigan [sic]) (Diptera: Tachinidae) parasitizing gypsy moth larvae feeding on tannin diets. *Canadian Entomologist*, 123, 1047–1055.
- Bourchier, R.S. & Smith, S.M. (1998) Interactions between large-scale inundative releases of *Trichogramma minutum* (Hymenoptera: Trichogrammatidae) and naturally occurring spruce budworm (Lepidoptera: Tortricidae) parasitoids. *Environmental Entomology*, 27, 1273–1279.
- Brooks, A.R. (1945) New Canadian Diptera (Tachinidae). *Canadian Entomologist*, 77, 78–96.
- Brown, A.W.A. (1941) Foliage insects of spruce in Canada. *Canada Department of Agriculture Publication*, 712 (Technical Bulletin 31), 1–29.
- Burgess, A.F. & Crossman, S.S. (1927) The satin moth, a recently introduced pest. *United States Department of Agriculture, Department Bulletin*, 1469, 1–22 + 1 pl.
- Caesar, L. (1916) Leaf-rollers attacking apples. *Annual Report of the Entomological Society of Ontario [for] 1915*, 46, 163–178.
- Cappuccino, N., Houle, M.-J. & Stein, J. (1999) The influence of understory nectar resources on parasitism of the spruce budworm *Choristoneura fumiferana* in the field. *Agricultural and Forest Entomology*, 1, 33–36.
- Cappuccino, N., Lavertu, D., Bergeron, Y. & Régnière, J. (1998) Spruce budworm impact, abundance and parasitism rate in a patchy landscape. *Oecologia*, 114, 236–242.
- Carolin, V.M. & Coulter, W.K. (1959) The occurrence of insect parasites of *Choristoneura fumiferana* (Clem.), in Oregon. *Journal of Economic Entomology*, 52, 550–555.
- Ciesla, W.M. (1964) Life history and habits of the elm spanworm, *Ennomos sibsigharius*, in the southern Appalachian Mountains (Lepidoptera: Geometridae). *Annals of the Entomological Society of America*, 57, 591–596.
- Clausen, C.P. (1978) Tortricidae. In: Clausen, C.P. (Ed.), *Introduced parasites and predators of arthropod pests and weeds: a world review*. *United States Department of Agriculture, Agriculture Handbook*, 480, 236–240.
- Coppel, H.C. (1947) The collection of spruce budworm parasites in British Columbia with notes on their overwintering habits. *Annual Report of the Entomological Society of Ontario [for] 1946*, 77, 38–40.
- Coppel, H.C. (1953) Effects of super, — multi, — and hyperparasitism on the abundance of *Phytodietus fumiferanae* Rohw. (Hymenoptera: Ichneumonidae), a primary parasite of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *Report of the Quebec Society for the Protection of Plants [for] 1950–1951*, 32–33, 189–193.
- Coppel, H.C. (1958) Studies on dipterous parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). VI. *Phorocera incrassata* Smith (Diptera: Tachinidae). *Canadian Journal of Zoology*, 36, 453–462.
- Coppel, H.C. (1960) Key to adults of dipterous parasites of spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). *Annals of the Entomological Society of America*, 53, 94–97.

- Coppel, H.C. & Maw, M.G. (1954a) Studies on dipterous parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). III. *Ceromasia auricaudata* Tns. (Diptera: Tachinidae). *Canadian Journal of Zoology*, 32, 144–156.
- Coppel, H.C. & Maw, M.G. (1954b) Studies on dipterous parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). IV. *Madremyia saundersii* (Will.) (Diptera: Tachinidae). *Canadian Journal of Zoology*, 32, 314–323.
- Coppel, H.C. & Smith, B.C. (1957) Studies on dipterous parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). V. *Omotoma fumiferanae* (Tot.) (Diptera: Tachinidae). *Canadian Journal of Zoology*, 35, 581–592.
- Coquillett, D.W. (1902) New Diptera from North America. *Proceedings of the United States National Museum*, 25 [= No. 1280], 83–126.
- Cossentine, J., Jensen, L., Deglow, E., Bennett, A., Goulet, H., Huber, J. & O'Hara, J. (2004) The parasitoid complex affecting *Choristoneura rosaceana* and *Pandemis limitata* in organically managed apple orchards. *BioControl*, 49, 359–372.
