Cow patty critters:

An introduction to the ecology, biology and identification of insects in cattle dung on Canadian pastures

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COW PATTY CRITTERS: AN INTRODUCTION TO THE ECOLOGY, BIOLOGY AND IDENTIFICATION OF INSECTS IN CATTLE DUNG ON THE CANADIAN PRAIRIES

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Foreword

When I first started looking at insects in cattle dung some 30 years ago, I was amazed at the abundance of life – flies, beetles, wasps and other critters in many different shapes, sizes and colours. My first question was "What is that?" My second question was "What does it do?"

Answers to these questions were scattered in scientific books and articles that were often hard to access and written in language not intended for the layperson. Most of the information was focused on the biology or morphology of relatively few insects – mainly dung beetles (scarabs) and pest flies affecting livestock. Only a few authors used a community-level approach to describe the inhabitants of dung pats and their interactions. Descriptions typically relied on line drawings or black and white photographs.

With this in mind, I undertook to write a guide that would serve as a 'doorway' through which readers could pass to learn more about the cow dung community. I set out to include a range of topics of interest to farmers and ranchers, but also to students wishing to pursue further study of dung-breeding insects. I took pains to include high-quality colour photographs to showcase the diversity and beauty of these insects, and I included an extensive list of references.

This guide focuses on insects associated with cattle dung in Canada, but it is my hope for the future that someone will undertake to expand its contents to make the guide equally useful throughout North America. A checklist of beetles associated with cattle dung in Canada and the United States has been published to help realize this possibility (Bezanson and Floate 2019).

This is the guide I wish I had when I started my career. If I have done my job right, readers will find it informative, interesting and enjoyable.

Kevin Floate
Lethbridge, Alberta
2023

Acknowledgements

This guide is the culmination of hundreds of hours spent with children, ranchers, undergraduate and graduate students, and fellow researchers looking at and talking about critters in cattle dung. For your enthusiasm, this experience, and the knowledge that I have gained, I thank each and every one of you.

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I especially thank the many photographers whose work appears in this guide and their foresight in making so much of it freely available under use of a creative commons license.

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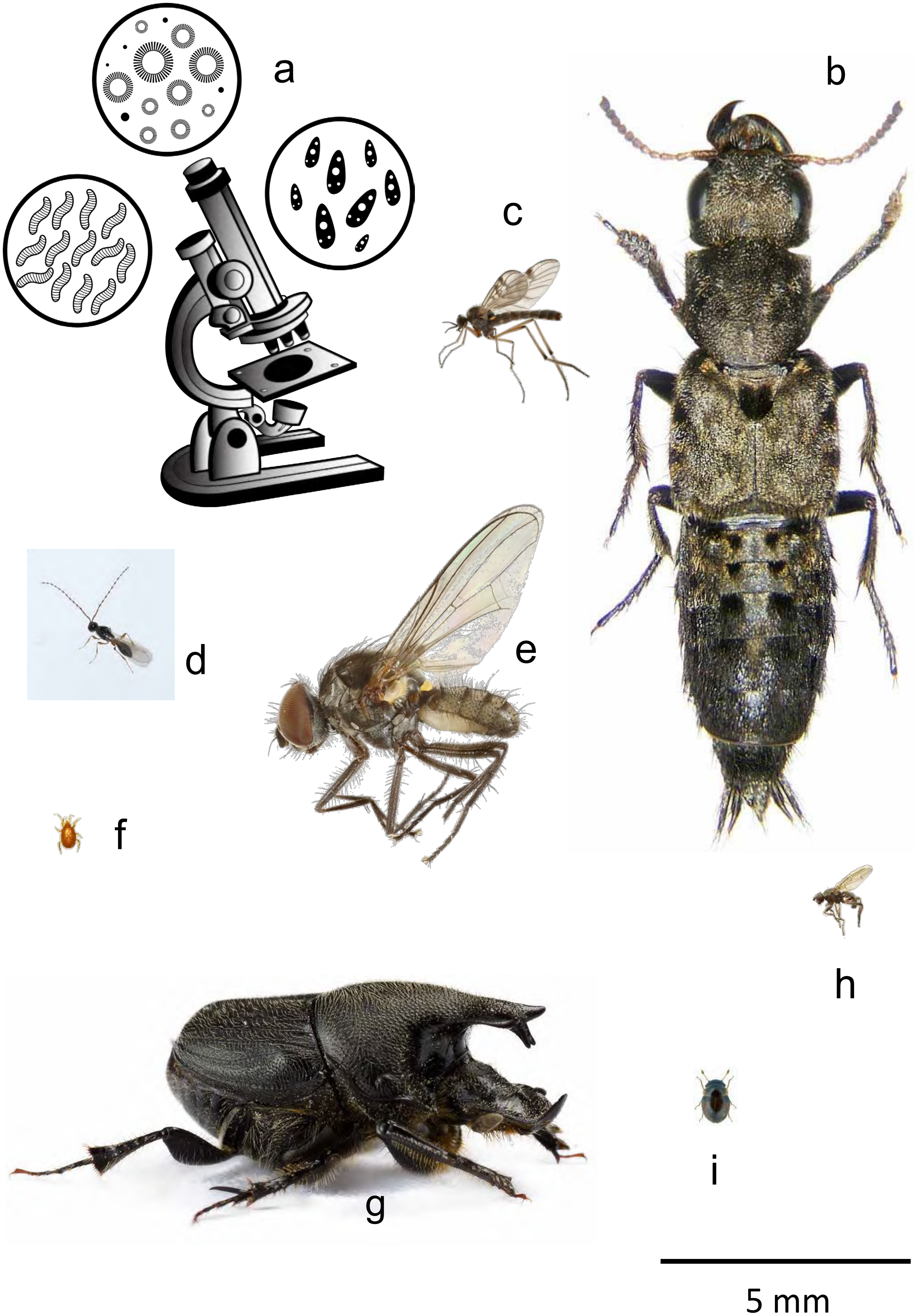
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Introduction

Hopping, flying, squirming and digging – cow pies are crawling with critters. Some of these are invisible to the naked eye – wee little beasties such as bacteria and nematodes that can only be seen under a microscope. Mites are not much bigger. Dung-dwelling insects may be as small as 1–2 mm or, in Canada, as large as 20 mm in length (Fig. 1).

More than 300 species of insects are found in cattle dung on Canadian pastures; mating, eating dung, laying eggs and eating each other. A veritable bee hive of activity changing in composition on a daily basis. Some insects are well-known and have been given both scientific and common names; for example, the livestock pest *Stomoxys calcitrans* (stable fly). Most other insects only have scientific names and a few remain undiscovered by science and have yet to be named.

Through their tunnelling and feeding activities, these insects provide valuable ecosystem services. They scatter dung to remove breeding sites for pest species and speed up the return of nutrients to the soil. Removing deposits from the surface of the pasture also increases available grazing area. By burying dung, they aerate the soil and improve water drainage. They disperse seeds, pollinate plants, eat the eggs and larvae of pest species and, in turn, are eaten by other insects, birds and small mammals. Because of these services, dung insects are of general interest to ranchers, land managers, naturalists and conservation groups.

But cow pies are also playpens for researchers. A dung pat is a discrete habitat that comes into existence in a matter of seconds. Fresh dung is plentiful, inexpensive and easily manipulated. Pats formed of different size and placed in the field at different locations, time of the day, or month of the year, can be used to study ecological processes including community structure, succession, competitive exclusion, species interactions and seasonal activity. Insights also can be gained into how the diet of the animal or its treatment with veterinary medicines affect the structure and function of the insect community that inhabits its dung.

Dung or manure?

'Dung' is animal excrement. The term is mainly used with reference to livestock; e.g., cow dung, horse dung, sheep dung.

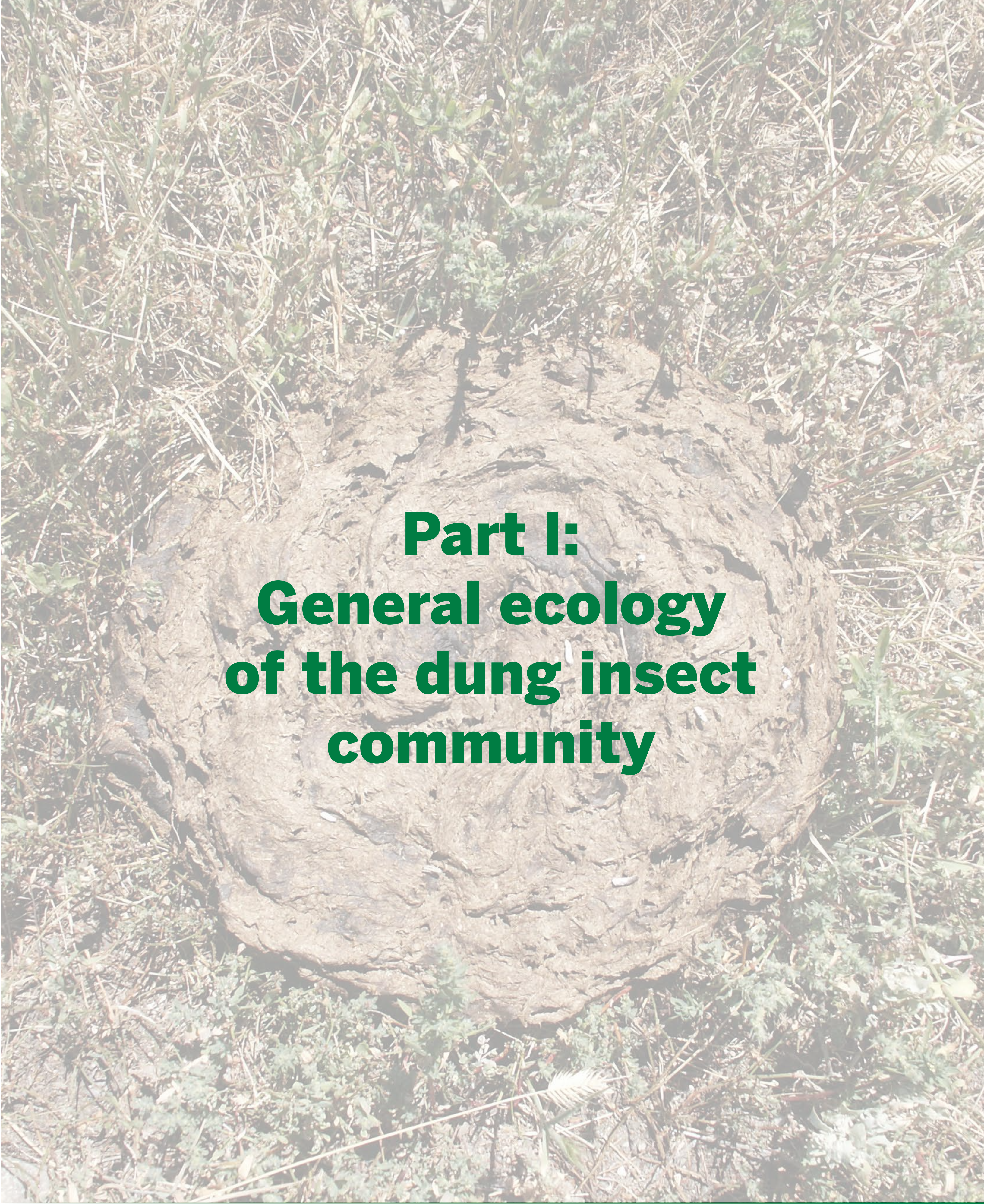
'Manure' is a mixture of dung and other plant material. It is used in agriculture to improve soil fertility.

Some species of insects that are common in dung cannot breed in manure and vice versa.

Figure 1. Variation in size among groups of organisms common in cattle dung. a – bacteria, fungi and nematodes; b – *Ontholestes murinus* (a predacious beetle); c – *Sylvicola punctatus* (a dung-feeding fly); d – *Trichopria* sp. (a parasitoid wasp); e – *Pegoplata patellans* (a dung-feeding fly); f – a macrochelid mite; g – *Onthophagus hecate* (a dung beetle); h – *Copromyza equina* (a dung-feeding fly); i – *Clambus pubescens* (a fungus-feeding beetle). Photos: b, i – Udo Schmidt, CC-BY-SA-2.0; c – © Malcolm Storey; d – Ilona Loser, CC-BY-ND-NC-1.0; e, h – Janet Graham, CC-BY-2.0; f – B. Lee, AAFC; g – © Kevin Stohlgren.

Written in two parts, this guide introduces the reader to the insects in cattle dung on pastures across Canada. Part I originated as a book chapter (Floate 2011) that has been updated and expanded. It focuses on general aspects of insect diversity and ecology. Part II is intended to help the reader identify insects. It provides information on the biology and morphology of different insect groups and is supplemented with colour photographs. For certain groups of beetles, lists are provided for those species known to occur in each province and territory. Although the species mentioned in this guide are specific for Canada, most of them also occur in the United States. A few species can be identified by the layperson without special equipment. Identification of most species requires use of a microscope, access to an insect reference collection, and comprehensive knowledge of insect body parts and structures. References are provided to taxonomic keys for readers wishing to pursue this level of detailed identification.

The guide concludes with an extensive list of references that allows the reader to explore topics in more depth and discover sources of information that might otherwise be overlooked. Many of these references were published decades ago, but are still valuable and are increasingly being made available online.



Part I: General ecology of the dung insect community

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What's in dung...

At the time of deposition, cattle dung is about 80% water (Lee and Wall 2006; Lysyk et al. 1985) and supports a matrix of undigested plant material rich in nutrients, microorganisms and their by-products. By dry weight (DW), dung contains about 0.8% potassium (K), 0.4% sodium (Na), 2.4% calcium (Ca), 0.7% phosphorus (P), and 0.8% magnesium (Mg) (Marsh and Campling 1970). Levels of nitrogen (N) in dung DW range from 2.5–4.0% N (Lysyk et al. 1985; Marsh and Campling 1970), which is comparable to that reported for many species of plants (Fig. 2.2 in Bernays and Chapman 1994). Unlike plants, however, much of the nitrogen in dung is in the form of bacteria, which may comprise 10–20% of dung DW (Lohnis and Fred 1923 – cited in Marsh and Campling 1970). Other organisms present in dung at the time of its deposition may include protozoa, parasitic nematodes (roundworms, lungworms), trematodes (flukes) and cestodes (tapeworms) passed from the cow.

Faecal factoid!

Fresh dung initially contains mainly anaerobic bacteria from the oxygen-poor environment of the cow's digestive tract.

These anaerobic bacteria become replaced by aerobic bacteria, free-living in the environment or carried to the dung by coprophilous insects.

The dung-loving or coprophilous organisms that colonize fresh dung include fungi, nematodes, earthworms, insects and mites. Blume (1985) lists more than 450 species of arthropods[1] reported from cattle dung in North America, but his list includes many species that do not breed in dung (see next paragraph). Studies in British Columbia (Macqueen and Beirne 1974) and Alberta (Floate 1998b) report a combined total of 112 taxonomic insect groups or taxa from cattle dung on pastures. However, this number does not include many species known to be common in dung in other parts of the country, rarer species, or species that colonize dung in later stages of decomposition. These two studies reported three species of pteromalid wasps, but at least 20 species in Canada are known to parasitize flies that breed in dung (Floate and Gibson 2004; see Table 6). Macqueen and Beirne (1974) report only four of the 36 species of coprophilous hister beetles (page 87) known from Canada (Bousquet and Laplante 2006). Examination of the published literature suggests that at least 300 species of insects are members of the dung arthropod community in Canada, representing close to 50 taxonomic families (see Part II of this guide, page 37). By comparison, Skidmore (1991) reports about 275 species of insects in dung of cattle in Britain.

Coprophilous or coprophagous?

Coprophilous = dung-loving

Coprophagous = dung-feeding

Dung beetles are coprophilous and coprophagous – they are attracted to and feed on dung. Insects that are parasitoids and predators are coprophilous – they are attracted to dung, but feed on other insects within the dung.

[1] The term 'arthropod' refers to insects and their relatives that include, in part, spiders, mites, woodlice, millipedes and centipedes

Other arthropod species may be associated with cattle dung, but are not considered to be members of the cow dung community. Instead, they are best viewed as 'visitors'. Some of these visitors include insects such as butterflies, which visit fresh dung to extract sodium and nitrogen – a behaviour known as 'puddling' (Molleman 2010). Other visitors will search in older deposits for prey or hosts, or shelter beneath pats, but are not specifically attracted to dung. Dung is also colonized in its latter stages of degradation by species more typically associated with rich organic soils or rotting vegetation. These late colonizers include centipedes, woodlice, millipedes, harvestmen, spiders, oribatid mites, earwigs, springtails, ants, click beetles, ground beetles and true bugs. Other common visitors include herbivorous insects present on grassland pastures and which use the pat as place upon which to perch.

Membership in the cow dung community is occasionally ambiguous. Adults of the dung beetles *Chilothorax distinctus* (page 103), *Calamosternus granarius* (page 102) and *Melinopterus prodromus* (page 108) are attracted to fresh cattle dung to feed, but not to breed (Floate 2007; Floate and Gill 1998). At certain times of the year, thousands of adults may arrive at a single pat (Bezanson and Floate 2020; Mohr 1943). In such large numbers, the tunnelling activity of the adults can scatter the pat to affect the survival and interactions of other species within. The larvae of these dung beetles, however, are detritivores and develop in organic-rich soils. In southern regions of the Prairie Provinces, composted manure from cattle feedlots is incorporated into agricultural fields in the spring. The odours associated with this manure attract large numbers of adults that lay their eggs in the soil. By early summer, these fields may contain scores of larvae ('white grubs') per square meter (Floate 2021). On several occasions, the author has reared these larvae in jars of soil to recover adults of predominantly *C. distinctus*, but also of *C. granarius* and *M. prodromus*.

Thousands of studies have reported on dung-breeding insects, but most of these have limited their attention to either one or only a few species (Bezanson and Floate 2019). In North America, the bulk of these studies have examined four species of muscid flies (page 65) that are important economic pests of livestock. By bothering or biting the animals, they can spread disease, cause dairy cattle to produce less milk and beef cattle to lose weight. A smaller number of studies have focused on different species of dung beetles, because of their role in degrading dung and reducing its suitability as breeding sites for pest flies. Other studies have examined natural enemies of pest flies or the response of insects to chemical residues in the dung of cattle treated with veterinary medicines. Only a handful of studies provide a more holistic view of the cow dung community and the interactions among its members; e.g., Hammer (1941), Mohr (1943), Laurence (1954), Hanski and Cambefort (1991) and particularly Skidmore (1991).

... And why should we care?

The role of insects and other organisms that accelerate dung degradation has important practical implications. In Canada, an estimated 110 million dung pats (= 242,000 tonnes of fresh manure) are deposited by cattle each day. This reflects an average daily deposition of ten pats (ca. 22 kg of fresh dung) per animal (references in Fincher 1981) for a national herd in 2020 of about 11 million cattle (Statistics Canada 2022). Assuming no overlap of dung pats, a cow will cover an area of 0.8 m^2 in dung each day. High levels of nitrogen and other nutrients released during dung decomposition cause the growth of unpalatable ('rank') vegetation immediately adjacent to the pat. Avoidance of this vegetation by cattle may remove an additional five-fold greater area from grazing (references in Fincher 1981).

That's a load of crap!

If cow pats do not overlap and cows avoid grazing near them, 100 head of cattle can potentially remove 7.2 ha of pasture from beef production during a grazing season of 150 days.

The cost of forage removed from grazing due to pat deposition in Canada has not been calculated, but data is available for the United States. In the foothills of northern California, undegraded dung on pastures totalling 2,024 ha and supporting 455 head of cattle was estimated, in 1984, to cost a cumulative US$ 4,858 over three years (= CDN$ 17,300 in 2022 dollars) (Anderson et al. 1984). This cost represented lost forage, which translated into a loss of 2,730 kg, 628 kg, and 112 kg of beef in the 1st, 2nd and 3rd growing season after dung deposition, respectively. This cost would occur for each group of 455 cattle grazed per year. The foothills of northern California have a dung fauna and hot, dry summers similar to those in southern regions of the Canadian Prairies (Anderson et al. 1984).

The loss of nitrogen and minerals from pasture soils is another cost of undegraded dung. Up to 80% of the nitrogen present in fresh cattle dung deposited on pasture may be lost to the atmosphere in the form of ammonia if the pats are allowed to fully dry in the sun without burial (Gillard 1967). Additional nutrients remain trapped in the undegraded pat and are unavailable for plant growth.

Cattle dung also provides breeding sites for pest flies and parasites that affect livestock. Face fly, horn fly and stable fly are dung-breeding muscid flies (page 65) that are pests of cattle in North America. Kunz et

The cow chip toss - yes, it's a sport!

When hard and disk-shaped, dry cow pats ('cow chips') can be thrown like a Frisbee. According to the Guinness Book of World Records (2021) and under the rule of `non-sphericalisation and 100 per cent organic', the longest cow chip toss is 81.1 m (266 ft).

al. (1991) estimated that the potential annual economic losses associated with these three pests in the United States totalled US$ 1.4 billion (= CDN$ 3.9 billion in 2022). Colautti et al. (2006) estimated the potential annual losses due to horn fly and stable fly in Canada totalled CDN$ 96 million (= CDN$ 151 million in 2022). Fresh dung of infected animals also may contain the immature stages of internal parasites. These parasites include nematodes that infect the gastrointestinal tract (roundworms) or lungs (lungworms), trematodes that infect the liver (liver flukes) or cestodes that infect the intestine (tapeworms). In the absence of rapid dung degradation, these immature stages are more likely to survive and reinfect beef and dairy cattle, contributing additional losses to meat and milk production (Fincher 1973; Lawrence and Ibarburu 2007).

The cumulative benefits associated with rapid dung degradation are difficult to assess with certainty, but they are potentially enormous. Fincher (1981) provides for the United States an estimate that takes into account the increased availability of forage otherwise lost to pasture contamination, the increased return of nitrogen to pasture soils, and the reduced incidence of pest flies (Moon et al. 1980) and internal parasites (Fincher 1973). Assuming a national herd of about 110 million animals, he calculated the annual potential savings due to accelerated dung degradation to be US$ 2 billion (= CDN$ 8.0 billion in 2022). Losey and Vaughan (2006) revisited these calculations and obtained a more modest estimate of US$ 380 million (= CDN$ 674 million in 2022). The cattle herd in Canada is roughly 1/10th the size of that in the United States. If we accept Losey and Vaughan's (2006) estimate, the benefits of rapid dung degradation in Canada equate to roughly CDN$ 67 million per year.

Did you know ...

... that the burrowing owl will line the walls of its underground burrow with fragments of cow dung, possible to attract dung beetles upon which it feeds (Levey et al. 2004)?

Photo: burrowing owl – Alan Vernon (CC-BY-2.0)

Dung-breeding insects also provide additional ecological services as seed dispersers, pollinators and as food resources for other insects, birds and small mammals (McCracken 1993; Nichols et al. 2008). Coprophilous insects are particularly important as food items for chicks of bird species that nest on or near pastures (Beintema et al. 1991; Hammer 1941; Horgan and Berrow 2004; Laurence 1954), including threatened and endangered species. In Europe, this includes the red-billed chough *Pyrrhocorax pyrrhocorax* (McCracken et al. 1992) and, in North America, the burrowing owl *Athene cunicularia* (Floate et al. 2008; Levey et al. 2004). Dung-breeding insects are regularly reported in the diet of different species of bats (Kervyn and Libois 2008; Robinson and Stebbings 1993; Rydell 1992).

Guild structure

Insects that colonize dung have been classified by Skidmore (1991) into one of seven main guilds based on their feeding habits (Fig. 2). Three of these guilds contain species of flies that are distinguished by differences in larval diet. Larvae of dung-feeding flies feed on microorganisms and tiny fragments of plant material. Most coprophagous flies are members of this guild. Early-instar larvae of mixed-diet flies have the same diet as dung-feeding flies – but then switch, usually in the 3rd and final larval instar, to feed on insects. Larvae of predatory flies feed only on insects. A fourth guild contains species of parasitoid wasps (page 143), which develop inside other insects – mainly species of flies. The final three guilds contain species of beetles. Fungivorous beetles colonize pats at later stages of decomposition to feed on fungal hyphae and spores. Predatory beetles feed on other insects, particularly the eggs and larvae of flies. The last guild is comprised of dung-feeding beetles that feed solely or primarily on dung. Adult dung beetles are filter-feeders (Holter 2004; Holter et al. 2002) and obtain nutrition mainly by ingesting the microorganisms present in the fluid component of fresh dung (Aschenborn et al. 1989). The larvae of dung beetles, however, feed mostly on undigested plant fibre.

Although this guild classification is useful to describe general features of dung insect communities, Skidmore (1991) himself acknowledges that it oversimplifies the complexity of interactions and excludes non-insect arthropods. The yellow dung fly is classified as a 'dung-feeding fly' by virtue of its coprophagous larvae, but the adults are voracious predators. Staphylinid beetles in the genus *Aleochara* are classified as 'predatory beetles', but their larvae are parasitoids of fly puparia. Hydrophilid beetles in the genus *Sphaeridium* are classified as 'dung-feeding beetles', but their larvae may feed on other insects. Mites are common in cattle dung, but are often overlooked because of their tiny size. Some species of mites feed on immature stages of insects or other mites, or on nematodes. Other species of mites are parasites of insects, feed on fungus or are both predators and scavengers. For this reason, mites are included in Figure 2 with both fungus-feeding beetles and predatory beetles.

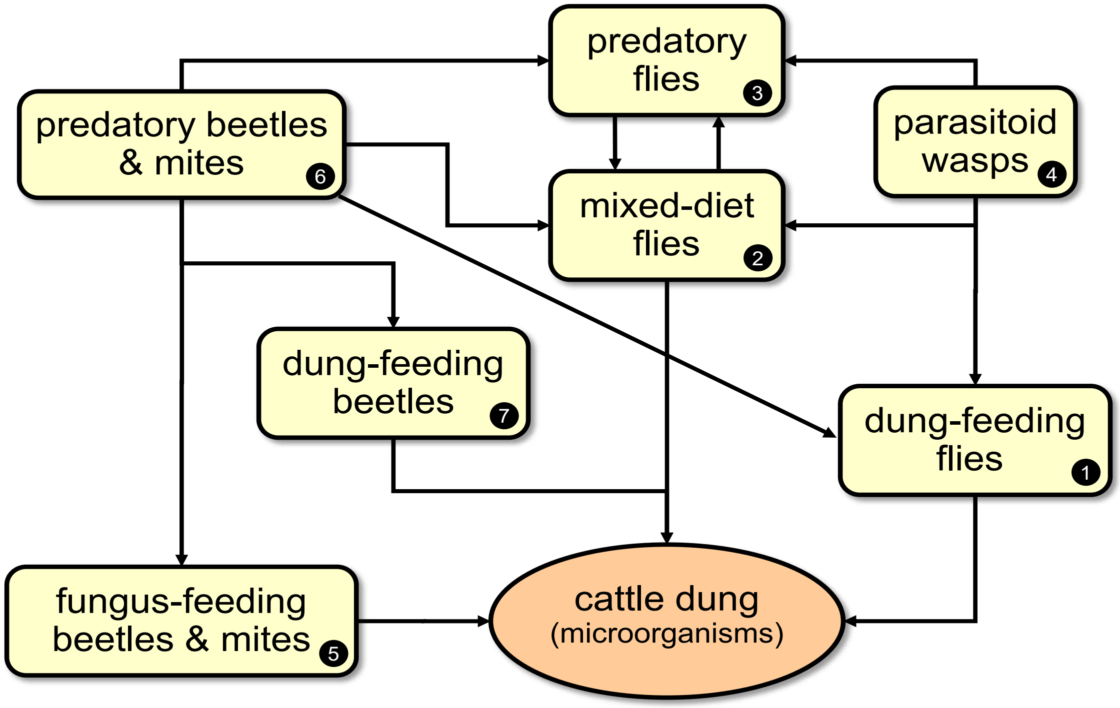


Figure 2. The microorganisms (bacteria, fungi, nematodes) in cattle dung support a food web of seven main insect feeding guilds; the direction of the arrows indicate what they feed on. 1 – the larvae of dung-feeding flies eat bacteria in the dung; 2 – the larvae of mixed-diet flies eat bacteria and insects; 3 – the larvae of predatory flies eat insects; 4 – parasitoid wasps develop inside the immature stages of flies; 5 – fungus-feeding beetles and mites eat fungal hyphae and spores; 6 – predatory beetles and mites eat other insects and nematodes; 7 – the larvae of dung-feeding beetles eat dung fibre, adults extract nutrients from the fluid component of fresh dung. Image modified and reprinted from Floate (2011).

The guild classification also overlooks key differences among dung beetles that are 'dwellers' (endocoprids), 'tunnellers' (paracoprids) or 'rollers' (telecoprids) (Cambefort and Hanski 1991; Figs. 3 and 4). Dung beetles include predominantly species of Scarabaeidae, but also some species of Geotrupidae. The adults of dwellers (Scarabaeidae: Aphodiinae) are attracted to fresh dung in which they feed and lay eggs. The larvae that hatch from these eggs tunnel and feed within the pat until they are ready to pupate, which is done either in the pat or at the interface between the pat and the soil surface. Larval feeding activity slowly fragments the pat into a light, dry, granular material. This material is scattered by wind, penetrated by vegetation growing from beneath, or worked into the soil by biotic (= living; e.g., earthworms, insects, bacteria) and abiotic (= non-living; e.g., rain) factors. Removal of the dung pat from the soil surface by dwellers normally takes weeks to months. However, at certain times of the year, large numbers of dweller may be attracted to fresh pats that they can scatter in a period of days (see section titled 'Seasonal activity'). Dwellers tend to be relatively small and nondescript beetles and are the dominant group in northern temperate regions including Canada.

The adults of tunnellers and rollers (Geotrupidae; Scarabaeidae: Scarabaeinae) remove portions of dung from the fresh pat and move it into more or less vertical burrows or nesting

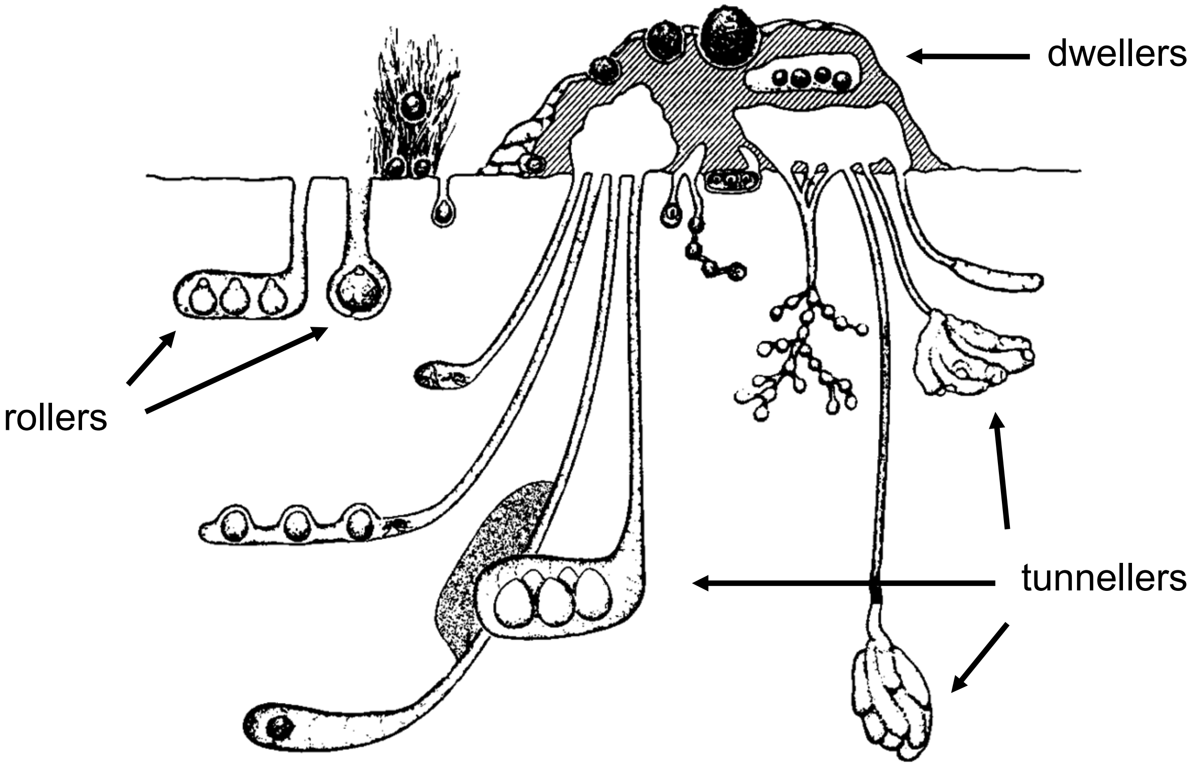


Figure 3. Dung beetles can be grouped into categories of 'dwellers', 'tunnellers' and 'rollers' based on their nesting behaviour. Within each category, different species of beetles may form different types of burrows. Image modified from Doube (1990) and reprinted from Floate (2011).

chambers (Fig. 3). The depth of these chambers varies with species and soil type, but may extend for tunnelling species in Canada (e.g., *Onthophagus nuchicornis*, Fig. 4b) to a depth of about 20 cm (Rojewski 1983; von Lengerken 1954). *Canthon pilularius* (Fig. 4c), a species of roller in Canada, will bury dung to a depth of 5–10 cm (Ritcher 1966). The burrows of larger tunnellers, such as species of *Heliocopris* in Africa, may extend into the soil to a depth of up to 120 cm (Kingston and Coe 1977). Whereas tunnellers form chambers that extend from directly beneath the pat, rollers will first shape small parcels of dung into balls that they roll away from the pat to the site of the future chamber. This process is often performed by the male and female working in tandem. Once the dung has been relocated into the nesting chamber, the female forms a small cavity within the packed mass of dung in which she lays an egg; the cavity is then sealed with an excrement cap. The egg and the associated mass of dung form the 'brood ball.' For smaller species of tunnellers and rollers, such as those that are endemic to Canada, no further care is given to the offspring and each brood ball constitutes the total quantity of food available to a single larva. Elsewhere, however, particularly for species endemic to warmer climates, adults may exhibit parental care – for example, by guarding the chamber against invasion by other insects. The nesting process for *Colobopterus erraticus* (page 104) (a tunneller) and for *C. pilularius* (page 114, Fig. 4c) is described in detail by Rojewski

(1983) and by Matthews (1963), respectively. Both of these species occur in Canada. Cambefort and Hanski (1991) provide descriptions of nesting behaviours for dung beetles in general. Halffter and Edmonds (1982) provide an excellent and detailed review on the nesting behaviour of mainly tropic and subtropic species of tunnellers and rollers.

In comparison with dwellers, tunnellers and rollers are much more effective degraders of dung and provide additional benefits to pasture health. Adults of these latter two groups can remove most of a fresh dung pat from the soil surface in less than a week. The burrowing activity associated with nest chamber formation increases soil aeration and water filtration. The relocation of dung from the pat into the soil improves soil fertility. Tunnellers and rollers typically are larger than dwellers, have more ornate morphologies (e.g., possess horns) and tend to dominate in subtropical and tropical climates. In Canada, species of tunnellers and rollers include species of *Onthophagus* and *Canthon*, respectively (Fig. 4).

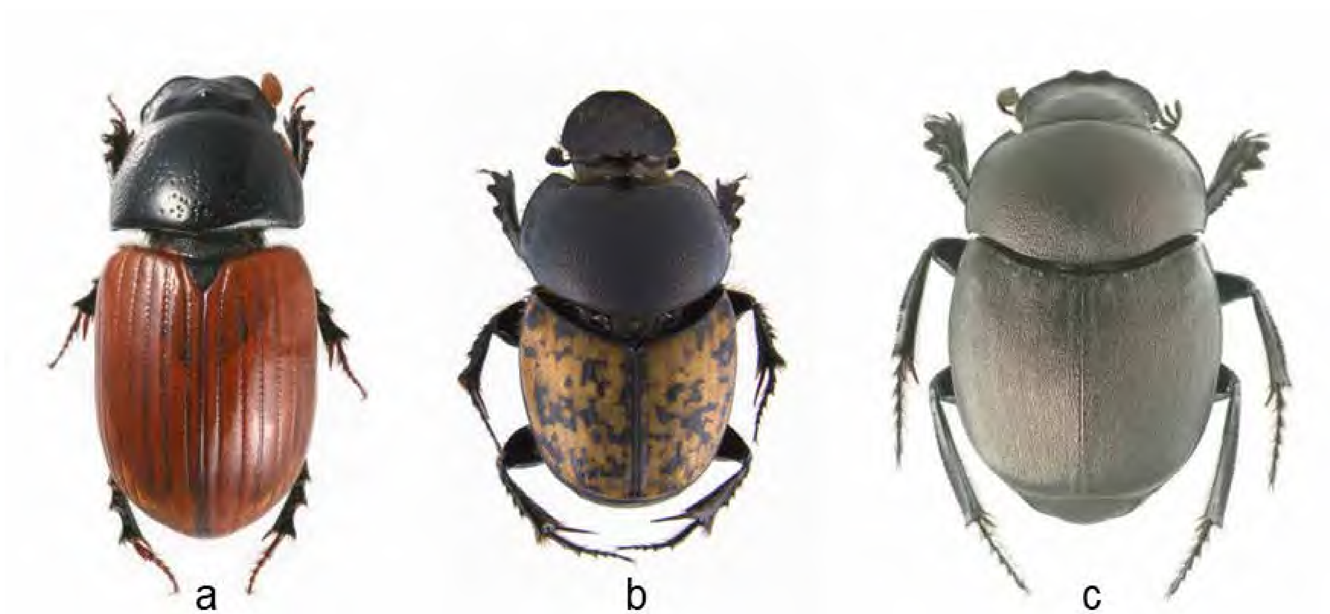


Figure 4. Three species of dung beetles with different nesting behaviours. a – *Aphodius pedellus* (6–8 mm) is one of the more colourful species of 'dweller' in Canada. b – *Onthophagus nuchicornis* (6–8 mm) is a species of 'tunneller' that locally can be very abundant. c – *Canthon pilularius* (12–17 mm) is a species of 'roller' and is perhaps the largest species of dung beetle in Canada. Whereas it is a native species, the other two are of European origin. Photos: H Goulet (retired), AAFC Ottawa, ON

Pattern of succession

The colonization of fresh dung by insects occurs in a series of sequential stages (known as *succession* by ecologists) that is heavily influenced by the age of the pat and weather conditions (Hammer 1941; Kessler and Balsbaugh 1972; Laurence 1954; Mohr 1943; Yoshida and Katakura 1986). The earliest colonists are mainly adult flies, which begin to arrive within minutes of dung deposition to oviposit. Horn flies, which normally rest on the backs and sides of cattle, may colonize dung literally within seconds of deposition (McLintock and Depner 1954). Colonization by adult flies usually declines within a few hours post-deposition. This coincides with the formation of a crust on the surface of the pat that slows the release of the volatile chemicals that attract flies and other coprophilous insects to the deposit. Eggs laid during this first stage generally will produce a new generation of adult flies in 10 to 20 days, varying with ambient temperatures. This rapid development time is facilitated by the feeding of larvae on nutrient-rich microorganisms or on other insects.

Faecal factoid!

Upon arriving at a fresh pat, 'dweller' dung beetles quickly tunnel below the crust to feed and lay eggs

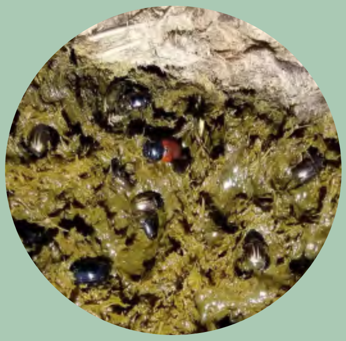


Photo: KD Floate, AAFC Lethbridge, AB

The arrival of adult dung beetles signals a second stage of colonization. It normally peaks between the first and fifth day after dung deposition with numbers of colonists declining rapidly thereafter (Holter 1975; Kessler and Balsbaugh 1972; Lee and Wall 2006; Mohr 1943; Rainio 1966; Tixier et al. 2015). Aphodiine dung beetles will reside within the dung for roughly 3 to 20 days to feed and (or) lay eggs, before leaving to colonize fresh dung elsewhere; residency times vary with the beetle species and season (spring vs. summer vs. autumn) (Holter 1982; Roslin 2000). In contrast to flies, the development of dung beetle larvae may take several weeks to months. This slower development time reflects the low nutrient value of the plant fibre upon which the beetle larvae feed. Larvae of the European species, *Acrossus rufipes* (formerly *Aphodius rufipes*) assimilate only 7–10% of the plant fibre consumed and may ingest 175–530% of their dry body weight each day to obtain the nutrients needed to complete development (Holter 1974). There is little further colonization of dung by coprophilous arthropods 2 to 3 weeks post-deposition.

The first and second stages of colonization coincide with the arrival of parasitoid wasps and predacious beetles (Kessler and Balsbaugh 1972; Mohr 1943) intent on parasitizing or eating other colonists and their offspring. Depending upon the species of wasp, they may lay their eggs in the eggs, larvae or pupae of the host insect species. Some parasitoid species are gregarious, laying several eggs in one host. Other species are solitary and lay only one egg in a host. Some species also may be hyperparasitoids; i.e., parasitizing immature stages of wasps that, in turn, are parasitic on other insects. Adult flies and beetles that colonize the dung frequently arrive carrying phoretic nematodes and mites (see Phoresy, page 15). The tunnelling and feeding activity of first- and second-stage colonists and their offspring accelerates the degradation of the pat to allow it to be more easily penetrated by vegetation and incorporated into the soil.

The final stage of colonization occurs with the breakdown of the interface between the dung pat and the surface of the soil. This process allows soil-dwelling organisms (e.g., earthworms, springtails, oribatid mites, nematodes) to enter the pat and complete the degradation of the dung to its component parts. Fungal spores, likely ingested by cattle and faecally excreted, germinate at various times during the decomposition process to further accelerate degradation and provide food for fungivorous species. The degradation process is aided by moist soil conditions that favour microbial activity. On pastures in Europe and moister regions of North America, earthworms are attracted to dung and can play a major role in its degradation (Bacher et al. 2018; Hirschberger and Bauer 1994; Holter 1979; James 1992). In contrast, earthworms are uncommon on grassland pastures on the Canadian Prairies and other arid regions in adjacent states in the United States. Native species of earthworms were eradicated during glaciation and are only slowing expanding their distributions northward from southern refugia (Tomlin and Fox 2003). Exotic species have been introduced into Canada following European settlement, but their populations are concentrated in urban centres and moister regions of the country (Bohlen et al. 2004).

Faecal factoid!

Dung beetle larvae have an enlarged hindgut that functions like the rumen of a cow. It contains specialized bacteria that produce cellulolytic enzymes, which allow the larvae to extract nutrients from otherwise indigestible plant fibre. The larvae acquire these bacteria when they feed on the brood ball, which is inoculated with secretions by the mother at the time the egg is laid (Shukla et al. 2016).

Photo: scarab larva – Gilles San Martin (CC-BY-SA 2.0)

Phoresy

The ephemeral and patchy nature of fresh dung favours organisms that can quickly locate fresh deposits over long distances (see Dung attraction, page 24. Most insects achieve this by directed flight, attracted by volatile cues emitted from the dung. Phoresy provides an alternate mechanism for small non-flying organisms (e.g., nematodes, mites) to achieve the same goal. In brief, an animal (the *phoretic* or *phoront*) actively seeks out and attaches to the outer surface of another animal, which carries the phoretic to more favourable habitat (Farish and Axtell 1971; Houck and OConnor 1991). Or restated another way, the phoretic hitchhikes on flying insects that carry it to a fresh cow pat.

Nematodes, because of their tiny size, are usually overlooked, but are among the most diverse and abundant of the organisms present in cow dung. Sudhaus et al. (1988) recorded 51 species of nematodes in dung aged up to 24 days. From dissections of 114 *Geotrupes stercorosus* dung beetles, Weller et al. (2010) reported the recovery of 5,002 nematodes in five taxonomic categories with close to 1,500 nematodes from one individual. The phoretic stage of nematodes are termed *dauer larvae*. Most coprophilous nematode species are non-selective and do not require a particular insect species on which to attach. The dauer larvae anchor their posteriors to the dung and wave their upper bodies, presumably to increase the likelihood of a chance encounter with a passing insect. When such an encounter occurs, the dauer larvae immediately attach to the insect. For other nematode species, the dauer larvae show a higher degree of specialization. Kiontke (1996) describes the relationship between the nematode *Diplogaster coprophila* and black scavenger flies (Sepsidae, page 73). The dauer larvae aggregate on the puparium of the fly and, upon emergence of the new adult, will enter through the fly's genital pore to occupy its reproductive system. When the female fly oviposits in fresh dung, the dauer larvae are passed with the eggs. The dauer larvae can only complete development if they have spent time in the fly host.

Why are they called dauer larvae?

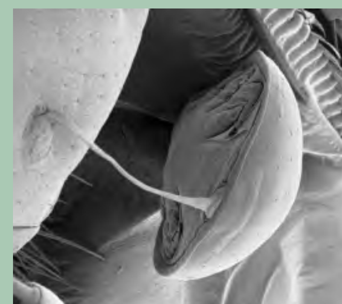
Dauer larvae are in a type of development stasis that helps them survive long periods of unfavourable conditions. The German word 'dauer' translates into English as 'duration.'

Photo: Nematodes – CSIRO

The phoretic associations between mites and arthropods are reviewed by Hunter and Rosario (1988) and by Houck and OConnor (1991). The degree of specialization exhibited by phoretic mites varies among species (Farish and Axtell 1971). Adult mites may use appendages to grasp onto insects during transport; e.g., Macrochelidae (Fig. 5b). Conversely, the phoretic stage may be an immature stage termed the *deutonymph*. The deutonymphs of uropodid mites have a specialized gland that secretes a substance to form an attachment stalk or *anal pedicel* between the mite and the carrier (Bajerlein and Witaliński 2012). The deutonymphs of other mites may attach to hosts using appendages (e.g., Parasitidae) or sucker-like discs (e.g., Acaridae). Deutonymphs can be extremely resistant to desiccation and starvation, surviving in one case for a minimum of 47 days on adult false stable fly, *Muscina stabulans*, with the flies dying before the mites (Greenberg 1961).

Deutonymph attachment stalk

Scanning electron micrograph showing the stalk formed by a uropodid deutonymph by which it has attached to the dung beetle *Aphodius pedellus*.



Micrograph: Lisa Lumley, Alberta Biodiversity Monitoring Institute, University of Alberta

To facilitate successful transmission from an aging to a fresh dung pat, most species of phoretic mites actively seek out potential hosts. Deutonymphs of *Myianoetus muscarum* are attracted to volatile chemicals emitted by the pupae of dung-breeding flies (Greenberg and Carpenter 1960). Although initially scattered throughout the pat, large numbers of deutonymphs aggregate on the fly puparium and then move onto the adult fly when it emerges. Deutonymphs of *Macrocheles mycotrupetes* and *M. peltotrupetes* are overwhelmingly attracted to certain species of dung beetles, orientating to chemical secretions emitted by the preferred species (Krantz and Mellott 1972). Upon arrival at the new habitat, chemical or mechanical cues that are often associated with egg-laying by the host will trigger the detachment of mites from the host. Once detached, the mites move into the dung to breed and feed on immature insects, mites and nematodes.

It is common to find several mites of one or more species on insects arriving at fresh dung. Twelve species of mites in eleven genera (ten taxonomic families) were recovered from adult stable flies on a cattle farm in Britain (McGarry and Baker 1997). An estimated 450 species of mites (representing 48 genera in 18 families) are associated with dung beetles, for which species in family Macrochelidae are most common (Krantz 1983). The number of mites carried by a host can be highly variable. In the British study, 150 mites were recovered from a single fly (McGarry and Baker 1997). Many hundreds of phoretic mites may attach to one dung beetle (Fig. 5).

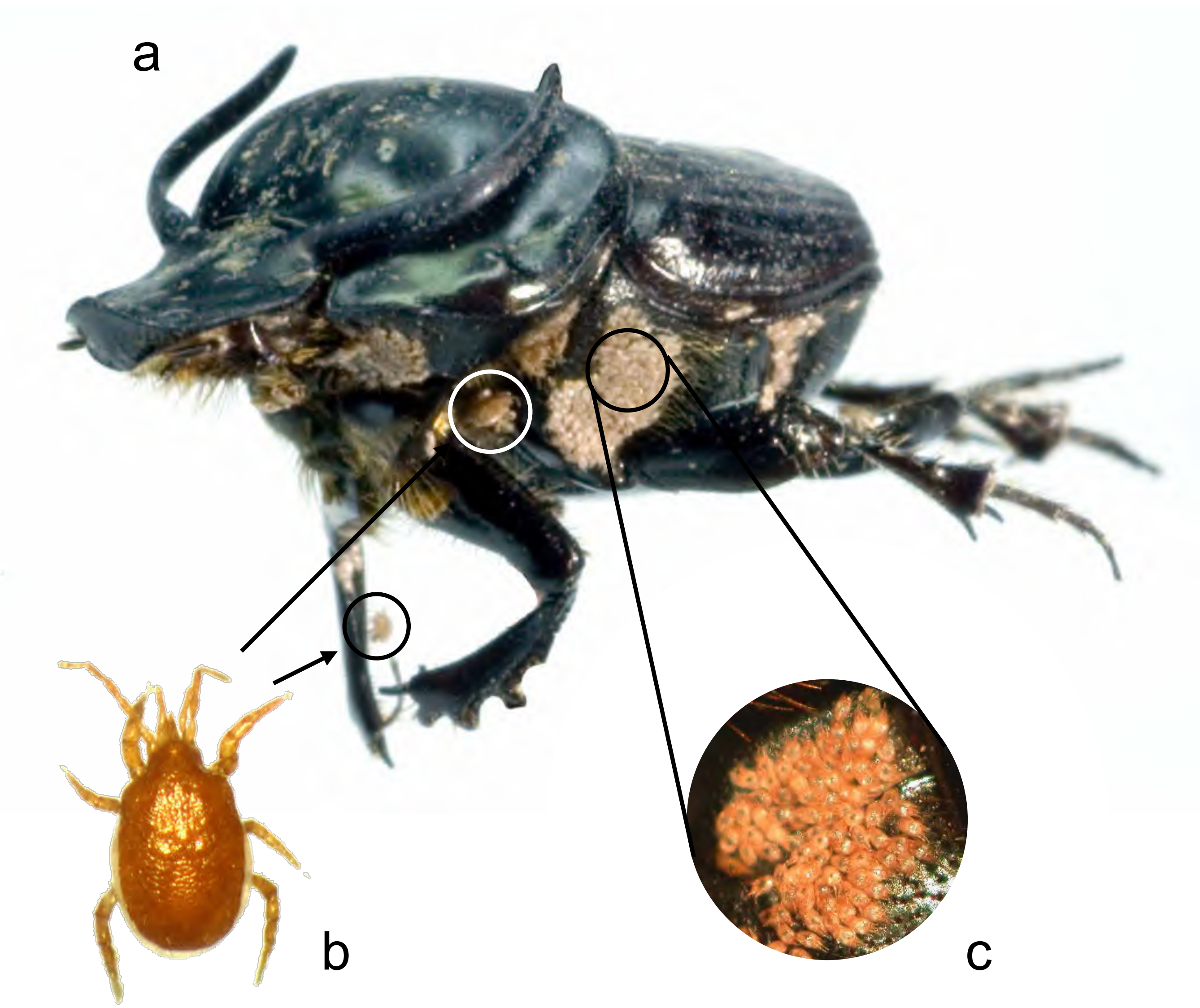


Figure 5. One insect can carry hundreds of phoretic mites to a fresh cow pie. a – the dung beetle, *Onthophagus taurus*. b – an adult mite in the family Macrochelidae. c – a cluster of immature mites.
Photos: a, c – B. Lee, AAFC; b – R. Spooner, AAFC.

Factors affecting succession

The speed of insect succession in a dung pat and its subsequent rate of degradation reflects a complex interaction of abiotic and biotic factors (Fig. 6). Climate, soil and economics dictate the type of pasture maintained by the rancher. Pasture type determines forage productivity, productivity affects stocking rate, and stocking rate affects both the frequency of dung deposition and the likelihood that pats will be disrupted by trampling. In grassland regions of Alberta, for example, stocking rates may be 17.5-fold higher on irrigated pastures planted to tame forages than on native pastures in excellent condition (Alberta Agriculture 1992).

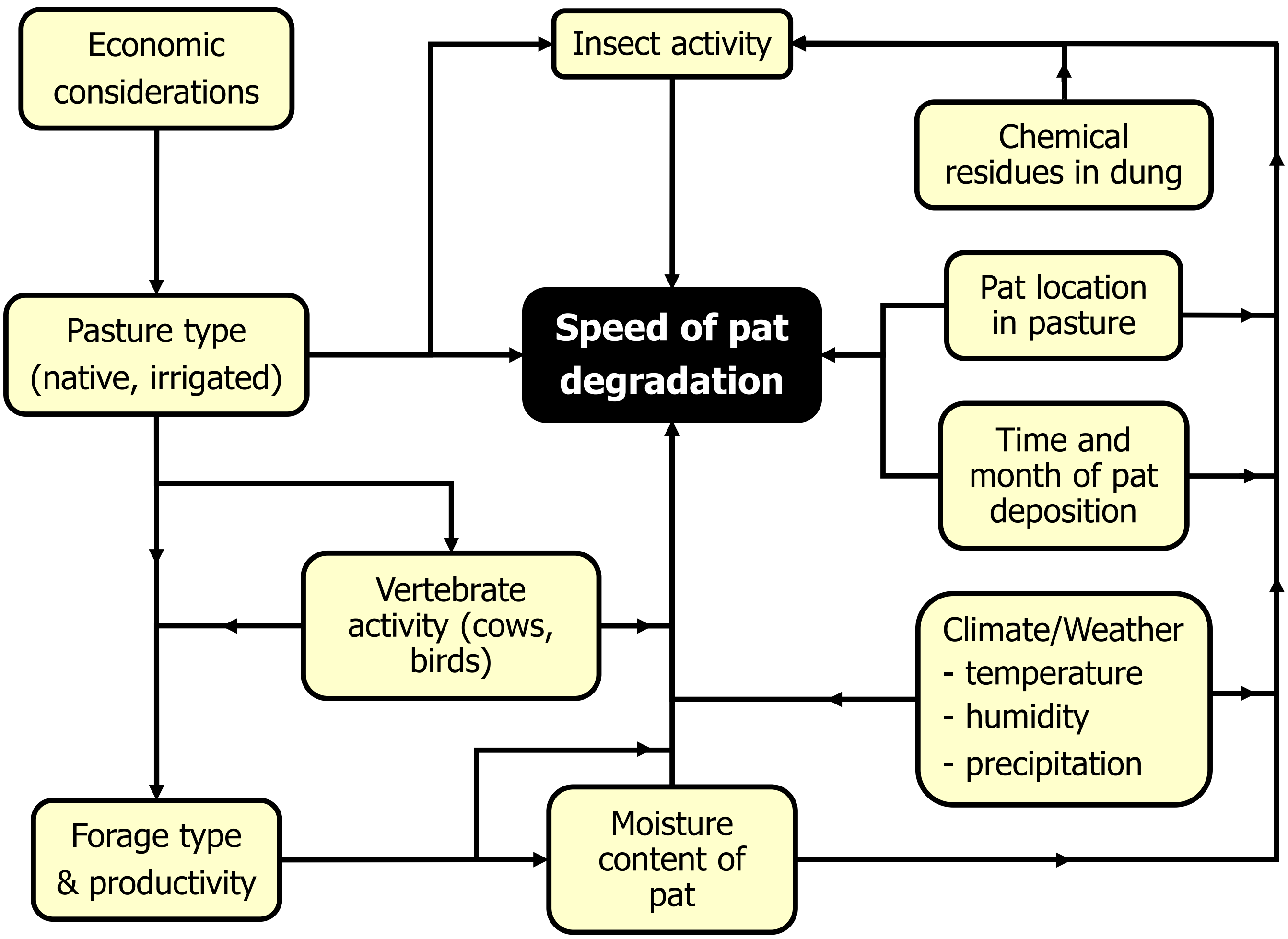


Figure 6. Simplified flow chart illustrating the interaction of abiotic and biotic factors that influence the degradation rate of cattle dung pats on grassland pastures. Modified from Floate (2006) as adapted from Merritt and Anderson (1977).

