


ARTICLE

# Two adventive species of European Chrysomelidae (Coleoptera) new to North America: *Cryptocephalus moraei* (Cryptocephalinae) and *Psylliodes dulcamarae* (Galerucinae: Alticini), and the origins of adventive Chrysomelidae in Canada and United States of America

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## Abstract

First North American records are presented for *Cryptocephalus moraei* (Linnaeus, 1758) (Coleoptera: Cryptocephalinae) and *Psylliodes dulcamarae* (Koch, 1803) (Coleoptera: Galerucinae: Alticini), as confirmed by morphology and DNA barcoding. Additional information is presented about phenology and host use for *C. moraei*, the first European Cryptocephalinae to be found elsewhere as conclusively adventive. *Cryptocephalus moraei* is expected to have no ecological impact on its host, the adventive *Hypericum perforatum* Linnaeus (Hypericaceae). However, *P. dulcamarae*, the second recently discovered flea beetle associated with the adventive *Solanum dulcamara* Linnaeus (Solanaceae), probably does harm that host. Both species are hypothesised to have arrived from Europe with woody plant material imported with soil during 1960–1965. A literature review of introduced Chrysomelidae found that Canada and the United States of America are together home to 68–78 species of adventive Chrysomelidae. All non-Bruchinae species among these are both native to Europe and occur either in Canada or both Canada and United States of America, except for intentionally introduced biological control agents and two species that feed on *Eucalyptus* L'Héritier de Brutelle (Myrtaceae). This suggests a dominant role of accidental introductions of cool-climate European species in recent unplanned additions to the fauna of leaf-feeding Chrysomelidae in North America.

## Introduction

Leaf beetles are drivers of ecological change in terrestrial biomes, acting as plant pests, biological control agents, and elsewhere as abundant herbivores (Myers and Sarfraz 2017). Québec, Canada has a tradition of collaboration between professionals and skilled amateur collectors in documenting its insect fauna, including economically important species (e.g., de Tonnancour *et al.* 2017). Here, we report establishment of two additional species of adventive Chrysomelidae found by independent scientific collectors in and near cities in Québec.

The first, *Cryptocephalus moraei* (Linnaeus, 1758) (Coleoptera: Cryptocephalinae), is native throughout Europe and western Asia (Lopatin *et al.* 2010). It has been found there in

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association with *Hypericum perforatum* Linnaeus (Hypericaceae), or St John's-wort (Rheinheimer and Hassler 2018). The second, *Psylliodes dulcamarae* (Koch, 1803) (Coleoptera: Galerucinae: Alticini), is native to western Eurasia, including Europe, Anatolia, Kazakhstan, Mongolia, and eastern Siberia (Döberl 2010). It has primarily been associated in Europe (Rheinheimer and Hassler 2018) with *Solanum dulcamara* Linnaeus (Solanaceae). We also discuss our findings in the context of the diversity and origins of accidentally introduced Chrysomelidae in North America.

## Methods

Co-authors CC and SD collected specimens during independent insect-collecting activities. CC noted that neither species matched known North American species and sent specimens to co-author HD for identification through the Agriculture and Agri-Food Canada National Identification Service, Canadian National Collection of Insects, Arachnids and Nematodes (Ottawa, Ontario, Canada). SD learned about the discovery of *Cryptocephalus moraei* from CC and recognised that he also had specimens of *C. moraei* from Québec. SD also searched near Montréal, Québec for additional specimens and further ecological associations during the summers of 2019 and 2020. Associated plants were identified visually, in some cases with supporting photographs. HD searched for specimens at three sites with *Hypericum* in Ottawa, Ontario, Canada during summer 2020. Specimens are deposited in the following Canadian insect collections: Claude Chantal Insect Collection (private collection), Varennes, Québec, Canada; Pierre de Tonnancour Insect Collection (private collection), Terrasse Vaudreuil, Québec, Canada; Stéphane Dumont Insect Collection (private collection), Montréal, Québec, Canada; and the Canadian National Collection of Insects Arachnids and Nematodes, Ottawa Ontario, Canada. HD and KS dissected and compared specimens to North American (White 1968; Quinn 2017) and European (Burlini 1955; Doguet 1994; Nadein 2010) taxonomic literature and expert-managed Internet sites (Borowiec 2010–2020) and identified the Canadian National Collection specimens, also sending images of Canadian specimens of *C. moraei* to J. Bezděk (Mendel University, Brno, Czech Republic) and images of *P. dulcamarae* to M. Gikonyo (Max Planck Institute for Chemical Ecology, Germany), who performed independent photo-based identifications.

