The parasitoid communities associated with *Ceutorhynchus* species (Coleoptera: Curculionidae) in Ontario and Québec, Canada*

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Abstract—Surveys were conducted in Ontario and Québec, Canada to determine the parasitoid communities associated with *Ceutorhynchus* Germar (Coleoptera: Curculionidae) weevil species that are potential nontarget hosts of candidate biological control agents of the cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham). New host plant associations are documented for *Ceutorhynchus americanus* Buchanan, *Ceutorhynchus neglectus* Blatchley, and *Ceutorhynchus omissus* Fall. More than 18 species of Chalcidoidea (Hymenoptera) were associated with six *Ceutorhynchus* species reared from siliques and stems of Brassicaceae plants. Silique-feeding *Ceutorhynchus* species supported a more diverse parasitoid community than stem-feeding or root crown-feeding species. The major components of the parasitoid assemblage of the native *C. neglectus* included *Mesopolobus gemellus* Baur and Muller, *Mesopolobus moryoides* Gibson, *Trichomalus lucidus* (Walker) (Hymenoptera: Pteromalidae) and a cryptic species complex previously reported as *Necremnus tidius* (Walker) (Hymenoptera: Eulophidae). These species, plus *Trimeromicrus maculatus* Gahan (Hymenoptera: Pteromalidae) were the main parasitoids attacking the native *C. omissus*. The major parasitoids associated with the accidently introduced *Ceutorhynchus erysimi* (Fabricius) and *Ceutorhynchus typhae* (Herbst) included *T. maculatus*, the *N. tidius* species complex, *M. gemellus*, and *M. moryoides*. *Trichomalus perfectus* (Walker) (Hymenoptera: Pteromalidae), a major parasitoid of *C. obstrictus* in Europe, is an accidental introduction first reared in Canada from that host in 2009 and first collected from *C. omissus* in 2011. *Mesopolobus gemellus* is shown to have a broad host range. These findings highlight the need for a cautious approach before introducing new biological control agents.

Résumé—Nous avons réalisé en Ontario et au Québec, Canada, un relevé de la faune de parasitoïdes associés aux espèces de charançons du genre *Ceutorhynchus* Germar (Coleoptera: Curculionidae) qui peuvent servir d'hôtes non-intentionnels d'agents de la lutte biologique contre le charançon de la graine du chou, *Ceutorhynchus obstrictus* (Marsham). De nouvelles plantes hôtes sont répertoriées pour *Ceutorhynchus americanus* Buchanan, *Ceutorhynchus neglectus* Blatchley et *Ceutorhynchus omissus* Fall. Plus de 18 espèces de Chalcidoidea (Hymenoptera) sont associées à six espèces de *Ceutorhynchus* qui se développent dans les siliques et les tiges de crucifères (Brassicaceae). Les espèces de *Ceutorhynchus* dont les larves se développent dans les siliques sont les hôtes d'un plus grand nombre d'espèces de parasitoïdes que celles qui se développent dans les tiges ou les couronnes de racine. Les principaux parasitoïdes de l'espèce indigène *C. neglectus* sont *Mesopolobus gemellus* Baur and Muller, *Mesopolobus moryoides* Gibson, *Trichomalus lucidus* (Walker) (Hymenoptera: Pteromalidae) et un groupe d'espèces cryptiques réunies dans la littérature sous le nom de *Necremnus tidius* (Walker) (Hymenoptera: Eulophidae). Ces espèces sont, en plus de *Trimeromicrus maculatus* Gahan (Hymenoptera: Pteromalidae), celles qui attaquent le charançon indigène *C. omissus*. Le complexe de parasitoïdes associés aux espèces introduites *C. erysimi* (Fabricius) et *C. typhae* (Herbst) comprend *T. maculatus*, le groupe d'espèces cryptiques près de *N. tidius*, *M. gemellus* et *M. moryoides*. *Trichomalus perfectus* (Walker) (Hymenoptera: Pteromalidae),

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important parasitoïde du charançon de la graine du chou en Europe, a été accidentellement introduit au Canada où il s'est développé dans *C. obstrictus* en 2009 et dans *C. omissus* en 2011. Le parasitoïde *M. gemellus* peut attaquer un grand nombre d'hôtes. Nos résultats démontrent la nécessité de procéder prudemment avant d'introduire de nouveaux agents de lutte biologique.

Introduction

The cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marsham) (Coleoptera: Curculionidae), is an invasive alien species of European origin and an important pest of canola, *Brassica napus* Linnaeus and *Brassica rapa* Linnaeus (Brassicaceae). It has become widespread in canola-growing regions of North America (Dosdall and Mason 2010) and costs Canadian canola producers in excess of $300 million (Canadian dollars) in losses annually (Colautti *et al*. 2006). A classical biological control project is assessing the need and potential for introduction of exotic parasitoids to suppress populations of *C. obstrictus* and provide a reduced-risk option to prevent losses. Previous studies documented the Hymenoptera parasitoid communities associated with *C. obstrictus* across Canada (Dosdall *et al*. 2006, 2009; Gillespie *et al*. 2006; Mason *et al*. 2011) and in Georgia, United States of America (Gibson *et al*. 2006). These show that the communities vary between regions and consist of multiple species, most being native or putatively Holarctic, although overall parasitism was low. Three Palaearctic species of Pteromalidae (Hymenoptera) were also reported: *Stenomalina gracilis* (Walker), introduced into British Columbia, Canada in the 1940s (Gillespie *et al*. 2006) and *Mesopolobus gemellus* Baur and Muller and *Trichomalus perfectus* (Walker), both accidental introductions into eastern Canada (Mason *et al*. 2011).

