AN ABSTRACT OF THE THESIS OF

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Title BIOLOGY AND FEEDING HABITS OF PLEOCOMA LARVAE (COLEOPTERA:SCARABAEIDAE) IN WESTERN OREGON CONIFEROUS FORESTS

Abstract approved [redacted] (Major Professor)

Food habits and biology of five species of Pleocoma larvae were studied at a dozen forested sites in western Oregon between May 1960 and December 1961.

First instar Pleocoma hatch in late summer and moult to second instars in early fall. Second and subsequent instars moult annually between mid-summer and early fall. Larvae appear to go through more than nine instars pupating after the seventh, in the upper 20 inches of soil, in mid-summer. Male larvae outnumber females by about 30 percent.

Larvae move through the soil primarily by use of the mandibles. This movement can exceed a rate of four inches a day.

Larval populations varied from none to 4.4 larvae per square foot and were distributed between two and 44 inches in depth. Soil temperatures and soil moisture influenced most larvae at some sites to leave the upper 16 inches of soil during the summer. At other

sites, however, a shallow silicate clay hardpan influenced larvae to remain at shallow depths throughout the year. A fungus disease killed from five to more than 20 percent of the larvae in some areas. Dipterous predators killed some larvae.

Coniferous roots comprise the major part of the larval diet throughout most of the year, being found exclusively in 86 percent of the larvae. Thirty percent of the roots in the guts were definitely identified as Douglas-fir, the predominant conifer at the sites of the collections. Larvae preferred smaller roots, mostly smaller than 2mm, many of them mycorrhizal rootlets. A few larvae merely girdled the roots, stripping the bark leaving the xylem in the soil. Most larvae, however, severed and consumed the entire root. Larvae either severed and ingested intact root segments or gnawed on root ends masticating them into very fine pieces before ingestion.

Except for last instar larvae, usually at shallower depths, and first stage larvae, neither of which appeared to feed on roots, all other larval stages at all depths were feeding on roots throughout the year, except during the moulting period. The cessation of root feeding extended over about a four-month moulting period from June to September, inclusive. The moulting period varied somewhat between species. Most larvae consumed the exuvia. Some soil, probably less than five percent by volume, was ingested.

Other material tentatively identified in larval guts was: remains of fungal hyphae, cast ventricular epithelium, gregarine parasites,

and bacteria.

Pleocoma larvae do not appear to be serious forest pests in old-growth and advanced second-growth coniferous forests because of the generally low and scattered larval populations. In newly-established forests, however, Pleocoma larvae are a potential pest as one or two feeding larvae can kill a small tree. Only further studies in re-generated areas will determine their role in these cut-over and re-established forests.

BIOLOGY AND FEEDING HABITS OF PLEOCOMA LARVAE (COLEOPTERA:SCARABAEIDAE) IN WESTERN OREGON CONIFEROUS FORESTS

by

DAVID GENE FELLIN

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APPROVED:

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Chairman of Department and Professor of Entomology
In Charge of Major

[redacted]

Dean of Graduate School

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Typed by Eula Weathers

This work is dedicated to

the memory of my Mother -

Mrs. Zilda Fellin

1905-1962

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BIOLOGY AND FEEDING HABITS OF PLEOCOMA LARVAE (COLEOPTERA: SCARABAEIDAE) IN WESTERN OREGON CONIFEROUS FORESTS

INTRODUCTION

The family Scarabaeidae has a long international history of economic damage to crops and trees, both above and below ground by adults and/or larvae. The subfamily Melolonthinae, for example, contains numerous species of serious pests. In Europe, Melolontha melolontha L. has been known for more than 100 years as a destructive pest of crop roots while May beetles, Phyllophaga spp., are perhaps the most destructive members of the subfamily in North America. The Japanese beetle (subfamily Rutelinae) has ravaged crops in the Northeast since its introduction into the U. S. in 1916.

Scarabs are also internationally well known for their destructiveness in coniferous forest nurseries and plantations. Abroad, second-year Anomala larvae are injurious to roots of young coniferour trees in Japan (46, p. 113-115; 48, p. 114), while in France, adult Melolontha melolontha L. injure forest trees (52, p. 674). In Canada, white pine transplants have been damaged in Manitoba, Saskatchewan, and Quebec (7).

In New York State, Phyllophaga larvae damage young evergreens both in nurseries and reforestation plantings (62, p. 176) often completely eliminating seedlings or transplants from relatively small areas (28, p. 944; 75, p. 842).

In the Lake States, increasing acreages of new plantings are being treated to control Phyllophaga grubs (2, p. 8) which frequently kill trees and are sometimes very destructive to forest plantations (59, p. 103). Many of these plantations were established in Michigan on vast areas of cut-over and burned land between 1932 and 1938 (21, p. 261-262). In Wisconsin, as much as 25 percent of entire stands in a nursery have occasionally been destroyed (64, p. 429) and the killing of 10 to 15 percent of the trees is not unusual.

In the Southeast, damage by white grubs, chiefly Phyllophaga spp., in forest nurseries has been a serious problem for many years (73, p. 148-149), annual losses having been variously estimated at from 25 to 40 percent of the original stock of pine seedlings (33, p. 1). Though serious white grub injury to field-planted pine seedlings has been reported (77, p. 77) damage to plantations is apparently an exception or has often gone unnoticed (81, p. 710).

In the Southwest, June beetle larvae were damaging western yellow pine in nurseries and field plantings at the Fort Valley Experiment Station north of Flagstaff, Arizona, in 1911 and 1912. Five to 15 percent of the transplants in the nursery reportedly were killed in 1912 (49, p. 354).

In the West, white grubs have not been considered important on forest trees but with much current investigation in forest management being concentrated around forest regeneration and young-growth

management (53), some damage has become apparent. In 1959, larvae of the 10-lined June beetle, Polyphylla decemlineata (Say) killed about 30 percent of the trees in a new plantation of Christmas trees near Olympia, Washington (6, p. 20). In 1961 June beetle larvae were responsible for the death of an estimated 1.9 million three-year-old Douglas-fir seedlings planted in 1959 in a forest nursery near Oakridge, Oregon.

In Oregon, Pleocoma (subfamily Pleocominae) larvae have been known for some ten years to be serious pests of orchard trees in the Hood River Valley (15, p. 3-10; 56, p. 41-42) and at The Dalles (13, p. 431).

In February, 1960, William I. Stein, a U. S. Forest Service Research Forester found Pleocoma larvae feeding on roots of one- and two-year-old conifer seedlings in experimental seedbeds east of Roseburg, Oregon (74, p. 134). This was the first confirmed record of Pleocoma larvae feeding on roots of forest tree seedlings.

Prior to 1960 there had been scattered and unconfirmed reports of larvae of the genus feeding on coniferous roots in other parts of the West, but evidence was only circumstantial. Of at least one species, it has been said that "Nothing at all is known about the feeding habits of Pleocoma dubitalis dubitalis larvae even though the species is found associated with Douglas-fir" (55, p. 183). This statement could apply to at least two other species, P. simi and

P. carinata, of the total of six species now known to occur in western Oregon.

Accelerated emphasis on forest regeneration in the West means that factors responsible for mortality of young trees will be increasingly important. Newly established seedlings are prone to insect damage, as they are to disease and drought. Hence any insect feeding on any part of young trees is a potential pest. Since little was known of the feeding habits or biology of Pleocoma larvae in the forest environment, and since they appear to be a potential forest pest, this study was initiated.

The study had two objectives. The first was to study the biology and ecology of Pleocoma larvae under forest conditions, especially their movement, habits, and distribution and the way in which environment affects this behavior. A second objective was to observe larval feeding habits under natural conditions in the soil of some western Oregon coniferous forests; specifically to determine what relationship exists, if any, between Pleocoma larvae and the roots of coniferous trees.

EXPERIMENTAL PROCEDURES

When the study began, P. dubitalis dubitalis Davis[1] was known from some three dozen sites in northwestern Oregon. Less than a dozen sites were known for P. simi, all between Eugene and Selma, south of Grants Pass, and only two sites, both east of Medford, were known for P. carinata. As the study progressed, new sites were located for P. simi and P. carinata by following up reports of adults in flight during the fall months submitted by amateur entomologists and foresters. With one exception, (Site #39)[2] P. dubitalis was studied only at McDonald Forest, five miles north of Corvallis (Site #32); P. simi and P. carinata were studied in several areas (Appendix Table 1).

Collection times differed for each species studied. Once a month, beginning January 1961 (a few collections were made prior to this date) and ending December 1961, P. dubitalis was collected at Site #32 (Appendix Figure 2). From June 1960 until December 1961, collections of P. simi and P. carinata were so timed that over a period of one calendar year collections were spaced every 1-1/2 months and every two months, respectively. Collections of P. minor and P. crinita in the Hood River Valley were made as time permitted.

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[1] Hereinafter referred to merely as P. dubitalis.

[2] Site numbers refer to Appendix Figure 1 and Appendix Table 1.

The exact spots at which the sample holes were dug were arbitrarily chosen in the general area where adults had been seen. The sampling unit, or sample hole, was three feet square and dug no less than 30 inches deep but at least six inches below where the last larva was found.[3] Any hole dug to a depth of 30 inches with no larvae having been found was abandoned and further holes dug until a minimum of six larvae had been collected. The depth at which larvae were collected was measured to the nearest inch and later grouped into four-inch classes. Other researchers collecting scarab larvae (14, p. 104; 67, p. 666; 25, p. 87; 76, p. 693) have followed similar procedures in determining depth of sample holes. A sample hole is shown in Figure 1.

Larvae collected were handled in one of two ways. Some larvae were killed and preserved so an analysis of their gut contents could be made. Other larvae were kept alive in metal salve tins for experimentation.

Studies of Larval Biology

In the laboratory, all larvae, and eggs from which small larvae were obtained, were reared in salve tins lightly packed with sifted soil. The salve tins were kept in a temperature cabinet

[3]Some sampling units, early in the study, were not according to these specifications.

consisting of an ordinary household refrigerator equipped with a fan and heating unit to maintain constant temperature. Cabinet temperature was changed periodically to simulate soil temperature 30 inches deep at the McDonald Forest study area. It was difficult to provide field conditions in the laboratory, because, as pointed out by Hayes (27, p. 7), white grubs have a unique habitat beneath the soil surface.

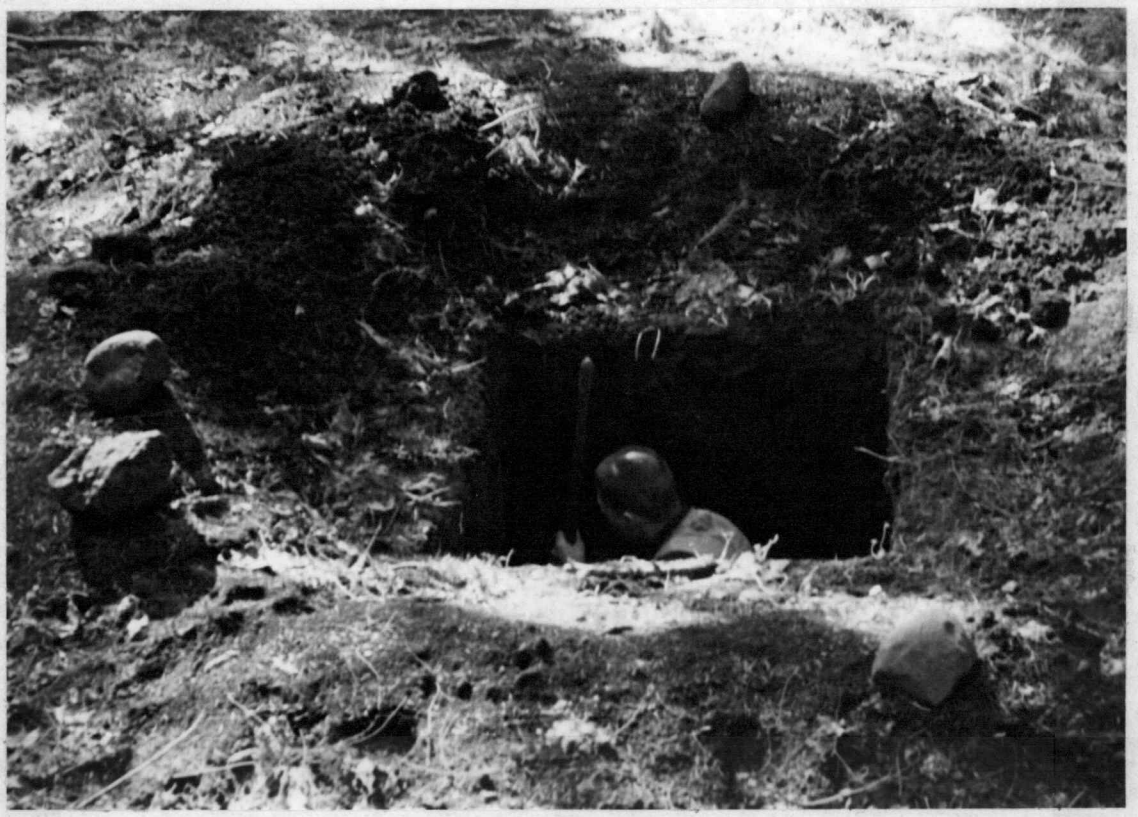

Figure 1. A typical larval sample collecting hole three feet square and 48 inches deep.

Head capsules of larvae were measured at the widest point on the dorsal aspect with a stereo dissecting microscope, one ocular of which was equipped with a calibrated micrometer ruled into ten

divisions of ten fine units each. Each fine unit was equivalent to 0.15mm. All head capsules of preserved specimens were dry when measured; no measurements were made with specimens submerged in preserving medium. Live and active larvae were subjected to a small amount of CO_2 to render them inactive while measuring.

The range of head capsule width for first and second instar Pleocoma larvae was established in a manner similar to that used by Ellertson and Ritcher (15, p. 22). That is, several larvae were preserved shortly after hatching and measured to establish a range for the first instar. Other larvae were allowed to moult after which they were preserved and the head capsules measured.

All larvae were sexed according to techniques described for some scarabaeid larvae by Menees (43, p. 97-100) and Hurpin (30, p. 104-107). Larvae in which that portion of the abdomen bearing sexual characters was damaged were not considered in determining sex ratios. The applicability of their methods with Pleocoma larvae was confirmed when sexed larvae pupated, in which stage sex is readily determined (15, p. 24).

Movement of Larvae

From 1 May to 31 October 1961, P. dubitalis larval movements through the soil were studied at McDonald Forest. Larvae were collected in the immediate area where the study was conducted and

brought to the laboratory. Here they were measured and marked so one could readily identify individual larvae in following their movements through the soil.

In marking the larvae, each was pierced in one of its many fleshy areas, particularly along the meso-ventral line of the thorax or abdomen, with a minuten nadeln (Figure 2A). The pin was removed immediately after the exoskeleton had been punctured. Darkening of the haemolymph upon exposure to air as a result of the action of phenol oxidase enzyme (tyrosinase) (86, p. 91) left a very obvious mark (Figure 2B) by which each larva could be definitely identified.

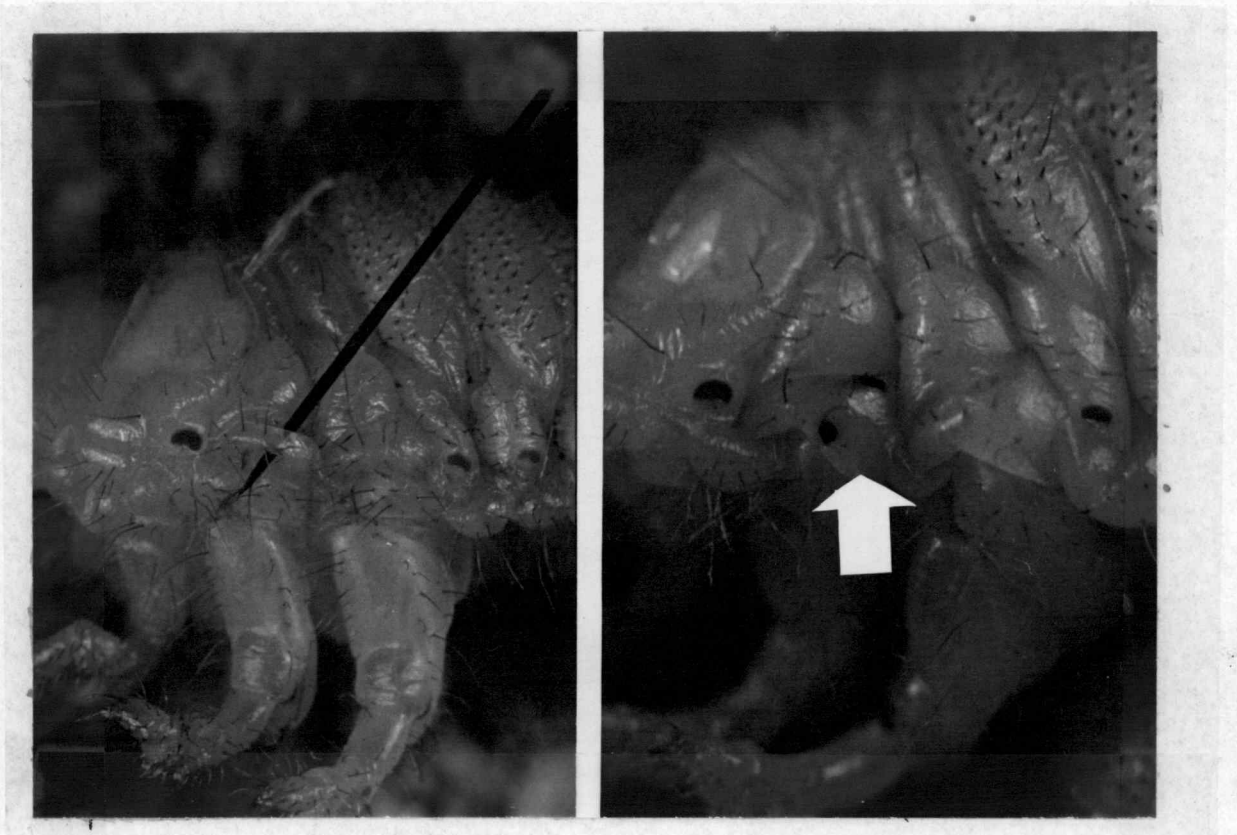

Figure 2. Technique used to mark Pleocoma larvae. (A) (Left)--Thoracic area of sixth-seventh instar P. dubitalis showing minuten nadeln thrust through fleshy lobes at base of mesothoracic leg (9X). (B) (Right)--Thoracic area of seventh-eighth instar P. dubitalis showing two black spots (arrow) in fleshy lobes near base of mesothoracic leg, caused by darkening of haemolymph where lobes were punctured by minuten nadeln (9X).

