REARING, IDENTIFICATION AND BIOLOGY OF PARASITOIDS AND PREDATORS ASSOCIATED WITH *PISSODES* WEEVILS IN CANADA

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ABSTRACT

Methods for collecting and rearing parasitoids of larvae and pupae of *Pissodes* species are discussed. Illustrated keys are provided for the identification of 31 species of Diptera and Hymenoptera, which are parasitoids, hyperparasitoids, and scavengers associated with *Pissodes* species. Twenty-six of these species are known to occur in Canada, and another 6 are widespread in the United States and probably occur in Canada. A list is provided of 33 other species which have been recorded as associates of *Pissodes* species, but whose records are suspect and have not been confirmed. A brief discussion of the biology and abundance of each species, which is included in the key, is given. A glossary is given.

RÉSUMÉ

Les auteurs traitent des méthodes de collecte et d'élevage des parasitoïdes des larves et des pupes des espèces du genre *Pissodes*. Ils présentent des clés d'identification illustrées de 31 espèces de diptères et d'hyménoptères parasitoïdes, hyper-parasitoïdes et détritivores associées aux espèces du genre *Pissodes*. Vingt-six de ces espèces sont présentes au Canada et six autres sont répandues aux États-Unis et sont probablement présentes au Canada. Les auteurs fournissent une liste de 33 autres espèces mentionnées comme apparentées au genre *Pissodes*, mais ces relevés sont douteux et restent à confirmer. Ils décrivent brièvement la biologie et l'abondance de chacune des espèces traitées dans la clé qui comprend également un glossaire.

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INTRODUCTION

The genus *Pissodes* includes 11 currently valid species known to occur in Canada. These bark weevils attack the stems and terminals of coniferous trees, and their larvae feed on phloem and pith. Most species attack weakened or dying trees, and they may be associated with primary pests such as bark beetles and root diseases. Some species attack living healthy trees, particularly the terminal-inhabiting *Pissodes strobi* (Peck) and *Pissodes terminalis* Hopping, which are known to have significant economic impact on regenerating stands (Hiratsuka et al. 1995). The literature on the taxonomy, biology, and control of *Pissodes* is extensive (Langor 1998), and there is continuing study of economically important species (Alfaro et al. 1994).

In the course of rearing *Pissodes* species from attacked trees, a large number of individuals of other insect species are inevitably recovered. Numerous species of the Hymenoptera families Ichneumonidae and Braconidae and the superfamily Chalcidoidea and Diptera families Lonchaeidae and Dolichopodidae have been associated with *Pissodes*-attacked trees. The nature of the association of many of these species is not well understood, although the biology of some species has been studied and their status as parasitoids or predators of *Pissodes* larvae confirmed. There remain many gaps in our understanding of the role of natural enemies in the regulation of *Pissodes* populations, and hence there are many opportunities to explore the use of natural enemies in controlling pest populations of *Pissodes*. Such studies could be aided by tools to help in identifying the complex fauna of parasitoid and predator species.

We have developed an identification key to adults of the 31 species of Hymenoptera and Diptera that are confirmed or highly likely natural enemies of *Pissodes* larvae or pupae (or both) in Canada, according to literature records and examination of reared specimens in various Canadian collections (Appendix 1). Biological information on the association of each species with *Pissodes* is summarized. Another 33 species have been cited in various literature sources as being associated with *Pissodes* (Appendix 2), but for a number of reasons have not been included in this key. Some of these records are probably erroneous, as they involve species that do not normally include *Pissodes* in their host range; in these cases, the specimens might have been misidentified, or they might have been attacking other wood-boring species co-occurring with *Pissodes*. Other records need confirmation; these include single rearings of small numbers of specimens of species that have not been encountered in other studies, rearing of species that attack many host species and may have attacked either *Pissodes* or some other host co-occurring in the reared material, reports of unconfirmed data on specimen labels in taxonomic works, and records of species that attack *Pissodes* in areas outside of Canada but that are unlikely to occur here.

The taxonomic literature on natural enemies of *Pissodes* is sparse. Most species belong to genera for which there are no identification keys, and the existing literature comprises isolated species descriptions, which may contain a few notes on biology. For species with taxonomic and biological literature, a brief summary and key references are given here. For most species, the best literature resources are taxonomic catalogs and overview syntheses. Catalogs for parasitic Hymenoptera are available in book (Krombein et al. 1979) and electronic (Noyes 1998; Yu 1999) form, and taxonomic overviews exist for Ichneumonidae (Townes 1969a, 1969b, 1969c, 1971), Braconidae (Wharton et al. 1997), Chalcidoidea (Gibson et al. 1997), and Hymenoptera (Goulet and Huber 1993). A taxonomic review of the Diptera (McAlpine et al. 1981) is also available, in which information on all Diptera taxa included here may be found.

COLLECTING AND REARING PARASITOIDS AND PREDATORS

Most parasitoid and predator species that attack *Pissodes* larvae and pupae are univoltine. They show a strong preference for mature larval or pupal hosts, overwinter as pupae or prepupae, and emerge as adults in late spring of the next year. However, some species may be multivoltine, particularly those with a wide host range, and these may occur on different hosts in different parts of the season. Most parasitoid species within an assemblage may be recovered by sampling when *Pissodes* larvae have begun to construct chip cocoons and form prepupae. This stage may be determined by removal of small sections of bark on the boles of trees or dissection of terminals. To recover parasitoids that attack earlier stages, or to determine which species may have more than one generation per year, samples should be taken earlier, when larvae are in middle instars.

Identification of *Pissodes*-infested host material is not difficult. Terminal leaders infested with *P. strobi* or *P. terminalis* wilt and discolor. Close examination of wilting terminals reveals numerous clumped oviposition marks on the bark of the previous year's terminal if attacked by *P. strobi* (Hiratsuka et al. 1995, Fig. 30C) and scattered oviposition marks on the current year's terminal if attacked by *P. terminalis* (Hiratsuka et al. 1995, Fig. 31B). *Pissodes* species that infest boles and branches attack only trees that are severely weakened or recently killed by other agents. Infested boles and branches show no outward signs that they contain *Pissodes*, and the bark must be removed to confirm the presence of these organisms. *Pissodes* larvae are legless grubs with creamy white, wrinkled bodies and reddish brown heads. Superficially they resemble bark beetle (Scolytidae) larvae. An easy, nonmorphological way to determine whether a larva fitting this general description is a bark beetle or a weevil is to determine if the larval feeding gallery originates from an egg gallery constructed by adults entering the bark (bark beetle) or not (weevil). Furthermore, all bole- and branch-inhabiting *Pissodes* larvae construct chip cocoons for pupation (Hiratsuka et al. 1995, Fig. 30E), but bark beetles do not. *Pissodes*-infested materials may be collected and transferred to containers that can accommodate single bole sections or terminals. Individual rearing of samples is the best approach for obtaining parasitoid information, as this reduces the chance of co-occurrence of other potential host insects for any given rearing.

When terminals attacked by *P. strobi* are collected, they must be snipped well below the first whorl of branches under the terminal. Most parasitoids do not attack *P. strobi* until near or during the time when host larvae are preparing chip cocoons for pupation, and this process usually occurs around the first branch whorl. Because *P. terminalis* usually confines its feeding to the current year's terminal, it suffices to collect only this part. Terminals are best reared individually in capped cardboard mailing tubes, hung vertically with a vial attached to a hole in the lower cap to facilitate collection of emerging specimens. Evidence of damage by other terminal- or shoot-boring insects may be checked by dissection of the terminal when rearing is complete or by observing the presence of hosts among reared samples.

Insects in infested boles may be reared in larger containers or cages fitted with collection devices. Many parasitoid species are minute, so care must be taken to seal larger containers adequately. Containers should be well vented to allow heat and moisture to escape and to retard fungal growth. Adult *Pissodes* emerge from damaged wood in late summer and autumn of that year, whereas most parasitoids do not emerge until spring of the following year, so provision should be made for ambient-temperature, long-term storage, to afford parasitoids the opportunity for diapause.

As field-collected damaged wood may contain a complex community of saproxylic species, confirmation of host identity is best achieved by rearing the individual parasitized host larvae (although this approach has not been used for predaceous Diptera larvae). With the help of the identification criteria provided above to discriminate between weevil and bark beetle larvae, parasitized weevil larvae may be extracted carefully from the wood for rearing. Hosts that have been paralyzed by hymenopterous parasitoids are easily identified, as they are plump and immobile, and the dark scar of the oviposition puncture can be seen under low-power magnification. Care must be taken in removing the host and any attached ectoparasitic larvae or eggs. On occasion, parasitoid larvae and eggs may become detached from the host. These should be placed gently back on the host in the rearing containers. Larvae that are thought to be paralyzed but that have no ectoparasitoids should also be reared, as they may contain endoparasitoids. It is also wise to remove healthy larvae and preserve them in 70% ethanol; these organisms can be used to help in species identification later, as the larvae of some species have been described (Williams and Langor 2002). Healthy prepupae and pupae may be placed on moistened tissue paper in petri dishes and allowed to continue development to adulthood.

Small (5- or 10-dram) plastic or glass containers or vials function well as rearing containers, with a thin layer of rearing medium (Robertson 1979) in the bottom to maintain humidity and prevent fungal and bacterial growth. This medium contains an artificial diet that will probably not be consumed, as parasitized larvae seldom return to normal activity; the user may therefore decide to alter the formula to eliminate unnecessary ingredients. Vials may be placed in plastic bags or larger containers with moist paper towels to maintain humidity. Rearing containers should be stored in the dark. For many species, diapause is facultative, and parasitoid larvae will develop, pupate, and eclose to adulthood without cold treatment. Species with obligatory diapause will require several months of cold treatment before they can complete development. Storage in a refrigerator or a cold room (5ºC) should suffice. In the field, parasitoid larvae occur in protected habitats, and hard freezing causes death.