- Culver, J.J. (1919) A study of *Compsilura concinnata*, an imported tachinid parasite of the gipsy moth and the brown-tail moth. *United States Department of Agriculture, Bureau of Entomology, Bulletin*, 766, 1–27 + 1 pl.
- Curran, C.H. (1933) The North American species of *Actia* in the American Museum of Natural History. *American Museum Novitates*, 614, 1–7.
- Cusson, M., Laforge, M., Régnière, J., Béliveau, C., Trudel, D., Thireau, J.C., Bellemare, G., Keirstead, N. & Stolz, D. (2002) Multiparasitism of *Choristoneura fumiferana* by the ichneumonid *Tranosema rostrale* and the tachinid *Actia interrupta*: occurrence in the field and outcome of competition under laboratory conditions. *Entomologia Experimentalis et Applicata*, 102, 125–133.
- Dang, P.T. (1992) Morphological study of male genitalia with phylogenetic inference of *Choristoneura* Lederer (Lepidoptera: Tortricidae). *Canadian Entomologist*, 124, 7–48.
- Daviault, L. (1946) Forest entomology. *Report of the Minister of Lands and Forests of the province of Quebec for the year ending March 31st, 1945*, 113–122.
- Daviault, L. (1950) Les parasites de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* Clem.) dans la province de Québec. *Report of the Quebec Society for the Protection of Plants*, 31, 41–45.
- Davis, J.J. (1912) Report on insects injurious to flowering and ornamental greenhouse plants in Illinois. *Report of the State Entomologist on the noxious and beneficial insects of the state of Illinois*, 27, 83–143.
- Dixon, J.C. & Benjamin, D.M. (1963) Natural control factors associated with the jack-pine budworm, *Choristoneura pinus*. *Journal of Economic Entomology*, 56, 266–270.
- Doganlar, M. & Beirne, B.P. (1978) Natural enemies of budworms, *Choristoneura* spp. (Lepidoptera: Tortricidae), on Douglas fir near Yale, British Columbia, in 1977. *Journal of the Entomological Society of British Columbia*, 75, 25–26.
- Dowden, P.B., Buchanan, W.D. & Carolin, V.M. (1948) Natural-control factors affecting the spruce budworm. *Journal of Economic Entomology*, 41, 457–464.
- Dowden, P.B., Carolin, V.M. & Dirks, C.O. (1951) Natural control factors affecting the spruce budworm in the Adirondacks during 1946–1948. *Journal of Economic Entomology*, 43 (1950), 774–783.
- Dowden, P.B., Jaynes, H.A. & Carolin, V.M. (1953) The role of birds in a spruce budworm outbreak in Maine. *Journal of Economic Entomology*, 46, 307–312.
- Drooz, A.T. & Benjamin, D.M. (1956) Parasites from two jack-pine budworm outbreaks on the Upper Peninsula of Michigan. *Journal of Economic Entomology*, 49, 412–413.
- Evans, D. (1962) Descriptions and life history of *Melanolophia imitata* (Walker) (Lepidoptera: Geometridae). *Canadian Entomologist*, 94, 594–605.

- Fitzpatrick, S.M., Troubridge, J.T. & Maurice, C. (1994) Parasitoids of blackheaded fireworm (*Rhopobota naevana* Hbn.) larvae on cranberries, and larval escape behaviour. *Journal of the Entomological Society of British Columbia*, 91, 73–74.
- Frankenhuyzen, K. van. (2002) *Choristoneura pinus pinus* Freeman, jack pine budworm (Lepidoptera: Tortricidae). In: Mason, P.G. & Huber, J.T. (Eds.), *Biological control programmes in Canada, 1981–2000*. CABI Publishing, Wallingford and New York, pp. 75–78.
- Franklin, H.J. (1943) Injurious and beneficial insects affecting the cranberry. *Massachusetts Agricultural Experiment Station Bulletin*, 398, 26–28.
- Franklin, H.J. (1950) Cranberry insects in Massachusetts. Part V. Insects and other animals beneficial in cranberry growing. *Massachusetts Agricultural Experiment Station Bulletin*, 445, 55–76.
- Gardiner, J.G. (1946) Report of the Minister of Agriculture [for] 1945–46. *Report of the Minister of Agriculture for the Dominion of Canada for the year ended March 31, 1946*, 235 pp.