By marking larvae on different segments or on different parts of similar segments, numerous marking combinations were achieved so larvae were not confused with one another. As long as the larva was not pierced too deeply, the puncture being kept as far out on the lobe as possible, no ill effects on the larvae were noticed.

Marked larvae were returned to the field, and placed in small niches in the side of an old sample hole which had not been refilled with soil. The niches were then covered with a salve tin lid (Figure 3A). After a week, lids were removed and the soil dug away until the larvae were recovered and identified (Figure 3B).

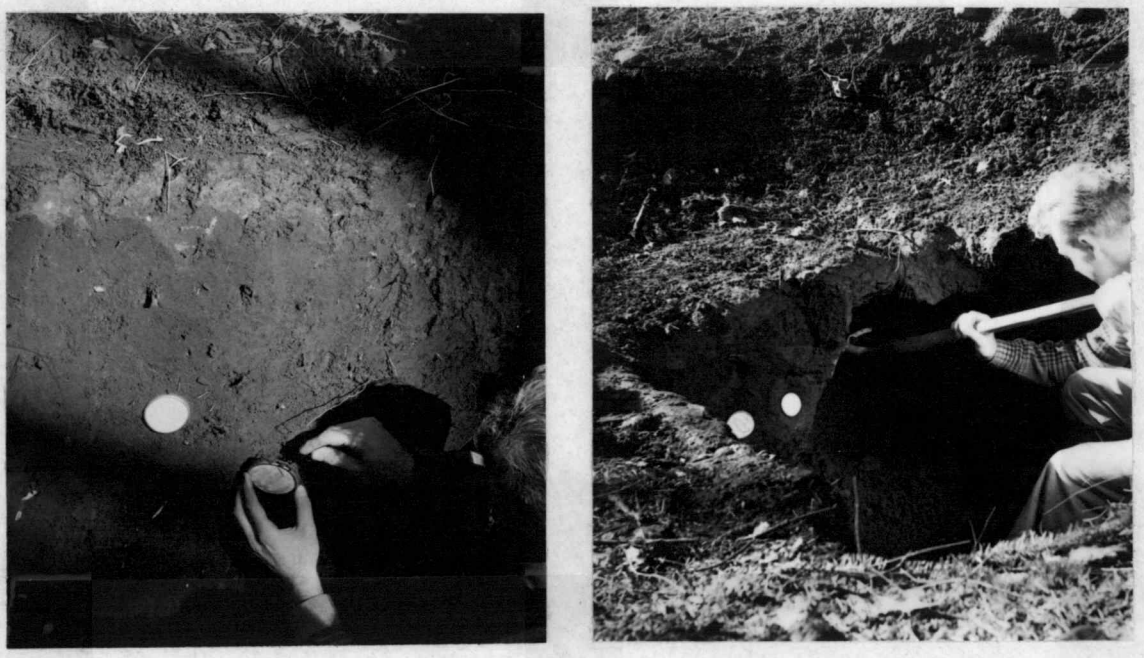

Figure 3. Technique used in studying movement of larvae in the soil. (A) (Left)--A larva being placed in a small niche provided for it in the side of an old sample hole and the niche being covered with a salve tin lid. (B) (Right)--Searching for Pleocoma larvae which had been marked and placed on the side of the sample hole one week prior.

Since one cannot follow the paths of Pleocoma larvae through the soil, an arbitrary method was used to determine how far larvae travelled. Vertical and lateral measurements were taken between the point at which larvae were released and the point of recovery and two distances computed: (1) the distance a larva would have travelled had it gone straight into the soil and then at a right angle downward, upward or to right or left, and (2) the distance travelled had it gone a direct route from the point of release to the point of recovery (the hypotenuse of the right triangle). I used the average of these two as an estimate of the distance travelled during the week, and then computed an average rate of movement per day. Because Pleocoma larvae often follow winding paths through the soil, the average rate of movement as computed is probably conservative.

Density of Larvae

The primary objective in collecting was to gather as many larvae as possible to study their feeding habits and biology. Therefore, the number and location of sampling units was purposively, not randomly selected. The sites at which larvae were collected were restricted to areas where larvae were known to occur or where adult males had been taken in flight. Recognizing the difficulty ".... of computing reliable population figures unless a proper statistical method is adopted to interpret the results" (36, p. 122), I agreed

that "Site selection and the size and number of samples and subsamples.....must largely be the responsibility of the individual worker" (36, p. 116) and that "....there should be purposeful selection of sample-unit placement to as full an extent as there is sound basis afforded by prior knowledge, accurate observation and good judgement;..." (34, p. 274).

Hence, with the disjunct distribution of Pleocoma larvae and the wide area over which the five species were collected, I was confronted with the rather common conflict, as discussed by Richards (54, p. 156), between a desirable sampling program and what is physically possible for the entomologist.

The difficulties and absence of optimum or suitable statistically designed sampling procedures notwithstanding, data were collected on absolute densities (frequency per unit area (45, p. 249)) as they are the only data available on abundance of Pleocoma larvae in forest soils.

Measurements of Soil Characteristics

Soil samples were collected at four depths from each sample hole dug, and analyzed for soil moisture content. The amount of water present in the soil was expressed in percentage based on dry soil as outlined by Lyon and Buckman (39, p. 151). Briefly their technique consists of mixing, weighing and air drying 100 grams of

soil which is then heated for 7-8 hours in an oven at 100-110°F., cooled in a dessicator and weighed.

Soil samples for determination of soil pH were collected in one-pint waxed cardboard containers at four depths in each sample hole dug. Measurements of pH were made with a Beckman model N portable pH meter equipped with micro electrodes. A two-gram soil sample was suspended in 2ml of distilled water in a 5ml beaker and allowed to stand for one hour. The electrodes were then immersed to within a millimeter or two of the bottom of the beaker, and the reading was made. All measurements were made using a buffer of pH 7, but any sample reading below 5.5 was rerun at once using a buffer of pH 4 to get a more accurate reading.

Soil temperatures were measured with an ordinary immersion type 110°C. etched-stem thermometer thrust laterally into the soil at least two inches, and left for at least five minutes before being read.

Studies of Larval Feeding Habits

Early in the study each larva, as it was removed from the sample hole, was killed in hot water and placed in a vial of 70 percent alcohol. Later, as the gut contents proved to be mostly woody material, the procedure was modified and the larvae were taken from

the hole and placed at once into FAA[4].

At the laboratory, each larva was dissected, and a qualitative examination made of the contents of the alimentary canal. Gross dissections were made under a dissecting microscope with magnifications of 9 to 27X, with specimens pinned out under FAA. Gut contents were classified into one of four groups; roots, exuvia, soil, and other material. Roots were identified, measured, and examined for type of damage done by the feeding larvae.

From the larvae taken at each collection, six larvae were purposively (8, p. 6) selected to represent the range in size of larvae and the range of depths over which they were collected. The stomodaeum was removed intact from each of the six larvae. Keeping the stomodaeum intact insured that none of its contents, expecially the small woody particles would be lost during dehydration and embedding processes (Figure 4).

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[4]Formalin-Aceto-Alcohol mixed as follows: ethyl alcohol (95%), 50cc; glacial acetic acid, 10cc; formalin (30-40%), 20cc; distilled water, 35cc. This mixture was modified from standard formulations often presented (60, p. 16) in that the amount of acetic acid was decreased and the formalin increased, a procedure recommended for hard woody material to increase the penetration of the fluid (32, p. 41).

Figure 4. Stomodaeum being transferred from vial to vial during dehydration procedures. Note large pieces of roots protruding from caudal end of crop held tightly and prevented from being lost by the thin almost transparent intima, the innermost membrane of the stomodaeal wall (2X).

Each stomodaeum was washed twice in 50 percent alcohol, dehydrated with Dioxan as outlined by Sass (60, p. 30) and embedded in 56-58° paraffin. The embedded stomodaea were soaked, to soften the woody material, in a solution of glycerin and a detergent[5] for four to six weeks at approximately 37°C.[6] after which they were sectioned immediately or stored in water in a refrigerator until needed. Longitudinal serial sections of the stomodaea were cut at ten microns on a rotary microtome, placed on one- by three-inch glass slides and stained with safranin and fast green as recommended and outlined by Johansen (32, p. 62, 80-82). Each slide was scanned with a low-power objective of a binocular compound microscope; important taxonomic characters were critically examined with higher-powered

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[5] Dreft, 1 gram; water, 90ml; glycerol, 10ml.

[6] Alcorn and Ark (1, p. 55-56) recommend exposing part of the embedded material by cutting away the paraffin and soaking in the softening solution for two or three days.

objectives. A slide bearing several stomodaeal serial sections is shown in Figure 5A. Approximately 775 such slides were prepared in order to identify all roots in the 150 Pleocoma stomodaea examined.

Roots were categorized into three classes in the phylum Tracheophyta subphylum Pteropsida:[7] Filicineae, ferns; Gymnospermae, gymnosperms; and Angiospermae, angiosperms or flowering plants, (further subdivided into Monocotyledoneae and Dicotyledoneae).

Gymnospermae were identified by the presence of large bordered pits[8] in the tangential walls of the xylem tissue (Figures 5C, 6), a well-known and characteristic feature of the class (50, p. 65) and the absence of wood vessels.[9] With the exception of only aberrant representatives in three families (31, p. 373), Angiospermae are characterized anatomically throughout by the presence of wood vessels. Filicinae also are characterized by the possession of vessels, but are distinguished from angiosperms in that fern

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[7] Classification after Simpson et al. (68, p. 478).

[8] Some angiosperms have bordered pits but they are not easily confused with bordered pits found in the gymnosperms. Angiosperm bordered pits are generally smaller. The torus, so characteristic of gymnosperm bordered pits, occurs only rarely in the angiosperms (16, p. 45) and when it does it is so thin it is hard to demonstrate.

[9] In the Gymnospermae, wood vessels are found in the Gnetaceae (Gnetales) but this family is restricted to the warmer parts of the Hemisphere and does not occur in the forests of western Oregon.

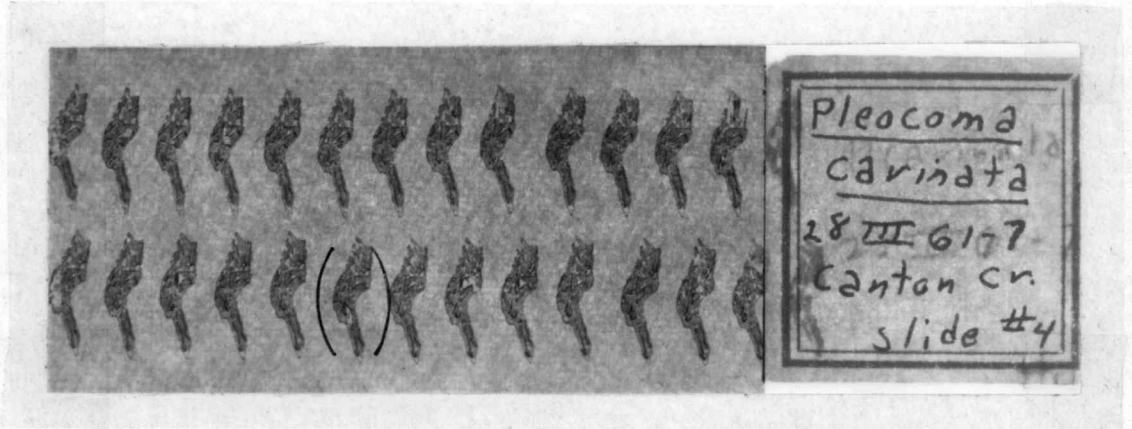
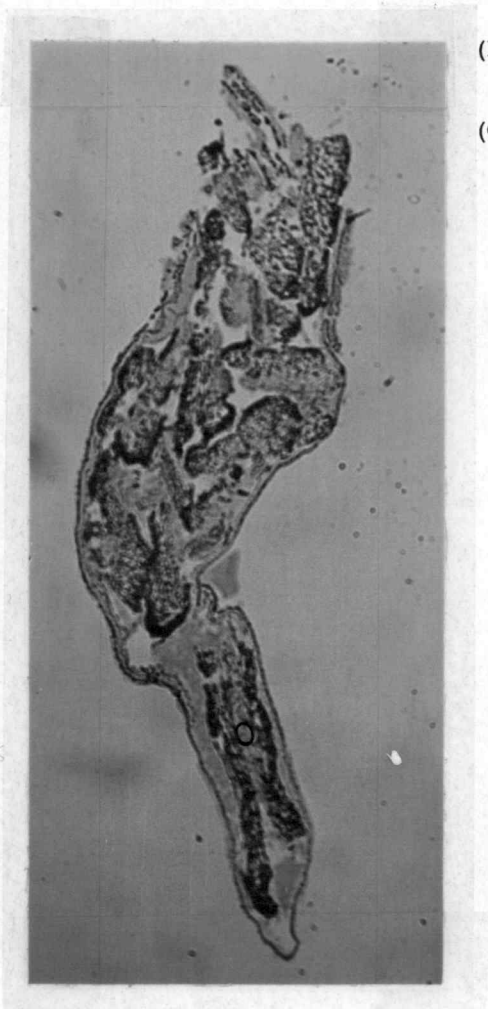


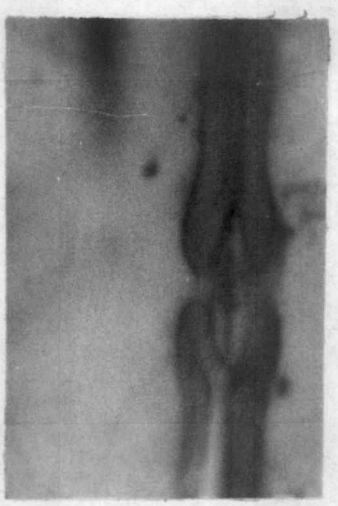
Figure 5. Sectioned Pleocoma larval stomodaeum mounted on glass slide.

(A) Above--One- by three-inch microslide with serial sections of a portion of the stomodaeum of a medium-sized P. carinata larva (1 3/4X).

(B) Left--An enlarged view of one of the sections (encircled) shown in the figure above (12X).

(C) Below--Photomicrograph of sectional view of a coniferous bordered pit-pair. Note the darker torus lying just to left of center on the vertical pit membrane between the pit apertures. This pit pair was observed under high magnification in the xylem tissue (encircled) of the root lying lengthwise in the oesophagaeal area of the stomodael section shown in the figure at left. These large bordered pits, with tori on the primary wall (pit membrane), are distinguishing features of the conifers (2800X).





vessel elements usually have scalariform perforations over the entire vessel while angiosperms usually have perforation elements confined to ends of vessels.

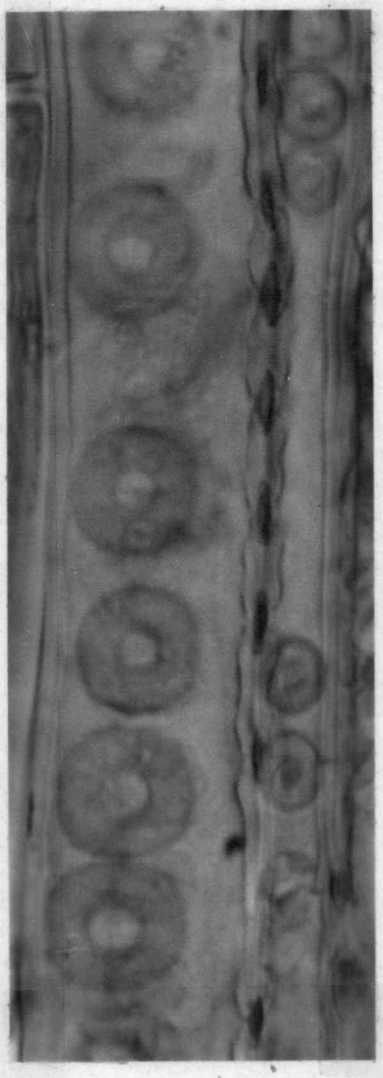


Figure 6. Photomicrograph of coniferous bordered pits in both face (left) and sectional (right of center) view observed in the xylem tissue of a coniferous root consumed by a Pleocoma larva. (1100X)

Several factors (i.e., small and masticated roots) made it difficult to identify most roots in the stomodaea more specifically than to the class level. One exception was the ability to distinguish Douglas-fir roots (Gymnospermae) by the presence of spiral thickenings which are "....a constant feature in the longitudinal (and ray) tracheids of Douglas-fir (5, p. 139). Although other species of conifers also possess spiral thickenings to some degree they either do not grow in Oregon or, if so, no larval collections were made within their range.

BIOLOGY OF THE LARVAE

Many aspects of the biology of P. dubitalis, P. carinata and P. simi investigated during this study were found to be similar to the biology of P. crinita, P. oregonensis and P. minor already investigated (14, 15). However, biological information presented is new, only a few observations having been published on the biology of P. dubitalis (55).

