

European ectoparasitoids of two classical weed biological control agents released in North America

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Abstract—The ceutorhynchine weevils *Hadroplontus litura* (F.) and *Microplontus edentulus* (Schultze) (Coleoptera: Curculionidae), are established in North America as biological control agents for Canada thistle, *Cirsium arvense* (L.) Scop., and scentless chamomile, *Tripleurospermum perforatum* (Mérat) M. Lainz (Asteraceae), respectively. In North America, both weeds occur sympatrically and in similar habitats as another ceutorhynchine, *Ceutorhynchus obstrictus* (Marsham) (cabbage seedpod weevil), an important pest of canola, *Brassica napus* L., and *Brassica rapa* L. (Brassicaceae). Ceutorhynchinae weevils released to control weeds in cultivated crops may serve as alternate hosts if agents released for biological control of *C. obstrictus* are not specific to that species. Parasitoids associated with *M. edentulus* and *H. litura* inflict similar levels of mortality on their hosts, yet a single species was associated with the latter host, whereas 13 species attacked the former. The stem-mining *M. edentulus* appears to be at some risk but not the root-crown feeding *H. litura*, should the parasitoids *Trichomalus perfectus* (Walker) and *Mesopolobus morys* (Walker) (Hymenoptera: Pteromalidae) be introduced as biological control agents of the silique-feeding *C. obstrictus*. These findings suggest that feeding niche may be an important criterion for developing a nontarget species test list for host-range testing of potential biological control agents.

Résumé—Les charançons *Hadroplontus litura* (F.) et *Microplontus edentulus* (Schultze) (Coleoptera : Curculionidae) sont établis en Amérique du Nord comme agents de lutte biologique contre le chardon des champs (*Cirsium arvense* (L.) Scop.) et la matricaire inodore (*Tripleurospermum perforatum* (Mérat) M. Lainz (Asteraceae)), respectivement. Ces deux mauvaises herbes sont sympatriques et poussent dans des milieux semblables à ceux occupés par le charançon de la graine du chou (*Ceutorhynchus obstrictus* (Marsham)), important ravageur du canola (*Brassica napus* L., *Brassica rapa* L. (Brassicaceae)) en Amérique du Nord. Les charançons de la sous-famille des Ceutorhynchinés lâchés dans les cultures pour lutter contre les mauvaises herbes peuvent aussi servir d'hôtes aux agents de lutte biologique utilisés contre le *C. obstrictus* si ces agents ne sont pas spécifiques à ce ravageur. On a observé que des parasitoïdes associés à *M. edentulus* et *H. litura* ont entraîné des taux de mortalité similaires chez leurs hôtes, mais qu'une seule espèce de parasitoïde était associée à *H. litura*, tandis que 13 espèces attaquaient *M. edentulus*. *Microplontus edentulus*, mineur des tiges, serait menacé alors que *H. litura*, qui s'attaque au collet, ne le serait pas si les parasitoïdes *Trichomalus perfectus* (Walker) et *Mesopolobus morys* (Walker) (Hymenoptera : Pteromalidae) étaient introduits comme agents de lutte biologique contre *C. obstrictus*, qui s'attaque aux siliques. Ces résultats laissent penser que la niche alimentaire pourrait être un critère important dans l'établissement de listes d'espèces non ciblées à considérer dans les essais visant à déterminer les gammes d'hôtes des agents de lutte biologique potentiels.

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Introduction

Classical biological control is an important strategy used against nonindigenous invasive weed populations (McFadyen 1998; Knight 2001; Wittenberg and Cock 2001). More than 50% of the 85 biological control agents released against weeds in Canada, the United States of America, Australia, and New Zealand belong to the Curculionidae, Chrysomelidae (Coleoptera), or Tephritidae (Diptera) (Gassmann 1995; Mason and Huber 2002; Coombs 2004). In Canada, 13 species of ceutorhynchine weevils have been released for biological control of 10 weeds. Among these are *Microplontus edentulus* (Schultze) and *Hadroplontus litura* (F.) (Coleoptera: Curculionidae) (McClay *et al.* 2002a).

Microplontus edentulus, a univoltine stem-mining weevil, was released to control scentless chamomile, *Tripleurospermum perforatum* (Mérat) M. Laínz (Asteraceae), a weed of cultivated land (Hinz and McClay 2000). Scentless chamomile forms dense, semipermanent stands in periodically disturbed sites such as pond margins, field depressions, or roadsides, from which seeds disperse into adjacent fields. Overwintered adult *M. edentulus* lay eggs into the upper parts of scentless chamomile stems in early summer. Larval feeding reduces both seed output and biomass (Bacher 1993). In North America *M. edentulus* has been reported as established in British Columbia, Alberta, and Saskatchewan (Anonymous 2009). However, only the Alberta population has been recently confirmed to be persisting, and *Microplontus edentulus* appears to have had minimal impact on scentless chamomile to date, owing to its very limited distribution, and damage caused by the larvae that does not directly impact plant reproduction (A. McClay, McClay Ecoscience, Edmonton, Alta., personal communication).