Climate also affects the composition of the local insect community. Dweller species of dung beetles are more cold-tolerant and tend to dominate on pastures in Canada and adjacent states in the United States, whereas tunnellers and rollers are less cold-tolerant and are more common in southern regions of the United States (Lobo 2000). Because dwellers are least able to quickly degrade dung, pats deposited on north temperate pastures may require months or years to fully breakdown (Merritt and Anderson 1977), whereas pats on pastures in the southern United States may be completely buried and (or) scattered in a matter of hours.

The moisture content of pasture forages declines during the grazing season to reduce the moisture content of fresh cattle dung (Edwards 1991; Lysyk et al. 1985) and affect the size and shape of the pat upon deposition. Cattle grazing on lush forage early in the season typically deposit thin, watery pats that readily degrade (Fig. 7a). Cattle grazing on dry forage later in the season deposit more substantial pats that resist degradation (Fig. 7b). This change in consistency is most noticeable on native grassland or dryland pastures. The difference is much less noticeable on tame pastures, where use of irrigation and fertilizer maintains a lush cover of forage.

Figure 7. Diet affects pat consistency. a – dung from cow grazing on lush forage; b – dung from cow grazing on drier forage.
Photo: © Marci Whitehurst

The moisture content of the pat also affects its suitability for dung-breeding insects. A study by Edwards (1991) in South Africa nicely illustrates this for wildebeest dung. The moisture content of fresh wildebeest dung ranges from 71 to 78% during the year and is significantly correlated with rainfall during the two weeks preceding dung deposition. Larvae of the African buffalo fly *Haematobia thirouxi potans* cannot complete development in dung with a moisture content below 73%, but exhibit a linear increase in survival when dung moisture content is increased from 73 to 76%. Females of the dung beetle *Euoniticellus intermedius* do not form brood balls when the moisture content of wildebeest dung is below 68%, but brood ball formation increases in an almost linear fashion when the moisture content is increased from 68 to 78% (Edwards 1991).

Other factors that affect succession include weather (temperature, humidity, precipitation), time (day vs night) and the location of pat deposition (shaded woodland vs open grassland) (Bezanson et al. 2022, Dickinson et al. 1981; Fincher et al. 1986; Merritt and Anderson 1977).

Landin (1961) reports temperature profiles beneath and on the surface of different types of livestock dung in exposed and shaded locations over the course of a 24-hr cycle. He found that over a 6-day period the moisture content of fresh cattle dung in an exposed location declined from 92 to 56% versus a decline from 92 to 76% for dung placed in a shaded location. Many insect species only fly during daylight hours (diurnal), by which time dung deposited the previous night will have formed a thin crust and be less attractive (Merritt and Anderson 1977). Other species only fly at dusk (crepuscular) or at night (nocturnal) and are less attracted to dung deposited during the day (Kamiński et al. 2015). For dung beetles in Texas, Fincher et al. (1986) identified 21 species as diurnal and 14 species as crepuscular/nocturnal. In Finland, specialist coprophages (*Aphodius, Sphaeridium*) and larger predators (Staphylininae) were found to generally exhibit diurnal activity, whereas generalist coprophages (*Cercyon, Megarthrus*, Oxytelinae) and smaller predators (Aleocharinae) tended to be crepusculular (Koskela 1979). The association of coprophilous species with different types of habitat in the presence of suitable dung has been reported by a number of authors (Bezanson et al. 2022; Fincher et al. 1986; Landin 1961; Rainio 1966). Landin (1961) describes these categories as eurytopic (species with no preference for habitat type), oligotopic (species preferring either shaded or exposed habitats) and stenotopic (species restricted to either shaded or exposed habitats).

Did you know ...

... fossilized dung (coprolites) from the Late Cretaceous period provides evidence that dung beetles co-existed with dinosaurs (Chin and Gill 1996)?

Seasonal activity

The type of species and number of insects available to colonize fresh dung depends greatly on the time of year, due to differences in patterns of seasonal activity. In addition to climatic factors, these patterns reflect differences in the overwintering stage of a given insect species and the number of generations it has each year. Insect activity is highest when conditions are warm and (or) wet, and lowest when conditions are cold and (or) dry. In Canada, peak visitation of fresh dung by insects occurs in spring to early summer followed by a secondary peak of activity beginning in late summer and extending into late autumn. Partially because of this greater activity, pats deposited in spring may largely degrade over the course of a couple of months. In contrast, dung deposited during winter months may not fully degrade for several years. Dung deposited in winter is not colonized by insects because they are inactive during this time. When insects become active in spring, winter-deposited pats are hard and dry and no longer attractive to coprophilous species. Degradation of winter pats, therefore, is more dependent on freeze-thaw cycles and microbial activity. Several authors have reported on the seasonal activity of coprophilous species in Canada (Floate and Gill 1998; Kadiri et al. 2014; Levesque and Levesque 1995; Matheson 1987) or in the northern United States (Coffey 1966; Mohr 1943; Price 2004; Rounds and Floate 2012; Rutz and Scoles 1989; Smith and Rutz 1991; Wassmer 2014; Wassmer 2020). Other authors report on patterns for these species in northern Europe (Hammer 1941; Hanski 1980; Holter 1982; Landin 1961; Roslin 2000; White 1960).

Flies and parasitoid wasps typically have two or more generations per year. They can be seen arriving at fresh dung pats from spring through autumn, varying in numbers and species composition during this time (Coffey 1966; Hammer 1941; Mohr 1943). The seasonal activities of pest flies are best known and show a common pattern. Each species attains peak adult density in late summer or autumn due to the increase of populations over several generations in the preceding three to four months (Lysyk 1993). The stage in which these flies overwinter is the most conspicuous difference. Horn flies overwinter as diapausing pupae, face flies overwinter as adults, and stable flies overwinter as slow-developing larvae. The wasps parasitic on dung-breeding flies overwinter as mature larvae or pupae within the puparium of the host fly (Floate and Skovgard 2004).

Dung beetles in Canada and in other northern countries typically have one generation per year, with adults exhibiting one of two general patterns of seasonal activity. These patterns are reflected by the recovery of adult beetles in dung-baited pitfall traps (Bezanson 2019; Floate and Gill 1998; Kadiri et al. 2014). The first pattern is bimodal with one peak of activity in spring and a second peak in autumn (Fig. 8a–d). Species that exhibit this bimodal pattern overwinter as adults that emerge in spring to colonize fresh dung, feed, and lay eggs. Those eggs develop into a new generation of adults that emerge in autumn of the same year. Seamans (1934) provides a description for autumn flights of *Chilothorax distinctus* (formerly *Aphodius distinctus*) in southern Alberta (see sidebar on next page). The second pattern is unimodal with only one peak of activity (Fig. 8e–g). These latter species overwinter as immature stages, complete their development and then emerge as adults in late spring to early summer to mate and lay eggs. Because their progeny do not complete development until the following spring, there is no autumn peak of adult activity. This separation in seasonal activity limits the number of species present in a local area that can co-occur in a given dung pat. Of 16 species of dung beetles recorded in the Northern Pennines in England, no more than four species may be common at any one time (White 1960).

> ***Chilothorax distinctus***
>
> *"The flight of beetles usually occurs on a still, bright, warm day. Without any preliminaries the beetles appear in countless thousands. The air to a height of ten or 15 feet seems filled with flying beetles. Clouds of them hover over manure piles or over horse droppings on the roads or fields. The manure itself is literally filled with beetles and in less than an hour fresh horse droppings are reduced to a coarse dust spread over a two or three foot circle on the surface of the ground."* (Seamans 1934)

Seasonal activity and overwintering stage also vary with latitude. In colder climates, new adults of *Melinopterus prodromus* may not emerge in the current year, but instead overwinter in pupal cavities (White 1960). In Oregon, *Planolinellus vittatus* overwinters as an adult and appears to have two generations per year (Jerath and Ritcher 1959). In Alberta, *P. vittatus* also appears to overwinter as an adult, but has only one peak of adult activity – indicative of one generation per year (Fig. 8f). In North Carolina, peak adult activity for *C. granarius* occurs in March through April, with the autumn peak of *C. distinctus* in late November through December (Bertone et al. 2005). In Canada, peak activity of *C. granarius* occurs in late May through early June (Fig. 8e), with that of *C. distinctus* in late September through early October (Fig. 8b) (Floate and Gill 1998; Kadiri et al. 2014). In Illinois, Mohr (1943) reported that *Aphodius fimetarius* lays eggs in autumn that hatch the following spring, such that eggs and adults may overwinter in the same dung pat. On pastures in southern Canada, overwintering adults (and possibly eggs) of the closely-related *Aphodius pedellus* can be recovered with adult *C. distinctus* (Figs. 8b and c) and *M. prodromus* from dung pats deposited in mid-October (KDF, pers. obs.).

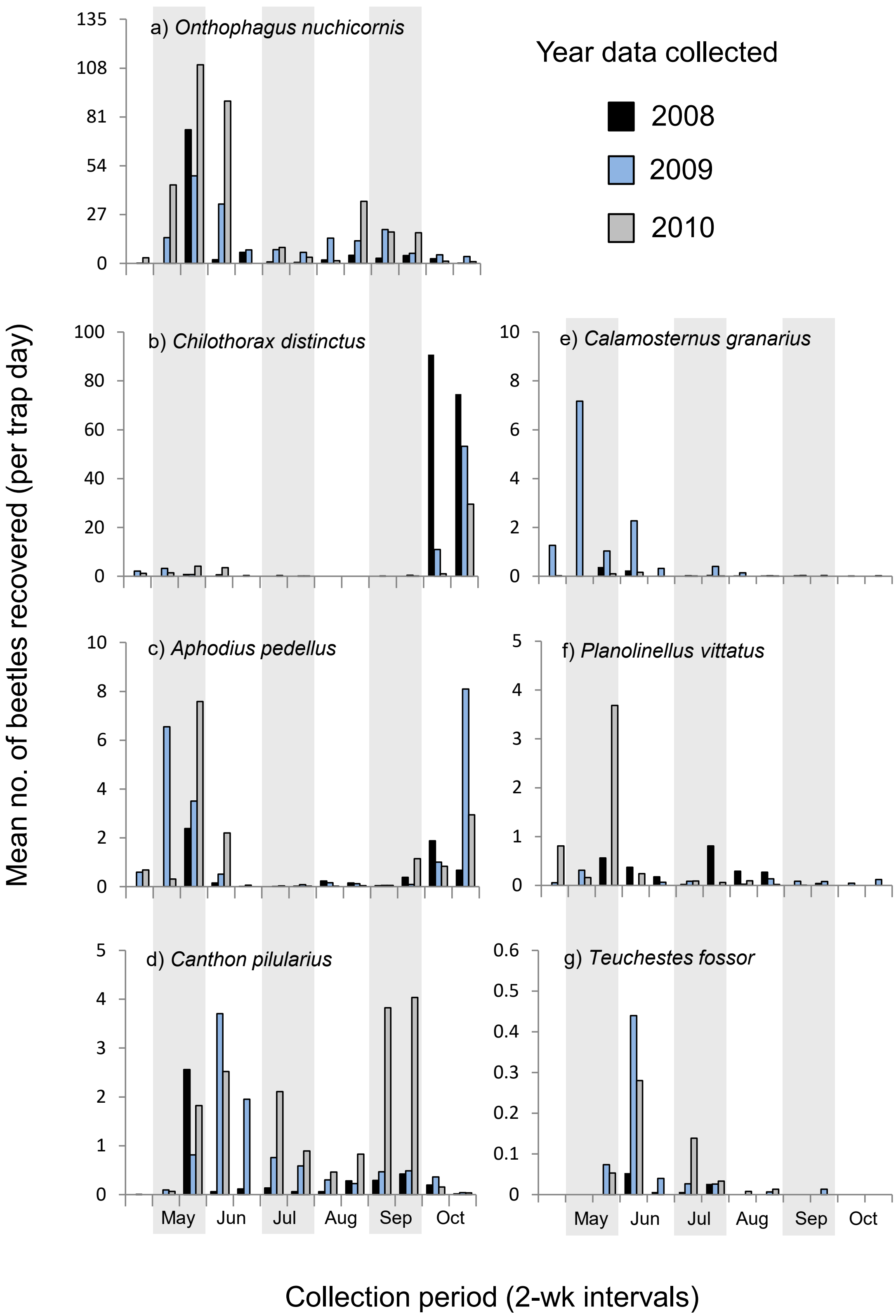


Figure 8. Seasonal activity of dung beetles reflected by their recovery in dung-baited pitfall traps from April through October (2008–2010) in southern Alberta, Canada. a–d: Species with peak flights of adults in spring and in autumn. The low recovery of *C. distinctus* (b) in spring is because overwintered adults of this species show little attraction to fresh dung. e–f: Species with peak flights of adults only in spring/early summer. Modified from Kadiri et al. (2014)

Dung attraction

Coprophilous insects are attracted to fresh dung by the volatile organic compounds (VOCs) that it emits. The physical and chemical properties of the deposit can only be assessed directly after the insect arrives. Frank et al. (2017) undertook a detailed analysis on the nutritional composition of dung for 23 species of animals (carnivores, omnivores, herbivores) and showed that, although different dung beetle species exhibited strong preferences for different types of dung, these preferences were not predicted by the dung's nutritional composition. Thus, fresh dung of different animals deposited at the same time and location will generally attract the same set of dung insect species, albeit in different numbers. In one such comparison, swine dung was identified as being most attractive to dung beetles, followed by dung of opossum, fox and cattle with chicken dung being least attractive (Fincher et al. 1970). Finn and Giller (2002) found dung of sheep to be more attractive to coprophilous beetles than dung of horse or cow. Dormont et al. (2004) reported cattle dung to be more attractive to dung beetles than horse dung. As further evidence of their response to VOCs, rather than to dung per se, dung beetles also may be attracted to butyric and propionic acids, isoamylamine, fermenting malt, rotting fruit and fungus, and carrion (Howden 1955; Matthews 1961; Stone et al. 2021; Weithmann et al. 2020).

The strength of insect attraction to the deposit reflects the composition and relative abundance of its associated VOCs, which change over time. Mackie et al. (1998), for example, reported that more than 160 VOCs may be associated with livestock manure. Sladecek et al. (2021) measured the concentrations of 54 VOCs released by cattle dung during a 1-wk period. Dung aged up to about 2 days released an early successional group of VOCs of mostly aliphatic alcohols and phenols that preferentially attracted flies (mainly due to 1-butanol). Older dung released a late successional group of VOCs of mostly aliphatic esters, nitrogen- and sulfur-bearing compounds that preferentially attracted beetles (mainly due to dimethyl trisulfide).

These compounds can attract insects at very low concentrations. Dung beetles in the genus *Geotrupes*, for example, respond to the chemical skatol at a concentration of parts per billion (Warnke 1931 – as cited in Dethier and Chadwick 1948). This sensitivity to low concentrations of VOCs allows dung beetles to locate fresh deposits from long distances. Using mark-recapture techniques, Silva and Hernández (2015) showed that dung beetles in a Brazilian forest readily flew several hundred meters to locate baits of human dung, with one beetle recovered 850 m from the site of release. On grassland sites in Finland, Roslin (2000) found that most aphodiine dung beetles flew relatively short distances to fresh cattle dung to remain within a pasture, but were capable of flying up to 1 km to move between pastures. His results also showed that beetles were more likely to fly further distances if they were of larger size or had a higher degree of specialization on cattle dung. Depending upon the species, the median residency time of beetles colonizing dung pats ranged from 7 to 12 days, suggesting that an individual beetle probably colonizes only a few pats during its lifetime (Roslin 2000).

Some species may even change their behaviour to make the best use of available dung. The dung beetle *Canthon praticola* has a particular association with prairie dog dung (Gordon and Cartwright 1974), which takes the form of small pellets that easily can be rolled by the beetles to suitable sites for burial. In the absence of its preferred dung, however, *C. praticola* will form balls of dung from fresh cattle dung (Gordon and Cartwright 1974).

Chemical residues in dung

Cattle are commonly treated with veterinary medicines to control pests and parasites; residues from these treatments can pass through the animal and be faecally excreted in metabolized or parent form to kill insect larvae developing in the dung. This phenomenon has been known for decades and has been explored as a 'larvicide' strategy to control pestiferous dung-breeding flies. Gallagher (1928) tested several compounds for their ability to control horn fly larvae by adding these compounds to the water and food of cattle. Other studies targeting horn fly explored the use of compounds including arsenic, phenothiazine and zinc oxide (Bruce 1939; Bruce 1940; Bruce 1942; Knipling 1938). Harris et al. (1973) examined the larvicidal properties of juvenile hormone analogues against horn fly, house fly and stable fly. Studies in the 1970s examined the larvicidal properties against house fly, of chlortetracycline, coumaphos, diethylstilbestrol, fenchlorphos and tetrachlorvinphos (Miller and Gordon 1972; Miller et al. 1970; Rumsey et al. 1977). Other compounds tested for larvicidal activity against pest flies include azadirachtin (Miller and Chamberlain 1989), diflubenzuron (Schmidt and Kunz 1980), ivermectin (Drummond 1985; Miller et al. 1981; Schmidt 1983; Schmidt and Kunz 1980) and methoprene (Moon et al. 1993).

The effect of chemical residues in dung on non-pest insects seems to have gone largely unnoticed until the pivotal work of Wall and Strong (1987). They showed that when ivermectin was applied to cattle as a parasiticide in a slow-release (SR) bolus formulation, dung insect activity and pat degradation was greatly reduced when compared to dung of untreated cattle. Ivermectin and related compounds (e.g., doramectin, eprinomectin, moxidectin) are effective against parasites within (e.g., nematodes, cattle grub) and on (e.g., lice, ticks, mites) the treated animal. Because they target both internal (endo) and external (ecto) parasites, these products are commonly termed *endectocides* and have global popularity.

Numerous studies in many countries have confirmed the insecticidal activity of ivermectin residues and that of other endectocides in dung to non-pest species of dung-breeding insects (Floate et al. 2005; Jacobs and Scholtz 2015; Junco et al. 2021; Lumaret et al. 2012). In Canada, recommended topical doses of ivermectin (Floate 1998b) or doramectin (Floate et al. 2008), respectively, have been shown to reduce numbers of insects developing in dung deposited by cattle up to 12 and 16 weeks post-treatment. A novel formulation of eprinomectin has been shown to reduce the survival of insects in dung of cattle treated 20 or more weeks previously (Fig. 9 and Backmeyer et al. (2023)). Use of pyrethroid products also has been shown to reduce insect activity in cattle dung (Sands et al. 2018; Vale et al. 2004; Wardhaugh et al. 1998). Flies in the suborder Cyclorrhapha and their parasitoid wasps appear to be most susceptible to residues, although reductions also are commonly observed for species of beetles (Hydrophilidae, Scarabaeidae, Staphylinidae) (Finch et al. 2020; Floate 1998b; Floate et al. 2008; Floate et al. 2002; Nieman et al. 2018).

In addition to being directly toxic to insects, residues may affect colonization of the dung pat or have sublethal effects. In a meta-analysis of 22 studies, results indicated that endectocide residues generally increased colonization of dung by aphodiine dung beetles (Finch et al. 2020). Other studies, however, show that insects may be repelled by residues, exhibit no response, or alter their response depending upon the type of parasiticide, residue concentration or season (Floate 1998a; Floate 2007; Holter et al. 1993). Sublethal effects associated with residue exposure have been reported to delay development, affect locomotion and odour perception, reduce body mass, reduce reproductive success, span trophic levels, and cause subtle

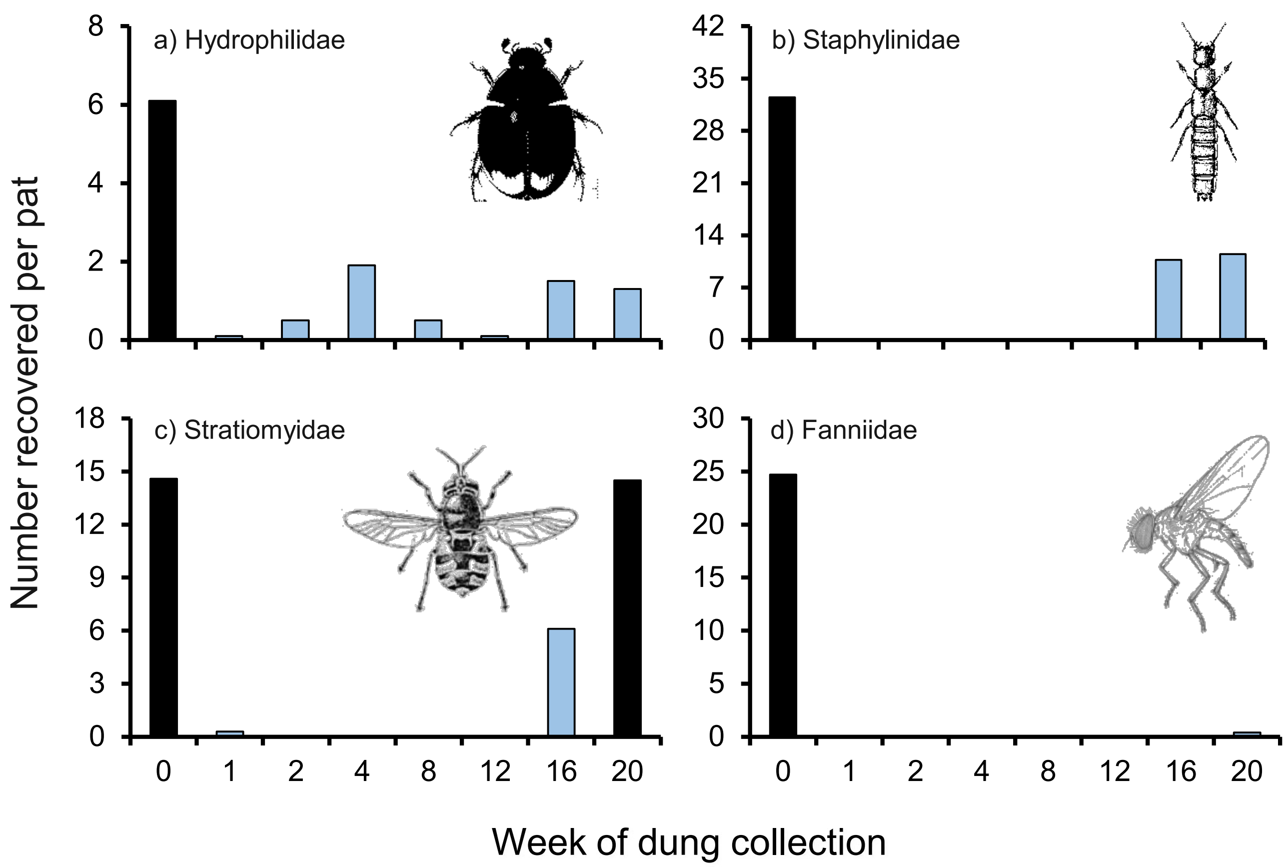


Figure 9. Number of insects developing from egg-to-adult in dung deposited by untreated cattle (Week 0) and by cattle treated up to 20 weeks previously with a recommended dose of an extended release formulation of eprinomectin. Values are means based on 12 dung pats per treatment and are shown in blue if they are significantly different from controls (Week 0). Panels a and b show results for two different groups of predacious beetles. Panels c and d show results for two different groups of dung-feeding flies. Data from Nieman et al. (2018).

morphological deformities (Clarke and Ridsdill-Smith 1990; Floate and Fox 1999; González-Tokman et al. 2017; Römbke et al. 2009; Sommer et al. 2001; Strong and James 1992; Strong and James 1993; Verdú et al. 2015; Webb et al. 2007). The effects of residues are not limited to the use of parasiticides. Dung beetles feeding on dung voided by cattle treated with antibiotics were shown to undergo a change in their gut microbes, albeit with no discernible effect on the beetle's biology or reproduction (Hammer et al. 2016). Jochmann et al. (2011) review methodologies and considerations when testing the insecticidal activity of residues in dung of cattle treated with veterinary products.

A key concern for cattle producers is whether, by reducing insect activity, chemical residues in dung slow the process of pat degradation to reduce pasture quality. This would seem to be a valid concern and has been shown in some studies (Madsen et al. 1990; Römbke et al. 2010a; Sands et al. 2018; Wall and Strong 1987). However, it is by no means a foregone conclusion (Basto-Estrella et al. 2016; McKeand et al. 1988; Tixier et al. 2016). Part of the challenge in documenting such an effect – if present – is that its detection may be confounded by the many other factors that affect insect activity and dung degradation (see Factors affecting succession, page 18). In one non-intuitive finding, use of ivermectin on cattle and sheep actually increased the number of dung beetles attracted to fresh manure to accelerate dung degradation, despite the insecticidal action of residues (Wardhaugh and Mahon 1991).

Another concern is the duration and extent of insect suppression following parasiticide application. At the level of the individual cow pat, residues can suppress insect numbers in fresh dung deposited by cattle treated weeks or months previously, depending upon the insect species, type of product and its formulation (e.g., injectable, pour-on, extended-release). However, this does not necessarily mean that insect populations at the level of the pasture will experience a significant and prolonged reduction in numbers. Not all cattle in the pasture may be treated. Coprophilous insects are typically strong fliers and may immigrate into pastures from adjacent areas (Roslin 2000). Insect species with multiple generations per year may quickly rebound in number. All of these factors will help mitigate the potential harmful effects of parasiticide use.

Earthworms and residues?

Earthworms are much less sensitive than insects to endectocide residues in dung (Halley et al. 2005; Römbke et al. 2010b; Scheffczyk et al. 2016; Svendsen et al. 2003; Svendsen et al. 2005). This sensitivity varies with earthworm species and the parasiticide to which it is exposed (Goodenough et al. 2019).

Ranchers concerned about the potential effect of parasiticide use on non-target species of dung-breeding insects can implement management practices to avoid or reduce the risk of residue exposure. Towards this end, consideration of the following questions may be helpful.

- *Is a parasiticide application necessary?* Application of parasiticides as a prophylactic places non-target species at unnecessary risk.
- *Is there a product or formulation available that will reduce the risk of non-target effects?* Some products and formulations may place non-target species at risk for particularly prolonged periods.
- *When can I apply treatments to minimize the risk to non-target species?* Insect populations on pastures are at greatest risk in spring or early summer when most species are colonizing fresh dung to feed and lay eggs. Treatments applied in autumn to cattle entering feedlots pose no risk to insects on pasture.

The expanding diversity of dung fauna

The number of coprophilous species associated with bovine dung in North America has perhaps more than doubled since European colonization.

Prior to European settlement, an estimated 40–60 million bison (American buffalo) (*Bison bison*) roamed North America, from northern Canada, south through much of the United States and into Mexico. By the 1880's, the species was all but exterminated (Soper 1941) and an abundant supply of fresh dung was removed from the landscape. *Where went the dung-breeding insects of the American bison?* This was the question addressed by Tiberg and Floate (2011), who concluded that these insects likely made a successful transition to breed in cattle dung and persist to the current day.

Prior to about 1640, there was an initial mass importation of cattle from Europe to the eastern United States with a subsequent increase in their numbers and distribution on the continent (Bowling 1942). Cattle and bison co-existed in some areas leaving faecal deposits of similar form and quality. As evidence of this similarity, Tiberg and Floate (2011) compared the attraction of insects to, and development in, dung of bison fed hay versus dung of cattle fed hay or barley

The American Bison

"Of all the quadrupeds that have lived upon the earth, probably no other species has ever marshaled such innumerable hosts as those of the American bison. It would have been as easy to count or to estimate the number of leaves in a forest as to calculate the number of buffaloes living at any given time during the history of the species previous to 1870." (Hornaday 1889)

silage. They found that insects were as likely to respond to differences in the diet of the animal as they were to the species of animal depositing the dung. As further evidence of their similarity, bison and cattle interbreed to form fertile progeny called *beefalo* or *cattalo*, depending upon their genetic composition (Peters and Slen 1966; Ward et al. 2001).

The sailing vessel used by Jacques Cartier

When settlers arrived in North America with their cattle, they unintentionally introduced species of insects that were present in the sand and soil used as ballast by ships sailing from Europe. Upon arrival in the New World, the ballast was discarded ashore at ports along the Atlantic coast with the ships returning to Europe with coal, lumber and other exports. From eastern ports, these adventive species subsequently spread westward across North America (Brown 1940; Brown 1950; Lindroth 1957). Cattle were first introduced into what is now Canada in the 1500s (MacLachlan 1996). In 1518, there was a failed attempt to establish a herd on Sable Island off the coast of Nova Scotia. In 1541, the French explorer Jacques Cartier brought the first cattle to Quebec (4 bulls and 20 cows) in a second failed attempt to establish a herd. By the early 1600s, however, herds were well-established in pastures along the St. Laurence River in Quebec. International shipments of goods, plants and livestock continue to introduce new species into the country; e.g., 639 of the beetle species in Canada are thought to be of exotic origin (Brunke et al. 2019).

In a survey of beetles, flies, wasps and mites in cattle dung in the interior of British Columbia, at least 25 of the 67 species recovered were known or suspected of being exotic (Macqueen and Beirne 1974). In two surveys of dung beetles (Scarabaeidae) on pastures in southern Alberta, eight of 17 (Floate and Gill 1998) and eight of 12 (Floate and Kadiri 2013) species were of European origin and collectively accounted for about 95% of the 345,000 beetles recovered.

A world traveller

Of African origin, *Digitonthophagus gazella* may have the widest distribution of any dung beetle species in the world. Because of deliberate introductions, it now occurs in Australia, New Zealand, Central America, North America and South America.

Photo: H. Goulet (retired), AAFC Ottawa, ON.

Adventive species of dung beetles are almost exclusively dwellers. Their reproductive behaviour – less complicated than that of rollers and tunnellers – was more conducive to surviving in soil ballast for the several weeks of a transatlantic voyage by sailing vessel. Across Canada, non-native species associated with dung include at least 12 species of dung beetles, six species of Histeridae (page 87) (Bousquet and Laplante 2006), 16 species of Hydrophilidae (page 91) (Smetana 1978) and 58 species of Staphylinidae (page 124) (Klimaszewski and Brunke 2018). There also are many species of introduced flies, most notably the pest species house fly, stable fly, horn fly and face fly.

Some insect species have been deliberately introduced into North America. Dung beetles (mainly tunnellers) were released to accelerate the degradation of cattle dung to improve pasture quality and eliminate pats as breeding sites for horn fly and face fly (Pokhrel et al. 2021). Predacious beetles and parasitoid wasps were released as natural enemies of these pest species. Most of the releases have been made on Hawaii, where cattle (and horn fly) were introduced prior to the 1900s and where native insects are incapable of degrading the mound-like deposits of cattle. Because the rest of North America has a diverse assemblage of native species capable of degrading cattle dung, only a few species have been deliberately released on the mainland. Pokhrel et al. (2021) review the rationale, history and rearing/release methods for dung beetle introduction programs in North America and elsewhere. They also discuss the regulatory requirements for these programs. These requirements include an assessment of the risk that the introduced species may displace native species (Filho et al. 2018), and ensure that safeguards are in place to prevent the accidental introduction of pathogens or parasites that might affect livestock into the country of dung beetle release. With rare exception, these programs have targeted regions that do not have native species capable of degrading cattle dung; e.g., Australia, New Zealand and island nations including Easter Island, New Caledonia and Vanuatu.

Ranchers may ask, *Where can I get dung beetles to accelerate dung degradation on my pastures?* If such beetles are not already present on your property, they are either making their way on their own or cannot survive in your part of the country. Dung beetles are strong fliers. In the absence of geographical barriers (e.g., mountains, oceans), they will spread out and establish in regions that support their survival. Consider the European species *Onthophagus nuchicornis*. Present in northeastern North America prior to the 1840s, it was first recorded in western Canada in British Columbia in 1945 (Hatch 1971); it is now one of the most common species in the Prairie Provinces (Floate and Gill 1998; Floate et al. 2017). *Colobopterus erraticus*, a European species not reported from west of Manitoba prior to 1991, is now common throughout southern Alberta (Floate and Kadiri 2013).

Experimental studies show how climate limits the distributions of three closely-related species of tunnellers in North America (Floate et al. 2015; Floate et al. 2017). *Onthophagus nuchicornis* has an obligatory diapause triggered in autumn by shorter days and cooler temperatures, which allows it to survive cold winter conditions in Canada and adjacent states to the south. However, because these environmental cues are absent in warmer regions, *O. nuchicornis* cannot establish in the southern United States. It also explains why releases of the species failed to establish in Hawaii (Anonymous 1911). The Afro-Asian species *Digitonthophagus gazella*, formerly *Onthophagus gazella*, was deliberated introduced in the southern United States in the 1970s (Blume and Aga 1978). It has been recovered as far north as Kansas, but is otherwise limited to regions further south extending into Mexico and Latin America (Noriega et al. 2020). Its lifecycle does not include a diapause and adults cannot survive for more than a few days at soil temperatures below 7 °C (Fincher and Hunter 1989). Because of these differences, the distributions of *O. nuchicornis* and *D. gazella* will never overlap. In contrast, *Onthophagus taurus* is a Mediterranean species with a facultative diapause. Diapause is not required to complete the lifecycle, but can be entered into if necessary to survive cold conditions (Floate et al. 2015). Because of this flexibility, the distribution of *O. taurus* overlaps with that of *O. nuchicornis* to the north and with that of *D. gazella* to the south (Floate et al. 2017). First recorded in North America in Florida in 1971 (Fincher and Woodruff 1975), *O. taurus* now occurs as far north as Michigan (Rounds and Floate 2012).

Diapause

Diapause is a period of suspended development normally triggered by changes in day length, temperature or available food. Insects in diapause can better survive unfavourable conditions and may do so as eggs, larvae, pupae or adults, depending upon the insect species.

<u>Obligatory diapause</u> – required to complete the life cycle; common for species with one generation per year.

<u>Facultative diapause</u> – not required to complete the lifecycle; common for species with two or more generations per year.

Climate change will further expand the diversity of coprophilous species in Canada. On the Prairies, observed seasonal mean temperatures (°C) from 1948–2016 increased as follows: winter (3.1), spring (2.0), summer (1.8) and autumn (1.1) (Zhang et al. 2019). Field cage studies show that *O. taurus* can complete egg-to-adult development in southern Alberta, but overwintering mortality prevents establishment (Floate et al. 2015). If this trend for warmer winter conditions continues, establishment of this species on the Prairies seems likely.

Celestial navigation

Some species of dung beetles roll balls of dung across the landscape in remarkably straight lines. If you think they do this by orientating to a landmark, you'd be wrong. Instead, the beetles orientate their movement using polarized light, the sun, the moon, and even the Milky Way (Byrne et al. 2003; Dacke et al. 2013; Dacke et al. 2014).

A fascinating video presentation by Dr. Marcus Byrne illustrates how dung beetles orientate to these celestial cues (Byrne 2012).

Taking a peek at critters in poop

The best way to learn about insects in dung is to observe them. With a bit of practice and Part II of this guide, you should be able to quickly distinguish between general categories of flies, dung beetles, predacious beetles, and wasps. Depending upon your intent, you may wish to collect some of these insects for further study. Methods used to collect coprophilous insects are briefly described in the following paragraphs. For more detailed information on how to collect, prepare and preserve insects of all types, I recommend Martin (1977) as an excellent place to start.

Crouch beside a fresh dung pat. Look at the species that arrive and watch how they interact[2]. You may see sarcophagid flies, whose eggs hatch inside the adult to be deposited as larvae ('larvipositing') on the surface of the pat. There may be male yellow dung flies fighting amongst themselves for mates. Staphylinid beetles are almost certain to be present, running about and searching crevices for something to eat. With a little luck, you may see dung beetles forming bits of dung into a ball and rolling it away. Many of the beetles that arrive will quickly tunnel through the crust forming on surface of the pat and out of sight. A hand trowel can be used to remove this crust to get a better idea of the number of beetles within and may reveal the immature stages of other insects; most likely fly larvae. Removing the crust also releases a fresh cloud of chemical volatiles that will attract more insects to the pat. It is always a good idea to wear gloves when handling fresh dung, which can harbour different types of human pathogens (Bicudo and Goyal 2003).

Use flotation to recover insects inside the pat. With a spade, transfer the dung into a bucket of water and gently stir. Tunnelling species of dung beetles may be present in the soil beneath the pat. To recover these, you'll need to scoop up the soil below the pat – for species of tunnellers in Canada, a depth of 10–15 cm should suffice. Most of the insects will float to the surface of the water where they can be recovered by hand, with a fine mesh dip net, or with forceps. Flotation works best with fresh dung, before the pat has formed a thick crust and begins to dry out in the centre. Adult beetles are mostly likely to be recovered; adult flies or wasps quickly leave the pat when it is disturbed. Flotation of older dung pats aged a few days to a couple of weeks will recover fly maggots and pupae as well as beetle grubs. Mechanical methods of extraction with flotation can be used to process large numbers of pats with relatively little effort (Fowler et al. 2020; Sutherst et al. 1987).

Dung-baited pitfall traps are the easiest way to collect coprophilous insects. In simplest terms, they consist of a container sunk into the ground with the opening level with the soil surface and baited with fresh dung (Fig. 10). To recover live insects, traps can be operated without a preservative ('dry') and the bait placed in the bottom of the container on a layer of soil. Dry traps should be checked daily and are best suited to recover dung beetles, which will

[2] There are several excellent videos online that show dung insect activity. Two that I highly recommend are by Jochmann (2017a, 2017b).

tunnel into the soil and dung. Traps can otherwise be operated with a preservative ('wet') and the bait suspended from a mesh screen over the opening of the container. The screen also reduces the likelihood of small rodents falling into the trap and will prevent animals from drinking the preservative. Add a drop of liquid dish detergent to the preservative to break the surface tension of the solution, so that insects entering the trap will sink below the surface of the preservative and drown. Use a non-toxic preservative as a further precaution to avoid poisoning small animals. A saturated solution of salt water works well if traps are checked every 2–3 days. A mixture of water and propylene glycol (1:1) is more suitable if traps are checked weekly[3]. Should researchers wish to use recovered insects for molecular analyses, the findings of Nakamura et al. (2020) suggest a high level of DNA preservation for specimens stored in

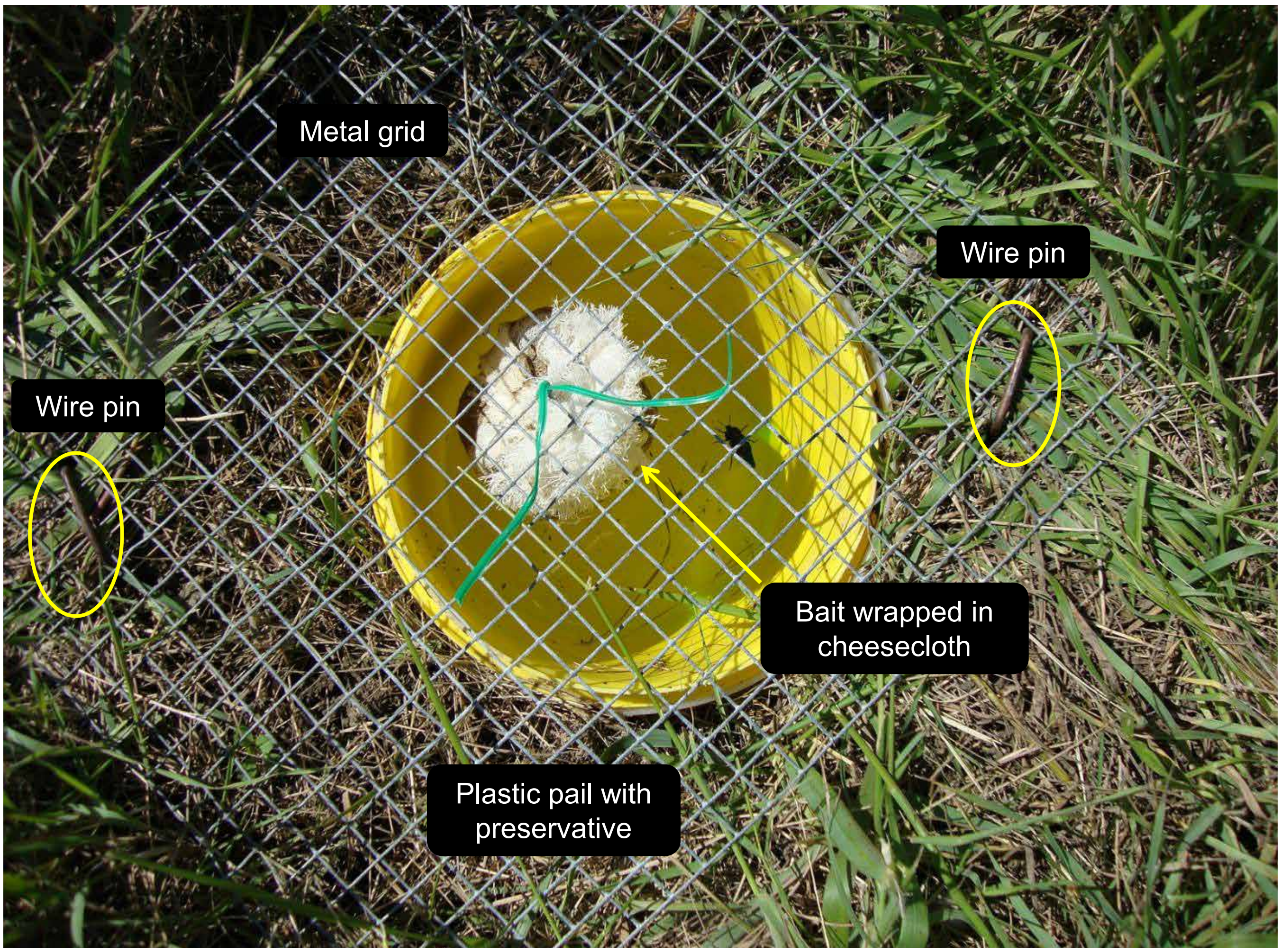


Figure 10. This dung-baited pitfall trap uses two plastic pails (2-litre capacity), one nested inside the other, buried with the lip of the trap level with the soil surface. The inner pail is easily removed to empty trap contents; the outer pail remains in the soil to prevent the hole from collapsing. A wire screen secured with metal pins over the mouth of the trap excludes rodents and birds, and supports a bait made from fresh cattle dung (ca. 250 ml) wrapped in 3-ply cheese cloth and secured with a twist tie. Baits can be made the day of use, or made in advance and frozen until needed. They remain effective for 2–3 days (Bezanson et al. 2020). Preservative (ca. 2 cm depth) in the inside pail drowns and preserves insects attracted to the bait. (Photo: KD Floate).

[3] Do not confuse propylene glycol with ethylene glycol. Propylene glycol has low toxicity and is used to winterize waterlines in cottages or recreational vehicles. Ethylene glycol has high toxicity and is sold as automotive antifreeze.

propylene glycol. Brown and Matthews (2016) review the different types of pitfall traps and preservatives that have been used by various researchers.

Thousands of dung beetles may be recovered in dung-baited traps in a few days (Fig. 11). In such cases, it may be easier to estimate the number of beetles recovered by their bulk weight rather than counting them individually (Bezanson and Floate 2020). Many non-coprophilous species also may be captured, either because they are attracted to the colour of the trap, to light reflecting off the preservative, or by simply falling in. These latter species commonly include leafhoppers, grasshoppers, plant bugs, butterflies, bees and miscellaneous flies.

Carrion beetles (Silphidae) are occasionally recovered in large numbers, attracted to volatile organic compounds released by rotting insects or dead animals that have fallen into the trap. Species in the genus *Nicrophorus* are particularly noticeable with their distinctive markings of black and orange (Fig. 12). Species of silphids in Canada can be identified using Anderson and Peck (1985).

Insect emergence cages can be used to recover insects developing within a specific dung pat or determine how long it takes for them to develop from egg-to-adult. This information can be used, for example, to assess the survival of insects developing in dung of cattle treated with

Figure 11. Dung beetles recovered from one dung-baited pitfall trap operated for one week in September on native grassland in southern Alberta, Canada. Contents include 5,069 *Chilothorax distinctus*, 20 *Onthophagus nuchicornis*, 15 *Aphodius pedellus*, nine *Melinopterus prodromus*, and one *Canthon praticola* (Photo: KD Floate).

parasiticides (see Chemical residues in dung, page 25). Fresh cattle dung is exposed in the field to allow insects to colonize and oviposit in the pat. The pat is then enclosed within a cage either by placing the cage over the pat in the field, or by removing the pat from the field and placing it in the cage. A common form of cage is a plastic container with solid sides and screened 'windows' for air circulation. Insects that complete development within the pat emerge as adults into the cage. The design of some cages requires the insects to be removed by hand, which can be time-consuming (Fig. 13a). The design of other cages includes a collection chamber with preservative into which the insects enter. The chamber can be fixed to the top of the cage to take advantage of the propensity for insects to crawl upwards (Fig. 13b). Conversely, the chamber can be attached to the side of the cage where insects are attracted to a light source (Fig. 13c, d).

Figure 12. The carrrion beetle, *Nicrophorus investigator*.
Photo: Stanislav Snäll – CC-BY-3.0

The first insects to emerge will be adult beetles that were present in the pat at the time it was placed in the cage. Excluding these colonizers, and depending upon the species and ambient temperatures, adults of insects developing from egg-to-adult within the pat may emerge within a matter of weeks (e.g., flies, parasitoid wasps) or several months (e.g., dung beetles).

Nocturnal species of dung beetles can be recovered with light traps. Blank et al. (1983) used light traps to monitor the effect of wind, cloud cover, precipitation and air temperature on the flight activity of the introduced species *Copris incertus* in New Zealand. De Clerck-Floate et al. (2012) used *Chilothorax distinctus* as a 'test' species to assess the effectiveness of light traps as a design feature to limit the movement of insects in an insect quarantine facility. In a particularly awe-inspiring example, a light trap was operated weekly for 26 years to examine how releases of the South African species *Digitonthophagus gazella* into Brazil affected the diversity of native dung beetle species (Filho et al. 2018). Battery-powered light traps are available for use in the field. As a bonus, many other types of nocturnal insects will be attracted to the light trap in addition to coprophilous species.

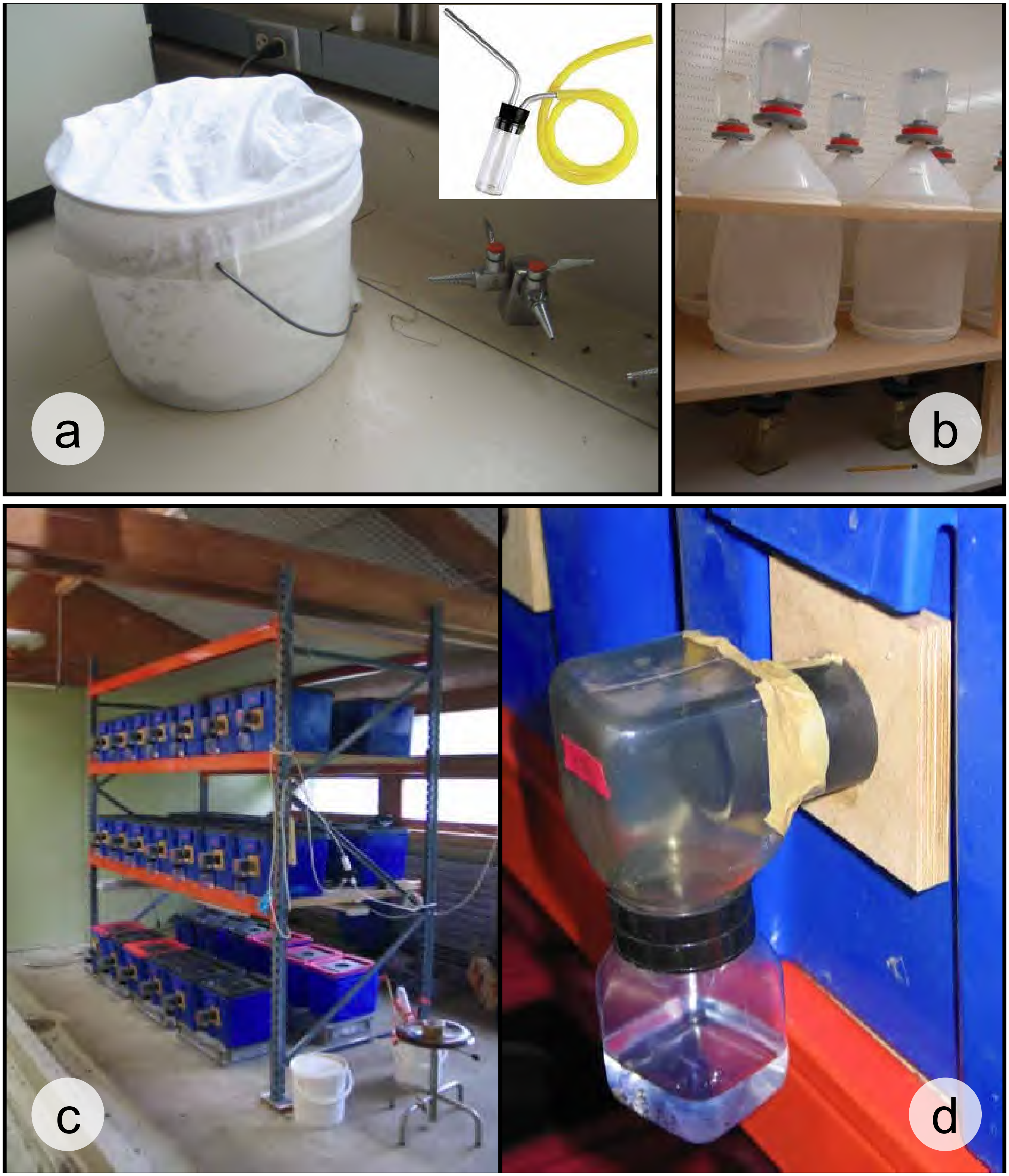


Figure 13. Different types of insect emergence cages. a – Insects emerge into a pail with a mesh 'sleeve'. An aspirator attached to a vacuum line is used to manually remove the insects from the cage. b – Insects fly up into a chamber at the top of the cage, or drop into a chamber affixed to the bottom of the cage. c – Attracted to light, insects fly into a chamber affixed to the side of an otherwise solid cage. d – collection chamber for traps shown in c.
Photos: a – KD Floate, AAFC; b – ©J Lahr; c and d – ©W Blanckenhorn

Part II: Identification of dung-breeding insects

photo: (c) Geoff Holroyd

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What's in a name?

Throughout this guide, insects are referred to by their scientific names. These names can be a mouthful and hard to remember, but their use unambiguously identifies an insect without confusing it with another species. Understanding some of the rules for taxonomic nomenclature can be useful when searching the scientific literature to find information on the biology and distribution of a particular species.

Scientific names have a binomial (2-part) nomenclature consisting of a genus epithet followed by a species epithet, which are normally written in italics; e.g., *Musca domestica*. Genus and species names are at the lower end of a hierarchical naming structure that has many levels including order, suborder, family, subfamily, tribe, genus and species. The further down in this hierarchy that species are grouped, the more similar they are in terms of their evolution, morphology and life history.

Consider the taxonomic hierarchy for the dung beetle, *Onthophagus nuchicornis*. If we refer to it as a 'beetle' (Coleoptera), we identify it as one of more than 8,200 species of beetles known to occur in Canada (Brunke et al. 2019). If we refer to it as a 'true dung beetle' (Scarabaeinae), we narrow its identity to one of 14 species of beetles in Canada that, in common with other members of this subfamily, breed in dung. If we identify it further as a species of *Onthophagus*, we know that it is one of five species of tunnelling dung beetles in Canada.

Each level of this hierarchy is associated with an Authority name and year. These identify the individual(s) who first described the group and the year in which they did so. The genus *Onthophagus* was described by Latreille in 1802; the species *nuchicornis* was first described by Linnaeus in 1758.

Historically, researchers working in different countries or languages often gave different names to the same insect species. Over the years, the dung beetle *Onthophagus taurus*

Onthophagus nuchicornis
(Linnaeus, 1758)

Order: Coleoptera Linnaeus, 1758
- beetles [8,237 species in Canada]

Family: Scarabaeidae Latreille, 1802 – scarab beetles [221 species in Canada]

Subfamily: Scarabaeinae Latreille, 1802 – true dung beetles [14 species in Canada]

Tribe: Onthophagini Burmeister, 1846 [5 species in Canada]

Genus: *Onthophagus* Latreille, 1802 [5 species in Canada]

Species: *nuchicornis* (Linnaeus, 1758) [1 species globally]
Synonyms
- *Scarabaeus nuchicornis* Linnaeus, 1758
- *Onthophagus rhinoceros* Melsheimer, 1846

has been given 24 scientific names and placed in four different genera (Smith 2009). You can imagine the confusion this causes when the same species has multiple names in the scientific literature. To sort this out, the International Code of Zoological Nomenclature (ICZN) was established to ensure a uniform system for use in assigning scientific names (https://www.iczn.org/the-code/the-international-code-of-zoological-nomenclature/).

By ICZN convention, the valid scientific name for a species is the name under which it was first described. All other names are recognized as synonyms or former names. However, there may be well-founded reasons to reclassify a species into a genus other than that in which it was originally placed. This might happen, for example, when closely-related species are newly discovered or when molecular studies reveal previously unsuspected relationships. In such cases, the Authority name and year appear in brackets. *Onthophagus nuchicornis* was first described as *Scarabaeus nuchicornis* by Linnaeus in 1758. In 1846, Melsheimer described this species as *rhinoceros* and placed it in the genus *Onthophagus*. However, because the species was first described by Linnaeus, he remains the Authority with his name and the year in which he described the species placed in brackets; i.e., *Onthophagus nuchicornis* (Linnaeus, 1758).

The scientific name often provides clues on the shape, colour or biology of the insect. Flies (Order Diptera), beetles (Order Coleoptera, and wasps (Order Hymenoptera) are the most common types of insects associated with dung. Flies have only one pair of wings ('di' = two, 'ptero' = wing). Adult beetles have a hardened first pair of wings that cover a second membranous pair of wings ('coleo' = sheathed, 'ptera' = wing). Wasps have two pairs of wings that are joined together with a series of fine hooks ('hymen' = married, 'ptero' = wing). Males of the beetle *Onthophagus rhinoceros* have a rhinoceros-like pronotal horn. *Haemorrhoidalis* ('haemo' = pertaining to blood, 'rrhoid' = flow) is the species name for the fly *Sarcophaga haemorrhoidalis*, and the beetles *Cercyon haemorrhoidalis* (Fig. 55a) and *Otophorus haemorrhoidalis* (Fig. 67), all of which have posterior reddish markings.

Because they have little value for most readers, I do not provide the Authority name and year of description for the various species mentioned in this guide. However, I do provide other names (synonyms) for the species of dung beetles (Scarabaeidae) featured in Part II of the guide. Many of these species recently were reclassified

For common names – a space makes all the difference

Insect common names can be confusing. Doodlebugs are not bugs, but are the larvae of antlions. Antlions are neither ants nor lions, but are easily mistaken for damselflies, which – you guessed it – are not flies.

