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ARTICLE

The history and current state of cluster flies (Diptera: Polleniidae: *Pollenia*) in North America, with new Canadian provincial records

K.A. Vezsenyi[1]*, S.V. Langer[1], B.A. Samkari[1], and D.V. Beresford[1,2]*

[1]Environmental and Life Sciences Program, Trent University, 1600 West Bank Drive, Peterborough, Ontario, K9J 7B8, Canada and [2]Biology/Trent School of the Environment Departments, Trent University, 1600 West Bank Drive, Peterborough, Ontario, K9J 7B8, Canada
*Corresponding authors. Email: kathrynvezsenyi@trentu.ca; davidberesford@trentu.ca

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Abstract
We provide a thorough historical account of the genus *Pollenia* Robineau-Desvoidy, 1830 (Diptera: Polleniidae) in North America through published records beginning in 1849. From this, we have gleaned insights into their presence on this continent, how they were perceived as pests, and studies of their biology to better frame current work on this genus. Further, we report on our own study of *Pollenia* spp. distribution across Canada from our collection of 2211 specimens that include all six North American species collected in seven provinces between 2011 and 2013. We report first provincial records for *Pollenia angustigena* Wainwright, 1940 and *P. labialis* Robineau-Desvoidy, 1863. We also discuss knowledge gaps and provide suggestions for future research.

Introduction

Cluster flies, or *Pollenia* Robineau-Desvoidy, 1830, are a commonly observed genus of true flies (Diptera: Polleniidae), readily distinguished by their dull-coloured bodies with golden setae on the thorax (Whitworth 2006). They are often disregarded beyond their role as house pests, and a quick search of their common name would produce endless results instructing how to rid your home of them. This view has remained unchanged throughout their history in North America, with one early account being typical, suggesting that "words fail to describe their general depravity; it is beyond expression. If you wish to be happy, be sure you don't introduce cluster flies into your family" (Dall 1882). These plentiful flies often cluster together on walls, ceilings, and windows, entering any cracks in walls and roofs of houses to overwinter (Oldroyd 1964).

Several hundred flies may gather in any one cluster (Lintner 1893), and in early spring, hundreds of flies may die in homes before they are able to find their way back outside (Shewell 1987). Aside from inside houses, *Pollenia* have been found overwintering in leaf sheaths of corn stalks, under bark (DeCoursey 1927), in trees using old woodborer galleries (Dennys 1927), in the abandoned galleries of darkling beetles in rotting hoof fungi (Will 1995), and in a bald-faced hornet (Hymenoptera: Vespidae) nest (Greenberg 1998). The flies are abundant in the spring and fall but are rarely noticed in the summer by the general public (DeCoursey 1927).

Pollenia are widely regarded as harmless nuisance pests (Goble 1972; Allen-McGill 1983). Despite this, there is evidence that these flies could spread bacterial pathogens

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(Thomson 1972; Faulde *et al.* 2001), the accumulation of dead flies can cause allergies, and their corpses may act as breeding material for dermestid beetles and other pests (Spencer 1928; Shewell 1987). *Pollenia* are suspected to have contributed to one case of faecal coliform bacterial contamination in a water reservoir in Martinborough, New Zealand, where massive numbers of the flies were present in and on the reservoir (Heath *et al.* 2004). In addition to spreading bacteria, spores of *Entomophthora schizophorae* S. Keller and Wilding, 1988 (Entomophthoraceae) are known to persist within *Pollenia* and to transmit between flies as they overwinter in unheated attics (Eilenberg *et al.* 2013).

History in North America: 1800s

It is unknown exactly when *Pollenia* were first introduced to North America (Gisondi *et al.* 2020). If all North American *Pollenia* species are found to be obligate earthworm parasites, cluster flies likely arrived when earthworms were introduced to North America by European settlers as early as the 1500s (Reynolds 1995), limiting the arrival of *Pollenia* to an approximate window of 350 years. Howard (1911) stated that the date of introduction to the United States of America was unknown. *Pollenia* were first reported in North America between 1820 and 1822 from Nova Scotia (Walker 1849; Piers 1917). More records soon followed: 1858 (Osten-Sacken 1858) and again in 1862 (Loew 1862), although no specific localities were reported in either case. The next Canadian reference appears to be from 1867, with specimens collected in Québec (van der Wulp 1867). Lintner (1893) recalled seeing flies in 1875 in Schenectady, New York, United States of America that he believed to be *Pollenia*, although he did not know how to classify them at the time of observation. Osten-Sacken (1878) included this record in an 1878 revision of his 1858 report, documenting the species *Pollenia rudis* (Fabricius, 1794). These specimens were, at least at the time, housed in the collection of Diptera of the Museum of Comparative Zoology in Cambridge, Massachusetts, United States of America (1878), but any *Pollenia* specimens belonging to this collector (Osten-Sacken) that currently remain in the collection could not be distinguished (C. Maier, personal communication). As such, modern species classifications for the *Pollenia* specimens in Osten-Sacken's publications could not be determined.

In 1882, Dall wrote about specimens of *Pollenia* he had received from a relative in Geneva, New York, in what appears to be the first North American reference to *Pollenia* as household pests (Dall 1882). That relative recalled "it is probably thirty years since the flies appeared in our neighbourhood" (Dall 1882), which puts their arrival somewhere in the early 1850s by their account, within the same decade as Osten-Sacken's (1858) publication. The flies were described as sluggish, cold, and oily, and as existing in the country, with few occurring in towns and villages (Dall 1882). They were reportedly hard to kill, unlike other house pests (Dall 1882), even when pyrethrum powder was used (Mann 1882); however, other authors reported that this method was successful (Lintner 1893). These reports from the late 1800s include Québec, Canada (van der Wulp 1867) and New England, Washington (Dall 1882), New Jersey (Smith 1890), and New York, United States of America (Dall 1882; Lintner 1893).