An important component of any biological control project is to assess the host-range of candidate agents as a measure of their safety (Bigler *et al*. 2006; van Lenteren *et al*. 2006). In an area of introduction, in this case Canada, an important first step is to document the parasitoid assemblage associated with potential nontarget species to provide baseline data that can be compared with post-release monitoring data to assess impacts on target and nontarget species should the candidate agent be released. Thus, the objectives of this study were to determine the larval parasitoid complexes associated with *Ceutorhynchus* Germar weevils that are potential nontarget hosts of candidate agents for biological control of *C. obstrictus* in Ontario and Québec, and to assess the host range of these parasitoids.

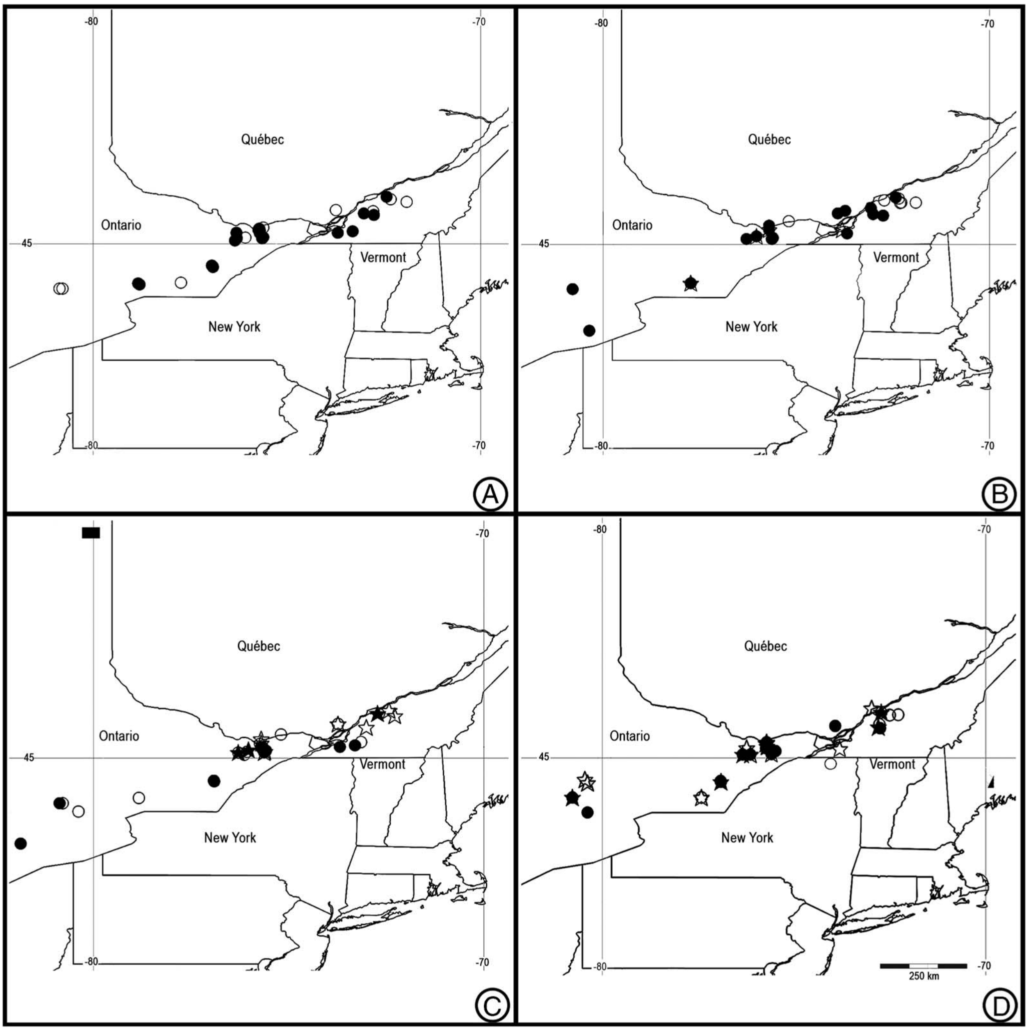
Materials and methods

Surveys were conducted from 2006 to 2011 in canola-growing areas in southern Ontario and southern Québec, Canada where *C. obstrictus* was present or could potentially occur (Mason *et al*. 2004, 2011). Locations sampled for weevils associated with Brassicaceae other than *B. napus* are shown in Figure 1.

