# The Insect Community of Dead and Dying Douglas-Fir
# I. The Hymenoptera

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# THE INSECT COMMUNITY OF DEAD AND DYING DOUGLAS-FIR: I. THE HYMENOPTERA

MARK AMIDON DEYRUP

University of Washington, Seattle

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## ABSTRACT

The insects that invade a dying or dead tree are the immediate cause of death and the principle mediators of early stages of decomposition of the tree. These insects form a large and complex community, the species components of which are restricted to particular habitats. A study of the insect community associated with dead Douglas-fir has revealed an intricate assemblage of species; in this publication only the 70+ species of the order Hymenoptera are discussed. Keys are provided for identification of all taxa, and there are discussions of the families, genera, and species represented. The known biology of each species is described, and an attempt is made to suggest the ecological role of each species within the dead tree. Table 1 and the appendix deal with the extent of tree-host specificity of the species of Hymenoptera.


KEYWORDS: BARK BEETLES--PARASITES, DOUGLAS-FIR, DOUGLAS-FIR INSECT COMMUNITY, HYMENOPTERA--DEAD CONIFERS, HYMENOPTERA--DOUGLAS-FIR, INSECT COMMUNITY, WOOD BORERS--PARASITES

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# INTRODUCTION

Douglas-fir, *Pseudotsuga menziesii,* is the dominant tree of western Washington and western Oregon, and is locally abundant throughout many other areas of western North America. It is obvious that a great array of insects has evolved to exploit this vast biomass. The phytophagous insects on Douglas-fir, with the associated parasites, predators, and scavengers, form a discrete insect community.

The community of insects supported by Douglas-fir may be further divided into two separate communities. One community is based upon those insects consuming the growing tree; they are the leaf consumers, the seed and cone insects, the sap consumers, and a few bark and wood consuming insects. The second community is based upon those insects that consume the bark and wood of the dead and dying tree. The community of insects upon a living, growing tree is normally a relatively long-term community, which remains in equilibrium with the host tree; the inroads made by insects upon tree biomass are compensated for by growth and replacement. It is to the advantage of the insect community that this system remains in balance. In contrast, the community of insects in the dead and dying tree causes a rapid and drastic change in the tree itself.

A moribund standing tree, a recent windfall, or a felled tree is living in the sense that the cells are alive, though perhaps functioning abnormally. Nevertheless, such a tree is rapidly abandoned by the live-tree insect community and is even more rapidly invaded by the dead-tree insect community. The first drastic change effected by the dead-tree insects is to kill a live tree, hence, the first vital role of these insects in a forest biome: a damaged or weakened tree is forced abruptly to end its competition with healthy trees for air, minerals, water, and sunlight.

This same ability to locate and kill moribund trees gives the insects a second important function: they may also kill trees undergoing temporary stress such as that caused by a severe drought. In this way, insects may kill basically healthy trees and in so doing change the composition of the Douglas-fir stand. This ability is most highly developed in one species of bark beetle, *Dendroctonus pseudotsugae,* which normally attacks moribund Douglas-fir, but under epidemic conditions will mass attack and kill healthy trees. In spite of its presence on healthy trees, even this species must be considered part of the dead-tree community, as the beetle larvae develop only in dead trees.

The community of insects that causes death of a Douglas-fir at the cellular level remains in the tree for some time, where it performs its third vital function, the recycling of minerals stored by the tree over the years and the conversion of tree biomass. After one year an insect-infested dead Douglas-fir in the proper environment is profoundly changed. The phloem has been reduced to a conglomeration of frass; the outer bark has become loosened and profusely perforated, allowing extensive leaching by rainwater; the sapwood contains numerous insect galleries from which spread fungal hyphae, extracting and concentrating nutrients from the xylem.

The peculiar economic and ecological significance of the insect community associated with dying trees has inspired several published studies. Graham (1925) produced a study of the different environmental conditions occurring in white pine logs, and described how these conditions determine the species of insects invading the logs. Savely (1939) published a monograph on the succession of insects in pine and oak logs, using trees that had been dead for various lengths of time and paying particular attention to the ecological role played by each insect species. The successor to Savely's work is Howden and Vogt's slightly less exhaustive study (1951) of the insect communities of standing dead Virginia pine. Finally, there is the work of Kimmy and Furniss (1943) on the deterioration of fire-killed Douglas-fir. This study is particularly relevant, not only because it deals with Douglas-fir, but also because insects are considered with fungi and weathering to give a total picture of the transformation of the trees from the time of their death.

In addition to these ecological studies, there are a number of published lists and biological studies of insects associated with dead and dying trees. The first of these is a monograph by Blackman and Stage (1924) on insects living in the bark and wood of dying and dead hickory. This study provided original descriptions of the biologies of many species of insects. In 1938, Bedard published a work of special interest, an annotated list of the insects associated with Douglas-fir in Idaho and Washington. The list includes many insects from dying and recently dead trees and indicates some of the faunal differences between our study area in western Washington and areas in the eastern range of Douglas-fir. Recently (1968), Ross produced an annotated list of beetles attacking freshly felled larch in British Columbia; many of the species that infest larch also attack Douglas-fir. Amman (1969) contributed an annotated list of the insects found in bark and wood of Fraser fir.

Only fragmentary knowledge is available of the insect community whose role discussed above is so important in the Douglas-fir forests. In 1972, a program was begun to compile all published information on insects of dying and recently killed Douglas-fir. At the same time, fieldwork was begun to elucidate the biology of these insects: their seasonal flight patterns, their target areas on fallen trees, their preferences as to the age and condition of the trees.

The first portion of this general study of the insect community of dead Douglas-fir deals with the Hymenoptera; additional portions will deal with the Diptera, Coleoptera, and a few small orders of insects, It should be possible to take the information in the completed general study and combine it with the data from the fieldwork to produce charts showing the ecological niche of each species of insect associated with the dead Douglas-fir tree.

The purpose of this volume is to provide easy identification of hymenopterans associated with dead and dying Douglas-fir and to compile all known information concerning the life histories of these insects. It is hoped the study will be of interest to those people dealing with the control of forest pests, to those examining the working of the forest ecosystem, and to those interested in the composition of discrete insect communities. Since there seems to be no similar study of any other conifer, tables are provided (see Table 1 and Appendix) showing alternate tree associations of Douglas-fir hymenopterans, for the benefit of those who are investigating the insect fauna of other conifers.

Over 60 species of Hymenoptera have been reported in various publications as associated with dead and dying Douglas-fir. In a year and one-half of work in western Washington, approximately 15 more species have been added to this list. Thus it seems realistic to expect that at least 20 or 30 more species of hymenopterans will be found in the dead Douglas-fir community, primarily in the eastern and southern range of Douglas-fir. Of the 70-odd species discussed here, only a few have ever been studied in any detail, and the life histories of some of the commonest species are virtually unknown. Thus there can be nothing definitive about this study, but it will be a useful tool for other investigators. Each taxonomic group is briefly introduced, and the introduction is followed by a key to the subgroups wherever necessary. Discussions and aids to identification are provided at the family, genus, and species levels.

## MATERIALS AND METHODS

The principal study site is at Cedar Falls, within the Cedar River watershed in King County, Washington. The area chosen is a predominantly Douglas-fir second-growth stand with trees mainly 30-60 cm dbh. The elevation is approximately 290 m. There is little natural windfall near the study site, therefore it was considered appropriate for the study of a strictly endemic population of Douglas-fir insects.

Beginning at the end of March, trees were felled at approximately three-week intervals. The serial felling was intended to test the theory that the date of felling, because of the limited flight season of certain insect species, might have a lasting effect upon the insect community invading the tree.

At each felling, two trees were cut in a dense portion of the stand and two in a small clearing. It was felt that the extreme temperature regimes and the great degree of direct insolation in an exposed tree might limit or modify its insect community.

At each felling, for two trees all living branches were removed and for two trees the crowns were left intact. It was postulated that the foliage would continue transpiring to some extent and thus cause more rapid drying of the tree, with a concomitant effect upon the invading insect community.

Immediately after the trees were felled, 30-$cm^2$, 6-mm mesh hardware cloth screens were suspended vertically straddling the bole, attached to two vertical metal rods so that the screening presented a barrier to insects flying up or down the length of the bole. The barriers were placed, three per tree, near the base of the tree, near the midpoint on the bole between the cut end and the crown, and in the crown itself. A total of 20 trees were cut, and 60 traps were in operation by the end of summer. The traps were coated with Stikem Special (Michel & Pelton Co., Emeryville, Calif.) and the adhering insects were removed at weekly intervals. The insects were washed with commercial solvent (Shell or Chevron) sold at service stations. The insects were then dried and their species were determined. In addition, insects other than scolytids, taken by a co-worker on traps similar to those described above, were examined and species were determined. The traps were placed above variously treated Douglas-fir bolts.

Samples of dead Douglas-fir from a few other areas of western Washington were also examined for insects, and other insects were reared from this material. Insect activity associated with the cut trees was observed throughout the two summers.

## KEY TO THE FAMILIES OF ADULT HYMENOPTERA ASSOCIATED WITH DEAD AND DYING DOUGLAS-FIR

1. Wingless . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

1'. Winged . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 4

2. Thorax and main part of abdomen connected by a small wedge-shaped segment . . . . . . . . . . . . Formicidae (ants)

2'. Thorax and main part of abdomen connected directly, no small wedge-shaped segment between them . . . . . . . . . . . . 3

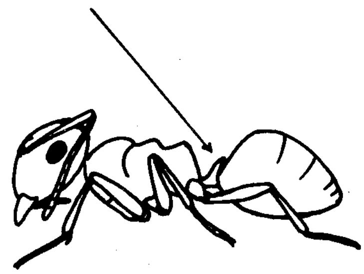


Figure 1. Ant, showing small wedge-shaped segment between thorax and gaster (genus *Lasius*).

3. Antennae elbowed; vestigial wings sharply bent . . . . . Eupelmidae

3'. Antennae not elbowed; vestigial wings if present not sharply bent . . . . . . . . . . . . . . . . . Braconidae

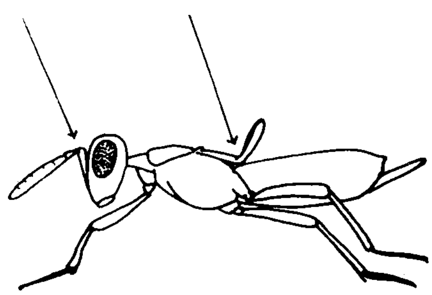


Figure 2. Wingless eupelmid, showing elbowed antennae and bent wings (genus *Eupelmella*).

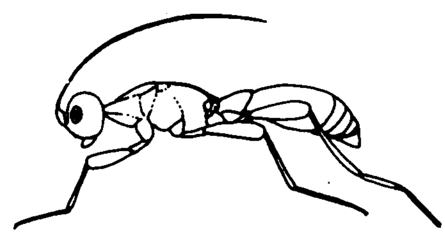


Figure 3. Wingless braconid, showing unelbowed antennae (genus *Ecphylus*).

4. Venation of forewing simplified as illustrated; small species, usually under 5 mm long (Chalcidoidea) . . . . . . . . . 5

4'. Venation of forewing usually complex, never simplified in the manner illustrated for Chalcidoidea . . . . . . . . . . . . 8

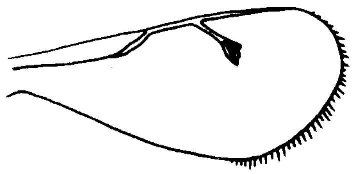


Figure 4. Forewing of chalcidoid, showing simplified venation.

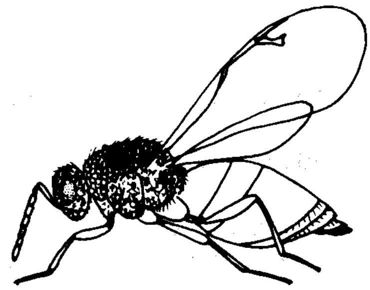


Figure 5. Eurytomid (genus *Eurytoma*).

5. Black; thorax roughly pitted and hairy . . . . . . . . . Eurytomidae

5'. Usually shining metallic; thorax finely sculptured and usually not hairy . . . . . . . . . . . . . . . . . . 6

6. Side of mesothorax appearing a single convex plate with a longitudinal furrow near the bottom . . . . . . . Eupelmidae

6'. Side of mesothorax divided by an oblique furrow running from top to bottom . . . . . . . . . . . . . . . . . . . . . . 7

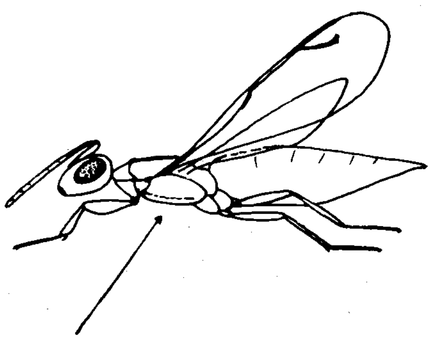


Figure 6. Eupelmid, showing side of mesothorax with longitudinal furrow (genus *Calosota*).

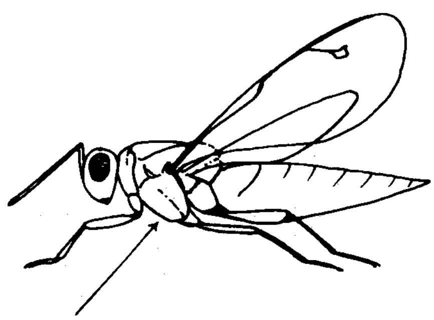


Figure 7. Female pteromalid, showing side of mesothorax with oblique furrow (genus *Cecidostiba*).

7. Female with a long ovipositor protruding from tip of abdomen; ovipositor more than half the length of abdomen . . . . . Torymidae

7'. Female without a long ovipositor protruding from tip of abdomen . . . . . . . . . . . . . . . . . . . . . . . . Pteromalidae

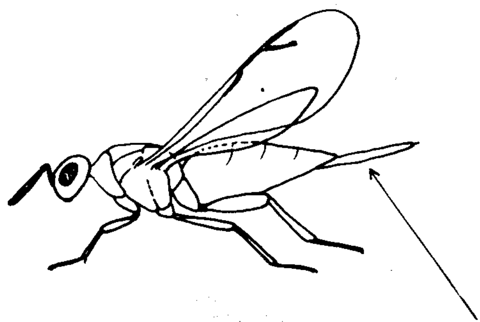


Figure 8. Female torymid, showing long ovipositor (genus *Roptrocerus*).

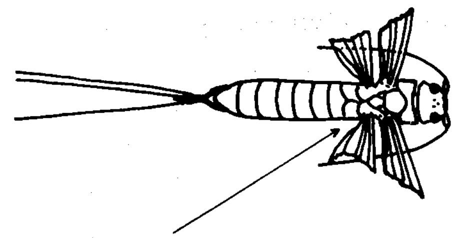


Figure 9. Siricid wood wasp (wings removed) showing no constriction between thorax and abdomen (genus *Xeris*).

8. No constriction between thorax and abdomen . . . . . . . . . . . . . 9

8'. Constricted "wasp-waist" present . . . . . . . . . . . . . . . . . 10

9. Abdomen tipped with a spear-shaped extension of the terminal segment; antennae long and slender . . . . . Siricidae (wood wasps)

9'. Abdomen rounded apically, without spear-shaped extension; antennae short and stout . . . . . Orussidae (parasitic wood wasps)

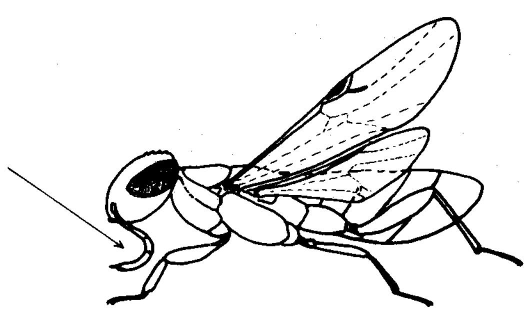


Figure 10. Orussid wood wasp, showing short antennae (genus *Orussus*).

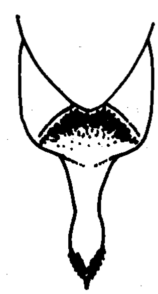


Figure 11. Last abdominal segment of siricid wood wasp.

10. First segment of hind tarsus extremely long, second segment with a projection . . . . . . . . . . . . . . . . Ibaliidae

10'. Hind tarsus not as above . . . . . . . . . . . . . . . . . . . . 11

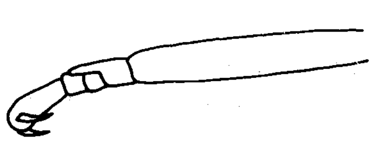


Figure 12. Segments of hind tarsus of ibaliid (redrawn from Borror and Delong 1970, p. 554).

11. Wings without veins . . . . . . . . . . . . . . . . . . . . Diapriidae

11'. Wings with veins . . . . . . . . . . . . . . . . . . . . . . . . 12

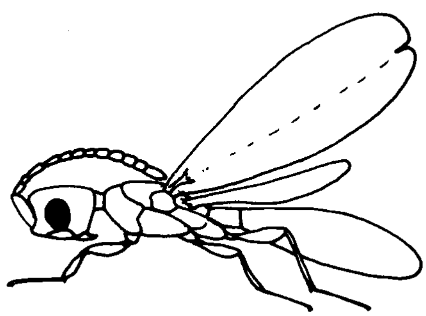


Figure 13. Diapriid, showing veinless wings; longitudinal line in forewing is a fold.

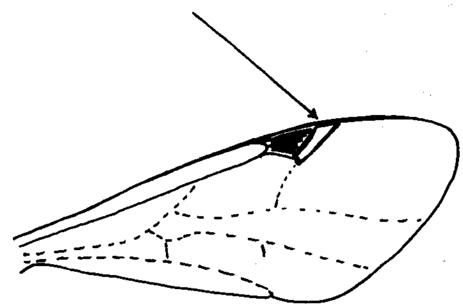


Figure 14. Proctotrupid wing, showing small cell following stigma (genus *Codrus*).

12. A very small cell following stigma of forewing; most veins in forewing weakly sclerotized . . . . . . . . Proctotrupidae

12'. Large cell following stigma of forewing; most veins in forewing well sclerotized . . . . . . . . . . . . . . . . 13

13. Leading edge of forewing before stigma with a long narrow cell above the long triangular cell . . . . . . . . Aulacidae

13'. Leading edge of forewing without a narrow cell above the long triangular cell; narrow cell has shrunk and vanished, leaving two veins lying together along edge of wing (Ichneumonoidea) . . . . 14

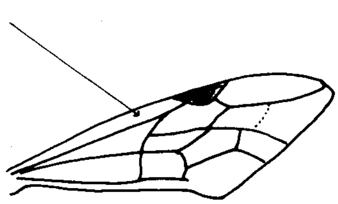


Figure 15. Forewing of aulacid; point of arrow located in the diagnostic cell (genus *Pristaulacus*).

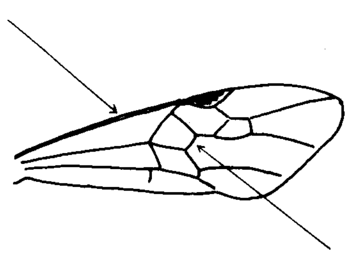


Figure 16. Wing of ichneumonoid (Braconidae), showing two veins together along edge of wing, as well as recurrent vein mentioned in couplet 14.

14. Only one "recurrent vein" (see illustration); wings often strongly tinted blackish or brownish . . . . . . . Braconidae

14'. Two "recurrent veins" (see illustration); wings not tinted . . . . . . . . . . . . . . . . . . . . . . . . . Ichneumonidae

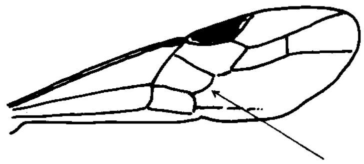


Figure 17. Wing of braconid, showing a single recurrent vein.

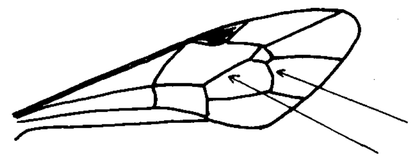


Figure 18. Wing of ichneumonid, showing two recurrent veins.

## PART I: NONPARASITIC HYMENOPTERA

### FORMICIDAE

Four species of ants belonging to four different genera were taken on recently felled Douglas-fir in the Cedar River watershed. These species were determined with the aid of Smith's key to the ants of the Pacific Northwest (1939), and this reference should be consulted for determination of those species that do not fit our key. There is undoubtedly a somewhat different ant fauna in dead Douglas-fir east of the Cascade Range.

This discussion of the ants of Douglas-fir follows Smith's nomenclature (1939), but omits the subspecific and variety names that could be applied to all the species found. By this omission, the construction of a complicated key to the subspecies and varieties is avoided; such a key would be necessary to identify the same species of ants in other faunal zones within the range of Douglas-fir.

The four species may be found simultaneously in considerable numbers on the same tree. All are apparently general predators and frequently may be seen attacking insects or carrying off pieces of dead insects. Attacks on live adult insects on Douglas-fir are usually unsuccessful because flies and parasitic Hymenoptera quickly fly away, while scolytids characteristically retract their legs and antennae and remain immobile or tumble off the log. Larvae, when available, as well as hymenopterans that are ovipositing through the bark, are quickly seized and carried off by the ants.

The four ant genera seem to have niches defined by nesting and feeding habits. *Leptothorax* and *Camponotus* live under bark, and queens of both genera were often taken on traps or cut logs. *Formica* and *Lasius* normally nest in the ground. *Leptothorax* and *Lasius* attack very small prey; *Leptothorax* is constantly searching crevices and entering scolytid galleries, while *Lasius* runs rapidly along the surface of the bole. *Formica* engages in hunting behavior much like that of *Lasius*, but is much larger than the latter. *Camponotus* was the scarcest of the ants observed. The only personal observation of its foraging behavior was that *Camponotus* moves much more slowly than *Formica*.

#### *Key to Genera and Species of Formicids Associated with Recently Felled Douglas-Fir*

1. A large pointed spine on the posterior end of the thorax; thorax and main part of abdomen connected by two segments . . . . . . . . . . . . . . . . . . . . . . . . . *Leptothorax acervorum*

1'. Thorax unarmed; only one segment between thorax and main part of abdomen . . . . . . . . . . . . . . . . . . . . . . . . . 2

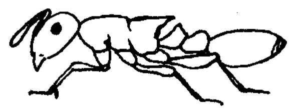


Figure 19. *Leptothorax acervorum.*

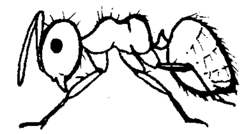


Figure 20. *Lasius niger.*

2. Small (4 mm or less) species; entire body yellowish brown . . . . . . . . . . . . . . . . . . . . . . . . . . . *Lasius niger*

2'. Larger (5 mm or more) species; body bicolored black and red . . . 3

3. Legs and thorax very dark red; thorax in lateral profile presenting an almost smooth curve . . . . . *Camponotus herculeanus*

3'. Legs and thorax more orange; thorax in lateral profile with two distinct humps . . . . . . . . . . . . *Formica truncicola*

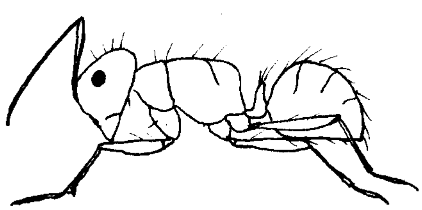


Figure 21. *Camponotus herculeanus.*

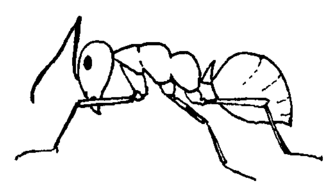


Figure 22. *Formica truncicola.*

*Leptothorax*

Two local members of the genus *Leptothorax* seem to be closely associated with dead trees. Smith (1939) reports that *L. acervorum* and *L. curvispinosus* both nest primarily in the soft wood and subcortical area of fallen trees. The two species are similar in appearance, but *L. curvispinosus* lacks the slight dorsal constriction that demarks the third lobe of the thorax as seen in lateral view. *Leptothorax curvispinosus* is usually found in somewhat drier regions (Smith 1939) and perhaps replaces *L. acervorum* in Douglas-fir east of the Cascade Range. DeLeon (1934) observed an unidentified species of *Leptothorax* on lodgepole pine attacked by *Dendroctonus ponderosae*. Savely (1939) found *L. curvispinosus* under the bark of pine and oak trees that had been dead for one to four years.

*Leptothorax acervorum*

*Leptothorax acervorum* was common in the plots in Cedar River watershed, running up and down fallen logs, exploring bark fissures and holes in the bark. Individuals were occasionally seen entering or leaving the galleries of *Dendroctonus pseudotsugae* and *Pseudohylesinus nebulosus*. There is some evidence *L. acervorum* may invade active scolytid galleries in order to establish colonies. Several alate queens were taken on traps on scolytid-infested trees in early August. A series of apterous queens emerged, probably to forage, from billets brought indoors and still containing *Dendroctonus pseudotsugae* adults. *Leptothorax acervorum* usually occurs in exposed trees. During the present study colonies of *L. acervorum* were found in *Pseudotsuga menziesii, Tsuga heterophylla,* and *Picea sitchensis*.

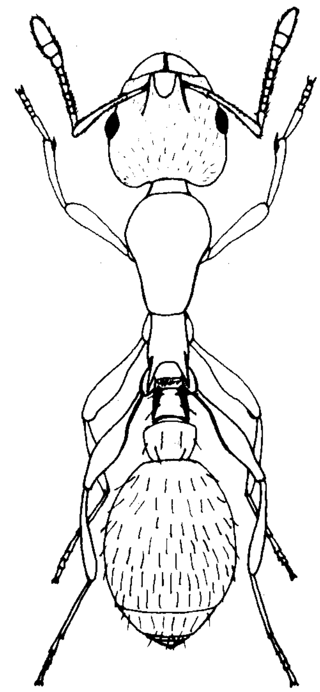


Figure 23. *Leptothorax acervorum*, worker.

A colony of *L. acervorum* was brought into the laboratory and placed in an observation nest formed by laying a pane of glass over a series of small, interconnected chambers excavated in a block of wood. This colony produced numerous workers and, eventually, a few winged adults. Workers repeatedly refused various sweet solutions, were indifferent to live aphids, and rejected larvae of *Scolytus unispinosus*. Small cerambycid larvae were stung and dragged into the nest. The workers gathered about the cerambycid larvae and apparently lapped up their body fluids, presumably drinking from small lacerations.

## *Lasius*

Only one species of *Lasius* has been taken on Douglas-fir.

*Lasius niger*

Unlike *Leptothorax acervorum, Lasius niger* gives no indication of any dependence on fallen trees. This species is an omnivorous scavenger and honeydew-feeder, which is found in many habitats and may even become a pest in houses. Smith (1939) reports colonies in logs, but implies that the trees had been dead for some years.

Aside from their continual harassment of other insects on the fallen trees, these ants seemed to be of some importance as predators of small insects. They were observed carrying off live sciarids and chalcidoid parasites of scolytids. On one occasion, a team of *L. niger* was seen systematically excavating frass from an active *Dendroctonus* gallery.

### *Camponotus*

One species of *Camponotus* has been taken on Douglas-fir. Members of this genus are often called carpenter ants because of their habit of excavating nests in solid wood. The establishment of a *Camponotus* colony in a dead log is the beginning of a greatly accelerated process of decomposition. It is thus not unusual to find a log that, in the course of a few years, has been reduced to little more than a mass of thin septa dividing the chambers and galleries of a large *Camponotus* colony.

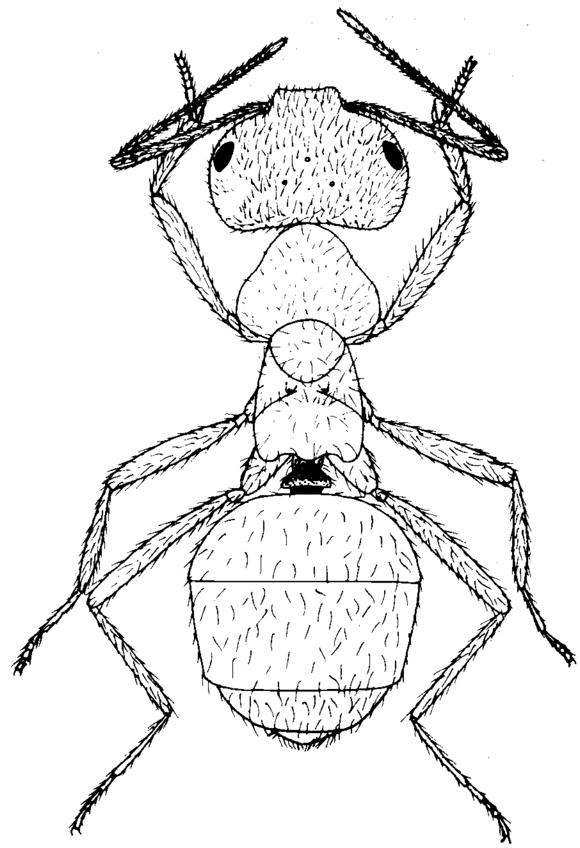


Figure 24. *Lasius niger*, worker.

#### *Camponotus herculeanus*

*Camponotus herculeanus* was the least common ant on the cut trees in the plots in Cedar River watershed; only one or two individuals were normally visible at any one time per tree. *Camponotus herculeanus* is one of the carpenter ants and thus clearly associated with sound and partly rotten wood. The colonies are usually initiated under the loose bark of dead trees (Smith 1939). Ayre (1963) studied the feeding habits of *C. herculeanus* using laboratory colonies. He found that *C. herculeanus* is a highly predacious species: in 44 trials, 98% of the live insects offered were killed and eaten. A slightly lower percentage of dead insects were taken and eaten. A wide variety of insects was offered. *Camponotus herculeanus* has been observed on the bark of *Pinus contorta* infested by *Dendroctonus ponderosae* (DeLeon 1934), and on *Pinus strobus* and *P. resinosa* attacked by various scolytids (Thomas 1955).

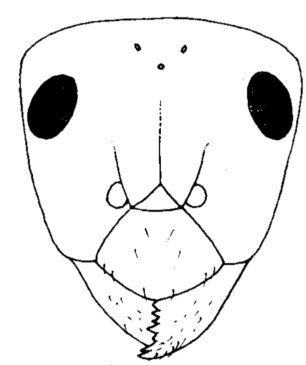


Figure 25. Head of *Formica truncicola*, worker.

### *Formica*

Only one species of *Formica* has been associated with Douglas-fir.

#### *Formica truncicola*

*Formica truncicola*, which frequently is found under the name of *F. rufa*, was common on all the cut trees. It is not typically a wood-inhabiting species, the nest usually occurring under stones or rotten wood (Smith 1939). Such observations as were made suggest that *F. truncicola* is an aggressive, predacious species. On one occasion, one of these ants was seen to seize an ovipositing *Spathius sequoiae,* pull it from the bark, and remove the wings. DeLeon (1934) found *F. rufa* on bark of lodgepole pine infested with *Dendroctonus ponderosae*.

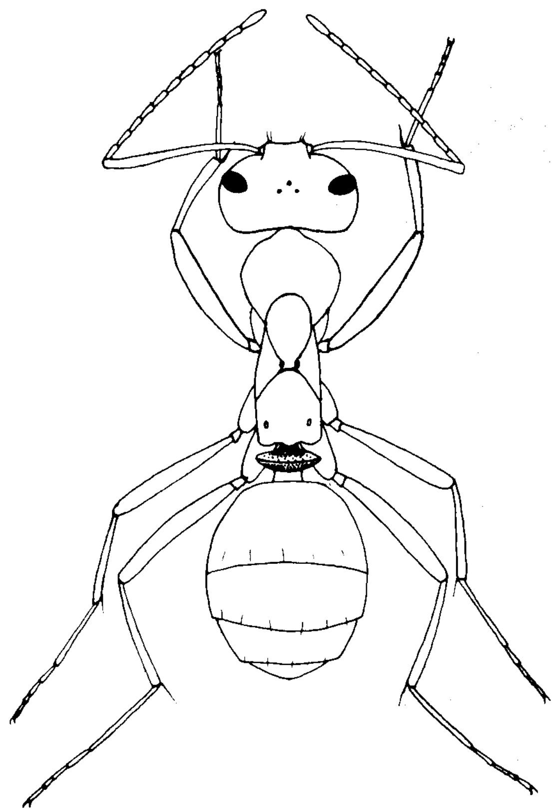


Figure 26. *Formica truncicola,* worker.

## SIRICIDAE

The siricids are the only Hymenoptera found upon dead Douglas-fir that are not predacious or parasitic. The larvae of siricids tunnel through sapwood and heartwood, but obtain nourishment from the mycelia of fungi that are introduced during oviposition.

Morgan (1968) has published a review of the known biological information concerning the Siricidae. This information deals mainly with *Sirex noctilio,* a species that has been intensively studied because it is an important pest, but Morgan believes the biologies of all conifer-infesting siricids are basically similar.

Adult siricids emerge in the late summer and early fall; in the Pacific Northwest, almost all specimens are taken between mid-July and late August (Morris 1967). Males usually emerge about a week before females and go to the crown area of surrounding trees, where they may display swarming behavior (Morgan 1968). Emerging females have a rather different behavioral pattern, flying first to areas of high light intensity before seeking mates and oviposition sites (Morgan 1968). Females use their long ovipositors to reach the sapwood; each egg is supplied with glandular secretions and a propagule of symbiotic fungus (Morgan 1968). *Sirex cyaneus* lays an average of about three eggs in each puncture (Middlekauff 1960); the number of eggs per puncture of other Douglas-fir siricids is apparently unknown. The development of most siricid larvae requires one to three years; this developmental time varies with the temperature and the moisture content of the infested trees: larvae develop fastest at high temperatures and low moisture content (Morgan 1968). Before emerging from its pupal chamber, the adult female moves the abdomen about in such a way as to transfer fungal propagules to the openings of two nutrient-producing mycangial sacs at the base of the ovipositor (Morgan 1968).

Because of their specialized feeding habits, siricids occupy a different niche in the Douglas-fir community from that of sapwood-feeding Coleoptera such as cerambycids and buprestids. The larvae of sapwood-feeding Coleoptera normally gnaw their way through outer bark and phloem to reach the wood, and sometimes even require a diet of phloem for a period before attacking the wood. The siricids are not usually found in the bark, and by virtue of their long ovipositors penetrate deeply into the sapwood before it has been invaded by any insects other than ambrosia beetles. Coleoptera that attack sapwood are usually able to digest the wood itself, and thus a larva may remain in a tree for many years enjoying a constant food supply, or successive generations of emerging adults may attack the tree from which they emerge as long as sound wood remains. Siricids, depending on a fungus that flourishes only under certain conditions, cannot develop in a tree that has become extremely dry; thus siricids seldom take more than two or three years to mature and are not likely to reattack the trees from which they emerged. It is also possible that the symbiotic fungus of siricids is unable to compete with some of the other fungi responsible for the deterioration of Douglas-fir. It would be interesting to know what interaction there may be between the symbiotic fungus of siricids and the fungi of the ambrosia beetles, which often occupy the same tree.

A single species of fungus, *Stereum chailletii,* is the symbiote associated with *Sirex cyaneus, S. juvencus, Urocerus gigas flavicornis,* and *Urocerus albicornis* (Stillwell 1966). It seems probable that the fungi of all Douglas-fir siricid species would tend to overlap in the wood, and if there were more than one fungus variety, the more vigorous variety would tend to displace the less vigorous varieties and would be transported by all the emerging siricids, hence a uniformity of symbiotic fungi would result.