For DNA analysis, a single leg was detached from each specimen and was placed in a well in a 96-well microplate prefilled with 10 µL of 96% ethanol. Each specimen was also photographed, and the resulting image was uploaded to the Barcode of Life Database (BOLD; Ratnasingham and Hebert 2007) along with the label data. The DNA extraction, polymerase chain reaction amplification, and Sanger sequencing of the cytochrome oxidase subunit 1 barcode region were performed for all specimens at the Centre for Biodiversity Genomics (University of Guelph, Guelph, Ontario, Canada), using standard protocols as outlined by Pentinsaari *et al.* (2019). Primers *LepF1* and *LepR1* (Hebert *et al.* 2004) were used for polymerase chain reaction amplification. Sequences were obtained through unidirectional analysis. Details on the polymerase chain reaction and sequencing protocols for each specimen are provided in the public BOLD dataset information below.

Detailed collection information for each specimen, including both DNA-barcoded material and other specimen records, as well as GenBank accession numbers for the barcode sequences, are listed in the text. All sequences, details on polymerase chain reaction and sequencing primers, photographs, and full collection data for the DNA-barcoded specimens are available through a public dataset on BOLD (<https://doi.org/dx.doi.org/10.5883/DS-CRYPPEYL>).

The total number of adventive Chrysomelidae in North America north of Mexico has not been defined, but Klimaszewski *et al.* (2020) found Canada hosted 61 species of adventive Chrysomelidae. The lack of current total estimates for North America may originate from a history of publications for Bruchinae that are separate from the remainder of Chrysomelidae

and the fact that the catalogue by Riley *et al.* (2003) did not focus primarily on adventive species. Here, we review the recent literature to assemble a list of adventive Chrysomelidae for North America.

## Results and discussion

### *Cryptocephalus moraei*

The external morphology and genitalia of Canadian specimens closely matched Burlini's (1955) taxon concept of *C. moraei*, as based on European specimens; J. Bezděk also confirmed our identification.

*Cryptocephalus moraei* was found at the following localities in **Canada, Québec**: Verchères, Varennes, 16.vii.2017, Claude Chantal 1 ex.; Laval, Rue St-Boniface, 45.5964, -73.6827, 6.vii.2013, swimming pool, 1 ex., S. Dumont; Laval, Boisé Papineau, 45.6078, -73.6849, 28.vi.2014, mixed meadow with *Equisetum arvense*-*Potentilla reptans*, 3 ex., S. Dumont; same except, 15.vii.2019, 6 ex. (including DNA-barcoded specimen CCDB19514\_CNC\_P1A10, CNC1053107; GenBank: MW564587); same except, 22.vii.2019, 5 ex. and *Lotus corniculatus*, 1 ex.; Montréal, Parc Zotique-Racicot, 45.5416, -73.6831, 24.vii.2015, *Plantago lanceolata*, 1 ex., S. Dumont; same except, 45.5426, -73.6903, 11.vii.2018, *Cirsium arvense*, 1 ex.; same except 45.5432, -73.6916, 17.vii.2019, *Medicago lupulina*, 4 ex. (including DNA-barcoded specimen CCDB19514\_CNC\_P1A9, CNC1053106; GenBank: MW564586); same except, 18.vii.2019, 1 ex. + *Hypericum perforatum*, 1 ex.; same except, 24.vii.2019, *Medicago lupulina*, 6 ex.; same except, 30.vii.2019, 3 ex.; same except, 1.viii.2019, 1 ex.; same except 14.vi.2020, 2 ex.; same except 19.vi.2020, 1 ex. + Montréal, Bois-de-Boulogne train station, 45.5407, -73.6754, *Potentilla reptans*, 6 ex.; Montréal, Parc Zotique-Racicot, 45.5432, -73.6916, 28.vi.2020, *Medicago lupulina*, 13 ex.; same except, 5.vii.2020, 6 ex., S. Dumont with P. de Tonnancour; same except, 18.vii.2020, 7 ex., S. Dumont; same except, 22.vii.2020, 2 ex.; same except, 24.vii.2020, 1 ex.; same except, 11.viii.2020, 1 ex.

Specimens were swept from *Equisetum* Linnaeus (Equisetaceae) and *Potentilla* Linnaeus (Rosaceae) stands and from individual plants of *Hypericum* Linnaeus (Hypericaceae), *Lotus* Linnaeus (Fabaceae), *Medicago* Linnaeus (Fabaceae) (Fig. 1D), *Plantago* Linnaeus (Plantaginaceae), and *Trifolium* Linnaeus (Fabaceae) growing in dry-mesic meadows on disturbed rocky subsoil (Fig. 1), with *Cryptocephalus venustus* (Fabricius, 1787) also present. No *C. moraei* specimens were found in wet-soil parts of one of the same sites. The earliest collection year for *C. moraei* was 2013 in Laval, Québec. Specimens from the Montréal, Québec sites were collected between 14 June and 11 August 2020. Searches were not conducted during 3–13 August 2019 or between 31 July and 7 August 2020. Searches by SD on 14, 18, and 31 August 2019, on 17, 20, 24, and 30 May 2020, and on 16 and 19 August 2020 yielded no specimens. The distances between collection site clusters were 36 and seven kilometres in the Montréal area, including the south shore of the St. Lawrence River and the two largest islands of the Hochelaga Archipelago. Collection of 74 specimens in three areas over seven years suggests that *C. moraei* is established at multiple sites in Canada. Searches at three similar sites in central Ottawa, Ontario, Canada yielded no specimens. No wider survey has been conducted to determine the full range of this species in North America.