Sites were visited when the plants (see Table 1) were in the silique stage of development (similar to canola Stage 73–79 of Lancashire *et al*. 1991). Plant samples were taken at different times during the season, depending on plant component and plant species. For example, wild mustard, *Sinapis arvensis* Linnaeus (Brassicaceae) is an annual with a single generation each year and siliques were present in early to mid-July (Mulligan and Bailey 1975). In contrast, shepherd's-purse, *Capsella bursa-pastoris* (Linnaeus) Medikus (Brassicaceae) flowers from early spring to late fall (Alex 1998) and siliques were present from June to September. Presence of adult weevils was determined with a standard sweep net when the plants were flowering (Stage 61–65) by sweeping 25–100 times (depending on stand size) in a 180° arc while walking through a stand of plants. Samples were placed in 70% ethanol and processed in the laboratory.

To determine larval weevil infestation levels and parasitism levels, whole plants at the silique stage (73–79) were randomly selected in each stand, bagged and processed in the laboratory where root crowns, stems, and siliques harvested from racemes were separated from plants. As described in Mason *et al*. (2011) samples (root crowns, stems, siliques) were placed in $30 \times 30 \times 30$ cm cardboard emergence boxes containing moistened fine vermiculite as a pupation substrate. A 2-cm hole in one side of the box allowed adult weevils and parasitoids to

Figure 1. Sample locations in 2006–2011 for Brassicaceae plant hosts of *Ceutorhynchus* species (A) *Erysimum cheiranthoides* – *Ceutorhynchus omissus*: ● (present), ○ (absent); (B) *Rorippa* species – *Ceutorhynchus neglectus*: ● (present), ○ (absent); *Erucastrum gallicum* – *Ceutorhynchus neglectus*: ★ (present), ☆ (absent); (C) *Sinapis arvensis* – *Ceutorhynchus americanus*: ● (present), ○ (absent); *Rorippa* species – *Ceutorhynchus americanus*: ★ (present), ☆ (absent); (D) *Capsella bursa-pastoris* – *Ceutorhynchus typhae*: ● (present), ○ (absent); *Capsella bursa-pastoris* – *Ceutorhynchus erysimi*: ★ (present), ☆ (absent).



exit into plastic containers. The emergence boxes were placed in a rearing room maintained at 22 ± 1 °C and 18L:6D (light:dark hours). Collection containers were inspected every one to two days until insects ceased to emerge from the boxes for 30 consecutive days. Emerged insects were placed in vials containing 70% ethanol, and weevils and parasitoids were sorted and counted. Percent parasitism was estimated based on numbers of dead weevil larvae and parasitoid pupae found in the vermiculite substrate and emerged weevil and parasitoid adults. Because of the large numbers of pods collected, it was impractical to dissect each pod to determine if weevil remains or parasitoid pupae were present. Thus, estimates of parasitism may be slightly lower than actual. Parasitoids were critical-point dried and identified by G.A.P. Gibson, and weevils identified by P. Bouchard. Voucher specimens of parasitoids

Table 1. Weevil species collected in Ontario and Québec, Canada in 2006–2011, host plants and feeding niche.

Species	Host plant(s)	Feeding niche
Curculionidae	Brassicaceae	
Ceutorhynchinae		
Ceutorhynchini		
Ceutorhynchus americanus Buchanan	*Raphanus raphanistrum* Linnaeus – wild radish; *Rorippa palustris* (Linnaeus) Besser – marsh-cress; *Sinapis arvensis* Linnaeus – wild mustard	Stem
Ceutorhynchus erysimi (Fabricius)*	*Capsella bursa-pastoris* (Linnaeus) Medikus – shepherd's-purse	Root crown
Ceutorhynchus neglectus Blatchley	*Erucastrum gallicum* (Willdenow) Schultz – dog-mustard; *Rorippa palustris* (Linnaeus) Besser – marsh-cress	Silique
Ceutorhynchus omissus Fall	*Erysimum cheiranthoides* Linnaeus – wormseed mustard	Silique
Ceutorhynchus pallidactylus (Marsham)*	*Raphanus raphanistrum* Linnaeus – wild radish	Stem
Ceutorhynchus rapae Gyllenhal*	*Capsella bursa-pastoris* (Linnaeus) Medikus – shepherd's-purse *Erysimum cheiranthoides* Linnaeus – wormseed mustard *Erysimum hieraciifolium* Linnaeus – tall wormseed mustard	Stem
Ceutorhynchus typhae (Herbst)*	*Capsella bursa-pastoris* (Linnaeus) Medikus – shepherd's-purse	Silique

*Accidentally introduced and established in North America.

and weevils are deposited in the Canadian National Collection of Insects, Arachnids, and Nematodes in Ottawa, Ontario, Canada. Specimen labels include site codes.

Means and standard errors were calculated using PROC Means of the SAS statistical software (SAS 2010).