The invasion of a dead or dying Douglas-fir by siricids is a turning point in the deterioration of the tree. Stillwell (1960) reported that balsam fir attacked by siricids is permeated by fungus to an average depth of 1 cm in less than a year, whereas balsam fir unattacked by siricids showed scarcely any decay after two years. This proliferation of fungal hyphae in recently killed trees must have a profound effect on the cerambycids, buprestids, melandryids, and other wood-feeding Coleoptera.

Apparently little or nothing is known about the mechanisms by which Douglas-fir siricids locate susceptible hosts. Observations of *Sirex noctilio* indicate that once a suitable host has been found, the ovipositing adult discovers the amount of resins and the moisture content in the wood by drilling with the ovipositor, which is equipped with what appear to be specialized sensilla (Morgan 1968).

There is little available information concerning the ecological differences between the three genera of siricids attacking Douglas-fir. Since most siricids apparently must oviposit in the sapwood, it appears that on thick-barked areas on trees only those species with long ovipositors would be able to oviposit. This hypothesis could be tested easily by enclosing a species with a relatively short ovipositor, such as *Urocerus albicornis,* with bolts whose bark is thicker than the measured length of the siricid ovipositor. Similarly, because of varying ovipositor lengths as well as larval habits, stratification of larvae of different siricids could occur within thin-barked material.

Ichneumonids of the genera *Rhyssa* and *Megarhyssa* are common parasites of siricids on Douglas-fir (Townes and Townes 1960). Species of the family Ibaliidae are also parasites of siricids (Morgan 1968); one species of this family has been taken on Douglas-fir (Bedard 1968).

Table 1 shows the known alternate host genera of siricids attacking Douglas-fir. Redwood, cedar, and cypress are apparently unusual alternate hosts for Douglas-fir siricids. Except for *Sirex areolatus*, all siricids that attack Douglas-fir also attack a wide range of hosts in the Pinaceae. Eight species of siricids, belonging to three genera, have been reported from Douglas-fir.

**Table 1. Alternate host genera of siricids associated with Douglas-fir.**

| | *Urocerus albicornis* | *U. californicus* | *U. gigas flavicornis* | *Sirex areolatus* | *S. cyaneus* | *S. californicus* | *Xeris spectrum* | *X. morrisoni* |
|---|---|---|---|---|---|---|---|---|
| ***Pinus*** | X | X | X | X | X | X | X | X |
| ***Abies*** | X | X | X | | X | | X | X |
| ***Picea*** | X | | X | | X | | X | X |
| ***Larix*** | X | X | | | | X | X | X |
| ***Tsuga*** | X | X | | | | | X | X |
| ***Thuja*** | X | | | X | | | | |
| ***Libocedrus*** | | X | | X | | | | X |
| ***Cupressus*** | | | | X | | X | | |
| ***Sequoia*** | | | | X | | | | |

*Key to the Genera of Siricidae Associated with Douglas-Fir (adapted from Bradley 1913)*

1. Head with a large white spot behind eye . . . . . . . . . . . . . . 2

1'. Head without a large white spot behind eye . . . . . . . . . . . *Sirex*

2. Posterior tibiae with two apical spurs; ovipositor shorter than abdomen . . . . . . . . . . . . . . . . . . . . . *Urocerus*

2'. Posterior tibiae with one apical spur; ovipositor longer than abdomen . . . . . . . . . . . . . . . . . . . . . . *Xeris*

*Sirex*

Three species of *Sirex* have been reported from Douglas-fir, but one species, *S. areolatus*, usually seems to be associated with Cupressaceae and Taxodiaceae and only rarely associated with the Pinaceae (Keen 1952).

There is some confusion about the taxonomy of the species of *Sirex* attacking Douglas-fir. Bradley (1913) considered *S. cyaneus* a subspecies of *S. juvencus*, but most recent publications (Muesebeck et al. 1951, Middlekauff 1960) indicate *S. cyaneus* and *S. juvencus* are discrete species. Since *S. cyaneus* introduced into Europe has long maintained its identify separate from that of the native *S. juvencus*, it seems likely the two species are distinct. More recently, Benson (1963) has synonymized *S. juvencus* and *S. californicus*.

*Key to the species of Sirex associated with Douglas-fir (adapted from Middlekauff 1960)*

1. All legs blackish or metallic blue-black . . . . . . . . . . . . . . 2

1'. Female with all legs mostly reddish brown; male with fore- and middle legs mostly reddish brown . . . . . . *cyaneus*

2. Female with ovipositor about as long as forewing; male entirely blue-black except for the last five segments of the abdomen, which are yellowish orange . . . *areolatus*

2'. Female with ovipositor much shorter than forewing; male unknown . . . . . . . . . . . . . . . . . . . . . . . *californicus*

*Sirex cyaneus*

Only one specimen of *S. cyaneus* was taken in the Cedar River watershed during 1972. This individual, a female, was walking along a felled log that had been infested by *Dendroctonus pseudotsugae*. The collection date is 7 October, an unusually late date for this species to be active.

*Sirex cyaneus* is reported from *Pseudotsuga menziesii* (Bedard 1938), *Abies lasiocarpa* (Morris 1967), *A. fraseri* (Amman 1969), *A. balsamea*, *A. concolor* (Middlekauff 1960), *Picea glauca* (Morris 1967), and *Pinus* sp. (Muesebeck et al. 1951).

Bedard (1938) found *S. cyaneus* ovipositing in August on Douglas-fir killed the previous year by *Dendroctonus pseudotsugae*. Morris (1967), working in British Columbia, found that *S. cyaneus* requires two years to complete its life cycle. Adults emerged during the last half of July and the first half of August. In his studies of Fraser fir in North Carolina, Amman (1969) found *S. cyaneus* emerging in June and ovipositing in July and August. This same study showed that no wood wasps emerged from trees that had been dead for more than three years, indicating that *S. cyaneus* needs fresh material.

Middlekauff (1960) summarized the results of several studies of *S. cyaneus* by European entomologists. Females of *S. cyaneus* produce about 300 or 400 eggs, which are laid in batches of one to seven in each puncture. After three to four weeks the eggs hatch and the larvae bore into the wood along the grain. When the larvae are 8-9 mm long, they turn and tunnel toward the heartwood, then turn again and bore toward the outer surface of the tree, finally constructing a pupal chamber about 2 cm below the surface of the wood. The pupal stage lasts five to six weeks.

The entire gallery is about 25-30 cm long. Two years are required for the life cycle of *S. cyaneus*. *Sirex cyaneus* is parasitized by *Rhyssa lineolata* (Middlekauff 1960).

*Sirex areolatus*

*Sirex areolatus* has not yet been collected in the Cedar River watershed, and according to Keen (1952) it does not usually attack Douglas-fir. *Sirex areolatus* has been associated with *Pseudotsuga menziesii, Sequoia sempervirens, Cupressus macrocarpa, Pinus contorta, P. jeffreyi, P. lambertiana, P. radiata, Libocedrus decurrens,* and *Thuja* sp. (Middlekauff 1960).

This species is unusual among siricids in that it is reported to oviposit in bark as well as in wood (Morgan 1968). *Sirex areolatus* and all its life stages are illustrated in Keen (1952). It is parasitized by *Ibalia ensiger* (Middlekauff 1960), *Rhyssa ponderosae*, and *R. persuasoria* (Townes and Townes 1960).

*Sirex californicus*

*Sirex californicus* has not yet been collected in the Cedar River watershed. Tree associations include *Pseudotsuga menziesii, Pinus jeffreyi, P. ponderosa, P. contorta, Cupressus macrocarpa* (Middlekauff 1960), and *Larix occidentalis* (Morris 1967).

Middlekauff (1960) considers the species fairly common, but the male has yet to be described, probably because of the habit of siricid males of swarming in the treetops. In the absence of any male specimens of *S. californicus*, it seems risky for Benson (1963) to synonymize this species with *S. juvencus*.

## *Urocerus*

Three species of *Urocerus* attack Douglas-fir. Nothing seems to be known about how the niches of these species differ, except that there is a possible geographic separation. *Urocerus gigas flavicornis* is primarily a northern species, while *U. californicus* is found in western alpine areas (Krombein 1958). *Urocerus albicornis* is a very widespread species but much less common than *Urocerus californicus* in California (Middlekauff 1960).

*Key to the species of Urocerus associated with Douglas-fir (adapted from Middlekauff 1960)*

Females

1. Abdomen black with at least two yellow segments . *gigas flavicornis*

1'. Abdomen entirely black or black with small lateral spots . . . . . 2

2. Wings golden yellow; light markings on legs and antennae yellow . . . . . . . . . . . . . . . . . . . . . *californicus*

2'. Wings dark brown; light markings on legs and antennae white or cream-colored . . . . . . . . . . . . . *albicornis*

Males

1. Abdomen entirely reddish brown; wings golden yellow . *californicus*

1'. Abdomen yellow and black; wings not yellow . . . . . . . . . . . . . 2

2. Basal segment of hind tarsus 4.1 to 5.6 times as long as broad . . . . . . . . . . . . . . . . . . . . . . . *albicornis*

2'. Basal segment of hind tarsus 6.4 to 8.1 times as long as broad . . . . . . . . . . . . . . . . . . . . *gigas flavicornis*

*Urocerus albicornis*

*Urocerus albicornis* was frequently observed in 1972 ovipositing on freshly cut Douglas-fir during late July and early August in the Cedar

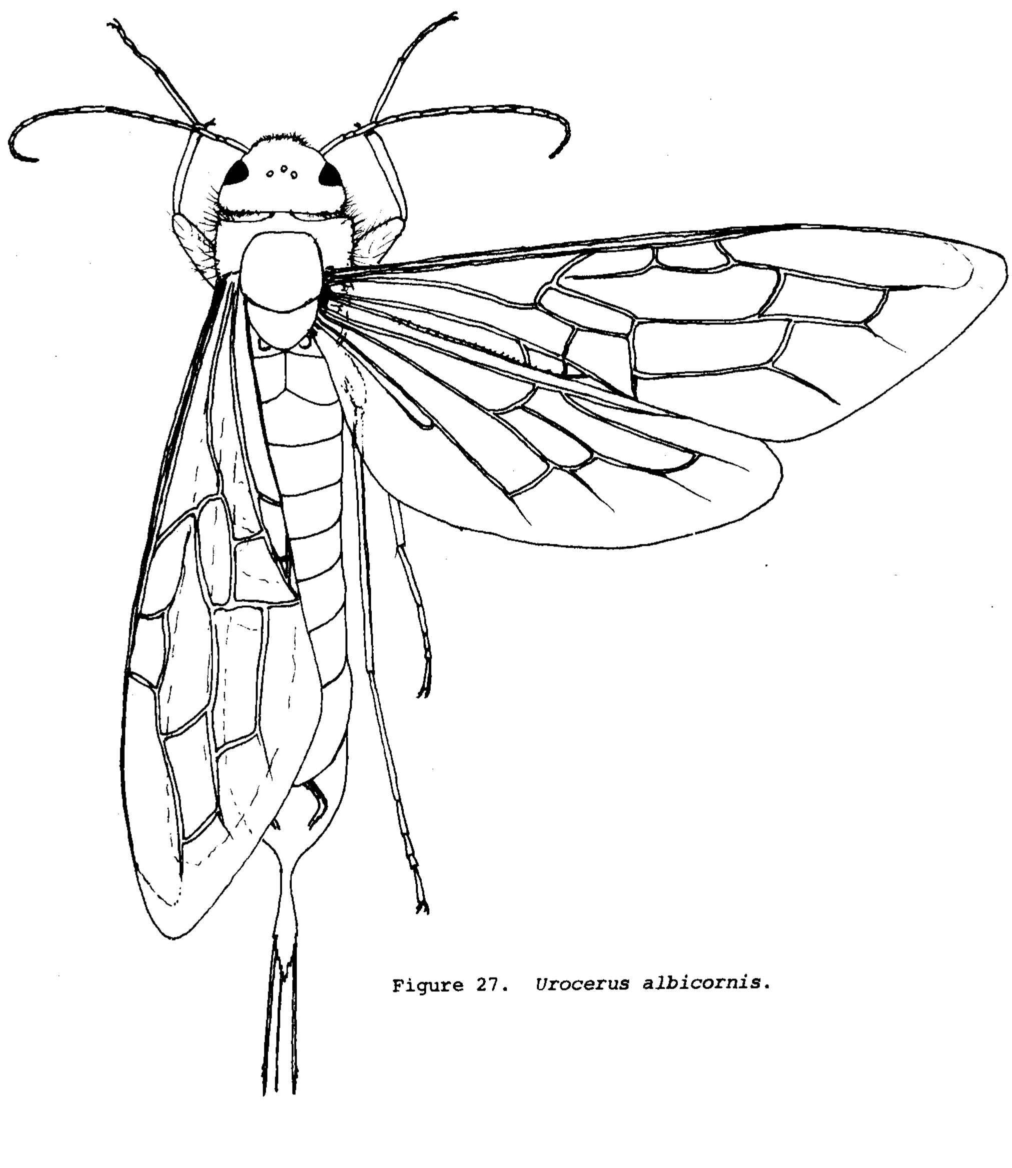


Figure 27. *Urocerus albicornis*.

River watershed. The diameter of the material attacked ranged from about 8 cm to about 33 cm. The earliest collection date was 5 July, the latest, 8 August.

*Urocerus albicornis* is reported from *Pseudotsuga menziesii* (Bedard 1938), *Abies fraseri* (Amman 1969), *A. balsamea* (Middlekauff 1960), *A. lasiocarpa, Larix occidentalis, Thuja plicata* (Morris 1967), *Tsuga* sp., *Pinus* sp. (Middlekauff 1960), and *Picea sitchensis*. Bedard (1938) found *U. albicornis* ovipositing in August on trees killed the previous year by *Dendroctonus pseudotsugae*. Morris (1967) found emergence dates in British Columbia extending from 21 June to 1 August; he also demonstrated that *U. albicornis* has a two-year life cycle. Parasites of this species include *Megarhyssa nortoni, Rhyssa lineolata* (Middlekauff 1960), and *R. crevieri* (Townes and Townes 1960).

*Urocerus californicus*

*Urocerus californicus* was not seen in 1972 in the Cedar River watershed. The hosts of *U. californicus* include *Pseudotsuga menziesii* (Bedard 1938), *Abies balsamea, A. concolor, A. magnifica* (Middlekauff 1960), *A. lasiocarpa, Tsuga heterophylla, Larix occidentalis, Pinus monticola* (Morris 1967), *P. contorta, Libocedrus decurrens* (Middlekauff 1960), and *Picea sitchensis*. Morris (1967) found *U. californicus* emerging from 11 to 28 July, with one specimen emerging on 19 June. In this same study, Morris reports a two-year life cycle for *U. californicus* in alpine fir and western white pine (seven specimens emerged), and a one-year life cycle on western hemlock and western larch (again, seven specimens emerged). This difference in developmental time may be due to the time of year when the eggs were laid or to the condition of the trees attacked.

*Urocerus gigas flavicornis*

*Urocerus gigas flavicornis* was not found on Douglas-fir by Bedard (1938), or Morris (1967), nor in the study of the Cedar River watershed in 1972. *Urocerus gigas flavicornis* is reported from throughout the range of Douglas-fir. Known hosts are *Pseudotsugae menziesii, Picea sitchensis, Abies lasiocarpa* (Krombein 1958), and *Larix occidentalis* (Morris 1967).

## *Xeris*

Two species of *Xeris* occur in Douglas-fir; neither species was taken in the Cedar River watershed in 1972, one species was observed in 1973. Little is known about the habits of the species of *Xeris* attacking Douglas-fir. Muesebeck et al. (1951) indicate that in the western United States the Holarctic *X. spectrum* is primarily an alpine species.

At least one species of *Xeris, X. spectrum,* has only vestiges of the abdominal mycangial sacs in which species of *Sirex* and *Urocerus* transport propagules of symbiotic fungi (Stillwell 1966). Morgan (1968) suggests that *Xeris spectrum* may attack trees that already have been inoculated with fungi by other siricids.

*Key to the species of Xeris associated with Douglas-fir (adapted from Bradley 1913)*

1. Abdomen mostly reddish . . . . . . . . . . . . . . . . . . . . *morrisoni*

1'. Abdomen black . . . . . . . . . . . . . . . . . . . . . . . . *spectrum*

*Xeris morrisoni*

Bedard (1938) found *X. morrisoni* ovipositing during August on Douglas-fir killed the previous year by *Dendroctonus pseudotsugae*. Other hosts include *Larix occidentalis* (Morris 1967), *Abies magnifica* (Middlekauff 1960), *A. grandis, A. lasiocarpa, Picea sitchensis, P. pungens, Tsuga heterophylla, Libocedrus decurrens* (Krombein 1958), *Pinus ponderosa*, and *P. contorta* (Middlekauff 1960).

The emergence date of the single specimen reported by Morris (1967) is 25 July and there was a one-year life cycle. *Megarhyssa nortoni* is a parasite of this species (Middlekauff 1960).

*Xeris spectrum*

Two specimens of *Xeris spectrum* were taken on 16 July in the Cedar River watershed on trees that had been cut the previous year. This species attacks *Pseudotsuga menziesii, Larix occidentalis* (Morris 1967), *Abies lasiocarpa, A. grandis* (Krombein 1958), *A. balsamea* (Stillwell 1966), *Picea sitchensis, P. pungens, Tsuga heterophylla, Pinus contorta* (Krombein 1958), and *P. ponderosa* (DeLeon 1934). Middlekauff (1960) states that *Pinus contorta* is probably the preferred host in California.

DeLeon (1934) found *X. spectrum* ovipositing in late July and in August. Morris (1967) found an unusually long and late emergence period, from 17 July to 7 September. In this same study, Morris found seven specimens with one-year life cycles and one specimen with a two-year life cycle.

## PART II: PARASITIC HYMENOPTERA

The families of insects that follow are traditionally considered parasitic Hymenoptera. There are various refinements of the concept of parasitism, and most species discussed below are actually external parasites, sometimes known as "parasitoids." The larval host of such a parasite is located and usually paralyzed by the ovipositing parasite. A single larva of the parasite attacks and entirely consumes the host larva.

There is a common belief that, whereas a species of predatory insect attacks a wide variety of hosts, a parasitic insect is exceedingly specialized and attacks only one or two host species. This generalization cannot be applied to insects found in freshly killed conifers. The great majority of parasites in these recently killed trees occur in several tree species and attack more than one genus of host insect. The ecological niches of most parasitic Hymenoptera in fallen conifers will probably be found to be defined indirectly by the host species and directly by other factors, such as the size of the host, the thickness of bark or wood above the host, the portion of the tree in which the host is located, the exposure of the tree, and the time since the death of the tree. This idea has been formulated by Townes (1960):

> Probably the most important single factor determining host selection, after those factors that limit the parasite to a very broad phyletic line of hosts, are the ecological factors. There are first the general ecological factors that limit the parasites to hosts within its geographic range, ecological habitat, and seasonal distribution. These are rather obvious, but it is commonly overlooked that the ovipositing female of each species of parasite searches for hosts of certain characteristics in a restricted ecological niche, and that a parasite may attack a variety of hosts which happen to meet its peculiar ecological requirements.

Since most parasitic Hymenoptera in dead conifers are not dependent upon a single host, it follows that the abundance of a parasite may not be closely correlated with that of a particular host that is being studied. This suggests that studies of the population dynamics of insects that are hosts of parasitic Hymenoptera should include a survey of the alternate hosts available to the parasites.

### AULACIDAE

The wasps of the family Aulacidae are sometimes, particularly in the older literature, referred to as the subfamily Aulacinae of the family Gasteruptiidae. Two genera of aulacids have been reported from Douglas-fir. In life, the members of this family are easily recognized by the curiously bent ovipositor, and the habit of rapidly flicking the wings, which are held vertically along the sides of the body. Almost nothing is known about the behavior or ecology of this group of wasps except that they parasitize cerambycid and buprestid larvae in bark or conifer cones. These wasps are not uncommon and can easily be reared from beetle-infested trees. A study to discover the oviposition behavior, the appearance of the larva, and the nature of the parasitism of a species such as *Pristaulacus minor,* which is abundant and has a short life cycle, could be accomplished relatively easily.

*Key to the Genera of Aulacidae Associated with Douglas-Fir (adapted from Townes 1950)*

1. Tarsal claws with two or more teeth; no conspicuous wrinkles in area between lower ocellus and antennae . *Pristaulacus*

1'. Tarsal claws with a single basal tooth, which is difficult to see; conspicuous wrinkles usually present in area between lower ocellus and antennae . . . . . *Aulacus*

*Aulacus*

Bedard (1938) reports "*Pammegishia* sp. near *minnesotae* Bradl." ovipositing on cerambycid and buprestid larvae in Douglas-fir during August. *Pammegishia minnesotae* has since been changed to *Aulacus pallipes*. *Aulacus pallipes* has no close relatives in the Northwest, and has been reared only from wood wasps of the genus *Xiphidria* in birch. It would be difficult to determine what species of *Aulacus* Bedard might have found, and there is a possibility the wasp was actually a *Pristaulacus*.

Figure 28. Tarsal claws of *Pristaulacus*.

*Pristaulacus*

Four species of *Pristaulacus* have been associated with Douglas-fir. Differences in the ecological roles played by these four species are little known. *Pristaulacus minor* and probably *P. rufitarsus* are found on exposed trees. Only one species has been taken in the Cedar River watershed.

*Key to the species of Pristaulacus associated with Douglas-fir (adapted from Townes 1950)*

1. Forewings with three darkish spots: at apex, below stigma, and near center of wing; four teeth on each tarsal claw . . . . . . . . . . . . . . . . . . . . . . . . *pacificus*

1'. Forewings with no dark spots; two teeth on each tarsal claw . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2. Hind femur blackish or very dark brown . . . . . . . . . *rufitarsus*

2'. Hind femur reddish or red-brown . . . . . . . . . . . . . . . . . . 3

3. Hind tibia darker than hind femur and tarsus, front and middle legs with second trochanters blackish red . . . . . *minor*

3'. Hind tibia same color as hind femur and tarsus; front and middle legs with second trochanter brownish red . . . . *editus*

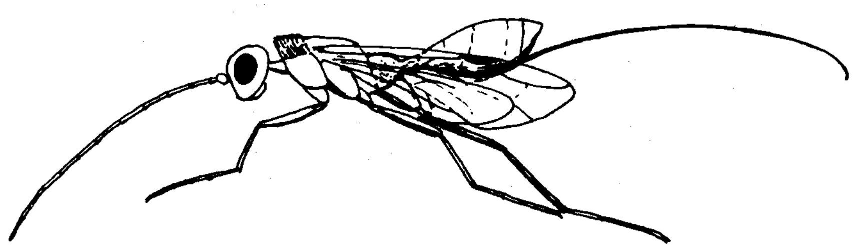


Figure 29. *Pristaulacus minor*; posture of live insect.

*Pristaulacus editus*

Bedard (1938) reared *P. editus* from the bark of Douglas-fir during June, and suggests that the hosts are buprestids and cerambycids. Other host records (Townes 1950), are *Trachykele blondeli* in *Thuja plicata*, and *Paratimia conicola* and *Chrysophana placida* in cones of *Pinus attenuata*. The host-searching behavior required for parasitizing larvae in pine cones appears so different from that required for parasitizing subcortical larvae in dead trees, that it seems likely that two behavioral races exist.

*Pristaulacus rufitarsus*

Bedard (1938) observed *P. rufitarsus* ovipositing on cerambycid and buprestid larvae in Douglas-fir during August. Other tree associations (Townes 1950) include *Pinus ponderosa, Tsuga canadensis, T. mertensiana, Abies concolor,* and *Populus tremuloides*. Known insect hosts (Townes 1950) are *Chrysobothris caurina, Melanophila drummondi, M. fulvoguttata,* and *Saperda calcarata*.

*Pristaulacus minor*

*Pristaulacus minor* is common in the Cedar River watershed, where it may be seen during late June and in July on logs infested by *Melanophila drummondi*. This species emerged from hemlock and Douglas-fir in the Cedar River watershed, and from an unspecified host, probably *M. gentilis*, in ponderosa pine from eastern Washington. Additional tree associations (Townes 1950) are *Abies concolor, A. magnifica, Picea sitchensis,* and

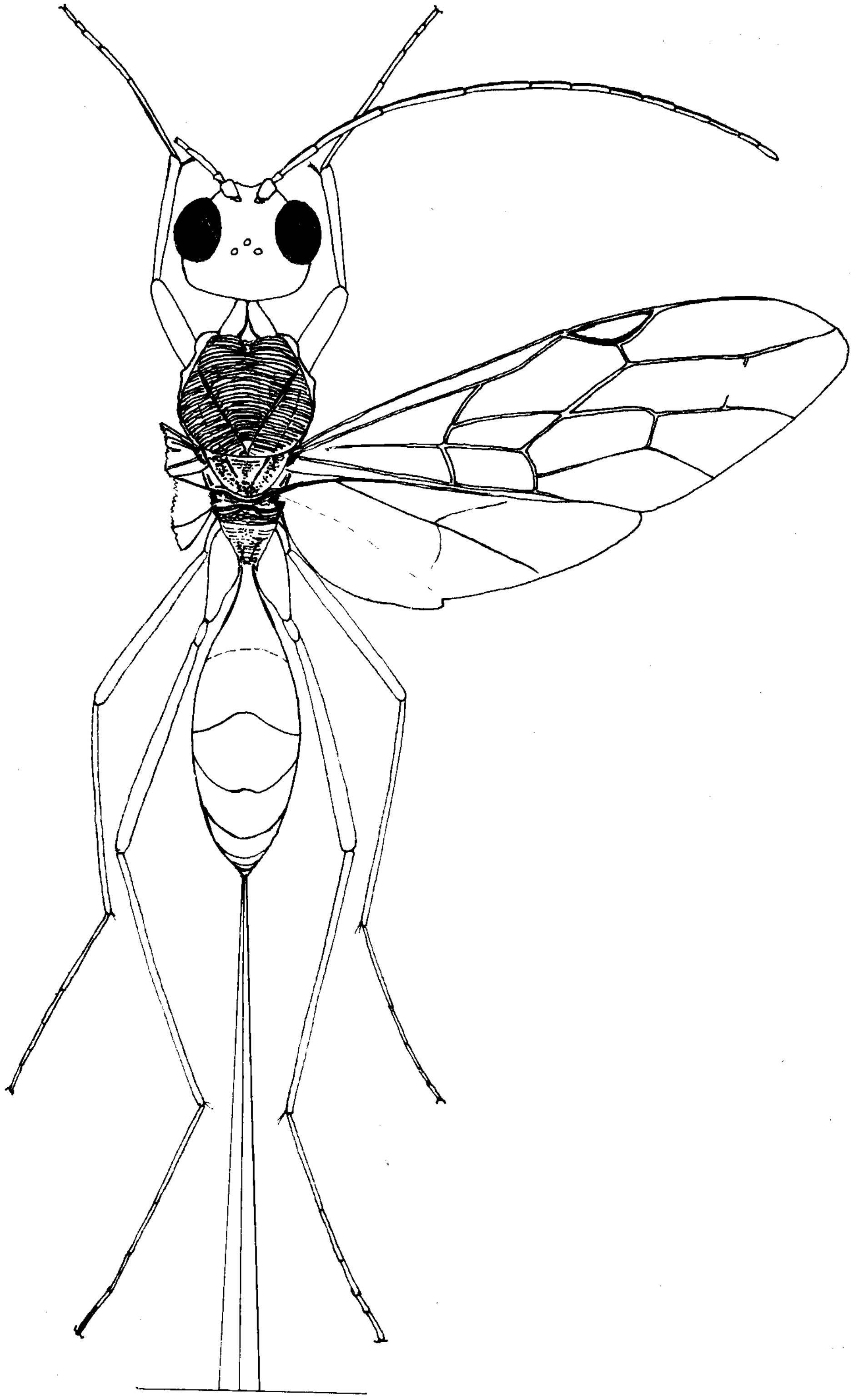


Figure 30. *Pristaulacus minor.*

*Pinus ponderosa*. Hosts of *P. minor* include *Melanophila intrusa* and *Hylotrupes ligneus* (Townes 1950).

*Pristaulacus minor* is found regularly on freshly cut trees on which *M. drummondi* is just beginning to oviposit. The long ovipositor of *P. minor* suggests this species oviposits through bark on host larvae, but observations indicate that *P. minor* oviposits into the eggs of its hosts and the parasite larva develops after its host larva has become mature. The long ovipositor of *P. minor* is probably adapted to reach host eggs hidden in deep bark fissures.

*Pristaulacus pacificus*

*Pristaulacus pacificus* is included here because Townes (1950), at the end of his discussion of *P. pacificus,* remarks significantly, "This species seems to have about the same range as *Pseudotsuga taxifolia* (Douglas-fir)." There are no known hosts.

## PROCTOTRUPIDAE

One genus of Proctotrupidae has been taken on traps on cut logs and bolts in the Cedar River watershed. The only published reference found on proctotrupids associated with freshly killed trees is DeLeon's (1934) observation of *Cryptoserphus abruptus* adults on trees attacked by *Dendroctonus ponderosae*. On one occasion, DeLeon saw a female *C. abruptus* entering a *Dendroctonus* gallery.

### *Codrus*

Three species of the genus *Codrus* were taken on traps on freshly killed Douglas-fir in the Cedar River watershed. Many specimens were so badly damaged that it was impossible to determine their species.

The only known hosts for members of the genus *Codrus* are staphylinids (Hedqvist 1963a). Williams (1932) has supplied a fine illustration of a *Codrus* pupa protruding from a staphylinid larva. Probable hosts for *Codrus* in Douglas-fir would be staphylinids of the genera *Quedius* and *Atrechus,* medium-sized beetles, the adults and larvae of which are frequently found under bark of Douglas-fir.

A key to most of the known species of *Codrus* and a brief description of *Cryptoserphus abruptus* appear in Brues' publication (1919). Masner (1961) has provided a key to the genera of the world.

*Key to the species of Codrus possibly associated with freshly killed Douglas-fir (adapted from Brues 1919)*

1. Antennal joints short, penultimate joint less than twice as long as wide, antennae pale at base, antennal joints unarmed . . . . . . . . . . . . . . . . . . . . *similis*

1'. Antennal joints long, penultimate joint more than twice as long as wide, antennae not pale at base, male with peculiar toothlike ridges on antennal joints . . . . . . 2

Figure 31. Antenna of *Codrus similis*.

Figure 32. Antenna of *Codrus placidus*.

2. Large (6-7 mm) . . . . . . . . . . . . . . . . . . . . . . . . *placidus*

2'. Small (about 3 mm) . . . . . . . . . . . . . . . . . . . . . *serricornis*

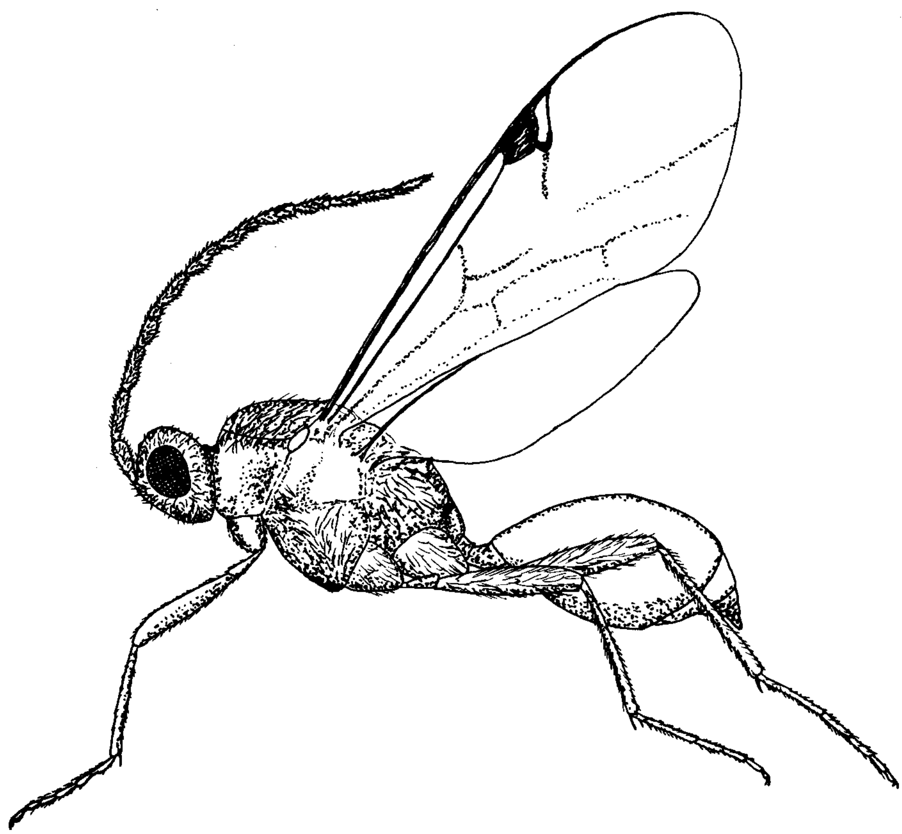


Figure 33. *Codrus placidus*.

*Codrus placidus*

In the Cedar River watershed, this large species was taken during the last half of July and in early August on traps. It was associated primarily with bolts that had been soaked in water or baited with alcohol. Most of the specimens taken were males. Coincidentally, large numbers of staphylinids of the species *Quedius laevigatus*, a known subcortical predator in dead and dying trees, appeared on the same traps at the same time. If indeed *C. placidus* is associated with Douglas-fir, the most probable host would be *Q. laevigatus* and both host and parasite might be attracted by fermentation products. This leaves open the puzzling question of how and when *C. placidus* might attack its large and aggressive host.

*Codrus similis*

Only two specimens (both females) of *C. similis* were taken in the Cedar River watershed during 1972. The collection dates are 5 and 19 July. If these species are actually associated with Douglas-fir, the probable host would be *Atrechus macrocephalus*.

*Codrus serricornis*

Three specimens of *C. serricornis* were taken during the summer in the Cedar River watershed, on 26 July and 1 August. *Atrechus macrocephalus* again is the possible host.

## ORUSSIDAE

The family Orussidae is easily recognized by the peculiar wing venation and the set of teeth on the top of the head, as well as the bizarre facies. There are two species described from the range of Douglas-fir; both belong to the genus *Orussus*.

The members of the family Orussidae are generally considered to be parasites of wood-boring beetles (Muesebeck et al. 1951), and in fact have been given the common name of "parasitic wood wasps." Arguments for this theory were marshalled by Burke (1917) in an article entitled "*Orussus* is parasitic." The evidence consists of finding a number of larvae and pupae of *Orussus* in the pupal cells of cerambycids, or more commonly buprestids; of finding the remains of beetle larvae associated with the *Orussus* larva; the observation of a female ovipositing into a buprestid gallery; and the occurrence of *Orussus* females on a number of species of dead trees that had been attacked by various insects. This evidence, though circumstantial, seems reasonably convincing.

More recently, Cooper (1953) made a thorough study of the anatomy and behavior of two eastern species of *Orussus*. The two oviposition sites examined both proved to be abandoned buprestid galleries. The female appeared to discover these galleries by tapping the wood with her abdomen. While not discounting the possibility that *Orussus* is parasitic, Cooper presents an alternative theory: the larva of *Orussus* lives on wood particles and fungi in the galleries of buprestids and follows the galleries out to the pupal cell, where the parasite perhaps attacks the beetle larva if it is present. This second theory fits in well with the habits of other members of the Siricoidea.