Hatching

In the laboratory, P. dubitalis larvae began hatching from 76 field-collected eggs on 21 August and continued until 21 September. P. dubitalis larvae emerged from laboratory-laid eggs between 29 August and 20 September. In 1954 Ritcher and Beer (55, p. 183) observed 24 P. dubitalis larvae to hatch from field-collected eggs between 28 August and 8 September. A year later these authors report 13 P. dubitalis larvae to emerge from laboratory-laid eggs between 1 and 24 September.

P. carinata larvae began hatching from 43 laboratory-reared eggs on 3 September and continued until 8 September.

Moulting

Pleocoma larvae prepare a cell in the soil in which they

moult. The cell is usually cylindrical, rounded on the ends and often horizontal. If sloped at all, larvae usually lie with the head in the higher end of the cell. P. dubitalis larvae almost always lie on their dorsa while moulting, often assuming this position a day or two before. Upon splitting the old head capsule, the newly-moulted larva extricates itself from the exuvia through movements of the body. Some larvae remained on their dorsa for two days after moulting.

Twenty-three first stage P. carinata larvae, hatching in the laboratory from eggs deposited by two field-collected females, moulted approximately 33.5 days following hatching. Larvae moulted between 5 and 12 October.

Seventy first instar P. dubitalis, 35 hatching from field-deposited eggs and 35 from laboratory-deposited eggs, moulted approximately 31 days after hatching. First instar P. dubitalis larvae from field-collected eggs moulted between 21 September and 20 October while those from laboratory-deposited eggs moulted between 30 September and 17 October.

Second instars and older P. dubitalis larvae usually moult at the time of year shortly before first instars begin hatching. About 55 P. dubitalis larvae, field-collected between 24 July and 22 August 1961, were placed in a constant temperature cabinet and observed daily to note dates of moult. The first larva moulted on 19 August and the last on 25 September. Most larvae, 46 out of 55 or 84

percent, moulted between 26 August and 17 September.

Younger larvae seem to be the first to moult. Of 16 larvae which moulted prior to 1 September, 94 percent were fifth instars or younger and 69 percent were fourth instars or younger.

All Pleocoma larvae may not moult each year. Out of 60 P. dubitalis larvae collected between 24 July and 22 August 1961, 14, or 23 percent, did not moult between the time they were collected and when observations were discontinued in the laboratory on 15 October. All but one of these non-moulting larvae were seventh instars or older and all were males.

Besides the apparent failure to moult by these older larvae, some first instars apparently failed to moult as well. First instar P. dubitalis and P. carinata were observed daily from eclosion until 30 October and 6 November, 10 and 25 days, respectively, after the last larva of each species moulted. Of 80 first instar P. dubitalis reared in the laboratory, five, or 6.3 percent, failed to moult. Twenty-one of 46, or 45.6 percent, first instar P. carinata failed to moult.

Hence, Pleocoma larvae foregoing a moult appear to be only the very young and the relatively old.

Sex Ratio

Male larvae of P. dubitalis, P. simi, and P. carinata

outnumbered female larvae by 31, 28, and 26 percent, respectively (Table 1). Sex ratios presented in Table 1 were computed on the basis of all larvae of the three species collected.

Table 1. Larval sex ratio of three species of Pleocoma collected in the field.

Species	Number of larvae examined	Number of males	Number of females	Sex ratio males: females
P. dubitalis	446	253	193	1.31:1.00
P. simi	114	64	50	1.28:1.00
P. carinata	77	43	34	1.26:1.00

To compute larval sex ratio for progeny of individual females, six groups of larvae were available, each group representing part of larger egg clutches collected from six different females. Male to female sex ratios for first instars of two species, (Table 2), range from a high of 2.22 to 1.00 to a low of 1.09 to 1.00.

Table 2. First instar sex ratio of two species of Pleocoma.

Species	Number of larvae examined	Number of males	Number of females	Sex ratio males:females	Oviposition in:
P. dubitalis	25	15	10	1.50:1.00	field
	41	22	19	1.16:1.00	field
	23	12	11	1.09:1.00	laboratory
	29	20	9	2.22:1.00	laboratory
P. carinata	22	12	10	1.20:1.00	laboratory
	22	14	8	1.75:1.00	laboratory

Number of Instars

Number of Instars of P. dubitalis

Head capsule measurements for 118 first instar P. dubitalis ranged from 1.95 to 2.55mm, and 92 second instars ranged from 2.25 to 2.55mm. The range of measurements for first and second instar P. dubitalis so overlap that there is no distinct difference between the two instars (Figure 7A).

Since the largest head capsule width for a second instar was found to be 2.55mm, the peak at 3.15-3.30mm (Figure 7A) is probably that for third instars. Though this is a relatively well-defined peak, an interpretation from the histogram of the range of any given instar beyond the second, for which we have defined the limits, would be somewhat subjective.

Though peaks may characterize some instars, extremes of the range for each instar tend to merge. It was possible, however, by rearing larvae through a moult, to get two head capsule measurements on individual larvae, one prior to and one after the moult. Assuming that the peak at 3.15-3.30mm represents third instars, and using this as a starting point, the head capsule measurements have been arranged into reasonably discrete groups (Table 3). From data in Table 3 and the frequency histogram in Figure 7A, P. dubitalis larvae are tentatively classified into instars in Table 4, with

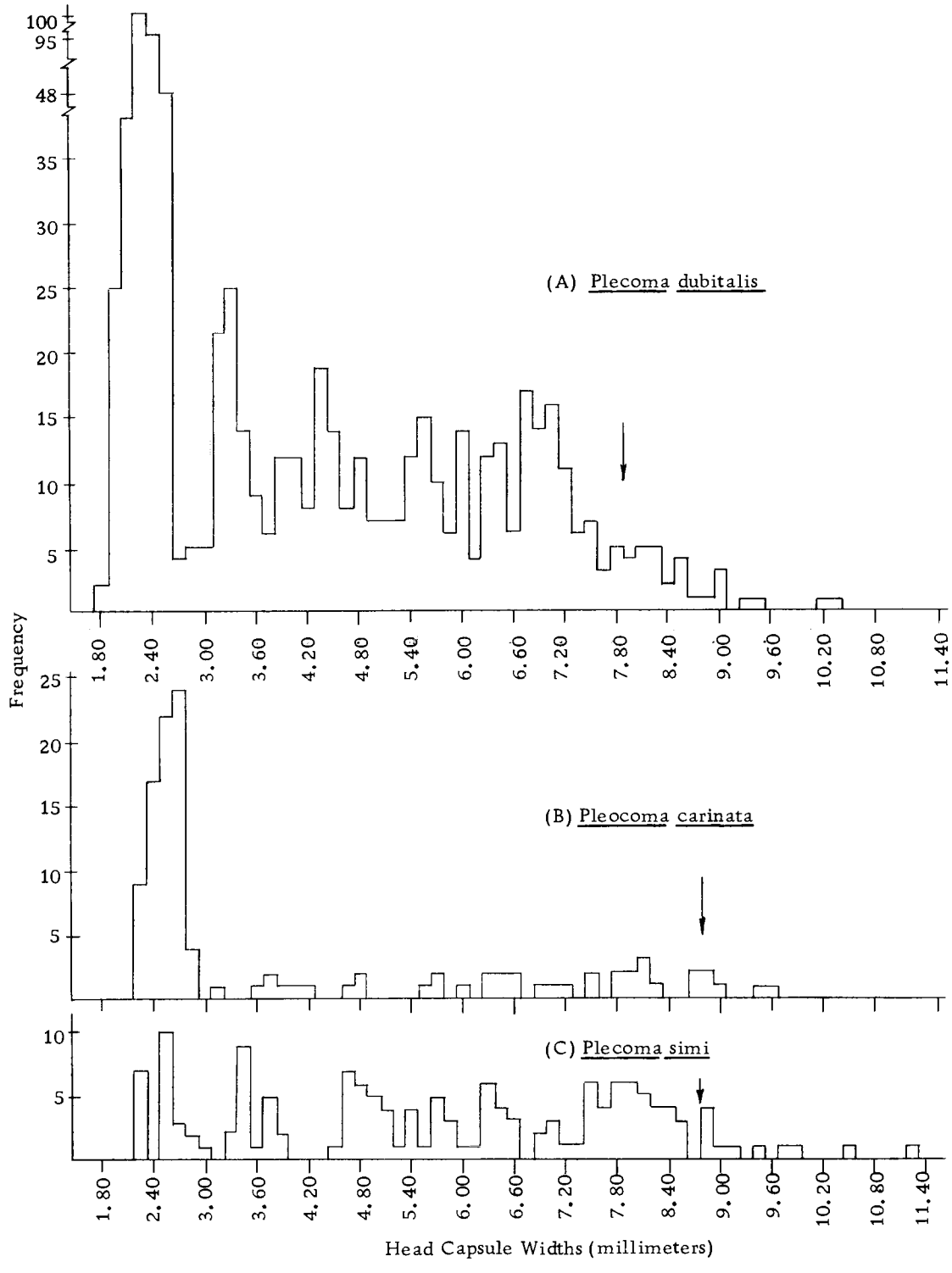


Figure 7. Frequency histograms of larval head capsule widths for three species of Pleocoma. Portions of histograms to left of arrows represent both male and female larvae, portions to right represent females only.

Table 3. Head capsule measurements of P. dubitalis larvae made before and after moulting during the summer of 1961.

Head capsule width (mm) and tentative instar--			Head capsule width (mm) and tentative instar--		
before moult	after moult	Increase (mm)	before moult	after moult	Increase (mm)
2nd instars	3rd instars		5th instars	6th instars	
2.40	2.85	0.45	4.35	5.55	1.20
			4.35	5.70	1.35
3rd instars	4th instars		4.35	6.00	1.65
3.00	3.75	0.75	4.50	5.40	0.90
3.00	3.75	0.75	4.50	5.55	1.05
3.15	3.60	0.45	4.50	5.70	1.20
3.15	3.90	0.75	4.50	5.70	1.20
3.15	3.90	0.75	4.65	5.85	1.20
3.15	4.05	0.90	4.95	6.00	1.05
3.15	4.05	0.90			
3.15	4.05	0.90	6th instars	7th instars	
3.15	4.20	1.05	5.55	6.00	0.45
3.15	4.20	1.05	5.55	6.60	1.05
3.30	4.35	1.05	5.70	6.75	1.05
3.30	4.50	1.20			
			7th instars	8th instars	
4th instars	5th instars		6.00	7.50	1.50
3.60	4.65	1.05	6.30	6.90	0.60
3.75	4.50	0.75	6.30	6.90	0.60
3.75	4.80	1.05	6.30	6.90	0.60
3.75	4.95	1.20	6.30	7.05	0.75
3.90	4.65	0.75	6.45	7.05	0.60
3.90	4.80	0.90			
3.90	4.95	1.05	8th instars	9th instars	
3.90	4.95	1.05	7.05	7.95	0.90
3.90	5.10	1.20			
4.05	4.80	0.75			
4.05	4.80	0.75			
4.05	5.40	1.35			
4.20	5.25	1.05			

minimum and maximum head capsule widths given. Data are too few to make even an estimate of the range of head capsule widths for instars beyond the eighth.

Table 4. Minimum and maximum head capsule widths for some tentative instars of Pleocoma dubitalis.

Tentative instars	Head capsule width (in mm) minimum	maximum
1	1.95	2.55
2	2.25	2.70
3	2.85	3.45
4	3.60	4.50
5	4.35	5.40
6	5.25	6.00
7	6.00	6.75
8	6.75	7.50

Number of Instars of P. carinata and P. simi

First and second instar P. carinata larvae appear to be generally larger than P. dubitalis. Range in head capsule measurements for 44 first instar P. carinata was 2.25 to 2.55mm, and 23 second instars ranged from 2.55 to 2.85mm. Like P. dubitalis, the range of measurements for first and second instar P. carinata overlap.

First and second instar P. simi larvae are generally smaller than P. carinata but larger than P. dubitalis. Head capsules of seven first instar P. simi measured 2.25mm. Head capsule width of thirteen second instars averaged 2.58mm.

It was not possible to categorize P. simi and P. carinata into

instars beyond second as only relatively few larvae were available for study. The wide range of head capsule measurements (Figure 7B and 7C) indicates that both species probably pass through many instars as do other species of Pleocoma.

Sexual Differences in Number of Instars

All larvae were sexed at the time head capsules were measured. There was no appreciable difference in larval head capsule widths between sexes in the earlier instars. However, without exception all larger larvae were females. Shown in Figure 7 are the head capsule widths above which all P. dubitalis, P. carinata and P. simi larvae were females.

Furthermore, all larger P. crinita and P. minor larvae collected were females. No male P. crinita larvae were collected with head capsules larger than 7.65mm (ninth or tenth instars according to Ellertson and Ritcher (15, p. 23)); three larger larvae were all females. The three largest P. minor larvae collected, all with head capsules greater than 7.95mm, were all females.

Since there appears to be no difference in larval head capsule widths between sexes in the earlier instars, these observations indicate that female Pleocoma larvae develop through more instars than males before pupation.

Pupation

Pleocoma dubitalis larvae appear to pass through at least seven or eight instars before pupating. Six larvae which pupated had head capsules ranging from 6.45 to 8.25mm as follows:

Sex	Head capsule width (mm)	Instars
male	6.45	7th
male	6.75	7-8th
male	7.05	8th
female	7.95	9th-larger
female	8.10	9th-larger
unid.	8.25	9th-larger

It is of interest to note from the tabulation that the three smallest larvae to pupate were all males and that two (possibly all three) of the largest were females.

P. dubitalis larvae pupate toward the end of July, becoming inactive several weeks prior to the transformation. In 1961, larvae pupated between 20 and 31 July. Two larvae became completely inactive 41 and 72 days, respectively, before pupating. There are indications that some larvae become inactive as much as six months prior to pupating.

In the forest environment, P. dubitalis larvae pupate at relatively shallow depths in the soil. On 22 July 1954, Ritcher and Beer (55, p. 184) found three P. dubitalis pupae at depths of 7, 7.5 and 9.5 inches, respectively, at McDonald Forest. Further observations at

McDonald Forest during this study show larvae pupated at the following depths:

Date of collection	Depth of pupae (inches)
27 July 1960	5.5
27 July 1960	5.5
25 August 1960	14.5
25 August 1960	20.0
28 January 1961	13.0
28 June 1961	16.0
13 September 1961	6.0

This depth of pupation is generally shallower in the soil than depths at which most larvae are found. With the exception of five prepupal larvae, all larvae collected at McDonald Forest between June and September in 1960 and 1961 were deeper than 17 inches.

Natural Control Factors

When this study began, no parasites or predators were known from any species of Pleocoma.[10] Observations made during this study indicate that a fungus disease and a larval predator may account for some larval mortality.

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[10] Collembola and mites have been reported associated with dead and living Pleocoma larvae in the vicinity of Hood River, Oregon, but whether either acted adversely toward the grubs was not known (14, p. 100).

Fungus Disease

A fungus identified as Beauvaria sp.[11] had killed from 5 to 22 percent of the P. dubitalis larvae collected in 1961 at McDonald Forest. Infected larvae were collected in situ in their soil burrows. Diseased larvae were collected at all times of the year and at depths ranging from 6 to 38 inches. All instars appeared to be susceptible to the disease. No diseased P. simi or P. carinata larvae were collected.

Some laboratory observations indicate that the fungus may develop quite rapidly in Pleocoma larvae even in the relatively cool forest soil. In from three to seven days at 48-52°F., Beauvaria infection progressed in some Pleocoma larvae from a state of apparent non-infection as shown by the larva in Figure 8B to a condition such as that shown by the larva in Figure 8A.

Predaceous Diptera

Some observations were made indicating Diptera can kill, or at least feed on, P. dubitalis larvae in the soil.

Occasionally P. dubitalis larvae were collected bearing

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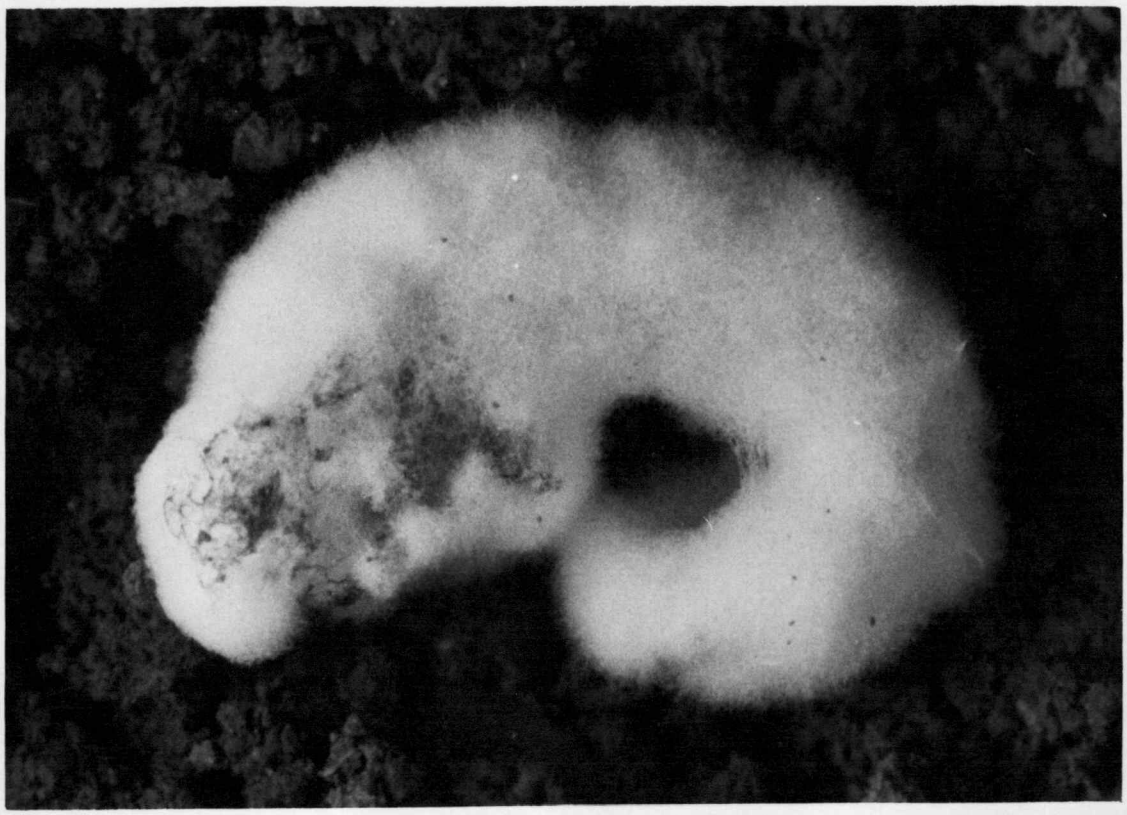
[11] Dr. Clarence A. Thompson, Insect Pathologist, Forestry Sciences Laboratory, U. S. Forest Service, Corvallis, Oregon, identified the fungus as Beauvaria globulifera (Spegazzini) Picard or B. bassiana (Balsama) Vuillemin.