History in Canada: 1900s

Canadian reports of *Pollenia* continued in the 1900s. In 1928, *Pollenia* were described as household pests that caused "considerable alarm" in Ontario (Ross and Caesar 1928). Although the journal volume in question (the 95th Annual Report of the Entomological Society of Ontario, 1928) contains articles with species lists from Prince Edward Island, Nova Scotia, New Brunswick, Quebec, Manitoba, Saskatchewan, Alberta, and British Columbia, Canada, *Pollenia* are mentioned only in the Ontario paper (Ross and Caesar 1928). Interestingly, they were excluded in a subsequent publication by Caesar (1941). For many years, the Annual Reports of the Entomological Society of Ontario published summaries of pest insects. A series by C.G. MacNay from 1950 to 1960

(Volumes 81–91) reported on Canadian infestations in which *Pollenia* were mentioned from 1951 onwards as a common household pest in Ontario and Québec. Other provinces, including British Columbia (MacNay 1953, 1954), Alberta (MacNay 1951), and the Gulf of St. Lawrence provinces (MacNay 1953), had less-consistent reports. None were found in the Prairie provinces (MacNay 1953). A similar series by W.C. Allan from 1967 (Allan 1967) to 1973 (Volumes 98–104) focussed exclusively on Ontario and stated that the flies were abundant pests each year.

Taxonomy

Despite the classifications of several species of *Pollenia* in Europe, nearly all of the early accounts of this genus in North America reported specimens as *P. rudis* (Cranshaw and Due 2018). Aldrich (1905) listed three species, at least one of which is synonymous with *P. rudis*; however, the other species names seem to have been largely disregarded in subsequent publications. Rognes (1987) also reported synonyms under *P. rudis* that could not be confidently traced to the new species he was naming. In Hall's (1948) monumental work on Calliphoridae (including *Pollenia*), only *P. rudis* was included. Later, Shewell (1961) reported *Pollenia vagabunda* (Meigen, 1826) from Prince Edward Island, Nova Scotia, and British Columbia. Nevertheless, the practice seems to have been to assume that all Canadian *Pollenia* were *rudis*, including life history studies (*e.g.*, Thomson 1972; Yahnke and George 1972; Thomson and Davies 1973a, 1973b, 1974). However, Thomson and Davies (1973b) did speculate that discrepancies in the literature with host interactions could be due to "various strains" of *Pollenia*.

Rognes (1987) examined the specimens collected from the same area as those reported in Yahnke and George (1972) and reported both *P. rudis* and a new species, *Pollenia pseudorudis* (Rognes 1987), which is now regarded as a synonym of *Pollenia pediculata* Macquart, 1834. Rognes (1987) noted that the majority of specimens used in Yahnke and George's (1972) paper were of this latter species. Rognes (1991) listed six species from North America in his revision of Scandinavian species.

Following this, Whitworth (2006) produced a key to the six species in North America, which was later used as the basis for a web-based illustrated key by Jewiss-Gaines *et al.* (2012). From specimens preserved in collections that could be re-evaluated for species identifications, Jewiss-Gaines *et al.* (2012) reported the earliest records as follows: 1904 – *P. pediculata*; 1906 – *P. angustigena* Wainwright, 1940; 1913 – *P. rudis*; 1925 – *P. griseotomentosa* (Jacentkovskỳ, 1944); 1958 – *P. vagabunda*; and 1969 – *P. labialis*. In terms of *P. vagabunda*, an earlier specimen from 1940 exists (Shewell 1961) and is housed at the Canadian National Collection of Insects, Arachnids, and Nematodes (Ottawa, Ontario, Canada). Recently, the subfamily Polleniinae of the Calliphoridae was elevated to family status, Polleniidae (Cerretti *et al.* 2019).

Pollenia and earthworms

Most of what is known about the life history of *Pollenia* in North America was studied under the catch-all species name *P. rudis*. As a result, we use only the genus name for this section. Most studies on the biology of the immature stages of *Pollenia* were undertaken in Europe. The first record of *Pollenia* parasitising worms came from a German earthworm publication in 1845 by W.F.L. Hoffmeister (cited in Thomson 1972). In 1909, the information was repeated by Keilin (1911; later republished in a North American journal in English in 1911). *Pollenia* larvae were not found in North America until 1916 (Webb and Hutchison 1916), and although Keilin's European research was built upon by North American researchers, the lumping of many species under the name of *P. rudis* makes it impossible to know which species the life history information applies to (Rognes 1987).

At minimum, at least one *Pollenia* species in North America is a parasitoid of earthworms (Oligochaeta: Lumbricidae) (Jewiss-Gaines *et al.* 2012). Gravid females insert their ovipositors

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into the soil (DeCoursey 1927) and deposit eggs in batches of up to seven at a time until 100–130 eggs have been laid (Thomson and Davies 1973a). Individual batches are placed about 30 cm apart over a large area, which is an advantage to larvae seeking earthworms (DeCoursey 1927). Larvae search for earthworm hosts by an apparent random movement through naturally occurring pore spaces (Thomson and Davies 1973a), with most encounters taking place as earthworms move to the surface at night or after light rains (Heath *et al.* 2004). *Pollenia* likely are free living in the soil when not feeding on earthworms (DeCoursey 1927). This behaviour, where eggs are laid away from a host and larvae navigate to their host unaided, is unusual for calyptrate Diptera (Wood 1987).

Parasitised earthworms have been collected in North America and have also been successfully parasitised under controlled laboratory conditions (Yahnke and George 1972; Thomson and Davies 1973b). Not all field-collected earthworm species were affected by larvae (Thomson and Davies 1973b), and earthworm species reported to be parasitised in Europe were not found to contain larvae in North America (Webb and Hutchison 1916). *Pollenia* may also be considered predators, with larvae sometimes exiting the worm to feed from the outside (Szpila 2003).