- Graham, A.R. (1965) A preliminary list of the natural enemies of Canadian agricultural pests. *Canada Department of Agriculture Research Institute Information Bulletin*, 4, 1–179.
- Graham, A.R. & Jones, P.A. (1962) Appendix I. Parasites and predators released against forest insects in Canada, 1910–58. In: McLeod, J.H., McGugan, B.M. & Coppel, H.C., A review of the biological control attempts against insects and weeds in Canada. *Commonwealth Institute of Biological Control, Technical Communication*, 2, 129–175.
- Hagley, E.A.C. & Barber, D.R. (1991) Foliage-feeding Lepidoptera and their parasites recovered from unmanaged apple orchards in southern Ontario. *Proceedings of the Entomological Society of Ontario*, 122, 1–7.
- Harris, J.W.E. & Dawson, A.F. (1979) Parasitoids of the western spruce budworm, *Choristoneura occidentalis* (Lepidoptera: Tortricidae), in British Columbia 1977–78. *Journal of the Entomological Society of British Columbia*, 76, 30–38.
- Harris, J.W.E. & Dawson, A.F. (1985) Parasitoids of the western spruce budworm in British Columbia. In: Sanders, C.J., Stark, R.W., Mullins, E.J. & Murphy, J. (Eds.), *Recent advances in spruce budworms research*. Proceedings of the CANUSA spruce budworms research symposium. Bangor, Maine, September 16–20, 1984. Canadian Forestry Service, Ottawa, p. 102.
- Hébert, C. & Cloutier, C. (1990a) Temperature-dependent development of eggs and larvae of *Winthemia fumiferanae* Toth. (Diptera: Tachinidae), a larval-pupal parasitoid of the spruce budworm (Lepidoptera: Tortricidae). *Canadian Entomologist*, 122, 329–341.
- Hébert, C. & Cloutier, C. (1990b) Host instar as a determinant of preference and suitability for two parasitoids attacking late instars of the spruce budworm (Lepidoptera: Tortricidae). *Annals of the Entomological Society of America*, 83, 734–741.
- Hébert, C., Cloutier, C. & Régnière, J. (1990) Factors affecting the flight activity of *Winthemia fumiferanae* (Diptera: Tachinidae). *Environmental Entomology*, 19, 293–302.
- Hébert, C., Cloutier, C., Régnière, J. & Perry, D.F. (1989) Seasonal biology of *Winthemia fumiferanae* Toth. (Diptera: Tachinidae), a larval-pupal parasitoid of the spruce budworm (Lepidoptera: Tortricidae). *Canadian Journal of Zoology*, 67, 2384–2391.
- Herting, B. (1984) Catalogue of Palearctic Tachinidae (Diptera). *Stuttgarter Beiträge zur Naturkunde Serie A (Biologie)*, 369, 1–228.
- Hewitt, C.G. (1913) Report of the Dominion Entomologist for the year ending March 31 1912. *Canada Department of Agriculture, Annual Report on Experimental Farms for the year 1911–12*, 173–189.
- Huber, J.T., Eveleigh, E., Pollock, S. & McCarthy, P. (1996) The chalcidoid parasitoids and hyperparasitoids (Hymenoptera: Chalcidoidea) of *Choristoneura* species (Lepidoptera: Tortricidae) in America north of Mexico. *Canadian Entomologist*, 128, 1167–1220.
- Ichiki, R. & Shima, H. (2003) Immature life of *Compsilura concinnata* (Meigen) (Diptera: Tachinidae). *Annals of the Entomological Society of America*, 96, 161–167.

- Jaynes, H.A. & Drooz, A.T. (1952) The importance of parasites in the spruce budworm infestations in New York and Maine. *Journal of Economic Entomology*, 45, 1057–1061.
- Johannsen, O.A. (1913) Spruce bud worm and spruce leaf miners. *Maine Agricultural Experiment Station, Bulletin*, 210, 13–36 + 3 pls.
- Johnson, C.W. (1925) Fauna of New England. 15. List of the Diptera or two-winged flies. *Occasional papers of the Boston Society of Natural History*, 7, 1–326.
- Knowlton, G.F. & Allen, M.W. (1937) Oblique-banded leaf roller, a dewberry pest in Utah. *Journal of Economic Entomology*, 30, 780–785.