Hadroplontus litura, a univoltine stem- and root-mining weevil, was established in Canada to control Canada thistle, *Cirsium arvense* (L.) Scop. (Asteraceae) (McClay *et al.* 2002a). Canada thistle causes extensive crop yield losses through competition (Stachon and Zimdahl 1980), but is also a major problem in disturbed noncrop areas (White *et al.* 1993). Eggs

are laid into the midveins of leaves of Canada thistle rosettes in early spring and larvae mine through the vein into the stem base and upper part of the taproot. Mature larvae emerge from the stem and pupate in the soil, and adults emerge to feed on Canada thistle foliage in late summer (Zwölfer and Harris 1966; Peschken and Wilkinson 1981). Adults overwinter in the soil. In North America, *H. litura* is established in British Columbia, Alberta, Saskatchewan, and Ontario (McClay *et al.* 2002a). Damage by *H. litura* larvae appears to reduce free sugars and fructose in roots of Canada thistle (Hein and Wilson 2004), contributing to the physiological stress that reduces its competitiveness with some native plants (Ferrero-Serrano *et al.* 2008), rather than directly reducing plant biomass or seed production.

Scentless chamomile and Canada thistle are major weeds in or near canola, *Brassica napus* L. and *Brassica rapa* L. (Brassicaceae), fields in Europe (Schroeder *et al.* 1993). In Canada, both weeds are widespread (Darbyshire 2003), including major canola production areas of Manitoba, Saskatchewan, and Alberta (Donald 1990; Woo *et al.* 1991). In these provinces and in Ontario and Quebec, where canola is also grown, another ceutorhynchine, the invasive alien cabbage seedpod weevil, *Ceutorhynchus obstrictus* (Marshall), is a serious pest of canola (Doddall and Mason 2010). Adults destroy flower buds and larvae damage seeds within siliques (Kuhlmann *et al.* 2002). In Europe, the parasitoids associated with *C. obstrictus* have been well documented (Williams 2003; Ulber *et al.* 2010) and two species, *Trichomalus perfectus* Walker and *Mesopolobus morys* Walker (Hymenoptera: Pteromalidae), are potential classical biological control agents. However, ceutorhynchines introduced to control weeds in cultivated crops could be at risk of attack if agents released for biological control of *C. obstrictus* are not specific to that species (Kuhlmann *et al.* 2006a). Because *M. edentulus* and *H. litura* are ceutorhynchines, they have been included in the proposed nontarget species test list for candidate biological control agents of *C. obstrictus* (Kuhlmann *et al.* 2006a). Despite a number of studies on *M. edentulus* and *H. litura*, host-parasitoid association records are limited, and it is unknown if

parasitoid species attacking *C. obstrictus* will also attack *H. litura* and *M. edentulus*.

To assess the potential for *C. obstrictus* parasitoids to attack related weed biological control agents, it is necessary to determine the host–parasitoid associations of ecologically and (or) taxonomically related nontarget species in the area of origin. Such studies provide important guidance when selecting nontarget species for host-specificity testing and facilitate better prediction of potential risks associated with candidate biological control agents. The objectives of our study were to *i*) assess the parasitism levels of *H. litura* and *M. edentulus*, and *ii*) determine the parasitoid assemblages associated with these biological control agents in their native European habitat.

Methods

Field collections

Scentless chamomile plants were collected from fallow fields, at field margins, and along roadsides from May to July at three sites in Austria (Burgenland county) in 2003, and at five sites in Hungary (Bekes, Csongrand, and Pest counties) in 2004 (Fig. 1). Canada thistle plants were collected in May and June in 2002, 2003, and 2004 at two sites in eastern France (Alsace région) and five sites in Germany (Baden-Württemberg, Bavaria, and Schleswig-Holstein states) (Fig. 1). These sites were chosen because they were in the regions where populations of *M. edentulus* and *H. litura* introduced to North America were collected (McClay *et al.* 2002a, 2002b).

At each site, 20–50 host plants were collected and dissected at intervals of 2–10 days. The ramet of Canada thistle plants, the main shoot, and three randomly chosen side shoots of scentless chamomile plants were dissected to detect weevil eggs and larvae. Prepupal larvae of *M. edentulus* and *H. litura* chew an exit hole through the parenchyma tissue to exit the plants and drop down into the soil where they pupate. Thus, the exit holes were recorded and taken into account to estimate the number of larvae that had left the plants. Where high larval infestations occur, several larvae can exit through the same hole, resulting in underestimation of these numbers.