Western orussids may be similar to eastern species in being dependent on bark-free areas for oviposition sites, especially if some sort of vibrational cue from tapping is necessary for oviposition. Several of the small number of specimens of *Orussus* from western North America were taken on logs that had been peeled for examination of scolytid broods (Burke 1917). Only one species has been associated with Douglas-fir.

*Key to the species of Orussus in western North America (adapted from Rohwer 1913)*

1. Thorax ferruginous; distinct sharp ridge present behind eye; length 5 mm . . . . . . . . . . . . . . . . . . *thoracicus*

1'. Thorax black; no distinct sharp ridge present behind eye; length 10 mm or more . . . . . . . . . . . . *occidentalis*

*Orussus occidentalis*

*Orussus occidentalis* has been taken from a cerambycid larval gallery in Douglas-fir, as well as from the pupal chamber of *Buprestis aurulenta* in Douglas-fir (Burke 1917). Other associations include *Buprestis laeviventris* in *Pinus ponderosa* and *B. confluens* in *Populus tremuloides* (Burke 1917). A single specimen was taken in the Cedar River watershed on Douglas-fir, 17 July 1972. This species is highly variable and includes six former species that were previously considered separate because of both morphological and color differences.

## TORYMIDAE

### *Roptrocerus*

*Roptrocerus xylophagorum* is apparently the only North American representative of the family Torymidae found in dead and dying trees. The species is readily separated from other Douglas-fir chalcidoids by the elongate ovipositor. Published records of *R. xylophagorum* may appear under the names *Pachycerus xylophagorum, P. eccoptogastri,* and *R. eccoptogastri*. All these names were synonymized in Hedqvist's (1963b) study of chalcidoid parasites of Swedish bark beetles. A good illustration appears in the same study.

*Roptrocerus xylophagorum*

*Roptrocerus xylophagorum* was found in the Cedar River watershed throughout the summer, from early June through mid-August. Individuals were seen to enter galleries of *Pseudohylesinus nebulosus*. During the present study *R. xylophagorum* was reared from *Pseudohylesinus nebulosus* in *Pseudotsuga menziesii*, *Pseudohylesinus sericeus* in *Tsuga heterophylla*, *Dendroctonus ponderosae* in *Pinus monticola*, *Pityophthorus confertus* in

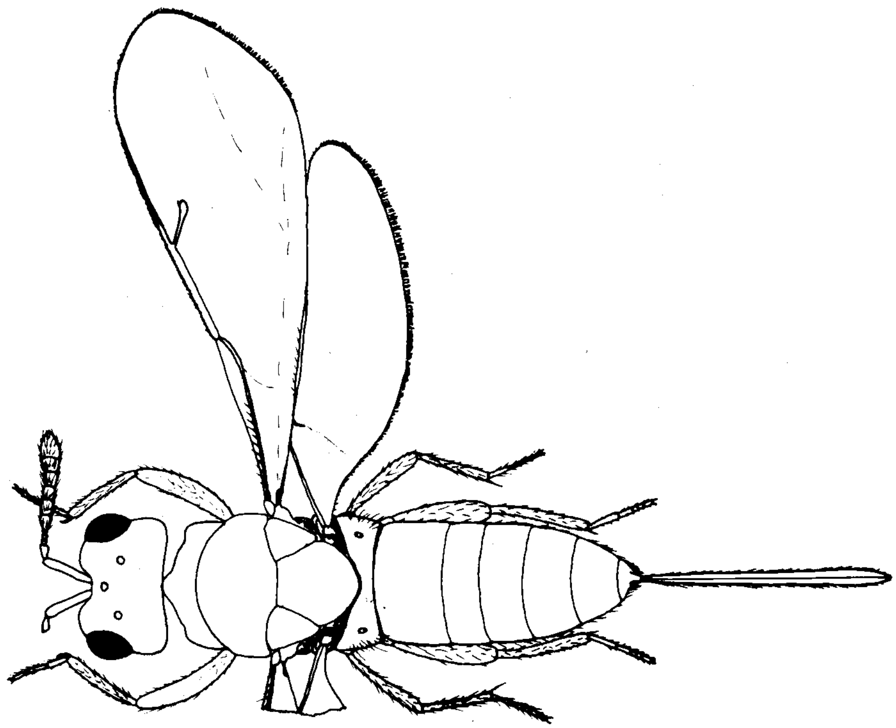


Figure 34. *Roptrocerus xylophagorum.*

*Pinus contorta,* and *Pityophthorus pseudotsugae* in *Abies procera*. Other hosts of *R. xylophagorum* are *Dendroctonus pseudotsugae* (Bedard 1938), *D. frontalis* (Franklin 1969), *Ips grandicollis, I. pini, I. calligraphus* (Berisford et al. 1970), *I. avulsus* (Berisford and Franklin 1972), *I. confusus, Polygraphus rufipennis, Scolytus rugulosus, S. quadrispinosus, Orthotomicus caelatus,* and *Phloeosinus dentatus* (Ashraf and Berryman 1969). The biology of *R. xylophagorum* has been investigated by DeLeon (1934), Reid (1957), Franklin (1969), and Berisford et al. (1970). The female wasp does not use the ovipositor to pierce the bark, but rather enters the galleries through the entrance hole of the parent scolytid (DeLeon 1934). The ovipositor penetrates the frass plug of the egg niche (Reid 1957). The wasp larva is an external feeder (Franklin 1969).

There seemed to be an emergence of *R. xylophagorum* in late July and early August in the Cedar River watershed from material attacked by *Pseudohylesinus nebulosus* in late April. It is not known whether these adults would immediately seek new hosts or whether they would wait until the following year. A few specimens that overwintered as larvae or pupae were reared from material from which *P. nebulosus* has emerged the previous summer. Overgaard (1968) found that in Texas, Louisiana, and Missouri, *R. xylophagorum* has two peaks of emergence, one in April and one in August. These emergence peaks coincide closely with those of the host, *Dendroctonus frontalis*.

Observations were made of courtship and mating behavior of numerous captive specimens reared from Douglas-fir from the Cedar River watershed. The male pursues the female, buzzing his wings. As soon as possible, the male mounts the female and begins rapidly bobbing his head, apparently touching the antennal scapes of the female, while simultaneously buzzing the wings at about 1-sec intervals. A receptive female raises the abdomen slightly, whereupon copulation takes place. After an average of about 10 sec, copulation ends and the female is no longer receptive to any males. Males mate several times, and frequently pursue females that have already mated.

In studies of *Dendroctonus frontalis* (Overgaard 1968, Franklin 1969) and in studies of *Ips* spp. (Berisford and Franklin 1972), *Roptrocerus xylophagorum* was the most important of the parasites studied because of its abundance throughout the season, its responsiveness to changes in host numbers, its independence of bark thickness with regard to oviposition, and its acceptance of a variety of hosts. In the Cedar River watershed, *Pseudohylesinus,* not *Dendroctonus,* is the normal host of *R. xylophagorum.* Competition with a variety of chalcidoids and the braconid *Spathius* is apparently strong, and *R. xylophagorum* is probably most successful in those areas of the bole that are too thin-barked for heavy infestation by *Dendroctonus,* but too thick-barked for *Spathius, Cecidostiba, Heydenia,* and *Eurytoma* to pierce the bark to reach the *Pseudohylesinus* larvae.

## EURYTOMIDAE

Two genera in the family Eurytomidae are associated with dead Douglas-fir. The keys to the members of this family deal only with females. Males can be identified by association with females, and in fact males placed with virgin females of their own species mate very readily.

*Key to the Genera of Eurytomidae (Females) Associated with Dead Douglas-Fir (adapted from Burks 1971)*

1. Both head and pronotum flattened dorsally and lying on the same plane when viewed from the side . . . . . *Ipideurytoma*

1'. Head and pronotum not flattened dorsally . . . . . . . . . *Eurytoma*

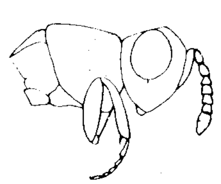


Figure 35. Head and pronotum of *Ipideurytoma* (after Peck et al. 1964).

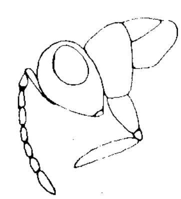


Figure 36. Head and pronotum of *Eurytoma*.

## *Ipideurytoma*

Only one species of *Ipideurytoma* occurs in North America. *Ipideurytoma* has not been observed in the Cedar River watershed.

### *Ipideurytoma polygraphi*

Female *I. polygraphi* enter scolytid galleries to oviposit, and thus lack the long abdomen and ovipositor of members of the genus *Eurytoma*. Known hosts are *Polygraphus rufipennis* (Muesebeck et al. 1951), *Xyloterinus politus* (MacLean and Giese 1967), and *Trypodendron lineatum* (Prebble and Graham 1957). In spite of the *Polygraphus* record, the normal hosts are probably ambrosia beetles.

MacLean and Giese (1967) have published photographs of larvae of *I. polygraphi* in the cradles of *Xyloterinus politus*. The larval eurytomid must have some adaptation that prevents it from being overwhelmed by the fungus that lines the galleries of the ambrosia beetles.

## *Eurytoma*

The species in the huge genus *Eurytoma* are particularly difficult to identify. Thus, in several records of *Eurytoma* attacking scolytids, the species name is not given. There are more than 80 species of *Eurytoma* reported from America north of Mexico. Some species attack subcortical insects, others are parasites or inquilines in various types of galls, still others are phytophagous in buds, stems, or seeds (Bugbee 1967). Other species besides the three in the key below will probably be found associated with recently felled Douglas-fir. They may be identified using Bugbee's key (1967).

*Key to the species of Eurytoma (females) associated with dead Douglas-fir (adapted from Bugbee 1967)*

1. Face covered with shining yellow hair . . . . . . . . . . *pissodis*

1'. Face with whitish hair . . . . . . . . . . . . . . . . . . . . . . . . . 2

2. Front and middle legs, including coxae, reddish yellow . . . . . . . . . . . . . . . . . . . . . . . . . . . *cleri*

2'. Front and middle legs blackish except for yellowish bases and apices of joints; coxae black . . . . . . . . . . *tomici*

### *Eurytoma cleri*

The known hosts of *E. cleri* are a larval clerid, *Ips oregoni, Dendroctonus ponderosae,* and possibly *Pissodes strobi* (Bugbee 1967). Dr. Bugbee has identified as *E. cleri* a pair of female eurytomids that were reared from *Pseudohylesinus*-infested Douglas-fir. One or two specimens of *Pissodes fasciatus* emerged from the same material, suggesting another possible host. *Eurytoma cleri* is larger than *E. tomici* and has a proportionally longer abdomen, hence the ovipositor may be able to reach hosts unavailable to *E. tomici*.

*Eurytoma pissodis*

Bedard (1938) found *E. pissodis* emerging from the cocoons of *Coeloides* (either *C. brunneri* or *C. dendroctoni*) during August. Other hosts are *Pissodes strobi* (Taylor 1929), and *P. terminalis* (R. E. Bugbee, personal communication). The behavioral sequence required to attack *Pissodes* in conifer leaders is so different from that required to attack *Coeloides* found in the bole of a *Dendroctonus*-infested tree, it seems probable that Bedard found a separate race or species. DeLeon (1934) writes of a *Eurytoma* species "close to *pissodis*" that attacks *Coeloides dendroctoni*, but the status of this *Eurytoma* has never been clarified.

Taylor, in his careful study of the biology of *E. pissodis* (1929), reports on the mating and oviposition behavior of this species. The male pursues and quickly mounts the female, then, standing on her thorax, rapidly vibrates his antennae against hers. This behavior may continue for some minutes before the female stops walking about and allows the male to curve his abdomen under and around hers to attempt copulation. The female *E. pissodes* seems normally to make several trial punctures before

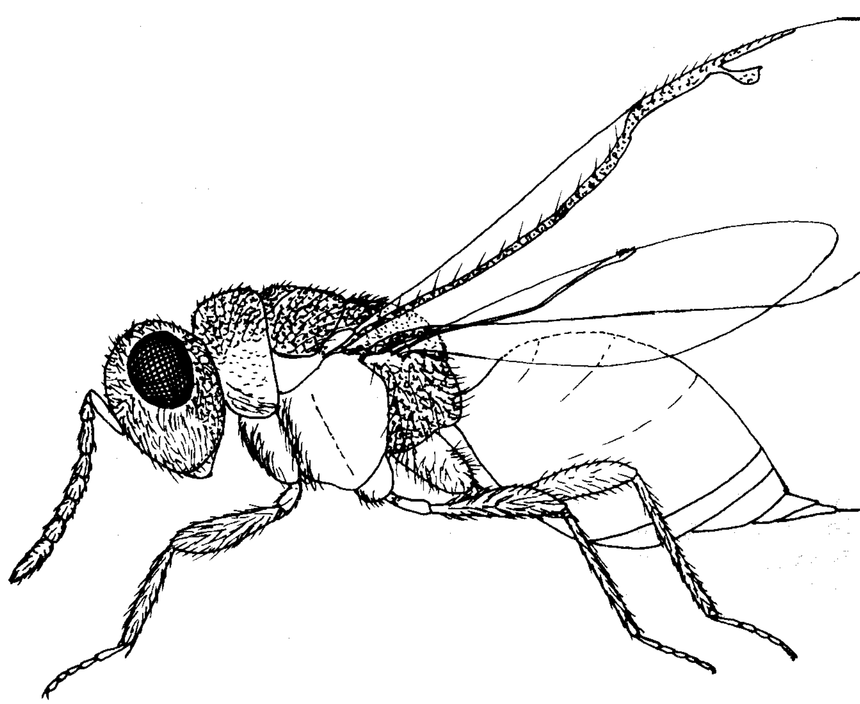


Figure 37. *Eurytoma tomici*, female. (Text, next page.)

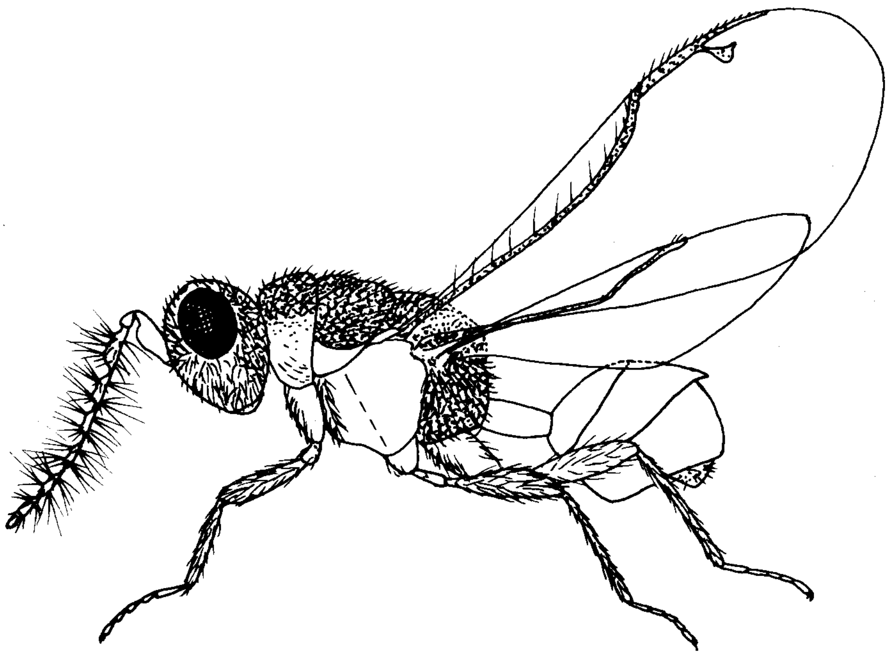


Figure 38. *Eurytoma tomici*, male.

attaching a stalked egg to a *Pissodes* within its pupal cell. There is only one parasite per host and there is normally one generation per year. The presumed *E. pissodis* associated with *Coeloides* must be able to distinguish parasitized *Dendroctonus*, perhaps using the same cues *Coeloides* uses to avoid multiple parasitism.

*Eurytoma tomici*

Host records for *E. tomici* include *Cylindrocopturus eatoni, C. furnissi, C. longulus, Epiblema strenauna, Phloeosinus* sp. (Bugbee 1967), *Dendroctonus brevicomis* (Bushing and Bright 1965), and *D. frontalis* (Overgaard 1968). Dr. Bugbee has identified as *E. tomici* several specimens that were reared from Douglas-fir infested by *Pseudohylesinus nebulosus*. A number of specimens that appear to be *E. tomici* were taken in the Cedar River watershed between the end of June and the second week of August. Nearly all were trapped on one *Pseudohylesinus*-infested tree.

The mating behavior of *E. tomici* differs from that of *E. pissodis* in that the male, while standing on the female, bobs his head rapidly, apparently touching the female's antennae as he does so, in a manner reminiscent of the courtship of *Roptrocerus xylophagorum*. Males were observed attempting copulation without going through this head-bobbing performance, but they were always repulsed until they had gone through the usual ritual.

*Eurytoma tomici* oviposits through the bark, and may parasitize hosts only in thin-barked material as the ovipositor is 1.5-2 mm long. In a single *Pseudohylesinus* gallery, *E. tomici* may be found with *Cecidostiba, Heydenia, Roptrocerus*, and *Spathius*. *Eurytoma tomici* overwinters in the larval or pupal stages.

# EUPELMIDAE

In this study, two genera of eupelmids have been associated with Douglas-fir. These genera had not previously been associated with dead trees in North America.

*Key to the Genera of Eupelmidae Associated with Douglas-Fir*

1. Wingless . . . . . . . . . . . . . . . . . . . . . . . . *Eupelmella*

1'. Winged . . . . . . . . . . . . . . . . . . . . . . . . . *Calosota*

## *Eupelmella*

One species of *Eupelmella* has been associated with Douglas-fir. It is the only wingless chalcidoid known from Douglas-fir.

### *Eupelmella vesicularis*

*Eupelmella vesicularis* is an ectoparasite attacking an extraordinary variety of hosts, including Diptera, Coleoptera, Hymenoptera, Lepidoptera, Homoptera, and Orthoptera (Gahan 1933). Winglessness notwithstanding, this species has achieved a Holarctic range (Krombein and Burks 1967). *Eupelmella vesicularis* is parthenogenetic, thus only females are found (Morris 1938).

One specimen was taken in April as a mature larva in galleries of *Orthotomicus caelatus* in the top of a small Douglas-fir in Montesano, Washington. The larva was in the pupal cell of a scolytid but was surrounded by small pieces of a mature *Cecidostiba,* which it had evidently devoured. This penchant of *E. vesicularis* for hyperparasitism has been carefully documented by Morris (1938). The larva pupated soon after it was brought indoors and the adult emerged in about two weeks.

A full description of *E. vesicularis* and a good illustration of the adult may be found in Gahan's study of the parasites of the hessian fly (1933). Morris (1938) has published beautiful drawings of the egg, larva, and pupa.

## *Calsota*

A single species of *Calosota* has been reared from Douglas-fir.

### *Calosota pseudotsugae*

Dr. B. D. Burks was willing to describe *Calosota pseudotsugae* from a series of specimens reared during the present study from Douglas-fir

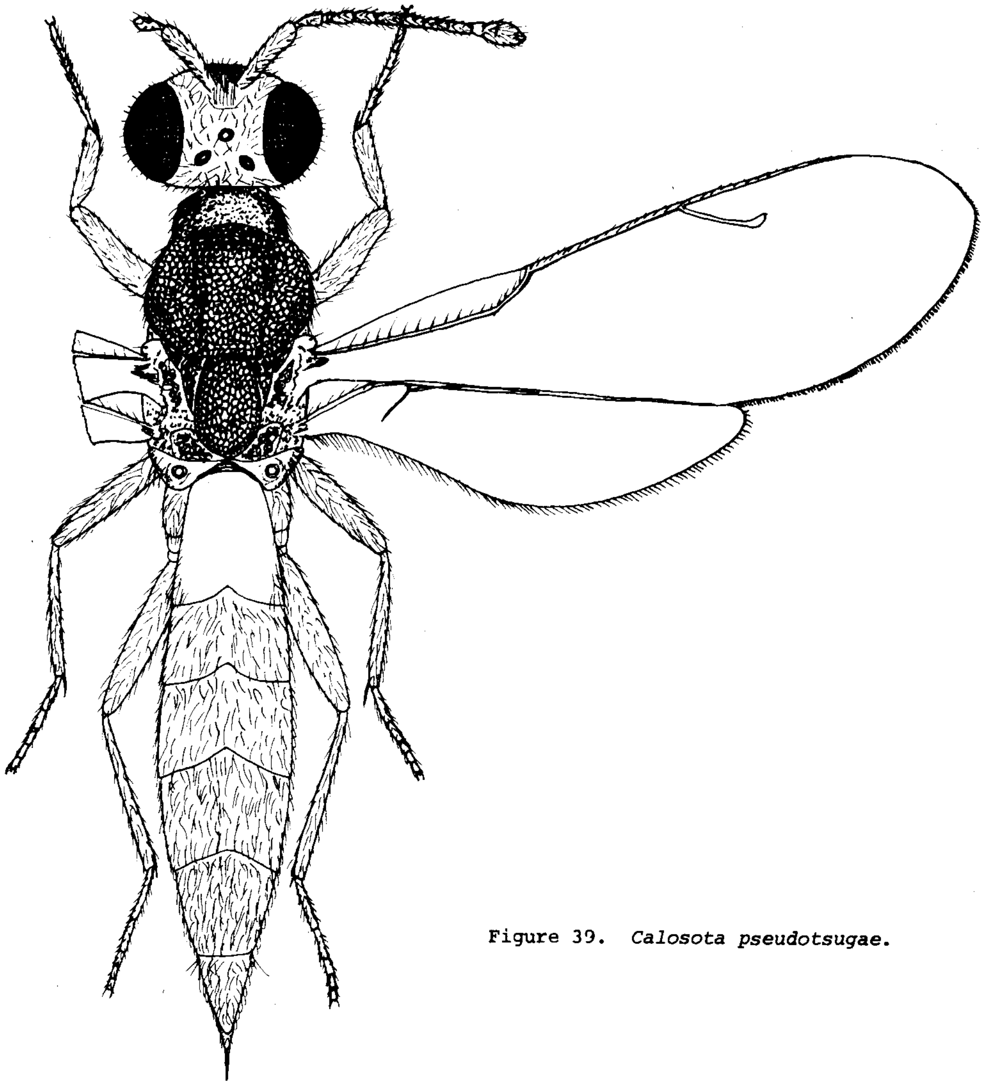


Figure 39. *Calosota pseudotsugae.*

infested with *Pseudohylesinus nebulosus* (Burks 1973). When *C. pseudotsugae* was described the probable host seemed to be *P. nebulosus,* but since that time a series of specimens has been reared from the cocoons of the braconid *Spathius sequoiae* parasitizing *P. nebulosus, Cryphalus pubescens, Lechriops californicus,* and *Alniphagus aspericollis*. *Calosota pseudotsugae* emerges considerably later than its host, and possibly parasitizes *Spathius* larvae, which have already spun their cocoons. The principal benefits that *C. pseudotsugae* gains from hyperparasitism are probably the acquisition of a protective cocoon, easy access through a previously formed oviposition hole, relative freedom from competition, and the opportunity to obtain hosts after scolytids such as *P. nebulosus* have emerged from the tree. The adult *C. pseudotsugae,* when pursued, can leap several centimeters.

## PTEROMALIDAE

Most species of chalcidoid Hymenoptera occurring on dead Douglas-fir are pteromalids. The lack of keys for the identification of North American pteromalids probably has discouraged entomologists from reporting their observations. There is relatively little published biological information about this group. Most genera of Nearctic pteromalids can be identified using Graham's (1969) or Nikol'skaya's (1952) keys to Palaearctic genera.

The majority of pteromalids on dead Douglas-fir are small insects that oviposit through the bark and whose larvae are external parasites of larval Coleoptera. These pteromalids are necessarily restricted to thin-barked areas of the upper boles and branches of dead trees. The genera *Cheiropachus, Heydenia,* and some species of *Cecidostiba* are apparently parasites of small scolytids such as *Pseudohylesinus*. Most records suggest that *Rhopalicus* and *Macromesus* are less specialized parasites, attacking not only a variety of scolytids, but also subcortical weevils, including weevils found in leaders. Two species of the genus *Cecidostiba* attack larger scolytids, such as *Dendroctonus pseudotsugae*.

Two genera of pteromalids, *Perniphora* and *Karpinskiella,* do not oviposit through bark; the females of these genera have short, rounded abdomens, while females of the other genera of pteromalids mentioned above have long, pointed abdomens. *Perniphora* is a parasite of ambrosia beetles, while the remarkable genus *Karpinskiella* attacks adult scolytids.

Omitted from the following keys and discussion of Douglas-fir pteromalids is an apparently undescribed species, probably belonging to the genus *Neocatolaccus* (B. D. Burks, personal communication). This species, which is an unusually large pteromalid, is an external parasite of *Melanophila drummondi,* and was taken in the Cedar River watershed in 1973.

*Key to the Genera of Pteromalidae Associated with Dead Douglas-Fir*

1. Front femur swollen . . . . . . . . . . . . . . . . . . . . . . . . . 2

1'. Front femur normal . . . . . . . . . . . . . . . . . . . . . . . . . 4

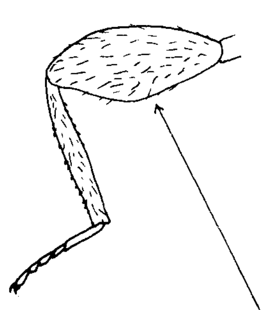


Figure 40. Front femur of *Cheiropachus* (*C. brunneri*).

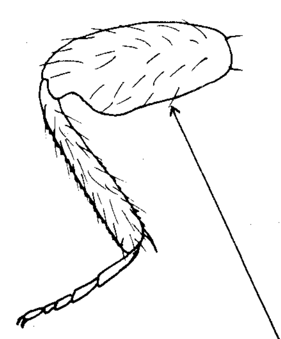


Figure 41. Front femur of *Heydenia* (*H. unica*).

2. Prothorax viewed from side much shorter than wide . . . . . . . . 3

2'. Prothorax viewed from side about as long as wide . . . . . *Heydenia*

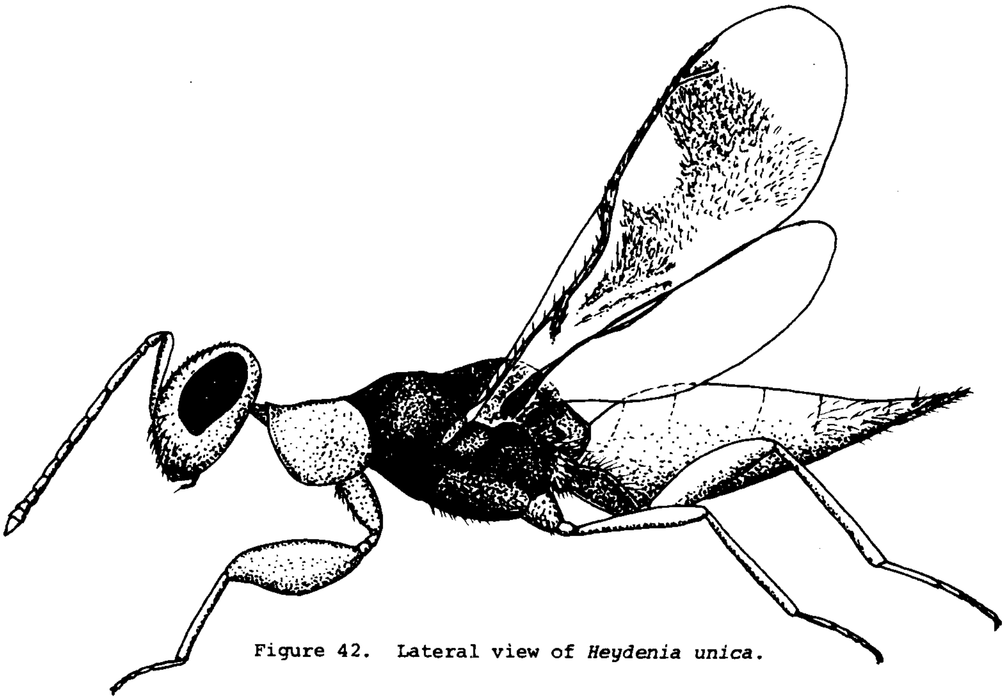


Figure 42. Lateral view of *Heydenia unica*.

3. Abdomen of female pointed at apex; forewing may have dark spots . . . . . . . . . . . . . . . . . . . *Cheiropachus*

3'. Abdomen of female rounded at apex; wings clear . . . . . *Perniphora*

4. Abdomen of female rounded at apex . . . . . . . . . . *Karpinskiella*

4'. Abdomen of female pointed at apex . . . . . . . . . . . . . . . . . 5

5. Stigmal vein (vein extending outward from leading margin of forewing) abruptly enlarged into a terminal knob . . . . . . . . . . . . . . . . . . . *Cecidostiba*

5'. Stigmal vein gradually enlarged into a terminal knob . . . . . . . 6

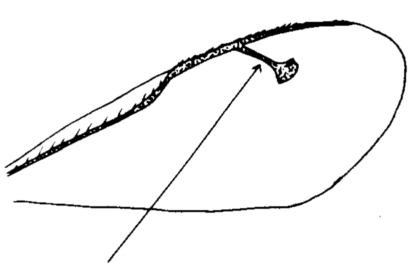


Figure 43. Forewing of *Cecidostiba*, showing stigmal vein.

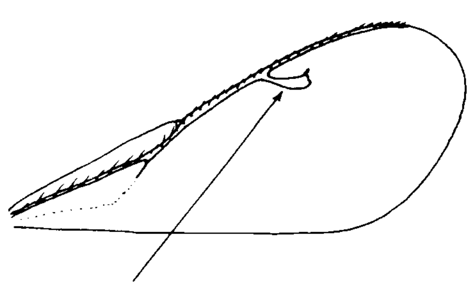


Figure 44. Forewing of *Macromesus americanus*, showing stigmal vein (redrawn from Hedqvist 1960, p. 141).

6. Large dark pigmented spot on wing; stigmal vein not shortened and thickened . . . . . . . . . . . . *Rhopalicus*

6'. No pigmented spot on wing; stigmal vein shortened and thickened . . . . . . . . . . . . . . . . . *Macromesus*

### *Perniphora*

There is only one known Nearctic species of *Perniphora;* this species was described by Miller (1965) from specimens reared from birch in Maine, New Hampshire, and New Brunswick. Bedard (1938) reports an undetermined species of *Perniphora* occurring in Douglas-fir in Washington; Miller (1965) mentions Bedard's specimens, but does not indicate whether these specimens are *P. americana*. In spite of the great geographic distance between Bedard's and Miller's collecting sites, and in spite of the disparity of tree hosts, it is not improbable that there is only one Nearctic species of *Perniphora*. The Palaearctic *P. robusta* has a very extensive geographic range and occurs in both coniferous and broadleaf trees (Hedqvist 1963b). No specimens of this genus were taken in the Cedar River watershed in 1972.

#### *Perniphora americana*

*Perniphora americana* has been associated with *Trypodendron betulae* in *Betula alleghaniensis* and *B. papyrifera*. The specimens were taken in June and August. Bedard reared his *Perniphora* sp. during May from the larval cradles of *Trypodendron lineatum*.

Little is known about the life cycle or behavior of *Perniphora*. The European species is an external parasite, matures in about two weeks, and overwinters as a larva (Graham 1969). The rarity of records of Nearctic specimens implies that *P. americana* has little effect on populations of ambrosia beetles. *Perniphora* and *Ipideurytoma* are the only insects known to prey upon any of the three species of ambrosia beetles that are so abundant in Douglas-fir.

Miller (1965) has published illustrations of portions of *P. americana*, showing diagnostic characters.

### *Macromesus*

There is only one species in the genus *Macromesus* associated with Douglas-fir. It was not taken in the Cedar River watershed in 1972.

#### *Macromesus americanus*

This species parasitizes *Cylindrocopturus longulus, C. eatoni, Pseudohylesinus nebulosus, Scolytus praeceps, S. unispinosus,* and *S. ventralis* (Krombein and Burks 1967). *Macromesus americanus* has been associated with *Pseudotsuga menziesii, Pinus lambertiana, P. ponderosa, P. montana,* and *Abies concolor* (Hedqvist 1960). Aside from its hosts, nothing seems to be known of the biology of *M. americanus,* or of the biology of the Palaearctic *M. amphiretus.* Illustrations of diagnostic characters of *M. americanus* appear in Hedqvist's description of the species (1960).

## *Karpinskiella*

There are two species in the genus *Karpinskiella* that are definitely known to occur on Douglas-fir. One species apparently attacks only a single host: *Dendroctonus pseudotsugae*. A second species of *Karpinskiella* parasitizing a much smaller scolytid host (*Pityophthorus pseudotsugae*) in California is apparently undescribed (Furniss 1968). The second species has not yet been reported from Douglas-fir. A third species, also undescribed, was recently discovered parasitizing *Cryphalus pubescens,* during the present study.

The unusual habit of parasitizing adult scolytids has several special advantages and disadvantages. There is almost no direct competition from other parasites, whereas several species of parasites usually seem to compete for scolytid larvae within a single tree. The scolytid host is exceedingly vulnerable when it is boring into a new host tree, and *Karpinskiella* females can probably parasitize several hosts in quick succession. Unlike parasites of larval scolytids, *Karpinskiella* is ovipositing at the time that scolytids are invading trees, and conceivably uses scolytids' pheromones to locate hosts. The major disadvantages of parasitizing adult scolytids are the shortness of the period in which the host is available, and the relative scarcity of adult scolytids on a tree compared with the abundance of larval scolytids, which appear later. In addition, the host of the larval *Karpinskiella* is not at the end of the long, narrow, frass-packed gallery of a larval scolytid, but in a more or less open parental gallery that is usually the home of a large number of predaceous and scavenging Coleoptera and Diptera. If scolytid pheromones are in fact used by *Karpinskiella* to locate hosts, efficiency in host finding must be paid for by specialization, so that *Karpinskiella* may be restricted to hosts that are perennially abundant.

*Key to the species of Karpinskiella associated with Douglas-fir*

1. Length 2.2 to 3.2 mm; parasitizing *Dendroctonus pseudotsugae* in southern Rocky Mountains . . . . . . . *paratomicobia*

2. Length 1.5 mm; parasitizing *Cryphalus pubescens* in western Washington . . . . . . . . . . . . . . *Karpinskiella* sp.

### *Karpinskiella paratomicobia*

*Karpinskiella paratomicobia* is unlike other pteromalids occurring in Douglas-fir in that it is an internal parasite. It is the only known internal parasite of *Dendroctonus pseudotsugae* (Furniss 1968). The following details of the biology of *K. paratomicobia* are taken from a study by Furniss (1968). *Karpinskiella paratomicobia* oviposits on *D. pseudotsugae* ent beetles are boring into the tree. This hypothesis also implies that in the study of Berisford and Franklin (1972), the indigenous pines happened to produce large amounts of α-pinene, whereas the introduced pines produced little α-pinene. It seems certain that Camors and Payne have discovered an attractant of *H. unica*, but it seems probable that additional attractants are involved.

## *Rhopalicus*

Two, possibly three, species of *Rhopalicus* occur in North America, but only *R. pulchripennis* is found in the range of Douglas-fir.