Pollenia larvae have also been found to parasitise caterpillars and bees (van Emden 1954). *Pollenia* of an unknown species were reported feeding in honeybee (Hymenoptera: Apidae) thoraces in Egypt (Ibrahim 1984), and some species have been reared on noctuid moths (Lepidoptera: Noctuidea) (Rognes 2010). Larvae of *Pollenia* are obligate predators or parasites, however, and although they can feed on crushed fresh earthworms, they are unable to survive when fed on cow dung, horse manure, loam soil, clay soil, grass sod, decaying roots of grass in soil, decaying wood, decaying meat, or dead earthworms (DeCoursey 1927, but see van Emden (1954) for one possible example where this was successful). The presence of *Pollenia* adults in buildings in areas far from suitable earthworm habitat suggests the need for further research into alternative hosts (Cranshaw and Due 2018).

Life history and overwintering

In North America, there are three to four generations per year of *Pollenia* (Thomson and Davies 1973a), with populations peaking with the third overwintering generation in about early October. Adult males and females seek shelter without requiring either food or water (DeCoursey 1927). From these, flies that emerge early die in the snow or feed as outdoor temperatures permit (DeCoursey 1927). Females from *P. pediculata* and *P. vagabunda* overwinter as virgins with undeveloped ovaries until the spring (Greenberg 1998), whereas males produce sperm continuously (DeCoursey 1927). After winter, when temperatures rise, adults copulate (Greenberg 1998), with females ovulating about a month later (DeCoursey 1927). The overwintering generation dies off by about mid-April, and their offspring appear in late May or early June, with numbers remaining low until mid-July and then increasing until fall (DeCoursey 1927).

Pollenia and agriculture

Adults of this genus are reported to be significant pollinators (Būda *et al.* 2009; Jewiss-Gaines *et al.* 2012), hence, the name *Pollenia*. There are reports of pollen-covered *Pollenia* (Robineau-Desvoidy 1863), and adults are commonly found during general surveys of insects on a number of plants in North America, including wind-pollinated plants such as wheat (Poaceae) (Webster 1900) and insect-pollinated plants such as carrot (Apiaceae) (Bohart and Nye 1960), ox-eye daisy (Asteraceae) (Judd 1964), flowering boneset (Asteraceae) (Allan 1967), and strawberry blossoms (Rosaceae) (Nye and Anderson 1974).

Although it is reasonable to assume that *Pollenia*'s nectar feeding results in pollination, neither the extent nor the importance of this is known. For example, in a comprehensive review of dipteran pollinators (Larson *et al.* 2001), *Pollenia*, while listed in a table, were not mentioned in the discussion of important dipteran pollinators. The insects' yellow hairs might give the appearance of carrying more pollen than is present. For example, during a field survey of insects associated with sugar beets (Amaranthaceae), individual Syrphidae (hover flies) were found to carry eight times as many pollen grains (11 619) as *Pollenia* (1421), which were also outclassed by Muscidae (1933) (Free *et al.* 1975). Adult *Pollenia* also feed on the exudates of plants, carrion, faecal matter, and refuse (Thomson 1972) and on natural oils from yarns and spun goods (Mann 1882).

Despite the potential importance to agriculture and wild ecosystems as both pollinators and parasitoids, little is known about the *Pollenia* species in North America, including their role in these ecosystems, their basic life history, and – the most fundamental question of all – where they are found. In this paper, we report on thousands of *Pollenia* collected from across Canada and update the known distributions based on our new records.

Materials and methods

All *Pollenia* specimens were collected as part of a large-scale collaboration with the Ontario Provincial Police and the Royal Canadian Mounted Police across Canada and are housed in the Entomology Lab at Trent University (Peterborough, Ontario, Canada). The initial study was designed to survey forensically important blow fly species (Diptera: Calliphoridae) of the subfamilies Calliphorinae, Luciliinae, and Chrysomyinae using baited bottle traps with the help of law-enforcement volunteers from across Canada. Details are provided in Langer *et al.* (2019). Briefly, volunteers were invited from each province; 32 individuals responded from detachments in seven provinces: British Columbia, Alberta, Saskatchewan, Ontario, New Brunswick, Nova Scotia, and Newfoundland and Labrador. The unexpected abundance of *Pollenia* spp. that were also captured provided the impetus for this paper. Typically, bycatch specimens remain unanalysed, but when possible, reporting is encouraged, especially for nationwide surveys (Spears and Ramirez 2015).

From 2011 to 2013, each volunteer was mailed two 2-L bottle traps baited with prerotted beef liver and four collecting bottles containing nontoxic plumbing antifreeze as a preservative. (See details of the bottle-trap design in Langer *et al.* 2016.) After being deployed for two weeks at each location, the four bottles of captured specimens (one per week per trap) were mailed back to us for processing. When received, specimens were transferred to bottles with 80% ethanol until they could be pinned and identified. The identifications were confirmed by KAV; the key used is that in Jewiss-Gaines *et al.* (2012).

New provincial records and range extensions are based on existing known range records reported in Jewiss-Gaines *et al.* (2012) and Gisondi *et al.* (2020) and on records in GBIF.org (Global Biodiversity Information Facility Secretariat 2021). Range maps shown here were created in ArcMap (Environmental Systems Research Institute 2011).

Results

We captured 2249 *Pollenia* specimens and identified 2211 of these to species level. Thirty-eight specimens were damaged and could not be identified. *Pollenia* were collected from 29 of the 32 locations surveyed and included all six species known from North America (Table 1). The most abundant species – and the only species found in all sampled provinces – was *P. pediculata* ($n = 1272$), followed by *P. rudis* ($n = 435$), *P. angustigena* ($n = 175$), *P. labialis* ($n = 146$), *P. vagabunda* ($n = 138$), and *P. griseotomentosa* ($n = 45$; Table 1).