KEY TO ADULT HYMENOPTERA AND DIPTERA ASSOCIATED WITH *PISSODES* SPECIES IN CANADA

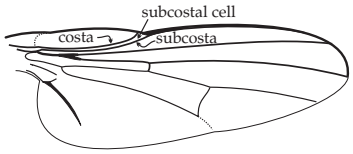

Fig. 1. ***Lonchaea corticis*** **Taylor wing.**

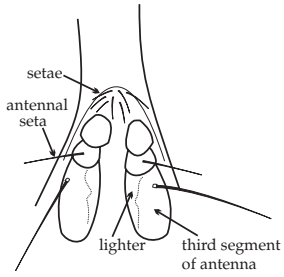

Fig. 2. ***Lonchaea corticis*** **Taylor antennal area of head.**

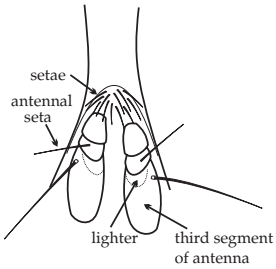

Fig. 3. ***Lonchaea furnissi*** **McAlpine antennal area of head.**

Fig. 4. ***Modetera vidua*** **Wheeler antenna.**

For an on-line version of this key, see the Biodiversity web page of the Northern Forestry Centre Internet site, <http://nofc.cfs.nrcan.gc.ca/biodiversity/>. Figures 1-63 comprise the key to adult Hymenoptera and Diptera associated with *Pissodes* species in Canada. Figures are not necessarily numbered in the order in which they appear in the key. In several instances figures are used more than once, to illustrate characters that help identify closely related groups of species and to illustrate differences among these closely related species. In these instances, the user is asked to refer to several parts of the key so that figures of closely related species may remain together.

1. Adult with two pairs of wings, forewings often much bigger than hindwings. Larva spins silken cocoon upon emergence from host or emerges as adult (Hymenoptera) 5

   Adult with one pair of wings, densely hairly on most of body. Larva hardens into a brown capsule upon emergence from host, with pupa inside (Diptera) 2

2. Body smooth and shiny. Forewing with costal and subcostal veins separate, subcostal cell extending to wing margin (Fig. 1). *Lonchaea* species. These species are very difficult to identify, especially the females 3

   Body with matte microsculpture. Forewing with costal and subcostal veins fused except near base; subcostal cell reduced (Fig. 5). *Medetera* species (key by Bickel 1985) 4

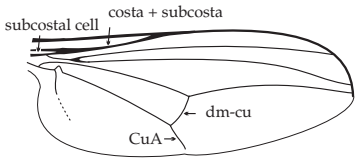

Fig. 5. ***Medetera vidua*** **Wheeler wing.**

3. Third antennal segment of male dark brown with orange or light brown area extending over most of length. Setae on area of head between antennal insertions thinner than large seta on second antennal segment (Fig. 2) ..... *Lonchaea corticis* Taylor

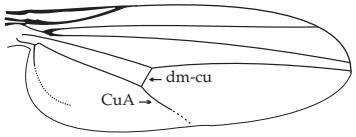

Fig. 6. ***Medetera apicalis*** **(Malloch) wing.**

Third antennal segment of male with orange or light brown area near base of segment only. Some setae on area of head between antennal insertions as stout as (although shorter than) seta on second antennal segment (Fig. 3) .... *Lonchaea furnissi* McAlpine

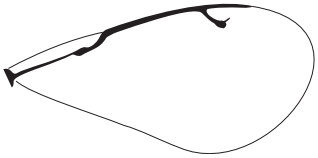

Fig. 7. ***Eupelmus pini*** **Taylor forewing.**

4. Antenna with scape and pedicel yellow (Fig. 4). Vein dm-cu of wing about as long as vein CuA. (Fig. 5) .... *Medetera vidua* Wheeler

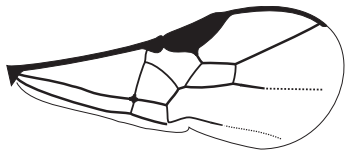

Fig. 8. ***Coeloides rufovariegatus*** **Provancher forewing.**

Antenna with scape and pedicel dark brown to black. Vein dm-cu about half as long as vein CuA (Fig. 6) .... *Medetera apicalis* (Malloch)

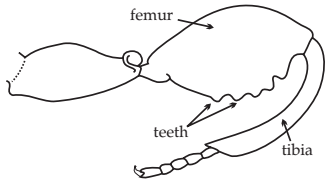

Fig. 9. ***Trigonura tarsata*** **(Dalla Torre) hind leg.**

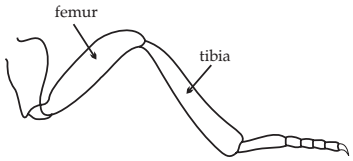

Fig. 10. ***Rhopalicus pulchripennis*** **(Crawford) hind leg.**

5.(1) Body usually < 4 mm long. Forewing with a single pigmented vein along anterior margin, (Fig. 7), some species with various faint veins or creases near base (Fig. 24). Chalcidoidea..... 6

Body usually > 4 mm long. Forewing with numerous veins enclosing several cells (Fig. 8). Ichneumonoidea..... 14

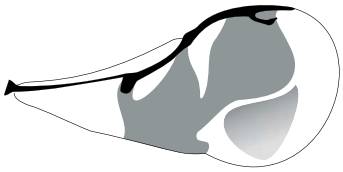

Fig. 11. ***Heydenia unica*** **Cook and Davis forewing.**

6. Femur of hind leg enlarged, toothed ventrally. Hind tibia curved, fitting into groove in ventral side of hind femur (Fig. 9) ..... *Trigonura tarsata* (Dalla Torre)

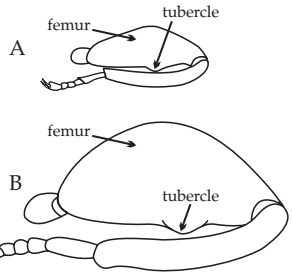

Fig. 12. ***Heydenia unica*** **Cook and Davis front leg.** **A.** Male. **B.** Female.

Hind femur and tibia similar to those of middle leg (Fig. 10)..... 7

Fig. 13. ***Eurytoma pissodis*** **(Girault) antenna, setae omitted.**

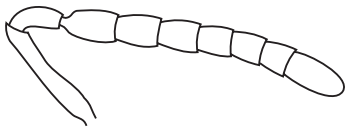

Fig. 14. ***Rhopalicus pulchripennis*** **(Crawford) antenna of female.**

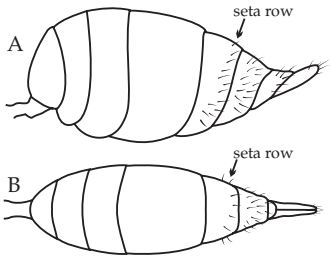

Fig. 15. ***Eurytoma cleri*** **Ashmead gaster. A.** Lateral view. **B.** Dorsal view.

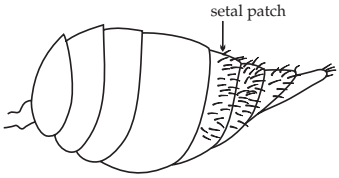

Fig. 16. ***Eurytoma picea*** **Bugbee lateral view of gaster.**

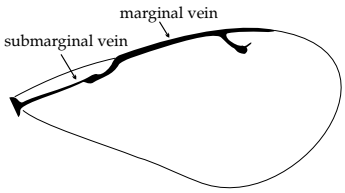

Fig. 17. ***Eupelmus pini*** **Taylor forewing.**

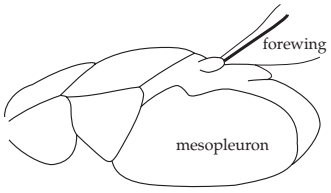

Fig. 18. ***Eupelmus pini*** **Taylor lateral view of thorax.**

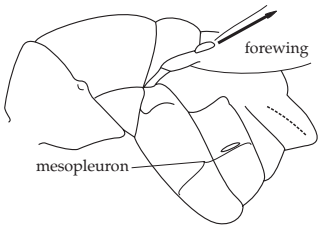

Fig. 19. ***Rhopalicus pulchripennis*** **(Crawford) lateral view of thorax.**

7. Forewing with a large darkened area consisting of pigment spots and stout, dark setae (Fig. 11). Femur of front leg enlarged, with a ventral tubercle (Fig. 12A, B) .... *Heydenia unica* Cook and Davis

Forewing clear (Fig. 17), or with small darkened spot on vein (Fig. 24). Femur of front leg similar to that of middle leg (similar to Fig. 10) 8

8. Body black. Head and thorax covered with coarse punctures. Antenna of male with segments constricted on ends (Fig. 13). Gaster of female somewhat laterally compressed, narrower in dorsal view than lateral view (Fig. 15A, B). *Eurytoma* species. These species are very uniform in appearance and difficult to identify, especially the males. (key by Bugbee 1967) 9

Head and thorax metallic green, usually with granular or striate sculpture. Antenna of male with segments cylindrical (similar to Fig.14). Gaster of female not laterally compressed, about as wide or wider in dorsal view as in lateral view (see Fig. 47) 11

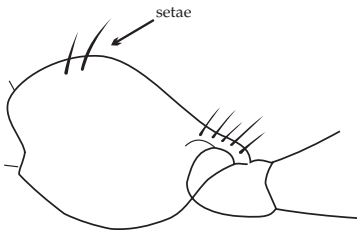

Fig. 20. ***Rhaphitelus maculatus*** **Walker hind coxa.**

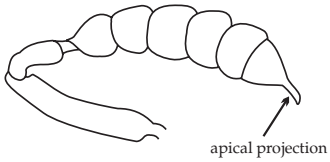

Fig. 21. ***Rhaphitelus maculatus*** **Walker antenna of female.**

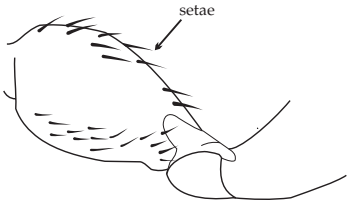

Fig. 22. ***Rhopalicus pulchripennis*** **(Crawford) hind coxa.**

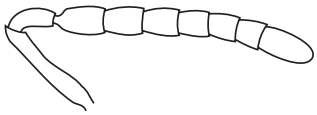

Fig. 23. ***Rhopalicus pulchripennis*** **(Crawford) antenna of female.**

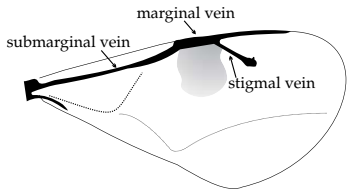

Fig. 24. ***Rhopalicus pulchripennis*** **(Crawford) forewing.**

9. Front and middle legs uniformly light brown, some specimens with middle femur slightly darkened dorsally..... ..... *Eurytoma pissodis* (Girault)

Front and middle legs with dark patches on femora and tibiae 10

10. Female with a single irregular row of setae on the fifth gastral tergum (Fig. 15A,B) ..... *Eurytoma cleri* Ashmead

Female with several rows or an irregular patch of setae on the fifth gastral tergum (Fig. 16)..... *Eurytoma picea* Bugbee

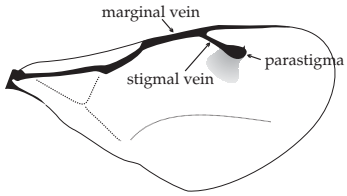

Fig. 25. ***Rhopalicus tutela*** **(Walker) forewing.**

11.(8) Forewing entirely clear, with marginal vein longer than submarginal vein (Fig. 17). Thorax of female elongate, with large, evenly sculptured and convex mesopleuron (Fig. 18) ..... *Eupelmus pini* Taylor

Fig. 26. ***Dolichomitus terrebrans nubilipennis*** **(Ratzeburg) forewing.**

Forewing with a small darkened spot on vein (Figs. 24, 25), marginal vein shorter than submarginal vein (Figs. 24, 25). Thorax of female with mesopleuron divided by areas of different convexity and sculpture (Fig. 19) ..... 12.