Results

Seven weevil species, *Ceutorhynchus americanus* Buchanan, *Ceutorhynchus erysimi* (Fabricius), *Ceutorhynchus neglectus* Blatchley, *Ceutorhynchus omissus* Fall, *Ceutorhynchus pallidactylus* (Marsham), *Ceutorhynchus rapae* Gyllenhal, and *Ceutorhynchus typhae* (Herbst) (Coleoptera: Curculionidae) were reared from siliques, stems, and root crowns of various Brassicaceae plants (Table 1). Among these species, *C. americanus*, *C. neglectus*, and *C. omissus* are native to North America and are associated with the native plants marsh-cress, *Rorippa palustris* (Linnaeus) Besser, dog mustard, *Erucastrum gallicum* (Willdenow) Schultz, and wormseed mustard, *Erysimum cheiranthoides* Linnaeus (Brassicaceae). *Ceutorhynchus americanus* was also associated with the nonnative wild radish, *Raphanus raphanistrum* Linnaeus (Brassicaceae) and wild mustard. The nonnative, *C. erysimi*, *C. rapae*, and *C. typhae*, were associated with shepherd's-purse, a nonnative weed associated with these species in Europe. *Ceutorhynchus rapae* was also reared from the native wormseed mustard and tall wormseed mustard, *Erysimum hieraciifolium* Linnaeus (Brassicaceae). *Ceutorhynchus pallidactylus* was reared from wild radish.

Collections of host plants did not yield *Ceutorhynchus* species at all sites and in all years (Fig. 1, Tables 2 and 3), indicating that distributions are not uniform and/or occurrence varied during the season (*i.e.*, samples collected from the same site at different times did not always yield specimens). Density was variable where weevils were present (Tables 2–3), possibly a reflection of small sample sizes or variable levels of attack. The stem-feeding *C. americanus* was rare, found in Ontario in marsh-cress in 2008 and 2010, and in the invasive wild radish in 2008, although it was found in wild mustard, in Ontario in 2007, 2008, and 2010, and in Québec in 2007. *Ceutorhynchus rapae*, also a stem feeder, occurred in shepherd's-purse in 2008, in wormseed mustard in 2010, and tall wormseed mustard in 2011 in Ontario, and in 2007 in Québec.

Parasitoids were recovered from all host plant species associated with all *Ceutorhynchus* species (Tables 2–3), except *C. americanus* and *C. pallidactylus* from wild radish. Parasitism levels were variable and the small sample sizes indicate that these do not necessarily reflect actual levels. At least 18 larval parasitoid species were collected from six putative[1] host weevil species (Table 4). Among these, the native *C. neglectus* and *C. omissus*, and the adventive *C. typhae* were associated with the highest numbers of parasitoids. Parasitoid species known to be associated with weevils were also reared from unidentified hosts in collections of siliques of the Brassicaceae species field pepper-grass, *Lepidium campestre* (Linnaeus) Aiton (*Necremnus tidius*[2] (Walker) (Hymenoptera: Eulophidae) and *Lyrcus* Walker species (Hymenoptera: Pteromalidae)), tumble mustard, *Sisymbrium altissimum* Linnaeus (*M. gemellus* Baur and Muller (Hymenoptera: Pteromalidae)) and siliques and stems (one species each) of yellow rocket, *Barbarea vulgaris* Aiton (*Eupelmus vesicularis* (Retzius) (Hymenoptera: Eupelmidae) and *Chlorocytus* Graham species (Hymenoptera: Pteromalidae)).

Mesopolobus gemellus was associated with the greatest number of *Ceutorhynchus* host species (six), followed by, an unnamed species of Eulophidae and *E. vesicularis* (five each), *N. duplicatus*, *Chlorocytus* species, and *Mesopolobus moryoides* Gibson (four each), *Trimeromicrus maculatus* Gahan[3] and *Pteromalus* Swederus species 1 (Pteromalidae) (three each), *N. tidius*, *Eurytoma tylodermatis* Ashmead, and *Eurytoma* Illiger species (Eurytomidae), and *Eurydinoteliodes perdubia* (Girault)[4] and *Trichomalus lucidus* (Walker) (Pteromalidae) (two each), an unnamed Encyrtidae species, *Euderus glaucus* Yoshimoto (Eulophidae), *Lyrcus nigroaeneus* Ashmead, *Lyrcus* species, and *T. perfectus* (Walker) (Pteromalidae) (one each). Not all species associated with weevil hosts were reared from that host in each year.

Parasitoids associated with native weevils

Ceutorhynchus americanus was host to six species of parasitoid. *Eupelmus vesicularis* and *T. lucidus* were reared from stems of marsh-cress collected in Ontario, whereas Eulophidae species, *Chlorocytus* species, *M. gemellus*, and *M. moryoides* were reared from stems of wild mustard (Table 4). Among these, *M. gemellus* was the most abundant, accounting for 50% of the 18 individuals reared from collections of wild mustard in Ontario. The only species reared from Québec collections of wild mustard was an unidentified Eulophidae.

Ceutorhynchus neglectus yielded parasitoids in all years, although the assemblage and proportions of species varied (Table 4). Overall, 12 parasitoid species were reared from this silique specialist. All species were present in Ontario and the greatest diversity was observed in 2010 when seven species were reared. Over all years,

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[1] Since no host remains were available to confirm its identity, the host is "putative" based on the findings that only one weevil species was reared from each plant species/feeding niche.

[2] Ongoing taxonomic research indicates that what previously has been identified as *N. tidius* in Europe and North America consists of several cryptic species, of which both *N. tidius* and *N. duplicatus* Gahan occur in North America.

[3] Listed as *Lyrcus maculatus* in recent literature related to the cabbage seedpod weevil, but *Trimeromicrus* Gahan resurrected from synonymy under *Lyrcus* by Gibson (2013).