- Knowlton, G.F. & Hansen, L.L. (1938) Notes on berry insects of Utah. *Proceedings of the Utah Academy of Sciences, Arts and Letters*, 15, 127–130.
- Kulman, H.M. & Hodson, A.C. (1961) Parasites of the jack-pine budworm, *Choristoneura pinus*, with special reference to parasitism at particular stand locations. *Journal of Economic Entomology*, 54, 221–224.
- Li, S.Y., Fitzpatrick, S.M., Hueppelsheuser, T., Cossentine, J.E. & Vincent, C. (2002) *Choristoneura rosaceana* (Harris), obliquebanded leafroller (Lepidoptera: Tortricidae). In: Mason, P.G. & Huber, J.T. (Eds.), *Biological control programmes in Canada, 1981–2000*. CABI Publishing, Wallingford and New York, pp. 78–83.
- Li, S.Y., Fitzpatrick, S.M., Troubridge, J.T., Sharkey, M.J., Barron, J.R. & O'Hara, J.E. (1999) Parasitoids reared from the obliquebanded leafroller (Lepidoptera: Tortricidae) infesting raspberries. *Canadian Entomologist*, 131, 399–404.
- MacDonald, D.R. & Webb, F.E. (1963) Insecticides and the spruce budworm. In: Morris, R.F. (Ed.), *The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada*, 31, 288–310 + figs. 39.1–39.6.
- Maw, M.G. & Coppel, H.C. (1953) Studies on dipterous parasites of the spruce budworm, *Choristoneura fumiferana* (Clem.) (Lepidoptera: Tortricidae). II. *Phryxe pecosensis* (Tns.) (Diptera: Tachinidae). *Canadian Journal of Zoology*, 31, 392–403.
- McAlpine, J.F. (1981) Morphology and terminology – adults. In: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Eds.), *Manual of Nearctic Diptera. Volume 1. Agriculture Canada Monograph*, 27, 9–63.
- McGugan, B.M. & Blais, J.R. (1959) Spruce budworm parasite studies in northwestern Ontario. *Canadian Entomologist*, 91, 758–783.
- McGugan, B.M. & Coppel, H.C. (1962) Part II — Biological control of forest insects, 1910–1958. In: McLeod, J.H., McGugan, B.M. & Coppel, H.C., *A review of the biological control attempts against insects and weeds in Canada. Commonwealth Institute of Biological Control, Technical Communication*, 2, 35–127.
- McKnight, M.E. (1974) Parasitoids of the western spruce budworm in Colorado. *Environmental Entomology*, 3, 186–187.
- Meigen, J.W. (1824) *Systematische Beschreibung der bekannten europäischen zweiflügeligen Insekten*. Hamm, Vol. 4, xii + 428 pp.
- Mellini, E. (1990) Sinossi di biologia dei Ditteri Larvevoridi. *Bollettino dell'Istituto di Entomologia "Guido Grandi" dell'Università di Bologna*, 45, 1–38.
- Miller, C.A. (1955) A technique for assessing spruce budworm larval mortality caused by parasites. *Canadian Journal of Zoology*, 33, 5–17.
- Miller, C.A. (1963) Parasites and the spruce budworm. In: Morris, R.F. (Ed.), *The dynamics of epidemic spruce budworm populations. Memoirs of the Entomological Society of Canada*, 31, 228–244 + figs. 34.1–34.7.
- Nealis, V.G. (1991) Parasitism in sustained and collapsing populations of the jack pine budworm, *Choristoneura pinus* pinus Free. (Lepidoptera: Tortricidae), in Ontario, 1985–1987. *Canadian Entomologist*, 123, 1065–1076.
- Neunzig, H.H. & Gyrisco, G.G. (1955) Some insects injurious to birdsfoot trefoil in New York.

- Journal of Economic Entomology*, 48, 447–450.
- O'Hara, J.E. (1985) Oviposition strategies in the Tachinidae, a family of beneficial flies. *University of Alberta, Agriculture and Forestry Bulletin*, 8(2), 31–34.
- O'Hara, J.E. (1988) Survey of first instars of the Siphonini (Diptera: Tachinidae). *Entomologica Scandinavica*, 18, 367–382.
