

AN ABSTRACT OF THE THESIS OF

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Title: A Biological and Systematic Study of the Armored Boreid,

Caurinus decetes, with Comparative Notes on Related Mecoptera

Redacted for privacy

Abstract approved: Dr. J. D. Lattin

Caurinus decetes Russell is a minute, brachypterous scorpionfly which was discovered at Marys Peak, Benton County, Oregon, in 1976, and subsequently described as the only representative of the subfamily Caurininae within the Boreidae (snow scorpionflies). Caurinus decetes is now known to range from the Olympic Peninsula and Northern Cascades in Washington, to northern Lane County, Oregon.

The habitats of C. decetes include moist, forested sites with both coniferous and deciduous canopies. Larvae and adults have been found in bryophytes occurring as epiphytes, or on logs and stumps, and in terrestrial stands of mosses and liverworts.

Feeding studies showed that both adults and larvae of Caurinus are specialized feeders on leafy liverworts (Jungermanniales). Twenty-five species of Jungermanniales in 15 genera were highly acceptable to adults, while 11 species in 10 genera were accepted

slightly, if at all. Adults of C. dectes fed to some degree on two of four genera of the thalloid Metzgeriales, while liverworts of the Marchantiales and Anthocerotae were not accepted at all. Larval feeding preferences paralleled those of adults.

The eggs of C. dectes are glued to the leaves of the host liverworts. Eggs hatch in spring, but some eggs may remain in diapause for a year or more. Larval feeding is within the shoot tissues, and is completed within 2 to 3 months of eclosion. There appear to be 3 larval instars. The fully grown larva constructs a silk-lined pupal cell within or under the substrate.

The pupal molt occurs between July 1 and August 15, adult emergence is between September 1 and October 15. The major period of adult activity extends from eclosion to April. Mating and oviposition may occur through most of this period. There is evidence that some fraction of the adult population may perenniate. The univoltine life cycle, probable perenniation of adults, and extended egg diapause all are unusual within the Boreidae.

The external morphology of larva and pupa, and internal and external morphology of adults are described. The larva is curculioniform, as compared with the scarabaeiform larvae of other Boreidae; the pupa is decticious and exarate.

The most aberrant structures of adult Caurinus (cf. other Boreidae), the short rostrum and retractable postabdomen of the female, are probably adapted to the dorsoventral organization of the host liverworts.

C. dectes is highly specialized, but a number of characters are primitive with respect to other boreids. These characters justify the recognition of Caurinus as the sister-group of all other boreids. Certain characters of C. dectes, including the free cerci of the female, support the view that the Boreidae are not closely related to other mecopteran families.

A Biological and Systematic Study
of the Armored Boreid,
Caurinus dectes, with
Comparative Notes on
Related Mecoptera

by

Loren Kenneth Russell

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". . . There is, however a prudent Moderation to be used in Studies of this kind. The Knowledge of Nature may be ornamental and it may be useful, but if to attain an Eminence in that, we neglect the knowledge and practice of essential Duties, we deserve Reprehension . . . Nicholas Gimcrack, therefore, who neglected the Care of his Family to pursue Butterflies, was the just object of Ridicule."

-Benjamin Franklin, in response to Polly Stevenson's question about the life history of a moth, 6/11/1765.

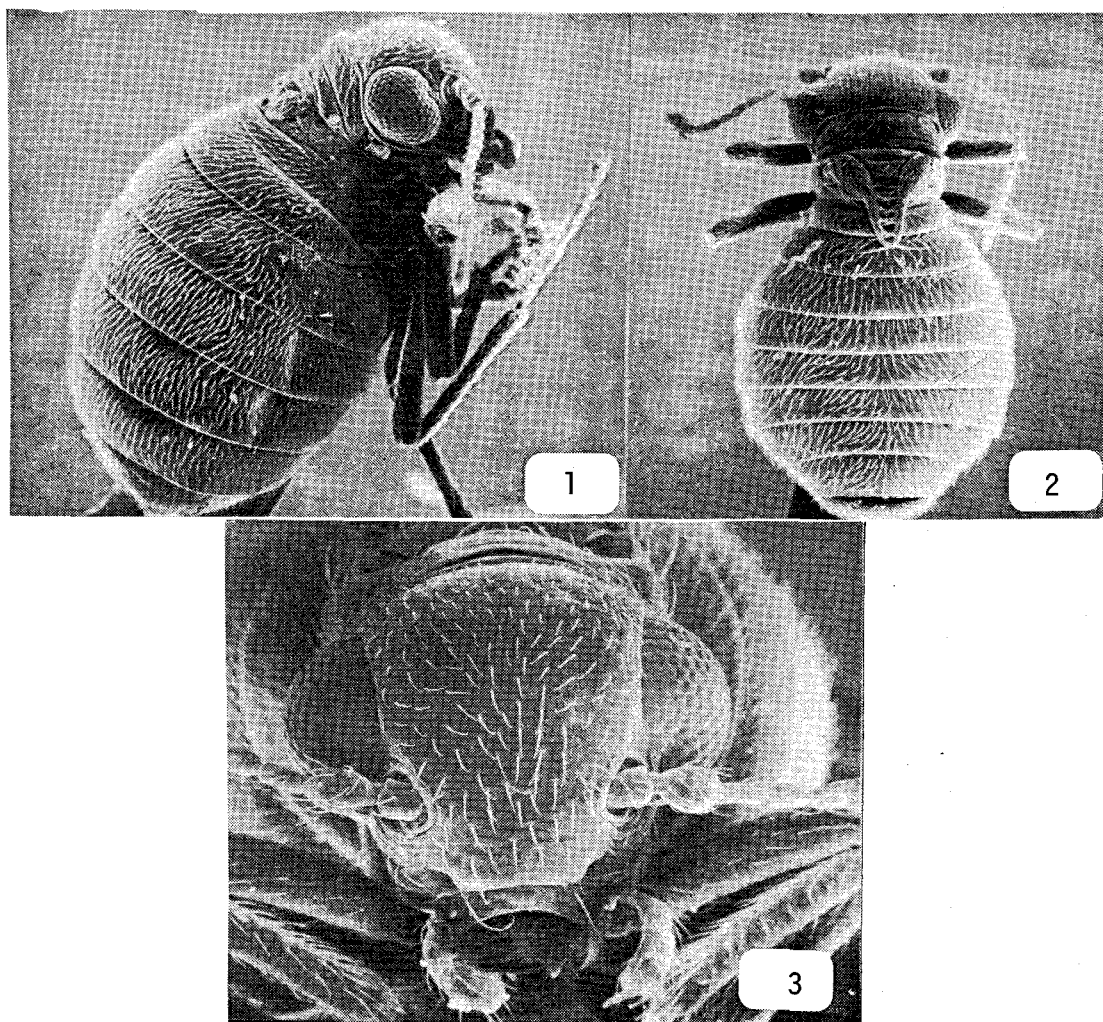
A BIOLOGICAL AND SYSTEMATIC STUDY OF THE
ARMORED BOREID, CAURINUS DECTES, WITH
COMPARATIVE NOTES ON RELATED
MECOPTERA

INTRODUCTION

This study has grown from my chance discovery in early 1976 of an enigmatic insect in forest floor material from the Oregon Coast Range. My initial taxonomic investigation showed that this insect represented an undescribed genus of Mecoptera most nearly related to the "snow scorpionflies" (Boreus, Hesperoboreus)¹ comprising the family Boreidae. This initial study resulted in my description of this insect as Caurinus dectes, and its separation as the only known species of the Caurininae, a new subfamily of the Boreidae (Russell, 1979). The previously known Boreidae belong to the nominate subfamily, the Boreinae; the term "boreine" is frequently used below to refer to attributes known to occur in species of Boreus and Hesperoboreus. Caurinus dectes adults are sharply set apart from other Mecoptera by an extensive list of characters (Table 1). The lack of the characteristic rostrate mouthparts found in most Mecoptera, and the absence of the exserted "ovipositor" of all female Boreinae, and the general extension of sclerotization have made Caurinus hardly recognizable as mecopteran.

Concurrently with the first study of the external morphology of C. dectes, the original site was sampled thoroughly to characterize the habitat occupied by this species as well as to obtain further specimens. Early success in these efforts led to a search for the immature stages and then an expanded study of the life history phenomena and ecological relationships of Caurinus. The discovery that C. dectes is specialized to feed on liverworts resulted in further study of its utilization of this unusual food substrate.

¹ Genera and species are cited in the text of this study without their authors. For the formal citation of these taxa, the faunal and floral lists, Appendix II, page 272, may be consulted.



Figures 1-3. Adult Caurinus dectes.

1) Female, lateral aspect (43X).

2) Male, dorsal aspect (45X).

3) Male, frontal aspect (100X).

The objectives for my study included the following: 1) to establish the habitat distribution, life cycle, and phenology for Caurinus dectes; 2) to investigate the host distribution of Caurinus and relate this to properties of the accepted hosts; 3) to observe feeding, mating, and other behavior of Caurinus; 4) to study the anatomy of all stages of Caurinus, and where possible relate structure to functional adaptations; 5) to compare the information gained with other boreids through the literature and my own observations on the co-occurring Hesperoboreus brevicaudus and other boreids. Additionally, I hoped to gather information on the distribution and feeding of other bryophagous insects of western Oregon. Some of the latter data has been placed in Appendix I (page 262) in order to present the study of Caurinus dectes as the body of this study.

Table 1. Some morphological traits differentiating Caurinus dectes from other known Mecoptera.

Structure	<u>Caurinus</u>	Character State	
		<u>Boreus</u> and <u>Hesperoboreus</u>	Other Mecoptera
Rostrum	very short, broad	very long	moderately long to very long; or short and attenual
Mandible	short; apical teeth large; with broad molar blade	elongate, rela- tively narrow; apical teeth moderate in size; molar blade not differentiated	usually very elongate and narrow
Maxillae	stipes fused medially with labium, trans- verse	stipes fused medially with labium, elongate	stipes not fused
Wings (male)	one pair apparent; short, clasping	two pairs present; elongate, clasping	two pairs; rarely apterous or brachypterous; without clasping modification
Abdomen	segments 2-6 symscleritous	segments 2-6 always with pleural membrane	anterior segments always with pleural membrane
Genitalia (male)	retracted into abdomen aedeagus eversible, with several large sclerites	exposed aedeagus eversible, membranous	exposed, often sting-like genital fold sclerotized, not eversible
Genitalia (female)	segments 9-11 telescoping, retracted into abdomen	segments 9-11 exposed forming rigid functional ovipositor	segments 9-11 exposed, partly telescoping

Specific Identity of Caurinus Populations

As noted above, the genus Caurinus is not closely similar in its morphology to other described Mecoptera. All adult specimens of Caurinus which I have seen to date can clearly be referred to the single species, C. dectes. This conclusion is well-based for the numerous specimens available from the central Oregon Coast Range (principally from localities in Benton, Lincoln, and southern Tillamook Counties). Several other clusters of localities are represented at the north and west sides of the Olympic Peninsula; an area southwest of Mt. Rainier in Pierce and Lewis Counties, Washington; the Nooksack and Stillaguamish River drainages in the North Cascades of Washington; and the western edge of the Columbia River Gorge at Crown Point, Multnomah County, Oregon (Map 1, Table 4).

Two of these population areas are known from very limited collections. Only three intact adults (all female) have been collected on the Olympic Peninsula, and another sample of three (two females, one male) has been taken at Crown Point.

The populations of Caurinus in northwestern and southwestern Washington are better represented in my collection. Sixteen adults have been collected from southwestern Washington, including a series of five males and five females from Morton, Lewis County. These specimens were closely compared with specimens from the type locality of Caurinus dectes (Marys Peak, Benton County, Oregon), and were judged to be conspecific. This comparison considered, but was not limited to, sculpture and vestiture, male wings and genital sclerites, the female abdomen, the head, antenna, and mouthparts. No considerable or consistent differences were found between these population samples.

The northwestern Washington localities (Whatcom and Snohomish Counties) were collected late in this study. A total of twelve adults and fifteen larvae were obtained from these samples. The adults also fall within the range of variation of Oregon Coast Range specimens in the characters examined. In Table 2, Washington

specimens (Snohomish and Lewis Counties) are compared with Caurinus dectes from Marys Peak for several morphometric characters. These small samples are very similar in most of the measurements, for same-sex comparisons. Only the rostrum length falls close to statistical significance; this character is difficult to record accurately, and the supposed difference between samples may be methodological.

In addition to the close agreement between populations in observed morphological characters of the adults, the Caurinus larvae collected in Snohomish County, Washington, closely resembles specimens from the Oregon Coast Range.

There are superficial differences in the ecological distribution of local populations; however, the full range of habitats known for Caurinus are occupied by some local populations where the appropriate substrates occur together. Both adults and larvae, under laboratory conditions, may be transferred from one host plant to another.

Although it is maintained that all observed Caurinus from western Washington and Oregon are conspecific, most of the morphological and behavioral data reported here are derived from Caurinus dectes collected at the type locality (Marys Peak, Benton County, Oregon). Reference to observations on "Caurinus dectes" or simply "Caurinus" without locality attribution, can be assumed to be specific to this population.

Table 2. Morphometric comparison of Caurinus dectes from the Oregon Coast Range and the Washington Cascades (All measurements are presented as means $\pm$ standard deviations in mm.).

Measurement	Oregon population Marys Peak, Benton Co.		Washington populations Snohomish and Lewis Counties	
	Males (n=6)	Females (n=7)	Males (n=8)	Females (n=5)
Body length	1.54 $\pm$.09	1.71 $\pm$.12	1.52 $\pm$.05	1.70 $\pm$.06
Head width	.51 $\pm$.03	.53 $\pm$.02	.49 $\pm$.02	.52 $\pm$.01
Head length (Vertex to labral apex)	.48 $\pm$.01	.50 $\pm$.02	.48 $\pm$.02	.53 $\pm$.02
Rostrum length (Ventral margin of eye to labral apex)	.16 $\pm$.02	.18 $\pm$.01	.145 $\pm$.01	.15 $\pm$.01
Rostrum width (at base of clypeus)	.20 $\pm$.005	.21 $\pm$.02	.20 $\pm$.01	.20 $\pm$.005
Forewing length	.30 $\pm$.01	.13 $\pm$.01	.31 $\pm$.01	.12 $\pm$.005
Abdomen length (base of second segment to apex)	.99 $\pm$.05	1.20 $\pm$.08	1.04 $\pm$.05	1.27 $\pm$.06
Abdomen width	.80 $\pm$.04	.99 $\pm$.06	.81 $\pm$.05	1.00 $\pm$.04
Body width / Body Length	.52	.58	.54	.59
Head Width / Head Length	1.06	1.06	1.02	1.00

METHODS

Most of the technical procedures used in this investigation are simple or well-known, so that little elaboration is required. The explanation of such procedures is integrated into the relevant presentation of results.

The techniques used to locate populations of Caurinus, and to obtain suitable living or preserved specimens, are more specific to this insect, as well as basic for the study as a whole. These methods, and the necessary cultural procedures for maintenance and observation of living specimens, are discussed below. Although most of the following chapters are concerned with Caurinus dectes alone, an effort was made to collect and observe other species of Boreidae in western Oregon. Accordingly, some of the special methods for the study of the boreines are also mentioned in this account.

Collection and Recovery

A number of methods were used to obtain Caurinus and other boreids in the course of this study. These methods included direct search, use of beating sheet or vacuum collector, and use of laboratory-based concentration and extraction techniques: sifting; wet-screening; flotation; and Tullgren funnel extraction. The method of choice at a given time depended on the nature and amount of substrate to be examined, the availability of equipment, and my experience with the various techniques and field situations.

The initial collection of Caurinus dectes was from a mixed sample of terrestrial and epixylic bryophytes from Marys Peak, Benton County, Oregon (22 January 1976). During the winter and spring of 1976 the major method for collection of adult Caurinus was Tullgren funnel extraction of various substrates collected at Marys Peak and other sites. The Tullgren funnel extraction of bryophyte samples continued to be the primary tool for survey for additional populations through the 1976-1977 winter season.

A wet-screening method was developed during the summer of 1976. Thereafter nearly all material from known Caurinus sites was processed in the lab by wet-screening. From June 1977 onward, when the battery of Tullgren funnels was not available for my work, wet-screening was also used as a survey tool.

A beating sheet (one-meter square of canvas supported with a wooden frame) was successfully used for collection of live adult Caurinus and Hesperoboreus during the period February to April 1976. Beating was effective only for recovery from clean, dry epiphytes, and was not time-effective once the wet-screening process was established. The beating sheet continued to be a useful tool for collection of Hesperoboreus and Boreus species.

A portable gasoline-powered vacuum collector was used in the during December 1976. This device, modified from a commercial leaf blower, was equipped with a 6-cm. diameter intake and nylon knee hose here used as sample bag. The vacuum collector was extremely effective for controlled sampling of known substrates for boreids, and unlike the beating sheet, was effectively used on many terrestrial sites. The vacuum sampler was not available on a permanent basis, and was not used further. An advantage for both the beating sheet and vacuum collection was the recovery of H. brevicaudus in good condition. Adults of this species were usually injured during the wet-screen extraction process.

The direct search of host material was useful for location and enumeration of eggs and feeding activity. This method became extremely efficient for survey as well once the general patterns of occurrence of Caurinus were well established by other sampling methods.

Each of the most used sampling methods will be discussed in detail below.

Wet-screening: The most extensively-used extraction method in this study was a wet-screening procedure. The material to be extracted was collected in the field, placed in polyethylene bags, and removed

to the laboratory. Extraction of these samples was often delayed for several days after collection. When the bagged bryophytes were stored at 10° to 12°C , they remained in fresh condition for a week or more. Caurinus and associated arthropods could be recovered in undiminished numbers as long as the substrate remained fresh and moist. These samples deteriorated rapidly if the moss was saturated with water; such samples were allowed to drain overnight before resealing the bags, or were processed immediately.

Each sample of epiphytes (usually from vine maple) was collected from several adjacent branches. Other samples were kept as uniform as possible and were normally taken from a single patch. The approximate area covered by each sample was recorded, where these were taken from large tree boles and log or terrestrial substrates. Samples of epiphytic bryophytes from stems smaller than 10 cm diameter were recorded by the length of stem sampled. Most epiphytic samples represented 2 to 6 meters of stem coverage. On most sample dates, 2 to 5 samples were taken from the Marys Peak Caurinus localities. The amount removed was determined both by the time constraints for processing, and by the need to ration substrates for this destructive sampling method. During 1976 and 1977 the samples were weighed before and after processing, and a sample was sometimes oven-dried to provide an estimate of the substrate dry weight.

Each field sample was divided into 2 to 4 batches for processing. Each batch was placed in a plastic tub, and cold water was sprayed over the moss until the tub was about one-half full. The sample was pulled apart in the water, agitated and removed after squeezing out excess water. The moss sample was then discarded. The remaining suspension was filtered by pouring the contents of the tub through a graded series of soil testing screens (20 cm diameter).

The series of screens which was most generally useful were the ASTM #4, #12, #18, #25, #30 and #40. The indicated numbers are the nominal meshes per inch; the dimensions of retained particles, and material typically retained in this application are listed in Table 3. The finest of the screens (#40) could not be used for samples

Table 3. Dimensions of testing screens used in wet-screen extraction, and material retained in each mesh size.

A.S.T.M. Number	Tyler Screen equivalent size	Mesh Size	Material retained during wet-screen process
4	4	4.75 mm	Coarse moss, wood fragments (discarded)
12	10	1.70 mm	Moss stem segments, large insects (discarded)
18	16	1.00 mm	Adults, large larvae of <u>Hesperoboreus</u> ; some <u>Caurinus</u> adult females
25	24	.71 mm	Most adult <u>Caurinus</u> ; large fragments of <u>Caurinus</u> small <u>Hespero-</u> <u>boreus</u> larvae, large <u>Caurinus</u> larvae
30	28	.59 mm	<u>Hesperoboreus</u> eggs (this screen rarely used)
40	35	.42 mm	Small <u>Caurinus</u> larvae; some <u>Caurinus</u> eggs; <u>Caurinus</u> head capsule; (<u>Caurinus</u> spermatophore, only one)

with large quantities of finely divided material. Adults and larger larvae of both Caurinus dectes and Hesperoboreus brevicaudus passed the #12 screen and were retained by the #18 or #25 screens; the #30 screen caught most of the smaller larvae, and all were recovered by the #40. After the samples were poured through, size-sorting was completed by gently spraying additional water through the screen stack.

Material retained in the #4 and #12 screens was discarded. The residue in each of the finer screens was rinsed into a 600-ml beaker; this graded suspension was concentrated onto an 11-cm filter paper disc in a Buchner funnel. This secondary filtration was manipulated to achieve nearly uniform thickness of the matted debris; the aim was to accumulate no more than a 1-mm thick mat on the filter disc. Surplus moisture was removed from the filter residue by two to five minutes continued suction after the supernatant water had filtered through. The filter disc was then transferred to a 12-cm Petri dish, and both upper and lower surfaces of the matted residue were examined at 6 to 10 X magnification with a stereo microscope. Recovery efficiency was high for boreid adults, pupae and larvae as well as skeletal parts of dead adults, when the mat was no more than 1-mm thick. When large quantities of fine detritus were included in the samples it was extremely tedious to keep the residual mats thin enough for efficient inspection. Under such conditions it was convenient to transfer filter residues to a "high-gradient litter extractor" after only cursory examination of thick mats. This extractor was quite effective in removing most of the active arthropods, including the boreids.

Most specimens of all stages of Caurinus and Hesperoboreus came through the wet-screening process intact, and could be transferred alive to small culture dishes for holding.

Although all material which passed the #12 screen and was retained by the #40 was searched, the intermediate screens were used to ensure more equal particle-size distribution in the residual samples. When the #18, #25 and #40 residues were concentrated and

searched separately, the incidence of clogging the finer screens was reduced, and the more uniform particles allowed easier handling of the fiber residues.

Tullgren funnel operation: The large Tullgren funnels used for the Caurinus survey were operated at the highest practical volume. With 100 W or 75 W incandescent bulbs used as the heat source, most of the boreids could be extracted from a 15 cm to 20 cm layer of loosely packed moss in three days. Very wet moss required four to six days for equivalent recovery.

Most samples were recovered in 70 percent ethanol, but some live specimens were obtained by replacing the preservative with several moist paper towels in the collection jar. Since wet-screening was a more efficient means of recovering live specimens this variant was not continued.

Direct search: It was rarely possible to locate Caurinus or Hesperoboreus adults in the field by examination of the substrate, although this is an effective means of collecting the much larger Boreus elegans and B. californicus. The eggs and feeding damage of C. decetes are more easily located in samples of the host liverworts than are the active stages of the insect. The eggs became a useful means of detecting new populations of Caurinus, since this stage is present on the substrate throughout the year. Search for the eggs can be rapid, and is often successful when very small samples are used. Under optimal conditions of adequate light and no precipitation, eggs could be located on liverwort samples in the field with a hand lens. Samples were selected which (to the unaided eye) appeared damaged by insect feeding; Scapania bolanderi was the most frequently selected substrate. Eggs could be recognized on the clean substrates as dark, elongate objects cemented to the underside of the liverwort leaves.

Samples brought to the laboratory for examination usually required rinsing before examination, since the liverworts were usually

soiled during transport, making the eggs less conspicuous. In samples of Scapania taken from areas of known Caurinus populations, at least one egg could usually be found on 20 shoots examined at random. By such rapid searches samples brought to the laboratory from new areas could be separated according to the likelihood that Caurinus adults were present. In addition, several localities were established through location of the egg alone, and sometimes from very small samples.

Culture methods

Adults and larvae of Caurinus dectes were held for study in Petri dishes of 11 cm diameter (glass) or 5 cm (plastic, with snap-on lid). The dishes were lined with filter paper discs; the paper was moistened and one or more small shoots of Porella navicularis or Scapania bolanderi was added before transferring the adults or larvae into the dish. Usually four to six adults were held in each small dish; up to twelve Caurinus were maintained in the large glass Petri dishes. The liverwort shoots were replaced as necessary, and the filter paper was changed every seven to ten days. The culture dishes were stacked near an east-facing window at my home; the lighting was always indirect during the day. Only dim room light reached the cultures at nights, except when the individual dishes were examined under the microscope.

The temperatures for these cultures during the winter averaged 15-18°C during the day and 10-12°C at night. During April and May, when most larval observations were made, the ambient temperature was higher, but rarely exceeded 22°C during the day, or 15°C at night. Since these temperatures are considerably higher than those experienced in the field populations at the same season, an environmental chamber was used for some cultures. This was less satisfactory than the open shelving. The frequent cooling cycles of the incubator increased the problems with condensation on the walls of the Petri dishes, and the forced air flow accelerated desiccation of the

cultures. Temperatures above 18°C appeared to greatly decrease adult longevity at lower temperatures; humidity control was the more important cultural factor.

The maximum longevity of adults was somewhat greater in the large Petri dishes; this was probably attributable to better ventilation and less exposure of the insects to condensation droplets. The smaller dishes were more convenient for observation of the adults and for confinement of the larvae, and did not dry out as quickly as the standard glass Petri dishes. The small dishes were used almost exclusively after October 1977.

The larvae were also maintained in the small plastic Petri dishes. Generally one shoot terminal of the liverwort host was provided for each larva in the dish; six to ten larvae could be accommodated in one container.

Adults were handled with an aspirator or with fine forceps, while the larvae were induced to cling to a piece of plant material, and then allowed to crawl onto the new substrate.

Pupae of Caurinus were also held in the small Petri dishes. Some were kept alive for up to three weeks, and two individuals initiated the imaginal molt, but none were reared to the adult stage. It appears that an artificial pupal cell would be necessary to allow the imago to free itself from the pupal skin.

Adults, larvae, and pupae of Boreus californicus, B. elegans, and Hesperoboreus brevicaudus were all maintained in the laboratory for observation. Adults of the two Boreus species were kept at 10-15°C in ventilated plastic boxes (20 X 10 X 8 (deep) cm) lined with a mat of host moss (Rhacomitrium heterostichum). Most specimens survived for about three weeks when the moisture level was maintained. Many H. brevicaudus adults were held for observation in the Petri dishes used for maintaining Caurinus. Survival was poor for most lots of Hesperoboreus, with much of the mortality attributable to fungal infection. This species is probably more subject to mechanical damage during the wet-screening extraction than is the more compact C. dectes. Hesperoboreus adults may also be less tolerant of very

high humidity or relatively high temperatures (around 20°C).

Larvae of Boreus elegans and B. californicus occurred together at the collected locality and were not separated in rearing attempts. These larvae can be kept alive for several months in large pads of the terrestrial mosses in which they were found. Only occasional watering of the moss was necessary to prevent desiccation of the larvae. Prepupal larvae and pupae of Boreus were removed to small, sealed plastic boxes (8 X 8 X 2.5 cm). Some adults emerged from these pupae, but there was difficulty in molting when the pupal cells had been damaged. Some Boreus larvae were kept in glass sandwich chambers (designed for study of symphylans, Berry, 1972). Movements of these larvae were observed over short period of time only because a viable moss cover could not be established. More attention was given to the study of H. brevicaudus larvae than Boreus larvae.

The Oregon Coast Range populations of Hesperoboreus occurred in epiphytic mosses, rather than in the soil. Larvae of H. brevicaudus were therefore kept in the small Petri dishes used for the Caurinus study. Both first-instar and grown larvae could be maintained by the addition of any of several pleurocarp mosses from their habitat. Rhytidiadelphus loreus was used most often to feed the Hesperoboreus larvae. The major problems encountered in maintaining these larvae was their tendency to become trapped in condensed water inside the plastic container, and the rapid desiccation of the dishes in warm weather. These problems in humidity control could be avoided by establishing the larvae in sods of Funaria hygrometrica growing in sawdust. Although this moss is unlikely to be available in Hesperoboreus habitats, it appeared to be fully adequate for survival and growth of the larvae. No oviposition was observed by any of the boreines in captivity, and of these, only H. brevicaudus was reared from field-collected eggs.

It is evident from the above account that success in maintenance of the immature boreids is related to the type of substrate utilized and the circumstances of humidity control. Other authors who have discussed rearing of soil-inhabiting larvae of Boreus include

Strübing (1950) and Withycombe (1922). Hesperoboreus notoperates (Cooper, 1974) was maintained in moss which was nearly free of soil. This species differs from H. brevicaudus in that the usual larval hosts (including species of Grimmia, Rhacomitrium and Orthotrichum) form dense cushions. Larvae within these cushions were therefore less subject to rapid desiccation and less likely to escape.

GEOGRAPHIC DISTRIBUTION OF CAURINUS

Caurinus is now known from 35 localities in Washington and Oregon (Map 1; Table 4). Twenty-four of these localities have been established by collection of at least one intact adult C. dectes; seven are known from identifiable skeletal fragments, sometimes associated with eggs and feeding damage; and six sites are recognized from eggs and damage only. All of these are considered to be definite records of occurrences of Caurinus. In addition, rather similar eggshell remains and feeding damage have been found on liverworts (mostly Calypogeja cf. neesiana) growing on redwood logs in north coastal California (Mendocino and Del Norte Counties). All of the eggs located in this material were too weathered to allow definite association with Caurinus. These eggs may be dipteran (possibly a species of Tipulidae; Alexander, 1920), but it is still possible that they indicate the occurrence of Caurinus dectes or a related species in northern California.

In Oregon, most Caurinus sites are near the coast. With the exception of Crown Point, on the Columbia River Gorge approximately 140 kilometers inland, the localities range from 43 kilometers inland (Marys Peak) to less than one kilometer from the open ocean at Fogarty Creek. These localities are within, or lie only a few kilometers inland from, the Picea sitchensis Zone as rather broadly defined by Franklin and Dyrness (1973). These Oregon populations of C. dectes are numerous and are probably continuously distributed near the central and north coast; fragmented and restricted to moist sites at moderate elevations in the eastern Coast Range; and rare if occurring at all in the Cascades and southern Coast Range.

C. dectes also occurs in the coastal forest zone on the west and northwest sides of the Olympic Peninsula in Washington, but has not been found in the few samples examined from the north-central and eastern sides of the peninsula. Another series of localities for Caurinus dectes is located southwest of Mount Rainier National Park in

the Nisqually and Chehalis River drainages. These latter localities have forest vegetation of the Puget Sound type of the Tsuga heterophylla Zone (Dyrness and Franklin, 1973).

Caurinus has not been sought throughout its potential range, so that its occurrence likely will be extended by additional collecting. For this reason the negative evidence for the occurrence of this species is indicated in Map 1. The incidence of C. dectes and of the often co-occurring Hesperoboreus brevicaudus, is tabulated by area and elevation in Table 5. Both boreids can be identified in samples from one-half or more of the ecologically suitable localities at suitable elevations in the northern Oregon Coast Range and the western Olympic Peninsula and southwestern Cascade Mountains of Washington. The absence of Caurinus from suitable collections in the Puget Sound region in Washington and the southern Coast Range and Cascades in Oregon shows that if this species is present, its range is more fragmented in these areas.

Elevation Range: In Oregon, Caurinus dectes occurs from sea level (less than 5 m elevation at Fogarty Creek) to about 650 m at Marys Peak. This species is commonly found at both low and moderate elevation near the coast; at distances more than 20 km inland, most populations occur above 150 m, while the lower elevational limit for the populations at Marys Peak is about 500 m. The known elevation range of C. dectes in the Olympic Peninsula is 50 to 400 m, while the inland localities in southwestern Washington range from 120 to 580 m.

Penny (1977) contrasted the elevational ranges of the "coastal" boreids, B. elegans and Hesperoboreus brevicaudus, with the "inland" species, including B. californicus. He believed the former to be restricted to elevations below 2000 feet (600 m) while he recorded B. californicus from more inland stations above 3000 feet (900 m). This distinction has been shown to be invalid through collections of these three boreids during the survey for Caurinus populations. The habitats and altitudinal zonation of all these species overlap in the Coast Range and Columbia River Gorge (The distribution of these

boreids in western Washington and Oregon is shown in Map 2).

Hesperoboreus brevicaudus has been collected on Marys Peak from the base (about 250 meters) to 1070 meters elevation (a ravine at the head of Parker Creek). Boreus elegans and B. californicus adults have been collected together at 900 m on Laurel Mountain (Polk County, Oregon), while H. brevicaudus and B. californicus occur together at Oneonta Gorge (Multnomah County, Oregon), at 160 m elevation, not far from the single Columbia Gorge site for C. dectes. Finally, three of these species (C. dectes, H. brevicaudus, B. elegans) also occur together between 450 and 500 m at Cascade Head (Tillamook County, Oregon).

Observations in the field and laboratory indicate that B. californicus adults are active at lower temperatures than the other boreids occurring in the Oregon Coast Range. However, the restricted coastal occurrence of B. californicus is not strictly related to altitude.

Climatic factors: For most of the coastally distributed invertebrates and cryptogams, the most important macroclimatic factor determining the range limit is probably the availability of moisture during the summer drought. This is higher near the coast, because of both reduced total evaporation (related to lower temperatures and greater cloud cover near the coast) and some increase in moisture input through fog capture near the coast and along ridgelines.

The temperature differences between the Picea sitchensis Zone and similar habitats in the Tsuga heterophylla Zone are probably not critical for most forest-floor invertebrates, including Caurinus dectes. Caurinus adults can survive in epiphytes exposed to continuous freezing temperatures for several days. The generally mild temperatures near the coast (January mean minimum 0° to +2.5°C, Franklin and Dyrness, 1973) would increase the scope for activity of Caurinus on the exposed host plants. The temperature regime in late winter and early spring (February to May) are also likely to be

favorable for the completion of larval feeding by Caurinus prior to the seasonal drying of its substrates.

A number of inland sites were located which appeared to be suitable for Caurinus in host availability and summer moisture retention, while the Columbia Gorge occurrence suggests that winter minimum temperatures are not the limiting factor in the inland range of Caurinus. Caurinus dectes, like many of the "Vancouverian" coastal invertebrates, appears to be limited in dispersal ability. Its usual occurrence in mid-successional habitats would require recolonization of suitable habitats. These factors may require that suitable habitats be extensive for the persistence of Caurinus populations, which may not be able to effectively colonize more widely dispersed but suitable habitats.

Discussion

Many insects are distributed similarly to C. dectes in Oregon, that is, largely restricted to coastal and Coast Range locality, but not associated with a specifically maritime habitat such as sand dunes or salt marsh. Some species, like Leistus ferruginosus (Coleoptera: Carabidae), resemble Caurinus in being mainly coastal in Oregon, but occurring frequently inland at low elevations in the Cascade Mountains of Washington (Russell, 1976). This distributional type is essentially the "Vancouverian element in its purest form" of Van Dyke (1926, 1929). Van Dyke, followed by Linsley (1958) and Hatch (1953) noted a high degree of endemism in the Coleoptera of the coastal forests of the Pacific Northwest. Species with similar distributional patterns occur in most insect orders.

In addition to Caurinus dectes, there are three other species of Mecoptera with a Vancouverian distribution: Hesperoboreus brevicaudus and Boreus elegans (Boreidae), and Brachypanorpa oregonensis (Panorpididae). In Oregon, both H. brevicaudus and B. oregonensis occur more widely in the Cascades than does Caurinus, although each is more continuously distributed in the Coast Range.

Generally, while endemism is relatively high in insects which are larger or not tied to the forest floor, the species diversity of these groups in the Coast Range is relatively low. The latter is also true of the vascular flora of the Coast Range, which is "relatively poor in species" but "very poor in endemic forms" (Peck, 1961). In the factors determining their distributional limits, the boreids probably have much in common with the smaller arthropods of the forest floor litter stratum. It is in the fauna of this habitat that coastal forest endemism and species richness is most marked, in comparison to similar inland communities. This pattern has been validated by systematic collecting only for the pseudoscorpions (Benedict, 1978). The coastal enrichment is evident in some other groups, however, including pselaphid beetles (Grigarick and Schuster; 1971, 1976) and opilionids (Briggs, 1971). The aggregate known range of the harvestman family Pentanychidae (2 genera, 5 species), as given by Briggs, is remarkably similar to that of Caurinus. Other non-vagile invertebrates also are distributed in this manner, including many of the large terrestrial oligochaete worms (William Fender, Forestry Sciences Laboratory, Corvallis, in conversation).

The western part of the Oregon Coast Range is also rich in cryptogamic plant species, many of which do not occur very far inland. Endemism in the mosses is not high (Schofield, 1968) but overall dominance is high, when compared to inland forest habitats. Coastal forms are numerous in the Basidiomycetes (J. M. Trappe, Forestry Sciences Laboratory, in conversation) and hepatics, not including any major hosts of Caurinus (David Wagner, University of Oregon, in conversation).

Some of the coastal invertebrate taxa resemble Caurinus in apparent failure to recolonize areas covered by late Pleistocene glaciation. This effect can be observed in the low species diversity of such groups as the pselaphid and scydmaenid beetles in the northern Puget Sound basin of Washington (personal collections) as well as the increased incidence of winged species in these taxa.

Howden (1968) and Ross (1965) have concluded that a number of insects of the coastal and foothill fauna of Oregon and California experienced little change in their ranges during or since the Pleistocene. Ross suggested that the slight northward movement of some caddisflies "might indicate that few temperature changes occurred in some of the lowland Pleistocene climates of that area".

Effect of Pleistocene Glaciation

The relationship of Caurinus records in Washington to the Pleistocene glacial limits is shown in Map 3. Most of the sites in Washington were occupied by glaciers at some stage of the Pleistocene. The Caurinus localities located in valleys on the west and northwest sides of the Olympic Peninsula and the southern Cascades of Washington, were occupied or approached by expanded alpine glaciers (Crandell, 1965). None of the above Caurinus localities is more than 30 km inside the extreme glacial limits shown by Crandell (Map 3). There are large unglaciated areas near these Caurinus localities which presumably served as refugia for many cold-tolerant organisms.

Recent collections from the Nooksack and Stillaguamish valleys of the Northern Washington Cascades extend the known range of C. deces into more extensively glaciated areas. These localities are up to 200 km north of the glacial limit, and the Nooksack River (Whatcom County) localities, at least, are some distance from any known unglaciated area. It should be noted, however, that the glaciated areas indicated in Map 3 were not all covered simultaneously in the later Pleistocene. By the time the Puget Lake of the cordilleran glaciers reached its maximum in the Vashon Stade (13,000 to 15,000 years ago), the alpine glaciers in the Cascade and Olympic Mountains had greatly decreased in size (Crandell, 1965). The alpine glaciers of northwestern Washington probably reached their maxima at various times from 20,000 to more than 50,000 years before present (Stuiver et al., 1978).

Most American boreid species occur widely both north and south of the glacial boundary (Penny, 1977). Hesperoboreus notoperates, (found only in southern California) is the only boreid restricted to areas south of the continental glaciers, while the two Boreus species endemic to Alaska, B. borealis and B. intermedius, are the only species not occurring south of the general glacial limit. Of the latter, Boreus borealis is known from St. Paul Island in the Pribilofs, while B. intermedius has been collected at two sites on the eastern slope of the Wrangell Range (Kennicott and McCarthy, Alaska). The latter localities are about 100 km from the western edge of the major unglaciated corridor in central Alaska (Péwé et al, 1965). Both Alaskan species are morphologically close enough to the widespread B. californicus to have originated during the Pleistocene (Penny, 1977; my interpretation). However, Coope (1978) has shown that the well-preserved fossil insect faunas of the Quaternary period do not support the frequent assertions (e.g., Ross, 1965) of widespread speciation of insects during the latter part of the Pleistocene.

These distributional patterns and the highest species diversity in the family in areas of the glacial margin (especially Western Montana and Southwest British Columbia) indicate that Boreus species, in spite of their lack of flight, dispersed easily along the glacial margin. The cold tolerance of the adults and utilization of pioneering mosses as hosts presumably facilitated this dispersal, although no Boreus are known to occur in high Arctic habitats. In the most boreal environments, adult activity occurs in spring or even mid-summer (B. borealis; Penny, 1977). The necessity for over-wintering of the pharate adult or unemerged adult would probably limit their occurrence in the true Arctic.

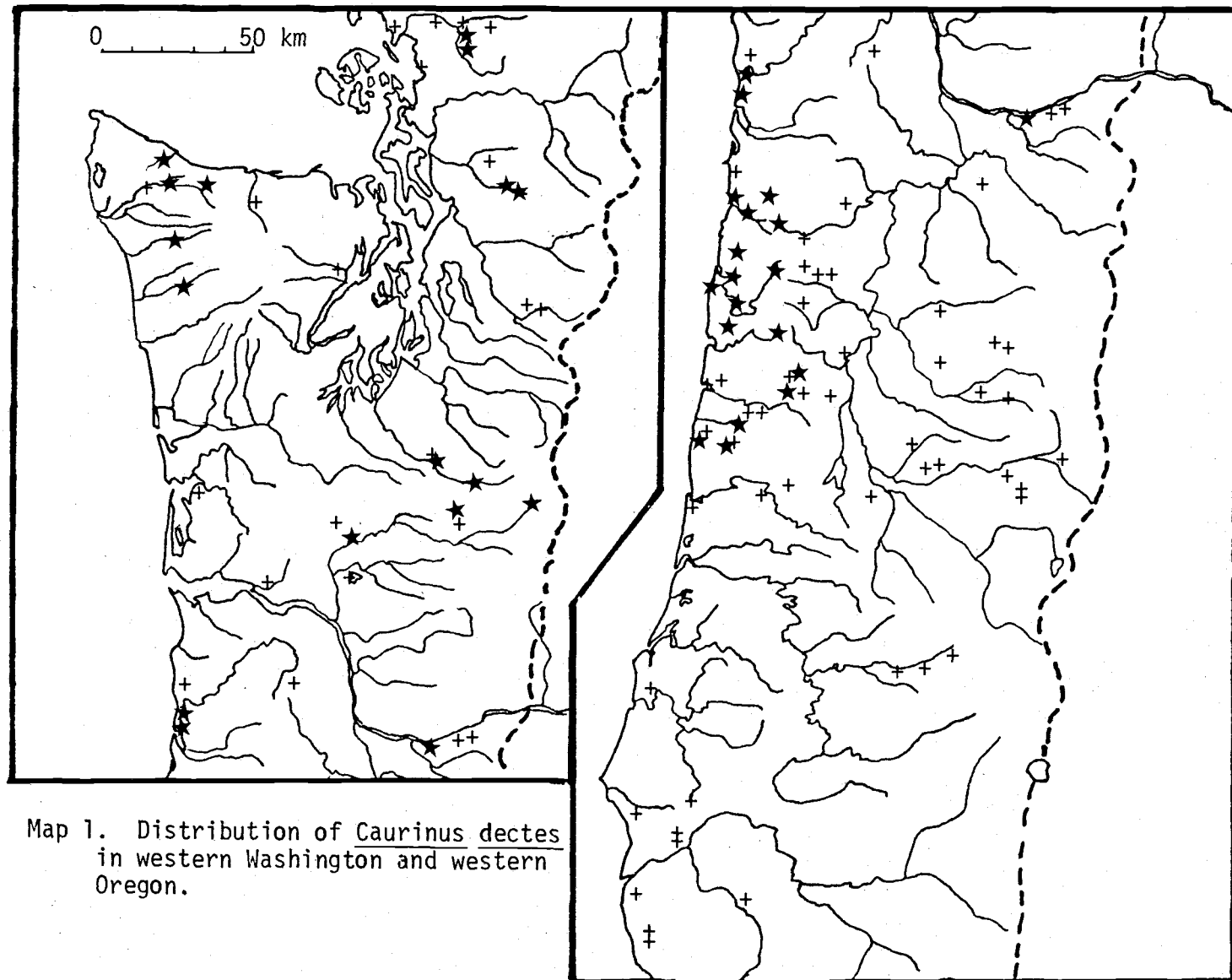
If Caurinus has penetrated only the southern edge of the glaciated area, this distribution can be explained most easily by its general restriction to forested habitation in this species than in many boreines, and by the larva feeding in aerial shoots rather than in the soil under thick mosses. This larval adaption requires

completion of larval development within one season, while the boreine larvae are capable of hibernation and can complete development in two or more years.

Some boreine species probably increased their latitudinal range during the Pleistocene, remaining in microthermal habitats in the south while recolonizing northern regions during interglacial times. Caurinus dectes probably survived the Pleistocene in much of the area known to be occupied today, including the western Olympic Peninsula and southern Cascades of Washington. Further collecting in northern Washington and British Columbia is required to establish the northern range limit for Caurinus dectes.

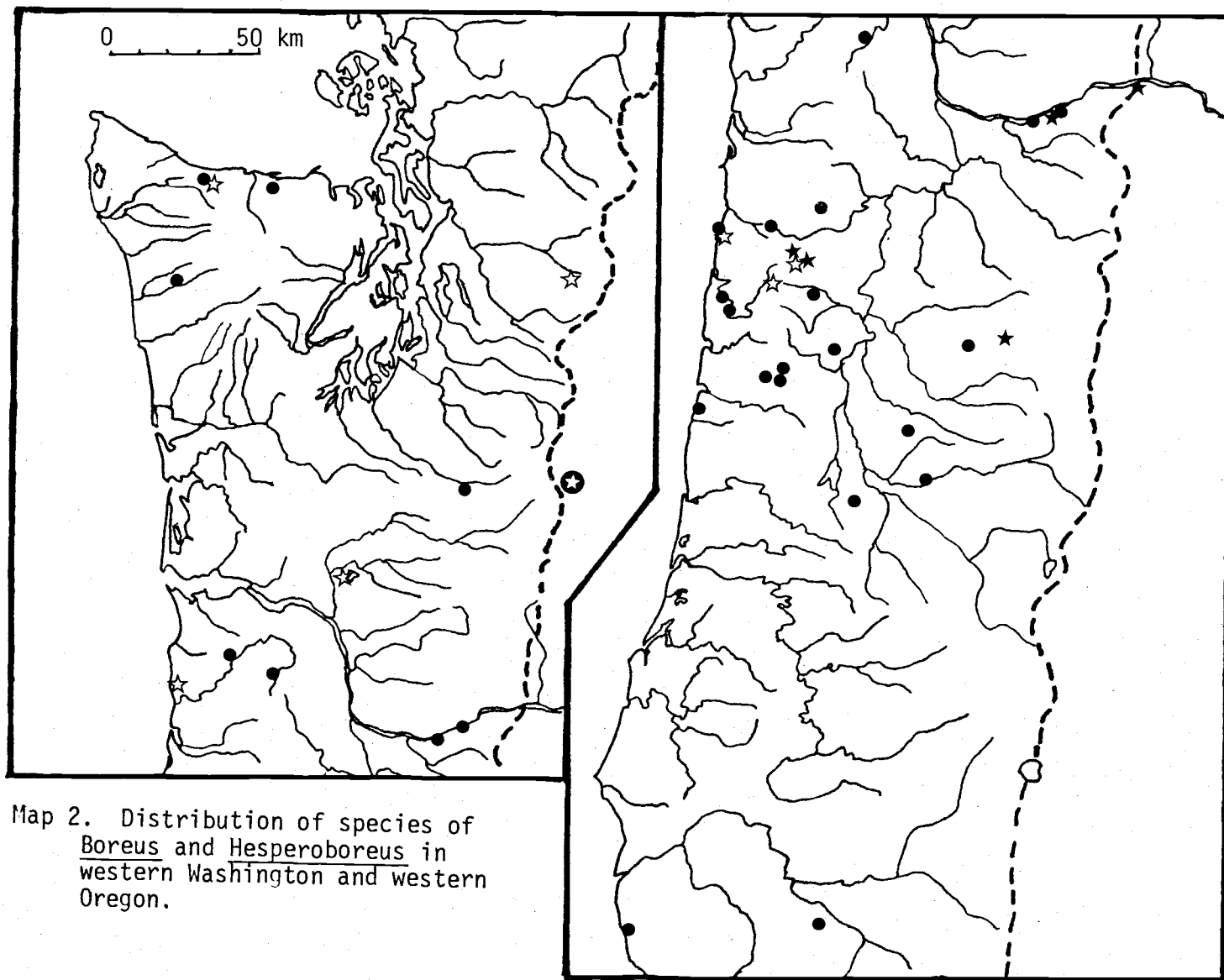
Map 1. Distribution of Caurinus dectes in western Washington and western Oregon.

- ★ - localities from which C. dectes has been collected (as intact adults, skeletal fragments, or eggs attached to host liverworts).
- + - negative records: localities or clusters of localities where Caurinus has not been detected in apparently suitable habitats.

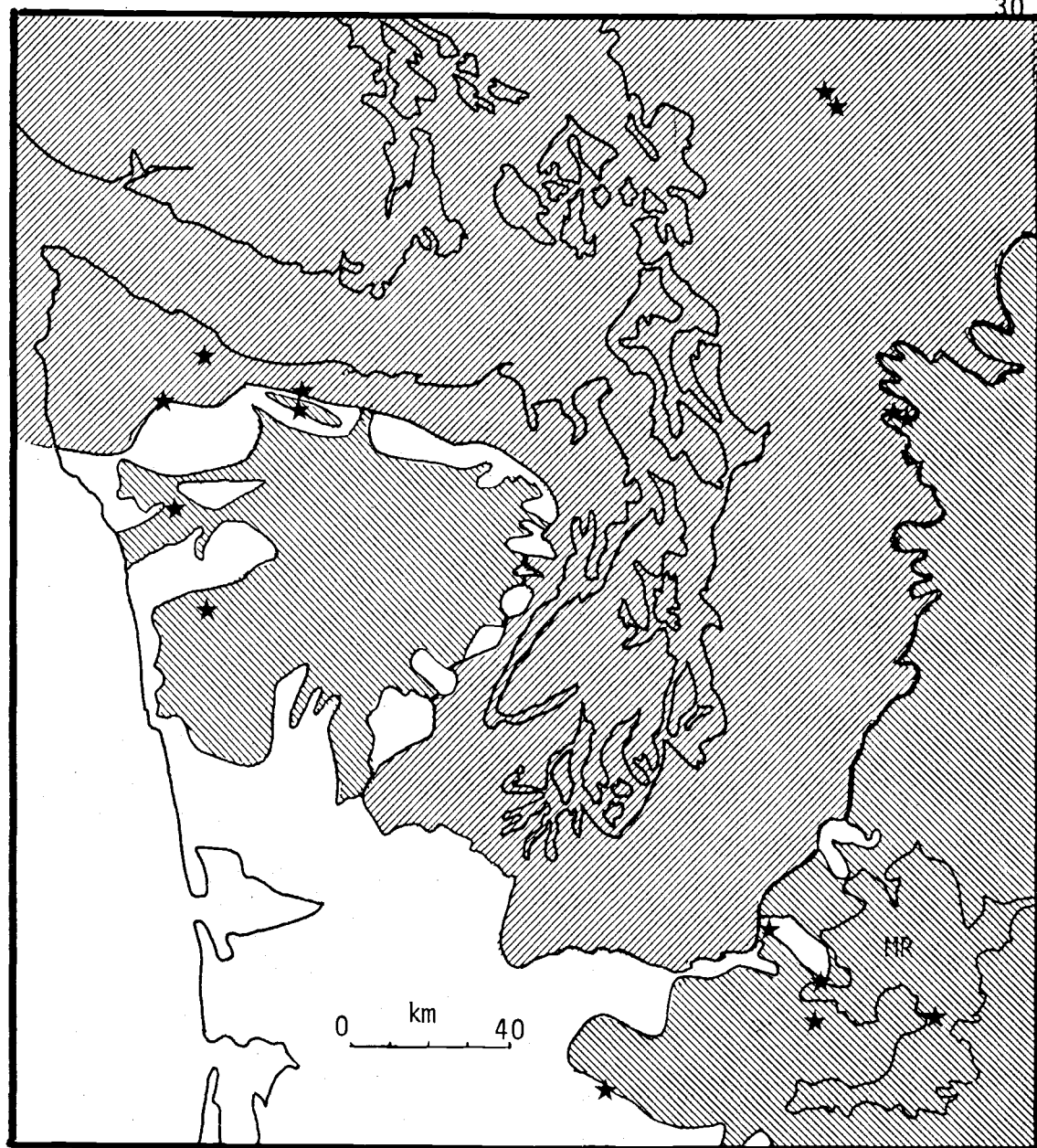


Map 2. Distribution of species of Boreus and Hesperoboreus in western Washington and western Oregon. (Map includes published records, as compiled by Penny (1977)).

- - localities or clusters of localities for Hesperoboreus brevicaudus (as adults or larvae).
- ★ - localities for Boreus californicus.
- ☆ - localities for Boreus elegans.
- ⊛ - locality for Boreus reductus.



Map 2. Distribution of species of Boreus and Hesperoboreus in western Washington and western Oregon.



Map 3. Occurrence of Caurinus decetes in western Washington in relation to late Pleistocene glacial maxima.

- ★ (filled stars) - localities from which C. decetes is known.
- ▨ - area occupied by Puget Lobe of Cordilleran glaciers at Vashon maximum advance.
- ▩ - area occupied in Olympic and Cascade mountains by alpine glaciers in late Pleistocene (mostly in Silver Springs time). The lines enclosing "MR" represent the glacial area near Mount Rainier at a later period (Evans Creek Stade).

1) Map is simplified from one in Stuiver et al. (1978).

Table 4. Localities from which Caurinus dectes has been collected.