### *Rhopalicus pulchripennis*

Recorded hosts of *R. pulchripennis* are *Cylindrocopturus eatoni, C. furnissi, Pissodes strobi* (Muesebeck et al. 1951), *P. terminalis, P. approximatus* (Krombein and Burks 1967), *Dendroctonus ponderosae* (DeLeon 1934), *Pseudohylesinus nebulosus, Scolytus unispinosus* (Bushing and Bright 1965), *Ips grandicollis, I. pini, I. avulsus* (Berisford et al. 1970). *Rhopalicus pulchripennis* has been associated with *Pinus contorta* (DeLeon 1934), *P. taeda, P. echinata, P. elliottii* (Berisford and Franklin 1972), *P. strobus* (Taylor 1929), and *Pseudotsuga menziesii* (Bushing and Bright 1965). *Rhopalicus pulchripennis* was not found in the Cedar River watershed in 1972.

*Rhopalicus pulchripennis* oviposits through the bark and the larva is an external feeder (Reid 1957). DeLeon (1934) in Montana found the adults present from the beginning of June to September. In Alberta, Reid (1957) found the adults emerging in August; it is not known whether these adults immediately attack new hosts or whether they hibernate until spring. Taylor (1929) suggests that there may be more than one generation per year when *Pissodes strobi* is the host. Taylor (1929) has published illustrations of the larva of *R. pulchripennis*.

## *Cheiropachus*

All three western species of *Cheiropachus* are reported from Douglas-fir. Each species attacks a variety of insects found on a variety of trees; each species shares hosts with another species. Little can be surmised at present about possible differences in the ecological niches of *Cheiropachus* species.

*Key to the species of Cheiropachus associated with dead Douglas-fir (adapted from Gahan 1938)*

1. Front femur with a shallow notch on underside near apex; female with two dark spots on forewing . . . . . . . . . . . . 2

1'. Front femur without notch on underside near apex; female without two dark spots on forewing . . . . . . . *arizonensis*

2. Posterior section of thorax between spiricles with definite reticulate sculpture; legs of male brownish black . . . . . . . . . . . . . . . . . . . . . . . . . . *brunneri*

2'. Posterior section of thorax between spiricles without definite reticulate sculpture; legs of male brownish yellow . . . . . . . . . . . . . . . . . . . . . . . *quadrum*

*Cheiropachus arizonensis*

Known hosts of *Cheiropachus arizonensis* are *Phloeosinus* sp. (Gahan 1938), and *Pseudohylesinus nebulosus* (Bushing and Bright 1965). There are undoubtedly unreported hosts, as *C. arizonensis* has been reared from *Cercocarpus ledifolias*, as well as *Thuja plicata*, *Juniperus occidentalis* (Gahan 1938), and *Pseudotsuga menziesii* (Bushing and Bright 1965). This species has not been reported north of Oregon (Muesebeck et al. 1951).

*Cheiropachus brunneri*

Hosts of *C. brunneri* are *Phloeosinus punctatus*, *Pseudohylesinus nebulosus*, *Scolytus unispinosus*, *S. ventralis* (Bushing and Bright 1965), and *Pissodes* sp. (Muesebeck et al. 1951). *Cheiropachus brunneri* has been associated with *Pseudotsuga menziesii*, *Abies concolor*, *Libocedrus decurrens*, and *Chamaecyparis lawsoniana* (Bushing and Bright 1965). Adults were taken on Douglas-fir in the Cedar River watershed from early June to early August of 1972. During the present study *C. brunneri* was found most abundantly in galleries of *Scolytus unispinosus*; exposed or partially exposed trees are preferred.

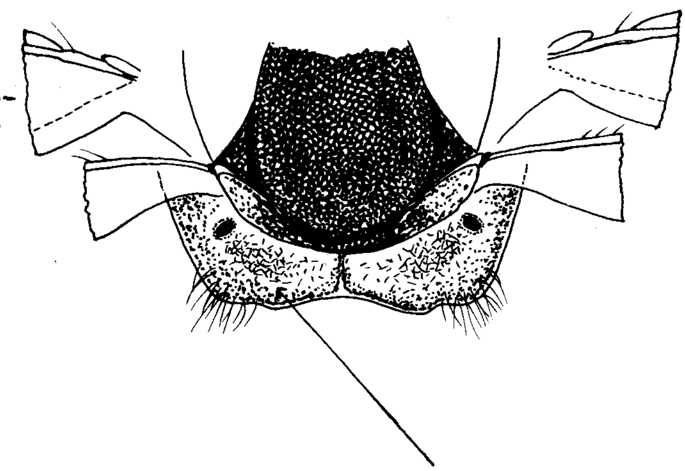


Figure 46. Posterior area of thorax of *Cheiropachus brunneri*, showing reticulate area between spiricles.

*Cheiropachus quadrum*

The Holarctic *Cheiropachus quadrum* has long been known as *C. colon*; the name was changed by Graham in 1969.

North American hosts of *C. quadrum* are *Scolytus ventralis*, *S. rugulosus*, *S. multistriatus* (Ashraf and Berryman 1969), *Phloeosinus canadensis*, and *Dendroctonus pseudotsugae* (Bushing 1965). This species has been associated with *Abies grandis* (Ashraf and Berryman 1969) and *Pseudotsuga menziesii* (Bushing 1965).

adults of either sex before the beetles have begun constructing their galleries. Since emerging *Dendroctonus* leave the tree from which they emerge almost immediately, Furniss suggests that the parasite seeks out freshly attacked trees where it finds its host. The parasite egg, inserted into the abdomen of the host, develops into a larva whose development in the female beetle causes a great reduction in the egg-laying potential of the host. The parasite overwinters under the Douglas-fir bark and emerges a few days before the peak of the flight season of *D. pseudotsugae*. Dead adults of *D. pseudotsugae* with round emergence holes cut in their hollow exoskeletons by the exiting parasites remain under the bark of the host tree.

Furniss (1968) postulates that *K. paratomicobia* may actually be beneficial to the host because a reduction of the number of host offspring causes a reduction in lethal competition between host larvae. Furniss notes that *K. paratomicobia* is known from only a few areas in the mountains of Utah and Arizona; these areas seem to suffer particularly intense infestations of *D. pseudotsugae*. It seems justified to conclude that in a heavily infested tree, *K. paratomicobia*, by reducing competition at the beginning of the *Dendroctonus* attack, may maximize the number of beetles that eventually emerge from this tree. This is in contrast to other hymenopteran parasites of scolytids, which tend to attack mature larvae after competition already has taken its toll, thus minimizing the number of emerging beetles. These other parasites, by reducing the number of beetles attacking new trees, seem to reduce the amount of competition between offspring of these beetles.

*Karpinskiella paratomicobia* has a pteromalid hyperparasite, *Amblymerus confusus* (Furniss 1968), which will not be included in this discussion of Douglas-fir pteromalids.

Furniss (1968) has published excellent drawings of the larva, pupa, and adult of *K. paratomicobia*, as well as a photograph of a female ovipositing on a *D. pseudotsugae*.

*Karpinskiella* sp.

During the present study a minute species of *Karpinskiella* was found parasitizing the adults of the small scolytid *Cryphalus pubescens*. A series of specimens of this undescribed *Karpinskiella* was reared from Douglas-fir twigs collected in three localities in western Washington. Most adult *C. pubescens* emerge a week or more earlier than their parasites, thus it appears that the female *Karpinskiella* sp. must search for Douglas-fir twigs recently attacked by *C. pubescens*.

### *Heydenia*

There is only one Nearctic species, *H. unica*, belonging to this genus (Muesebeck et al. 1951). DeLeon (1934) discusses the habits of *Heydenia hubbardii*; this species is actually a eupelmid, *Eusandalum hubbardii*, which has not been reported from Douglas-fir.

*Heydenia unica*

*Heydenia unica* may be recognized instantly by the swollen front femora and the elongated prothorax, a combination of characteristics that give this species a mantidlike appearance. It is apparently not known whether these peculiarities of the adult wasp are related to raptorial habits or to species recognition.

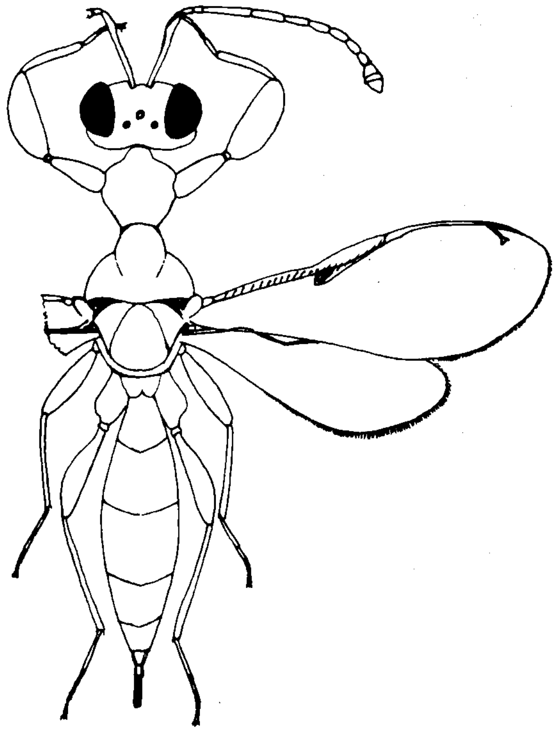


Figure 45. Female of *Heydenia unica*.

Hosts of *H. unica* include *Ips grandicollis, I. avulsus* (Berisford and Franklin 1972), *Dendroctonus frontalis* (Franklin 1969), *Pseudohylesinus nebulosus* (Bushing and Bright 1965), and *Scolytus rugulosus* (Muesebeck et al. 1951). During the present study, *H. unica* was reared in the laboratory from galleries of *Pseudohylesinus nebulosus* and occasionally *Scolytus unispinosus*. In western Washington *H. unica* is usually found in shaded trees.

*Heydenia unica* has been associated with *Pinus taeda, P. echinata, P. palustris, P. elliottii* (Berisford and Franklin 1972), and *Pseudotsuga menziesii*. Berisford and Franklin (1972), in an interesting study of the influence of tree hosts on parasites of *Ips* in Georgia, have shown that of the four *Pinus* species listed above *H. unica* prefers *P. taeda* and *P. echinata* regardless of the number or species of scolytid hosts present. It is perhaps significant that the two preferred pines are indigenous to the experimental area, while the other two pines were introduced. It seems logical that local populations of parasites that use the odors of infested trees to locate their hosts are most sensitive to odors characteristic of local tree species.

The host selection behavior of *H. unica* has been further elucidated in a study by Camors and Payne (1972). This study showed that *H. unica,* given a choice of trees containing various developmental stages of *Dendroctonus frontalis,* greatly preferred those trees that contained larvae, particularly third instar larvae. Bolts that contained only eggs and adults of the host were not attractive. Additional experiments showed that $\alpha$-pinene was attractive to *H. unica*. Pheromones of scolytid hosts were not attractive to *H. unica,* nor were combinations of $\alpha$-pinene and pheromones more attractive than $\alpha$-pinene alone.

From these data, Camors and Payne (1972) suggest that *H. unica* locates its host by responding to the $\alpha$-pinene that is released from the *Dendroctonus*-infested tree at the time when larvae are present. This hypothesis implies that production of $\alpha$-pinene is minimal at the time when the par-

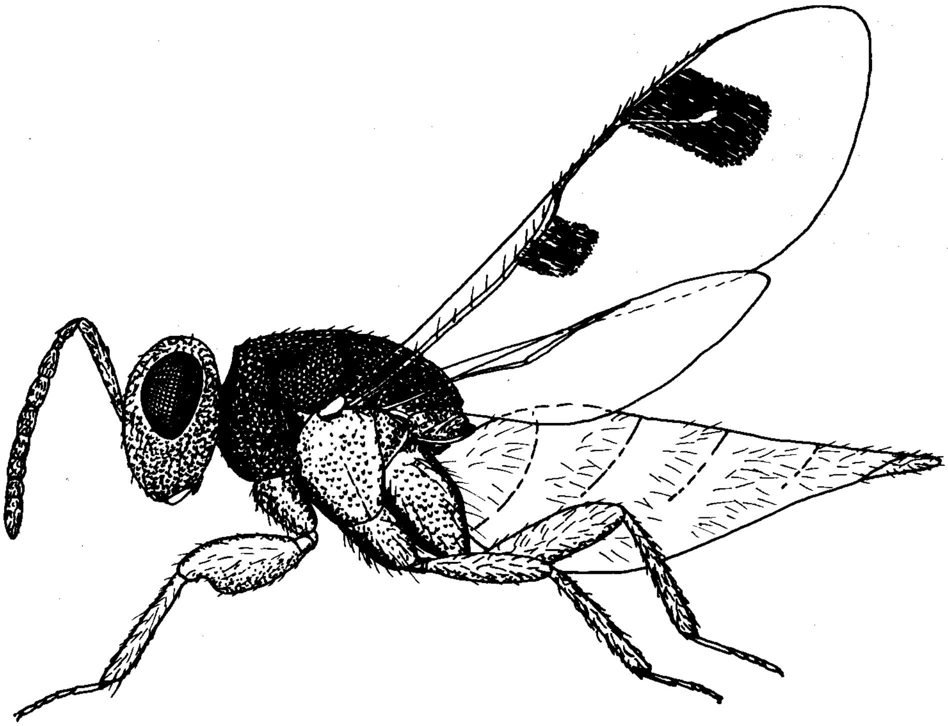


Figure 47. *Cheiropachus brunneri*.

*Cecidostiba*

North American species of the genus *Cecidostiba* eventually will be removed to a different genus. Crawford (1914) states that the Nearctic species placed in the genus *Cecidostiba* probably do not belong to the same genus as European species of *Cecidostiba*. Graham (1969) considers that North American species of *Cecidostiba* should be placed in or near the genus *Dinotiscus*. Palaearctic species of *Dinotiscus* are very similar to Nearctic species of *Cecidostiba*, not only in appearance, but also in hosts and habits (Hedqvist 1963b).

The four species of *Cecidostiba* found on Douglas-fir divide into two groups. *Cecidostiba dendroctoni* and *C. burkei* are large species with particularly elongated abdomens. They attack the larger scolytids, particularly *Dendroctonus*. *Cecidostiba thomsoni* and *C. acuta* are smaller species and tend to attack smaller hosts, such as *Pseudohylesinus* and *Scolytus*. *Cecidostiba thomsoni* and *C. acuta* may be found together on a single tree. Observations of three species of *Cecidostiba* in the Cedar River watershed indicate that the larval parasite devours a single host larva. Berisford et al. (1970) suggest that the larva of one species of *Cecidostiba, C. polygraphi*, moves about in the scolytid gallery and may attack more than one host larva.

*Key to the species of Cecidostiba associated with dead Douglas-fir (adapted from Crawford 1913)*

1. Side of mesothorax with a shining smooth triangular area below base of forewing . . . . . . . . . . . . . . . . . . . . 3

1'. Side of mesothorax with a nonshining sculptured triangular area below base of forewing . . . . . . . . . . . . . . . 2

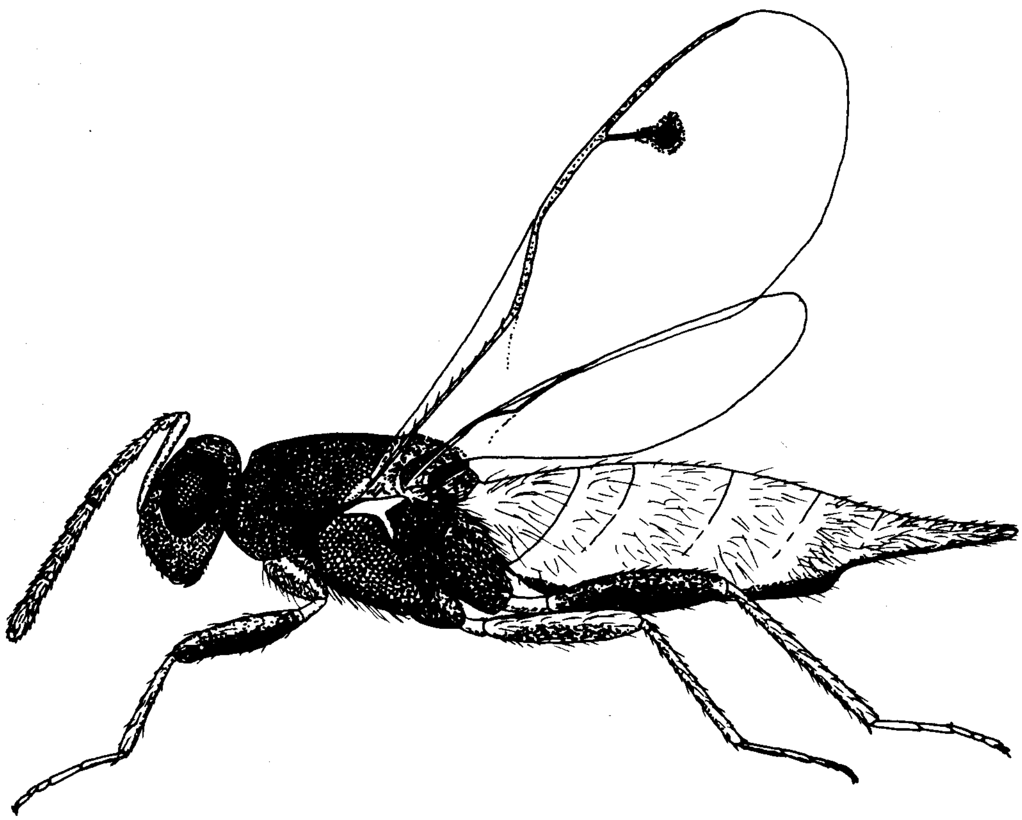


Figure 48. Lateral view of *Cecidostiba thomsoni*, showing shining smooth triangular area below base of forewing.

2. Marginal and postmarginal veins almost equal in length . . . . . . . . . . . . . . . . . . . . . . . . . *dendroctoni*

2'. Marginal vein much shorter than postmarginal vein . . . . . . . . . . . . . . . . . . . . . . . . . . . . *burkei*

3. Stigma of forewing surrounded by a pigmented area; body usually dark blue-green; fore and middle femora usually blue . . . . . . . . . . . . . . . . . . . . . *thomsoni*

3'. Stigma of forewing not surrounded by a pigmented area; body usually yellow-green; fore and middle femora usually yellowish . . . . . . . . . . . . . . . . . . . . . *acuta*

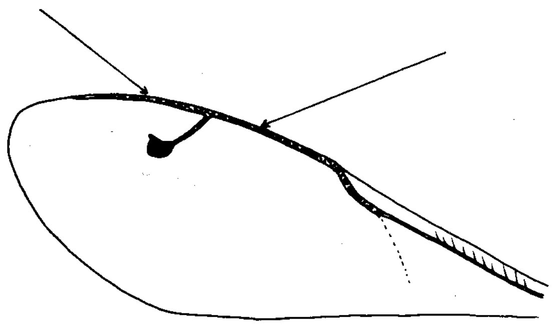


Figure 49. Wing of *Cecidostiba dendroctoni*, indicating marginal vein (arrow on right) and postmarginal vein (arrow on left).

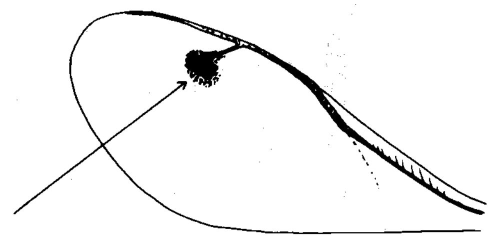


Figure 50. Wing of *Cecidostiba thomsoni*, showing pigmented area surrounding stigma.

*Cecidostiba dendroctoni*

Hosts of *C. dendroctoni* include *Dendroctonus pseudotsugae* (Bedard 1938), *D. ponderosae* (DeLeon 1934), *D. frontalis* (Franklin 1969), *Ips grandicollis, Polygraphus rufipennis,* and *Cylindrocopturus furnissi* (Muesebeck et al. 1951). In the Cedar River watershed, a specimen of *C. dendroctoni* was seen ovipositing into a gallery of *Pseudohylesinus nebulosus,* but neither scolytid larva nor parasite egg was visible when the bark was removed. *Cecidostiba dendroctoni* has been associated with *Pseudotsuga menziesii* (Bedard 1938), *Pinus contorta, P. monticola* (DeLeon 1934), *P. taeda, P. echinata,* and *P. palustris* (Berisford and Franklin 1972).

*Cecidostiba dendroctoni* is presumably restricted to relatively thin-barked portions of Douglas-fir trees. In such portions of the tree, *C. dendroctoni* apparently competes with *Coeloides brunneri*. In this competition, *Cecidostiba dendroctoni*, being considerably smaller than a normal *Coeloides brunneri,* would probably benefit from the ability to utilize smaller host larvae than those required by *Coeloides brunneri*.

*Cecidostiba dendroctoni* was taken in the Cedar River watershed in early July and first half of August of 1972. DeLeon (1934) found *C. dendroctoni* adults active through the summer, beginning in May.

*Cecidostiba thomsoni*

*Cecidostiba thomsoni* is known to parasitize *Pissodes* sp. (Crawford 1913), *Scolytus ventralis* (Ashraf and Berryman 1969), *S. unispinosus,* and, occasionally, *Pseudohylesinus nebulosus*. *Cecidostiba thomsoni* is associated with *Abies grandis* (Ashraf and Berryman 1969) and *Pseudotsuga menziesii*. In western Washington *C. thomsoni* is usually found on exposed or semiexposed trees, and only rarely attacks scolytids such as *P. nebulosus* living in shaded trees. *Cecidostiba thomsoni* overwinters as a mature larva.

*Cecidostiba acuta*

*Cecidostiba acuta* has been reported parasitizing *Dendroctonus ponderosae* (DeLeon 1934), *Polygraphus rufipennis* (Crawford 1913), *Pityophthorus*

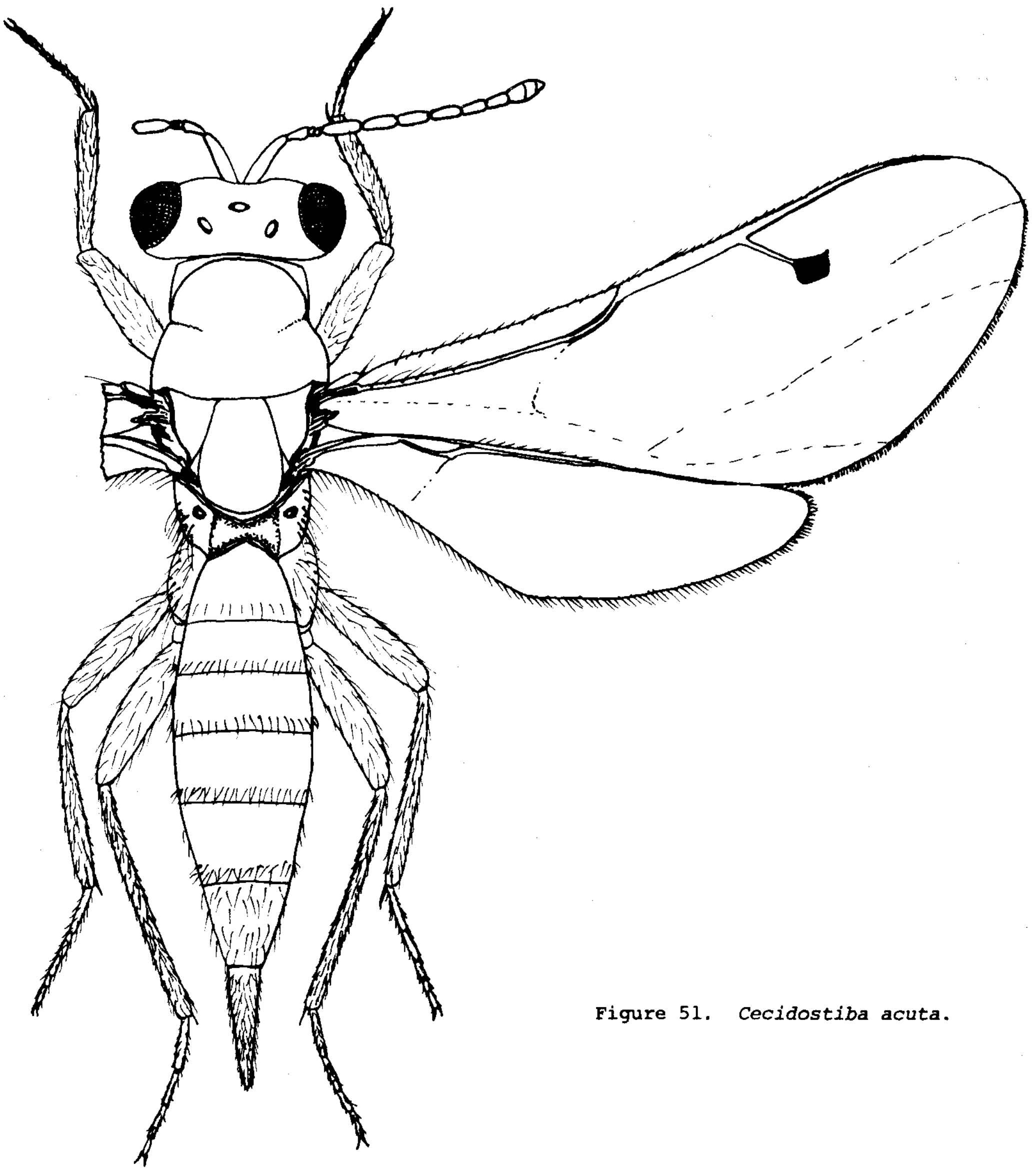


Figure 51. *Cecidostiba acuta.*

*carmeli, Pseudohylesinus nebulosus*, and *Scolytus ventralis* (Bushing and Bright 1965). During the present study *C. acuta* was reared from *Pseudohylesinus sericeus, P. nebulosus, P. granulatus, P. sitchensis, P. tsugae, Hylurgops rugipennis, Scolytus unispinosus, Phloeosinus punctatus, Cryphalus pubescens, Pityophthorus nitidulus*, and *Alniphagus aspericollis*. *Cecidostiba acuta* is associated with *Pinus monticola* (DeLeon 1934), *P. radiata, P. ponderosa, Pseudotsuga menziesii, Abies concolor* (Bushing and Bright 1965), *A. grandis* (Ashcraft and Berryman 1964), *Tsuga heterophylla, Picea sitchensis, Thuja plicata*, and *Alnus rubra*.

In western Washington *C. acuta* is the most common pteromalid parasite of scolytids in shaded tops and branches. It is unusual to find *C. acuta* in exposed material, thus *Scolytus unispinosus* is not a normal host. *Pityophthorus nitidulus* and *Cryphalus pubescens* are regularly attacked by *C. acuta*, but these small scolytids almost never produce female *C.*

*acuta;* it is probable that only male eggs are laid on small hosts. It is surprising to find *C. acuta* parasitizing *Alniphagus aspericollis* in a deciduous tree, but *Alniphagus* seems to be a normal host. *Cecidostiba acuta* frequently produces two generations per year in western Washington; the second generation overwinters as mature larvae.

*Cecidostiba burkei*

Hosts of *C. burkei* are *Dendroctonus brevicomis* (Muesebeck et al. 1951) and *D. pseudotsugae* (Kline and Rudkinsky 1964). *Cecidostiba burkei* has been reported from *Pseudotsuga menziesii* (Kline and Rudinsky 1964), *Picea sitchensis* (Crawford 1913), and *Pinus ponderosa* (Bushing and Bright 1965).

## ICHNEUMONIDAE

The ichneumonids associated with dead Douglas-fir tend to parasitize large subcortical and woodboring insects. These hosts are usually present in relatively small numbers and frequently require a period of years to attain maturity; hence their ichneumonid parasites are not readily reared in the laboratory. For this reason, there is little published information concerning the host preferences and behavior of ichneumonids associated with dead Douglas-fir. Most of this information has been summarized in a monograph on the ichneumonids by Townes and Townes (1960). This work also includes excellent keys and illustrations.

Ichneumonids associated with dead Douglas-fir attack their hosts by piercing the bark (or bark and wood) with a long ovipositor, paralyzing the host larva, and laying an egg on or near the host. The scanty information available about the host preferences of these ichneumonids suggests the following generalizations:

> *Megarhyssa* and *Rhyssa* attack siricids and beetles deep in the sapwood.
>
> *Helcostizus* attacks various beetles in branches.
>
> *Apistephialtes* attacks subcortical clerids.
>
> *Aplomerus, Odontocolon,* and *Coleocentrus* attack unknown hosts in the bole; it is not known whether these hosts are in the sapwood or subcortical region.
>
> *Xorides, Neoxorides,* and *Dolichomitus* probably attack only subcortical beetles; one species of *Dolichomitus* apparently specializes in parasitizing the genus *Pissodes;* the other species in these genera attack several host genera, or the host data are too scanty for conclusions.

The degree of specialization the wood-dwelling Ichneumonidae may obtain is demonstrated in Heatwole and Davis' study (1965) of *Megarhyssa* species. Three species in this genus all attack the same host in the same tree at the same time, but a single species can attack hosts only at a particular depth in the log because there are differences in the respective lengths of the ovipositors of three *Megarhyssa* species. While the ovipositors of the various species of ichneumonids attacking Douglas-fir insects vary in length from species to species, it is necessary to secure a good series of each species before describing ecological niches. Within a species, ovipositor length of individuals varies with size, which itself may vary radically depending on the amount of food available to the developing wasp larva.

Since the ichneumonids associated with Douglas-fir usually parasitize hosts that have been developing in the tree for at least a year, they presumably would be little attracted to recently cut trees. Perhaps for this reason few ichneumonids were taken in our study in 1972, the same year that the trees were cut. Many ichneumonids were taken ovipositing on these same trees in the summer of 1973.

*Key to the Ichneumonidae (Females) Associated with Dead Douglas-Fir*

1. Ovipositor much shorter than abdomen; front tibia swollen and cylindrical . . . . . . . . . . . . . *Helcostizus*

1'. Ovipositor longer than abdomen; front tibia not swollen and cylindrical . . . . . . . . . . . . . . . . . . . 2

2. Hind femur with a large tooth on underside . . . . . . . *Odontocolon*

2'. Hind femur without tooth on underside . . . . . . . . . . . . . . 3

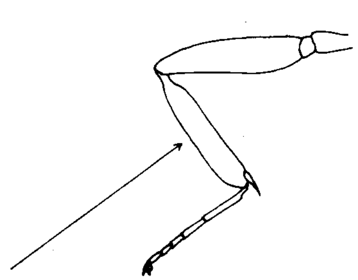


Figure 52. Foreleg of *Helcostizus*, showing swollen tibia.

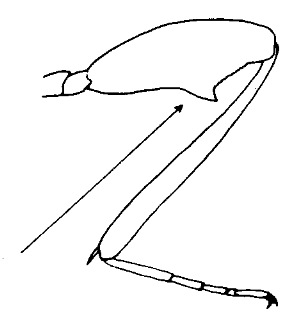


Figure 53. Hind leg of *Odontocolon*, showing tooth on femur.

3. Apical third of forewing with a small triangular or pentagonal cell . . . . . . . . . . . . . . . . . . . . . . . 4

3'. Apical third of forewing without small triangular or pentagonal cell . . . . . . . . . . . . . . . . . . . . . . . 8

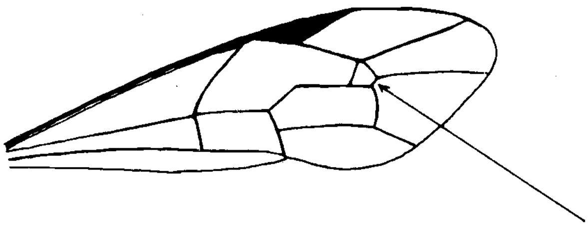


Figure 54. Forewing of ichneumonid (*Dolichomitus*), showing small triangular cell in apical third.

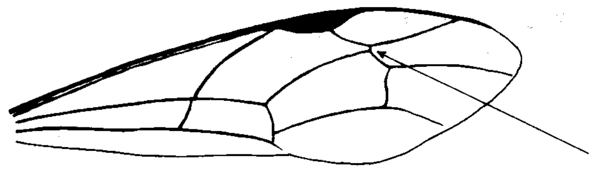


Figure 55. Forewing of ichneumonid (*Aplomerus*), lacking small cell in apical third.

4. Mesothorax with many conspicuous transverse ridges dorsally; yellow spots present on abdominal tergites . . . . . . . . . . . . . . . . . . . . . . . . 5

4'. Mesothorax without dorsal transverse ridges; no yellow spots on abdominal tergites . . . . . . . . . . . . . . 6

5. Background color of abdomen reddish brown to blackish brown . . . . . . . . . . . . . . . . . . . . . *Megarhyssa*

5'. Background color of abdomen black . . . . . . . . . . . . . *Rhyssa*

6. All tarsal claws with conspicuous broad basal lobes . . . . . . . . . . . . . . . . . . . . . . . . . . . . . 7

6'. Tarsal claws without broad basal lobes . . . . . . . . *Coleocentrus*

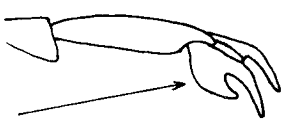


Figure 56. Tarsal claws of an ichneumonid (*Dolichomitus*) showing basal lobes.

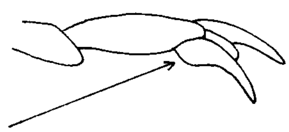


Figure 57. Tarsal claws of *Coleocentrus* without basal lobes.

7. Front coxae mostly white; first segment of abdomen shorter than second segment . . . . . . . . *Apistephialtes*

7'. Front coxae orange colored; first segment of abdomen as long as second segment . . . . . . . . . . *Dolichomitus*

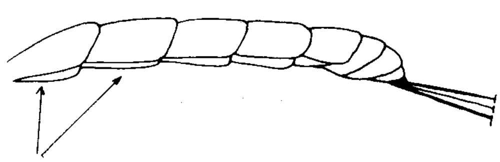


Figure 58. Abdomen of *Dolichomitus*, showing first segment of abdomen as long as second segment.

8. Body somewhat flattened; hind femur short and swollen; mandibles with two teeth . . . . . . . . . . *Aplomerus*

8'. Body not flattened; hind femur not swollen; mandibles chisel shaped, without teeth . . . . . . . . . . . . . . 9

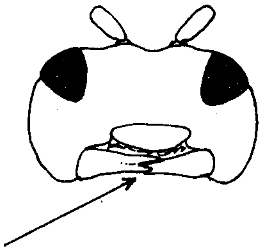


Figure 59. Head of *Aplomerus*, showing toothed mandibles.

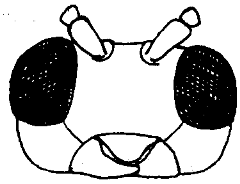


Figure 60. Head of *Xorides*, showing simple mandibles.

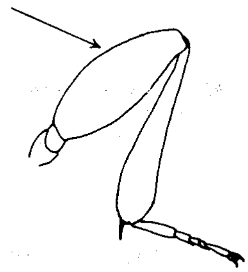


Figure 61. Hind femur of *Aplomerus*.