[4] Listed as *Lyrcus perdubius* in recent literature related to the cabbage seedpod weevil, but transferred to *Eurydinoteloides* Girault by Gibson (2013).

Table 2. Mean density (±SE) and mean parasitism (±SE) of *Ceutorhynchus* species weevils collected from *Capsella bursa-pastoris* (Linnaeus) Medikus, *Erysimum cheiranthoides* Linnaeus, *Erucastrum gallicum* (Willdenow) Schulz, *Rorippa palustris* (Linnaeus) Besser, and *Sinapis arvensis* Linnaeus in Ontario, Canada 2006–2011* (*n* indicates the number of samples from which the value was calculated; and "." signifies data not collected).

Host plant	Niche	Weevil species	Year	Density (*n*)[†]	Parasitism (*n*)
Capsella bursa-pastoris (Linnaeus) Medikus	Root crown	*Ceutorhynchus erysimi* (Fabricius)	2006	.	.
			2007	.	.
			2008	0.7 (3)	0
			2009	5.2 ± 2.8 (4)	0
			2010	8.0 (1)	4.9 (1)
			2011	5.7 ± 2.8 (4)	6.3 ± 3.3 (3)
	Silique	*Ceutorhynchus typhae* (Herbst)	2006	0.4 ± 0.2 (6)	79.3 ± 11.2 (6)
			2007	0.1 (1)	8.3 (1)
			2008	1.1 ± 0.5 (8)	45.8 ± 17.6 (6)
			2009	0.2 ± 0.05 (4)	42.7 ± 11.6 (5)
			2010	0.04 (1)	.
			2011	1.4 ± 0.9 (2)	7.5 ± 4.6 (2)
Erysimum cheiranthoides Linnaeus	Silique	*Ceutorhynchus omissus* Fall	2006	0.4 ± 0.1 (4)	95.5 ± 4.6 (6)
			2007	0.1 (1)	20.0 (1)
			2008	0.8 ± 0.7 (3)	79.7 ± 11.8 (3)
			2009	0.3 ± 0.1 (6)	66.5 ± 15.5 (4)
			2010	1.3 ± 0.3 (11)	48.0 ± 8.5 (11)
			2011	1.6 ± 0.4 (6)	32.9 ± 7.8 (6)
Erucastrum gallicum (Willdenow) Schulz	Silique	*Ceutorhynchus neglectus* Blatchley	2006	.	.
			2007	.	.
			2008	1.4 (1)	45.7 (1)
			2009	0.1 (1)	0 (1)
			2010	0.2 (1)	86.7 (1)
			2011	.	.
Rorippa palustris (Linnaeus) Besser	Silique	*Ceutorhynchus neglectus* Blatchley	2006	0.2 ± 0.1 (3)	9.5 ± 3.8 (3)
			2007	0.7 ± 0.5 (2)	59.6 ± 32.0 (2)
			2008	0.4 ± 0.2 (3)	15.1 ± 9.8 (3)
			2009	0.1 (1)	12.5 (1)
			2010	0.04 ± 0.02 (4)	57.1 ± 24.8 (4)
			2011	0.9 ± 0.1 (2)	6.8 ± 0.7 (2)
	Stem	*Ceutorhynchus americanus* Buchanan	2006	.	.
			2007	.	.
			2008	1.3 (1)	15.4 (1)
			2009	.	.
			2010	0.3 ± 0.2 (3)	28.6 (1)
			2011	0 (2)	.
Sinapis arvensis Linnaeus	Stem	*Ceutorhynchus americanus* Buchanan	2006	0.7 ± 0.6 (3)	81.5 ± 9.8 (3)
			2007	0.6 ± 0.5 (2)	70.0 ± 30.0 (2)
			2008	.	.
			2009	.	.
			2010	0.3 (2)	.
			2011	.	.

*Not shown are results for: *C. americanus* from *Raphanus raphanistrum* Linnaeus in 2008 [3/stem ($n = 1$)]; *C. rapae* from *Capsella bursa-pastoris* in 2008 [0.3 ± 0.1/stem ($n = 2$)]; *C. rapae* from *Erysimum cheiranthoides* in 2010 [0.5 ± 01/stem ($n = 2$)]; *C. rapae* from *Erysimum hieraciifolium* Linnaeus in 2011 [0.1/stem ($n = 1$)].

[†] Number per root crown, per stem or per 10 siliques.

Table 3. Mean density (±SE) and mean parasitism (±SE) of *Ceutorhynchus* species weevils collected from *Capsella bursa-pastoris* (Linnaeus) Medikus, *Erysimum cheiranthoides* Linnaeus, *Rorippa palustris* (Linnaeus) Besser, and *Sinapis arvensis* Linnaeus in Québec, Canada 2007–2010* (*n* indicates the number of samples from which the value was calculated; and "." signifies data not collected).