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Table 1. *Pollenia* species collected in each province (west to east) from 2011 to 2013 by sex (M, male; F, female). An asterik (*) denotes a first provincial record. From left to right, *P. angustigena, P. griseotomentosa, P. labialis, P. pediculata, P. rudis,* and *P. vagabunda.*

	Species													
	P. ang.		*P. gris.*		*P. lab.*		*P. pedic.*		*P. rudis*		*P. vaga.*		Total	
Province	M	F	M	F	M	F	M	F	M	F	M	F	M	F
British Columbia		13		3	10	6		7	3	63	7	21	20	113
Alberta		1*			3*	1*	7	7	20	23	1	3	31	35
Saskatchewan							6	25					6	25
Ontario	65	91	10	18	48	52	315	678	75	197	14	23	527	1059
New Brunswick				2	3		97	118	13	9	13	29	126	158
Nova Scotia	1				10	12	6	5	3	4			20	21
Newfoundland and Labrador	1*	3*		12		1		1	3	22	3	24	7	63
Total	67	108	10	35	74	72	431	841	117	318	38	100	737	1474

Distribution

Despite the commonness of *Pollenia* and the low number of North American species, our collections resulted in three new provincial records: two from Alberta and one from Newfoundland and Labrador (Table 1; Figs. 1–6). The new record from Newfoundland and Labrador was a range extension, extending the known population further to the east (*P. angustigena*). Of the new records from Alberta, *P. labialis* served as a gap infill between records in the west, in British Columbia, and in the east, in Ontario.

The known distributions of all species, with the exception of *P. pediculata* and *P. rudis*, are based largely on pockets of records from the west coast, from the east coast, and in southern Ontario and Québec. Comparatively few records are reported from Alberta, Saskatchewan, Manitoba, and western Ontario (Jewiss-Gaines *et al.* 2012). This holds true when regarding North American *Pollenia* populations as a whole: although their populations extend south into the United States of America, large gaps remain towards these middling latitudes (Jewiss-Gaines *et al.* 2012). Our records fill some of these gaps for *P. angustigena* (Alberta), *P. labialis* (Alberta and western Ontario), and *P. rudis* (western Ontario).

We caught more *Pollenia* in the first of the two sampling weeks (week 1: 1270; week 2: 941). Collection bottles were changed between weeks, but the liver bait was not refreshed. We also caught more females than males (females: 1474; males: 737), nearly twice as many each week (week 1 – females: 854, males: 416; week 2 – females: 620, males: 321). By species, we caught more females for all species except *Pollenia labialis,* for which two more males than females were caught (Table 1).

Across all sampling sessions and locations, 37% of traps contained one or more *Pollenia* specimens, with the mean being 11.46 specimens per trap. The most caught in any one trap was 195 specimens, from Peterborough, Ontario. Although per-trap catches were low in most cases, *Pollenia* were a consistent bycatch of our liver-baited bottle traps. Approximately three times fewer *Pollenia* were collected than blow flies – the original target of these traps: 2211 *Pollenia versus* 7272 blow flies (Langer *et al.* 2019; 0.304), which is far more *Pollenia* than we had expected from traps designed for carrion specialists.

All six species were caught in British Columbia, Newfoundland and Labrador, and Ontario, with 150 specimens or less each (Table 1). Provinces with the fewest species were Nova Scotia

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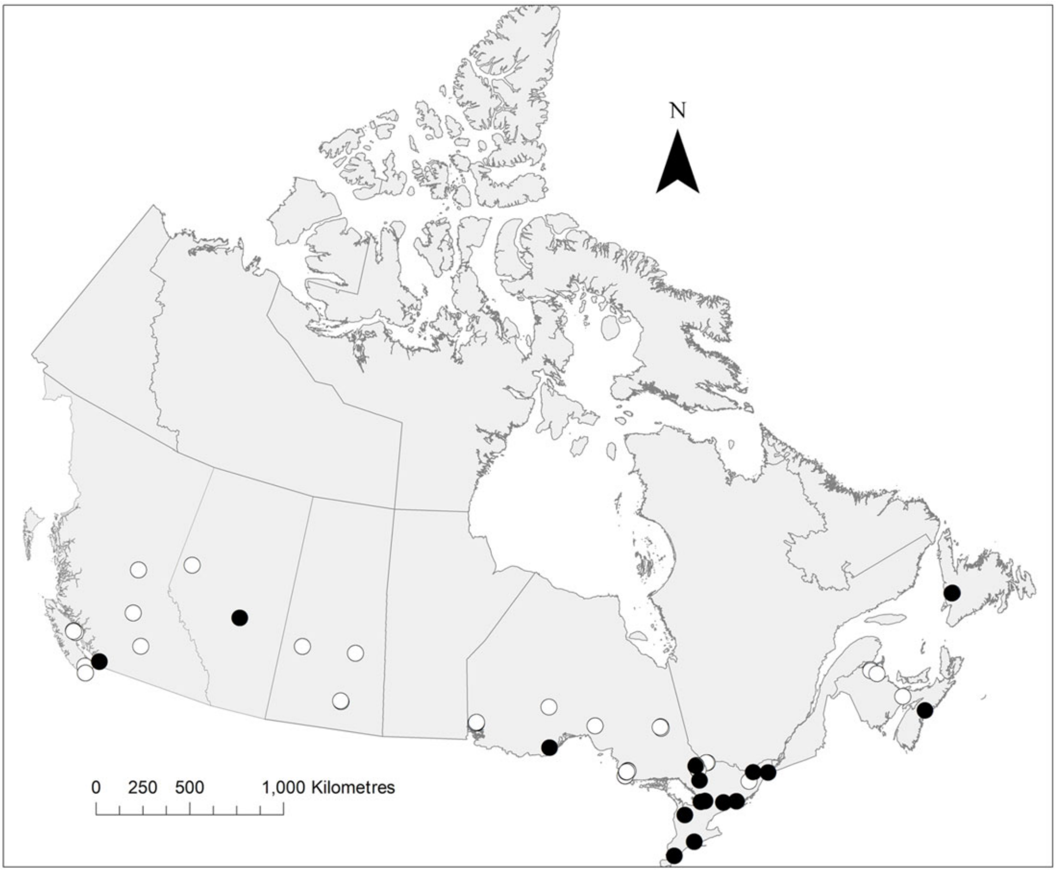

Fig. 1. Distribution of *P. angustigena* collected during the present study. The map notes traps from which this species was collected (black circles) and absent (white circles). Map created in ArcMap.

and Saskatchewan. Even with 284 specimens, only five species were captured in New Brunswick. Regionally, the Prairie provinces have the fewest species of *Pollenia*.