*Cryptocephalus moraei* can be distinguished from other North American and European *Cryptocephalus* by body length, 3–5 mm, with nonmetallic and mainly black dorsal and ventral colouration (Fig. 2A, B), body glabrous dorsally; head with pale markings on frons (X-shaped in male, Fig. 2C; female with two red longitudinal lines in most); pronotum pale at anterior edge and hind angles in male (Fig. 2A, C, D) and in some females, pronotal lateral carina not visible in dorsal view, punctures not forming striae; elytra striate with pale patches near humeri and apices (Fig. 2A, B), humeral pale patches not reaching elytral base or suture; legs with ventral side of profemora pale (Fig. 2A), tibiae and tarsi pale (modified from



**Fig. 1.** Habitat and resting plants used by *Cryptocephalus moraei* from Québec, Canada: **A**, Boisé Papineau, Laval, Québec, Canada; **B**, Parc Zotique-Racicot, Montréal, Québec; **C**, on leaf (possibly of *Pastinaca sativa* Linnaeus (Apiaceae)); and **D**, under leaf of *Medicago lupulina*.

Mohr 1966). The aedeagal shape (Fig. 3A–C) also distinguishes this from previously illustrated North American *Cryptocephalus* species (White 1968). The prosternum also has pale peg-like postcoxal projections (Fig. 2D) not observed in other North American *Cryptocephalinae*. Females can be distinguished from males by dark anterior edge of the pronotum and a mesal depression on ventrite 5. The eastern North American *Cryptocephalus quadruplex* Newman, 1841 is similar, but pale markings are absent from the head and pronotum, and most specimens have the humeral pale spot reaching the elytral base.

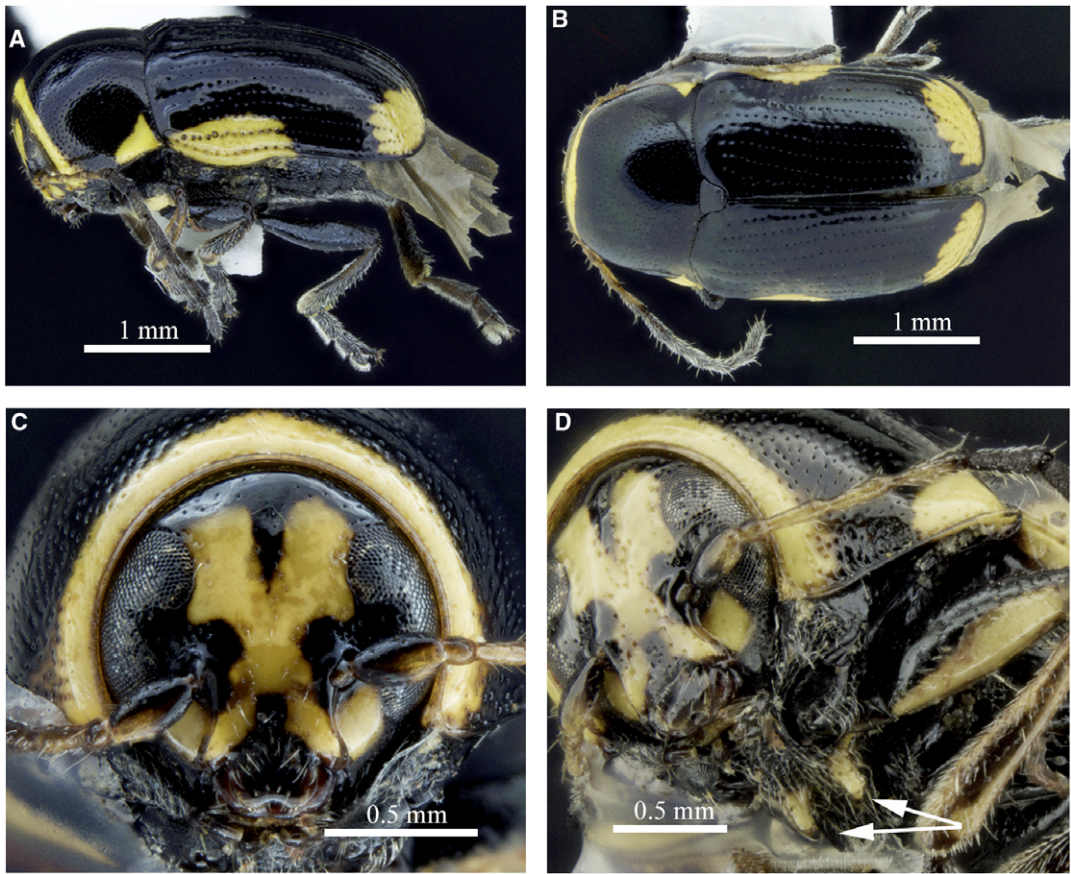


Fig. 2. Morphology of a male of *Cryptocephalus moraei* from Québec, Canada: **A**, lateral habitus; **B**, dorsal habitus; **C**, anterior view of head; and **D**, ventrolateral view of prosternum with arrows to postcoxal projections.