Host plant	Niche	Weevil species	Year	Density (*n*)	Parasitism (*n*)
Capsella bursa-pastoris (Linnaeus) Medikus	Root crown	*Ceutorhynchus erysimi* (Fabricius)	2007	.	.
			2008	0.45 (1)	53.3 (1)
			2009	0.2 ± 0.1 (1)	0
			2010	.	.
	Siliques	*Ceutorhynchus typhae* (Herbst)	2007	0.1 (1)	100 (1)
			2008	0.5 (1)	53.3 (1)
			2009	.	.
			2010	.	.
Erysimum cheiranthoides Linnaeus	Silique	*Ceutorhynchus omissus* Fall	2007	0.9 ± 0.3 (3)	76.2 ± 15.7 (3)
			2008	0.4 ± 0.2 (2)	33.3 (1)
			2009	0.4 (1)	100 (1)
			2010	.	.
Rorippa palustris (Linnaeus) Besser	Silique	*Ceutorhynchus neglectus* Blatchley	2007	0.3 ± 0.02 (2)	39.7 ± 4.0 (2)
			2008	0.5 ± 0.4 (3)	67.5 ± 32.5 (2)
			2009	1.2 (1)	31.3 (1)
			2010	.	.
Sinapis arvensis Linnaeus	Stem	*Ceutorhynchus americanus* Buchanan	2007	0.2 ± 0.05 (2)	83.3 ± 16.7 (2)
			2008	.	.
			2009	.	.
			2010	.	.

*Not shown are results for *Ceutorhynchus rapae* from *Erysimum hieraciifolium* in 2007 [0.2/stem ($n = 1$)].

T. lucidus was most prevalent, representing 22.1% of the 12 parasitoid species ($n = 77$ individuals) reared from marsh-cress in Ontario. In Québec, 71 individuals of six species, *N. duplicatus*, Eulophidae species, *E. vesicularis*, *M. gemellus*, *M. moryoides*, and *T. lucidus* were also reared on marsh-cress. Among these, *M. moryoides* constituted 45.1% of the parasitoids reared, followed by *N. duplicatus* at 33.8%. The dominant species differed among years, for example *T. lucidus* was most abundant in 2007, *N. duplicatus* in 2008, and *M. moryoides* in 2009. Parasitoids were only reared ($n = 76$ individuals) from dog mustard collected in Ontario and of the five species *M. moryoides* represented the greatest proportion at 75%.

Ceutorhynchus omissus was host to the greatest diversity of parasitoids, accumulating 13 species in Ontario and five in Québec populations (Table 4). *Mesopolobus gemellus* was the dominant species, comprising 41.6–75% of parasitoids reared from siliques collected in Ontario in 2006 and 2008–2011. In 2010, 142 of 300 individuals reared were *M. gemellus*, while *M. moryoides* (77 individuals) and *N. duplicatus* (56 individuals) were also abundant. *Necremnus duplicatus* was reared in 2006 and 2008–2011 in Ontario. A single individual of *T. perfectus* was reared from siliques of wormseed mustard in Ontario in 2011. In Québec, samples in 2007 yielded five parasitoid species ($n = 26$ individuals), *M. gemellus* (42%), *N. duplicatus* (15%), an unidentified Eulophidae and *T. lucidus* (11.5% each), and *E. tylodermatis* (4%). Only *M. gemellus* was collected from Québec samples in other years (2008 and 2009) and overall, of the 46 individuals reared, it was the most prevalent parasitoid at 63%. *Trichomalus lucidus* was collected in Québec in 2007 (three individuals) and 2010 (two individuals).

Parasitoids associated with nonnative weevils

Ceutorhynchus erysimi yielded three parasitoid species (Table 4), all from Ontario collections in 2010 and 2011, and all introduced species.

Table 4. Parasitoid species (number of specimens) reared from *Ceutorhynchus* species hosts collected from Brassicaceae plant hosts 2006–2011.

	C. americanus		*C. erysimi*	*C. neglectus*		*C. omissus*	*C. rapae*		*C. typhae*
	Rorippa palustris marsh cress	*Sinapis arvensis* wild mustard	*Capsella bursa-pastoris* shepherd's-purse	*Rorippa palustris* marsh cress	*Erucastrum gallicum* dog mustard	*Erysimum cheiranthoides* wormseed mustard	*Capsella bursa-pastoris* shepherd's-purse	*Erysimum hieraciifolium* tall wormseed mustard	*Capsella bursa-pastoris* shepherd's-purse
Encyrtidae									
Unidentified species						ON (1)			
Eulophidae									
Euderus glaucus Yoshimoto				ON (1)					
Necremnus duplicatus Gahan				ON (5) QC (24)	ON (5)	ON (79) QC (4)			ON (68)
Necremnus tidius (Walker)†			ON (24)						ON (30)
Unidentified species		ON (3) QC (2)		ON (20) QC (1)	ON (7)	ON (22) QC (3)	ON (2)		ON (6) QC (1)
Eupelmidae									
Eupelmus vesicularis (Retzius)*	ON (2)		ON (1)	ON (4) QC (2)	ON (1)	ON (11)			ON (4)
Eurytomidae									
Eurytoma tylodermatis Ashmead				ON (1)		ON (1)			
Eurytoma species				ON (6)		ON (1)			
Pteromalidae									
Chlorocytus species		ON (1)		ON (6)	ON (6)	ON (5)			ON (5)
Eurydinoteloides perdubia (Girault)							ON (1)		ON (7)
Lyrcus nigroaeneus (Ashmead)						ON (5)			
Lyrcus species									ON (3)
Mesopolobus gemellus Baur and Muller†		ON (9)	ON (1)	ON (9) QC (1)		ON (297) QC (29)		ON (1) QC (1)	ON (94) QC (24)
Mesopolobus moryoides Gibson		ON (5)		ON (6) QC (32)	ON (57)	ON (81)			ON (21)
Pteromalus species 1				ON (1)		ON (1)			ON (3)
Trichomalus lucidus (Walker)*	ON (2)			ON (17) QC (11)		QC (5)			
Trichomalus perfectus (Walker)†						ON (1)			
Trimeromicrus maculatus Gahan				ON (1)		ON (31) QC (4)			ON (45)
Total number of parasitoids	4	20	26	148	76	581	3	2	311