- O'Hara, J.E. (1991) Revision of Nearctic species of *Actia* Robineau-Desvoidy (Diptera: Tachinidae). *Canadian Entomologist*, 123, 745–776.
- O'Hara, J.E. (2002) Revision of the Polideini (Tachinidae) of America north of Mexico. *Studia dipterologica, Supplement*, 10, 170 pp.
- O'Hara, J.E. & Cooper, B.E. (1992) Revision of the Nearctic species of *Cyzenis* Robineau-Desvoidy (Diptera: Tachinidae). *Canadian Entomologist*, 124, 785–813.
- O'Hara, J.E. & Wood, D.M. (2004) Catalogue of the Tachinidae (Diptera) of America north of Mexico. *Memoirs on Entomology, International*, 18, 410 pp.
- Osten Sacken, C.R. (1887) Some North American Tachinae. *Canadian Entomologist*, 19, 161–166.
- Otvos, I.S. (1991) Tortricids in forestry. North American species in forestry. In: van der Geest, L.P.S. & Evenhuis, H.H. (Eds.), *Tortricid pests. Their biology, natural enemies and control*. World Crop Pests 5, Elsevier, Amsterdam, pp. 719–756.
- Pfannenstiel, R.S. & Unruh, T.R. (2003) Conservation of leafroller parasitoids through provision of alternate hosts in near-orchard habitats. In: Van Driesche, R.G. (Ed.), *Proceedings of the International Symposium on Biological Control of Arthropods. Honolulu, Hawaii, 14–18 January 2002*. United States Department of Agriculture, Forest Service, Morgantown, WV. FHTET-2003-05, pp. 256–262.
- Prebble, M.L. (1935) *Actia diffidens* Curran, a parasite of *Peronea variana* (Fernald) in Cape Breton, Nova Scotia. *Canadian Journal of Research*, 12, 216–227.
- Pree, D.J., Whitty, K.J., Pogoda, M.K. & Bittner, L.A. (2001) Occurrence of resistance to insecticides in populations of the obliquebanded leafroller from orchards. *Canadian Entomologist*, 133, 93–103.
- Prentice, R.M. (1955) The life history and some aspects of the ecology of the large aspen tortrix, *Choristoneura conflictana* (Wlkr.) (n. comb.) (Lepidoptera: Tortricidae). *Canadian Entomologist*, 87, 461–473.
- Raizenne, H. (1952) *Forest Lepidoptera of southern Ontario and their parasites received and reared at the Ottawa Forest Insect Survey Laboratory from 1937 to 1948*. Canada Department of Agriculture, Science Service, Division of Forest Biology, Ottawa, v + 277 pp.
- Reeks, W.A., Forbes, R.S. & Cuming, F.G. (1948) Maritime provinces and Newfoundland. *Canada Department of Agriculture, Science Service, Annual Report of the Forest Insect Survey, Forest Insect Investigations, 1947*, 9–23.
- Richmond, H.A. (1938) Forest insects of the season 1937 in Manitoba and northern Ontario. *Canadian Insect Pest Review*, 16, 45–46.
- Richmond, H.A. (1940) Review of forest insects of the season 1939 from the Winnipeg laboratory. *Canadian Insect Pest Review*, 18, 49–54.
- Richmond, H.A. (1941a) Forest insects of the season 1940 in central Canada. *Canadian Insect Pest Review*, 19, 57–60.
- Richmond, H.A. (1941b) [Untitled.] *Canadian Insect Pest Review*, 19, 209.
- Roland, J., Evans, W.G. & Myers, J.H. (1989) Manipulation of oviposition patterns of the parasitoid *Cyzenis albicans* (Tachinidae) in the field using plant extracts. *Journal of Insect Behavior*, 2, 487–503.
- Ross, D.A. (1952) Key to the puparia of the dipterous parasites of *Choristoneura fumiferana* Clem. *Canadian Entomologist*, 84, 108–112.
- Royama, T. (1984) Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecological Monographs*, 54, 429–462.

- Sabrosky, C.W. & Arnaud, P.H., Jr. (1965) Family Tachinidae (Larvaevoridae). In: Stone, A., Sabrosky, C.W., Wirth, W.W., Foote, R.H. & Coulson, J.R. (Eds.), A catalog of the Diptera of America north of Mexico. *United States Department of Agriculture, Agriculture Handbook*, 276, 961–1108.