Although *C. moraei* is primarily associated with *Hypericum perforatum* Linnaeus (Hypericaceae) (also called St John's-wort; Rheinheimer and Hassler 2018), only one Canadian adult specimen was also found on *H. perforatum*. *Hypericum perforatum* is an adventive weed in North America that has been subject to biological control efforts. However, *C. moraei* is not expected to substantially damage *Hypericum* plants because its larvae consume senescent leaves (Rheinheimer and Hassler 2018).

Analysis of the two DNA-barcoded Canadian specimens of *C. moraei* through the BOLD Identification Engine resulted in a 98.78% match with *Cryptocephalus moraei*. The BOLD Barcode Index Number (Ratnasingham and Hebert 2013) cluster assignments were not available for our specimens at the time of publication. Comparison of sequences of our specimens to publicly available specimens from European barcoding initiatives (Pentinsaari *et al.* 2014; Hendrich *et al.* 2015) indicated sequence divergences of 1.2–4.3% among 26 specimens from barcode index numbers ACE2080 and AAN3893. The barcodes from the Canadian specimens were closer to barcode index number ACE280, with specimens from Finland and Estonia, than to barcode index number AAN3893, with specimens from Germany, Italy, Spain, France, Austria, Netherlands, and Norway. Clustering of the Canadian specimens within European sequences of *C. moraei* is consistent with our morphological identification.

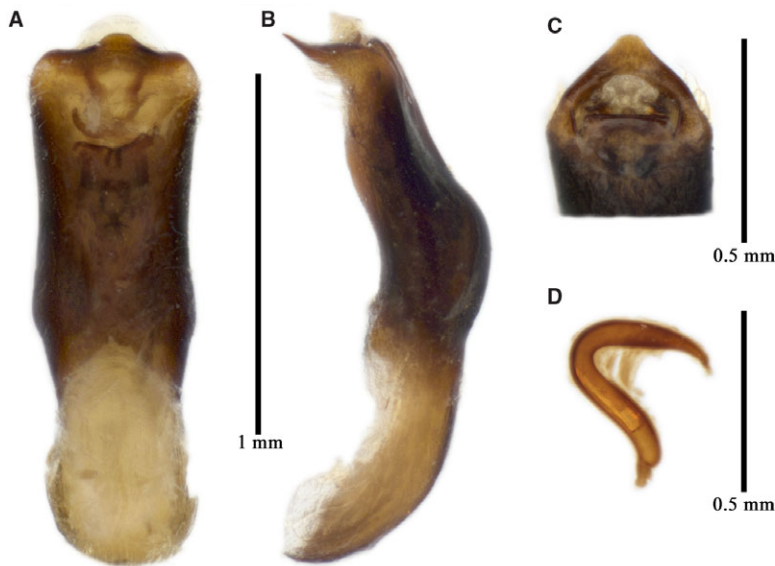


Fig. 3. Genitalia of *Cryptocephalus moraei* from Québec, Canada: **A**, aedeagus, dorsal view; **B**, aedeagus, lateral view; **C**, aedeagus apex in apico-dorsal view; and **D**, spermatheca.