Locality	Elevation	Canopy	Stratum	Specimens collected
WASHINGTON: CLALLAM CO.				
1. Pysht (5 km E Clallam Bay Junction) (48° 11' N; 124° 17' W)	90 m	Deciduous (shrubs)	Epiphytes	Adult
2. Bear Creek Campground (3 km E Sappho) (48° N; 124° W)		Conifer	Logs (Scbo)	Eggs
3. Lake Crescent (Fairholm Campground) (48° 04' N; 123° 55' W)	140 m		Epiphytes	Eggs, Fragments
4. Aurora Park trailhead (Olympic N. P.) (48° 04' N; 124° 00' W)	400 m		Logs	Eggs, Fragments
5. Hoh River (16 km E U.S. 101) (47° 49' N; 124° 07' W)	105 m	Conifer	Epiphytes, Logs	Fragments
6a. Queets Campground (Olympic N. P.) (47° 37' N; 124° 01' W)	90 m	Conifer	Logs (Scbo)	Adults
6b. Queets Campground (2 km SW) (47° 37' N; 124° 02' W)	80 m	Conifer	Logs	Eggs
WASHINGTON: WHATCOM CO.				
7. Mosquito Lake (4 km N) (48° 47' N; 122° 07' W)	180 m	Conifer	Logs (Scbo)	Eggs
8. Blue Mountain (6 km E Acme) (48° 44' N; 122° 06' W)	215 m	Mixed (stream)	Logs, Terrestrial	Adults, Eggs
WASHINGTON: SNOHOMISH CO.				
9a. Lake Twentytwo trail (5 km E Verlot) (48° 05' N; 121° 44' W)	335 m	Conifer	Logs	Adults, Eggs

Table 4. Caurinus dectes localities (continued)

Locality	Elevation	Canopy	Stratum	Specimens collected
WASHINGTON: SNOHOMISH CO.				
9b. Bear Creek (7 km E Verlot) (48° 05' N; 121° 41' W)	340 m	Conifer	Terrestrial	Eggs, Larvae
9c. Schweitzer Creek (8 km E Verlot) (48° 05' N; 121° 40' W)	370 m	Conifer, Open	Terrestrial (Gyun)	Adult, Larvae
WASHINGTON: PIERCE CO.				
10. Pack Forest (2 km S Eatonville) (46° 05' N; 122° 49' W)	380 m	Conifer (boggy)	Logs (Scbo)	Adults, Eggs
WASHINGTON: LEWIS CO.				
11. Lewis and Clark State Park (46° 31' N; 122° 49' W)	120 m	Deciduous, Conifer	Epiphytes, Logs	Adults, Eggs
12. Morton (8 km N) (46° 37' N; 122° 14' W)	365 m	Mixed	Logs (Scbo)	Adults
13. Big Creek Campground (Snoqualmie N. F.) (46° 43' N; 122° 00' W)	490 m	Deciduous	Logs (Scbo, Caly)	Eggs, Fragments
14. Catt Creek (46° 43' N; 121° 59' W)	580 m	Conifer, Open	Terrestrial	Adult
15. Packwood (15 km N) (46° 42' N; 121° 35' W)	550 m	Conifer	Logs	Fragments
OREGON: MULTNOMAH CO.				
16. Crown Point (1 km E) (45° 32' N; 122° 15' W)		Deciduous	Logs, Terrestrial	Adults

Table 4. Caurinus dectes localities (continued)

Locality	Elevation	Canopy	Stratum	Specimens collected
OREGON: TILLAMOOK CO.				
17. Wheeler (0.5 km S) (45° 41' N; 123° 53' W)	10 m	Mixed (stream)	Log (Caly)	Eggs, Fragments
18. Rockaway (45° N; 123° W)	10 m	Mixed	Epiphytes	Adults
19. Little Nestucca County Park (45° 07' N; 123° 54' W)	30 m	Mixed	Epiphytes	Adult
20. Cascade Head (summit) (45° 04' N; 123° 59' W)	490 m	Spruce, Open	Terrestrial (Nasc), Logs	Adults, eggs,
21. Neskowin Creek Campground (Siuslaw N. F.) (45° 04' N; 123° 54' W)	130 m	Deciduous	Epiphytes	Fragments
OREGON: YAMHILL CO.				
22. Hanchet Creek (45° 06' N; 123° 44' W)	180 m	Deciduous (stream)	Epiphytes	Adults
OREGON: LINCOLN CO.				
23. Otis (1.3 km NE) (45° 02' N; 123° 56' W)	20 m	Mixed	Epiphytes	Adults
24. Schooner Creek Campground (Siuslaw N. F.) (44° 57' N; 123° 55' W)	110 m	Conifer (stream)	Logs (Scbo)	Eggs, Fragments
25. Kernville (5 km E) (44° 52' N; 123° 55' W)	20 m	Mixed	Terrestrial	Adult
26. Fogarty Creek State Park (44° 50' N; 124° 03' W)	10 m	Mixed	Logs (Scbo, Caly)	Eggs

Table 4. Caurinus dectes localities (continued)

Locality	Elevation	Canopy	Stratum	Specimens collected
OREGON: LINCOLN CO.				
27a. Siletz (1.5 km N; (44° 44' N; 123° 55' W)	40 m	Mixed	Epiphytes	Adult
27b. Siletz (Euchre Creek, 5 km N) (44° 46' N; 123° 55' W)	40 m	Conifer (stream)	Epiphytes	Adult
28. Depot Creek (8 km N Toledo) (44° 41' N; 123° 57' W)	20 m	Deciduous (stream)	Epiphytes, Logs	Adults, Eggs, Larvae
29. Nashville (3 km N) (44° 41' N; 123° 37' W)	110 m	Deciduous (swamp)	Epiphytes	Fragments
30. Grass Mountain (4 km W summit) (44° 26' N; 123° 44' W)	170 m	Deciduous	Logs	Adult
31. Fisher (1.5 km SW) (44° 17' N; 123° 51' W)	200 m	Conifer	Terrestrial (Gyun)	Adult
OREGON: POLK CO.				
32. Valsetz (5 km NW) (44° 52' N; 123° 41' W)	290 m	Conifer (stream)	Logs	Eggs
OREGON: BENTON CO.				
33. Marys Peak (3 km N summit) (44° 32' N; 123° 33' W)	500- 620 m	Conifer, Deciduous	Epiphytes, Logs, Terres- trial	Adults, Eggs, Larvae, Pupae

Table 4. Caurinus dectes localities (continued).

Locality	Elevation	Canopy	Stratum	Specimens collected
OREGON: LANE CO.				
34. Cape Ridge (8 km E Cape perpetua) (44° 16' N: 124° 02' W)	400 m	Conifer	Logs, Terres- trial	Adult
35. Klickitat Mountain (Buck Creek) (44° 14' N; 123° 33' W)	490 m	Conifer (boggy; open banks)	Logs (Caly), Terrestrial (Gyun)	Adults, Larvae

Abbreviations for liverwort associations:

On logs: Caly - Calypogeja spp and associates.

Scbo - Scapania bolanderi association

Terrestrial: Gyun - Gyrothyra underwoodiana association

Nasc - Nardia scalaris association

Table 5. Summary of occurrence of Caurinus dectes and Hesperoboreus brevicaudus in apparently suitable sites in western Washington and Oregon.

Area	Elevation	No. of Sites Collected	No. with <u>C. dectes</u>	No. with <u>H. brevicaudus</u>
<u>A. Western Washington</u>				
Olympic Peninsula	0-150m	7	5	3
	150-650m	5	1	0
North Cascades & Puget Sound Lowland	0-150m	7	0	0
	150-650m	13	5	0
Southwest Washington	0-150m	3	1	0
	150-650m	7	4	1
<u>B. Western Oregon</u>				
Northern Coast Range: Northern Lane Co. to Clatsop Co.				
Distance from Coast				
0-10km	0-150m	16	8	2
	150-650m	4	2	1
10-20km	0-150m	7	2	2
	150-650m	5	1	1
	650+m	2	0	0
20-50km	0-150m	25	1	7
	150-650m	17	5	3
	650+m	14	0	2
Southern Coast Range and Siskiyou	0-150m	13	0	0
	150-650m	10	0	2
	650+m	3	0	0
Columbia River Gorge	0-150m	5	1	3
Western Cascades and foothills east of Willamette Meridian	0-150m	9	0	4
	150-650m	14	0	1
	650+m	4	0	0

HABITAT OF CAURINUS DECTES

A detailed description is given here of the Caurinus dectes habitat on Marys Peak (Benton County, Oregon). Less extensive notes are included on each of several other localities, with comparison of the apparent utilization of these habitats by Caurinus.

The Marys Peak sites were visited one to four times each month from January 1976 to October 1978. The other known Caurinus populations have been sampled on one to six dates each. The Marys Peak populations are the best known in time and space, and much of the accessible area on Marys Peak has been surveyed for the occurrence of Caurinus. The distribution of Caurinus dectes and the areas sampled in this study, are shown in Map 4.

All but one of the collections of Caurinus on Marys Peak have been made within Section 16 of Township 12 South, Range 7 West, Willamette Meridian. A detailed survey was made of the plant communities and the distribution of hosts of Caurinus dectes within this section. The canopy type, shrub and herb understory, and occurrence of dead wood substrate was noted for each sampled site. This reconnaissance was made along the road and trail system, by observation from viewpoints, and by cross-country traverses. Accurate mapping was not achieved due to the large area involved, but location of many ground features was possible by reference to landmarks and contour lines on topographic maps (Marys Peak quadrangle, 1: 62,500, U.S.G.S., 1969, revised 1954, 1957; unpublished maps on file at the Siuslaw National Forest Headquarters, Corvallis, Oregon).

The southwest corner of the section, above 650 meters elevation (about 30 percent of the area) was observed only at sites adjacent to the Marys Peak trail. The vegetation of this higher area was described by Merkle (1951) in his study of the plant communities of Marys Peak above 2500 feet (760 m). Smaller areas on the west and east edges of the section were not traversed on foot. Information for these is entered from Forest Service site classification maps, and by observation from viewpoints.

Topography and soils

The elevation range of sites visited is from about 470m along the north and east edges of the section, to 1000m at the southwest corner. Slopes average 40 to 50 percent in the upper (southwest) quadrant; below 630m elevation most slopes average a 20 percent gradient to the north or east.

Several branches of Mulkey Creek and the North Fork of Rock Creek originate in springs near the 600m contour line. These streams drain to the north and east, respectively. Soils in the more level lower areas are fairly deep, dark brown clay loams; the upper slopes have thin, rocky soil.

Vegetation

This section is almost entirely forested. Much of the area below 600m has an open canopy of Douglas fir (Pseudotsuga menziesii) averaging 40 to 50cm DBH. On the upper slopes, to about 800m, and on part of the northeast-exposed lower slopes, the canopy is a dense mixture of western hemlock (Tsuga heterophylla), red cedar (Thuja plicata), and Douglas fir. Most of the trees are rather small on the lower slopes (averaging 25 to 30cm DBH), but larger specimens occur above.

The understory on open mesic sites is largely sword fern (Polystichum munitum) on slopes, or sword fern and Oxalis oregana on more level sites. Vine maple, when it occurs in the understory, has a very heavy cover of bryophytes, including Porella navicularis, on the horizontal stems.

The understory of Douglas fir stands on drier sites is dominated by salal (Gaultheria shallon). Where vine maple occurs this constitutes the AGs community described by Anderson (1969). Epiphytic cover on the shrubs in this community is much sparser than in the moist coniferous stands.

Dense stands of Douglas fir, and the hemlock-red cedar stands generally lack a vascular understory. Bryophytes are largely restricted to sparse growth on rotting wood, and grow abundantly only in lightspots (the surface under small canopy openings), where the mosses Eurhynchium oregonum and Plagiothecium undulatum sprawl over the ground and low woody debris. Scapania bolanderi, a liverwort, also grows on rotting wood on the ground stratum in these lightspots.

Less than ten percent of the section has a deciduous or mixed deciduous-coniferous canopy, according to Forest Service stocking maps, but these areas are of special importance for the occurrence of Caurinus. The deciduous stands are located in moist locations at the head of small streams, as well as in narrow stringers along parts of Rock Creek and Mulkey Creek. In each of the significant deciduous stands, the canopy was formed by large or over-mature red alder (Alnus rubra), commonly of 35 to 45 cm DBH. A few bigleaf maple (Acer macrophyllum) of similar size, are present in each of these stands. Two of the alder groves include central, parklike areas on nearly level ground with only a few shrubs; here the herbaceous stratum (dominated by Oxalis oregana), with large patches of the terrestrial moss Mnium insigne is interrupted only by a number of large coniferous logs and stumps. The open aspect of these sites is apparently maintained through heavy browsing by deer.

The remainder of the alder stands, along streams and in the boggy areas at the head of streams, have a well developed shrub stratum. Vine maple (Acer circinatum) is abundant; most specimens show the arched growth form (Anderson, 1969), and are very heavily covered with epiphytic bryophytes. Salmonberry (Rubus spectabilis) and red elderberry (Sambucus racemosa var. arborescens) are abundant in this section only near the streams, while Devil's club (Oplopanax horridum) occupies very wet north-facing slopes. The herbaceous layer varies from site to site, but Oxalis oregana and Mnium insigne dominate over the largest area. Along the stream corridors, lady fern (Athyrium felix-femina) and skunk cabbage (Lysichitum americanum) are conspicuous.

Map 4. Distribution of Caurinus dectes at Marys Peak, Benton County, Oregon, in relation to vegetation types. (Area shown in map is Section 16, R7W, T12S, Willamette Meridian).

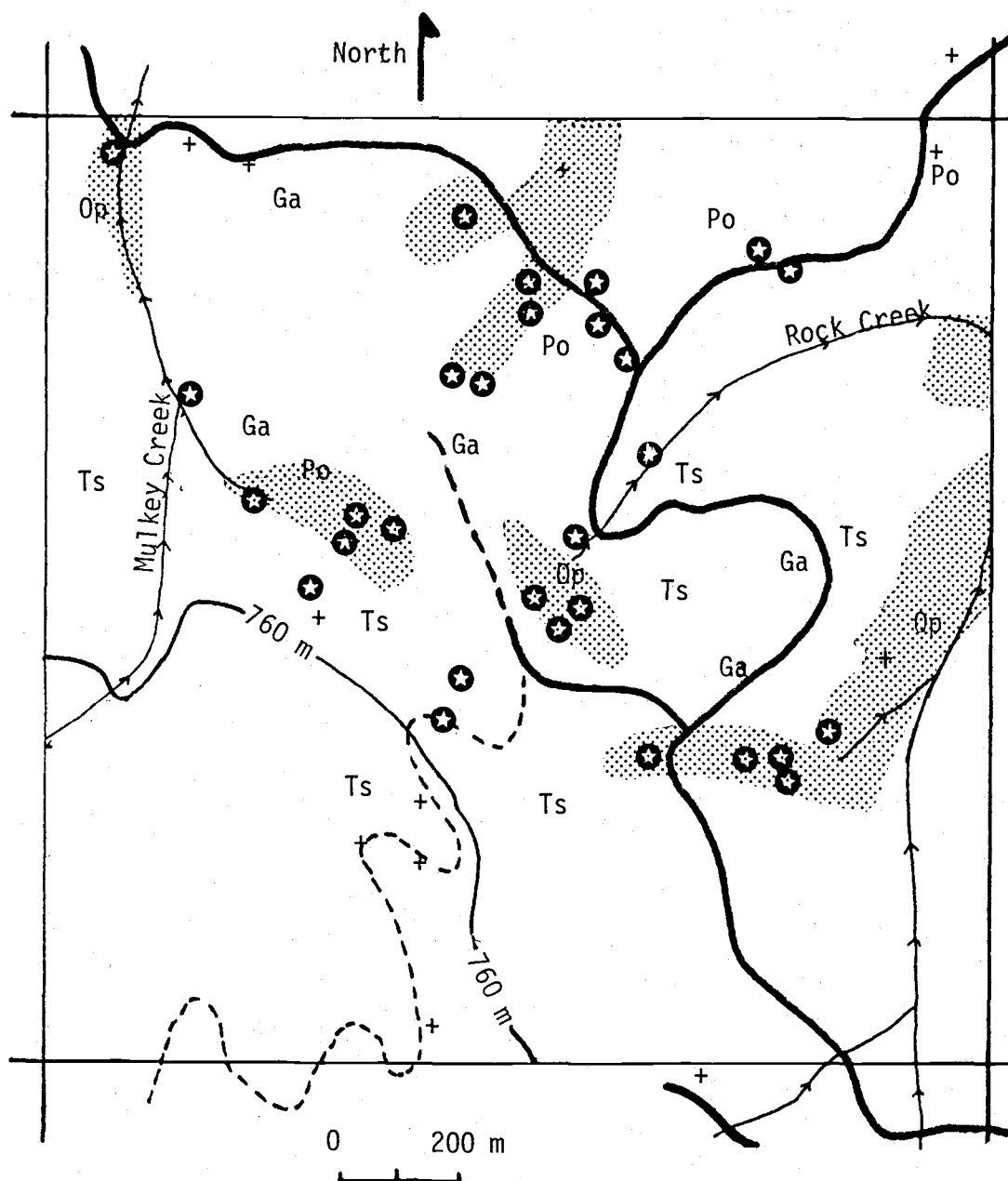
- ★ - site where Caurinus has been collected
- + - negative record (Caurinus not found in liverworts)

Plant associations:

-  - predominately deciduous canopy (determined from U.S. Forest Service site maps, with alterations)
- Po - mesic understory; Polystichum munitum and/or Oxalis oregana abundant
- Op - very moist, boggy; Oplopanax horridum present
- Ga - relatively xeric understory; Gaultheria shallon abundant
- Ts - vascular understory absent or nearly so; mostly dense cedar-hemlock canopy

Other symbols:

-  - roads
-  - trail
-  - stream (permanent or intermittent)



Map 4. Distribution of *Caurinus dectes* at Marys Peak, Benton County, Oregon, in relation to vegetation types.

Distribution of *Caurinus* host substrates

On Marys Peak *Caurinus decetes* feeds on liverworts which occur in several distinct assemblages; these can be identified by the most important liverwort species as the *Porella navicularis*, *Scapania bolanderi*, *Gyrothya underwoodiana*-*Diplophyllum obtusifolium*, and *Calypogeja trichomanis*. The distribution of these hepatics is apparently not directly determined by the higher vegetation, but appears to be mediated by the light and moisture regime and availability of suitable substrates.

The *Porella navicularis* association is especially abundant on horizontal vine maple stems in the moist deciduous and coniferous stands where *Polystichum* or *Oxalis* is abundant (Figure 5). *Porella* usually occurs in large sprays, in a context of pleurocarpous mosses; the latter include *Metaneckera menziesii*, *Antitrichia curtipendula* and *Isothecium spiculiferum*. A similar epiphytic association also occurs on the lower boles of alder and bigleaf maple (Figures 9, 10). *Porella* appears to be most abundant in the middle canopy in the deciduous stands. It occurs on horizontal major branches to at least seven meters above the ground, and frequently has a greater cover frequency than mosses at the mid-canopy levels. In addition to vine maple, older stems of Devil's club and elderberry are colonized by *P. navicularis*. *Caurinus* adults, eggs, and larvae or larval mines, have been located in *Porella* taken from fallen alder branches. It is not known whether these branches were occupied by *Caurinus* before they fell, although no *Caurinus* were found in a few samples of the *Porella* association collected from alder and bigleaf maple at three to five meters above the ground.

Porella navicularis and the associated liverworts also occurred in lesser amounts on vine maple in the drier sites at Marys Peak (where *Gaultheria* and *Corylus cornuta* were present), but *C. decetes* has not been taken from epiphytic material collected in such stands. I have no evidence that the liverworts associated with *P. navicularis* (principally *Frullania tamarisci* var. *nisquallensis* and *Radula*

bolanderi are utilized by Caurinus at Marys Peak.

Scapania bolanderi is very abundant on coniferous logs and stumps, both with and without bark (Figures 7,8). Scapania bolanderi often occurs in small patches among liverworts of the Calypogeja and Lepidozia associations. However, the distinctive growth form of Scapania, with its tendency to occur in very extensive single-species stands, make it desirable to consider S. bolanderi separately from other xylicolous liverworts in this discussion. S. bolanderi was found on wood debris in all of the deciduous stands, and was very abundant in the moister coniferous stands. Scapania was less frequent and often stunted, on wood substrates in the drier Douglas fir stands. In the densest hemlock-cedar and Douglas fir stands, this species was for the most part restricted to small lightspots at the ground layer. Scapania bolanderi probably occurs as an epiphyte in the mid-canopy in many of these stands, but it is questionable whether the micro-climate of the canopy would allow use of these sites by Caurinus.

Caurinus was very abundant on S. bolanderi in moist sites with many old logs or stumps, under an open canopy. Where such conditions occurred S. bolanderi frequently grew in extensive pure stands, either on bark or on bare wood. Samples of Scapania from accumulations of logging debris next to the streams showed feeding damage caused by adult C. dectes on most of the shoots; counts of Caurinus eggs as high as two to five per ten shoots of Scapania were noted in these streamside sites.

Caurinus also occurred on S. bolanderi growing on wood within the closed hemlock stands up to 250 m from the main openings. Most of the Scapania noted in these stands occurred in lightspots less than 10 m across, which had often originated from a single windthrown tree. Feeding by Caurinus was less extensive in most of these isolated sites than in the extensive stands of Scapania mentioned above.

Calypogeja association: Liverworts of the genus Calypogeja are common in the study area, but rarely form extensive patches. One female Caurinus was found in a small patch of Calypogeja fissa near

the soil surface on a partly burned log. This collection was in an open swale in the south-central part of the study section (Figure 7). Caurinus eggs and feeding were found on C. fissa, C. trichomanis, and Scapania bolanderi taken from this log.

Other xylicolous liverworts, often associated with Calypogeja spp., were collected in the Marys Peak study area. These liverworts, including Riccardia spp., Cephalozia spp., Lepidozia reptans are not known to be utilized by Caurinus in the field.

Gyrothyra association: Terrestrial hepatics at Marys Peak are almost entirely limited to road cuts and verges with eroding or very compacted soil. Eggs and larvae of C. dectes were found on shoots of Gyrothyra underwoodiana from two of four road bank sites collected. Eggs and feeding damage were quite sparse in terms of the amount of material examined. Samples of Diplophyllum obtusifolium from the edge of one of the Gyrothyra mats with Caurinus showed no sign of eggs or feeding damage. Terrestrial liverworts also were found on little used trails; several species grew together, including Jungermannia rubra, Riccardia latifrons, Blasia pusilla, G. underwoodiana and D. obtusifolium. Adults and eggs of Caurinus were found on J. rubra and G. underwoodiana in these associations.

A single Caurinus egg was discovered on the dorsal surface of a large thallus of Conocephalum conicum (Marchantiales) from the Rock Creek ravine. Other collections and feeding trials seem to discount this liverwort as a potential host.

Distribution of Caurinus dectes in relation to plant communities and succession

In addition to the section mapped in some detail, the Marys Peak area was surveyed along most of the road and trail network around the mountain. Within the area just discussed the distribution of Caurinus dectes can be explained by environmental variables that are reflected by the understory vegetation. On Marys Peak Caurinus is apparently absent from the drier sites characterized by the

presence of Gaultheria shallon; in these communities the host liverworts are scarce, and the environmental conditions are comparatively harsh.

In the denser hemlock-cedar stands, the hepatics are apparently shaded out from the ground layer, as are nearly all vascular understory species. The lightspots in this forest site are favorable for the growth of Scapania bolanderi and a number of other xylicolous liverworts; such sites are colonized by Caurinus at least a few hundred meters from more extensive habitats. The usually low level of utilization (in terms of feeding incidence and egg numbers on the hosts) in the small lightspots may indicate that these are marginal sites which may function more as stepping stones for dispersal than as breeding sites for viable populations.

Populations of Caurinus dactes are usually found in rather extensive habitats with intermediate ground level light intensity, and high moisture availability throughout the year. On Marys Peak as well as nearer the coastline, these sites are usually found in seepage areas or along streams, or at least in well-shaded ravines with intermittent stream flow. The most extensive suitable habitats are mid-successional, where the canopy has opened through mortality of the pioneer tree species (red alder or Douglas fir).

The duration of this seral stage is not established. The alder groves on the north slope of Marys Peak were established following disturbance from forest fire, logging, or windthrow of the coniferous canopy. The most recent major fire which affected this site in September 1902 burned over much of the north slope of Marys Peak below 2500 feet (760 m) (Morris, 1934). High-cut stumps in the two "park-like areas" mentioned above indicate that railroad logging occurred within the study area early in this century.

The presence of large (about 100 cm DBH) windthrown logs in the wettest part of one site, suggests that it was opened to colonization by alder by windthrow (Figure 6). On all sites the alder stands are even aged, about 60 to 75 years old, and limited to some of the moistest sites in the area. The sequence of development of the

possible hosts of Caurinus can not be inferred from the literature. Scapania bolanderi, under appropriate microclimatic conditions, can colonize intact coniferous logs within a few years of the disturbance, and this liverwort evidently persists for decades on some wood or bark substrates. This species eventually is crowded out by growth of robust mosses (such as Rhytidiadelphus triquetris) on horizontal bark surfaces. Scapania can persist for some time on such substrates since aerial shoots of S. bolanderi from the tops of logs in the Rock Creek ravine had up to 13, probably annual, growth increments (interpretation supported by David Wagner, in conversation). I have attributed the abundant branching of the potentially monopodial Scapania shoots at the Rock Creek site to damage to the apical meristem through feeding by Caurinus. If this is so, the pattern of branching implies that Caurinus has been present on these logs throughout the period of growth of the aerial shoots.

S. bolanderi apparently persists over many decades on the weathered, decorticated vertical surfaces of coniferous stumps. The aerial shoots of Scapania are usually not very old, and the extensive cover on stumps (mostly red cedar) estimated to be at least 60 to 70 years old, is attained through recolonization of the substrate following delamination of the earlier bryophytic cover.

The persistence of the Porella association is also related to the opening of the original canopy, and on Marys Peak, primarily to the spread and growth form of vine maple. According to Anderson (1969), vine maple persists indefinitely in the understory by vegetative reproduction in the "Acer/Polystichum" communities, but is ultimately shaded out almost completely in the "Oxalis" communities on Marys Peak by development of the dense hemlock-cedar canopy. The maximum age recorded for a vine maple stem in the Acer/Polystichum community was 117 years, while persistence was presumably less in the shaded community. The oldest vine maples in the Acer/Polystichum stands were still classed as having a "heavy" (more than 80 percent) cover of bryophytes. From my field reconnaissance, it appears that older vine maple stems maintain a heavy cover including Porella and

associates as long as the maple stems remain vigorous. Vine maple stems which were obviously decadent, had very sparse epiphytes. These stems usually bore no Porella navicularis, and were never occupied by Caurinus.

On Marys Peak vine maple, with accompanying epiphytes, can be expected to persist indefinitely in the mesic Acer/Polystichum community by lateral growth and rooting in lightspots (Anderson, 1979). In these communities, Caurinus could be expected to persist as well until major disturbance by forest fire or clear-cutting. The fragmentation of the inland range of Caurinus and the close association of this species with streams and boggy areas, may be related to the very extensive contemporaneous forest fires in the Coast Range in the period following 1850 (See map, page 150 in Loy and Patten, 1976). Unburned refuge sites were more frequent within major burns near the coast, where Caurinus dectes is more continuously distributed.

Other Caurinus Populations

The area on Marys Peak described above includes most of the known range of habitats for Caurinus dectes. This species does appear however to vary in its utilization of the possible substrates at different localities. Aside from the Marys Peak populations the best information on the occurrence of Caurinus is available for several populations near the Oregon coast; these habitats are described briefly and contrasted with the Marys Peak sites.

The Cascade Head area: Three of the cited localities (Table 4) are within or adjacent to the Cascade Head Experimental Forest. The locations of these collections are shown in Map 1. Two of these sites, at Neskowin Creek Campground and at Deer Creek (0.8 km north of Otis), are closely comparable to the stream corridor vine maple communities on Marys Peak. As in this community type on Marys Peak, Caurinus appears largely confined to epiphytes of the shrub layer where Porella navicularis is the predominant hepatic species. The most striking difference from the Marys Peak sites is the abundance

of vascular epiphytes (Selaginella oregana and Polypodium scolieri) on vine maple and bigleaf maple at the Cascade Head sites. The fibrous roots of these plants contribute to more tightly woven and better attached epiphytic mats than those usual inland in the Porella-Metaneckera association. In addition to P. navicularis, Frullania, Radula, and Metzgeria conjugata are the usual epiphytic hepatics at these sites.

The other site where Caurinus dactes has been collected at Cascade Head is at the north summit area of Cascade Head Ridge. This site, at 490 meters elevation, is less than three kilometers from the ocean, and is strongly influenced by fog interception (Isaac, 1946) and storm winds. The summit vegetation is quite different from that at the other sites discussed. Just below the summit on the north side is a nearly impenetrable growth of young (about 10 year-old) Sitka spruce with almost no understory vegetation except at the verge of a road. This road bank is covered by a thick mat of moss, largely Rhytidiadelphus loreus, which also sprawls over rocks, logs, and the bases of trees and shrubs. The Caurinus specimens from this site were recovered from moss from this road bank, although no hepatics could be located in this substrate. Further inspection disclosed two types of breeding substrate within the Cascade Head summit area. The more extensive is a terrestrial Nardia scalaris-Diplophyllum albicans association. These hepatics occur in small patches on the road verge at the initial collection site, but cover many square meters in pure stand (mostly Nardia) about 150 meters east on rock and soil in a disused quarry. At the latter site, D. albicans is apparently utilized by Caurinus more than N. scalaris although the latter species is much more abundant here. Mats of these liverworts in partial shade at the edge of the quarry show more signs of Caurinus activity than the same species in the open quarry wall.

The other hepatic substrate available at the summit site is a Porella navicularis-Frullania nisquallensis epiphytic assemblage growing at the base of salmonberry stems in one open area above the road. Six apparently teneral adult Caurinus were taken

from a sample of these epiphytes, but no search was made for eggs or larvae in this situation. The presence of any significant epiphytic cover on salmonberry is itself unusual: Coleman et al. (1956) found salmonberry one of the least frequently colonized shrubs in their study of epiphytic associations on the Olympic Peninsula, Washington.

Although the Porella on salmonberry appears to be fed on by Caurinus, this substrate is not abundant enough to account for the Caurinus population. Most of the local population of C. dectes is assumed to be associated with the terrestrial liverworts along the margin of the quarry and the road.

Other coastal populations: Most of the sites where Caurinus has been collected fit into the habitats discussed above. In some cases, as at the extensive Depot Creek site (Lincoln County, Oregon), the shrubby understory is considerably denser than at Marys Peak. One of the mixed vine maple-salmonberry stands at Depot Creek is shown in Figure 12.

At two of the southern-most sites where Caurinus dectes has been found in Oregon, this boreid has been located in terrestrial liverworts (Fisher, Lincoln County), and in both terrestrial and xylicolous hepatics (Klickitat Mountain, Lane County). Caurinus has not been found in epiphyte collections at the two latter localities, although these are similar in aspect to the Porella associations which are utilized elsewhere in the Oregon Coast Range. The major habitat at Klickitat Mountain is the boggy head of a stream (Buck Creek). Although this is very similar to the corresponding areas on Marys Peak the open Douglas fir canopy at Klickitat Mountain has a transgressive understory of western hemlock. Vine maple is common somewhat downstream, but not at all extensive in cover at the bog site. The terrestrial hepatics are again largely confined to soil banks resulting from road building. At Klickitat Mountain (Figures 14,15) and at Fisher, the dominant terrestrial species is Gyrothyra underwoodiana, with Diplophyllum taxifolium the most abundant associate at the former site. At both sites the hepatics grew over areas of many square meters without significant numbers of mosses or

vascular plants.

At Klickitat Mountain, large logs in the boggy area supported Caurinus on hepatics of the Scapania bolanderi and Calypogeja associations (Figure 16). No Caurinus were found in the large cushions of the semiaquatic Scapania undulata.

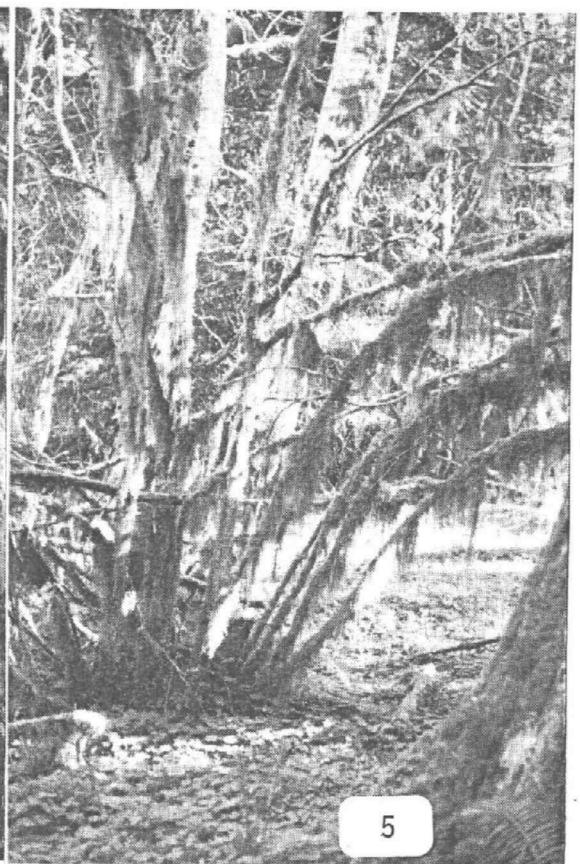
Populations in Washington: The occurrence of Caurinus at the Olympic Peninsula and Packwood sites in Washington were established by extraction of samples supplied by Paul J. Johnson. I have not visited these sites since the collections were made. The Olympic Peninsula collections were all from epiphytic bryophytes. The Clallam Junction collection was taken largely from stems of red elderberry (Sambucus racemosa var. arborescens in a dense, Sambucus-Rubus spectabilis thicket. The liverworts and mosses present appeared to be very similar to the species composition of the Porella-Metaneckera association in the Oregon Coast Range. The Hoh River (Washington) collection was of two fragments of adults from material taken from low branches of western hemlock. This site was adjacent to a more open stringer of alder along a stream. The corticolous Porella-Frullania association was well represented on the alder boles. Nearly all of the Hoh River collection was composed of the moss Isoetecium spiculiferum although some fragments of Porella navicularis and Radula bolanderi were encountered during processing of the sample.

The Packwood (Lewis County, Washington) collection is established from a single female abdomen. Larvae of Hesperoboreus were also present in this sample, which was a composite of bryophytes from the tops of well-rotted logs and from low branches of vine maple. A large number of liverwort species were present, including Scapania bolanderi, Calypogeja trichomanis, Lophocolea cuspidata, Blepharostoma trichophyllum and small quantities of Porella navicularis and Radula bolanderi. A large number of shoots of S. bolanderi were searched in this sample. No eggs of C. dectes were found, although insect feeding damage was evident on many shoots. The small amount of Porella was not adequate to determine whether the Caurinus population was associated with this epiphyte.

Crown Point population: The only known site for Caurinus on the Columbia River Gorge is a steep hillside with an open canopy of bigleaf maple and Douglas fir. The ground is covered with a thick mat of Rhytidiadelphus loreus, much like that described for the summit area of Cascade Head. The original specimen was obtained from the R. loreus, although liverworts could not be located in this material. A second collection showed that Porella navicularis, on low, horizontal branches of bigleaf maple; and several species of hepatics growing on wood (especially S. bolanderi and Jungermannia atrovirens were utilized by C. dectes at this site.

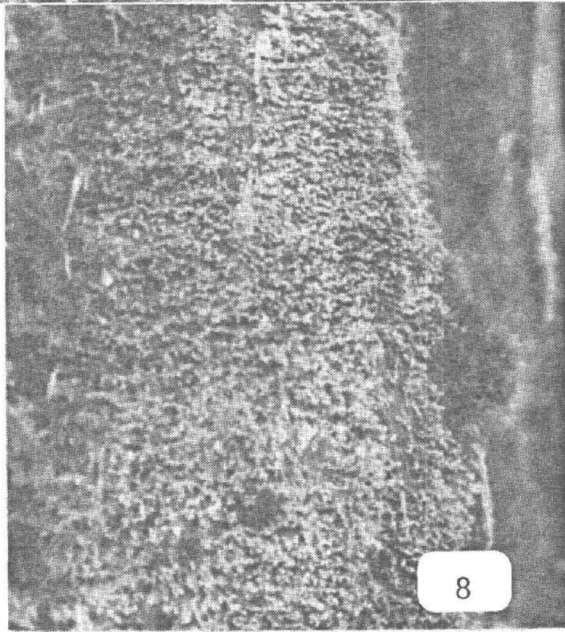
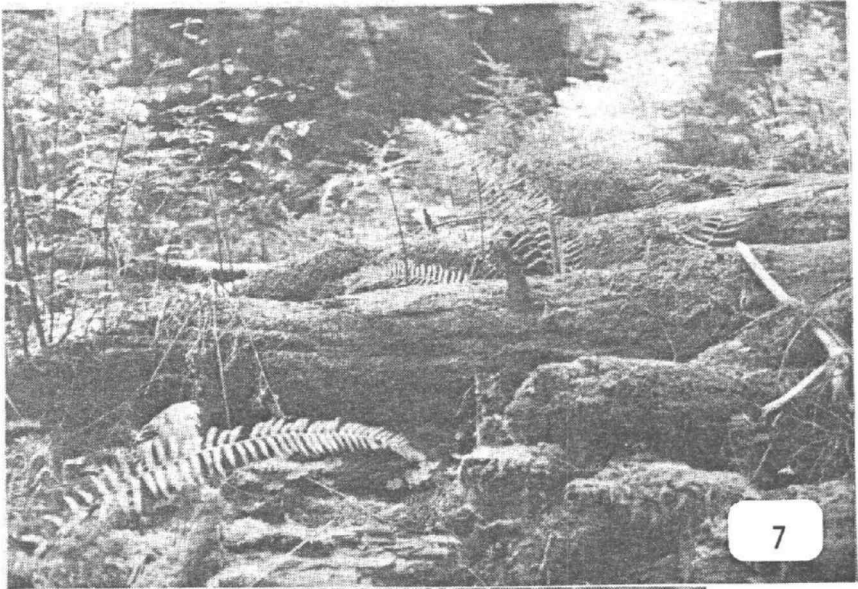
Figures 4-6. Habitat of boreids at Marys Peak (Benton County, Oregon).

- 4) Epiphytic moss (principally Isothecium spiculiferum) on lower branches of western hemlock. Adults and larvae of Hesperoboreus brevicaudus present in epiphytes.
- 5) Epiphytic bryophytes (Porella-Metaneckera association) on arched stems of vine maple. Adults and larvae of Caurinus dectes and H. brevicaudus present.
- 6) Open grove of red alder and bigleaf maple with old coniferous windthrow in foreground.



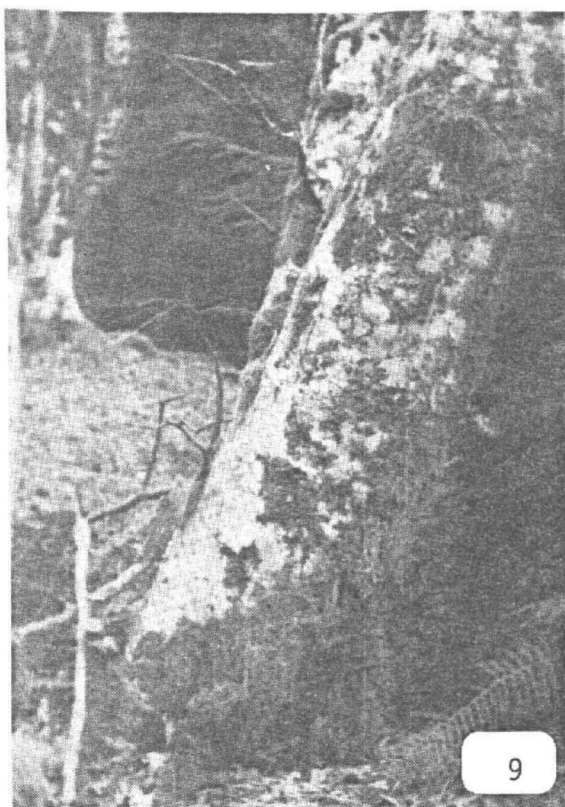
Figures 7, 8. Habitat of Caurinus dectes at Marys Peak.

- 7) Logs in depression, with Scapania bolanderi and Calypogeja associations.
- 8) Close-up of Scapania bolanderi growing near base of decorticated red cedar stump. (The dark tuft is the moss Dicranum fucescens).



Figures 9-11. Habitat of Caurinus dectes at Marys Peak.

- 9) Base of mature red alder in open grove with abundant Porella-Frullania epiphytic association.
- 10) Close-up of stem in Figure 9, showing patches of mosses, liverworts, and lichens on bark surface.
- 11) Logging debris in small tributary of Mulkey Creek, northern exposure. C. dectes is abundant in Scapania bolanderi growing on logs.



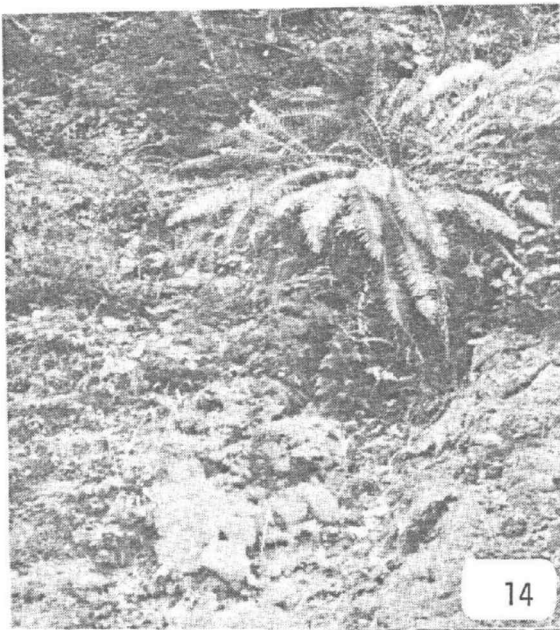
Figures 12, 13. Habitat of boreids near coast (Lincoln County, Oregon).

- 12) Habitat of Caurinus dectes in stream corridor at Depot Creek.
- 13) Tangle of vine maple near Siletz, Oregon. C. dectes and Hesperoboreus brevicaudus present in epiphytes.

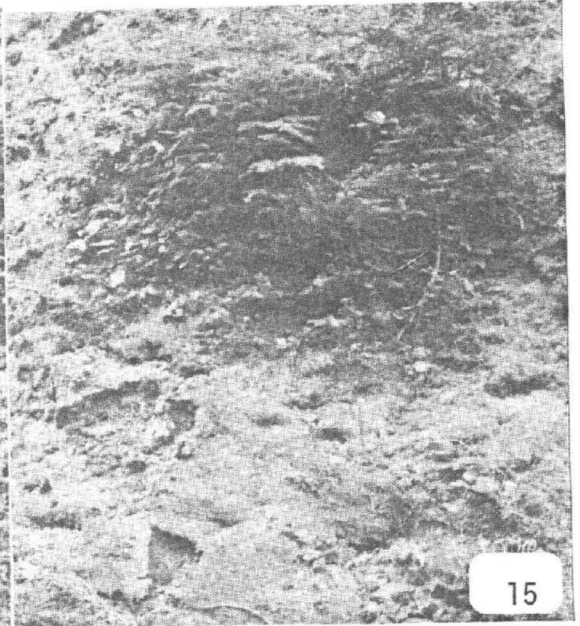


Figures 14-16. Habitat of Caurinus dectes at Klickitat Mountain
(Lane County, Oregon).

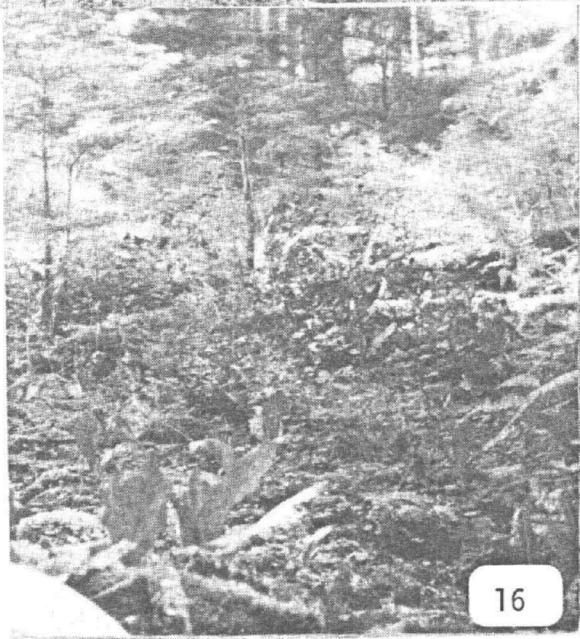
- 14) Terrestrial Gyrothya underwoodiana association
growing on clay of north-exposed road bank.
- 15) Gyrothya underwoodiana and Diplophyllum
taxifolium growing on soil. Larvae of
C. dectes found at this site.
- 16) Bog at head of stream. C. dectes and
Epimartyria larvae present on xylicolous
liverworts in bog.



14



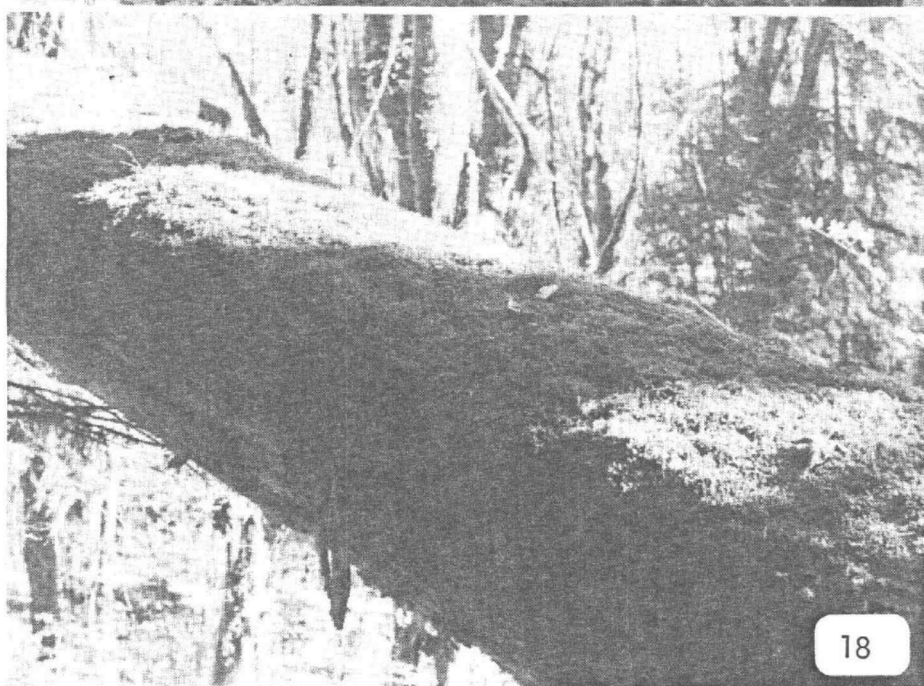
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16

Figures 17, 18. Habitat of Caurinus dectes in southwestern Washington (Morton, Lewis County, Washington).

- 17) General aspect of site with mixed canopy and abundant understory vegetation including Oplopanax horridum and Athyrium felix-femina.
- 18) Section of split log with upper surface covered by Scapania bolanderi.



FEEDING BIOLOGY OF CAURINUS DECTES

One of the main goals of this study was to determine the substrates used as food by adults and larvae of Caurinus. The feeding relationships were considered of special interest because the very unusual mouthparts of adult Caurinus (compared with other Mecoptera) suggested a novel diet. Conversely, if Caurinus had been found to feed on mosses, as is usual for the family Boreidae, the comparison of host utilization by C. dectes with the ecologically sympatric Hesperoboreus brevicaudus would be an interesting study.

An attempt to identify the food of Caurinus was made in March 1978 with the first living adults obtained after discovery of this species. At that time, I supposed that Caurinus was specifically associated with one or more of the epiphytic bryophytes occurring on vine maple, or at least fed on some substrate available in this habitat. The epiphytes were checked closely for possible food sources which could be presented to Caurinus adults in a controlled setting. The feeding association with mosses is well established for most or all other adult Boreidae (Cooper, 1974; Penny, 1977). For this reason, the Caurinus were first confined with shoots of some of the conspicuous epiphytic mosses: Metaneckera menziesii, Rhytidiadelphus loreus, Antitrichia curtispindula and Isoetecium spiculiferum.

Caurinus specimens were confined with these mosses for three weeks. These individuals were most frequently observed resting on the mosses. Although seven of ten individuals survived three weeks, no evidence was found of any feeding on the mosses.

The search for an acceptable food substrate was next broadened to include other types of naturally occurring or artificial substrates: Mnium glabrescens (moss); Peltigera canina (foliose lichen); Agaricus campestris (field mushroom, cap fragment); apple slices; Collembola (Entomobryidae: wounded, immobilized springtails).

These materials were presented to two or more Caurinus in small Petri dishes. Small fragments (less than 4 mm diameter) of the plant

materials, and two to four immobilized springtails were arranged near the Caurinus specimens. These were observed continuously for at least one hour, and checked several times in the following 24 hours. No indication of feeding was observed in this case. Most materials, including the springtails, appeared to be completely ignored.

One of the last collections of Caurinus for spring 1976 included a male, recovered in 70 percent ethanol, which had a green precipitated regurgitate in the oral region. Dissection of this specimen also showed green plant material in the proventriculus.

Since Caurinus was evidently phytophagous, presentations were resumed in October 1976. The liverwort, Porella navicularis was immediately accepted when it was included in this series of trials.

For some time it was assumed that P. navicularis, and to some extent Frullania tamarisci ssp. nisquallensis were the only significant hosts of Caurinus dectes. Sampling strategy for this species emphasized the epiphytic Metaneckera-Porella association. A reappraisal of this assumption was made necessary when a numerous C. dectes population was found at Cascade Head summit where the epiphytic liverworts, including Porella and Frullania, were very limited in occurrence. (The Caurinus were first collected in terrestrial, almost pure, stands of Rhytidiadelphus loreus.) This find led to a general survey for additional host plants for Caurinus, with emphasis on other species of liverworts.

Liverwort survey

The sites where Caurinus had been found were searched for other species of liverworts. Collections of the latter were submitted to Dr. David Wagner (Department of Biology, University of Oregon), and samples of identified liverworts were used in the feeding experiments described below. Many later collections were identified by myself, with the help of reference specimens and a manuscript key to hepatics of Oregon, supplied by Dr. Wagner. The synonymy and taxonomic

arrangement of the most recent checklist of North American liverworts (Stotler and Crandall-Stotler, 1977) is used throughout.

Forty-two species of hepatics, representing four orders and 21 families, were collected between November 1977 and October 1978, in or near known Caurinus habitats. All of the above were used at least once in feeding experiments involving adult or larval Caurinus.

These hepatics are listed in Table 7. An idea of the taxonomic coverage is given in Table 6. The hepatics which have been identified to date probably represent most of the species available to Caurinus dectes within its known range.

Table 6 . Coverage of Oregon liverwort flora in feeding experiments.

Order	Number of Genera			Number of Species		
	In Expt.	In Oregon		In Expt.	In Oregon	
Class Hepaticae:						
Sphaerocarpaceae	0	1	0%	0	1	0%
Marchantiales	2	11	22%	2	17	12%
Metzgeriales	4	7	57%	5	15	33%
Jungermanniales	20	29	69%	34	ca.75	45%
Class Anthocerotae	1	2	50%	1	?	?
Total	27	49	55%	42	ca.110	38%

The coverage is least for the thalloid liverworts (Sphaerocarpaceae, Marchantiales) and is greatest for the leafy liverworts (Jungermanniales). It will be shown below that the latter group includes the hosts of Caurinus. Many of the Oregon species of leafy liverworts not found in my survey occur only more inland or at higher elevation than any known Caurinus dectes populations.

Feeding tests - adult and larval Caurinus

Feeding acceptance and preference by Caurinus was evaluated by presenting small amounts of various substrates to field-collected Caurinus. Most trials used two to five Caurinus confined in 5 cm

Table 7. Liverworts collected during survey for Caurinus habitats.

JUNGERMANNIALES

1. <u>Blepharostoma trichophyllum</u> (L.) Dum.	Pseudolepicoleaceae
2. <u>Ptilidium californicum</u> (Aust.) Underw.	Ptilidiaceae
3. <u>Lepidozia reptans</u> (L.) Dum.	Lepidoziaceae
4. <u>Kurzia makinoana</u> (Steph.) Grolle	"
5. <u>Bazzania ambigua</u> (Lindenb.) Trev.	"
6. <u>B. tricrenata</u> (Wahl.) Trev.	"
7. <u>Calypogeja fissa</u> (L.) Raddi	Calypogejaceae
8. <u>C. muelleriana</u> (Schiffn.) K.Mull.	"
9. <u>C. suecica</u> (H.Arnell et J.Perss.) K.Mull.	"
10. <u>C. trichomanis</u> (L.) Corda	"
11. <u>C. cf. neesiana</u> (Mass. et Carest.) K.Mull.	"
12. <u>Cephalozia bicuspidata</u> (L.) Dum.	Cephaloziaceae
13. <u>C. lunulifolia</u> (Dum.) Dum.	"
14. <u>Geocalyx graveolens</u> (Schrud.) Nees	Geocalycaceae
15. <u>Lophocolea cuspidata</u> (Nees) Limpr.	Lophocoleaceae
16. <u>L. heterophylla</u> (Schrud.) Dum.	"
17. <u>Chiloscyphus pallescens</u> (Ehrh. ex Hoffm.) Dum.	"
18. <u>C. polyanthos</u> (L.) Corda	"
19. <u>Plagiochila porelloides</u> (Torrey ex Nees) Lindenb.	Plagiochilaceae
20. <u>Gyrothyra underwoodiana</u> M. A. Howe	Gyrothyraceae
21. <u>Lophozia incisa</u> (Schrud.) Dum.	Jungermanniaceae
22. <u>Jamesoniella autumnalis</u> (DC.) Steph.	"
23. <u>Nardia scalaris</u> S. Gray	"
24. <u>Jungermannia atrovirens</u> Dum.	"
25. <u>J. rubra</u> Gott. ex Underw.	"
26. <u>Diplophyllum albicans</u> (L.) Dum.	Scapaniaceae
27. <u>D. obtusifolium</u> (Hook.) Dum.	"
28. <u>D. taxifolium</u> (Wahlenb.) Dum.	"

Table 7. Liverworts collected during survey (continued)

29. <u>Diplophyllum plicatum</u> Lindb.	Scapaniaceae
30. <u>Scapania americana</u> K.Mull.	"
31. <u>S. bolanderi</u> Aust.	"
32. <u>S. umbrosa</u> (Schrad.) Dum.	"
33. <u>S. undulata</u> (L.) Dum.	"
34. <u>Radula bolanderi</u> Gott.	Radulaceae
35. <u>Porella cordaeana</u> (Hub.) Moore	Porellaceae
36. <u>P. navicularis</u> (Lehm et Lindenb.) Lindb.	"
37. <u>P. roellii</u> Steph.	"
38. <u>Frullania tamarisci</u> (L.) Dum. subsp. <u>nisquallensis</u> (Sull.) Hatt.	Jubulaeaceae
METZGERIALES	
39. <u>Pellia neesiana</u> (Gott.) Limpr.	Pelliaceae
40. <u>Metzgeria conjugata</u> Lindb.	Metzgeriaceae
41. <u>Blasia pusilla</u> L.	Blasiaceae
42. <u>Riccardia latifrons</u> Lindb.	Aneuraceae
43. <u>R. multifida</u> (L.) S.Gray	"
MARCHANTIALES	
44. <u>Conocephalum conicum</u> (L.) Lindb.	Conocephalaceae
45. <u>Athalamia hyalina</u> (Sommert.) Hatt.	Cleveaceae
ANTHOCEROTAE (Anthocerophyta)	
46. <u>Anthoceros punctatus</u> L.	

Petri dishes with discs of moist filter paper lining the bottom of the dish. At least four small (2 cm or less maximum dimension) examples of the feeding substrates were presented in each trial. At least one shoot of a highly-accepted host (usually gametophytes of the liverworts Scapania bolanderi or Porella navicularis) was included at the start of each trial. In addition to this "standard", one to four test substrates were included on each occasion. Activity of the Caurinus and feeding traces were usually checked at 2, 12 and 24 hours after introduction. At 24 hours the extent of feeding on each substrate was noted, and the standard was removed.