9. Small ridge present at anterior end of large sclerite on side of mesothorax . . . . . . . . . . . . . . . *Xorides*

9'. No ridge at anterior end of large sclerite on side of mesothorax . . . . . . . . . . . . . . . . . . . . *Neoxorides*

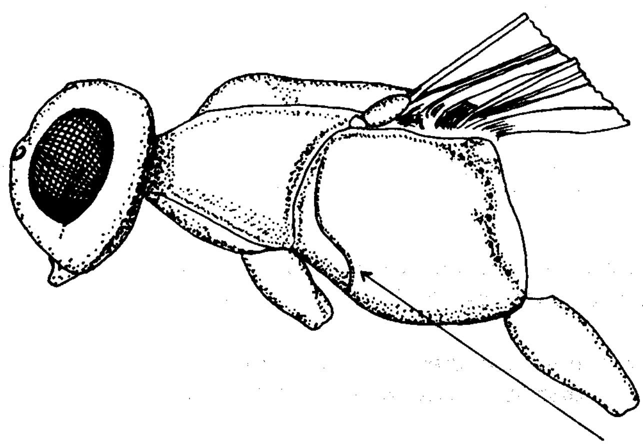


Figure 62. Side of mesothorax of *Xorides* indicating diagnostic ridge.

## *Aplomerus*

There are four species of *Aplomerus* found within the geographic range of Douglas-fir, but only one species has been associated with Douglas-fir. Very little is known about the tree hosts of the other species of this genus (Townes and Townes 1960). The flattened appearance of *Aplomerus* species is undoubtedly related to their habit of parasitizing buprestids, which make low, wide galleries.

### *Aplomerus robustus*

*Aplomerus robustus* may be recognized by the fine striae that completely cover the third and fourth abdominal tergites. These striae are absent or cover only part of the tergites in the other species of *Aplomerus* (Townes and Townes 1960).

This species has been associated with *Pinus radiata* and is found in Douglas-fir stands (Townes and Townes 1960). One specimen of *A. robustus* was taken on 9 August 1972 on a trap on a recently cut Douglas-fir in the Cedar River watershed. The only known insect host is a buprestid, species unknown (Townes and Townes 1960).

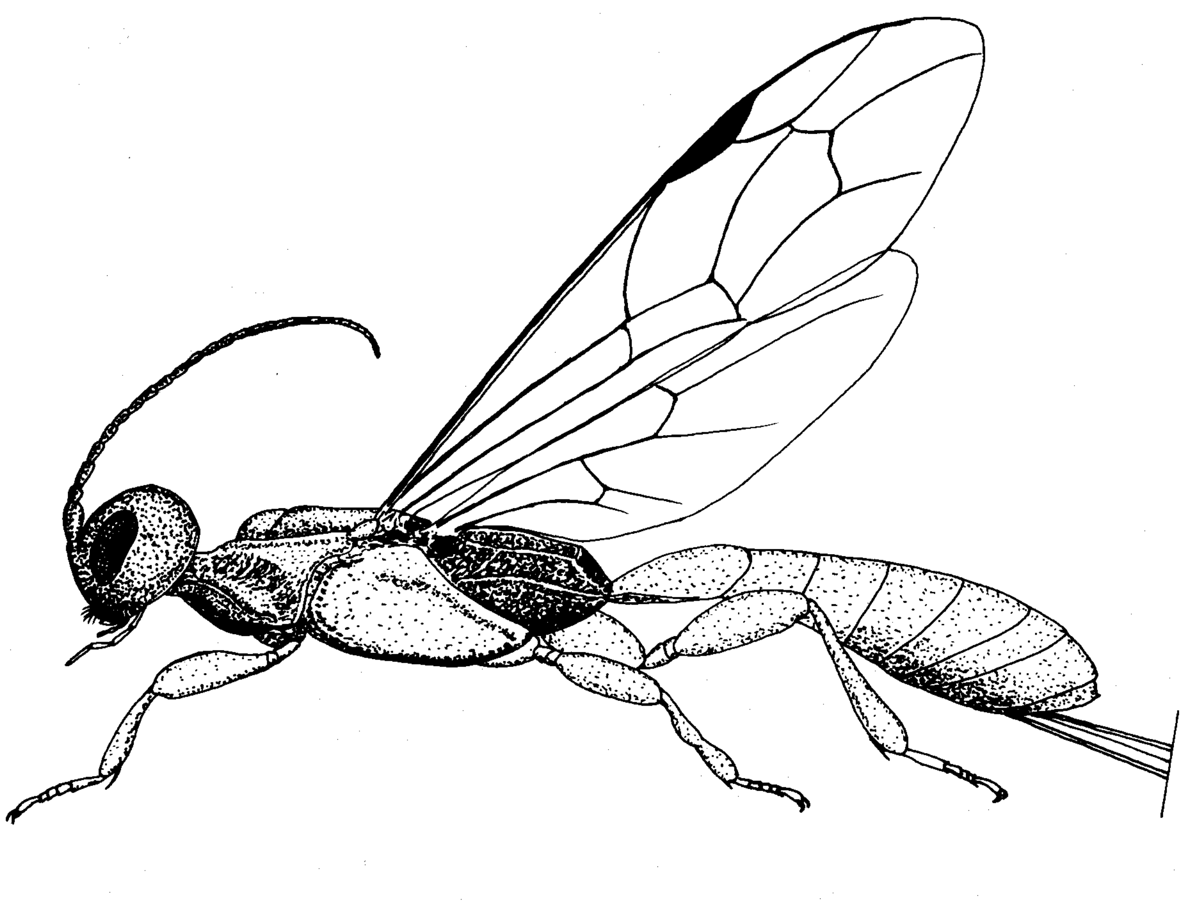


Figure 63. *Aplomerus robustus*.

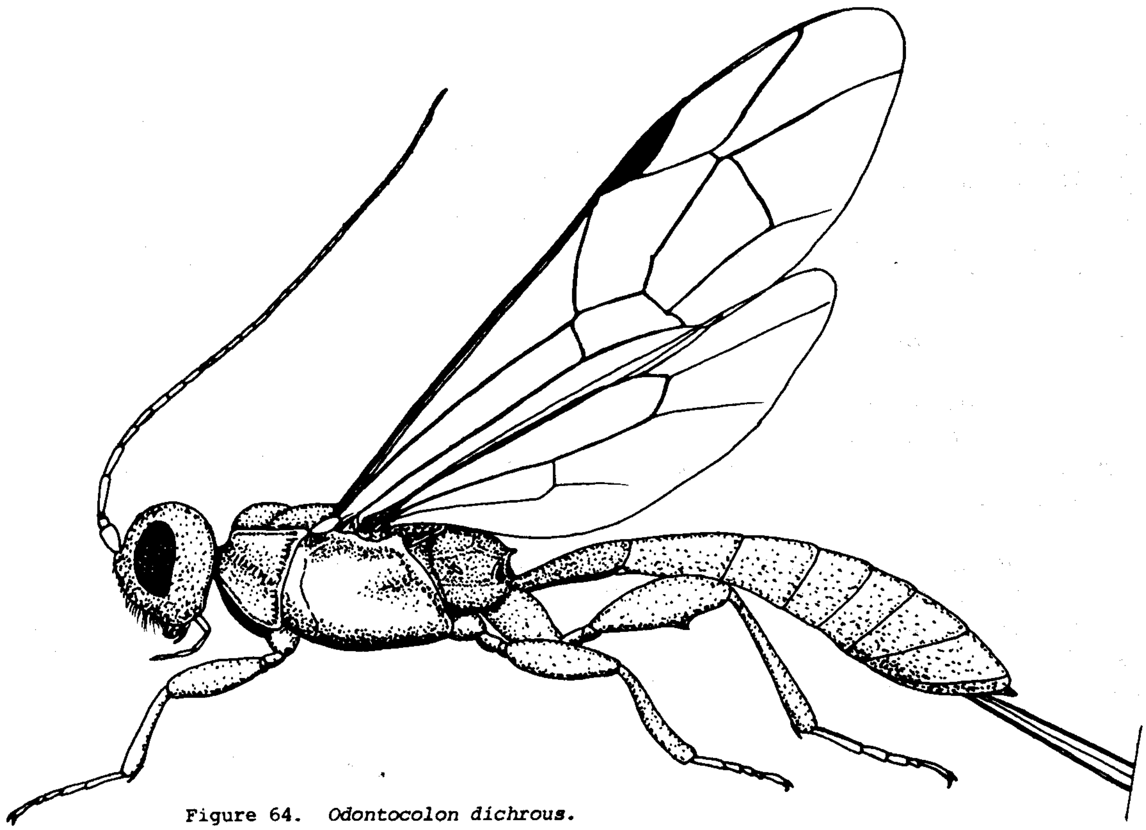


Figure 64. *Odontocolon dichrous.*

## *Odontocolon*

There are numerous western species of *Odontocolon;* most of these species have not been associated with any tree species or insect host. A single species is reported from Douglas-fir; however, it should not be assumed that this is the only species occurring on Douglas-fir. Specimens of *Odontocolon* may be identified using the key in Townes and Townes' monograph on the ichneumonids (1960).

### *Odontocolon dichrous*

Specimens of *O. dichrous* were taken on traps on cut Douglas-fir in the Cedar River watershed on 15 June, 22 July, and 8 August 1972. This wasp has not previously been associated with any tree; no insect hosts have been reported (Townes and Townes 1960). *Odontocolon dichrous* has several races. In specimens from high altitudes and from California the abdomen is red, while in specimens from low altitudes in the Vancouver area the abdomen is black (Townes and Townes 1960). The specimens from the Cedar River watershed are of the latter race.

Bedard (1938) reports *Odontomerus tibialis* ovipositing in larvae of *Tetropium velutinum* in Douglas-fir. The name *Odontomerus tibialis* has since been changed to *Odontocolon canadense,* which is found only in eastern North America (Townes and Townes 1960). It seems probable that Bedard's *O. canadense* is actually the very closely related *O. punctatum,* or the similar *O. dichrous.*

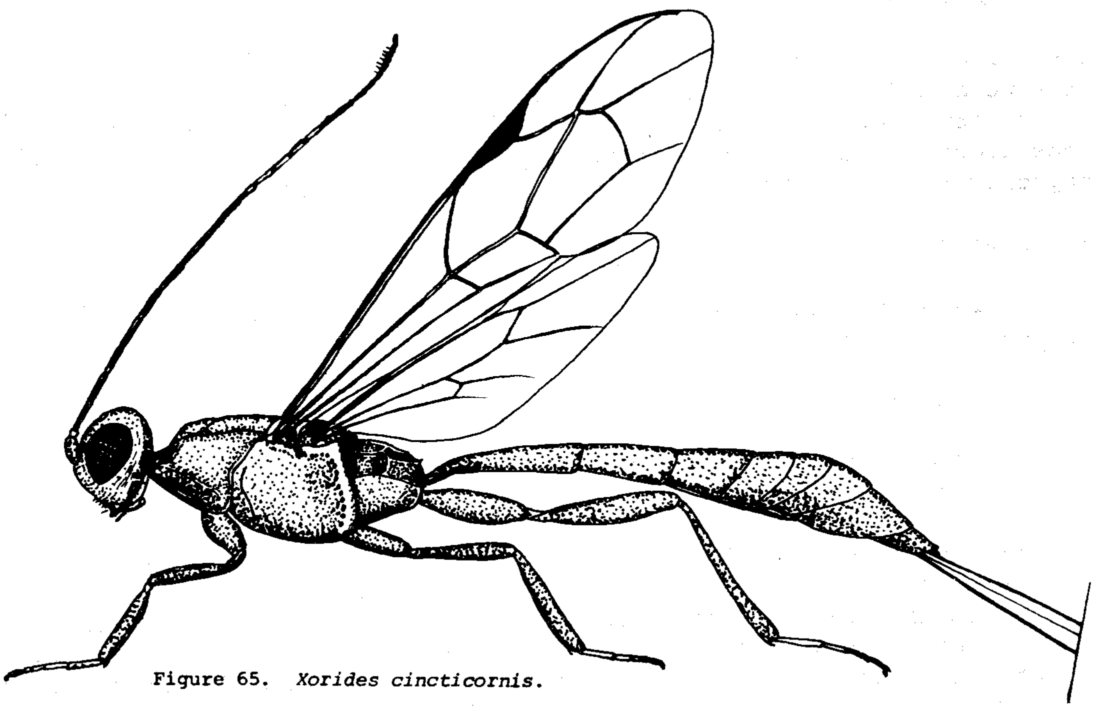


Figure 65. *Xorides cincticornis.*

## *Xorides*

There are 21 Nearctic species of *Xorides,* and a few besides the three species discussed below are likely to be found associated with Douglas-fir. They do not have the combinations of identifying characters used in the following key. Townes and Townes (1960) have published a complete key and detailed descriptions of all Nearctic species of *Xorides*.

Relatively little is known about the insect hosts or tree associations of the many species of *Xorides*. There is some evidence that the species of this genus are unusually catholic with respect to their hosts. Available host records suggest that a single species of *Xorides* usually attacks hosts belonging to at least two different genera. It is unusual for an insect species to live in both deciduous trees and conifers (see Appendix), yet this situation occurs in at least four species of Nearctic *Xorides*.

*Key to the species of Xorides associated with Douglas-fir.*

1. Conspicuous white band covering about 4.5 segments of antenna of female; body black or reddish brown . . *cincticornis*

1'. No white band on antenna . . . . . . . . . . . . . . . . . . . . . . 2

2. Body black with white markings on head and thorax . . . . *insularis*

2'. Body reddish brown with white markings on head and thorax . . . . . . . . . . . . . . . . . . . . . . . . . *maudae*

*Xorides cincticornis*

One specimen of *X. cincticornis* was taken on a trap on a Douglas-fir bolt in the Cedar River watershed on 1 August 1972. The only other known tree host is *Pinus ponderosa;* there are no records of insect hosts (Townes and Townes 1960). There are two subspecies of *X. cincticornis;* the northern subspecies is black, and the southern subspecies is reddish brown.

*Xorides maudae*

*Xorides maudae* has been reared from Douglas-fir. There are no records of insect hosts (Townes and Townes 1960).

*Xorides insularis*

Bedard (1968) found *X. insularis* ovipositing on cerambycid and buprestid larvae during August. Townes and Townes (1960) report *X. insularis* parasitizing *Hylotrupes ligneus, Melanophila drummondi,* and *Scolytus* sp. The last host seems much too small to produce *X. insularis* unless a large number of host larvae were consumed by the wasp larva. Tree associations include *Pseudotsuga menziesii, Pinus ponderosa, P. edulis, P. monticola, Thuja plicata, Libocedrus decurrens, Tsuga heterophylla, Abies amabilis, A. concolor, Picea engelmannii, P. parryana, P. sitchensis, Chamaecyparis lawsoniana, Cupressus macrocarpa,* and *Sequoia sempervirens* (Townes and Townes 1960).

## *Coleocentrus*

Two species of *Coleocentrus* have been associated with Douglas-fir. The insect hosts of Nearctic species of *Coleocentrus* are unknown, but "are almost certainly in dead (probably decaying) wood . . ." (Townes and Townes 1960). Several specimens of *Coleocentrus* were seen in the Cedar River watershed on standing, partly rotten Douglas-fir trees that had been dead for at least three years. Just a few yards away were trees that had been cut that spring, but no specimens of *Coleocentrus* were seen on those trees.

*Coleocentrus occidentalis* and *C. manni* are the only species of *Coleocentrus* found within the range of Douglas-fir. According to Townes and Townes (1960), *C. manni* usually prefers drier habitats than those preferred by *C. occidentalis.*

*Key to the species of Coleocentrus associated with Douglas-fir*

1. Yellowish red areas present on face; clypeus with a transverse band of 30 to 50 hairs . . . . . . . . . *occidentalis*

1'. Face black; clypeus with a transverse band of about 18 hairs . . . . . . . . . . . . . . . . . . . . . . . . *manni*

*Coleocentrus occidentalis*

*Coleocentrus occidentalis* is reported as common around logs and stumps of Douglas-fir, and there is one specimen reported from *Pinus contorta* (Townes and Townes 1960).

*Coleocentrus manni*

*Coleocentrus manni* was taken on Douglas-fir in the Cedar River watershed in 1973. There are apparently no published records of tree hosts of *C. manni*.

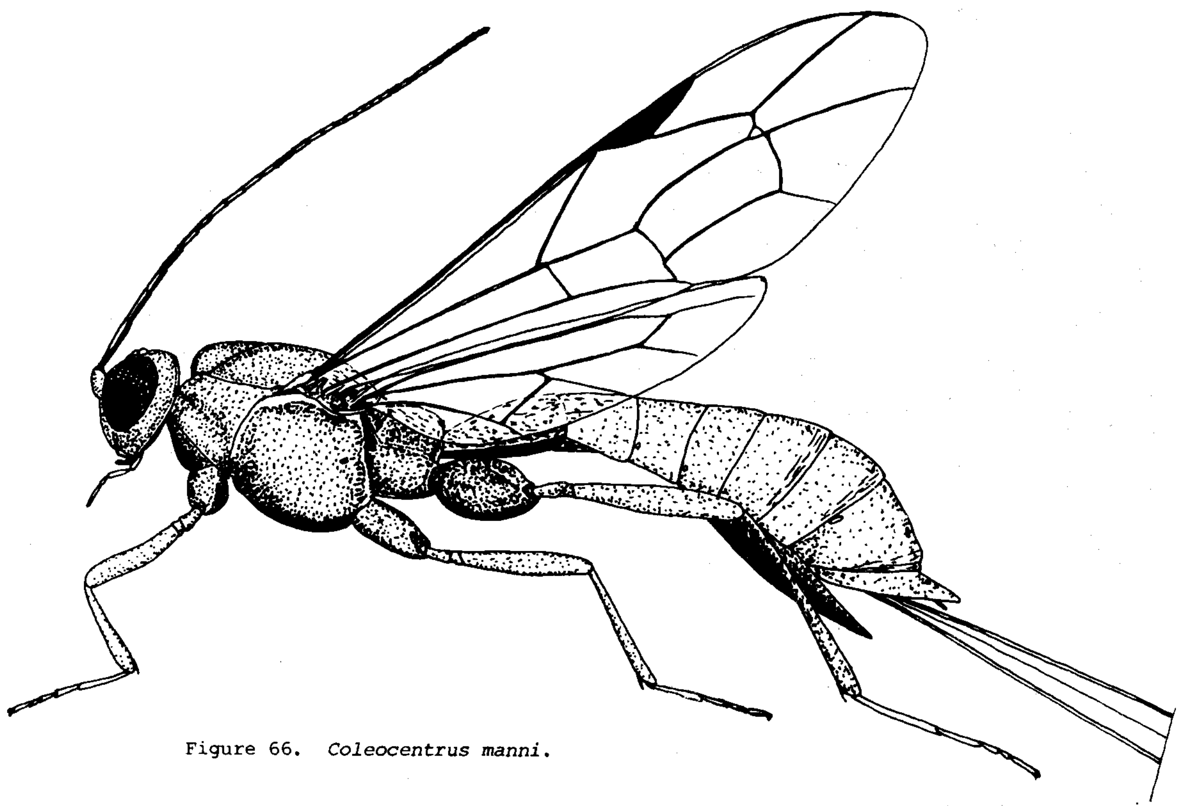


Figure 66. *Coleocentrus manni*.

## *Apistephialtes*

Only one species of *Apistephialtes* is likely to be found on Douglas-fir.

*Apistephialtes dentatus*

*Apistephialtes dentatus* attacks larvae of *Enoclerus sphegeus*, *E. lecontei*, and *Thanasimus nigriventris*. Tree hosts include *Pseudotsuga menziesii*, *Picea engelmannii*, *Pinus lambertiana*, and *Libocedrus decurrens* (Townes and Townes 1960). One specimen was taken in the Cedar River watershed in May of 1973 on a dead *Tsuga heterophylla* cut the previous year.

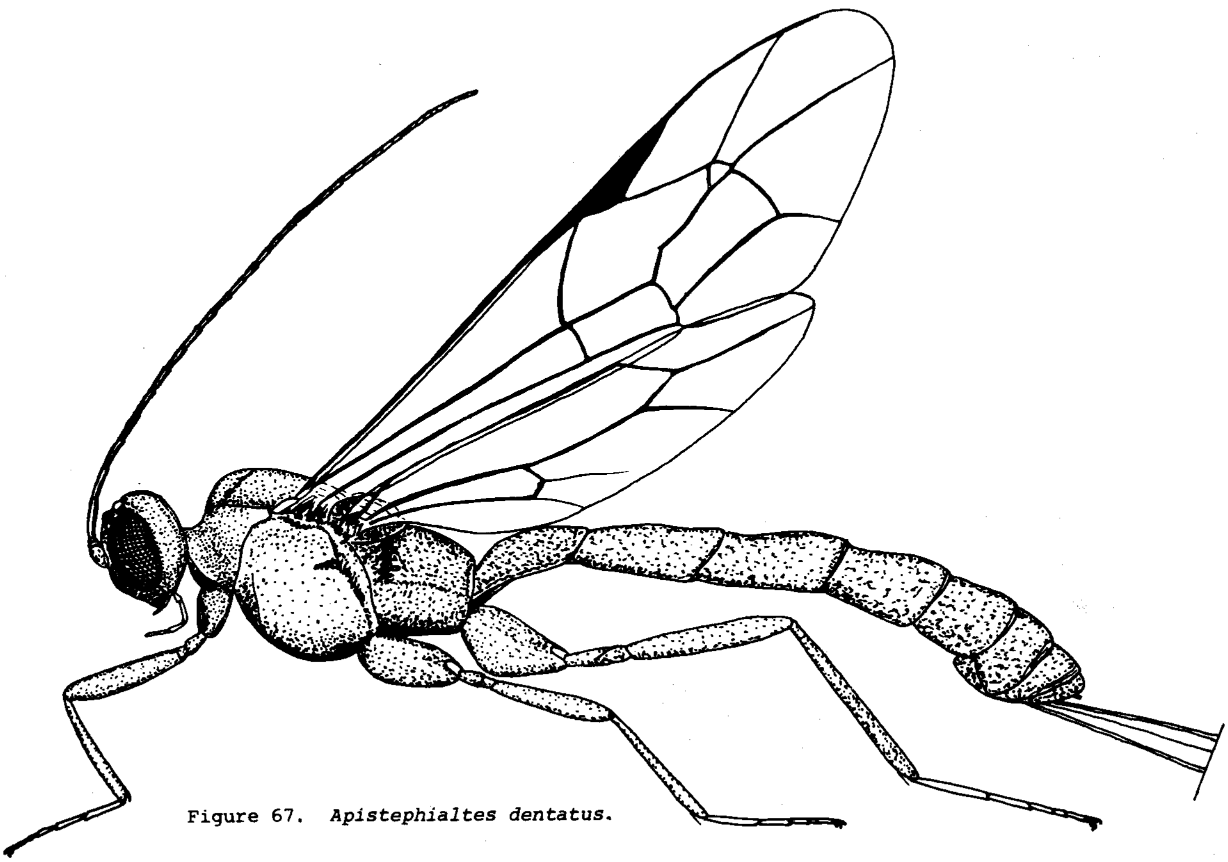


Figure 67. *Apistephialtes dentatus*.

*Dolichomitus*

*Dolichomitus* is a large genus whose species are usually exceedingly difficult to identify. A few species are definitely reported from Douglas-fir; there are a few additional species for which the tree host records are sufficiently broad or vague as to suggest that Douglas-fir is a possible host. These species do not have the combinations of diagnostic characters used in the key that follows. For a complete key and detailed descriptions of all 19 Nearctic species of *Dolichomitus,* see Townes and Townes (1960).

Three species of *Dolichomitus* are known to occur on Douglas-fir. *Dolichomitus terebrans* clearly specializes in parasitizing subcortical weevil larvae; these hosts are found primarily in shaded areas of the tree bole. *Dolichomitus foxleei* is known to attack *Melanophila* and is therefore found in more exposed areas on the host tree. Nothing is clearly known about the host or habitat preferences of *D. pygmaeus*.

A Japanese species of *Dolichomitus* seems to have evolved a system whereby male and female larvae utilize separate hosts and thus avoid competition. Male eggs are usually laid upon larvae of *Pissodes* and *Shirahoshigo* weevils, while female eggs predominate on larvae of *Niphades,* a larger species of weevil (Kishi 1970). This is a refinement of the ability, probably widespread among the Ichneumonoidea, to distinguish between large and small hosts.

*Key to the species of* Dolichomitus *(females) associated with Douglas-fir (adapted from Townes and Townes 1960)*

1. Hind and middle tibiae (when seen from side) with a whitish base, followed by a dark brown band, tibiae distal of this band lighter brown; ovipositor sheath about 1.45 as long as forewing . . . . . . . . . . . . . . *pygmaeus*

1'. Hind tibia may be brown with a light base, but no discrete dark brown band present . . . . . . . . . . . . . . . . . . . . 2

2. Last four segments of maxillary palpi yellowish white; ovipositor sheath about 1.2 as long as forewing; front wing shorter than 12 mm, usually shorter than 19 mm . . . *terebrans*

2'. Maxillary palpi brown; ovipositor sheath about 1.6 as long as forewing . . . . . . . . . . . . . . . . . . . . . . *foxleei*

*Dolichomitus pygmaeus*

One specimen of *Dolichomitus pygmaeus* emerged in the early spring from Douglas-fir bolts brought indoors in February from the Cedar River watershed. Probable hosts include *Melanophila drummondi, Pissodes fasciatus,* and one or more species of unidentified cerambycids. The only host record is one specimen from the borings of *Plectrura spinicauda* (Townes and Townes 1960), presumably in a deciduous tree.

*Dolichomitus foxleei*

*Dolichomitus foxleei* is associated with *Pseudotsuga menziesii, Abies concolor, Pinus ponderosa,* and *P. monticola;* most records are from Douglas-fir (Townes and Townes 1960). The only definite host is *Acanthocinus* sp., but female *D. foxleei* have been taken ovipositing on logs infested with *Melanophila drummondi* and *Semanotus ligneus* (Townes and Townes 1960). In the Cedar River watershed, one female was taken in May on a large hemlock containing *Melanophila drummondi* and a second was reared from Douglas-fir bark. A male that is probably *D. foxleei* was reared from galleries of *Melanophila drummondi* in Douglas-fir from Willard, Washington. Since the male of *D. foxleei* apparently never has been seen (Townes and Townes 1960), there are no descriptions of it, so this record must be confirmed by an expert.

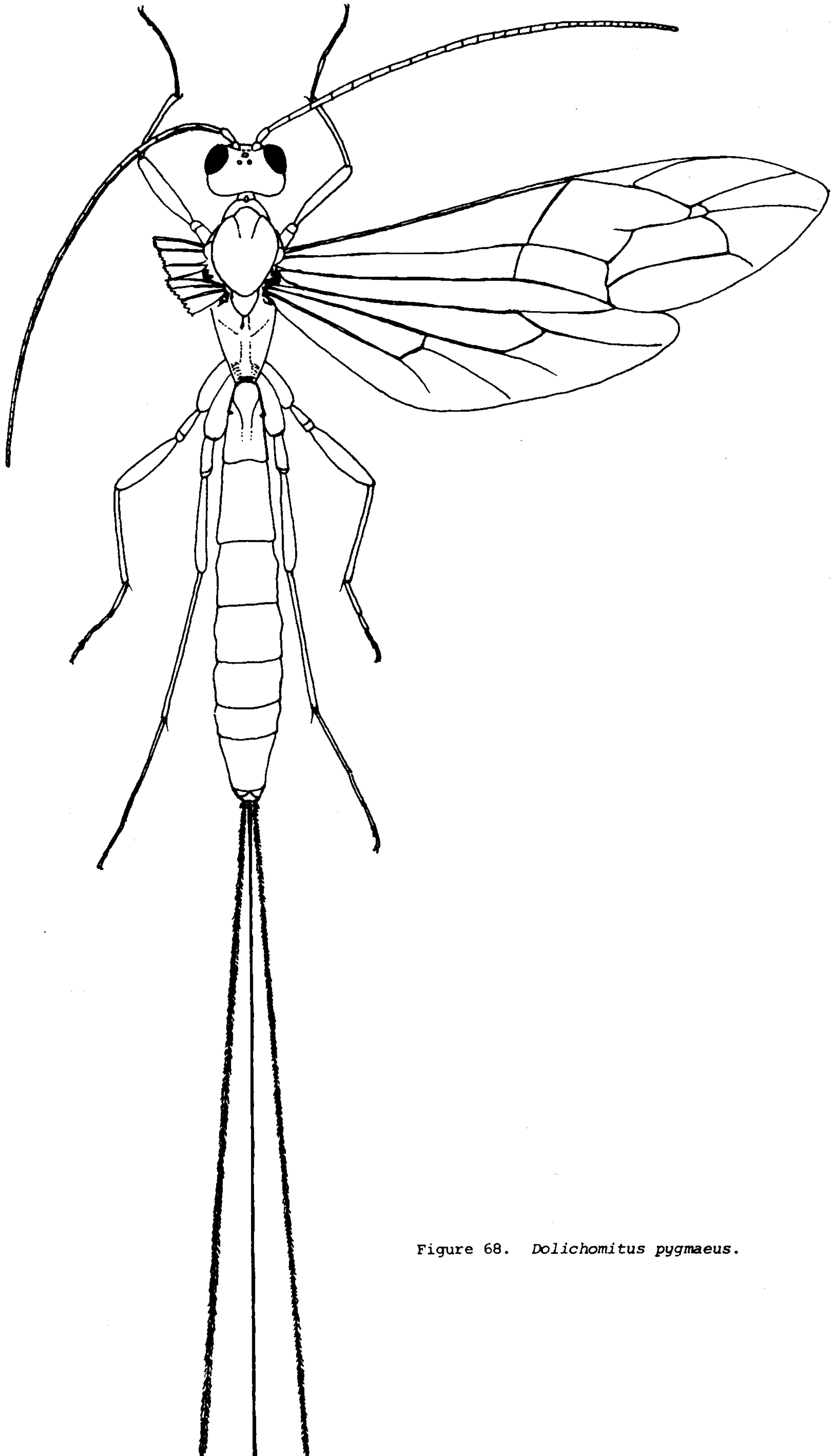


Figure 68. *Dolichomitus pygmaeus*.

*Dolichomitus terebrans*

The insect hosts of *D. terebrans* include *Pissodes fasciatus*, *P. engelmannii*, *P. dubius*, *P. rotundatus*, *P. strobi*, and *Scolytus* sp. (Townes and Townes 1960). The *Scolytus* host record is probably an error, as the host would be much too small. *Dolichomitus terebrans* is associated with *Pseudotsuga menziesii*, *Abies lasiocarpa*, *A. magnifica*, *Picea engelmannii*, *Pinus contorta*, *P. virginiana*, and *Larix* sp. (Townes and Townes 1960).

*Dolichomitus terebrans* is unusual in that it attacks a single host genus in a variety of different tree species and in radically different sites on the trees. *Pissodes strobi* and *P. engelmannii* are found in the leaders of living trees, while *P. fasciatus*, *P. rotundatus*, and *P. dubius* inhabit boles of dead and dying trees (Smith and Sugden 1969). One is tempted to suspect there may be two races of *D. terebrans*, one of which seeks hosts high in the crowns of living trees, while the other searches the lower boles of dead trees. A few specimens of *D. terebrans*, which were reared from *Pissodes sitchensis*, differ in small ways from specimens reared from *P. fasciatus* in Douglas-fir, but there is even more variation within the Douglas-fir series.

On Douglas-fir, *D. terebrans* must compete for hosts with *Coeloides brunneri*, but the latter, because of its relatively short ovipositor, is confined to thin-barked areas of the Douglas-fir bole. Perhaps more serious competition is offered by *Eubadizon crassigaster*, which oviposits into the eggs of *Pissodes fasciatus* before the weevil larvae hatch and bore into the bark.

In the Cedar River watershed, *D. terebrans* was reared from *P. fasciatus* in Douglas-fir, and was taken from May to August 1973 on trees cut in 1972.

## *Neoxorides*

Two of the three species of *Neoxorides* are reported from Douglas-fir. The hosts of these ichneumonids include a variety of subcortical hosts in trees belonging to many different genera. No wasps of this genus were taken in the Cedar River watershed in 1972.

*Key to the species of Neoxorides associated with Douglas-fir*

1. Ovipositor sheath about 0.7 as long as forewing; forewing 4.4 to 9.5 mm long . . . . . . . . . . . . . . . . . *pilulus*

1'. Ovipositor sheath about 1.4 as long as forewing; forewing 8 to 15.5 mm long . . . . . . . . . . . . . . . . . *borealis*

*Neoxorides borealis*

*Neoxorides borealis* is the current name for *Deuteroxorides occidentalis*, which Bedard (1968) found parasitizing buprestid larvae in Douglas-fir.

The known host insects are *Atimia confusa, Semanotus ligneus, Tetropium velutinum* (Muesebeck et al. 1951), *Melanophila drummondi,* and *Lespeyresia toreuta,* a subcortical moth (Townes and Townes 1960). Trees associated with *N. borealis* are *Pseudotsuga menziesii, Abies lasiocarpa, Juniperus scopulorum, Libocedrus decurrens, Pinus ponderosa, Picea* sp., and *Larix* sp. (Townes and Townes 1960). During the present study a male *N. borealis* was reared from an unidentified species of *Pissodes* in a dead *Tsuga heterophylla.* An illustration of *N. borealis* appears in Townes and Townes (1960).

*Neoxorides pilulus*

The only known host of *Neoxorides pilulus* is an unspecified buprestid in Douglas-fir; additional tree associations are *Castanea dentata, Picea engelmannii,* and *Abies concolor* (Townes and Townes 1960).

### *Helcostizus*

There is only one species of *Helcostizus* found within the geographic range of Douglas-fir.