For each plant dissected, the eggs and larvae of ectoparasitoids found on the larvae and pupae of host weevils or near the remains of a consumed weevil host, were recorded. Mortality due to host feeding by ectoparasitoid adults was considered to be an indirect effect of parasitism and recorded independently. Parasitism was determined as follows:

$$\% \text{ parasitism} = \frac{\sum_1^n \text{paras.}}{\sum_1^n \text{avail. hosts}} \times 100 = \frac{\sum_{\text{larv}}^{\text{par}} + \sum_{\text{larv}}^{\dagger} + \sum_{\text{par}}^{\text{alone}}}{\sum_{\text{larv}}^{\text{healthy}} + \sum_{\text{larv}}^{\text{par}} + \sum_{\text{larv}}^{\dagger} + \sum_{\text{holes}} + \sum_{\text{par}}^{\text{alone}}} \times 100$$

where $\sum_1^n \text{paras.}$ is the total number of parasitoids found in the plant; $\sum_1^n \text{avail. hosts}$ is the total number of hosts available for parasitism (second- and third-instar larvae) found in the plant; $\sum_{\text{larv}}^{\text{par}}$ is the number of larvae found parasitized by an ectoparasitoid; $\sum_{\text{larv}}^{\dagger}$ is the number of larvae found dead with traces of host feeding like brownish punctures on the tegumen; $\sum_{\text{par}}^{\text{alone}}$ is the number of parasitoids found alone near the remains of a consumed host, either as a pupa, or as a newly emerged adult that had not yet exited the plant; $\sum_{\text{larv}}^{\text{healthy}}$ is the number of healthy host larvae; \sum_{holes} is the number of exit holes (made by healthy third-instar larvae that have left the plant) found on the shoots during dissections.

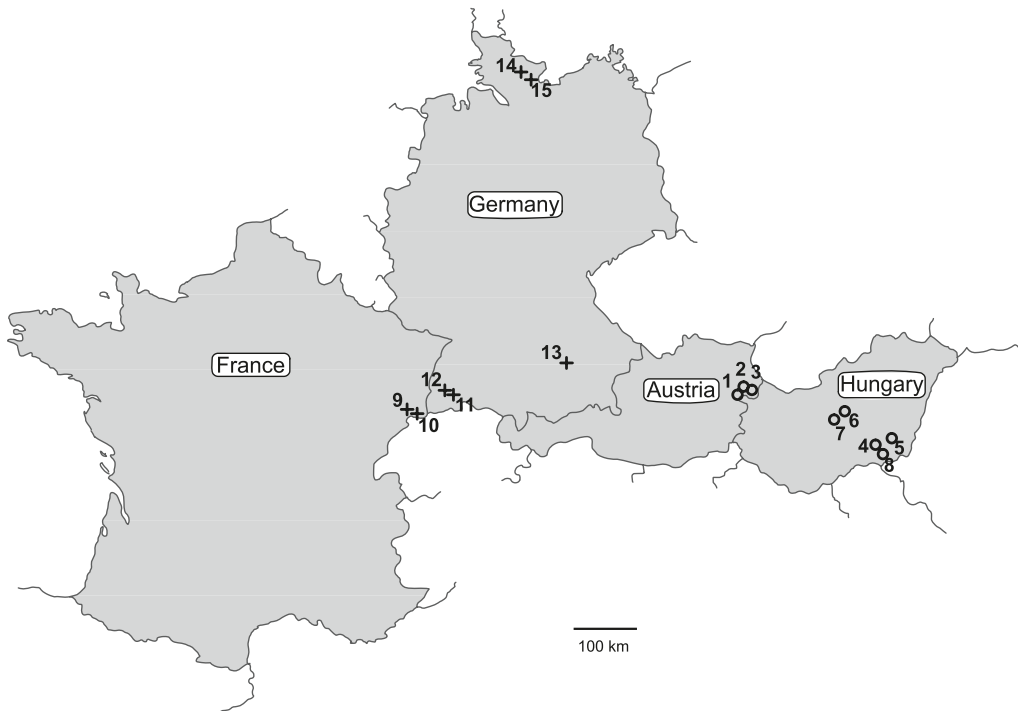
A representative parasitism level was estimated for each site, for the date on which the maximum number of healthy larvae still available for parasitism were present in the plant, *i.e.*, just before the number of exit holes started to increase.

Host density was defined as the maximum number of hosts parasitized or available for parasitism during the season. Thus, only second- and third-instar larvae were used for calculations. Exit holes were recorded as equivalent to a single third-instar larva that had exited the plant.

Parasitoid rearing and identification

Parasitoid eggs and larvae were reared on the host larvae on which they were found, and pupae were reared individually on filter paper in 5.5 cm diameter Petri dishes. Insects were reared at $20 \pm 2^\circ\text{C}$, $70\% \pm 10 \text{ RH}$, and

Fig. 1. Locations of field collection sites of *Tripleurospermum perforatum* and *Cirsium arvense* surveyed for *Microplontus edentulus* (o) and *Hadroplontus litura* (+), respectively, in 2002, 2003, and 2004.