- Sanders, C.J. (1991) Tortricids in forestry. Biology of North American spruce budworms. In van der Geest, L.P.S. & Evenhuis, H.H. (Eds.), *Tortricid pests. Their biology, natural enemies and control*. World Crop Pests 5, Elsevier, Amsterdam, pp. 579–620.
- Schaffner, J.V., Jr. (1959) Microlepidoptera and their parasites reared from field collections in the northeastern United States. *United States Department of Agriculture, Miscellaneous Publication*, 767, iv + 97 pp.
- Schaffner, J.V., Jr. & Griswold, C.L. (1934) Macrolepidoptera and their parasites reared from field collections in the northeastern part of the United States. *United States Department of Agriculture, Miscellaneous Publication*, 188, 1–160.
- Schaupp, W.C. Jr., Volney, W.J.A. & Waters, W.E. (1991) Parasitoids of endemic and epidemic populations of *Choristoneura occidentalis* Freeman and *Choristoneura retiniana* (Walsingham) (Lepidoptera: Tortricidae) in southern Oregon. *Canadian Entomologist*, 123, 1095–1102.
- Schmid, J.M. (1981) Distribution of western spruce budworm (Lepidoptera: Tortricidae) insect parasites in the crowns of host trees. *Canadian Entomologist*, 113, 1101–1106.
- Schoenmaker, A., Cusson, M. & Frankenhuyzen, K. van. (2001) Interactions between *Bacillus thuringiensis* and parasitoids of late-instar larvae of the spruce budworm (Lepidoptera: Tortricidae). *Canadian Journal of Zoology*, 79, 1697–1703.
- Schröder, D. (1969) *Lypha dubia* (Fall.) (Dip.: Tachinidae) as a parasite of the European pine shoot moth, *Rhyacionia buoliana* (Schiff.) (Lep.: Eucosmidae) in Europe. *Commonwealth Institute of Biological Control, Technical Bulletin*, 12, 43–60.
- Schuh, J. & Mote, D.C. (1948) The oblique-banded leaf roller on red raspberries [*Archips rosaceana* (Harris)]. *Oregon Agricultural Experiment Station, Technical Bulletin*, 13, 1–43.
- Sellers, W.F. (1930) The identity of *Zenillia blanda* O.S. and *Zenillia virilis* A. & W. with notes on *Zenillia blandita* Coq. (Diptera, Tachinidae). *Annals of the Entomological Society of America*, 23, 569–576.
- Sellers, W.F. (1943) The Nearctic species of parasitic flies belonging to *Zenillia* and allied genera. *Proceedings of the United States National Museum*, 93 [= No. 3157], 1–108.
- Shima, H. (1996) A systematic study of the tribe Winthemini from Japan (Diptera, Tachinidae). *Beiträge zur Entomologie*, 46, 169–235.
- Smith, H.E. (1912) A contribution on North American dipterology. *Proceedings of the Entomological Society of Washington*, 14, 118–127.
- Smith, S.M., Frankenhuyzen, K. van, Nealis, V.G. & Bouchier, R.S. (2002) *Choristoneura fumiferana* (Clemens), eastern spruce budworm (Tortricidae). In: Mason, P.G. & Huber, J.T. (Eds.), *Biological control programmes in Canada, 1981–2000*. CABI Publishing, Wallingford and New York, pp. 58–68.
- Tilles, D.A. & Woodley, N.E. (1984) Spruce budworm parasites in Maine: a reference manual for collection and identification of common species. *United States Department of Agriculture, Forest Service, Cooperative State Research Service, Agriculture Handbook*, 616, 35 pp.
- Thompson, W.R. (1953) The tachinid parasites of *Archips cerasivorana* Fitch. (2) *Eusisyropa blanda* O.S. (Diptera). *Canadian Entomologist*, 85, 393–404.
- Torgersen, T.R. (1985) Parasitoids and western budworm dynamics. In Sanders, C.J., Stark, R.W., Mullins, E.J. & Murphy, J. (Eds.), *Recent advances in spruce budworms research*. Proceedings of the CANUSA spruce budworms research symposium. Bangor, Maine, September 16–20, 1984. Canadian Forestry Service, Ottawa, pp. 104–105.