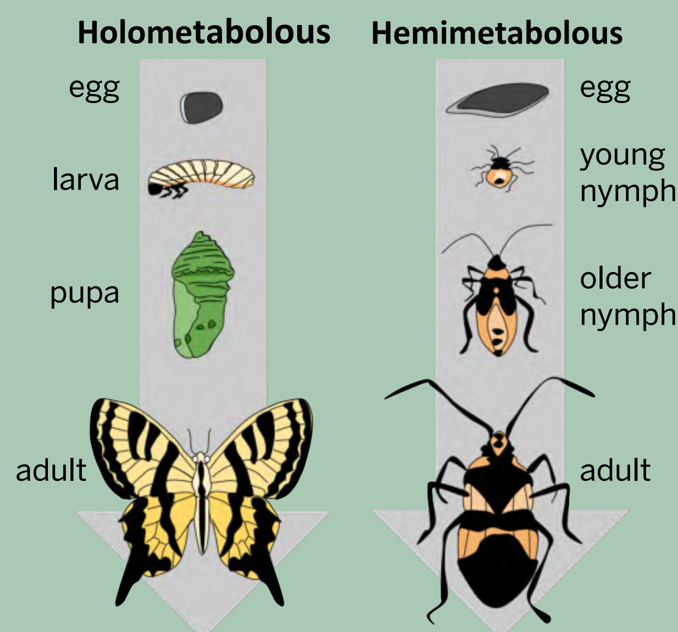
To help make sense of this mess, entomologists insert a space in the common name if it identifies the taxonomic group to which the insect belongs; i.e.,

- bumble bee (space) = a type of bee
- butterfly (no space) = not a fly
- ladybird beetle (space) = a type of beetle
- ladybug (no space) = not a bug
- bed bug (space) = a type of bug
- snakefly (no space) = not a fly

from the genus *Aphodius* into other genera (Gordon and Skelley 2007), such that information on their biology and distribution appears in the contemporary literature under different scientific names. I also make reference to other names in Table 6, for species of wasps (Order Hymenoptera) parasitic on dung-breeding flies. Occasionally, I have inserted notes to explain changes affecting higher levels of taxonomy such as subfamily or family; e.g., see Empidoidea (page 61) and Muscidae (page 65).

Did you know that insects have two types of life cycles?

Holometabolous metamorphosis – an insect life cycle with four developmental stages (egg, larva, pupa, adult); also called complete metamorphosis. The larva and adult have very different body forms and often different feeding habits. Examples of insects with this type of life cycle include butterflies and moths, wasps, flies and beetles. This is the type of life cycle common to insects that breed in dung.



Hemimetabolous metamorphosis – an insect life cycle with three developmental stages (egg, nymph, adult); also called simple or incomplete metamorphosis. The nymph and adult have the same general body form and often have similar eating habits. Examples of insects with this type of life cycle include aphids, cockroaches, true bugs and grasshoppers.

Image: Username1927 CC BY-SA 4.0, https://commons.wikimedia.org/wiki/File:Holometabolous_vs._Hemimetabolous.svg

Identification of immature insects

Most of the insects in cattle dung are present in an immature form, especially for pats older than a few days. The residency time of the adult insects that colonize the fresh pat to feed and lay eggs normally ranges from a few minutes to perhaps a week or so. But the offspring that hatch from those eggs remain within the pat for weeks or months as they pass through a series of larval stages, pupate, and then emerge as adults (Fig. 14).

It can be difficult if not impossible to identify an insect to species from its immature form. But the morphological characteristics of the larva and pupa can be used to identify insects to order, suborder and sometimes to family (Zhu 1949). The common types of insects in dung are flies (Diptera: suborders Brachycera and Nematocera[4]), beetles (Coleoptera: e.g., families Histeridae, Hydrophilidae, Scarabaeidae, Staphylinidae) and wasps (Hymenoptera).

The larvae of beetles recovered from dung have a well-defined head capsule with well-developed mouthparts and antennae. With some exceptions, they also have conspicuous legs. The body shape of beetle larvae will be of one of three general types:

- *campodeiform* – flattened body with long legs; usually with short spike-like projections (termed 'cerci' or 'caudal filaments') projecting from the tail end (abdomen). This is the larvae form for many species of beetles whose larvae are active predators, including Staphylinidae (Fig. 15a).

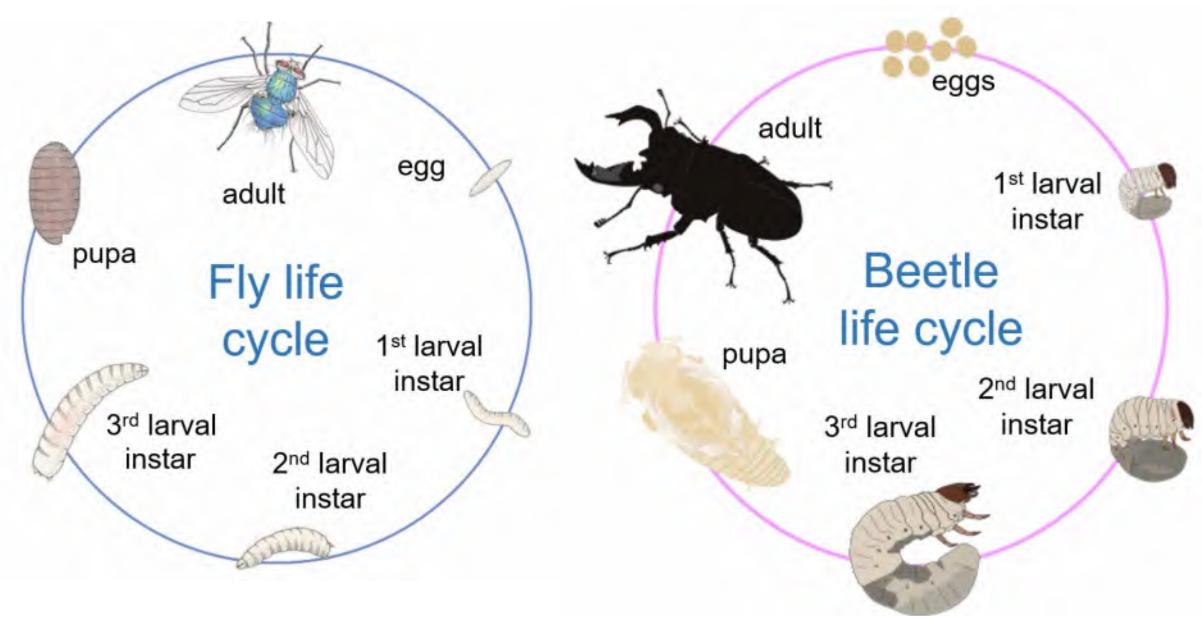


Figure 14. Generalized life cycles of flies and beetles.
(Fly life cycle imageImage: created by Cara Gibson (https://www.caragibson.com/); Beetle life cycle image: Bug-boy52.40 CC-BY-SA 3.0)

[4] Flies traditionally have been placed in either Suborder Nematocera or Brachycera. The former group comprises slow-moving flies with long antennae (e.g., mosquitoes), whereas the latter group comprises fast-moving flies with short antennae (e.g., house flies).

- *platyform* – flattened body with legs absent or extremely short. Species of Histeridae and Hydrophilidae (subfamily Sphaeridiinae) have this larval form (Fig. 15b).
- *scarabaeiform* – body cylindrical and curved in a 'C' shape; well-defined head and usually with short but readily visible legs. As the name suggests, this is the larval form common to true dung beetles (Scarabaeidae) (Fig. 15c).

Fly larvae have a body shape that is vermiform or wormlike (Figs. 15d and e). The shape is cylindrical with no appendages for locomotion, such that the absence of legs distinguishes them from beetle larvae. In addition, the fly larvae most commonly recovered from dung are members of suborder Brachycera, which lack head capsules (Fig. 15d). This provides a second way to distinguish the larvae of flies from those of beetles. Species of flies in suborder Nematocera do have a head capsule (Fig. 15e), but this is much less prominent than that of beetle larvae.

The larvae of parasitic wasps also have vermiform bodies. However, the larva and pupae of these wasps can only be recovered by dissecting the body of their host.

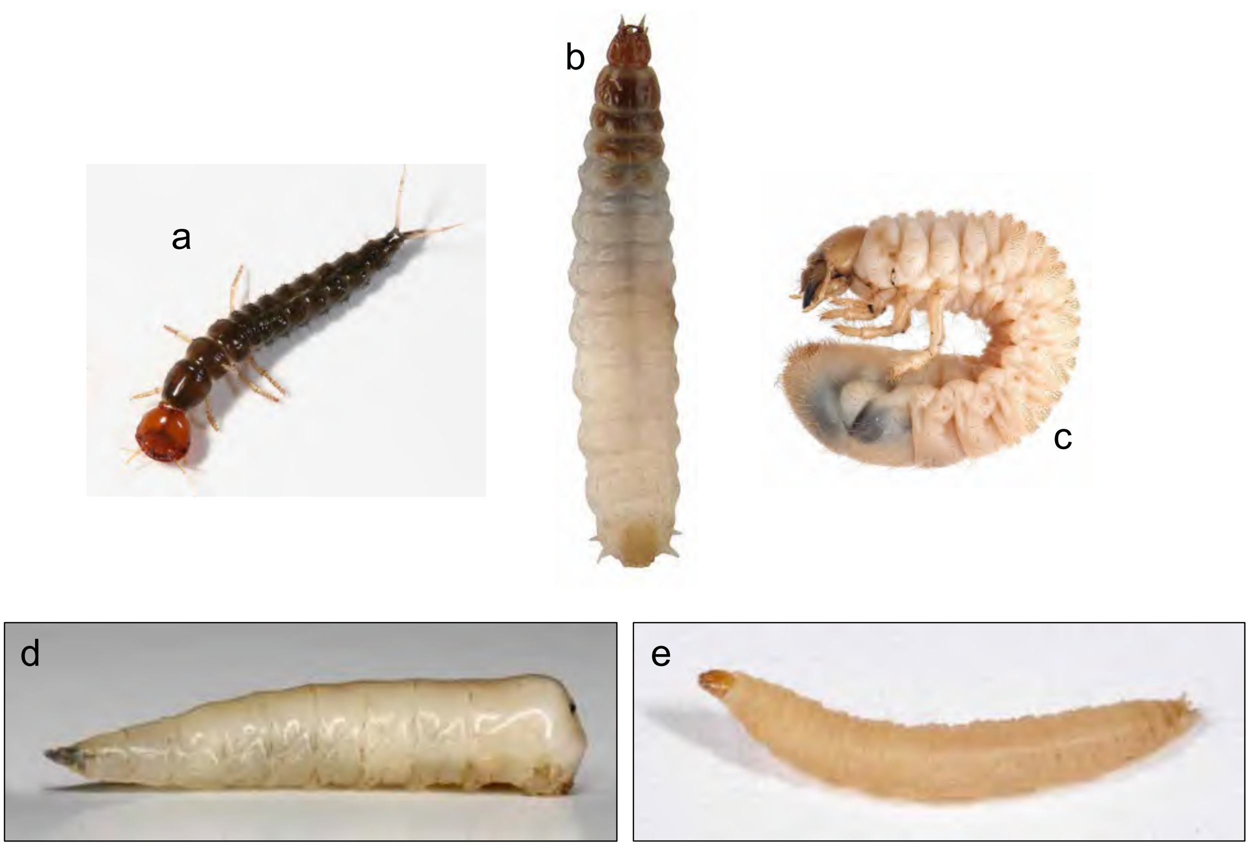


Figure 15. Different larval body forms: a – campodeiform larva of a staphylinid beetle; b – platyform larva of a hydrophilid beetle; c – scarabaeiform larva of the Japanese beetle; d – vermiform larva of the false stable fly; e – vermiform larva of a winter crane fly.
Photos: a – Tom Murray; b – A.A. Zaitsev, https://www.zin.ru/animalia/Coleoptera/eng/index.html; c – Gilles San Martin CC BY-SA 2.0; d – Håkon Haraldseide; e – Matt Bertone

Difference in morphology also can be used to distinguish between the pupae of beetles and flies. Three pupal forms are recognized, based on the degree to which the appendages are held tight (appressed) to the body.

- *obtect* (Figs. 16a and b) – appendages held tight to the body, which is covered with a thin transparent membrane. The pupae of butterflies and moths (Lepidoptera), many species of beetles (including staphylinid beetles in subfamily Staphylininae), and flies in suborder Nematocera have this form.
- *exarate* (Fig. 16c) – appendages are not held tight to the body. The majority of beetle species (including most other subfamilies of staphylinids) have exarate pupae.
- *coarctate* (Fig. 16d) – the appendages are not visible; the insect pupates within the skin of the final larval instar, which forms a hard capsule termed the 'puparium' (puparia = plural). This form is common to flies in suborder Brachycera.

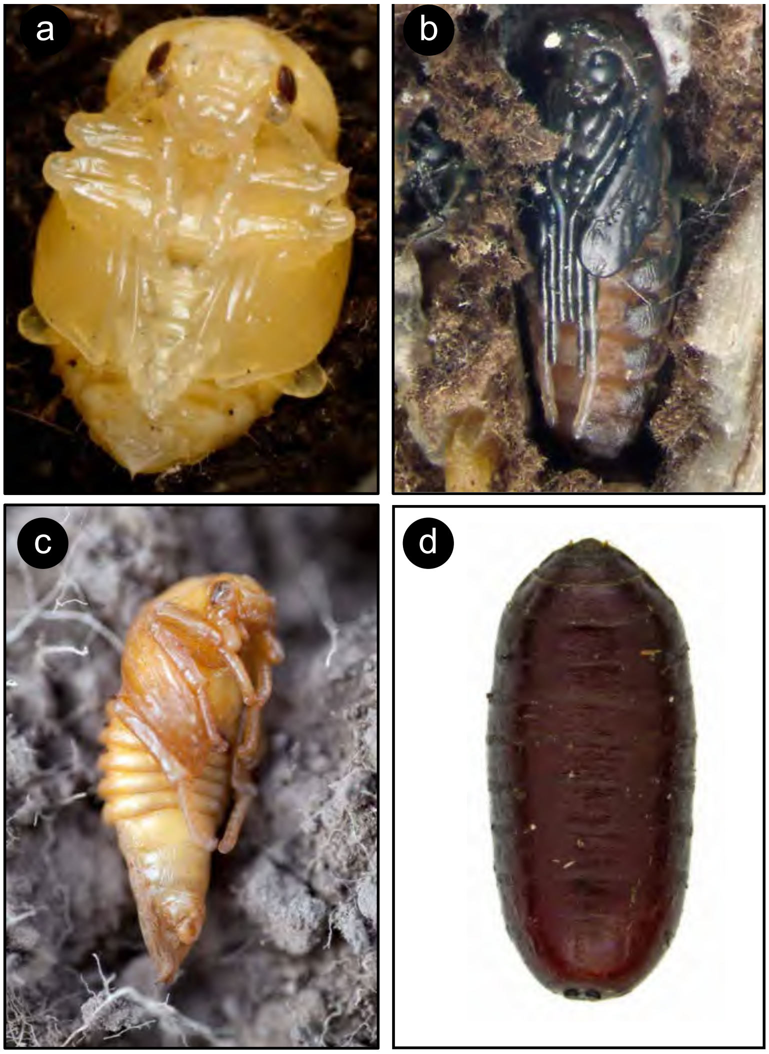
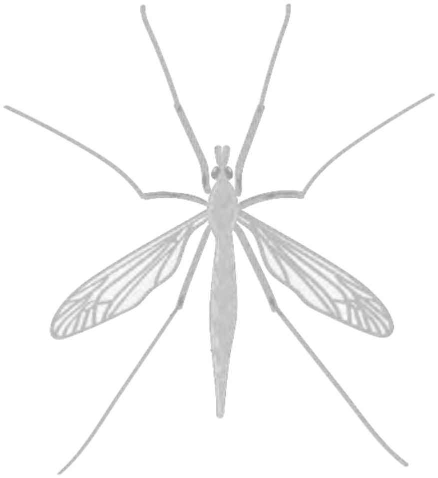
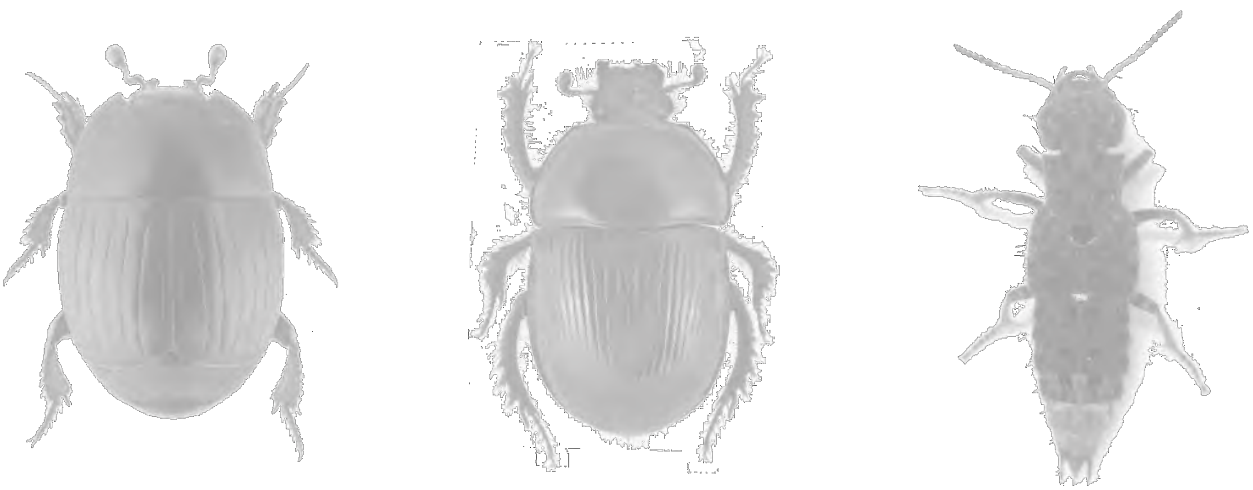


Figure 16. Different pupal body forms. a – obtect pupa of the rosemary beetle; b – obtect pupa of a cecidomyid fly; c – exarate pupa of a cockchafer beetle; d – coarctate pupa of the house fly.
Photos: a – Alessandro Strano (CT – Italy); b – MJ Hatfield CC-BY-ND-NC 1.0; c – Julian Black (CC BY-NC 2.0; d – © Salvador Vitanza



Diptera (flies):
Suborder Nematocera

Diptera (flies):
Suborder Brachycera



Coleoptera (beetles)

Hymenoptera (wasps)

Arachnida (mites)

Identification of adult insects (and mites)

Insects recovered from cattle dung are usually identified from their adult forms and will most often be flies, beetles, or wasps that are parasitoids (page 143) of flies (Fig. 1). Phoretic mites are frequently present on these insects, which they use to travel from one cow pie to the next (see Phoresy, page 15). The current section introduces the reader to the dung-loving (coprophilous) organisms in these four groups.

For each group, there are summaries of morphology, biology and ecology for those taxonomic families that contain at least a few members in Canada that breed in dung. An estimate for the number of Canadian species in the family is provided along with references to taxonomic keys that can be used for genus or species-level determinations. Additional families are included whose members might be mistakenly thought to breed in cattle dung, based on their presence on fresh dung pats on pasture, in dung-baited pitfall traps, or their association with livestock and livestock facilities; e.g., the dipteran families Calliphoridae, Chloropidae, Ephydridae, Oestridae and Syrphidae. Other families are included whose members are unlikely to breed in fresh cattle dung, but do breed in dung in more advanced states of decomposition; e.g., the dipteran families Stratiomyidae and Ulidiidae, and the beetle families Cryptophagidae and Latridiidae.

Taxonomic families for flies are presented first for suborder Nematocera (with thread-like antennae) and then for suborder Brachyptera (with short antennae). Most authorities recognize flies as being members of one of these two suborders.

To help identify beetles, tables are provided for families Clambidae, Histeridae, Hydrophilidae, Scarabaeidae and Staphylinidae. These tables list the size and Canadian distributions of species that are reported in the literature to be coprophilous. Species that are most likely to be recovered from fresh cattle dung are identified in the tables using bold font. Dung beetles (Scarabaeidae) have been particularly well-studied, which allows for more detailed information to be provided for species common in cattle dung. This information is presented first for members of subfamily Aphodiinae and then for members of suborder Scarabaeinae. Information for rove beetles (Staphylinidae) is presented for each subfamily containing members likely to occur in fresh cattle dung.

Information for wasps is presented for taxonomic families with species that are parasitoids of dung-breeding flies. A table is provided that lists the distributions of these species with citation to references providing details of biology and ecology.

Despite being among the most common residents in cattle dung, coprophilous mites have been poorly studied in Canada and cannot be identified with any accuracy without the use of a microscope. The information provided for this group is mainly a list of those species reported to occur in cattle dung in Canada.

Flies (Diptera: Suborder Nematocera)

Suborder Nematocera (= thread-horns) is one of two recognized suborders of flies (Order Diptera). Adults in this group typically have long, thin antennae with many segments, and elongate bodies with long legs.

Black flies, crane flies, gnats, midges, and mosquitoes are among the members of this group.

Anisopodidae (wood gnats)

Adult anisopodids are small to medium-sized flies (2–10 mm in length) with slender bodies and long legs. The head is small and round with three simple eyes (ocelli) in close proximity that nearly form an equilateral triangle. The antennae are threadlike with a length about the same as that of the combined length of the head and thorax (Fig. 17). They are reported to feed on nectar and are often attracted to flowing sap. Adults are often observed in shady wooded habitats, giving rise to the common name wood gnats.

Anisopodids breed in decaying organic material, including rotting leaves, wood, fermenting sap and dung. Rare cases of larvae infesting humans have been reported; probably arising from the accidental ingestion of eggs or larvae (Morris 1968; Smith and Taylor 1966). In Britain, *Sylvicola punctatus* is the only anisopodid reported from dung (identified as *Sylvicola punctata* in Skidmore 1991), but it may be among the most abundant of dipteran larvae present. Adults of this species are characterized by distinctive cloudy patches on the wings. Due to taxonomic revision, what is identified as *Anisopus* by Laurence (1954) is now recognized as *Sylvicola*. Cervenka and Moon (1991) list *S. punctata* as a synonym of *S. marginatus*.

Only five species of anisopodids are known from Canada with perhaps another 2–5 species remaining to be reported or described (Savage et al. 2019). A key for genus-level identifications is provided by Peterson (1981).

Figure 17. Anisopodidae. *Sylvicola punctatus*.
Photo: © Malcolm Storey

Cecidomyiidae (gall midges, gall gnats)

Cecidomyiids are small delicate flies (generally 1–5 mm in length) with long legs and long threadlike antennae. Wings are typically hairy with weak and reduced venation (Fig. 18b, c).

Most of the known species of cecidomyiids have larvae that live in plants and induce atypical swellings of plant tissues called *galls* or *cecidia*, which gives rise to the family name (Fig. 18a). The larvae of other species live in plants without inducing galls, or feed on fungus and develop in decaying wood and vegetation. Still other species are free-living predators or parasitoids. Hammer (1941) reports cecidomyiids as being common in dung. Skidmore (1991) reports that species in the genera *Monardia* and *Mycophila* breed in manure; *Monardia illinoensis* has been reported from cattle dung (Mohr 1943). Several species are economically-important pests of crops including clover, cereals, hops, cabbage, turnips, and mushrooms (Smith 1989).

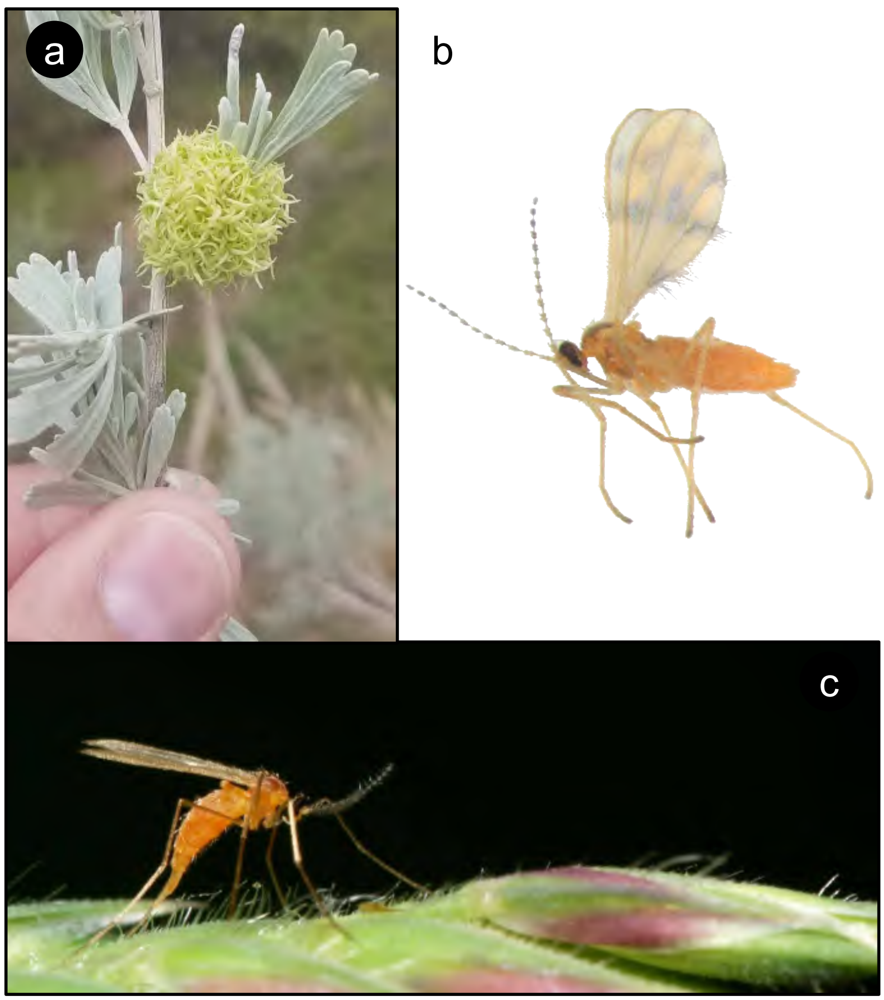


Figure 18. Cecidomyiidae. a – gall formed by a cecidomyid larva on sage brush (*Artemisia* sp.); b – unidentified adult cecidomyid fly; c – unidentified cecidomyid fly laying eggs on grass.
Photos: a – Frost Entomological Museum CC-BY-2.0; b – MJ Hatfield CC-BY-ND-NC-1.0; c – Sarefo CC-BY-SA-4.0

Several cecidomyiid species have the unusual ability to reproduce through a process termed *paedogenesis*, whereby immature stages produce offspring (Wyatt 1960; Wyatt 1961). Under optimal conditions, larva or pupa develop functional ovaries that produce larvae. These larvae develop inside of the "mother" larvae or pupae, feeding on her tissues and then emerging from her body. Under suboptimal conditions, the larvae complete a normal metamorphosis, passing through a pupal stage and then emerging as an adult able to fly to a new location with more favourable conditions (Fig. 19).

A total of 243 species are known from Canada (Savage et al. 2019), but Hebert et al. (2016) estimates the Canadian fauna may be closer to 16,000 species. A key for genus-level identifications is provided by Gagne (1981).

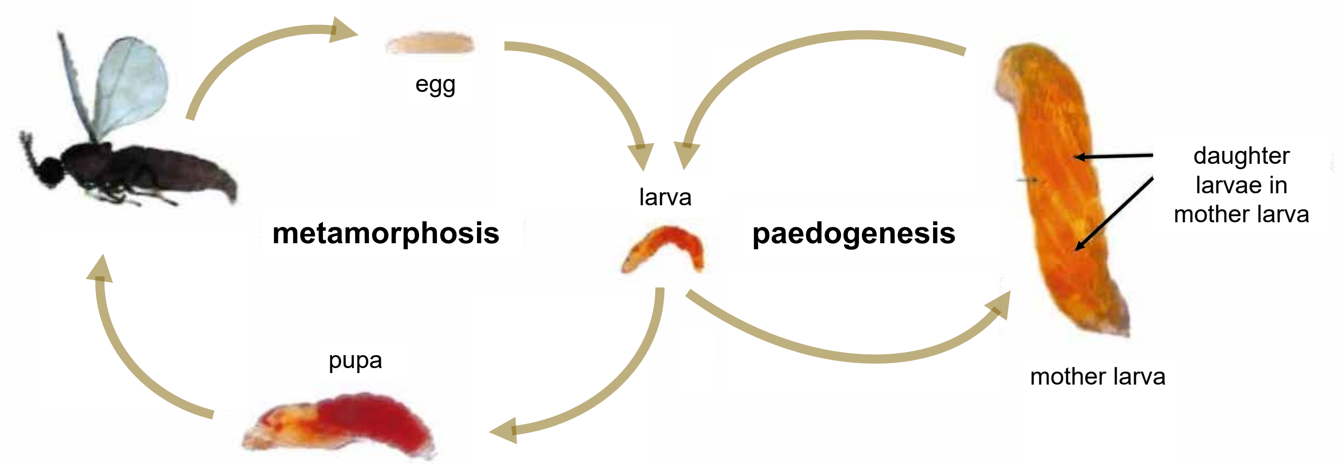


Figure 19. The cecidomyid fly, *Mycophila speyeri*, can reproduce by complete metamorphosis (egg-larva-pupa-adult) or by paedogenesis (larva-larva). Image modified by the author from an original drawing by Jason Hodin appearing in Hodin and Riddiford (2000).

Ceratopogonidae (biting midges, punkies, no-see-ums)

Ceratopogonids are small flies (generally 1–3 mm in length) that are slender to moderately robust in shape. The antennae are long and threadlike. The antennae of males are covered with fine filaments, which gives the antennae a feathery appearance. The feathery antennae for males of certain nematoceran species helps them locate females for mating. Wings may be strongly patterned and are held overlapping one another and flat over the back when adults are at rest (Fig. 20a). Adults are often found near the larval breeding habitat.

Ceratopogonids breed in wet or moist habitats that may include moss, accumulations of rotting organic material, under bark, wet soil, and pools of water. The larvae of some species are predacious, whereas those of other species feed on fungi, algae or plant debris. Adult males and females visit flowers to feed on nectar, but the females of many species also require protein to mature their eggs. Depending upon the species, this protein is obtained by taking blood meals from insects or vertebrates. Bites can be painful and can transmit the causative agents (e.g., nematodes, protozoa, viruses) of diseases that affect people and other animals (Linley 1985). Bluetongue virus (BTV) is a disease of ruminants that is vectored by certain species of *Culicoides*. It is of particular concern in sheep where it can cause high levels of mortality (Mullen and Murphree 2019).

A total of 263 species are known from Canada, but an estimated 300 additional species may be present (Savage et al. 2019). Ceratopogonids that are reported to breed in cattle dung include *Forcipomyia brevipennis* and *F. bipunctata*, plus two species of *Culicoides* (Macqueen and Beirne 1975b; Skidmore 1991). None of these species are known to attack people (Skidmore 1991). The body and wings of *Forcipomyia* species are usually densely covered with tiny black hairs; the body of *Culicoides* species is much less hairy and the wings are almost clear. A key for genus-level identifications is provided by Downes and Wirth (1981).

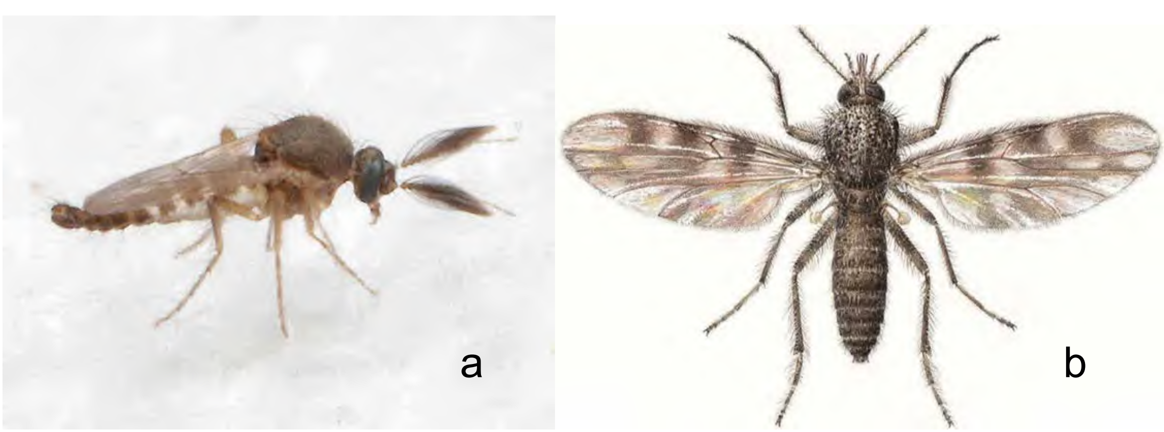


Figure 20. Ceratopogonidae. a – *Forcipomyia* sp. (♂) – note the feathery appearance of the antennae (© Ken Childs); b – *Culicoides* sp. (♀) (Siama et al. 2017, CC-BY 3.0)

Chironomidae (midges)

Adult chironomids are delicate, small to medium sized flies (1–10 mm in length) with long slender legs of which the first pair are often the longest. Wings are narrow, whitish in colour and, at rest, are positioned flat or form a peak over the abdomen. The antennae are long and threadlike; those of males are covered with fine filaments to give their antennae a feathery appearance. Chironomids do not have biting mouthparts and are sometimes called non-biting midges. At rest, adults typically hold their first pair of legs stretched out in front of the head and upwards. Swarms of males are commonly seen at dusk, often positioned over some type of marker; e.g. a fence post or bush. Females are attracted to these swarms to mate.

Chironomids breed in nearly every type of wet or moist habitat, including standing water, soil, sewage and dung. Larvae are typically detritivores, but may feed on small plants or are carnivores. Some species have haemoglobin (the same molecule in human blood) that allows them to survive in oxygen-poor environments. The distinctive red colour of these larvae give rise to their common name *bloodworms*. Chironomids are important sources of food for insects, birds, and fish and are often studied as bioindicators of environmental pollution.

Figure 21. Chironomid larva (B. Schoenmakers – CC-BY-3.0).

A total of 798 species are known from Canada, but an estimated 1,000 species remain to be reported or described (Savage et al. 2019). Species associated with cattle dung include *Camptocladius stercorarius*, *Krenosmittia* sp., *Mesosmittia flexuella* and *Smittia* spp. (Floate 1998b; Skidmore 1991). All of these species are members of subfamily Orthocladiinae and are similar in appearance with a wing length of 1.5–2.5 mm. A key for genus-level identifications is provided by Oliver (1981).

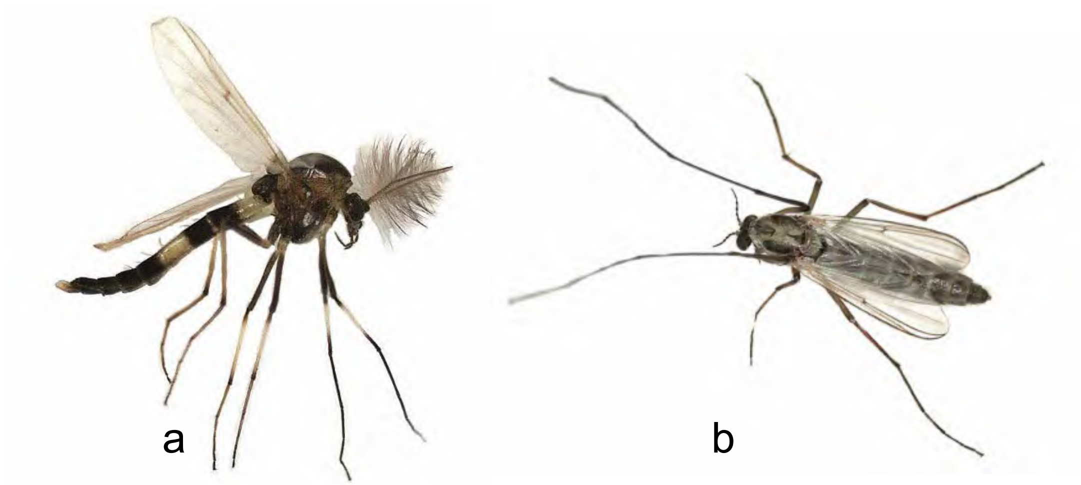


Figure 22. Chironomidae. a – *Cricotopus bicinctus* (♂) – note the feathery appearance of the antennae (B. Schoenmakers – CC-BY-3.0); b – *Chironomus* sp. (♀) (B. Schoenmakers – CC-BY-3.0).

Psychodidae (moth flies, sand flies)

Adult psychodids are tiny to small flies (< 5 mm in length) with short bodies covered by a thick coat of hairs. The antennae are long and threadlike. The wings are typically broad and are laid flat or form a peak over the abdomen when the adults are at rest. Their hairy appearance and wing shape gives rise to the common name of *moth flies*. Wing venation consists mainly of a series of parallel veins; crossveins are absent or restricted to the basal half of the wing. Adults tend to be nocturnal and rest during the day in shaded habitats. The pattern of flight is characteristically short and erratic.

Psychodids breed in moist habitats (e.g., decaying vegetation, mud, dung) and feed on organic matter including bacteria. Species that breed in sewer drains are commonly called *drain flies* or *sewer gnats*. Only a few species of psychodids are pest species. Cases of psychodid larvae infesting humans are occasionally reported (Hyun et al. 2004; Rasti et al. 2016). Species in subfamily Phlebotominae breed in soil, often in semi-desert regions and are called *sand flies*. Sand flies are the only species of psychodids with biting mouthparts; females take blood meals and can vector causative agents of diseases that affect humans; e.g. leishmaniasis.

There are 34 species known from Canada, with perhaps a further 10–50 species yet to be described or reported (Savage et al. 2019). Taxa reported to breed in dung include species of *Pericoma* and *Psychoda* (subfamily Psychodinae) (Skidmore 1991). *Psychoda* larvae can be among the most abundant insects in cattle dung (Laurence 1954), but are often overlooked because of their small size. A key for genus-level identifications is provided by Quate and Vockeroth (1981).

Figure 23. *Psychoda* sp. (© Nick Block)

Scatopsidae (minute black scavenger flies)

Scatopsids are tiny to small flies (0.5–4 mm in length) with stout oblong bodies. They are usually blackish in colour, but may range from brown to black, and may include some yellow. The antennae are threadlike, but relatively short. Wing venation is somewhat reduced; veins near the front margin are conspicuous, with the remaining veins much less evident.

Scatopsids breed in rotting plant and animal material. *Coboldia* (*Scatops*) *fuscipes* has been reported as a nuisance pest when present in large numbers at wineries and canneries (Meade and Cook 1961). Scatopsids are otherwise of no known economic importance.

There are 30 species known from Canada, with an estimated 15–20 species yet to be recorded or described (Savage et al. 2019). Scatopsids associated with dung include species of *Anapausis*, *Coboldia*, *Cookella*, *Reichertella* and *Scatopse* (Laurence 1954; Skidmore 1991). A key to identify scatopsid genera is provided by Cook (1981).

Figure 24. Scatopsid fly (© John Maxwell)

Sciaridae (dark-winged fungus gnats)

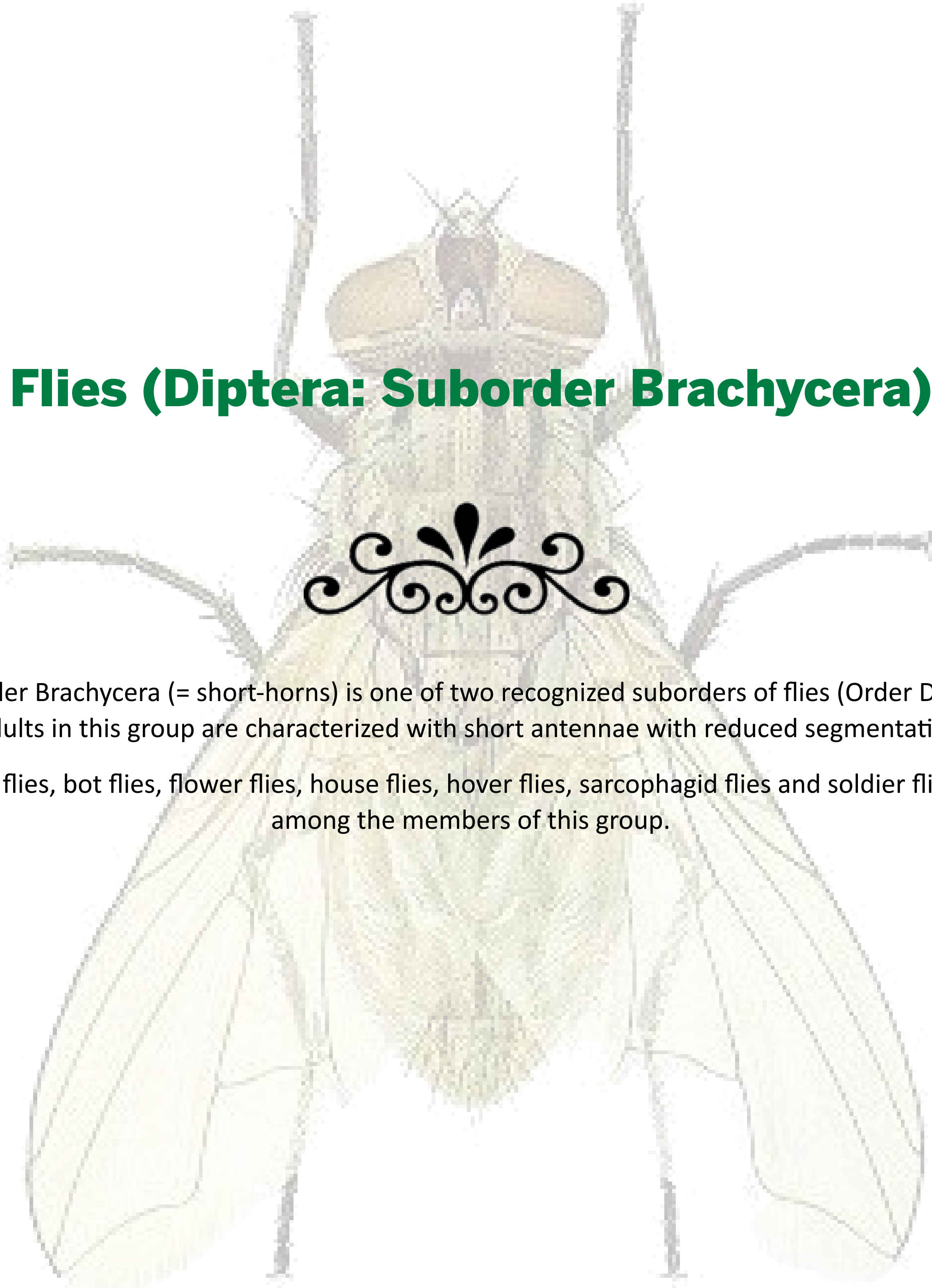
Adult sciarids are tiny to medium-sized flies (1–11 mm in length) with long legs and threadlike antennae. The head has three simple eyes (ocelli) with the two compound eyes connected, or nearly so, above the base of the antennae. The colour of the body and wings is dark, ranging from yellowish to blackish. Adults are short-lived and do not bite.

Sciarids breed in moist shady habitats where they feed on fungus, dung and decaying plant material. They are common in the soil of potted plants with adults emerging indoors to become nuisance pests when present in large numbers. Larvae of *Bradysia* spp. feed on rotting organic matter and fungus, but also on the healthy tissues of young plants; they are common pests in greenhouses and mushroom farms (Cloyd 2015). Larvae of *Sciara* spp. form aggregations that migrate over land. Termed *snake-worms*, these aggregations can extend for more than one-third of a meter with a width of 1–2 cm (Brues 1951).

Savage et al. (2019) reports 129 described species of sciarids in Canada with an estimated 100–200 additional species present. Large numbers have been reported in cow dung, particular dung in an advanced stage of decomposition. However, it is unknown if any species breed solely in dung. A key for genus-level identifications is provided by Steffan (1981)

Figure 25. Scatopsid fly **–** male (left) and female (right) *Odontosciara nigra* (© Matt Bertone).

Figure 26. Snake-worm of migrating sciarid larvae (*Sciara* sp.) (© Derek Sikes).



Flies (Diptera: Suborder Brachycera)

Suborder Brachycera (= short-horns) is one of two recognized suborders of flies (Order Diptera). Adults in this group are characterized with short antennae with reduced segmentation.

Blow flies, bot flies, flower flies, house flies, hover flies, sarcophagid flies and soldier flies are among the members of this group.

Anthomyiidae (flower-flies)

In size (2–12 mm in length), colour and body shape, adult anthomyiids are reminiscent of house flies and other members of family Muscidae. They are non-metallic and drab; generally yellowish or brownish-grey to greyish-black in colour. They are active fliers, feed on nectar and are important as pollinators.

Anthomyiid larvae have diverse feeding habits. The larvae of some species feed on plants and are economically important as pests; e.g., *Delia antiqua* (onion maggot), *D. floralis* (turnip maggot) and *D. radicum* (cabbage maggot). The larvae of other species feed in dung or other decaying material. The larvae of species in dung can be classified into three groups based on their feeding habits: i) coprophagous; i.e., feed only on dung, ii) semi- or facultative carnivores; i.e., may feed only on dung, but will eat other insects if the opportunity arises, iii) obligate carnivores; i.e., need to eat other insects to survive (Thomson 1937).

A total of 515 species of anthomyiids have been reported for Canada; possibly 10–30 species are not yet described or recorded (Savage et al. 2019). Species associated with dung include members in the genera *Adia*, *Anthomyia*, *Eutrichota*, *Hylemya*, *Hylemyza*, *Lasiomma*, *Paregle* and *Pegoplata* (Griffiths 1997). A key for genus-level identifications is provided by Huckett (1987).

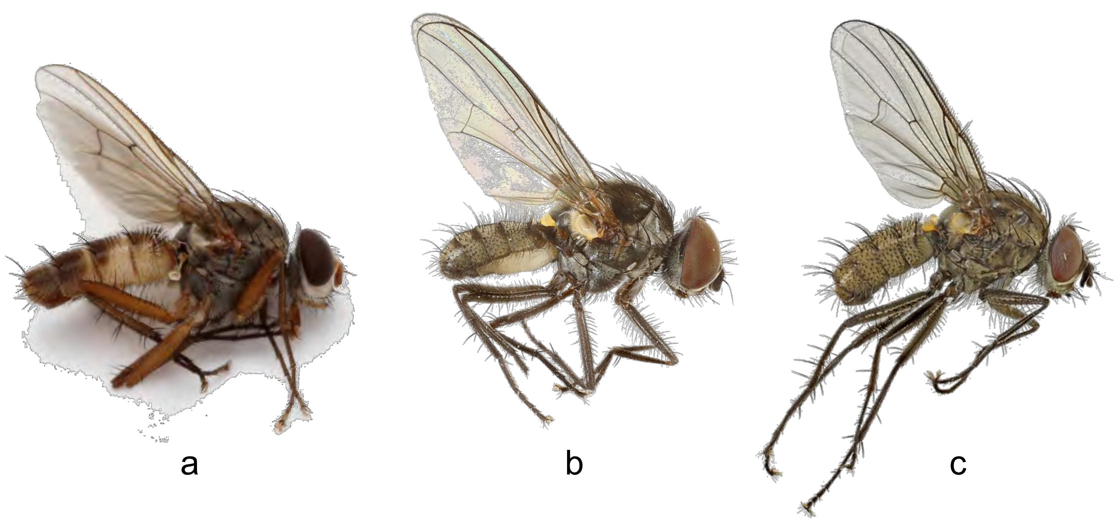


Figure 27. Anthomyiidae. a – *Eutrichota* sp. (♂) (© Dave Almquist); b – *Pegoplata patellans* (Janet Graham – CC-BY-2.0); c – *Hylemya variata* (© Matt Bertone).

Calliphoridae (blow flies)

These common flies are similar in shape to a house fly and about the same size or a bit larger (4–16 mm in length). Many species are metallic green or blue, including the common green bottle fly, *Lucilia sericata*. Other species may be shiny black or brass in colour. Adults will visit flowers and often rest on low foliage in bright sunlight. They are reminiscent of Sarcophagidae (flesh flies), but the latter are blackish with grey stripes on their thorax.

Adults are frequently seen on fresh dung or recovered in dung-baited pitfall traps, but they typically breed in carrion. Some species lay eggs in fresh lesions or on soiled wool around orifices of livestock where the larvae (termed screwworms) feed on healthy tissue to cause large wounds (myiasis). Larvae of bird blow flies (*Protocalliphora* spp.) develop in bird nests where they feed on the blood of nestlings. Larvae of cluster flies (*Pollenia* spp.) are parasitoids of earthworms; large numbers of adults will enter buildings in autumn and become nuisance pests. Many calliphorid species are of interest to forensic entomologists for use in death investigations. Tomberlin et al. (2016) review the literature on blow flies with a specific emphasis on their interactions with different types of bacteria.

A total of 62 and 93 species of calliphorids are reported for Canada (Savage et al. 2019) and North America (Jones et al. 2019), respectively. A key for genus-level identifications is provided by Jones et al. (2019), who also includes information allowing for identification of 41 species of possible forensic importance.

Figure 28. Calliphoridae. a – *Lucilia sericata* (© Salvador Vitanza); b – *Calliphora vomitoria* (© Blake Layton, Mississippi State University Extension).

Chloropidae (grass flies, frit flies)

Chloropids are tiny to small flies (1.5–5 mm in length). The body is generally yellow and black in colour; the virtual absence of hairs gives it a shiny appearance. The head usually has a prominent plate-like triangle pointing downwards from between the eyes. Because of their abundance on grasslands, adults are often seen sitting on cattle dung or are recovered in dung-baited pitfall traps.

The diversity of larvae and their feeding habits is reviewed by Nartshuk (2014). Most species are phytophagous and develop in grasses. Some of these species are economically important pests of cereal crops and turf grass. A few species form galls, whereas others are predators of insects. A number of species develop in fungi or rotting organic matter. Species of *Elachiptera*, *Hippelates* and *Liophippelates* develop in decomposing dung (Nartshuk 2014); *Siphunculina aenea* develops in fresh bear scat (Kanmiya 1982).

In Canada, 140 species are known with an estimated 260 species remaining to be described or reported (Savage et al. 2019). Few, if any, of these species breed in fresh cattle dung. A key provided by Sabrosky (1987a) can be used for genus-level identifications.

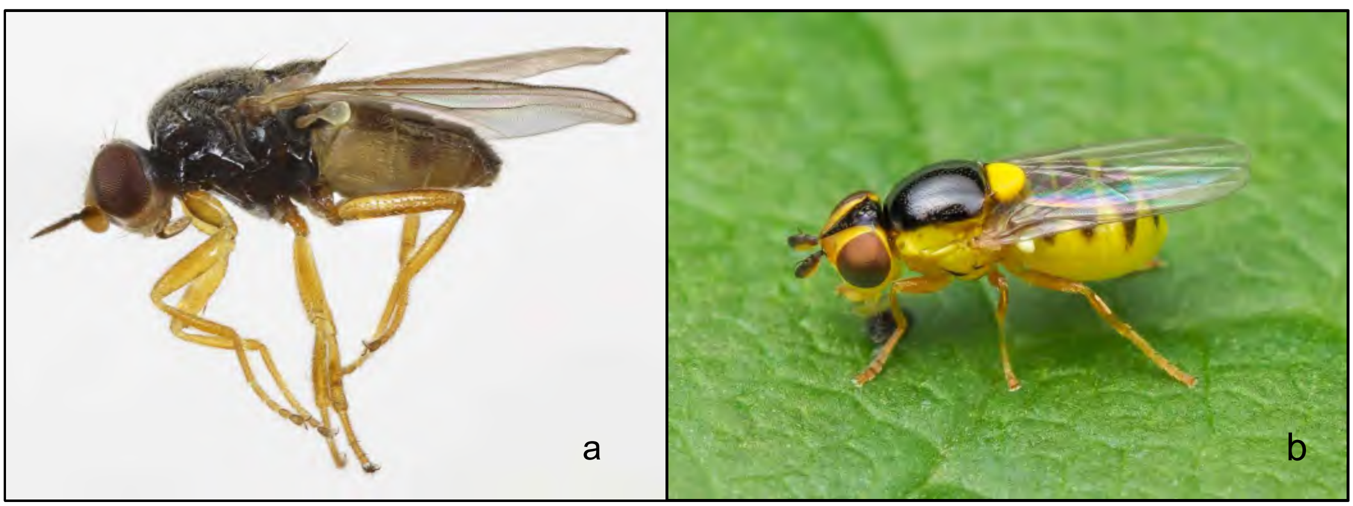


Figure 29. Chloropidae. a – *Elachiptera tuberculifera* (© Janet Graham – CC-BY-2.0); b – *Thaumatomyia* sp. (© C. Perkins).

Empidoidea (dagger flies, balloon flies, dance flies)
(Empididae – dagger flies, balloon flies; Hybotidae – dance flies)

Hybotinae previously was recognized as a subfamily within family Empididae (Steyskal and Knutson 1981), but since been elevated to family Hybotidae (Sinclair and Cumming 2006). Both families are discussed here under the superfamily Empidoidea.

Empidoids are tiny to medium sized flies (1.5–12 mm in length). Their body shape tends to be elongate and cylindrical, but is short in some genera; e.g., *Crossopalpus* and *Drapetis*. Body colouration is usually dark, occasionally yellowish or light brown; none of the North American species are metallic. Adults are predaceous or visit flowers to feed on nectar and pollen. Legs are slender and may be thickened or otherwise modified to help capture prey.

Many empidoids have highly ritualized mating behaviours. Adults of some species form mating swarms within which their synchronized movements give rise to the common name *dance flies*. Within Empididae, males of certain species will present females with nuptial gifts consisting of prey, inedible objects, or balloons of silk or froth to attract their attention. The latter behaviour is the source of the common name *balloon flies*. Species in several genera of Empididae have long and strong piercing mouthparts, which gives rise to their other common name *dagger flies* (see image of *Empis trigramma* below).

Larvae breed in habitats that range from aquatic to terrestrial. Females of most species lay eggs. The eggs of *Ocydromia glabricula* (Hybotidae) hatch within the body of the female and are deposited as larvae on dung; a phenomenon termed *larviposition*. Larvae are predators. Steyskal and Knutson (1981) report that the larvae of a few species have been reared from dung, but do not specify the genera. Skidmore (1991) and Laurence (1954), respectively, identify *Empis trigramma* (Empididae) and *Drapetis* spp. (Hybotidae) as empidoids that breed in cattle dung.

In Canada, 251 species of Empididae are known with perhaps a further 200 species yet to be described or reported (Savage et al. 2019). Canada's insect fauna also includes 155 reported species of Hybotidae, with an estimated 200 further species to be reported. The key provided by Steyskal and Knutson (1981) allows for genus-level identifications.