Host plant / <i>Ceutorhynchinae</i> species	Country	Region / Town	Site #	Geographic coordinates		Elevation (m.)	
				Lat. N	Long. E		
<i>Tripleurospermum perforatum</i> / <i>Microplontus edentulus</i>	Austria	Burgenland / Eisenstadt	1	47°49'22.57"	16°32'18.77"	148	
			2	47°50'01.50"	16°34'01.95"	138	
			3	47°48'54.06"	16°32'16.45"	149	
	Hungary	Csongrad / Hodmezovasarhely	4	46°22'01.13"	20°13'17.51"	74	
			5	46°27'45.83"	20°32'37.14"	79	
			6	47°11'28.20"	19°04'20.10"	93	
			7	47°11'15.66"	19°02'38.58"	96	
			8	46°19'07.44"	20°17'23.10"	85	
<i>Cirsium arvense</i> / <i>Hadroplontus litura</i>	France	Alsace / Lucelle	9	47°26'23.93"	07°18'06.15"	480	
			10	47°26'21.93"	07°19'12.99"	525	
	Germany	Baden-Württemberg / Grissheim	11	47°52'02.78"	07°36'33.27"	213	
			12	47°52'28.23"	07°34'51.26"	205	
			13	48°30'00.32"	11°28'01.02"	492	
			Schleswig-Holstein / Stolpe	14	54°09'00.00"	10°46'58.08"	19
				15	54°08'49.93"	10°47'31.67"	21

16L:8D. The insects were checked daily until adult parasitoid emergence. Some species emerged in the same summer season they were collected. Others, such as the Braconidae, overwintered in cocoons maintained at ambient temperatures in an outdoor bunker and emerged the following spring. Identification was possible only for adults that were killed using

ethyl acetate directly after they had emerged. Specimens were individually card-mounted, labelled, and stored for later identification. Pteromalidae and Braconidae specimens were identified to species, whereas specimens of other hymenopteran families were identified to genus. Voucher specimens for the study are deposited in the collections of the Natural

Table 1. Numbers (mean \pm SE) of second- and third-instar larvae of *Microplontus edentulus* available for parasitism before the third instars started to exit from plants, and percent parasitism observed in Austria in 2003 and Hungary in 2004.

Location	Mean number (\pm SE)	Percent parasitism
Austria		
Burgenland / Eisenstadt 1	4.9 \pm 0.60	23.0
Burgenland / Eisenstadt 2	7.5 \pm 0.92	52.3
Burgenland / Eisenstadt 3	4.0 \pm 0.57	1.9
Hungary		
Csongrad/Hodmezovasarhely	1.9 \pm 0.46	3.1
Bekes/Kardoskut	5.2 \pm 0.63	11.6
Pest/Bugyi	3.7 \pm 0.30	17.8
Pest/Kiskunlachaza	4.7 \pm 0.51	26.3
Csongrad/Maroslele	7.1 \pm 0.82	4.7

History Museum of Bern, the Natural History Museum of Leiden, and the CABI Europe—Switzerland in Delémont.

Host range for each parasitoid species was determined by reviewing the literature. Where a specific name could not be assigned, the families known to be hosts for the genus were reported.

Results

Microplontus edentulus

At all study sites, *M. edentulus* larvae were present in shoots until the first week of July. Weevil densities ranged from 4.0 \pm 0.6 (mean \pm SE) to 7.5 \pm 0.9 larvae per plant in Austria in 2003, and from 1.9 \pm 0.5 to 7.1 \pm 0.8 larvae per plant in Hungary in 2004 (Table 1).

Ectoparasitoids were present from the third week of May until the first week of July. Parasitism levels ranged from 1.9% to 52.3% in Austria in 2003 and from 3.1% to 26.3% in Hungary in 2004 (Table 1). A total of 14 parasitoid species were reared from *M. edentulus* larvae, and the species present differed among sites (Table 2). The most common parasitoids were *Eurytoma curculionum* Mayr (Hymenoptera: Eurytomidae) and *Stenomalina gracilis* (Walker) (Hymenoptera: Pteromalidae), which occurred at six and five, respectively, of the seven sites sampled. Six species, one species of each of *Closterocerus* Westwood (Hymenoptera: Eulophidae), *Eupelmus* Dalman (Hymenoptera: Eupelmidae), and *Triaspis* Haliday (Hymenoptera: Braconidae), an unidentified ichneumonid

(Hymenoptera), and *Trichomalus* cf. *gynetelus* (Walker) and *T. cf. perfectus* (Walker) (Hymenoptera: Pteromalidae) occurred at only one of the sites.

All parasitoids are ectoparasitoids, except *Triaspis* sp., which is likely an endoparasitoid (Yu 2009); the single specimen was found as a pupa alongside the remains of its weevil host. All species are broad generalists, some being both primary and hyperparasitoids. The *Trichomalus* spp. are primary parasitoids of only some beetle families. *Trichomalus perfectus*, however, has been associated with *Dasineura brassicae* (Winnertz) (Diptera: Cecidomyiidae) (Vidal 1993), a secondary invader of the siliques damaged by the primary host, *C. obstrictus* (Table 3).