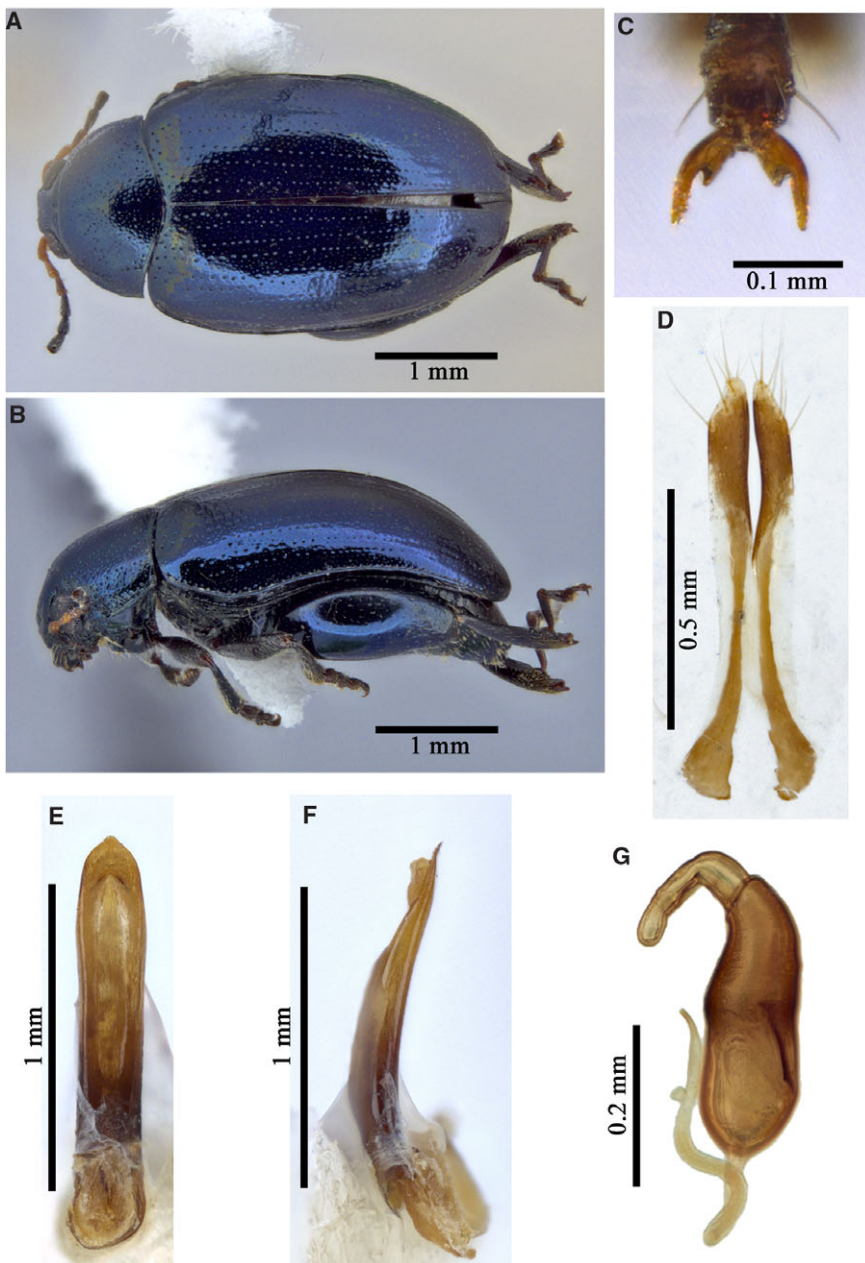
### *Psylliodes dulcamarae*

The external morphology and male genitalia of Canadian specimens closely matched Nadein's (2010) taxon concept of *P. dulcamarae*, as based on European specimens; M. Gikonyo also confirmed our identification. We identified *Psylliodes* specimens as *P. dulcamarae* using Nadein (2010) and Doguet (1994). They also matched Canadian National Collection specimens identified by Doguet in body shape, frons morphology and colour pattern, punctuation of the pronotum and elytra, aedeagus shape, and spermatheca shape. The spermatheca matches the image published by Doguet (1994, Fig. 223i) in the shapes of the pump and duct; however, the receptacle is about one-third narrower than in the specimen illustrated. This suggests that there may be undocumented spermathecal receptacle-shape variability in the native range of this species.

Analysis of the DNA-barcoded Canadian specimen of *P. dulcamarae* through the BOLD Identification Engine resulted in a 99.69% match with *Psylliodes dulcamarae*. The BOLD barcode index number assignments were not available for our specimens at the time of publication.

Comparison of sequences of our specimen to specimens from the German Barcode of Life project (Hendrich *et al.* 2015) indicated sequence divergences of 0.3–0.9% among the eight specimens with publicly available data compared. This result is consistent with morphological identification of *P. dulcamarae*.

One author (CC) found *P. dulcamarae* at the following localities in **Canada, Québec**: Verchères, Varennes, 9.vi.2010, 1 ex.; 15.v.2012, 2 ex.; 27.vi.2013, 1 ex.; 11.v.2014, 1 ex.; 21.v.2014, 1 ex.; 23.v.2014, 2 ex.; 11.vi.2014, 4 ex.; 30.vi.2014, 1 ex.; 8.vii.2014, 1 ex.; 30.vii.2014, 2 ex.; 15.v.2015, 1 ex. (DNA-barcoded specimen CCDB19514\_CNC\_P1A11, CNC1053108; GenBank: MW564584); 18.v.2015, 1 ex.; 1.vi.2015, 1 ex.; 7.vi.2015, 2 ex.; 2.vii.2015, 1 ex.; 24.v.2018, 1 ex.; Boucherville, woodland edge by industrial area, 45.55, –73.42, 25.v.2012, 3 ex.; same data except 19.v.2014, 1 ex. Collection of 27 specimens from two sites on the south shore of the St. Lawrence River, Québec separated by 25 km over eight years suggests that populations of *P. dulcamarae* are established in Canada. No survey has been conducted to determine the full range of this species in North America.