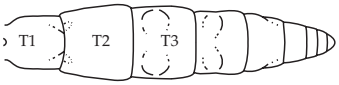

Fig. 27. ***Calliephialtes comstockii*** **(Cresson) dorsal view of gaster.**

Hind coxa bare dorsally or with a few erect setae (Fig. 20). Antenna of female short and club-like, with an apical finger-like projection (Fig. 21) ..... *Rhaphitelus maculatus* Walker

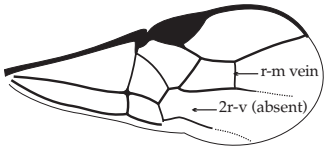

Fig. 28. ***Bracon pini*** **(Muesebeck) forewing**

Hind coxa with scattered reclining setae dorsally (Fig. 22). Antenna of female more elongate, without apical projection (Fig. 23). *Rhopalicus* species 13

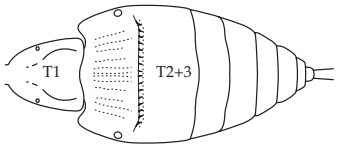

Fig. 29. ***Bracon pini*** **(Muesebeck) dorsal view of gaster.**

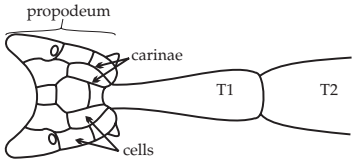

Fig. 30. ***Labena grallator*** **Say dorsal view of propodeum and first two gastral segments.**

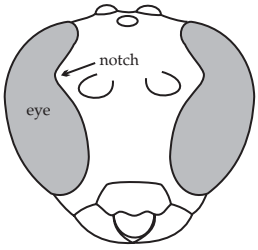

Fig. 31. ***Labena grallator*** **Say anterior view of head.**

13. Forewing with marginal vein slightly longer than stigmal vein, with dark pigmented spot near wing margin (Fig. 24)..... ..... *Rhopalicus pulchripennis* (Crawford)

Forewing with marginal vein much longer than stigmal vein, with dark pigmented spot around parastigma (Fig. 25) ..... *Rhopalicus tutela* (Walker)

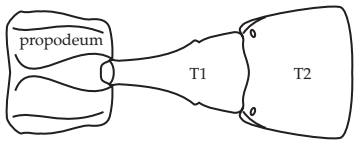

Fig. 32. ***Cubocephalus occidentalis*** **(Provancher) dorsal view of propodeum and first two gastral segments.**

14.(5) Second recurrent vein (2r-v) of forewing present (Fig. 26). Second and third gastral terga (T2 and T3) separate (Fig. 27). Ichneumonidae..... 15

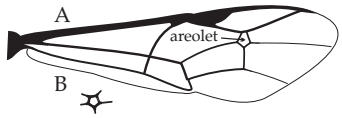

Fig. 33. **A.** ***Cubocephalus occidentalis*** **(Provancher) forewing. B.** ***Helcostizus contortae*** **Townes areolet.**

Second recurrent vein (2r-v) of forewing absent (Fig. 28). Second and third gastral terga fused (T2+3), joint marked by a groove in some species (Figs. 29, 47A, B). Braconidae..... 21

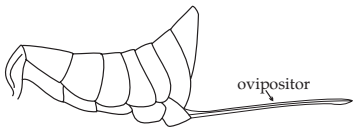

Fig. 34. ***Helcostizus contortae*** **Townes lateral view of gaster.**

Fig. 35. ***Dolichomitus terrebrans nubilipennis*** **(Ratzeburg) forewing.**

Fig. 36. ***Dolichomitus terrebrans nubilipennis*** **(Ratzeburg) lateral view of gaster.**

15. Propodeum with well-developed carinae enclosing several cells (Fig. 30). Inner margin of eyes notched near antennae (Fig. 31) ..... *Labena grallator* Say

Propodeum with few carinae and without closed cells (Fig. 32). Inner margin of eye straight or sinuate..... 16

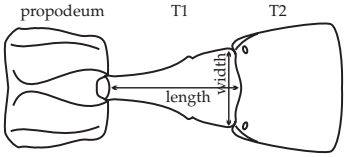

Fig. 37. ***Cubocephalus occidentalis*** **(Provancher) dorsal view of propodeum and first two gastral segments.**

16. Areolet five-sided, with one side shorter than the others (Fig. 33A) or partially faint or missing (Fig. 33B). Ovipositor shorter than gaster (Fig. 34) 17

Areolet four-sided and diamond-shaped (Fig. 35). Ovipositor longer than gaster (Fig. 36)..... 20

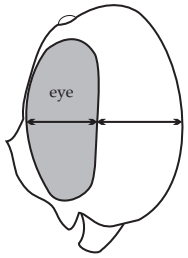

Fig. 38. ***Cubocephalus occidentalis*** **(Provancher) lateral view of head.**

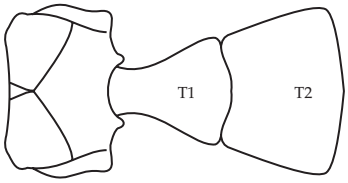

Fig. 39. ***Helcostizus contortae*** **Townes dorsal view of propodeum and first two gastral segments.**

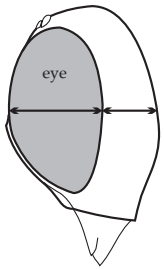

Fig. 40. ***Helcostizus contortae*** **Townes lateral view of head.**

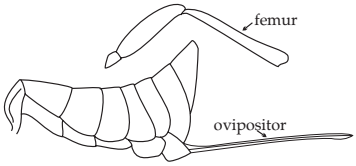

Fig. 41. ***Helcostizus contortae*** **Townes lateral view of gaster and hind leg.**

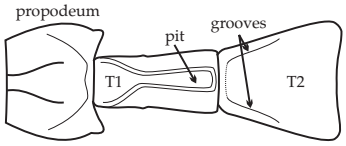

Fig. 42. ***Dolichomitus terrebrans nubilipennis*** **(Ratzeburg) dorsal view of propodeum and first two gastral segments.**

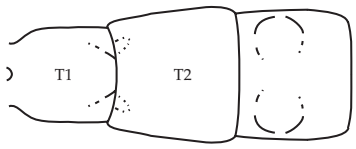

Fig. 43. ***Calliephialtes comstockii*** **(Cresson) dorsal view of anterior end of gaster.**

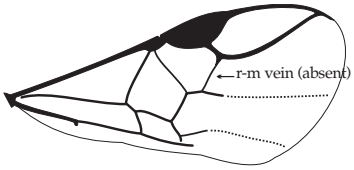

Fig. 44. ***Eubazus calyptoides*** **(Martin) forewing.**

17. First gastral tergum (T1) much longer than apical width (Fig. 37). Eye narrower than posterior part of head in lateral view (Fig. 38)..... *Cubocephalus occidentalis* (Provancher)

First gastral tergum (T1) slightly longer than apical width (Fig. 39). Eye wider than posterior part of head in lateral view (Fig. 40). *Helcostizus* species (key by Townes 1983) 18

18. Thorax with large brown area midventrally .... *Helcostizus albator rufiscutum* Cushman

Thorax black 19

19. Ovipositor about 1.5 times as long as hind femur (Fig. 41). Tegula white. Hind tibia uniformly dark brown .... *Helcostizus contortae* Townes

Ovipositor more than twice as long as hind femur. Tegula white with brown apex. Hind tibia darker apically than basally .... *Helcostizus subrectus* Townes

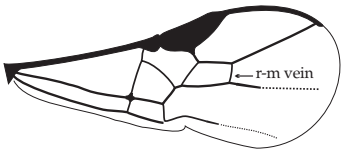

Fig. 45. ***Coeloides rufovariegatus*** **Provancher forewing.**

20.(16) Gastral tergum 1 (T1) longer than tergum 2 (T2), with a pair of dorsal carinae surrounding an apical pit, tergum 2 with a pair of lateral oblique grooves at base (Fig. 42)..... ..... *Dolichomitus terrebrans nubilipennis* (Ratzeburg)

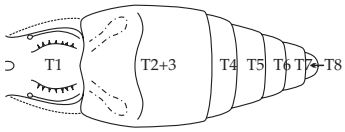

Fig. 46. ***Coeloides rufovariegatus*** **Provancher dorsal view of gaster.**

Gastral tergum 1 (T1) shorter than tergum 2 (T2), with incomplete carinae, tergum 2 without lateral oblique grooves (Fig. 43) ..... *Calliephialtes comstockii* (Cresson)

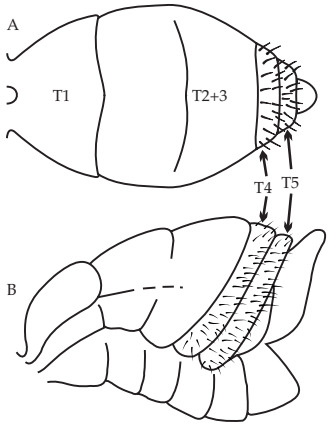

Fig. 47. ***Eubazus crassigaster*** **(Provancher) gaster.**
A. Dorsal view.
B. Lateral view.

21.(14) Second submarginal cell open, r-m vein absent (Fig. 44). Gaster with first three terga forming a carapace that covers most of dorsal surface (Figs. 47A, 48A). *Eubazus* species 22

Second submarginal cell closed, r-m vein present (Fig. 45). Gaster with at least six large terga visible dorsally (Fig. 46) 23

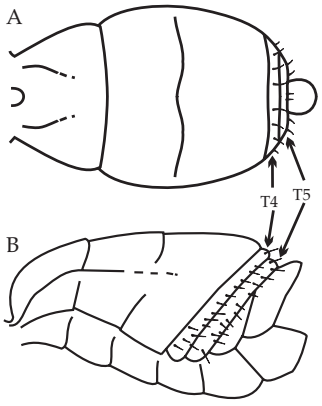

Fig. 48. ***Eubazus calyptoides*** **(Martin) gaster.**
A. Dorsal view.
B. Lateral view.