Hadroplontus litura

At all study sites, *H. litura* larvae were observed in shoots of Canada thistle during the first week of May, and third-instar larvae left the plant beginning in the second week of May. Although densities observed in France and Germany in 2004 were similar to those observed in 2003, the average temperatures in 2004 were in the normal seasonal range compared with 2.0–3.5 °C higher temperatures observed in 2003. Consequently, the phenology of *H. litura* was 1 week later in 2004. Overall infestation levels were rather low, with densities between 1.2 \pm 0.4 and 2.4 \pm 0.8 larvae per plant in France, and between 0.4 \pm 0.2 and 1.6 \pm 0.4 larvae per plant in Germany (Table 4).

Table 2. Parasitoid species associated with *Microplitis edentulus* and proportions (%), with the number in parentheses, of total parasitoids collected at each sample site in 2003 and 2004.

Parasitoid species	Austria			Hungary		
	Eisenstadt 1	Eisenstadt 2	Eisenstadt 3	Bekes	Pest	Csongrad
Braconidae						
<i>Bracon atrator</i> Nees	—	—	—	—	—	22.2 (2)
<i>Bracon intercessor</i> Nees	25.0 (2)	4.8 (1)	—	10.5 (2)	—	20.0 (3)
<i>Triaspis</i> Haliday sp.	—	—	16.7 (1)	—	—	—
Eulophidae						
<i>Closterocerus</i> Westwood sp.	—	—	—	5.3 (1)	—	—
Eupelmidae						
<i>Eupelmus</i> Dalman sp.	37.5 (3)	—	—	—	—	—
Eurytomidae						
<i>Eurytoma curculionum</i> Mayr	—	23.8 (5)	50.0 (3)	26.3 (5)	11.1 (1)	22.2 (2)
Ichneumonidae						
	—	—	—	10.5 (2)	—	—
Pteromalidae						
<i>Chlorocytus</i> Graham sp.1	—	—	—	36.8 (7)	22.2 (2)	22.2 (2)
<i>Chlorocytus</i> sp.2	—	—	—	10.5 (2)	22.2 (2)	—
<i>Sphegigaster</i> Spinola sp.	—	—	—	—	22.2 (2)	11.1 (1)
<i>Stenomalina gracilis</i> (Walker)	25.0 (2)	66.6 (14)	16.7 (1)	—	11.1 (1)	—
<i>Syntomopus</i> Walker sp.	—	—	16.7 (1)	—	11.1 (1)	22.2 (2)
<i>Trichomalus cf. gynetelus</i> (Walker)	—	14.8 (1)	—	—	—	—
<i>Trichomalus cf. perfectus</i> (Walker)	12.5 (1)	—	—	—	—	—
Total number of specimens	8	21	6	19	9	9

Table 3. Species, feeding niche, and known host range of parasitoids reared from *Microplontus edentulus* infesting scentless camomile, *Tripleurospermum perforatum*.

Parasitoid	Feeding niche	Hosts	Reference
Braconidae			
<i>Bracon atrator</i> Nees	Ectoparasitoid	<i>Apion buddenbergi</i> Bedel [Coleoptera: Brentidae]; <i>Gymnetron antirrhini</i> (Paykull); <i>G. campanulae</i> Schoenherr; <i>G. villosulum</i> Gyllenhal [Coleoptera: Curculionidae]; <i>Anauromyza flavifrons</i> Meigen [Diptera: Agromyzidae]; <i>Tephritis neesii</i> Meigen, <i>T. separata</i> Rondani [Diptera: Tephritidae]; <i>Coleophora coronillae</i> Zeller [Lepidoptera: Coleophoridae] <i>Atelabus nitens</i> (Scopoli), <i>Rhynchites bacchus</i> Linnaeus [Coleoptera: Attelabidae]; <i>Apion opeticum</i> Bach [Coleoptera: Brentidae]; <i>Agapanthia villosoviridescens</i> (DeGeer), <i>A. violacea</i> (Fabricius), <i>Phytoecia coerulescens</i> (Scopoli) [Coleoptera: Cerambycidae]; <i>Anthonomus pedicularius</i> (Linnaeus), <i>A. punorum</i> (Linnaeus), <i>A. sorbi</i> Germar, <i>Curculio crux</i> Fabricius, <i>C. salictivorus</i> Paykull, <i>Lixus brevisstris</i> Boheman; <i>L. incanescens</i> Boheman; <i>L. juncii</i> Boheman, <i>Microlarinus lareynii</i> Jacquelin du Val, <i>Microlarinus lypriformis</i> Wollaston, <i>Sibinia femoralis</i> Germar [Coleoptera: Curculionidae]; <i>Liriomyza haidobrensis</i> (Blanchard) [Diptera: Agromyzidae]; <i>Tetramesa hyalipennis</i> Walker, <i>T. rossica</i> Rimsky-Korsakov [Hymenoptera: Eurytomidae]; <i>Pontania acutifoliae</i> Zinovjev, <i>P. bella</i> (Zaddach), <i>P. kriechebaumeri</i> Konow, <i>P. nigricantis</i> Kopelke, <i>P. pedunculi</i> (Hartig), <i>P. vesicator</i> (Bremi), <i>P. viminalis</i> Linnaeus [Hymenoptera: Tenthredinidae]; <i>Augsma atraphaxidellum</i> Kuznetsov [Lepidoptera: Coleophoridae]; <i>Scrobipalpa obsoletella</i> (Fisher von Roeslerstamm) [Lepidoptera: Gelechiidae]; <i>Parametriotes theae</i> Kuzn. [Lepidoptera: Momphidae]; <i>Chamasphlecta hungarica</i> Tomala, <i>C. astatifformis</i> Herrich-Schaeffer, <i>Paranthrene tabaniformis</i> Rottemburg, <i>Synanthedon culiciformis</i> (Linnaeus) [Lepidoptera: Sesiidae]; <i>Sparganothis pilleriana</i> Denis & Shiff. [Lepidoptera: Tortricidae]; <i>Argyresthia conjugella</i> Zeller [Lepidoptera: Yponomeutidae].	Yu 2009
<i>Bracon intercessor</i> Nees	Ectoparasitoid		Yu 2009