(A) Second instar P. dubitalis killed by Beauvaria sp. (12X).

(B) Normal and healthy small P. simi larva (11X).

Figure 8. Diseased and healthy Pleocoma larvae.



discolored or blackened areas on one or more parts of the abdomen. On two occasions a dead or dying larva was collected with an asilid[12] larva in the burrow immediately adjacent to the grub. In both cases the Pleocoma larva appeared as that shown in Figure 9. One grub had a hole in its thorax where the predator had been feeding.

Figure 9. A seventh-eighth instar P. dubitalis showing discoloration in the abdominal midsection and several blackened areas apparently caused by feeding of a predaceous asilid larva (6X).

[12] Identification of this asilid larva was confirmed by Dr. P. O. Ritcher, Head, Department of Entomology, Oregon State University, Corvallis, Oregon.

Asilid larvae may exert some natural control on Pleocoma larvae in the soil. Though only two grubs were found to have been killed, asilid larvae were collected in eleven sample holes representing four sites. The asilids were generally found in the same general strata where Pleocoma larvae were collected. Asilids are a natural enemy of Phyllophaga larvae (10, p. 89-96) and are known to feed chiefly on larvae of other insects in the soil (4, p. 615).

Other Factors

There are some indications that ants and centipedes may kill some Pleocoma larvae in the soil. During this study, both of these arthropods killed grubs placed in the soil for experimentation. Whether they kill grubs in the soil under natural conditions is not known. Ants are known to feed on white grubs in the Southeast (78).

Movement of Larvae

Method of Movement

Larvae move through the ground by biting away soil in front of them with their mandibles and depositing it to their rear as they move. Each bite of soil is held beneath the thorax by the thoracic legs. When a sufficient quantity of soil is deposited there, the larva, holding the soil by its legs, mandibles and maxillae, turns 180° and

deposits this soil in the rear of the burrow. Here it is packed against the back wall, presumably with the aid of secretions from the mouth which help cement this soil to fill the burrow behind. The movement of Pleocoma larvae is very similar to that observed with Phyllophaga (22, p. 379). Cells removed intact from the soil reveal on their edges an interesting pattern of marks made by mandibles of the larvae (Figure 10).

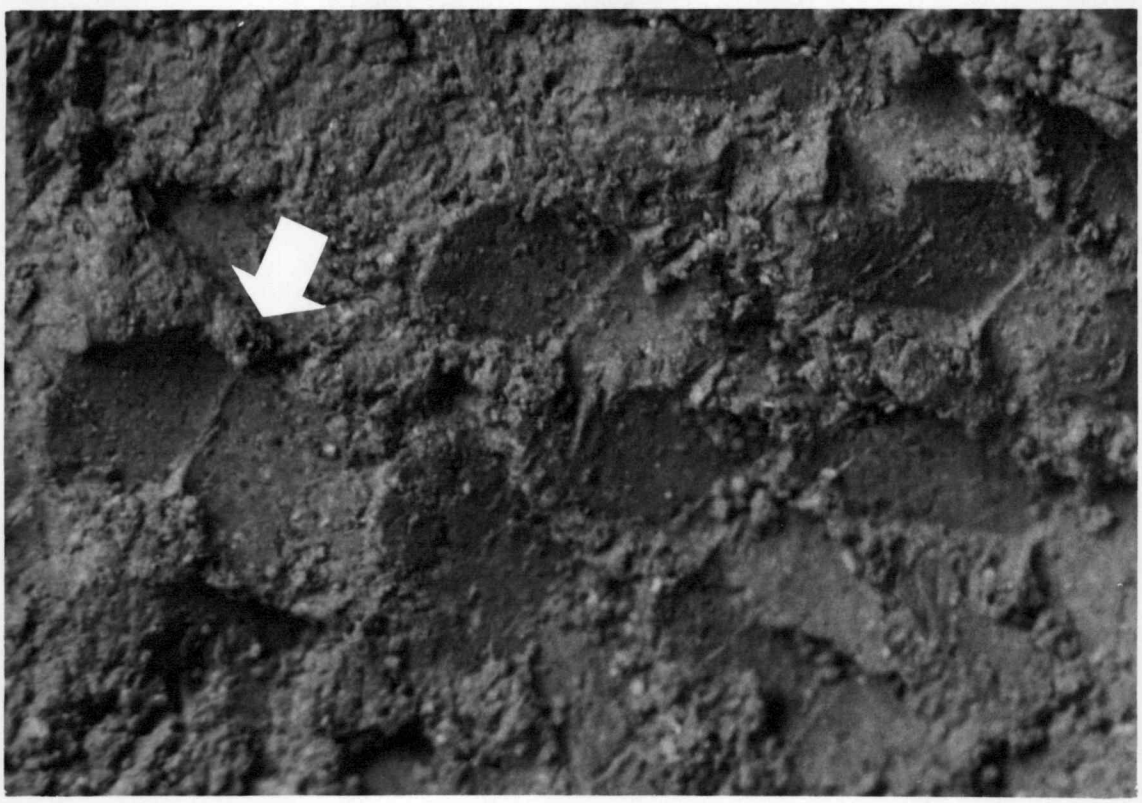
Body movements through the soil are dependent mainly on a sort of three-point touch. By manipulating the dorsum of the abdomen, the anal area and the thoracic legs the larva is able to move through an open burrow fairly rapidly by pressure of these three points against the walls of the burrow (see Figure 24). Larvae are well adapted for this type of movement by possessing many spine-like setae dorsally on most abdominal segments and around the anus where the caudal segments contact the soil. Necessity of three-point contact is realized when one observes the helplessness of larvae in trying to move on a flat surface.

Larvae maintain some distance of open burrow behind them, the length of which often varies with depth, direction, size of larva, or time of year. Fifth instar Pleocoma have been found with as much as four inches of open burrow behind them.

(A) Portion of a P. simi larval cell halved lengthwise to show the pattern made along the edges of the cell by the mandibles of the larva (2.5X).

(B) Close-up view of a portion of the cell pictured above to show marks made by individual pairs of mandibles. The arrow points to a narrow ridge of soil formed at the point where each mandible of a pair come together (12X).

Figure 10. Larval cell showing pattern made by mandibles while larva moved through the soil.



Rate of Movement

Rate of movement of various instars of P. dubitalis through the hard compact forest soil is presented in Table 5.

Table 5. Rate of movement of P. dubitalis larvae through the soil from early May to late October 1961 at McDonald Forest.[a]

Approximate instar	No. of larvae	Average rate of movement (inches per day)
2	9	0.33
3	6	1.55
4	2	0.27
5	2	3.48
6	3	0.68
7	3	1.96
8	4	1.83
9-larger	8	1.18

[a]No data are included for larvae preparing for, or recovering from, a moult.

The fastest movement was by a fifth instar which, during the period from 27 April to 18 May moved an average of 4.36 inches per day. Two other larvae moving more than three inches per day were a seventh and an eighth instar which travelled 3.59 and 3.09 inches per day, respectively, during June.

Time of Year of Movement

A rather slow rate of movement for second instar P. dubitalis explains why one often finds these young larvae in groups, often not

having dispersed[13] much from the area of oviposition. First stage larvae do not burrow away from the egg niches. Second instar P. dubitalis were found in egg niches in mid-November 1960. Hence second instars do not begin movement until sometime after mid-November.

Most larvae were active during the period from 1 May to 31 October when movement was intensively studied, and periodic observations from 1 November to 31 April indicate most larvae to be active during this period as well. Between early August and late October, especially during September, there is a general period of larval inactivity when larvae are moulting or pupating. However, the period during which larvae are moulting and pupating is so long that some larvae are in movement at all times even during this period.

There was considerable variation between larvae in the number of days each ceased and resumed burrowing before and after moulting, respectively. Some larvae slowed little in their movements prior to moulting; others ceased movements entirely for as much as 21 days prior to the moult. Following the moult, some larvae began burrowing almost immediately while others remained motionless for as much as 24 days before they travelled again.

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[13] The word 'dispersal' is used here as defined by Schneider (61, p. 223) to mean a lengthening of the mean distance between neighboring individuals.

Moulting, especially the shedding of the hind and fore portions of the alimentary canal and tracheae ". . . . is a difficult operation which compels the insect to cease activities for a short period of time" (20, p. 109).

Direction of Movement

Of 46 larvae studied, 31 travelled predominantly downward during their period of movement. Two travelled down and then up and one larva went up first and then down. Six larvae travelled horizontally and the direction which six travelled is not known.

Pleocoma larvae do not travel for any length of time in any particular direction. Open burrows behind larvae indicate that in a relatively short distance of two to four inches they may have travelled several directions. For example, one medium-sized P. simi larva was found with four inches of open burrow behind it. In this distance it had travelled upward, turned a bit, leveled off, then turned twice more on a generally flat plane. Other Scarabaeidae larvae also change direction of movement, often doubling back in the direction from which they had burrowed (23, p. 414; 26, p. 504).

There is no evidence that Pleocoma larvae migrate, in the sense of recent reviews (85, p. 163; 61, p. 223) that there is a continued or prolonged movement in a direction and at a rate over which they have control with a temporary or permanent change of

habitat. Movement of Pleocoma larvae beneath the ground could probably be explained in a more realistic way in terms of dispersal, defined (61, p. 223) as a lengthening of the mean distance between neighboring individuals.

Vertical Distribution of Larvae

P. dubitalis larvae were collected at McDonald Forest once each month during 1961. The depths at which larvae were collected, with some data from 1960, and the number of larvae in each four-inch depth class are presented in Figure 11. Concerning the data in Figure 11: (1) Larvae were generally absent from the upper 16 inches of soil during the summer months from May to September, inclusive; (2) Only five larvae, all of a size large enough to pupate, were found shallower than 16 inches between May and September; (3) Larvae were generally deeper in the soil in July than in any other summer month. In July no larvae were encountered shallower than 24 inches, with the exception of two; (4) Between October and April, inclusive, December excepted, most larvae were fairly well distributed vertically through the soil. The general accumulation of larvae at lower depths in December is unexplained; (5) Out of 176 larvae represented in Figure 11, 134, or 76 percent were collected in a 20-inch stratum between 17 and 36 inches in depth.

Vertical distribution of P. simi larvae from eight collections

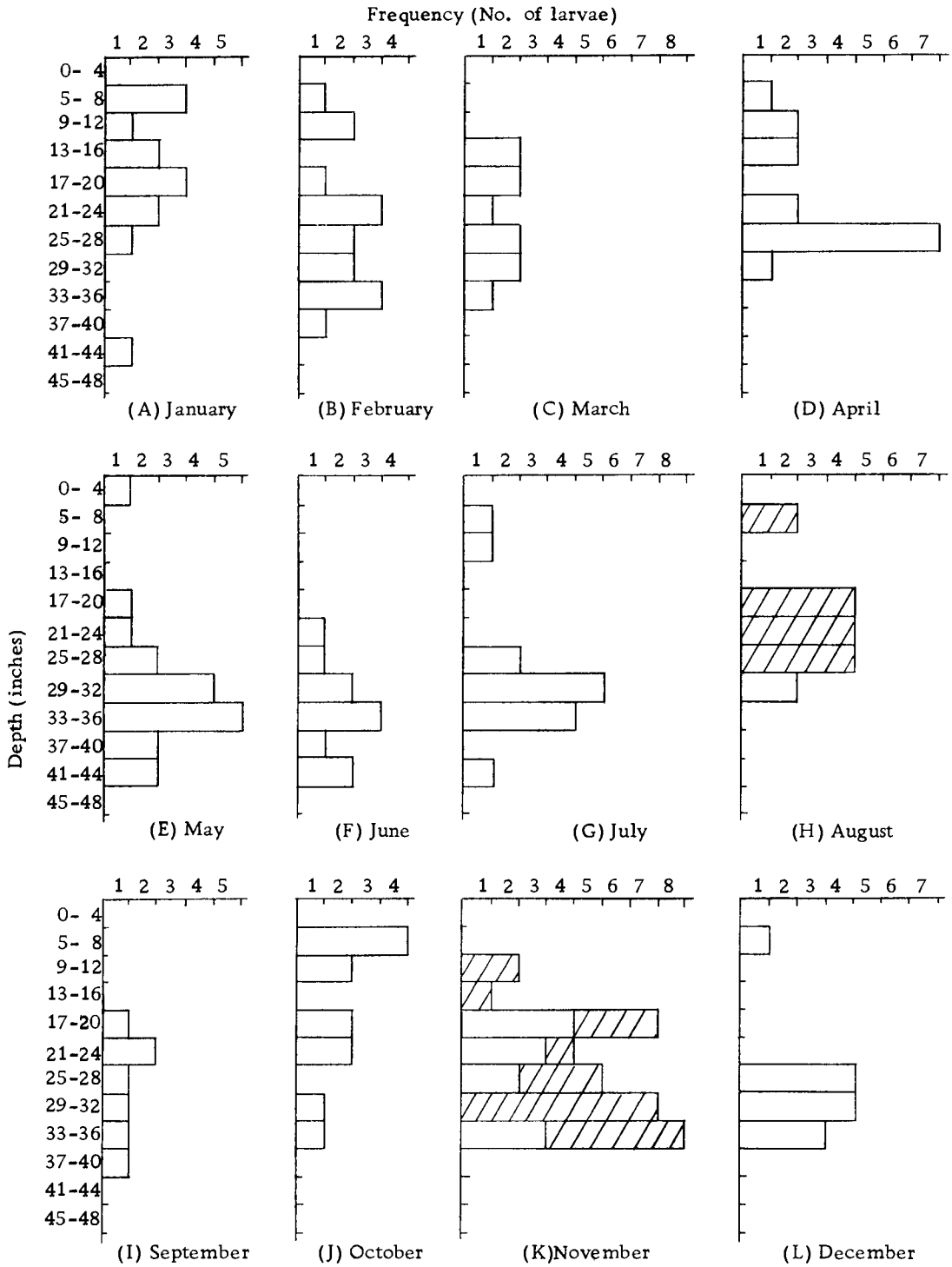

Figure 11. Vertical distribution of Pleocoma dubitalis larvae in the soil at McDonald Forest in 1961. (Hatched blocks indicate larvae collected in 1960).

at five sites is presented in Figure 12. These data too, reveal some interesting characteristics: (1) Frequency distributions A and B in March and May, respectively, show an extreme congregation of larvae at an eight-inch stratum between 25 and 32 inches. In no other P. simi collection was there such a striking example of larval accumulation by depth. (2) Larvae presented in distribution C were taken in December at the same site as those in distributions A and B. No accumulation of larvae at the lower depths was evident in December. Larvae collected at this time were generally evenly distributed by depth between 9 and 44 inches. (3) Though collected in five different months and from four different sites, larvae presented in distributions D-H are all generally shallow, mostly above 24 inches in depth. (4) P. simi larvae collected in the four summer months (June to September) were generally shallow in the soil (mostly above 20 inches) while P. dubitalis larvae collected during the summer months were generally deeper in the soil, usually below 16 inches (Figure 11 F-I).

P. carinata larvae were collected at relatively shallow depths in the soil. Nineteen larvae collected at site #2 were generally less than 20 inches deep in the soil and seven collected at site #8 were shallower than 28 inches.