At 3-4 days the trial was terminated, and the relative feeding on each substrate was recorded. Where possible, all substrates which were not fed on in initial trials were tested under deprivation conditions (in the absence of any readily accepted substrate).

These data were used to evaluate possible hosts on a five point scale:

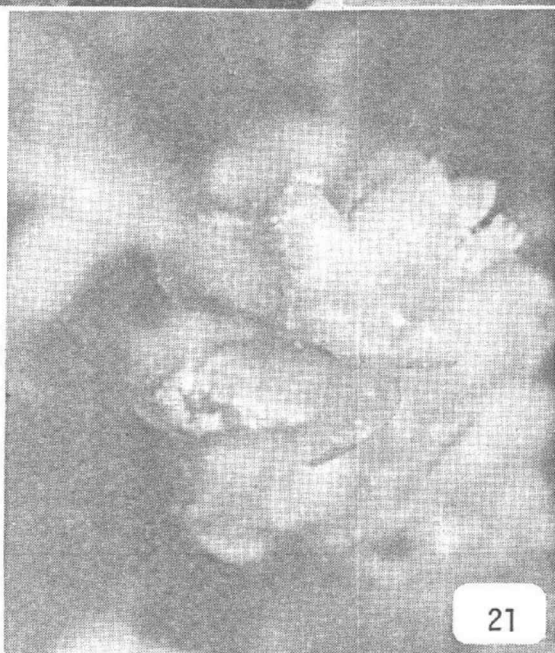
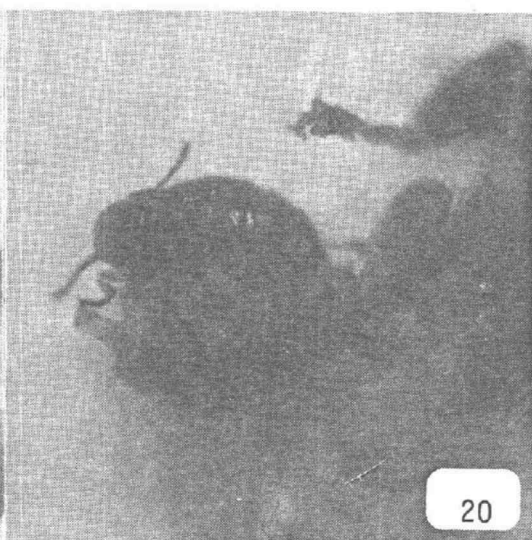
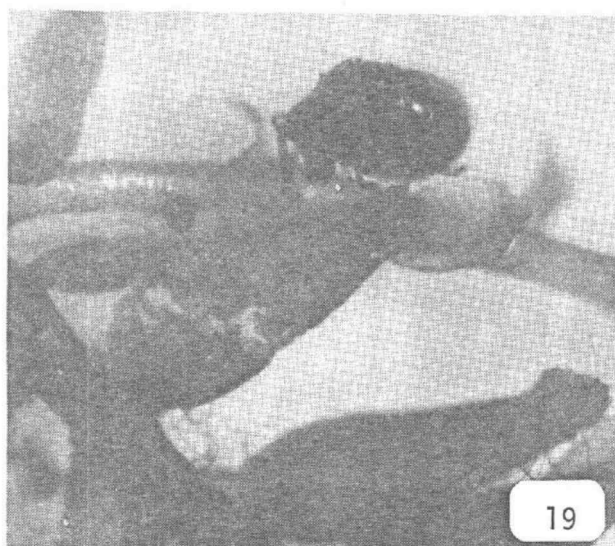
1. immediate acceptance (first 24 hours, usually first 12 hours); feeding usually extensive.
2. acceptance limited while preferred host present, then feeding extensive as in #1.
3. acceptance delayed and feeding less extensive than in #1, 2.
4. feeding very localized, not continued.
5. no feeding detected.

Results expressed on this qualitative scale were usually consistent in separate trials when both the offered substrates and the number of Caurinus were varied. This was associated with the feeding behavior of adults during the main reproductive season (December - March), when most individuals would feed frequently, and move about between periods of feeding.

Feeding trials with teneral or old adults (September, October, April, May) were often inconclusive because many of the individuals were in poor condition, and fed and moved less regularly. Results of tests with such material is recorded here only if not repeated under better conditions.

Figures 19-22. Feeding activities of adult Caurinus dectes.

- 19) Male C. dectes feeding on leaf of Plagiochila porelloides. Feeding damage is visible at base of leaf.
- 20) Female C. dectes feeding on Geocalyx graveolens.
- 21) Shoot of Scapania bolanderi with adult Caurinus feeding damage; collected at Marys Peak, Benton County, Oregon.
- 22) Scapania bolanderi heavily damaged by Caurinus adults in culture.



The more sedentary Caurinus larvae required a somewhat different approach for evaluation of the host range. Rather than using a choice trial, I placed larvae on or next to a clump or shoot of the bryophyte substrate. Criteria for host acceptance were: initiation of feeding (usually penetration of the tissues); short-term survival and persistence (vs. absconding), to three or four days; and growth.

Fewer bryophyte taxa were examined for larval acceptance than were surveyed for the adults. These data were augmented by observation of larvae discovered in situ in field-collected bryophytes. The acceptance was rated on the same scale used for adults. However, all taxa found to be utilized in the field were rated as "1" - fully acceptable.

Field records of oviposition and apparent adult or larval feeding damage by Caurinus were also utilized to evaluate the actual host range. Records were also kept of feeding on bryophytes by other insects.

Results of feeding

The results of the feeding acceptance trials for Caurinus adults and larvae are given in Tables 8 and 9. The assignment of grades of acceptance, although qualitative, was usually in agreement between trials. Variation between trials was highest for adults exposed to species of Cephalozia, Calypogeja, and Diplophyllum. This variation may be due to differences in the behavior of individual Caurinus, or reflect differences in host material. The latter includes the possibility of misidentifications in the above genera, where similar-appearing species may grow in close proximity. Additionally, there may be environmental or seasonal influences on host quality. The single instance of adult Caurinus feeding on Cephalozia lunulifolia occurred on the perianth of a fertile shoot while other trials utilized only sterile shoots of this species.

The significance of feeding acceptance under laboratory conditions requires substantiation by field observations. Caurinus

Table 8. Feeding acceptance of liverwort species by Caurinus dectes adults.

Liverwort species	Source ¹	Caurinus		Extent of feeding		Reference species ²	Rating ³
		#(M/F)	Source ¹	1 day	2-5 days		
<u>Blepharostoma trichophyllum</u>	KM	2/0	KM	none	none	Sbol	
	PF	1/2	MO	none	none?	Ppor	5?
<u>Ptilidium californicum</u>	MP	1/1	MP	none	min.	Sbol	3-4
<u>Lepidozia reptans</u>	MP	5/3	MP	none	none	Pnav	
	KM	0/2	KM	none	none	Sbol	
	PF	1/3	MO	none	none	Sbol	5
<u>Bazzania ambigua</u>	PF	0/1	MO	mod.	----	Sbol	
	PF	2/2	MP	min.	mod.	Sumb	2
<u>Bazzania tricrenata</u>	LT	1/2	LT	mod.	much	Sbol	1
<u>Calypogeja fissa</u>	MP	4/3	MP	mod.	much	Pnav	1
<u>Calypogeja muelleriana</u>	KM	1/3	KM	mod.	mod.	Sbol	1
<u>Calypogeja seucica</u>	PF	1/1	PF	none	min.	Sbol	4
<u>Calypogeja trichomanis</u>	MP	2/1	MP	min.	min.	Sumb	
	MP	2/2	MP	mod.	much	Sbol	2-3
<u>Cephalozia bicuspidata</u>	MP	1/5	MP	none	none	Pnav	5
<u>Cephalozia lunulifolia</u>	MP	2/1	MP	none	none	Sbol	
	PF	0/2	MO	none	none	Ppor	5
<u>Geocalyx graveolens</u>	KM	1/3	KM	none	mod.	Sbol	3
<u>Lophocolea cuspidata</u>	CP	1/1	MP	mod.	mod.	Pcor	2
<u>Lophocolea heterophylla</u>	PF	1/2	PF	much	much	Ppor	
	PF	3/3	MO	min.	much	Sbol	1

Table 8. (Continued)

Liverwort species	Source ¹	Caurinus		Extent of feeding		Reference species ²	Rating ³
		#(M/F)	Source ¹	1 day	2-5 days		
<u>Chiloscyphus pallescens</u>	MP	2/1	MP	none	none	Sumb	5
<u>Chiloscyphus polyanthos</u>	MP	2/1	MP	min.	mod.	Pnav	2
<u>Plagiochila porelloides</u>	CP	6/5	MP	much	much	Sbol	
	PF	2/0	MO	much	much	----	
	MP	1/1	MP	mod.	much	----	1
<u>Gyrothya underwoodiana</u>	MP	3/2	MP	none	mod.	Sbol	
	KM	1/1	KM	mod.	mod.	Sbol	2-3
<u>Lophozia incisa</u>	KM	1/5	MP	min.	min.	Sbol	3-4
	PF	3/5	MO	mod.	mod.	Ppor	1
<u>Jamesoniella autumnalis</u>	PF	1/1	MP	none	mod.	Sbol	3
<u>Nardia scalaris</u>	LT	1/2	LT	min.	mod.	Sbol	2
<u>Jungermannia atrovirens</u>	CP	1/1	MP	none	mod.	Ppor	3
<u>Jungermannia rubra</u>	MP	3/7	MP	mod.	mod.	Pnav	1
<u>Diplophyllum albicans</u>	CH	1/3	MP	none	mod.	Pnav	3
<u>Diplophyllum obtusifolium</u>	MP	0/3	MP	mod.	much	Ppor	1
<u>Diplophyllum taxifolium</u>	KM	1/3	KM	none	none	Sbol	5
<u>Diplophyllum plicatum</u>	LT	1/2	LT	min.	much	Sbol	2
<u>Scapania americana</u>	CP	1/5	MP	mod.	much	Pcor	1

Table 8. (Continued)

Liverwort species	Source ¹	Caurinus		Extent of feeding		Reference species ²	Rating ³
		#(M/F)	Source ¹	1 day	2-5 days		
<u>Scapania bolanderi</u>	MP	10/16	MP	much	much	----	
	PF	3/3	MO	mod.	mod.	----	1
<u>Scapania umbrosa</u>	MP	2/4	MP	mod.	mod.	Ppor	1-2
<u>Scapania undulata</u>	KM	2/1	MP	none	none	Sbol	
	MP	2/0	MP	none	none	Sbol	5
<u>Radula bolanderi</u>	MP	5/5	MP	min.	none	Pnav	4-5
<u>Porella cordaeana</u>	CP	6/7	MP	mod.	much	----	1
<u>Porella navicularis</u>	MP	11/20	MP	much	much	----	
	PF	3/3	MO	mod.	much	----	1
<u>Porella roellii</u>	CP	3/4	MP	mod.	min.	Ppor	Toxic?
<u>Frullania tamarisci</u>	MP	3/3	MP	min.	mod.	Pnav	
	CH	2/0	CH	mod.	much	Pnav	2
<u>Pellia neesiana</u>	KM	1/1	KM	none	none	----	5
<u>Metzgeria conjugata</u>	QU	0/3	MP	none	none	Ppor	5
<u>Blasia pusilla</u>	MP	0/3	MP	none	mod.	Ppor	3
<u>Riccardia latifrons</u>	MP	0/4	MP	min.	mod.	----	2
<u>Riccardia multifida</u>	MP	2/1	MP	none	mod.	Pnav	3

Table 8. (Continued)

Liverwort species	Source ¹	<u>Caurinus</u>		Extent of feeding		Reference species ²	Rating ³
		#(M/F)	Source ¹	1 day	2-5 days		
<u>Conocephalum conicum</u>	MP	1/3	MP	none	none	----	
	CP	0/4	MP	none	none	Ppor	5
<u>Athalamia hyalina</u>	CP	2/4	MP	none	none	Ppor	5
<u>Anthoceros punctatus</u>	MP	2/2	MP	min.	none	----	
	PF	1/3	MO	none	none	Ppor	4-5

Observations used in table

¹Localities:

CH: Cascade Head (Tillamook County, Oregon)
 CP: Crown Point (Multnomah County, Oregon)
 KM: Klickitat Mountain (Lane County, Oregon)
 LT: Lake Twentytwo trail (Snohomish County, Washington)
 MO: Morton (Lewis County, Washington)
 MP: Marys Peak (Benton County, Oregon)
 PF: Pack Forest (Thurston County, Washington)
 QU: Queets (Jefferson County, Washington)

²Reference species:

Pcor: Porella cordaena
 Pnav: Porella navicularis
 Ppor: Plagiochila porelloides
 Sbol: Scapania bolanderi
 Sumb: Scapania umbrosa

³Acceptance ranking:

1 - highly acceptable
 5 - never eaten

Table 9. Feeding acceptance of liverwort species by Caurinus dectes larva, including observations in larvae collected in situ.*

Liverwort species	Source	Caurinus larvae		Source	Found in field	Extent of feeding	Growth	Rating
		No.	(Instar)					
<u>Calypogeja</u> <u>fissa</u>	MP	2	?	MP	no	mod.	?	2
<u>Cephalozia</u> <u>bicuspidata</u>	MP	3	2	MP	no	mod.	?	3
<u>Cephalozia</u> <u>lumulifolia</u>	MP	5	2	MP	no	none	none	5
<u>Gyrothya</u> <u>underwoodiana</u>	MP	3	2,3	MP	yes	mod.	?	
	KM	2	3	KM	yes	mod.	good	1-2
<u>Lophozia</u> <u>incisa</u>	KM	2	3	KM	no	none	none	5
<u>Nardia</u> <u>scalaris</u>	CH	3	3	CH	yes	mod.	good	1
<u>Jungermannia</u> <u>rubra</u>	MP	3	2	MP	no	much	good	1
<u>Diplophyllum</u> <u>albicans</u>	CH	2	3	CH	yes	mod.	good	1
<u>Scapania</u> <u>bolanderi</u>	MP	14	1-3	MP	yes	much	good	1
<u>Porella</u> <u>navicularis</u>	MP	17	1-3	MP	yes	much	good	1
<u>Frullania</u> <u>tamarisci</u>	MP	12	2	MP	no	mod.	poor	3
<u>Conocephalum</u> <u>conicum</u>	MP	3	?	MP	no	none	none	5
<u>Anthoceros</u> <u>punctatus</u>	MP	4	2	MP	no	none	none	5

*Abbreviations are defined in Table 8.

Table 10. Field associations of Caurinus dectes with leafy liverworts (Jungermanniales).

Liverwort species	Locality	With <u>Caurinus</u> eggs	With adult feeding	With larvae or larval galleries
<u>Bazzania</u> <u>ambigua</u>	Lewis Co., WA	+	+	-
<u>Bazzania</u> <u>tricrenata</u>	Snohomish Co., WA	-	+	-
<u>Calypogeja</u> <u>fissa</u>	Benton Co., OR	+	+	-
<u>Lophocolea</u> <u>heterophylla</u>	Lewis, Co., WA	-	+	-
<u>Plagiochila</u> <u>porelloides</u>	Benton Co., OR	+	+	+ (?)
<u>Gyrothyra</u> <u>underwoodiana</u>	Benton Co., Lincoln Co., OR	+	-	-
<u>Lophozia</u> <u>incisa</u>	Snohomish Co., WA	+	-	-
<u>Nardia</u> <u>scalaris</u>	Tillamook Co., OR	+	+	+
<u>Diplophyllum</u> <u>albicans</u>	Tillamook Co., OR	+	-	+
<u>Diplophyllum</u> <u>obtusifolium</u>	Benton Co., OR	+	+	-
<u>Scapania</u> <u>umbrosa</u>	Benton Co., OR	-	+	-
<u>Scapania</u> <u>bolanderi</u>	many localities, Wash., Oregon	+	+	+
<u>Porella</u> <u>navicularis</u>	Benton Co., Lincoln Co., OR	+	+	+

(+) Association known from at least one locality

(-) No field evidence for association

have rarely been located without disturbance in the field, and have not been observed feeding under such conditions. Only a few liverworts have been found in pure stands of sufficient extent to establish a host association by location of Caurinus in a bulk sample.

The best evidence of patterns of adult feeding in the field is the location of feeding damage similar to that produced by Caurinus in the laboratory. Similar damage is caused by feeding of chironomid and micropterygid larvae, so that I have been reluctant to use such damage as evidence of Caurinus host associations. Citation of field association has therefore been limited to association of the damaged liverworts with eggs or adults of Caurinus.

In contrast to the adults, Caurinus larvae have been located within their feeding sites. The location of larvae in their feeding galleries provide direct evidence of utilization of some liverwort species. Unfortunately, it was difficult to identify abandoned larval galleries. The destruction of the central axis causes the affected shoot segment to disintegrate within a short period of time. Truncated shoots found in the field were thought to be damaged by Caurinus larvae, but this association is too weak to admit for identification of the host range. The relevant field records of larval feeding, adult feeding, and oviposition are given in Table 10.

A comparison of laboratory and field observations indicates that liverworts which are highly accepted in the presentation experiments (grades "1" and "2") are likely hosts of Caurinus if they occur in appropriate habitats. Species classified as "4" or "5" (no feeding, or feeding only when deprived of preferred hosts) are likely to be unavailable to Caurinus, while the intermediate grade includes species which may occasionally be utilized by Caurinus. As noted above, there is a possibility that the acceptance levels given here are not representative of all growth forms of the liverwort species.

Additional presentations were made of several species of mosses during the feeding trials described here. Adult Caurinus fed

sparingly (producing small perforations of the leaf lamina) on two species: Mnium glabrescens (Mniaceae), and Hookeria lucens (Hookeriaceae). Each occurrence was under deprivation (no preferred liverworts available) and only H. lucens was accepted under similar conditions in a second trial. Each of these would correspond to the lowest acceptance level ("4") used in Tables 8 and 9, and neither is included in the list of Caurinus host plants.

From the evidence given above, it appears that in nature Caurinus decetes feeds only on hepatics of the order Jungermanniales (the leafy liverworts). Although liverworts of the related order Metzgeriales have been eaten under laboratory conditions, there is no evidence that these, or other unrelated bryophytes are of any significance as adult or larval hosts of Caurinus decetes.

A number of species of leafy liverworts are strongly indicated to be hosts utilized by field populations of Caurinus. These are distributed among genera representing several of the suborders of Jungermanniales, as defined by Stotler and Crandall-Stotler (1977). Most of the hepatic species sampled in this study are decidedly stenotopic, but in the aggregate they occupy a number of different substrates. Caurinus decetes is active over several strata of the forest habitat. Accordingly the species composition in the diet of an individual or population of C. decetes varies according to the distribution of substrates colonized by liverworts.

Although other environmental factors affect the distribution of hepatics, a classification by substrate appears the most useful means of depicting the acceptance spectrum of Caurinus among co-occurring species.

Most of the hepatic species available to Caurinus populations can be associated with one or more of these major substrate types: epiphytic; xylicolous (on decaying wood); on rock surfaces; on soil; and aquatic or semiaquatic.

The distribution of liverworts among these substrate groupings and by their apparent significance as hosts for Caurinus is shown in Table 11. Both laboratory and field evidence are incorporated in the

Table 11. Status of liverwort species as hosts for Caurinus decetes, and their distribution by habitat associations. (Status as host inferred from field and laboratory observations).

Habitat group	Highly accepted hosts	Secondary hosts	Not accepted
Epiphytic on deciduous trees and shrubs	<u>Porella navicularis</u> -AL	<u>Frullania tamarisci</u> -AL	<u>Radula bolanderi</u> -A <u>Metzgeria conjugata</u> -A
On decaying logs, stumps (early stage, with bark)	<u>Scapania bolanderi</u> -AL <u>Bazzania tricrenata</u> -A	<u>Ptilidium californicum</u> -A <u>Bazzania ambigua</u> -A <u>Lophocolea cuspidata</u> -A <u>Porella roellii</u> -A ¹	<u>Lepidozia reptans</u> -A
On decaying logs (advanced stage, decorticated)	<u>Calypogeja fissa</u> -A <u>C. muelleriana</u> -A <u>C. trichomanis</u> -A <u>Scapania bolanderi</u> -AL <u>S. umbrosa</u> -A <u>Lophocolea heterophylla</u> -A	<u>Geocalyx graveolens</u> -A <u>Lophozia incisa</u> -A <u>Cephalozia bicuspidata</u> -L <u>C. lunulifolia</u> -A <u>Calypogeja fissa</u> -L <u>Jamesoniella autumnalis</u> -A <u>Jungermannia atrovirens</u> -A <u>Riccardia latifrons</u> -A	<u>Cephalozia bicuspidata</u> -A <u>C. lunulifolia</u> -L <u>Blepharostoma trichophyllum</u> -A <u>Chiloscyphus pallescens</u> -A <u>Lepidozia reptans</u> -A

Table 11. (continued)

Habitat group	Highly accepted hosts	Secondary hosts	Not accepted
Terrestrial, on compacted soil	<u>Gyrothya underwoodiana</u> -L	<u>Gyrothya underwoodiana</u> -A	<u>Pellia neesiana</u> -A
	<u>Nardia scalaris</u> -AL	<u>Jungermannia rubra</u> -AL	<u>Athalamia hyalina</u> -A
	<u>Diplophyllum albicans</u> -L	<u>Blasia pusilla</u> -A	<u>Conocephalum conicum</u> -A
	<u>D. obtusifolium</u> -A		<u>Anthoceros punctatus</u> -AL
Terrestrial, on forest litter	<u>Plagiochila porelloides</u> -A		
	<u>Diplophyllum plicatum</u> -A		
On boulders, rock outcrops	<u>Plagiochila porelloides</u> -A	<u>Porella cordeana</u> -A	
		<u>P. roellii</u> -A ¹	
		<u>Scapania americana</u> -A	
Semiaquatic, in streams and seepages ²		<u>Chiloscyphus polyanthos</u> -A	<u>Scapania undulata</u> -A
		<u>Riccardia multifida</u> -A	<u>Anthoceros punctatus</u> -AL
		<u>Blasia pusilla</u> -A	

A - adult association; L - larval association

1) accepted, but probably toxic to C. dactylus. 2) habitat probably not entered by C. dactylus.

ranking in this table, but the latter is emphasized. Where results from adult and larval feeding trials differ markedly, the liverwort is placed in separate cells in Table 11.

The xylicolous grouping, including most of the listed species, is subdivided into early and late successional sections. This separates species occurring on intact logs from those on more decayed, often decorticated, wood surfaces. All species of the early successional group also occur as epiphytes on conifers. With the exception of the hydric group, each of the hepatic substrates is accessible to Caurinus adults within the known range of this species. However, there is no definite association of Caurinus with hepatics growing on rock outcrops.

The host associations shown in Table 11 are discussed briefly below by substrate grouping.

Epiphytic hepatics: Much of my earlier work on Caurinus centered on Oregon Coast Range populations which were principally associated with epiphytic bryophytes of the forest understory and lower canopy. The heavy mats of epiphytes on the lower branches and boles of deciduous trees and shrubs are the most favorable sites for Caurinus in this stratum. All of these populations are apparently dependent on Porella navicularis as the only significant larval and adult host. P. navicularis is apparently not utilized at some Caurinus sites where it occurs. This is presumably due to marginal physical factors in the canopy for Caurinus, for all collections of P. navicularis used for feeding Caurinus were highly acceptable.

The only other epiphytic hepatic of any probable importance to Caurinus is Frullania tamarisci. This hepatic was possibly fed on by C. decetes where it occurred on salmonberry stems at Cascade Head; there is no indication of larval feeding on this liverwort in the field. No acceptance has yet been recorded for samples of the other epiphytic genera, Radula and Metzgeria.

Hepatics growing on logs and stumps (xylicoles): In Table this group is divided into an early and a late successional section. The early successional species occur on the back of relatively intact

wood. All of those listed also occur as epiphytes on living coniferous trees (Coleman et al. 1958), but such occurrences are not known to be utilized by Caurinus. Scapania bolanderi is by far the most important hepatic in terms of coverage in a number of coniferous bark sites. S. bolanderi often occurs in dense, more or less pure stands over large areas on stumps or fallen logs, although it also occurs in tufts among other bryophytes. Scapania bolanderi is frequently heavily damaged by adult and larval Caurinus feeding activity. Like P. navicularis, this species has been used to maintain Caurinus cultures, and as a standard in the feeding trials.

None of the favored liverworts listed from the later successional flora of rotting logs is as generally abundant as S. bolanderi in the earlier stages, and none has been conclusively shown to support Caurinus populations. Caurinus decetes has been found on rotten-log substrates where S. bolanderi is absent or not utilized, however. In such associations, one or more of the Calypogeja species are most likely to serve as alternate hosts. The shoots of C. fissa, C. muelleriana, and C. trichomanis frequently show leaf damage and abnormal intercalary branching as evidence of insect feeding.

Hepatics occurring on rock surfaces: Collections of the liverworts Porella roellii and Plagiochila porelloides were made on moist rocky substrates near known Caurinus habitats in the Columbia River Gorge and in Thurston County, Washington, but actual Caurinus contact with these hepatics was not demonstrated. Plagiochila porelloides is as acceptable to C. decetes adults as the best host species (Porella navicularis and Scapania bolanderi). Although Plagiochila porelloides is a very conspicuous species it was difficult to locate in areas occupied by Caurinus. Collections were finally made at the Marys Peak site in October 1978 and heavy Caurinus feeding damage was demonstrated.

Porella roellii is interesting because of its apparent toxicity. Caurinus adults readily began feeding on this species, but showed distress, including regurgitation and repeated mouthpart grooming, beginning within 30 seconds of the initial feeding. It should be

noted that the field character for identification of P. roellii is its violent, burning taste, experienced after a few seconds delay.

Terrestrial hepatics: A number of the thalloid liverworts of the orders Marchantiales and Metzgeriales are terrestrial in wet places; these are apparently not hosts to Caurinus and are not considered further. The terrestrial Jungermanniales are chiefly mat-forming species, and frequently cover relatively large areas on compacted or rapidly eroding clay or sand banks in shaded, moist sites. Some of the Oregon Coast Range hepatics growing abundantly on soil are:

Jungermannia rubra

Diplophyllum albicans

Gyrothya underwoodiana

D. taxifolium

Nardia scalaris

Blasia pusilla

Partly because of the large amount of host material present, it is difficult to evaluate the state of the relatively sparse terrestrial Caurinus populations. Eggs and larvae, as well as adult feeding damage, have been found in field collected G. underwoodiana, N. scalaris, and D. albicans at some distance from other host substrates. In spite of the lack of visible feeding impact on terrestrial hosts, the scarcity of other hepatics at such sites as Cascade Head, Fisher, and Klickitat Mountain (all in the Oregon Coast Range, see Table 4) implies that these populations are chiefly associated with one or more of the terrestrial liverworts listed above.

Aquatic hepatics: Although some of the hygic liverworts are accepted in the laboratory, there is no evidence that Caurinus enters this habitat.

Discussion

The data presented above show that adults and larvae of Caurinus are quite similar in overall habitat utilization and in host range. The host spectrum is related to plant taxonomy in that the only known highly acceptable hosts are species of Jungermanniales, while some species of the similar Metzgeriales are eaten occasionally and a few

mosses are rarely accepted.

Within the Jungermanniales however, the pattern of utilization is erratic. The most favorable host species are distributed among several unrelated families, while some genera include species of widely different palatability. This pattern is probably determined by phytochemical differences in bryophytes, possibly through interaction of host-recognition and feeding-deterrent materials.

The major groups of bryophytes are characterized biochemically by quite different secondary metabolites. A number of mosses are known to produce triterpenoid compounds or considerable quantities of phenolic materials (Hegnauer, 1962). Most liverworts sequester lipophilic materials in intracellular "oil bodies", which occur in some or all tissues of the gametophytes (Schuster, 1966). The contents of the oil bodies commonly range between one and two percent of the tissue dry weight in leafy liverworts. Recent work has shown the oil bodies of most leafy liverworts to be largely composed of complex mixtures of sesquiterpenoid material, frequently resembling chemicals elaborated in essential oils of higher plants (Andersen, et al., 1973, 1977).

All species of Jungermanniales investigated to date are characterized by presence of α - or β -barbatene or anastreptene (Andersen et al., 1977). Neither compound is known to occur outside the leafy liverworts, and these or related sesquiterpenoids could provide host identification for Caurinus or other specialists of this group. A number of leafy liverwort species are known to have extremely bitter or "hot" tastes (like Porella roellii), while some species of Frullania (including F. tamarisci, Knoche et al., 1969) and Radula (Asakawa et al., 1978) cause contact dermatitis in humans. The active materials, where known, are chemically diverse, and these again could contribute to reduced palatability for Caurinus.

Stahl (1888) and Lohmann (1903) suggested that herbivore defense is based on toxic substances in liverworts, while mosses were thought to be relatively indigestible. This presumed dichotomy closely parallels recent ideas of vascular plant-herbivore interactions,

Table 12 . Characteristics of host plants of Boreidae related to insect feeding.

Leafy liverworts	Mosses
Shoots with bilateral symmetry, often depressed	Shoots with radial symmetry
Leaves unistratose	Leaves with 1 or 2 cell layers
Leaves without cuticle	Cutin waxes frequently present
Cell walls not thickened in most tissues	Cell walls frequently thickened in older tissues and outer layer of stem
Cell walls with little true cellulose	Cell walls with high cellulose content
Cell walls not mineralized (terrestrial spp.)	Cell walls frequently with silica deposits
Cell size large on average ($>30\mu$)	Cell size frequently small ($<15\mu$)
Sesquiterpenoids present in most species, localized in intracellular "oil-bodies"	Oil-bodies absent, few reports of toxic phytochemicals
Phenolic content low	Frequently with high phenolic content (both tannin-like and lignin-like compounds known)

including the qualitative and quantitative defense scheme of Feeny (1975). Since Caurinus is univoltine and the moss-feeding boreines are semivoltine (i.e., with a two-year life cycle) it was thought that the nutrient quality of hepatics might be relatively high, as predicted for chemically well-protected plants. This is probably not the case, as indicated by the elemental nutrient analysis of nine co-occurring bryophytes (3 liverworts, 6 mosses) from Marys Peak (Table 13). The most striking feature of these analyses is the generally low level of nitrogen (therefore, of protein) for the Caurinus hosts P. navicularis and S. bolanderi, as well as in Frullania tamarisci and five of the six moss species. Mnium glabrescens had over twice the nitrogen content of any other species tested, and was high in the other inorganic nutrients, as well. This is evidently due to a low cell wall/cell contents ratio in this moss; it is worth noting that both M. glabrescens and Mnium insigne are relatively heavily grazed by the generalist slug Ariolimax columbiana (observed at Marys Peak).

Although Caurinus adults, and to some extent the larvae, are capable of excluding cell wall material and feeding on the cell contents, it seems unlikely that Jungermanniales are generally higher quality food than the mosses utilized by boreine adults and larvae. The life cycle difference is more likely due to primary utilization of detritus (rather than living moss tissues) by Boreus or Hesperoboreus larvae. There is some indication that the micro-ptyergid larvae (Epimartyria sp.) occurring with Caurinus, and feeding on the same liverworts, may require two years to mature.

The liverworts most frequently utilized by Caurinus are principally of West Coast distribution (Schofield, 1968), although Plagiochila porelloides, and a number of secondary hosts are widely distributed Holarctic species. Caurinus is apparently too generalized in its diet for host distribution to be significant in determining its geographical range. Similarly, there is no indication that Caurinus or any other contemporaneous herbivore has selected the phytochemical spectrum of leafy liverworts. Although Schuster (1972) supposed that

Table 13. Macronutrient composition of gametophytes of some bryophytes collected at Marys Peak.

	Element (percent dry weight)					
	P	N	Na	K	Ca	Mg
Mosses						
<u>Dicranum fucescens</u>	.142	.932	.038	.546	.418	.145
<u>Mnium glabrescens</u>	.251	2.083	.043	1.125	.972	.261
<u>Eurhynchium oreganum</u>	.146	.829	.056	.741	.518	.190
<u>Isoetecium spiculiferum</u>	.142	.949	.034	.512	.526	.177
<u>Antitrichia curtispindula</u>	.151	.686	.028	.631	.430	.170
<u>Rhytidiadelphus loreus</u>	.164	.727	.072	.770	.440	.171
Liverworts						
<u>Scapania bolanderi</u>	.072	.748	.035	.659	.275	.111
<u>Porella navicularis</u>	.155	.890	.026	1.040	.426	.156
<u>Frullania tamarisci</u> ssp. <u>nisquallensis</u>	.107	.874	.030	.904	.515	.134
Average mosses (6 species)	.166	1.034	.045	.721	.551	.186
Average liverworts (3 species)	.111	.834	.030	.868	.405	.134

most families and genera of liverworts had evolved by the early Cretaceous, the "defensive" chemicals are quite similar in a number of distantly related genera. The dependence on the oil-bodies, containing sesquiterpenoids, is in fact found in all the major subgroups of the Hepaticae. These facts suggest that the disruptive selection, leading to evolution of unique secondary chemicals in related groups of vascular plants, has been less of a factor in the evolution of the liverworts.

BEHAVIOR

Several aspects of the behavior of Caurinus dectes are described in sections dealing with the ecological context of the behavior, or are covered in association with morphological description of the effector systems. Accounts are given elsewhere of mating (page 236), oviposition (page 104), and locomotion (page 215) in the adult; locomotion (page 112) and feeding (page 113) in the larva; and the activity of the pupa and pharate adult (page 123).

With the functional allocation of the above topics, the present section is restricted to a discussion of general activity rhythms in C. dectes, and to a description of grooming behavior in this species. The latter is somewhat extended because of the ethological value of this maintenance behavior (Jander, 1966).

Adult feeding behavior

Feeding activity of Caurinus adults was observed on many occasions and on a number of host liverworts, both during inspection of cultures and in the feeding preference tests.

Feeding behavior was relatively uniform, and I consider the following account typical of many observations.

Five adult Caurinus which had been held without food for 3 days were placed in a small petri dish with two 2 cm Porella shoots, one with dorsal side up and the other ventral side up. Within ten minutes, all of the Caurinus had climbed onto the Porella, and were feeding or were examining the liverwort with antennae and maxillary palps.

Feeding activity was observed for two males and a female. Each initiated feeding shortly after reaching the Porella. Feeding bouts of two to five minutes were interspersed with quiescent periods. Feeding was initiated by one male at the base of an underleaf (inverted shoot) 4 mm from the shoot apex. The rostrum of the Caurinus was extended anteriorly and the body was elevated

posteriorly. The insect remained immobile in this pose, except for probing movements of the maxillary palps, for several seconds. Then the head was thrust forcefully to each side several times. This movement was powered by the legs with the entire body bobbing from side to side, and the head often twisting back against the thrust as the open mandibles caught on the substrate. Within 20 seconds a laceration appeared on the Porella stem transverse to the Caurinus body axis. At this point an anterior thrusting movement was introduced, with the Caurinus still frequently thrusting laterally with vigorous body movements. The feeding site was enlarged toward the body as the rostrum was brought into a more vertical position; the foothold rarely was changed during this sequence. Five minutes after feeding commenced, a drop of clear liquid was expressed from the anus. This droplet remained attached to the abdomen and grew by increments to 0.25 mm diameter before it was removed by contact with the Porella substrate. Pumping movements of the abdomen occurred each time the droplet enlarged, but there was no active attempt to remove it; the hypandrium was open, exposing the gonopods and proctiger, throughout the feeding bout. During 18 minutes of feeding activity (including pauses) an area about 1 mm in diameter was excavated through the underleaf and into the stem of the Porella. The Caurinus remained in the vicinity of the feeding site, circling it several times. It resumed feeding at this site after 30 minutes of inactivity. During feeding the site was deepened, until the rostrum was pressed into the tissue nearly to eye level. The antennae were held erect and nearly vertical to the substrate.

A second male initiated feeding on the basal lateral margin of a dorsal leaf of Porella. A head-down posture and lateral thrusting along the ventral surface of the leaf occurred as above. After initial laceration of this surface the Caurinus moved astride of the leaf edge and produced a 0.25 mm deep cut in the leaf margin, which was then enlarged distally, and anteriorly away from the insect. In this case it was possible to observe the movement of the mandibles during feeding. These were fully abducted during the initial thrusts, and

during these movements the apical mandibular teeth "stabbed" the leaf surface. After the initial incision was produced the mandibles were abducted widely as the insect thrust at the incision, and then were fully adducted to bite into the leaf tissues. Whenever the mandibles met resistance, the Caurinus twisted or shook its body. The maxillary palps appeared to bend passively as the rostrum pushed into the liverwort tissues. There was no evidence of the rhythmic movement of the maxillolabial complex which Boreus adults execute during feeding.

A female Caurinus fed in a manner similar to that described for the males. Feeding began with laceration of the basal ventral surface of a Porella leaf and proceeded from lateral gouging to more rhythmic anterior thrusting and biting. The initial feeding stance was again head-down and the twisting and thrusting effected through leg movements. As feeding continued, the body returned to a more horizontal stance.

Liquid was eliminated by an exertion of the proctiger and evacuation of a 0.1 mm droplet which was flicked away by a rapid retraction of the proctiger with closure of the eighth segment. These small clear droplets were produced frequently during feeding. During 30 minutes of feeding this individual removed approximately 0.8 mm² of leaf surface.

Caurinus fed freely on dorsal and ventral along most of the length (often 5 cm or more) of living Porella navicularis stems. Feeding continued into the central axis only on the apical 5 to 10 cm of a shoot. When fresh food was not provided, feeding proceeded to skeletization of the entire shoot and the calyptra and outer tissues of the developing spore capsule were sometimes consumed. The non-photosynthetic fertile tissue of the capsule was apparently never consumed, even under deprivation.

The extent of feeding on different tissues of host liverworts appeared to depend largely on the toughness of the tissues. Caurinus maintained on Scapania bolanderi usually fed first on leaves of the one or two growth nodes, and often failed to feed at all on living

leaves more than four or five nodes from apex. The Scapania shoot apex was fed on by Caurinus, but stem tissues, which are tough in the species, are otherwise immune to attack.

At the other extreme, both leaves and outer stem tissues of Plagiochila porelloides were frequently eaten to the base (as much as 4 cm of the stem were used for feeding Caurinus). However, Caurinus on P. porelloides concentrated their feeding on the leaves and shoot apex (Figure 19).

The elimination of a clear urine occurs only when Caurinus feed on very wet substrates. This was observed for Caurinus feeding on several genera of liverworts, but was rarely seen in individuals feeding on Scapania bolanderi.

Elimination of solid material from the gut has not been observed directly, although many green, circular stains appeared on filter paper in the observation containers. Mouthpart-wiping, combined with regurgitation, was observed on several occasions. As discussed elsewhere, there are structural grounds for supposing that regurgitation - "back-flushing" - may be used in Caurinus to clear the foregut of solid particles.

Caurinus feeding freely in the field are of course not confined to feed on one shoot. Field collections indicate that feeding is well dispersed, frequently with only one feeding incision on a shoot. In Scapania bolanderi, in which the shoots grow erect in dense turfs, most adult feeding is terminal and conspicuous (Figure 21). This field-collected feeding damage usually consists of linear or arcuate, ragged-edged incisions in the liverwort leaves, with abundant, white, cell wall debris remaining in the cut. This is nearly specific: larvae of Epimartyria pardella (Micropterygidae) also leave cell wall fragments, but rarely produce the transverse feeding pattern.

Diurnal Cycle

The daily activity cycle of Caurinus was not observed under natural conditions. The culture dishes containing the insects were exposed to indirect natural light from an east-facing window, but also received dim illumination from room lights. Although adult Caurinus are active during short-day conditions (circa 8-11 hours), the cultures received a combined (natural and artificial) photoperiod of about 16 hours (approximately 0730 to 2330 P.S.T. Increased activity (fewer adults in resting posture) was observed around sunset after a mid-afternoon low in feeding and locomotory activity. It is unclear whether the evening activities which compose most of the available observations correspond to crepuscular or to nocturnal activity in the field. The few specimens which were found in situ in the field during the day were in resting posture, and it therefore seems probable that this species is least active during midday in the field.

In the laboratory, feeding activity was very high for C. dectes adults during the evening period of artificial illumination (1800 to 2400 hours). However, oviposition and probably mating, are apparently restricted to the hours of darkness. The former was never observed, although several hundred eggs were laid by females under observation; and mating in the two pairs found in the cultures was apparently initiated in the early morning hours.

Mating is frequently observed in Boreus and Hesperoboreus during the day, and males of several boreine species have been observed orienting visually to the females (Cooper, 1974; Crampton, 1940; Steiner, 1937). Cooper (personal communication) reports however that both Hesperoboreus notoperates and H. brevicaudus mate "in large numbers shortly after dark in the field, as well as in the lab". In view of this observation, and the fact that pairing persists up to 20 hours in Boreus (Mickoleit, 1974), the rhythm of mating in Boreus spp. may require more careful study. I observed only a few matings in Boreus elegans and B. californicus held in a dark incubator at 15°C

for eight days. Of special interest however was the formation of a mixed pair (B. elegans male mating with a female B. californicus) in this culture. Apparently no mixed-species pairs have been reported although two or more species occur together over wide areas (Penney, 1977). Since elegans and californicus are not closely related, and are contrasting in color, vision may normally be used in species recognition where these species are sympatric.

The metallic colors of most Boreus and Hesperoboreus species are frequently associated with diurnal activity in insects. The bright metallic green of B. californicus and H. brevicaudus is also decidedly cryptic against a moss background.

A nocturnal bias in activity in Caurinus dectes is unlikely to be subject to many visual predators. The difference in activity between Caurinus and Boreus is more likely to be the result of environmental permissiveness. Over most of the range of C. dectes, there are likely to be relatively few nights of frost during a winter. In contrast, most Boreus species typically occur in areas of heavy winter snowfall (Cooper, 1974), where diurnal activity would ensure more reliable conditions above a behavioral threshold temperature. During the drier periods of the adult emergence, nocturnal bias in Caurinus may allow feeding and other activities at high humidities allowing escape in time from the most xeric conditions in the canopy.

Grooming Behavior

Grooming activity was observed frequently in the adults held for study. Grooming occurred as one or a few iterations of a simple movement, and also as extended bouts involving the cleaning of all appendages and much of the body surface. Single behavioral bits, most frequently the cleaning of one antenna, an eye, or rubbing the front legs together, were often observed within the context of ongoing feeding or locomotion. Longer bouts of grooming were observed, ranging from around 15 seconds to 25 minutes or more. Bouts of grooming sometimes followed feeding, but also began in individuals

which were previously inactive. Cleaning was more frequent within the first day after the Caurinus adults were obtained by the washing-screening techniques. Aside from this artifact, no attempt was made to elicit grooming behavior.

The grooming behavior of Caurinus can be described according to the surfaces cleaned by the activity. The observed patterns included cleaning of the antenna, the head, eyes, and mouthparts, the legs, and sides, venter, and apex of the abdomen. With the exception of two unusual action patterns (described here as "head-butting" and "mouthpart-dragging"), the effector surfaces were always the distal half of the tibiae, including the small tibial spurs, and the tarsi, principally the plantar surface of the basitarsus.

Antenna cleaning: Three, usually distinct, modes of cleaning the antenna were seen. In all cases the tibial-tarsal surfaces were the cleaning structures. These antennal cleaning patterns in C. dectes can be described as a) unilateral wipes with corresponding foreleg, b) cleaning of one antenna between the two front tarsi, and c) cleaning of one or both antenna between the corresponding foreleg and the substrate. The unilateral wipe (a) is accomplished by raising and anterior rotation of the front femur to place the basitarsus on the ipsilateral antennal scape. The wiping action resulting from abduction of the tibia is confined to the basal half of the antenna; the antenna is supported by the front or side of the rostrum during this action. This wipe is repeated one to five times. During more intensive bouts of cleaning this antennal wiping may become bilateral, the combing strokes of the two forelegs commonly alternated. Occasionally both forelegs may move together as in the two-legged unilateral antennal cleaning (b).

Either antenna may be cleaned by both forelegs (b). This action is initiated as in (a), but the antenna is directed more medially, and the contralateral protibia is brought to meet the antenna, usually after contact has been made in the starting position for (a). The antenna is drawn between the two appressed basitarsi as the legs are straightened. The length of the stroke is increased by

rotation of the head, usually with raising of the forebody. The forelegs rather frequently fail to catch the antenna at the beginning of this movement; when this occurs, the insect follows through the full stroke before returning to the starting position.

The least frequently seen method of antennal cleaning was the use of the ipsilateral protarsus against the substrate (c). This was begun by lowering the head with the antenna spread laterally and downward. The insect then stepped on one or both antennae (at the midlength, around segments 8-10), and drew the antenna between basitarsus and substrate by abruptly raising the forebody with accompanying protraction of the head.

The significance of this diversity of cleaning methods, against the usual high monotony of antennal cleaning in major taxonomic groups (Jander, 1966), can be seen in the overall context of their occurrence. The "one-handed" wipe can be viewed as a low-intensity action which is both a simplified precursor of (b), and also differs little from the movements involved in cleaning the eyes and anterior and lateral portions of the rostrum. It usually acts to clean only the basal segments of the antennae, which are frequently soiled in feeding, due to the short rostrum and rather messy feeding of Caurinus. The "crossed-tarsi" position for antennal cleaning (b) is very similar to that described for Panorpa (Jander, 1966), and is the characteristic action for Mecoptera in general. It is therefore viewed as the "normal" antennal cleaning action, modified from the general pattern only by the reduction of the tibial spurs and use of the basitarsal planta as the abrasive surface. Motion (c) described above is apparently unusual among Mecoptera or related orders, although one or both tarsi may come to the substrate at the end of the usual "two-handed" action in Panorpa and other mecopteroids (Jander, 1966). This movement seems discontinuous from the others in Caurinus, however. It was most frequently seen in individuals which had been covered with water droplets (after "washing-screening", when freed from entrapment in condensate in culture dishes, or when water was replaced in the cultures with a plant sprayer). This action is a

high-intensity cleaning mode which is effective in freeing the terminal segments of the antenna from water droplets. Although a novelty among mecopteroid insects, this action pattern (especially the bilateral variant) is very similar to the usual mode of antennal cleaning in several families of Coleoptera.

Cleaning of the head and mouthparts: Grooming of the eyes and the lateral and frontal areas of the rostrum is done with simple wipes by the front legs. The body attitude and motion of the legs is similar to that adopted in the "one-handed" antennal cleaning; both the distal internal surface of the tibia and the basitarsal planta are effectors.

The mouthparts and posterior surface of the rostrum are cleaned by movements akin to the foreleg rubbing described below. As in the other actions bringing both forelegs off the substrate, the body is rocked backward, often (especially the females) bringing the abdomen in contact with the substrate. The head is protracted, and both fore basitarsi are applied to its ventral or posterior surface. Strokes by the two legs are usually alternate. The mandibles gape, usually motionless, and the maxillolabial complex is protracted; the maxillary palps can be seen to move forward and back in time with strokes of the protarsi. The principal effector surfaces here appear to be the tibial apex and edge of the basitarsus although precise observation is difficult.

Cleaning of the legs: All of the legs were cleaned by mutual rubbing. The combinations of leg-to-leg contacts were quite numerous. The most frequent of all grooming activity was mutual rubbing of the forelegs. This action almost always preceded and followed episodes of cleaning the antennae (types a and b), head, and other legs. It also occurred as an isolated action pattern.

As mentioned above, the foreleg-rubbing pose was usually maintained throughout a bout of cleaning the head and its appendages: the body is elevated anteriorly 20° to 40° from the usual resting position as the forelegs are brought off the substrate. Frequently the abdomen is propped against the substrate. The forelegs are

extended anteriorly with the tarsi crossed or in linear contact. (This is similar to the corresponding position of muscoid flies as well as other mecopteroid insects.) There follows a rapid series of scraping movements. Probably both move actively in each stroke, although this has not been clearly observed.

Other leg-cleaning movements are less commonly seen. One of the mesothoracic legs may be taken into the ongoing foreleg-rubbing where it is apparently always passively cleaned. A female was once observed balanced only on her metathoracic legs and abdominal tip, while the four anterior legs were actively rubbed together for 6-8 seconds. The hind legs are usually rubbed together with the body pitched down anteriorly. The middle legs (one at a time) may be joined with the hindleg-rubbing action, although this is less frequent than the use of the front legs. All of the leg-rubbing seen was mainly associated with the tibial and tarsal segments. The more proximal legs are not regularly cleaned in Caurinus.

Cleaning of the abdomen: The abdominal surface was occasionally cleaned, with one or both hind tarsi working at a time. This was usually preceded and followed by hindleg-rubbing. It was regularly elicited by spraying water on the insects. Usually, only the venter and sides of segments 4-8, and the caudally facing eighth tergum, were cleaned.

Other cleaning behavior: Grooming of the thorax, wings, and the retracted segments of the abdomen was not seen in Caurinus of either sex. Two unusual action patterns were observed which can be associated with the cleaning routine in Caurinus. The first, previously referred to as "mouthpart-dragging", was observed in full intensity in one, obviously distressed, individual (22 March 1978). This male fed normally for a short period on the toxic Porella roellii (page 85). It then began wiping its mouthparts from side to side on the substrate, while walking a short distance backward. During this backing and wiping behavior the Caurinus appeared to regurgitate. The backing phase was alternated several times with foreleg cleaning of the mouthparts; head-bobbing during the latter phase was much more

pronounced than in the usual form of this behavior. Duration of the of the high-intensity cleansing behavior in this case was about five minutes. Some components of the mouthpart-wiping behavior were seen on other occasions, but only as fragments and without an obvious irritant.

The second unusual cleansing pattern was observed in several individuals; it can be referred to as "head-butting". This maneuver was seen only in a feeding or post-feeding context. This peculiar action appeared to be a modified escape hop, which was effected with the body inclined downward anteriorly to bring the frons nearly in contact with the liverwort substrate. A sudden extension of the hind legs without tarsal release "butted" the head into the substrate. This maneuver was often repeated very rapidly several times; repetition of two to four butts sometimes followed after a brief rest. In one observation several large fragments of Porella navicularis had adhered to the frons during feeding; these were removed during the head-butting activity. Since there were no indications of degraded behavior in these specimens, this peculiar head-butting is evidently part of the normal repertoire of grooming in Caurinus.

Grooming behavior has been found to be frequently very conservative in evolution, so that certain behavioral bits are uniform at the ordinal or superordinal level. In the Mecoptera, full grooming repertoires have been described for Panorpa communis (Jander, 1966; generalized to some other European Panorpa with "identical" behavior) and Bittacus stigmaterus (Setty, 1931). I have seen the full cleaning sequence in Bittacus chlorostigma, but antennal cleaning only in Boreus californicus and Hesperoboreus brevicaudus.

The cleaning repertoire described for Caurinus above generally resembles that of Panorpa communis (Jander, 1966). Caurinus lacks the elaborate wing-cleaning routine (also found in Bittacus), while the antenna-cleaning in Panorpa, Boreus, and Hesperoboreus is apparently constantly of the "one antenna-two crossed tarsi" type. Grooming activities in Bittacus are somewhat unusual because of the extremely long legs and the habit of hanging suspended by the front

legs. The middle legs, rather than the forelegs, are most frequently used to clean the head and appendages in this genus; the leg to head movements are restricted to unilateral wipes by the femora. Leg-to-leg rubbing is the most frequent grooming activity of Bittacus, especially following prey capture and feeding.

Jander (1966) has emphasized the detailed correspondence of the entire grooming repertoire in Panorpa to that occurring in Diptera (specifically comparing it to the behavior of the syrphid, Volucella inflata). This agreement was presented as further evidence of the close relationship between these two orders. Other similarities extend to the other mecopteroid orders. According to Jander (1966) the "Mecopteria" differ consistently from the "Neuropteria" by disuse of the mouthparts in cleaning the legs. Among the mecopteroids, only Micropteryx (M. calthella), is known to groom its forelegs with the mouthparts. (All appendages may be cleaned with the mouthparts in more primitive arthropods.) Since Caurinus dectes, with the Micropterygidae, is one of the few mecopteroid insects with relatively unmodified biting mouthparts, it is worth noting that these are not employed in grooming. The chief peculiarities of the cleaning sequence in Caurinus are the diverse means of antennal cleaning, the reductions related to aptery and the very compact, inflexible body, the ability to free as many as four legs at a time for cleaning, and the inclusion of the "head-butting" maneuver, presumably a derivative of the escape hop in these boreids.

LIFE HISTORY OF CAURINUS DECTES

This account is largely based on observations made on field-collected specimens which were either preserved or held for study. The association of the immature stages with Caurinus dectes was determined through observation of oviposition, unhatched larvae and eclosion, and the larval-pupal ecdysis. The association of the pupa with the adult of Caurinus is obvious.

The pupa and all larval stages are easily distinguished from any other insects in the Pacific Northwest. Further, it is possible to identify unhatched or hatched eggs of C. dectes when these are located undisturbed on the host plant. The characters permitting recognition of these stages are given in the following descriptions and discussions. Although it is assumed that at least all of the known Oregon Coast Range populations of Caurinus are conspecific, the morphological accounts are based only on material from the Marys Peak type locality of C. dectes.

Egg

Newly laid Caurinus eggs are elongate-oval, and almost spindle-shaped with narrowly rounded (parabolic) ends (Figures 23, 24). There is no noticeable polar or dorso-ventral asymmetry. The eggs average 0.60 x 0.25 mm (length by width) when laid; moderate swelling occurs later in development.

The eggs appear black and are micro-reticulate over most or all of their surface. A few eggs are less pigmented at one pole, and show that the chorion itself is cream-colored, but covered with a dark cementing material which usually fills in the angles where the egg joins the substrate. Eggs which are lightly covered with cement show dark spots where this fills the punctures in the chorion surface, as well as parallel longitudinal streaks. This suggests that this material is applied during oviposition before the egg leaves the body.

The cement layer is usually very thin, the microreticulate surface appears to be developed on the chorion. Occasional thicker areas of cement covering appear quite smooth at 250X magnification. Eggs with an incompletely pigmented surface were commonly observed in cultures both early and near the end of the season of activity of adult Caurinus.

The cement is presumably the secretion of the colleterial glands of the female, and is probably a protein which is tanned after secretion. The coating of the colorless egg with dark cement may protect the exposed egg from ultraviolet light damage. Intact eggs remaining on the liverwort substrate become bleached to a dark brown color by late July to August. A thick, pigmented chorion is usual among Heteroptera which lay their eggs on exposed plant surfaces, and in Zicrona coerulea (Pentatomidae) the effective pigmentation is a layer of black cement over a colorless chorion (Southwood, 1956).

The chorion is very tough and leathery, and it is difficult to puncture or tear open an egg with sharp forceps. This is not a result of the tanning of the cement layer, for the colorless, mature ovarian eggs are frequently found intact in detached, skeletal abdomens recovered in wet-screened samples.

Oviposition

Oviposition was never observed during the two years adult Caurinus were held for study even though several hundred eggs were laid by captive females. Oviposition may have been missed by its being a largely nocturnal activity in Caurinus. However it is also likely that it is more rapid and involves a less conspicuous posture by the female than that occurring in Boreus species (Aubrook, 1939; Maréchal, 1939). This discussion is based both on observations of Caurinus in culture, and on examination of field collected host material.