Table 3 (continued).

Parasitoid	Feeding niche	Hosts	Reference
<i>Triaspis</i> Haliday sp.	Endoparasitoid	Anobiidae, Attelabidae, Bostrichidae, Brentidae, Buprestidae; Cerambycidae, Chrysomelidae, Curculionidae [Coleoptera]; Chlorophidae, Lonchaeidae, Tephritidae [Diptera]; Choreutidae, Tischeridae, Tortricidae [Lepidoptera]	Yu 2009
Pteromalidae			
<i>Chlorocyttus</i> Graham sp.	Larval or pupal ectoparasitoids, and in some cases hyperparasitoids	Cerambycidae, Curculionidae [Coleoptera]; Agromyzidae, Tephritidae [Diptera]; Cephidae, non-gall forming Eurytomidae [Hymenoptera]	Graham 1969; Yu 2009; Tremblay 1968; Charlet <i>et al.</i> 2002
<i>Closterocerus</i> Westwood sp.		leaf-miners and gall-formers;	Hansson 1990, 1994, 1996;
<i>Eupelmus</i> Dalman sp.	Ectoparasitoids, endoparasitoids, facultative hyperparasitoids, predators	Argidae, Diprionidae [Hymenoptera]; Diaspididae, Psyllidae [Hemiptera]	Gumovski 2001; Schauff 1991; Yu 2009
<i>Eurytoma</i> <i>curculionum</i> Mayr	Ectoparasitoids, hyperparasitoids	Lepidoptera, Hemiptera, Hymenoptera, Coleoptera, Neuroptera and Orthoptera	Yu 2009
		<i>Apion violaceum</i> Kirby [Coleoptera: Brentidae]; <i>Baris chlorizans</i> Germar, <i>B. cupirostris</i> Germar, <i>B. laticollis</i> (Marshall), <i>Brachonyx pineti</i> Tourmier, <i>Ceutorhynchus obsstrictus</i> (Marshall), <i>Ethelcus verrucatus</i> (Gyllenhal), <i>Gymnetron asellus</i> (Gravenhorst), <i>G. campanulae</i> Schoenherr, <i>Hypolixus truncatulus</i> (Fabricius), <i>Lixus juncii</i> Boheman, <i>L. scrobicollis</i> Neresheimer & Wagner, <i>Pissodes validirostris</i> (Sahlberg) [Coleoptera: Curculionidae]; <i>Bracon intercessor</i> Nees [Hymenoptera: Braconidae]; <i>Norbanus cerastops</i> (Masi) [Hymenoptera: Pteromalidae]	Boucek 1977; Dmoch 1975; Vidal 1997
<i>Sphegigaster</i> Spinola sp.	Ectoparasitoids, hyperparasitoids	Curculionoidea [Coleoptera]; Agromyzidae, Anthomyiidae, Chloropidae, Drosophilidae and Tephritidae [Diptera]; Braconidae [Hymenoptera]; Lyonetiidae [Lepidoptera]	Graham 1969; Yu 2009

Table 3 (concluded).