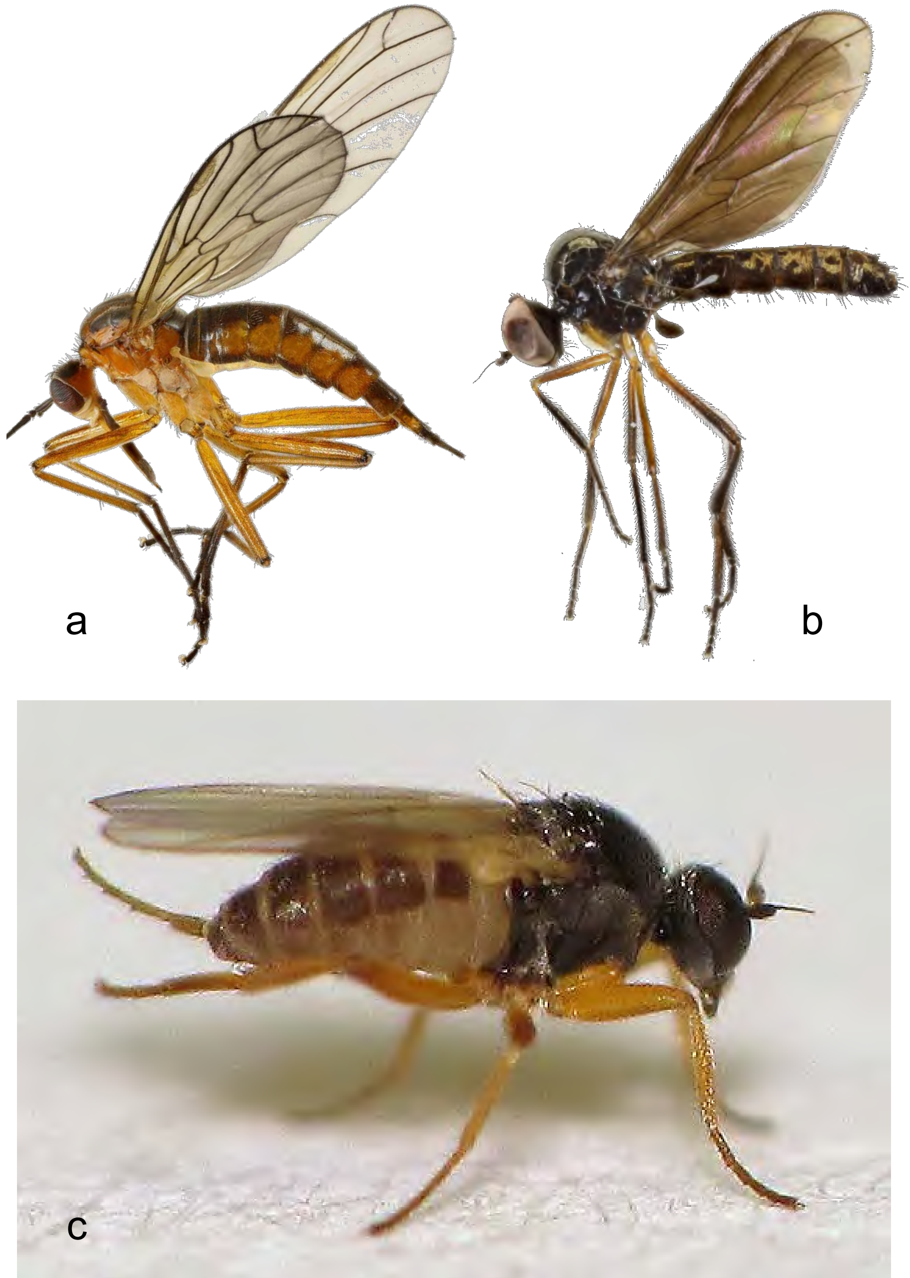


Figure 30. Empidoidea. a – *Empis trigramma* (Empididae) (Janet Graham – CC-BY-2.0); b – *Ocydromia glabricula* (Hybotidae) (Janet Graham – CC-BY-2.0); c – *Crossopalpus* sp. (Hybotidae) (© John Schneider).

Ephydridae (shore flies)

Ephydrids are tiny to medium sized (1–11 mm in length) flies with diverse body shapes and bristle patterns. Body colour is generally dull and dark. Wings of some species are patterned. Adults of *Ochthera* spp. are predators and have swollen forelegs that help them capture small insects (Fig. 31b). Adult shore flies occur in large swarms along the shores of maritime marshes, salt water tidal pools, or along the shores of highly alkaline or salt lakes. They are important sources of food for many insects and animals, in particular, waterfowl.

The larvae of most species breed in semi-aquatic or aquatic habitats and feed on microorganisms. The larvae of some species are predacious or mine within the leaves and stems of various plants. *Hydrellia griseola* is an economic pest of rice (Grigarick 1959), whereas other *Hydrellia* species are being studied as biological control agents of invasive aquatic weeds (Purcell et al. 2019). A number of ephydrid species develop in brackish, saline or alkaline waters, with some species exhibiting a remarkable ability to thrive in extreme environments. *Ephydra brucei* and *Paracoeni* sp. develop in hot springs with water temperatures of 30–45°C (Brock et al. 1969). *Helaeomyia petrolei* (formerly *Psilopa petrolii*) breeds in pools of crude petroleum (Thorpe 1930).

There are 197 species of ephydrids known from Canada, with an estimated 10–15 additional species not yet recorded (Savage et al. 2019). No species are reported to breed in dung, but many species of *Hydrellia* species develop in the stems of grasses and can be among the most abundant insects on pastures (Skidmore 1991). Because of this abundance, adults are often seen resting on cattle dung or are recovered in dung-baited pitfall traps. Wirth et al. (1987) can be used to identify species to genus.

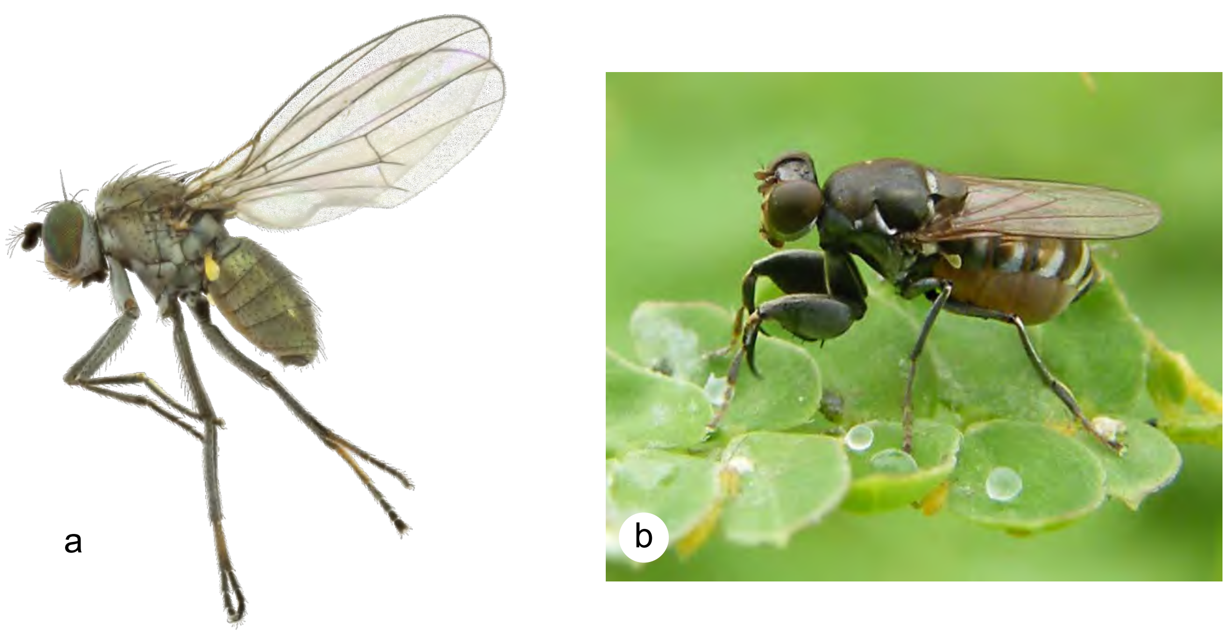


Figure 31. Ephydridae. a – *Hydrellia maura* (Janet Graham – CC-BY-2.0); b – *Ochthera* sp. (Ian Jacobs – CC-BY-NC-2.0).

Milichiidae (milichiid flies)

Milichiids are small inconspicuous flies 1–5 mm in length. They typically have red eyes, dull black body colouration, and a dense layer of tiny hairs on the dorsal surface of the thorax. Depending upon species, their sucking mouthpart or *proboscis* may be short, or long and quite evident. The wings are clear with easily discernible venation.

Milichiid flies breed in rotting organic material, including decaying fruit, compost, manure and dung. Some species develop in fungal gardens maintained by certain species of ants. Adults often visit flowers and may be kleptoparasites; i.e., they stay in close contact with spiders and predatory insects to feed on fluids oozing from prey items (Fig. 32a). Because of this behaviour, members of this group are sometimes called *freeloader flies*.

Members of this group have only infrequently been identified as associates of cattle dung. Coffey (1966) reared large numbers of *Madiza glabra* and *Meoneura prima* (formerly *Meoneura seducta*) from swine dung and chicken manure; smaller numbers of these two species and individual specimens of *Desmometopa sordida* and *Hemeromyia washingtona* were collected on cattle dung. *Meoneura polita* was recorded by Poorbaugh et al. (1968) with cattle dung in California.

Thirteen species of milichiids are known from Canada, with perhaps another 20–30 species remaining to be recorded (Savage et al. 2019). Sabrosky (1987b) provides a key to genera.

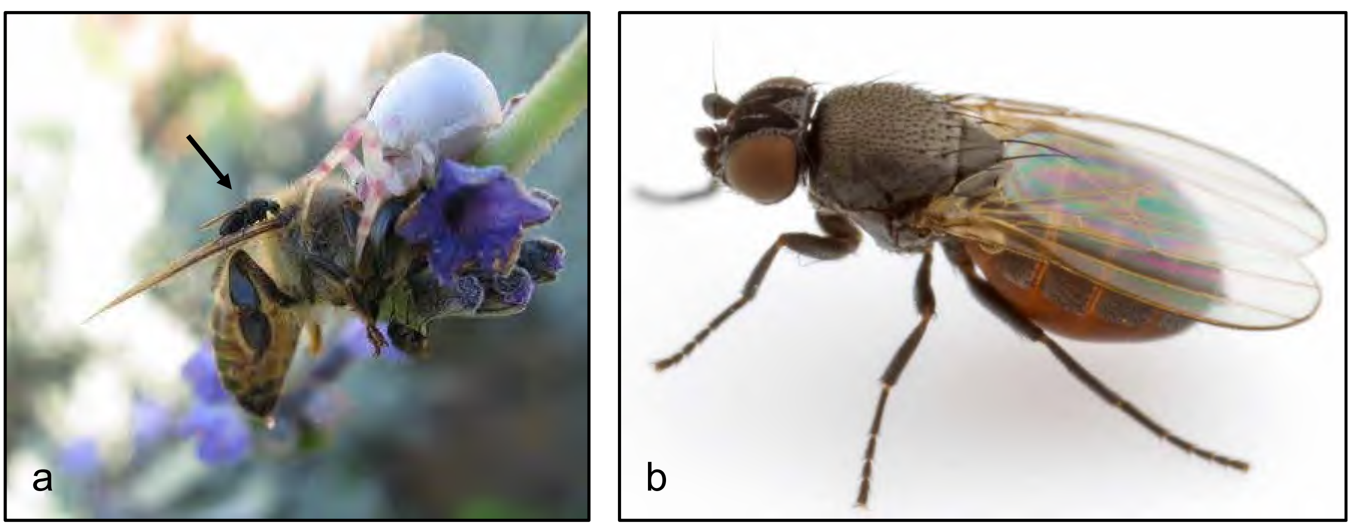


Figure 32. Milichiidae. a – Milichiid (see arrow) waiting to feed on the fluids of a bee killed by a spider (Jon Richfield – CC-BY-3.0); b – *Desmometopa* sp. (© Salvador Vitanza).

Muscidae (muscid flies)

The convention of Huckett and Vockeroth (1987) is followed here, who include Fanniinae as a subfamily within family Muscidae. However, McAlpine (1989) advocated for the elevation of Fanniinae to family Fanniidae, which is now the general convention.

Adult muscids are common flies with slender to robust bodies (2–14 mm in length) that often have long, distinct large bristles. The body colour is usually dull black or grey, but some muscids may be yellowish or bright metallic green or blue. The legs tend to be slender. Wings have well-developed venation and rarely have markings.

The larvae of most species are coprophagous or saprophagous, but some species are obligatory or facultative predators on the immature stages of other insects. Breeding habitat includes dung, rotting vegetation, fungi, bird and insect nests, carrion, and soil. *Filth-breeding* flies or *filth flies* is the common term for species that breed in rotting accumulations of feed, manure, and straw in livestock confinements; e.g., feedlots, dairies, swine barns, poultry houses. Few species appear to develop in living plant tissues. Depending upon the species, adults may feed on the exudation of vertebrates (especially large mammals), on blood or pollen, are predaceous on other insects, or feed on microorganisms in rotting vegetation and in dung.

Among the families of coprophagous Diptera, muscids have received by far the greatest amount of attention. This is partially because they are common and diverse in dung, but mainly because some species of dung- and filth-breeding *Haematobia*, *Musca* and *Stomoxys* are global pests of livestock. In North America, this list includes horn fly (*Haematobia irritans*) (Fig. 33h), stable fly (*Stomoxys calcitrans*) (Fig. 33i), face fly (*Musca autumnalis*) (Fig. 33a) and house fly (*Musca domestica*) (Fig. 33f). Horn fly and stable fly feed on the blood of vertebrates. Horn fly generally only attack cattle, whereas stable fly attack cattle, horses, people, dogs and swine. Both species deliver painful bites that interrupt feeding of the hosts and trigger avoidance behaviour that reduces weight gains in beef cattle and milk production in dairy cattle. Face fly do not bite, but feed on exudations near the mouth, eyes and nostrils of the host animal. They transmit the causative agent for pinkeye (infectious bovine keratoconjunctivitis) to cattle, and the eyeworm nematode *Thelazia rhodesi* to cattle and horses. They also overwinter as adults. In rural areas close to pastured animals, large numbers of face flies can enter buildings in late autumn to become nuisance pests. House fly also do not bite, but are nuisance pests and can vector the causative agents of anthrax, dysentery, and typhoid. Details on the biologies of face fly, horn fly and stable fly are provided by Lysyk (2011).

There are 524 species of muscids (including 84 species of Fanniinae) known from Canada; an estimated 48–50 species (including 8–10 species of Faniinae) remain to be recorded (Savage et al. 2019). Muscids reported in association with cattle dung in the northern hemisphere include species of *Azelia*, *Drymeia*, *Eudasyphora*, *Haematobia*, *Haematobosca*, *Hebecnema, Helina, Hydrotaea* (formerly *Ophyra*), *Mesembrina, Morellia, Musca, Mydaea, Myospila, Neomyia* and *Polietes* (Cervenka and Moon 1991; Hammer 1941; Skidmore 1991). Macqueen and Beirne (1974)'s list of muscids from cattle dung in British Columbia includes *Orthellia caesarion* (now recognized as *Neomyia cornicina*) (Fig. 33c) and *Pyrellia cyanicolor* (now recognized as *Eudasyphora cyanicolor*) (Fig. 33j). Huckett and Vockeroth (1987) can be used for genus-level identifications.

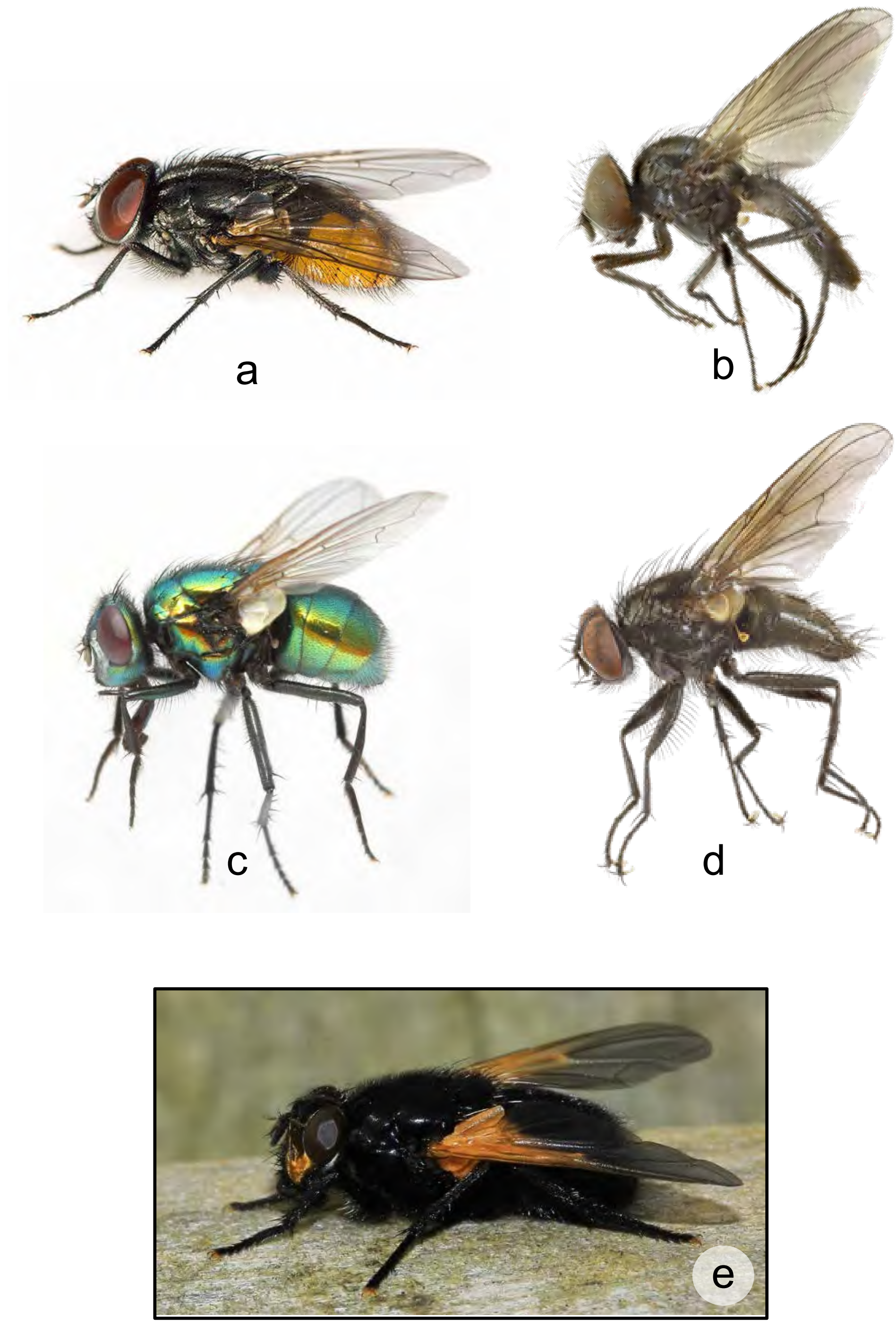
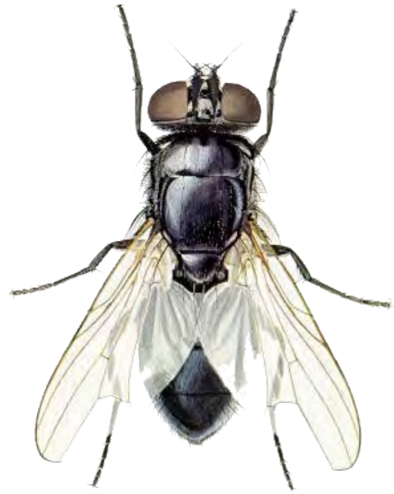


Figure 33. Figure 33. Muscidae. a – *Musca autumnalis* (Scott T. Smith / ScottSmithPhoto.com); b – *Fannia* sp. (Janet Graham – CC-BY-2.0); c – *Neomyia cornicina* (© J. Kahanpää); d – *Myospila meditabunda* (Janet Graham – CC-BY-2.0); e – *Mesembrina meridian* (© Richard Collier); f - *Musca domestica*; g - *Hydrotaea aenescens*; h - *Haematobia irritans*; i - *Stomoxys calcitrans* (image credit for f-i: illustrations by F. Gregor in Greenberg (1971), reprinted with permission of Princeton University Press); j – *Eudasyphora cyanicolor* (© Steve Scholnick).


f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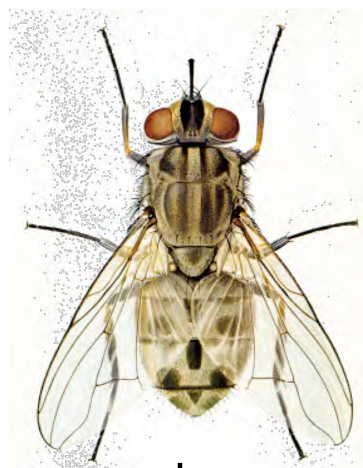
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Oestridae (bot flies, warble flies)

The convention of Wood (1987) is followed here, in which Cuterebrinae, Gasterophilinae, Hypodermatinae and Oestrinae are recognized as subfamilies within order Oestridae. Other publications may have placed these subfamilies in different orders or elevated them to the status of family; e.g., Gastrophilinae as Gastrophilidae (Skidmore 1991).

Oestrids are medium-sized to very large (9–25 mm in length) flies with a stout and hairy appearance reminiscent of bumble bees. The head is typically broad and flattened, with short antennae and small, non-functional mouthparts. The thorax and abdomen are covered with hairs; legs are short, stout and also hairy.

Larvae are obligate endoparasites of mammals; i.e., they develop inside the body of their host. Females typically oviposit or larviposit on the host animal. The larvae then enters the host, completes development, and then exits the host to pupate in the soil. For some species, the larvae enter through the nose and develop in the nasal cavity (nose bots). For other species, the larvae are ingested and develop in the gastrointestinal tract (stomach bots). Of particular importance in the Northern Hemisphere are *Hypoderma bovis* and *H. lineatum*, which are parasites of cattle. Larvae penetrate through the skin of the host and migrate to the back where they develop in swellings or warbles just below the skin (warble flies, cattle grub). Infestations can affect the health of the animal and the damage caused by warbles can reduce the quality of the hide. The economic impact of *Hypoderma* species has diminished greatly since the introduction of avermectin parasiticides onto the market in the early 1980s (Scholl 1993). Detailed information on the biology of oestrids globally is provided by Colwell et al. (2006). Information for species affecting livestock in Canada is provided by Lysyk (2011). Although rarely encountered and not associated with dung, oestrids are included in this guide as members of the insect community intimately associated with cattle.

Seventeen species of oestrids occur in Canada (Savage et al. 2019). Wood (1987) provides a taxonomic key to genera.

Figure 34. Oestridae. a – *Cephenemyia* sp. (♂) (© Robyn Waayers); b – *Oestrus ovis* (© Dr. Cosmin-O. Manci).

Sarcophagidae (flesh flies)

Sarcophagids are robust flies of small to large size (2–18 mm in length). Their bodies are mostly dull grey (never metallic) in colour; the thorax typically bears longitudinal stripes. The abdomen may be marked with a pattern of checks, stripes or bands; it may be partially or completely red, particularly the terminal segments.

Sarcophagids do not lay eggs. Instead, the embryos develop within the body of the female and are deposited on suitable substrate as larvae; a phenomenon termed 'larvipositing'. Such substrates normally comprise some form of animal material. Many species are parasitoids and develop in the bodies of snails, insects, spiders and animals. Females in the genus *Wohlfahrtia* larviposit on healthy animals and human infants whereupon the larvae penetrate the skin to feed subcutaneously (cutaneous myiasis) (Haufe and Nelson 1957). Infestations of *Neobellieria* (formerly *Sarcophaga*) *citellivora* in Richardson's ground squirrels are often fatal to the host (Michener 1993) (Figure 35).

Many species of *Oxysarcodexia* and *Ravinia* develop in dung (Cervenka and Moon 1991; Macqueen and Beirne 1974; Mohr 1943; O'Hara et al. 2000). Blume (1985) also lists species of *Blaesoxipha*, *Boettcheria*, *Camptops, Helicobia, Metopia, Sarcodexia* and *Sarcophaga* as associated with dung. However, this association may reflect a reliance on grassland insects as hosts, rather than an indication that they breed in dung. *Blaesoxipha* spp. frequently parasitize grasshoppers, giving rise to their common name of grasshopper maggots (O'Hara et al. 2000; Smith 1958).

There are 135 species of sarcophagids known from Canada with an estimated 5–15 species that remain to recorded (Savage et al. 2019). Shewell (1987) provides a key to genera. Identification of *Ravinia* species can be done with Dahlem (1989). Pape (1996) provides an update of taxonomic revisions within Sarcophagidae.

Figure 35. Lethal myiasis in Richardson's ground squirrel caused by *Neobellieria citellivora* (© Gail Michener).

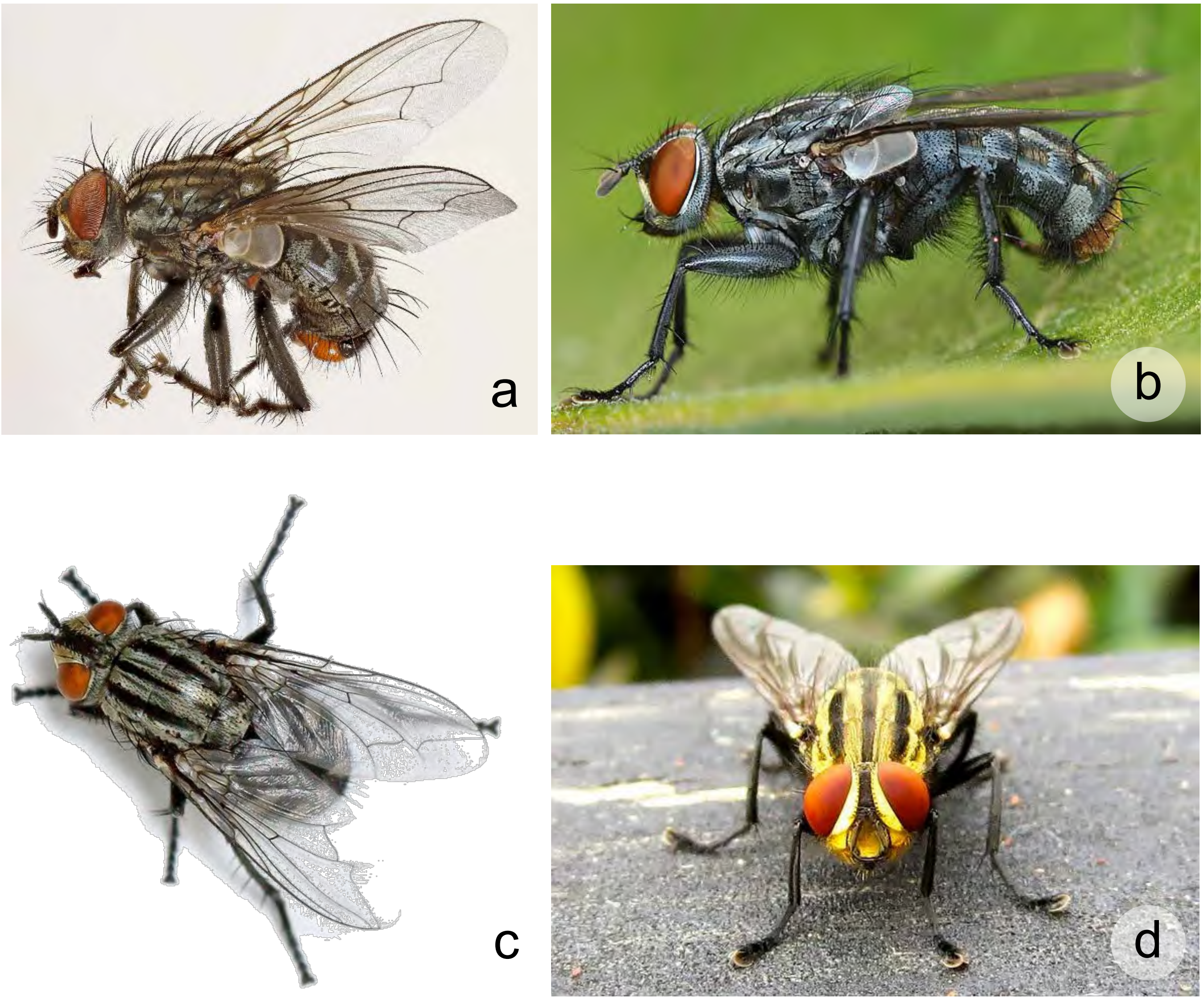


Figure 36. Sarcophagidae. a – *Sarcophaga vagans* (Janet Graham – CC-BY-2.0); b – unidentified species (Ryan Hodnett – CC-SA-4.0); c – *Sarcophaga carnaria* (© Marcello Consolo); d – *Sarcophaga aurifrons* (Geoff Shuetrim – CC-BY-2.0).

Scathophagidae (dung flies)

Scathophagidae is recognized in some publications as a subfamily within family Anthomyiidae or family Muscidae. The convention of Vockeroth (1987) is followed here, who elevates it to family status. The genus Scathophaga (formerly Scopeuma) occasionally appears in the literature as Scatophaga.

Scathophagids are small to large flies (3–11 mm in length) with slender legs. They have a slender body shape, with the apical end of the male abdomen strongly enlarged in some species. Bodies are typically yellow, brown, grey or black in colour and may be sparsely to thickly bristled; some species are densely covered in hair. Wings are usually clear, but may have patches of colour.

Depending upon the species, larvae develop in plants, rotting organic material or may be predators. Larvae of *Scathophaga* spp. breed in dung. Adults of all species are predators of other insects. The yellow dung fly, *Scathophaga stercoraria* (*stercorarium* in some literature), is locally abundant in many regions of the Northern Hemisphere. Males are typically furry and yellow. However, smaller males may appear more similar to females, which are greenish and bristly (not furry).

Figure 37. *Scathophaga stercoraria* – male (top) mating with female (© Conall McCaughey, www.flickr.com/people/conall).

Scathophaga stercoraria is perhaps the most widely studied of the non-pest coprophilous flies. It has been examined as a potential biological control agent for blow flies (Cotterell and Lefroy 1920) and is widely used as a model species to examine reproductive behaviour and ecological questions (Hosken et al. 2000; Jann and Ward 1999; Parker 1970; Parker 1971 – and see other references in Blanckenhorn et al. 2010). More recently, it has become a bioassay species used to assess the toxicity of insecticidal residues in dung of livestock treated with veterinary parasiticides (OECD 2008; Römbke et al. 2009; Strong and James 1992; Webb et al. 2007; West and Tracy 2009).

There are 126 scathophagid species recorded from Canada with an estimated 29 species yet to be recorded (Savage et al. 2019). Reports of scathophagids reared from cattle dung in Canada and the United States of America are limited to *Scathophaga furcata* (*furcatum* in some literature) and *S. stercoraria* (Cervenka and Moon 1991; Floate 1998b; Macqueen and Beirne 1974; Mohr 1943; Skidmore 1991). A key to genera is provided by Vockeroth (1987); keys to identify *Scathophaga* spp. are provided by Malloch (1935) and James (1950). A key to British species of Scathophagidae, nicely illustrated with drawings and photographs, is available online (Ball 2014).

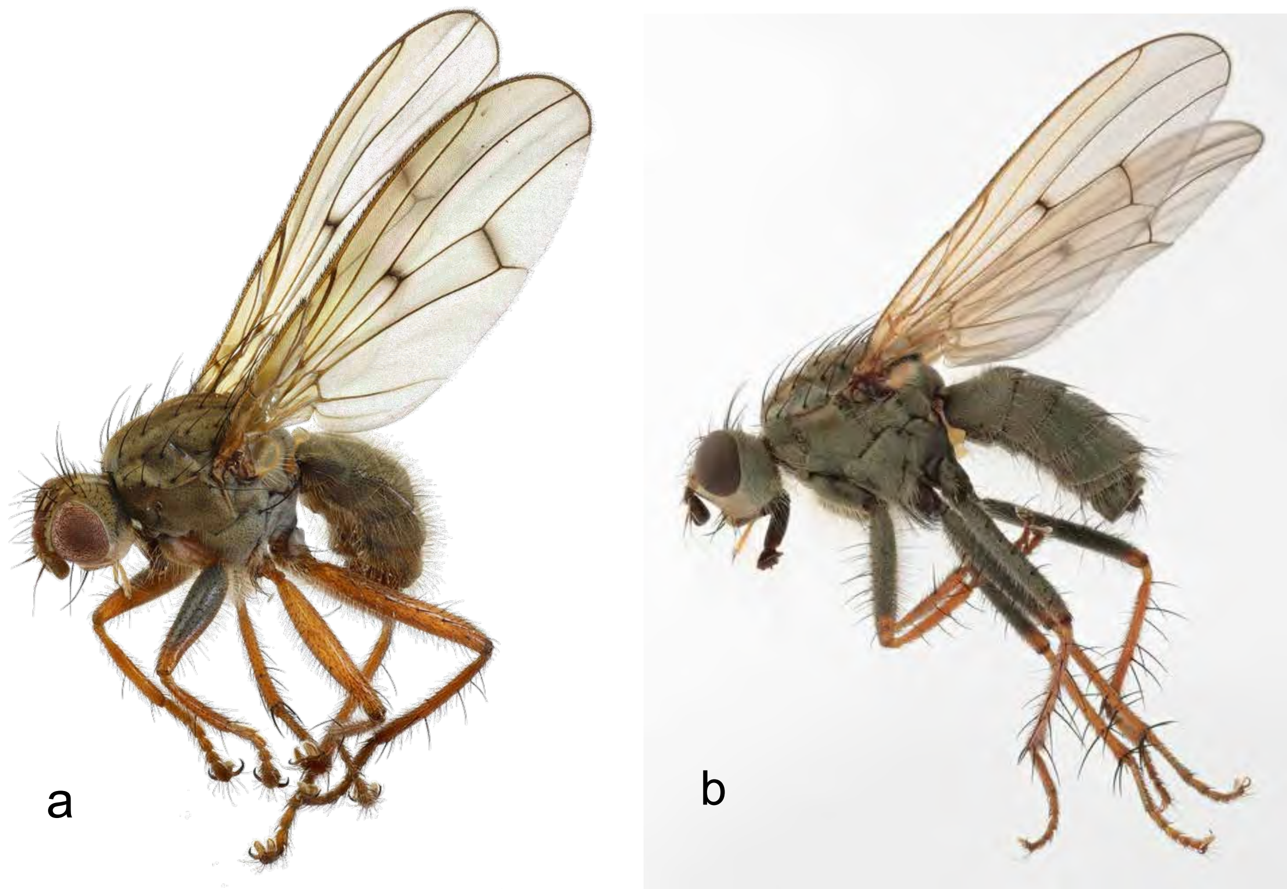


Figure 38. Scathophagidae. a – *Scathophaga furcata* (♂) (Janet Graham – CC-BY-2.0); b – *Scathophaga stercoraria* (♀) (© Malcolm Storey, www.discoverlife.org).

Sepsidae (black scavenger flies)

Sepsids are flies of small to medium size (2–6 mm in length). Colouration is typically purplish-black and metallic, but may be shades of yellow or brown and (or) dull. They have a somewhat ant-like shape with a round head, slender legs and a narrow waist. Wings tend to be narrow and clear, but often have a dark spot at the tip of each wing. Adults characteristically flick their wings outwards when walking about, a behaviour made more obvious by the spotted wing tips.

Although some species of sepsids breed in decaying plant or animal material, most species breed in dung. The biology of some of the dung-breeding sepsids is discussed by Hammer (1941). They are among the earliest arrivals to fresh dung, where large numbers of males wait along the periphery of the pat for the arrival of females towards which the males rush. Parker (1972) provides further detailed information on the mating strategies of *Sepsis cynipsea* and *S. punctum*. Pont and Meier (2002) provide a detailed overview on the morphology and natural history of European species of sepsids, including breeding substrates, parasitoids, and a key to species, much of which is relevant to the North American fauna.

There are 19 species of sepsids recorded for Canada with a further 5–10 species that may yet to be recorded (Savage et al. 2019). Species can be keyed to genera for North America using Steyskal (1987b) or for Europe using Pont and Meier (2002). Ozerov (2005) provides a world checklist of sepsid species with synonymies and updated genus/species names. The online digital reference collection Sepsidnet (https://sepsidnet.biodiversity.online/) can be used to help identify sepsid species of the world.

Dung-breeding species of sepsids recorded for North America include A*rchisepsis ecalcarata* (formerly *Sepsis insularis*), *Archisepsis pleuralis* (formerly *Sepsis pleuralis*), *Decachaetophora aeneipes, Saltella sphondylii* (syn. *scutellaris*), *Sepsis* (*biflexuosa, flavimana* (formerly *vicaria*), *luteipes, neocynipsea, punctum, secunda* (formerly *brunnipes*/*piceipes*), *violacea*), and *Themira putris* (Blume 1985; Cervenka and Moon 1991; Macqueen and Beirne 1974; Matheson 1987; Mohr 1943).

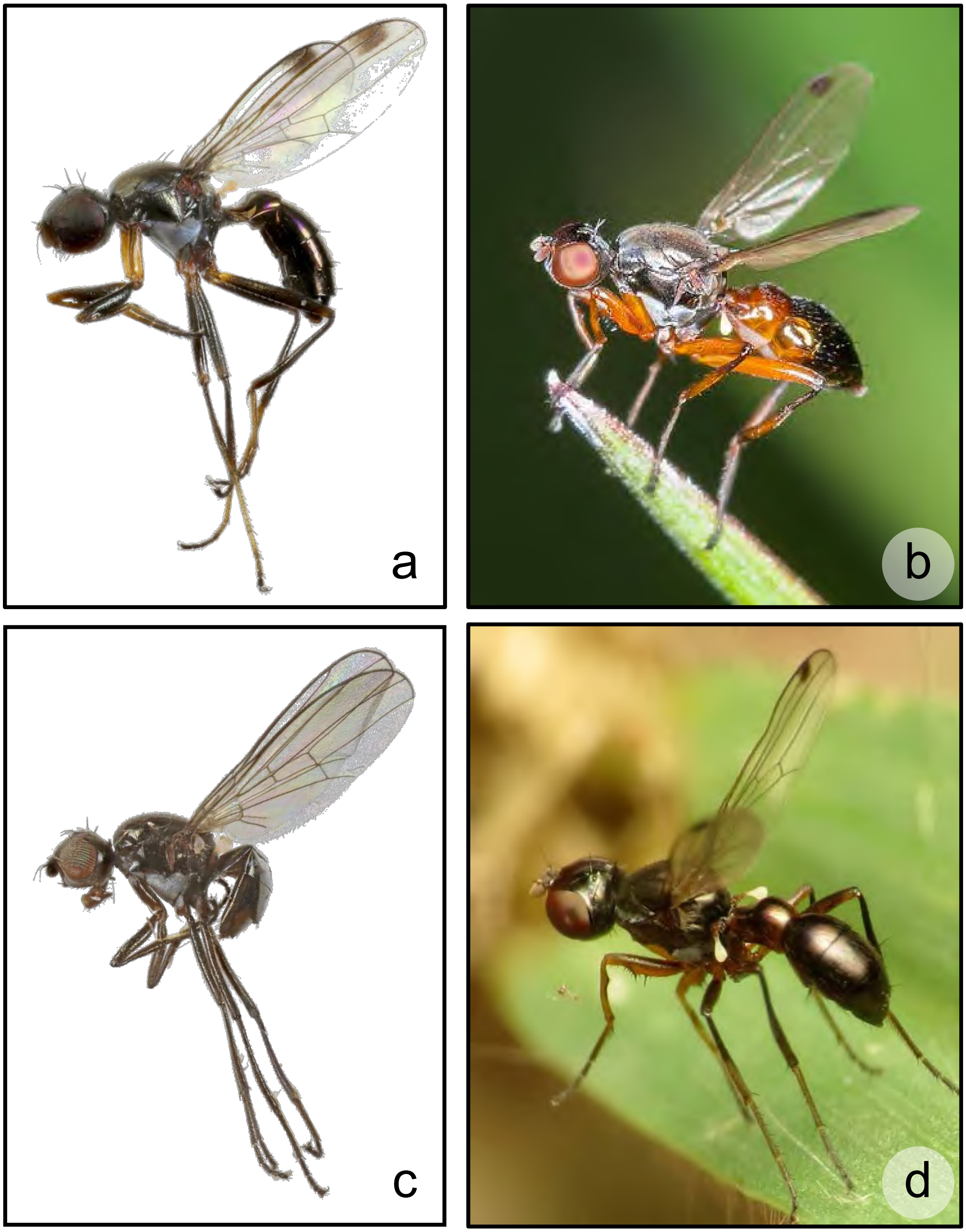


Figure 39. Sepsidae. a – *Sepsis cynipsea* (♂) (Janet Graham – CC-BY-2.0); b – *Sepsis punctum* (© Jessica Joachim); c – *Themira minor* (Janet Graham – CC-BY-2.0); d – *Sepsis neocynipsea* (© Katja Schulz – CC-BY).

Sphaeroceridae (small dung flies)

Sphaerocerids are tiny to small-sized flies (1–5 mm in length) with stout bodies. Typically black or dark brown, some species are brown or have yellowish legs and heads. The wings rarely have markings and may be reduced or lacking in some species. The first tarsomere on the hindleg of all species is characteristically short and thick (Fig. 40). The top of the thorax is usually covered with fine hairs, but occasionally with bumps.

Sphaerocerids breed in moist rotting organic material. Suitable habitats include fungi, carrion, compost, decaying vegetation, nests, burrows, dens, manure and dung. They are among the most common of the dung-breeding flies and are often seen scuttling on the surface of fresh pats, or entering into the pat via openings made by larger insects. Observations on the occurrence and seasonal activity of sphaerocerids associated with cattle dung are provided by Laurence (1955) and by Mohr (1943), the latter identifying them under the previous family name of Borboridae.

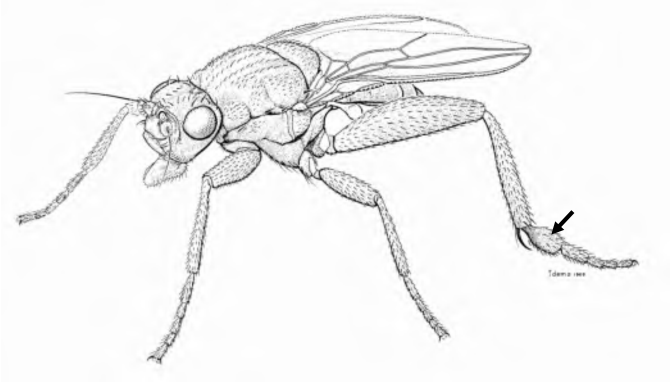


Figure 40. *Sphaerocera curvipes* with arrow indicating the first tarsomere of the hindleg (image from Marshall and Richards 1987).

No species appear to be of direct importance as pests of crops or livestock. However, they have been identified as vectors of pathogenic nematodes affecting commercial mushroom production (Haglund and Milne 1973). They are nuisance pests when present in large numbers in livestock confinements; e.g., feedlots and poultry houses. Fredeen and Taylor (1964) report infestations of sphaerocerids in schools and homes associated with large numbers breeding in septic tanks.

A total of 184 species of sphaerocerids are known from Canada with an estimated 20 species yet to be described or reported (Savage et al. 2019). Marshall and Richards (1987) provide a key for North American genera; Marshall and Buck (2010) can be used to identify most of the Canadian species of sphaerocerids. Several authors provide records of sphaerocerid species associated with dung in Canada and adjacent states (Blume 1985; Cervenka and Moon 1991; Floate 1998b; Matheson 1987). Updated taxonomic names for sphaerocerids globally are provided by Rohácek et al. (2002) and Marshall et al. (2011).

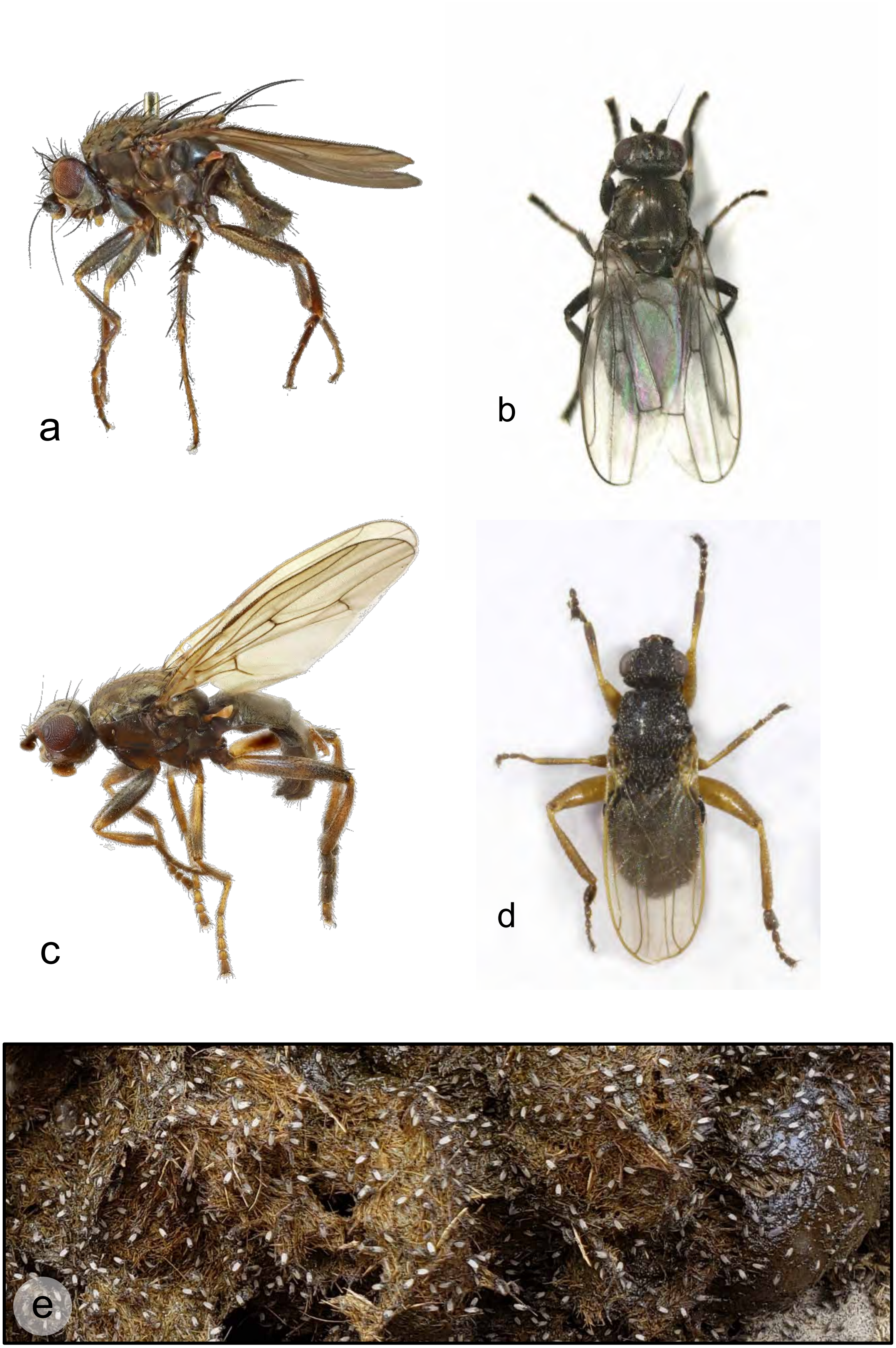


Figure 41. Sphaeroceridae. a – *Leptocera fontinalis* (♂) (Janet Graham – CC-BY-2.0); b – *Lotophila atra* (B. Schoenmakers – CC-BY-3.0); c – *Copromyza equina* (Janet Graham – CC-BY-2.0); d – *Ischiolepta denticulate* (Janet Graham – CC-BY-2.0); e – fresh horse dung covered with sphaerocerid flies appearing as white specks (KD Floate).

Stratiomyidae (soldier flies)

Stratiomyids are robust flies with a body length of 2–18 mm. Overall colouration may be black, blue, green or yellow and occasionally metallic; frequently with patches or streaks of colour on the abdomen. Some species are wasp or bee mimics. Wings are fully developed; legs do not have any unusual modifications. Adults of many species are attracted to flowers, but otherwise occur in association with the breeding habitat.

All stratiomyids that develop in dung in North America appear to be species of *Sargus* and *Microchrysa* (subfamily Sarginae) (McFadden 1972; Skidmore 1991). Members of this subfamily are readily distinguished from other stratiomyids by their metallic colouration and (or) elongate bodies. *Microchrysa* spp. have a relatively broad body shape (3–6 mm in length) with the abdomen shining black or the body completely metallic green. *Sargus* spp. have a relatively narrow body shape (6–12 mm in length) with an abdomen that is never shining black.

Figure 42. Stratiomyid larva (© Julian Smart).

Species in subfamily Stratiomyinae are aquatic; all other species are terrestrial and generally breed in rotting organic material. A small number of species are pests on plants or are predacious on other insects. Larvae have a flattened, leathery appearance with a long and conical head capsule. They are slow growing and are most often found in old dung. The black soldier fly, *Hermetia illucens* develops on a large variety of organic waste materials including poultry and swine manure. It has been the subject of extensive study as a biological agent to convert this material into larvae as a high quality protein source for use as livestock feed (Wang and Shelomi 2017).

A total of 114 species of stratiomyids are known from Canada with perhaps a further 5–10 species yet to be recorded (Savage et al. 2019). Species in North America reported from dung include *Microchrysa* (*flavicornis, polita*) and *Sargus* (*cuprarius, decoris, elegans, viridis*) (Blume 1985; Cervenka and Moon 1991; Coffey 1966; Macqueen and Beirne 1974; McFadden 1972). A report of *Nemotelus* spp. (subfamily Nemotelinae) associated with cattle dung (Blume 1970) is assumed here to be an artefact of the collecting method, and not an indication that this genus breeds in dung. A key to genera is provided by James (1981). McFadden (1972) can be used to identify species of *Sargus* and *Microchrysa* in Canada. Woodley (2001) provides a world catalogue with updated taxonomic revisions.

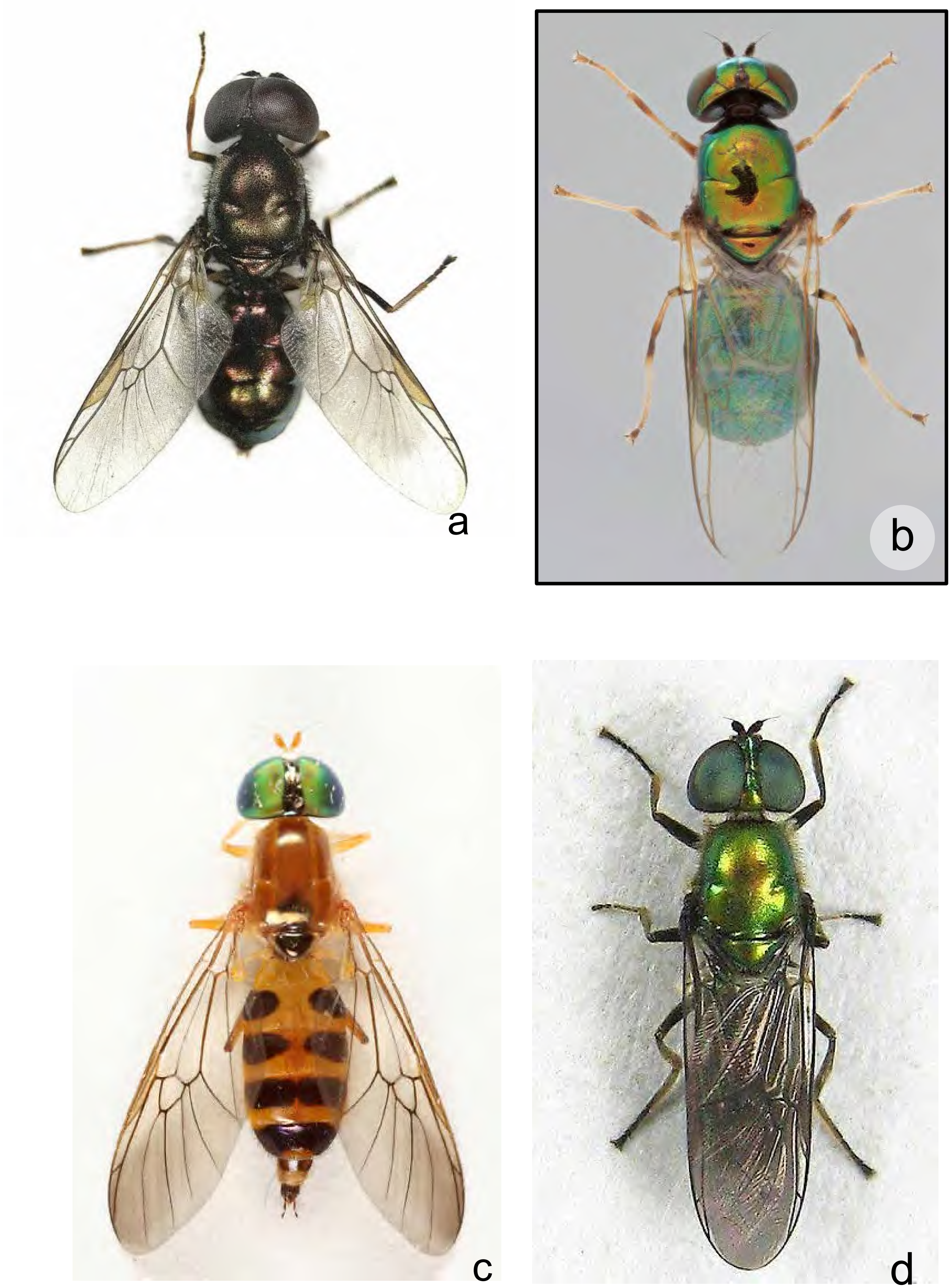


Figure 43. Stratiomyidae. a – *Microchrysa polita* (B. Schoenmakers – CC-BY-3.0); b – *Microchrysa flavicornis* (© Malcolm Storey, www.bioimages.org.uk – CC-BY-NC-SA-4.0); c – *Sargus elegans* (Tom Murray – CC-BY-ND-NC-1.0); d – *Sargus viridis* (Jim Moore – CC-BY-ND-NC 1.0).

Syrphidae (hover flies)

Syrphids are among the most numerous and conspicuous of flies. Adults range in size from 4–25 mm in length with slender to robust body shape. They are frequently seen hovering near flowers where they feed on nectar or pollen, giving rise to their common name. Typical colouration is black with yellow or orange markings; many species are excellent mimics of bees or wasps.

Larvae have diverse life histories. Depending upon the species, some larvae feed on aphids or other insects, some larvae feed within plants, and others live in waters with a high organic content. The larvae of *Rhingia*, *Syritta* and *Tropidia* develop in dung or similar rotting organic material (Vockeroth and Thompson 1987). However, none of these species are likely to be found in dung in Canada. *Rhingia campestris* is the only syrphid reported to breed in cattle dung in Britain (Skidmore 1991), but does not occur in North America. No syrphids are listed in Blume's (1985) list of insects associated with cattle dung in North America.

I mention this family mainly to inform readers of the drone fly, *Eristalis tenax*. This is a common syrphid with cosmopolitan distribution. The adults are similar in size (10–12 mm in length) and colouration to honey bees and are frequent visitors to flowers. The larvae are often present in large numbers on farms and livestock facilities where they breed in wet areas rich in organic matter. Suitable habitats include water tanks, sewage lagoons, rotting carcasses, the edge of silage pits and the base of composting piles of manure. To allow them to develop in these wet environments, the larvae have a long posterior siphon that functions as a snorkel and which gives rise to the common name *rat-tailed maggot*. Adults are often seen in pastures where they may be observed resting on dung pats and may be recovered in dung-baited pitfall traps.