The spindle-shaped eggs are laid singly and are cemented by their sides to the bryophyte leaf. Both in culture and in the field,

the eggs were almost always attached to the ventral surface of liverwort leaves (Figures 23, 24). Especially in the case of eggs deposited on Porella navicularis, the eggs are frequently inserted between two overlapping leaves. (The egg is sometimes cemented to both leaves in this position.) Both in Porella and Scapania bolanderi, where the eggs are usually within the leaf overlap, but adherent only to the underside of the upper leaf, the leaves are sufficiently close and rigid to necessitate considerable extension of the membranous segments 9-11 of the female Caurinus for insertion of the egg.

Eggs were invariably deposited on bryophytes, usually on leafy liverworts, but occasionally on mosses. One egg was found in the field on the upper surface of the thallus of Conocephalum conicum (Marchantiales). The placement of the eggs is normally on leaves of the host liverworts, and adult feeding is usually found on the same shoot. In the laboratory, eggs were frequently deposited within a few mm of the site of feeding of the previous day, and some individuals spent several days on the same shoot, feeding intermittently and laying several eggs.

There was some selectivity of egg substrate in the laboratory, although this was largely concordant with the time spent on different hosts through feeding preferences. Females oviposited more frequently on Scapania bolanderi than on Porella navicularis when both were present in the culture dish. Oviposition never occurred on Frullania tamarisci although both adult and larvae of C. dectes feed sparingly on this liverwort. Oviposition did occur occasionally on mosses which were rejected as food, but readily used for resting sites. In one case, three females deposited nine eggs on a single one-cm shoot of the moss Isoetecium spiculiferum, over a four-day period. A shoot of P. navicularis was also present; although it was eaten extensively, only three eggs were laid on it over the same period. Eggs were also found deposited on moss shoots in the field, but these were always intermingled with liverwort hosts of Caurinus.

Egg Hatching

Although several hundred eggs were obtained in culture, and many more from the field, very few have hatched in culture. The hatching process was not observed and the following account is based on observation of many eggs recovered from field samples of liverworts. The opening of eggs by hatching larvae is very different from Boreus and Hesperoboreus. The egg is slit in a neat longitudinal line on the surface directly opposite the cemented surface. This straight slit extends nearly the entire length of the egg, and is not widened or frayed at any point. It is unknown whether the chorion is cut along its length, or if there is a line of weakness to facilitate hatching.

The hatching Caurinus larva probably cut through the chorion with the very fine, serrate ridge on the frons which appears to be an egg-burster (page 142). The chorion is not eaten by the larva of Caurinus. The eggshell retains its normal shape and it is often difficult to distinguish hatched from unhatched eggs without manipulation.

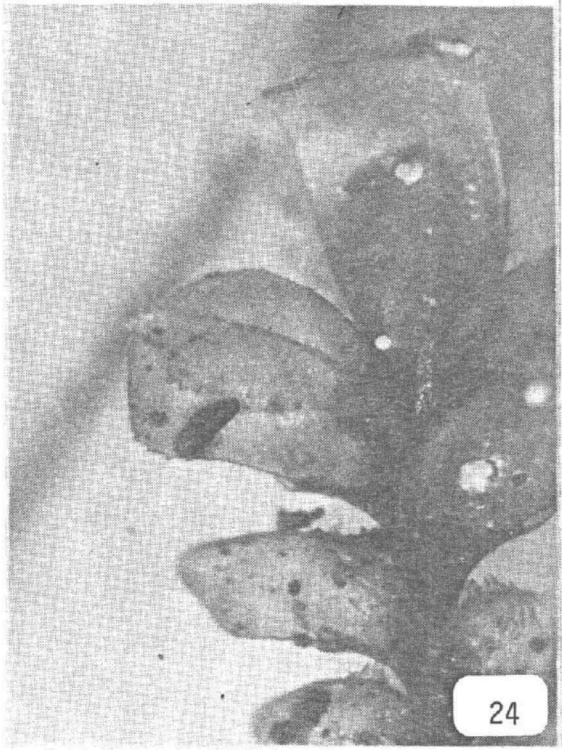
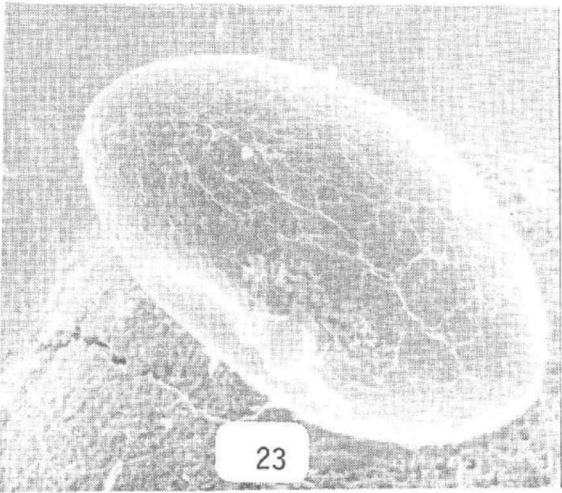
Eclosion has been described in Hesperoboreus notoperates (Cooper, 1976). In this species and in H. brevicaudus (personal observation), the larva perforates the chorion with its mandibles, leaving an irregular apical cap.

My inability to obtain eclosion in C. dectes eggs from culture is probably an indication of obligate egg diapause in this species. A high rate of infertility would be unlikely, since some matings occurred in the culture dishes, and most eggs were obtained from females which had been active in the field for one to several months. In addition, few of the undisturbed eggs were attacked by fungus and most remained plump unless the culture dishes were allowed to dry out.

Groups of eggs were held at 16 to 20°C for up to four months (January to May, 1977) without evidence of development other than swelling of the eggs. The culture temperature should have allowed

Figures 23, 24. Eggs of Caurinus dectes.

- 23) Egg of C. dectes on leaf of Porella
navicularis (somewhat foreshortened)
(135X).
- 24) Egg of C. dectes on underside of leaf of
Scapania bolanderi.



development, since hatching in the field occurs as early as late February, while temperatures (at the Marys Peak site) rarely exceed 20°C until late spring. Investigation of egg development was hindered by the opaque eggshell until April, 1978 when immersion for 15-30 seconds in sodium hypochlorite bleach was used to make the chorion transparent (Gassner, 1963).

Development without diapause is reported for other boreid eggs although the reported developmental rates vary. Hatching occurred in eggs of B. hyemalis in three weeks at 20°C, but took up to one and a half months at 7°C (Strübing, 1950). Cooper (1974) observed little development in eggs of H. notoperates held for 30 days at 9°C, but the latter developed to a stage with visible head capsule within 15 days after transfer to 20°C. (Eclosion "spread out over a period of 36 days", however.)

My interpretation of the egg diapause is largely based on field collections and will be covered in my discussion of the phenology of field populations of C. dectes. A different type of delayed egg hatch in H. brevicaudus will also be discussed on the basis of field evidence.

Fecundity

Dissections of mature female Caurinus showed that a maximum of seven or eight mature eggs could be present at one time. This, coupled with the very extended season of activity, indicated that potential fecundity was not indicated by the clutch size.

Only a few females were held for observation of egg production over a period of time. Five, 11 cm Petri dishes were each stocked with one male and one female C. dectes between 23 December 1976 and 6 January 1977. The temperature averaged 16 to 18°C. Four of the five females, but only one male, survived until 31 March 1977. The periods of observation for these females ranged from 61 to 98 days; one female produced only seven eggs, but the other four laid from 27 to 43 eggs (average 37) during the 84 to 98 days they were isolated (Table 14).

There was a general pattern of decline in oviposition rates from December through March. The mean daily egg production per female was 0.71 from 23 December to 9 January; 0.55 from 9 January to 13 February; 0.36 from 13 February to 27 February; and 0.31 to 31 March.

Egg production was observed for another group of females over a shorter period in March 1978. Eighteen female Caurinus which were observed from six to nine days, laid 92 eggs, for an average production of 0.65 eggs per female per day. The 1977 figures probably are more representative of sustainable production, since there appears to be an initial period of increased oviposition when the females are placed under culture conditions.

The fecundity under these conditions is probably higher than for field populations where lower temperatures or nutritional factors may contribute to lower egg production.

Since egg production in the field begins in early November, and continues through winter and early spring, 40 to 50 eggs is a reasonable estimate of average fecundity through the entire season.

The maximum egg production previously reported for a boreid under laboratory conditions is 11.6 (Hesperoboreus notoperates; Cooper 1974), representing 186 eggs laid by 16 females in 10 days. Cooper took the production of 1.16 egg per day for the maximum laboratory life span of four weeks to obtain an estimate of 32 eggs for the expected fecundity over this period.

Other authors (Strübing, 1950; Withycombe, 1922) have also given very low estimates of fecundity for Boreus hyemalis, probably partly due to difficulty in locating eggs in the moss turfs utilized by Boreus. Oviposition has not been reported over periods nearly as long as those given here for Caurinus in the laboratory.

Table 14 . Egg production by individual Caurinus dectes females.

	Observation Periods				Totals
	12/23-1/9	1/9-2/13	2/13-2/27	2/27-2/31	
Female #					
77-A(12/9/76)					
Eggs	10	18	5	10	43
Days	14	38	14	32	98
Oviposition rate	.71	.47	.36	.31	.44
Female #					
77-B(1/6/77)					
Eggs	--	27	5	4	36
Days	--	38	14	32	84
Oviposition rate	--	.71	.36	.12	.43
Female #					
77-C(1/6/77)					
Eggs	--	12	0	0	12
Days	--	38	14	9	61
Oviposition rate	--	.32	0	0	.20
Female #					
77-D(12/27/76)					
Eggs	--	19	4	20	43
Days	--	48	14	32	94
Oviposition rate	--	.40	.29	.63	.46
Female #					
77-E(1/6/77)					
Eggs	--	8	11	8	27
Days	--	38	14	32	84
Oviposition rate	--	.21	.79	.25	.32
Average for five females	.71	.42	.36	.31	.37

Larvae of Caurinus - Behavior

All observations on live Caurinus larvae were made from first and second instar larvae collected on Marys Peak in 1977 and 1978. Most larvae were obtained by wet screening, but a few were located by direct search of the host liverworts brought back to the lab.

Small Caurinus larvae survive the screening and filtration of the extraction process remarkably well. Over 80% of first instar larvae are viable when recovered and much of the loss is due to failure of the larvae to establish feeding galleries in the observation dishes.

Locomotion

The Caurinus larva is more mobile than might be expected for a nearly apodous larva. Locomotion on a level, porous surface (moist filter paper) is accomplished by waves of contraction of the trunk segments passing anteriorly. Each wave is initiated by pronounced retraction of the last three abdominal segments (9-11). The elongate pygopod (segment 11) is brought to its maximal retraction anteriorly, and placed in contact with the substrate. At this point it appears to push off to start the wave of progression. This wave produces a dorsal and lateral bulging of the 2-3 segments contracted, and a constriction and elongation of the several following segments. As the wave progresses, the thoracic pedal lobes also are carried forward in sequence. When the larva is creeping slowly there is no perceptible raising of the body off the substrate. When the larva moves more rapidly however, it appears to throw its body forward with the contracted segments of at least the anterior abdominal region clearly raised off the substrate. At high speed, the head is also more actively involved in extending forward and propping the anterior body with the closed mandibles. An early second-instar larvae, with relaxed body length of 1.2 mm, crept 20 mm in 2 mins. 10 sec. when placed on illuminated, moist filter paper at 16°C ambient temperature.

Larvae placed on moist filter paper appear to be scototactic under moderate illumination. There is apparent visual orientation toward small dark objects at distances of 5 - 10 mm. Larvae will turn, approach and climb onto fragments of liverworts (Porella, Scapania, Jungermannia), moss (Dicranum), or moist soil particles. When the larvae reached any of these objects it attempted to climb onto it. If the point of first contact was inclined and in contact with the paper surface, the larva continued creeping onto it without a pause. If no convenient ramp was available the larva paused, raised its head and anterior 1 or 2 thoracic segments and probed to either side.

In most cases whether the larva had reached a steeply sloping surface or a liverwort or moss leaf within 0.5 mm of the surface of the paper, the probing behavior passed into a climbing behavior. The abdomen was strongly contracted and the pygopod brought forward and in contact with the paper, and then the body was arched dorsally bringing more of the anterior trunk off the surface. After 2 or 3 more iterations the larva stood erect on its pygopod.

When this maneuver brought the leaf or soil surface within reach of the forebody, the thoracic venter contacted the surface. The thoracic pedal lobes moved over the surface, as the larva appeared to search for a purchase with these appendages. Finally the larva released its hold with the pygopod, and climbed onto the substrate, with the head and pedal lobes used as the initial anchors.

Larval Feeding

Small Caurinus larvae usually began feeding activity within a few minutes after being placed on, or climbing onto a stem of Porella or Scapania.

The first action of larvae placed on the dorsal leaf surface of the liverwort shoot was to move to a sheltered site either between overlapping leaves or on the ventral surface of the large leaf lobe. The structure of the liverworts apparently determined different

methods of entry. Larvae on Scapania simply crawled between the overlapping leaves, while those on Porella most frequently chewed a hole through one of the upper leaves. Relatively few forced their way between the closely appressed leaves of Porella, while other apparently crawled around the lateral leaf margin to reach the ventral side. Some larvae then rested on the ventral surface of a leaf, sometimes remaining stationary with little or no feeding, for one or two days. Larvae sometimes wandered, usually eating circular holes through leaves as they moved. Most larvae soon began construction of a gallery in the Porella shoot. This was initiated either by extending feeding from an initial perforation of a dorsal leaf near the midline to the upper stem tissues. In Porella, such a gallery retained openings at one or both ends. Periodically frass was pushed out these openings, or intermittently they were sealed with this material. Within a week of initiation, a gallery would extend for the apical 2.5 - 5 mm of stem in the Porella terminal shoot (main axis, or major branch).

Larvae which reach the ventral surface of the Porella shoot normally move to a position in a leaf axil, and begin to chew their way into the stem in the axil. Large quantities of outer stem tissue accumulate at the site of the entry, apparently without passing through the gut of the larva.

By the end of the second instar, the Caurinus larva expanded its tunnel by eating out most of the stem tissues. As this enlargement proceeds, the leaves are plastered together with frass. The mine is also enlarged basad on the Porella shoot. Fully fed second-instar larvae are found in the mine with head oriented apically.

The above sequence occurs when terminal growth (probably less than 2 years increment) is available. Caurinus larvae which cannot enter a terminal usually fail to penetrate the stem, but continue to eat out a gallery within the overlapping leaves. In most cases, most of the leaf tissue roofing the feeding gallery is left intact.

Larval feeding in other boreids

Larval feeding of Boreus species which have been studied is normally confined to terrestrial or boulder-sited, sod-forming mosses. Apparently most or all Boreus larvae feed actively on the rhizoids and lower parts of the mosses, and trapped organic matter in and under the mosses. Cooper's (1974) observations on Hesperoboreus notoperates show that the larvae of this species feed in moss cushions (of Grimmia, Tortula, and Racomitrium) on granite boulders, much as do many Boreus larvae.

Larvae of Hesperoboreus brevicaudus are apparently more active than most boreine larvae. Larvae of H. brevicaudus are usually found in loose, epiphytic mosses. When placed among shoots of common, pleurocarpous mosses, the larvae readily ascend the stems, and move actively among the leaves.

While feeding on Antitrichia curtipendula, the H. brevicaudus larvae typically rest curled within the leaf axil initially with the dorsum against the inner leaf surface. In this position they bite at the outer layer of the stem. Periodically, somersaulting movements bring the mouthparts in contact with the enclosing leaf. Apparent attempts are made to bite any of the moss surfaces as the larva contacts them. Ultimately the larva bores through the leaf base, or several in succession, leaving a trail of fibrous borings. In contrast to this external movement and feeding, H. brevicaudus larvae bore within the stem axis of Plagiothecium undulatum while leaving the outer surface of overlapping leaves untouched.

Both types of feeding by H. brevicaudus larvae are similar to feeding activity of Caurinus larvae. It can be assumed that a switch to feeding on the aerial portions of bryophytes preceded the morphological specializations of Caurinus larvae.

Molting

First and second instar larvae of C. decetes molt within one to three days after becoming turgid and stretched out. The ecdysis occurs within the larval gallery, and is usually rapid. Some specimens were observed which had failed to complete the molt. In these, the epicranium had split along the length of the coronal and both frontal lines, so that the frontal apotome was free to the clypeal apex. No split was observed in the cuticle posterior to the head in these specimens or in recovered exuviae.

After the molt the exuviae are pushed out of the feeding gallery; the head capsule is intact, with the frontal apotome still attached on its anterior margin. There is no ventral ecdysial line (Hinton, 1963) and the narrow postgenal bridge remains intact. The post-cranial cuticle is left rolled up like the finger of a glove.

Within two or three hours of the ecdysis, the head of the second or third instar larva is fully pigmented and feeding activity has resumed.

Post-feeding Larvae and Pupa

Little direct information is available for the late larval and pupal stages. It was difficult to obtain these stages during my study. Only five pharate pupae and thirteen pupae were collected, most of which were recovered by washing. The sharp drop in larval collection at the end of the feeding period (around 1 June) in both 1977 and 1978 seemed to indicate that the larvae were no longer in the loosely constructed feeding galleries. However, until midsummer of 1978 none could be located in situ by search and dissection of the hosts. Most of the earlier search was in Porella navicularis, both from Marys Peak and from the coast, but Scapania bolanderi, Gyrothyra underwoodiana, and Nardia scalaris from stands which supported large numbers of young larvae were also examined.

Construction of the Pupal Cell

Large larvae (late feeding phase of third instar in culture often left feeding galleries and appeared to seek out crevices. In culture, these larvae sometimes entered the lumen of perianths of Porella or Scapania, but no larvae were located in the perianths of field collected liverworts during the estival period. The exposed terminal position of the perianth of a leafy liverwort makes it an unlikely site for estivation.

The first indication of the circumstances of pupation in Caurinus was provided by recovery from Scapania turf, of a pharate pupa which was inside an intact, secreted envelope (Figure 54). The pupal molt was completed by this individual the next evening (20 August 1978).

This secreted cell, or cocoon, was off-white, translucent, and of a stiff, parchment-like consistency, without an apparent fibrous context. The dimensions of the cocoon were 1.75 mm (long), and .80 mm (greatest diameter). When recovered, the cocoon was laterally flattened. Lateral clearance for the pupa averaged 0.1 mm, with approximately 0.25 mm clearance at the anterior pole. Small fragments of wood, and of material resembling the rhizoidal mat of horizontal "runners" of Scapania bolanderi were attached all about the outer wall of the cocoon.

Two more Caurinus pupae were found in situ in Scapania turf collected at Marys Peak (4 September 1978). The material containing these pupae was collected from the nearly vertical surface of an old, decorticated red cedar stump, between 20 cm and 50 cm above the ground. This stump was located in one of the Alnus-Acer openings within the study area (page 39). Approximately 75 percent of the area sampled was occupied by Scapania bolanderi, while there were smaller amounts of the mosses Hypnum circinale and Dicranum fucescens.

Both Caurinus pupae found in this collection were in cells constructed in soft, fibrous rotted wood underlying the Scapania. Both cells were about 3 mm within the rotted wood. In one of these

cells, the silk lining was continuous with the wood matrix. The second cell was constructed with the anterior pole of the cocoon free from the substrate. The appearance and texture of the exposed silk surface was similar to that of the cocoon isolated by screening.

The initial excavation of pupal cells by fully grown Caurinus larvae was observed on 2 May 1979, when 8 larvae washed from Scapania turf were placed in a Petridish with a 10 x 30 x 3 mm piece of wood from a Pseudotsuga log, the upper surface sparsely covered with Bazzania tricrenata and Scapania bolanderi. Six hours later there were two entrance holes in the upper surface of the wood, and one of three larvae observed on the wood surface was excavating a tunnel. Small fragments of wood were cast to the side, apparently without any being ingested. One hour after first observation, this larva had also disappeared into the wood, leaving a loose plug of wood fragments in the tunnel. One day later a fourth larva had tunneled into the wood, while three larvae were found dead in the dish and one larva was unaccounted for.

It appears that mature Caurinus larvae, after leaving their final feeding gallery, normally tunnel into the substrate to construct a pupal cell, which is then lined with a substantial amount of silk. However, I have little information in the type of pupal cell or cocoon constructed by Caurinus larvae which have fed in non-xylicolous liverworts. One dead Caurinus larva was found in a cell-like structure in a mat of the terrestrial Gyrothyra underwoodiana which had been dried for herbarium deposition (29 April 1978; Klickitat Mountain, Lane County, Oregon). This cell was apparently secreted and was constructed in the basal rhizoidal layer of the Gyrothyra, rather than the underlying clay soil.

It is particularly unfortunate that I have not located cocoons or pupal cells from the epiphytic Porella-Metaneckera association. Caurinus successfully completes its life history in this substrate, although there is usually no substrate available for the excavated pupal cells which have been found under Scapania. In the epiphytic associations Caurinus larvae probably either construct free cocoons

attached to bryophyte stems, or cement together loose debris to form the pupal chambers. The large amount of silk used to line cells formed within substrates may then be related to behavioral plasticity allowing Caurinus to pupate whether pupal cells can be excavated, or a free cocoon is required.

Pupal cells have been described for several soil-inhabiting boreid larvae (e.g., Boreus hyemalis, Strübing, 1950; Boreus brumalis, Williams, 1916). I have collected larvae, pharate pupae, and pupae of Boreus elegans and B. californicus from pupal chambers formed in soil under mosses. These pupal cells are elongate cylinders and extend almost vertically to near the soil surface. The walls are smooth, packed earth. These cells are quite different from the chambers occupied by feeding larvae of these species, which are short, ovoid, and often extend deeper into the soil.

Withycombe (1922) described a similar pupal cell in Boreus hyemalis, but he stated further that these cells are frequently lined with a sparse covering of silk threads:

"As pupation approaches the larva makes a vertical tube leading almost to the surface, and it is presumably at this period that the fine silk thread is spun which sometimes sparsely lines the walls. The silk lining is, in my opinion, by no means always present, although being never very noticeable I may have overlooked it."

A lining of the pupal cell was not reported in other studies of B. hyemalis (Strübing, 1950) nor in recent studies of other species of Boreus. This point requires further clarification; it is possible that Withycombe was influenced by his assumption that a spinneret was present in this larva, "similar to that of lepidopterous larvae", located on the labium and connected with the salivary glands. This supposed spinneret, reported by Withycombe (1922) and Brauer (1863) was shown by Potter (1938) to be a pair of convergent setae inserted on the mentum, which present the illusion of a conical process of the labium.

Although it is still not known if any Boreus larvae have functional silk glands, both species of Hesperoboreus appear to produce a cementing secretion. Cooper (1974) reported that

Hesperoboreus notoperates larvae form estival and pupal cells in moss which cleave away from the dry moss as intact pellets. The substance cementing the walls of these cells is evidently soluble or disrupted in water, for the cells are said to split open readily when the mosses are broken apart a few minutes after being soaked with water. The first-year larvae of H. brevicaudus are not known to form estival cells, and these larvae appear to feed throughout the summer. Pupal cells of H. brevicaudus have been found in rotted wood (under Hypnum circinale), and appear to have cemented walls. Like Caurinus, H. brevicaudus can complete its life cycle in epiphytic mosses.

Although estival or pupal cells of H. brevicaudus have not been recovered from field collected epiphytes, second-year larvae of this species have been observed to produce cells in culture dishes. These cells are produced under drying conditions by larvae feeding along the axis of robust pleurocarpous mosses (Antitrichia curtipendula, Rhytidiadelphus loreus, and Plagiothecium undulatum). These cells are produced by destruction of the stem axis, and packing the fibrous fragments into walls of an ovoid cell. When the cell is breached, the walls are rapidly repaired by the larva with a plug of fibers. No evidence was noted for presence of a cementing secretion, although this may be present.

The production of silk or silk-like materials by larvae of boreids and other Mecoptera has been debated. A cocoon-like structure is not known outside the Boreidae in this order. Naked pupae, in earth cells, have been described in the Choristidae (Chorista australis; Tillyard, 1926), Nannochoristidae (Microchorista philpotti; Pilgrim, 1972), Bittacidae (e.g., Bittacus stigmaterus; Setty, 1931), Panorpidae (e.g., Panorpa nuptialis; Byers, 1963), and Panorpodidae (Brachypanorpa oregonensis, my observation). Pupation in all of the above species occurs in chambers constructed near the soil surface by the last-instar larvae. Byers (1963) stated that the pupal cell of P. nuptialis "appears to be formed by compression of moist soil particles by the body of the larva". According to Setty's (1931) description, the pupal cell of Bittacus stigmaterus is formed in the same manner. Against Byers' (1963) statement, Tillyard (1935)

claimed that mecopteran larvae produce a "gluey mass" from the labial "silk" glands to line the pupal cells. It is probable that the secretion forming the "cocoon" of Caurinus is also a product of the labial glands, since these are large in the mature larvae. The source of this material is evidently not the malpighian tubules. The size, structure, and the dark brown contents of the latter remain remarkably constant throughout the larval, pharate pupal, and adult stages in Caurinus. Although silk production is little known in larva of Mecoptera, the labial glands are specialized for secretion of a rapidly solidifying liquid in males of the Panorpidae (Mercier, 1951; Gassner, 1963); this material is a substrate for courtship feeding in this family.

The production of silk-like material from the labial glands is apparently a primitive trait of the mecopteroid orders (Lepidoptera, including Zeugloptera, Trichoptera, Diptera (Nematocera), and Siphonaptera). Larval silk in all these orders (as well as in the Hymenoptera) is a product of the labial glands.

The cocoons secreted by Caurinus are especially similar in structure to those of another primitive mecopteroid group, the Micropterygidae (Lepidoptera: Zeugloptera). In the latter group, cocoons are attached to the host liverworts (Sabatinka incongruella; Tillyard, 1923) or line excavated pupal cells in the soil (Micropteryx calthella; Lorenz, 1961).

Development of the pharate pupa

In the following discussion of the larva-pupa-adult metamorphosis of Caurinus, I have followed the practice of Hinton (1971) in dating the pupal and adult instars from the apolysis rather than from the ecdysis as is the usual practice. The pharate pupa and pharate adult are both easily recognized and of long duration in the Boreidae (Cooper, 1974) so that this distinction may be applied for Caurinus.

Transformation from fully-grown third-instar larva to pharate pupa was not observed in live Caurinus specimens. Recovery of recognizable pharate pupae from as early as 11 July (Depot Creek, Lincoln County, Oregon) indicates that apolysis may occur several weeks before the larval-pupal ecdysis.

The specimens reported here were washed from field collected bryophytes of the Porella-Metaneckera, Scapania bolanderi, and Calypogeja associations.

The pharate pupa can be recognized first by the posterior migration of the eye pigment from the larval to the pupal eye position. This process resembles that described by Cooper (1974) in the pharate pupa of Hesperoboreus, and appears to be general throughout the Boreidae. With the posterior shift of the pigment, the seven stemmata are easily seen on each side of the head. There is no change in body pigmentation at this time, although boreine "larvae" frequently change from white to a dirty yellowish color at the time of eye pigment migration (Cooper, 1974). The body is shortened somewhat through contraction of the terminal trunk segments (7-11). Mandibles are slightly agape and may be incapable of movement. The trunk segments remain tensescent with the pedal lobes inflated at the base and poorly demarcated from the thorax. Later in this stage the pupal head is visibly retracted from the larval cuticle.

The pharate pupa is apparently incapable of directed locomotion. In contrast to feeding third-instar larvae, individuals at this stage could not be induced to crawl on the ventral surface, or to climb onto or adhere to liverworts or other surfaces. When disturbed by contact

or strong light the pharate pupae are able to roll about by undulatory movements of the abdomen.

Pharate adult and eclosion

The adult apolysis apparently begins shortly after the pupal molt. From examination of the preserved specimens, the development of the pharate adult takes the following course. First, the adult cuticle separates from the pupal cephalic appendages and legs. The outlines of the adult antenna, labrum, maxillary palps, and tarsi are established; the postorbital ridge is well defined. Later, the sets of the antennae, and setae, spines, and tarsal claws of the legs darken and become evident, and the adult mandibles are visible within the pupal mandibles. Darkening of the postoccipital rim of the head and the notal sclerites of the pterothorax also occurs at this stage. Pigmentation of the shorter setae of the body surface proceeds posteriorly from head to abdomen. A transverse series of somewhat larger setae is visible on each of abdominal segments before the remaining fine setae are pigmented.

Separation and development of the genital structures occur late in the pupal stage. The gonopophyses of the female and genital styles of the male, with associated setae, turn brown a few days before the imaginal molt. The large spines of the male forewings also become apparent late in pupal development, well after most of the large setae of the body are pigmented.

Two specimens had completed development of the pharate adult, but failed to molt successfully. In each of these, the head turned brown laterally from the clypeus to vertex near the eyes, and in a large, acute triangle extending from the occipital rim to near the upper border of the eyes.

Adult eclosion: The adult molt was not completed by any of the pupae under observation. The robust, toothed mandibles of Caurinus pupae are probably employed by the pharate adult to cut an opening in the pupal cell. However, it has not been observed whether the final ecdysis occurs within the intact or opened cell, or if the pharate

adult emerges from the cell before ecdysis, as is usual among endopterygotes with decticous pupal mandibles (Hinton, 1946).

The Caurinus pupa does exhibit action patterns similar to those performed by pharate adults of Panorpa falsa in digging to the soil surface (Yie, 1951). A Caurinus pupa placed on moist filter paper drags itself forward by a vigorous levering action of the head with the mandibles providing the points of contact with the substrate. The Caurinus pupa is able to roll on its long axis, but does not use wriggling movements of the abdomen to aid in progression, as do the pupae of Boreus, Hesperoboreus, Panorpa, and Bittacus. The latter is not surprising since the pupal abdomen of Caurinus is short and compact, and the abdominal muscles are presumably reduced to the vestigial adult condition early in the pupal stage. Since possibilities for movement are very limited within the pupal cells, it can be guessed from this behavior that Caurinus adults retain the ability to move through the substrate.

It has been suggested (Williams, 1916) that Boreus brumalis also uses the pupal mandibles to break out of the pupal cell, but this was not observed. The adult ecdysis of both Panorpa (Yie, 1951) and Bittacus (Setty, 1940) occur at the soil surface, and in each case the pupal skin is frequently left protruding from the emergence opening of the pupal cell. Microchorista philpotti (Nannochoristidae) also has robust, decticous pupal mandibles, although the adult mandibles are vestigial. In those individuals of Microchorista which have formed pupal cells in damp soil, the pharate adult probably digs its way to the surface before molting. However, some individuals of M. philpotti pupate "without any special cell" in damp moss (Pilgrim, 1972). It can be concluded that Caurinus has not diverged from other Mecoptera in the process of adult emergence, in spite of some differences in pupal morphology and position and composition of the pupal cell.

The adult ecdysis in Caurinus should be a simple process, since this species is brachypterous and the pupal morphology is very similar to that of the adult. By contrast, the rostrum, as well as the wings,

must be expanded in the Panorpidae. A special circumstance of the adult molt in Caurinus as related to the rigid abdominal structure (page 216). The abdomen of the female must expand greatly to allow space for growth of the reproductive system in the adult. The molting adult probably swallows air to "inflate" the abdomen through distension of the midgut. Several otherwise normal females have been observed which had abdomens almost as slender as in the male. It is possible that this variation is due to a failure in the eclosion process.

Mortality Factors

Little was learned in this study of natural mortality factors affecting Caurinus at any stage of its life cycle. As noted before, the adults are long-lived, and appear to survive frequently for more than a year. The apparently high mortality in late winter may be due to physiological causes. Adults are usually infrequent in the sampled habitats before high temperatures or ground-layer desiccation would create unfavorable physical conditions. The high mortality of C. dectes adults in culture appears to be related to water-balance factors. Some individuals drowned in condensed droplets of water, while many moribund individuals appear to be unable to eliminate water rapidly enough in wet surroundings. Fungal disease may also occur under holding conditions. Survival is progressively poorer at temperatures of 18°C and above.

Caurinus adults may be relatively free from predation and parasites. No instance of an internal parasitoid was discovered in the several hundred adults held for varying periods of time.

One recently dead female of C. dectes, recovered from a moss sample from Otis (Lincoln County, Oregon), contained a bright orange, cecidomyiid (Diptera) larva which was feeding on the tissues of the dead Caurinus. The larva was inside the intact abdomen of the Caurinus, the forebody of which was partially disarticulated, and telescoped into the anterior opening of the abdominal cavity. Within two days of the first observation, the fly larva produced a brown cocoon, still

within the Caurinus abdomen. A few cecidomyiid species are parasitoids of aphids and other insects (Clausen, 1940), but the above appeared to be an instance of saprophagous feeding, or at most, predation on a moribund Caurinus. Larvae which appeared to be the same species of cecidomyiid were frequent in samples of epiphytes from the Oregon Coast Range. These larvae are very active, and resemble predatory syrphid larvae in their constant side-to-side searching behavior. Both small and full grown larvae of this cecidomyiid occurred in the moss samples, suggesting the assumption that this is a free living predator or saprophage rather than a parasitoid.

Predation of adults is probably not important in the population dynamics of C. decetes. Most invertebrate predators found in the epiphytic communities were as small or smaller than C. decetes. Many species of mesostigmatid mites, pseudoscorpions, micryphantid spiders, and small lithobiid centipedes were recovered in the filtered moss samples. All of these predators frequently captured and fed on immobilized, soft-bodied arthropods (mostly springtails), but none were observed to interact with Caurinus. The hard, smooth exoskeleton and lack of exposed membranes in this genus probably protect C. decetes from most small, generalized predatory arthropods.

Parasitism is also unknown in the immature stages of Caurinus, but ectoparasitoids of larvae could be disassociated by the screening method, and only a few larvae and pupae have been observed in situ. Hymenopterous parasites specific to boreid larvae are known: Dyscoletes lancifer feeds on mature larvae of Boreus hyemalis in Europe (Fraser, 1943); D. canadensis has been reared from B. brumalis (Mason, 1976); and Conostigmus quadratogenalis (Ceraphronoidea) is parasitic on Hesperoboreus notoperates (Cooper and Dessart, 1974). Caurinus larvae are apparently more exposed to predation than the soil inhabiting boreines. Presumably some of the spiders, pseudoscorpions and mites mentioned above are able to capture the larvae in their open feeding galleries. Some other predators, including staphylinid beetle adults and larvae are also abundant in the substrates occupied by Caurinus, and may feed on the larvae.

All stages of C. dectes have been subject to fungal infection in the laboratory. I have not seen infection of Caurinus by the pathogenic genus Cordyceps, although this fungus is frequent in the soil inhabiting larvae and pupae of Boreus (Cooper, 1974). Presence of the host liverworts may be prophylactic against overgrowth of the eggs by fungi. Caurinus eggs, which generally remain free from fungal attack while they remain attached to live shoots of liverworts, often become moldy after they are removed to filter paper. The fungi affecting isolated eggs usually spread over the paper surface, while the living liverworts appear to inhibit such growth.

The pattern of occurrence in the field and lack of evidence for specifically adapted parasites or predators of Caurinus dectes suggest that this species is adapted for high survival of all stages except the relatively exposed feeding larva. Both biological and physical mortality factors (especially desiccation of the substrate) are most likely to affect the larva. The egg diapause and adult perenniation postulated for this species may be adaptations to high, unpredictable mortality in the larval stage.

There seems to be little loss of the diapausing eggs, while the post-feeding larvae and pupae are well insulated from most physical and biological mortality factors in the silk-lined pupal cells.

Extreme conditions of the physical environment may be supposed to be the major mortality factor in adults during their winter period of activity, although Caurinus adults can survive for days in exposed sites with air temperatures remaining around -2° to -4°C ; the adults are apparently also tolerant of drying conditions at temperatures near 0°C .

Phenology

The seasonal occurrence of life history phenomena of Caurinus dectes is best known from field collections of the Marys Peak populations. Collections were made one or two times a month between April 1976 and October 1978. These indicate the seasonal distribution

and relative numbers of the adults and immature stages of C. dectes, and of Hesperoboreus brevicaudus within the same substrates.

Nearly all the boreids collected at Marys Peak from January 1976 through February 1978 were extracted from samples of epiphytes of vine maple (most) and of big leaf maple and alder (few samples). The goal through much of the sampling program was to obtain live specimens of C. dectes for study, and to explore utilization of the available habitats by the species. The sampling was not designed for precise population estimation. The quantity of moss sampled was also limited by processing time and by rationing of available substrates through the study.

The number of boreids recovered from these epiphytic samples can be related to weight of the substrate or to some area measure. Although fresh weights were recorded for the bryophyte samples, these were inconsistent since moisture content could not be determined routinely to establish "sample dry weight" as a population base. Since most of the collections were of the vine maple epiphytes, a more convenient base for the population estimates was one related to area or volume, which could be represented by the stem length sampled. Moss samples from logs and epiphytes of trees (stem diameter greater than 20 cm) were recorded as the approximate area removed, and a constant relation of three "linear feet" to one "square foot" was assumed from relative weights of these substrates.

The monthly collection effort at Marys Peak was usually in the range of 7 to 12 meters of vine maple stems, or the equivalent area of other substrates. The collection data were reduced to the monthly mean recovery (of each stage) per 10 meters length of epiphytes. These values are represented for both C. dectes and H. brevicaudus in Figures 25 and 26. It is evident from this representation that the two species are very similar in patterns of seasonal occurrence. Specifically, in both species, young larvae are first noted in February or March, pupae have been collected August through October, and most adult activity is in the period from October through March. The major life-cycle differences appear in the presence of Hesperoboreus

Figure 25. Abundance of larvae, pupae, and adults of Caurinus
dectes recovered from samples of epiphytic bryophytes
at Marys Peak. (Monthly mean density from April 1976
to October 1978, as number per 10 meters of vine maple
stems.)

Figure 25

Caurinus dectes

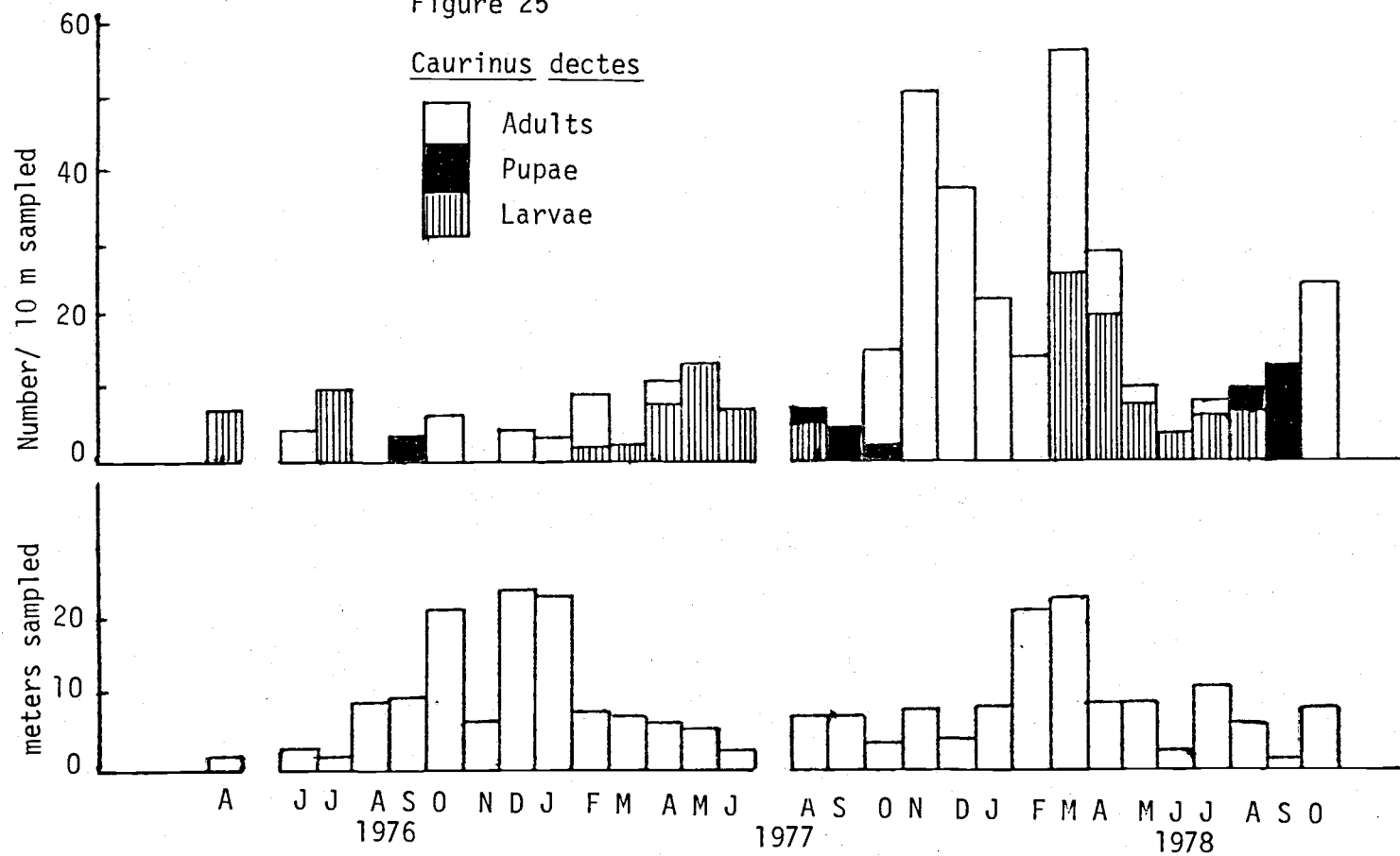
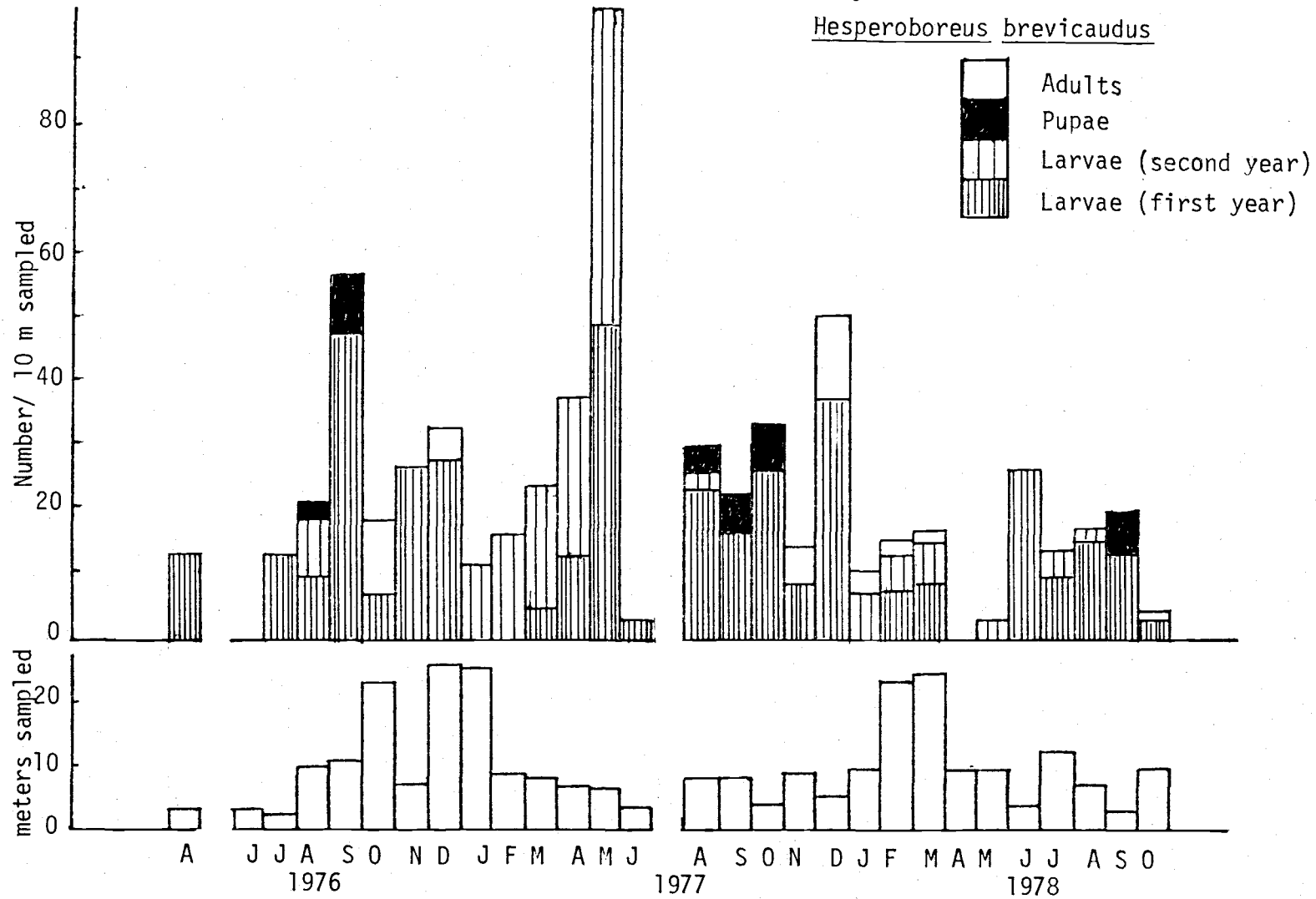


Figure 26. Abundance of larvae, pupae, and adults of Hesperoboreus brevicaudus recovered from samples of epiphytic bryophytes at Marys Peak. (Monthly mean density from April 1976 to October 1978, as number per 10 meters of vine maple stems.)

Figure 26

Hesperoboreus brevicaudus



larvae through the year, with two size classes evident in the spring and summer months, and in the scattered collections of Caurinus adults through the summer months. Caurinus was indicated as univoltine from partial rearing data, and this is confirmed in the regular succession of larvae, pupae, and adults through the annual cycle. Hesperoboreus brevicaudus, however, is generally semivoltine (requiring two years to complete its life cycle), as has been inferred for all other boreines examined to date (Cooper, 1974). Semivoltinism was demonstrated by rearing for Boreus hyemalis by Strübing (1950). It is not known whether the two-year life cycle is obligatory in species of Boreus and Hesperoboreus or if some adults may emerge a year earlier or later.

The large increase in capture of adults of Caurinus from 1976-7 to 1977-8 was due in part to improved collecting skill, but Caurinus were more abundant in the sampled substrate in 1977-8 than the previous year. Collections of adult H. brevicaudus and C. dectes were approximately equal at Marys Peak in 1976-7 (and in late winter of 1976), but Caurinus was much more abundant than Hesperoboreus in the following year.

My largest collections of adult boreids are those of C. dectes in 1977-8. The records for that season show an increase in the population in the epiphytes during October and November, and a steady decline in numbers through February 1978. The increased number of adults in March was due to inclusion of some samples of pure stands of Scapania bolanderi growing on logs and stumps. Late spring and summer collections (May through August) of adult Caurinus have yielded only a few specimens. These were all taken near the ground and were generally found during periods of wet weather. My collecting effort was reduced during the summer, and I believe that these few occurrences underestimate the survival of Caurinus past the normal season of activity for boreid adults. It seems likely that many adults leave the normal breeding habitats, especially the rapidly desiccated epiphytic stratum, and resume activity whenever weather conditions are favorable. It is likely, but not proven, that these adults survive long enough to overlap a new generation of adults. To

date, live Caurinus adults have been collected at Marys Peak in every month except September.

There is no indication that H. brevicaudus is capable of perenniation in the adult stage, and I have collected adults of this species only during the period from October through March. Some Boreus species have been collected during the summer months; B. borealis, endemic to St. Paul Island in the Pribilof group, has been collected only in July. Summer collections have also been reported in more southern populations, but these are quite sporadic. Penney (1977) reported, with reservation, a collection of both B. brumalis and B. nivoriundus on the same date (15 August 1935) in Ohio. Lubomir Masner (in conversation) collected one of the European species (B. hyemalis or B. westwoodi) "under stones" in July. Such collections (that is, not from pupal cells) quite possibly represent survivors from the previous winter generation of adults. Cooper (personal communication) has interpreted similar occurrences as instances of precocious emergence of new adults.

The seasonal pattern of adult emergence is nearly constant among mid-latitude boreid populations. The population curves estimated from collections of H. brevicaudus and C. dectes at Marys Peak (Figure 27) are similar to the seasonal record of abundance of a population of B. hyemalis on coastal sand dunes in Wales (Cotton, 1970). Other, subjective accounts of European and North American boreids generally agree in the dates of first emergence (around mid-October), peak emergence (late November or December) and last occurrence (March). Caurinus dectes has not departed from this pattern except in its ability to perenniate as an adult.

There is little information available on the effect of latitude and altitude on emergence patterns within a single species of Boreidae. Teneral adults of Caurinus dectes were collected at several localities in Thurston and Lewis Counties, Washington, on 20 September 1978. This date is at least two weeks before the median date for eclosion of adults at Marys Peak. The range of elevations at the Washington localities overlap with the altitudes at Marys Peak,

suggesting that this earlier emergence of the Washington populations may be a response to the latitudinal separation (2° latitude, about 250 km).

Another unusual life history characteristic which is inferred for C. dectes from the field data is an extended egg diapause. An obligatory egg diapause would explain why eggs laid in culture fail to hatch (page 106) and would fit field observations of eggs. The main breeding season for Caurinus is known to extend from late October to early April, although oviposition was observed as late as May 8, by a female collected May 5. However, unhatched and apparently viable eggs are abundant on the host liverworts throughout the year. The hatching period, as known from collections of first-instar larvae, is mid-February to early March. From observations of the development of field collected eggs in culture and the presence of feeding larvae at least as late as mid-June, egg hatching may extend into mid-April.

My interpretation of the field data is that some of the eggs laid within the approximate six-month period of oviposition produce larvae in that season, while others do not hatch until the following year. This pattern could be produced by a cold-exposure termination of diapause, which would allow only those eggs produced early in the winter to hatch the same year.

In other boreids, egg development apparently proceeds without diapause, although development is slow at low temperatures. Boreus hyemalis eggs require three weeks to hatch at 20°C , and one and one-half months at 7°C (Strübing, 1950). Hesperoboreus notoperates eggs held for a month at 9°C showed little development; these eggs began to hatch three weeks after transfer to 20°C (Cooper, 1974). Cooper further noted that egg hatch was spread over 36 days for this batch of identically treated H. notoperates eggs. Variation in hatching probably accounts for the extended seasonal occurrence of H. brevicaudus eggs at Marys Peak in 1977, during a winter and spring drought. All eggs recovered from mid-March through mid-June of that year were near hatching condition, and all hatched within one week at 20°C after their extraction. The eggs of H. brevicaudus and

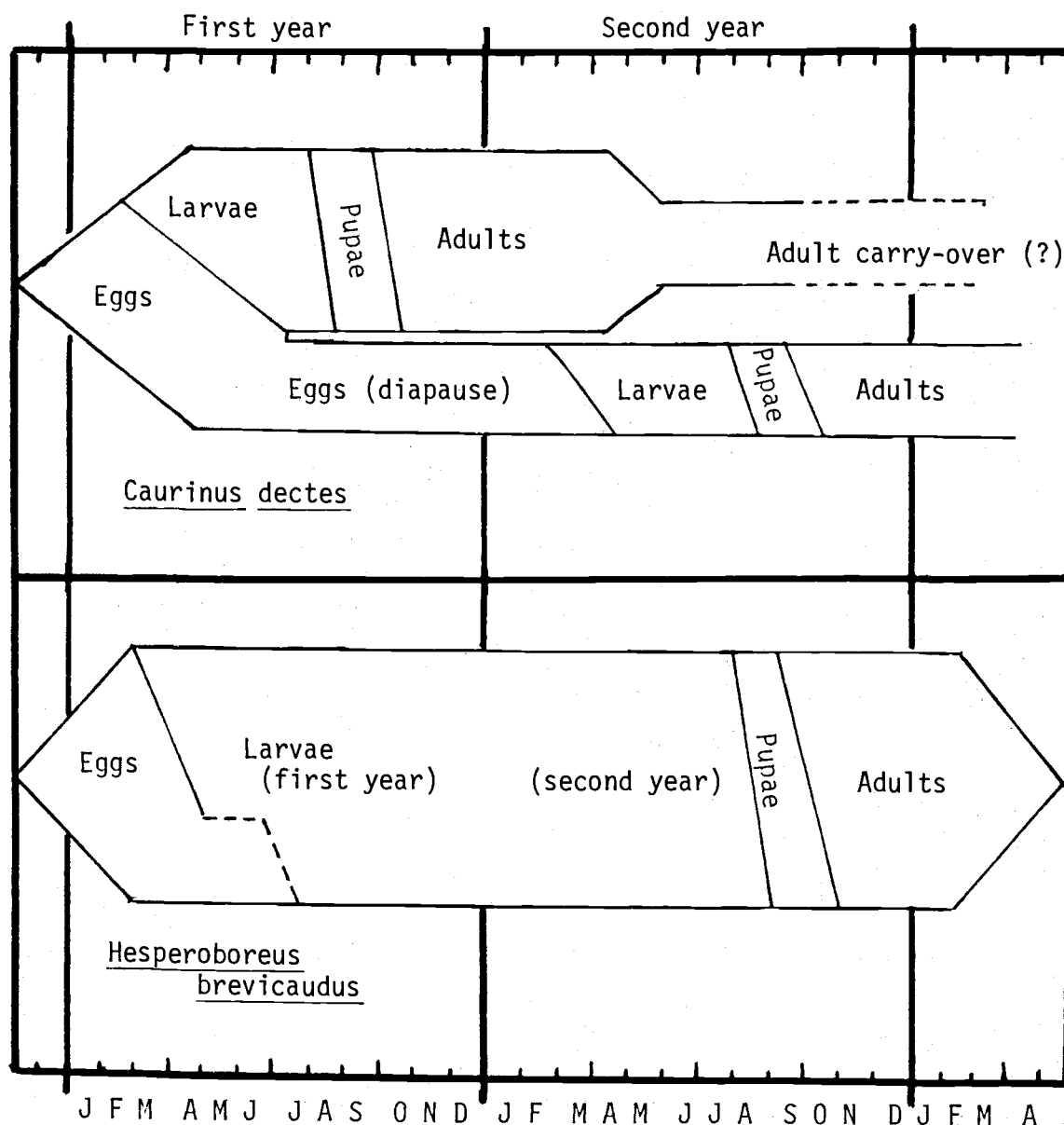


Figure 27. Comparison of the life-history patterns of Caurinus decetes (above), and Hesperoboreus brevicaudus (below). The timing of stage to stage recruitment is representative of the earliest and latest dates observed for the Marys Peak populations. Mortality is represented for seasonal adult die-off only.