*Putatively Holarctic.
†Accidentally introduced and established in North America.

Among the 26 individuals reared, *N. tidius* was most prevalent at 92.3%. The native *N. duplicatus* was not reared from *C. erysimi*. Collections were not made from 2006–2009 as the feeding niche was not known.

Ceutorhynchus rapae yielded single specimens of *E. perdubia* and *M. gemellus* from stems of shepherd's-purse and tall wormseed mustard, respectively, from two sites in Ontario and one in Québec. In addition, two Eulophidae species specimens were reared from stems of shepherd's-purse in Ontario.

Ceutorhynchus typhae was host to 10 parasitoid species (Table 4); the entire assemblage was reared from samples collected in Ontario in 2008. *Necremnus duplicatus* and *N. tidius* as well as *M. gemellus* were present in all years. In 2006 *M. gemellus* dominated, comprising 43.3% of the 127 parasitoid individuals reared, followed by *N. duplicatus* plus *N. tidius* at 33.9%, *T. maculatus* at 18.1%, *E. vesicularis* (2.4%), *Chlorocytus* species (1.6%), and *M. moryoides* (0.8%). Similarly, in 2008 *N. duplicatus* plus *N. tidius* dominated, comprising 36.8% of the 133 parasitoid individuals reared, followed by *M. gemellus* at 18%, *T. maculatus* at 16.5%, *M. moryoides* at 13.5%, *E. perdubia* (4.5%), unidentified Eulophidae (3.0%), *Chlorocytus* species (2.3%), *Lyrcus* species (2.3%), *Pteromalus* species (2.3%), and *E. vesicularis* (0.8%). In Québec, only *M. gemellus* (24 individuals in 2008) and an unidentified Eulophidae (one individual in 2007) were reared from shepherd's-purse siliques.

Discussion

The larval host plant associations and feeding niches determined for *C. neglectus* and *C. omissus* are reported for the first time. The association of *C. americanus* with the native marsh-cress and the alien wild mustard are also new. Previously this species was reported to feed on roots and stems of turnip, *B. rapa* Linnaeus, cultivated radish, *Raphanus sativus* Linnaeus (Brassicaceae) (Beirne 1971), whitetop, *Lepidium draba* Linnaeus (Cripps *et al*. 2006), all alien species, and the native poor-man's-peppergrass, *L. virginicum* Linnaeus (Buchanan 1937). Further work is needed to clearly define the life cycles of *C. americanus*, *C. neglectus*, and *C. omissus* in order to develop rearing methods for host-range studies of potential biological control agents and to track the impact of accidentally or intentionally introduced natural enemies of the cabbage seedpod weevil, *C. obstrictus*. The documentation here of *C. americanus* emerging from wild mustard combined with earlier reports of this species feeding on turnip, cultivated radish and whitetop suggests that some native weevils are capable of adapting to new host plants. Although as Cripps *et al*. (2006) report, *C. americanus* was the least abundant of the 11 species encountered during surveys for natural enemies of whitetop. Of the 73 known *Ceutorhynchus* species in North America details of the biology of only a handful of species are known, as Scheibner (1963; 5) stated "… primarily because many of the species are apparently uncommon…. Knowledge is more nearly complete for the species which occur more commonly, among which are those of economic importance". However, even for these latter species, such as the invasive *C. erysimi*, *C. pallidactylus*, *C. rapae*, and *C. typhae*, comprehensive information is not available and documentation that the species was reared from the host plant(s) noted is lacking. In addition to *C. obstrictus*, details of the life cycle of the stem-feeding *C. subpubescens* LeConte, a western species, and the silique-feeding *C. neglectus*, both on the alien flixweed, *Descurainia sophia* (Linnaeus) Webb (Brassicaceae), were provided by Dosdall *et al*. (1999, 2007). The *C. neglectus* reported in this study is probably a different species than that studied by Dosdall *et al*. (1999) and studies using molecular methods are under way to verify this hypothesis (P.B., personal observation; see also Laffin *et al*. 2005).