22. Body dark brown, with gaster lighter apically. Fourth and fifth gastral terga (T4 and T5) wide in dorsal view, together about a third to half as wide as third gastral terga (Fig. 47A), with abundant hairs (Fig. 47B)..... *Eubazus crassigaster* (Provancher)

Body black. Fourth and fifth gastral terga (T4 and T5) hidden beneath third gastral terga or visible as narrow strips in dorsal view (Fig. 48A), with few, scattered hairs (Fig. 48B)..... ..... *Eubazus calyptoides* (Martin)

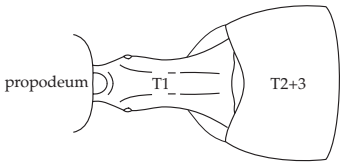

Fig. 49. ***Spathius brachyurus*** **Ashmead dorsal view of anterior end of gaster.**

23. Body uniformly light golden brown. First gastral tergum (T1) narrow and elongate (Fig. 49). *Spathius* species (key by Matthews 1970) 24

Body dark brown, or with dark and light patches, or gaster lighter than head and thorax. First gastral tergum (T1) rectangular (Fig. 50A) or triangular (Fig. 53A) 25

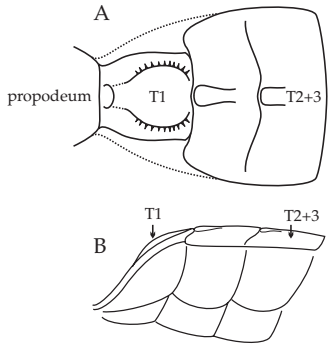

Fig. 50. ***Coeloides pissodis*** **(Ashmead) anterior end of gaster. A.** Dorsal view. **B.** Lateral view.

24. Propodeum with a pair of lateral tubercles (propodeal tubercle, Pt) (Fig. 51). Ovipositor slightly longer than hind tibia ..... *Spathius brachyurus* Ashmead

Propodeum without tubercles (Fig. 52). Ovipositor nearly twice as long as hind tibia ..... *Spathius sequoiae* Ashmead

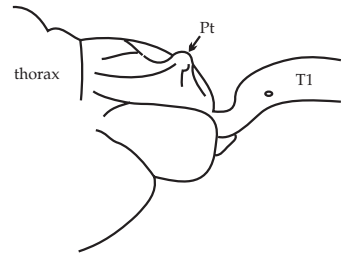

Fig. 51. ***Spathius brachyurus*** **Ashmead lateral view of propodeum.**

25. First gastral tergum (T1) covering entire surface of segment 1 in dorsal view (Fig. 53A), convex in lateral view (Fig. 53B). Gastral terga 1–3 mostly striate (Fig. 53A) ..... *Doryctes* sp.

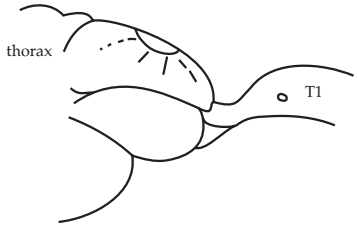

Fig. 52. ***Spathius sequoiae*** **Ashmead lateral view of propodeum.**

First gastral tergum (T1) with membraneous areas of segment 1 visible laterally in dorsal view (Fig. 50A), platelike, narrow in lateral view (Fig. 50B). Gastral terga with striate area limited to middle of second tergum or absent (Fig. 50A) 26

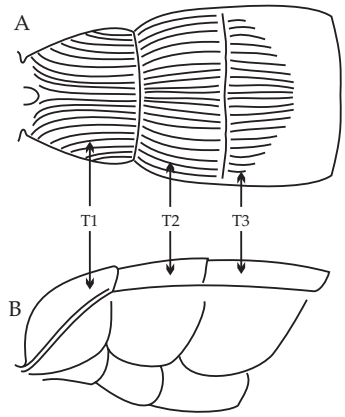

Fig. 53. ***Doryctes*** **sp. anterior end of gaster. A.** Dorsal view. **B.** Lateral view

26. Antennal flagellum with 1–3 basal segments concave ventrally and with flared rim, clearly different in shape from other flagellar segments (Fig. 54). *Coeloides* species (key by Mason 1978) 27

Antennal flagellum with basal segments sometimes a different length than other flagellar segments, but otherwise similar in shape (Fig. 55). *Bracon* species 30

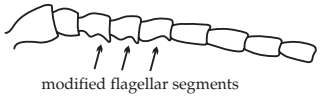

Fig. 54. ***Coeloides pissodis*** **(Ashmead) base of antenna.**

27. Coxa and femur of hind leg, and in some specimens middle leg, red or lighter in color than remainder ..... *Coeloides pissodis* (Ashmead)

Legs uniform dark brown to black 28

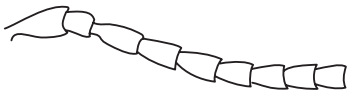

Fig. 55. ***Bracon pini*** **(Muesebeck) base of antenna.**

28. Head mostly or entirely orange–red, with variable dark markings on or near the occelli ..... *Coeloides vancouverensis* (Dalla Torre)

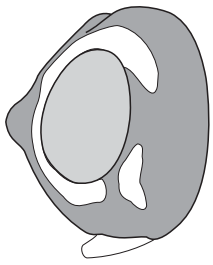

Fig. 56. ***Coeloides rufovariegatus*** **Provancher lateral view of head.**

Head black or brown, some specimens with pale markings around eye margin (Figs. 56, 58) 29

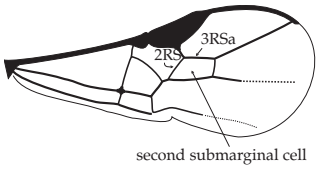

Fig. 57. ***Coeloides rufovariegatus*** **Provancher forewing.**

29. Head with distinct pale markings around eye, including inner margin between antennae and mandibles (Fig. 56). Second submarginal cell of forewing long, 3RSa vein longer than 2RS vein (Fig. 57) ..... *Coeloides rufovariegatus* Provancher

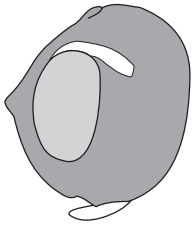

Fig. 58. ***Coeloides secundus*** **(Dalla Torre) lateral view of head.**

Head without pale markings, or with faint markings around dorsal eye margin, markings absent between inner margin between antenna and mandible (Fig. 58). Second submarginal cell of forewing short, 3RSa vein as long as or shorter than 2RS vein (Fig. 59)..... *Coeloides secundus* (Dalla Torre)

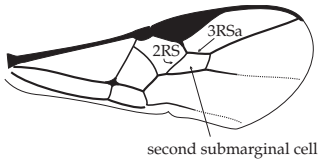

Fig. 59. ***Coeloides secundus*** **(Dalla Torre) forewing.**

30.(26) Head bicolored, with approximately equal areas of light and dark patches (Fig. 60) ..... *Bracon nanus* Provancher

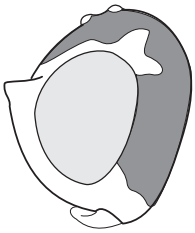

Fig. 60. ***Bracon nanus*** **Provanchr lateral view of head.**

Head uniformly dark brown to black, some specimens with pale markings around dorsal eye margin (Fig. 61)..... ..... *Bracon pini* (Muesebeck)

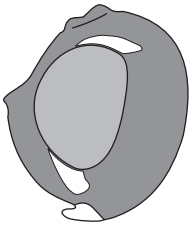

Fig. 61. ***Bracon pini*** **(Muesebeck) lateral view of head.**

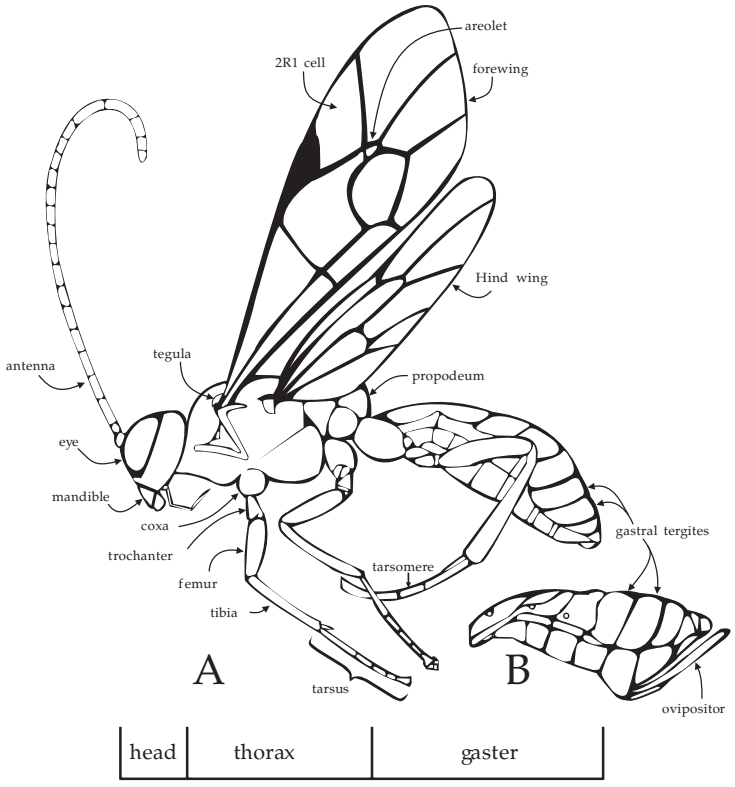

Fig. 62. Adult Hymenoptera
A. Lateral view of habitus of adult male. B. Lateral view of gaster of adult female.