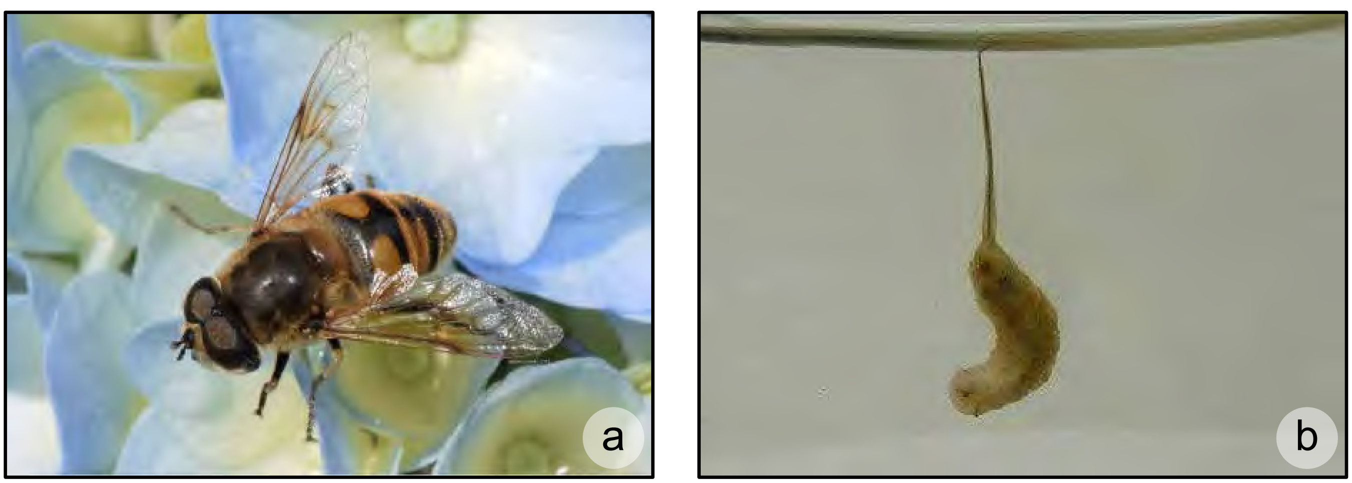


Figure 44. Syrphidae. a – *Eristalis tenax* (© Dianne Clarke); b – larva (photo courtesy of www.uksafari.com).

Ulidiidae (picture winged flies)

Family Ulidiidae is reported as Otitidae in much of the earlier literature.

North American species of ulidids are small to large flies (3–12 mm in length) varying in shape. The body is typically metallic and bright in colour. The wings are often marked with some type of pattern.

The larvae of most species seem to be saprophagous. Reported breeding habitats include moist cavities beneath the bark of dead trees, decaying plant bulbs and cacti, fungi, composing manure and other types of rotting organic material (Allen and Foote 1967). *Physiphora demandata* (formerly *Chrysomyza demandata*) has been reported from manure heaps and horse dung (Skidmore 1991). Allen and Foote (1967) found that *P. demandata* could be reared only on dung or vegetation mixed with dung; larvae of *Seioptera vibrans* appeared to exhibit a preference for the same substrates.

The Canadian fauna of ulidiids consists of 35 reported species with perhaps an additional 20 species yet to be described or reported (Savage et al. 2019). The Otitiidae key provided by Steyskal (1987a) allows for identification to genera. Kameneva and Korneyev (2016) provide a key to identify species of *Physiphora*.

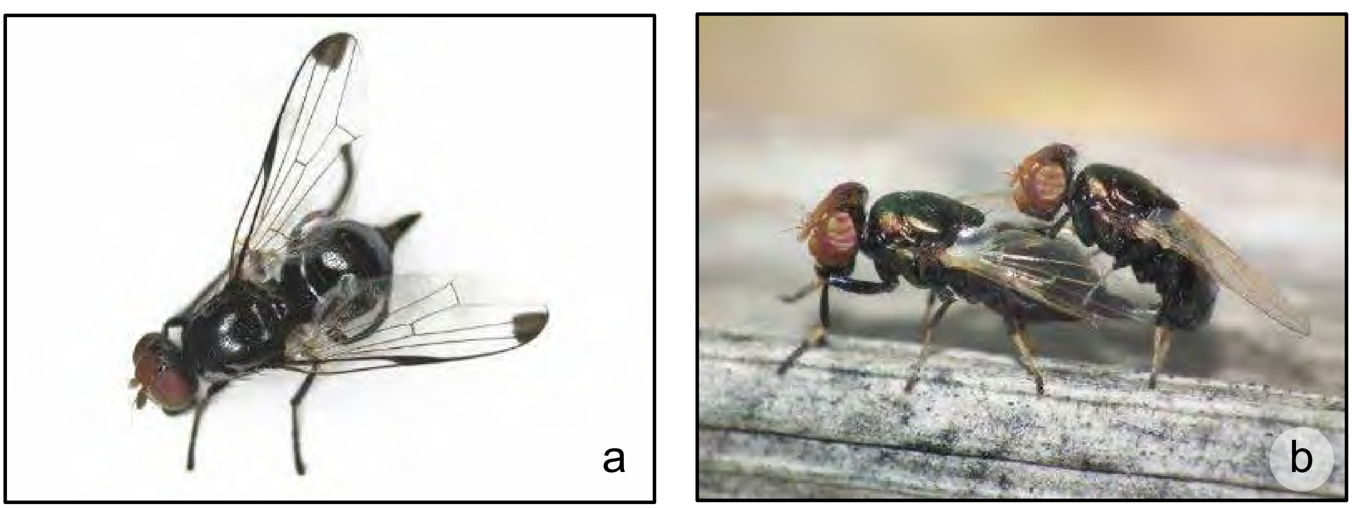
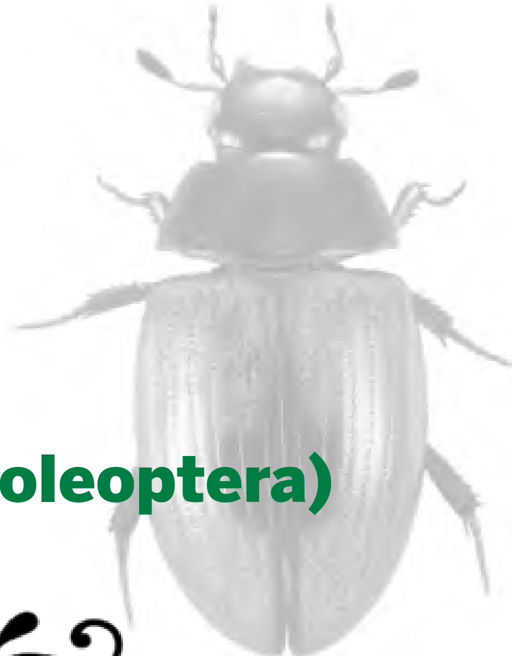
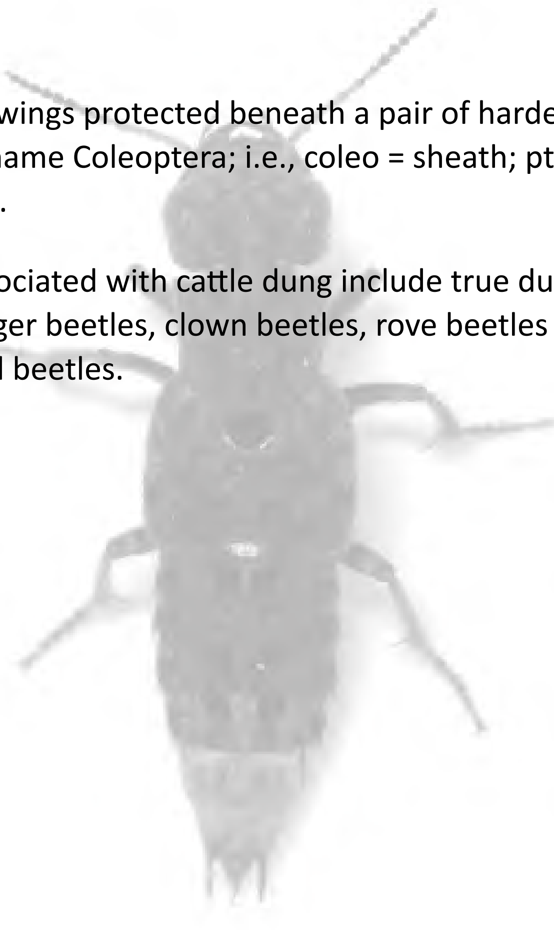


Figure 45. Ulidiidae. a – *Seioptera vibrans* (© B. Schoenmakers – CC-BY-3.0); b – *Physiphora alceae* (© Rui Andrade).

Beetles (Coleoptera)

Adults normally have a membranous hind pair of wings protected beneath a pair of hardened shield-like forewings. This gives rise to the order name Coleoptera; i.e., coleo = sheath; pteron = wing.

Some of the members of this group that are associated with cattle dung include true dung beetles, earth-boring dung beetles, water scavenger beetles, clown beetles, rove beetles and feather-winged beetles.

The following section occasionally mentions morphological features of beetles using terms that will not be recognized by all readers. These terms are described below, illustrated with reference to family Scarabaeidae (true dung beetles) for which many species-level descriptions are provided. However, several of these terms are also relevant to beetles in other taxonomic families. The ***clypeus*** is the broad plate that forms the front of the head. ***Tubercles*** are large bumps on the head. In place of tubercles, the males of some species have well-developed horns. The ***antennae*** (antenna = singular) of the Scarabaeidae are usually tightly tucked under the head and not readily visible. The antennae of other beetle species may be threadlike and readily apparent (e.g., Staphylinidae). The ***pronotum*** is the prominent plate-like structure behind the head. Punctures are shallow pits that often appear on the head, pronotum and elytra. ***Granules*** (not shown) are small bumps on the head, pronotum and (or) elytra of some species. The ***basal marginal line*** may appear as either an engraved line or as a narrow ridge along the rear margin of the pronotum. The ***scutellum*** is a small triangular plate-like structure. Located behind the pronotum and between the point of attachment for the elytra, it is readily visible in some species of dung beetles. The ***elytra*** (elytron = singular) are the harden forewings that lie above and protect the membranous hindwings, which are used for flight. The ***elytral suture*** denotes the margin along which the elytra meet when closed. The ***elytral striae*** are linear grooves on the elytra that run somewhat parallel to the elytral suture.

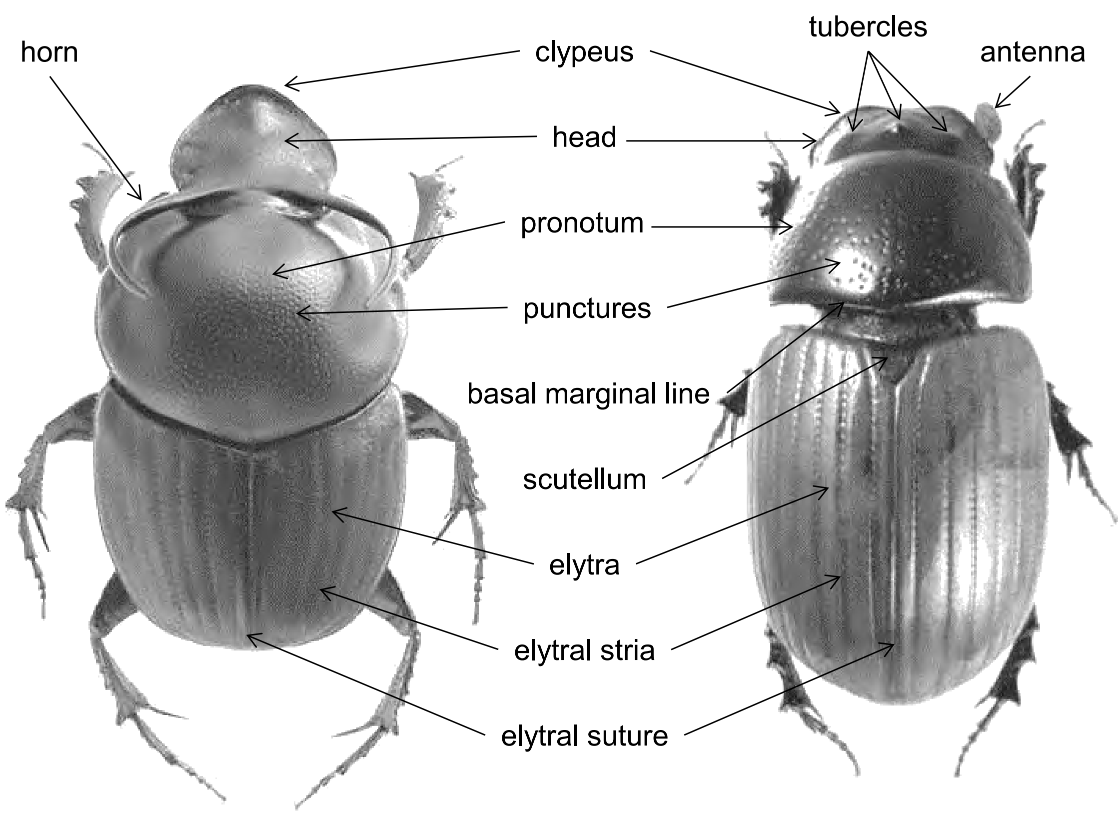


Figure 46. Terms used to describe different morphological features of beetles

Clambidae (minute beetles, fringe-winged beetles)

Clambids are tiny beetles that range in length from 1–2 mm. The eyes are partially to completely divided. The last two segments of the antennae are distinctly expanded to form a club. Adults are black to yellowish-brown in colour and covered with a thick mat of hair. The bodies of adults are also oval-shaped and convex, which allows the beetles to roll themselves into a ball. The hindwings have a fringe of hairs.

Little is known about the biology of these beetles. They are typically found in decaying plant material where they are thought to feed on fungal hyphae and spores. They are most likely to be encountered in partially degraded cattle dung that is rich in fungal growth.

Because of their small size, they seem to be overlooked as members of the dung insect community. They are absent from extensive lists of coprophagous insects for Britain (Skidmore 1991) and North America (Blume 1985), but an unidentified species of *Clambus* was reared from cattle dung in southern Alberta (Floate 1998b). In Canada, they are represented by seven species in the genera *Calyptomerus* and *Clambus* (Table 1). At least one of these species, most likely *Clambus gibbulus* or *Clambus pubescens*, has been associated with cattle dung. A key for the identification of clambid beetles in North America is provided by Endrödy-Younga (1981).

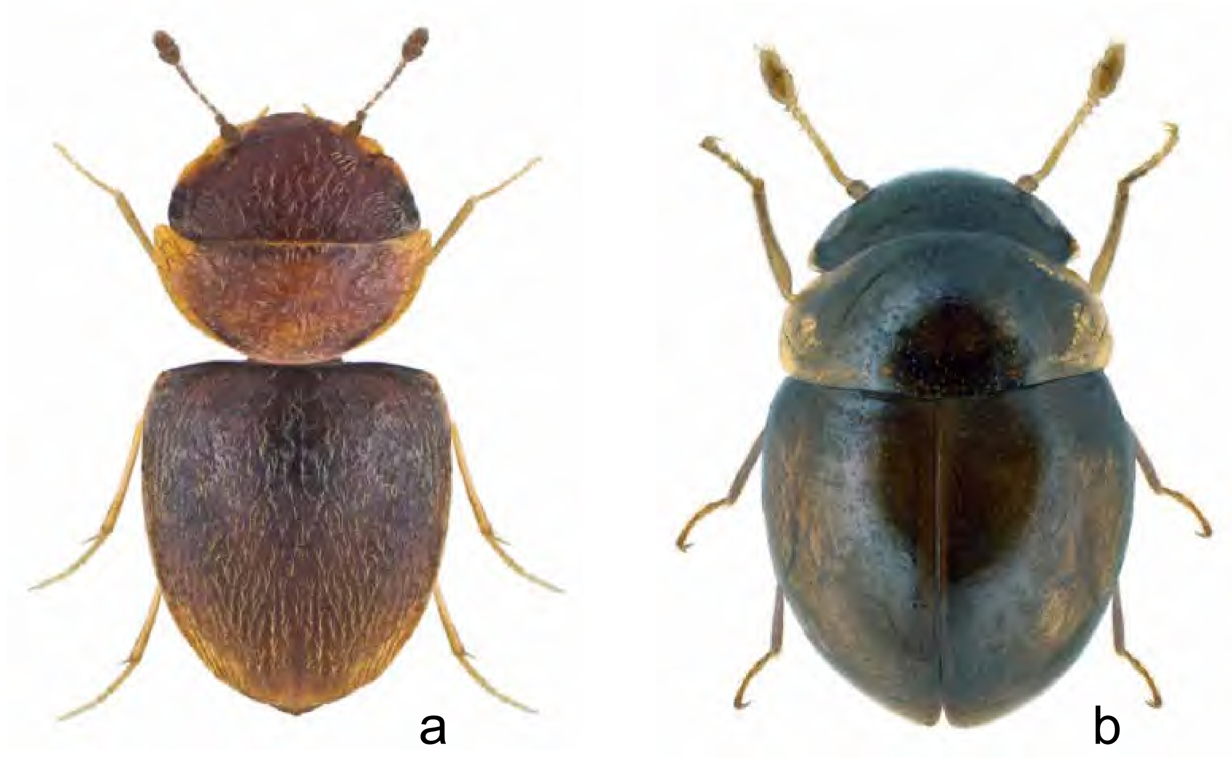


Figure 46. Clambidae. a – *Calyptomerus dubius* (Udo Schmidt – CC-BY-SA-2.0); b – C*lambus pubescens* (Udo Schmidt – CC-BY-SA-2.0).

Table 1. Checklist, size and Canadian distribution for species of Clambidae[1].

Genus	Species	Length (mm)	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
Calyptomerus	*oblongulus*	1.8–2.3	BC	AB									
Clambus	*armadillo*[*]	1.0–1.3					ON	QC	NB				NF
Clambus	*gibbulus*	1.0–1.1	BC	AB	SK	MB		QC					
Clambus	*howdeni*	1.0–1.1					ON	QC	NB	NS			
Clambus	*pubescens*[*]	0.9–1.2	BC	AB	SK	MB	ON	QC					NF
Clambus	*smetanai*	1.0–1.1						QC					
Clambus	*vulneratus*	1.2						QC					

[1] Species and distributions are from Bousquet et al. (2013); size measurements are Endrödy-Younga (1981).
[*] Exotic.

Cryptophagidae (silken fungus beetles)

Cryptophagid beetles are tiny to small beetles that typically range in length from about 1–5 mm. The last three (rarely two) segments of the antennae are somewhat expanded to form a loosely-shaped club. The bodies of adults are oval to elongate-oval in shape and are commonly covered with fine silk hairs. The elytra are irregularly punctured and lack elytral striae or rows of punctures.

These beetles feed on fungi and are common in moist habitats rich in fungal growth; e.g., dead or dying trees, decaying vegetation, stores of moldy grain or food products. Species of *Atomaria* and *Cryptophagus* are frequently recovered in granaries (White et al. 2011). *Ootypus globosus, Hypocoprinus latridioides* and species of *Atomaria* have been reported from cattle dung in Britain (Anonymous 2018; Skidmore 1991), but reports of cryptophagids from cattle dung in North America are lacking (Blume 1985). They are most likely to be found in cattle dung in later stages of degradation.

All species known to occur in Canada and Alaska are reviewed by Pelletier and Hébert (2019). This impressive work includes updated taxonomies, an interactive key with high resolution photographs, and description pages for each species.

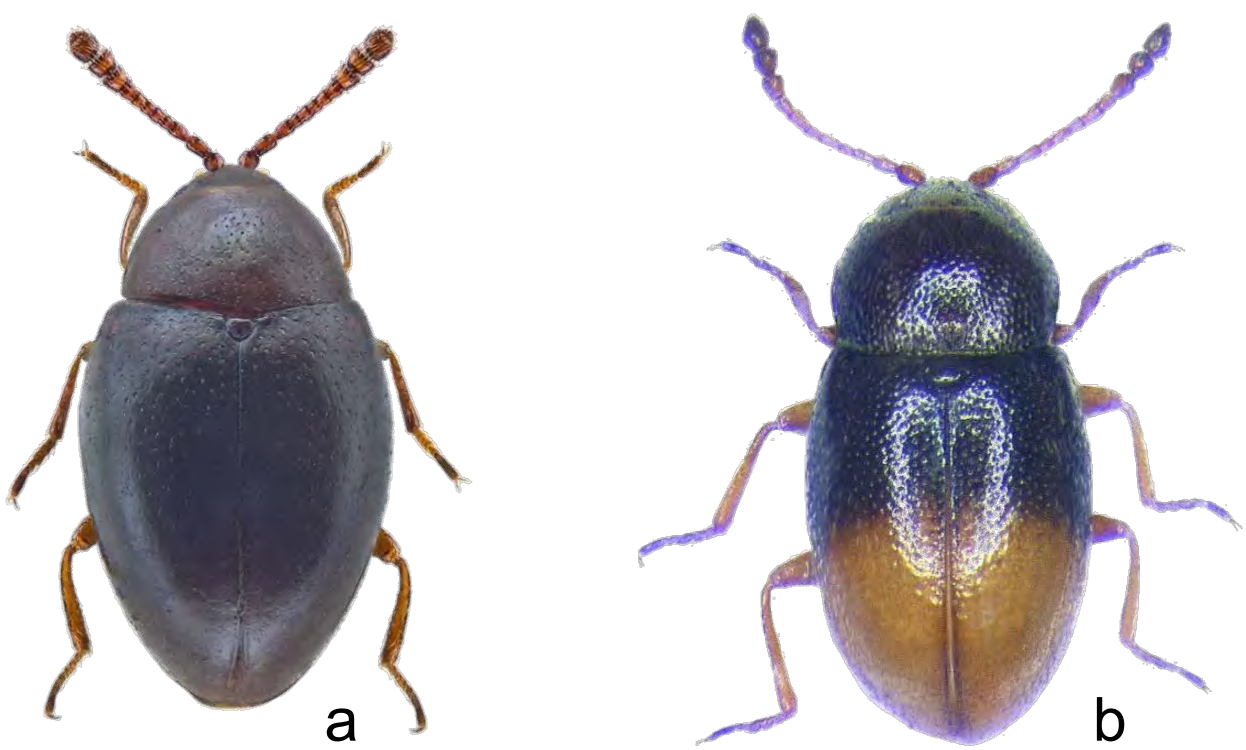


Figure 47. Cryptophagidae. a – *Ootypus globosus* (Udo Schmidt – CC-BY-SA-2.0); b – *Atomaria mesomela* (Udo Schmidt – CC-BY-SA-2.0).

Geotrupidae (earth-boring dung beetles)

Once recognized as subfamily Geotrupinae in family Scarabaeidae, this group has since been elevated to family status with two subfamilies; i.e., Bolboceratinae and Geotrupinae (Smith 2006). However, the taxonomy of the group is still the subject of considerable debate.

Adult geotrupines range in size from 5–40 mm. The head does not tilt downward, but rather projects forward with the mandibles readily visible when viewed from above. The antennae have 11 segments or *antennomeres* with the three terminal segments expanded to form a club. (In contrast, members of family Scarabaeidae typically have 10-segmented antennae with a terminal club formed of 3–5 segments.) The clypeus often carries a horn or tubercle. The base of the pronotum is broader than, or of similar width to, the base of the elytra. The body is round or oval and may range in colour from shades of yellow, brown, reddish or black; it may or may not have a metallic sheen. Larvae are scarabaeiform (Fig. 15C), similar in shape to that of scarabaeid larvae.

Referred to as dor beetles in the United Kingdom, adult geotrupines spend most of their lives in burrows that extend to a depth of 15–200 cm (potentially as deep as 3 meters). They provision these burrows with decomposing plant material (e.g., decaying leaves, cow or horse dung) or fungus, which provides food for the developing larvae.

The 11 species of geotrupines reported in Canada comprise three genera in subfamily Bolboceratinae (*Eucanthus* – 2 species; *Bolbocerosoma* – 1 species; *Odonteus* – 3 species) and the genus *Geotrupes* (5 species) in subfamily Geotrupinae (Bousquet et al. 2013). Of these species, only *Geotrupes stercorarius* is considered here to be a member of the cow dung community. This is a large European species (20–26 mm in length) that is now established in Quebec and the Atlantic Provinces. Its use of fresh dung by adults and larvae is well-documented (Howden 1955; Skidmore 1991). The native species *Geotrupes hornii* is reported to normally feed on fungi as adults, but only on “old cow dung” as larvae (Howden 1955). Keys for the identification of geotrupine beetles in North America are provided by Howden (1955; 1964). None of the other geotrupid species in Canada appear to feed in, or provision burrows with, fresh dung.

Figure 48. *Geotrupes stercorarius* (Udo Schmidt – CC-BY-SA-2.0).

Histeridae (clown beetles)

Hister beetles are usually < 12 mm in length (range from 0.5–25 mm) with sturdy compact bodies. The head is much smaller than the pronotum, underneath which it is often tucked to give beetles a 'headless' appearance. The mandibles are short, stout and protruding. The antennae are relatively short with the last three segments forming a compact club; the antennae are positioned out of sight under the pronotum when the beetle is at rest. Body shape may be oval to elongate-oval or flattened top-to-bottom (dorso-ventrally); many species are convex. Most species are black or dark reddish-brown in colour and lack hairs on the upper surface. Each elytron has fewer than six striae; the apical end of the elytra are abruptly shortened (truncate) to expose usually the last two abdominal segments. Legs are short and robust with prominent teeth on the outward facing edge of the first pair of legs.

Little is known about the biology of most species of hister beetles, although general information is provided in Kovarik and Caterino (2000) and in Bousquet and Laplante (2006). There is one generation per year in more northerly regions; e.g., southern Canada. Adults overwinter to emerge in spring and lay eggs. Newly-hatched larvae pass through two instars, pupate, and complete their development to emerge as new adults by late summer.

Most species feed on the egg and larval stages of soft-bodied insects and are common in moist decaying plant material that support large populations of fly larvae; e.g., fresh dung. Several species of hister beetles have received attention as natural enemies of dung-breeding flies that are pests of livestock. *Carcinops pumilio* has been studied as a biological control agent for house flies in poultry facilities (Achiano and Giliomee 2005; Geden and Axtell 1988). Species of *Atholus, Hister* and *Phelister* have been studied (Summerlin et al. 1990; Summerlin et al. 1991a; Summerlin et al. 1991b) or have been introduced outside of their native range (Legner 1978) as biological control agents of horn flies, which affect cattle on pasture. Summerlin (1989) provides information on how to collect and rear hister beetles.

Hister beetles can be classified into five groups based on their habitat associations; i.e., xylophiles (dead or dying trees), psammophiles (sandy soils), inquilines (bird and mammal nests), myrmecophiles (ant colonies) and saprophiles (rotting vegetation, carrion and dung) (Bousquet and Laplante 2006). Members of this latter group in Canada include most species of *Atholus, Hister, Margarinotus* and many species of Saprininae.

There are at least 136 species of hister beetles in Canada (Bousquet et al. 2013). Species-level keys and additional information on biology and Canadian distributions are provided by Bousquet and Laplante (2006). Table 2 lists 34 species for which dung is reported in the literature as a possible habitat. Only a fraction of these, however, seem to be recovered in surveys of the cow dung community.

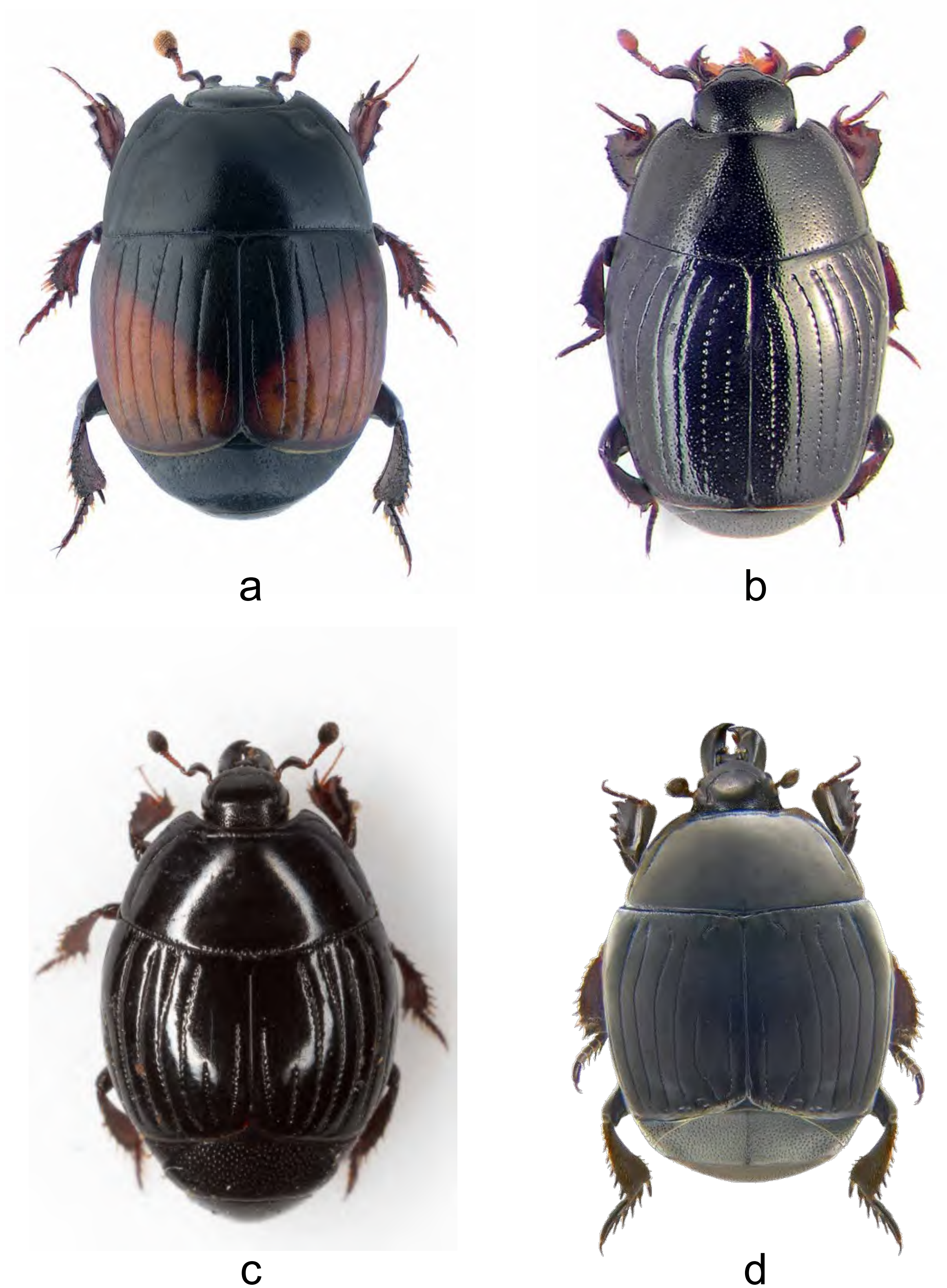


Figure 50. Histeridae. a – *Atholus bimaculatus* (Udo Schmidt – CC-BY-SA-2.0); b – *Carcinops pumilio* (© Lech Borowiec); c – *Hister abbreviatus* (© Chris Rorabaugh); d – *Margarinotus brunneus* (Udo Schmidt – CC-BY-SA-2.0).

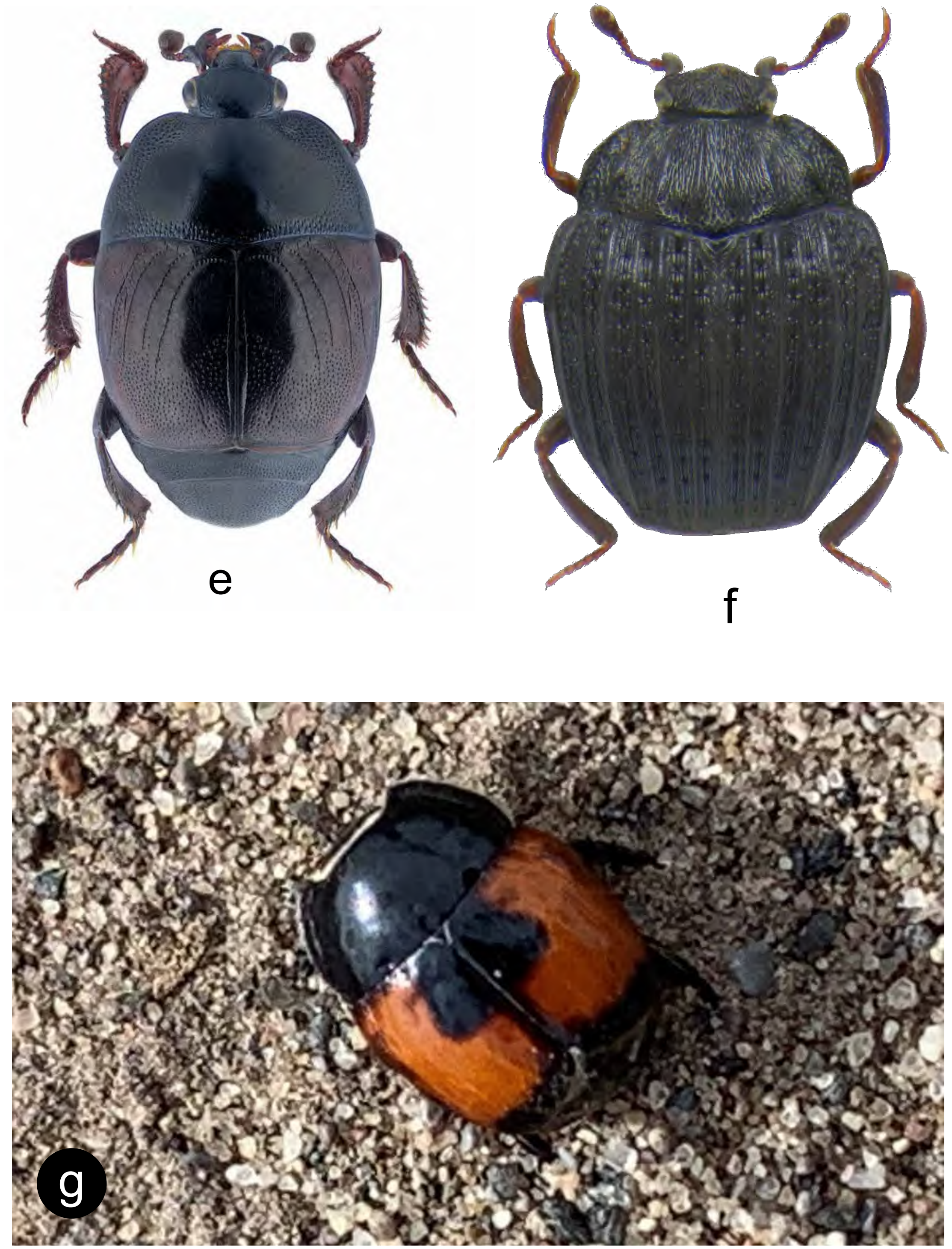


Figure 50. Histeridae (continued). e – *Saprinus subnitescens* (Udo Schmidt – CC-BY-SA-2.0); f – *Onthophilus* sp. (Udo Schmidt – CC-BY-SA-2.0); *Spilodiscus* sp. (Jacqueline M. Richard – CC-BY-NC-4.0).

Table 2. Checklist, size and Canadian distribution for coprophilous species of Histeridae[1]. Species identified in bold font regularly occur in fresh cattle dung. Other species are occasional visitors to fresh cattle dung or information is insufficient to make a determination.

Genus	Species	Length (mm)	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
Acritus	*nigricornis*[*]	0.9–1.0	BC	AB	SK	MB		QC					
Atholus	*americanus*[2]	2.7–4.2					ON	QC					
Atholus	*bimaculatus*[3,*]	4.0–4.8	BC	AB		MB	ON	QC	NB				
Atholus	*perplexus*	3.5–4.9			SK	MB	ON	QC	NB	NS	PE		
Atholus	*sedecimstriatus*	4.2–4.9					ON	QC	NB				
Carcinops	*pumilio*[*]	2.1–2.6	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Euspilotus	*assimilis*[4]	3.5–5.5				MB	ON	QC	NB	NS	PE		
Geomysaprinus	*moniliatus*	2.5–3.6				MB	ON	QC	NB				
Hister	***abbreviatus***	4.1–6.0	BC	AB	SK	MB	ON	QC	NB				
Hister	*depurator*	5.9–7.8					ON						
Hister	*furtivus*	5.5–8.0	BC	AB	SK	MB	ON	QC	NB	NS	PE		
Margarinotus	*egregius*	4.8–7.0				MB	ON	QC	NB	NS			
Margarinotus	*faedatus*	4.2–5.8					ON	QC	NB	NS	PE		
Margarinotus	*harrisii*	4.0–6.0	BC	AB	SK	MB	ON	QC	NB				
Margarinotus	*hudsonicus*	5.2–7.0				MB	ON	QC	NB	NS			
Margarinotus	*interruptus*	5.2–8.0			SK	MB	ON	QC	NB	NS	PE		
Margarinotus	*lecontei*	3.4–4.2		AB	SK	MB	ON	QC	NB	NS	PE		
Margarinotus	*merdarius*[*]	6.0–8.5	BC	AB		MB	ON	QC	NB	NS			
Margarinotus	*obscurus*	5.0–5.8	BC										
Margarinotus	*purpurascens*[*]	3.5–4.1	BC										
Margarinotus	*rectus*	5.8–7.5	BC										
Margarinotus	***umbrosus***	4.0–6.0	BC	AB									
Onthophilus	*deflectus*	1.8–2.2					ON						
Onthophilus	*pluricostatus*	2.2–2.7						QC					
Phelister	***subrotundus***	1.8–2.4					ON	QC					
Saprinus	*distinguendus*[5]	3.2–4.8			SK	MB	ON	QC					
Saprinus	*lugens*	4.8–7.2	BC	AB	SK	MB	ON	QC					
Saprinus	***oregonensis***	3.0–4.8	BC	AB	SK	MB							
Saprinus	*profusus*	3.3–6.6				MB	ON						
Saprinus	*subnitescens*[*]	4.9–5.7					ON	QC					
Spilodiscus	*Ulkei*	4.4–5.5		AB	SK								
Xerosaprinus	*acilinea*[6]	2.5–3.8	BC	AB	SK	MB							
Xerosaprinus	***lubricus***[7]	2.4–4.0	BC										
Xestipyge	*conjunctum*	2.2–2.5					ON						

[1] Species and size measurements are from Bousquet and Laplante (2006); distributions are from Bousquet et al. (2013).

[2] Reported in Blume (1985) as *Hister americanus*.

[3] Reported in Blume (1985) as *Peranus bimaculatus*.

[4] Reported in Blume (1985) as *Saprinus assimilis.*

[5] Also reported from the Northwest Territories.

[6] Reported in Blume (1985) as *Xerosaprinus fimbriatus*.

[7] Reported in Blume (1985) as *Saprinus lubricus*.

[*] Exotic

Hydrophilidae (water scavenger beetles)

Hydrophilid beetles range in size from 1–40 mm. Adults are broadly oval in shape with a convex dorsal surface; there are few if any hairs on the upper surface. Antennae are short with the last three segments expanded to form a loose or moderately compact club. The body colour is dull and typically black or with black and brown markings; rarely with cream-coloured markings. In contrast to hister beetles, the elytra completely cover the abdomen. Legs are somewhat short and flattened.

The common name "water scavenger beetle" is misleading. Larvae are fierce predators of soft-bodied insects, including eggs and larvae of dung-breeding flies that are pests of livestock (Abdel-Gawaad et al. 1976). Adults occasionally may be predators or scavengers, but also may be omnivores, vegetarians or cannibalistic. Most species of hydrophilids occupy aquatic habitats, but members of the subfamily Sphaeridiinae are adapted to terrestrial environments where they live in rotting organic material, including cattle dung. The mouthparts of adult *Sphaeridium lunatum* allow them to filter out and ingest small particulate matter (Holter 2004).

Figure 52. Hydrophilid larva – dorsal and side view (A.A. Zaitsev, https://www.zin.ru/animalia/coleoptera/eng/sphscaaz.htm).

Adult hydrophilid beetles, primarily species of *Cercyon* and *Sphaeridium*, can be found in fresh dung from spring through autumn. Because of their larger size (4–7 mm), species of *Sphaeridium* can be easily distinguished from other genera of hydrophilid beetles found in dung.

Numbers of adult hydrophilids in dung are highest in mid-May to mid-June with a secondary peak later in August (Levesque and Levesque 1995; Wassmer 2014). Adult *Sphaeridium* are among the first insects to arrive at fresh dung. As they crawl over the surface of the pat, they penetrate the thin 'skin' that forms on the surface of the fresh deposit. These points of penetration give older pats a 'shot-holed' appearance and provide entry points for other coprophilous species to enter the pat (Fig. 54d).

Life history information is sparse. Species of *Cercyon* in Canada are assumed to have only one generation per year (Levesque and Levesque 1995), whereas these same species may have multiple generations per year in warmer locations in Europe (Hanski 1980). At least some species overwinter as adults (Mohr 1943). In Illinois, *Sphaeridium scarabaeoides* breeds continuously from early spring into late fall and has been reported to complete larval and pupal stages in as little as 12 days (Mohr 1943). Abdel-Gawaad et al. (1976) describes the life history of *Sphaeridium bipustulatum* based on laboratory studies. Mated females lay 2–5 eggs in chambers that they form within the dung pat (lifetime production of 68 eggs/female). The eggs hatch into larvae (with atrophied legs) that feed on fly larvae. When mature, the larvae form cocoons within the dung pat in which they pupate. Time from egg to egg-laying adult is 44 days at 27 °C (Abdel-Gawaad et al. 1976).

In Canada, this family is represented by at least 151 species (Bousquet et al. 2013). Van Tassell (2000) provides a key that allows identification of hydrophilid beetles to genus. Smetana (1978) provides a key that allows for species-level identification of North American species in subfamily Sphaeridiinae. Coprophilous species of hydrophilids reported in Canada are listed in Table 3. Only a subset of these species appear to occur in cattle dung with any regularity (Cervenka and Moon 1991; Floate 1998b; Macqueen and Beirne 1974; Mohr 1943; Rounds and Floate 2012; Wassmer 2014).

Only three species of *Sphaeridium* occur in Canada. They have a transcontinental distribution and are common in fresh cattle dung. The elytra of *S. bipustulatum* (3.9–5.2 mm in length) have an apical pale spot that is not divided by a dark stripe. *Sphaeridium lunatum* (4.3–7.0 mm) and *S. scarabaeoides* (4.0–7.1 mm) are larger with an apical pale spot on the elytra that is divided by a dark stripe. For *S. scarabaeoides*, the side margins of the pronotum are typically pale and the apical pale spot is usually prolonged along the side margins of the elytra to at least the midpoint. For *S. lunatum*, the side margins of the pronotum are dark, the apical spot is not or only slightly prolonged along the side margin of the elytra.

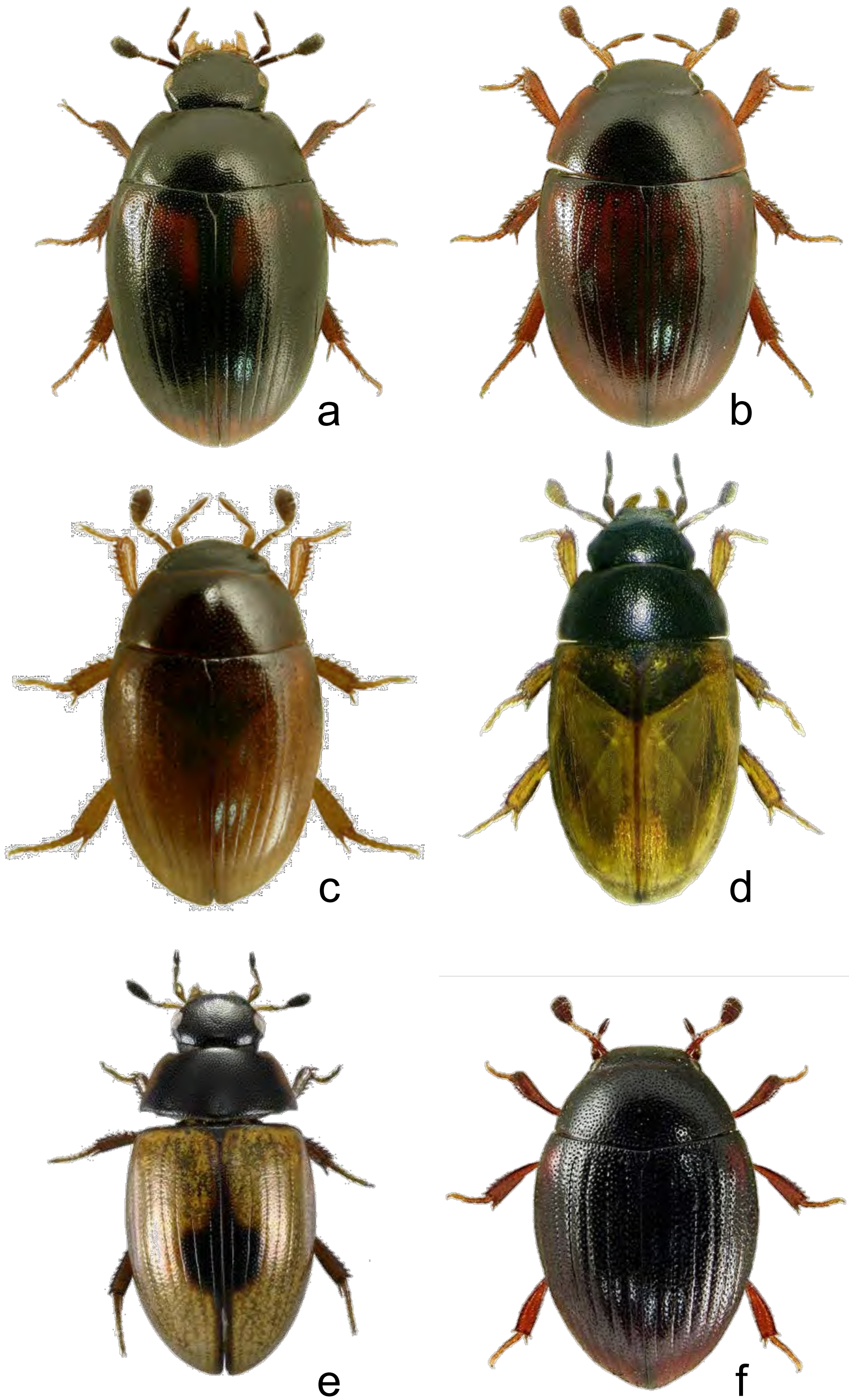


Figure 53. Hydrophilidae. a – *Cercyon haemorrhoidalis* (© Lech Borowiec); b – *Cercyon lateralis* (© Lech Borowiec); c – *Cercyon pygmaeus* (© Lech Borowiec); d – *Cercyon quisquilius* (Udo Schmidt – CC-BY-SA-2.0); e – *Cercyon unipunctatus* (J.-H. Yvinec – CC-BY-NC); f – *Cryptopleurum minutum* (© Lech Borowiec).

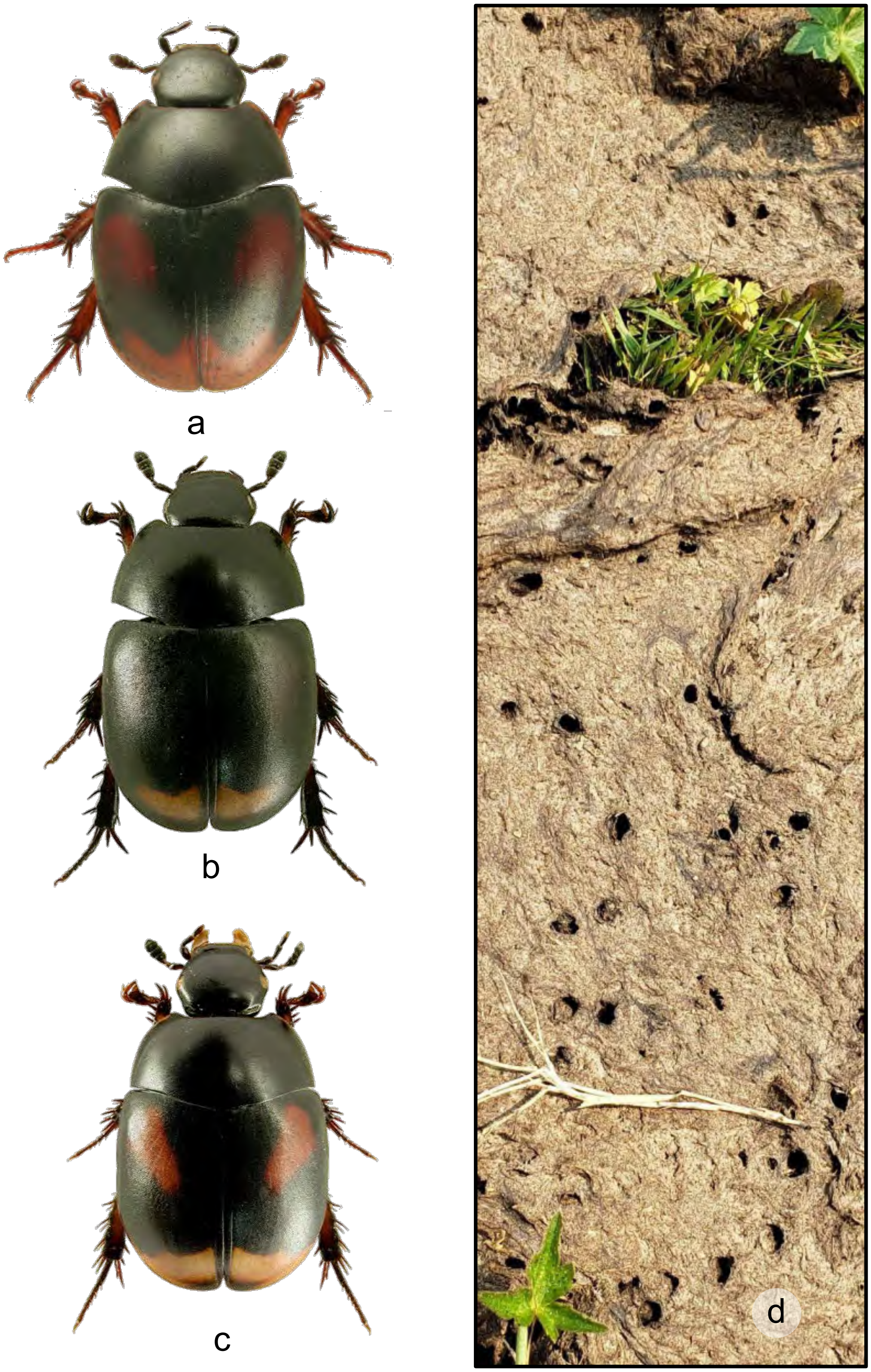


Figure 54. Hydrophilidae (continued). a – *Sphaeridium bipustulatum* (© Lech Borowiec); b – *Sphaeridium lunatum* (© Lech Borowiec); c – *Sphaeridium scarabaeoides* (© Lech Borowiec); d – holes in crust of cattle dung formed by the activity of adults of *Sphaeridium* spp. (KD Floate).

Table 3. Checklist, size and Canadian distribution for coprophilous species of Hydrophilidae[1]. Species identified in bold font regularly occur in fresh cattle dung. Other species are only occasional visitors to fresh cattle dung or information is insufficient to make a determination.

Genus	Species	Length (mm)	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
Cercyon	*assecla*	1.9–2.5		AB	SK		ON	QC	NB	NS	PE		
Cercyon	***haemorrhoidalis***[*]	2.0–3.2	BC				ON	QC	NB	NS	PE		
Cercyon	*impressus*[*]	2.8–3.5	BC										
Cercyon	***lateralis***[2,*]	2.0–3.0	BC	AB	SK		ON	QC	NB	NS			NF
Cercyon	*limbatus*[2,3]	2.0–3.0	BC	AB									
Cercyon	*marinus*[2,3]	2.0–3.0	BC	AB	SK	MB	ON	QC					
Cercyon	*minusculus*	1.3–1.9	BC		SK	MB	ON	QC	NB	NS			NF
Cercyon	*nevadanus*	1.4–2.2	BC										
Cercyon	*nigriceps*[4,*]	1.0–1.9		AB	SK			QC		NS			
Cercyon	***praetextatus***	2.4–3.5				MB	ON	QC		NS			
Cercyon	***pygmaeus***[*]	1.0–1.6	BC	AB	SK	MB	ON	QC	NB	NS			NF
Cercyon	***quisquilius***[*]	1.8–2.5	BC	AB	SK	MB	ON	QC	NB	NS			NF
Cercyon	*terminatus*[*]	1.7–1.9				MB	ON	QC	NB				
Cercyon	***unipunctatus***[*]	2.0–3.2	BC	AB	SK	MB	ON	QC	NB	NS			
Cercyon	*ustulatus*[*]	2.6–3.3						QC					
Cryptopleuron	***minutum***[*]	1.3–2.1	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Cryptopleuron	*subtile*[*]	1.4–1.8	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Helophorus	*orientalis*[2]	3.0	BC	AB	SK	MB	ON	QC	NB	NS	PE		
Megasternum	*concinnum*[5,*]	1.6–2.0	BC										
Megasternum	*posticatum*[*]	1.6–2.0	BC										
Phaenonotum	*exstriatum*	2.3–4.0					ON						
Sphaeridium	***bipustulatum***[*]	3.9–5.2	BC	AB	SK	MB	ON	QC	NB	NS	PE		
Sphaeridium	***lunatum***[*]	4.3–7.0	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Sphaeridium	***scarabaeoides***[*]	4.0–7.1	BC	AB	SK	MB	ON	QC	NB	NS			NF

[1] Species and size measurements are from Smetana (1978); distributions are from Bousquet et al. (2013).

[2] Also reported from the Northwest Territories.

[3] Also reported from the Yukon.

[4] Reported in Smetana (1978) and Blume (1985) as *Cercyon atricapillus*.

[5] Reported in Smetana (1978) as *Megasternum obscurum*.

[6] Reported in Smetana (1978) and Blume (1985) as *Cercyon pubescens*.

[*] Exotic.

Latridiidae (minute brown scavenger beetles)

Species in this group have elongated oval bodies that are somewhat convex and range in size from 1–3 mm. Adults are yellowish-brown to brownish-black in colour. The antennae are slender, but end with a 'club' formed from two or three segments. The head is narrower than the pronotum, which in turn is narrower than the base of the elytra. The elytra have regularly spaced rows (striae) of punctures with bristles or hairs. The spaces between these rows (interstriae) may form ridges that may be smooth or also have hairs. Wings may be present or absent.

Adults and larvae feed on fungus and are also known as fungus beetles. They are most often encountered in moist habitats that include rotting vegetation, the underside of bark and stones, and occasionally the nests of ants and termites. Several species are common in stores of mouldy human food products and now have global distribution. Taxonomic keys and life history information for these latter species is provided by Hinton (1941). Species in the genera *Cartodere* and *Enicmus* have been recovered from dung heaps (Hinton 1941); Floate (1998b) reported an unidentified latriid from cattle dung. Not strictly coprophilous; species recovered in dung are likely attracted from adjacent habitats in search of prey.

In Canada, this family is represented by at least 64 species in 11 genera (Bousquet et al. 2013). A key for the identification of latriid beetles in North America is provided by Andrews (2002).