**Fig. 4.** Morphology of *Psylliodes dulcamarae* from Québec, Canada: **A**, male dorsal habitus; **B**, male lateral habitus; **C**, male tarsal claw; **D**, vaginal palpi; **E**, aedeagus, dorsal view; **F**, aedeagus, lateral view; and **G**, spermatheca.

Genus *Psylliodes* requires taxonomic revision; however, *P. dulcamarae* can be distinguished from other eastern North American *Psylliodes* by the following combination of characters: metallic-blue colouration and uniformly dark legs (Fig. 4A, B). Its aedeagus and female genitalia also appear unique among described North American species (Fig. 4D–G).

*Psylliodes dulcamarae* has primarily been associated in Europe with *Solanum dulcamara* (Rheinheimer and Hassler 2018), a species with red berries that are probably toxic to humans

in large quantities (Alexander *et al.* 1948; Hornfeldt and Collins 1990) and possibly also to livestock (Waggy 2009). Although *Solanum dulcamara* is not native to North America, it has apparently not been a subject of biological control research efforts (Mason and Huber 2002; Mason and Gillespie 2013). It has perhaps not received biological control research attention because of its low stand density in nature and because it is congeneric with potato, tomato, and peppers. Its relatedness to cultivated vegetables presents a risk that herbivorous biological control agents could also attack crops. However, to date, *P. dulcamarae* has not been found associated with important damage to crop species. This species may benefit agriculture, human safety, and native plant communities in North America by harming *S. dulcamara* plants.

### Adventive species biology

Interestingly, *P. dulcamarae* is the second pest of *Solanum dulcamara* to be discovered recently in North America. Deczynski (2014, 2019) recently reported *Epitrix pubescens* (Koch, 1803) (Coleoptera: Chrysomelidae) from the northeastern United States of America and eastern Canada, with specimens known from as early as 1975. It seems likely that these two flea beetle species that feed on the same host may have come to North America along the same trade pathway. One possible pathway for such introductions is importation of woody plants with soil. For example, some populations of Elateridae (Coleoptera) that were detected as larvae in shipments of woody plants shipped with soil during 1960–1965 have only recently been detected as adventive in North American cities (Douglas 2011). Many flea beetle larvae also develop around the roots of weedy hosts, which are likely to also have been shipped to North America in soil with woody ornamental plants.

*Cryptocephalus moraei* is the first Palearctic species of Cryptocephalinae introduced elsewhere in the world (although the Nearctic *Diachus auratus* Fabricius, 1801 now has a cosmopolitan distribution; Reid 1988; Regalin and Medvedev 2010; Schöller *et al.* 2010). Cryptocephalinae with larvae mainly inhabiting leaf litter are probably less prone to accidental transport by humans via plant tissue than are herbivores feeding on or in growing plant tissues. Finding such an introduction in a northeastern North American city is also consistent with the former practice of importing European plants in soil to North America.

### Origins of adventive Chrysomelidae in North America

Before these findings, Canada and the United States of America were together known to host 66–76 species of adventive Chrysomelidae (Table 1). This estimate is based on 44 adventive and possibly adventive Chrysomelidae reported from North America by Riley *et al.* (2003). Riley *et al.* (2003) also reported three additional nonnative species of uncertain population-establishment status in North America. Kingsolver (2004) added 14 adventive Bruchinae and two North American Bruchinae of possible adventive origins to these numbers. Klimaszewski *et al.* (2020) reviewed recent records of adventive Chrysomelidae in Canada (including recent additions by Pentinsaari *et al.* 2019), finding seven additional species for the North American fauna. Five additional species are reported from the United States of America in four other publications (see Table 1). These sources, together with our findings, indicate that 68–78 species of adventive Chrysomelidae are known from Canada and the United States of America. Of these, 51–59 are known from Canada, and 56–66 are known from the United States of America. These numbers include 21 species intentionally introduced as biological control agents. The numbers also capture uncertainty about the presence of six nonnative species and about nonnative status of four recorded species. Unverified Internet reports suggest that at least two additional species of Palearctic Chrysomelidae occur in the United States of America. It is also likely that some species reported from only the United States of



**Table 1.** Adventive Chrysomelidae reported from Canada and the United States of America. Unless noted otherwise, all are established, accidentally introduced nonnative species that are present in both countries. References cited are numbered as follows: (1) Riley *et al.* 2003; (2) Clark *et al.* 2004; (3) Kingsolver 2004; (4) Hoebeke *et al.* 2009; (5) Overholt *et al.* 2009; (6) Tracy and Robbins 2009; (7) Overholt *et al.* 2016; and (8) Klimaszewski *et al.* 2020.