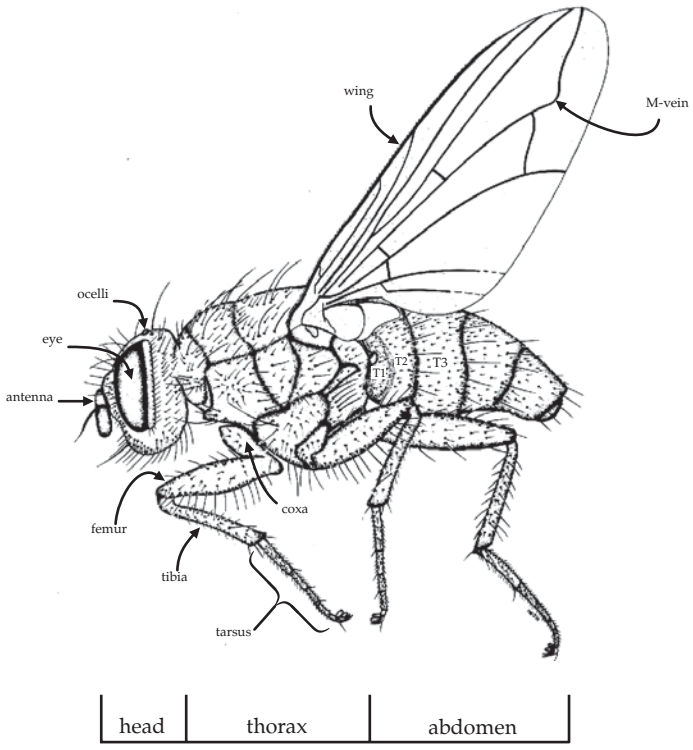

Fig. 63. Lateral view of habitus of adult dipteran parasitoid.

NOTES ON BIOLOGY AND ABUNDANCE OF REARED TAXA

Diptera

Diptera associated with *Pissodes* are predaceous, and they may also act as scavengers. Eggs are laid in adult weevil feeding and oviposition punctures, and fly larvae search for prey. Each larva remains free ranging, probably attacking several living or recently dead *Pissodes* larvae before development is complete.

***Lonchaea corticis* Taylor**

Also as *Lonchaea polita* Say, *Lonchaea rufitarsus* Maccquart, *Lonchaea hirta* Malloch, *Lonchaea laticornis* Meigan

Host: *P. strobi*

The biology of this species has been studied in British Columbia by Alfaro and Borden (1980) and Hulme (1989), and specimens have been reared from terminals attacked by *P. strobi* and collected from across Canada and the northern United States. It is a common predator of *P. strobi* larvae wherever they occur in Canada. It is recovered in almost all rearing studies (Langor 1998), and it may have a significant role in regulating weevil populations at some sites (Nealis 1998). The fly larvae attack weevil larvae gregariously, usually penetrating the posterior of the host, and eat the entire internal contents, leaving an empty skin with a posterior hole. They may also feed on dead larvae. Predation by this species can destroy most of the larvae in a terminal.

***Lonchaea furnissi* McAlpine**

Host: *Pissodes fasciatus* LeConte

This species has been reared only once from *Pissodes* (Deyrup 1978), but the record is considered confirmed. Specimens have been collected from the western United States and British Columbia, and it may attack *Pissodes* species there, although this occurrence is probably rare. No information on the biology of this species was given by Deyrup (1978), but it is probably similar to that of *L. corticis*.

***Medetera apicalis* (Malloch)**

as *Medetera arctica* Van Duzee

Host: *P. fasciatus*

This species has been reared only once from *Pissodes* (Deyrup 1978), but the record is considered confirmed. Specimens have been collected or reared from the boles of coniferous and deciduous trees throughout North America and Europe. Little is known about the biology of this species, but like other species in the genus it is probably predaceous on a variety of bark- and wood-boring beetle larvae (McAlpine et al. 1981).

***Medetera vidua* Wheeler**

Host: *P. fasciatus*

This species has been reared only once from *Pissodes* (Deyrup 1978), but the record is considered confirmed. Specimens have been collected from across Canada and the United States in coniferous forests. This species is primarily associated with bark beetles (Bickel 1985), and attack on *Pissodes* appears rare.

Hymenoptera

Hymenoptera associated with *Pissodes* are parasitoids or hyperparasitoids. *Pissodes* larvae are attacked directly by ovipositing female parasitoids. The female parasitoid stings the host larva with the ovipositor to inject venom, which immobilizes the larva. Eggs are laid in, on, or very near the host. There is no or minimal host searching by the parasitoid larva, and it remains associated with a single host larva. This pattern is also the behavior of hyperparasitoids, which attack the parasitoid species associated with *Pissodes*. There are two types of parasitism: Idiobiont and Koinobiont. In idiobiosis, adult females attack later larval host instars or pupae. Immobilization of the host is protracted and may be permanent or result in death. Idiobiont species

are usually ectoparasitic, with eggs deposited on or near the host and parasitoid larvae feeding externally through a rupture in the host integument. If the host regains mobility after being stung, it quickly becomes moribund again as a result of parasitoid feeding. It is unlikely that host larvae will resume normal development. Most Hymenoptera associated with *Pissodes* exemplify of this type of parasitism.

Koinobiosis requires a longer and more intimate association between parasitoid and host and is considered more specialized or derived than idiobiosis. Adult females often attack earlier-instar larvae. Immobilization is temporary, and the host usually returns to activity after attack, in some cases resuming feeding and growth for an extended period. Koinobiont species are usually endoparasitic, with eggs deposited inside the body of the host. The parasitoid larva remains inside the host for an extended period, either developing slowly to allow the host to remain active or feeding on nonessential organs such as the fat body. The host may remain active until parasitoid emergence is imminent and may not be killed until it is ruptured by the mature parasitoid larva. Most hyperparasitoids and some parasitoids are of this type.

***Bracon nanus* Provancher**

Also as *Microbracon nanus* Provancher

Host: *P. strobi*

This species has been recorded as an uncommon idiobiont parasitoid of *P. strobi* larvae in the eastern United States (Harman and Kulman 1967). Specimens of this species have also been collected in Quebec, and it probably also occurs in Ontario and the Maritimes. Although it has been misidentified as the more common *Bracon pini* (Muesebeck) (Harman and Kulman 1967), the record is confirmed. Little is known about the biology of *B. nanus*, but it is probably similar to that of *B. pini*.

***Bracon pini* (Muesebeck)**

Also as *Microbracon pini* Muesebeck

Hosts: *P. fasciatus, Pissodes schwarzi* Hopkins, *P. strobi, P. terminalis*

The biology of this common idiobiont species was examined by Deyrup (1978) and Taylor (1929). It is recovered in most studies of *Pissodes* parasitoids throughout the United States and Canada (Langor 1998). It attacks middle- to late-instar host larvae and occasionally pupae. Several eggs may be laid per host, with one to five parasitoid larvae per host feeding gregariously. Several larvae can successfully mature from one host because of the small size of the adult parasitoid. Most individuals overwinter as prepupae and emerge as adults in the spring. About one-third of individuals emerge the same year and may attack new hosts. Note: Identification of *Bracon* specimens should not be considered definitive. This genus contains many species of common parasitoids, described and undescribed. Confirmation of the identity of *Bracon* specimens should be made by a specialist.

***Calliephialtes comstockii* (Cresson)**

Also as *Exeristes comstockii* Cresson

Host: *P. strobi*

This species is a common idiobiont parasitoid of numerous species of shoot- and terminal-boring Lepidoptera and Coleoptera across the United States and Canada (Yu 1999). Parasitism of *Pissodes* is rare but has been confirmed by Stevenson (1963) and Williams and Langor (unpublished) in Alberta. References to parasitoid biology are numerous for lepidopterous hosts (Arthur 1963), and this species has been the subject of experimental research on host–parasite interactions (Thompson and Barlow 1972). Several eggs may be laid per host, but usually only one larva develops. Most individuals overwinter in terminals as prepupae and complete development the following spring.

***Coeloides pissodis* (Ashmead)**

Hosts: *Pissodes nemorensis* Germar, *Pissodes striatulus* (Fabricius), *P. strobi*

This species is an uncommonly encountered idiobiont parasitoid of *Pissodes* species and some bark beetles. It has been recovered several times from *Pissodes* species in the eastern United States at low incidence, often below 1% (Taylor 1929; MacAloney 1930). Higher attack rates have been observed for some bark beetle hosts. Specimens have been collected from eastern Canada as far west as Manitoba, although this species has not been recovered from Canadian *Pissodes* populations to date. Females attack mature larvae and prepupae, laying one egg per host. Parasitoid prepupae overwinter in a cocoon inside the host gallery, and there is one generation per year.

***Coeloides rufovariegatus* Provancher**

As *Coeloides dendroctoni* Cushman

Host: *P. strobi*

This species is a common idiobiont parasitoid of wood-boring Coleoptera throughout North America. It is associated with various bark beetle species of economic importance, and it may be a factor in regulating host populations. Parasitism of *Pissodes* is rare but has been confirmed by Stevenson (1967) and Williams and Langor (unpublished) in Alberta. Little is known about the biology of this species in *Pissodes* hosts. It is probably similar to that of *C. pissodis*, although the incidence of *C. rufovariegatus* is significantly higher in bark beetle hosts.

***Coeloides secundus* (Dalla Torre)**

Host: *P. striatulus*

This species has been reared several times from fir logs containing *Pissodes dubius* Randall and *Pissodes fraseri* Hopkins (synonyms of *P. striatulus*) in the eastern United States and Ontario, Quebec, and the Maritimes. Specimens have been collected as far west as Michigan. Records are limited to a list of specimens examined by Mason (1978) in his taxonomic treatment of the genus. This species is rarely collected, but the repeated occurrences support its inclusion in the key. Little is known about the biology of this species, but it is probably similar to that of other *Coeloides* species.

***Coeloides vancouverensis* (Dalla Torre)**

As *Coeloides brunneri* Viereck

Hosts: *P. fasciatus, P. strobi*

This species is a common idiobiont bark beetle parasitoid in the western United States, British Columbia, and Alberta. There have been some investigations of the biology of this species attacking bark beetles (Ryan and Rudinsky 1962 [as *C. brunneri*]), for which it may be a factor in regulating host populations. Parasitism of *Pissodes* is rare but has been confirmed by rearing from individual *P. fasciatus* larvae (Deyrup 1978) and from terminals attacked by *P. strobi* (Stevenson 1967). In bark beetles, a single egg is laid per host, and parasitized host larvae are permanently immobilized. Larval development is complete within 1 month, and adults may emerge and begin another generation if suitable hosts are still available. Otherwise, prepupae overwinter in a cocoon inside the host gallery, completing development to pupae and adults the following spring.