The maximum depth at which P. simi and P. dubitalis larvae were found--44 inches--is considerably shallower than the maximum

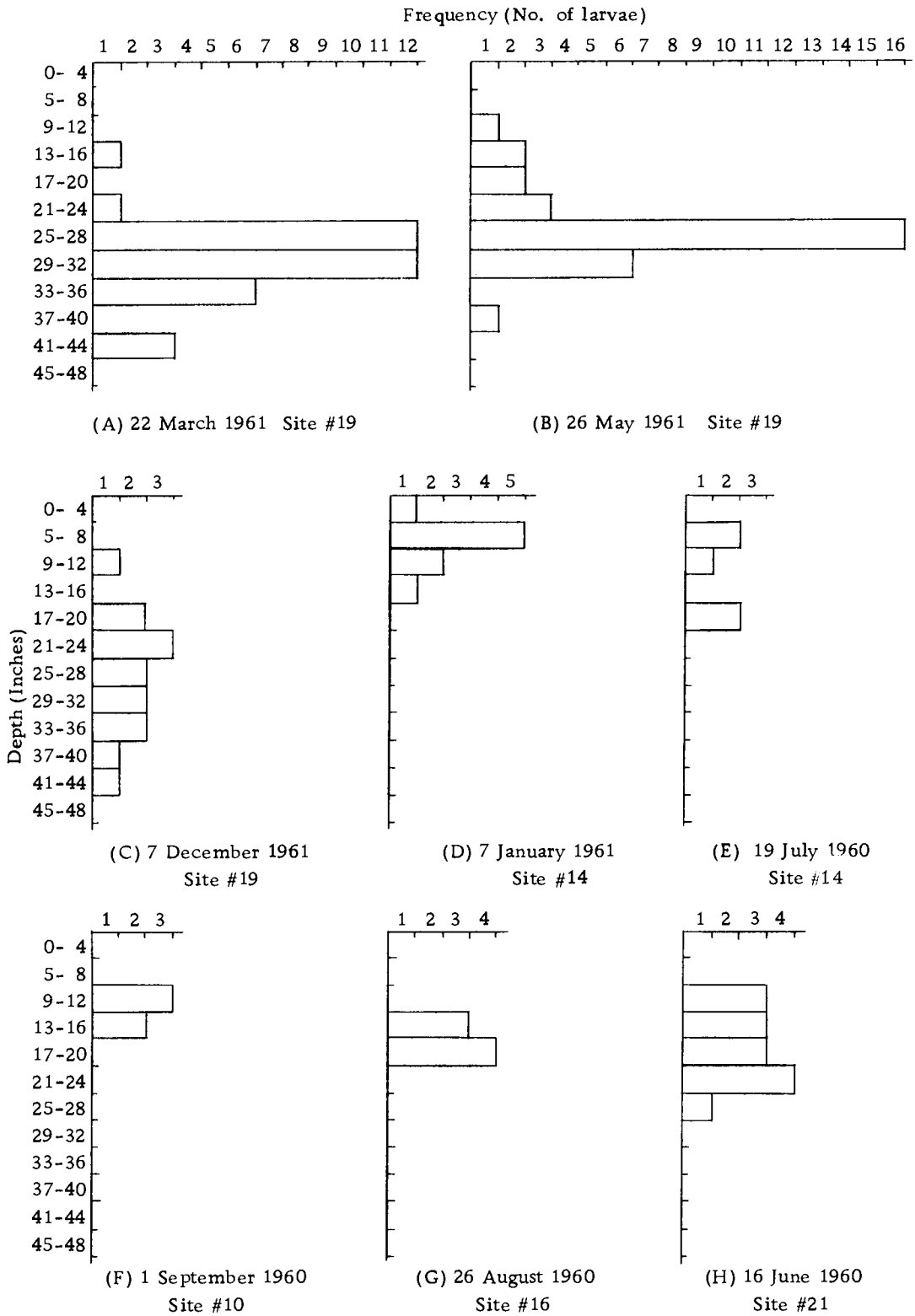

Figure 12. Vertical distribution of Pleocoma simi larvae in the soil at several sites in 1960 and 1961.

depth at which larvae of other Pleocoma species and other white grubs have been dug. P. minor has been found as deep as 59 inches (15, p. 18) and P. puncticollis as deep as eight feet (38, p. 102). Phyllophaga grubs have been found at 74 inches in Canadian soil (27, p. 61).

Factors Affecting Vertical Distribution of Larvae

Vertical distribution of Pleocoma larvae in the soil seems to be influenced by several environmental factors. During this investigation four factors--soil temperature, soil moisture, soil pH, soil profile--were studied and/or observed. On the basis of other scarabaeid research, they were considered most likely to influence, directly or indirectly, the vertical distribution of Pleocoma larvae in the soil. Each of these factors is discussed below.

Soil Temperature

At McDonald Forest, soil temperatures at all depths were highest during summer and lowest in winter. Temperatures were higher, however, at the shallower depths during the summer months and higher at the lower depths during the winter months (Figure 13). Such a relationship is responsible for two temperature overturns, one in spring and one in fall. At the time of the spring overturn in 1961, the temperature at all four depths was 9^{o}C., and during the

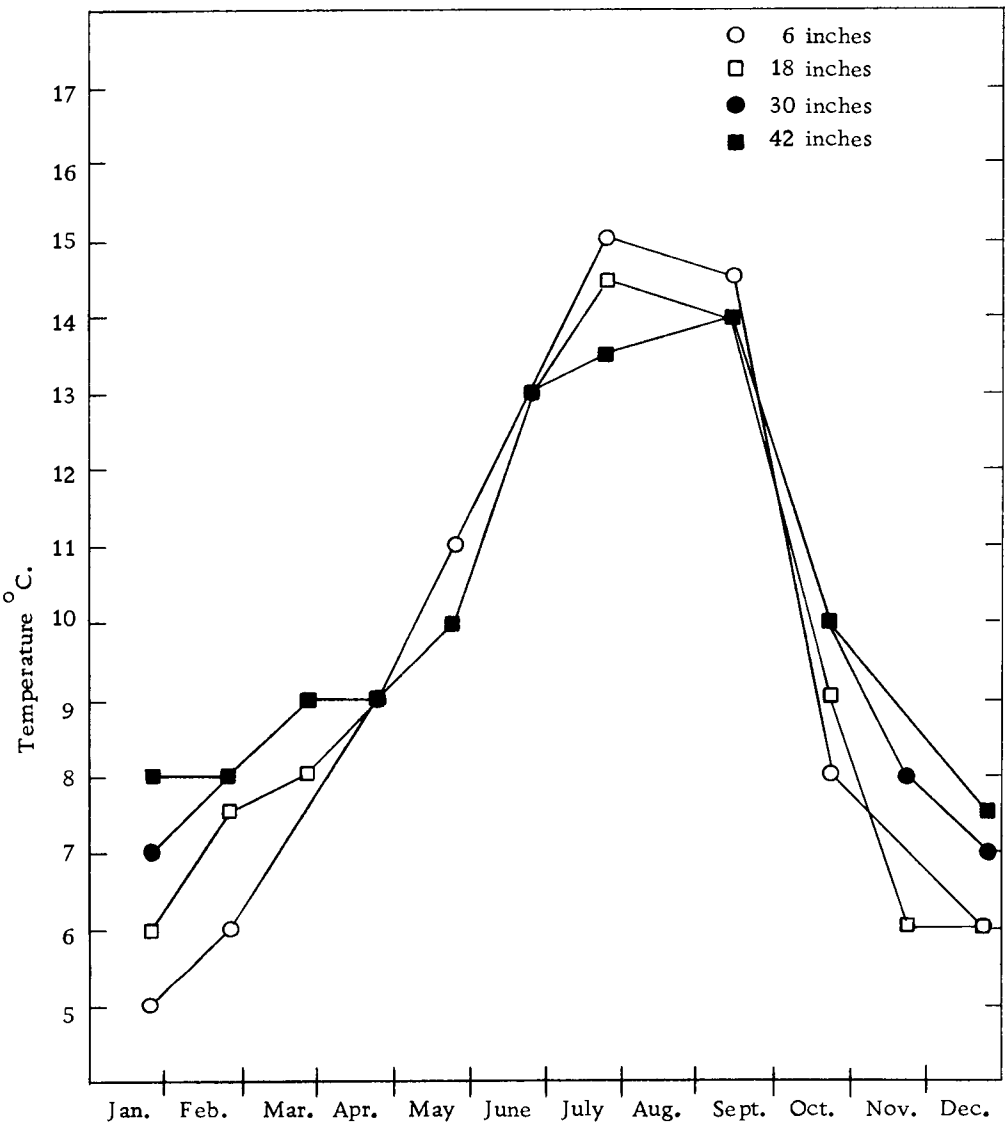

Figure 13. Soil temperatures at McDonald Forest during 1961.

fall overturn temperatures at the four depths were near 13°C.

Larvae were absent from the upper 16 inches of soil from May to September, inclusive, the five months when soil temperatures at shallower depths were the highest. This indicates that most larvae are deeper in the soil in summer because of higher soil temperatures at the shallower depths. In fall, some larvae begin moving upward with the onset of cooler temperatures at shallower depths.

Temperature does not appear to be the sole factor responsible for the absence of larvae at shallower depths since temperatures at 18 inches and 30 inches were, during these five months, the same or within 1.0-1.5°C., of those at the six-inch level. In May, July, and September, three of the five months showing definite absence of larvae above 16 inches, the difference in soil temperature between the six-inch and the 18-inch levels was only 0.5°C.

Pleocoma dubitalis larvae did not appear to seek the soil environment with the least temperature fluctuation. Had they done so, one would expect to have found them congregated at a depth of 42 inches or deeper where soil temperatures throughout the year fluctuated the least (Table 6).

Table 6. Maximum and minimum soil temperatures at McDonald Forest in 1961.

Depth (inches)	Temperature (°C.)		
	maximum	minimum	difference
6	15.0	5.0	10.0
18	14.5	6.0	8.5
30	14.0	7.0	7.0
42	14.0	7.5	6.5

Soil temperatures were also taken with most collections of P. simi and P. carinata during 1960 and 1961. These soil temperatures followed the same general seasonal pattern discussed above for soil temperatures at McDonald Forest.

Pleocoma simi and P. carinata larvae, however, were generally at relatively shallow depths, usually less than 24 inches, during the summer months when soil temperatures were highest at the shallow depths.

Soil temperature does not seem to be correlated with vertical distribution of P. simi larvae from three collections at site #19 in March, May and December, 1961 (Figure 12A, B, and C). In May, larvae were generally deep when shallow soil temperatures were highest. However, in March shallow soil temperatures were cooler than soil temperatures at greater depths but larvae were congregated at lower depths then as well, even a more pronounced congregation than in May. In December, larvae were rather evenly distributed between 9 and 44 inches even though soil temperatures varied from

5.5°C., at six inches to 8.0°C., at 42 inches.

Soil temperatures no doubt influence vertical distribution of P. dubitalis, P. simi, and P. carinata larvae. However, evidence presented here indicates in some cases no apparent correlation between seasonal soil temperature changes and vertical movement of Pleocoma larvae.

Soil Moisture

At McDonald Forest, soil moisture percentages generally were highest in winter and lowest in summer (Figure 14). There was an overturn of percent soil moisture twice a year very similar to that found with soil temperatures. In 1961 at McDonald Forest, percent soil moisture overturned in spring in May and June and in fall in October and November.

The drier soil at the shallower depths in summer is also generally correlated with the movement of larvae deeper into the soil during summer months. This relationship has also been found with other scarabaeid larvae (59, p. 104; 67, p. 667).

The soil moisture percentages fluctuated least at the 42-inch level at McDonald Forest in 1961 (Table 7). P. dubitalis larvae did not search out the depth at which soil moisture was most stable or one would expect to have found them congregated at 42 inches or deeper in the soil.

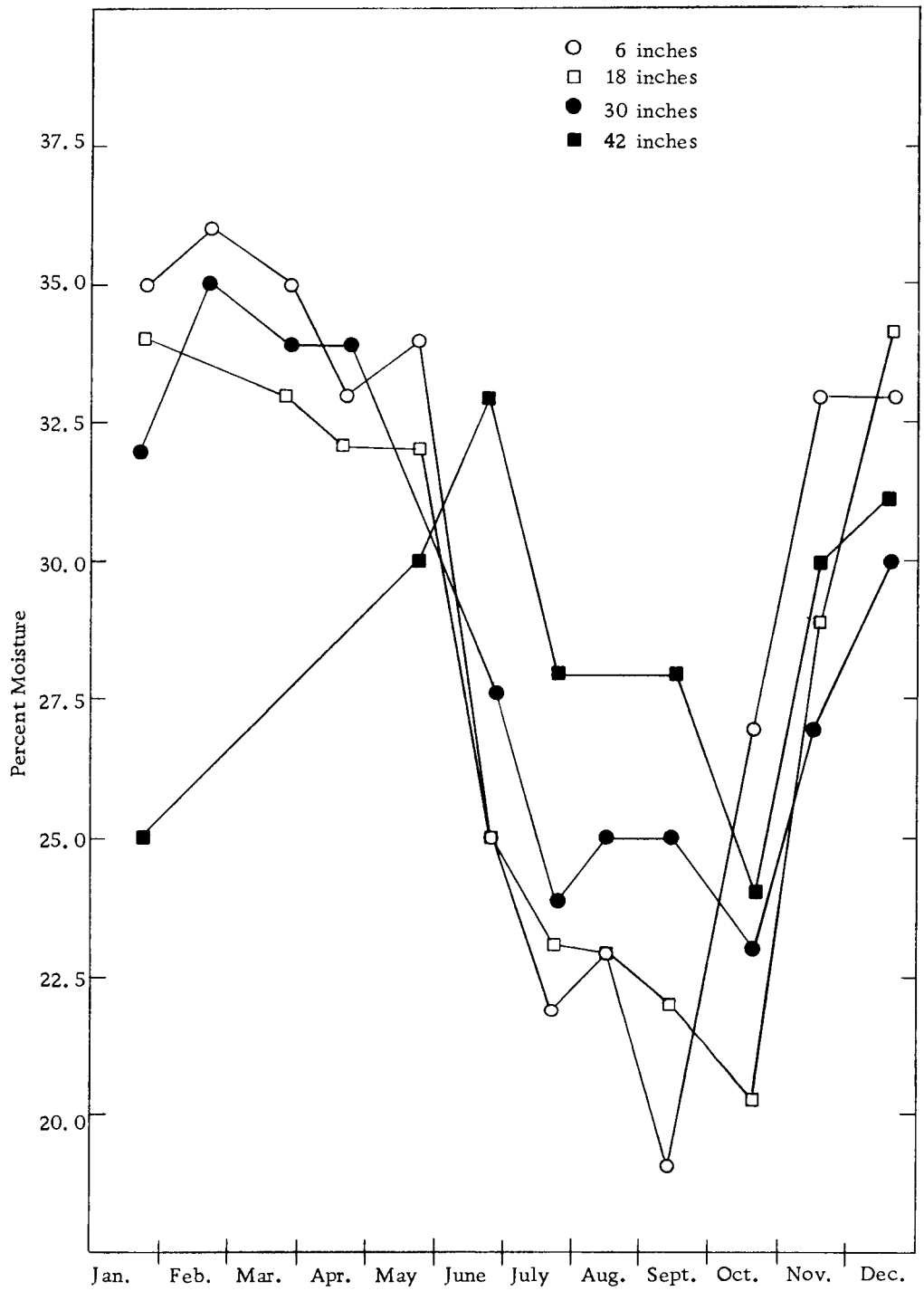

Figure 14. Soil moisture at McDonald Forest during 1961.

Table 7. Highest and lowest soil moisture percentage at McDonald Forest in 1961.

Depth (inches)	Soil moisture (percent)		
	driest	wettest	difference
6	19	36	17
18	20	34	14
30	23	35	12
42	24	33	9

Soil moisture percentages were taken also with most collections of P. simi and P. carinata. These percentages followed the same general pattern as percentages shown in Figure 14. However, as was found with soil temperatures, P. simi and P. carinata were generally at relatively shallow depths during that period of the year when soil there was the driest.

It appears then, that soil moisture alone may not be solely responsible for vertical distributions of Pleocoma larvae in the soil. Although in some cases soil moisture and soil temperature together are reasonably correlated with some larval movement, other factors must be involved in the vertical distribution of Pleocoma larvae.

Soil pH

Soil pH did not appear to be a factor affecting the vertical distribution of P. dubitalis larvae at McDonald Forest or P. simi or P. carinata at the various sites where they were collected. There was an increase in acidity with depth but the increase was relatively

slight, averaging about 0.3, between 6 and 42 inches in depth.

Soil Profile

Vertical distribution of Pleocoma larvae in the soil appears to be influenced by the presence of a silicate clay horizon at some sites. When a clay horizon was present, larvae were often found congregated just above it and when the horizon was absent there was usually no significant congregation of larvae, by depth.

No horizon of silicate clay was encountered at the McDonald Forest study site and the vertical distributions of P. dubitalis larvae collected there attest to this. There was no congregation of larvae, at any time, either at the shallower or at the lower depths. Even in those months when only a few larvae were collected the larvae were rather well distributed vertically.

P. simi and P. carinata larvae were collected in Lane, Douglas, and Jackson counties, counties lying in a major soil type characterized by horizons of silicate clay accumulation (35, p. 43). Depth of clay hardpan varied considerably between sites. At some sites it was fairly deep, 32-34 inches, and fairly regular; at other sites it was as shallow as six inches and generally irregular and undulating. It is not uncommon for horizons of some soils to have tongues or pockets protruding into the horizon below making the horizon boundaries very irregular (79, p. 187).

The presence of a silicate clay hardpan at most sites where P. simi larvae were collected is reflected in the vertical distribution of larvae from these sites. At site #19, for example, a definite silicate clay hardpan was encountered at about 34 inches and the horizon boundary was fairly regular. In all three collections at that site (Figure 12 A-C) the majority of the larvae were found above 36 inches. At other P. simi sites the hardpan was encountered at relatively shallow depths. Without exception, larvae collected at these sites were above the hardpan (Figure 12 D-H).

As noted previously, all P. carinata larvae were taken at relatively shallow depths. The depth of these larvae was also apparently influenced by the silicate clay stratum.

A silicate clay horizon may also affect oviposition depth, thus indirectly affecting the vertical distribution of larvae, at least soon after hatching. In 1960, a female P. dubitalis and 64 eggs were collected at site #39. The female was taken at exactly 19 inches and the clutch of eggs extended below her to a depth of 23 inches. At about 24 inches a horizon of clay accumulation was encountered. The female probably began ovipositing just above this layer after having encountered it in burrowing downward.

Clay hardpans and other soil characteristics also affect the vertical movements of Phyllophaga larvae (76, p. 694; 22, p. 377).

Interaction of Factors

From the foregoing discussion it is apparent that several factors influence the vertical distribution of Pleocoma larvae in forest soils. Under certain conditions one factor may be more influential than others but generally the interaction of two or more factors is involved. For example, during summer, higher soil temperatures and lower soil moistures acting jointly at the shallower depths seem to cause some larvae to burrow deeper into the soil. If no silicate clay layer is encountered, or if the hardpan is relatively deep, larvae are reasonable free to burrow as deep as necessary to find moisture and temperature conditions more suitable than near the surface. In some areas, however, larvae encounter a higher clay horizon as they are retreating downward away from unfavorable conditions in the shallower soils. Since larvae were not generally found in the silicate clay soil, they apparently prefer to bear suboptimum temperature and moisture rather than penetrate an unfavorable soil horizon. This would account for finding many P. simi and P. carinata at very shallow depths in those sites where the silicate clay horizon was high, especially during summer when most larvae in soils without shallow hardpans are deeper in the soil.