C. dectes resist desiccation under field conditions in the Oregon Coast Range; the prolonged presence of Hesperoboreus eggs nearly ready to hatch was probably an adaptive response to the dry conditions. Just as the collected eggs hatched soon after the wet-screening treatment, all remaining eggs in the field evidently hatched following a rainy period in July.

Following the discovery of the association of C. dectes with Scapania bolanderi at Marys Peak, samples of Scapania were taken to determine the frequency and distribution of eggs and feeding damage. These are both conveniently determined on this substrate.

LARVAL MORPHOLOGY

The following description is based on larger larvae, which are regarded on the basis of head measurements as the third (last) larval instar (page 160). Approximately 65 larvae were available for study, including some poorly preserved specimens which died in culture dishes while being used in feeding tests. About 40 of these specimens were last-instar larvae. Observations on head structures were drawn from samples of all last-instar larvae. Post-cranial structures, however, were studied primarily on fully grown, extended larvae, because most features were better displayed at this stage.

Description of full-grown larvae of *Caurinus dectes*

A lot of seven extended, final instar larvae averaged 2.06 mm (range 1.81 to 2.33 mm) in length and 0.65 mm (range 0.63 to 0.67 mm) in maximum width. The larva (Figure 28) is curculioniform; that is, with well-developed head; orthognathus, biting mouthparts; and unsclerotized, ventrally curved body. Thoracic legs are very reduced, and abdominal prolegs are absent. There are 14 post-cranial segments; the thoracic and anterior abdominal segments are similar in size and form, while abdominal segments 8 to 10 are more slender. Segment 11 forms a simple four-lobed adhesive organ. Setae of the head and post cranial body are very short and reduced in number.

Color: The post cranial body is white; the head capsule medium tan, with an olive-green tint in live larvae. Sclerites of the mouthparts and antennae, and cervical sclerites are brown, the mandibles and mesal bands of the maxillae darker. The large eyespots are black; the reddish malpighian tubes are visible through the body wall.

Texture: Head capsule obscurely rugose, the meshes tending to unite in an irregular polygonal network (Figure 29). Unsclerotized surface of thorax and abdomen densely set with uniform conical protruberances (about 10 μ diameter); these in transverse rows on

much of the dorsal and ventral surfaces, whorled or irregularly aligned elsewhere.

Head: Orthognathous, oval in frontal view, widest slightly behind eyes, vertex narrowed at occipital sutures; occiput extending caudad as large bluntly angulate lobe. Head proportions (Width/Length/Height) 1.0/1.2/0.6. Head capsule completely sclerotized dorsally except for extensive articulation membranes of labrum and antenna, ventrally with very narrow sclerotized postgenal bridge continuous between the large occipital foramen and the maxillo-labial complex, ventral ecdysial line absent. Epistomal and occipital sutures present, as are dorsal ecdysial cleavage lines (epicranial suture). Thickened cuticular bands circle the antennal coria and are continuous with the anterior tentorial arms and strengthening bands (pleurostomata) joining the dorsal and ventral mandibular articulations and the posterior margin of the head capsule. Anterior tentorial arms stout, originating at inner margin of antennal sclerite posterior to visible part of epistomal suture.

Labrum transverse, most of anterior margin membranous, basal margin with narrow median lobe. Labral sclerite with four sensory pits on dorsal surface, apical membrane with setal brush. Clypeus transverse, apical margin not sharply set off from labral articulation membrane, basally bounded by epistomal suture, which ends near the anterior medial angles of the antennal membrane. A break in pigmentation separates the main clypeal area from the sclerotized pleurostomal band.

Ecdysial stem extending slightly anterior to occipital sutures; the ecdysial arms enclose 120° and extend obliquely anterior, then directly anterior to the inner margin of antennal membrane and the anterior tentorial pits. Frontal apotome (Figure 30) elongate and anteriorly parallel-sided. Lateral eyes (sternmata) seven on each side, equally spaced and arrayed as a question-mark pattern. The four ventral lenses are adjacent to the external margin of the antennal membrane, and three other lenses are recurved posteriorly from this group. Each lateral eye cluster underlain by a large oblong

black pigment spot. Antennae (Figure 32) short, prominent, two-segmented, set in extensive membrane. Basal segment very short, broad; with membranous apex; second segment elongate, cylindrical, with elongate membranous excavation on mesal surface of apical half. Membrane between first and second segments extensive, with three large placoid sensilla on medial surface. Second segment with four apical peg-shaped sensilla, without larger apical setae. Antennal proportions (Length 1 : Width 1 : Length 2 : Width 2) are 1 : 3 : 3 : 1.

Mandible (Figure 40) stout, triangular, with three large, transversely placed apical teeth, the middle tooth the largest. One or two smaller teeth are proximal to these; the proximal half of the mesal edge sharp, slightly arcuate. The mesal and dorsal apical teeth and molar blade are in one plane, the ventral apical tooth defined from this. In lateral aspect the mandible is basally broad, with large hypocondyle and robust adductor and abductor tendons. Mandible with two setae on ectal surface, at basal one-fourth and two-fifth of mandibular length, respectively.

Maxillolabial complex large, ventrally prominent, maxilla with curved sclerotized mesal band extending from the posterior articulation with the head capsule, to the apical mesal border of the maxillary endite.

Stipes weakly sclerotized, continuous with mesal sclerotized band. Palpifer and two-segmented maxillary palps well sclerotized. Palpifer large, approaching sclerotized band where this turns dorsad along mesal border of maxilla. Maxillary palps similar to antenna, 2-segmented with basal segment short, stout; second segment cylindrical, truncate at apex. Two punctiform sensilla in membrane between palpal segments; basal segment with two setae, second segment with two dorsal pits and with numerous basiconic sensilla on apical membrane. Maxillary endite not divided into lacinia and galea; with dense, fine setae on mesal and dorsal surfaces, ventral surface with two larger setae and four sensory pits, laterally near palpifer.

Labium with postmental field membranous. Distally, an elongate unpaired median lobe (Figure 43, apparently the fused prementum and hypopharynx) is supported by lateral sclerotized bands which are

continuous basally. Distal to the basal bridge of this sclerite on the ventral membrane are two annular sclerites which are probably the labial palps, which are reduced to one segment and flattened onto the submental membrane.

Thorax and abdomen: Fourteen postcranial segments are evident in Caurinus. Thoracic segments, each with small, conical legs, ventrally oriented and widely separated from the ventral midline. In expanded larva, the body is nearly cylindrical and slightly curved ventrally. Body broadest at metathorax and first abdominal segment, strongly tapered from seventh to eleventh abdominal segments.

Prothorax relatively long; its anterior dorsal lobe covers the occiput. The mesothorax and metathorax and abdominal segments 1 to 7 nearly uniform in length and diameter. Segments 8-10 when extended each slightly longer than the anterior abdominal segments. Segment 11 short, one-third length of segment 10. Segment 10 about one-fourth the diameter of segment 6.

The thoracic and anterior abdominal segments with transverse dorsal and ventral folds. Ventral folds evident to the seventh abdominal segment; the dorsal folds reduced between the fifth and seventh segments, absent on segments 8-11.

The only distinct postcranial sclerites are the cervical sclerites, borne laterally on the prothorax. The cervical sclerite posteriorly expanded as triangular plate and extending obliquely anteriorly to the postgena, flexed at mid-length. The thoracic legs frequently retracted and unrecognizable in preserved specimens; the two anterior pairs somewhat better developed than metathoracic pair. Leg apex somewhat nipple-like, but otherwise unsegmented. The thoracic sterna each traversed by folds extending between and diverging anterior and posterior to the leg. The abdominal sterna divided into anterior and posterior folds. The anterior folds elevated, bearing asperities that apparently function as creeping welts.

The slender apical segments (8-11) of the abdomen form a proleg-like structure. Segment 11 (Figure 31) apically divided into four equal, rounded lobes, forming an adhesive organ.

Distinct pleural folds on all segments from prothorax to the eighth abdominal segment only (Caurinus larvae are amphipneustic). The spiracles (Figures 46,48) each externally a U-shaped structure, the two arms each a sclerotized peritreme with transverse bars separating 7-8 pores. Each spiracle continuous with an elongate atrium lined with many long setae. Each peritreme bar 20-25 μ long and 4-5 μ wide.

Discussion

The description of the grown larva applies equally well to the earlier larval stages. No differences were noted between the large larvae and presumed first instar larvae in mandibular shape, cranial sutures, and setation, antennal proportions and sensory structures and the number and position of ocelli. The leg structure also is constant through larval development. The smaller larvae may be relatively more slender, and the head relatively larger than larvae of comparable growth in the last instar. The only structural difference noted in the small larvae is the sharp median longitudinal keel on the posterior half of the frontal apotome (Figure 30). This has been found only in the three smallest preserved larvae and in eight preserved exuviae. The frontal ridge is very thin, but its position, restriction to the smallest larvae, and the linear chorion split in Caurinus eggs, suggest that this structure is an egg-burster. Since the larvae bearing the egg-burster are uniform in size, this structure is also taken to be a reliable stage marker, present only in the first larval instar.

Conical or spine-like frontal egg-bursters have been reported on first instar larvae of the Panorpidae (Panorpa nuptialis; Gassner, 1963), and Bittacidae (Bittacus pilicornis; Setty, 1940), but apparently do not occur in other Boreidae. Frontal egg-bursting spines or ridges are apparently a primitive feature of the pronymphal cuticle in exopterygotes and are known to occur in the Megaloptera, Neuroptera, and Trichoptera as well. Persistent frontal egg-bursters, which are structures of the first larval instar, are known to occur in

a number of nematoceran Diptera, Siphonaptera, Coleoptera (most Adephaga), and Thysanura (van Emden, 1946), in addition to the Mecoptera mentioned above. The distribution of this structure indicates that it is a primitive feature of the first instar in Mecoptera, and probably of the Antliophora (Hennig, 1969).

Comparison of *Caurinus* larvae with other Mecoptera

Previously described larvae of Mecoptera are of a uniform type in each family: eruciform in the Bittacidae, Choristidae, and Panorpididae (and probably in the Apteropanorpididae also); elateriform and aquatic in Nannochoristidae; and scarabaeiform in Panorpididae (*Brachypanorpa*) and Boreidae. The larvae of Notiothaumidae and Meropeidae are still unknown (Kaltenbach, 1978). The curculionoid larva of *Caurinus* is far more similar to those of *Boreus* and *Hesperoboreus* than to any other Mecoptera. Superficially however, *Caurinus* is very divergent from the boreine larvae. Some of the characters separating *Caurinus* from boreine larvae are listed in Table 15. Many of those differences can be attributed to the *Caurinus* larva having adaptations typical of stem-miners or other internal-feeding phytophagous insect larvae. *Boreus* and *Hesperoboreus* larvae, on the other hand, resemble some other sedentary soil larvae, such as those of the Scarabaeidae.

The *Caurinus* characters which are typical of endophytophagous larvae include the almost straight, cylindrical, unsclerotized body with deeply set head; the very reduced legs and presence of dorsal and ventral folds adapted for movement within a gallery; and the reduction or loss of long setae. The large, mobile head and blunt mandibles of *Boreus*, as well as its general body form are all associated with the larvae tunneling in the soil.

The amphipneustic condition of *C. dectes* is unusual for a terrestrial insect larva. "With rare exceptions (Diptera, *Eneocyla*,²

²Hinton probably refers here to *Enoicyla* (Trichoptera: Limnephilidae). *Enoicyla pusilla* has a terrestrial larva, which retains the closed tracheal system of aquatic caddis fly larvae.

Table 15. Morphological attributes separating larvae of Caurinus from other boreid larvae.

CHARACTER STATE	
in <u>Caurinus</u>	in <u>Hesperoboreus</u> , <u>Boreus</u>
General	
Form curculioniform:	Form scarabaeiform:
Head well-developed, orthognathous	Head well-developed orthognathous
Body slightly curved	Body C-shaped
Legs very reduced, 1-segmented	Legs large, 3-segmented fleshy
Setae of head and body few, short (15-25 μ in 2mm larva)	Setae more numerous on body, many setae long (50-60 μ in 2-3mm larvae)
Head	
Deeply set in thorax mouthparts fairly short	Head mobile, ventrally prominent
With 7 ocelli	With 3 ocelli
Labrum with dorsal apical brush of setae	Labrum with 2-4 large setae
Frontal arms of ecdysial line complete	Frontal arms of ecdysial line incomplete anteriorly
Frontal egg-burster present in first instar	No egg-burster
Antenna 2-segmented without large apical seta	Antenna 2-segmented with 2 large apical setae
With 3 placoid sensilla in membrane at apex of first segment	Without placoid sensilla
Mandible with 3 large, 1-2 smaller teeth and sharp mola	Mandible with 2-3 apical teeth
Cardo not distinct	Cardo well developed sclerite
Prementum and hypopharynx large, extending near apex of maxillae	Prementum short
Labial palps very reduced	Labial palps large, 2-segmented

Table 15 . Morphological attributes (Continued)

in Caurinusin Hesperoboreus, Boreus

TrunkThoracic segments simple,
similar to abdominal
segmentsAmphipneustic (1 thoracic,
1 abdominal spiracle)Mesothoracic spiracle
single, similar to
spiracle on abdominal
segment 8Abdominal segment 11
exposed, 4-lobedThoracic segments with
prominent setose dorsal
and lateral lobesPeripneustic (1 thoracic and 8
abdominal spiracles)Mesothoracic spiracle with
double peritreme and atriumAbdominal segment 11 not
exposed

and a few others) terrestrial insect larvae are polypneustic in all instars" (Hinton, 1947). The reduction to two functional spiracles in Caurinus probably reflects reduced efficiency of intermediate spiracles through adherence of wet host tissues, as well as small size and possible cuticular respiration in these larvae.

Aside from the reduction or loss of structures, only a few characters are diagnostic for both types of boreid larvae. Among these, the antennal and maxillary structure and the elateroid spiracles (Hinton, 1947, definition) are unique among mecopteran larvae. Hinton (1958) could not determine the molting process associated with the complex spiracles of Boreus, but noted that "it is either panorpoid or elateroid." Potter (1938b) described the spiracles of the larva of B. hyemalis as consisting of single (the abdominal spiracles), or double (the mesothoracic spiracle), "circular apertures". Given Hinton's (1958) remarks, which were probably based on observation of B. hyemalis also, it may be assumed that the larval spiracles of this species are divided by cuticular bars, as in American boreines and in Caurinus. I have not observed stigmatic scars associated with either functional or non-functional spiracles in Caurinus larvae. However, I found tracheal scars in larvae of H. brevicaudus similar to those described next to the spiracles of larval Boreus hyemalis by Potter (1938b). In Hesperoboreus, these scars are attached by a collapsed cuticular tube to the trachea at the base of the spiracular atrium, and indicate the elateroid molting process. Since the structure of the spiracle and atrium of C. dectes is similar to that of the boreines, the stigmatic scars presumably occur in all segments bearing spiracles in the adult, but are obscured by the pebbly surface of the cuticle.

Some other comments are required on the implied homologies used in the larval description. These include my treatment of the epistomal suture, the stemmata, the antennal segmentation, the labial structures, and the eleventh abdominal segment.

Epistomal suture: As noted in the description, this suture is incomplete laterally and isolated from the anterior tentorial pits in

Caurinus larvae. Hinton (1958) noted that "the larvae of the Mecoptera (excluding Boreidae) are exceptional in that there is a very distinct transverse suture between the frontal region of the head and clypeus". Its identity with the frontoclypeal suture of primitive exopterygotes was left open, however. Cooper (1974) showed that a similar suture is present in several boreid larvae, including those of Hesperoboreus notoperates, Boreus brumalis, and B. westwoodi. In these larvae, and in H. brevicaudus, the suture is complete, extending to near the base of the mandible.

The position of this suture in Caurinus is more similar to that of Panorpa (examined in P. lugubris (?) from North Carolina) than of H. brevicaudus. In Panorpa and Brachypanorpa, the position of the epistomal suture is more anomalous. In these larvae, the anterior tentorial pits lie at the end of a short suture posterior and parallel to the epistomal suture, which originates in the antennal sclerite. In Brachypanorpa oregonensis, the epistomal suture curves forward laterally and ends well anterior to the mandibular articulation, clearly within the clypeal field. From these data, it appears that the apparent epistomal suture of larval Mecoptera (including Caurinus) is not necessarily homologous with the epistomal suture of adults of the order (which does end in the tentorial pits), or with the similar structure in other insects.

Larval eyes: The larval eyes of Caurinus differ from those of Boreus and Hesperoboreus in the larger numbers of lenses (seven on each side, as compared to three in the boreine larvae). These eyes resemble typical stemmata (Hinton, 1958), but are underlain by a large common pigment spot, and are rather closely clustered in Caurinus. Most other mecopteran larvae have compound eyes with numerous (15-30+) ommatidia (Bierbrodt, 1942; Riek, 1970), although typical compound eyes are otherwise unknown among endopterygote larvae. Eyes are absent in Brachypanorpa larvae, while Microchorista larvae (Nannochoristidae) have large ocular pigment spots, but no corneal lenses (Pilgrim, 1972). The lateral eye of bittacid larvae is a ring of seven "ocelliform structures" (Applegarth, 1939), quite similar in external

appearance to the eyes of micropterygid larvae (Tillyard, 1923). The bittacid eyes were believed to be stemmata by Applegarth, but most recent authors have considered them to be compound eyes (Kaltenbach, 1978).

The large number and close spacing of the stemmata in Caurinus are probably primitive features relative to the eye structure of boreine larvae. The arrangement of the lenses along the periphery of the large pigment spots suggests a derivation from the type of compound larval eye in this order, through loss of the central ommatidia. The reduction to stemmata in the Boreidae could therefore be viewed as convergent with the usual eye structure of other endopterygote larvae.

Antennal segmentation: The antenna of Caurinus and of boreine larvae are described here as two-segmented. This is clear in Caurinus larvae, but the antenna of Boreus and Hesperoboreus larvae have been described both as three-segmented, and as two-segmented with an apical bristle. The identification of the large apical bristle of boreine larvae with the antennal flagellum (third segment of panorpids and others) is credible, given the reduction of this joint in some Bittacidae (Setty, 1940). However, the following observations on the larva of C. dectes and H. brevicaudus make the three-segment construction untenable. In H. brevicaudus larvae (Figure 34), there are two apical bristles, and these are only slightly better developed than the four large apical setae on the third antennal segment of Brachypanorpa oregonensis. These setae, usually short, are also constantly found in described panorpid larvae. The nature of the antennal reduction in boreids is shown by the three large placoid sensilla in the membrane at the apex of the first antennal segment of C. dectes. These are identical with the more numerous sensilla of the membrane at the apex of the second segment of panorpids, Brachypanorpa, bittacids, and possibly other mecopteran larvae (Figures 36-39). It is therefore likely that reduction of the number of antennal segments in Boreidae came through complete incorporation of the pedicel in the membrane between scape and flagellum, rather than through fusion of the scape and flagellum.

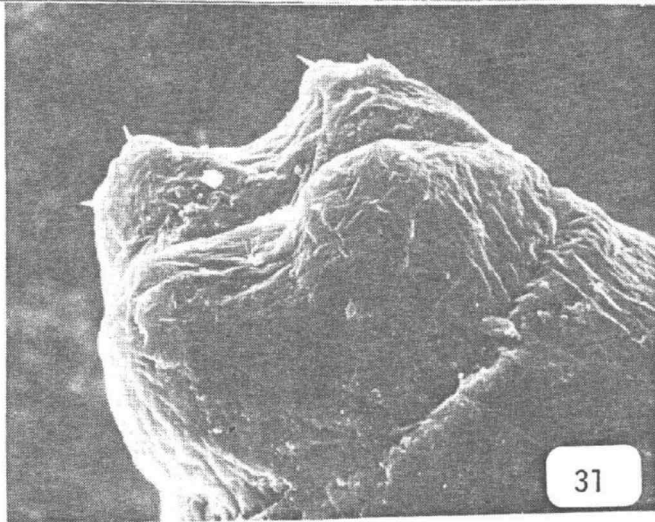
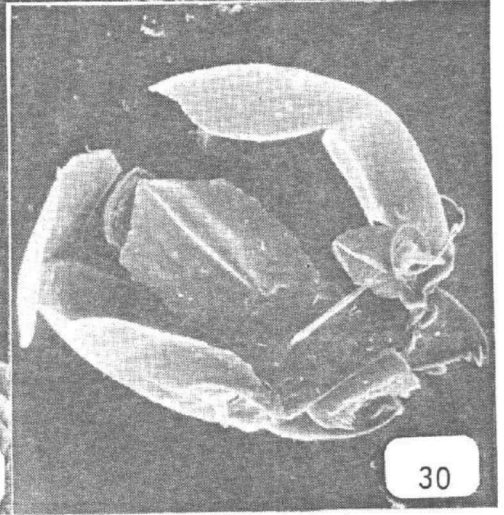
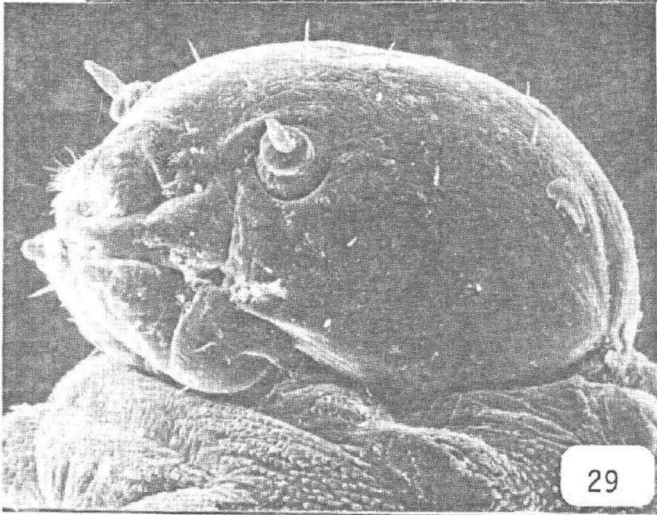
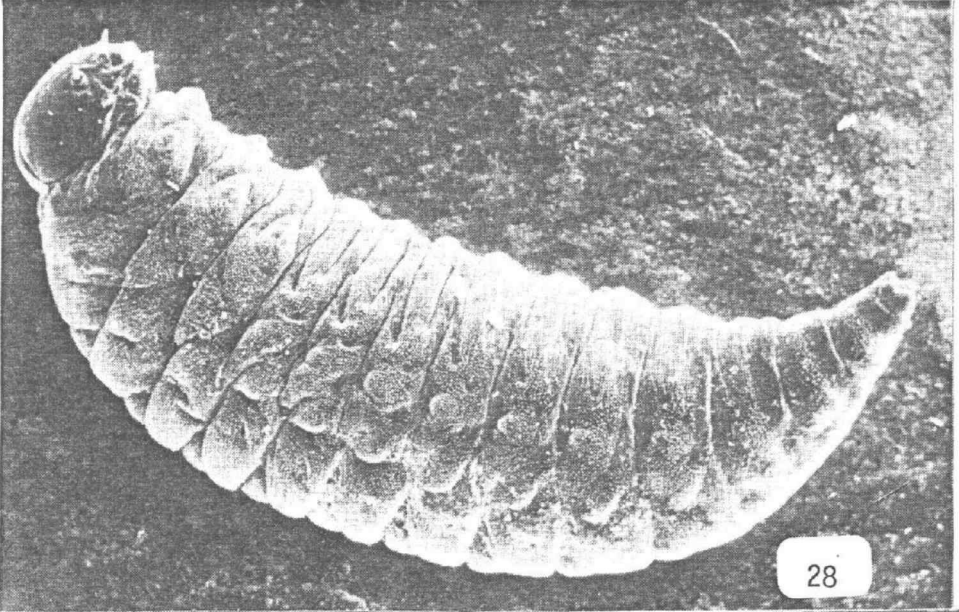
Labium and hypopharynx: The elongate median lobe lying between the maxillae represents a fusion of the prementum and hypopharynx. This follows from the assumption 1) that the ligular elements are absent from the larval labium of C. dectes, as in all other Mecoptera; 2) that the annular structures lying at the base of this structure are the reduced labial palps; and 3) that the large sclerite supporting it and extending across its base is in part homologous with the cuticular hoop of the prementum positioned basal to the labial palps in Boreus hyemalis (Potter, 1938b).

The complex structures, apparently sensory, associated with the pair of annular sclerites identify these as reduced palps rather than the two convergent setae which are basal to the palps on the prementum of boreines (Cooper, 1974). The salivary orifice was not located in Caurinus, but most of this lobe is likely to represent the hypopharynx, and the distal portion of the supporting sclerite are therefore to be compared with the lingual sclerites of orthopteroid insects (Matsuda, 1965).

The eleventh abdominal segment: This is short, and four-lobed in Caurinus, and functions as an adhesive organ. Hesperoboreus larvae (and probably Boreus as well) also adhere to the substrate by their anal segment, but these larvae have only ten apparent abdominal segments and their terminal segment lacks the finger-like lobes of Caurinus. The eruciform mecopteran larvae (of the Panorpidae, Bittacidae, and Choristidae) all have a large, eversible, four-lobed anal holdfast (Kaltenbach, 1978). The external basal margin of this holdfast bears a series of sclerites which, in Apterobittacus (Applegarth, 1939), fold together to conceal the anal membranes. This structure is usually identified as the eleventh segment (Byers, 1963). However, Matsuda (1976) homologized this "anal fork" with the anal papilla of nematoceran larvae, and therefore (following Christophers, 1923, from Culicidae) regarded it as representing the cerci only. This interpretation is associated with Matsuda's assumption that the apicalisation of cerci in adult Mecoptera (except Bittacidae) results from loss of the supraanal and subanal lobes (the twelfth segment

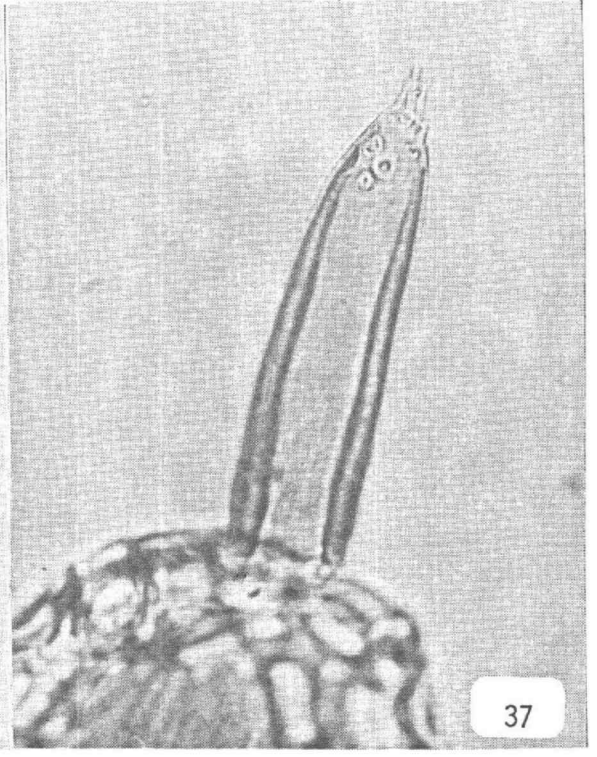
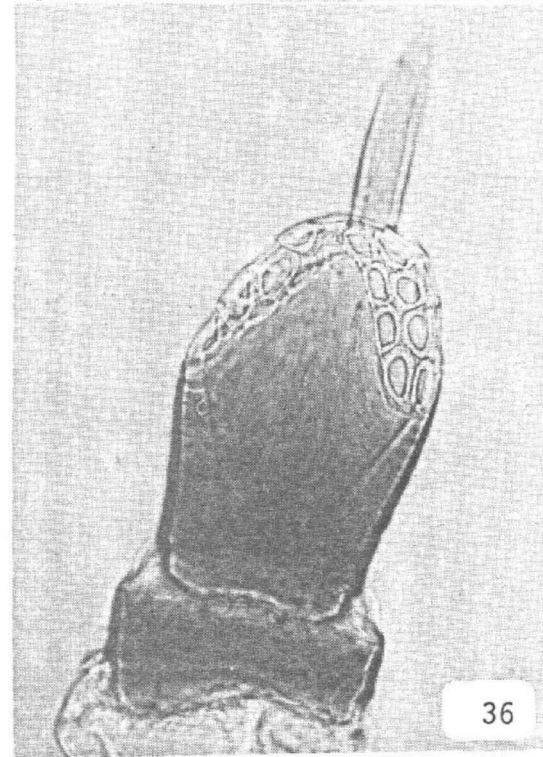
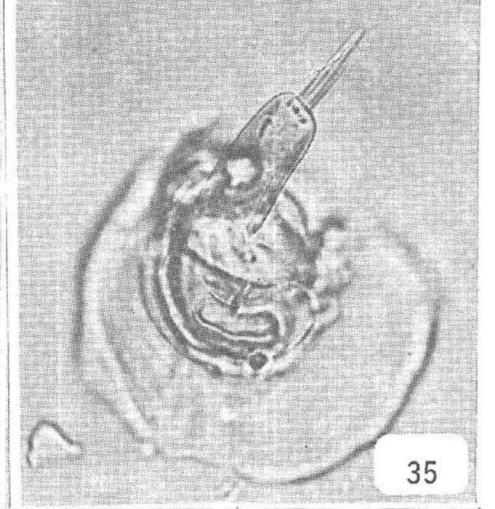
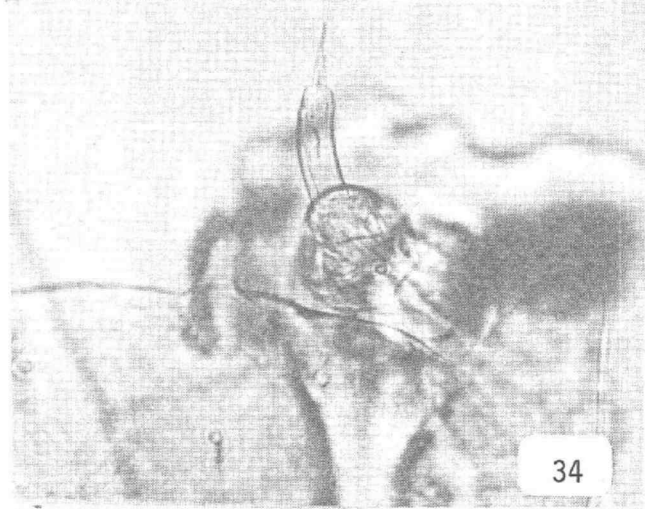
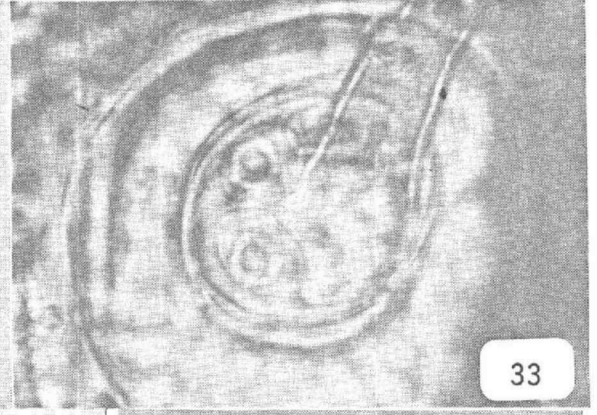
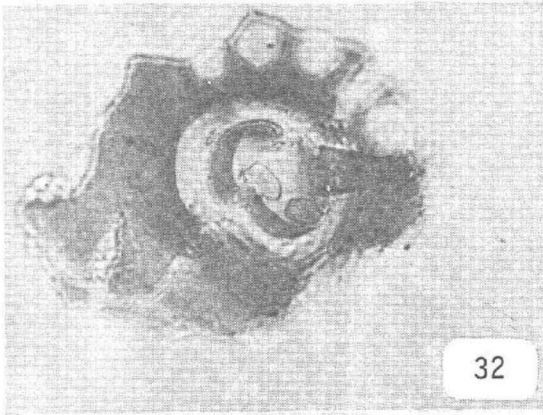
Figures 28-31. Larva of Caurinus dectes.

- 28) Fully grown third-instar larvae, ventro-lateral aspect (49X).
- 29) Head of third-instar larva; frontolateral aspect (150X).
- 30) Exuvial first-instar head capsule showing frontal ridge (190X).
- 31) Eleventh segment of third-instar larva, lateral aspect (450X).



Figures 32-37. Antennae of larvae of Mecoptera.

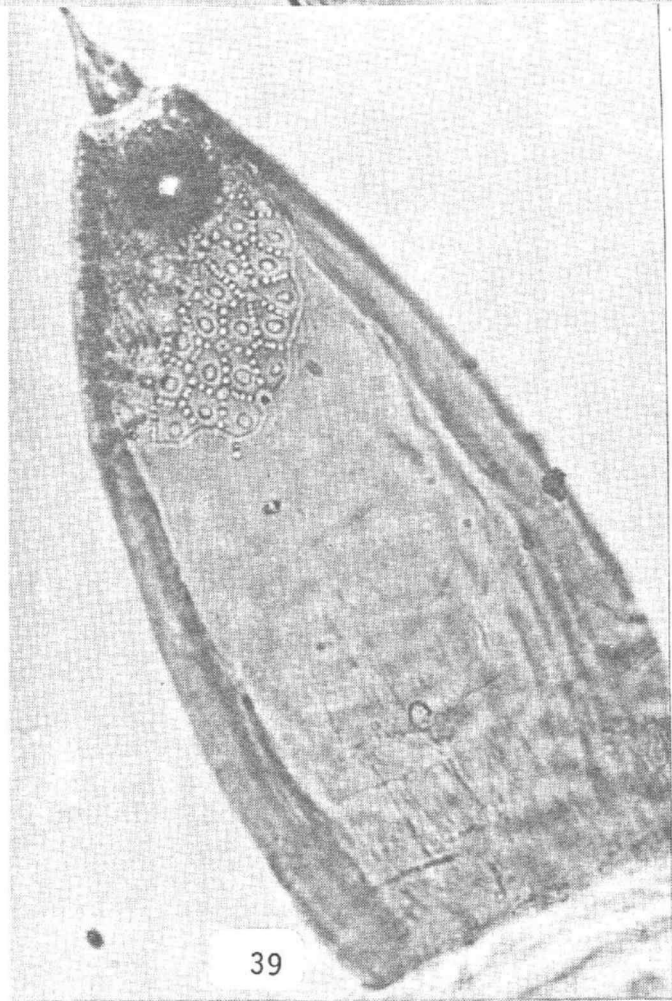
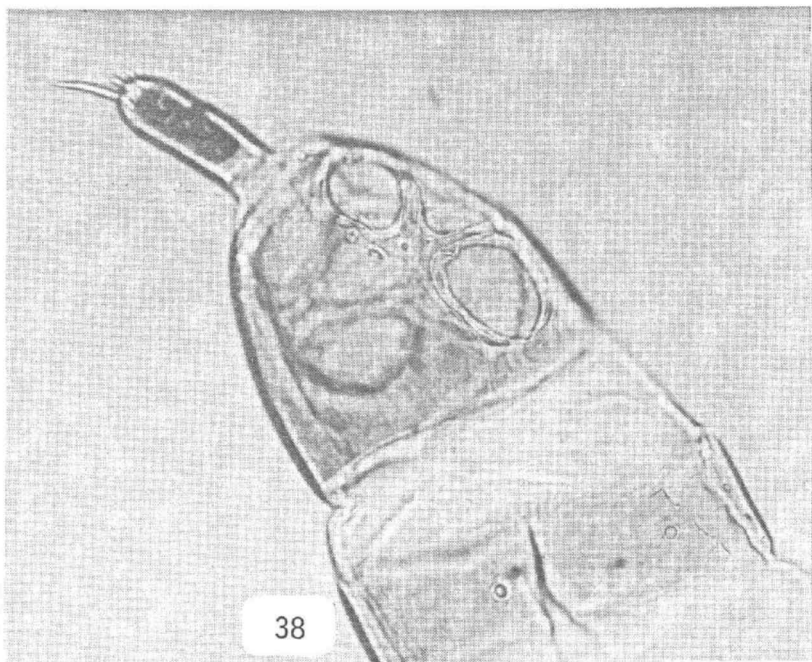
- 32) Antenna of larva of Caurinus dectes, mesal aspect (400X).
- 33) Antenna of larva of C. dectes, showing three placoid sensilla (1000X).
- 34) Antenna of larva of Hesperoboreus brevicaudus (400X).
- 35) Antenna of larva of Boreus reductus (Idaho) (400X).
- 36) Antenna of larva of Panorpa sp. (North Carolina) (160X).
- 37) Apical segment of antenna shown in Figure 33 (Panorpa sp.) (400X).



Figures 38, 39. Antennae of larvae of Mecoptera.

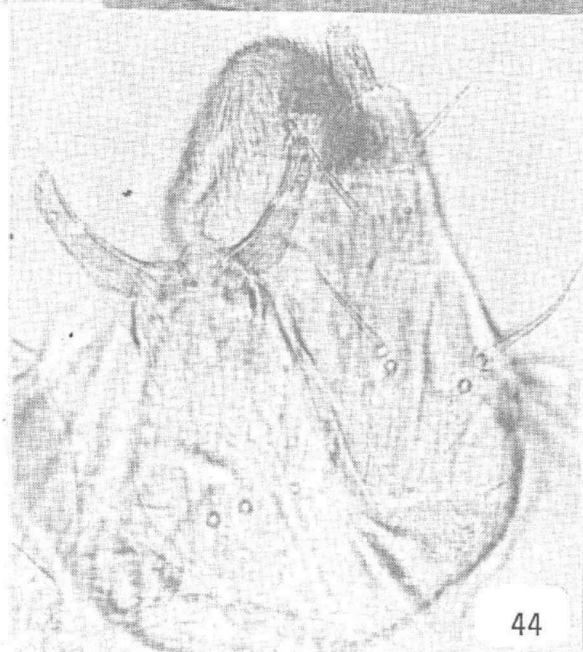
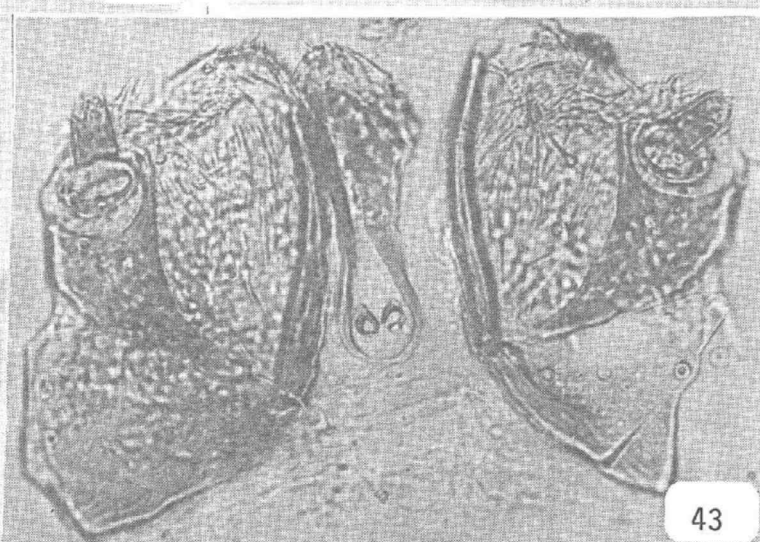
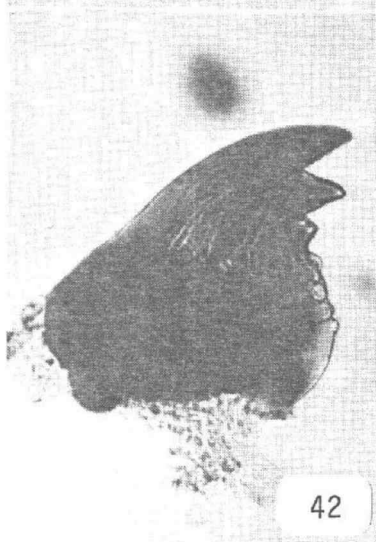
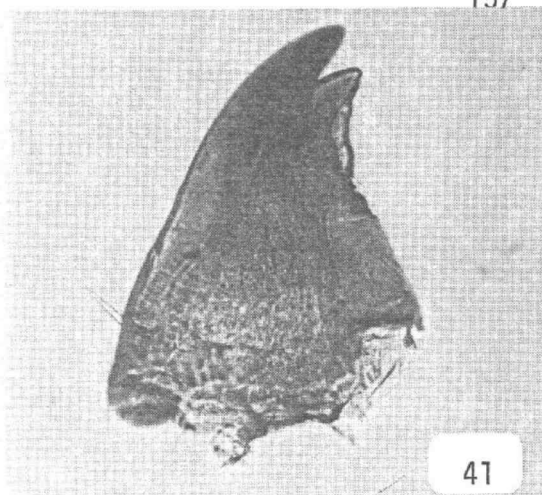
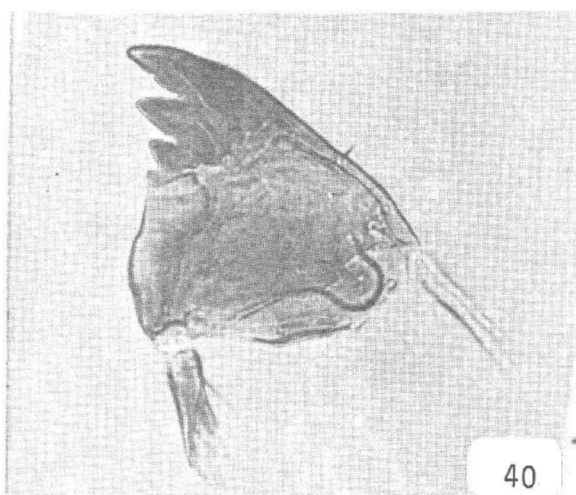
38) Antenna of mature larva of Brachypanorpa oregonensis (Panorpididae) Benton County, Oregon (250X).

39) Antenna of larva of Apterobittacus apterus (Bittacidae) San Mateo County, California (250X).



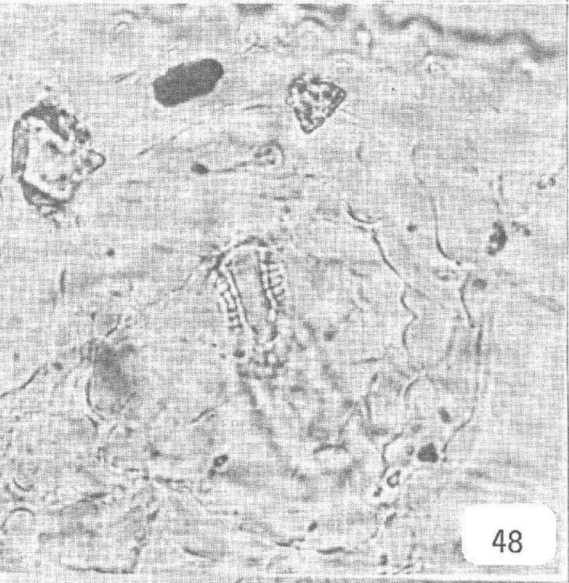
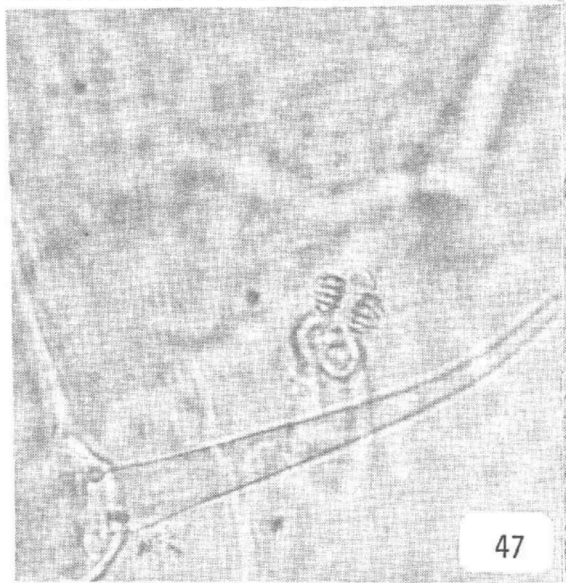
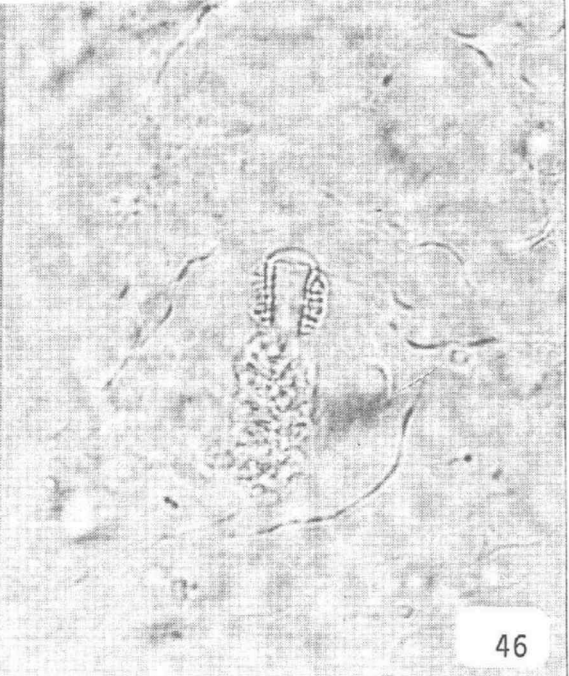
Figures 40-44. Mouthparts of larvae of Boreidae and of Micropterygidae.

- 40) Left mandible of mature larva of Caurinus dectes, posterior aspect (250X).
- 41) Left mandible of larva of Hesperoboreus brevicaudus, anterior aspect (250X).
- 42) Right mandible of Epimartyria pardella (Micropterygidae), posterior aspect (250X).
- 43) Maxillae, labium, and hypopharynx of larva of C. dectes, posterior aspect (250X).
- 44) Left maxilla and labium of larva of H. brevicaudus, posterior aspect (right maxilla removed) (250X).



Figures 45-48. Spiracles of larvae of Caurinus dectes and Hesperoboreus brevicaudus.

- 45) Mesothoracic spiracle of mature larva of H. brevicaudus (1100X).
- 46) Mesothoracic spiracle of third-instar larva of C. dectes (1100X).
- 47) Spiracle of sixth abdominal segment of H. brevicaudus larva (1100X)
- 48) Spiracle of eighth abdominal segment of C. dectes larva (1100X).



according to Matsuda). The four lobes of the anal holdfast in Mecoptera circle the anus, and in Caurinus, form a well-defined segment. The cerci and supraanal lobe are both well-developed in adult females of Caurinus, so that there is no good reason to accept Matsuda's restricted interpretation of the anal segment of the larva.

Number of larval instars in Caurinus

Since the larvae of C. dectes were not reared from egg to pupa, it was necessary to use indirect means to identify the stages of larval development. The available forms of instar analysis rely on 1) statistical analysis of some dimension of the larval population, 2) computation from Dyar's constant, which in strict sense is extrapolation from an observed interstadial growth increment, and 3) analysis based on meristic or other non-continuous variation in the observed population. Obviously many factors could interfere with accurate instar counts through any of these approaches. The more important of these are the failure of the assumption of a growth constant (perhaps through interpolation of a non-feeding instar), non-inclusion of either first or last larval stage, underrepresentation of some stages, and any polymorphism not related to growth stages. Instar analysis by any means other than rearing is also likely to be inaccurate if there are many instars or a variable number.

My analysis of Caurinus larvae is based on all three lines of evidence listed above. Most of the preserved larval material was examined and several measurements taken on each specimen, using a micrometer eye-piece at magnification of 24X to 100X. Head-width, measured in dorsal aspect at the widest part of the head just posterior to the eyes, was the most satisfactory measurement for statistical analysis which could be made on the intact larvae. Head length, in lateral aspect, and maximum body length and width, were also recorded for each larva.

The head width of the 63 larvae measured, varied from .247 to .350 mm. Measurements of heads of exuviae and unhatched first instar

larvae are not included in these totals. Histograms of the head widths, plotted as nominal values, or by .01 mm classes, show two strong modalities (Table 16), including one group of individuals (L2; N=19) with head width ranging from .277 to .290 mm, and a second group (L3; N=11) ranging from .306 to .350 mm. Three smaller larvae (L1) ranged between .247 and .256 mm.³

The mean head widths for the three classes above are .252, .287, and .325 mm, which if successive instars, give growth ratios (Dyar's constant) of 1.15 and 1.13 for the successive molts. Although these data indicate that three larval instars are represented in my material, it is necessary to use other morphological cues in identifying the smallest and largest class. The three smallest larvae each have the previously mentioned egg-burster. Since egg-bursting structures are normally confined to the first instar (van Emden, 1946), I have concluded that these three larvae are a sample of the first larval instar.

The larger larvae (L3) are more numerous in this sample, and more variable than the other two classes identified here. However, the coefficient of variability (C.V.) for L3 is still quite low (3.3%); Cooper (1979) reported a C.V. of 9.7% for last-instar larvae of H. notoperates. In addition to the difficulty in accommodating two instars within this sample, the dispersion of this group is symmetrical to the mean, as shown in the plot of probability function of the ranked data (Figure 49). The rank-probability transformation is useful in detecting growth stages if the sample sizes of adjacent groups are not greatly unequal (Wightman, 1978). This group (L3) is taken to represent the last larval instar, since three pharate pupae are near the mean for this class (mean (L3) = .325 mm; pharate pupae: .316, .328, .329 mm).

³ These measurements are reported only for the Marys Peak population. The validity of the sample is supported by measurements on a collection of larvae from Snohomish County, Washington. Ten larvae with egg-bursters (recovered 28 March 1979) had head widths ranging from .246 to .258, with a mean of .2515 (L1). Two larvae recovered from part of the same sample on 3 April had head widths of .322 and .328 (L3).

If Caurinus has three larval instars, this is the first species of Mecoptera found to have other than four or five larval instars. Four instars are known for all mecopteran species reared to date. These include the nannochoristid Microchorista philpotti (Pilgrim, 1972), many panorpids, including 13 Nearctic species of Panorpa (Boese, 1973) and several Formosan species of Panorpa and Neopanorpa. Setty (1940) indicated that Bittacus larvae have four feeding larval stages plus a prepupal molt within the pupal chamber.

The existence of a fifth (prepupal) instar in Bittacus should be investigated. Since Setty (1940) did not mention whether exuviae were found in the pupal cell, it is possible that he based his conclusion on a marked change of appearance at the pupal apolysis, together with shedding of the soil cover borne by the feeding larvae. Four instars have been suggested for Boreus hyemalis (Withycombe, 1922) and Hesperoboreus notoperates (Cooper, 1974), but the evidence is not conclusive in either case. Cooper (1974) measured known first-instar and last-instar larvae which had mean head-lengths of .32 mm and .68 mm, respectively. The principal uncertainty in his data was the identification of smaller larvae collected with the mature larvae in August and September as the penultimate instar; these were used to estimate a Dyar's constant of 1.29 for this species. This is probably correct, although it indicates that the duration of the last larval instar is almost a year in most boreines. I have not found head measurements sufficient for an instar analysis of H. brevicaudus larvae (Figure 50); any number from three to seven instars could be fitted into the data.

Early authors (Felt, 1896; Miyaké, 1913) erroneously predicted seven instars in Panorpa debilis and P. klugi, respectively, from applying Dyar's rule to the young larvae. These species were later found to have four instars (Byers, 1963).

Although the occurrence of three larval instars in Caurinus should be checked by rearing, the reduced number would not be surprising given the relatively large eggs of C. dectes. Further, should four larval instars be found characteristic of other Boreidae,

the duration of larval development in Caurinus is less than the duration of the first three larval stages in boreines.

The body length and width data in Table 16 represent only those larvae which appeared to have reached full growth in a given instar. These were recognized as stretched out and turgid in appearance (as in Figure 28). Some larvae of lesser growth were included to provide a larger sample. These data indicate that the very small Dyar's constants computed from head measurements are the result of negative allometry of the head versus the postcranial structures. The growth ratios based on maximum length and width for each instar all are near 1.3. This is near the growth ratio reported by Cooper (1974) for the head of H. notoperates larvae where such head-body allometry is not noticeable.

The dimensional growth ratios from Table 16 were used to estimate increase in volume, or weight, between instars. Since the shape of larvae at the end of an instar is similar between the three larval stages, the ratio of weight increase from the end of the first instar to the end of the third should be near the 5.6 value given here. With allowance for growth during the first instar, larvae could be expected to grow to 12 to 15 times the weight at hatching. Actual weights are available for diapausing eggs (mean weight .026 mg, N = 10) and for live adults early in the breeding season (15 November 1977) (mean weight: males .498 mg; females .677 mg). The egg weight is 4% that of the mature female, and 5% of the mature male. The discrepancy between these weights and the stated larval growth (12 to 15 times hatching weight) can be accounted for by the great increase in water content of the egg prior to hatching and by adult feeding and growth in weight.

Figure 49. Ranked head widths ($n = 66$) of Caurinus dectes larvae on a probability scale; $\bar{x}$ = mean head widths for L1, L2, and L3; $\odot$ = data points for pharate pupae.

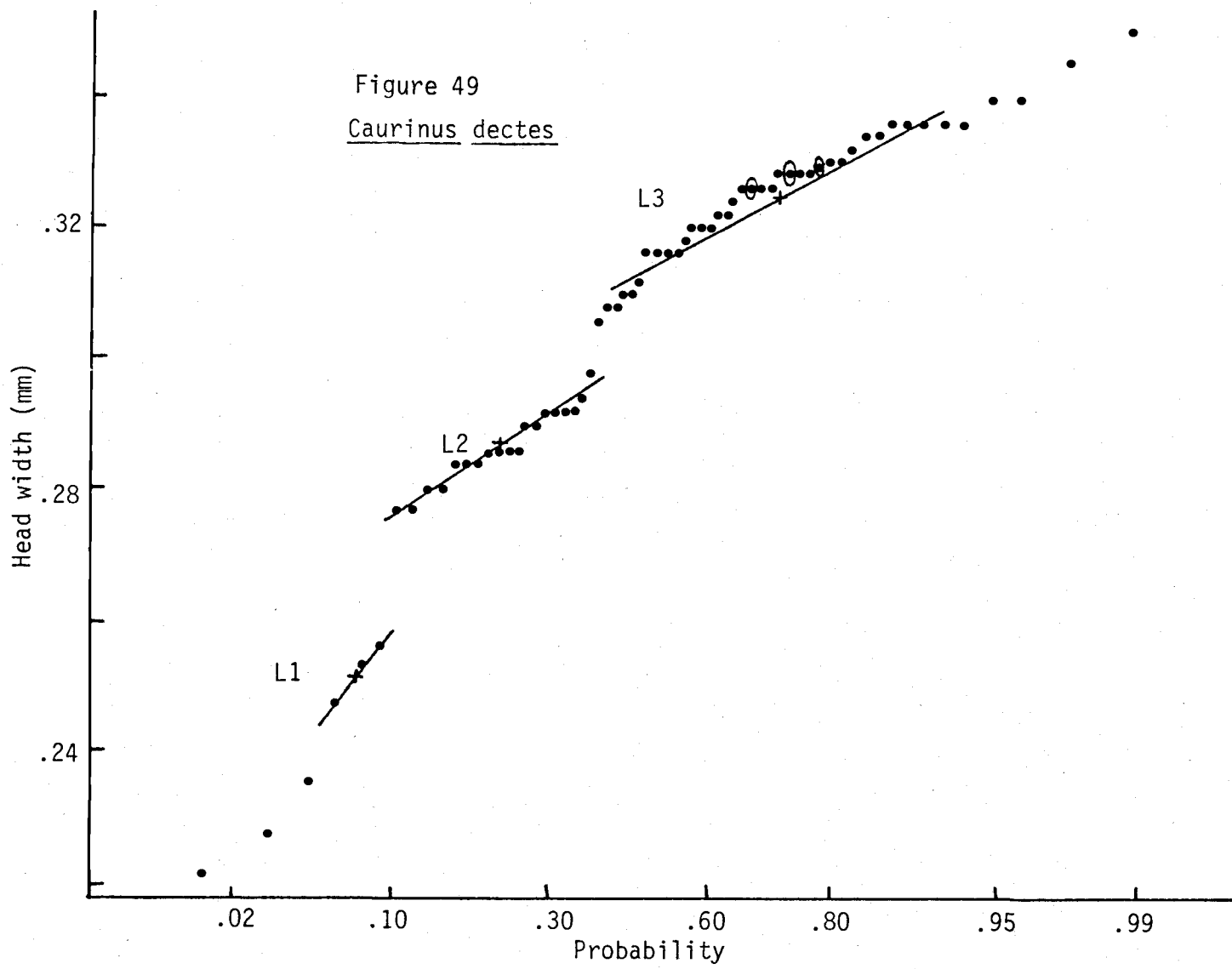


Figure 50. Ranked head widths ($n = 107$) of Hesperoboreus brevicaudus larvae on a probability scale.