The parasitoid assemblages of the Nearctic weevil species, *C. americanus*, *C. neglectus*, and *C. omissus* in Ontario and Québec comprised complexes of species that vary from year to year. Of the 19 species reared, 16 are also associated with the cabbage seedpod weevil, *C. obstrictus* (Mason *et al*. 2011), which is an invasive alien species established in these provinces in the 1990s (Brodeur *et al*. 2001; Mason *et al*. 2004). Among the 16 species shared with *C. obstrictus*, 12 are putatively Nearctic and may form an assemblage that has adapted to this nonnative invader. These include *N. duplicatus*, now determined to be the only species of *Necremnus* reared from *C. obstrictus* in North America (G.A.P.G., personal observation). Recognition that *N. duplicatus* and not *N. tidius* parasitises *C. obstrictus* in North America helps explain the absence of *Necremnus* species from rearings of *C. obstrictus* in Europe. Among the remaining four parasitoid species, two, *E. vesicularis* and *T. lucidus*, are putatively Holarctic or Palaearctic species that invaded North America some time ago. We hypothesise that *M. gemellus* and *T. perfectus* are recent introductions, the latter thought to have been introduced into Québec with *C. obstrictus* (Mason *et al.* 2011).

The parasitoid assemblage of the European invader *C. typhae* consists of 10 species. It is the only *Ceutorhynchus* species from which both the Palaearctic *N. tidius* and Nearctic *N. duplicatus* were reared. The only other *Ceutorhynchus* species from which *N. tidius* was reared is *C. erysimi*, suggesting that *N. tidius* was introduced into North America along with one of these two Palaearctic weevil species and that it has not adapted to attack native weevils. The two *Necremnus* species along with *M. gemellus* (a probable introduction) are the dominant parasitoids of *C. typhae*. The Nearctic species *T. maculatus* and *M. moryoides* are also abundant and appear to have adapted to *C. typhae*. Muller *et al.* (2011) studied the parasitoids associated with *C. typhae* in Germany, Switzerland, and France, and found that only *M. gemellus* and *S. gracilis* were associated with this seed-feeding weevil. The former species comprised 98% of individuals, whereas only a single specimen of *S. gracilis* was reared. Our results show that the Palaearctic *N. tidius* and *E. vesicularis*, both widely distributed and highly polyphagous, also parasitise *C. typhae* and suggest that these parasitoids may not occur in the region where Muller *et al.* (2011) conducted their European study. Furthermore, our study supports the Muller *et al.* (2011) findings that *T. lucidus* is not associated with *C. typhae*.

The parasitoid assemblages of the stem-feeding *C. americanus* (six species) and *C. rapae* (three species),[5] and the root crown/leaf mid-rib feeder *C. erysimi* (three species) are small compared with the diversity associated with weevils that feed in the siliques of their host plants (10–14 species). This suggests that the latter weevil species are more vulnerable to attack by parasitoids, although the small sample sizes for these species may have underestimated the diversity of associated parasitoids.

The finding that *M. gemellus* is associated with all *Ceutorhynchus* species reared during our study is remarkable. This European species, when originally described was thought to be associated with *C. typhae*, except for a single female from *Ceutorhynchus turbatus* Schultze (Coleoptera: Curculionidae) (Baur *et al.* 2007). It was recently associated with *C. obstrictus* in eastern Canada (Mason *et al.* 2011) and our results suggest *M. gemellus* is a generalist parasitoid of silique-infesting and stem-infesting and possibly root crown-infesting *Ceutorhynchus* species weevils. *Mesopolobus gemellus* may have been introduced with *C. typhae*, although molecular studies are needed to substantiate this hypothesis. Given this broad host range, that *M. gemellus* has not been reported elsewhere in North America (including from *C. obstrictus* [Mason *et al.* 2011]) suggests it may be a recent invader and tracking the spread and impact of this species on native *Ceutorhynchus* species will be important. Furthermore, if its primary host is indeed *C. typhae* and attack of other *Ceutorhynchus* species is a spillover effect due to high populations of this host, *M. gemellus* may not establish in western North America because *C. typhae* does not occur there (Bousquet *et al.* 2013), despite the ubiquitous distribution and abundance of its host plant, *C. bursa-pastoris* (United States Department of Agriculture 2013).

Mesopolobus gemellus, thought to be a recent adventive introduction, has a broad host range in North America, attacking all host species collected, including the native *C. americanus*, *C. neglectus*, and *C. omissus*. In contrast, only a single specimen of *T. perfectus*, a candidate biological control agent, was collected from the native *C. omissus*. *Trichomalus perfectus* may be a more recent adventive introduction than *M. gemellus* and thus yet to manifest its potential impacts fully. Tracking of *M. gemellus* and

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[5] Scheibner (1963) reports one additional species, *Euderus lividus* (Ashmead) (Hymenoptera: Eulophidae).

T. perfectus is recommended to monitor their spread and impacts on nontarget species.

The findings reported here provide new information on the host plants and feeding niches of the native *C. americanus*, *C. neglectus*, and *C. omissus* and the first documentation of parasitoids associated with each species. The results also show that the parasitoid assemblage of silique feeders is more diverse than those of stem or root crown feeders (although additional data is needed to verify this hypothesis), that native parasitoids adapt to introduced weevil hosts, and some, not all, introduced parasitoids adapt to native weevil hosts. These have important implications for programmes involving the introduction of weevils for biological control of weeds as well as for biological control of pest weevils.

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