Most likely the silicate clay layer only indirectly restricts the downward movement of Pleocoma larvae through the direct effect

of the clay layer on tree roots. Pleocoma larvae are known to be capable of burrowing into very hard soils (9, p. 129). However, an obstructing layer such as a fragipan will cause a proliferation of Douglas-fir roots resulting in a greater density of rooting, hence a greater concentration of food, just above the fragipan (42, p. 117). Where the silicate clay layer is shallow, larvae probably prefer to bear sub-optimum temperature and moisture conditions in the presence of abundant food at shallower depths than to burrow down into the hardpan and be without food even though soil temperature and soil moisture, and perhaps other factors, may be more suitable. Ellertson and Ritcher (15, p. 16) found the character of the subsoil to affect the penetration of orchard tree roots and the vertical distribution of P. crinita and P. minor larvae.

At McDonald Forest some P. dubitalis larvae, without exception those of pupating size, were found at shallow depths (less than 12 inches) during the summer months when most other larvae had burrowed deeper into the soil. Unfavorable soil temperature and soil moisture apparently did not outweigh the intrinsic factors which caused these larvae to remain in the upper layers of soil immediately prior to pupation.

A complex interaction of factors is responsible for the vertical migrations of other scarabaeid larvae (17, p. 345; 70, p. 33; 46, p. 104; 41, p. 30; 22, p. 377).

Density of Larvae in the Soil

Thirteen collections were made of P. dubitalis larvae at McDonald Forest in 1961. The site at which each of these thirteen collections was made, the date of collection and the relative position of each sample is shown in Appendix Figure 2. Larval population densities averaged 1.5 larvae per square foot and ranged from 0 to 3.2 (Table 8) in sample holes varying between 30 and 52 inches in depth.

Table 8. Density of P. dubitalis larvae in the soil at McDonald Forest during 1961

Date	Size of Hole			No. larvae collected	Larvae per sq. ft.
	length	width	depth		
28 January	36	36	48	17	1.9
25 February	36	36	38	18[a]	2.0
31 March	36	36	39	29[b]	3.2
28 April	36	36	30	0	0.0
29 April	36	36	36	17	1.9
29 May	36	36	52	17	1.9
28 June	36	36	48	9	1.0
28 July	36	36	48	14	1.6
15 August	36	36	40	2	0.2
13 September	36	36	50	9	1.0
21 October	36	36	44	12	1.3
21 November	36	36	42	12	1.3
22 December	36	36	42	16	1.8

[a]Unavoidable circumstances prevented the sampler from completing this hole. Had further digging been possible more larvae may have been collected.

[b]Fifteen of these 29 larvae were young second stage larvae congregated in the hole and probably all of the same "clutch."

Between May 1960 and October 1961, 17 collections of P. carinata were made at three different sites in southwestern Oregon. The number of larvae taken at each collection is presented in Table 9. The most dense larval population was 1.2 larvae per square foot. Six of the 17 collections, about 35 percent, produced no larvae.

Table 9. Density of Pleocoma carinata larvae in southwestern Oregon coniferous forest soils in 1960 and 1961.

Date	Site No.	Size of hole			No. larvae collected	Larvae per sq. ft.
		length	width	depth		
21 May 1960	2	36	36	20	0	0.0
21 May 1960	2	36	48	18	14	1.2
2 September 1960	2	36	48	24	3	0.3
2 September 1960	2	48	48	24	7	0.4
12 May 1961	2	36	36	32	2	0.2
18 July 1961	2	36	36	36	3	0.3
19 July 1961	2	36	36	24	3	0.3
2 January 1961	3	36	36	36	0	0.0
3 January 1961	3	24	24	36	0	0.0
3 January 1961	3	36	48	42	4	0.3
10 May 1961	3	36	36	30	0	0.0
10 May 1961	3	36	36	36	2	0.2
11 May 1961	3	36	36	30	0	0.0
11 May 1961	3	36	36	42	1	0.1
28 March 1961	8	36	36	36	5	0.6
27 October 1961	8	36	36	30	1	0.1
27 October 1961	8	36	36	24	0	0.0

From May 1960 to December 1961, 31 sample holes were dug at eight different sites in southwestern Oregon searching for P. simi larvae. The number of larvae taken at each of these collections is presented in Table 10. Fifteen of the 31 collections produced no larvae and five yielded only a single larva. The most dense larval population was 5.1 larvae per square foot.

Table 10. Density of Pleocoma simi larvae in southwestern Oregon coniferous forest soils in 1960 and 1961.

Date	Site No.	Size of hole			No. larvae collected	Larvae per sq. ft.
		length	width	depth		
9 June 1960	14	36	36	18	1	0.1
9 June 1960	14	36	36	18	0	0.0
9 June 1960	14	36	36	18	0	0.0
9 June 1960	14	36	36	18	0	0.0
19 July 1960	14	36	36	24	0	0.0
19 July 1960	14	24	24	24	0	0.0
19 July 1960	14	36	48	30	3	0.3
19 July 1960	14	36	36	30	2	0.2
7 January 1961	14	36	36	24	10	1.1
20 May 1960	55	36	36	18	0	0.0
20 May 1960	55	36	36	31	0	0.0
16 June 1960	21	48	48	18	2	0.1
16 June 1960	21	18	24	18	1	0.3
16 June 1960	21	36	36	30	11	1.2
16 June 1960	21	36	36	24	7	0.8
16 June 1960	21	36	36	18	1	0.1
19 May 1960	10	36	36	18	0	0.0
19 May 1960	10	36	36	18	1	0.1
1 September 1960	10	36	36	18	0	0.0
1 September 1960	10	36	36	24	5	0.6
26 August 1960	11	30	30	18	1	0.2
26 August 1960	11	36	36	30	0	0.0
26 August 1960	11	36	36	18	0	0.0
26 August 1960	16	24	24	30	6	1.5
22 May 1961	27	36	36	30	0	0.0
22 May 1961	27	36	36	36	0	0.0
22 May 1961	27	36	36	30	0	0.0
22 March 1961	19	36	36	52	46[a]	5.1
22 March 1961	19	36	36	26	0	0.0
26 May 1961	19	36	36	48	28	3.1
7 December 1961	19	36	36	48	17	1.9

[a]Thirteen of these 46 larvae were small second instars congregated near the place where the eggs had been laid.

P. minor and P. crinita were collected in forested areas adjacent to the orchards in the Hood River Valley. Four P. crinita collections produced seven larvae for an average of 0.19 larvae per square foot. Four P. minor collections produced 19 larvae for an average of 0.48 larvae per square foot.

It is of interest to compare larval density of the five species of Pleocoma discussed above under forest conditions with density of Pleocoma larvae in some orchard soils. Relative densities of larval populations for each of the six Oregon species of Pleocoma under varied conditions of orchard and forest soil are presented in Table 11.

Table 11. Larval densities of the six western Oregon species of Pleocoma in forest and orchard soils.

Species	No. larvae per sq. ft. minimum	No. larvae per sq. ft. maximum	Site
P. dubitalis	0.0	3.2	Douglas-fir forest
P. simi	0.0	4.4	Douglas-fir forest
P. carinata	0.0	1.2	Mixed conifer forest
P. oregonensis[a]	0.0	1.67	Beneath western yellow pine
P. oregonensis[a]	0.06	0.33	Beneath cherry tree
P. crinita[a]	0.44	7.78	Apple orchard
P. crinita	0.0	0.44	Mixed conifer forest
P. minor[a]	----	21.00	Apple orchard
P. minor	0.11	1.00	Mixed conifer forest

[a]Data from Ellertson and Ritcher (15, p. 23-24).

It appears from Table 11 that Pleocoma larval populations are generally much denser in some Hood River Valley orchards than

they are in most forest soils. However, "There are," according to Ritcher[14] "many orchards in the Hood River Valley which have few or no Pleocoma. All of our digging was done in orchards known to be injured or infested." Likewise all collecting during the present investigation was done at sites where Pleocoma larvae were expected to be found as indicated by adults having been collected at the site. Yet out of 69 holes dug in search of Pleocoma larvae, 22 produced no larvae.

Several factors, acting independently or in combination with one another, are probably responsible for the variation in the density of Pleocoma larvae in the soil. Though the influence of these factors on larval density was not studied here, we may infer, from the results of other scarabaeid research, that the following factors might be involved:

1. Soil moisture.--Excessive soil moisture is detrimental to other root-feeding scarabaeid larvae, infestations often being light in poorly drained locations (66, p. 257; 48, p. 114; 18, p. 476; 70, p. 22). On the other hand, excessively dry soil is also detrimental at times (76, p. 695; 70, p. 36). Rainfall, being a major factor controlling moisture content of the soil (44, p. 187) could indirectly influence development and survival of some larvae.

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[14] Personal correspondence with Dr. P. O. Ritcher in 1964.

2. Soil pH.--A low soil pH seems to be correlated with higher larval populations. This relationship has been found with the Japanese beetle (51, p. 476; 82, p. 733), Phyllophaga sp. (24, p. 18) and the European Chafer (66, p. 257).

3. Food of the Larvae.--If larval food were depleted, the ability of Pleocoma larvae to move through the soil would enable them to search out, and congregate near, a food supply.

4. Biological Factors.--Several biological and/or behavioral factors could contribute to larval density. Among these are: deposition of many eggs in a relatively small area, the wingless condition of Pleocoma females, and high populations of vertebrate predators in some areas.

5. Soil type.--Some species of Pleocoma have been associated with certain types of soils (29, p. 217-218; 57, p. 24-25; 71, p. 115). Lighter soils are more heavily infested with Phyllophaga than heavier ones (63, p. 328) and highly impervious soils are detrimental to Japanese beetle larvae (70, p. 8).

The difficulty in trying to isolate environmental factors and their respective influence on the density of larval populations is complicated by the fact that most insect species "....can survive and maintain their numbers in environments which differ considerably from one another" (9, p. 126).

FEEDING HABITS OF THE LARVAE

Identification and Analysis of Gut Contents

Several types of material were found in the alimentary canals of the more than 400 Pleocoma larvae examined. These materials included tree roots, larval exuvia, soil and material tentatively determined to be fungal hyphae, cast ventricular epithelium, and bacteria. Each of the types of material is discussed below.

Roots

Coniferous roots were the most abundant material found in the guts of Pleocoma larvae; some guts were packed with roots while others contained only a trace of woody material.

Identity of Roots. Of the 150 Pleocoma stomodaea examined, 131 contained gymnosperm roots, 3 contained angiosperm roots, 11 contained two classes of roots and five contained roots which I was unable to identify. The identification of these roots found in the stomodaea is presented by species of larvae in Table 12.

Of the 66 P. dubitalis larvae which had eaten gymnosperm roots, 24 had definitely eaten Douglas-fir roots. Although gut contents of the remaining 42 larvae were identifiable only as gymnosperms, most of them were probably Douglas-fir as well. This is so since the only conifer growing, with the exception of a few small

Table 12. Identifications of roots from alimentary systems of Pleocoma larvae collected in western Oregon coniferous forests in 1960 and 1961.

Identification of root	Number of larvae feeding on each class of root				
	P. dubitalis	P. simi	P. carinata	P. minor / P. crinita	Total
Gymnospermae	42	23	19	6	90
Douglas-fir[a]	24	11	4	2	41
Angiospermae					
Dicotyledonae			1		1
Oregon White Oak[b]		1			1
Angiospermae					
Monocotyledonae			1		1
Gymnospermae-					
Angiospermae	1	3		2	6
Gymnospermae-					
Filicinae		1	4		5
Unidentifiable	3	1	—	1	5
	70	40	29	11	150

[a] Pseudotsuga menziesii (Mirb.) Franco var. menziesii

[b] Quercus garryana Dougl.

scattered Grand fir (Abies grandis Lindl.), where the P. dubitalis collections were made at McDonald Forest (Appendix Figure 2) was Douglas-fir.

It is also possible to identify more specifically which gymnosperms were eaten by P. simi, P. carinata, P. minor, and P. crinita larvae since we know what conifer species were growing at each site where these larvae were collected. Table 13 shows, for example, that the only conifer species recorded at sites #14 and #19 was Douglas-fir. One might infer, then, that Douglas-fir was the gymnosperm eaten by P. simi larvae collected at these two sites. Likewise, one can be reasonably sure that the gymnosperm eaten by P. simi larvae collected at site #10 was either Douglas-fir or incense cedar.

Angiosperms in six of the nine larvae which had fed on this class of root were distinguishable only to class. Angiosperms in the remaining three larvae were identifiable to subclass; one was a monocot and two were dicots (one identified as Oregon White Oak, Quercus garryana Dougl.).

No stomodaeum contained exclusively fern roots although ferns were intermixed with gymnosperms in five stomodaea, one of P. simi and four of P. carinata. Although there are many species of ferns in Oregon (58, p. 1-16), the species on which the five larvae had fed was probably either bracken fern, Pteridium aquilinum or

Table 13. Conifers growing at the 12 sites where Pleocoma larvae were collected in western Oregon in 1960 and 1961.[a]

Site number	Conifers recorded at site*
2	A, C, D, E
3	A, B, C, D, E
8	A, B, D, E, F
10	A, E
11	A, B
14	A
16	A, E
19	A
21	A, B, C, D, E, F, G
32	A, B
39	A, B, C
Hood River	A, B, C

*Species represented by each letter are as follows:

A.	Douglas-fir	Pseudotsuga menziesii (Mirb.) Franco
B.	grand fir	Abies grandis Dougl.
C.	ponderosa pine	Pinus ponderosa Laws.
D.	sugar pine	Pinus lambertiana Dougl.
E.	incense-cedar	Libocedrus decurrens Torr.
F.	Pacific yew	Taxus brevifolia Nutt.
G.	western hemlock	Tsuga heterophylla (Raf.) Sarg.

[a]Conifers recorded at sites #27 and #55 are not recorded in this table. Attempts made to collect larvae at these two sites were unsuccessful.

sword fern, Polystichum munitum.

These data (Table 12) document evidence that five species of Pleocoma larvae found in the soil in old-growth or second-growth coniferous forests in western Oregon were feeding primarily on roots of coniferous trees. The first known record of Pleocoma larvae feeding on conifers was established in early February, 1960. At site #21, Stein (74, p. 126) found P. simi larvae feeding on conifer seedlings--ponderosa pine, sugar pine, Douglas-fir, and grand fir--in seedbeds located in a then recently logged area in southwestern Oregon (Appendix Figure 4A). Prior to 1960 there was only circumstantial evidence that Pleocoma larvae were feeding on the roots of forest trees.

Host Preferences. Although 86 percent of the Pleocoma larvae examined had fed exclusively on gymnosperm roots, this frequency of occurrence cannot be construed as an indication of food preference since all larvae were collected in forest soils, where coniferous roots were most abundant. Since other classes of roots were not as plentiful in these soils, conifer roots might be considered as an important, though maybe not preferred food by Pleocoma larvae.

Those larvae in each of whose stomodaeum more than one class of root was found did not seem to have exercised a feeding preference; in each stomodaeum two classes of roots were lying

contiguous indicating they may have been ingested simultaneously or in close succession (Figure 15).

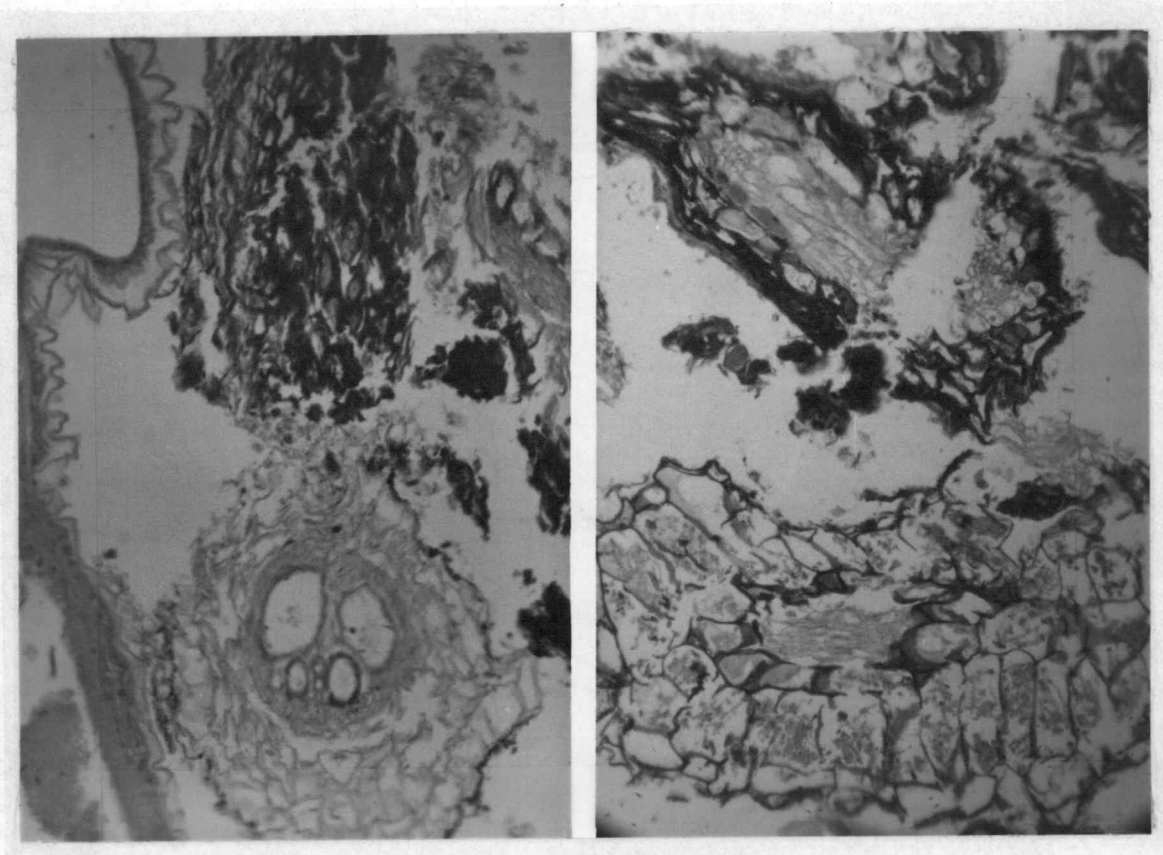

Figure 15. Photomicrographs showing two classes of root in the same stomodaeum. Left--Sections of gymnosperm (above) and angiosperm (below) lying contiguous in the stomodaeum of a fifth-sixth instar P. dubitalis (130X). Right--Section of a gymnosperm (above) and fern (below) lying adjacent in the stomodaeum of a large P. carinata larva (100X).