***Cubocephalus occidentalis* (Provancher)**

As *Phygadeuon nitidulus* (Provancher)

Host: *P. strobi*

Little is known about the biology of this species. It is a rare primary parasitoid of *P. strobi* in the eastern United States (Taylor 1929; MacAloney 1930; Mott 1930), and specimens have been collected across Canada. The authors cited have listed this species as a potential hyperparasitoid because other *Cubocephalus* species attack Hymenoptera species, but these hosts are free-living, usually defoliators, not parasitic. *Cubocephalus* is a large genus, which attacks a wide range of free-living and concealed Coleoptera and Lepidoptera. The species for which biology is known are solitary koinobiont endoparasitoids.

***Dolichomitus terrebrans nubilipennis* (Ratzeburg)**

Hosts: *P. fasciatus*, *Pissodes rotundatus* LeConte, *P. striatulus*, *P. strobi*, *P. terminalis*

This species is a common idiobiont parasitoid of a wide range of bark- and shoot-boring Lepidoptera and Coleoptera throughout the northern hemisphere, and there are numerous references to its taxonomy, biology, and hosts (Taylor 1929; Stevenson 1967; Alfaro et al. 1985; Langor and Williams 1998; Yu 1999). It is one of the largest of the *Pissodes* parasitoids, and females show a preference for attacking fourth-instar host larvae, tending to delay attack until later than other parasitoid species. When parasitizing *P. strobi* and *P. terminalis*, this species is one of few that successfully attack larvae that have burrowed into the pith, which females can access with their very long ovipositors. A single egg is laid on the host larva. The mature larva spins a distinctive, semi-translucent cocoon, in which it overwinters. This species can occur in large numbers and may be a factor in regulating local host populations.

***Doryctes* sp. or spp. (undetermined)**

Hosts: *P. schwarzi*, *P. strobi*

This record is considered confirmed, although the identity of this rare species is unknown, and it is not certain that specimens reared from *P. schwarzi* in California (Stevens 1966) represent the same species as those reared from *P. strobi* in New England (Plummer and Pilsbury 1929; MacAloney 1930). The New England species probably also occurs in Quebec and the Maritimes. It is clear from details in the records that one or several species of *Doryctes* are solitary idiobiont parasitoids of *Pissodes* species, although these hosts were not recorded in a taxonomic study of the genus by Marsh (1969). There is little information on the biology of this genus aside from fragmentary observations and host data on specimen labels, but observations by Stevens (1966) indicate that incidence can be moderately high locally.

***Eubazus calyptoides* (Martin)**

As *Allodorus calyptoides* Martin

Hosts: *P. schwarzi*, *P. strobi*, *P. terminalis*

We have repeatedly recovered this species as a common parasitoid of *P. strobi*, *P. terminalis* (Langor and Williams 1998), and *P. schwarzi* in the Prairie provinces. Alfaro et al. (1985) mention *Allodorus* sp. nr. *crassigaster*, which may be *A. calyptoides*, as a parasitoid of *P. strobi* in British Columbia. Specimens have also been collected in Wisconsin. Nothing is known about the biology of this species, but it is probably similar to that of *Eubazus crassigaster* (Provancher).

***Eubazus crassigaster* (Provancher)**

As *Allodorus crassigaster* (Provancher), *Eubazidon strigitergum* (Cushman)

Hosts: *P. fasciatus*, *P. striatulus*, *P. strobi*

This species is a common and important koinobiont parasitoid of *Pissodes* species throughout North America (Stevenson 1967; Deyrup 1978; Alfaro et al. 1985) and has been investigated as a potential biological control agent for *P. strobi* (Hulme 1994). The genus *Eubazus* belongs to a tribe of braconids that is noteworthy for oviposition in host eggs. Parasitoid larvae remain associated with the host for a protracted period after the egg hatches, allowing them to go through most of the larval period of feeding and growth with minimal interference. *Eubazus crassigaster* apparently follows this habit, as Deyrup (1978) observed adult female parasitoids waiting near ovipositing female weevils. Note: There is currently no key to species of *Eubazus*, and the two species discussed here are difficult to identify. The identity of specimens of *Eubazus* should be confirmed by an expert.

***Eupelmus pini* Taylor**

Host: *P. strobi*

This species has occasionally been recovered in low numbers in rearings of *P. strobi* in New England (Taylor 1929; MacAloney 1930; Harman

and Kulman 1968) and may occur in Quebec and the Maritimes. Little is known about its biology except that mature larvae and pupae have been recovered from host chip cocoons. Oviposition probably occurs on middle-instar host larvae, as adults are active mainly in June. Most other species of *Eupelmus* are endoparasitic, and evidence shows that host larvae remain active, continue to feed, and construct a chip cocoon for pupation after being parasitized by *E. pini*, which indicates that this species is probably a koinobiont.

***Eurytoma cleri* Ashmead**

Host: *P. strobi*

Hopkins (1899) collected specimens of this rare species directly from chip cocoons produced by *P. strobi* larvae in Virginia and West Virginia, and we have examined specimens reared by Alfaro et al. (1985) from British Columbia, so the record is considered confirmed. Little is known about the biology of this species, but it is probably similar to that of *Eurytoma pissodis* (Girault).

***Eurytoma picea* Bugbee**

Hosts: *P. strobi, P. terminalis*

This rare species has been collected from terminals attacked by *P. strobi* in British Columbia (Bugbee 1967; Alfaro et al. 1985; several series of specimens the authors have examined) and *P. terminalis* in the western United States (Stevens and Knopf 1974). Little is known about the biology of this species, but it is probably similar to that of *E. pissodis*, and it may act as a hyperparasitoid of other *Pissodes* associates.

***Eurytoma pissodis* (Girault)**

Hosts: *P. strobi, P. terminalis, Ceoloides vancouverensis*, *Coeloides* sp.

This species is an abundant and common idiobiont parasitoid of terminal-inhabiting *Pissodes* that is recovered in most surveys throughout North America (Taylor 1929; Stevenson 1967; Harman and Kulman 1968; Alfaro et al. 1985; Langor and Williams 1998). Adults of this species are active in July, and females prefer to attack host prepupae after construction of the chip cocoon, laying one to four distinctive black eggs on the host. Only one parasitoid larva per host survives, overwintering as a prepupa and completing pupation and adult emergence the following spring. *Eurytoma pissodis* apparently attacks any species present in chip cocoons, acting as a hyperparasitoid on other species of parasitoids that have killed the host larva. Note: Species of the genus *Eurytoma* are very similar to one another in appearance. Even though a key to species is available (Bugbee 1967), identification is difficult and should be confirmed by an expert.

***Helcostizus albator rufiscutum* Cushman**

Host: *P. strobi*

Little is known about the biology of this rare species. The genus *Helcostizus* belongs to a tribe of Ichneumonidae for which there is little host data. Those species of the tribe for which hosts are known are parasitoids of the prepupae and pupae of Coleoptera larvae. Specimens have been reared from conifer boles or collected in California and Arizona. Stevenson (1967) reared this species from individual hosts in British Columbia, a record that is considered confirmed, but provided no other details about life cycle.

***Helcostizus contortae* Townes**

Host: *P. terminalis*

See comments for *H. a. rufiscutum*, above. Stevenson and Petty (1968) and Langor and Williams (1998) have reared small numbers of this species from lodgepole pine tips containing *P. terminalis* larvae from several different localities in Alberta. Townes (1983) also examined specimens of this species reared from lodgepole pine containing *P. terminalis* in British Columbia and Oregon.

***Helcostizus subrectus* Townes**

Host: *P. terminalis*

See comments for *H. a. rufiscutum*, above. Stevens and Knopf (1974) recovered this species in several locations in the western United States, and a few specimens have been collected from Arizona to Alberta.

***Heydenia unica* Cook and Davis**

Host: *P. strobi*

This species is a common idiobiont parasitoid of numerous species of bark beetles. It has been recovered from conifers or collected throughout the United States and probably occurs in southern Canada, at least in British Columbia and Ontario. Parasitism of *Pissodes* is rare (Taylor 1929) but has been confirmed by Hopkins (1899), who obtained specimens from *P. strobi* chip cocoons. There have been some investigations of the biology of this species attacking bark beetles (Dix and Franklin 1983), but little is known about attack on *P. strobi*. This species prefers to attack late-instar larvae and frequently attacks pupae. A single egg is laid per host, and the parasitoid larvae overwinter, completing development the following year.

***Labena grallator* Say**

Also as *Labena apicalis Cresson*

Host: *P. strobi*

This species is a common parasitoid of a wide range of wood-boring Coleoptera, primarily Cerambycidae, in the southern and eastern United States. It probably also occurs in Ontario and Quebec. Little is known about the biology of this species, except that it is rare in *Pissodes* (Barnes 1928; Taylor 1929; Harman and Kulman 1968) and seems to have low incidence on all known hosts.

***Spathius brachyurus* Ashmead**

Hosts: *P. nemorensis, P. strobi*

This rare idiobiont parasitoid species has been recovered several times in studies of *Pissodes* in the eastern United States, at low incidence (Britton 1920; Peirson 1922). Specimens have also been collected in Quebec, and this species is probably also present in Ontario and the Maritimes. Parasitoids attack prepupae, usually laying several eggs, with the number depending on the size of the host. Larvae feed gregariously, and several can successfully mature from one host because of the small size of the adult parasitoid. Matthews (1970) recorded as many as seven *S. brachyurus* cocoons associated with the remains of a single host larva. Parasitoids overwinter as prepupae in cocoons spun in the host gallery. Adults emerge in late spring and are active throughout the summer. There may be several generations per year if suitable hosts are available, either *Pissodes* species or several species of bark beetles that are also attacked by this parasitoid.

***Spathius sequoiae* Ashmead**

Host: *Pissodes* sp.

This idiobiont parasitoid species attacks primarily bark beetles in the western United States, and parasitism of *Pissodes* is rare (Matthews 1970). Specimens have also been collected from Alaska, British Columbia, and Alberta, and it probably occurs in the Yukon and Northwest Territories as well. There are few records of attack on *Pissodes*, and available specimens have been reared from host larvae in boles. The biology of this species attacking bark beetles resembles that of *S. brachyurus*, although it is not known if the larvae feed gregariously.

***Rhaphitelus maculatus* Walker**

Hosts: *P. strobi, Pissodes* sp.

This species is a common and abundant idiobiont parasitoid of bark beetles and other wood-boring Coleoptera occurring worldwide (Yu 1999). Parasitism of *Pissodes* is rare, although it can be locally common in the Prairie provinces (Williams and Langor, unpublished). There has been some investigation of the biology of this species attacking bark beetles (Campos and Gonzalez 1993), but little is known about attack on *P. strobi*. This species is flexible in both host range and behavior. It attacks both prepupae and pupae and will facultatively act as a hyperparasitoid on other *P. strobi* parasitoids, presumably those occurring in chip cocoons. Adults are active in July, and females will deposit one or several eggs on a host. A single parasitoid larva survives per host, overwintering as a prepupa. Development is completed the following year.