Discussion

Although this genus is commonly encountered in general surveys, we were able to report a few first provincial records (Table 1). This likely reflects the relatively little attention that has been paid to the genus. For example, our records expand the known range of two of the six North American species, which is unprecedented for such large-bodied insects with potential importance in agricultural systems and as pests. There are very few records from Manitoba and Saskatchewan. *Pollenia* are present in Manitoba, listed in pest prevention reports for the province as cluster flies (Ellis 2002), with records for *P. pediculata* and *P. rudis* available online (Global Biodiversity Information Facility Secretariat 2021). However, the species present in Manitoba have yet to be published. The situation in Saskatchewan is similar: we recorded *P. pediculata*, which was previously recorded from Saskatchewan in 2020 (Gisondi *et al.* 2020). The dearth of records from the Canadian prairies is likely due to a combination of fewer collections and of fewer *Pollenia* species being present.

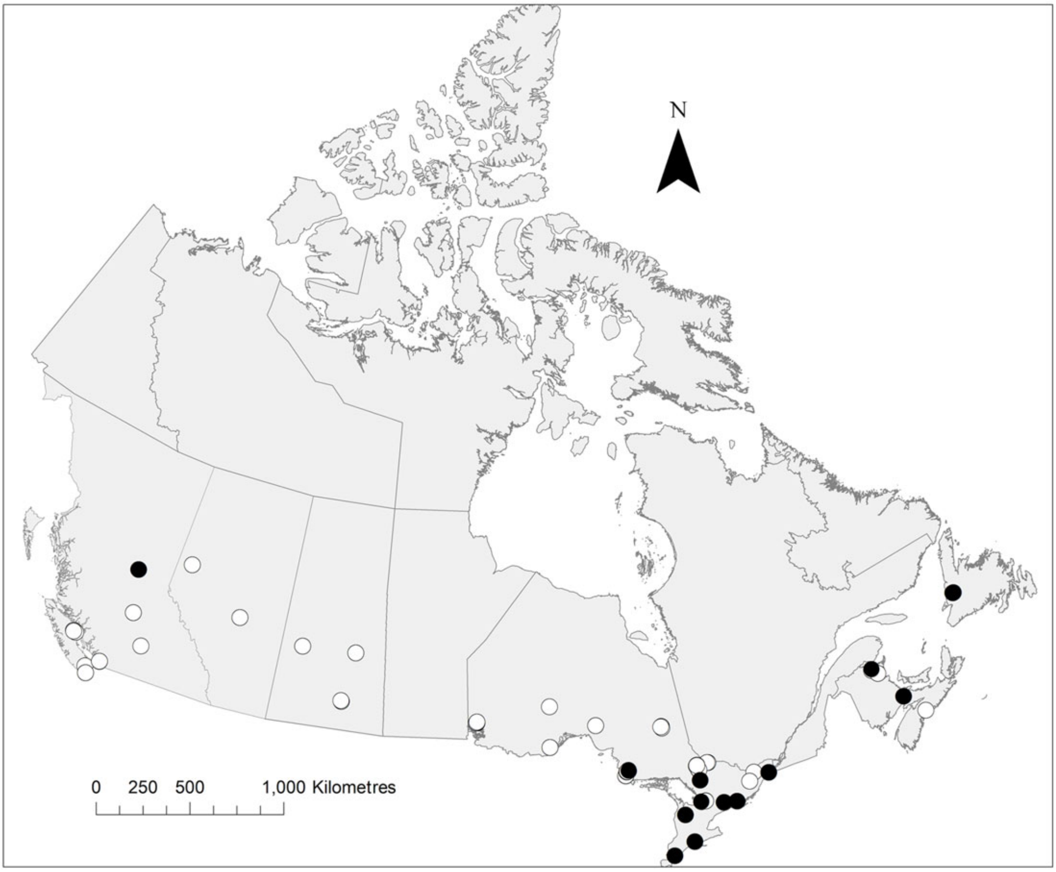

Fig. 2. Distribution of *P. griseotomentosa* collected during the present study. The map notes traps from which this species was collected (black circles) and absent (white circles). Map created in ArcMap.

Introduction and spread

If *Pollenia* were brought to the Nearctic through shipping, their earliest occurrences would have been near port and coastal cities (British Columbia coast, Atlantic coast, and Great Lakes region), with *Pollenia* dispersing inland towards land-locked regions (Alberta, Manitoba, and Saskatchewan). Although this account of the genus's spread is speculative, it appears to be consistent with what we see from their current distribution maps. Dall's (1882) account of *Pollenia* appearing in Geneva, New York in about the 1850s is especially interesting because it is not far from Oswego, in the same state, home of one of the busiest shipping ports on the Great Lakes during the 1850s (Palmer 2010). Howard (1911) believed that *Pollenia* may have first arrived on ships while hibernating, a reasonable assertion because *Pollenia* have successfully crossed oceans on cargo ships. For example, in 1981, they were intercepted in New Zealand on cargo ships from the United States of America (Dear 1986). The spread of *Pollenia* in North America continues even now, with *P. vagabunda* recently reported in Alaska (Bowser 2015).