Parasitoid	Feeding niche	Hosts	Reference
<i>Stenomalina gracilis</i> (Walker)	Ectoparasitoids	<i>Ceutorhynchus alliariae</i> Gyllenhal, <i>C. obstructus</i> (Marsham), <i>Microplontus rugulosus</i> Herbst [Coleoptera: Curculionidae]; <i>Agromyza Apfelbecki</i> Strobl, <i>Napomyza lateralis</i> (Fallen), <i>Phytomyza rostrata</i> Hering, <i>P. ramunculi</i> (Schränk) [Diptera: Agromyzidae]; <i>Lucilia caesar</i> (Linnaeus) [Diptera: Calliphoridae]; <i>Dasineura brassicae</i> (Winnertz) [Diptera: Cecidomyiidae]; <i>Urophora cardui</i> (Linnaeus) [Diptera: Tephritidae]	Bauer 2005; Yu 2009
<i>Syntomopis</i> Walker sp.	Ectoparasitoids	Agromyzidae [Diptera]; Pterophoridae [Lepidoptera]	Yu 2009
<i>Trichomalus</i> cf. <i>gynetelus</i> (Walker)*	Ectoparasitoid	<i>Apion carduorum</i> (Kiry) [Coleoptera: Brentidae]; <i>Hachroplontus litura</i> Fabricius [Coleoptera: Curculionidae]	Bauer 2005; Graham 1969
<i>Trichomalus</i> cf. <i>perfectus</i> (Walker)†	Ectoparasitoid	<i>Ceutorhynchus constrictus</i> Marsham, <i>C. obstructus</i> (Marsham), <i>C. marginatus</i> Germar, <i>C. pleurostigma</i> Stephens [Coleoptera: Curculionidae]; <i>Dasineura brassicae</i> (Winnertz) [Diptera: Cecidomyiidae]‡; § <i>Megastigmus bipunctatus</i> (Swederus) [Hymenoptera: Torymidae]	Bauer 2005; Graham 1969; Mitroiu 2001; Vidal 1993; Yu 2009

*Host records for *Trichomalus gynetelus* (Walker).†Host records for *Trichomalus perfectus* (Walker).‡Ulber et al. (2010) do not include *T. perfectus* in their comprehensive list of parasitoids of *D. brassicae*.

§This is a dubious record; Graham (1969) reported that "Possibly the parasite was misidentified ... the record needs to be checked".

Table 4. Numbers (mean \pm SE) of second- and third-instar larvae *Hadroplontus litura* available for parasitism, and percent parasitism observed at sites in France and Germany in 2002, 2003, and 2004.

Location	Mean number (\pm SE)	Percent parasitism
France		
Alsace / Lucelle 1	1.21 \pm 0.41	12.5
	1.90 \pm 0.63	6.9
Alsace / Lucelle 2	2.35 \pm 0.81	47.1
	1.25 \pm 0.33	15.4
	0.85 \pm 0.38	43.8
Germany		
Southern Rhine Valley / Grissheim 1	0.40 \pm 0.22	37.5
Southern Rhine Valley / Grissheim 2	0.65 \pm 0.23	35.3
Bayern/Scheyern	1.55 \pm 0.44	9.3
Schleswig-Holstein / Stolpe 1	0.56 \pm 0.18	18.8
Schleswig-Holstein / Stolpe 2	0.48 \pm 0.20	15.4

Ectoparasitoids were already present when collections began during the second week of May 2003 and reached maximum levels by the second week of June. Parasitism levels were between 6.9% and 47.1% in France and between 9.3% and 37.5% in Germany (Table 4). Healthy host larvae started to leave the plant when sampling began, and only parasitized larvae and a low number of unparasitized third-instar larvae were still in the shoots. Ectoparasitoids found in shoots on the final sampling dates (the beginning of June) in 2003 and 2004 had already built cocoons. Twenty-five and 15 adults emerged from these cocoons over a 1-month period in April of 2003 and 2004, respectively.

Bracon intercessor Nees (Hymenoptera: Braconidae) was the only species found associated with *H. litura* larvae and was present at all sites sampled in both years. This species was also associated with *M. edentulus* at four of the seven sites where that species was collected.

Discussion

Hadroplontus litura and *M. edentulus* are present in their respective host plants at the same time of year (Zwölfer and Harris 1966; Hinz *et al.* 1996; McClay *et al.* 2002a, 2002b; this study), yet the parasitoid complexes associated with each herbivore are very different. As well, overall parasitism levels were similar between *M. edentulus* and *H. litura*, 17.6%

(1.9%–52.3%) and 24.2% (6.9%–47.1%), respectively, yet 13 and 1 species were associated with *M. edentulus* and *H. litura*, respectively. Differences in feeding niche may explain this, because a correlation exists between parasitoid species richness and host-larval feeding site in phytophagous insects (Mills 1994). Furthermore, plant species that are highly exposed are subject to highest colonization levels by herbivorous insects, and parasitoids should find the greatest range of hosts on such plants (Askew and Shaw 1986). *Hadroplontus litura* is a stem- and root-feeder that mines Canada thistle rosettes, at ground level in spring, and feeds downward into the root (*i.e.*, it is subterranean and difficult to find). *Microplontus edentulus* mines the aerial stems of scentless chamomile plants and larvae move upward to the seed heads (*i.e.*, it is easy to find). On a scale of increasing concealment within the host plant or soil, borers (miners) generally support more parasitoid species than do root-feeders (Hawkins 1994), a relationship clearly evident in this study.