In the laboratory, Pleocoma larvae were held without food for several days, then offered a choice of two species of freshly-cut roots. There was an indication from these feeding tests that

Pleocoma larvae may prefer ponderosa pine to Douglas-fir and Douglas-fir to either incense cedar or oak.

P. simi larvae feeding on conifer seedlings in experimental seedbeds damaged twice as many pines as firs, when the two species were equally available, and appeared to reject incense cedar (74, p. 136).

A rejection of incense cedar by Pleocoma larvae may not be surprising; other conifer-feeding insects make a sharp host plant distinction between the group represented by the Taxodiaceae-Cupressaceae and that of the Pinaceae. Pines and firs are in the Pinaceae; incense cedar is in the Cupressaceae.

Pleocoma larvae feeding on the roots of orchard trees do not seem to show any preference. Pear trees in the Hood River Valley orchards showed some sign of immunity in 1953 (56, p. 41-42). Later, however, Ellertson and Ritcher (15, p. 9-10) found P. crinita and P. minor larvae to be oligophagous in their feeding habits in that they fed on Malus, Pyrus and Prunus and shifted their feeding from Prunus to Malus and from Malus to Prunus.

Some species of Phyllophaga feeding on roots of forest trees seem to be selective, and others not. Eastern white pine and red pine suffer about twice as much grub injury as do jack pine and Scotch pine (59, p. 103-104) in experimental plantations in Wisconsin. Yet in New York, Stone (75, p. 842-844) states, "Well-marked food

preferences are not yet known, but feeding on the roots of tree seedlings by Phyllophaga appears incidental, rather than selective." In the South, Speers (73, p. 149) says that because Phyllophaga ".... larvae are not selective in their feeding habits, they will damage most roots with which they come in contact."

Non-host-selectivity by Pleocoma and Phyllophaga larvae feeding on roots of forest trees would seem to be advantageous when one considers their relatively slow rate of travel through the soil. In relating movement of soil insects to food habits, King (34, p. 271), indicating general feeders have an advantage over all other types of feeding, says, ".... the slowness of movement within the soil renders flexibility of food habits of great significance for species or stages confined there."

Type of Damage to Roots. Pleocoma larvae feed on roots in coniferous forest soils of western Oregon in several ways. In some cases one type of damage is quite distinct and does not intergrade with another type; at other times, however, more than one type of damage can be found on a single root. One can almost always find, in the same larval gut, roots representing more than one type of damage. Each of the types of damage observed is discussed below.

1. Many Pleocoma larvae follow roots through the soil and

feed only on the soft bark[15] as they burrow along. This type of feeding, though for the most part confined to the tissues outward from the vascular cambium, usually scores the xylem tissue inward from the cambium. A segment of root exhibiting this type of damage is shown in Figure 16A. The largest root found to have been damaged in this way measured 13mm in diameter. This was also the largest root known to have been damaged in any manner by Pleocoma larvae in the forest soils studied.

Pleocoma larvae, in removing the soft phloem and outer bark, do not always confine their damage to one side of a root. Roots will often be completely girdled as larvae feed on all sides of the root (Figure 17B). This type of damage is most severe when larvae completely strip all phloem and outer bark from a root leaving only stringers of xylem in the soil. The remains of two roots which were found in a larval cell are shown in Figure 17C. The larva had completely stripped the bark from the xylem of both roots, leaving only a bit of bark tissue attached to the xylem of the larger root.

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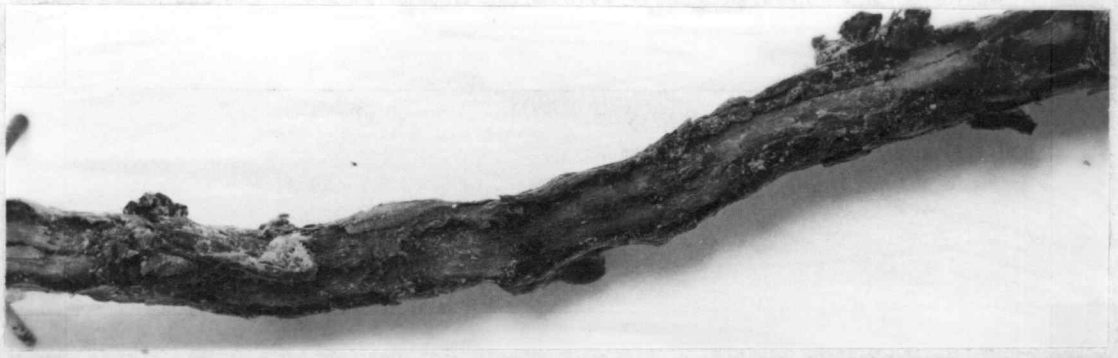
[15] When used here, the non-technical term "bark" is meant to include the phloem and all the tissues located outward from it. The term is frequently employed for this purpose (16, p. 267). However, the term "phloem and outer bark" also is frequently used. In this case, "phloem" refers to the living primary phloem between the vascular cambium and the cork cambium (phellogen) while "outer bark" refers to the cork (phellem) and the dead secondary phloem lying outside of the cork cambium.



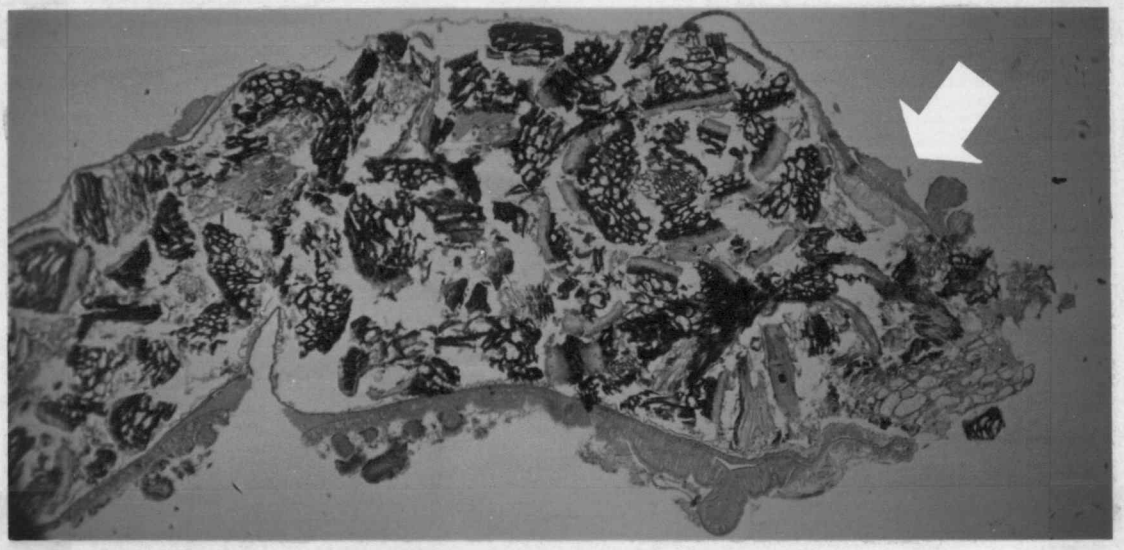


Figure 16. Douglas-fir root damaged by small P. simi larva.

(A) Top--Phloem and outer bark eaten from one side of root but larva barely touched the xylem (5X).

(B) Center--Stomodaeal section of larva which fed on above root. Nearly all material to right of arrow is phloem and outer bark, evidence of type of damage shown in root above. Roots in rest of crop indicate larva had fed on a small branch root (45X).

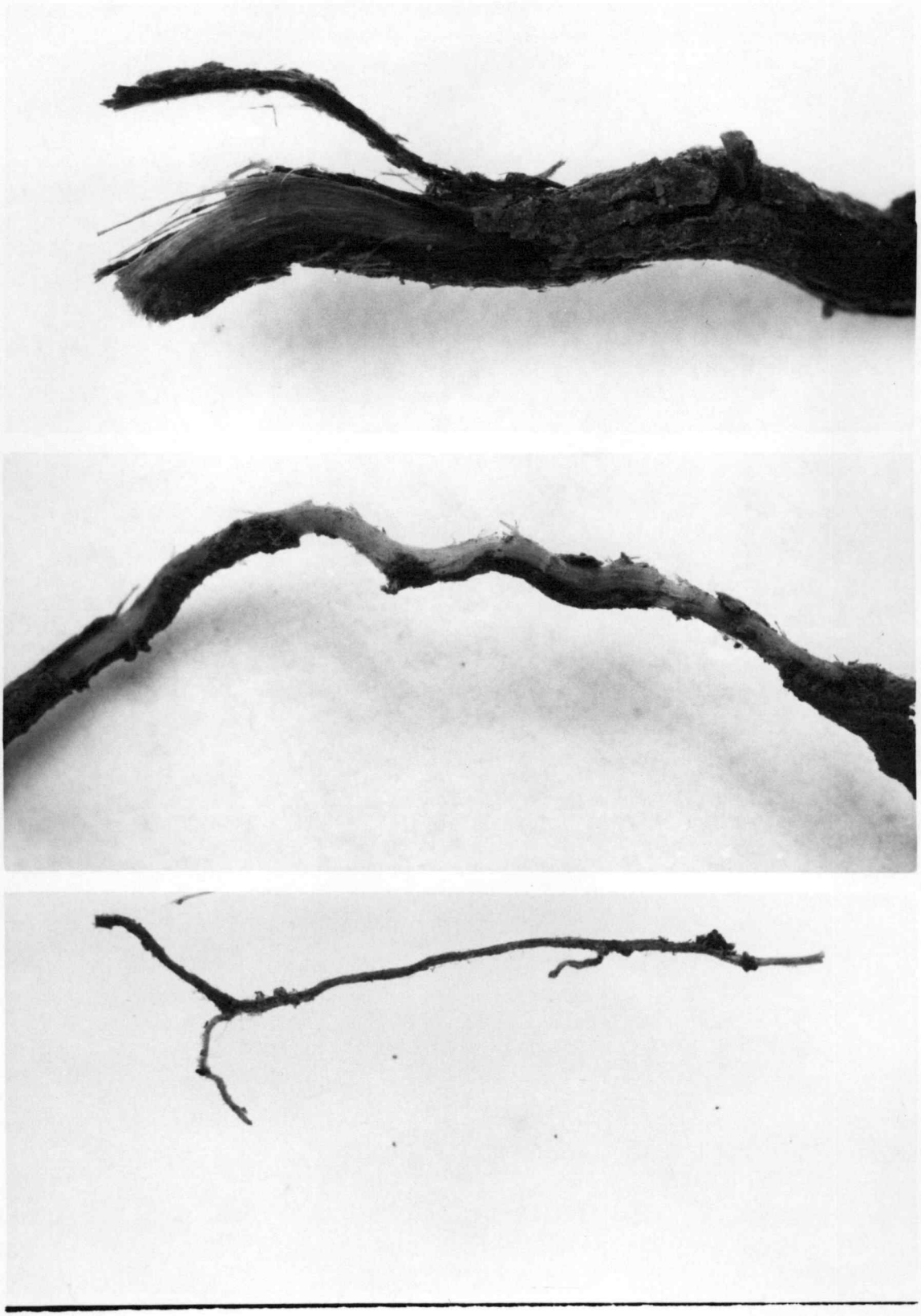
(C) Lower--Photomicrograph of tangential section of root shown in (A). Root identified as Douglas-fir on three characteristics: (1) thick-walled epithelium cells of the transverse resin canal, (2) large bordered pits in both face and lateral view, and (3) tracheary spiral secondary thickenings (280X).

(A) Medium-sized P. carinata larva had gnawed the left end of this root. The larva also had split off a portion of the root (which protrudes above the main root) and fed on the phloem and outer bark (13X).

(B) Damage to root (1.10mm in diameter) by third instar P. dubitalis in the laboratory. Larva girdled the root by removing much phloem and outer bark. Xylem was not severed though fractured in several places (5.5X).

(C) Stringers of xylem found in larval cell of large P. carinata. Larva had completely stripped phloem and outer bark from lower root and most of that from upper root (0.15mm in diameter) (7.5X).

Figure 17. Coniferous roots showing feeding damage by Pleocoma larvae.



The same type of root damage was also observed by larvae feeding in the laboratory. A P. dubitalis larva confined with a Douglas-fir root, 1.05mm in diameter, followed along the root and stripped away all phloem and outer bark (Figure 18A). The root was taken from the larva, sectioned in two places and the cross sections photographed (Figures 18B and 18C). Figure 18B is a photomicrograph of the root at a point where the larva had just begun to feed. Most of the phloem and outer bark encircles the harder xylem tissue in the center of the root. The larva had already begun feeding on one side of the root. The xylem having been stripped of the phloem and outer bark tissue by the feeding larva, is shown in cross section in Figure 18C.

Stomodaea of larvae which have fed exclusively on phloem and outer bark of coniferous roots appear as shown in Figure 19B. The woody material in, and protruding from, the caudal end of the crop is entirely phloem and outer bark.

2. Some larvae, as they burrow through the soil, encounter roots and begin feeding on the outer bark. However, instead of paralleling the roots, they feed at right angles to the root, through the outer bark and phloem, into the xylem and completely sever the root.

A large P. simi larva was found in its soil burrow with a root 6mm in diameter which had been severed in this manner (Figure 20).

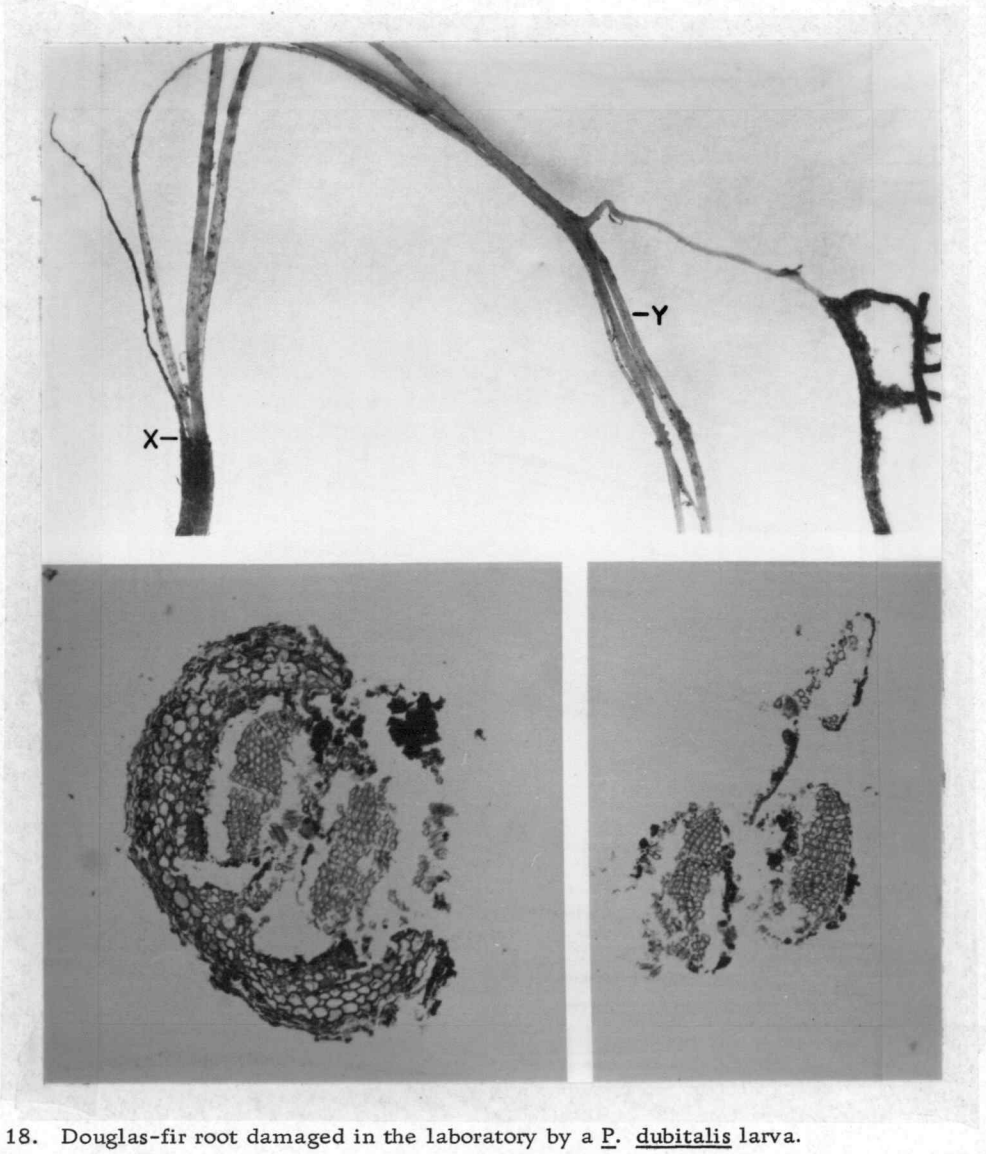


Figure 18. Douglas-fir root damaged in the laboratory by a P. dubitalis larva.

(A) Top--Larva stripped phloem and outer bark from most of root. Darker portions in lower left and far right are undamaged (4X).

(B) Lower left--Photomicrograph of cross section of root shown in (A) above, at point 'X' where larva commenced feeding on one side of root. Most of phloem and outer bark still encircle harder xylem in center of root (50X).