***Rhopalicus pulchripennis* (Crawford)**

Hosts: *P. strobi, P. terminalis, Coeloides rufovariegatus*

This species is a common and abundant idiobiont parasitoid of *Pissodes*, bark beetles, and other wood-boring Coleoptera throughout North America (Plummer and Pilsbury 1929; Taylor 1929; Stevenson 1967; Harman and Kulman 1968; Langor and Williams 1998). Adult females attack middle- to late-instar host larvae and may have more than one generation per year. In areas where studies have been conducted, there are two periods of adult activity, in early June and late July. Females that have parasitized middle-instar host larvae early in the season may emerge on time to attack later instars. A single egg is deposited per host, and the larva, if it overwinters, does so as a prepupa. This species will facultatively act as a hyperparasitoid on other *P. strobi* parasitoids.

***Rhopalicus tutela* (Walker)**

Also as *Rhopalicus tutela suspensus* (Ratzeburg)

Host: *P. strobi*

This species is a common and abundant idiobiont parasitoid of bark beetles and other wood-boring Coleoptera worldwide. Parasitism of European species of *Pissodes* is common, but uncommon in *P. strobi*, although the parasitoid has been recovered several times (Britton 1920; Plummer and Pilsbury 1929). Some information is available on the biology of this species attacking bark beetles (Berisford et al. 1970), but little is known about attack on *P. strobi*. Adults attack middle- to late-instar bark beetle larvae and are active over much of the season, and there might be more than one generation per year. A single egg is laid per host, and the larva, if it overwinters, does so as a prepupa. In studies of parasitism of *Ips*, larvae and pupae of this species have been found separate from host remains, having moved from one part of the host gallery to another. It is possible that individuals of this species attack more than one host, facultatively acting as predators.

***Trigonura tarsata* (Dalla Torre)**

Host: *P. strobi*

Little is known about the biology of this rare species. Specimens have been collected from the eastern United States as far west as North Dakota, and this species is probably also present in Ontario and Quebec. It was reared by Barnes (1928) and Taylor (1929), and these records are considered confirmed, although this species has not been recovered since. Other hosts include several species of the genus *Magdalis*, which are bark-boring weevils with similar biology to that of *Pissodes*.

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APPENDIX 1

PARASITOIDS, HYPERPARASITOIDS, AND PREFATORS ASSOCIATED WITH *PISSODES* SPECIES IN CANADA

Family	Species	Host	Role[a]	Distribution
Diptera				
Lonchaeidae	*Lonchaea corticis* Taylor	*P. strobi*	Pred	Transcontinental
Lonchaeidae	*Lonchaea furnissi* McAlpine	*P. fasciatus*	Pred	Western North America
Dolichopodidae	*Medetera apicalis* (Malloch)	*P. fasciatus*	Pred	Western North America
Dolichopodidae	*Medetera vidua* Wheeler	*P. fasciatus*	Pred	Western North America
Hymenoptera				
Braconidae	*Bracon nanus* Provancher	*P. strobi*	Par	Eastern North America
Braconidae	*Bracon pini* (Muesebeck)	*P. fasciatus*, *P. schwarzi*, *P. strobi*, *P. terminalis*	Par	Transcontinental
Braconidae	*Coeloides pissodis* (Ashmead)	*P. nemorensis*, *P. striatulus*, *P. strobi*	Par	Transcontinental
Braconidae	*Coeloides rufovariegatus* Provancher	*P. strobi*	Par	Transcontinental
Braconidae	*Coeloides secundus* (Dalla Torre)	*P. striatulus*	Par	Transcontinental
Braconidae	*Coeloides vancouverensis* (Dalla Torre)	*P. fasciatus*, *P. strobi*	Par	Western North America
Braconidae	*Doryctes* sp.	*P. schwarzi*, *P. strobi*	Par	Transcontinental
Braconidae	*Eubazus calyptoides* (Martin)	*P. schwarzi*, *P. strobi*, *P. terminalis*	Par	Western North America
Braconidae	*Eubazus crassigaster* (Provancher)	*P. fasciatus*, *P. striatulus*, *P. strobi*	Par	Transcontinental
Braconidae	*Spathius brachyurus* Ashmead	*P. nemorensis*, *P. strobi*	Par	Eastern North America
Braconidae	*Spathius sequoiae* Ashmead	*Pissodes* sp.	Par	Western North America
Chalcididae	*Trigonura tarsata* (Dalla Torre)	*P. strobi*	Par	Northeastern North America
Eupelmidae	*Eupelmus pini* Taylor	*P. strobi*	Par	Eastern U.S.A.

Family	Species	Host	Role[a]	Distribution
Eurytomidae	*Eurytoma cleri* Ashmead	*P. strobi*	Par Hyp	Transcontinental
Eurytomidae	*Eurytoma picea* Bugbee	*P. strobi*, *P. terminalis*	Par Hyp	British Columbia
Eurytomidae	*Eurytoma pissodis* (Girault)	*P. strobi*, *P. terminalis*	Par Hyp	Transcontinental
Ichneumonidae	*Calliephialtes comstockii* (Cresson)	*P. strobi*	Par	Transcontinental
Ichneumonidae	*Cubocephalus occidentalis* (Provancher)	*P. strobi*	Par Hyp	Transcontinental
Ichneumonidae	*Dolichomitus terrebrans nubilipennis* (Ratzeburg)	*P. fasciatus*, *P. fasciatus*, *P. rotundatus*, *P. striatulus*, *P. strobi*, *P. terminalis*	Par	Transcontinental
Ichneumonidae	*Helcostizus albator rufiscutum* Cushman	*P. strobi*	Par	Western North America
Ichneumonidae	*Helcostizus contortae* Townes	*P. terminalis*	Par	Western North America
Ichneumonidae	*Helcostizus subrectus* Townes	*P. terminalis*	Par	Western North America
Ichneumonidae	*Labena grallator* Say	*P. strobi*	Par	Transcontinental
Pteromalidae	*Heydenia unica* Cook and Davis	*P. strobi*	Par	Transcontinental
Pteromalidae	*Rhaphitelus maculatus* Walker	*P. strobi*, *Pissodes* sp.	Par Hyp	Transcontinental
Pteromalidae	*Rhopalicus pulchripennis* (Crawford)	*P. strobi*, *P. terminalis*	Par Hyp	Transcontinental
Pteromalidae	*Rhopalicus tutela* (Walker)	*P. strobi*	Par Pred	Holarctic (Eastern North America)

[a]Pred = predator, Par = parasitoid, Hyp = hyperparasitoid. Species with more than one designation may take either role or both.

APPENDIX 2

UNCONFIRMED RECORDS OF OTHER PARASITOIDS ASSOCIATED WITH PISSODES SPECIES

Order and species	Host	Distribution	References	Comments
Diptera				
Compsilura concinnata (Meigan)	*P. strobi*	Transcontinental	MacAloney 1930, Harman and Kulman 1967	Host unconfirmed. Both sources sources cite the same incidence of emergence from a terminal. All other records from Lepidoptera.
Lonchaea spp. (see Appendix 1)	*P. strobi*	Various	Various	All citations of *Lonchaea* species in literature, except for *L. furnissi* (see Appendix 1), should be attributed to *L. corticis*. Other records are due to synonymy or misidentification.
Muscina stabulans (Fallén)	*P. strobi*	Transcontinental	MacAloney 1930	Host unconfirmed. This species is a detritus feeder, not a predator or parasitoid.
Hymenoptera				
Amblymerus sp.	*P. strobi*	Transcontinental	Stevenson 1963	Host unconfirmed. Recorded hosts include several holometabolous orders.
Barycnemis simplicicornis (Viereck)	*Pissodes* sp.	Northwestern U.S.A.	Krombein et al. 1979, Yu 1999	Catalog citations only, with no other information.
Brasema cleri Ashmead	*P. strobi*	Southeastern U.S.A.	Krombein et al. 1979, Noyes 1998	Catalog citations only, with no other information.
Cecidostiba thomsoni (Crawford) as *Dinotiscus*	*Pissodes* sp.	Western N. A.	Krombein et al. 1979, Noyes 1998	Catalog citations only, with no other information.
Cheiropachus brunneri Crawford	*Pissodes* sp.	Montana	Krombein et al. 1979, Noyes 1998	Catalog citations only, with no other information.

Order and species	Host	Distribution	References	Comments
Conura igneoides (Kirby) as *Spilochalcis*	*P. strobi*	Transcontinental	Harman 1966, Harman and Kulman 1968	Listed with no other information. Recorded hosts are Lepidoptera, as a hyperparasitoid.
Coeloides crocator (Kirby) as *C. promontorii*	*P. strobi* as *P. engelmanni*	Transcontinental	Stevenson 1967	Possibly a correct association, but unconfirmed. Record not accepted by later reviser (Mason 1978).
Copidosoma bakeri (Howard)	*P. strobi*	Transcontinental	Taylor 1929, MacAloney 1930, Mott 1930	Recorded from a very wide range of Lepidoptera, probably as a hyperparasitoid. Records from *P. strobi* are suspect as this is the only beetle host.
Cyanopterus laevis (Provancher)	*P. strobi*	Transcontinental	Britton 1920, Barnes 1928	Possibly a correct association, but unconfirmed, probably rare. Not accepted as a host in catalogs.
Dolichomitus imperator (Kriechbaumer)	European *Pissodes*	Holarctic	Yu 1999	Associated with *Pissodes* in Europe and present in Canada, but not recovered from *Pissodes* here.
Dolichomitus tuberculatus (Geoffrey)	European *Pissodes*	Holarctic	Yu 1999	Associated with *Pissodes* in Europe and present in Canada, but not recovered from *Pissodes* here.
Ephialtes manifestor (L.)	European *Pissodes*	Holarctic	Yu 1999	Associated with *Pissodes* in Europe and present in Canada, but not recovered from *Pissodes* here.
Habrocystis sp.	*P. strobi*	Transcontinental	Barnes 1928, Harman 1966	Host unconfirmed. Recorded from a very wide range of Hymenoptera, Lepidoptera, and Coleoptera.