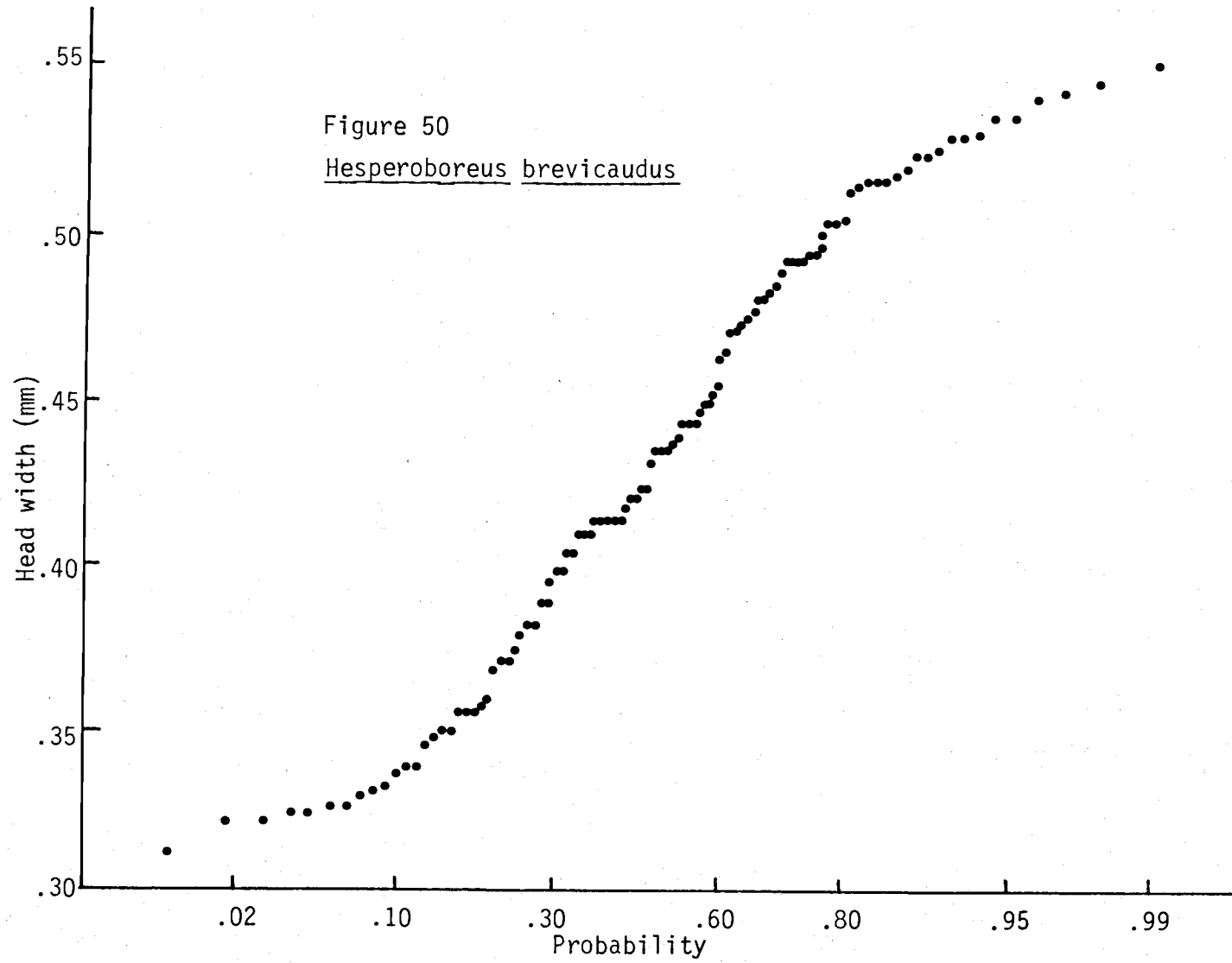


Table 16. Instar analysis of Caurinus dectes larvae, and growth parameters. (All measurements are in mm).

A. Data description for larval head width measurements.

Parameter	Instar grouping		
	L1	L2	L3
Number assigned	3	19	41
Mean $\pm$ standard deviation	.252 $\pm$.005	.287 $\pm$.006	.325 $\pm$.010
Range	.247 .256	.277 .298	.306 .350
Confidence interval of mean ($\bar{X} \pm (t_{.05} s_{\bar{X}})$)	.241 $\leq \bar{X} \leq$.263	.284 $\leq \bar{X} \leq$.290	.322 $\leq \bar{X} \leq$.328
Coefficient of variation	1.8%	2.1%	3.3%

Growth ratios (Dyar's constants) for head width of Caurinus larvae:

$$L2/L1 = 1.14 \quad L3/L2 = 1.13 \quad (L3/L1 = 1.30)$$

B. Growth parameters based on "fully fed" larvae of each instar (i.e., larvae appearing "stretched out")

Parameter	Instar grouping		
	L1	L2	L3
Number assigned	2	4	7
Mean body length (BL)	1.25	1.64	2.06
Mean body width (BW)	.36	.48	.65

Growth ratios (Dyar's constants) for trunk measurements of Caurinus larvae:

Body length (fed): $L2/L1 = 1.31$ $L3/L2 = 1.26$ ($L3/L1 = 1.64$)

Body width (fed): $L2/L1 = 1.33$ $L3/L2 = 1.38$ ($L3/L1 = 1.81$)

Estimated volume increase during instar (from volume $BL \cdot (BW)^2$)

during second instar: $V(L2)/V(L1) = 2.32$

during third instar: $V(L3)/V(L2) = 2.40$

Volume increase from end of first instar to end of third instar: 5.6 X

MORPHOLOGY OF THE PUPA

Twelve pupal specimens (5 males, 7 females), representing both pupae and pharate adults, were available for study. The description below is of the pupa prior to obvious signs of the adult apolysis. Notes are made of the development of adult features. It should be noted that some features of the pupal cuticle are most easily observed in specimens where retraction of the adult cuticle has occurred.

Description of the pupa of *Caurinus* *dectes*

The pupa closely resembles the adult of *C. dectes*, and specifically so in the general proportions of the head, thorax, and appendages.

Form: exarate, dectitious. Length 1.4 to 1.8 mm; width .50 to .61 mm. Color: cream white, eyes lavender to dark purple, mandibular teeth and articulation point brown. Surface glabrous, generally with sparsely pebbled texture. Body straight, apical segments of abdomen not upturned in female, slightly so in male.

Head free, large, .54 to .60 mm, with five pairs of long (80-90) setae: two pairs placed medially and laterally on vertex, one pair on frontal apotome above antennal base, one pair on frons below antenna. One seta on subgena above posterior mandibular articulation.

Head, antennae, and mouthparts otherwise without setae. Coronal and basal, divergent arms of frontal sutures present; epistomal suture complete; clypeolabral suture indicated laterally, obliterated at middle. Frons and vertex convex; labrum bilobed. Mandibles (Figure 53) large, functional, considerably exceeding labrum, distally thin (lateral view) with five teeth. Sheaths of maxillary palps as long as mandibles, with four evident segments; penultimate segment enlarged, apical segment small, conical. Maxillary endite and two-segmented labial palps smaller, not prominent. Antenna with scape and pedicel not clearly separated, with 14 flagellar articles distinct.

Thorax and legs similar to those of adult, meso- and metanota equal, simple. Mesothorax with wing-pads in female similar to adult in size and position; in male, wing sheaths lanceolate; costal margin arcuate, directed caudad, wing appressed to mesopleuron. Abdomen short, with tergum 1 and annular segments 2-8 about equal in length, slightly tapered apically. Apical segments in male with large ninth sternum (hypandrium); short, undivided gonopods; and upturned small, cylindrical proctiger. Female with segments 9 and 10 fused, conical. Small, cylindrical segment 11 flanked laterally by short cerci.

The pupa of Caurinus can be compared with more or less detailed descriptions of Panorpa nuptialis (Byers, 1963), P. falsa and Neopanorpa sauteri (Yie, 1951), Bittacus punctiger (Setty, 1940), Microchorista philpotti (Pilgrim, 1972) (Nannochoristidae), and Boreus brumalis (Williams, 1916). The chaetotaxy is not recognisable in detail in the two latter descriptions. I have examined pupae of Boreus (B. elegans or B. californicus), Hesperoboreus brevicaudus, Brachypanorpa oregonensis, and Apterobittacus apterus.

The most striking differences between the pupa of Caurinus and other boreid pupae are characters of the adult stage: the short rostrum and short, compact abdomen are among these. Boreine pupae have elongate rostra, while the corresponding region in panorpids is little more elongate than in Caurinus. However, adult panorpids have rostra of similar length to those of Boreus or Hesperoboreus. The pupal cerci of female Caurinus are inserted basolaterally on the eleventh segment, while those of female pupae in the Boreinae, Panorpidae and Panorpididae are as specialized as in the adults of those taxa.

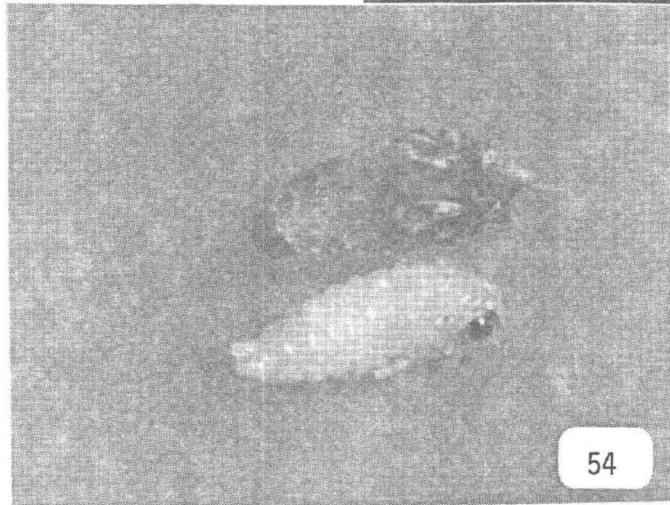
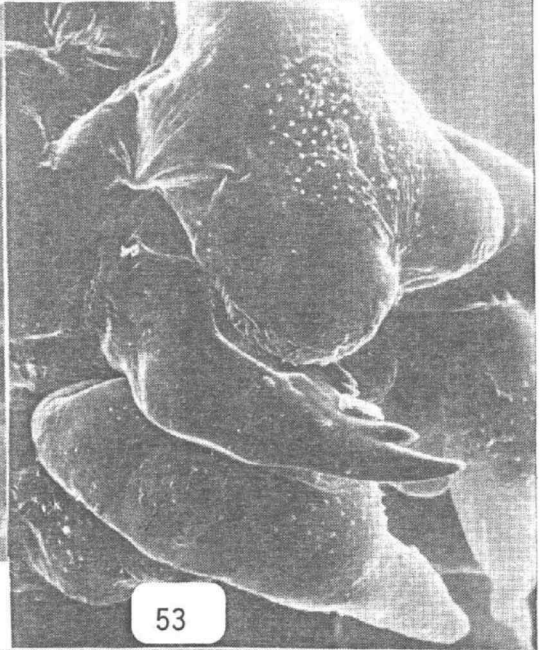
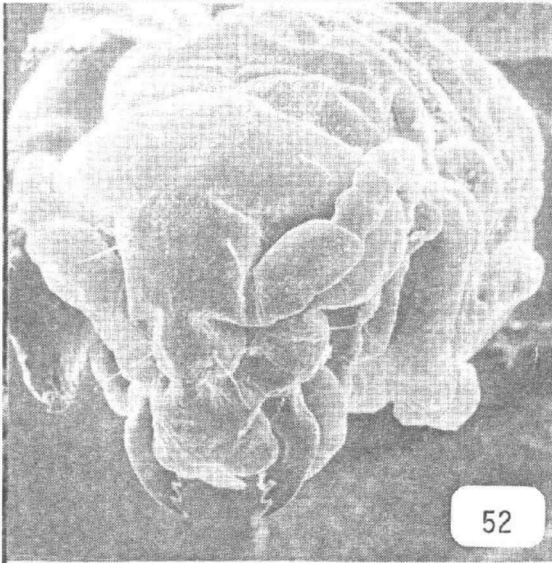
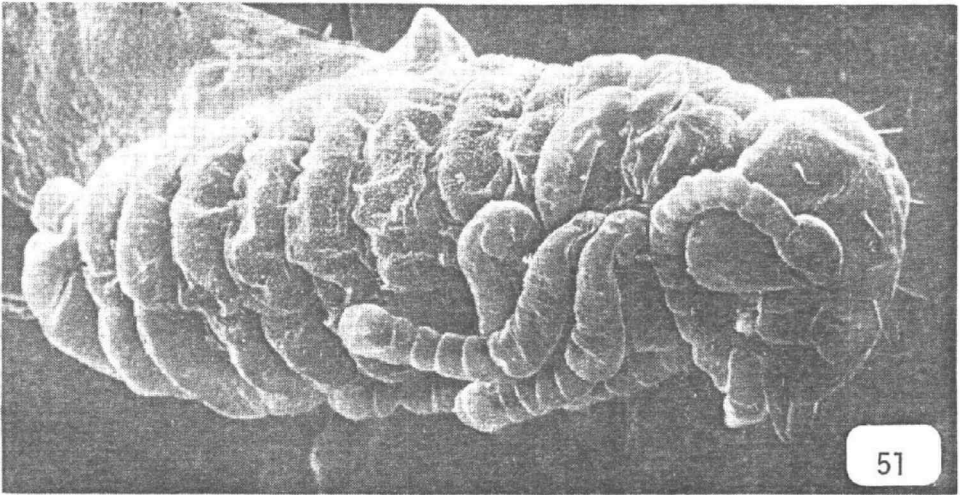
Characters specific to the pupal stage are chiefly those of the mandibles and of the chaetotaxy. The pupal mandibles of Caurinus differ from those of boreines in being wider in the basal half; this difference is related to the broad adult mandibles in C. dectes. The setae are greatly reduced in number in Caurinus pupae. Suspensory setae are present only on the head, there limited to four dorsal pairs of setae and one ventrolateral pair. All other known pupae of

Mecoptera have more extensive setation of the head, and have setae present on the thorax and abdomen, as well as on the second antennal segment. The loss of setae in the Caurinus pupa is presumably related to the small size of this species, since these long seta in Mecoptera and other groups with exarate pupae, function to suspend the pupa free from contact between its body surface and the wall of the pupal chamber (or cocoon). The body setae of the Boreus (elegans ?) pupae (body length 6 mm) are quite prominent, but those of H. brevicaudus (3 mm) are so short that they probably no longer constitute a suspensory system.

The chaetotaxy of the head of Caurinus pupae, although reduced, can be easily derived from the panorpid pattern (Yie, 1951). The pupal setation is relatively consistent among the Panorpididae, Panorpodidae, and Boreidae, and apparently also to the Bittacidae.

Figures 51-54. Pupa of Caurinus dectes.

- 51) Male pupa of C. dectes, lateral aspect (75X).
- 52) Male pupa of C. dectes, frontal aspect (112X).
- 53) Male pupa of C. dectes, detail of mouthparts, to show articulated mandible (280X).
- 54) Pupa of C. dectes (below) and intact pupal cell (above) washed free from Scapania bolanderi turf (25X).



ADULT MORPHOLOGY

The external morphology of adult Caurinus dectes is described in detail in the species description (Russell, 1979). The following discussion will describe the internal anatomy, which was not covered in the previous publication. In addition, the mouthparts and male and female genitalia are described in greater detail here in association with the functionally associated internal structures. The discussion of functional anatomy covers original and published data on related Mecoptera, and the evolutionary significance of these structural adaptations is addressed.

Internal anatomy - methods of study

Caurinus adults are difficult objects for dissection, due to their small size, lack of membranous areas, and hard, brittle exoskeleton.

The best dissections were those performed on live or freshly killed adults early in the season (September, October), before the females contained mature oocytes. The reproductive system and posterior portion of the digestive system could be studied by a method based on that described by Kamm and Ritcher (1972) for inspection of ovaries in beetles and leafhoppers. The abdomen was squeezed with one pair of forceps to press the retracted abdominal segments into view; the caudal segment was then grasped with another fine forceps and the end of the abdomen was pulled caudally. The ovaries and associated structures could frequently be pulled out intact in reproductively immature specimens. The best preparations were obtained by cutting away the abdominal cuticle after freeing the reproductive organs and hindgut. With care the major abdominal organs could then be exposed without damaging the midgut, or breaking the systems away from the forebody. In all specimens dissected by pulling out the posterior viscera, the ventral nerve cord was broken. The nervous system was therefore not studied intact.

The male internal genital structures broke away from the genital capsule when treated in the above manner. The best dissection method for this system required removal of the abdomen from the forebody and cutting the lateral abdominal cuticle with a fine scalpel inserted into the abdominal cavity.

The internal structures of the head and thorax were studied from sagittal razor blade sections of this region which were stained with 0.5% Congo red in 90 percent ethanol. Several specimens were also prepared for microtome sectioning, and some information on the organization of the internal structures was gained in this way. For this procedure, specimens were killed in Brasil-Bouin's fixative, washed in 70% ethanol, and transferred through absolute ethanol, toluene, and paraffin oil, to be embedded in Paraplast wax (melting point 56-57°C). Sections were cut at 6 μ , and stained with Delafield's haematoxylin and Eosin Y (Galigher and Kozloff, 1971).

Internal anatomy of adults of *Caurinus* *dectes*

The most extensive review of the comparative anatomy of adult Mecoptera is given in Kaltenbach (1978). This is based largely on the work of Potter (1938a) on the gross structure of the digestive tract, nervous system, internal reproductive organs, and associated structures; and by Hepburn on the proventriculus (1969a), and on the skeleto-muscular system of the head (1969b) and thorax (1970). Potter studied eight genera of Mecoptera, representing six families, while Hepburn studied specimens of the nine families presently recognized in this order (Byers, 1965).

More detailed anatomical and histological descriptions are given by Grell (1938, 1942) for the gut and reproductive system, Hasken (1938, the thoracic muscles) and Heddergott (1938, the head and foregut), all of these dealt with *Panorpa communis* only.

The morphology and histology of sex pheromone secreting glands have been described in males of *Harpobittacus* by Crossley and Waterhouse (1969) and in *Panorpa* and *Brachypanorpa* by Thornhill (1973).

The only comparative studies of internal structures within the Boreidae are the accounts of the male and female reproductive systems by Cooper (1940, 1974).

The following account generally considers only the gross structures of Caurinus dectes, and most comparative statements are keyed to the corresponding descriptions of boreids by Potter (1938a) and Cooper (1974).

The digestive system

The salivary (labial glands (Figure 56): These are simpler in structure than in most of the Mecoptera described by Potter (1938a). The short common salivary duct extends from the anterior surface of the labium almost to the cervix, where it divides into the two lateral ducts. The lateral ducts lie to either side of the esophagus; they extend into the second abdominal segment, where each divides into three glandular branches. Two branches continue caudad along the lateral wall of the midgut. The dorsal branch of the salivary gland is recurved anteriorly into the thorax and lies alongside the salivary duct. The salivary glands of Caurinus are relatively shorter and thicker than those of Boreus hyemalis and also differ in their irregular branching, the apparent lack of a reservoir on each lateral duct, and the shorter common duct; they are otherwise closely comparable. There is no apparent sexual dimorphism, as occurs in the Panorpidae (Mercier, 1915).

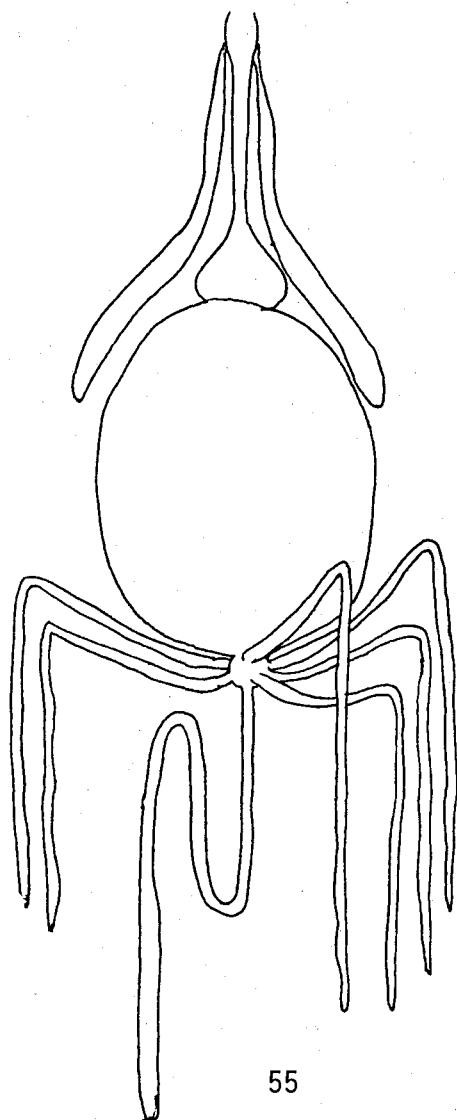
The foregut (stomodeum): The pharynx has been observed only in longitudinal razor-blade sections, which did not permit observation of the muscular attachments. The lumen is widest posterior to the nerve ring; the ventral wall is somewhat sclerotized and the dorsal wall is membranous. The esophagus is narrow (outside diameter, 40μ) and elongate, extending through the thorax from the caudal surface of the head.

The proventriculus is located in the metathorax and first abdominal segment; it is a rounded, caudally truncated cone, 170μ

Figures 55, 56. Digestive system of Caurinus dectes.

55) Alimentary tract of female, with salivary glands and malpighian tubules.

56) Left salivary gland, in lateral aspect.



wide and 150μ long. The walls are thick and muscular, and the interior surface is densely lined with fine cuticular spines or "acanthae" (Richards and Richards, 1969). The acanthae form an unusual filtration-valve which is found in all families of Mecoptera (Hepburn, 1969a). The shape of the acanthae in Caurinus conforms to the "boreid type" which Hepburn found only in the three Boreus species studied. However, the basis of Hepburn's acanthal types is the distribution of meso- and endocuticle, which I did not observe in Caurinus.

The midgut (mesenteron): The proventriculus is joined to the midgut through the five-lobed cardiac valve, which extends caudally into the midgut lumen. The midgut is a short, broad sac. Its external surface has a rather conspicuous irregular polygonal pattern formed by a network of pale lines; these meshes are about 100μ to 150μ in diameter. In males the midgut, when engorged, is almost spherical (about .65 mm in diameter) and occupies most of the anterior half of the abdominal cavity. The midgut is usually a more elongate shape in female Caurinus; the observed dimensions range from 400μ X 600μ when nearly empty, to 650μ X 900μ in a distended midgut. The internal epithelium of the midgut is a layer of large, cuboidal cells, arranged in a hexagonal pattern. Crypts of regenerative epithelial cells, which are numerous in the midgut of Panorpa communis (Grell, 1938), are generally absent in sections of the midgut of Caurinus. Regenerative cells were present in a ventral fold near the pyloric valve.

The muscular investment of the midgut of Caurinus is principally composed of transverse and oblique fibers. A peritrophic membrane is absent, as in other Mecoptera (Hepburn, 1969a). A few cell wall fragments were found in the fluid midgut contents of one C. dectes, which had fed on Scapania bolanderi. Other specimens which had fed on liverworts had fluid or semisolid gut contents composed entirely of cell contents. Hepburn (1969a) reported that the Mecoptera typically form a solidly packed food bolus in the midgut (except for the Nannochoristidae, which have reduced mouthparts and

probably do not take solid food as adults). Such boli are apparently not formed in Caurinus.

Hindgut (proctodeum) and malpighian tubules: The narrow, cylindrical hindgut is sharply set out from the sac-like midgut. Short, lamellar structures project from the pyloric attachment into midgut; although these resemble a valvular structure, I am not sure that the lumen is continuous from midgut to hindgut. The pyloric region of the hindgut (Figure 61) is short and slightly enlarged where the six malpighian tubules open on the gut. The distal end of the malpighian tubules lie along the rectum; a loop of each tubule reaches anteriorly along the posterior wall of the midgut. The malpighian tubules are reddish-brown for most of their length, but are colorless near their point of origin.

The regions of the hindgut are only weakly differentiated. The ilium, about 0.6 mm long, is very narrow ($30-40\mu$). The transition to the rectum is marked only by a noticeable increase in diameter (to $50-70\mu$). The rectal glands, which are characteristic of all previously investigated Mecoptera except Boreus, are also absent in Caurinus. The entire hindgut is about 1.5 mm, and is coiled about twice, lying with the malpighian tubules against the dorsal surface of the midgut. A short terminal section of the hindgut is slightly narrowed as it near the anus. The solid material in the hindgut resembles, and may be completely derived from, the contents of the malpighian tubules.

Since very little solid, indigestible material reaches the midgut of adult Caurinus, there would be little fecal material whether the pyloric connection is, or is not, functional. Any solids entering the gut could be removed by "back-flushing" with selective filtering through the proventriculus, and the production of green stains on the substrate by feeding adults apparently indicates frequent regurgitation. The mechanism for the elimination of large quantities of clear liquid from the anus cannot be specified on structural grounds. It can be assumed that the malpighian tubules or the hindgut, or both, regulate the composition of the hemolymph by production of hypotonic

urine, when excess water enters the midgut. Gerson (1973) suggests the same mechanism to explain the tolerance of Ledermuelleria (a moss-feeding stigmaeid mite) to prolonged immersion in water.

The central nervous system

The brain and ventral nerve cord are similar in form to that described for Boreus hyemalis (Potter, 1938a). The brain is transverse, with well-developed optic lobes and inconspicuous antennal lobes. The paraesophageal connectives are short and very broad, and the subesophageal ganglion is large and rather elongate. The connectives between the subesophageal and prothoracic ganglia, and between the abdominal ganglia are closely appressed and appear fused.

The three thoracic ganglia are large and nearly coalesced, especially the meso- and metathoracic ganglia. There are six abdominal ganglia in female Caurinus; the first five are of equal size, while the sixth is about twice the size of the others. The first abdominal ganglia is separated from the metathoracic ganglion only by a constriction; the remaining connectives are distinct, but short, so that the ganglionic chain resembles a beaded string. In male C. dectes the large last abdominal ganglion is teardrop-shaped rather than oval, and is almost fused to the next anterior ganglion. The number of abdominal ganglia was not established and may be 6 or 7 in male Caurinus. There are seven abdominal ganglia in both sexes of B. hyemalis. In other Mecoptera there are usually seven free ganglia in the male and six in the female; male and female Merope tuber possess eight and seven respectively.

The shortening and fusion of the connectives make the ganglia of the central nerve cord of Caurinus more concentrated than any other known mecopteran. This can be attributed to the very compact body shape of Caurinus, and especially to the very short thoracic region, which has crowded the large thoracic ganglia together.

The stomadeal sympathetic nervous system, including the frontal ganglion, recurrent nerve, and associated structures, was described

for most of the Mecoptera studied by Potter. I have not studied this system in Caurinus.

The male reproductive system

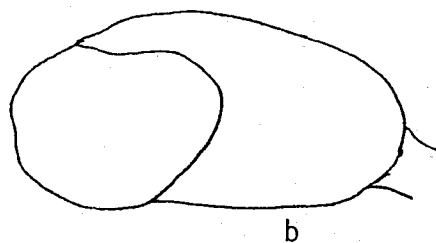
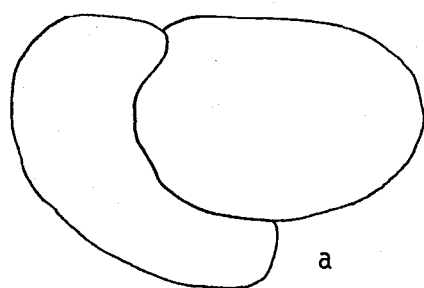
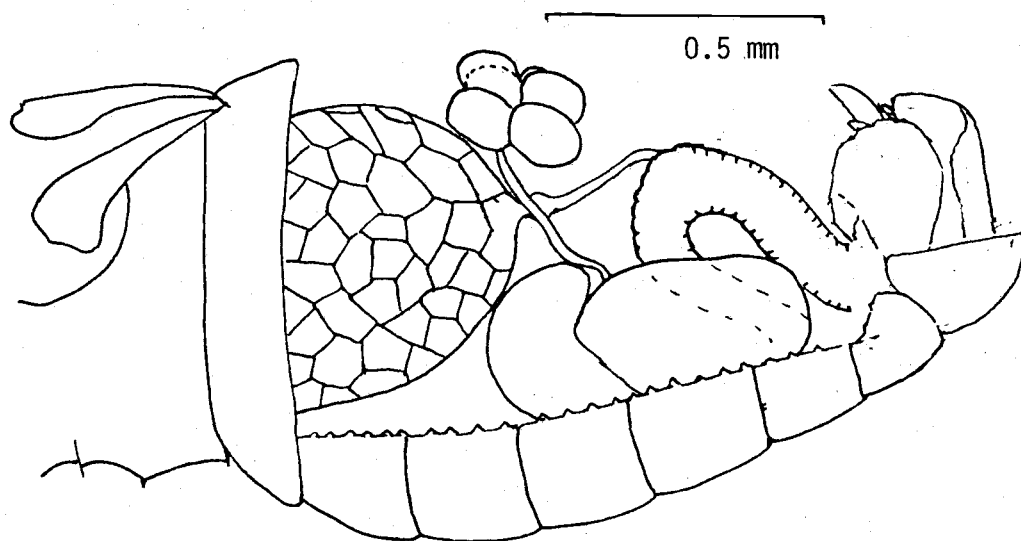
The internal genitalia of male Caurinus (Figure 57, 58) are similar in organization to those of other boreids (Potter, 1938a; Cooper, 1972). The testes are united and lie embedded in fatty tissue on the dorsal midline of the abdomen. There are six lobes (follicles) in the conjoined testes. The two vasa deferentia loop around the hindgut and each joins one of the large, paired accessory glands at its mesal surface at midlength. Each accessory gland is an elongate ellipsoid with a large, laterally compressed cap enveloping its anterior pole. The main part of the accessory gland and the anterior lobe (cap) are each coated by a tough membrane. The anterior lobe contains a long, greatly looped duct, which is probably a prolongation of the vas deferens. The large lumen of the main lobe of the accessory gland contains a highly refractive, light blue material, which hardens soon after exposure to air or tissue fixatives. This material evidently forms most of the spermatophore.

The accessory gland opens by a very short, broad lateral ejaculatory duct into the large, muscular, U-shaped median ejaculatory duct. The male reproductive tract of Boreidae, including Caurinus, is very different in structure from other Mecoptera; this is undoubtedly related to the occurrence of spermatophores in this family only.

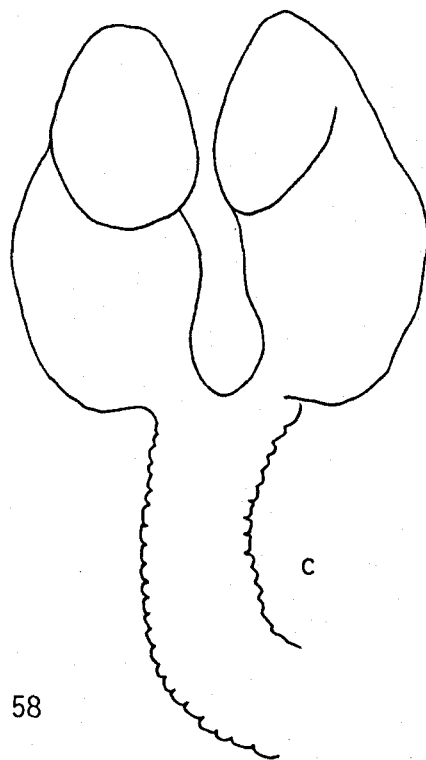
The reproductive tract of male Caurinus is generally similar to that of the Boreinae. The three lobes per testis and close association of the testes, are characters falling within the range of variation among species of the Boreinae. There are one to five follicles per testis in Boreus, and four lobes per testis in Hesperoboreus. The accessory gland of Caurinus are most similar to those in Hesperoboreus; both of these genera lack a basal lobe which occurs in Boreus. Caurinus differs from the Boreinae in the less differentiated calyces

Figures 57, 58. Male genital system of Caurinus dectes.

- 57) Dissection of abdomen of male C. dectes, showing position of midgut and male genital structures.
- 58) Male accessory glands, a) lateral aspect; b) dorsal aspect; c) ventral aspect.



0.5 mm



of the testes.

The female reproductive system

This system is most conveniently studied in teneral adults. Within a few weeks after adult emergence the reproductive system is greatly distorted by the very large mature oocytes. The ovaries (Figure 84) each are composed of four ovarioles which originate close together on the lateral oviduct. Four to ten apparently panoistic egg chambers can be recognized in each ovariole. The germarium and associated tissue taper to a thin strand. The ovarioles of each ovary are usually separated apically; the apical filaments are often parallel, and lie dorsal to the midgut and malpighian tubules.

The lateral oviducts merge in the short broad oviduct; the sixth abdominal ganglion is closely attached to the crura of the oviducts. The spermatheca is reniform, without lateral lobes, and lies ventral to the ovaries. The spermathecal duct is about five times the length of the spermatheca and lies tightly coiled between the spermatheca and common oviduct. The spermathecal duct enters the common oviduct some distance anterior to the genital opening. That portion of the oviduct distal to the spermathecal duct has been termed the vagina (Potter, 1938a). A large (up to 0.45 by 0.35 mm) paraboloid sac enters the oviduct caudal to the spermathecal duct; this structure, often containing loose, granular material, may be the accessory gland or a glandular reservoir.

The ovariole number in Caurinus (invariably four) is the least recorded for Mecoptera. Females of Hesperoboreus notoperates have six ovarioles per ovary, while the number varies from seven to ten in Boreus (sometimes within a single species). The ovariole number in other Mecoptera varies from seven to ten in the more primitive families (Meropeidae, Choristidae) to as many as 14 in Panorpa and 14 to 19 in Apterobittacus apterus. The large, oblong spermatheca and elongate duct of Caurinus are similar to those of Boreus and most other Mecoptera, but are unlike the peculiar many chambered, almost sessile

spermatheca of Hesperoboreus. All other Mecoptera have paired, tubular accessory glands emptying into the oviduct by a short common duct, although Panorpa communis females have a small median saccate gland in addition to the paired structure. The structure in Caurinus is most probably formed by a fusion of the paired glands, however.

The ovarioles of Caurinus are stated to be panoistic on the basis of their resemblance to those of Boreus (Cooper, 1940), from examination of whole slide mounts and transverse serial sections of the female. They are definitely not polytrophic, as are those of Panorpa (Ramamurty, 1967), and Bittacus (Setty, 1940), and presumably all Mecoptera other than the Boreidae.

Among holometabolous insects, only the Boreidae and Siphonaptera are known to have panoistic ovaries. Heming (1977) infers from the distribution of ovarian types among the insect orders that the Siphonaptera, and possibly the Thysanoptera also, have secondarily regained the panoistic type. (Heming was apparently unaware of the occurrence of panoistic ovarioles in Boreidae.) The evolutionary success of the orders with meroistic ovarioles may have been contributed to directly by their ability to grow oocytes faster and in greater numbers than those with panoistic ovarioles, because of the greatly increased amount of template DNA in the polyploid nuclei of the nurse cells.

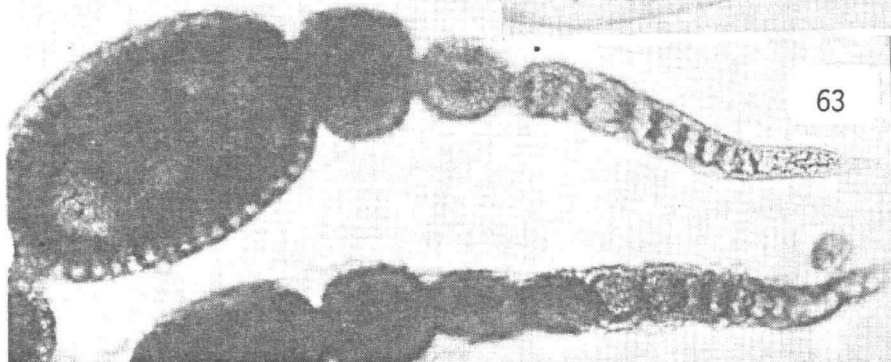
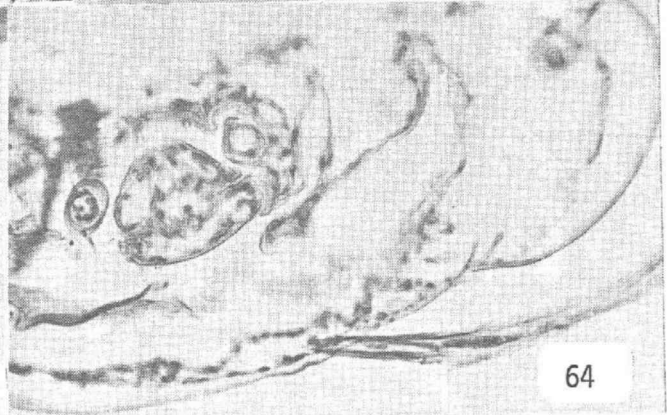
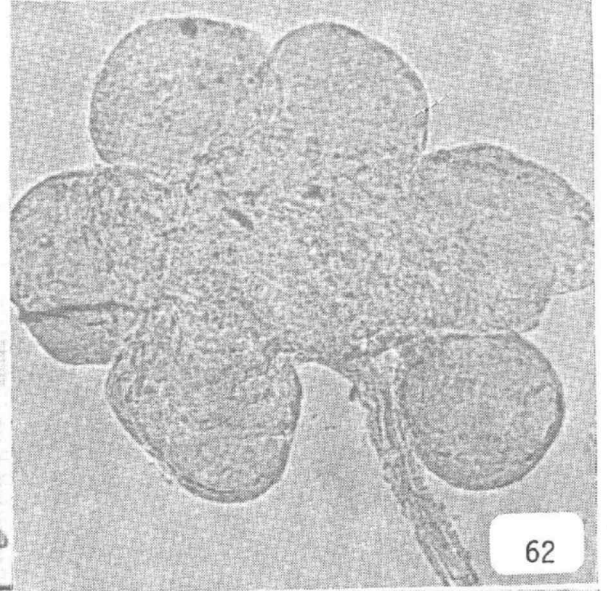
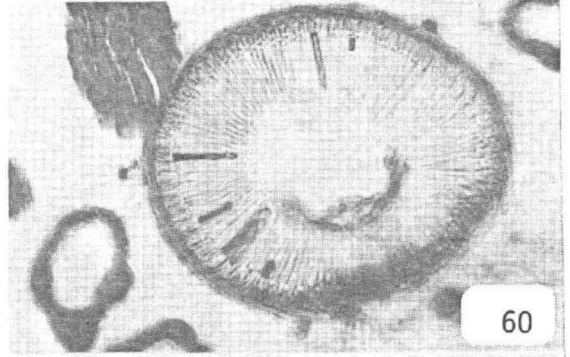
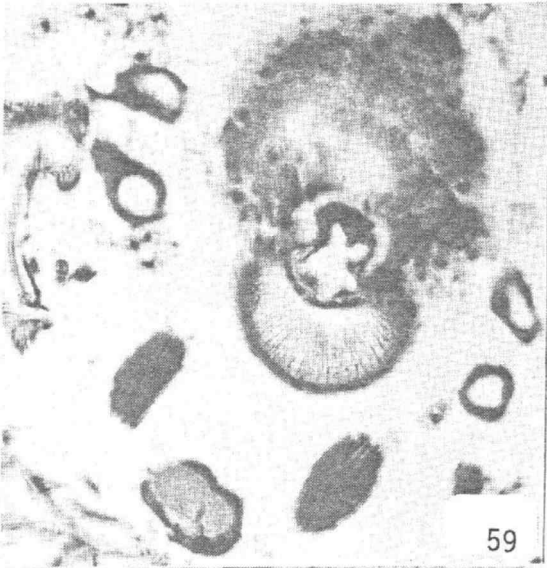
In contrast, the regaining of panoistic ovarioles in boreids might be explained by the peculiarities of their life cycle, with reproduction constrained by low nutrient availability, low temperature, and occurring over an extended season. If panoistic ovarioles in Boreidae are a derived rather than primitive trait, the sharing of this trait with the Siphonaptera becomes more significant. The question of any relationship between Boreidae and Siphonaptera will be reviewed later.

Tracheal system

There are eight pairs of functional spiracles in adult Caurinus. The mesothoracic spiracles are inserted in the posterior fold of

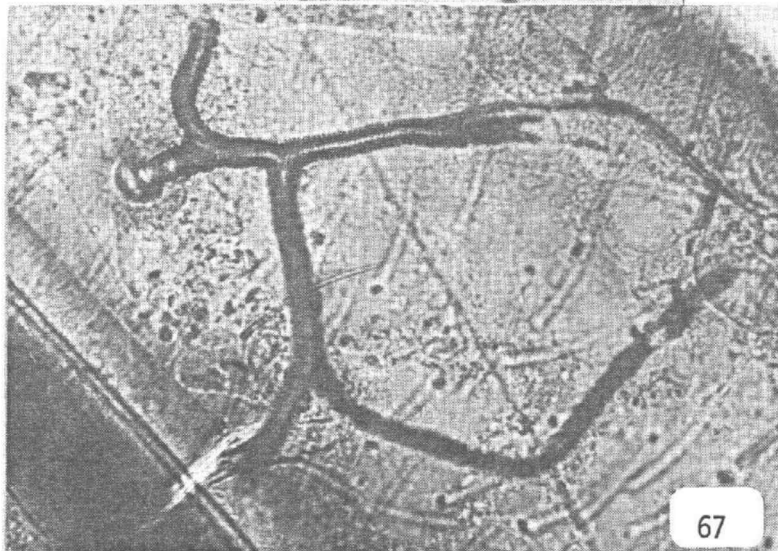
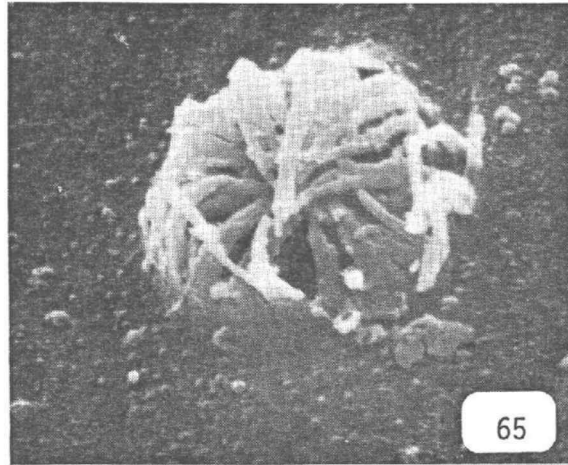
Figures 59-64. Internal structures of adult Caurinus dectes.

- 59) Oblique cross-section of female C. dectes at level of metacoxae, showing juncture of proventriculus and midgut (160X).
- 60) Section of proventriculus, showing acanthae (250X).
- 61) Junction of midgut and hindgut, with proximal and distal segments of malpighian tubules (whole mount, 250X).
- 62) Conjoined testes showing six lobes, and one vas deferens; the other vas deferens is torn away. Whole mount, distorted by compression (250X).
- 63) Two ovarioles of C. dectes. The most basal oocyte of each is visible (160X).
- 64) Cross-section of terminal segments of abdomen of female C. dectes, showing invaginated segments and cerci (160X).



Figures 65-67. Tracheal system of adult Caurinus dectes.

- 65) Spiracle of third abdominal segment in male C. dectes, external aspect (5600X).
- 66) Cross section of mesothoracic spiracle of female C. dectes, showing external filter, atrium, and principle trachea (250X).
- 67) Fourth abdominal spiracle of male C. dectes, internal aspect, with major tracheal connections (400X).



the pronotum, the remaining spiracles are in the terga (or segmented rings) of abdominal segments 2 to 8. The small, closed metathoracic and first abdominal spiracles are also evident. All functional spiracles are circular and protected by converging cuticular processes externally (Figure 65). The spiracular stria are also lined with fine hairs. The atrium is constricted at its juncture with the trachea; a very fine muscle inserts at this point in the abdominal spiracles (Figure 67). The contraction of this muscle closes the spiracle, apparently opposed by elastic forces. The closing mechanism of the mesothoracic spiracle was not observed in Caurinus.

Most adult Mecoptera are holopneustic. The two thoracic and first abdominal spiracles are usually large and slit-like, with an external closing apparatus. The remaining abdominal spiracles in most families are small and oval; frequently all spiracles are located in the pleural membranes (Kaltenbach, 1978).

The Boreidae and Apteropanorpidae differ from this pattern in the incorporation of the mesothoracic spiracle in the pronotum, and lack of external lips closing the thoracic spiracles. This similarity is presumably convergent, resulting from reduction of membranes in these flightless mecopterans.

The spiracles in Caurinus are further modified from those of Boreus and Hesperoboreus only in the reduction of the first abdominal spiracle. This is second in size to the mesothoracic spiracle in Boreines, but is closed and non-functioning in Caurinus.

In Panorpa, the closing mechanism of the thoracic spiracles includes a single occlusor muscle, while there are two occlusor muscles for each abdominal spiracle (Hassan, 1944). Hepburn (1970) stated that "those families which lack the normal external lids and in which the spiracles are firmly imbedded in the nota (Boreidae and Apteropanorpidae) also lack occlusor muscles". However, Fuller (1955) demonstrated the presence of single occlusor muscles on both the mesothoracic and first abdominal spiracles of Boreus westwoodi. These are similar in arrangement to those observed on the abdominal spiracles of Caurinus.

The tracheal system was observed in fresh specimens of Caurinus dissected in glycerine. Several large tracheae radiate from the mesothoracic spiracle into the thorax, and two of these on each side pass into the head.

The abdominal trachea are not enlarged into air sacs, and there are no pronounced longitudinal tracheal trunks. Fine ventral commissures connect each pair of abdominal spiracles, while an anterior branch from each tracheal base joins the next interior spiracle (Figure 67). There are no evident specializations in the tracheation of the abdominal viscera; the tracheal knots associated with the rectal papilla of most Mecoptera are absent in Caurinus as in Boreus hyemalis (Potter, 1938a).

THE SKELETOMUSCULAR SYSTEM

The external morphology of adult Caurinus dectes was described in considerable detail in the species description (Russell, 1979). My present account does not repeat, in full, descriptions of structures covered adequately in the previous paper.

Emphasis is given in the following account to the skeletal elements of the mouthparts and genitalia in greater detail than was possible when the paper describing Caurinus was prepared. The musculature of the mouthparts, and of the thorax (in part), is discussed for the first time. The skeletomuscular systems of the mouthparts and thoracic appendages are considered in a functional context. Finally, this discussion encompasses many comparisons of the anatomical data for Caurinus with that known for other boreids, and for the Mecoptera as a whole. These comparisons are possible because of several recent comprehensive studies of structural variation within the Mecoptera; most of this information is reviewed by Kaltenbach (1978).

The head

The head and mouthparts of adult Mecoptera were studied by Otanes (1922; cuticular structures only) and by Hepburn (1969b; skeleto-muscular system). Within the Boreidae, Penny (1977) noted the distribution of some superficial characters of the head and mouthparts of species of the Boreinae. Each of the authors mentioned apparently based their description of the mouthparts of Boreidae on a single species of Boreus. Since I have noted considerable variation of the mouthparts among species of Boreus and Hesperoboreus, I have attempted to verify through observation, all comparisons of this system for Caurinus and the Boreinae.

The head of Caurinus dectes contrasts greatly with the boreines in its "normal" proportions for a mandibulate insect. In this sense, whether primary or not, Caurinus approaches the generalized condition

for insects more closely than any other mecopteran. Caurinus is unusual among the Mecoptera in its highly convex vertex and frons, the deeply impressed epistomal suture distant from the ventral eye margins, the laterally placed antennal sockets which lack exposed membranes; the strongly carinate postorbital ridges, and the absence of a prominent subgenal process. The rostrum, comprising the clypeolabral region and the ventral mouthparts (maxillolabial complex), is very short in Caurinus. These rostral structures are more elongate in other Mecoptera, including other genera with short rostra.

The dorsal cranial sutures, including the ecdysial cleavage line (epicranial suture) and the temporal sutures are absent in Caurinus adults. The subantennal (or frontogenal) suture is recognizable as a depressed line in some specimens, but there is no suture or apodeme on this line. As a result, the occiput, vertex, frons, and genae cannot be bounded precisely. A reduced epicranial suture is present in Panorpidae, Panorpididae, and Choristidae, while subantennal sutures are present in Panorpidae, Panorpididae, Meropeidae, and Boreidae. The temporal sutures bound the occiput laterally in other Mecoptera with the exception of Nannochoristidae and Bittacidae (Hepburn, 1969b), and they apparently are homologous with similar sutures occurring in the Micropterygidae (Lepidoptera) and Rhyacophilidae (Trichoptera) (Issiki, 1933). The temporal sutures are well-developed in the larva of Caurinus (page 139), as they are in most other mecopteran larvae.

In contrast to the dorsal sutures, the sutures of the oral region are well developed in Caurinus. The epistomal, subgenal, clypeogenal, and clypeolabral sutures are all visible both as external inflections and as internal ridges. These sutures are variable in other Mecoptera. The epistomal suture is difficult to trace externally in most genera, while the clypeolabral suture is otherwise unknown in adult Mecoptera. The subgenal suture in Caurinus is nearly horizontal through its length. In most other Mecoptera, this suture is strongly descending at its posterior end; in these genera the subgenal and occipital sutures are confluent at the apex of the subgenal process.

The only cranial sclerites which require detailed discussion are those of the clypeolabral and subgenal regions. The sutures of this region are complete and well defined. The shape and arrangement of the rostral sclerites differ from other Mecoptera however. In all other Mecoptera, the clypeus is evidently constricted at the anterior mandibular articulation. Some workers, including Heddergott (1939) and Denis and Bitsch (1973) have considered the clypeus to be subdivided into an anteclypeus and postclypeus at this line. In Caurinus, the short clypeolabral region is evenly convergent from the base of the mandibles to its broadly emarginate apex. The suture line termed the clypeolabral suture here alternatively can be interpreted as an intraclypeal suture, as there is a large transverse membranous lobe inserted distally and internally to the sclerotized clypeolabrum. This lobe is normally almost completely concealed by the clypeolabrum, but its course distad can be discerned by manipulation of dissected specimens. If my identification of the clypeolabral suture is correct, the labium is basally defined by the suture, and is immovably fused to the clypeus. The membranous lobe must then be identified as a modified fold of the epipharynx. This movable lobe is equivalent to the membranous lobes on the lateral margin of the clypeolabrum of many Mecoptera, including Boreus and Hesperoboreus. Similar lateral labral membranes are found in Tipula reesi (Diptera), where the clypeolabral suture is well defined (Rees and Ferris, 1939).

These lateral lobes are absent in the Panorpididae and Bittacidae. The basal boundary of the labrum in Mecoptera was believed to be the constriction between the mandibular bases by Otanes (1922) and Miyake (1913). However, Issiki (1933) and Hepburn (1969b) limit the labrum to the lateral membranous lobes distal to the clypeolabral apodemes (tormae) and displaced laterally by the ventral extension of the clypeus. Heddergott (1939) recognized the same lateral basal limit for the labrum of Panorpa communis, but indicated that the median area of the labrum is concealed by the clypeal extension. The membranous lobes of Boreus appear to lack such a median fold.

Although the precise interpretation of the labral base is in doubt in Caurinus and in other Mecoptera, it should be noted that this suture is continuous with the clypeolabral apodemes. The suture, whether the primitive clypeolabral suture or a new structure, is found in no other Mecoptera.

The free lobe of the epipharynx (labrum) is supported by 10-16 fine rods, each ending in an apparently sensory structure. The epipharynx lacks the two or four large sclerotized rods occurring in its oral surface in Panorpidae and Boreinae. The prominent round sensory pits of the epipharynx of a number of Mecoptera are also lacking.

Cranial endoskeleton

The endoskeleton of the head includes the robust corporatentorium which, through reduction of the posterior arms, divides the occipital foramen. The anterior tentorial arms are robust at the base, but could be traced less than half the distance to the corporatentorium. Short dorsal processes originate near the base of the anterior arms.

The "Apodemalwalze" (Heddergott, 1939) peculiar to the Mecoptera, appears to be completely absent in Caurinus. This structure, which is present but somewhat reduced in Boreus, is formed by involutions of the cuticle near the mandibular bases, and is a sclerotized bridge joining the sclerotized ventral pharyngeal wall.

The mandibles

The shape and dentition of the mandibles of Caurinus were emphasized in the species description (Russell, 1979). The mandible (Fig. 68) is unusually short and broad in frontal aspect for a mecopteran, while the three long, sharp teeth could be taken (falsely) to indicate raptorial habits in Caurinus. The mandibles are also broad at the base in lateral view; the hypocondylar and epicondylar articulations

are both well developed. The epicondyle articulates with a heavily sclerotized involution of the clypeus; the hypocondyle is articulated with a short process of the postgena.

Both the adductor and abductor tendons of the mandibles are large, the adductor tendon is folded with a corresponding division of the adductor muscles. However, all adductors are tergal in origin, arising on the vertex, postgena, and frons. A clypeo-apodemal adductor (Hepburn, 1969b) was not observed; tergal adductors originate on the vertex.