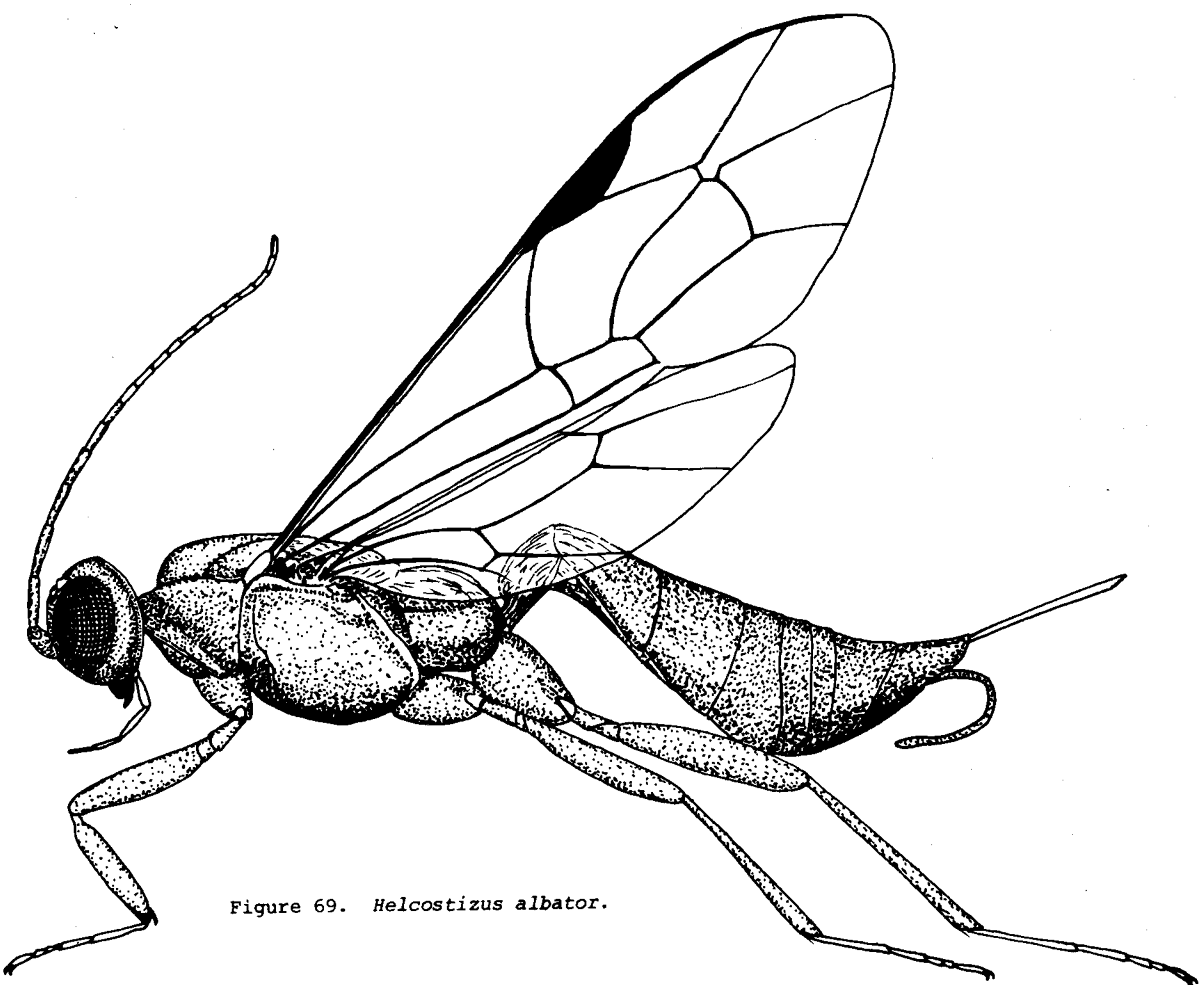


Figure 69. *Helcostizus albator.*

*Helcostizus albator*

Insect hosts of *H. albator* are *Callidium glabratum* and *Saperda calcarata* in Europe, and in North America *Callidium* sp., possibly *Pissodes terminalis*, and possibly *Plectrura spinicauda* (Townes and Townes 1962). Tree associations include *Pinus contorta*, *Rhus diversiloba*, *Cupressus macrocarpa*, and *Chamaecyparis* (Townes and Townes 1962). During the present study one specimen of *H. albator* was reared from *Pissodes fasciatus* in Douglas-fir, and several specimens were reared from *Dicentrus bluthneri*, also in Douglas-fir. Most of the specimens that developed from the small cerambycid *D. bluthneri* were males; larvae of somewhat larger cerambycids are probably preferred by the ovipositing *H. albator* for the production of females.

## *Rhyssa*

Three species of *Rhyssa* have been associated with Douglas-fir. There is one additional species that might be found on Douglas-fir; this species, *R. ponderosae*, may be distinguished by its lack of large white spots on the sides of the meso- and metathorax.

Characteristic of the genus *Rhyssa* is the long ovipositor with which the female is able to parasitize a host deep within the sapwood of a dead tree. The hosts of *Rhyssa* species may be either wood wasps or beetles. Apparently most species of *Rhyssa* accept a wide variety of hosts and host trees. It appears that nothing is known about ecological differences between the species of *Rhyssa* reported from Douglas-fir.

*Key to the species of Rhyssa associated with Douglas-fir (adapted from Townes and Townes 1960)*

1. Antenna with a conspicuous white band . . . . . . . . . . . *lineolata*

1'. Antenna without a white band . . . . . . 2

2. Head of female viewed from side with a sharply defined white stripe next to eye; second to fourth sternites of male each consisting of a single convex undivided sclerite . . . . . . . . . . . . . . . . . . . . *persuasoria*

2'. Head of female viewed from side without sharply defined white stripe next to eye; second to fourth sternite of male each consisting of a broad median sclerite and two narrower lateral sclerites . . . *alaskensis*

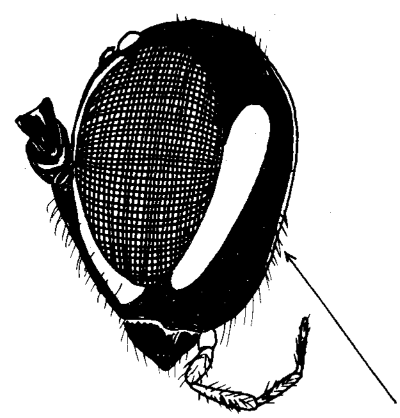


Figure 70. Head of *Rhyssa lineolata*, showing white stripe similar to that of *R. persuasoria*.

*Rhyssa lineolata*

Bedard (1938) found *R. lineolata* on Douglas-fir parasitizing larvae of *Serropalpus substriatus* and siricids. Other insect hosts of *R. lineolata* are *Monochamus scutellatus, M. titillator, Phymatodes dimidiatus, Sirex edwardii, S. cyaneus, Urocerus albicornis,* and *Xeris* sp. (Muesebeck et al. 1951). Tree associations of *R. lineolata* include *Picea sitchensis, Tsuga canadensis, Abies lasiocarpa,* and *A. balsamea* (Townes and Townes 1960). Specimens were taken in the Cedar River watershed in July and August 1973 on trees that had been cut in 1972.

The hosts of *R. lineolata* are notably similar to those of *R. persuasoria* as listed in Muesebeck et al. (1951). Differences in ovipositor length or differences in general habitat preferences seem the most promising factors to be considered when defining the ecological niches of these two species. An illustration of the head and body of *R. lineolata* showing the pattern of white markings appears in Townes and Townes (1960).

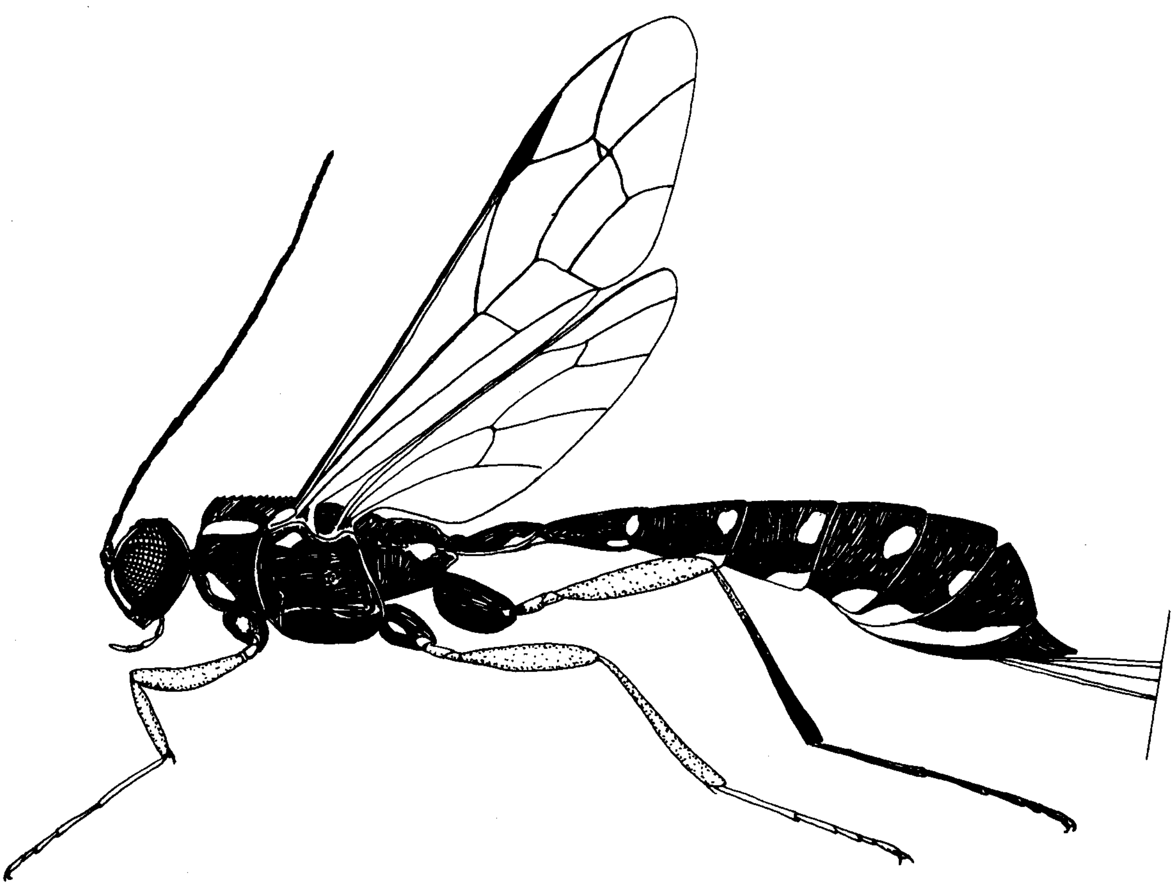


Figure 71. *Rhyssa alaskensis,* showing white markings; these markings may be considerably expanded on large specimens.

*Rhyssa persuasoria*

*Rhyssa persuasoria* occurs in North America and Europe and has been introduced into Australia to combat *Sirex noctilio*. North American insect hosts include *Monochamus notatus*, *M. scutellatus*, *M. titillator*, *Xeris* sp. (Muesebeck et al. 1951), and *Sirex areolatus* (Townes and Townes 1960). Bedard (1938) found *R. persuasoria* parasitizing larvae of *Serropalpus substriatus* and siricids in Douglas-fir. Additional North American tree hosts are *Abies balsamea*, *A. concolor*, *Pinus edulis*, and *P. ponderosa* (Townes and Townes 1960).

There have been two studies of the host selection of *R. persuasoria*. Madden (1968) found that extracts of the symbiotic fungus associated with *Sirex* larvae stimulated females of *R. persuasoria* to investigate the odor source with their antennae and probe the substrate with their ovipositors. Spradbery (1968) discovered that *Serropalpus* larvae and fly maggots, when placed in cavities filled with *Sirex* frass, were stung but not parasitized by *R. persuasoria*. Bee larvae and cerambycid larvae were readily accepted for oviposition. Thus it appears certain information about the host must be received by sensors on the ovipositor before oviposition can occur.

Exceedingly detailed illustrations of the larva and pupa of *R. persuasoria* appear in Spradbery's study (1970a) of the parasites of European siricids. Townes and Townes (1960) have supplied a figure of the adult wasp.

*Rhyssa alaskensis*

The insect hosts of *R. alaskensis* are unknown; tree associations include *Picea sitchensis*, *Pinus contorta*, and *Abies lasiocarpa* (Townes and Townes 1960). Specimens were taken in the Cedar River watershed in July 1973 on Douglas-fir that had been cut in 1972.

In the Cedar River watershed, specimens of *R. alaskensis* and *R. lineolata* were taken on the same Douglas-fir trees on the same dates. As the ovipositor of *R. alaskensis* is about the same length as that of *R. lineolata*, it seems probable that *R. alaskensis* and *R. lineolata* differ in their host preferences, or in their selection of oviposition sites on the trees.

## *Megarhyssa*

Only one species of *Megarhyssa* occurs within the geographic range of Douglas-fir.

*Megarhyssa nortoni*

*Megarhyssa nortoni* has been associated with many tree species, including *Pseudotsuga menziesii*, *Abies concolor*, *A. grandis*, *A. lasiocarpa*, *A. magnifica*, *Picea sitchensis*, *Pinus contorta*, *P. jeffreyi*, *P. ponderosa*, and *Thuja* sp. (Townes and Townes 1960). Hosts of *M. nortoni* are *Xeris morrisoni*, *Urocerus albicornis*, *Sirex* sp. (Muesebeck et al. 1951), and possibly *Chrysobothris* sp. (Townes and Townes 1960). *Megarhyssa nortoni* was taken in the Cedar River watershed in late July 1973 on a Douglas-fir cut in 1972.

The ability of *Megarhyssa* species to unerringly locate hosts that are hidden beneath 2-3 cm of solid wood is still unexplained. Madden's study (1968) of *M. nortoni* suggests that important stimuli for oviposition may be substances produced by a symbiotic fungus associated with the larva of the siricid host. Extracts of fungus cultures in various solvents including water elicit from female wasps antennal investigation and probing with the ovipositor. Madden also obtained some positive responses from *M. nortoni* females to acetaldehyde, a compound released by the symbiotic fungus. Heatwole et al. (1964), in a study of three *Megarhyssa* species (not including *M. nortoni*), concluded that the only known senses that *Megarhyssa* might use to locate its prey would be olfaction or ultrasound. Since then it has been shown (Richerson and Borden 1972b) that *Coeloides brunneri* uses minute heat gradients to locate its subcortical host, and it seems possible that *Megarhyssa* species might likewise use heat gradients. Platelike sensory organs on the antennae of *Coeloides brunneri* probably function as the heat receptors (Richerson and Borden 1972b); the antennae of *Megarhyssa* are also covered with platelike sensory organs (Heatwole et al. 1964).

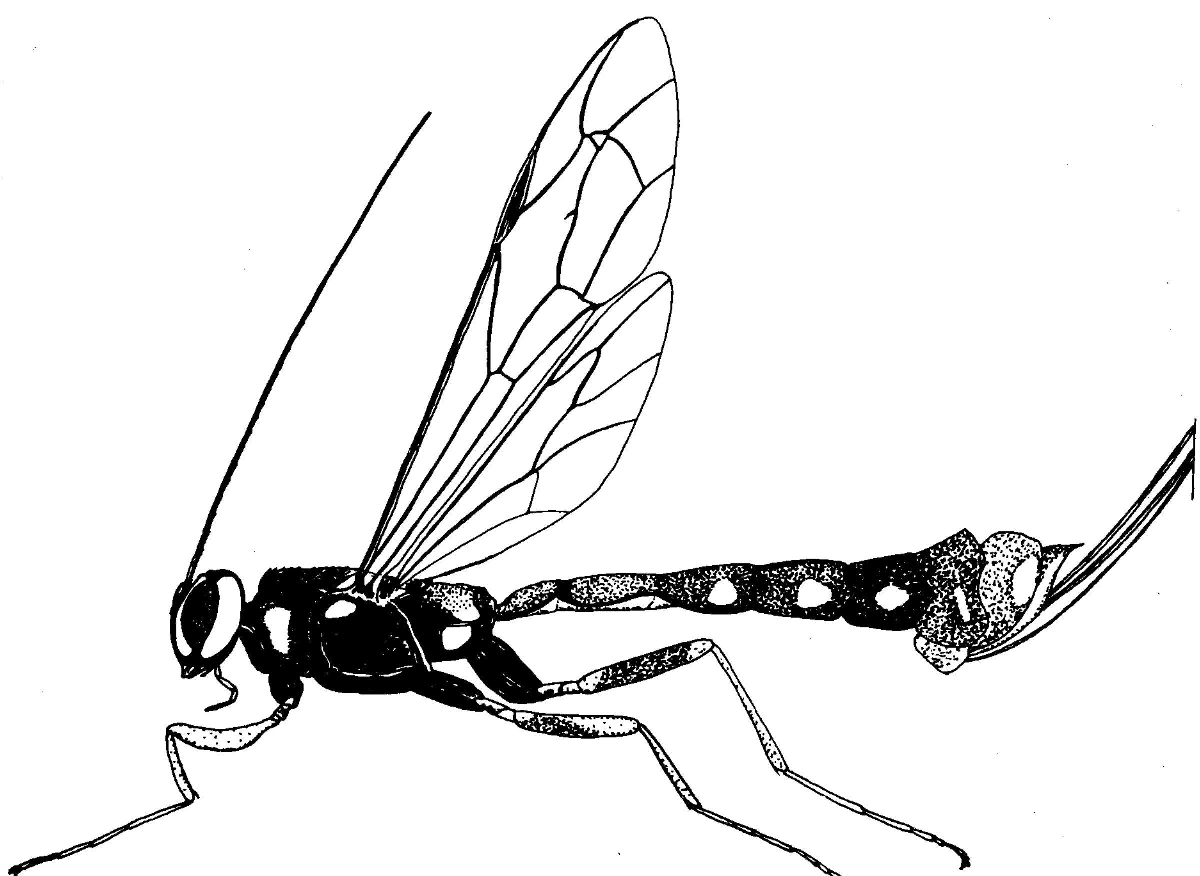


Figure 72. *Megarhyssa nortoni*, showing extent of yellow markings.

*Megarhyssa* males apparently find their mates by the sound of the emerging female gnawing its way out through the wood. After the female emerges, mating is apparently induced by a temporary species-specific pheromone of the female (Heatwole et al. 1964).

## BRACONIDAE

The numerous species of braconids found on dead Douglas-fir are similar to the related ichneumonids in appearance and in oviposition behavior. Unlike the ichneumonids, the braconids tend to attack scolytids and buprestids present in the dead tree only during the first year after the death of the tree. Exceptions to this rule are the genera *Helcon*, *Helconidea*, and possibly *Doryctes*, which may be found on a dead tree for at least two or three consecutive years.

*Coeloides* and *Spathius*, attacking *Dendroctonus* and *Pseudohylesinus*, respectively, are the hymenopterans most commonly reared from dead Douglas-fir. The much less abundant *Dendrosoter* and *Ecphylus* seem to specialize in parasitizing the smallest scolytids and those in exposed bark. *Atanycolus* is common on exposed tree trunks containing *Melanophila drummondi*. *Doryctes* has been associated with buprestids and cerambycids, but must be limited in its choice of hosts by the shortness of the ovipositor, unless the host is attacked in the egg stage. *Helcon* and *Helconidea* are large braconids strongly resembling ichneumonids; these two genera parasitize cerambycids. *Eubadizon* lays its eggs in those of *Pissodes* weevils, hosts which are also attacked by the genus *Bracon*. An undescribed species of *Blacus* parasitizes predatory or scavenger beetle larvae living in the galleries of scolytids.

Two genera of braconids observed on dead Douglas-fir by Bedard (1938) are probably not normally found on dead or dying trees. *Macrocentrus aegeriae*, which Bedard reported ovipositing on cerambycid and buprestid larvae, is apparently exclusively a parasite of Lepidoptera (Muesebeck et al. 1951); the insects seen by Bedard may have been searching for pitch moths. An undescribed species of *Opius* is reported as a parasite of *Pseudohylesinus nebulosus;* the adults emerge from bark during June. A large mass of biological information concerning the genus *Opius* indicates that all members of this genus parasitize flies in fruits or in herbaceous plants (Fischer 1964, 1965). A search through a monograph on the Opiinae (Fischer 1964, 1965) has not revealed any mention of Bedard's noteworthy specimens. It seems probable that Bedard's specimens belong to some genus other than *Opius*.

### *Key to the Genera of Braconidae Associated with Dead Douglas-Fir*

1. Large circular opening present between clypeus and closed mandibles (illustrated p. 68) . . . . . . . . . . . . . . 5

1'. No large opening above mandibles; closed mandibles and clypeus practically contiguous (illustrated p. 68) . . . . . . 2

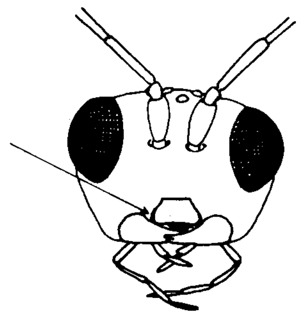


Figure 73. Head of braconid (*Eubadizon*) showing no large gap above mandibles.

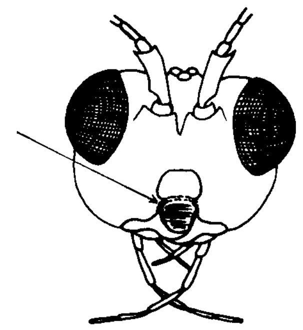


Figure 74. Head of braconid (*Atanycolus*) showing large circular opening above mandibles.

2. Large tooth present on underside of hind femur . . . . . *Helconidea*

2'. No tooth on hind femur . . . . . . . . . . . . . . . . . . . . . . . 3

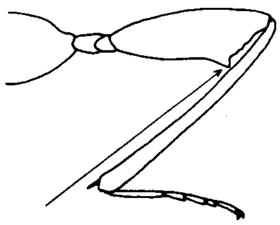


Figure 75. Leg of *Helconidea*, showing tooth on underside of femur.

3. Body usually at least 10 mm long; forewing with three cubital cells . . . . . . . . . . . . . . . . . . . . *Helcon*

3'. Length of body 5 mm or less; forewing with no cubital cells . . . . . . . . . . . . . . . . . . . . . . . . . 4

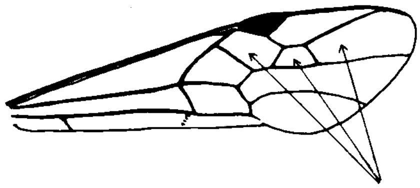


Figure 76. Forewing of *Helconidea*, showing three cubital cells like those of *Helcon*.

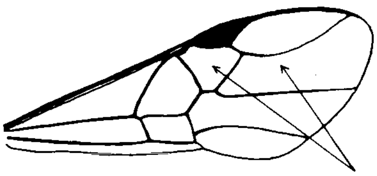


Figure 77. Forewing of *Eubadizon*, showing two cubital cells.

4. Body about 4 or 5 mm long; antennae with more than 25 segments; legs orange-brown . . . . . . . . . . . *Eubadizon*

4'. Body about 3 mm long; antennae with fewer than 20 segments; legs yellow-brown . . . . . . . . . . . . *Blacus*

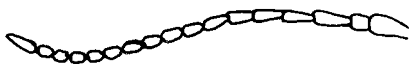


Figure 78. Antenna of *Blacus* (female).

Figure 79. Antenna of *Eubadizon* (female).

5. Forewing more or less darkened, with a transverse clear stripe in the middle; small species, less than 5 mm long; body entirely dark brown . . . . . . . . . . . . . 6

5'. Forewing may be darkened, but no clear stripe present; a few species wingless; various sizes and color patterns . . . . . . . . . . . . . . . . . . . . . . . . 7

6. Lower margins of second and third cubital cells almost equal in length; hind wing of male without swollen veins . . . . . . . . . . . . . . . . . . *Spathius*

6'. Lower margin of second cubital cell much longer than that of the third; hind wing of male with a greatly swollen vein in its leading edge . . . . . . . *Dendrosoter*

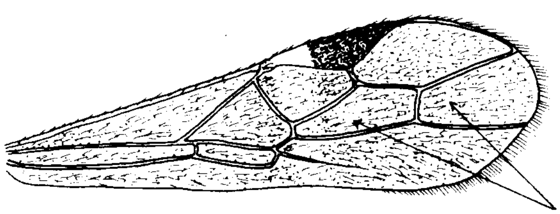


Figure 80. Forewing of *Spathius sequoiae*, showing second and third cubital cells with lower margins almost equal.

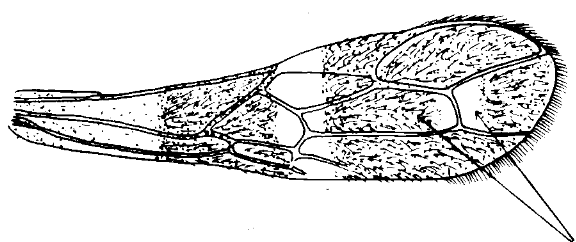


Figure 81. Forewing of *Dendrosoter scaber*, showing second and third cubital cells having unequal lower margins (redrawn from Muesebeck 1938, p. 284).

7. May be wingless; if winged, hind edge of forewing with a single, long, narrow cell; only one cubital cell (illustration p. 70) . . . . . . . . . . . . *Ecphylus*

7'. Always winged; two cells near hind edge of forewing; three cubital cells (illustration p. 70) . . . . . . . . 8

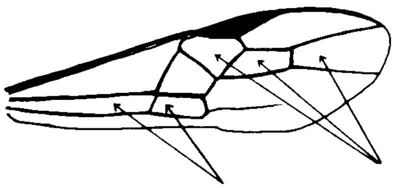


Figure 82. Forewing of *Atanycolus*, showing two cells at hind edge of wing, and three cubital cells.

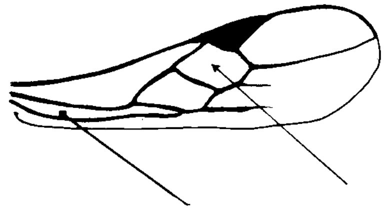


Figure 83. Forewing of *Ecphylus*, showing single cell at hind edge of wing, and single cubital cell (redrawn from Marsh 1965, p. 684).

8. Wings blackish; usually some scarlet on thorax . . . . . *Atanycolus*

8'. Wings colorless or only slightly tinted; no scarlet thorax . . . . . . . . . . . . . . . . . . . . . . . . . 9

9. Small triangular cell at base of hind wing at least half the length of the lower margin of the cell immediately above it . . . . . . . . . . . . . . *Doryctes*

9'. Small triangular cell at base of hind wing much less than half the length of the lower margin of the cell immediately above it . . . . . . . . . . . . . . . . 13

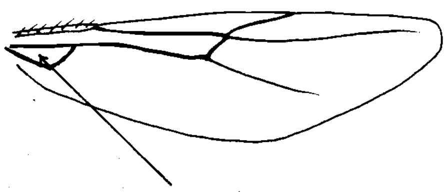


Figure 84. Hind wing of *Coeloides*, showing small triangular cell much less than half the length of the cell above it.

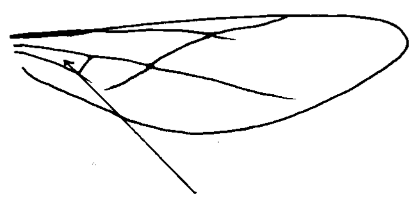


Figure 85. Hind wing of *Doryctes*, showing small triangular cell more than half the length of the cell above it.

10. Ovipositor of female longer than abdomen; most of abdomen orange; head may be orange . . . . . . . . *Coeloides*

10'. Ovipositor of female shorter than abdomen; head and body completely dark brown except for base of abdomen, which may be yellowish brown . . . . . . . . . . . . . . . . . . . . . . . . . . *Bracon*

## *Helconidea*

Two species of *Helconidea* have been associated with Douglas-fir. A number of other species occur within the range of Douglas-fir and have not yet been associated with any host trees. These species do not have the characteristics mentioned in the key that follows, and may be identified using Cresson's key (1873); the names so obtained should be checked for changes in the Hymenoptera catalog (Muesebeck et al. 1951).

The hosts of *Helconidea* are various cerambycids. The species found on Douglas-fir apparently fly considerably later in the year than most of the several species of ichneumonids that might compete with *Helconidea* for hosts. Douglas-fir and western larch seem to be the only tree hosts reported for any species of *Helconidea*. Nothing seems to be known about the behavior of any species of *Helconidea*.

*Key to the species of Helconidea associated with Douglas-fir*

1. Body entirely black . . . . . . . . . . . . . . . . . . . *occidentalis*

1'. Abdomen reddish brown; hind tarsus reddish brown . . . . . . . . . . . . . . . . . . . . . . . . *necydalidis*

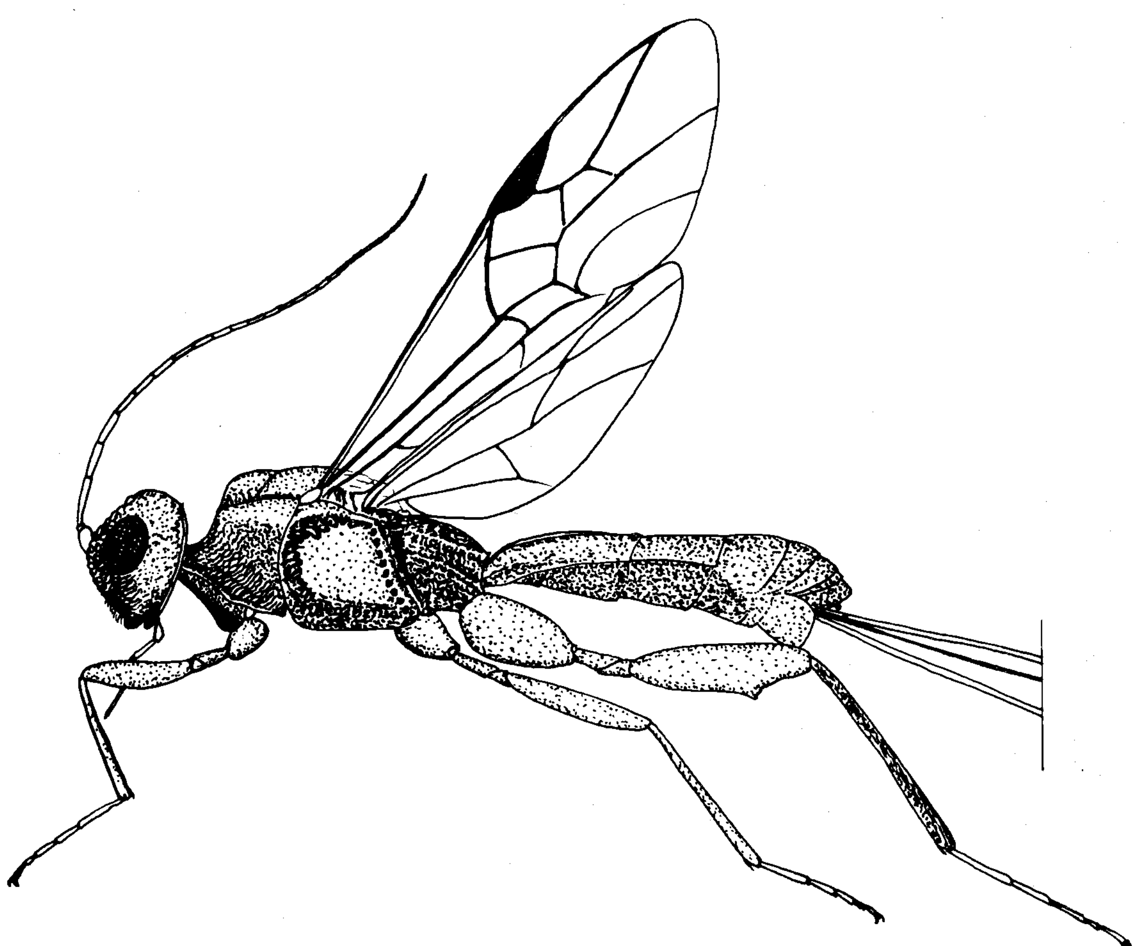


Figure 86. *Helconidea necydalidis*.

*Helconidea necydalidis*

Nine specimens of *H. necydalidis,* including five females, were captured on traps on recently cut Douglas-fir in the Cedar River watershed between 26 July and 16 August 1972. Additional specimens were taken on the same trees in late July and in August 1973; no males were observed during 1973.

There are apparently no published records of the host trees of *H. necydalidis.* The type specimens of this species were reared from *Necydalis laevicollis* (Cushman 1931). During the present study several specimens of *H. necydalidis* were reared from the cerambycid *Leptura obliterata* in a large, exposed Douglas-fir stump.

*Helconidea occidentalis*

Bedard (1938) found *H. occidentalis* ovipositing on cerambycid and buprestid larvae in Douglas-fir. Finlayson (1969) reared this species from *Tetropium velutinum* in western larch. *Serropalpus* galleries in the same larch logs did not contain cocoons of *H. occidentalis.* One specimen was captured on freshly cut Douglas-fir in the Cedar River watershed in 1972.

*Helconidea occidentalis* is much larger than the preceding species, and has an ovipositor more than twice the length of that of *H. necydalidis.* *Helconidea necydalidis* and *H. occidentalis* probably parasitize larvae at different depths from the surface of the log. An illustration of the cephalic structure of the larva of *H. occidentalis* appears in Finlayson's study (1969).

## *Helcon*

Apparently almost nothing is known about the Nearctic species of *Helcon.* This genus is very similar to *Helconidea,* but lacks the femoral tooth. Three species occur in the range of Douglas-fir, but only one is definitely associated with Douglas-fir. No specimens of *Helcon* have been taken in the Cedar River watershed.

*Helcon yukonensis*

*Helcon yukonensis* is distinguished from other species of *Helcon* in the range of Douglas-fir by the following characters: abdomen reddish at sides, hind femur red-brown with black apex, hind tibia and tarsus black (Cresson 1873).

Bedard (1938) found this species ovipositing on Douglas-fir. There seems to be no other published information concerning the habits of *H. yukonensis.*

## *Eubadizon*

*Eubadizon* has a wide host range, including species of Lepidoptera, Hymenoptera, and Coleoptera (Muesebeck et al. 1951). Martin (1956) has made a separate genus, *Calyptus*, for the species of *Eubadizon* that parasitize beetles, but this distinction has not been generally accepted. Only one species of *Eubadizon* has been reported from Douglas-fir.

*Eubadizon crassigaster*

*Eubadizon crassigaster* was by far the commonest braconid on traps on Douglas-fir in the Cedar River watershed in 1972. More than 2000 specimens were captured between June and the middle of August. Constantly flying and walking up and down the length of the logs, *E. crassigaster* seemed exceedingly vulnerable to the trapping system used.

In Douglas-fir *E. crassigaster* is a parasite of *Pissodes fasciatus;* the egg of *E. crassigaster* is injected into the *Pissodes* egg, but the larval parasite does not begin to grow until the host larva is mature. On several occasions, females of *E. crassigaster* were observed ovipositing in the punctures made by ovipositing *P. fasciatus*. In one instance, two female parasites were seen waiting while a *Pissodes* was excavating the oviposition niche.

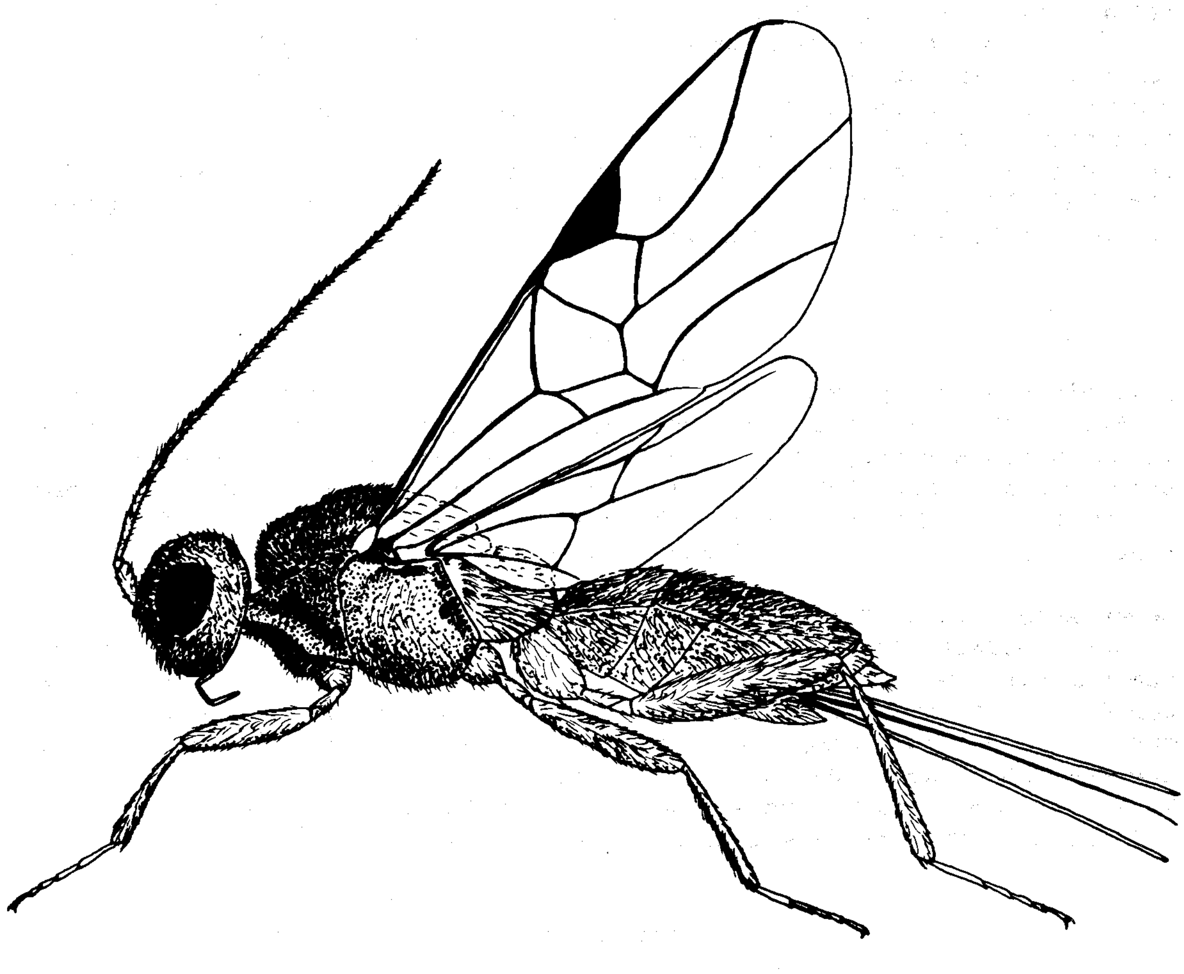


Figure 87. *Eubadizon crassigaster*.