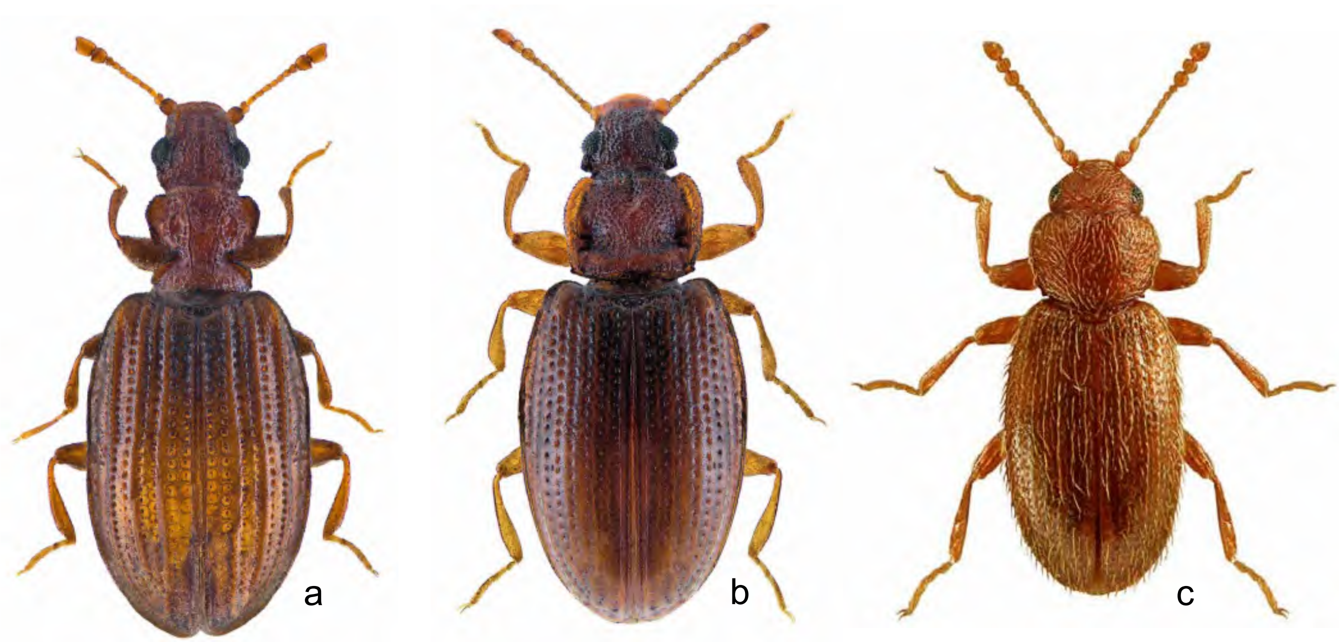


Figure 55. Latridiidae. a – *Cartodere constricta*; b – *Enicmus transversus*; c – *Corticaria fulva* (all photos Udo Schmidt – CC BY-SA-2.0).

Ptiliidae (feather-winged beetles)

Ptiliids are about 0.25–1 mm in length and include the world's smallest beetles. Adults are dark in colour, round to oval in shape, and densely covered with hair. Their antennae are long and narrow; the first two segments are enlarged with the last three segments expanded to form a loosely-shaped club; the apical end of each antennal segment has a whorl of long hairs. Adults may have either normal eyes and hindwings ('normal' morph), or more commonly have eyes and hindwings that are reduced or absent ('vestigal' morph) (Dybas 1978). The hindwings of the normal morph are usually folded and hidden beneath the leathery forewings (i.e., the elytra). When unfolded, the hindwings can be seen to have a distinct border of long hairs. Because of this feature, aerial dispersal is believe to be passive; e.g., similar to that of dandelion seeds.

Ptiliid beetles are found in moist environments with rotting vegetation suitable for the growth of fungi upon which they feed. Because of their small size, they are often overlooked as members of the dung insect community, but may be very common (Floate et al. 2002).

In Canada, they are represented by at least 49 species in 14 genera (Bousquet et al. 2013). A key for the identification of ptiliid beetles in North America is provided by Hall (2000).

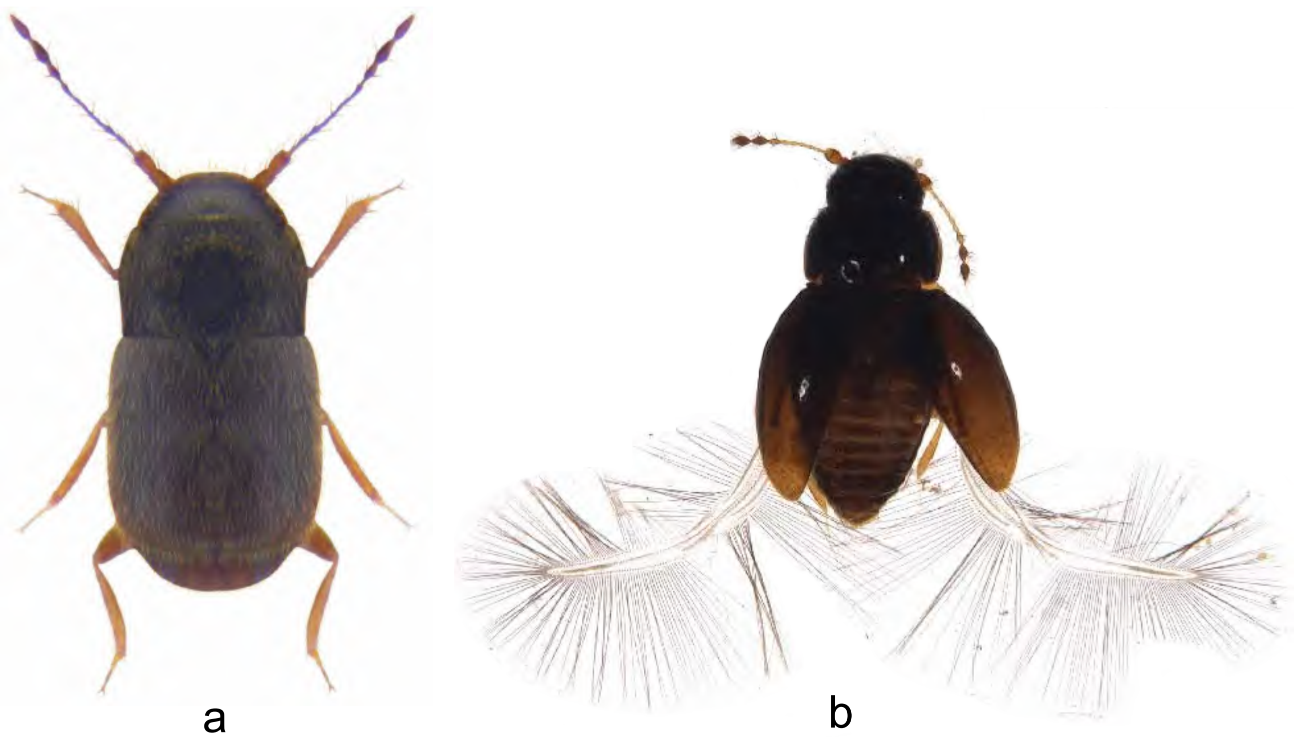


Figure 56. Ptiliidae. a – *Smicrus filicornis* (Udo Schmidt – CC – BY-SA-2.0); b – *Ptenidium* sp. (note the feathery hindwings) (Centre for Biodiversity Genomics. CBG Photography Group – CC-BY-NC-SA-3.0).

Scarabaeidae (dung beetles)

Scarabaeidae or 'scarabs' are represented in Canada by at least 220 species (Brunke et al. 2019) in seven subfamilies; i.e., Aegialiinae (18 species), Aphodiinae (95), Cetoniinae (17), Dynastinae (8), Melolonthinae (62), Rutelinae (6) and Scarabaeinae (14) (Bousquet et al. 2013). Many species in this group have been well-studied, either because of their large size, bright colours, morphological features, interesting reproductive behaviour and (or) their status as pests of economic concern. The Japanese beetle (*Popillia japonica*), for example, is a pest on more than 300 species of plants in North America.

Figure 57. *Popillia japonica* (Gilles San Martin – CC-BY-SA-2.0).

Scarabs are stout-bodied beetles with a general oval or squarish shape. North American species range in length from 2–60 mm. The head may or may not have a slight downward tilt. Most species have 10-segmented antennae with the last 3–5 segments forming a distinct club. Depending upon the species, the clypeus (Fig. 46) may have prominent bumps (tubercles) or a horn and the mandibles may not be visible from above. There may be tubercles or horns on the pronotum, the scutellum may or may not be visible, and elytra may or may not have striae (Fig. 46). The larvae of all species are scarabaeiform, white or yellowish in colour (Fig. 15b), with some species (Scarabaeinae) bearing a hump.

The biology of scarabs is quite diverse. Some species feed on living plant tissues (leaves, roots, fruit, pollen), whereas others feed on decomposing organic matter (compost, dung, carrion) or on fungi. However, only subfamilies Aphodiinae (aphodiine or 'small' dung beetles) and Scarabaeinae (true dung beetles) contain species that require fresh dung to complete their life cycle. Aphodiines are typically < 8 mm in length (rarely > 15 mm), with the body length of individuals of the same species differing by up to 60% (Landin 1957 – cited by Vessby 2001). They have 9-segmented antennae with a 3-segmented club; the hindmost segment of the abdomen (the pygidium) is partially or full-covered by the elytra. Scarabaeines have antennae with 8 or 9 segments with a 3-segmented club; the pygidium is not concealed by the elytra. The mandibles of both aphodiines and scarabaeines are hidden beneath the clypeus.

Dung beetles show different levels of specialization. Some species are typically associated with the small, hard pellet-like dung of rodents or deer, whereas other species are generalists on the mound-like deposits left by large grazing herbivores (Gordon 1983; Gordon and Cartwright 1974). Aphodiines associated with cattle dung typically breed within the deposit and are termed 'dwellers'. In contrast, adult scarabaeines remove fresh dung that they bury in tunnels below the deposit ('tunnellers') or which they form into balls that are rolled away from the deposit and then buried ('rollers') (see section titled 'Guild structure').

Scarabs can be identified to genus using taxonomic keys in Ratcliffe et al. (2002). The vast majority of species in subfamily Aphodiinae are in tribe Aphodiini for which species can be identified using Gordon and Skelley (2007). The latter taxonomic revision resulted in many species originally in the genus *Aphodius* being reclassified into other genera, which may cause some confusion when reviewing the older literature. Species of scarabaeine dung beetles can be identified for different genera using the following references: *Canthon* – Robinson (1948), *Copris* – Matthews (1961), *Onthophagus* – Howden and Cartwright (1963).

Many of the dung beetles regularly found in cattle dung have been well-studied. Information on these species is provided in the following pages. Information for three species of *Diapterna* also is provided. These latter species do not breed in, but may be attracted to, fresh dung (Bezanson 2019; Floate and Gill 1998). Table 4 lists species of scarabs in Canada with reported associations to dung. However, as is the case for *Diapterna*, many of these species may be attracted to dung in response to volatile organic compounds that they associate with rotting organic material and not with fresh dung per se. To distinguish between these groups, species that are routinely recovered from fresh dung and are considered as true dung beetles are identified in the table using bold font.

Scarabaeidae, subfamily Aphodiinae: *Agoliinus leopardus*

Other names: *Aphodius leopardus*

Common name: None

Functional group: Dweller

Pest status: None

Description: 5–7 mm in length. Head dark brown with punctures, forward margin lighter in colour. Pronotum dark brown with fine and coarse punctures, forward and side margins lighter in colour. Elytra generally light brown with pattern of dark brown markings (maculate), but can be variable. In some cases, the markings may be almost absent or almost completely cover the wing covers. Scutellum small; 1/6th or less the length of the elytra.

Geographic distribution: Native to North America. Transcontinental in Canada and the northern United States. In the eastern United States, extending south to North Carolina (Bousquet 1991; Gordon and Skelley 2007).

Seasonal adult activity: July to October. Peak activity in August (Gordon 1983).

Figure 58. *Agoliinus leopardus* (© Guy A. Hanley, Northern Plains Entomology).

Biology: Overwinters as an adult, emerging in the spring to oviposit in dung. The new generation of adults emerges in mid-summer. One generation per year.

Notes:

- Adults are general dung feeders with a strong preference for dung of elk, sheep and deer; mainly restricted to forest habitats (Gordon 1983).
- Warmer temperatures at the southern extent of its distribution, allow for peak flights of adults to occur during winter months (Gordon 1983).
- Similar in general appearance and size to *Chilothorax distinctus*, but with a dark brown head and pronotum (not black), elytra (= wing covers) with a background colour of light brown (not golden), has peak flights in August (not October), and is associated with forests (not open pastures).

Scarabaeidae, subfamily Aphodiinae: *Aphodius pedellus*

Other names: *Aphodius fimetarius* (see Notes)

Common name: None

Functional group: Dweller

Pest status: Occasional (see Notes)

Description: 6–10 mm in length. Head black. Pronotum black with reddish-yellow front corners; coarsely punctate. Elytra reddish. Scutellum small; 1/6th or less the length of the elytra. Unlikely to be mistaken for any other dung beetle species in Canada.

Geographic distribution: Introduced from Europe and now widely distributed in North America. Present in southern Canada from coast-to-coast (Floate and Gill 1998); likely present wherever cattle are grazed. In Alberta, as least as far north as Manning (KDF pers. obs.)

Seasonal adult activity: March into December. Peak recovery of adults in cattle dung in April to early May with a larger peak in September and October (Floate and Gill 1998; Kadiri et al. 2014).

Figure 59. *Aphodius pedellus* (H. Goulet (retired), Agriculture and Agri-Food Canada).

Biology: Details of this species' life history are provided by Mohr (1943) and by Christensen and Dobson (1977). Overwintering occurs as adults and as eggs. Adults emerge in spring and preferentially tunnel into dung pats aged 3–10 days to lay eggs. Overwintered eggs hatch with warmer temperatures. Larvae feed within the pat until they complete development and then tunnel into the soil beneath the pat to a depth of 2–3 cm to pupate. New adults emerge in autumn and may or may not lay eggs prior to winter. One generation per year.

Notes:

- Adults are general dung feeders with a preference for open pastures and cattle dung (Gordon 1983). One of the most common dung beetles in Canada.
- Larval feeding has been associated with damage to potatoes in Germany; adult feeding has been associated with damage to mushroom caps in England (Jerath and Ritcher 1959). Morphology of larvae described by Jerath (1960).
- Originally described as a subspecies of *Aphodius fimetarius*, but now recognized as a genetically distinct species (Miraldo et al. 2014; Wilson 2001). Morphologically, however, the two species are almost indistinguishable.
- Both *A. fimetarius* and *A. pedellus* co-occur in parts of North America; *A. pedellus* is likely the only species in Canada and the northern United States (Floate et al. 2022; Miraldo et al. 2014).
- In an area of co-occurrence, Miraldo et al. (2014) reported adult *A. pedellus* to have two peaks of activity (spring, early autumn), whereas *A. fimetarius* only had only one peak of activity (spring).
- At a constant 22 °C, I have observed an average of 67 days from oviposition in fresh cattle dung to emergence of new adults at (n = 128 beetles; KDF unpub. data).

Scarabaeidae, subfamily Aphodiinae: *Calamosternus granarius*

Other names: *Aphodius granarius*

Common name: None

Functional group: Dweller/detritivore

Pest status: Occasional (see Notes)

Description: 3–6 mm in length. Head, pronotum and elytra glossy brownish black to black in colour. Head moderately to densely punctate, pronotum with mix of coarse and fine punctures. Scutellum small; 1/10th to 1/8th the length of the elytra, slightly depressed below the level of the wing covers and pentagonal in shape.

Geographic distribution: Introduced from Europe and now widely distributed in North America from southern Canada to Mexico (Floate and Gill 1998; Gordon and Skelley 2007); likely present wherever cattle are grazed.

Seasonal adult activity: March to November. Peak activity in late May to early June (Floate and Gill 1998).

Figure 60. *Calamosternus granarius* (H. Goulet (retired), Agriculture and Agri-Food Canada).

Biology: Adults overwinter and emerge in early spring. Eggs are laid directly in the food material, wherein the larvae develop. Pupation occurs in the soil beneath the food source. One generation per year.

Notes:

- Adults are general dung feeders with a preference for open pastures and cattle dung (Gordon 1983). One of the most common dung beetles in Canada.
- Larvae develop in dung, also in carrion, compost material, rotting vegetables and similar decaying organic materials (Landin 1961). Larval feeding has been reported on sprouting corn seeds (Lugger 1899 – as cited in Ritcher (1966)); high larval densities (ca. 100–200 larvae/m^2) have been associated with damage to turf grass on golf courses (Sears 1978). Morphology of larvae described by Jerath (1960).

Scarabaeidae, subfamily Aphodiinae: *Chilothorax distinctus*

Other names: *Aphodius distinctus*

Common name: Maculated dung beetle

Functional group: Detritivore

Pest status: Occasional (see Notes)

Description: 4–6 mm in length. Head and pronotum black; lightly to moderately punctate. Elytra gold in colour with distinctive black markings (= maculate). Scutellum small; 1/10th to 1/8th the length of the elytra.

Geographic distribution: Introduced from Europe and now widely distributed in North America. Present in southern Canada from coast-to-coast (Floate and Gill 1998); likely present wherever cattle are grazed. In Alberta, as far north as Grande Prairie (KDF pers. obs.).

Seasonal adult activity: March into December. Peak recovery of adults in cattle dung in April to early May with a larger peak in October (Floate and Gill 1998; Kadiri et al. 2014).

Figure 61. *Chilothorax distinctus* (H. Goulet (retired), Agriculture and Agri-Food Canada).

Biology: Overwinter as adults. Females apparently mate in autumn and emerge in spring with mature eggs (Christensen and Dobson 1976) that they lay in soil. Larvae complete development in late June, pupate in July, and emerge as adults in autumn where they are attracted to fresh dung in enormous numbers to feed and presumably mate. One generation per year.

Notes:

- Adults are general dung feeders with a preference for open pastures and cattle dung (Gordon 1983). One of the most common dung beetles in Canada.
- Larvae do not develop in dung, but rather in rotting organic material (Landin 1961) and may feed on plant roots. Damage to mint has been reported (Jerath and Ritcher 1959); Christensen and Dobson (1976) conclude that *C. distinctus* has the potential to be a pest of pastures and lawns. Densities can exceed 100 larvae / m^2 in agricultural fields; often in association with thinning stands of canola, corn, dry bean, onion, and pea. In southern Alberta, occasional but predictable reports of such damage are received in mid- to late June (Floate 2021).
- Flights of adults in autumn are abrupt and triggered by precipitation and cold temperatures (Christensen and Dobson 1976; Seamans 1934).
- Similar in general appearance and size to *Agoliinus leopardus*, but has elytra with a background colour of yellow (not light brown), has peak flights in October (not August), and is associated with open pastures (not forests).

Scarabaeidae, subfamily Aphodiinae: *Colobopterus erraticus*

Other names: *Aphodius erraticus*

Common name: None

Functional group: Tunneller

Pest status: None

Description: 6–8 mm in length. Head and pronotum black; densely punctate. Elytra yellowish-brown with a black band along the elytral suture. Scutellum large; 1/5th to 1/3rd the length of the elytra.

Geographic distribution: Introduced from Europe and now widely distributed in North America. Present in southern Canada from coast-to-coast (Floate and Gill 1998) and possibly wherever cattle are grazed. In Alberta, as far north as Grande Prairie (KDF unpub. data).

Seasonal adult activity: April to October. Peak recovery of adults in cattle dung in late May/early June and in late July/early September (Kadiri et al. 2014).

Figure 62. *Colobopterus erraticus* (H. Goulet (retired), Agriculture and Agri-Food Canada).

Biology: Rojewski (1983) provides a detailed description of this species' life history; details of nesting behaviour are provided by Vitner (1998). Adults fly to fresh dung pats in spring where they feed and mate. Females form tunnels beneath the pat to a depth of about 3–5 cm (but as deep as 10 cm). Eggs are laid in cavities at the lower depth of the tunnels. The female then fills the lower portion of the tunnel with dung removed from the pat. Newly-hatched larvae feed on the dung, complete larval development and pupate. The new adults emerge in late July or early August and feed in fresh dung until September. With the arrival of colder temperatures, they tunnel into the soil to depths of 20–27 cm and overwinter. One generation per year.

Notes:

- Adults are general dung feeders with a preference for open pastures and cattle dung (Gordon 1983). One of the most common dung beetles in Canada.
- One female can bury 20–23 g of dung in about 8 days, equating to about 500–600 times their own weight (Rojewski 1983).
- Egg-to-adult development in 35–40 days at 19–20 °C (Gittings and Giller 1997). Morphology of larvae described by Jerath (1960).
- Apparently absent in western North America until the 1980s (Blume 1985; Macqueen and Beirne 1974). In the mid-1980s, recovered as far south as Georgia, USA (Hunter et al. 1987). Recorded in eastern Canada prior to 1940, but not reported west of Manitoba until 1991. First report from Alberta may be a single individual collected in 1995 during a 3-year survey in southern Alberta (Floate and Gill 1998) where it is now common (Floate and Kadiri 2013).

Scarabaeidae, subfamily Aphodiinae: *Diapterna hamata*

Other names: *Aphodius hamata, A. hamatus*

Common name: None

Functional group: Detritivore

Pest status: None, but see Notes

Description: 6–8 mm in length. Head black without punctures or weakly punctate; pronotum black with sparse scattering of fine and coarse punctures. Scutellum large; 1/5th to 1/3rd the length of the elytra. Elytra are usually coloured with an intermix of yellow and brown, but occasionally entirely yellow or brown.

In common with other species of *Diapterna*, males have a characteristic 'fish-hook' structure on the last pair of legs (Fig. 63b).

Geographic distribution: Native to North America; typically associated with northern, boreal forests. In Canada, reported from British Columbia east into Quebec (Bousquet et al. 2013). In the United States, reported from Washington east to Minnesota, and south along the Rocky Mountains into the northern regions of Arizona, Nevada and California (Gordon and Skelley 2007).

Seasonal adult activity: May to August.

Figure 63. a – *Diapterna hamata* (Guy A. Hanley, Northern Plains Entomology); b – close-up showing 'fish-hook' structure on rear leg of male (arrow) (© Paul Skelley).

Biology: Adults attracted to cattle dung to feed; larvae likely develop in organically rich and moist soils. Jerath (1960) reported recovery of last (3rd) instar larvae in mid-November in Nevada, indicating the species overwinters as larvae or pupae.

Notes:

- Excluding one report from Nevada of larval damage to grass roots (Jerath and Ritcher 1959), no other reports of pest damage are known.
- For larval descriptions, see Jerath (1960), Ritcher (1966), or Helgesen and Post (1967).
- Adults may have a preference for open versus forested pastures. In Cypress Hills Interprovincial Park in southern Alberta, adults were commonly recovered in dung-baited pitfall traps on open grassland, but were rarely collected in similar traps 100 m distant in stands of conifer trees (Bezanson et al. 2022).

Scarabaeidae, subfamily Aphodiinae: *Diapterna pinguella*

Other names: *Aphodius pinguellus*

Common name: None

Functional group: Detritivore

Pest status: Occasional (see Notes)

Description: 5–7 mm in length. Head dark brown to black in colour. Pronotum and elytra coloured as per head. Pronotal disc (i.e., centre portion) usually shiny with mixture of fine and coarse punctures, increasing in density towards sides. Basal marginal line absent. Scutellum large; 1/5th to 1/3rd the length of the elytra.

In common with other species of *Diapterna*, males have a characteristic 'fish-hook' structure on the last pair of legs (Fig. 63b).

Geographic distribution: Native to North America. In Canada, reported from British Columbia east into Manitoba (Bousquet et al. 2013). In the United States, reported from Idaho and North Dakota south into Wyoming, Colorado and Nebraska (Ratcliffe and Paulsen 2008).

Seasonal adult activity: March to October; in Alberta, peak emergence in mid-July.

Figure 64. *Diapterna pinguella* (Guy A. Hanley, Northern Plains Entomology).

Biology: Common to moist locations (e.g., near swamps or ponds). Adults are attracted to dung, but larvae likely develop in organically rich and moist soils (Helgesen and Post 1967).

Notes:

- Occasionally reported as a pest of golf courses in Alberta. Larvae develop underground on golf course greens. Upon completing development, the new adults emerge onto the greens where they and the emergence holes they form interfere with the roll of the ball. Adult densities of 10–20 m^2 have been observed (KDF pers. obs.). The larvae themselves do not seem to damage the turf. However, the turf may be damaged by birds and animals foraging for larvae.

Scarabaeidae, subfamily Aphodiinae: *Diapterna pinguis*

Other names: *Aphodius pinguis*

Common name: None

Functional group: Detritivore

Pest status: None

Description: 6–7 mm in length. Head shiny black with fine punctures. Pronotum and elytra coloured as per head; pronotum with even distribution of fine punctures. Basal marginal line distinct and either complete or with a narrow interruption at middle. Scutellum large; 1/5th to 1/3rd the length of the elytra.

In common with other species of *Diapterna*, males have a characteristic 'fish-hook' structure on the last pair of legs (Fig. 63b).

Geographic distribution: Native to North America. In Canada, reported from the Northwest Territories, and from Alberta east into New Brunswick and Newfoundland and Labrador (Bousquet et al. 2013). In the United States, reported from Montana, North Dakota and Minnesota, south into northern Iowa and Nebraska (Helgesen and Post 1967; Ratcliffe and Paulsen 2008).

Seasonal adult activity: May to July.

Figure 65. *Diapterna pinguis* (Guy A. Hanley, Northern Plains Entomology).

Biology: Common to moist locations (e.g., near swamps or ponds). Adults are occasionally attracted to dung, but larvae likely develop in organically rich and moist soils (Helgesen and Post 1967).

Notes:

- Distinguished from *D. pinguella* by a distinct basal marginal line (absent in *D. pinguella*) and the even pattern of fine punctures on the pronotum (mix of fine and coarse punctures in *D. pinguella*).

Scarabaeidae, subfamily Aphodiinae: *Melinopterus prodromus*

Other names: *Aphodius prodromus*

Common name: None

Functional group: Detritivore

Pest status: None

Description: 5–8 mm in length. Head and pronotum black; scattered fine and coarse punctures. Sides of pronotum with a broad yellow margin. Elytra slightly alutaceous and shiny; yellowish; each with a large light brown spot that does not extend to the tip or base. Short stiff hairs on the elytra are particularly evident along the sides and end. Yellowish legs. Scutellum small; 1/10th to 1/8th the length of the elytra.

Geographic distribution: Introduced from Europe and now widely distributed in North America. Present in southern Canada from coast-to-coast (Floate and Gill 1998). In the United States, in states adjacent to Canada (excluding Alaska) and south to Iowa, Nebraska and Virginia (Gordon and Skelley 2007).

Seasonal adult activity: March to May, September to November (Floate and Gill 1998).

Figure 66. *Melinopterus prodromus* (H. Goulet (retired), Agriculture and Agri-Food Canada).

Biology: Information on the life history of this species has been reported for Europe (Gittings and Giller 1997; Landin 1961; White 1960). Adults fly to fresh dung in early spring, but only to feed and presumably mate. Larvae do not develop in dung. Instead, eggs are individually laid in rotting organic material (e.g., decayed vegetables, compost) in which larvae develop, pupate, and emerge as new adults in late autumn. In localities with more severe climate, adults may remain in the pupal chambers and emerge the following spring (White 1960). Observations from Ireland indicate that females overwinter without mature eggs. One generation per year.

Notes:

- Adults are general dung feeders with a preference for open pastures. Because of its distinctive colouration, it is unlikely to be mistaken for another species. Attracted to dung of horse, sheep, and cattle. Has been reared in small numbers from agricultural fields (KDF pers. obs.), possibly developing on composted manure or crop debris incorporated into the soil. Morphology of larvae described by Jerath (1960).
- Likely overlooked in many areas, due to its particularly early and late periods of adult activity. Its first report from Alberta arose from a dung-baited pitfall study (Floate and Gill 1998). With the same trapping efforts at the same sites, < 400 individuals were recovered between 20 May – 26 October (in 1993), versus about 54,000 individuals between 22 March – 30 November (in 1995).
- Overwinters as an adult (Jerath and Ritcher 1959).

Scarabaeidae, subfamily Aphodiinae: *Otophorus haemorrhoidalis*

Other names: *Aphodius haemorrhoidalis*

Common name: None

Functional group: Dweller

Pest status: None

Description: 4–6 mm in length. Head and pronotum black; moderately to densely punctate. Elytra black, but with apical 1/3rd reddish in colour. Scutellum punctate and large; 1/5th to 1/3rd the length of the elytra. Unlikely to be mistaken for any other dung beetle species in North America.

Geographic distribution: Introduced from Europe and now widely distributed in North America. Present in southern Canada from coast-to-coast (Floate and Gill 1998) and possibly wherever cattle are grazed.

Seasonal adult activity: April to October in northern latitudes (Floate and Gill 1998; Kadiri et al. 2014), with peaks in mid-June and in late July to early August (Yoshida and Katakura 1986).

Figure 66. *Otophorus haemorrhoidalis* (H. Goulet (retired), Agriculture and Agri-Food Canada).

Biology: In northern Japan, adults fly to fresh dung pats in spring, lay eggs mainly in June with larvae completing development, pupating, and emerging as new adults in late July or early August; the species overwinters as adults that mate before and after hibernation (Yoshida and Katakura 1986). The life cycle is similar elsewhere, although 3rd instar larvae are reported to be the overwintering stage in Finland (Landin 1961). One generation per year.

Notes:

- Adults are general dung feeders with a preference for open pastures and cattle dung (Gordon 1983). They may occur, however, in either exposed or shaded locations wherever suitable dung (e.g., cow, sheep, horse, etc.) is present (Landin 1961).
- Regularly collected in Canada. Adults are not attracted to lights (Yoshida and Katakura 1986).
- For larval descriptions, see Jerath (1960), Ritcher (1966), or Helgesen and Post (1967); information on nesting behaviour is provided in Vitner (1998).

Scarabaeidae, subfamily Aphodiinae: *Planolinellus vittatus*

Other names: *Aphodius vittatus*

Common name: None

Functional group: Dweller

Pest status: None

Description: 3–5 mm in length. Head and pronotum black, with a uniform pattern of small punctures. Elytra variable in colour – typically reddish-brown with a black strip down the middle and from side to side, but may range from entirely piceous (glossy brown to black) to entirely reddish brown. Scutellum small; 1/10th to 1/8th the length of the elytra.

Geographic distribution: Native to North America (but see Notes). Present in southern Canada from coast-to-coast (Floate and Gill 1998). Present throughout most of the United States south into Florida and northern Mexico (Gordon and Skelley 2007).

Seasonal adult activity: In Canada, from April to October; peak activity in spring (Kadiri et al. 2014). Year-round in more southern parts of its range.

Figure 68. *Planolinellus vittatus* (Guy A. Hanley, Northern Plains Entomology).

Biology: Adults are general dung feeders (including rodent pellets) with a preference for open pastures (Gordon and Skelley 2007). As many as 220 *P. vittatus* have been reared from one (500 gram wet weight) cattle dung pat, colonized naturally in the field (KDF unpub. data). Time to development (egg to emergence of new adults from the dung pat) averages an estimated 58 days (n = 812 beetles) at 22 °C (KDF unpub. data). Assumed to have one generation per year in Canada (KDF), but two or more generations per year in warmer climates (Cabrero-Sañudo et al. 2007; Jerath and Ritcher 1959). Overwinters as an adult (Jerath and Ritcher 1959).

Notes:

- Morphology of larvae described by Jerath (1960).
- Can be collected at lights, but not in the large numbers observed for other species of dung beetles (Ratcliffe and Paulsen 2008).
- Considered to be a species native to North America, but present in Europe and Asia (Gordon and Skelley 2007).

Scarabaeidae, subfamily Aphodiinae: *Planolinoides borealis*

Other names: *Aphodius borealis*

Common name: None

Functional group: Dweller

Pest status: None

Description: 4–6 mm in length. Head and pronotum black; pronotum uniformly punctate. Elytra dark, but usually with a small reddish area on the apical 1/3rd tip and on either side of the base (point of attachment). Scutellum small; 1/10th to 1/8th the length of the elytra.

Geographic distribution: Present through northern regions of the world (= holarctic). In Canada, reported from all provinces and territories, excluding Prince Edward Island and Nunavut (Bousquet et al. 2013).

Seasonal adult activity: April to November (Gordon and Skelley 2007).

Figure 69. *Planolinoides borealis* (Udo Schmidt – CC-BY-NC-SA).

Biology: Mainly associated with forest habitats, but occasionally recovered on open pastures. Adults are generalists and likely or are known to feed in dung of sheep, deer, elk, moose, and cattle (Gordon and Skelley 2007; Landin 1961). Landin (1961) only recovered larvae from sheep droppings, which he attributed to the preferences of adults for this type dung; larvae can be successfully reared in cattle dung. Overwinter as adults (Landin 1961).

Notes:

- Very similar to *Planolinus tenellus*. Without close examination and depending upon the degree of reddish colouration, specimens potentially also could be mistaken for *Calamosternus granarius* or for dark-coloured specimens of *Planolinellus vittatus*.

Scarabaeidae, subfamily Aphodiinae: *Pseudagolius coloradensis*

Other names: *Aphodius coloradensis*

Common name: None

Functional group: Dweller

Pest status: None

Description: 6–7 mm in length. Most of upper surface dark brown to nearly black; tip of head a paler reddish brown. Head densely punctate. Pronotum densely punctate with a mix of coarse and fine punctures. Elytra slightly alutaceous, shiny. Scutellum small; 1/10th to 1/8th the length of the elytra.

Geographic distribution: Native to North America. In Canada, reported from southern regions of Alberta, Saskatchewan and Manitoba. In the United States, present in the central and southwestern states south to Mexico City, Mexico (Blume 1985; Gordon 1976).

Seasonal adult activity: April to August.

Figure 70. *Pseudagolius coloradensis* (Guy A. Hanley, Northern Plains Entomology).

Biology: Adults are attracted to fresh cattle dung and lights (Ratcliffe and Paulsen 2008). Gordon (1976) collected many specimens at lights in a given area, but few specimens from cattle dung in the same area. From this observation, he suggested that *P. coloradensis* may preferentially feed and breed on decaying vegetation in upper soil layer.

Notes:

- Widest reported distribution of any native North American species of aphodiine dung beetle, with the exception of *Planolinellus vittatus* (Gordon 1976).

Scarabaeidae, subfamily Aphodiinae: *Teuchestes fossor*

Other names: *Aphodius fossor*

Common name: None

Functional group: Dweller

Pest status: None

Description: 8–12 mm in length. Head and prothorax shiny black, moderately punctate. Elytra shiny black. Scutellum large; 1/5th to 1/3rd the length of the elytra.

Geographic distribution: Introduced from Europe and now widely distributed in North America. Present in southern Canada from coast-to-coast (Floate and Gill 1998) and possibly wherever cattle are grazed. In Alberta, as far north as Grande Prairie (KDF unpub. data).

Seasonal adult activity: April to October. Peak recovery of adults in fresh cattle dung in late May/early June (Floate and Gill 1998; Kadiri et al. 2014).

Figure 71. *Teuchestes fossor* (H. Goulet (retired), Agriculture and Agri-Food Canada).

Biology: The reproductive biology of this species is described by Gittings and Giller (1997) and by Vitner (1998). Adults fly to fresh dung pats in spring where they feed and mate. Females form shallow chambers of < 1 cm depth in which they lay single eggs; the chambers are formed in the lower portion of the dung pat or in the soil immediately below the dung pat (Vitner 1998). Newly-hatched larvae feed within the dung pat, complete larval development, and pupate in the soil. Pupae become adults in autumn, but the new adults typically do not feed or fly prior to overwintering. One generation per year.

Notes:

- Adults are general dung feeders with a preference for open pastures and cattle dung (Gordon 1983). One of the most common dung beetles in Canada and, by virtue of its large size, unlikely to be mistaken for another species.
- Adults are not attracted to lights (Ratcliffe 1991).
- Egg-to-adult development in 40–55 days at 19–20 °C (Gittings and Giller 1997); a female can lay at least 50 eggs (Vitner 1998).
- Adults that colonize fresh dung remain in the pat for a longer period as it ages, relative to other dung beetle species (Holter 1982).

Scarabaeidae, subfamily Scarabaeinae: *Canthon pilularius*

Other names: *Canthon laevis*

Common name: None

Functional group: Roller

Pest status: None

Description: 12–17 mm in length. Head, pronotum and elytra black, occasionally with a weak purple or bronze hue; upper surface with a dense pattern of large and small granules intermixed. The clypeus is characterized by two small teeth (= bidentate; see arrows in Fig. 72). The scutellum is not visible. The elytra leave the last abdominal segment (the pygidium) exposed. Unlikely to be mistaken for any other dung beetle species in western Canada by virtue of its large size.

Geographic distribution: Native to North America. In Canada, reported from southern regions of Alberta and Saskatchewan (Bousquet et al. 2013). In the United States, reported from essentially all states east of the Rocky Mountains (Blume 1985).

Seasonal adult activity: May into October. Peak recovery of adults in cattle dung in mid-May to mid-June and again in September (Kadiri et al. 2014).

Figure 72. *Canthon pilularius* (H. Goulet (retired), Agriculture and Agri-Food Canada).

Biology: Overwinter as adults. The biology of this species is reported by Lindquist (1935) and Ritcher (1966), the former referring to this species as *Canthon laevis*. Adults fly to fresh deposits of horse, sheep, cattle or bison dung. The adults remove dung from the deposit, form it into a ball (2–3 cm diameter), roll the dung ball away from the deposit, and then bury it in a tunnel 5–10 cm in depth; there is only one ball per tunnel. The female makes a cavity on the surface of the buried dung into which she lays an egg that is covered by a layer of soil to give the dung ball a pear-shape. In Canada, one generation per year.

Notes:

- Typically associated with open habitats; may have evolved in association with bison, but readily uses dung of cattle (Lindquist 1935; Tiberg and Floate 2011).
- Stone et al. (2021) reports recovery of large numbers in traps baited with carrion; presumably in response to the release of volatile organic compounds that the beetles associate with dung.
- On a 'per beetle' basis, probably the most effective species in Canada for dung removal. Lindquist (1935) reports from 50 to up to 600 beetles congregating in dung pats. Assuming 200 burrows per acre (Lindquist 1935), this equates to the burial of about 9.5 kg of air-dried dung and about 57 kg of excavated soil per acre (Cooper 1938).

Notes (continued):

- Eggs hatch in 4–8 days, the pupal period is 10–14 days; time from egg hatch to adult emergence under laboratory conditions ranges from 29–44 days (Lindquist 1935).
- Detailed observations (with illustrations) on the formation, rolling and burial of dung balls are provided by Matthews (1963).

Scarabaeidae, subfamily Scarabaeinae: *Canthon praticola*

Other names: *Canthon vetustus*

Common name: None

Functional group: Roller

Pest status: None

Description: 5–10 mm in length. Head, pronotum and elytra black. Pronotum and elytra with dense pattern of small granules intermixed with larger granules. The clypeus is characterized by four small teeth (= quadridentate; see arrows in Fig. 73). The scutellum is not visible. The elytra leave the last abdominal segment (the pygidium) exposed.

Geographic distribution: Native to North America. In Canada, reported from southern British Columbia east into Manitoba (Bousquet et al. 2013). In the United States, extending south from Canada through the central states into Texas and Arizona (Ratcliffe and Paulsen 2008).

Seasonal adult activity: Early May into October (Kadiri et al. 2014).

Figure 73. *Canthon praticola* (H. Goulet (retired), Agriculture and Agri-Food Canada).

Biology: Little is known about the biology of this species. In Canada, one generation per year.

Notes:

- Can be collected from cattle dung, but has a preference for dung of prairie dogs, *Cynomys ludovicianus* (Gordon and Cartwright 1974).

Scarabaeidae, subfamily Scarabaeinae: *Copris fricator*

Other names: *Copris cartwrighti, Copris tullius*

Common name: None

Functional group: Tunneller

Pest status: None

Description: 10–18 mm in length. Head, pronotum and elytra black. Clypeus with a median notch; rear angles of the head are acute (Fig. 74a). Upper surface of the head and the pronotum are densely punctured. On the elytra, punctures are reduced or absent and the striae are shallow and broad. The scutellum is not visible.

The head of large males (male majors) carries a spike-like horn that may curve slightly backwards; the pronotum has a median pair of prominent protuberances with an additional protuberance on either side (Fig. 74b). These features on small males (male minors) are reduced or lacking.

Geographic distribution: Native to North America. In Canada, reported from southernmost regions of Ontario and Quebec (Bousquet et al. 2013). Present in central and northeastern regions of the United States (Matthews 1961).

Seasonal adult activity: Using the name *Copris tullius*, Lindquist (1933) reported peak activity of adults in Kansas in the United States to occur from May through June, and then again through September into October.

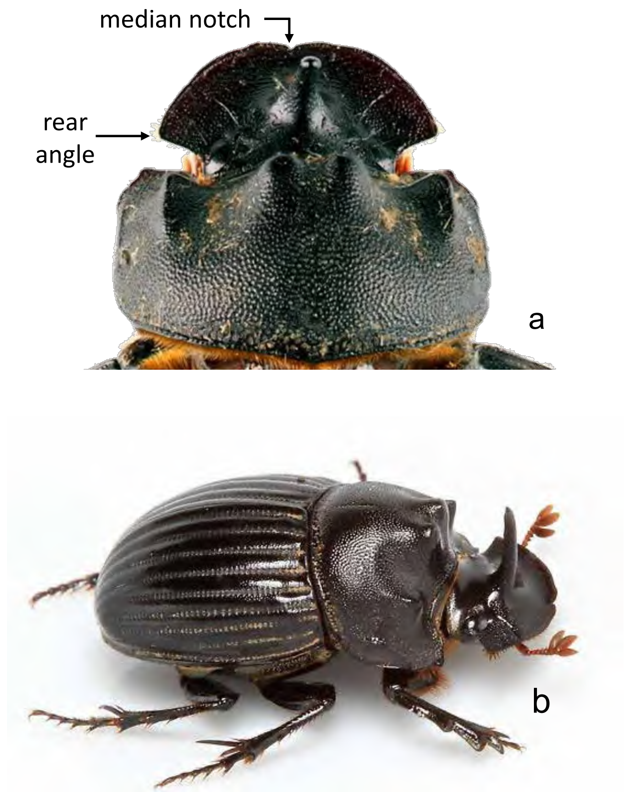


Figure 74. *Copris fricator* (♂). a – dorsal view of head showing the median notch of the clypeus and the acute rear angle of the head (© Tim Christensen); b – side profile providing a better view of the horn on the head and protuberances on the pronotum (© Marlin E. Rice).

Biology: The biology and nest-building (nidification) behaviour of this species is described by Lindquist (1933) (as *C. tullius*) and by Matthews (1961). Adults emerge in spring from overwintering tunnels devoid of dung and which extend vertically to an average depth of about 20 mm. Working independently, adults feed on fresh cattle dung that they first bury in a shallow chamber beside or below the deposit. Nest-building behaviour occurs later in spring, with male and female beetles working together to bury a single mass of dung in nests 5–12 cm below the soil surface. The female shapes this dung into several brood balls, each with a small cavity in which she deposits one egg. The female remains in the nest during larval development to maintain the integrity of the brood balls, which otherwise become overgrown with mold.

Notes:

- For each nest, the average weight of soil removed, and dung buried, is 38 and 7 grams, respectively (Lindquist 1933).
- Whereas feeding and nesting chambers are located beside or under the pat, overwintering tunnels are often located up to several meters away from the deposit (Lindquist 1933)
- *Copris minutus* is the only other species in this genus reported to occur in Canada (in southernmost Quebec). It can be distinguish from *C. frictator* using morphological features described in Matthews (1961).

Scarabaeidae, subfamily Scarabaeinae: *Onthophagus hecate*

Other names: None

Common name: Scooped scarab

Functional group: Tunneller

Pest status: None

Description: 5–10 mm in length. Head, pronotum and elytra dull purplish-black. Head with fine scattered punctures. Pronotum with dense pattern of small oblong tubercles (= bumps; each associated with a short stiff hair (Fig. 75a). Elytra with tubercles, each associated with a small stiff hair. All hairs are whitish, many may be broken off in older specimens. The scutellum is not visible. Unlikely to be mistaken for any other dung beetle species in Canada.

The forward edge of the pronotum in large males (male majors; 8–10 mm) forms a flattened shelf-like projecting extending over the head (Fig. 75b). This projection is underdeveloped in small males (male minors; 5–8 mm) and may be barely visible. Females (6–8 mm) lack the projection.

Geographic distribution: Native to North America. In Canada, reported from southern locations in all provinces east of British Columbia excluding Newfoundland and Labrador; recorded from all states in the United States, excluding Oregon, Washington, California and Nevada (Howden and Cartwright 1963).

Seasonal adult activity: April to October in northern parts of its range; peak recovery of adults in cattle dung in late May to early June with a larger peak in August and September (Rounds and Floate 2012).

Figure 75. *Onthophagus hecate* (♂). a – dorsal view (Guy A. Hanley, Northern Plains Entomology); b – side view (© Kevin Stohlgren).

Biology: Limited information is provided by Lindquist (1933) and by Ritcher (1966). Adults colonize fresh dung pats in spring. Females form tunnels beneath the pat that extend to depths of 5–23 cm; tunnels are nearly vertical but are bent at the end to form a short horizontal chamber. Dung is packed into this chamber to form a brood ball (the dung mass) with a single egg laid adjacent to it. The larva that hatches from the egg feeds on the dung, completes its development and then pupates within the remnants of the brood ball. The new generation of adults emerges from the soil in late summer. In Canada, one generation per year.

Notes:

- The most widely distributed species of *Onthophagus* in North America and one of the most common (Ratcliffe and Paulsen 2008).
- Preference for cattle dung, but also commonly attracted to dung of humans, horses, rabbits and dogs; adults also attracted to light, rotting fungi and fruit (Howden and Cartwright 1963); Stone et al. (2021) reports recovery of large numbers in traps baited with carrion.
- Dimensions of brood balls have been reported to average 17 x 8.5 mm, with an average weight of 0.26 g (Lindquist 1933).

Scarabaeidae, subfamily Scarabaeinae: *Onthophagus nuchicornis*

Other names: *Onthophagus rhinoceros*

Common name: None

Functional group: Tunneller

Pest status: None

Description: 6–8 mm in length. Head and pronotum black; densely punctate, each puncture with a short stiff hair. Elytra light brown with black mottling. The scutellum is not visible. Unlikely to be mistaken for any other dung beetle species in Canada.

Large males (male majors; 7–8 mm) have a pronounced horn that projects upward from the center back of the head (Fig. 76b). Small males (male minors; 6–7 mm) have an underdeveloped horn that may be barely visible. Females (6–8 mm) lack the horn (Fig. 76c).

Geographic distribution: Introduced from Europe and now widely distributed in southern Canada and the northern United States; likely present wherever cattle are grazed (Floate et al. 2017).

Seasonal adult activity: April to October. Peak recovery of adults in cattle dung in May to early June with a larger peak in August and September (Floate and Gill 1998; Kadiri et al. 2014; Rounds and Floate 2012).

Figure 76. *Onthophagus nuchicornis.* a – dorsal view (♂); b – side view (♂); c – side view (♀) (H. Goulet (retired), Agriculture and Agri-Food Canada).

Biology: Burmeister (1930) and von Lengerken (1954) provide detailed descriptions of this species' life history (in German). Adults arrive at fresh dung pats in spring. Females form branched tunnels beneath the pat to a depth of about 5 to 15 cm. The female packs the end of a branch (i.e., a 'cell') with dung until it is almost full to form a brood ball (the dung mass). She then forms a small cavity at the end of the brood ball in which she lays a single egg. The top of the cavity is covered with dung and soil, the remainder of the cell is filled with soil, and the entire process then repeated in another cell. The larvae that hatch from the eggs feed on the dung, complete their development and then pupate within the cell. The new adults emerge in early autumn to feed on fresh dung before overwintering. One generation per year.

Notes:

- Present in northeastern North America prior to the 1840s, but unknown from western North America until specimens were collected in 1945 in British Columbia (Hatch 1971). The species has since spread east into the Prairie Provinces and adjacent states (Floate and Gill 1998; Floate et al. 2017; Hoebeke and Beucke 1997; Howden and Cartwright 1963; Tinerella and Fauske 1999). Now one of the most common dung beetles in Canada.

- The formation of one brood ball removes about 2.5 g of fresh dung from the cow pat (Macqueen and Beirne 1975a). Studies indicate that the burial of dung by *O. nuchicornis* on pastures is unlikely to reduce horn fly populations (Macqueen and Beirne 1975a), but does enhance levels of soil nitrogen and subsequent plant growth (Macqueen and Beirne 1975b).
- Preference for cattle dung, but also associated with dung of horses, sheep, and dog.
- Common in its North American range, this European species is in decline or extirpated in much of its native range (Bistrom et al. 1991; Coope 2000; Lane and Mann 2016).
- Introduced into Hawaii to accelerate the degradation of cattle dung, but failed to establish (Legner 1978). This failure may reflect the requirement for a cold period, corresponding to the winter months of its native range, which *O. nuchicornis* survives by entering an obligatory diapause (Floate et al. 2015).

Scarabaeidae, subfamily Scarabaeinae: *Onthophagus taurus*

Other names: *Smith (2009) lists 23 other names by which this species has been formerly known*

Common name: Bull-headed dung beetle

Functional group: Tunneller

Pest status: None

Description: 6–11 mm in length. Head and pronotum dull black, occasionally with a faint metallic reflection; dense pattern of punctures. Elytra dull black, but also may have a brown or reddish hue. The scutellum is not visible.

Large males (male majors) have two large curved horns that project upward from the center back of the head (Fig. 77a). Small males (male minors) have much shorter underdeveloped horns or horns may be absent; females lack horns (Fig. 77b).

Geographic distribution: Introduced from Europe. Not reported from Canada, but may be present in southern Ontario and Quebec (see Notes). In the western United States, reported from California. In the eastern United States, reported from Texas, Arkansas, Missouri and Michigan east to the Atlantic Ocean (Floate et al. 2017).

Seasonal adult activity: : In Michigan, from May into early October (Rounds and Floate 2012). In North Carolina, from March to late November (Bertone et al. 2005).

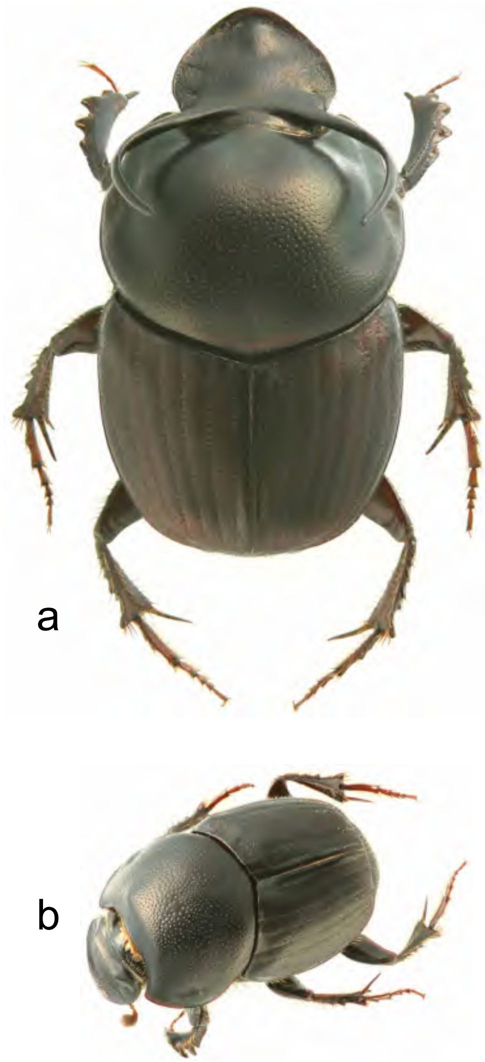


Figure 77. *Onthophagus taurus*. a – dorsal view (♂); b – side view (♀) (H. Goulet (retired), Agriculture and Agri-Food Canada).

Biology: Adult beetles colonize fresh dung pats to mate and feed on microorganisms. Beetles remove portions of dung from the pat and pack it into the blind end of tunnels constructed beneath the pat. An egg chamber is formed within the packed mass of dung into which one egg is laid. The chamber is then sealed with an excrement cap. The egg and the associated mass of dung form the 'brood ball'. No further care is given to the offspring, and each brood ball constitutes the total quantity of food available to a single larva.

In the laboratory, soil temperatures above 14 °C are required to complete development; average egg-to-adult development times range from 25 (at 30 °C) to 105 days (16 °C) (Floate et al. 2015; Wardhaugh et al. 2001). Under optimum conditions, females attain sexual maturity in about 1–2 weeks and will lay 1–2 eggs daily for four or more weeks. One generation per year in more northern localities; multiple generations further south.

Notes:

- Preference for open pastures and cattle dung, but also attracted to dung of horses, sheep, dog, and other animal species.
- First recovered in North America in 1971 (in Florida), presumed to have been accidentally introduced onto the continent (Fincher and Woodruff 1975), and now widely-distributed in the eastern United States and California (Floate et al. 2017).
- Deliberately relocated to different locations in the United States (Hoebeke and Beucke 1997) and different countries to accelerate the degradation of dung on pastures (Tyndale-Biscoe 1990).
- Can overwinter and reproduce in field cages in southern Alberta, but the death rate exceeds the birth rate such that populations cannot establish (Floate et al. 2015). The recovery of *O. taurus* in northern Michigan (Rounds and Floate 2012) supports predictions for its establishment in southern regions of Ontario and Quebec (Floate et al. 2017)

Table 4. Checklist, size and Canadian distribution for coprophilous species of Scarabaeidae[1]. Species identified in bold font are expected to regularly occur in fresh cattle dung, particularly in open (untreed) pastures. Other species are either occasional visitors to fresh cattle dung or information is insufficient to make a determination.