Subfamily	Name	Notes
Bruchinae	<i>Acanthoscelides modestus</i> (Sharp, 1885)	Not Canada (3)
Bruchinae	<i>Acanthoscelides obtectus</i> (Say, 1831)	Native? (3; 8)
Bruchinae	<i>Amblycerus nigromarginatus</i> (Motschulsky, 1874)	Not Canada (3)
Bruchinae	<i>Amblycerus obscurus</i> (Sharp, 1885)	Not Canada (3)
Bruchinae	<i>Borowiecius ademptus</i> (Sharp, 1886)	Not Canada (3)
Bruchinae	<i>Bruchidius cisti</i> (Fabricius, 1775)	(3; 8)
Bruchinae	<i>Bruchidius terrenus</i> (Sharp, 1886)	Not Canada (4)
Bruchinae	<i>Bruchidius villosus</i> (Fabricius, 1792)	(3; 8)
Bruchinae	<i>Bruchus brachialis</i> Fåhraeus, 1839	(3; 8)
Bruchinae	<i>Bruchus pisorum</i> (Linnaeus, 1758)	(3; 8)
Bruchinae	<i>Bruchus rufimanus</i> (Boheman, 1833)	(3; 8)
Bruchinae	<i>Callosobruchus chinensis</i> (Linnaeus, 1758)	(3; 8)
Bruchinae	<i>Callosobruchus maculatus</i> (Fabricius, 1775)	(3; 8)
Bruchinae	<i>Callosobruchus phaseoli</i> (Gyllenhal, 1833)	Not Canada (3)
Bruchinae	<i>Callosobruchus pulcher</i> Pic, 1922	Not Canada (3)
Bruchinae	<i>Caryedon serratus</i> (Olivier, 1790)	Not Canada (3)
Bruchinae	<i>Megacerus ripiphorus</i> (Fahraeus, 1839)	Native? (3), not Canada (3)
Cassidinae	<i>Cassida azurea</i> Fabricius, 1801	Biocontrol (1; 8), not United States of America
Cassidinae	<i>Cassida flaveola</i> Thunberg, 1794	Native? (8)
Cassidinae	<i>Cassida rubiginosa</i> Muller, 1776	(1; 8)
Cassidinae	<i>Cassida viridis</i> Linnaeus, 1758	Not United States of America? (8)
Cassidinae	<i>Gratiana boliviana</i> Spaeth, 1926	Biocontrol (4), not Canada
Chrysomelinae	<i>Chrysolina hyperici</i> (Forster, 1771)	Biocontrol (1; 8)
Chrysomelinae	<i>Chrysolina quadrigemina</i> (Forster, 1771)	Biocontrol (1; 8)
Chrysomelinae	<i>Chrysolina staphylaea</i> (Linnaeus, 1758)	Not United States of America
Chrysomelinae	<i>Chrysolina varians</i> (Schaller, 1783)	Biocontrol, established? (1; 8)
Chrysomelinae	<i>Gastrophysa polygoni</i> (Linnaeus, 1758)	(1; 8)
Chrysomelinae	<i>Parapsisterna m-fuscum</i> (Boheman, 1859)	Not Canada (2)
Chrysomelinae	<i>Plagioderia versicolora</i> (Laicharting, 1781)	(1; 8)
Chrysomelinae	<i>Trachymela sloanei</i> (Blackburn, 1896)	Not Canada
Criocerinae	<i>Crioceris asparagi</i> (Linnaeus, 1758)	(1; 8)
Criocerinae	<i>Crioceris duodecimpunctata</i> (Linnaeus, 1758)	(1; 8)
Criocerinae	<i>Lema cyanella</i> (Linnaeus, 1758)	Biocontrol, established? (1; 8)
Criocerinae	<i>Lilioceris cheni</i> Gressitt and Kimoto, 1961	Biocontrol (7), not Canada

(Continued)

Table 1. (Continued)