Because *Pollenia* are earthworm parasitoids, earthworm hosts likely must be common in an area for *Pollenia* to exist, although which species are parasitoids is not yet known. Currently, only four species of earthworms known to host *Pollenia* exist in Canada and are found in all provinces: *Allolobophora chlorotica* (Savigny, 1826) (Crassiclitellata: Lumbricidae), *Aporrectodea rosea* (Savigny, 1826) (Crassiclitellata: Lumbricidae), *Aporrectodea trapezoides*

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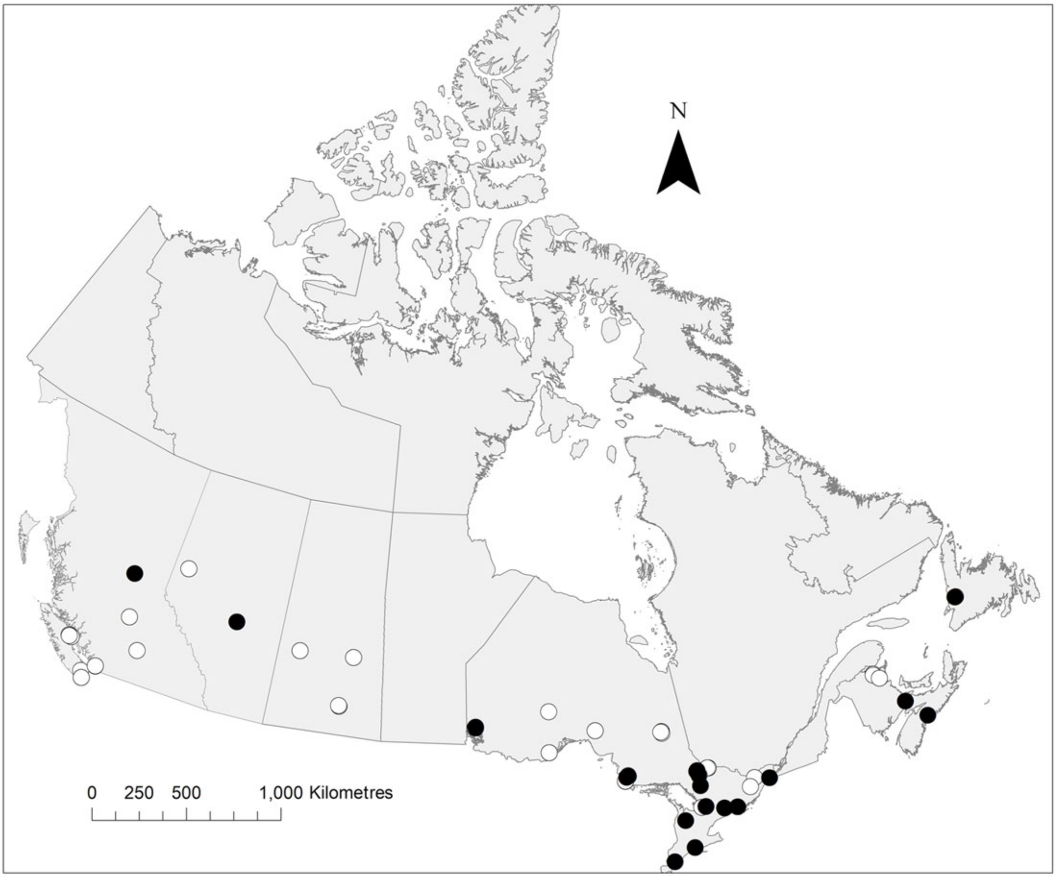

Fig. 3. Distribution of *P. labialis* collected during the present study. The map notes traps from which this species was collected (black circles) and absent (white circles). Map created in ArcMap.

(Duges, 1828) (Crassiclitellata: Lumbricidae), and *Lumbricus terrestris* Linnaeus, 1758 (Opisthopora: Lumbricidae) (Tomlin and Fox 2003; Reynolds 2021).

Sex ratio

We captured more females with the carrion-baited bottle traps. Estimates of *Pollenia* sex ratios from overwintering flies suggest that populations of *P. pediculata* and *P. rudis* have more males and that *P. angustigena* and *P. vagabunda* have more females (Greenberg 1998). In New Zealand, sex ratios in overwintering flies are closer to 50:50 (Heath *et al.* 2004). This might reflect overwintering behaviour: females tend to overwinter in outdoor refugia such as corn stubble, whereas males tend to overwinter in buildings (DeCoursey 1927), but this is not conclusive. Summer sex ratio records are few: Hall (1948) reported mostly males found on wild parsnip. Our results likely represent a trapping bias of our methods.

Sampling bias

Although blow flies were the original target for our liver-baited traps, they captured a surprising number of *Pollenia*. *Pollenia* are not unusual in carrion-baited traps (Feddern *et al.* 2018), but the reasoning for this is not yet known (Baz *et al.* 2007). *Pollenia* spp. have

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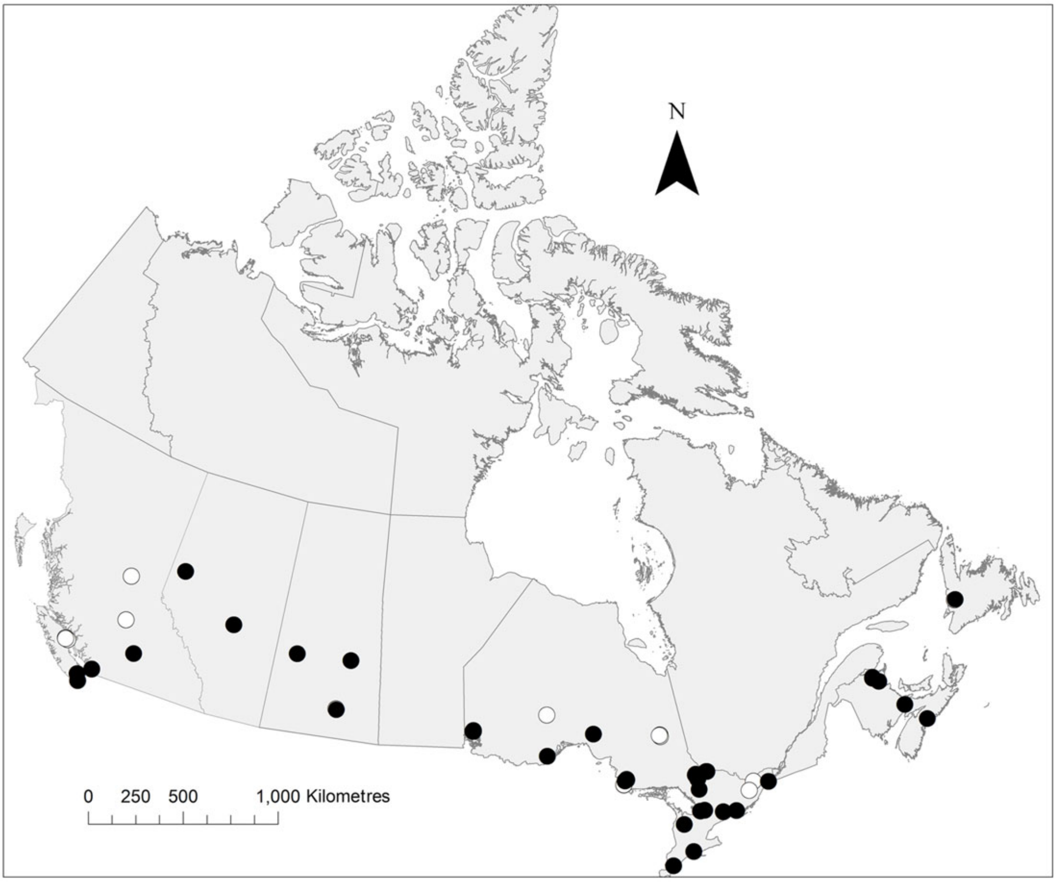