Genus	Species	Length (mm)	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
						Subfamily Aphodiinae							
Acrossus	*rubripennis*	6–9					ON	QC	NB	NS			
Acrossus	*rufipes*[*]	10–13					ON	QC					
Agoliinus	*albertanus*[2,3]	5–6	BC	AB	SK								
Agoliinus	*aleutus*	5–8	BC	AB									
Agoliinus	*anthracus*	6–10		AB									
Agoliinus	*bidentatus*	6–8	BC	AB	SK		ON						
Agoliinus	*congregatus*	5–8	BC	AB									
Agoliinus	*guttatus*[3]	4–7	BC	AB	SK	MB	ON	QC		NS			
Agoliinus	***leopardus***[2,3]	5–7	BC	AB	SK	MB	ON	QC	NB	NS			NF
Agoliinus	*manitobensis*	4–5		AB		MB	ON	QC	NB	NS			
Agoliinus	*sigmoideus*	8–11	BC										
Aphodius	***pedellus***[2,*]	6–10	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
Ataenius	*spretulus*	3–5					ON	QC					
Ataenius	*strigatus*	4–6					ON	QC	NB				
Blackburneus	*lentus*	3–5					ON	QC					
Blackburneus	*rubeolus*	3–5					ON						
Blackburneus	*stercorosus*	3–5					ON	QC					
Calamosternus	***granarius***[*]	3–6	BC	AB	SK	MB	ON	QC	NB	NS			
Chilothorax	***distinctus***[*]	4–6	BC	AB	SK	MB	ON	QC	NB	NS			
Colobopterus	***erraticus***[*]	6–8		AB	SK	MB	ON	QC	NB	NS			NF
Diapterna	***hamata***	5–8	BC	AB	SK	MB	ON	QC					
Diapterna	***omissa***[2,3]		BC	AB	SK	MB	ON		NB				
Diapterna	***pinguella***	5–7	BC	AB	SK	MB							
Diapterna	***pinguis***[2]	6–7		AB	SK	MB	ON	QC	NB				NF
Drepanocan-thoides	*walshii*	5–6		AB	SK	MB							
Eupleurus	*subterraneus*[*]	7					ON	QC	NB	NS			
Melinopterus	*femoralis*	4–6		AB[5]			ON	QC					
Melinopterus	***prodromus***[*]	5–8	BC	AB	SK	MB	ON	QC	NB	NS	PE		
Oscarinus	*rusicola*	3–5		AB	SK	MB	ON	QC	NB	NS			NF
Otophorus	***haemorrhoidalis***[*]	4–5	BC	AB	SK	MB	ON	QC	NB	NS			NF
Planolinellus	***vittatus***[*]	3–4	BC	AB	SK	MB	ON	QC	NB	NS		LB	
Planolinoides	***borealis***[2,3]	4–6	BC	AB	SK	MB	ON	QC	NB	NS		LB	NF
Planolinus	*tenellus*[2,3]	4–6	BC	AB	SK	MB	ON	QC					
Pseudagolius	*bicolor*	5–7					ON	QC					
Pseudagolius	***coloradensis***	5–8		AB	SK	MB							
Tetraclipeoides	*denticulatus*	5–8		AB									
Teuchestes	***fossor***[*]	8–12	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
Trichonotulus	*scrofa*[*]	3–4					ON	QC	NB				NF

Table 4 (continued). Checklist, size and Canadian distribution for coprophilous species of Scarabaeidae[1]. Species identified in bold font are expected to regularly occur in fresh cattle dung, particularly in open (untreed) pastures. Other species are either occasional visitors to fresh cattle dung or information is insufficient to make a determination.

Genus	Species	Length (mm)	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
						Subfamily Scarabaeinae							
Canthon	***praticola***	5–10	BC	AB	SK	MB							
Canthon	*simplex*	5–8	BC	AB									
Canthon	*chalcites*	14–19					ON						
Canthon	***pilularius***	12–17		AB	SK								
Canthon	*vigilans*	13–20					ON						
Canthon	*viridis*	3–5					ON						
Copris	***fricator***	10–18					ON	QC					
Copris	*minutus*	8–13						QC					
Melanocanthon	*bispinatus*	6–10					ON						
Onthophagus	***hecate***	5–10	BC	AB	SK	MB	ON	QC	NB	NS			
Onthophagus	***nuchicornis***[*]	6–8	BC	AB	SK	MB	ON	QC	NB	NS			NF
Onthophagus	*pennsylvanicus*	4–5					ON						
Onthophagus	***taurus***[4,*]	6–11											

[1] Species list and distributions are from Bousquet et al. (2013); size measurements are from Howden and Cartwright (1963), Gordon and Skelley (2007), and Ratcliffe and Paulsen (2008).

[2] Also reported from the Northwest Territories.

[3] Also reported from the Yukon Territory.

[4] Not yet reported in Canada, but expected to occur in southern ON and QC if not already present.

[5] Reported in Bezanson (2019).

[*] Exotic.

Staphylinidae (rove beetles)

Represented in Canada by over 1,800 species, staphylinids are the most diverse group of beetles in the country (Brunke et al. 2019). The length of some species may reach 35 mm, but for most species is 2–8 mm. Colouration may range from black to reddish-brown or yellowish. The body may be smooth or covered with a dense layer of hairs. Despite this diversity, most staphylinids generally can be distinguished from other species of beetles by the following combination of characteristics: i) adults have long and generally narrow bodies (but sometimes oval), ii) threadlike antennae (but sometimes moderately clubbed), and iii) short elytra that leaves most of the flexible abdomen exposed (Fig. 78).

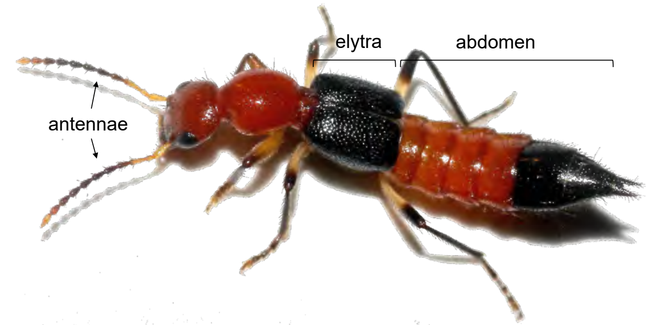


Figure 78. *Paederus gratiosus* (Satish Nikam – CC-BY-NC-SA-2.0).

Staphylinids occur almost anywhere and feed on almost everything excluding (with rare exception) the living tissues of vascular plants. Larvae pass through two or three instars, pupate, and then emerge as adults. The larvae and adults of predatory species have well-developed legs and actively search their environment for suitable prey items (Fig. 79). In dung pats, such items include mites, nematodes, immature insects (eggs, larvae, pupae), adult flies and beetles, and even other staphylinids. A notable exception to this general lifecycle is exhibited by species in the genus *Aleochara*, whose larvae are parasitoids of fly pupae (Maus et al. 1998). Many other species feed on pollen, fungi and decaying organic matter.

Figure 79. Staphylinid larva (Katja Schulz – CC-BY-2.0). The thin paired appendages attached to the last segment of the abdomen are termed cerci (singular cercus). They usually have a sensory function and are common to many species of insects.

Very few, if any, staphylinids strictly rely on dung for survival, but many species are attracted to dung to feed and breed. Adults arrive by flight and use crevices or holes formed by other insects to penetrate into the dung in search of food and breeding sites. The arrival and residency times of adult staphylinids attracted to fresh cattle dung was studied at length by Koskela (1972). He found that the species attracted to fresh dung was strongly influenced by the surrounding environment. Thus, dung of the same age in forested versus open pastures attracted a different but overlapping set of species. He also found that numbers of adult staphylinids was highest in dung aged 2–8 days, but peaked in dung aged 4 days (and see Hunter et al. 1986). He further identified five general groups of staphylinid species, based on their preference for dung of a certain age. Arrival and residency times partially reflect the availability of food items (Koskela 1972) which, for many staphylinid species, includes the eggs and young larvae of flies. Most of these flies oviposit in fresh dung with their eggs hatching in 1–2 days and larvae becoming pupae in 1–3 weeks. The pupae of muscoid-type flies are coarctate, meaning that they develop inside the final skin of the last instar larva which forms a hard-walled puparium to protect the pupa from predators (Fig. 16d). Because of this rapid chain of events, the preferred food for staphylinids is most abundant in dung aged < 1 week (Hammer 1941; Laurence 1954; Mohr 1943).

Identifying staphylinids can be difficult. Many species are quite small, similar in size and shape, and require close examination of morphological features under a microscope. Suitable keys are lacking for some groups or are woefully out of date. Partially for these reasons, the value of staphylinids as bioindicators of environmental change is rarely realized despite their abundance and diversity in many different habitats (Bohac 1999). In Finland, 133 species of staphylinids (ca. 50,000 individuals) were recovered from cattle dung over a 30-day period (Koskela 1972). In Minnesota, 31 species of staphylinids comprised 25% of the total number of insects (n = 52,520 individuals) recovered from cattle dung at two sites from mid-May through October (Cervenka and Moon 1991).

In Canada, there are at least 87 species of staphylinids that are identified in the literature as coprophilous. These include members of the subfamilies Aleocharinae, Omaliinae, Oxytelinae, Paederinae, Pselaphinae, Staphylininae and Tachyporinae (Table 5). Most of these species are infrequently recovered from fresh dung and are probably more attracted to rotting organic material than specifically to fresh dung. The remainder of these species – mainly Aleocharinae, Oxytelinae and Staphylininae – are repeatedly reported from dung, often in large numbers (Cervenka and Moon 1991; Floate 1998b; Koskela 1972; Paliy et al. 2020; Sanders and Dobson 1966; Skidmore 1991; Valiela 1969).

Taxonomic keys available to help identify specimens include those of Klimaszewski (2000) (limited to subfamilies in Canada and Alaska), Newton et al. (2001) (limited to subfamilies and genera in North America north of Mexico) and Brunke et al. (2011) (limited to subfamilies in eastern Canada and adjacent states, and to species of Staphylininae in subtribe Staphylinina). The latter key is free online and well-illustrated with photographs. Other references that may prove useful include Moore and Legner (1979) and Seevers (1978).

Staphylinidae: Subfamily Aleocharinae

Members of this diverse subfamily can be distinguished from almost all other species of staphylinids by the point at which the antennae attach to the head. When viewed from directly above, the antennae of aleocharines can be seen to be attached on the surface of the head between the eyes, and either slightly behind or level with an imaginary line extending across the front margin of the eyes (Fig. 80a). In contrast, species of staphylinids in other subfamilies (except Steninae) have antennae that, when viewed directly above, can be seen to be attached in front of the eyes and often on the sides of the head (Fig. 80b). The typical aleocharine has a roundish head with a slender body that may be densely punctured. Body colour may be black, reddish-brown, light to dark brown or occasionally with contrasting colours of black, red or yellow. Aleocharines are tiny to small beetles, typically 2–6 mm in length (range of 1–15 mm).

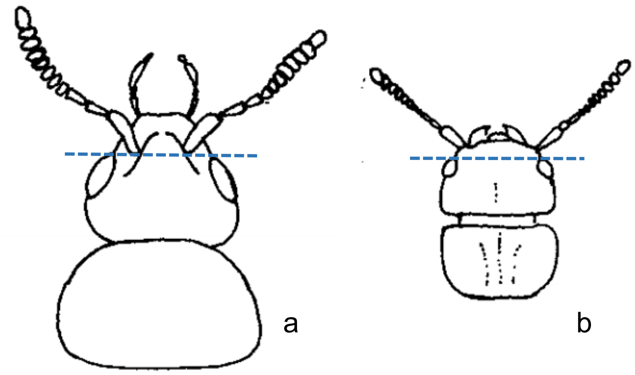


Figure 80. Antennal attachment of Aleocharinae (a) versus other staphylinid species (b). Image modified from Skidmore (1991) Insects of the cow dung community. Field Studies Council, Shrewsbury, UK.

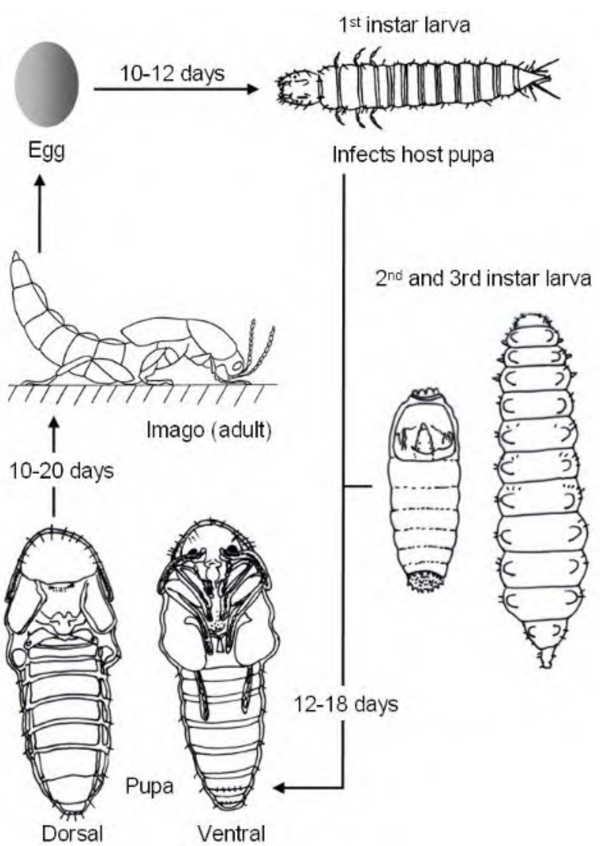


Figure 81. Life cycle of *Aleochara bilineata*. (www.cronodon.com)

Many species of aleocharines are predators. They are common in moist rotting organic material (including dung) where there is an abundance of the fly larvae and other soft-bodied insects upon which they feed. The larvae of *Aleochara* species are unusual among staphylinids in that they are ectoparasitoids (Fig. 81). A newly-hatched 1st instar larva will chew a small hole through the wall of a host fly puparium to penetrate inside. Once inside the puparium, the larva feeds externally on the fly pupa and continues to grow, first moulting to become a 2nd instar and then moulting again to become a 3rd instar. Depending upon the *Aleochara* species, the mature 3rd instar larva will either pupate inside the fly puparium, or exit the puparium to form a cavity nearby in the dung or underlying soil in which to pupate and ultimately to complete development and emerge as an adult (= imago).

Because they feed on all immature life stages of flies (eggs, larvae, pupae), some species of *Aleochara* have been extensively studied as biological control agents of pest flies that affect crop and livestock production (Fournet et al. 2000; Greene 1997; Wright and Muller 1989). Colhoun (1953) describes the biology of *Aleochara bilineata*, which overwinters as a 1st instar larvae inside the fly puparium. Whistlecraft et al. (1985) reports a method for the mass-production of 10,000 adult *A. bilineata* per week.

Among the subfamilies of Staphylinidae, subfamily Aleocharinae contains the greatest number of species. In Canada and Alaska, over 600 species in 125 genera are known and many more species are likely to be reported (Brunke et al. 2021; Klimaszewski 2000; Klimaszewski et al. 2021). Aleocharines associated with cattle dung include species of *Aleochara, Autalia* and *Falagria* (Table 5). Species-level keys are provided for *Aleochara* by Klimaszewski (1984), for *Autalia* by Hoebeke (1988) and for *Falagria* by Hoebeke (1985).

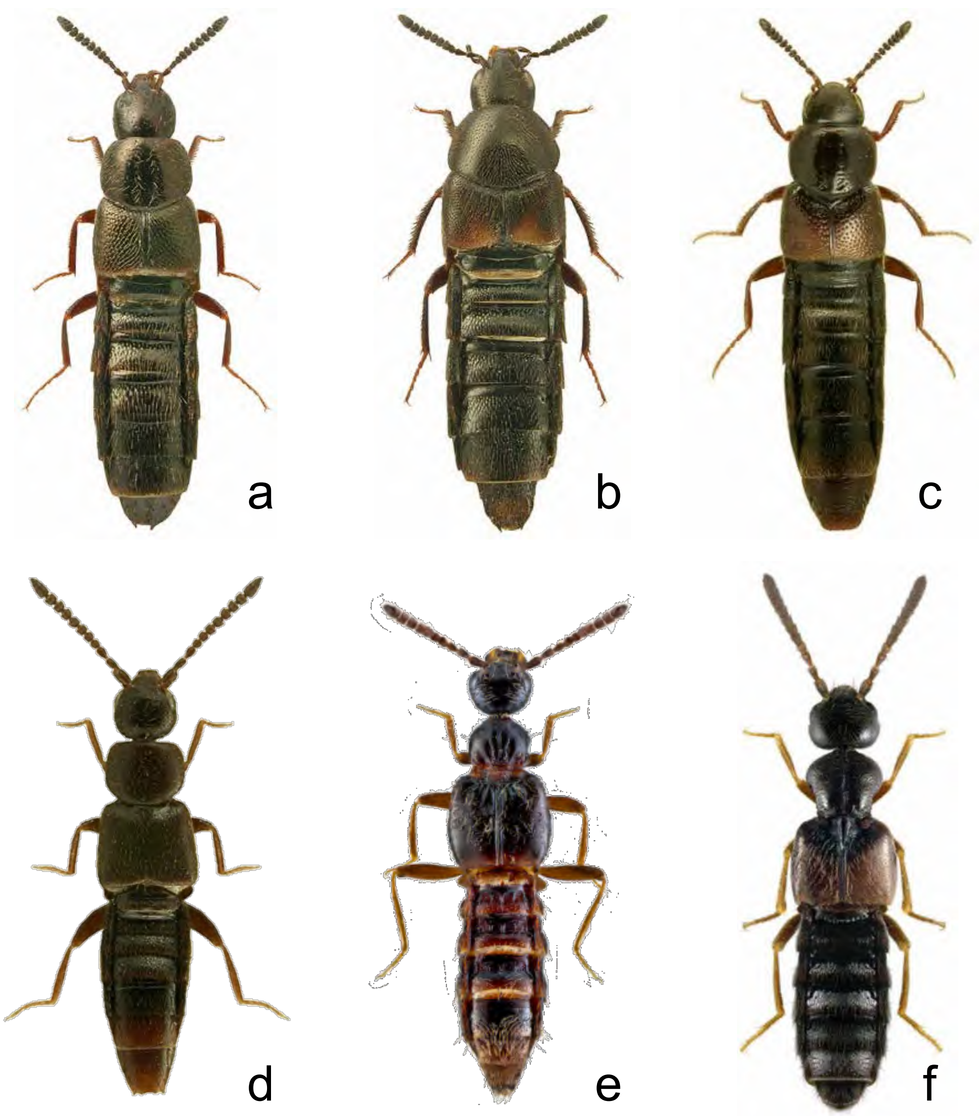


Figure 82. Subfamily Aleocharinae. a – *Aleochara bilineata*; b – *Aleochara bimaculata*; c – *Aleochara verna*; d – *Atheta nigra*; e – *Autalia rivularis*; f – *Falagria caesa*. Photos a-d and f (© Lech Borowiec); photo e (Udo Schmidt – CC-BY-NC-SA).

Staphylinidae: Subfamily Omaliinae

Omaliines can be readily identified by the presence of a pair of simple eyes or ocelli (singular = ocellus) that is positioned behind the compound eyes and present in most (but not all) members of this subfamily (Fig. 83). Body length ranges from 2–6 mm and, compared to most other species of staphylinids, is broader with a shorter and less flexible abdomen. Several genera of omaliines have species with relatively long elytra that, in some cases, may completely cover the abdomen (Newton et al. 2001).

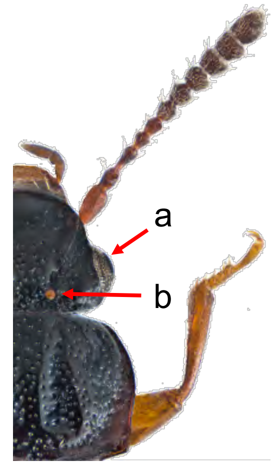


Figure 83. Head of an omaliine. a – compound eye; b – ocellus (© Udo Schmidt (CC BY-NC-SA).

Omaliines are common across North America, living in organic detritus on the forest floor, in grasslands or in wetland and riparian habitats. Most species are thought to be predators or omnivorous. However, some species may feed solely on pollen or are saprovores.

There are about 132 species of omaliines in 44 genera known from Canada and Alaska (Bousquet et al. 2013). These can be identified to genera using keys in Newton et al. (2001). Three of these species are reported to be associated with dung; i.e., *Omalium rivulare, Phyllodrepa floralis* and *Xylodromus concinnus* (Klimaszewski and Brunke 2018).

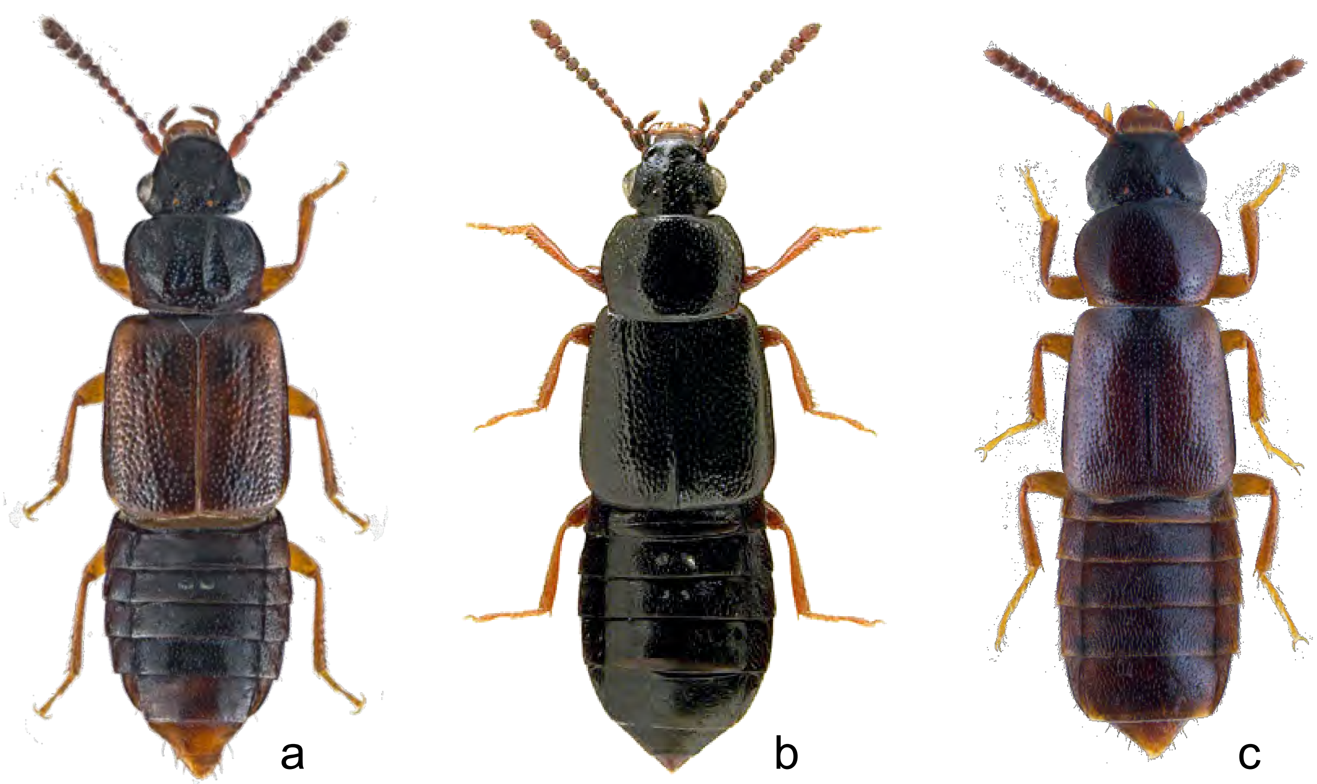


Figure 84. Subfamily Omaliinae. a – *Omalium rivulare* (Udo Schmidt – CC-BY-NC-SA); b – *Phyllodrepa floralis* (© Lech Borowiec); c – *Xylodromus concinnus* (Udo Schmidt – CC-BY-NC-SA).

Staphylinidae: Subfamily Oxytelinae

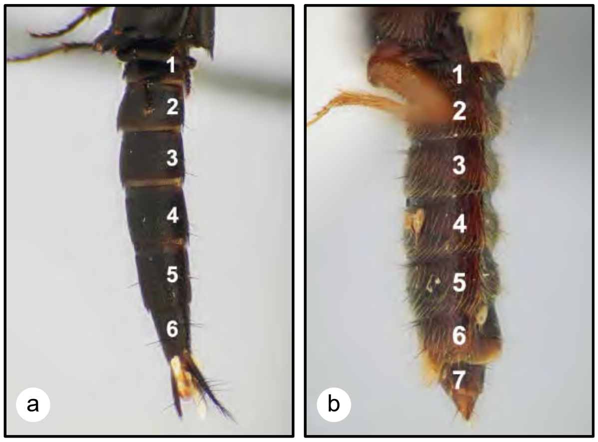


Figure 85. Number of abdominal sternites for: a – species in subfamily Staphylininae; b – species in subfamily Oxytelinae (b). Reprinted with permission from Brunke et al. (2011).

Abdominal sternites can be used to distinguish members of subfamily Oxytelinae (spiny-legged rove beetles) from most other species of staphylinids. A sternite is the ventral or underside of a segment that forms part of an insect's body. Most species of staphylinids have six fully developed and visible sternites (Fig. 85a). In contrast, most species of oxytelines have seven fully developed and visible sternites (Fig. 85b). In addition, the legs of oxytelines – particularly the forelegs – may be modified for tunnelling; the legs of most other staphylinid species are adapted for running or walking, (Klimaszewski 2000). The point at which the antennae are inserted onto the head is often located under a prominent ridge (Klimaszewski 2000). Oxytelines are tiny to small beetles, usually 3–4 mm in length (range of 1–10 mm) with well-developed mandibles. Their bodies are often broad and strongly flattened (top to bottom), with ridges or other sculpture. Body colour can be variable, but is typically black to brown.

Most members of this subfamily feed on living or decaying plant material (Klimaszewski 2000). In dung, oxytelines probably feed on bacteria and fungi, although they also may be facultative predators (Skidmore 1991). Hu and Frank (1995) studied the biology of the oxyteline *Platystethus americanus*. When reared in dung in the absence of potential prey items, *P. americanus* completed egg-to-adult development to show that dung, or fungi growing in the dung, provided an adequate diet. However, both larval and adult *P. americanus* consumed immature flies when provided the opportunity.

In Canada and Alaska, at least 83 species in 14 genera of oxytelines are known (Klimaszewski 2000). Oxytelines reported to be associated with cattle dung include species of *Anotylus, Oxytelus* and *Platystethus* (Table 5). *Platystethus americanus* is the only species listed for the latter genus, but it is often among the most abundant species of staphylinid recovered from dung (Cervenka and Moon 1991; Floate 1998b; Matheson 1987).

Species-level keys are provided for *Oxytelus* by Frank and Thomas (1981) and for *Platystethus* by Moore and Legner (1971). Klimaszewski et al. (2013) can be used to help identify species of *Anotylus* adventive in Canada.

Figure 86. Subfamily Oxytelinae. a – *Anotylus tetracarinatus* (© Lech Borowiec); b – *Oxytelus sculptus* (© Lech Borowiec); c – *Platystethus spinosus* (Udo Schmidt – CC-BY-NC-SA).

Staphylinidae: Subfamily Paederinae

Members of this subfamily mainly range in size from 3–7 mm. They have elongate bodies that are cylindrical or partially flattened. The head may be broadly oval or somewhat rectangular in shape. The antennae are attached near the forward margin of the head with the point of attachment concealed when viewed from above. The mandibles are curved, long and slender. The back of the head may be somewhat truncated and is attached to a distinct neck. The abdomen have six visible sternites (Fig. 85a). Body colour ranges from blackish-brown to reddish; some species may be brightly coloured (Fig. 78) and (or) spotted (e.g., blue, green, red, orange).

Paederines are predators with wide distribution in North America and associated with damp habitats; e.g., forests or near bodies of water (Thayer 2016). Frank and Kanamitsu (1987) review the taxonomy, biology and agricultural/medicinal importance of species in the genus *Paederus*. Members of this genus produce the chemical pederin that, when placed in contact with skin, can cause symptoms ranging from a skin rash (erythema) to fever and neuralgia and scars that may persist for more than a month. In Canada, however, no species of paederines appear to induce severe symptoms. Experimental studies indicate that pederin is biosynthesised by symbiotic bacteria living within the insect host (Kellner 1999; Kellner 2002).

There are at least 113 species of paederines known from Canada and Alaska (Bousquet et al. 2013; Pentinsaari et al. 2019). Paederines reported to be associated with cattle dung include species of *Lithocharis, Lobrathium* and *Rugilus* (Table 5). Species-level keys are provided for *Lithocharis* by Klimaszewski et al. (2013) and for *Lobrathium* by Casey (1905) and Watrous (1980).

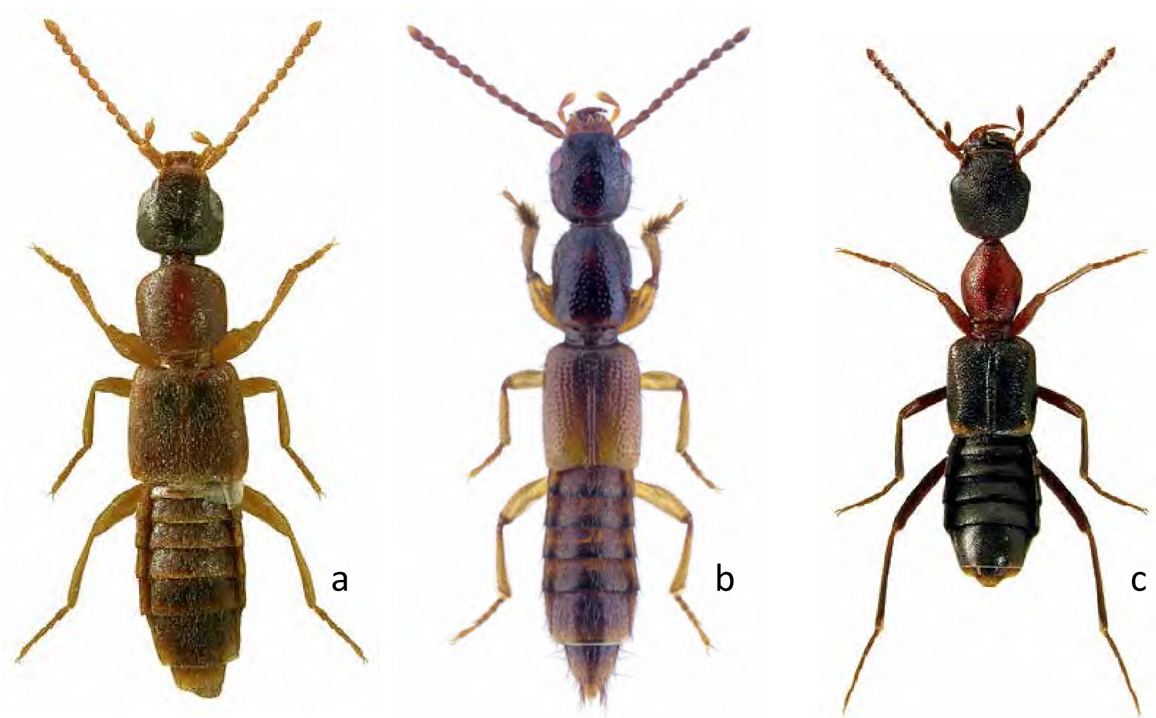


Figure 87. Subfamily Paederinae. a – *Lithocharis ochracea* (© Lech Borowiec); b – *Lobrathium multipunctum* (Udo Schmidt – CC-BY-NC-SA); c – *Rugilus angustatus* (© Lech Borowiec).

Staphylinidae: Subfamily Pselaphinae

Commonly called short-winged mold beetles, members of this group were recognized as family Pselaphidae, until reclassified in 1995 as subfamily Pselaphinae in family Staphylinidae. Adults of most species are about 1.5 mm in length (range of 0.5–5.5 mm) and are yellowish or brownish in colour. Antennae typically have a distinct club. Elytra are wider than the pronotum and are shortened, not covering the first abdominal segment.

Pselaphines are often encountered in moist habitats that include rotting vegetation, decaying logs, the underside of bark and stones, moss, and occasionally the nests of ants, termites or mammals. They are predators of collembolans (springtails) and oribatid mites (Thayer 2016). They are not strictly coprophilous; species recovered in dung are likely attracted from adjacent habitats in search of prey.

At least 107 species of pselaphines in 35 genera are reported in Canada (Bousquet et al. 2013). These can be identified to genus using keys in Newton et al. (2001). Two of these species are reported to be coprophilous and are members of the genus *Euplectus*; i.e., *E. karstenii* and *E. signatus*. A species-level key for *Euplectus* is provided by Wagner (1975).

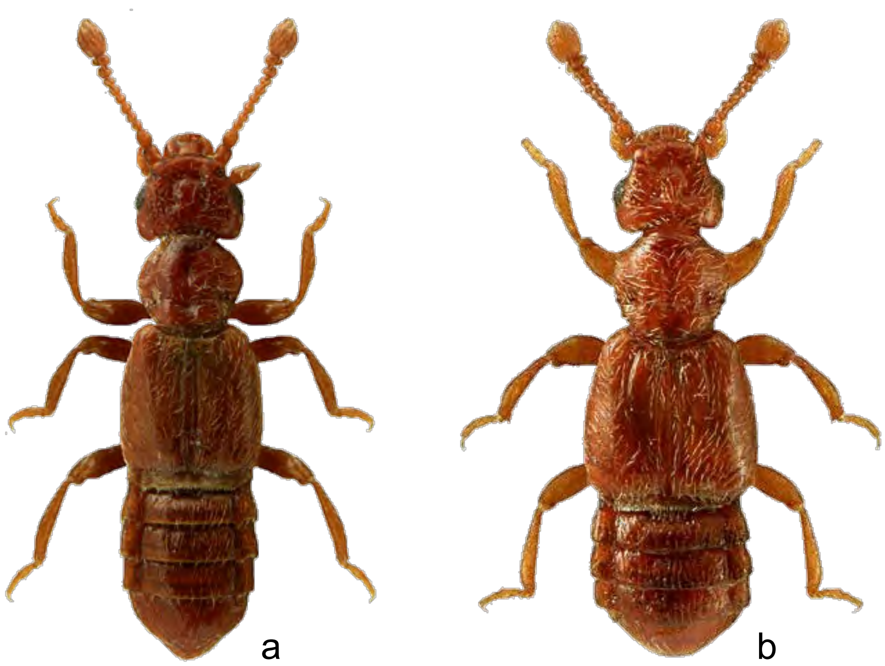


Figure 88. Subfamily Pselaphinae. a – *Euplectus karstenii*; b – *Euplectus signatus*. Images © Lech Borowiec.

Staphylinidae: Subfamily Staphylininae

Previously included within Staphylininae, the tribes Xantholinini, Diochini and Othiini are now treated together as subfamily Xantholininae (Smetana 1982).

This subfamily shares many of the morphological features of subfamily Paederinae. The body is typically 4–8 mm in length (range of 2–30 mm) and may be elongate, oval or spindle-shaped. The antennae are attached along or near the forward margin of the head and close to the base of the long, slender and curved mandibles. When viewed from above, the point of attachment for the antennae is either entirely or at least partially visible (Fig. 80a); the head usually has a distinct neck. Body colour ranges from black to brown and often has a glossy sheen; some species are brightly coloured with metallic purple, blue and green. The body may be hairy or bare.

Staphylinines are common in rotting organic material, including compost, decomposing fruit, dung, carrion, forest litter and decaying mats of aquatic weeds along shorelines. The adults and larvae of most species are predators and feed on other insects (including fly larvae), nematodes and snails. The largest of the staphylinids likely to be found in cattle dung anywhere in Canada is *Ontholestes cingulatus* (12–19 mm), whose abdomen has a distinct yellow tip (Fig. 89a). It is unlikely to be mistaken for any other species except possibly *Ontholestes murinus* (10–15 mm), which is a European species accidentally introduced to Canada and still only known from the island of Newfoundland (Brunke et al. 2011) (Fig. 89b). *Creophilus maxillosus* (12–18 mm) is of similar size, but is more often associated with carrion (Fig. 89c). Probably at least in part because of their impressive size, numerous authors have published on the biology and life history of these species (Alcock 1991; Greene 1996; Jefson et al. 1983; Schmidt 1999; Voris 1939).

Young (1998) describes predation on adult dung beetles by the tropical staphylinine *Gauropterus chalybaeus* in which the predator first cuts off the legs of the prey to prevent its escape and then chews into its body to consume the contents. Young (1982) hypothesizes that perching behaviour by dung beetles, wherein the beetle perches on vegetation for a period of time before landing on the dung resource, may have evolved as a mechanism to avoid predation by staphylinid beetles.

In Canada and Alaska, there are at least 309 species of staphylinines in 48 genera (Bousquet et al. 2013; Klimaszewski 2000), which makes this group the second most diverse subfamily of staphylinids after subfamily Aleocharinae. Members of at least 14 genera are reported to be coprophilous and can be identified to genus using Newton et al. (2001). However, only perhaps ten species in three genera (*Gyrohypnus, Ontholestes, Philonthus*) are likely to be frequently recovered from fresh cattle dung in Canada (Table 5). *Gyrohypnus* is represented by three species in Canada that can be identified to species using keys in Smetana (1982). The two species of *Ontholestes* that occur in Canada can be distinguished using Smetana (1981) or Brunke et al. (2011). A species key to *Philonthus* is provided by Smetana (1995).

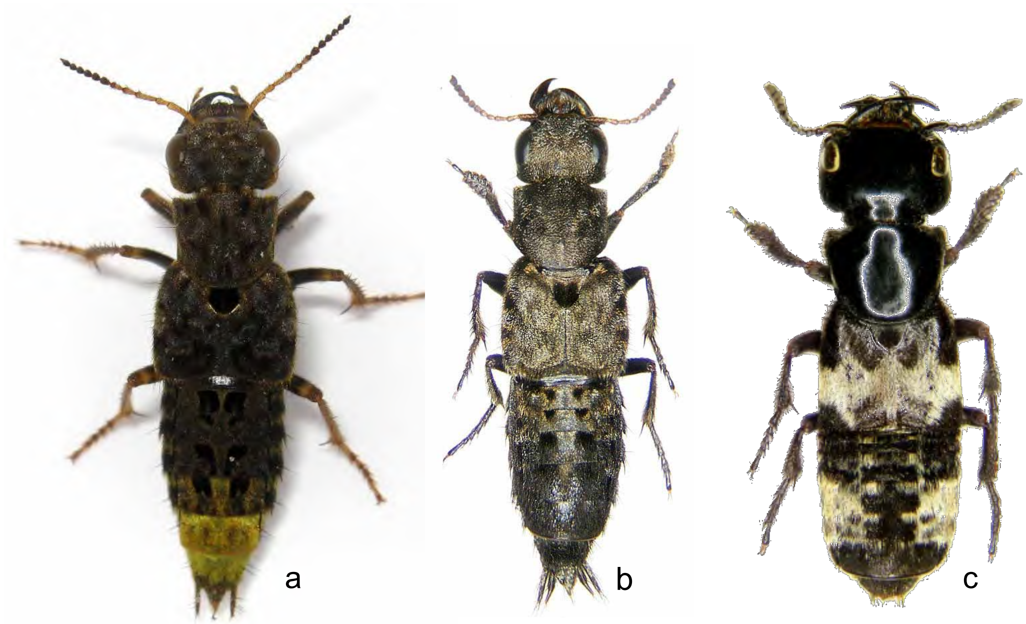


Figure 89. Subfamily Staphylininae. a – *Ontholestes cingulatus* (© Chris Rorabaugh); b – *Ontholestes murinus* (Udo Schmidt – CC-BY-NC-SA); c – *Creophilus maxillosus* (Udo Schmidt – CC-BY-NC-SA).

Figure 90. Subfamily Staphylininae (continued). d – *Gyrohypnus angustatus*; e – *Gyrohypnus fracticornis*; f – *Philonthus cruentatus*; g – *Philonthus debilis*; h – *Philonthus sanguinolentus*; i – *Philonthus varians*. photos d and e (Udo Schmidt – CC-BY-SA-4.0); photos f-i (© Lech Borowiec).

Staphylinidae: Subfamily Tachyporinae

Originally in subfamily Tachyporinae, Tribe Mycetoporini recently has been elevated to subfamily Mycetoporinae (Yamamoto 2021). For the purposes of Table 5, genera originally in tribe Mycetoporini (e.g., Ischnosoma and Bryoporus) are retained in Tachyporinae.

Members of this subfamily are commonly called crab-like rove beetles. Adults are generally 3–6 mm in length and range in colour from black to brown or yellowish. The bodies may have spotted markings, particularly on the elytra. The head is small with the antennae attached in front of the eyes; there is no distinct neck. The body shape ranges from broadly oval (e.g., *Tachyporus* spp.) to elongate (e.g., *Ischnosoma* spp.) with a broad prothorax and elytra. The abdomen tapers to a point, often with long, protruding setae; there are six well-defined abdominal sternites (Fig. 85a).

Tachyporines are common in moist forest habitats with rotting vegetation. Most species are thought to be predators, but other species feed on fungi or may be opportunists that feed on both arthropods and fungi. They appear to be only infrequently recovered from fresh cattle dung and are likely attracted there from adjacent habitats in search of prey.

At least 137 species of tachyporines in 15 genera are reported in Canada (Bousquet et al. 2013). These can be identified to genus using keys in Newton et al. (2001). One species in each of four genera have been identified in the literature as being associated with dung (Table 5). Species-level keys are provided for *Bryoporus* by Campbell (1993), for *Cilea* by Campbell (1975), for *Ischnosoma* by Campbell (1991) and for *Tachyporus* by Campbell (1979).

Figure 91. Subfamily Tachyporinae. a – *Bryoporus rufescens* (Mike Quinn, http://texasento.net/); b – *Cilea silphoides* (Udo Schmidt – CC-BY-NC-SA); c – *Ischnosoma splendidum* (© Lech Borowiec); d – *Tachyporus nitidulus* (© Lech Borowiec).

Table 5. Checklist, size and Canadian distribution for coprophilous species of Staphylinidae[1]. Species identified in bold font regularly occur in fresh cattle dung. Other species are either only occasional visitors to fresh cattle dung or information is insufficient to make a determination.

Genus	Species	Length (mm)	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
Subfamily Aleocharinae													
Aleochara	***bilineata***[*]	2–6	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Aleochara	***bimaculata***[2]	4–8	BC	AB	SK	MB	ON	QC	NB	NS		LB	NF
Aleochara	*curtula*[*]	4–7	BC				ON	QC	NB	NS	PE		NF
Aleochara	*lacertina*	3–6	BC	AB	SK	MB	ON	QC	NB	NS			NF
Aleochara	***lanuginosa***[*]	3–7	BC	AB			ON	QC	NB	NS			NF
Aleochara	*lata*[3,*]	4–9					ON	QC					
Aleochara	***morion***[*]	1.5–3	BC	AB	SK		ON	QC	NB	NS			NF
Aleochara	***tristis***[*]	4–8					ON	QC	NB				NF
Aleochara	***verna***[3]	2–4	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
Aloconota	*sulcifrons*[*]	3.5–4				MB	ON	QC	NB				NF
Atheta	*amicula*[*]	1.5–2					ON			NS			NF
Atheta	***atramentaria***[*]	ca. 3										LB	NF
Atheta	*dadopora*[2,3,*]	1.5–2	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
Atheta	***longicornis***[*]	3–3.5	BC					QC	NB	NS			NF
Atheta	***nigra***[*]	ca. 2			SK								
Autalia	***puncticollis***[*]	2–2.5	BC										
Autalia	***rivularis***[*]	1.5–2.5	BC	AB	SK[4]		ON	QC	NB	NS		LB	NF
Cordalia	*obscura*[*]	2–3	BC				ON	QC	NB	NS			
Crataraea	*suturalis*[*]	2–3	BC		SK		ON	QC	NB	NS		LB	
Falagria	*caesa*[*]	2–3		AB	SK[4]		ON	QC	NB				
Falagria	*dissecta*	2–3	BC	AB	SK	MB	ON	QC	NB	NS			
Nehemitropia	*lividipennis*[*]	3–3.5	BC		SK		ON	QC	NB	NS	PE		NF
Oligota	*parva*[*]	ca. 1					ON		NB		PE		
Subfamily Omaliinae													
Omalium	*rivulare*[*]	3–3.5	BC				ON	QC	NB	NS			NF
Phyllodrepa	*floralis*[*]	3.5–4	BC	AB		MB	ON	QC		NS			NF
Xylodromus	*concinnus*[*]	3–3.5	BC	AB	SK								
Subfamily Oxytelinae													
Anotylus	*insignitus*[*]	2.5–3					ON	QC					
Anotylus	*rugosus*[*]	4–5	BC		SK	MB	ON	QC	NB	NS	PE		NF
Anotylus	*sobrinus*[2]	ca. 3	BC	AB	SK	MB							
Anotylus	*suspectus*	1.5–2				MB	ON		NB				
Anotylus	***tetracarinatus***[*]	1.5–2	BC	AB			ON	QC	NB	NS			
Coprophilus	*striatulus*[2,3,*]	5–9					ON	QC	NB	NS			
Oxytelus	***laqueatus***[*]	3.5–5	BC	AB	SK	MB	ON	QC	NB	NS		LB	
Oxytelus	*incisus*	2.5–3.5					ON	QC	NB				
Oxytelus	*sculptus*[*]	3.5–4.5	BC			MB	ON	QC	NB	NS			
Platystethus	***americanus***[3]	2.5–3	BC	AB	SK	MB	ON	QC	NB				
Subfamily Paederinae													
Lithocharis	*ochracea*[*]	4–5	BC		SK		ON	QC	NB	NS			
Lobrathium	*longiusculum*	ca. 11					ON						
Rugilus	***ceylanensis***[*]	4–5					ON	QC					

Table 5 (continued). Checklist, size and Canadian distribution for coprophilous species of Staphylinidae[1]. Species identified in bold font regularly occur in fresh cattle dung. Other species are either only occasional visitors to fresh cattle dung or information is insufficient to make a determination.

Genus	Species	Length (mm)	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
Subfamily Pselaphinae													
Euplectus	*karstenii*[*]	ca. 1.5	BC		SK	MB	ON	QC	NB		PE		
Euplectus	*signatus*[*]	ca. 1.5			SK	MB	ON	QC					
Subfamily Staphylininae													
Bisnius	*cephalotes*[*]	6–7	BC		SK	MB	ON	QC		NS			NF
Bisnius	*fimetarius*[*]	6–7.5						QC	NB				NF
Bisnius	*inquietus*	4.5–7.5					ON	QC					
Bisnius	*parcus*[*]	7.5–9	BC				ON	QC					
Bisnius	*sordidus*[*]	ca. 5.5	BC	AB	SK	MB	ON	QC	NB	NS			NF
Creophilus	*maxillosus*[*]	12–18	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
Gabronthus	***thermarum***[*]	3–4					ON	QC					
Gauropterus	*fulgidus*[*]	9–11.5					ON						
Gyrohypnus	***angustatus***[*]	6–8.5	BC	AB[5]			ON	QC	NB	NS			NF
Gyrohypnus	***fracticornis***[*]	6–8.5	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Leptacinus	*intermedius*[*]	4.5–5.5	BC	AB	SK	MB	ON	QC	NB		PE		
Leptacinus	*pusillus*[*]	4.5–5.5			SK		ON	QC					
Neobisnius	*sobrinus*	ca. 2					ON	QC	NB	NS			NF
Neohypnus	*fragilis*	ca. 3	BC				ON						
Neohypnus	*obscurus*	ca. 5	BC	AB	SK	MB	ON	QC	NB	NS			NF
Ontholestes	***cingulatus***[2]	12–19	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Ontholestes	***murinus***[*]	10–15											NF
Phacophallus	*parumpunctatus*[*]	6–8					ON	QC	NB				
Philonthus	*carbonarius*[3,*]	ca. 5	BC		SK	MB	ON	QC	NB	NS	PE		NF
Philonthus	*caucasicus*[*]	ca. 11	BC	AB	SK	MB	ON	QC					
Philonthus	*cognatus*[*]	8–10	BC	AB			ON	QC	NB	NS	PE		NF
Philonthus	*concinnus*[*]	ca. 5	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Philonthus	***cruentatus***[*]	7–8	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Philonthus	***debilis***[*]	ca. 5	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Philonthus	*discoideus*[*]	5–6					ON	QC	NB				
Philonthus	***hepaticus***	4.5–6	BC						NB				
Philonthus	*jurgans*[*]	6–8	BC				ON	QC	NB			LB	NF
Philonthus	*longicornis*[*]	6.5–7.5				MB	ON	QC		NS			
Philonthus	*politus*[2,*]	9–13	BC	AB	SK	MB	ON	QC	NB	NS		LB	NF
Philonthus	***rectangulus***[*]	8.5–10.5	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Philonthus	*rufulus*	4.5–6	BC				ON	QC		NS			
Philonthus	***sanguinolentus***[*]	7–8	BC	AB[5]			ON						
Philonthus	*sericans*	5.5–6.5					ON	QC	NB				
Philonthus	***tenuicornis***[*]	11–14	BC										
Philonthus	*umbrinus*	ca. 4					ON						
Philonthus	***varians***[*]	6.5–7.5	BC	AB	SK	MB	ON	QC	NB	NS	PE		NF
Philonthus	*ventralis*[*]	5.5 – 6.5					ON	QC					

Table 5 (continued). Checklist, size and Canadian distribution for coprophilous species of Staphylinidae[1]. Species identified in bold font regularly occur in fresh cattle dung. Other species are either only occasional visitors to fresh cattle dung or information is insufficient to make a determination.

Genus	Species	Length (mm)	BC	AB	SK	MB	ON	QC	NB	NS	PE	LB	NF
Platydracus	_maculosus_	22–35					ON	QC					
Quedius	_cinctus_*	5.5–8.5					ON		NB				
Quedius	_fulgidus_*	7–11.5	BC		SK	MB	ON						
Quedius	_mesomelinus_*	6.5–11	BC	AB	SK	MB	ON	QC	NB	NS		LB	NF
Stenistoderus	_rubripennis_	ca. 8					ON						
Subfamily Tachyporinae													
Bryoporus	_rufescens_	3–8	BC	AB	SK	MB	ON	QC	NB	NS			
Cilea	_silphoides_*	2.5–3.5	BC	AB			ON	QC	NB				
Ischnosoma	_flavicolle_	3–5					ON	QC	NB				
Tachyporus	_nitidulus_[2, 3]	2–2.5	BC	AB	SK	MB	ON	QC	NB	NS		LB	NF

[1] Species list and distributions are compiled mainly from Skidmore (1991), Bousquet et al. (2013), Klimaszewski and Brunke (2018) and Bezanson and Floate (2019), with corrections and updates provided by A.J. Brunke.

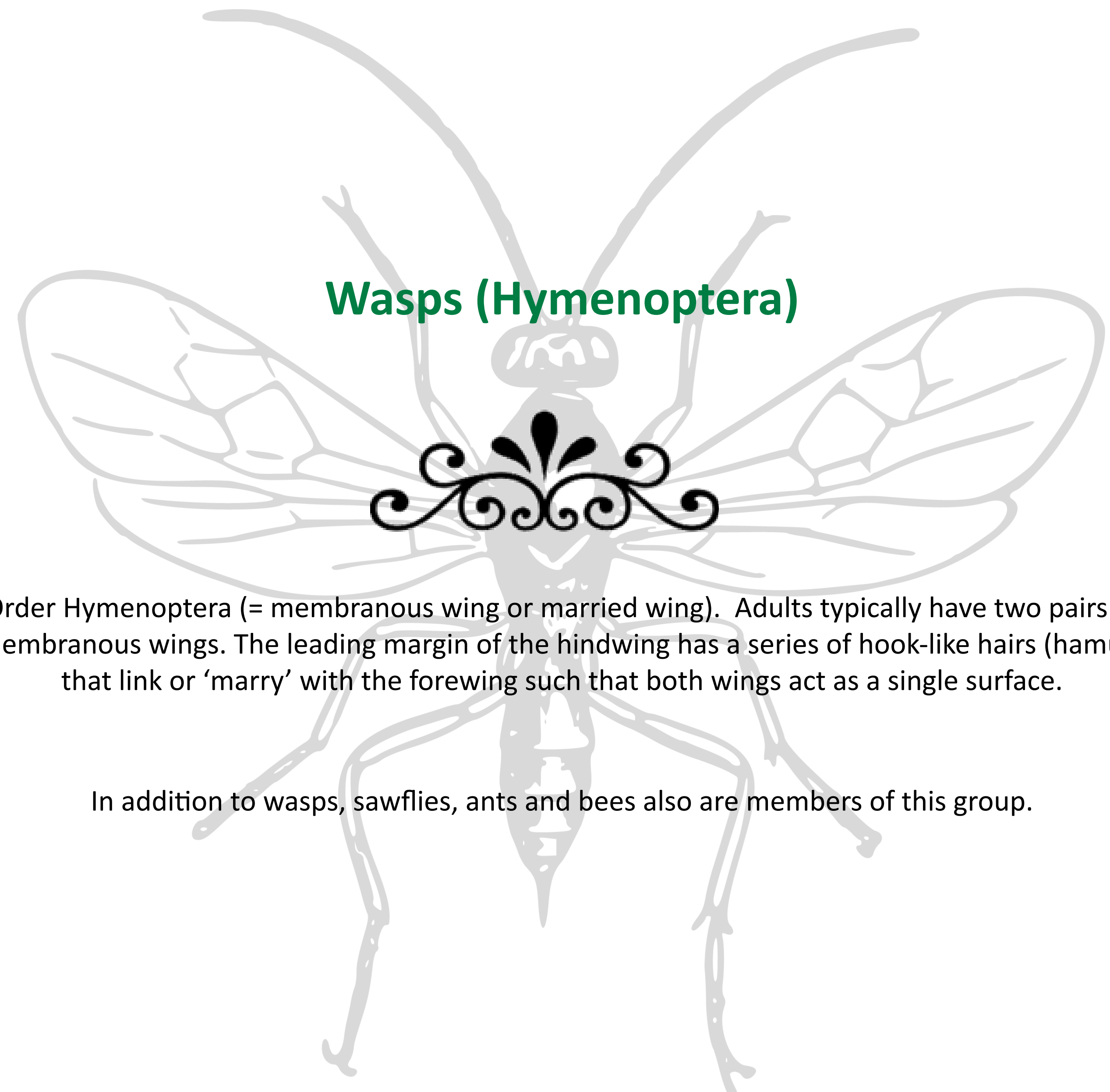
[2] Also reported from the Northwest Territories.

[3] Also reported from the Yukon Territory.

[4] Reported in Klimaszewski et al. (2016).

[5] Reported in Floate (1998b).

[*] Exotic.



Wasps (Hymenoptera)

Order Hymenoptera (= membranous wing or married wing). Adults typically have two pairs of membranous wings. The leading margin of the hindwing has a series of hook-like hairs (hamuli) that link or ‘marry’ with the forewing such that both wings act as a single surface.

In addition to wasps, sawflies, ants and bees also are members of this group.

Wasps

Parasite or parasitoid?

Parasites and parasitoids both spend part of their life cycle developing in or on a host organism. Parasites may feed on more than one host and don't normally kill the host. Parasitoids only develop in one host and almost always kill it.

Many people associate the word 'wasp' with paper wasps, hornets or yellowjackets. These types of wasps form colonies of dozens or hundreds of individuals and are called social wasps. But other types of wasps are solitary and live alone. This latter group includes parasitoid species that develop inside dung-breeding flies. Most of these wasps are quite small (1–3 mm in length) and easy to overlook. But if you pay close attention, you can see them running about on the surface of fresh dung pats, or entering the pat through holes in the crust made by other insects, to locate suitable hosts in which to lay their eggs.

Figure 92. A pteromalid wasp, *Muscidifurax* sp., on a house fly puparium (AAFC).

Understanding the different life histories of these wasps can aid in their identification. Some species oviposit in the egg of the host, whereas other species oviposit in the host larva and (or) pupa. *Ectoparasitoids* develop on the outside of the host; *endoparasitoids* develop within the host. *Idiobionts* are parasitoids that immobilize the host and prevent it from developing further. This strategy, common for ectoparasitoids, prevents the parasitoid from being dislodged from the host. *Koinbionts* are typically endoparasitoids and allow the host to continue development while the parasitoid feeds within. *Hyperparasitoids* (also termed *secondary parasitoids*) parasitize other parasitoids, that is, the hyperparasitoid develops on a second species of parasitic wasp (the primary parasitoid) that is itself developing on a fly host. *Solitary parasitoids* lay one egg per host, whereas *gregarious parasitoids* lay many eggs per host.

The complex of wasps parasitic on dung and filth-breeding flies is well-known, chiefly because of their role as natural enemies of the muscid flies that are pests of livestock (see Muscidae, page 65). In particular, a disproportionate amount of research has been devoted to wasps in the family Pteromalidae, for which species of *Muscidifurax* and *Spalangia* have been commercialized for sale as biocontrol agents of filth flies in livestock confinements (Rueda and Axtell 1985; Cranshaw et al. 1996; Gibson 2009).