Subfamily	Name	Notes
Criocerinae	<i>Liliceris lilii</i> (Scopoli, 1763)	(1; 8)
Criocerinae	<i>Oulema melanopus</i> (Linnaeus, 1758)	(1; 8)
Cryptocephalinae	<i>Cryptocephalus moraei</i> (Linnaeus, 1758)	Present study, not United States of America
Galerucinae	<i>Agasicles hygrophila</i> Selmán and Vogt, 1971	Biocontrol (1; 8), not Canada
Galerucinae	<i>Altica carduorum</i> (Guérin-Ménéville, 1858)	Biocontrol, established? (1; 8)
Galerucinae	<i>Aphthona cyparissiae</i> (Koch, 1803)	Biocontrol (1; 8)
Galerucinae	<i>Aphthona czwalinae</i> Weise, 1881–1893	Biocontrol (1; 8)
Galerucinae	<i>Aphthona flava</i> Guillebeau, 1894	Biocontrol (1; 8)
Galerucinae	<i>Aphthona lacertosa</i> Rosenhaur, 1840	Biocontrol (1; 8)
Galerucinae	<i>Aphthona nigriscutis</i> Foudras, 1860	Biocontrol (1; 8)
Galerucinae	<i>Chaetocnema concinna</i> (Marsham, 1802)	(1; 8)
Galerucinae	<i>Chaetocnema hortensis</i> (Geoffroy, 1785)	Not United States of America? (8)
Galerucinae	<i>Diorhabda carinulata</i> (Desbrochers des Loges, 1870)	Biocontrol (6), not Canada
Galerucinae	<i>Diorhabda elongate</i> (Brullé, 1832)	Biocontrol (6), not Canada
Galerucinae	<i>Epitrix pubescens</i> (Koch, 1803)	(8)
Galerucinae	<i>Longitarsus ferrugineus</i> (Foudras, 1859)	(1; 8)
Galerucinae	<i>Longitarsus flavicornis</i> (Stephens, 1831)	Biocontrol, established? (1; 8)
Galerucinae	<i>Longitarsus ganglebaueri</i> Heikertinger, 1912	Native? (8)
Galerucinae	<i>Longitarsus jacobaeae</i> (Waterhouse, 1858)	Biocontrol (1; 8)
Galerucinae	<i>Longitarsus lewisii</i> Baly, 1874	Not United States of America? (8)
Galerucinae	<i>Longitarsus luridus</i> (Scopoli, 1763)	(1; 8)
Galerucinae	<i>Longitarsus pellucidus</i> (Foudras, 1859)	Not United States of America?
Galerucinae	<i>Longitarsus pratensis</i> (Panzer, 1794)	(1; 8)
Galerucinae	<i>Longitarsus quadriguttatus</i> (Pontoppidan, 1763)	Biocontrol (1; 8), not United States of America
Galerucinae	<i>Longitarsus rubiginosus</i> (Foudras, 1859)	Not United States of America?
Galerucinae	<i>Longitarsus succineus</i> (Foudras, 1859)	Not United States of America
Galerucinae	<i>Lythriaria salicariae</i> (Paykull, 1800)	Not United States of America (8)
Galerucinae	<i>Mantura chrysanthemi</i> (Koch, 1803)	(1; 8)
Galerucinae	<i>Neocrepidodera ferruginea</i> (Scopoli, 1763)	Not United States of America? (8)
Galerucinae	<i>Neogalerucella californiensis</i> (Linnaeus, 1767)	Biocontrol (1; 8)
Galerucinae	<i>Neogalerucella pusilla</i> (Duftschmid, 1825)	Biocontrol (1; 8)
Galerucinae	<i>Phyllotreta armoraciae</i> (Koch, 1803)	(1; 8)
Galerucinae	<i>Phyllotreta cruciferae</i> (Goeze, 1777)	(1; 8)
Galerucinae	<i>Phyllotreta punctulata</i> (Marsham, 1802)	(1; 8)
Galerucinae	<i>Phyllotreta striolata</i> (Fabricius, 1801)	(1; 8)
Galerucinae	<i>Psylliodes affinis</i> (Paykull, 1799)	(1; 8)

(Continued)

**Table 1.** (Continued)

Subfamily	Name	Notes
Galerucinae	<i>Psylliodes chalconeris</i> (Illiger, 1807)	Biocontrol, established?, not Canada (1)
Galerucinae	<i>Psylliodes chrysocephalus</i> (Linnaeus, 1758)	Established? (8)
Galerucinae	<i>Psylliodes cucullatus</i> (Illiger, 1807)	(1; 8)
Galerucinae	<i>Psylliodes dulcamarae</i> (Koch, 1803)	Present study, not United States of America
Galerucinae	<i>Psylliodes napi</i> (Fabricius, 1792)	(1; 8)
Galerucinae	<i>Psylliodes picinus</i> (Marsham, 1802)	(1; 8)
Galerucinae	<i>Pyrrhalta viburni</i> (Paykull, 1799)	(1; 8)
Galerucinae	<i>Sphaeroderma testaceum</i> (Fabricius, 1775)	Not United States of America? (8)
Galerucinae	<i>Xanthogaleruca luteola</i> (Muller, 1776)	(1; 8)

America (northern parts) or only Canada also occur in the other country because detection surveys have not been done.

Except for seed-feeding Bruchinae, nearly all accidentally introduced species both originated in Europe and occur in Canada (Klimaszewski *et al.* 2020). The exceptions to this are two species that feed on Australian *Eucalyptus* L'Héritier de Brutelle (Myrtaceae) that are known from southwestern United States of America and which may have been introduced intentionally (Paine *et al.* 2010). This abundance of European adventive species indicates that although Asia is the source of some important recent introductions of beetles in other families, most newly discovered adventive Chrysomelidae species in North America continue to originate from Europe. This is consistent with the hypothesis that recent discoveries of introduced species represent expanding populations of species established 50–60 years earlier via former trade-related introduction pathways carrying larger numbers of soil-dwelling insects. Findings of accidentally introduced species in Canada but not in adjacent areas of the United States of America suggest that the fauna of the northeastern United States of America may include several undocumented adventive chrysomeloid species.

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