Fig. 4. Distribution of *P. pediculata* collected during the present study. The map notes traps from which this species was collected (black circles) and absent (white circles). Map created in ArcMap.

little to no forensic importance (Greenberg 1998; Brundage *et al.* 2011; Feddern *et al.* 2018). *Pollenia* have been captured at whole carcasses (Tabour *et al.* 2005; Bugajski *et al.* 2011; Benbow *et al.* 2013; Šuláková and Barták 2013; Weidner *et al.* 2017), leading to suggestions that earthworms near the carrion could be the attracting source (Šuláková and Barták 2013). However, *Pollenia* do not deposit eggs on earthworms but on soil, making this explanation unlikely. *Pollenia* have also been collected in baited bottle traps that use beef liver (Brundage *et al.* 2011; Weidner *et al.* 2015; Feddern *et al.* 2018) and pig liver (Hwang and Turner 2005; Farinha *et al.* 2014). Weidner *et al.* (2017) suggested that some unknown specific chemical released by beef liver but not unique to it could attract species that do not use the bait for colonisation.

Other successful baits for capturing *Pollenia* include bananas (Webb and Hutchison 1916; Yahnke and George 1972), especially when combined with milk and vanilla extract (Hall 1948), and apples (DeCoursey 1927), consistent with the need to feed from flowering plants, rotten fruits, and souring tree sap (Hall 1948). Only two plant compounds are known to attract *Pollenia*; these are methyl eugenol and methyl salicylate (Būda *et al.* 2009; El-Sayed 2021). Methyl eugenol is released when damage occurs to the leaves, stems, roots, fruits, or flowers of more than 450 plant species and can deter animals from feeding on plant tissues (Tan and Nishida 2012). Methyl salicylate is also released as a response to plant

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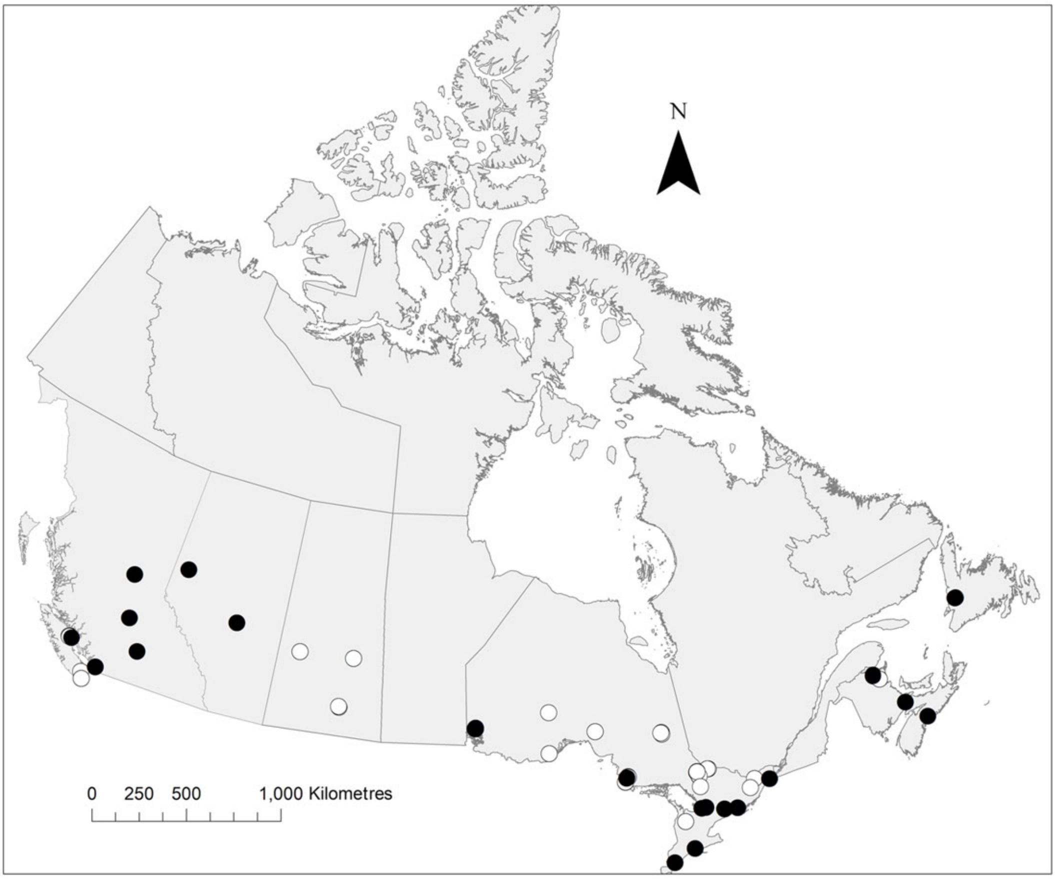

Fig. 5. Distribution of *P. rudis* collected during the present study. The map notes traps from which this species was collected (black circles) and absent (white circles). Map created in ArcMap.

damage and is attractive to many predator insects that prey upon insect herbivores (Stepanycheva *et al.* 2016). Methyl salicylate is emitted by many flowers and could signal a nectar source for *Pollenia,* which would allow the plant to be pollinated (Būda *et al.* 2009). None of these compounds are known to attract members of Calliphoridae (El-Sayed 2021).