The form and articulation of the mandibles in Caurinus are of great interest, in view of Mickoleit's (1971) description of apparent synapomorphic characters in the basic structure of the mandibles of Mecoptera and primitive Diptera. According to Mickoleit, the sister-group relationship of these orders is supported by the occurrence in each of flattened, "leaf-shaped" mandibles with a greatly reduced anterior mandibular articulation and the posterior condyle articulating with a long, slender subgenal "pillar". Although the blade of the Caurinus mandible is thin, the well-developed articulations are similar to the usual state in mandibulate insects. The firm articulations are presumably required to allow a close, precise shearing action of the molar blades.

The maxillae

The skeletal elements of the maxillae and labium are fused together basally in Caurinus as is the case in Boreus and Hesperoboreus. The maxillolabial structures of Caurinus dectes, Hesperoboreus brevicaudus, and Boreus elegans are shown in caudal view in Figures 71-73. In all three genera the stipes are fused at the midline, probably incorporating labial elements; this composite structure is the zygostipes. The boreid zygostipes is linked to the postgenal bridge by the medially approximated or fused cardines. The distal lateral angles of this sclerite are prolonged in an anteriorly curved process (the galea?) supporting the posterior and lateral surfaces of the

maxillary endites.

In Caurinus, the zygostipes is transverse and lacks a median suture. A conspicuous apodeme extends obliquely basad from the mesal margin of the sclerotized "galea" lobes on each side. In this genus, the cardines are separate, very slender sclerites. In Boreus and Hesperoboreus the cardines are fused together as an oval or quadrate sclerite. In some species, the line of fusion is evident as a median suture or an emargination of the distal margin. The elongate zygostipes of boreines have a prominent median longitudinal apodeme, in Boreus or in Hesperoboreus, a Y-shaped suture with the stem doubled along the line of fusion of the stipites.

There are two apical maxillary lobes in Caurinus (Fig. 74,75). The membranous mesal lobe appears to be the lacinia, while the larger outer lobe, supported laterally by the stipital extension, would be the galea. However, the homologies of the maxillary endites in Mecoptera are less straight-forward when the maxillae of the Panorpidae are considered. In Panorpa, there are two main apical lobes, obviously equivalent to the division in several other families. In addition, however, at least some Panorpa species have a very small, membranous lobe on the mesal basal margin of the apparent lacinia (Issiki, 1933; Heddergott, 1939). Both Issiki and Otanes (1922) believed that this rudiment represented the lacinia, and that outer two large lobes were a subdivided galea. This does not seem supportable, since the smaller mesal lobe is completely absent in the more generalized maxillae of Panorpodes (Heddergott, 1939) and Brachypanorpa. Since the apodemal framework usual in Mecoptera is completely absent in Caurinus, it is best to assume that the mesal, smaller lobe is the lacinia. The absence of this lobe in Boreus and Hesperoboreus implies that the lacinia has been lost, or fused with the galea, in the Boreinae. Hepburn (1969b) stated that the Boreidae, along with the Choristidae and Panorpididae, have both apical lobes, although these are "shorter" and with "more fusion of the lobes" than in Notiothauma, Merope, and Apteropanorpa. Hepburn gave no indication of his criteria for separating the galea and lacinia in Boreus. The division recognized

by Otanes (1922) between the outer "triangular plate" and the inner membranous, setiferous lobe is obvious, but it seems likely that the membranous lobe is a composite structure. The apodemes associated with the lacinial tendon used to recognize the apical lobes in other families occur in Boreus, but are modified in association with the prominent maxillary spines in this genus. By contrast, in Hesperoboreus, the lacinial tendon cannot be traced and the spines are inserted in an elongate sclerite. These spines are peculiar to the boreines, and are not found on the maxilla of Caurinus, or of any other Mecoptera.

The labium

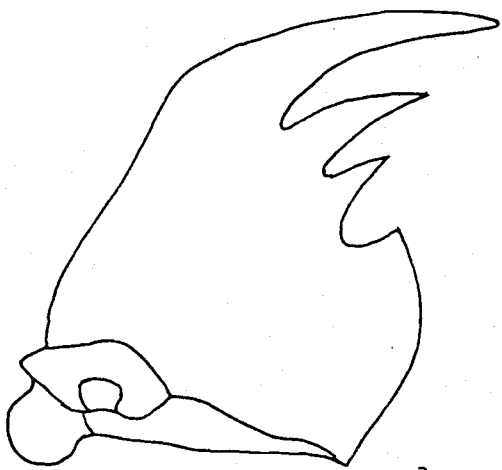
The labium of generalized Mecoptera is divided into a proximal postmentum and a distal prementum. In the Boreidae, including Caurinus, the postmentum is presumably incorporated into the zygostipes while the prementum occurs as a free shield-shaped sclerite bearing the two-segmented labial palps at its apex. The subapical transverse suture of the zygostipes in Hesperoboreus possibly indicates the fusion of the postmentum to the stipes.

The broad basal membrane of the prementum in Caurinus and the insertion of this sclerite under the apical margin of the zygostipes permits its movement in the longitudinal plane. In Boreus and Hesperoboreus, the prementum is separated from the zygostipes by a narrow band of membrane permitting flexion, but little protraction, of the labium.

The ligula is absent in Caurinus, as is the case in all other Mecoptera. The labial palps are contiguous basally, where they articulate with a sclerotized anterior lobe of the prementum. They are separated from the prementum laterally by broad membranes ("palpifers"; Hepburn, 1969b). In Caurinus the basal palpal segment is very large, flattened, and membranous on its median surface, where it bears a series of four specialized setae. The basal segments diverge laterally so that the awl-shaped apical segments are widely separated.

Figures 68-70. Mandibles of adult Boreidae.

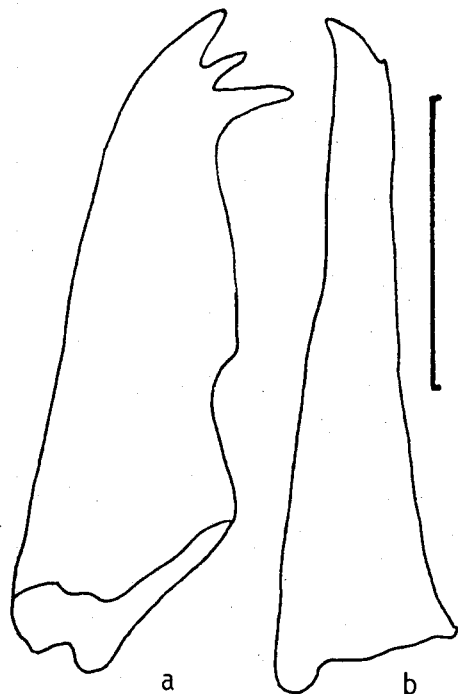
- 68) Mandible of Caurinus dectes, a) posterior aspect; b) lateral aspect.
- 69) Mandible of Hesperoboreus notoperates, a) posterior aspect; b) lateral aspect.
- 70) Mandible of Boreus elegans, a) posterior aspect; b) lateral aspect.



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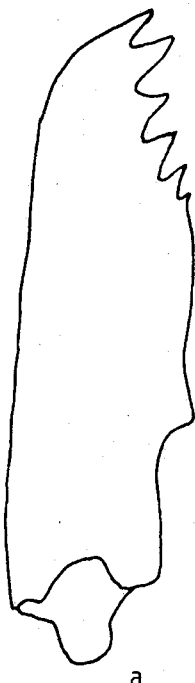


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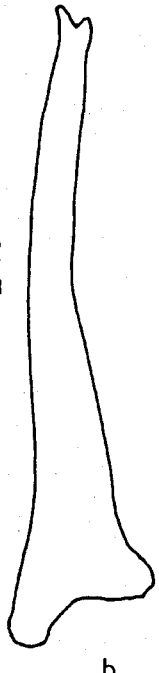


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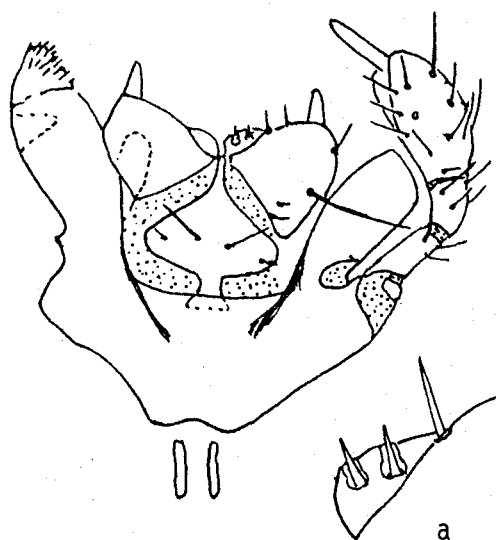
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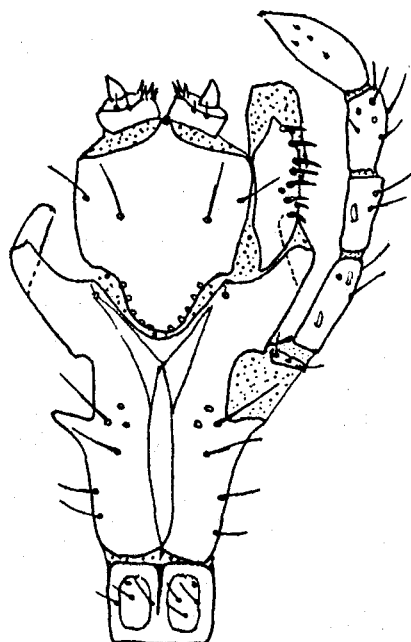
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Figures 71-73. Maxillolabium of adult Boreidae.

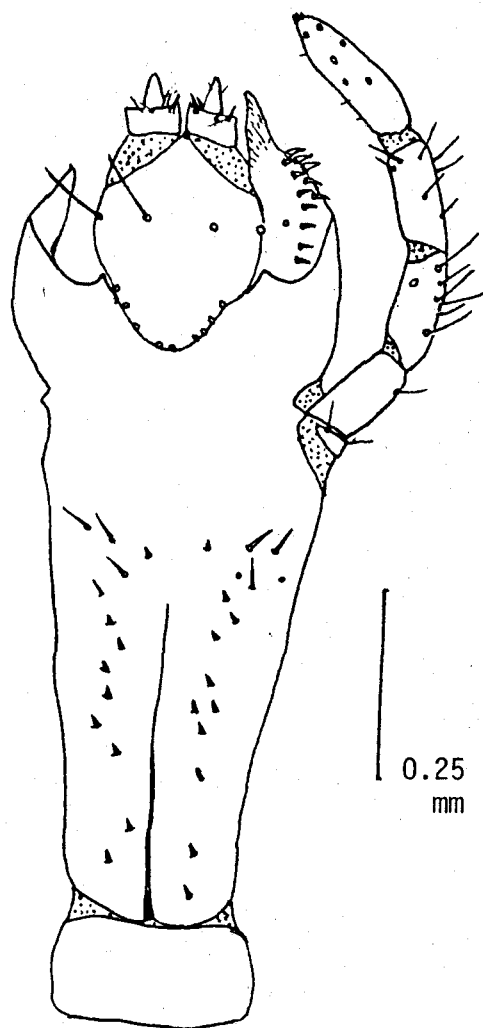
- 71) Maxillolabium of Caurinus dectes,
a) detail of membranous lobe of basal
labial palp segment.
- 72) Maxillolabium of Hesperoboreus brevicaudus.
- 73) Maxillolabium of Boreus nivoriundus.



71



72



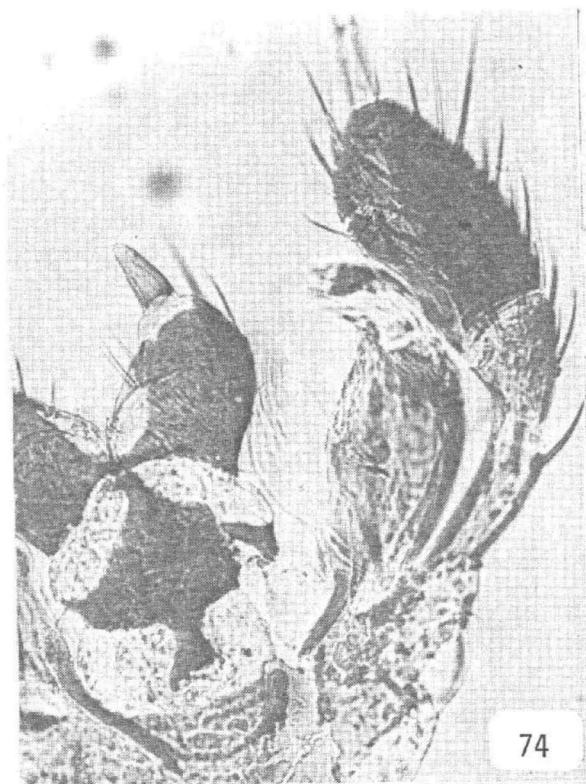
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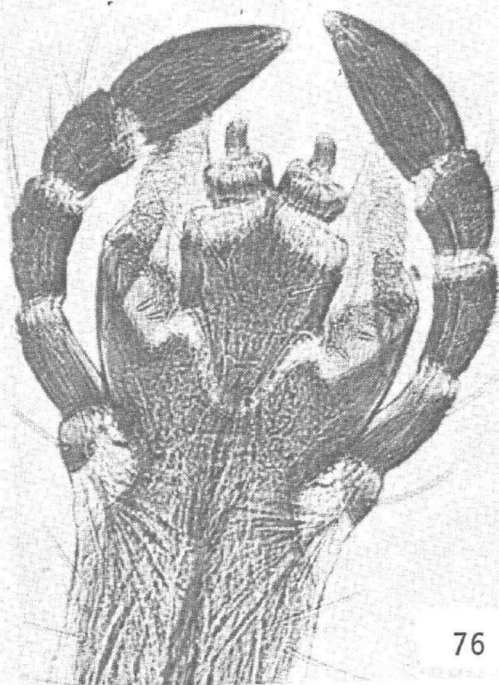
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Figures 74-76. Mouthparts of adult Boreidae.

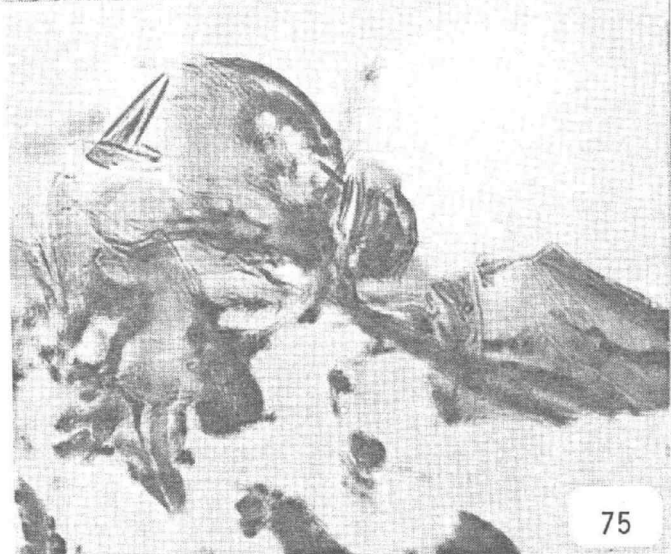
- 74) Maxillolabium of Caurinus dectes; left maxilla broken to show position of lacinia (250X).
- 75) Section of head of C. dectes, showing insertion of tergolacinial muscle in lacinia and galea (250X).
- 76) Maxillolabial complex of Boreus nix, posterior aspect. (Idaho) (125X).



74



76



75

The labial palps of the Boreinae consist of a short cylindrical basal segment and a robust peg-shaped, sometimes curved, apical segment. The mesal margins of the basal segments are sclerotized and only slightly divergent. A series of small sensory pits occurs on the basal margin of the prementum of Boreus and Hesperoboreus, but not Caurinus.

Muscles of the maxillolabial complex

The intrinsic muscles of the posterior mouthparts could be studied from whole mounts of the maxillolabium. The muscles originating on the cranium and tentorium were best observed in hemisected specimens. Many of the muscles are very small and easily damaged, and are difficult to observe. Some structures require further study. The names of the muscles follow the usage of Hepburn (1969b).

The maxillary muscles which have been identified in Caurinus include the tentoriocardinal, tergolacinial, stipitopalpal, and palpal groups. The tentoristipital muscles appear to be absent or are found with the tentoriocardinal, as occurs in the primitive Lepidoptera (Micropterygidae and Eriocraniidae; Kristensen, 1968). The tentoristipital muscles are very prominent in Boreus, and are the major retractors of the ventral mouthparts in other Mecoptera. The tentoriocardinal muscles include two strands originating on each anterior tentorial arm; they function as the adductors or depressors of the maxillolabium. The homologous muscles in Boreus originate on the clypeus well below the tentorium. The tergolacinial muscles appear to be present but the point of origin has not been established (Figure 75).

The muscles of the labium in Caurinus include the retractor of the prementum, extensor of the labial palp, and distal flexor of the palp. The proximal flexor of the palps, which occurs in some Mecoptera, is absent in Caurinus, as in Boreus.

The retractors of the prementum are small, elongate paired muscles which originate on the postgenal bridge near the occipital foramen and insert on the basal process of the prementum in Caurinus. The basal process is apparently homologous to the labial retractor apodeme in other Mecoptera, since the palpal extensors also insert on its base. This structure differs from the usual retractor apodeme in being exposed in its basal expansion. According to Hepburn the cranial premental retractors are absent in the Boreidae. However, while there is no cranial muscle inserting on this sclerite, I found short muscles extending from the zygostipes to the prementum in both Boreus and Hesperoboreus.

Mouthpart function

The differences between Caurinus and the Boreinae in head and mouthpart structure are striking since the food substrates are similar (Table 17), Caurinus feeds on the leaf and shoot surfaces of the bilaterally symmetrical, usually flattened, leafy liverworts, while Boreus and Hesperoboreus feed by preference on the internal tissues of the shoot apex of mosses (Fraser, 1943). The difference in rostrum length may therefore be related to the morphology and "defenses" of the host bryophytes. This divergence in the head structure of the Boreidae can be compared with the familiar case among phytophagous beetles of the leaf-eating Chrysomelidae (with normal head) and the rostrate Curculionidae, which often feed on protected internal plant tissues.

If the mouthparts of Boreus and Hesperoboreus are interpreted as principally used in boring or "puncture feeding", several morphological features can be given a functional significance. Among these are the transversely placed apical mandibular teeth and decussate mandibles and the united structure, large spines, and strong protractor and retractor muscles of the maxillolabium. In boring into a shoot of moss it appears that the rostrum is first forced between leaf bases of the moss. The puncture is enlarged by a nipping action of the mandibles, and the crossed mandibles and maxillary spines are used in

Table 17. Comparison of feeding mechanisms in adult Caurinus and the Boreinae.

<u>Caurinus</u>	<u>Boreus and Hesperoboreus</u>
Hosts: leafy liverworts	Hosts: mosses
Superficial feeder, eats primarily leaf tissues	"Puncture" feeders, frequently bore into shoot apex or leaf axil, also scrape softer tissues (e.g., leaf lamina of <u>Polytrichum</u>)
Structures	
Short snout	Long rostrum
Mandibles short, broad	Mandibles long, blade-like
Apical teeth long, sharp in longitudinal plane of mandible	Apical teeth short, set transverse
Molar blade large, arcuate, extending to base of mandible	Mesal edge of mandible with one to several teeth; proximal third of mesal surface weakly sclerotized
Maxillae short, inflexible	Maxillae elongate, with large membranous apical lobe
Without large lateral spines	With several large laterally projecting spines
Lacinia small, membranous, lying free in preoral cavity	Lacinia not developed as a free medial lobe
Prementum mobile	Prementum not retractile
Labial palps: first segment membranous mesally, without large apical spines	Labial palps: first segment not membranous mesally, with large apical spines
Gripping function provided by apical teeth of mandibles	Gripping function provided by lateral wedging of maxillary spines

succession to anchor the rostrum and allow the rostrum to penetrate further into the feeding puncture. The weak basal portions of the mandibles, and development of the marginal membranous lobes about the mouth cavity suggest predominately liquid feeding among the Boreinae. It is not possible, on the basis of published information, to suggest that solids are excluded from the gut.

In Caurinus, feeding is initiated by mandibular thrusting (page 91) and the structure of the mandibles makes it likely that the apical teeth are most important in grasping the food tissues. The maxillolabium moves during feeding, but in addition to the lack of anchoring spines, the muscles invoked in protraction and retraction of these structures are small and their orientation would not allow much leverage of the host tissues. Feeding on liverwort cell fluids has been demonstrated for Caurinus, and the lobes of the epipharynx and maxillolabium would contribute to effective pharyngeal suction. The molar blade of the mandible of Caurinus is used in chopping individual cells, as opposed to the probable bruising or crushing of moss cells by the apical mandibular teeth of Boreus.

The thorax

The thoracic skeleton is similar to that of Boreus and Hesperoboreus in its basic structure. Like the boreines, Caurinus is brachypterous, has a large prothorax, and the sclerites of the pterothoracic pleura and sterna are fused into a single sclerotized structure. Similar pterothoracic fusions have occurred in the apterous Apteropanorpa (Hepburn, 1970). In Caurinus, this process of reduction of membranes and fusion of sclerites has proceeded further than in the Boreinae. Most of the trunk, from the prothorax to the sixth abdominal segment is essentially a single mechanical unit, with little or no freedom of movement between segmental areas, and hardly any exposed membrane. The thoracic muscles of Caurinus also appear to be generally organized as in Boreus (Füller, 1955), although the preparations at hand did not permit study of all muscles in the

thorax of Caurinus.

Cervix: The cervical membrane is concealed by the pronotum dorsally, and laterally by the postorbital ridges, which fit closely to the prothorax when the head is retracted. The lateral cervical sclerites are well sclerotized but more slender in Caurinus than in boreines. These sclerites articulate with the middle anterior margin of the propleuron, while they are more vertically disposed in Boreus and Hesperoboreus where the cervical sclerites insert on the episternum near the procoxal articulation. The dorsal cervical sclerites, which are usually inconspicuous in Boreus and Hesperoboreus, are absent in Caurinus.

Prothorax: The prothorax of Caurinus is relatively shorter and more transverse than in Boreus, but is larger than usual in the Mecoptera. Mickoleit (1967) regarded the large prothorax of Merope as a plesiomorphic character in common with primitive neuropteroids (Megalopectera, Ithonidae). He considered the pronotum of the Boreidae to be secondarily enlarged by sclerotization of the intersegmental membrane, so that the mesothoracic spiracle is located on the pronotum in this family. The pronotum of Caurinus is immovably joined to the mesonotum, while in the boreines a ventral process of the pronotum is articulated on each side with a mesepisternal fovea. The remaining prothoracic structures except the procoxae, have not diverged greatly from the condition in boreines. The procoxae and pterothoracic coxae are much shorter and more cylindrical than those of Boreus.

Pterothorax: This region is also foreshortened in comparison to its size in the Boreinae. Specialization in Caurinus include reductions of the pleural and intersegmental sutures, as well as of the hind wing of the male and the first abdominal spiracle. The line of fusion of the first abdominal tergite to the metathorax is effaced, and the free apical tergite of the first segment of the Boreinae does not occur in Caurinus. The meso- and metathoracic coxae are deeply set in coxal cavities and are relatively immobile.

The pteronota are also further specialized from the boreine grade in male Caurinus. The nota are partly membranous, and the

sclerites thinner than the cuticle of the pleurosternal region. The scutellum is well developed and the scutum reduced to a narrow band in both pterothoracic segments. The front wing of the male extends only to the second abdominal segment and the hind wing is apparently represented by a minute peg-like sclerite.

The wing mechanism in male *Caurinus dectes*

The elongate, spiny wings of *Boreus* and *Hesperoboreus* have been recognized as accessory sexual claspers. Withycombe (1926) reported, probably incorrectly, their direct use in seizing the female, while Cooper (1940) and Mickoleit and Mickoleit (1976) described their use in grasping the female abdomen while positioning her for copulation. The wings are apparently also used by *Boreus* males (not *Hesperoboreus*) to support the female by grasping one or more appendages during the prolonged copulation (Cooper, 1940; Crampton, 1940). The functional morphology of the wings of *Boreus westwoodi* was described by Fuller (1954, 1955); I have applied his analysis to my observations on *Caurinus*.

The behavior of *Caurinus dectes* during courtship and pairing is still unobserved. However, I have established that the forewing of the male is used to clasp one of the female's antennae (page 239). The forewing of *Caurinus* agrees with that of boreines in the restriction of the wing movement to rotation in a plane nearly parallel to the longitudinal axis of the insect. However, the wing of *Caurinus* is capable of 180° forward rotation, while the clamping action of *Boreus* and *Hesperoboreus* appears to be feasible through only a 40° to 50° arc.

Spontaneous movements of the wings have not been noticed in *Caurinus*, but several males have been collected in fixative with both wings rotated forward to a position over the eyes, with the spines also rotated to a laterodorsal direction from the mesally projecting resting position (Fig. 80). The extended position of the wings indicates that both wings are frequently (necessarily ?) moved together, and that there are two stable positions: fully closed (the position in repose) and

fully extended. The size and shape of the wings, and possibly of a rapid closure with the long spines rotating mesally to interlock, lend this mechanism the appearance of a "snap-trap".

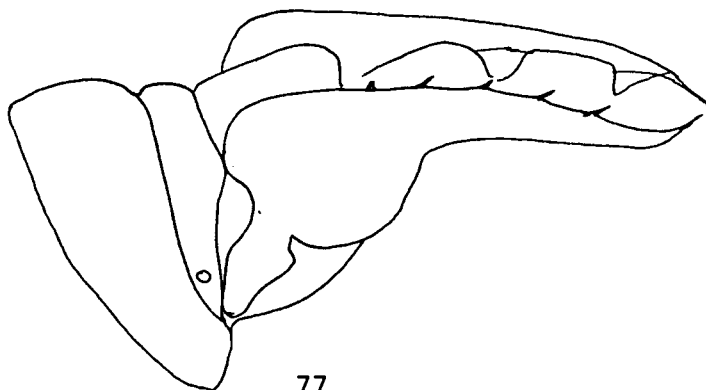
The key modifications of the Caurinus wing permitting this 180° rotation are the loss of the direct articulation of the wing base with the pleural wing process, and the free posterior margin of the basalare. As in Boreus, elevation of the wing (abduction) is apparently produced by a single pleural muscle inserting on the basalare, which is near this sclerite in the anterior episternal wall. The basalare is dorsally linked to the expanded lateral wing base, and anteriorly articulates with the narrow wall of the episternum.

Lowering, or adduction, of the wing is apparently produced by a more dorsally inserted pleural muscle inserted on a small sclerite near the dorsal wing process (the functional pivot). In addition, it is apparent that the wings of Caurinus and other boreids are "spring-loaded" resisting movement from the position of repose in the absence of muscle tonus (even when the muscles are dissected away). This elastic joint mechanism is probably the function of the large pad of resilin found in the wing ligament by Rothschild and Schlein (1975), rather than involvement in the hopping mechanism.

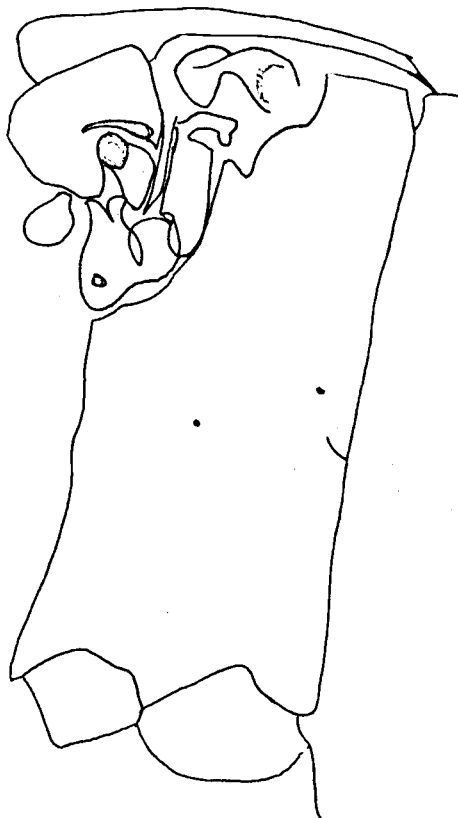
A third pleural muscle in Boreus effects rotation of the wing on its long axis and assists in adduction of the wing. I did not observe this muscle in Caurinus. If it is absent, the wing rotation of Caurinus can be adequately explained by the linkage of the basalare and lateral wing margins.

Figures 77-80. Wing mechanisms of male Caurinus dectes.

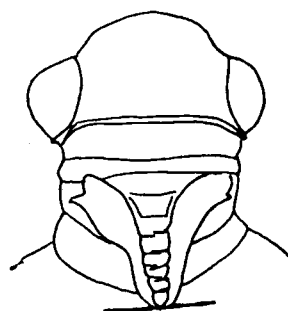
- 77) Lateral aspect of wing.
- 78) Pterothorax, lateral aspect, with left wing removed.
- 79) Head and thorax in dorsal aspect with wings in repose.
- 80) Head and thorax in dorsal aspect with wings fully abducted (observed only in specimens fixed in ethanol).



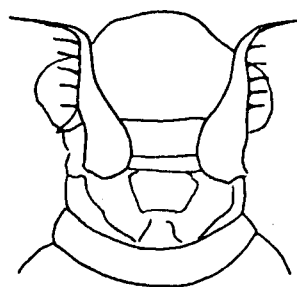
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78



79



80

Locomotion

The leg structure of boreids, including Caurinus, is adapted both for walking, and for execution of a sudden hop. The movements of Caurinus on a level surface are notably more sluggish and awkward appearing than those of Boreus and Hesperoboreus. The relatively short legs of Caurinus presumably help make this insect rather agile in climbing over the stems of its host, despite its bulky shape and fixed pterothoracic coxae.

The jumping ability of Boreus is well known and is usually mentioned in the numerous accounts of their activity. The jumping mechanism was described in Boreus westwoodi by Füller (1954, 1955). The major effectors of the jump are the large dorsoventral muscles of the meso- and metathoracic segments. These muscles are the strongest in the body, and represent the former indirect wing muscles now only functioning as leg muscles.

The thoracic structure of Caurinus differs from that of boreines in the differentiation of pterothoracic segments. The appendages and muscles are essentially similar in the mesothorax and metathorax of boreines (Füller, 1955). In Caurinus, the hind wings and metanotum are reduced in both sexes, while the metacoxae and the metathoracic dorsoventral muscle are both much larger than the structures of the mesothorax.

The presence in the brachypterous Boreus of large dorsoventral muscles inserted on the trochanteral apodeme, was cited by Füller (1955) as a point of resemblance to the Siphonaptera. He remarked that in the structure of these "spring-muscles" as well as in other details of the thoracic musculature "the German name 'Schneefloh' (snow-flea) characterizes Boreus very well". It should be noted that one of the four dorsoventral muscles in the pterothoracic segments of Panorpa communis also inserts on the trochanteral apodeme, and is probably involved in the pronounced jump-takeoff in this species (Hasken, 1939).

More recent investigations of the thoracic structure of fleas (Rothschild and Schlein, 1975; Rothschild et al, 1975) have revealed that energy from the large coxotergal muscles is stored in a resilin cap derived from the wing ligament of alate ancestors. This elastic recoil is suddenly released by a catch mechanism in the "explosive" hop of the flea. Since Rothschild et al (1975) found large resilin caps in the wing hinges of Boreus, it has been suggested that boreids store energy for their hop in a similar manner.

Rothschild (personal communication) believes that the boreid mechanism is "not very similar" to that in fleas, since the long femora in Boreus indicate a takeoff as in grasshoppers (energy transmitted through tarsal and tibial contact), not the explosive impact of the trochanters as in fleas. The best indication for energy storage in the Boreus hop lies in Cooper's (1940) observation that Boreus appear capable of only one hop at low temperature, but can perform several in rapid succession at higher temperatures. Rothschild et al (1975) observed that a significant advantage of the resilin system in host-seeking by fleas is the temperature independence of the elastic recoil of resilin. Finally, there is difficulty in crediting the lack of function to the large quantity of resilin present in Boreus.

My own observations of pupae and pharate adults of Boreus californicus, B. elegans, Hesperoboreus brevicaudus, and Caurinus dectes are based on only a few specimens. Using methylene blue staining (1% in ethanol) and fluorescent illumination of halved fresh thoraxes (Weis-Fogh, 1960), I have detected resilin in male pupae of all three boreines, but not in the single Caurinus examined (a male), nor in single female pupae of B. elegans and H. brevicaudus. If further investigation shows that this resilin pad is sexually dimorphic in boreines, the function may be clarified. When judged only by the position of the wing hinge and other thoracic structures, the resilin appears to me to function as a wing-hinge. The wings of all boreid males are used as a clamp at some stage of mating, and I have

found that the wings of relaxed, dead specimens are held elastically against the dorsum of the insect.

If resilin is missing from the wing-hinge of Caurinus, this has not affected their ability to hop. Since the legs are relatively shorter, and the thorax smaller than in Boreus and Hesperoboreus, it is not surprising that Caurinus jump less readily, and for shorter distances than the boreines. Both sexes of Caurinus normally respond to disturbance by walking away, pulling the appendages in while retaining a foothold, or either dropping or springing away. The falling individuals usually land in the common boreid "catatonic" pose (i.e., motionless, legs drawn in).

The longest observed hops performed by Caurinus were about 5 cm, by freshly collected males held at 18⁰ to 20⁰C. By comparison, large Boreus species (B. californicus, for instance) may hop more than 15 cm. Penny (1977) reports hops of 30 cm by boreids, as a means of locomotion on soft snow. There is no indication that Caurinus ever use the hop as simple locomotion.

The abdomen

The abdomen of Caurinus, in both sexes, is remarkable for the synscleritous, interlocking structure of segments 2-6. There is no remnant of the pleural membrane in any of these segments, as the terga and sterna are united in evenly sclerotized segmental rings. The anterior margin of each ring is recurved externally to provide a wedging lock over which the unmodified posterior margin of the preceding segment fits. These segments are not fused together, but the intersegmental membranes are so short that little or no movement is possible between adjacent segments in this region.

Anteriorly, the tergum of the first abdominal segment is incorporated in the fused pleurosternal region of the pterothorax. There is no suture separating the abdominal tergite and the metapleuron, but these regions can be recognized by differences in vestiture and by the position of the non-functional first abdominal spiracle. The

first abdominal sternum is represented by a pair of short sclerites fused to the ring-sclerite of the second segment. The main abdominal unit is linked to the pterothorax and first abdominal tergite by an elongate, finger-like process projecting anterodorsally from the externally-rolled anterior margin of the second segment. This process originates slightly above the lateral limit of the first sternite; this process locks under the ventral edge of the inward rolled posterior margin of the first abdominal tergite.

The exposed segments posterior to this interlocked thoraco-abdominal complex are discleritous: the tergum and sternum are separated by the pleural membrane for the length of the segment. In both sexes, the terga and sterna of segments 7 and 8 are large and sclerotized. In male Caurinus, the terminal exposed sclerite is the hypandrium (sternum 9), which closes against the eighth tergum. In females, no structures are normally exposed caudad to the tergum and sternum (incorporating the gonocoxites) of the eighth segment. The remaining structures of the genital and post-genital segments (9-11), including the male genital capsule, are enclosed within the abdominal cavity. These terminal abdominal structures will be discussed separately in conjunction with the male and female genitalia.

It is not surprising that the anterior abdominal musculature is reduced in Caurinus. The intersegmental muscles which extend from the metathoracic-first abdominal boundary to the anterior margin of the second segment, are similar to those described in Boreus westwoodi (Füller, 1955). These include a dorsal longitudinal, a lateral oblique, and two ventral pairs of muscles. In Caurinus, as compared to Boreus, these muscles are very small, and the two dorsal pairs are ventrally displaced. No remnants of the segmental and intersegmental muscles were found in the region of the second to sixth segments.

In male Caurinus the seventh and eighth segments have large muscle bands at the basal angles of the terga and sterna. The seventh segment in the female, though discleritous, is not very mobile, and its musculature is poorly developed. In the eighth segment there are very strong fan-shaped muscles joining the basal angles of the

tergum and sternum.

The type of segmental fusion occurring in Caurinus is not in itself unusual within the Mecoptera, but the position of these fused segments is unique. The primitive type of segmental structure in this order has simple tergite and sternite separated by a rather broad pleural membrane; the spiracle is borne either in the pleuron or the tergite. Most male Mecoptera also have one to four synscleritous abdominal segments. These may retain pleural membranes, with only the anterior margin of the segment continuously sclerotized, or the segmental structure may be fully equivalent to the condition in Caurinus.

Except for Caurinus, however, this ring structure occurs only in the modified pregenital segments. In its extreme condition (male Panorpidae), the three or four synscleritous pregenital segments form a constricted "postabdomen" sharply set off from the broader, normal segments of the preabdomen.

The abdominal structure of Caurinus is efficient for the rigid enclosure of the abdominal contents. With the retraction of the terminal segments and genitalia, the exoskeleton has no evident vulnerable points. In spite of its apparent value as defensive armor, few insects have evolved mechanically similar structures. Many insects, especially among the Coleoptera, Hymenoptera, and Siphonaptera, have eliminated most or all exposed membranous cuticle. Each of the latter groups retains the ability to adjust the abdominal volume -- through the membranous abdominal terga and subelytral spaces in the beetles, and through a wide overlap of the pleural membrane by the abdominal terga in most other armored insects. An approach to the Caurinus structure does occur in Osorius and related genera of rove beetles (Coleoptera, Staphylinidae), which have rigid ring-segments. The intersegmental membranes do not seem to be reduced in these beetles and would allow a considerable adjustment of abdominal volume.

The rigid structure of Caurinus appears to remove the possibility of adjusting to changes in volume of the abdominal contents during adult life. The growth of the reproductive system and of increase in

gut volume during feeding are apparently accommodated principally through changes in the hemolymph volume. The other possible solution would be the expansion and collapse of tracheal air sacs. However, histological sections and gross dissections of teneral individuals of both sexes showed that the viscera at this stage are largely restricted to the anterior abdomen and to a median dorsal chord of tissue. Most of the abdominal cavity was then occupied by a space without evident tracheal connections or cuticular walls; and no air-filled spaces were noted in dissected specimens. The significance of this "growth space" can be judged by my estimate that the maximum number of mature oocytes observed in a dissected female (8) represent about 35% of the weight of that individual.

There is no comparable excess volume of hemolymph in the pupa of Caurinus equivalent to that in teneral females. I have suggested (page 125) that the spherical expansion of the female abdomen is very likely accomplished through forcing of air into the greatly distensible midgut.

The change in the volume of enclosed systems can be visualized in mechanical (not to say physiological) terms through the assumption of an ability to decrease the hemolymph volume during adult growth. A second mechanical consequence arising from the rigid abdominal shell of Caurinus is the use of the hemocoel in transmitting hydraulic force. Both male and female terminalia are of structures requiring hemolymph pressure for their protrusion. Yet, such pressure would require that some compensating compression of the hemolymph volume. The male genital capsule is a much larger volume than the female postabdomen, but there are more apparent means of compensation and direct muscular action for its protrusion. The female caudal segments may be extended through maintenance of a positive pressure in the abdomen, through a non-apparent reduction in abdominal volume as the eighth segment gapes open, or it is possibly forced outside the sclerotized pre-abdomen by the movement of an egg into the common oviduct.

In addition to the protraction of the caudal segmental structures in connection with mating (male) and oviposition, the proctiger is exposed when "urine" drops are ejected during and after feeding (page 93). In this situation the idea of a positive abdominal pressure is credible, given the rapid absorption and excretion of excess water from the food.

Male genitalia

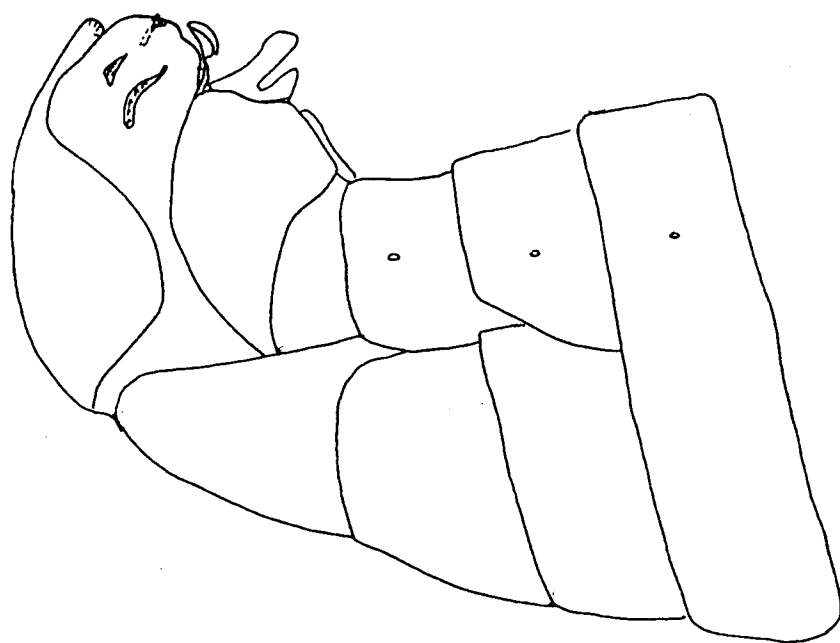
The genitalia and associated structures of the apical segments (9-11) of the abdomen of male Caurinus differ greatly from the corresponding structures of Boreinae and of other Mecoptera. In the present account, I describe these structures, compare the genital morphology with other Mecoptera, and interpret the peculiarities of Caurinus in functional terms.

The genital capsule of Caurinus is concealed by the closure of the ninth sternum (hypandrium) against the eighth tergum. The genital capsule (Figures 81, 82) comprises 2-segmented genital claspers, the gonostyles; a large aedeagus, with conspicuous dorsal and ventral sclerites; and a small, membranous proctiger (segments 10 and 11), borne dorsally between the gonostyles. The exertion of the genital capsule during mating is facilitated by extension of the pleural and intersegmental membranes of segments 7 and 8; these membranes are entirely concealed when the genital capsule is in repose.

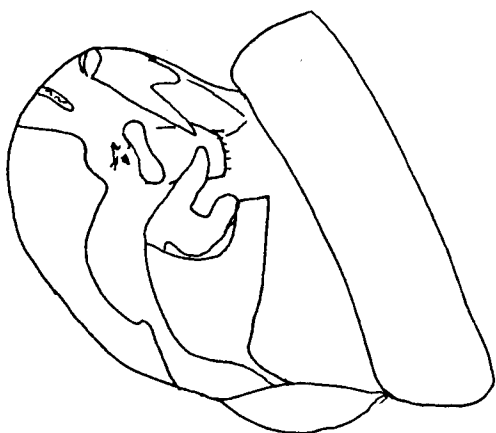
The gonocoxites are stout and somewhat compressed in the sagittal plane. They taper to a narrow basal process almost as long as the body of the sclerite, lying free in the lateral membrane above the ventral aedeagal trough. Medially, each gonocoxite bears a pillar-like basal apodemal process which articulates with a basal wing of the dorsal aedeagal apodeme (Fig. 83). These are the only points of articulation of the sclerites within the genital field. The gonostyle is strongly sclerotized with a curved elongate external tooth and a short broad median tooth. The median tooth bears 6 long setae, 2 of which are set dorsally and are conspicuous. The external tooth bears numerous

Figures 81-83. External genitalia of male Caurinus dectes.

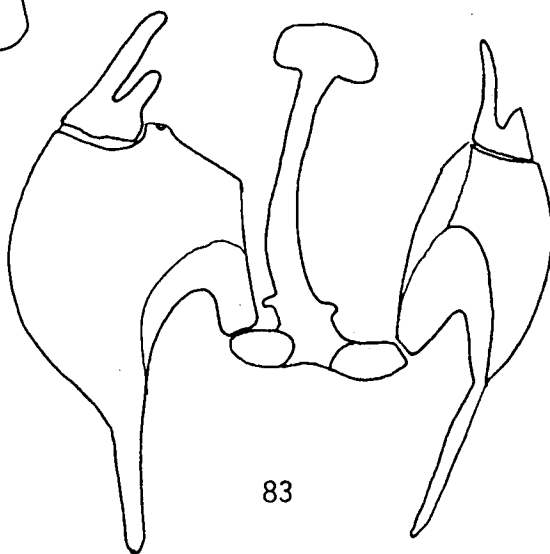
- 81) Terminal segments of abdomen with genital capsule everted, in lateral aspect.
- 82) Everted genital capsule, showing proctiger (segments 10 and 11), in dorsolateral aspect.
- 83) Gonopods and dorsal aedeagal sclerite in dorsal aspect, showing articulation between these sclerites.



81



82



83

transverse low ridges. The gonostyles, with the genital capsule fully everted, are oriented medially and their tips lie slightly anterior to the distal process of the dorsal apodeme.

The proctiger is short and membranous with the very lightly sclerotized eleventh tergum and sternum bearing very long, fine terminal setae. An oval sclerite lying in the dorsal membrane between the gonocoxites may represent the tenth tergite. If so, the ninth tergum is completely membranous. (A small sclerite was found at one side of the basal genital membranes in one male Caurinus; and may represent a vestige of the ninth tergum.)

The aedeagus is bounded ventrally by the large ventral trough and dorsally by the dorsal apodeme. Two linear, spinose sclerites are present in the lateral membrane between these structures on each side.

The distal ejaculatory duct is flanked by a pair of linear sclerites which are apically hooked and proximally form flattened apodemes. A small median dorsal sclerite is associated with these. The dorsal apodeme is a large, curved sclerite which is free from the membrane apically as a spoon shaped process. At its base it is broader and forms stout processes which articulate with the gonocoxites. A smaller pair of internal processes arise on the base of this sclerite distal to the articulation processes.

In dead specimens, independent movement can be produced between the dorsal apodeme and ventral trough, and between these and the sclerites of the ejaculatory duct.

Anatomical correlations during mating

The ejaculatory duct can be everted nearly to the bases of the linear aedeagal sclerites (Figure 92). In this position, the everted portion of the aedeagus extends some distance beyond the apex of the ventral trough and a space is defined between the paired ventral sclerites and the projecting median sclerite of the ejaculatory duct. The spermatophore (page 228) lies in the duct between these sclerites.

During mating the gonostyles lock into lateral notches of the female's eighth sternite, while the dorsal aedeagal sclerite lies against the mesal shelf of the female eighth sternite. The aedeagus is only partly inserted into the genital chamber, where the lateral spinose sclerites engage the chamber walls. The morphology of the female chamber in Caurinus is too poorly known to understand the function of the sclerites of the gonoduct; the paired rods probably position the apical pore of the spermatophore at the spermathecal duct. These rods may also aid in retaining the spermatophore at the termination of mating, or the ejection from the male after separation of the pair.

Discussion

The genitalia of Boreus and Hesperoboreus are of little aid in understanding the origin of the aedeagal structures of Caurinus. In contrast to the complex sclerites of the Caurinus aedeagus, a simple strap-shaped "dorsal plaque" is the only constantly present sclerite in the boreine aedeagus (Cooper, 1972, 1974). While the aedeagus in other mecopteran families is a rigid structure with complex lobes, the boreines have a membranous and erectile penis which is normally retracted into the endandrium (Cooper, 1974).

The aedeagus of Caurinus is actually similar in shape and position to the everted boreine structure, but the sclerites, in part at least, can be identified with structures of more typical Mecoptera. The most generalized mecopteran genitalia apparently are those of Notiothauma reedi (Crampton, 1931; Mickoleit, 1971). Three main sclerites together form a sperm pump. Two lateral sclerites are joined along the midline as the pump chamber, while a median sclerite, hinged anteriorly to the gonopod base and posteriorly to the pump body, acts as the pump piston. The aedeagal apodeme of Caurinus seems to be homologous with the piston-bearing sclerite (Pistillträgersklerit) of Notiothauma. This is indicated by the similar position and shape of the basal structures of these sclerites

and especially by the articulation with the gonocoxites in both genera. The aedeagal rods of Caurinus are most likely the remnants of the pump-body sclerites (Pumpenkörperskleriten) of Notiothauma since they lie in the walls of the distal gonoduct. The structures present in Caurinus are probably equivalent to the median distal lobes of the pump-body. These are modified in various ways in different families of Mecoptera, ranging in structure from short lobes to an elongate, tubular penisfilum (Tjeder, 1970) in the Bittacidae.

The homologies of the remaining aedeagal sclerites of Caurinus are less evident. The large "ventral trough" may be peculiar to Caurinus, although it is possible that this is a detached apical fragment of the hypandrium (such as that occurring in Notiothauma) which has become fused to the ventral aedeagal wall. There is little merit in attempting to identify the spinose sclerites of the lateral aedeagal membranes of Caurinus with any of the paired lateral processes of the aedeagus in other Mecoptera.

The presence of at least one of the sperm-pump sclerites in Caurinus is of special significance since there is a divergence between the functional sperm pump of all Mecoptera except the Boreidae; and its total absence in Boreus and Hesperoboreus. Sperm transfer in the Boreidae is by means of a spermatophore (described in Boreus westwoodi; Mickoleit, 1974; and for Caurinus in the present study. This means of sperm transfer is ostensibly primitive, but as Mickoleit demonstrates, this assessment in Boreidae would require that Boreidae be the basal branch of the Mecoptera, as maintained by Hinton (1958), and Diptera a paraphyletic derivative of the Mecoptera; or that the sperm pump is not homologous in the two orders. The structure of the Caurinus genitalia and production of a spermatophore in this genus make it evident that the spermatophore is secondarily regained in the Boreidae.

The remaining structures of the genital capsule in Caurinus are less modified from the usual condition in the Boreidae. The gonopods are unusual in being free at the base. All other Mecoptera have the gonocoxites fused dorsally and ventrally. Similarly, the ninth segment

Table 18. Comparison of the male genital segments in Caurinus, the Boreinae, and other Mecoptera.

<u>Caurinus</u>	<u>Boreus</u> and <u>Hesperoboreus</u>	Other Mecopteran Families
Genital capsule concealed	Genital capsule exposed	Genital capsule exposed
Gonobases not fused dorsally or ventrally	Gonobases with narrow dorsal and ventral bridges	Gonobases usually broadly fused
Aedeagus eversible, with dorsal and ventral sclerites present	Aedeagus eversible, usually with weakly sclerotized dorsal plaque only	Without eversible aedeagus, with complex sclerotized genital fold
Sperm pump absent	Sperm pump absent	Sperm pump present
Ninth segment disscleritous, ninth tergum not sclerotized	Ninth segment disscleritous or synscleritous	Ninth segment usually synscleritous
Dististyles without stylar organ	Stylar organ present	Stylar organ present in Nannochoristidae and Meropeidae
Cerci absent	Cerci absent	Cerci usually present

is almost always synscleritous in Mecoptera, and it is usually lobed posteriorly to support the genital structures. In Caurinus the genital capsule is free from the hypandrium (ninth sternum) and the ninth tergite is mostly or entirely membranous.

The two apical lobes of the gonostyles are flattened in Caurinus, while these structures often bear mesal teeth or granules in other Mecoptera, notably so in the boreines. The styler organ (Crampton, 1931) is absent in Caurinus; this vesicular structure occurs in the gonostyles of boreines, and is otherwise found only in the Meropeidae, Notiothaumidae, and Nannochoristidae (Mickoleit, 1971),

A study of the musculature of the genital capsule may allow some of the suggested homologies of the Caurinus genitalia to be reassessed. Since the muscles are described only for Panorpa (Grell, 1942), and superficially for Hesperoboreus notoperates (Cooper, 1974), these structures presently are of little comparative value.

The spermatophore

In addition to the spermatophore discarded by the male following the copulation described above, three other spermatophores were observed. Two were noted in culture dishes containing male and female C. dectes, before mating had been observed in this species. These were not recognized as spermatophores at the time. One other spermatophore was later recovered by wet-screening from field samples.

The spermatophore of Caurinus is a hardened gelatinous structure. It resembles a thick, curved sausage with a bent, finger-like appendage at its apex (Figure 91). The dimensions of the spermatophore recovered from the culture are (main structure) .55 by .20 mm; the apical appendage is .12 mm long. Its outer walls are transparent and colorless, while much of the internal volume is occupied by two lateral chambers of granular, gray material. An opaque white channel extends to an orifice on the apical appendage; it was not observed whether this sperm channel was continuous with the two granular chambers. The spermatophore was retained within the male aedeagus until after the pair separated. At the termination of copulation it appeared that

only the apical appendage protruded from the everted aedeagus.

A spermatophore similar in structure to that of Caurinus was described for Boreus westwoodi by Mickoleit (1974), who predicted that sperm transfer by means of a spermatophore would be a constant feature of the Boreidae. Mating has been observed in several species of Boreus and Hesperoboreus (Cooper, 1974), but no other author has noted the occurrence of a spermatophore. However, Withycombe (1926) figured the everted aedeagus of B. hyemalis, which obviously held a spermatophore of similar shape to that of B. westwoodi. Other observers have also probably failed to recognize spermatophores in the Boreidae.

The presence of spermatophores in the Boreidae raises some uncertainty about the evolution of sperm transfer within the Mecoptera and related orders. It is characteristic of the Mecoptera, Diptera, and Siphonaptera, that sperm is transferred as a fluid by means of a sperm pump. The sperm pump of each of these three orders differs in its structure, but this structure is believed to be homologous at least in the Mecoptera and Diptera (Mickoleit, 1971), and is cited as a major character supporting the supra-ordinal group, the Antliophora (Hennig, 1969). Hennig excluded the fleas from the Antliophora, but other authors (Kristensen, 1975; Rothschild, 1975) have included them. In the other holometabolous orders a spermatophore is usually present; in those species with fluid sperm transfer there is no structure similar to the sperm pump of the Mecoptera and Diptera (Davey, 1960; Khalifa, 1949). Among the neuropteroid orders the spermatophores are frequently of the simple type found in Caurinus and in B. westwoodi (Khalifa, 1949).

Mickoleit (1974) suggested that the secondary evolution of a spermatophore remains possible in Mecoptera (and Diptera) possessing a sperm-pump since the male accessory glands remain well-developed, and their secretion may retain a role in sperm transfer. Spermatophores are also known to occur, presumably secondarily, in a number of Diptera, including species of Ceratopogonidae, Chironomidae, and Bibionidae, as well as Glossina among the Brachycera (Downes, 1968;

Pollock, 1972). A sperm pump is absent in these groups, as well as in the sister-group of the Antliophora, the Amphiesmenoptera (Lepidoptera and Trichoptera). However, among the mecopteroid orders, the sperm are transferred to the female "by means of" the spermatophore only in the Boreidae. In the dipteran families mentioned above, as well as in the Amphiesmenoptera, the spermatophores are "formed within the female ducts by the hardening of a secretion ejaculated by the male" (Kristensen, 1975).

Mickoleit (1974) suggested that the spermatophore in Boreus, and the lack of a sperm pump, are the adaptive consequences of the long secondary ovipositor of boreines. The spermatophore was supposed to function as an extension of the aedeagus. This argument is not applicable to Caurinus, where the genital chamber is quite short, and there is no evidence that this represents a reduction from the boreine ovipositor (page 232). The aedeagus of Caurinus is also apparently more primitive than the completely membranous penis of boreines; although the sperm pump of other Mecoptera is lost in Caurinus, some of its elements are apparently retained. The extensive sclerotization of the aedeagus in C. decetes also makes a "supporting" function of the spermatophore unlikely.