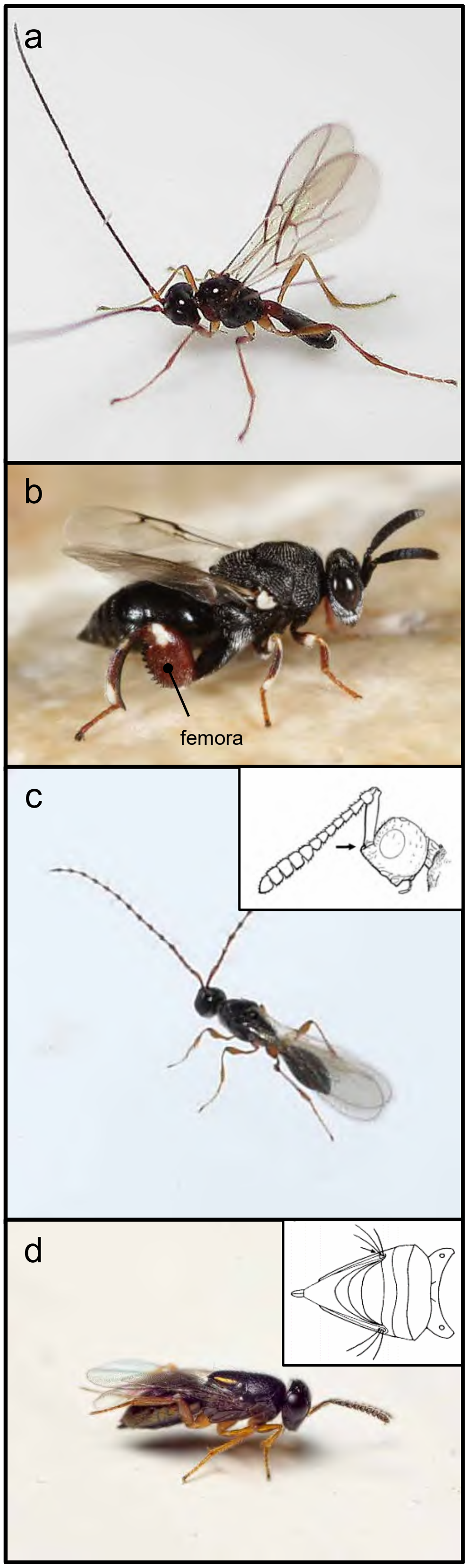
Members of this parasitic wasp complex for North America are listed in Table 6. This list builds upon the work of Blume (1985), supplemented with more recent literature. For the species most likely to be encountered, references are provided to direct the reader to more information on geographic distributions, synonymies, host associations, biology and taxonomic keys.

A reminder that taxonomic names are updated from time to time as new knowledge becomes available. This seems to be particularly true for the Hymenoptera and it can create confusion when referencing older literature. For example, *Striatovertex impatiens,* a species in the subfamily Eucoilinae (family Figitidae) (Schick et al. 2011) was formerly named *Eucoila impatiens* (Blume 1985). Similarly, species in the genus *Trichomalopsis* (Pteromalidae) (Gibson and Floate 2001) were once included in *Eupteromalis* (Blume 1985). A species initially described from Europe as *Eupelmus vesicularis*, but often treated in the literature as *Macroneura vesicularis*, is now recognized in North America as *Eupelmus messene* (family Eupelmidae) and as a complex of four species in Europe (Fusu 2017). Table 6 uses the most current species names.

In writing this section of the guide, I found a number of resources to be particularly useful and freely available online. Krombein et al. (1979) lists all species of wasps for America north of Mexico, with information on synonyms, host associations, and references to biological information. Pickering (2009) digitized Krombein et al. (1979), allowing for online access and rapid searches for particular taxa. The online database of Noyes (2019) is much more up-to-date, but is restricted to families of wasps in the superfamily Chalcidoidea; e.g., Chalcididae, Encyrtidae, Eupelmidae, Pteromalidae.

The taxonomic key of Goulet and Huber (1993) can be used to identify any species of wasp to family and subfamily. This handy resource also includes an illustrated glossary to help the reader navigate their way through an often confusing maze of morphological terms. Wharton et al. (1997) allows for identification to genus, but is restricted to species in the family Braconidae (superfamily Ichneumonoidea). The illustrated key of Gibson (2000b) is specific for wasps parasitic on filth-breeding flies, but is restricted to species in the superfamily Chalcidoidea.

The value of Table 6 is maximized if the species is first identified to its taxonomic family. To aid this process, the following pages provide brief summaries for the families of wasps with members parasitic on dung and filth-breeding flies. Table 6 follows thereafter.



a – Braconidae (superfamily Ichneumonoidea). Typically < 15 mm in length with wasp-like appearance. Body usually brown or black, sometimes with red markings. Antennae threadlike with at least 16 segments; not elbowed. Forewing usually with some closed cells. Female with ovipositor permanently extruded. Endoparasites or ectoparasites, primary or hyperparasitoids, solitary or gregarious.

Aphaereta sp. (♂) (© John Maxwell).

b – Chalcididae (superfamily Chalcidoidea). Typically 2–7 mm in length. Body black, brown, yellow or reddish, never metallic. Thorax coarsely sculptured. Wing venation reduced, without closed cells. Antennae usually elbowed, with 13 or fewer segments. Hind femora enlarged and with teeth ventrally (see photo). Parasitoids of Coleoptera, Diptera and Lepidoptera; some are hyperparasites.

Brachymeria podagrica (© Graham Montgomery).

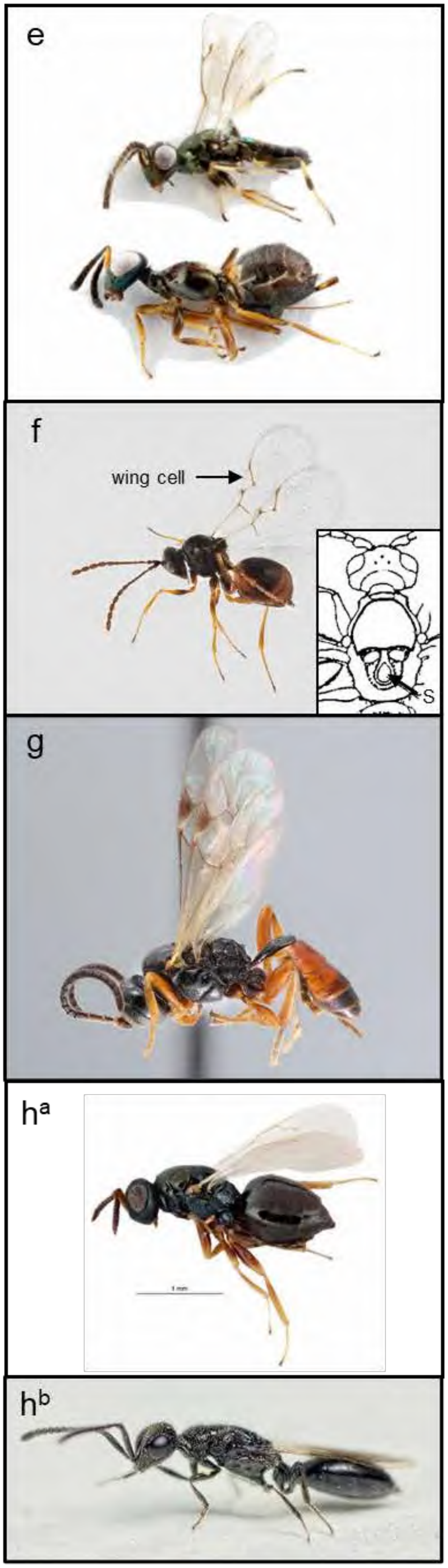
c – Diapariidae (superfamily Proctotrupoidea). Typically 2–4 mm in length. Body usually black, non-metallic, with a smooth appearance. Wing venation reduced. Antennae with more-or-less distinct elbow, 12 to 14 segments and usually attached to a prominent shelf-like ridge high on the head (see inset). Mainly parasitoids of Diptera.

Trichopria sp. (Ilona Loser – CC-BY-ND-NC-1.0); inset (Mason 1993).

d – Encyrtidae (superfamily Chalcidoidea). Typically 1–2 mm in length. Reduced wing venation without closed cells. Antennae usually elbowed, with 13 or fewer segments. Mesopleuron uniformly convex, cushion-like. Dorsal edges of abdominal segments often stretched forward to form a U-shape (see inset).

Unidentified encyrtid species (Pierre Bornand – CC-BY-NC-2.0), inset (Gibson 1993).

Figure 93. Images and summaries for parasitoid wasps in the families: a – Braconidae; b – Chalcididae; c – Diapridae; d – Encyrtidae.



e – Eupelmidae (superfamily Chalcidoidea).
Sexes highly dimorphic; females similar to Encyrtidae except without U-shaped abdominal segments; males similar to Pteromalidae. The one eupelmid species reported from dung and filth flies in North America has fully winged males and short-winged (brachypterous) females (see photo).

Eupelmus vesicularis: ♂ (top), ♀ (bottom) (© The Trustees of the Natural History Museum, London – CC-BY-4.0).

f – Figitidae (superfamily Cynipoidea).
Body dark, non-metallic, with a smooth appearance. Abdomen laterally compressed. Margin of forewing with a distinctive, triangular, cell; all other venation reduced or absent. Species in the subfamily Eucoilinae are characterized by a round or teardrop-shaped plate on the scutellum (S) (see inset).

Kleidotoma sp. (Arnstein Staverløkk – CC-BY-4.0); inset modified from Skidmore (1991) Insects of the cow dung community. Field Studies Council, Shrewsbury, UK.

g – Ichneumonidae (superfamily Ichneumonoidea).
Highly variable in size, colour and form, but similar to Braconidae except usually larger. Most species are solitary; some are hyperparasitoids.

Phygadeuon fumator (Andy Bennett, Agriculture and Agri-Food Canada).

h – Pteromalidae (superfamily Chalcidoidea). Highly variable, with wing venation and antennae as for other families of Chalcidoidea, but without their other described features. Body usually mainly metallic green or blue (h^a), but *Spalangia* spp. are black with flattish appearance (h^b) in contrast to most other pteromalids.

h^a – *Nasonia vitripennis* (Public domain).

h^b – *Spalangia drosophilae* (♀) (Pierre Bornand – CC-BY-NC-2.0).

Figure 93 (continued). Images and summaries for parasitoid wasps in the families: e – Eupelmidae; f – Figitidae; g – Ichneumonidae; h – Pteromalidae.

Table 6. Wasps parasitic on dung and filth-breeding flies in North America north of Mexico[1].

Taxa	North American distribution, notes and useful references
Family Braconidae	
Aphaereta pallipes	Distribution – transcontinental. Other names and host associations – Krombein et al. (1979). Biology – Salkeld (1959); Houser and Wingo (1967).
Alysia ridibunda	Distribution – Canada: ON; USA: FL, MI, KS, TX (Blume 1985). Other names and host associations – Krombein et al. (1979). Biology – Roberts (1935); Burgess and Wingo (1968). • with a body length of 5–9 mm, this is the largest parasitoid species likely to be reared from a dung-breeding fly.
Asobara fungicola	Distribution – USA: CA, CT, IL, OH (Blume 1985). Other names and host associations – Krombein et al. (1979). Description – Ashmead (1894).
Family Chalcididae	
Brachymeria podagrica	Distribution – cosmopolitan. Other names and host associations – Krombein et al. (1979); Noyes (2019). Biology – Roberts (1933). Taxonomic key – Burks (1960). • 3–6 mm in length; among the largest parasitoids likely to be reared from a dung-breeding dung. • common parasitoid of blow flies (Calliphoridae).
Family Encyrtidae	
Tachinaephagus zealandicus	Distribution – USA: CA, FL, GA, IL IN, KS, KY, MO, NY, NC, OH, SC, TN (Geden and Skovgård 2014). Other names and host associations – Krombein et al. (1979); Noyes (2019). Biology – Olton and Legner (1974); Geden and Moon (2009). Description – Johnston and Tiegs (1921). Taxonomic key – Gibson (2000b). • introduced into North America (CA) as a biocontrol agent for filth-breeding flies (Olton and Legner 1974).
Family Eupelmidae	
Eupelmus messene	Distribution – cosmopolitan. Other names and host associations – Krombein et al. (1979); Noyes (2019). Taxonomic keys – Gibson (1990); Fusu (2017). • accidentally introduced into North America from Europe by early settlers and called *Eupelmus* or *Macroneura vesicularis* before Fusu (2017).

Table 6 (continued). Wasps parasitic on dung and filth-breeding flies in North America north of Mexico[1].

Taxa	North American distribution, notes and useful references
Family Figitidae (includes subfamily Eucoilinae, formerly recognized as family Eucoilidae)	
Kleidotoma spp.	Distribution – cosmopolitan. Other names and host associations – Krombein et al. (1979); Forshage et al. (2013). Taxonomic key – Forshage and Nordlander (2008) (European genera of Eucoilinae). • Forshage et al. (2013) list the species described for North America. • *Kleidotoma* sp. has been reported from dung in Canada from AB, BC (*K. fossa*) and QC; in the USA from CA (*K. fossa*), IL and MO.
Striatovertex rufocincta	Distribution – USA: western and southwest states (Blume 1985). Other names and host associations – Krombein et al. (1979); Schick et al. (2011). Taxonomic key – Forshage and Nordlander (2008) (European genera of Eucoilinae). • = *Eucoila rufocincta* in previous literature. • rarely reported in surveys.
Leptopilina spp.	Distribution – cosmopolitan. Other names and host associations – Forshage et al. (2013). Taxonomic key – Lue et al. (2016) (species in the eastern USA). • Forshage et al. (2013) list the species described for North America. • = *Cothonaspis* in Valiela (1969). • rarely reported in surveys.
Neralsia hyalinipennis	Distribution – Canada: ON, QC; USA: AL, FL, IL, MD, MO, NM, NY, VA (Matheson 1987; Jiménez et al. 2008). Other names and taxonomic key – Jiménez et al. (2008) (species in North America). • rarely reported in surveys.
Trischiza atricornis	Distribution – USA: NE, NM. Description – Ashmead (1896) (as *Figitodes atricornis*). • = *Trichisza atricornis* in Blume (1985). • rarely reported in surveys, but large numbers recovered from horn fly pupae in Nebraska (Schreiber 1985).
Xyalophoroide quinquelineata	Distribution – transcontinental. Host associations – Blickle (1961); Turner et al. (1968). Other names and taxonomic key – Jiménez et al. (2008). • = *Xyalophora quinquelineata* in previous literature.
Family Ichneumonidae	
Phygadeuon fumator	Distribution – transcontinental. Biology – McKay and Galloway (1999). • several reports of *Phygadeuon* sp., but the lack of a recent revision impedes species' determinations (Schwarz and Shaw 2011). • provisional identifications of *P. fumator* appear in the literature as *P. ?fumator* (Gibson and Floate 2004; Noronha et al. 2007).

Table 6 (continued). Wasps parasitic on dung and filth-breeding flies in North America north of Mexico[1].

Taxa	North American distribution, notes and useful references
Family Pteromalidae	
Dibrachys microgastri	Distribution – widespread. Other names and host associations – Krombein et al. (1979); Peters and Baur (2011); Noyes (2019). Biology and description – Hoebeke and Rutz (1988); Peters and Baur (2011). Taxonomic key – Gibson (2000b) (to genus); Peters and Baur (2011) (to species). • = *D. cavus* in most previous literature. • Peters and Baur (2011) included three species as part of the *Dibrachys cavus* species complex, but recognized *D. microgastri* as the valid name for what formerly had been named *D. cavus*.
Muscidifurax raptor	Distribution – cosmopolitan. Other names and host associations – Krombein et al. (1979); Noyes (2019). Biology, description and (or) taxonomic key – Kogan and Legner (1970); Rueda and Axtell (1985); Gibson (2000b). • commercialized as a biocontrol agent for filth-breeding flies. • many studies on aspects of biology; e.g., Legner (1979); Capehart et al. (1981); King and Seidl (1993); Geden (1997).
Muscidifurax raptorellus	Distribution – see bullet points below. Other names and host associations – Krombein et al. (1979); Noyes (2019). Description and (or) taxonomic key – Kogan and Legner (1970); Gibson (2000b). • commercialized as a biocontrol agent for filth-breeding flies. • established in parts of the United States, but unlikely to establish in Canada (Floate et al. 2000; Floate and Skovgard 2004). • many studies on aspects of biology; e.g., Petersen and Currey (1996); Floate et al. (2000); Lysyk (2001a); Geden and Moon (2009).
Muscidifurax zaraptor	Distribution – cosmopolitan. Other names and host associations – Krombein et al. (1979); Noyes (2019). Biology, description and (or) taxonomic key – Kogan and Legner (1970); Rueda and Axtell (1985); Gibson (2000b). • commercialized as a biocontrol agent for filth-breeding flies. • many studies on aspects of biology; e.g., Wylie (1971); Coats (1976); Rivers et al. (1998); Lysyk (2001b).
Nasonia vitripennis	Distribution – cosmopolitan. Other names and host associations – Krombein et al. (1979); Noyes (2019). Biology – Whiting (1967). Description and taxonomic key – Rueda and Axtell (1985); Darling and Werren (1990); Gibson (2000b). • widely studied as a 'model' species for research on insect biology and genetics (Werren and Loehlin 2009).
Pachycrepoides vindemiae	Distribution – cosmopolitan. Other names and host associations – Krombein et al. (1979); Noyes (2019). Biology, description and (or) taxonomic key – Crandell (1939) (as *Pachycrepoides dubius*); Rueda and Axtell (1985); Gibson (2000b).

Table 6 (continued). Wasps parasitic on dung and filth-breeding flies in North America north of Mexico[1].

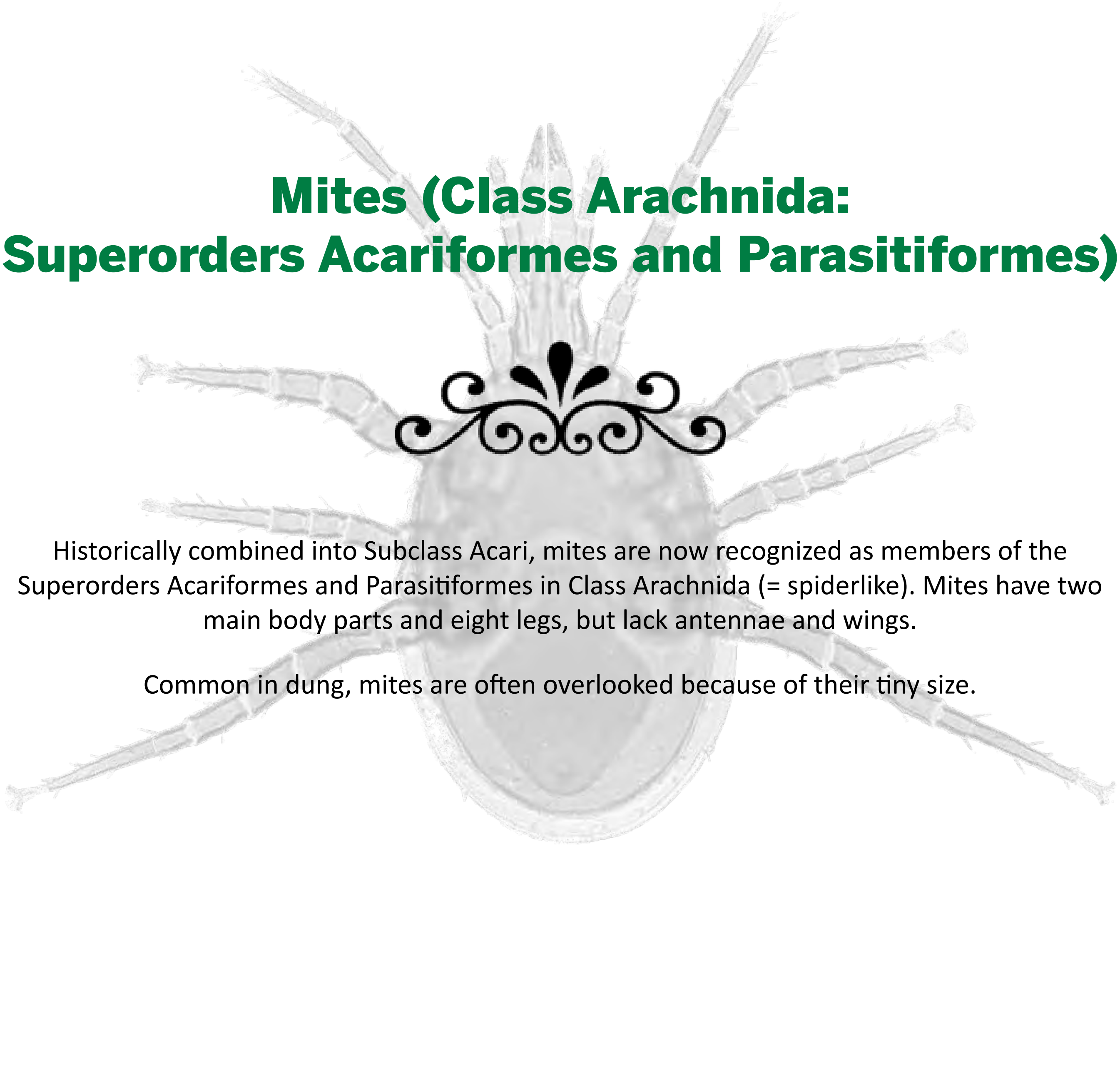
Taxa	North American distribution, notes and useful references
Spalangia cameroni	Distribution – cosmopolitan. Other names and host associations – Krombein et al. (1979); Gibson (2009); Noyes (2019). Description and (or) taxonomic key – Rueda and Axtell (1985); Gibson (2000b); Gibson (2009). • commercialized as a biocontrol agent for filth-breeding flies. • many studies on aspects of biology; e.g., Legner (1967); Moon et al. (1982); Morgan et al. (1989); Machtinger et al. (2016).
Spalangia drosophilae	Distribution – widespread in North and South America. Other names and host associations – Krombein et al. (1979); Gibson (2009); Noyes (2019). Biology – Lindquist (1936); Simmonds (1953). Description and (or) taxonomic key – Rueda and Axtell (1985); Gibson (2000b); Gibson (2009).
Spalangia endius	Distribution – cosmopolitan. Other names and host associations – Krombein et al. (1979); Gibson (2009); Noyes (2019). Description and (or) taxonomic key – Rueda and Axtell (1985); Gibson (2000b); Gibson (2009). • commercialized as a biocontrol agent for filth-breeding flies. • many studies on aspects of biology; e.g., Lindquist (1936) (as *S. muscidarum stomoxysiae*); Ables and Shepard (1974); Morgan et al. (1978); King (2002); Betelman et al. (2017).
Spalangia erythromera	Distribution – widespread in North America. Other names and host associations – Krombein et al. (1979); Gibson (2009); Noyes (2019). Description and (or) taxonomic key – Gibson (2000b); Gibson (2009). • rarely recovered from dung or livestock confinements; e.g., Peck (1974); Romero et al. (2010). • some interest on its use to control non-dung pest flies (Knoll et al. 2017).
Spalangia haematobiae	Distribution – transcontinental. Other names and host associations – Krombein et al. (1979); Gibson (2009); Noyes (2019). Description and (or) taxonomic key – Gibson (2000b); Gibson (2009).
Spalangia nigra	Distribution – cosmopolitan. Other names and host associations – Krombein et al. (1979); Gibson (2009); Noyes (2019). Biology – Legner (1969); Hall and Fischer (1988); King et al. (2018). Description and (or) taxonomic key – Rueda and Axtell (1985); Gibson (2000b); Gibson (2009).
Spalangia nigroaena	Distribution – cosmopolitan. Other names and host associations – Krombein et al. (1979); Gibson (2009); Noyes (2019). Description and (or) taxonomic key – Rueda and Axtell (1985); Gibson (2000b); Gibson (2009). • studied for use as a biocontrol agent of pest flies in livestock confinements (Hoelscher and Combs 1969; Greene et al. 1998; Weinzierl and Jones 1998).
Spalangia subpunctata	Distribution – transcontinental. Other names and host associations – Gibson (2009); Noyes (2019). Description and (or) taxonomic key – Gibson (2000b); Gibson (2009).

Table 6 (continued). Wasps parasitic on dung and filth-breeding flies in North America north of Mexico[1].

Taxa	North American distribution, notes and useful references
Trichomalopsis americana	Distribution – transcontinental. Other names and host associations – Gibson and Floate (2001); Noyes (2019). Biology – Best and Simpson (1975) (as *Eupteromalus americanus*). Description and (or) taxonomic key – Gibson and Floate (2001).
Trichomalopsis dubia	Distribution – transcontinental. Other names and host associations – Gibson and Floate (2001); Noyes (2019). Biology – Wylie (1976) (as *Eupteromalus dubius*). Description and (or) taxonomic key – Gibson and Floate (2001).
Trichomalopsis sarcophagae	Distribution – Canada: AB, MB, SK; USA: AZ, CA, ID, KS, MI, NB, WA. Other names and host associations – Gibson and Floate (2001); Noyes (2019). Biology – Dobesh et al. (1994); Lysyk (1998); Rivers et al. (1998). Description and (or) taxonomic key – Gibson and Floate (2001). • common in surveys of house fly parasitoids in Alberta, but not elsewhere (Floate et al. 2002). • Alberta strain studied for use as a biocontrol agent of pest flies in livestock confinements (Floate and Spooner 2002; Floate 2003; Floate and Skovgard 2004).
Urolepis maritima	Distribution – Canada: AB, QC; USA: AK, MI. Other names and host associations – Gibson (2000a); Noyes (2019). Biology, description and (or) taxonomic key – Gibson (2000a).
Urolepis rufipes	Distribution – transcontinental. Other names and host associations – Gibson (2000a); Noyes (2019). Biology – Smith and Rutz (1985); Smith and Rutz (1986); Smith and Rutz (1987); Cooper et al. (2013). Description and (or) taxonomic key – Gibson (2000a). • studied for use as a biocontrol agent of pest flies in livestock confinements (Pawson et al. 1987; Matthews and Petersen 1989; Kyei-Poku et al. 2003).

[1] Species rarely reported include: Bethylidae (*Laelius*), Braconidae (*Apanteles, Blacus, Idiasta, Pentapleura*), Chalcididae (*Dirhinus texanus*), Diapriidae (*Trichopria haematobiae*), Figitidae (*Eutrias tritoma, Figites, Melanips*), Ichneumonidae (*Orthocentrus*), Pteromalidae (*Psycophagus omnivorus, Trichomalopsis tachinae, Trichomalopsis viridescens*), Tiphiidae (*Myzinum*).

Mites (Class Arachnida: Superorders Acariformes and Parasitiformes)



Historically combined into Subclass Acari, mites are now recognized as members of the Superorders Acariformes and Parasitiformes in Class Arachnida (= spiderlike). Mites have two main body parts and eight legs, but lack antennae and wings.

Common in dung, mites are often overlooked because of their tiny size.

Mites

Mites are among the most diverse, but least known groups of animals on the planet (Fig. 95). Only about 54,000 of a worldwide estimate of 0.4–1.0 million species have been described. In Canada, almost 3,000 species have been named, but the national total is conservatively estimated at about 10,000 and may exceed 15,000 species (Beaulieu et al. 2019). Species determinations are confounded by their small size; typically < 1 mm and often smaller than the '.' at the end of this sentence. Use of a high powered microscope is needed for their identification. Identification is also confounded by a need for taxonomic revisions and species-level identification keys. Identification keys are also incomplete for most groups (Beaulieu et al. 2019). Krantz and Walter (2009) provide keys for family-level identifications with limited general information on mite biology and ecology. Walter and Proctor (2013) is more specifically focused on the latter two topics. Identification of mites is best left to a specialist.

Mites and insects are both members of Phylum Arthropoda, but otherwise have distinct differences. Insects (Class Insecta) have three main body parts (head, thorax, abdomen); mites (Class Arachnida: Superorders Acariformes and Parasitiformes) have two; i.e., the mouthparts (= *gnathosoma*) and the main body (= *idiosoma*). Adult insects have three pairs of legs; adult mites have four pairs of legs. Adult insects have antennae and many species have wings; mites have neither antennae nor wings. Insects have a pair of mouthparts termed *mandibles* that they use to bite, hold or chew their food; mites have a pair of pincher-like *chelicerae* that can only be used to pierce or grasp their prey. Mites may completely change in morphology during the transition from juvenile to adult, but – unlike many insects – lack a pupal stage. Instead, the newly-hatched mite passes through one or two larval stages (having six legs), and then through one to three nymphal stages (having eight legs) before completing its development to become an adult.

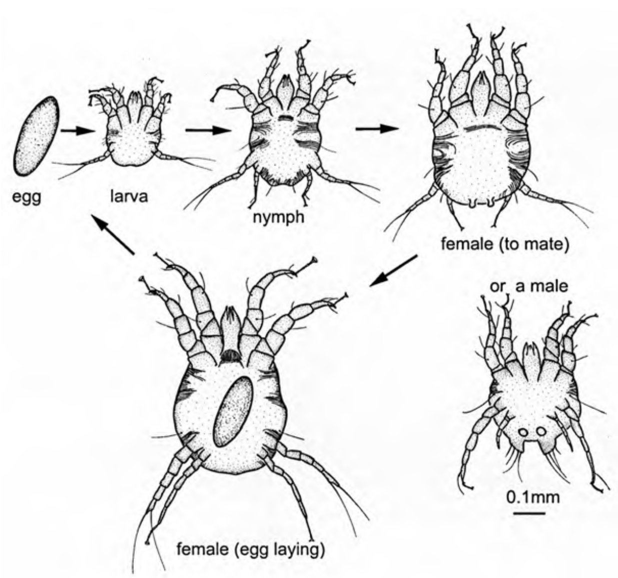


Figure 94. Life cycle of *Psoroptes ovis*, a mite parasitic on sheep and cattle (Daktaridudu CC BY-SA 3.0).

Fewer than 20 species of coprophilous mites have been reported from livestock dung in Canada so far (Lindquist 1988; Macqueen and Beirne 1974; Majka et al. 2007). All of these species appear to be free-living predators, phoretic on dung insects and common in rotting organic material where they feed on immature insects, nematodes and (or) fungi. Further studies will increase this number. For example, about 280 species of macrochelid mites have been reported globally as phoretic on beetles and flies (Krantz 1983). Macrochelid mites are of particular interest because of their potential to suppress populations of dung-breeding flies affecting livestock (Axtell 1961;

Azevedo et al. 2015; Halliday and Holm 1987; Halliday 1990; Krantz 1998; Rodriguez and Wade 1961).

The Canadian records identify representatives of the following main taxonomic groups:

- Eviphididae (e.g., Fig. 95b) – *Scarabaspis inexpectatus*.
- Histiostomatidae – *Pelzneria* sp. and *Spinanoetus* sp.
- Macrochelidae – *Glyptholaspis confusa, Macrocheles glaber* (Fig. 95c), *Macrocheles matrius, Macrocheles merdarius, Macrocheles muscaedomesticae, Macrocheles perglaber, Macrocheles subbadius* and *Macrocheles vernalis*.
- Parasitidae (e.g., Fig. 95d) – *Cornigamasus lunaris, Parasitus beta, Parasitus coleoptratorum, Parasitus fimetorum* and *Pergamasus longicornis*.
- Pyemotidae – *Pediculaster mesembrinae*.
- Uropodoidea (Figs. 95a, e) – *Uroobovella marginata* and *Uropoda orbicularis*.

As the dung ages, coprophilous mites are replaced by oribatid (Oribatidae) mites (Fig. 95g, h). The former group are most common in dung in the first few weeks after the pat has been deposited. They arrive at the fresh pat attached to dung-breeding insects and then disembark to colonize the dung and produce offspring. As the pat begins to dry out and degrade, it becomes colonized from the surrounding soil by oribatid mites. Oribatid mites, also known as beetle mites, are extremely common in soils and are important degraders of organic material. Walter et al. (2014) provides information on the biology and distribution of oribatid mite species in Alberta and keys for their identification.

It is also common to see red velvet mites (Trombidiidae) on older degraded pats actively searching for insect prey. Abundant in plant litter, they are particularly noticeable because of their large size (normally about 4 mm) and bright red colour (Fig. 95f).

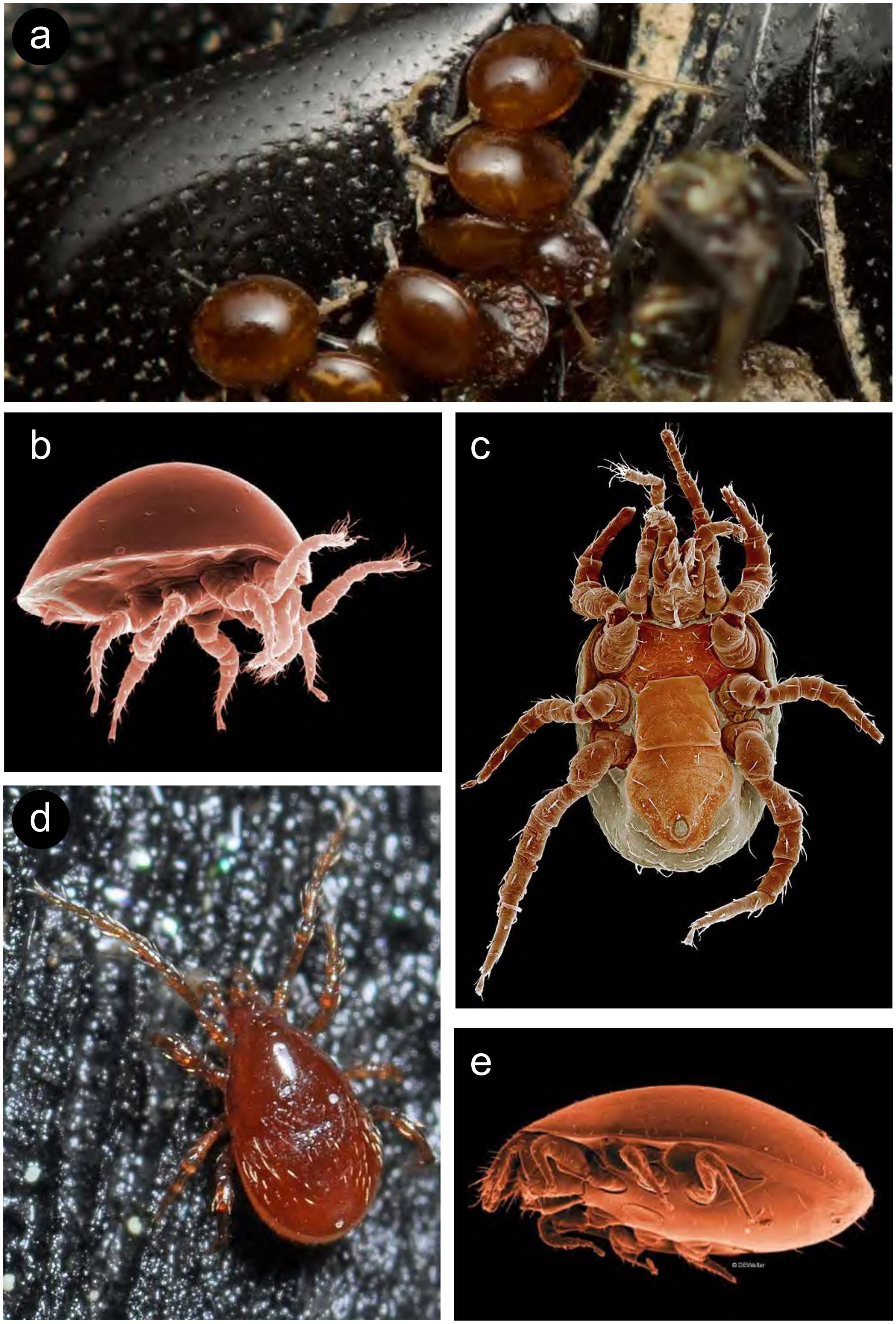


Figure 95. Examples of mites associated with dung and (or) soil: a – deutonymphs attached to the underside of a dung beetle (*Copris* sp.) (© Craig Biegler, CC BY-NC [image cropped from original); b – Eviphididae (© David E. Walter); c – *Macrocheles glaber* (Macrochelidae) (© Zsolt Ujvári); d – *Pergamasus* sp.? (Parasitidae) (Christophe Quintin, CC BY-NC 2.0); e – Uropididae (© David E. Walter).

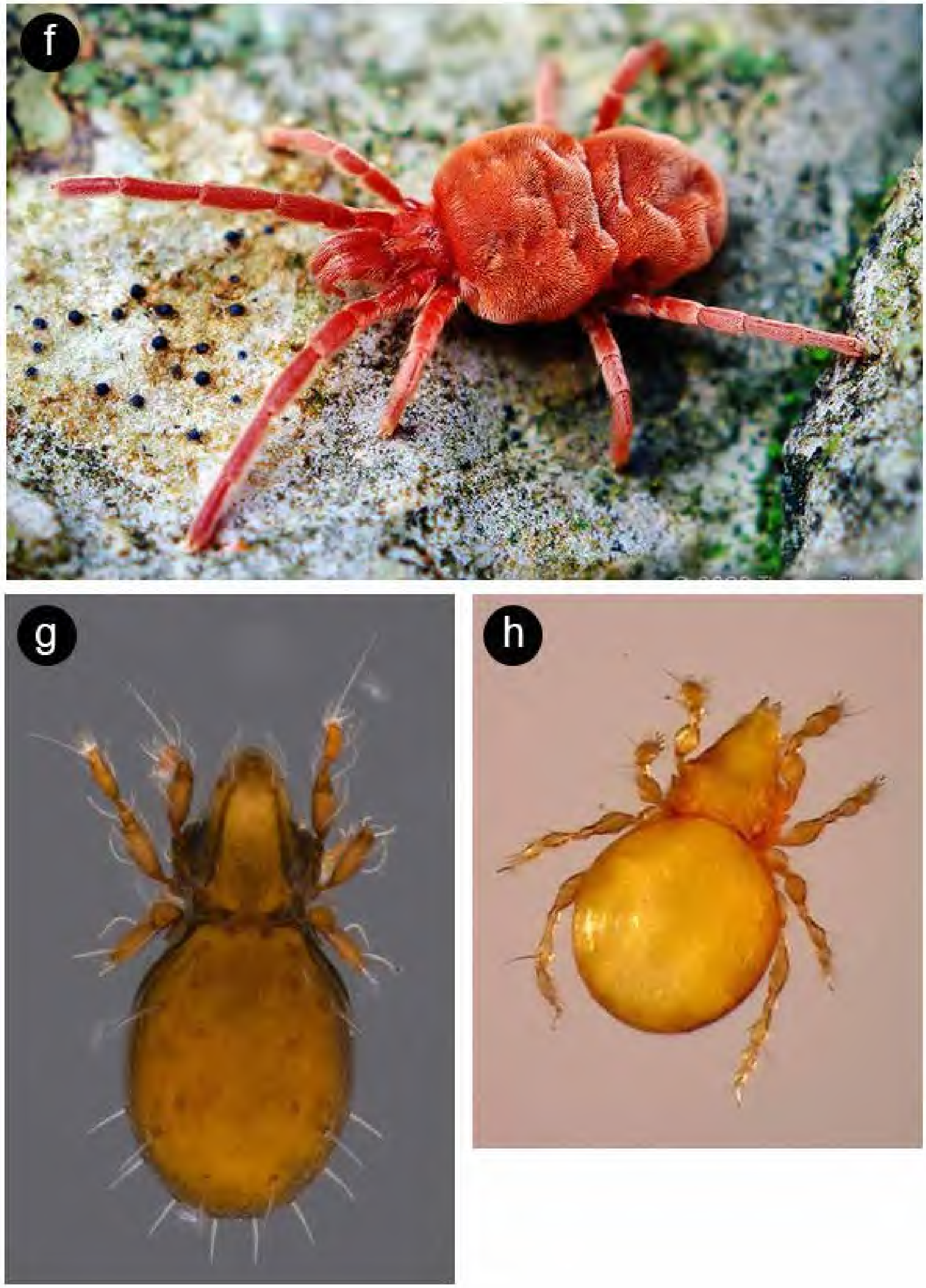


Figure 95 (continued). Examples of mites associated with dung and (or) soil: ; f – red velvet mite (Trombidiidae) (Thomas Shahan, CC BY-NC-ND 2.0); g – *Oribatida* sp. (Oribatida) (Donald Hobern – CC BY 2.0); h – *Ramusella* sp. (Oribatida) (© Natural England/Matthew Shepherd, CC BY-NC-ND 2.0).

Part III: References

Glossary of terms as used in this guide

Acarina – scientific name given to mites.

adventive – a species living outside of its native geographic range; e.g., European species of insects are adventive in Canada.

aerobic bacteria – bacteria that survive and reproduce when oxygen is present (compare with “anaerobic bacteria”).

alutaceous – characterized by small wrinkles or tiny cracks, similar to the texture of leather; sometimes used to describe the surface of elytra.

anaerobic bacteria – bacteria that do not require oxygen and may die in its presence. The digestive tract of cattle contains anaerobic bacteria that are passed out in fresh dung and replaced with aerobic bacteria as the pat is exposed to oxygen.

anal pedicel – a stalk formed by deutonymphs of uropodid mites that allows them to attach to an insect (page 16). This phoretic association with the carrier allows coprophilous mites to colonize fresh dung pats.

antenna (pl. antennae) – one of a pair of sensory appendages on the head of an insect; often long and thin (Fig. 78).

antennomere (pl. antennomeres) – a segment that forms part of the antennae. Their shape and number is used in insect identification; e.g., the apical antennomeres of dung beetles are expanded to form club-shaped antennae.

apical – the direction away from the point of attachment; e.g., the apical antennomere is the segment of the antennae furthest from the head (compare with "basal").

authority – the individual who first described a taxonomic group; usually accompanied by the year in which this was done; e.g., *Onthophagus nuchicornis* (Linnaeus, 1758).

basal – towards the point of attachment; e.g., the basal antennomere is the antennal segment closest to the head (compare with “apical”).

basal marginal line – may appear as either an engraved line or a narrow ridge at the base of the pronotum; used in insect identification (Fig. 46).

beefalo – fertile hybrid offspring between cattle (*Bos taurus*) and American bison (*Bison bison*); breed associations define a full beefalo as having 3/8th bison genetics (compare with “cattalo”).

bidentate – having two teeth or structures suggestive of teeth (Fig. 72).

bimodal – two peaks of activity; e.g., some species of insects have a bimodal pattern of seasonal adult activity (Fig. 8c).

binomial nomenclature – the naming system by which each species is uniquely recognized by a combination of two names, the first being the genus and the second being the species; e.g., *Musca domestica*.

biological control (aka biocontrol) – use of natural enemies (predators, parasitoids, pathogens) by humans to suppress pest populations. Suppression of pest populations without human intervention is defined as natural control.

bioindicator – a living organism used to monitor changes in the environment; e.g., the presence of chemical residues or climate change.

bloodworms – common name given to the bright red larvae of certain species of midge (Diptera: Chironomidae) (Fig. 21).

bluetongue – a disease of ruminants carried by certain species of *Culicoides* (Diptera: Ceratopogonidae); mainly affects sheep, but also cattle.

boreal – related to northern regions; often characterized by coniferous forest.

Brachycera – means "short-horns"; one of two recognized suborders of flies (Diptera). Adults are characterized with short antennae having reduced segmentation (compare with "Nematocera").

brood ball – a mass of dung formed by dung beetles and in which they have laid an egg. A similar mass of dung, but without an egg is called a "food ball".

campodeiform – larval form with a long body, long legs and often with terminal cerci (compare with "platyform", "scarabaeiform" and "vermiform"); common to many species of beetles; e.g., Staphylinidae (Fig. 15a).

cattalo – hybrid offspring between cattle (*Bos taurus*) and American bison (*Bison biso*n). Defined in the United States by law as having a bison appearance; no such requirement in Canada (compare with "beefalo").

cecidia (aka galls) – atypical swellings of plant tissue caused by the actions of certain species of insects including gall midges (Diptera: Cecidomyiidae).

cell – (1) a chamber formed by dung beetles that contains a brood ball; (2) a portion of an insect's wing surrounded by wing veins; i.e., a wing cell.

cercus (pl. cerci) – one of a pair of short, spike-like projections that extends from the terminal end of an insect's abdomen; also called caudal filaments.

chelicerae – the pincher-like mouthparts of mites used to grasp and pierce their food (compare with "mandibles").

clypeus – the broad plate that forms the front of an insect's head (Fig. 46).

coarctate – a type of pupal body form in which the appendages are not visible. The larva pupates inside the final larval instar, which forms a hard capsule called the puparium; common to flies in suborder Brachycera (Fig. 16d).

Coleoptera – means "sheath wing"; scientific name given to beetles.

compound eye – an eye formed of many simple eyes (ocelli) functioning together; most insects have compound eyes (Fig. 83a).

convex – rounded outwards or upwards like a sphere; many species of beetles have a convex body shape.

coprolites – fossilized dung.

coprophagous – means "dung-feeding"; refers to insects that feed on dung.

coprophilous – means "dung-loving"; refers to insects that live in dung.

crepuscular – appearing or active at twilight (compare with "diurnal" and "nocturnal"); e.g., crepuscular species of dung beetles begin to fly at dusk.

dauer larvae – phoretic stage of nematodes

detritivore – an organism that feeds on dead organic material, most often on plant detritus.

deutonymph – phoretic stage of immature mites (page 16).

diapause – a developmental resting period providing a mechanism to survive harsh environmental conditions. Many insects overwinter in a diapause state.

Diptera – means 'two wings"; scientific name given to flies.

diurnal – active during the day (compare with "crepuscular" and "nocturnal").

dorso-ventrally – flattened from back (dorso) to belly (ventral).

dung – animal excrement; mainly used in reference to livestock (compare with "manure"). Insects that thrive in dung may be uncommon or absent in manure and vice versa.

dweller – a category of dung beetle that breeds within the dung deposit (compare with "roller" and "tunneller") (Fig. 3).

ectoparasitoid – a parasitoid that develops on the outer surface of the host (compare with "endoparasitoid").

elytron (pl. elytra) – means "sheath" or "cover"; the harden forewings of beetles that lie above and protect the membranous hindwings, which are used for flight (Fig. 46).

elytra striae – grooves that run lengthwise along the elytra; used in beetle identification (Fig. 46).

elytral suture – the midline along which the two elytra meet on the back of the beetle (Fig. 46).

emergence cage – a cage in which insects emerging from dung or other substrate are recovered (Fig. 13).

endectocide – a veterinary drug applied to livestock to kill both internal (endo) and external (ecto) parasites.

endocoprid – a term used to describe species of dung beetles that are dwellers.

endoparasitoid – a parasitoid that develops within the host (compare with "ectoparasitoid").

entomologist – a person who studies insects; typically someone who does so for a living and often has a advanced degree.

eurytopic – an organism with a wide tolerance for different habitats or environmental conditions (compare with "oligotopic" and "stenotopic").

exarate – a type of pupal body form in which the appendages are not held tight to the body. The majority of beetle species have exarate pupae (compare with "coarctate" and "obtect") (Fig. 16c).

filth flies – a general term for flies that breed in rotting organic matter including compost and carrion; not applied to flies that breed in fresh dung.

formulation – the manner in which a product is prepared for application; e.g., endectocides are available as injectable, topical (pour-on) or extended-release formulations.

fungivore – an organism that feeds on fungal hyphae or spores.

galls – see cecidia.

granulate – small bumps or granules on the head, pronotum and (or) elytra; a trait used in beetle identification

hemimetabolous metamorphosis – an insect life cycle with three developmental stages (egg, nymph, adult); also called simple or incomplete metamorphosis (compare with "holometabolous metamorphosis")

holometabolous metamorphosis – an insect life cycle with four developmental stages (egg, larva, pupa, adult); also called complete metamorphosis (compare with "hemimetabolous metamorphosis")

horns – used to refer to the hornlike projections on the head or pronotum of dung beetle species (Figs. 74, 75, 76 and 77).

Hymenoptera – means 'married wings"; scientific name given to wasps and their close relatives (i.e., bees, ants, sawflies).

hyperparasitoid – a parasitoid that develops on another parasitoid.

idiobiont – a parasitoid that immobilize its host and prevent it from developing further. (compare with "koinbiont").

imago – the final stage of insect development; the adult, typically winged.

International Code of Zoological Nomenclature (ICZN) – a widely accepted convention that sets the rules for the formal scientific naming of insects and other animals.

koinbiont – a parasitoid that allows the host to continue development while the parasitoid feeds within (compare with "idiobiont").

larvicide – a chemical or substance that kills larvae. Residues of some parasiticides applied to cattle act as larvicides in dung of treated animals.

larviposition – the laying of larvae instead of eggs. In such cases, the eggs hatch within the body of the female.

maculate – having dark markings. Some species of dung beetles can be identified by a pattern of maculate elytra (e.g., *Chilothorax distinctus* – Fig. 61).

male major – one of two morphological categories of males associated with certain species of dung beetles; has well-developed horns (Figs. 74, 75, 76b and 77a) and is normally larger than male minors of the species (compare with “male minor”).

male minor – one of two morphological categories of males associated with certain species of dung beetles; has poorly-developed or absent horns and is normally smaller than male majors of the species (compare with “male major”).

mandibles – a pair of mouthparts that insects use to grasp, pierce and chew their food (compare with “chelicerae”).

manure – mixture of dung and other plant material. Insects that thrive in dung may be uncommon or absent in manure and vice versa (compare with “dung”).

median notch – a notch at the midpoint of the clypeus; used to identify certain species of dung beetles (Fig. 74).

myiasis – an infection of fly larvae in living tissue (Fig. 35).

Nematocera – means “thread-horns”; one of two recognized suborders of flies (Diptera). Adults are characterized with long, thin antennae with many segments, and elongate bodies with long legs (compare with “Brachycera”).

nidification – nest building; e.g, tunnelling and rolling categories of dung beetles have different patterns of nidification (Fig. 3).

nocturnal – active at night (compare with “diurnal” and “crepuscular”).

obtect – a type of pupal body form in which the appendages are held tight to the body, which is covered by a thin transparent membrane. Common form for butterflies and moths, many beetles, and nematoceran flies (compare with “coarctate” and “exarate”) (Fig. 16a and b).

ocellus (pl. ocelli) – means “little eye”; a light-detecting structure that consists of a single lens and a few photoreceptor cells (compare with “compound eye”) (Fig. 83b).

oligotopic – an organism with a reduced tolerance for different habitats or environmental conditions intermediate between that exhibited by eurytopic and stenotopic organism.

paedogenesis – a phenomenon in which the larvae or pupae of an insect develop functional ovaries that produce larvae (Fig. 18).

paracoprid – a term used to describe species of dung beetles that are tunnellers.

parasite – an organism that may feed on more than one host, but does not normally kill the host (compare with “parasitoid”).

parasiticide – a veterinary drug applied to livestock to kill parasites; e.g., cattle grubs, flukes, mites, nematodes, and tapeworms.

parasitoid – an organism that only develops on one host and almost always kills it (compare with “parasite”). Solitary parasitoids normally lay one egg per host; gregarious parasitoids normally lay multiple eggs per host.

pederin – a chemical produced by certain species of staphylinid beetles; skin contact can cause rashes, fever, neuralgia (nerve pain) and scarring.

phoresy – a phenomenon in which an animal (the phoretic) actively seeks out and attaches to the outer surface of another animal, which carries the phoretic to more favourable habitat (see section titled "Phoresy" – page 15).

piceous – glossy brownish black in colour; trait used to identify beetles.

pitfall trap – a container buried in the ground with the rim even with the soil surface allowing animals to fall in. Dung-baited pitfall traps are often used to catch dung beetles (Figs. 11 and 12).

platyform – larval form with a flattened body and extremely short or absent legs (compare with “campodeiform”, “scarabaeiform” and “vermiform”); common to certain groups of beetles; e.g., Histeridae, Hydrophilidae (Sphaeridiinae) (Fig. 15b).

pronotal disc – upper (highest) part of the pronotum with characteristics of texture and colour that may differ from the sides of the pronotum; used in beetle identification.

pronotum – prominent platelike structure behind the head of the insect; its shape, texture and colour are used in beetle identification (Fig. 46).

prophylactic – applied as a preventative measure; e.g., the prophylactic use of antibiotics to prevent disease in livestock.

propylene glycol – a non-toxic solution that is used as a preservative in pitfall traps; commonly sold to winterize waterlines in recreational vehicles and summer cottages. Do not confuse with ethylene glycol, which is highly toxic and commonly sold as automotive antifreeze.

puncture – small impression on the hard outer surface of insects. The presence and pattern of punctures on the head, pronotum and elytra is used for insect identification (Fig. 46).

puddling – behaviour in which insects (most commonly butterflies) visit fresh dung to extract moisture and nutrients.

punctate – studded with punctures; texture used in insect identification

puparium (pl. puparia) – the hardened larval skin in which the larva pupates (Fig. 16d); see "coarctate".

pygidium – the hindmost body segment for certain species of insects; left uncovered by the elytra in some species of dung beetles; e.g., Figs. 72 and 73).

quadridentate – having four teeth or structures suggestive of teeth (Fig. 73).

refugia – a region where organisms can survive unfavourable conditions such as glaciation.

roller – a category of dung beetle that removes dung from the fresh deposit and rolls it away for burial (compare with "dweller" and "tunneller") (Fig. 3).

saprophagous – feeding on decaying organic matter. Different from coprophagous, which implies a specific association with fresh dung.

scarabaeiform – larval form with a cylindrical and curved body, and usually with short but visible legs (compare with "campodeiform", "platyform" and "vermiform"); common to true dung beetles; i.e., Scarabaeidae (Fig. 15c).

scutellum – in beetles, refers to the small triangular plate-like structure behind the pronotum and between the point of attachment for the elytra; may or may not be visible depending upon the species (Fig. 46).

snake-worm – a rope-like procession of sciarid larvae formed during mass-migration (Fig. 26).

stenotopic – an organism with a narrow tolerance for different habitats or environmental conditions (compare with "eurytopic" and "oligotopic").

sternite – ventral portion of an insect's segment.

succession – a sequential and predictable pattern of change in a biological community; e.g., the succession of insect species in cattle dung as it ages.

synonym – in taxonomy, the formal scientific name for an organism that is no longer used; e.g., the dung beetle *Canthon pilularius* was previously known under the synonym *Canthon laevis*.

tarsomere – one of several small movable segments that form the apical-most portion of an insect's leg; tarsomere number and shape are used in insect identification (Fig. 40).

taxonomic hierarchy – the ranking of different groups (taxa) of organisms on the basis of their morphological similarity; e.g., by increasing similarity: phylum, class, order, family, genus, species.

taxonomic key – a tool or guide used to identify organisms; provides a series of choices normally based on morphological features that eventually allow for species-level identification.

telecoprid – a term used to describe species of dung beetles that are rollers.

truncate – shortened.

tubercle – prominent bump or rounded protuberance; used for some dung beetles to identify their sex and species.

tunneller – a category of dung beetle that removes dung from the fresh deposit and buries it below the deposit (compare with "dweller" and "tunneller") (Fig. 3).

unimodal – one peak of activity; e.g., some species of insects have a unimodal pattern of seasonal activity (Fig. 8g).

vermiform – larval form that is cylindrical and has no appendages (wormlike) (compare with "campodeiform", "platyform" and "scarabaeiform"); common form for larvae of flies and wasps (Figs. 15d and e).

VOCs (Volatile Organic Compounds) – gases emitted by certain liquids or solids. Changes in VOCs over time affect the number and type of coprophilous insects attracted to fresh dung.

warbles – swellings under the skin of animals infected by larvae of oestrid flies.

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