Our captures of *Pollenia* might be due to methyl salicylate in the propylene glycol antifreeze that was used as a trap preservative (Thomas 2008). Methyl salicylate is added as a scent so that antifreeze can be detected in plumbing (Cook 1998). Propylene glycol is a nontoxic alternative to ethylene glycol (Skvarla *et al.* 2014) and is an effective preservative for a range of insect studies (Weigand *et al.* 2021). We were unable to determine if methyl salicylate was added to the brand of plumbing antifreeze that we used. However, this compound does not explain *Pollenia*'s prevalence in other studies that did not use plumbing antifreeze in their traps (*e.g.*, Hwang and Turner 2005; Brundage *et al.* 2011; Farinha *et al.* 2014; Fremdt and Amendt 2014; Weidner *et al.* 2015; Feddern *et al.* 2018) and why fewer *Pollenia* are captured when whole animals are used as carrion bait.

Knowledge gaps

Because most of our understanding of the natural history of *Pollenia* comes from research that lumped several species as *P. rudis* (*e.g.*, Thomson 1972; Yahnke and George 1972; Thomson and

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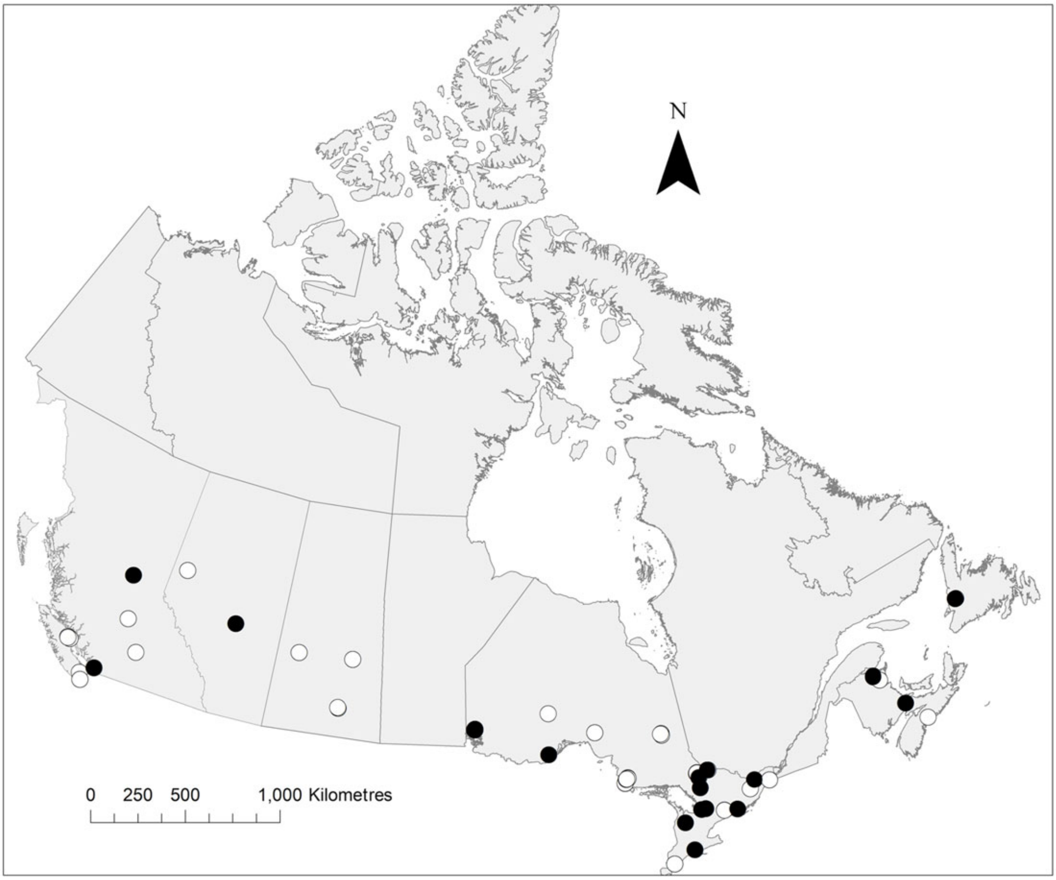

Fig. 6. Distribution of *P. vagabunda* collected during the present study. The map notes traps from which this species was collected (black circles) and absent (white circles). Map created in ArcMap.

Davies 1973a, 1973b, 1974), the basic natural history needs to be re-examined for each species (Rognes 1987). Our knowledge gaps include such basic information as (1) which North American *Pollenia* species are earthworm parasitoids; (2) how important this is for each species; (3) what other earthworms can host immature *Pollenia*; (4) whether *Pollenia* species differ in terms of earthworm host species; (5) how important *Pollenia* are for earthworm population dynamics and mortality; (6) whether *Pollenia* exist outside of regions with earthworms; (7) how important *Pollenia* species are for pollination services in agriculture; (8) how important *Pollenia* species are for transporting pathogens; and (9) what species of *Pollenia* exist across Canada.

Conclusion

We hope that this work spurs interest in this genus and leads to future studies aimed at better understanding the distribution and biology of *Pollenia* species. Although our work summarises what we know of their biology in North America and fills gaps in their distribution in Canada, much more can be done. The gaps in our understanding are curious and perhaps reflect the common state of entomological and biodiversity studies in general – that there is much that we do not know and much that we take for granted.

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