- Torgersen, T.R., Campbell, R.W., Srivastava, N. & Beckwith, R.C. (1984) Role of parasites in the population dynamics of the western spruce budworm (Lepidoptera: Tortricidae) in the North-

- west. *Environmental Entomology*, 13, 568–573.
- Tothill, J.D. (1912) Systematic notes on North American Tachinidae. *Canadian Entomologist*, 44, 1–5.
- Tothill, J.D. (1913) Tachinidae and some Canadian hosts. *Canadian Entomologist*, 45, 69–75.
- Tothill, J.D. (1923) Notes on the outbreaks of spruce budworm, forest tent caterpillar and larch sawfly in New Brunswick. *Proceedings of the Acadian Entomological Society [for] 1922*, 8, 172–182.
- Townsend, C.H.T. (1908) The taxonomy of the muscoidean flies, including descriptions of new genera and species. *Smithsonian Miscellaneous Collections*, 51 (2 [= pub. 1803]), 1–138.
- Townsend, C.H.T. (1926) New holarctic Muscoidea (Diptera). *Insector Inscitiae Menstruus*, 14, 24–41.
- Vakenti, J.M., Cossentine, J.E., Cooper, B.E., Sharkey, M.J., Yoshimoto, C.M. & Jensen, L.B.M. (2001) Host-plant range and parasitoids of obliquebanded and three-lined leafrollers (Lepidoptera: Tortricidae). *Canadian Entomologist*, 133, 139–146.
- Walker, F. (1849) *List of the specimens of dipterous insects in the collection of the British Museum*. London, Vol. 4, pp. 689–1172.
- Webber, R.T. & Schaffner, J.V., Jr. (1926) Host relations of *Compsilura concinnata* Meigen, an important tachinid parasite of the gipsy moth and the brown-tail moth. *United States Department of Agriculture, Department Bulletin*, 1363, 1–31.
- Wilkes, A. (1946) The introduction of insect parasites of the spruce budworm, *Archips fumiferana* Clem., into eastern Canada. *Canadian Entomologist*, 78, 82–86.
- Wilkes, A. (1949) Notes on the transfer of budworm parasites from British Columbia to eastern Canada. *Report of the Quebec Society for the Protection of Plants [for] 1945–1947*, 30, 111–112.
- Wilkes, A. & Anderson, M. (1947) Notes on recovery of the introduced spruce budworm parasite, *Phytodietus fumiferanae* Rohw. in eastern Canada. *Annual Report of the Entomological Society of Ontario [for] 1946*, 77, 40–44.
- Wilkes, A., Coppel, H.C. & Mathers, W.G. (1949) Notes on the insect parasites of the spruce budworm *Choristoneura fumiferana* (Clem.) in British Columbia. *Canadian Entomologist*, 80 (1948), 138–155.
- Wilkinson, T.K., Landis, D.A. & Gut, L.J. (2004) Parasitism of obliquebanded leafroller (Lepidoptera: Tortricidae) in commercially managed Michigan apple orchards. *Journal of Economic Entomology*, 97, 1524–1530.
- Williston, S.W. (1889) The dipterous parasites of North American butterflies. In: Scudder, S.H., *The butterflies of the eastern United States and Canada with special reference to New England*. Published by the author, Cambridge. Vol. 3, pp. 1912–1924 + pl. 89.
- Winn, A.F. & Beaulieu, G. (1915) A preliminary list of the insects of the province of Quebec. Part II — Diptera (two-winged flies). *Supplement to Report of the Quebec Society for the Protection of Plants*, 7, 108–159.
- Wishart, G. (1945) *Aplomya caesar* (Aldrich), a tachinid parasite of the European corn borer. *Canadian Entomologist*, 77, 157–167.
- Wood, D.M. (1987) Tachinidae. In: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Eds.), *Manual of Nearctic Diptera*. Volume 2. *Agriculture Canada Monograph*, 28, 1193–1269.
- Zeller, S.M. & Schuh, J. (1944) Diseases and insect pests of cane fruits in Oregon. *Oregon Agricultural Experiment Station Bulletin*, 418, 1–58.
- Zwölfer, H. (1961) A comparative analysis of the parasite complexes of the European fir budworm, *Choristoneura murinana* (Hub.) and the North American spruce budworm, *C. fumiferana* (Clem.). *Commonwealth Institute of Biological Control, Technical Bulletin*, 1, 162 pp.