Host location by *E. crassigaster* seems to require at least two steps. Tree odors probably attract the female wasps, as the parasites were caught in large numbers on bolts screened from insect attack. A few minutes after cutting, trees were already being examined by *E. crassigaster*. Once on the tree, the braconids explore it methodically, flying up and down the length of the tree, frequently alighting to traverse on foot, the antennae vibrating rapidly. In the few cases *E. crassigaster* was observed discovering a *Pissodes* puncture, host recognition occurred only about a centimeter from the oviposition site. Several (up to five) females have been observed ovipositing simultaneously in the same site. No more than one parasite seems to develop on a *Pissodes* larva.

Males of *E. crassigaster* emerged from Douglas-fir in the insectary, but were not trapped on freshly cut trees. Apparently mating takes place on the tree from which the wasps emerged, or at some aggregation site other than freshly cut trees. *Eubadizon crassigaster* overwinters as mature larvae in cocoons.

*Eubadizon crassigaster* must consist of at least two behavioral races or closely related species. One series of hosts, including *Pissodes dubius* (Krombein 1958), *P. fasciatus*, and an unidentified *Pissodes* in *Tsuga heterophylla*, inhabit the boles of dead trees. A second series of hosts, including *Pissodes engelmannii* (Stevenson 1963) and *P. sitchensis*, inhabit leaders of live trees. It is probable that there are two or more species of *Eubadizon* that, like their hosts, are exceedingly difficult to separate morphologically but easy to separate biologically. The record of *E. crassigaster* parasitizing *Pseudohylesinus nebulosus* (Krombein 1958) is based on an incorrect identification of the parasite (P. M. Marsh, personal communication).

## *Blacus*

A single species, probably belonging to the genus *Blacus* has been associated with Douglas-fir. The species is undescribed, as are many species in the genus *Blacus*. Dr. Paul Marsh, who was willing to examine the specimens of *Blacus* taken in this study, writes that these specimens are somewhat intermediate between *Blacus* and *Hysterobolus*. The subfamily Blacinae is in great need of revision (Muesebeck et al. 1951).

Seven specimens of *Blacus* sp. were reared from Douglas-fir infested by *Pseudohylesinus nebulosus*. The larval skins attached to the cocoons of the parasites were those of *Lasconotus intricatus*, a beetle that is common in the galleries of small scolytids. An adult female *Blacus* was seen pursuing and attempting to oviposit on a *Lasconotus* larva placed in the same container. Because of the shortness of its ovipositor, the female wasp must enter the scolytid gallery to seek its host. All specimens of this parasite are from Bear Lake, Kitsap County, Washington.

## *Dendrosoter*

*Dendrosoter* may be recognized by the heavily darkened forewing crossed by a sharp transparent band, and by the curiously swollen vein on the lead-

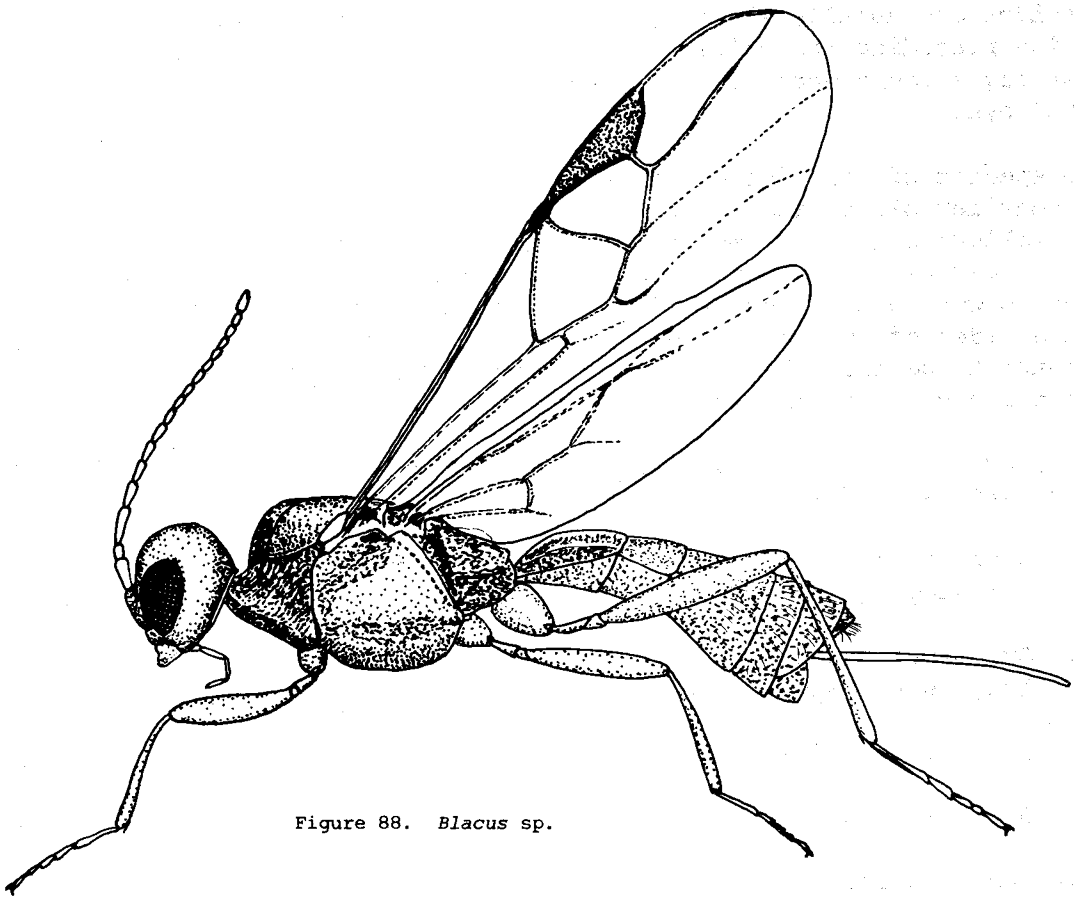


Figure 88. *Blacus* sp.

ing edge of the hind wing of the male. Specimens of this genus have not been taken in the Cedar River watershed. One species is associated with Douglas-fir.

*Dendrosoter scaber*

*Dendrosoter scaber* has been reared from *Pityophthorus* sp. in *Pinus monophylla* and from an unidentified scolytid in Douglas-fir (Muesebeck 1938). *Cylindrocopturus longulus* is an additional host (Krombein and Burks 1967).

### *Spathius*

The genus *Spathius* has been carefully reviewed in Matthews' monograph (1970), which includes a key to the 21 Nearctic species. All these species are parasites of bark- and wood-boring beetles, but only three species, those belonging to the *S. sequoiae* group, occur within the range of Douglas-fir. Two species of *Spathius* have been associated with Douglas-fir. The third species, *S. canadensis*, has been reared from several scolytids in a variety of conifers, not including Douglas-fir.

This genus is easily recognized by its small size, red-brown body color, and the distinctive appearance of the forewings. The forewings of

*Spathius* are usually slightly darkened, with an untinted transverse stripe preceding the stigma. In western species, this character is scarcely evident under the microscope, but rather conspicuous to the naked eye.

The species of *Spathius* are difficult to distinguish, but there seems to be considerable overlap of characters between closely related species. The following key has been much simplified from Matthews (1970). The reader may wish to refer to Matthews' descriptions and remarks. It is best to work with a series of specimens reared from the same material to get an idea of the variation within the population. *Spathius sequoiae* appears to be the only species abundant in Douglas-fir in areas where extensive collections have been made.

*Key to species of Spathius found in the range of Douglas-fir (adapted from Matthews 1970)*

1. Ovipositor shorter: 0.32-0.46 as long as forewing . . . . . . . . . . . . . . . . . . . . . . . . . *aphenges*

1'. Ovipositor longer: usually at least 0.5 as long as forewing . . . . . . . . . . . . . . . . . . . . . . . . . . 2

2. Ovipositor 0.45-0.65 as long as forewing . . . . . . . . *canadensis*

2'. Ovipositor 0.60-0.80 as long as forewing . . . . . . . . . *sequoiae*

*Spathius sequoiae*

*Spathius sequoiae* has long been known as *S. brunneri*. It is very closely related to *S. canadensis;* Matthews states the two species may eventually be combined. Cedar River specimens of *S. sequoiae,* particularly the larger individuals, show sculpturing on the head and abdomen similar to that described for *S. canadensis,* but the ovipositor is long. The usual hosts for *S. sequoiae* are small and produce small wasps; however, when a large host such as a Douglas-fir beetle is attacked, the resultant *Spathius* is almost twice as large as normal specimens, and at first glance appears to be a distinct species.

The life history of *S. sequoiae* at the Cedar River watershed is fairly well known. The adults emerge in late June, the males preceding the females by a day or two, and mating takes place on the log from which the wasps emerged. The females fly to new host material and may be seen ovipositing from late June through the middle of August. In the Cedar River watershed, there are at least two generations each year. The number of generations per year in other areas is not known. Oviposition takes place through the bark and the larvae are ectoparasites of bark beetles (Matthews 1970). Presumably the female *S. sequoiae* stings the beetle larva before ovipositing. There is only one parasite per host.

*Spathius sequoiae* is known from many insect hosts, including *Phloeosinus sequoiae, P. punctatus, Pseudohylesinus nebulosus, Scolytus ventralis,*

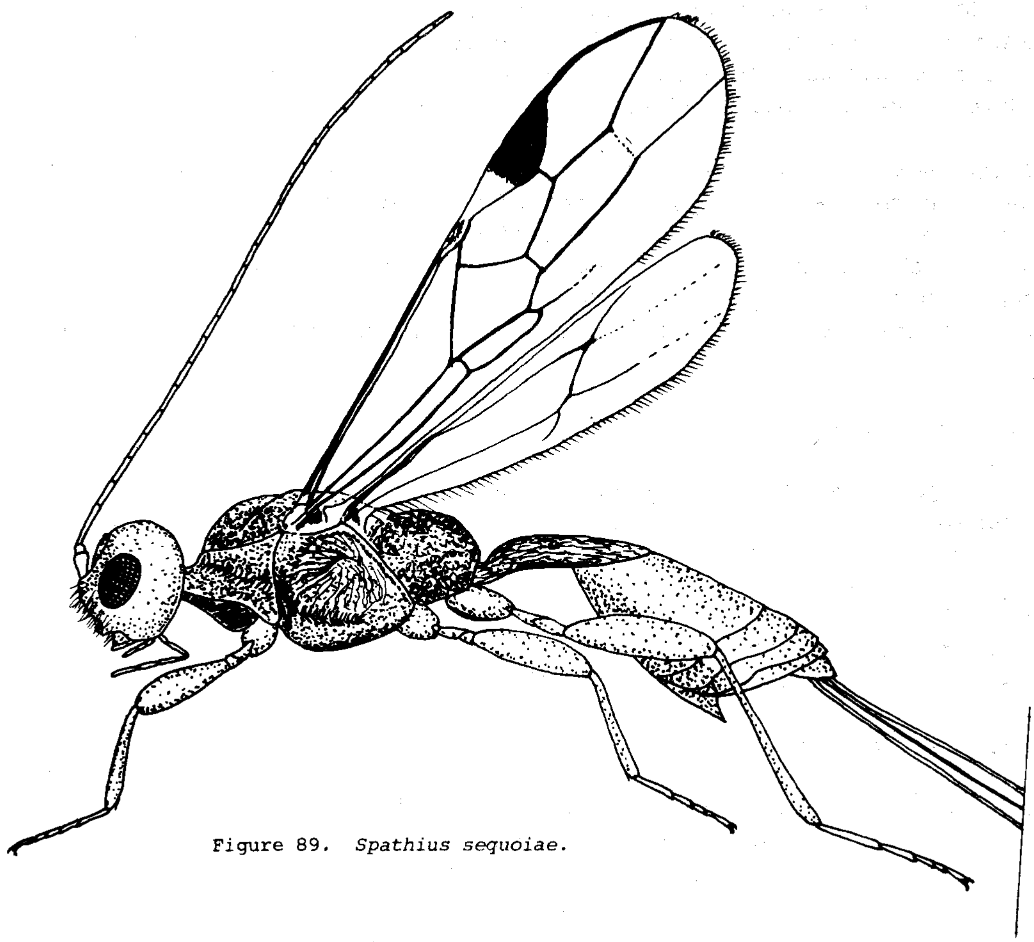


Figure 89. *Spathius sequoiae*.

*S. tsugae*, *Dendroctonus pseudotsugae*, *D. obesis*, and a *Pissodes* in Douglas-fir, presumably *P. fasciatus* (Matthews 1970. Additional hosts encountered during the present study are *Scolytus unispinosus*, *Pseudohylesinus sericeus*, *Cryphalus pubescens*, *Lechriops californicus*, and *Alniphagus aspericollis*. *Scolytus unispinosus* is a normal host in partially exposed trees; *Alniphagus aspericollis* is a normal host that occurs in a deciduous tree (*Alnus rubra*); *Cryphalus pubescens* is too small to be a normal host, and produces only male parasites. Because of the shortness of its ovipositor, *S. sequoiae* can attack only those hosts found in tops and branches. *Spathius sequoiae* has been taken on species of *Larix*, *Abies*, *Picea*, *Sequoia*, *Libocedrus*, and *Pseudotsuga* (Matthews 1970).

With such a wide range of tree hosts, one must assume that *S. sequoiae* is attracted either by many different substances, or by a single, rather universal substance produced by moribund conifers of many species. If a number of diverse substances are long-range attractants for *S. sequoiae*, there might well be different races of *S. sequoiae* attacking scolytids on different tree hosts. The actual pinpointing of the host larvae might be accomplished through heat perception, as has been demonstrated for *Coeloides brunneri* (Richerson and Borden 1972b).

In the Cedar River watershed and in other areas sampled in western Washington, *S. sequoiae* was by far the most abundant parasite of *Pseudohylesinus nebulosus*, as well as the most common hymenopteran to emerge from thin bark of Douglas-fir.

*Spathius sequoiae* is itself parasitized by the eupelmid *Calosota pseudotsugae*. In the laboratory, *C. pseudotsugae* emerges from the cocoons of *S. sequoiae* about three weeks after its host. It is not known whether the larval *S. sequoiae* is attacked after it has already spun its cocoon. A less important enemy of *S. sequoiae* is the larva of the colydiid *Lasconotus intricatus*, which was observed attacking the cocoons of *S. sequoiae*.

*Spathius aphenges*

*Spathius aphenges* is most commonly associated with scolytids attacking pine cones, but also has been reported from thin-barked tops and branches (Matthews 1970). Insect hosts are *Ips latidens*, *Conophthorus coniperda*, *Phthorophloeus puberulus*, and *Scolytus abietis*; tree associations include *Pinus lambertiana*, *P. ponderosa*, *P. contorta*, *Abies grandis*, and *Pseudotsuga menziesii* (Matthews 1970). *Spathius aphenges* was not encountered in the Cedar River watershed in 1972.

*Spathius canadensis*

Although *S. canadensis* has not been reported from Douglas-fir, its diverse tree associations (see Matthews 1970) suggest that it may be found in Douglas-fir. There is a possibility that *S. canadensis* and *S. sequoiae* are races of a single species.

## *Ecphylus*

There are three species of *Ecphylus* associated with Douglas-fir; all occur on a wide variety of trees. Apparently no details are known of the life cycle of any North American species of *Ecphylus*. The female pierces the bark of scolytid-infested trees to paralyze and lay an egg upon a host larva; the *Ecphylus* larva develops as an external parasite (Marsh 1965).

*Key to species of Ecphylus associated with Douglas-fir*

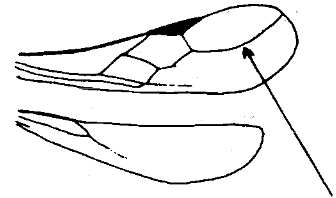
1. Body yellow; head brown; both sexes winged . . . . . . *californicus*

1'. Body, head dark brown; males apterous . . . . . . . . . . . . . . . 2

2. Male with short wing pads; radius in forewing of female strongly curved . . . . . . . . . . . . . . . . . *arcuatus*

2'. Male completely wingless; radius in forewing of female not strongly curved; female may be wingless . . . . *pacificus*

Figure 90. Wing of *Ecphylus arcuatus*, showing curved radius (redrawn from Marsh 1965, p. 684).



*Ecphylus californicus*

According to Marsh (1965), *E. californicus* has been associated with *Pseudotsuga menziesii, Sequoia sempervirens, Tsuga mertensiana, Libocedrus decurrens,* and probably *Thuja plicata;* the known insect hosts are *Phloeosinus sequoiae, P. punctatus, Pseudohylesinus nebulosus, Scolytus unispinosus,* and *Scolytus* sp., probably *praeceps*. During the present study great numbers of *E. californicus* were reared from *Scolytus unispinosus* in thin bark of Douglas-fir. The *S. unispinosus* larvae are attacked when they are far too small to be adequate hosts for *Spathius sequoiae, Rhopalicus pulchripennis, Cecidostiba burkei,* and most other parasites of *S. unispinosus*. Cocoons of *E. californicus* brought indoors during late winter usually do not hatch for at least two months.

*Ecphylus arcuatus*

Marsh (1965) reports *E. arcuatus* associated with *Tsuga mertensiana, Abies concolor,* and *Pseudotsuga menziesii;* during the present study a single specimen of *E. arcuatus* emerged from the gallery of *Scolytus unispinosus*.

The male *E. arcuatus* is apterous, a condition that might be expected in a male insect that emerges and waits for females to emerge from the same material. The lack of wings prevents the wasp from straying or being blown from the tree that contains females, and provides an antlike appearance that might deter some predators.

*Ecphylus pacificus*

*Ecphylus pacificus* parasitizes *Pityophthorus* sp. in *Pinus ponderosa* and *Picea sitchensis,* and *Pityophthorus carmeli* in *Pinus radiata* (Marsh 1965). During the present study numerous specimens of *E. pacificus* emerged from the galleries of *Cryphalus pubescens* in Douglas-fir branches. Adjacent colonies of *Pseudohylesinus nebulosus* had not been attacked by *E. pacificus*.

The males of *E. pacificus,* like those of *E. arcuatus,* are wingless; the females are sometimes wingless as well (Marsh 1965). The most plausible explanation for female aptery in this insect, which must periodically colonize new host trees located a long distance away, is that some broods of *E. pacificus* contain wingless females, which attack scolytids in the tree from which the parasite emerged, while other broods are winged to allow dispersal over long distances. Since a new supply of scolytid larvae of suitable size is constantly produced through much of the summer in a single tree, one would expect broods of wingless females in the summer, minimizing dispersal losses and maximizing efficiency in host utilization, followed by an overwintering generation in which the females would be winged. All specimens that emerged from the galleries of *Cryphalus pubescens* had overwintered and all were winged.

## *Doryctes*

The host records cited by Marsh (1969) indicate that *Doryctes* parasitizes buprestids and cerambycids. Two species have been definitely associated with Douglas-fir. No specimens of this genus were taken in the Cedar River watershed in 1972.

*Key to the species of Doryctes associated with Douglas-fir*

1. Ovipositor at least as long as body . . . . . . . . . . . . *pacificus*

1'. Ovipositor only slightly longer than abdomen . . . . . . . . *fartus*

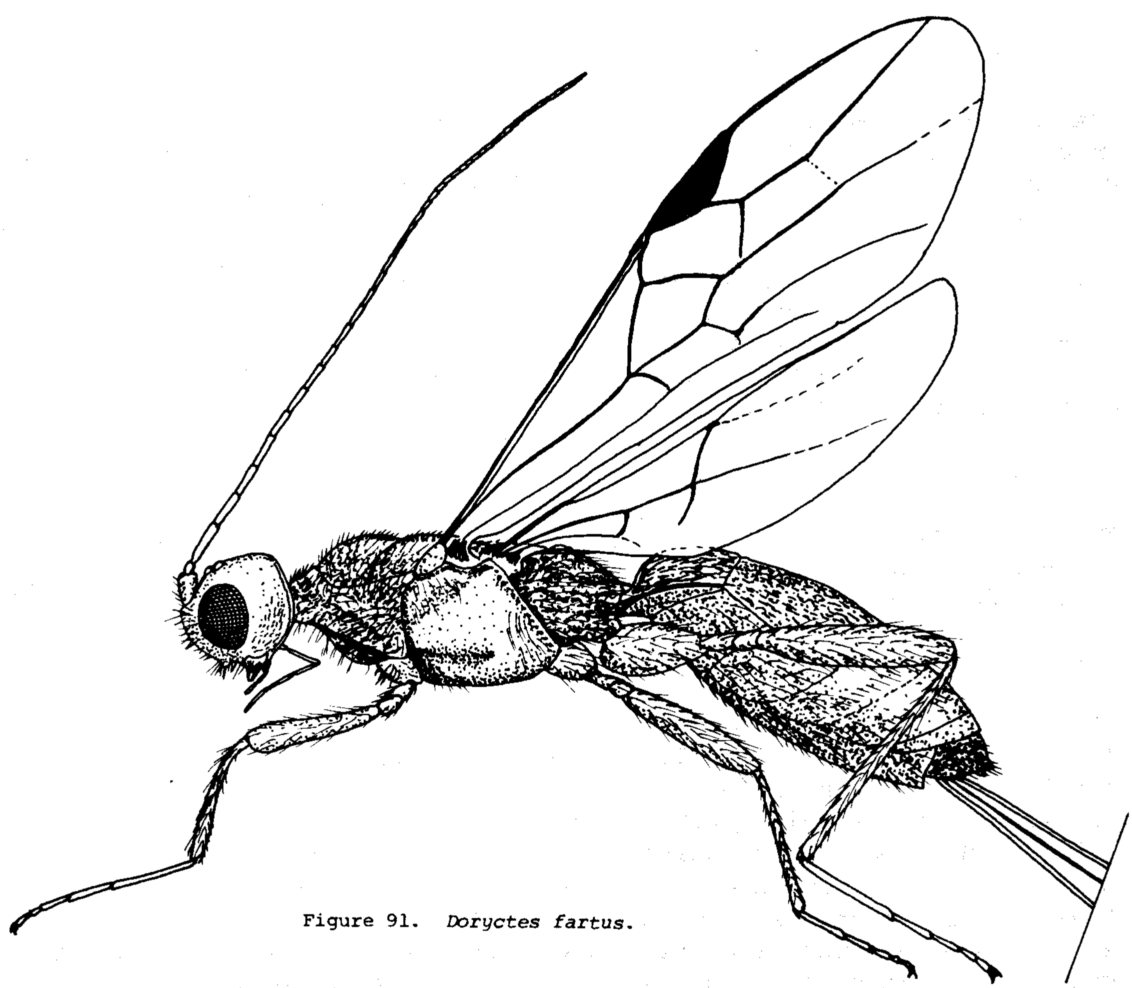


Figure 91. *Doryctes fartus*.

*Doryctes pacificus*

The only known host of *Doryctes pacificus* is *Dicerca* sp. in *Cercocarpus ledifolius;* the insect hosts of specimens associated with Douglas-fir and *Pinus attenuata* are unknown (Marsh 1969).

*Doryctes fartus*

Bedard (1938) reared *D. fartus* from white papery cocoons found in the galleries of unspecified buprestids. During the present study about 20 specimens of *D. fartus* were reared from small, unidentified cerambycids and buprestids under the bark of semiexposed Douglas-fir and *Tsuga heterophylla*. In western Washington the male of *D. fartus* is completely black except for the legs, which are partially fulvous. The abdomen of the female is dark-brown apically and basally instead of red.

## *Bracon*

There are more than 80 Nearctic species in the genus *Bracon*, formerly known as *Microbracon*. Hosts include numerous species of Lepidoptera, Coleoptera, and Hymenoptera. *Bracon pini* is the only species reported from dead Douglas-fir.

*Bracon pini*

*Bracon pini* previously has been associated with a number of weevil hosts in leaders of live conifers. These hosts include *Cylindrocopturus longulus*, *Pissodes strobi* (Muesebeck et al. 1951), *P. terminalis* (Krombein and Burks 1967), *P. sitchensis*, and *Podapion gallicola* (Krombain 1958). These insect hosts imply certain tree hosts: *Pinus strobi, P. contorta,* and *Picea sitchensis*.

In the present study numerous specimens of *B. pini* were reared from *Pissodes fasciatus* in Douglas-fir, and one specimen from an unidentified species of *Pissodes* in *Tsuga heterophylla*. These specimens were determined using Muesebeck's key (1925). A series of specimens reared from *Pissodes sitchensis* in the terminal leaders of *Picea sitchensis* were also determined as *B. pini*, and comparison of these specimens with those from Douglas-fir did not reveal any obvious differences.

Superficially, it seems unlikely that a parasite would be found both in leaders of live trees and under bark of dead trees, but there is additional evidence that *B. pini* is an unusually unspecialized parasite. In a very thorough study of *B. pini* parasitizing *Pissodes strobi*, Taylor (1929) remarks that *B. pini* does not seem highly specialized for effective parasitism of *Pissodes strobi*. The peak of emergence of *B. pini* is several weeks to a month before the optimum time for oviposition on host larvae. Newly emerged wasps are ready to oviposit and often attack undersized larvae. Studies of the oviposition of *B. pini* showed that eggs were sometimes laid in cells lacking weevil larvae or in cells containing dead larvae. The eggs are easily dislodged by the host and may be left

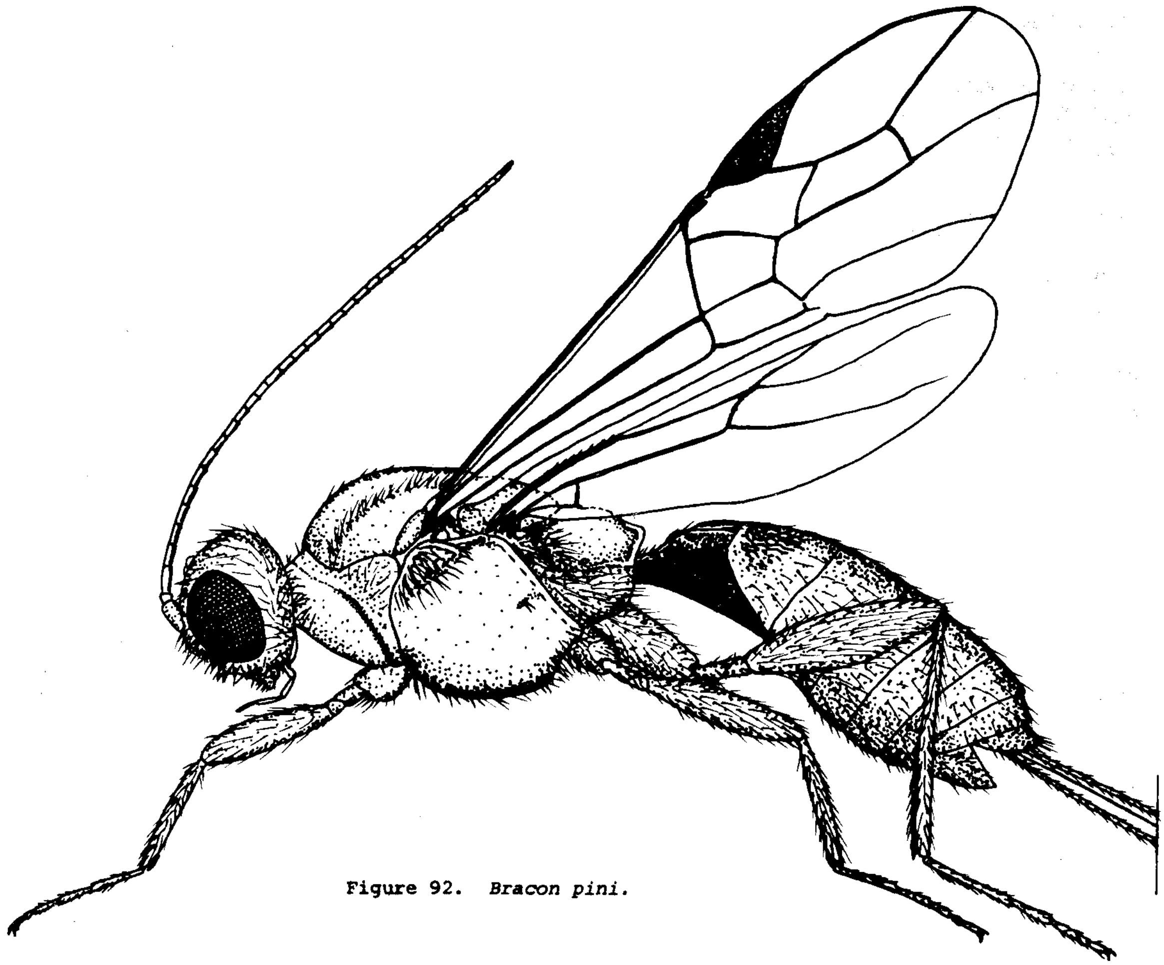


Figure 92. *Bracon pini.*

behind in the frass as the weevil continues its gallery. More eggs may be laid on the host larva than can develop to maturity on the limited food supply. The cocoons of *B. pini* are particularly vulnerable to predation by birds.

This apparently unadaptive behavior is more understandable if it is assumed that *B. pini* normally attacks both *Pissodes* that are subcortical in dead trees, and *Pissodes* that attack leaders. Since the subcortical host, such as *P. fasciatus,* overwinters in the larval stage as well as in the adult stage, there is an abundant supply of hosts in early spring for the emerging *Bracon pini,* although many of the host larvae may be concealed by bark that is too thick for the parasite to penetrate. Emerging from these hosts a few weeks later, the second generation of parasites is ready to attack the much more accessible larvae of a *Pissodes* that lives in leaders, such as *Pissodes sitchensis.* Since subcortical *Pissodes* are usually much larger than *Pissodes* found in leaders, it would not be surprising if the wasp tended to overparasitize the smaller host.

It is also possible that the specimens of *Bracon* taken on Douglas-fir are a different species from those reared from spruce leaders. The various species of *Pissodes* are so similar that it is often almost impossible to separate them by morphological characteristics, and it would not be remarkable if sibling species of *Bracon* had evolved along with each of several *Pissodes* species.

Taylor (1929) has published a careful report of the mating and oviposition behavior of *B. pini*. The description of mating suggests that the male is attracted at short range by a pheromone that immediately induces attempts at copulation. Taylor mentions that the females tend to strongly resist the mating attempts of the male, but it is possible that these resisting females were no longer virgins and thus were unreceptive. In a report of the oviposition behavior of *B. pini*, Taylor (1929) states that the female *B. pini* taps the bark with her ovipositor and applies the maxillary and labial palpi to the surface of the bark, while the antennae alternately wave and are motionless. This description suggests a wide range of stimuli are used by *B. pini* to locate its host. Illustrations of the egg, larva, and adult of *B. pini* appear in Taylor's study (1929).

When *B. pini* parasitizes *Pissodes fasciatus* up to four parasites develop on each host larva. Since *B. pini* has a short ovipositor, it can attack only host larvae that are under thin bark. In such situations *Coeloides brunneri*, normally a parasite of scolytids, also attacks *P. fasciatus* and apparently competes with *B. pini*.

## *Atanycolus*

Members of *Atanycolus*, a genus of braconids associated with Douglas-fir, may be distinguished by the black wings and scarlet abdomen. Small specimens of *Atanycolus* resemble large specimens of the closely related genus *Coeloides*, but the thorax of *Atanycolus* is usually partly orange, while that of *Coeloides* is always completely black. The first antennal segment of *Atanycolus* is very different from that of *Coeloides*.

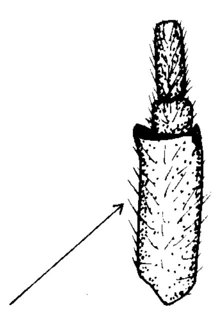


Figure 93. Frontal view of first antennal segment of *Atanycolus*.

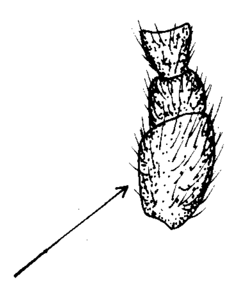


Figure 94. Frontal view of first antennal segment of *Coeloides*.

The taxonomy of the species of *Atanycolus* has been reviewed in detail by Shenefelt (1943) in a monograph that also includes most of the collection data associated with specimens collected in the United States up to 1934. From these collection data, it appears that the life cycle of *Atanycolus* is similar to that of *Coeloides*. The female wasp pierces the bark and stings a wood-boring beetle larva, or perhaps occasionally a pupa. The egg is laid on or near the paralyzed host. The mature larva spins a tan-colored cocoon and overwinters before transforming into a pupa. Adults have been taken all through the summer, suggesting the possibility of more than one generation per year.

Males of *A. longifemoralis* have been taken on trees too recently felled to be producing adult wasps. Thus *Atanycolus* apparently differs from *Coeloides* in that the male leaves its natal tree to search for females. Fragmentary observations of the mating of *Atanycolus* in aspirator bottles indicate that the male advances upon the female with buzzing wings and mounts and mates immediately. Attempts to induce mating behavior in reared specimens were uniformly unsuccessful, even when virgin females of various ages were introduced into containers with numerous males. It is possible that there is a premating requirement for exercise or for the presence of a host tree.

*Key to the species of Atanycolus associated with Douglas-fir (adapted from Shenefelt 1943)*

1. Last segment of antenna conical, apex not shining but covered with fine hairs; first segment of antenna with an emargination at apex when viewed from front (there is a much larger emergination seen from the posterior, or dorsal view) . . . . . . . . . . . . . . . *anocomidis*

1'. Last segment of female truncate and shining; apical segment of antenna of male more pointed, but strongly shining at apex; first segment of antenna of both sexes with emargination on posterior side but lacking emargination in front . . . . . . . . . . . . . . . . . . . . . . . 2

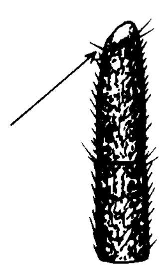


Figure 95. Apical segments of antenna of *Atanycolus longifemoralis*, male.