Order and species	Host	Distribution	References	Comments
Helcostizus restaurator (Fabricius)	European *Pissodes*	Holarctic	Yu 1999	Associated with *Pissodes* in Europe and present in Canada, but not recovered from *Pissodes* here.
Hemiteles bipunctator (Thunberg)	*P. strobi*	Holarctic	Taylor 1929, Taylor 1929, Mott 1930	Host unconfirmed. Attacks a wide range of hosts as a parasitoid, hyperparasitoid, and egg predator.
Hemiteles hydrophilus (Ashmead)	*P. strobi*	Eastern North America	Plummer and Pilsbury 1929	Host unconfirmed. Recovered only once. Has a wide range of hosts as a parasitoid and hyperparasitoid.
Heterospilus sp.	*P. strobi*	Transcontinental	Stevenson 1967	Host unconfirmed. This genus attacks many species of wood- and bark-boring Coleoptera.
Kranophorus suborbicularis (Provancher) as *Coelopisthia*	*P. strobi*	Northeastern North America	Plummer and Pilsbury 1929, Mott 1930	Mass reared from unconfirmed host. Recorded hosts are all Lepidoptera.
Lamennaisia sp. as *Mercetencyrtus*	*P. strobi*	West coast North America	Alfaro et al. 1985	Host unconfirmed. Only encountered once. Recovered from several coleopteran and hemipteran species.
Mesopolobus sp.	*P. terminalis*	Transcontinental	Stevens and Knopf 1974, Alfaro et al. 1985	See *Amblymerus*, above.
Microtypus sp.	*P. strobi*	California	Taylor 1929	A second-hand report of a record for a genus that is otherwise known only from Lepidoptera.
Monodontomerus aereus Walker	*P. strobi*	Eastern N. A.	Harman and Kulman 1968	Host unconfirmed. Recovered from many lepidopterous and hymenopterous hosts. Hyperparasitoid of *Dolichomitus* spp.

Order and species	Host	Distribution	References	Comments
Pediobius sp.	*P. strobi*	Transcontinental	Harman 1966, Harman and Kulman 1968	Listed with no other information. The genus is very large with a vast host range.
Scambus brevicomis (Gravenhorst)	European *Pissodes*	Holarctic	Yu 1999	Associated with *Pissodes* in Europe and present in Canada, but not recovered from *Pissodes* here.
Schenkia sp.	*P. strobi*	Holarctic	Taylor 1929, MacAloney 1930, Mott 1930	Host unconfirmed. Listed as "incidental" in publications. Record not accepted in catalogs.
Spathius pallidus Ashmead, also as *S. canadensis*	*P. nemorensis*	Southeastern North America	Barnes 1928, Taylor 1929, MacAloney 1930	Species has not been recorded north of Massachussetts and does not occur in Canada.
Spathius parvulus Matthews	*P. strobi*	Eastern North America	Matthews 1970	Recorded from label data in Matthews revision of the genus. Host unconfirmed.
Terastichus sp.	*P. terminalis*	Transcontinental	Stark and Wood 1964	Listed with no other information.
Trathala granulata (Davis)	*P. strobi*	Transcontinental	Dasch 1979	Catalog citations only, with no other information.
Triaspis pissodis Viereck	*Pissodes* sp.	Northwestern U.S.A.	Martin 1956	Host unconfirmed. Known only from type material, some of which cites *Pissodes* sp. on the specimen label.

APPENDIX 3

GLOSSARY

Abdomen (*see also* Gaster): The most posterior body section of an insect, containing digestive and reproductive organs in adult insects (Fig. 63).

Antenna: A sensory structure on the front of the head, which is thread-like on Hymenoptera (Fig. 62A), and club-like on Diptera (Fig. 63).

Anterior: Pertaining to the front or headward edge or surface of a body section or appendage.

Areolet: The first radial sector cell in the forewing of Ichneumonidae adjacent to the large 2R1 cell (Fig. 62A).

Carapace: A hard dorsal shell formed by the fusion of several abdominal tergites, which covers and protects the gaster of some Hymenoptera.

Carina (pl. carinae): A ridged type of sculpture. Carina length and placement can be highly variable among species.

Cell: An area of clear wing membrane that is surrounded on all sides by pigmented veins or the wing margin (Fig. 62A), or an area of sclerite surrounded and defined by carinae.

Chip cocoon: A structure prepared by *Pissodes* larvae from wood shavings taken from the host tree in which they pupate.

Cocoon: A construction of silk spun by the larvae of some insects, in which they pupate. Parasitic Hymenoptera larvae emerge from the host and spin white, oblong cocoons covered with loose fibers. Some spin cocoons inside the host, which are not visible unless the host cadaver is dissected.

Coxa: The first section of the leg, attached directly to the thorax (Figs. 62A, 63).

Diapause: A period in the life cycle of an insect during which development is temporarily suspended.

Dorsal: Pertaining to the upper surface of a body section or appendage.

Ectoparasitic: Pertaining to a parasitoid larva that lives outside the host's body, but feeds on the host's internal tissues and body fluids.

Endoparasitic: Pertaining to a parasitoid larva that lives entirely within the host's body.

Eye: The large, multifaceted visual organs on either side of an adult insect's head (Figs. 62A, 63).

Femur (pl. femora): The third section of the leg, between the trochanter and the tibia (Figs. 62A, 63).

Flagellum: The third section of the antenna of Hymenoptera, comprising the third to end segments, which resemble one another in size and shape and are different from the first two segments (see Scape and Pedicel).

Forewing: The larger, anterior pair of wings in Hymenoptera (Fig. 62A), or the only visible pair of wings (commonly referred to as simply the wings) in Diptera (Fig. 63).

Gaster (*see also* Abdomen): The most posterior body section of Hymenoptera, which consists of all abdominal segments except the first. The first abdominal segment is fused to the thorax and forms the propodeum (Fig. 62A).

Granular: A pebbled type of microsculpture that imparts a matte surface to a sclerite.

Generation: The time required to complete one full life cycle, including all stages.

Habitus: A drawing or photograph intended to display the general shape and feature of a species, upon which specific morphological characters may be highlighted.

Hair: Filaments that occur all over the bodies of flies and come in a variety of sizes. Setae are enlarged hairs, but for this purpose the term

hair is used to refer only to the smallest size class.

Head: The most anterior body section of an insect, containing sensory organs and mouthparts in adult insects (Figs. 62A, 63).

Hind wing: The smaller, posterior pair of wings in Hymenoptera (Fig. 62A). The hind wings in Diptera are reduced to small clubs and not easily visible (Fig. 63).

Hyperparasitoid: A parasitoid that attacks another parasitoid inside a host, not the host itself.

Idiobiont (Idiobiosis): A type of parasitism in which later host stages are parasitized, host activity is arrested following attack, and association of the host and parasitoid is relatively brief (see Koinobiont).

Instar: A stage in an insect's development.

Integument: The hard outer skeleton of an insect.

Koinobiont (Koinobiosis): A type of parasitism in which earlier host stages are parasitized, host activity continues following attack, and association of the host and parasitoid is prolonged (see Idiobiont).

Larva: An immature stage in the life cycle of an insect.

Lateral: Pertaining to the side surfaces of a body section or appendage.

Mandible: The chewing mouthpart of many insects (Fig. 62A).

Mesopleuron: A sclerite of the side of the thorax of Hymenoptera.

Microsculpture: Very fine surface texture of a sclerite that is visible only under very high magnification.

Multivoltine: Having several generations per year.

Occelli: A group of light-sensing organs on the top of the head of some insects (Fig. 63).

Oviposition mark: A small puncture in the bark of a terminal of a host tree left by an egg-laying *Pissodes* female.

Ovipositor: The egg-laying structure visible at the apex of the gaster in Hymenoptera. It is usually covered by a hairy sheath (Fig 62B).

Parasitoid: An insect that feeds on the internal tissues and body fluids of another insect, eventually killing the host.

Parastigma: An enlarged bulb on the end of the stigmal vein in some Hymenoptera.

Pedicel: The second segment of the antenna, which is often small, cylindrical, and drumlike, between the scape and the flagellum.

Posterior: Pertaining to the rear surface of a body section or appendage.

Predator: A free-living insect that attacks and consumes another or several other insects.

Prepupa (pl. prepupae): A stage of the last larval instar, just before molting to the pupa.

Propodeum: The first segment of the abdomen of Hymenoptera, which is fused to the posterior end of the thorax and which appears to be a thoracic sclerite (Fig. 62A).

Punctate: Referring to a part of the integument with distinct pits or circular impressions, often with a hair attached in the middle.

Pupa (pl. pupae): A stage (usually quiescent) in the development of an insect during which larval structures are lost and adult structures created.

Puparium (pl. puparia): An oblong, cylindrical structure composed of the skin of the mature larva of flies, which hardens and turns brown. The pupa is formed inside the puparium, and the adult fly emerges from this structure.

Scape: The first segment of the antenna, which attaches directly to the head and which is usually larger and more rounded than the remaining segments.

Sclerite: A distinct section of the body integument that is distinguished from other such sections by a ridge or groove.

Sculpture: Fine surface structures on the integument. These may be fine or coarse wrinkles, pebbling, pits or punctures, large ridges, or other features that otherwise alter the smooth, shining surface.

Seta (pl. setae): Very large, dark hairs that are often arranged in specific patterns.

Striate (pl. striae): A type of sculpture which comprises numerous parallel fine wrinkles.

Tarsus: The fifth and end-most section of the leg, which is attached to the tibia and which comprises four or five segments called tarsomeres (Figs. 62A, 63).

Tegula: A flap-like sclerite in Hymenoptera that covers the base of the wing where it attaches to the thorax (Fig. 62A).

Tergum (pl. terga or tergites): The dorsal sclerites of body segments. The posterior edge of a tergum is also called the apex or the margin, and the anterior edge is called the base.

Terminal: The topmost growing point of the main stem of a conifer tree.

Thorax: The middle body section of adult insects where the wings and legs are attached. In Hymenoptera the apparent thorax is composed of the true thorax plus the first abdominal segment (propodeum) (Fig. 62A). In Diptera the thorax is a true thorax (Fig. 63).

Tibia (pl. tibiae): The fourth section of the leg, between the femur and the tarsus (Figs. 62A, 63).

Trochanter: The second section of the leg, between the coxa and femur (Fig. 62A).

Tubercle: A swelling or bump on the surface of a sclerite.

Univoltine: Having only one generation per year.

Vein: The thickened, pigmented lines of the wings, which provide a supporting frame for the thin, membraneous remainder. The arrangement of veins and the cells they surround may be distinct among species (Figs. 62A, 63).

Ventral: Pertaining to the lower surface of a body section or appendage.