Female postabdomen

The genital and postgenital segments of female Mecoptera have been studied extensively by Mickoleit (1974, 1975, 1978). The modifications of this complex, and especially of the structures of the eighth sternum, the genital chamber, and the eleventh segment and cerci, are of considerable value for the classification at the higher categories in this order. The structure of these segments in Caurinus is of special interest because of the great divergence from the structure in Boreus and Hesperoboreus. In some respects Caurinus and the Boreinae represent opposite extremes in the development of these structures within the Mecoptera.

The terminal exposed segment in female Caurinus is the eighth abdominal segment; segments 9 to 11 are largely membranous and fully retracted within the abdomen. The tergum of the eighth segment is not modified. The eighth sternum is relatively short and completely sclerotized; on its apical margin is a broad, short process regarded here as the medially fused gonocoxites of the eighth segment. This sternal process is emarginate at the middle of its posterior margin, and it extends anteriorly as an internal shelf.

Each of the caudal segments (9-11) telescopes into the preceding one. The segments of the extended postabdomen can be delimited by the transverse series of long seta along the caudal margins of the ninth and tenth segments. The sterna of both segments are completely membranous. There are two pairs of sclerites on the lateral and dorsal surface of the ninth segment. These could be, respectively, tergite and laterotergite; tergite and gonocoxite; or laterotergite and gonocoxite. The median pair of sclerites in some specimens are continuous with a weakly sclerotized transverse band, and are probably tergal fragments. The more ventral pair of sclerites were previously identified as laterotergites (Russell, 1979) principally because these elements are of frequent occurrence in the Mecoptera (Mickoleit, 1975). However, these sclerites most closely resemble, in their position on the posterior half of the ninth segment, their elongate shape, and apparent function as hoop-like supports of the genital chamber, the second pair of gonocoxites of Notiothauma reedi (Mickoleit, 1975). In the Mecoptera, the second pair of gonocoxites are known only from N. reedi and the Nannochoristidae.

The eleventh segment of Caurinus is very generalized (Figures 86, 87). The tergum and sternum each bear oval, medially placed sclerites; the base of the segment is broadly membranous. The one-segmented cerci are inserted at the basal lateral angles of the eleventh segment, and are oriented caudolaterally.

The posterior abdomen of female Caurinus differs remarkably from the type of ovipositor found in the boreines. In Boreus and

Hesperoboreus, the eighth sternum is membranous basally and along the midline, while the gonocoxites are very elongate. Segments 9 to 11 are exerted and do not telescope at all. The cerci are fused medially and form the dorsal apical sclerite of the functional ovipositor. The ovipositor of Hesperoboreus differs significantly from Boreus, and in several (presumably synplesiomorphic) characters matches the structures of Caurinus (Table 19).

The female genital and postgenital segments in Caurinus probably resemble those of the hypothetical stem-species of Boreidae more than does the modified ovipositor of the boreines. If the separate cerci, and the basally-sclerotized, undivided eighth sternum are primitive structures, the ground-plan of the Boreidae approaches that of the Bittacidae rather closely, and is little different from the hypothetical ancestral form for the Mecoptera (Mickoleit, 1975). The boreid ancestor would resemble Caurinus in these structures, except with more extensive sclerotization of segments 9 and 10; and only partial telescoping of these segments, while the eighth sternum may have been membranous along the midline.

Mickoleit (1975) appears to have been correct in assuming that the boreines evolved their rigid ovipositor from the partly-telescoping structure typical for the Mecoptera. However, the structure of the eleventh segment and cerci in Caurinus make it unlikely that the mesal fusion of the cerci and the modification of the eleventh tergite in boreines are synapomorphic with the equivalent structures in the Panorpidae and related families. In my view, the cerci of Boreus and Hesperoboreus represent one-segmented cerci fused along their length, while retaining a basal articulation with the eleventh segment (Byers, 1962). This contrasts with Mickoleit's assumption (1978) that the cerci represent a reduction from 3-segmented cerci in which only the basal segments are fused along the midline and to the segment stem.

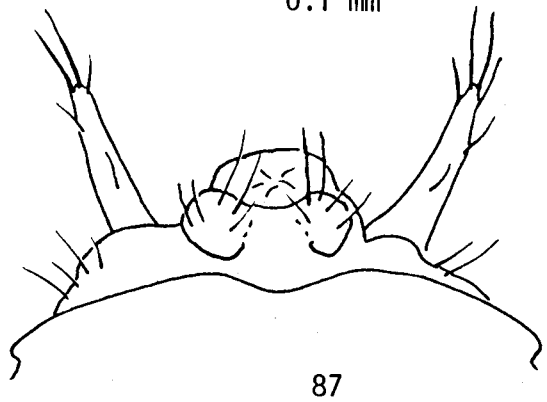
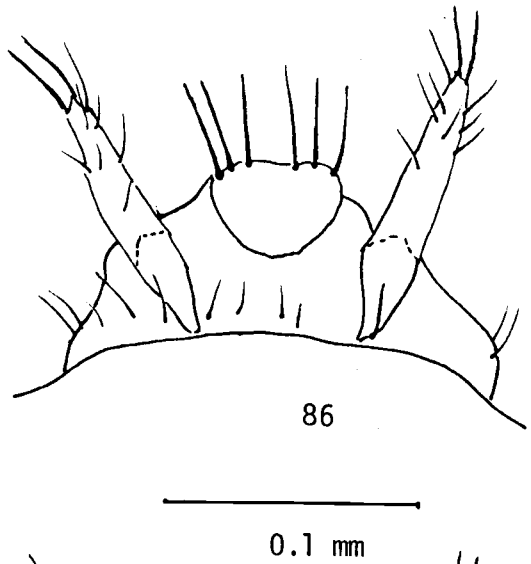
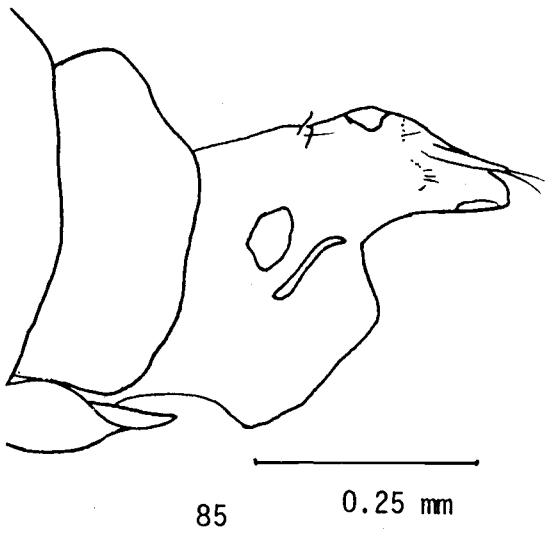
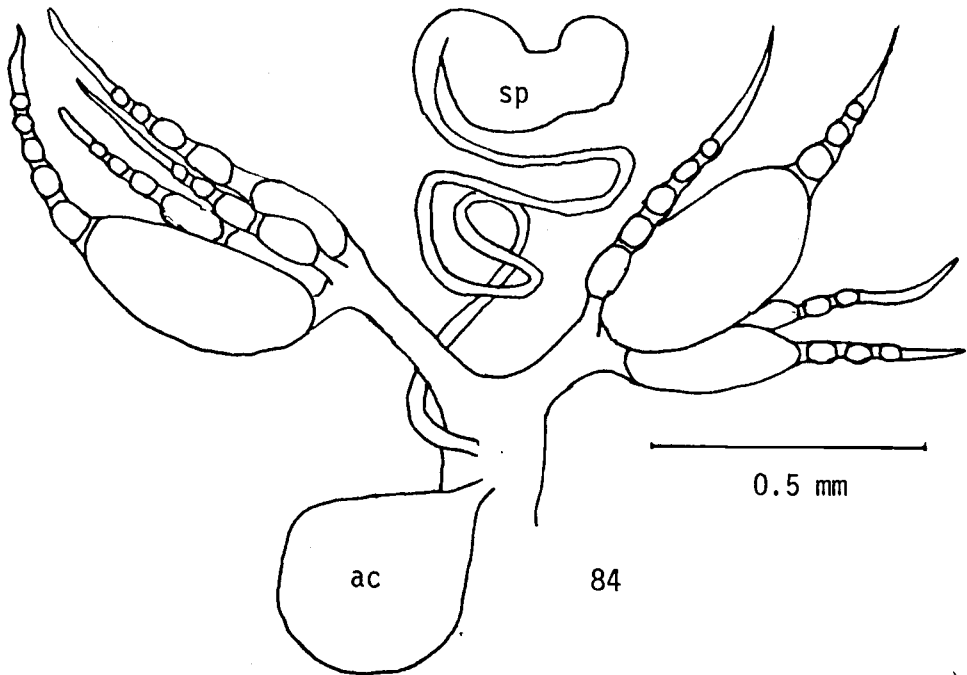
The resemblance of the female genitalia of Caurinus to those of the Bittacidae appears to rest largely on synplesiomorphic characters. Only the one-segmented cerci, and possibly the lateral notch of the eighth sternite can be mentioned as possible synapomorphic characters

Table 19. Structures of the genital and post-genital segments in female Boreidae.

	<u>Caurinus</u>	<u>Hesperoboreus</u>	<u>Boreus</u>
Eighth tergum	Not extended laterally	Extended laterally	Approximated ventrally
Eighth sternum	Sclerotized at base	Membranous at base and along midline	Membranous at base and along midline
First gonocoxites (of eighth sternum)	Short, fused medially and continuous with eighth sternum	Long, joined by membrane on midline	Long, joined by membrane at midline
Lateral notch of first gonocoxites	Present	Present	Absent
Insertion of eighth sternum and gonocoxites	Hinged at base	Articulate with lateral margin of eighth tergum	Articulate with caudal margin of eighth tergum
Ninth tergum	Largely membranous	Fully sclerotized	Fully sclerotized
Tenth tergum	Short, largely membranous	Sclerotized, prolonged caudad at lateral angles	Sclerotized, elongate
Second gonocoxites (?)	Present	Absent	Absent
Linkage of segments 9 - 11	Fully telescoping	Rigid	Rigid
Cerci	Separate, inserted at base of segment	Fused, suture evident, partly fused to tergum ₁₁	Fused, suture reduced, partly fused to tergum ₁₁
Eleventh tergum	Oval, not projecting laterad to bases of cerci	Circumapical sclerite entire prolonged laterad of cercal bases	Circumapical sclerites (often fragmented)
Eleventh sternum	Large, medially emarginate	Moderate in size	Small
Anus	Terminal	Terminal	Subventral

Figures 84-87. Female reproductive system and terminal segments of female Caurinus dectes.

- 84) Female reproductive system of C. dectes,
ac: accessory gland, sp: spermatheca.
- 85) Segments 9-11 of female C. dectes extruded,
in lateral aspect.
- 86) Eleventh segment of female C. dectes,
dorsal aspect.
- 87) Eleventh segment of female C. dectes,
ventral aspect.



linking Caurinus, and the Boreidae, with the Bittacidae. Mickoleit (1978) gave convincing grounds for separating the Bittacidae and Nannochoristidae from the remaining seven families of Mecoptera. Removal of Boreidae from the residual complex seems to be required on the basis of the female postabdomen of Caurinus. These matters will be discussed in the context of other proposed classifications of the Mecoptera.

Mating behavior of Caurinus dectes

Courtship and initial pairing was not observed. All close encounters between males and females during normal activities seemed entirely neutral, and this behavior did not seem to differ from interactions of individuals of the same sex. Either a male or female approaching another Caurinus would stop, antennate, and in most cases change its course of movement parallel to or away from the stationary individual. Late in this study it seemed possible that courtship behavior is typically nocturnal in this species. During February to April 1978, approximately 8 hours observation of Caurinus was made at night with a red filter on the microscope light source. No behavior was observed which might have been courtship-oriented.

Two pairs were found in copulation during observation of my cultures (14 March 1978, 0715 PST; 25 March 1978, 1300 PST). The first pair (14 March) was observed for 15 minutes, and then were fixed by immersion in warm (50°C) Bouin's preservative. The second pair was observed continuously from discovery until the insects terminated copulation, and the pair separated (1 hour 25 minutes elapsed time). This description is based on notes of direct observation, examination of the pair fixed in copulation, and photographs made of the second pair.

Caurinus mate in a position with the female on the dorsum of the male (Figures 88-90); intromission is accomplished by a dorsal and anterior curving of the aedeagus of the male. The female's body is horizontal or slightly inclined (less than 20°) to the male. In both pairs

observed, the left antenna of the female was held by the left wing of the male. (In pair 2 the right antennal flagellum had been lost.) The clasped antenna appeared to be held taut throughout the observation in both pairs, and this hold was maintained after fixation in the pair which was sacrificed.

Both males moved about intermittently during copulation, but seemed less agile than mating male Boreus or Hesperoboreus. Both females moved their mouthparts almost continuously throughout the observation period. These were slow movement of the maxillary palpi, and protraction of the maxillolabium. The female of pair 2 occasionally opened and closed her mandibles.

The first female (14 March) rested her pro- and mesotarsi on the dorsum of the male, while her free (right) antenna was directed posteriad, and held immobile. Her metatarsi appeared to rest on the sides of the male's abdomen without supporting her.

The posture of female 2 during the first hour of observation was more typical of that described for other boreids (Cooper, 1974). Her pro- and mesothoracic legs were drawn against her body and the hind legs were partly retracted with the tarsi resting in the area of the third abdominal segment of the male.

Rhythmic anterior-posterior movements of the female could be seen for most of the observation period. These movements of small amplitude and with a frequency around 1/second were produced by pumping movements of the posterior segments and genitalia of the male.

During the last hour of observation of pair 2 the male increased his locomotory activity. During this time the male began to "kick" the female with his metathoracic legs. These kicks were delivered with the tibial apex and basitarsus, usually one to five strokes at a time, and often with alternation of the right and left legs. The female responded to most bouts of kicking by more active movements of the mouthparts, and eventually she extended her two anterior pairs of legs to take a stance on the male's dorsum similar to that observed for female 1.

All this activity was episodic, but became more frequent in the 15 minutes preceding separation of the pair. On three occasions, kicking by the male appeared to elicit a pushing or batting movement of the prothoracic legs of the female. This was a repetitive unilateral or bilateral thrusting of the tibial apex against the pronotal or head region of the male.

Separation occurred shortly after the male walked under a small Porella fragment which was then carried around held between the pair. An impression was given of an attempt by the male to lever the female off his back; it was only at this point that the female's antenna was freed. When the pair disengaged, the female walked away immediately. The male rolled on his side with the appendages drawn in for 8-10 seconds, during which the everted part of the aedeagus was retracted and the spermatophore which had been enclosed in the aedeagus was discarded. Pair 2 was kept together, but showed no further interaction. The female did not increase her oviposition activity after mating.

Discussion of mating behavior

The copulatory position observed in Caurinus is similar to the final position in all recorded Boreus species (B. hyemalis, B. westwoodi, B. brumalis, B. californicus, and B. vlasovi, all referenced in Cooper (1974), and B. elegans, my observation). These species all adopt a "female vertical" copulatory position (Lamb, 1922) with "inverse correlation" of the genital ducts of the mating pair. Caurinus dectes also resembles Hesperoboreus notoperates, and apparently also H. brevicaudus, in the insertion of the gonostylar tooth into a lateral notch of the female gonapophysis. Both Hesperoboreus species differ from Caurinus and known Boreus in their retention of a "female perpendicular" position as the final copulatory attitude (Cooper, 1974). This position is morphologically equivalent to the usual Boreus position; however, in Hesperoboreus, the female is oriented nearly vertically throughout the copulation, and the male's

wings are folded in repose and not used in supporting the female. The position observed in both Hesperoboreus species is identical to the initial copulatory pose reported in species of Boreus. In Boreus, this position is necessary for the insertion of the female's gonapophyses into the endandrial pockets of the male (Cooper, 1974). Cooper (1974) termed this condition a "reciprocal intromission".

Since the precopulatory behavior of Caurinus has not been observed, it is necessary to resort to morphological inference for comparison with the curious mating behavior of the boreines. It certainly appears clear from structure, that the male Caurinus does not capture the female by jumping upon her, and certainly not by snaring an appendage with his gonostyles (as described for all the boreines above). Some form of interactive courtship, actively involving the female prior to mating, seems more likely than the rapine mating of Boreus and Hesperoboreus. This seems to follow from the lack of the modifications of the male wings and gonopods associated with this trait in the boreines. Caurinus lacks the granular medial apical field of the gonostyles, as well as the opposing granular excavations of the ninth tergum, which are characteristic of all boreines, and together form the gripping surfaces used in capture of the female. The short wings of Caurinus are used to hold one of the antennae through the entire copulation; they could not be used to transfer the female to the proper position on the male's dorsum as in B. hyemalis (Mickoleit and Mickoleit, 1976). Given the lack of the associated structural modifications in the boreines and other mechanical considerations (K. Cooper, in conversation, has imagined pairing in C. dectes as akin to "two billiard balls mating"), I believe that the female actively mounts the dorsum of the male. If this supposition is true, mounting could occur either prior to, or after, the grasping of her antenna by the male's forewing. In either case, if the grip observed in the two matings reported above represents the initial one, it is necessary that the antenna was grasped with the couple oriented parallel and facing the same direction. An initial grip could be changed after the copulatory position is assumed, but this apparently could not be

accomplished without fully releasing such a hold.

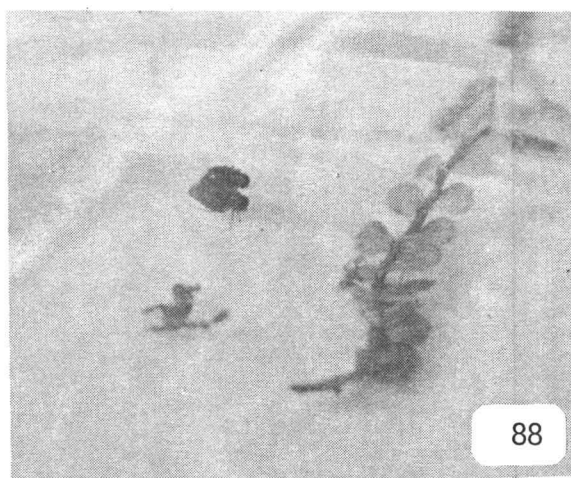
The female-vertical position found in the Boreidae is unusual among holometabolous insects. This position, and mating poses morphologically equivalent to it, are more widespread among primitive insects, especially the orthopteroids. Alexander and Brown (1963) consider the female mounting the dorsum of the male as the primitive state in ancestral pterygote insects. Within the Orthopteroidea this position is often associated with attractant glands opening on the dorsum of the male (Barth, 1964). The diversity in structure and position of these attractant (or trophic? -- Thornhill, 1976) glands suggests polyphyletic origin of this mating behavior in its extant form. It can be assumed from the distribution of mating types, that the female vertical and side-by-side mating positions are easily exchanged during evolution in groups with the same basic morphological relationships (inverse correlation of ducts) (Lamb, 1922). Scudder (1971) apparently accepts the polyphyletic origin of these two related forms of mating, and adds a functional interpretation. He believes that the female-above position may be retained throughout copulations if this is brief. Where copulation is prolonged (normally for the secretion of a complex spermatophore) an alternate position (side-by-side) is usually assumed after coupling (Scudder, 1971).

The female vertical position in Boreus and Hesperoboreus is the consequence of capture of the female, rather than her active mounting of the male. The passive role of the female at this stage, and the clasping structures associated with female capture, are probably the reasons that boreines fail to fit Scudder's prediction. Copulation is of long duration in the Boreidae, as long as 24 hours in B. hyemalis (Mickoleit, 1974). In B. hyemalis and C. dectes, at least, this prolonged copulation is necessitated by the secretion of a spermatophore which is retained within the male genitalia until the sperm is emptied into the female's genital tract.

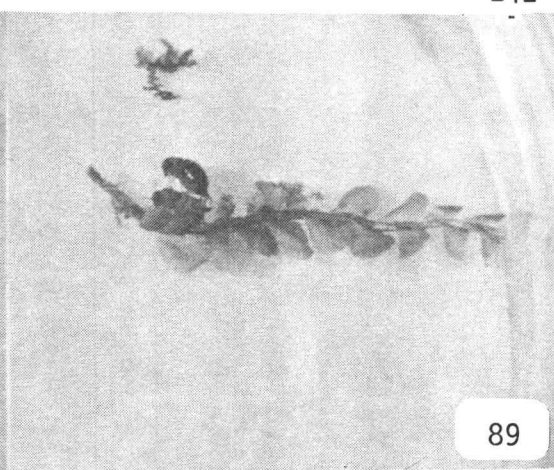
Although the behavior of the boreines precludes the existence of courtship feeding, this and other forms of male investment in

Figures 88-92. Mating and spermatophore of Caurinus dectes.

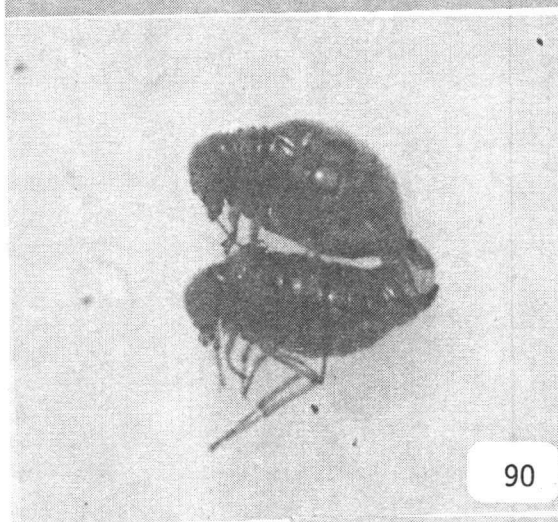
- 88) Mating pair of C. dectes, 30 minutes after first observation (25 March 1978).
- 89) Same pair, 1 hour later and just before separation.
- 90) Mating pair of C. dectes, preserved in copula. The left antenna of the female is grasped by the left wing of the male (250X).
- 91) Spermatophore of C. dectes, recovered from male after separation of mating pair (63X).
- 92) Everted aedeagal sac of C. dectes (160X).



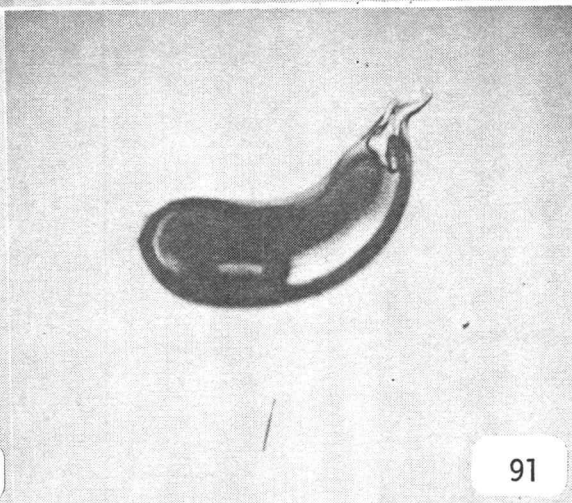
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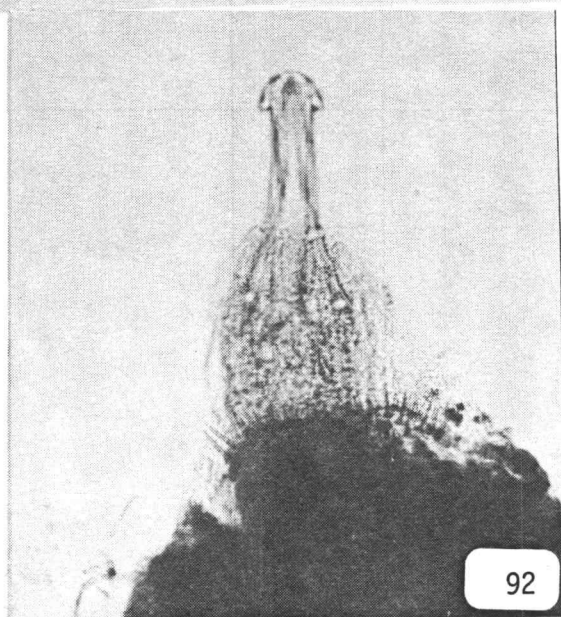
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reproduction are frequent in the Mecoptera (Thornhill, 1976). In addition to the well-documented presentation of prey in the Bittacidae (Thornhill, 1977), and production of saliva pellets by mating male Panorpa (Mercier, 1915; Gassner, 1963), there apparently is oral exchange of fluids in the Choristidae and Nannochoristidae (Tillyard, 1926). Male-produced sexual pheromones occur in the nuptial-feeding families Bittacidae (Bornemissza, 1964) and Panorpidae (Thornhill, 1973), and probably the Panorpididae (Brachypanorpa carolinensis males have an identical structure to the gland producing the pheromone in Panorpidae (Thornhill, 1973)). From the involvement of the female antenna with the dorsum of the male thorax in mating Caurinus, it is worth looking for evidence of a male pheromone in this genus also.

Cytology

The cytology of several species of Boreus and Hesperoboreus has been studied by Cooper (1940, 1951, 1974). Haploid autosomal complements in the species studied range from 11 to 14 in Boreus, while H. notoperates has 9 pairs of autosomes. The sex determination is via male heterogamety; males are X_1X_2Y in B. brumalis, but are XO in other known boreines, as in all other Mecoptera studied (Table 20).

An effort was made to determine the karyotype of Caurinus decetes (as well as, unsuccessfully, Boreus californicus and B. elegans) by means of lactic acid/orcein squash preparations. Since meiosis is precocious in this family (Cooper, 1951), it is necessary to examine last-instar larvae to obtain meiotic figures. Only one third-instar Caurinus larva was available for these preparations, and its gonads were not located by dissection. Although meiosis (and therefore the nature of the sex chromosomes) was not observable, mitotic figures were obtained by incubating brain tissue from this larva in insect Ringer's solution containing 0.5 percent colchicine.

The tissue was fixed in a drop of 45 percent acetic acid on a microscop slide, to which a drop of lactic acid-orcein was then added. A cover slip was placed on the preparation, and the slide

inverted on a pad of absorbent paper and the tissue squashed by steady pressure with the thumb until no further stain was expressed from the preparation. These preparations are not permanent, but can be studied for several weeks when ringed with fingernail polish. (This method was compiled from suggestions by P. R. Roberts, Oregon State University; and K. W. Cooper, University of California, Riverside, California).

Only a few metaphase mitotic figures could be located in the single preparation of Caurinus brain tissue. Figure 93 shows one of the two most complete and clearly spread figures. The karyotype cannot be definitely established from so few observations, but if this figure is complete, the diploid complement of this individual is 19. This odd number would indicate a male; if sex determination is $X0$ in C. decetes, the karyotype of this species would be n (male) = $9 + X(0)$, as it is in Hesperoboreus notoperates. Caurinus decetes and H. notoperates apparently differ in their chromosome morphology. In H. notoperates "the acrokinetic X is the largest chromosome of the set (from $7-9\mu$ long), being respectively two to five times the lengths of the largest and smallest autosomes" (Cooper, 1974). In the C. decetes individual reported here, there are two pairs of larger chromosomes; if this is a male, the X chromosome is quite short (Figure 93).

The chromosome number of Hesperoboreus and Caurinus is the lowest reported in Mecoptera (Table 20), although one "population of Nannochorista dipteroides also has a haploid number of about 9 (Bush, 1967). Only Panorpa spp., among reported Mecoptera, fall outside the range of chromosome numbers known in the Boreidae. The higher numbers of Panorpa, $n = 20-22 + X(0)$, were considered relatively specialized by Cooper (1951), although this was discounted by Atchley and Jackson (1970).

Table 20. Haploid chromosome complements in males of some Mecoptera. (from Kaltenbach, 1978, except for C. dectes).

<u>Species</u>	<u>n (male)</u>
<u>Merope tuber</u>	about 10 + X(0)
<u>Chorista australis</u>	14 + X(0)
<u>Nannochorista dipteroides</u> (two populations):	about 13 + X(0) 9
<u>Panorpa communis</u>	22 + X(0)
<u>P. cognata</u>	21 + X(0)
<u>P. germanica</u>	20 + X(0)
<u>Bittacus italicus</u>	13 + X(0)
<u>B. pilicornis</u>	14 + X(0)
<u>B. stigmaterus</u>	14 + X(0)
<u>Boreus hyemalis</u>	about 14 + X(0)
<u>B. nivoriundus</u>	15 + X(0)
<u>Hesperoboreus notoperates</u>	9 + X(0)
<u>Boreus brumalis</u>	11 + X_1X_2Y
<u>Caurinus dectes</u>	9 + X(0) (?)



Figure 93. Chromosomes of Caurinus dectes at metaphase in mitosis. From squash preparation of brain of third instar larva, treated with colchicine (0.5% in insect saline, 18 hours).

DISCUSSION AND CONCLUSIONS

Most of my goals for the description of the bionomics and morphology of Caurinus decetes (page 3) have been achieved in the foregoing chapters. I have shown that C. decetes is in many respects anomalous among the Mecoptera.

Caurinus is the smallest known mecopteran and is unique within the Mecoptera in many features of the adult anatomy. The nearly apodous larva is also quite distinct from all other known mecopteran larvae.

The life cycle and behavior of C. decetes can be considered more typically boreid than is the anatomy of this species. Caurinus resembles other boreids in the winter activity of adults, and in the bryophagous habits of adults and larvae. Caurinus differs from other Boreidae in feeding on liverworts rather than mosses, and in the endophytophagy of the larvae. The latter habit may be approached in the larvae of Hesperoboreus brevicaudus, however. In the laboratory the larvae of H. brevicaudus form feeding galleries in pleurocarpous mosses in a manner reminiscent of the feeding activities of Caurinus larvae in the apical growth of liverworts.

The information base developed here for Caurinus decetes can be summarized in functional terms as a likely series of co-adapted traits. These data can also be used to re-examine the phylogenetic position of Caurinus and to test previous opinions of the relationship of the Boreidae to other mecopteran families.

The functional and phylogenetic viewpoints are both involved in an assessment of evolutionary trends within the Boreidae. The presumed adaptive significance of some aspects of the life history, host relationships, and morphology of Caurinus decetes has been discussed separately in previous chapters.

A number of characters of Caurinus appear to represent the culmination of trends identified with the Boreidae as a whole. In several instances such characters can be linked in functionally related complexes. One important set of characters in which Caurinus has exceeded other boreids is reduction in overall size, number of

antennal segments, male ninth tergum and male wings. These reductions, together with the female ovipositor and "moss-feeding larvae" were cited by Penny (1975) as the major apomorphic characters separating Boreidae from panorpid-like ancestors. Although reduction in size often leads to reduction in meristic characters, it is actually unclear whether the antennal segmentation and male ninth tergites of the boreid ground plan are reduced from the condition occurring in Panorpididae and related families (see below).

Another extension of boreid trends in Caurinus is the great reduction of exposed membranes (Füller, 1954). This is expressed in Caurinus by the synscleritous abdomen, retracted genital segments and further obliteration of thoracic sutures. Finally, the curculioniform, internally-feeding larva of Caurinus is evidently derived from the scarabeiform boreine larva, which is itself reduced from the typical eruciform mecopteran larva.

A number of structural complexes have been discussed in functional terms above. Perhaps the two most remarkable departures in structure from the boreines, the rostrum and female genital segments, have both been related functionally to the dorsiventral differentiation of the liverwort hosts of Caurinus.

Phylogenetic position of Caurinus

In the description of Caurinus dectes (Russell, 1979) I placed it as the only species of the new subfamily Caurininae; the two other boreid genera (Boreus and Hesperoboreus) thereby constituted the subfamily Boreinae. This separation of Caurinus at a higher rank than genus was justified by the magnitude of the "morphological gap" and by a distribution of relatively generalized characters which "make a paraphyletic origin of Caurinus within the Boreus - Hesperoboreus lineage unlikely".

It is clear that Caurinus differs widely from other Boreidae in its holomorphology. The other implication of the above separation -- that the two subfamilies of Boreidae are each monophyletic -- can

not be inferred from the degree of morphological separation. In many respects Caurinus appears to differ from the Boreinae by further specialization from the boreine structural grade. Taxa which are exclusively defined through relatively primitive characters (synplesiomorphies) are often found to be paraphyletic with respect to the more specialized related group (Hennig, 1965).

One previous attempt to trace the phylogeny of the Boreidae (Lestage, 1940), resulted in the paraphyletic division of the relatively specialized Boreus (four European species including B. hyemalis) from Euboreus, including the American and most of the Asian species. However, Cooper (1972) showed that the grouping proposed by Lestage was artificial. Penny (1977) described Hesperoboreus with two western American species, leaving 21 species in Boreus. Penny defined each boreine genus with relatively advanced characters not found in the other. In addition to characters cited by Penny, I have found differences in the mouthparts of Hesperoboreus and Boreus (page 207). With Caurinus, Boreus, and Hesperoboreus each defined as a monophyletic taxon, there are three possible cladistic relationships of Caurinus to the other two genera (Figure 94).

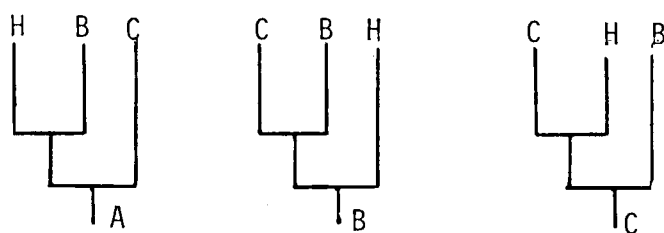


Figure 94. The possible cladistic relationships between the three boreid genera (C = Caurinus; B = Boreus; H = Hesperoboreus).

Of these possibilities, only "A", with Caurinus as the sister group of Boreus and Hesperoboreus would be consistent with the division of Boreidae into Boreinae and Caurinae. Possibility "B" is unlikely, since I have found no apomorphic characters linking Caurinus and Boreus, or Caurinus and any species group within Boreus.

On the other hand there are a number of characters common to Caurinus and Hesperoboreus, but not Boreus. Several of these characters are presumed to be apomorphic with reference to Boreus. Most of the latter are reductions (in antennal segments, ocelli, loss of outer spines of male forewing) which may be related to the small size of Caurinus and Hesperoboreus species. In several cases (number of ocelli and antennal segments; cerci of female), Hesperoboreus is intermediate between Caurinus and Boreus. The karyotypes of Caurinus dectes and Hesperoboreus notoperates may be similar, but this requires confirmation.

Although there is some morphological basis for placing Hesperoboreus as the sister-group of Caurinus, the characters which are plesiomorphic in Caurinus and synapomorphic in Boreus and Hesperoboreus (Table 21) are more numerous. The apparent plesiomorphies in Caurinus include some complex characters (free female cerci; dorsal sclerite of male genitalia) which are unlikely to have reverted to an ancestral condition. There is no consistent explanation for convergent evolution of the apomorphic states of these characters in Boreus and Hesperoboreus. It is extremely likely from these data, that the sister-group of Caurinus is Hesperoboreus and Boreus. Characters shared by Caurinus and Hesperoboreus are therefore either convergent, or were present in the boreid stem-species.

Relationship of Boreidae to other Families of Mecoptera

From the first separation of Mecoptera (as Panorptatae) from the Neuroptera, there has been frequent reference to the fossil record in the classification of the living forms. The correlation of fossil and living Mecoptera and their important position in the evolution of the Endopterygota was summarized by Tillyard (1935). Tillyard indicated a paraphyletic origin of the other panorpoid orders from within the Permian Eumecoptera after separation of the Protomecoptera (Meropeidae and Notiothaumidae). The Boreidae were

Table 21. Characters which are presumed to be relatively plesiomorphic in Caurinus and synapomorphic in Boreus and Hesperoboreus.

<u>Caurinus</u>	<u>Boreus</u> and <u>Hesperoboreus</u>
<u>Adult:</u>	
female cerci free, basally inserted	female cerci fused together; articulated with 10th tergum
female tergum ₁₁ entire	female tergum ₁₁ divided into two lateral "circum- apical sclerites".
dorsal aedeagal articulated with gonobases (homolog of "piston" of mecopteran sperm group).	dorsal aedeagal sclerite much reduced, not articulated.
prementum retractible, cranial labial retractor muscle and premental retractor apodemes present	prementum free but not retractable, cranial labial retractor muscle and retractor apodeme absent.
clypeolabral suture present (?)	clypeolabral suture absent.
<u>Larvae:</u>	
frontal hatching spine present	no egg-bursting structure present
placoid sensilla present in apical membrane of first antennal segment	no placoid sensilla on antenna
eyes composed of 7 stemmata	with 3 stemmata on each side of head
eleventh abdominal segment well-developed, forming clinging organ	eleventh segment not differentiated

supposed to have originated from small Permochoristidae.

A polyphyletic origin of the extant Mecoptera was also assumed by Hinton (1958), who placed the Boreidae in a separate order, the Neomecoptera. Cooper (1972) and Penny (1975) have shown that several of the characters emphasized by Hinton (e.g., supposed absence of cerci in Boreus) are not valid.

More recent authors (Byers, 1965; Penny, 1975, 1977; Mickoleit, 1978) have associated the Boreidae more or less closely with the Panorpidae and related families. Penny regarded the Boreidae as the sister group of the Panorpididae (Panorpodes and Brachypanorpa) on the basis of the scarabaeiform larva and phytophagous adults in these two families.

The principal reason for the varying treatments of the Boreidae in these classifications is the emphasis on characters of wing venation in determining the phylogeny of the Mecoptera. The cladistic analysis of the Mecoptera by Mickoleit (1978) (Figure 95) is based on characters of the female postabdomen, and is largely independent of previous classifications. As discussed above (page 232) these structures are apparently more plesiomorphic in Caurinus than in the Boreinae. I have accepted the basic argumentation by Mickoleit as probably correct. With data from Caurinus (present study), it seems appropriate to regard Boreidae as excluded from the "monophyletic assemblage" of the Panorpidae, Panorpididae, Apteropanorpidae, Notiothaumidae, and Choristidae. The possibility of a sister group relationship with the Meropeidae is not supported, while a sister-group relationship between Boreidae and Bittacidae seems possible. However, the latter grouping is hardly suggested by any other character complex.

The morphological isolation of the Boreidae is otherwise little affected by the addition of characters of Caurinus. Almost all of the morphological peculiarities of Boreus cited by Potter (1938) also occur in Caurinus. These include the lack of rectal glands, the panoistic ovarioles, and peculiarities of the male genital system associated with the production of spermatophores. Each of these could

be viewed as a primitive characteristic, compared with the state in other Mecoptera. The form of the dorsal aedeagal apodeme strongly suggests that absence of a sperm pump is not primary in the Boreidae.

Other character complexes, including the larval spiracles of the Boreidae, and the normally articulated mandibles of adult Caurinus are also difficult to evaluate as primitive or advanced characters. Although the relationships within the Mecoptera are becoming better known, the position of the Boreidae has yet to be established.

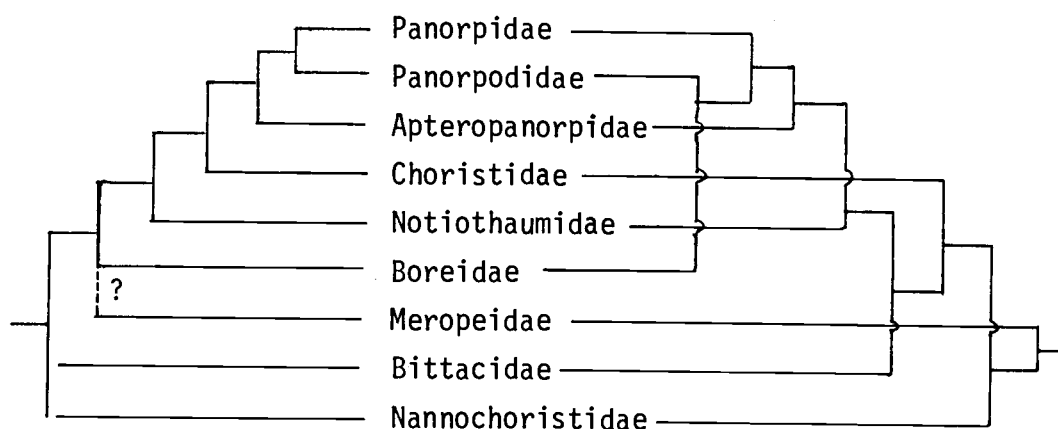


Figure 95. Comparison of phylogenetic classifications of the families of Mecoptera, by Mickoleit (1978) (left), and Penny (1975) (right). My study of Caurinus dectes supports a more isolated position of Boreidae, as posited by Mickoleit. The relative position of Boreidae and the other outlying families (Meropeidae, Bittacidae, and Nannochoristidae) remains indeterminate.

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APPENDIX I
AN ANNOTATED LIST OF BRYOPHAGOUS INSECTS
AND MITES IN WESTERN OREGON AND WESTERN WASHINGTON.

I have appended this list to my study of Caurinus dectes as a result of the numerous other insects encountered in bryophytes, and because of the general scarcity of information on bryophagous arthropods. (I have defined bryophagy here as the inclusion of mosses and liverworts as the principal food items for a species at one or more stages of its life history.) Most of the published records of bryophagy in insects are in the form of biological notes included in taxonomic papers. Such records are usually not indexed bibliographically, and it is frequently impossible to determine whether a feeding relationship may be assumed from such notes as "associated with mosses". I know of only one review of bryophagous arthropods (Gerson, 1969). The omission of such a major taxon as the Byrrhidae (Coleoptera) by the latter author emphasizes our incomplete knowledge of the bryophagous insect fauna.

I have included below only taxa which are known to occur in the Pacific Northwest, and which are known to occur in physical association with bryophytes. Most of these records are based on my personal observations. The arthropods cited here either have been observed feeding on mosses or liverworts in the laboratory, or meet one or both of the following criteria: 1) the taxon has been reliably shown to be narrowly bryophagous by previous workers, or 2) bryophytes have been identified in the gut contents of field collected specimens. My review has been limited to terrestrial insects and bryophytes. A number of aquatic insects are known to include mosses in their diets, but such feeding can rarely be separated from a generalized grazing habit (Glime and Clemons, 1972).

Bryophagous insects and mites:

ACARI

STIGMAEIDAE: Ledermuelleria spp. Adult and immature stages of one or more species of this genus are frequent in Tullgren funnel collections in western Oregon, but no species identifications are available. Gerson (1973) indicates that many if not most of the species of this world-wide genus are specialized to feed on mosses; frequently species of Ledermuelleria have narrow host spectra encompassing only one or a few genera of mosses.

PENTHALEIDAE: Penthaleus sp. The large, brightly colored mites of this genus are apparently all phytophagous, but none has previously been reported to feed on bryophytes. A Penthaleus species has been repeatedly encountered in bryophyte samples from western Oregon and western Washington. Specimens collected in Orthotrichum sp. at Marys Peak (Benton County, Oregon) were held for up to two weeks, and both adults and nymphs were observed feeding on the moss.

HOMOPTERA

APHIDIDAE: Aphids were collected from bryophytes on a number of occasions. The two species cited here identified by David Voegtlin (Department of Biology, University of Oregon), and are among the aphids cited as bryophagous by Mueller (1972).

Myzodium modestum. Many overwintering nymphs were collected on Polytrichum sp. at Waldo Lake, Lane County, Oregon on 10 September 1977.

Aspidaphium escherichi. This species was collected in mixed bryophytes, largely Rhytidiadelphus loreus, at Klahowya Campground, near Sappho, Clallam County, Washington, by Paul Johnson.

HEMIPTERA

TINGIDAE: Acalypta barberi
Acalypta saundersi

Both of these species are widespread in Oregon and Washington, and are recorded as "feeding and breeding in mosses" (Drake and Lattin, 1963). Adults and nymphs of A. barberi collected in Eurhynchium oreganum at

Heceta Head, Lane County, Oregon, fed on this moss for several weeks in the laboratory.

COLEOPTERA

BYRRHIDAE: Most species of this small family of beetles feed on mosses, although there are a few records of byrrhids feeding on liverworts and on vascular plants. In the Pacific Northwest only the genus Amphicyrta is known to feed principally or entirely on vascular plants. Paul Johnson (Corvallis, Oregon) has specialized in the study of the Byrrhidae, and many of the records below were provided by him or are based on work done by Mr. Johnson and the author jointly.

Exomella pleuralis

This species has been recorded from Rhacomitrium heterostichum (Johnson and Russell, 1978). Adults have also fed and oviposited on Eurhynchium oreganum.

Curimopsis albonotata

Curimopsis brevicollis

Both species of Curimopsis seem to be limited to higher elevations in this region. Curimopsis albonotata has been collected on Mt. Hood, Oregon, and C. brevicollis is known from Mt. Rainier, Washington. One specimen of C. brevicollis from northern Idaho was found to have moss in its gut.

Lioligus nitidus

Lioligus striolatus

It is questionable whether these forms represent separate species. Both forms occur in most mossy sites in the coastal forests of the Pacific Northwest; specimens referable to L. striolatus are more abundant in northwest Washington, while L. nitidus is the usual form in western Oregon. Observations of feeding in the laboratory indicate that Lioligus from both areas have very broad host ranges as adults and larvae. Adults and larvae from the Oregon Coast Range (mostly L. nitidus) feed freely on the following mosses in culture: Hylocomium splendens, Rhytidiadelphus loreus, R. triquetris, Eurhynchium oreganum, Hypnum circinale, Rhacomitrium heterostichum, and Plagiothecium

undulatum. Metaneckera menziesii was found to be unpalatable to adult Lioligus. A single specimen of Lioligus (referable to L. striolatus) was reared from egg to adult on the liverworts Diplophyllum plicatum and Scapania bolanderi. The Lioligus egg and the liverworts were collected at Verlot, Snohomish County, Washington. Adult Lioligus have otherwise failed to feed on S. bolanderi and other liverworts in the laboratory.

Lioon puncticeps

Lioon simplicipes

The two Lioon species are closely related and are nearly parapatric in their distribution. Both are eurytopic in coastal forests; adults and larvae occur in mosses in situations ranging from very wet, boggy soil to dry, epiphytic assemblages. The range of probable host mosses is also broad. Adults and larvae of L. puncticeps have fed on Dicranum fucescens, Rhytidiadelphus loreus, Antitrichia curtipendula, Eurhynchium oreganum, and Plagiothecium undulatum in the laboratory. The leaf lamellae and parts of the leaf tips of Polytrichum commune are also eaten by Lioon, but the tougher parts of this moss are not consumed by either adults or larvae of Lioon.

Listemus acuminatus

Listemus formosus

Both species of Listemus are usually found in mosses growing on soil, rocks, or logs, but do not occur in epiphytes as Lioon and Lioligus often do. Adults and the putative larvae of L. acuminatus have been maintained on Hypnum circinale, Plagiothecium undulatum, and Eurhynchium oreganum. The larvae of L. acuminatus have been found in nearly pure mats of Gyrothya underwoodiana and Nardia scalaris, but I have not seen them feeding on liverworts. In each occurrence it was possible that the larvae were feeding on the mosses which were present at low density in the mats.

Cytilus alternatus

This widely distributed boreal insect usually is found in open rocky sites in western Oregon, and often near seepages or waterfalls. Adults

of C. alternatus were reared by G. L. Peters (Corvallis, Oregon) from larvae found in moss at Marys Peak.

Byrrhus americanus

Byrrhus concolor

Byrrhus kirbyi

The genus Byrrhus is characteristic of the northern parts of the Holarctic Region, and each of the three species cited above has been collected only a few times in western Oregon. Moss has been noted in the guts of dissected museum specimens of all three of these Byrrhus species. One specimen of B. kirbyi, collected at Chinook Pass, Washington, continued to feed for some time on an unidentified moss (Paul Johnson).

ARTEMATOPIDAE: The two North American genera of this family, Eurypogon and Macropogon, have also been placed in the Dascillidae and as the Eurypogonidae. It is likely that all species of these two genera feed on mosses in the larval stage.

Macropogon testaceipennis

Macropogon piceus

Both Macropogon species occur in western Washington and western Oregon. Adults are usually found on trees or shrubs near moss-covered boulders or rock outcrops. Adults of M. testaceipennis are sometimes very abundant in prairie-forest ecotone on terminal glacial moraines in Thurston County, Washington. Macropogon larvae (species not determined) have been collected near Corvallis, Oregon, under Ceratodon purpureus; and under moss in sandy loam on a stream bank at Viento State Park, Hood River County, Oregon.

Eurypogon californicus

Larvae of Eurypogon have been collected under moss on exposed, south or southwest-facing rocks of road cuts at Marys Peak, Oregon, and along the Alsea River (Lincoln County, Oregon). The species occurring in the Pacific Northwest may not be E. californicus (fide K. W. Cooper, Riverside, California).

MECOPTERA

BOREIDAE: All boreids are apparently primarily bryophagous as adults and larvae; however there are a few records of Boreus larvae occurring under Selaginella (Lycopodiophyta). The distribution of species of Boreus and Hesperoboreus in western Washington and Oregon is shown in Map 2, page 29. Additional notes on the habitats and host ranges of these species are given below.

Hesperoboreus brevicaudus

This is primarily a forest species, where the larvae are usually found in epiphytic mosses. However, adult H. brevicaudus have also been found in thick, matted mosses on exposed rocks (Carpenterville, Curry County, Oregon; Oneonta Gorge, Multnomah County, Oregon); and larvae have been collected from moss on boulders in forest at Spencer's Butte (Lane County, Oregon). Adult H. brevicaudus have been observed feeding on Polytrichum sp. (leaf lamellae only), Mnium glabrescens, and Dicranum fuscens in the laboratory. Larvae have fed extensively on Funaria hygrometrica, Rhytidiadelphus loreus, Antitrichia curtipendula, and Plagiothecium undulatum in cultures (see page 115).

Boreus elegans

Adults of this species have been collected on moss on a north-facing road cut, in mosses near a hillside spring, and in moss growing on logs in a coastal forest. Adults have fed on Rhacomitrium heterostichum in the field and in the laboratory. Larvae and pupae were collected in deep soil under a mat of Brachythecium sp. and other mosses at Laurel Mountain, Polk County, Oregon.

Boreus californicus

The principal range of this species is east of the Cascades. In its occurrence in western Oregon, B. californicus appears to be more restricted to open, rocky sites than is B. elegans, although the two species occur together at Laurel Mountain, Oregon. Adults of B. californicus feed on Rhacomitrium heterostichum at Laurel Mountain. Larvae of B. californicus occurred in soil under mosses in the crevices of jointed basalt at Laurel Mountain, and in deep sandy loam of a

stream bank at Viento State Park, Hood River County, Oregon. The larvae were found under an unidentified moss growing in small patches among grasses.

Boreus reductus

Although B. reductus is chiefly known from semi-arid parts of the Pacific Northwest, specimens have been taken near the Cascade crest in eastern Washington (24 km east of Chinook Pass, Yakima County). Larvae of B. reductus have been collected in mats of Selaginella near Pullman, Washington (Penny, 1977), but also occur in association with mosses.

Caurinus decetes

As documented in this dissertation, C. decetes feeds in its adult and larval stages on many species of leafy liverworts (Jungermanniales).

DIPTERA

TIPULIDAE: Crane fly larvae are often common within mats of semiaquatic or terrestrial mosses. In some cases, as in some genera of the Cylindrotominae (Alexander, 1920), and in the tipuline genus Dolichopeza (Byers, 1963), the larvae are known to be bryophagous, feeding on live tissues of mosses or occasionally liverworts. Although I have no pertinent laboratory observations, I noted some crane fly larvae in apparent feeding association with mosses and liverworts in western Oregon. One tipulid larva was abundant within a mat of Nardia scalaris at Cascade Head, Tillamook County, Oregon. Several of the latter specimens were found to have green material in their guts, which was evidently derived from Nardia or from associated mosses.

CHIRONOMIDAE: Cricotopus sp.?

A large (to about 6 mm), yellow chironomid larva is abundant in samples of terrestrial, epixylic, and epiphytic liverworts in western Oregon and Washington. These larvae have fed on Porella navicularis, Calypogeja spp., Scapania bolanderi, Gyrothya underwoodiana, and Jungermannia rubra in the laboratory. In addition, Cricotopus larvae have been found in association with their feeding damage in Calypogeja fissa and J. rubra in the field. The generic identification of these larvae as Cricotopus is based on one female reared from J. rubra from Corvallis.

LEPIDOPTERA

MICROPTERYGIDAE: Epimartyria pardella

This is the only described species of micropterygid in western North America. However, at least one undescribed species of Epimartyria is included with E. pardella in my observations (fide John Heath, Merlewood Research Station, England). Larvae of Epimartyria feed on thalloid as well as leafy liverworts. The larvae are usually most abundant in seepage areas, where Pellia neesiana and Conocephalum conicum are the most conspicuous liverworts. Epimartyria also occur on moist rotting logs with Scapania bolanderi or with Calypogeja-Riccardia associations present. A single collection has been made from epiphytes, dominated by Porella navicularis, at Lewis and Clark State Park, Lewis County, Washington. All of the liverworts mentioned above, as well as Calypogeja fissa, Riccardia latifrons, Jungermannia obovata, and J. rubra, are fed on by Epimartyria larvae in the laboratory.

PYRALIDAE: SCOPARIINAE

Pyralid larvae and larval head capsules have repeatedly been found in moss from logs and deciduous tree trunks in the Oregon Coast Range. Feeding galleries, with webbing and fecal pellets among the damaged mosses, have also been located, in two instances with the larvae present. Hypnum circinale and Tetraphis pellucida are among the mosses which have been damaged in these galleries. The association of these pyralid larvae with the Scopariinae is based on the citation of European and Hawaiian species as bryophagous, and on the abundance of several species of Eudonia, Scoparia, and Cosipara as adults in mossy habitats of Vancouverian forests (Munroe, 1972). None of the American species of Scopariinae has been reared or associated with the larval food plants.

Summary:

With the inclusion of partially identified forms, the bryophagous insects listed above for western Oregon and Washington include at least 26 species, representing 18 genera, 11 families, and six orders. In addition, bryophagous mites belonging to two genera are listed from this region. Of the above, only three species (Caurinus dectes, Epimartyria pardella, and Cricotopus sp.) are definitely associated with liverworts. The single rearing of Lioligus striolatus from liverworts, and the occurrence of tipulid larvae in mats of terrestrial liverworts, show that it is possible for bryophagous species to include both major groups (mosses and liverworts) in their dietary spectrum.

The true diversity of bryophagous arthropods in the Pacific Northwest is certainly much greater than indicated by the list above. Only the Coleoptera and the Boreidae have been approached in a systematic manner; additional bryophagous species undoubtedly occur among the aphids, nematoceran flies, and Lepidoptera, while microarthropods have hardly been considered here. It is clear however, that even in this local fauna the incidence of bryophagy in insects is greater than is generally recognized.

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APPENDICES

APPENDIX II

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