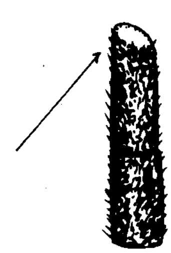


Figure 96. Apical segments of antenna of *Atanycolus longifemoralis*, female.

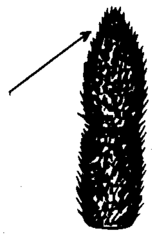


Figure 97. Apical segments of antenna of *Atanycolus anocomidis*, male.

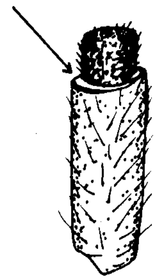


Figure 98. First segment of antenna of *Atanycolus longifemoralis*, showing no apical emargination in frontal view.

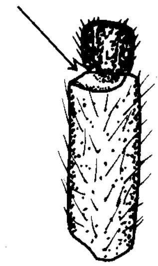


Figure 99. First segment of antenna of *Atanycolus anocomidis*, showing an apical emargination in frontal view.

2. Pronotum and sides of mesothorax darker red than red on middle lobe of mesonotum . . . . . . . . . . . . . *montivagus*

2'. Pronotum and sides of mesothorax same shade of red as red on middle lobe of mesonotum . . . . . . . . . . *longifemoralis*

*Atanycolus anocomidis*

*Atanycolus anocomidis* is associated with *Pseudotsuga menziesii, Abies concolor, A. lasiocarpa, A. amabilis, Pinus lambertiana, P. ponderosa, P. contorta, Picea parryana, P. sitchensis, Larix occidentalis,* and "cedar" (Shenefelt 1943). Known insect hosts are *Melanophila drummondi, Graphisurus* sp., *Semanotus ligneus,* and *Buprestis subornata* or *B. rusticorum* (Shenefelt 1943). During this study, a single specimen of *A. anocomidis* was taken in May on a small, standing, dead Douglas-fir near Bremerton, Washington.

*Atanycolus longifemoralis*

*Atanycolus longifemoralis* has been reported from *Pseudotsuga menziesii, Abies concolor, A. magnifica, Pinus ponderosa,* and *Larix occidentalis* (Shenefelt 1943). In the Cedar River watershed, *A. longifemoralis* was observed on *Tsuga heterophylla* and Douglas-fir. Insect hosts include *Melanophila drummondi, M. gentilis, Chrysobothris* sp., and *Hylotrupes* sp. (Shenefelt 1943).

Numerous specimens of *A. longifemoralis* were reared from Douglas-fir infested with *Melanophila drummondi;* the material was obtained in Willard, Washington. *Atanycolus longifemoralis* and the majority of the buprestid hosts emerged almost simultaneously, suggesting the possibility that the female parasites may emerge early in the spring, parasitize all available hosts, and thus produce a second generation that attacks hosts in midsummer. There is no known information that would indicate the ecological differences between *A. longifemoralis* and *A. anocomidis*.

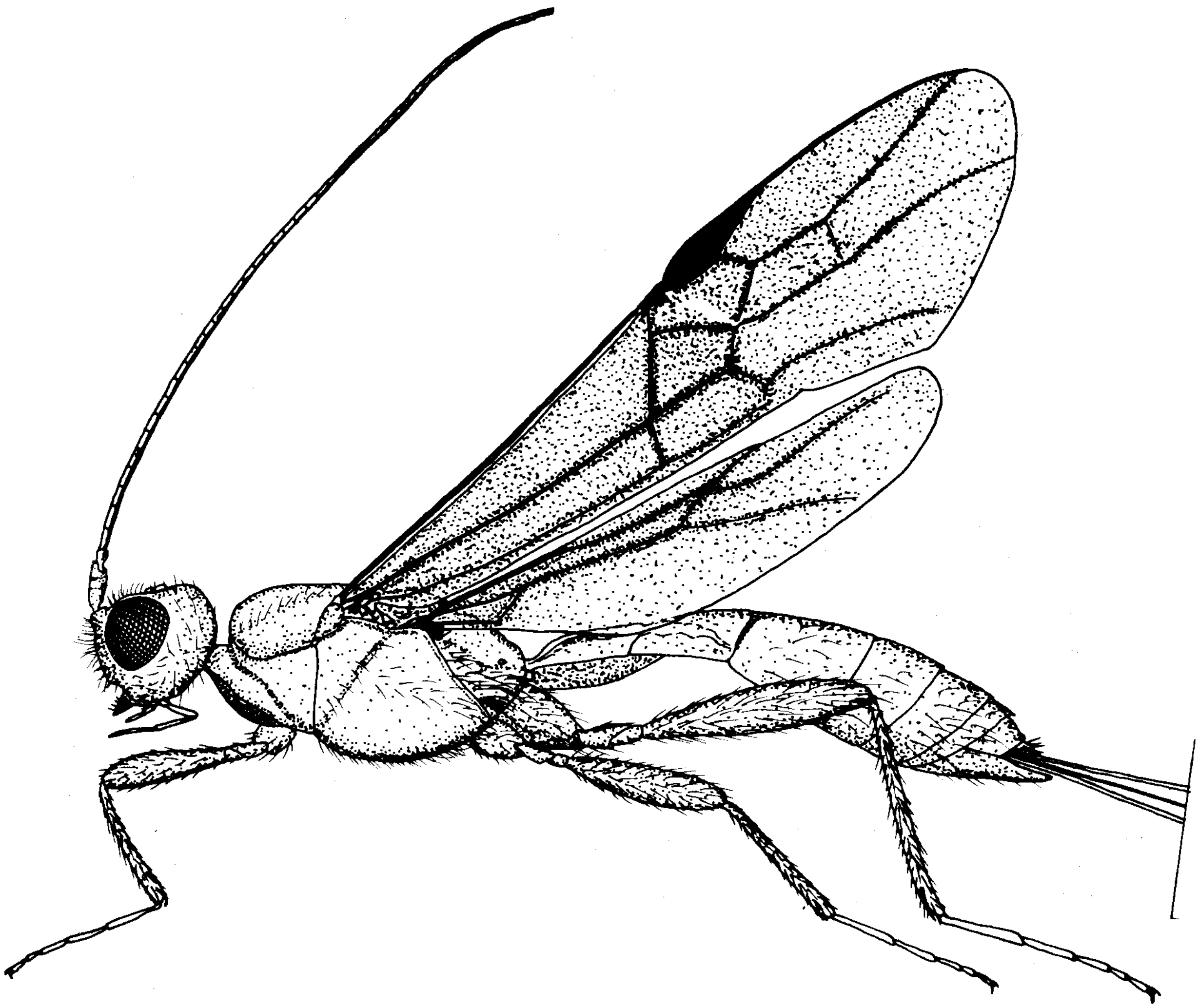


Figure 100. *Atanycolus longifemoralis.*

*Atanycolus montivagus*

*Atanycolus montivagus* is reported by Bedard (1938) from Douglas-fir; there are no other reported associations with trees or host insects. Shenefelt, who seems to have examined many of Bedard's specimens, makes no mention in his monograph (1943) of the occurrence of this species in Douglas-fir; moreover, the known distribution of *A. montivagus* seems outside of Bedard's collecting range. *Atanycolus montivagus* very closely resembles *A. longifemoralis,* not described at the time of Bedard's report, and has been confused with *A. anocomidis,* as some of the *A. montivagus* paratypes at the time of Shenefelt's investigation were actually *A. anocomidis.* Although Bedard lists three *Atanycolus,* two of them unnamed, associated with Douglas-fir, it seems probable that his *A. montivagus* specimens may actually have been *A. anocomidis* or *A. longifemoralis* and that the extreme variability in coloration among these latter species resulted in their being interpreted as three species.

## *Coeloides*

Because of its great importance as a parasite of scolytids, *Coeloides* is the most thoroughly studied genus of Hymenoptera occurring on dead and dying Douglas-fir. Two species occur on Douglas-fir.

*Key to species of Coeloides associated with Douglas-fir*

1. Head partially or entirely red-orange . . . . . . . . . . *brunneri*

1'. Head completely black . . . . . . . . . . . . . . . . . . *dendroctoni*

*Coeloides brunneri*

*Coeloides brunneri* shows great variation in sculpturing and coloration, variations that are correlated with differences in size, which in turn are dependent upon the size of the host consumed by the braconid larva. This variation has caused some confusion and synonomy, hence Bedard (1938) lists four different species of *Coeloides* on Douglas-fir. Large specimens, such as those that have developed on mature larvae of *Dendroctonus pseudotsugae*, tend to have completely red-orange heads, mostly red abdomens, and more abdominal sculpturing. Smaller specimens, such as those that occasionally emerge from galleries of *Pseudohylesinus nebulosus*, tend to have dark heads, dull orange-brown abdomens, and reduced abdominal sculpturing. When viewed from above, these small specimens might easily be confused with *C. dendroctoni*, as the top of the head is almost completely black.

*Coeloides brunneri* attacks a long series of hosts. Published records of hosts (Richerson and Borden 1972a) include *Melanophila drummondi*, *Conophthorus monophyllae*, *Dendroctonus ponderosae*, *D. pseudotsugae*, *Ips calligraphus*, *Ips paraconfusus*, *Pseudohlesinus granulatus*, *P. nebulosus* (Richerson and Borden 1972a cite *P. menziesii*, undoubtedly a misprint for *P. nebulosus*), *Scolytus tsugae*, and *S. ventralis*. In the Cedar River watershed, one additional host, *Pissodes fasciatus*, has been found. *Coeloides brunneri* was observed on *Pseudotsuga menziesii*, *Tsuga heterophylla*, and *Pinus ponderosa*; there are undoubtedly many other tree associations.

*Coeloides brunneri* is not the indiscriminate parasite the above host records suggest; on the contrary, the ovipositing female has highly specific habitat and host size preferences that limit its range of normal hosts. Oviposition normally takes place only in fairly deep shade (Ryan and Rudinsky 1962); this observation means that *Melanophila drummondi*, *Scolytus ventralis*, and other hosts occurring in sunlit portions of the tree bole are abnormal hosts. Of course, only those hosts can be parasitized that occur under bark no thicker than the length of the *Coeloides*

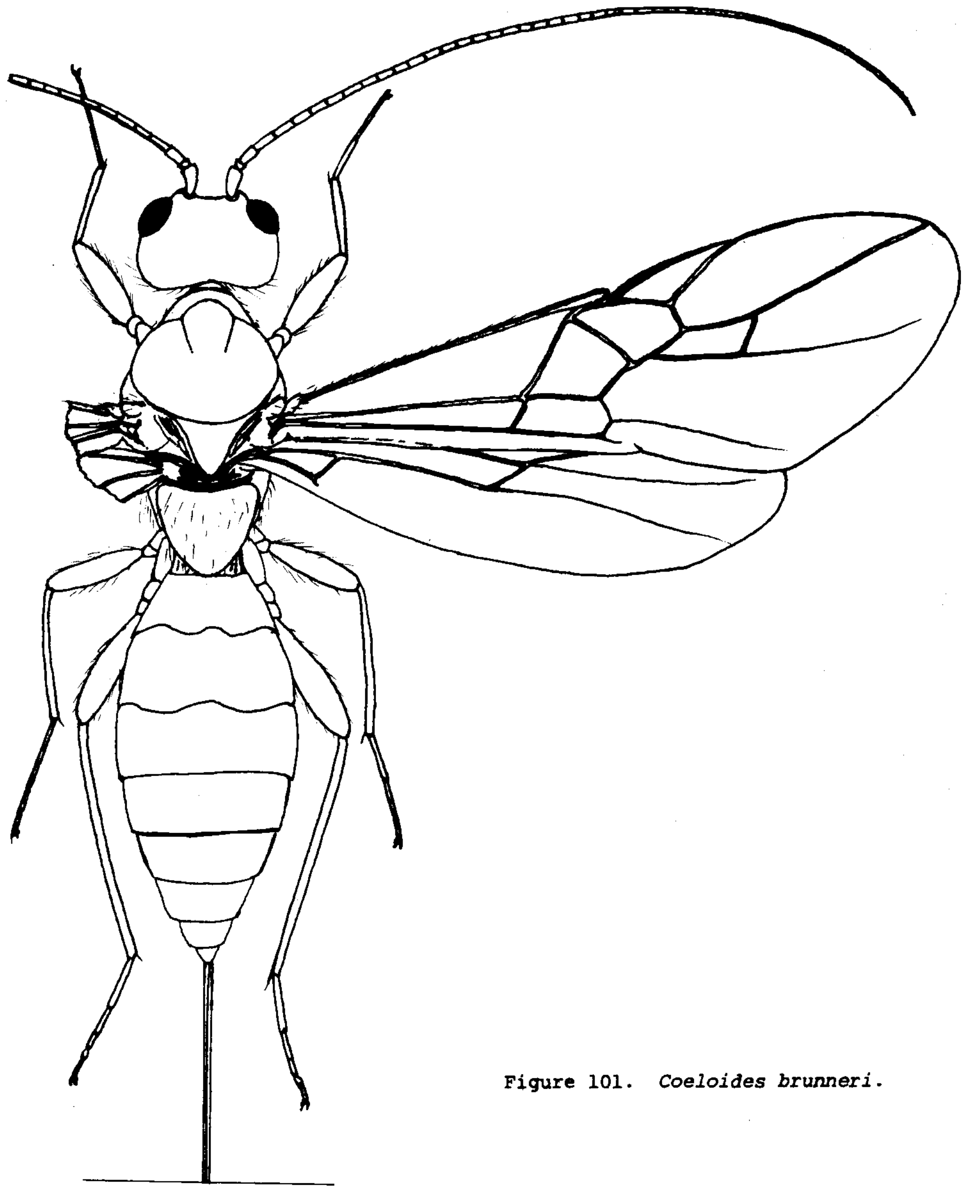


Figure 101. *Coeloides brunneri*.

ovipositor. Finally, the ovipositing *Coeloides* usually requires that the host be a certain size, approximating that of a third or fourth instar larva of *Dendroctonus pseudotsugae* (Ryan and Rudinsky 1962). This means that larvae of *Scolytus tsugae*, *S. ventralis*, *Conophthorus monophyllae*, and *Pseudohylesinus nebulosus*, and perhaps others of the hosts mentioned above, are not normal hosts. The diminutive *C. brunneri* males that were reared from *Pseudohylesinus nebulosus* undoubtedly would be at a severe disadvantage competing for mates with other males three times their size. The few females that have emerged from galleries of *Pseudohylesinus nebulosus* have ovipositors proportional to their body size, which means that the ovipositor would be too short to attain the galleries of their staple host, *Dendroctonus pseudotsugae*. The evolution of a small *Coeloides* species normally parasitizing small scolytids probably has been precluded by prior occupation of that niche by *Spathius*.

The life history of *C. brunneri* has been very nicely worked out by Ryan (1961), and a summary of this information has been published (Ryan and Rudinsky 1962). *Coeloides brunneri* is an external parasite; the larvae devour a beetle grub that has been paralyzed by the parent wasp just before oviposition. Only one parasite develops in each host larva. The mature larva spins a light tan cocoon.

Ryan (1961) found that in Oregon *C. brunneri* is multibrooded, with some larvae of each generation going into diapause until spring. These diapausing larvae comprise 5%, 50%, and 95%, respectively, of the first, second, and third generations. The system ensures a supply of ovipositing females throughout the time when suitable *Dendroctonus* larvae are available, a supply of females that is actually proportional to the number of susceptible hosts. Ryan (1961) suggests that light regimes during oviposition somehow determine whether the offspring, upon maturity, spin a thicker cocoon, go into diapause, and overwinter as larvae; or whether they spin a thinner cocoon, pupate immediately, and emerge during the latter part of the summer.

Ryan (1961) reports that mating occurs as soon as the female emerges; the males, at least those of the diapausing brood, emerge slightly earlier. The female mates only once, and becomes unattractive and unreceptive if she remains unmated for more than a day (Ryan 1961).

The method employed by *Coloides* to find a host has been the subject of an interesting series of investigations. It was at first suggested (Ryan 1961) that the sound of the host larva eating was the clue needed for oviposition. This theory was disproved by Richerson and Borden (1971), who demonstrated that *C. brunneri* was able to locate dead host larvae. A second article by the same authors (1972a) ruled out involvement of odor, magnetism, and sound. In a third publication, Richerson and Borden (1972b) showed that the bark immediately above a feeding larva of *D. pseudotsugae* is about a degree warmer than surrounding areas, and that *C. brunneri* attempted to oviposit on artificially created warm areas obtained by heating the bark from below by wire coils the same size as a *Dendroctonus* larva. Richerson and Borden (1972b) postulate that oviposition on dead larvae (Richerson and Borden 1971) was prompted by heat resulting from decomposition of the larvae. It seems unlikely that such delicate temperature gradients could be detected unless the temperature of the bark surface as a whole was particularly uniform, thus further restricting oviposition to shaded areas of the bark. It would be interesting to know whether *Atanycolus*, a close relative of *Coeloides*, normally waits until the sun is off the tree bole before ovipositing on its host, *Melanophila drummondi*, an insect confined to exposed portions of the tree.

Yet a further refinement of host selection is practiced by *Coeloides*. The female is able to distinguish between larger and smaller host larvae and, by retention of sperm, tends to lay male eggs upon the smaller larvae (Ryan 1961). As mentioned above, smaller hosts produce smaller parasites; small size is much less of a handicap for the male than it is for the female, who must have energy supplies to find a new host and to manufacture eggs, and whose ovipositor must be of a certain length or the choice of host larvae will be severely limited.

Two questions remain about the host-seeking activities of *C. brunneri*. The first is the problem of how this parasite locates an infested tree. The observation in the Cedar River watershed of *C. brunneri* patrolling freshly cut trees not yet attacked by any scolytids suggests tree odors may be important. The other question is, how does this species avoid multiple parasitism? Presumably the ovipositing female releases a pheromone that notifies other females that the host is already parasitized, but the presence of such a pheromone has yet to be demonstrated.

*Coeloides dendroctoni*

Like *C. brunneri, C. dendroctoni* has a long series of recorded hosts. These include (Richerson and Borden 1972a) *Dendroctonus ponderosae, D. piceaperda, D. engelmanni, D. pseudotsugae, Ips emarginatus, I. montanus, I. perturbatus, I. pilifrons, Orthotomicus caelatus*, and *Pityogenes* sp.

Although *C. dendroctoni* and *C. brunneri* share numerous hosts, it is clear (DeLeon 1935) *C. dendroctoni* is primarily a parasite of *Dendroctonus ponderosae* and is uncommon in Douglas-fir. Likewise, *C. brunneri* is the most important parasite of *Dendroctonus pseudotsugae,* a host attacked only occasionally by *C. dendroctoni* (Ryan 1961). It seems logical to assume that when *C. dendroctoni* is locating a tree that may contain hosts it might be principally attracted to pines, and only occasionally light upon Douglas-fir.

It seems obvious that *Dendroctonus ponderosae* and *D. pseudotsugae* cannot be parasitized efficiently by the same braconid. *Dendroctonus ponderosae* overwinters primarily in the larval stage; this determines the attack strategy of *C. dendroctoni* as described by De Leon (1935). The first generation of *C. dendroctoni* on a tree recently infested by *Dendroctonus ponderosae* attacks such mature host larvae as are present in the late summer. A second, larger generation of parasites emerges the following spring and immediately attacks the mature larvae present in the same tree. Of the resulting female offspring, some emerge late that same summer and fly to new host trees, but most overwinter as larvae and emerge the following summer, when they fly to trees that had been attacked by beetles the previous year. This attack strategy of *C. dendroctoni* is much more complex than that of *C. brunneri,* which may be summarized by stating that all overwintering female parasites must fly to new trees, while all nonoverwintering females can find hosts in the tree from which they emerged. *Coeloides dendroctoni* and *C. brunneri* will continue to be reported in the literature as parasites of the same *Dendroctonus* species, but in the field *Coeloides* normally will continue to discriminate between hosts (or between host trees) in order to benefit from the delicate synchronization of life cycles of each parasite and its respective host.

The bionomics of *C. dendroctoni* have been described by DeLeon (1935); the basic biology of this species seems to resemble closely that of *C. brunneri* discussed above. It seems justified to assume that the two species use similar mechanisms to find their host larvae.

# DIAPRIIDAE

Only one genus in the family Diapriidae is associated with dead Douglas-fir.

## *Psilus*

Frequently discussed under the name *Galesus,* the genus *Psilus* differs from all other northwestern diapriids in having both a folded forewing and an elongated head. *Psilus silvestrii* is the only species in this genus that has been studied in any detail. *Psilus silvestrii* oviposits through the puparium of its trypetid host; the egg hatches into a larva that has a large sclerotized head and strong curved mandibles lacking in instars that follow (Clausen 1940). Pupation takes place within the host puparium, which is eventually abandoned by splitting along the sutures intended for the use of the adult host (Clausen 1940). Illustrations of the larva and adult of *P. silvestrii* may be found in Clausen (1940). Only one species of *Psilus* is reported from Douglas-fir; a key to most of the known species of Nearctic *Psilus* appears in Brues (1906).

### *Psilus atricornis*

Bedard (1938) reports *P. atricornis* emerging in August from the cocoons of *Lonchaea corticis* in Douglas-fir. DeLeon (1934) mentions *Psilus*

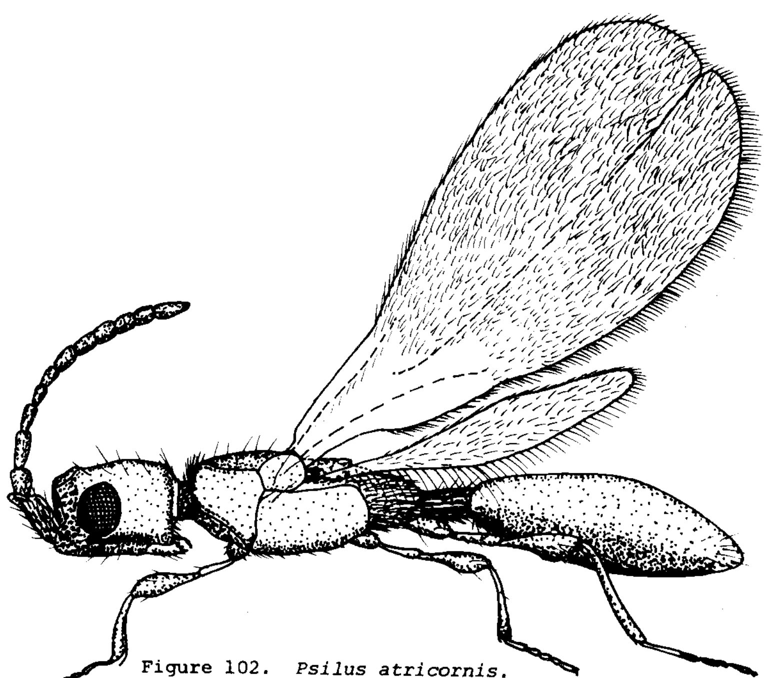


Figure 102. *Psilus atricornis.*

*"nigricornis"* in Ponderosa pine. It seems certain that *"nigricornis"* is the same as *"atricornis,"* as the names are similar in appearance and meaning, and there never has been a species named *Psilus nigricornis*. DeLeon's specimens were reared in October from the skin of a fly, probably a psychodid. This evidence suggests that *P. atricornis* may attack a wide range of dipterous hosts, perhaps including *Medetera*.

In the Cedar River watershed, *P. atricornis* was captured on traps on cut Douglas-fir from May through early August of 1972. One specimen was taken under the bark of *Tsuga heterophylla*, and another was observed entering and leaving a *Dendroctonus* gallery in Douglas-fir.

## IBALIIDAE

There is only one North American genus in the family Ibaliidae.

### *Ibalia*

Members of *Ibalia* are parasites of siricids and as such have received considerable attention in Europe and Australia. A study of a European species of *Ibalia* shows that the female wasp inserts her ovipositor down the oviposition hole made by the host and lays an egg inside the egg or small larva of the host (Spradbery 1970b). The *Ibalia* larva develops inside the siricid larva, emerging only when mature (Spradbery 1970b). Good illustrations of the egg, larva, and adult of *Ibalia*, as well as photographs of oviposition behavior, appear in the study by Spradbery 1970b).

*Ibalia* species have been shown to be strongly attracted by substances associated with the symbiotic fungus of the siricid host (Spradbery 1970b, Madden 1968). In a study (Madden 1968) that involved both *Ibalia* and the ichneumonids *Rhyssa* and *Megarhyssa* parasitizing siricids, it was shown that all three parasites are attracted and stimulated to oviposit by substances present in the same fungal cultures; but in tests with actual billets infested with siricids, *Ibalia* preferred those billets that had been infested for two to three weeks, while the ichneumonids showed little response to billets that had been infested for less than five months. Only one species of *Ibalia* is associated with Douglas-fir.

#### *Ibalia ensiger*

Bedard (1938) reports that one specimen of *Ibalia ensiger* was collected in June on a Douglas-fir infested with *Dendroctonus pseudotsugae*. Wickman (1964) found large numbers of *I. ensiger* associated with *Sirex areolatus* in *Libocedrus decurrens* killed by fire. Wickman (1964) mentions that *I. ensiger* is also found in other tree hosts. *Ibalia ensiger* probably has a life cycle lasting two or three years (Wickman 1964). It appears that *I. ensiger* is normally a rather rare insect; it has not been taken in the Cedar River watershed.

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## APPENDIX

### I. ALTERNATE TREE HOSTS OF SPECIES OF HYMENOPTERA ASSOCIATED WITH DEAD DOUGLAS-FIR

#### *Pinus attenuata*

*Doryctes pacificus*
*Pristaulacus editus*

#### *Pinus contorta*

*Atanycolus anocomidis*
*Bracon pini*
*Camponotus herculeanus*
*Cecidostiba dendroctoni*
*Coleocentrus occidentalis*
*Dolichomitus terebrans*
*Eurytoma pissodis*
*Formica rufa*
*Helcostizus albator*
*Megarhyssa nortoni*
*Rhopalicus pulchripennis*
*Rhyssa alaskensis*
*Roptrocerus xylophagorum*
*Sirex areolatus*
*S. californicus*
*Spathius aphenges*
*Urocerus californicus*
*Xeris morrisoni*
*X. spectrum*

#### *Pinus echinata*

*Cecidostiba dendroctoni*
*Heydenia unica*
*Rhopalicus pulchripennis*

#### *Pinus edulis*

*Rhyssa persuasoria*
*Xorides insularis*

#### *Pinus elliottii*

*Heydenia unica*
*Rhopalicus pulchripennis*

#### *Pinus jeffreyi*

*Megarhyssa nortoni*
*Sirex areolatus*
*S. californicus*

#### *Pinus lambertiana*

*Apistephialtes dentatus*
*Atanycolus anocomidis*
*Macromesus americanus*
*Sirex areolatus*
*Spathius aphenges*

#### *Pinus monophylla*

*Dendrosoter scaber*

#### *Pinus montana*

*Dolichomitus foxleei*
*Macromesus americanus*

#### *Pinus monticola*

*Cecidostiba acuta*
*C. dendroctoni*
*Roptrocerus xylophagorum*
*Urocerus californicus*
*Xorides insularis*

#### *Pinus palustris*

*Cecidostiba dendroctoni*
*Heydenia unica*

*Pinus ponderosa*

*Atanycolus anocomidis*
*A. longifemoralis*
*Cecidostiba acuta*
*C. burkei*
*Coeloides brunneri*
*C. dendroctoni*
*Dolichomitus foxleei*
*Ecphylus pacificus*
*Macromesus americanus*
*Megarhyssa nortoni*
*Neoxorides borealis*
*Orussus occidentalis*
*Pristaulacus minor*
*P. rufitarsus*
*Psilus atricornis*
*Rhyssa persuasoria*
*Sirex californicus*
*Spathius aphenges*
*Xeris morrisoni*
*X. spectrum*
*Xorides cincticornis*
*X. insularis*

*Pinus radiata*

*Aplomerus robustus*
*Cecidostiba acuta*
*Ecphylus pacificus*
*Sirex areolatus*

*Pinus resinosa*

*Camponotus herculeanus*

*Pinus strobus*

*Bracon pini*
*Camponotus herculeanus*
*Eurytoma pissodis*
*Rhopalicus pulchripennis*

*Pinus taeda*

*Cecidostiba dendroctoni*
*Heydenia unica*
*Rhopalicus pulchripennis*

*Pinus virginiana*

*Dolichomitus terebrans*

*Abies amabilis*

*Atanycolus anocomidis*
*Xorides insularis*

*Abies balsamea*

*Rhyssa lineolata*
*R. persuasoria*
*Sirex cyaneus*
*Urocerus albicornis*
*U. californicus*
*Xeris spectrum*

*Abies concolor*

*Atanycolus anocomidis*
*A. longifemoralis*
*Cecidostiba acuta*
*Cheiropachus brunneri*
*Dolichomitus foxleei*
*Ecphylus arcuatus*
*Macromesus americanus*
*Megarhyssa nortoni*
*Neoxorides borealis*
*Pristaulacus minor*
*P. rufitarsus*
*Rhyssa persuasoria*
*Sirex cyaneus*
*Urocerus californicus*
*Xorides insularis*

*Abies fraseri*

*Sirex cyaneus*
*Urocerus albicornis*

*Abies grandis*

*Cecidostiba acuta*
*C. thomsoni*
*Cheiropachus quadrum*
*Megarhyssa nortoni*
*Spathius aphenges*
*Xeris morrisoni*
*X. spectrum*

*Abies lasiocarpa*

*Atanycolus anocomidis*
*Dolichomitus terebrans*
*Megarhyssa nortoni*
*Neoxorides borealis*
*Rhyssa alaskensis*
*R. lineolata*
*Sirex cyaneus*
*Urocerus albicornis*
*U. californicus*
*U. gigas flavicornis*
*Xeris morrisoni*
*X. spectrum*

*Abies magnifica*

*Atanycolus longifemoralis*
*Dolichomitus terebrans*
*Megarhyssa nortoni*
*Pristaulacus minor*
*Urocerus californicus*
*Xeris morrisoni*

*Abies procera*

*Roptrocerus xylophagorum*

*Picea engelmannii*

*Apistephialtes dentatus*
*Dolichomitus terebrans*
*Eubadizon crassigaster*
*Neoxorides pilulus*
*Xorides insularis*

*Picea glauca*

*Sirex cyaneus*

*Picea parryana*

*Atanycolus anocomidis*
*Xorides insularis*

*Picea pungens*

*Xeris morrisoni*
*X. spectrum*

*Picea sitchensis*

*Atanycolus anocomidis*
*Bracon pini*
*Cecidostiba acuta*
*C. burkei*
*Dolichomitus terebrans*
*Ecphylus pacificus*
*Eubadizon crassigaster*
*Leptothorax acervorum*
*Megarhyssa nortoni*
*Pristaulacus minor*
*Rhyssa alaskensis*
*R. lineolata*
*Urocerus albicornis*
*U. californicus*
*U. gigas flavicornis*
*Xeris morrisoni*
*X. spectrum*
*Xorides insularis*

*Tsuga canadensis*

*Pristaulacus rufitarsus*
*Rhyssa lineolata*

*Tsuga heterophylla*

*Apistephialtes dentatus*
*Atanycolus longifemoralis*
*Bracon pini*
*Cecidostiba acuta*
*Coeloides brunneri*
*Dolichomitus foxleei*
*Doryctes fartus*
*Eubadizon crassigaster*
*Leptothorax acervorum*
*Neoxorides borealis*
*Psilus atricornis*
*Roptrocerus xylophagorum*
*Spathius sequoiae*
*Urocerus californicus*
*Xeris morrisoni*
*X. spectrum*
*Xorides insularis*

*Tsuga mertensiana*

*Ecphylus arcuatus*
*E. californicus*
*Pristaulacus rufitarsus*

*Larix occidentalis*

*Atanycolus anocomidis*
*A. longifemoralis*
*Urocerus albicornis*
*U. californicus*
*U. gigas flavicornis*
*Xeris morrisoni*
*X. spectrum*

*Libocedrus decurrens*

*Apistephialtes dentatus*
*Cheiropachus brunneri*
*Ecphylus californicus*
*Ibalia ensiger*
*Neoxorides borealis*
*Sirex areolatus*
*Urocerus californicus*
*Xeris morrisoni*
*Xorides insularis*

*Thuja plicata*

*Cecidostiba acuta*
*Cheiropachus arizonensis*
*Ecphylus californicus*
*Pristaulacus editus*
*Urocerus albicornis*
*Xorides insularis*

*Cupressus macrocarpa*

*Helcostizus albator*
*Sirex areolatus*
*S. californicus*
*Xorides insularis*

*Sequoia sempervirens*

*Ecphylus californicus*
*Sirex areolatus*
*Xorides insularis*

*Chamaecyparis lawsoniana*

*Cheiropachus brunneri*
*Xorides insularis*

*Juniperus occidentalis*

*Cheiropachus arizonensis*

*Juniperus scopulorum*

*Neoxorides borealis*

*Populus tremuloides*

*Orussus occidentalis*
*Pristaulacus rufitarsus*

*Alnus rubra*

*Calosota pseudotsugae*
*Cecidostiba acuta*
*Spathius sequoiae*

*Cercocarpus ledifolius*

*Cheiropachus arizonensis*
*Doryctes pacificus*

*Betula alleghaniensis*

*Perniphora americana*

*Betula papyrifera*

*Perniphora americana*

*Castanea dentata*

*Neoxorides pilulus*

*Rhus diversiloba*

*Helcostizus albator*

II. ALTERNATE TREE HOST GENERA OF HYMENOPTERA ASSOCIATED WITH DEAD DOUGLAS-FIR

| Genus of tree | Number of species of Hymenoptera shared with Douglas-fir |
|---|---|
| *Pinus* | 40 |
| *Abies* | 26 |
| *Picea* | 22 |
| *Tsuga* | 21 |
| *Larix* | 10 |
| *Libocedrus* | 9 |
| *Thuja* | 7 |
| *Cupressus* | 4 |
| *Sequoia* | 3 |
| *Chamaecyparis* | 3 |
| *Juniperus* | 2 |
| *Alnus* | 2 |
| *Populus* | 3 |
| *Cercocarpus* | 2 |
| *Betula* | 1 |
| *Castanea* | 1 |
| *Rhus* | 1 |

## III. ALTERNATE TREE HOSTS OF HYMENOPTERA ASSOCIATED WITH DEAD DOUGLAS-FIR: HIGHER TAXA AND CONCLUSION

| Family of host tree | Number of species of Hymenoptera shared with Douglas-fir[1] |
|---|---|
| Pinaceae | 52 |
| Cupressaceae | 15 |
| Taxodiaceae | 3 |
| Salicaceae | 2 |
| Rosaceae | 2 |
| Fagaceae | 1 |
| Betulaceae | 4 |
| Anacardiaceae | 1 |

| | |
|---|---|
| Conifers | -54 |
| Broad-leaved trees | -10 |

[1]Predictably, alternate tree hosts of Hymenoptera found in dead Douglas-fir are usually rather closely related to Douglas-fir. About two-thirds of the species of Hymenoptera found in dead *Pseudotsuga* also occur in at least one other genus of conifer. Only a few species are found in both conifers and broad-leaved trees. Relatively few species are reported from conifers other than the Pinaceae. Only two species of Hymenoptera are reported only from Douglas-fir and members of the Cupressaceae or Taxodiaceae. Almost all families, most genera, and many species of Hymenoptera reported from dead Pinaceae are discussed in this study. Most families, many genera, and some species of Hymenoptera reported from other dead conifers are discussed. Most families, but few genera and very few species of Hymenoptera occurring in dead broad-leaved trees are discussed.