Askew and Shaw (1986) stated that similar ectoparasitoid complexes attack taxonomically and ecologically related hosts in widely separated geographic areas. If they are correct, then our findings, despite being collected in only one region of their range, indicate that the parasitoid complex associated with *M. edentulus* consists of a large number of species, among which at least four, *B. intercessor*, *E. curculionum*,

S. gracilis, and a species of *Syntomopus* Walker (Hymenoptera: Pteromalidae), are widespread (Yu 2009). We could find no published studies of the parasitoids associated with *M. edentulus*, thus we could not determine if this parasitoid assemblage occurs over the entire range of its host.

In the case of *H. litura*, the single parasitoid collected in this study, *B. intercessor*, was also associated with *M. edentulus*. This parasitoid is widespread across the Palaearctic and it has a very broad host range (Table 3; Yu 2009). However, Freese (1994, 1997) reported one possible hyperparasitoid, a species of *Gelis* Thunberg (Hymenoptera: Ichneumonidae) and four ectoparasitoids, *Phaonia trimaculata* (Bouché) (Diptera: Muscidae), *Bracon immutator* Nees (reported as *Lucobracon erraticus* Wesmael in Freese 1994) (Hymenoptera: Braconidae), an unidentified species of *Chlorocytyus* Graham (Hymenoptera: Pteromalidae), and *S. gracilis* associated with *H. litura* in Germany. The *Chlorocytyus* species was associated with *H. litura* from western Poland, and the other species with *H. litura* in thistles in the Nordbayern region of Germany.

These findings suggest that there is geographic variation in the parasitoid complex associated with at least *H. litura*. The presence of a braconid species, and the pteromalids *Chlorocytyus* sp. and *S. gracilis* in the parasitoid assemblage of both *M. edentulus* and *H. litura* supports the hypothesis that parasitoid complexes are similar for taxonomically and ecologically related hosts over broad geographical areas (Askew and Shaw 1986). Furthermore, Freese (1997) also recorded 24% parasitism by *B. immutator* at various sites in three regions of Germany, which is similar to the findings in this study for *B. intercessor*.

Hadropontus litura, *M. edentulus*, and *C. obstrictus* occur sympatrically in Europe and overlap in their periods of larval development (Bonnemaison 1957; Zwölfer and Harris 1966; Peschken and Wilkinson 1981; Hinz *et al.* 1996; McClay *et al.* 2002b; Dossdall and Moisey 2004), suggesting that parasitoids of *C. obstrictus* could attack *H. litura* and *M. edentulus* (Kuhlmann *et al.* 2006a). *Trichomalus perfectus* and *M. morys* are the two most common parasitoids of *C. obstrictus* in Europe (Williams 2003) and

both are considered to be potential biological control agents for release in Canada (Kuhlmann *et al.* 2002). In this study, we found *T. cf. perfectus* also associated with *M. edentulus*. If this parasitoid is confirmed to be *T. perfectus*, it indicates that release of *T. perfectus* in North America could result in nontarget impact on *M. edentulus*. However, such nontarget impact would likely be negligible because only a single specimen was found at one of the seven locations sampled in our study.

Our study documented several new host–parasitoid associations: *Chlorocytyus* spp., *E. curculionum*, *S. gracilis*, *Syntomopus* sp., and *T. cf. gynetelus* with *M. edentulus* larvae; and *B. intercessor* with *H. litura* larvae. *Stenomalina gracilis* has a broad host range, associated with several ceutorhynchine species such as *C. obstrictus* (Dmoch 1975), *H. litura* (Vidal 1997), *C. napi* Gyllenhal, *C. pallidactylus* (Marsham), and *C. roberti* Gyllenhal (Kuhlmann and Mason 2002; Ulber 2003), so it is not surprising to find it also associated with *M. edentulus*. Our results indicated that *Syntomopus* sp. is a primary larval ectoparasitoid, whereas other *Syntomopus* spp. have been recorded only as primary pupal ectoparasitoids (Graham 1969). The braconid *B. intercessor*, one of the four most common parasitoids associated with *M. edentulus*, was the only species to attack *H. litura* in our study, a new association.

In conclusion, parasitoids associated with *M. edentulus* and *H. litura* inflict similar levels of mortality on their hosts, yet a single species is associated with the latter host, whereas 13 species attack the former. The stem-mining *M. edentulus* appears to be at greater risk than the root-crown-feeding *H. litura*, should biological control agents of *C. obstrictus* be introduced. These results indicate that feeding niche may be an important criterion for developing a nontarget species test list for host-range testing of potential biological control agents, supporting the methods proposed by Kuhlmann *et al.* (2006a, 2006b). Furthermore, understanding the population dynamics of economically important species is still hampered by insufficient knowledge of the natural enemy complexes that may be important in regulating herbivorous insects (Vidal 2003). If *T. perfectus*, with only a single specimen found in this study, and *M. morys*,

with none found, are introduced to Canada, it appears that they would pose low risks to either *M. edentulus* or *H. litura*.

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