(C) Lower right--Photomicrograph of cross section of root shown in (A) above at point 'Y'. Larva stripped all phloem and outer bark leaving only stringers of hard secondary xylem (50X).

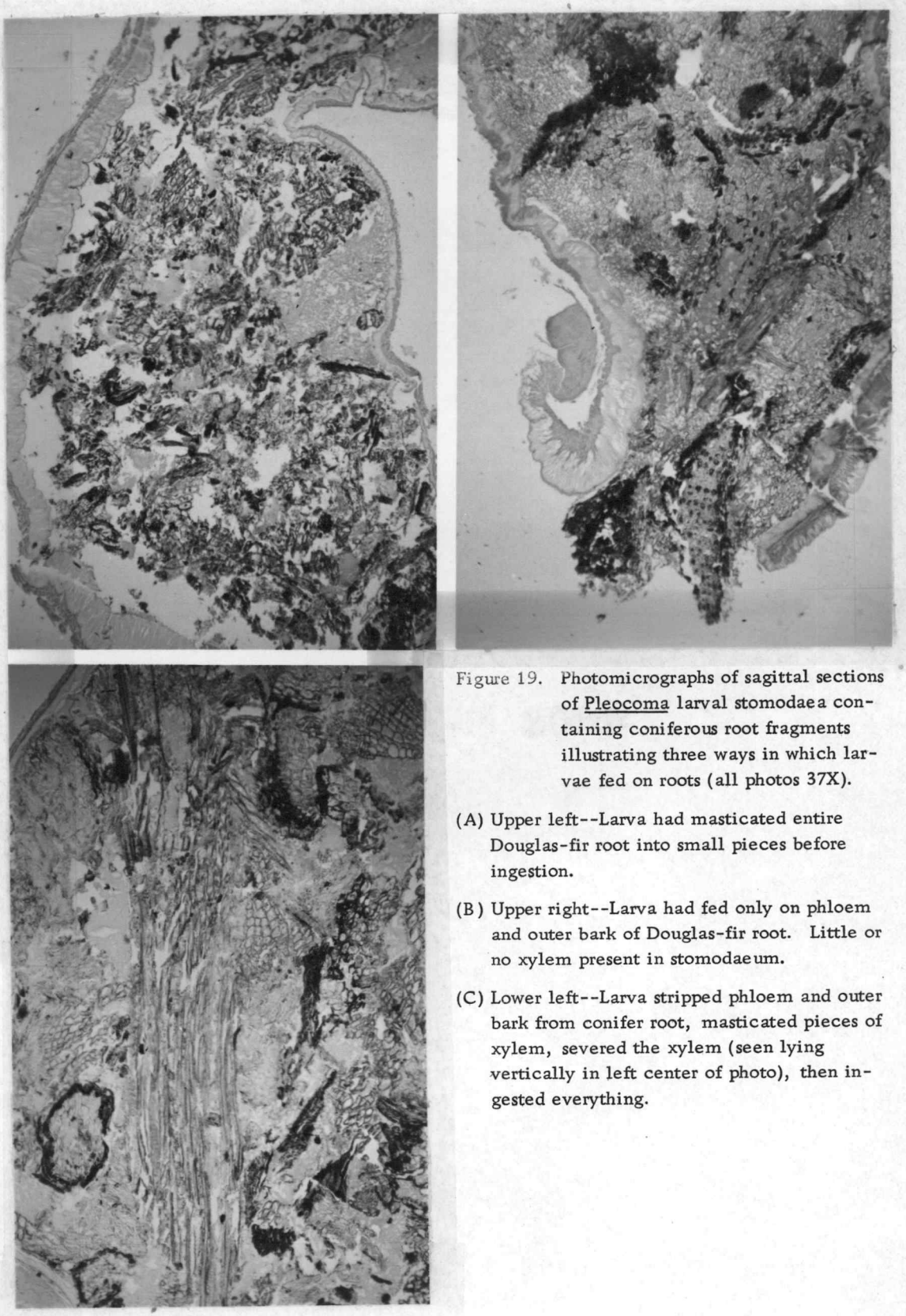


Figure 19. Photomicrographs of sagittal sections of Pleocoma larval stomodaea containing coniferous root fragments illustrating three ways in which larvae fed on roots (all photos 37X).

(A) Upper left--Larva had masticated entire Douglas-fir root into small pieces before ingestion.

(B) Upper right--Larva had fed only on phloem and outer bark of Douglas-fir root. Little or no xylem present in stomodaeum.

(C) Lower left--Larva stripped phloem and outer bark from conifer root, masticated pieces of xylem, severed the xylem (seen lying vertically in left center of photo), then ingested everything.

This is the largest root found during this study to have been damaged in this manner.

Figure 20. A large P. simi larva in its burrow with a Douglas-fir root, to its right, which had been severed. (The other end of severed root was displaced when larva was unearthed.) (1.5X).

3. Having severed a root as described above, many larvae no doubt continue burrowing through the soil. Other larvae, however, begin feeding on one end of the root which they have severed, and follow the root through the soil biting off intact lengths of root as they move along. The intact segments are ingested and pass through the alimentary system without further mastication. Intact segments of roots from which the outer phloem and bark has not been stripped can be seen in Figure 21A.

An intact root segment is shown passing through a stomodaeum in Figure 5B. The root segment is lying lengthwise in the

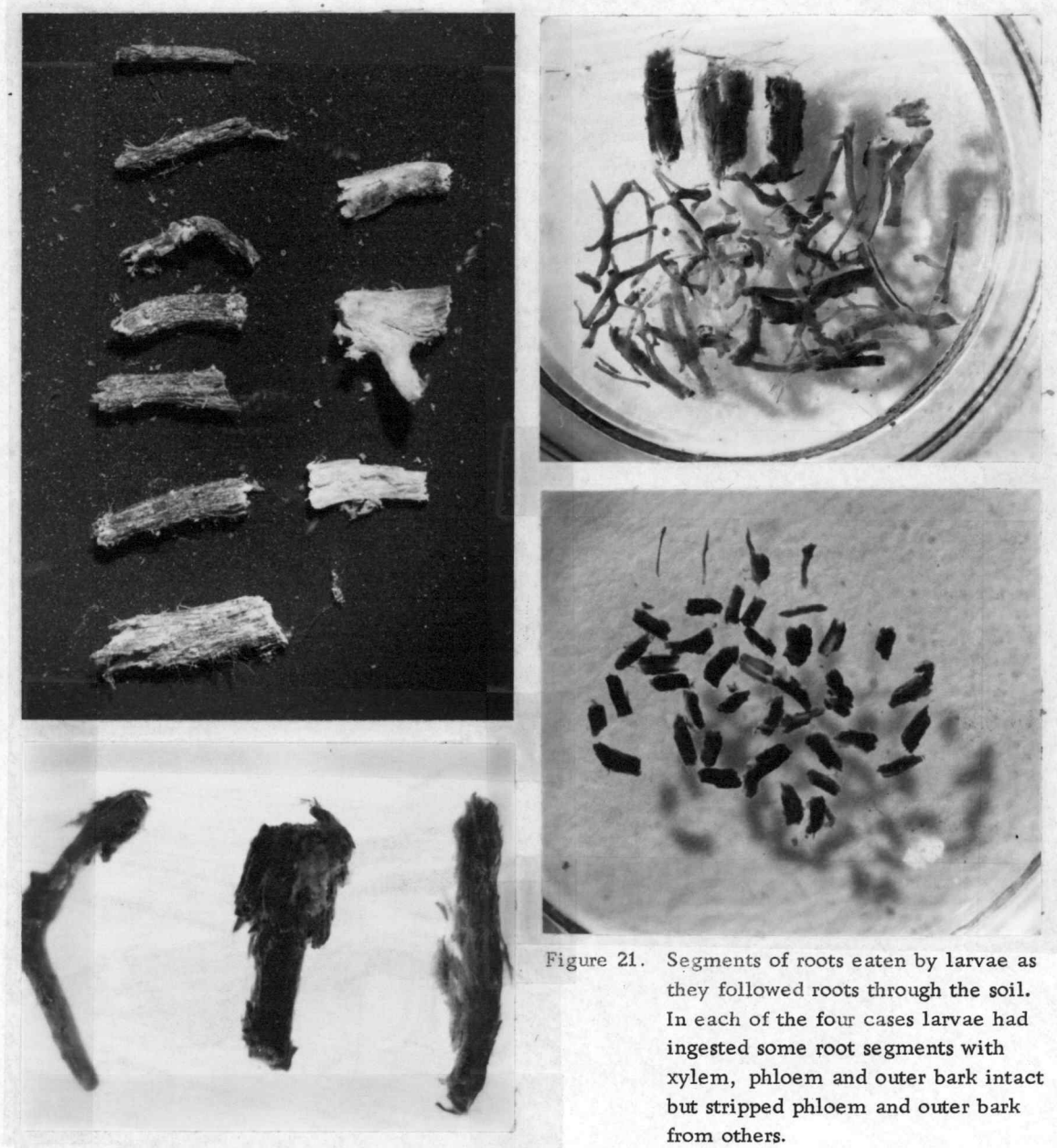


Figure 21. Segments of roots eaten by larvae as they followed roots through the soil. In each of the four cases larvae had ingested some root segments with xylem, phloem and outer bark intact but stripped phloem and outer bark from others.

(A) Upper left--Root segments from ninth-larger instar P. dubitalis gut. Phloem and outer bark removed from three segments at right (6X).

(B) Upper right--Roots from mesenteron of large P. carinata larva. Three larger root segments above had been eaten intact (4X).

(C) Lower right--Root segments, a little more than 1mm in length eaten by small (probably second instar) P. simi. Four roots in top of photo have had phloem and outer bark stripped from them (4X).

(D) Lower left--Root segments from colon of large P. carinata larva. Phloem and outer bark completely removed from roots on right and left but remain intact on half of root shown in center (14X).

oesophagus in the lower part of the photo.

The largest piece of intact root segment, found in the stomodaeum of a ninth-larger instar P. dubitalis measured 1.90mm in diameter and 3.10mm in length. The next largest intact root, 1.70mm in diameter and 3.00mm in length, was eaten by a medium-sized P. carinata larva. Five larvae had ingested intact root segments measuring 1.50mm in diameter and varying from 2.00mm to 4.50mm in length.

4. Some larvae bit off root segments as they follow roots through the soil, but instead of ingesting the segments intact, as larvae discussed above had done, they strip the softer phloem and outer bark from the severed xylem before ingestion. Whether the stripping is done before or after the segment is bitten off is not known. Roots from which the bark has been stripped from the xylem can be seen in the photographs in Figure 21.

In the same gut one will find root segments in which the phloem and outer bark has been stripped, intermingled with segments which are intact. Furthermore, both types of damage not only occur on roots in the same gut but also on the same segment of root (Figure 21D).

The type of damage discussed here is similar to that discussed under #1 above in that the hard xylem has been stripped of the phloem and outer bark. Some larvae, however, bite off and ingest

segments of xylem while others leave the long stringers of xylem in the soil.

5. At times, usually with the larger roots, some larvae, after having severed a segment of root and removing the bark from the xylem, split the xylem lengthwise into two or more fragments before ingestion. A large fragment of gymnosperm xylem from which phloem and outer bark have been stripped is shown in Figure 19C. Some relatively large pieces of xylem which have been split lengthwise before being ingested are shown lying exposed in the alimentary canal illustrated in Figure 34A. Two fragments of xylem which were ingested in this manner, and passed through the alimentary system, are shown in the frass pellet in Figure 38A.

The largest xylem fragments ingested by Pleocoma larvae measured from 3.00 to 4.80mm in their longest dimension and 1.20 to 2.00mm in their narrowest dimension. What was probably the largest fragment, 4.70mm X 1.80mm, was eaten by a ninth-larger instar P. dubitalis. Another large fragment, 4.80mm X 1.20mm was ingested by a large P. simi larva.

6. Other larvae following roots through the soil do not appear to bite off intact segments of the root as larvae discussed above had done, but apparently chew the entire root into fine pieces prior to ingestion. Ends of roots so eaten give the appearance of having been gnawed on (Figure 17A and Figure 22). This type of

damage probably is most frequent with larger roots. The largest root, 2.85mm in diameter, found with this type of damage is that root shown in Figure 22. Figure 19A depicts, photomicrographically, how roots so eaten appear in the stomodaea after having been ingested.

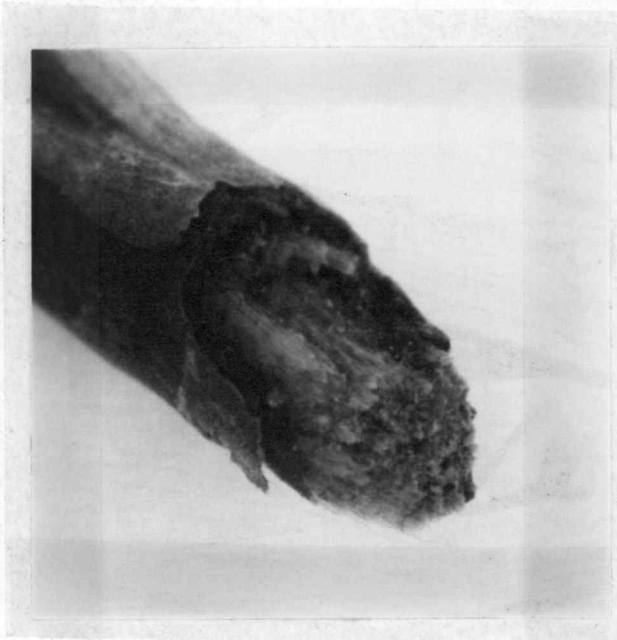


Figure 22. End of conifer root upon which a large P. carinata larva had been feeding. The larva had apparently been gnawing at end of root and had also eaten away a portion of the upper surface of the root (11.5X).

The longest segment of root eaten by any larva was 7.40mm long (Figure 23). It was consumed by a ninth-larger instar P. dubitalis. At the large end where it measures 1.20mm in diameter, the root segment is intact but the portion to the left is mostly phloem and outer bark. Shown above the root in Figure 23 is an empty proctodaeum from a larva of a size comparable to that from which the root was removed. The convoluted hind gut must be quite

flexible and expandable to accommodate and pass roots of this size without rupturing.

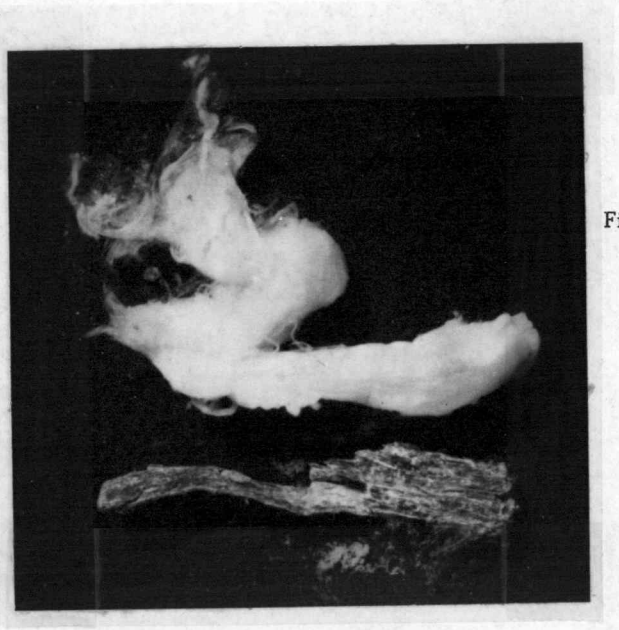


Figure 23. The longest piece of root (7.40mm) found in the alimentary canal of any Pleocoma larva examined. Above the root is shown the empty proctodaeum from a larva of comparable size (7.5X).

The second longest piece of root eaten, 7.00mm long, was ingested by a large P. carinata larva. This root was much thinner than that shown in Figure 23, measuring only 0.15mm in diameter. These were the only two segments of root consumed that were longer than 7.00mm. There were many roots eaten intact, however, which were longer than 4.00mm and a few 5.00mm and longer.

Elsewhere in the United States, white grubs damage the roots of young trees in much the same manner as Pleocoma larvae were observed to feed on the roots of conifers in western Oregon. White grubs, chiefly Phyllophaga, damage roots of conifers in nurseries

and plantations both by cutting and by stripping the roots (49, p. 354; 62, p. 176; 64, p. 429; 65, p. 651; 73, p. 149).

Preference for Type of Damage or Size of Root. Pleocoma larvae seem to consume more roots by masticating them and/or chewing off the phloem and outer bark before ingestion than by following roots through the soil and biting off intact segments. Roughly, only 30 percent of the larvae consumed roots in intact segments while following roots through the soil.

Many larvae tended to strip roots. The preference of some larvae to strip roots rather than eat them intact is supported by the observations that even very small roots, which could easily have been ingested in intact segments, were oftentimes stripped rather than eaten intact.

Although the softer bark would be relatively easy to strip from, and much easier to masticate than, the hard xylem, there are undoubtedly nutritional differences between the wood and the phloem which could be responsible for some larvae stripping the xylem, regardless of whether the xylem was ingested or not.

Moreover, the fact that larvae will damage a root in different ways indicates they do not necessarily prefer to feed in any certain way, or on any certain portion of roots. For example, a small P. simi larva was found feeding on a small Douglas-fir root (Figure 16). The mesenteron, and proctodaeum and posterior stomodaeum

were full of phloem and outer bark. Most of the stomodaeum, however, was filled with segments of a smaller branch root. This indicated that the larva was feeding on the phloem and outer bark along the periphery of the larger root but on encountering the branch root severed it and consumed part of it as well.

Another larva gnawed on the end of a root, fed on the phloem and outer bark along one side and split off a piece of bark and shredded some of the xylem tissue (Figure 17A). The gut contents of many other larvae attested to the fact that larvae feed indiscriminantly on roots, generally paying little attention to the manner in which they are feeding.

Though Pleocoma larvae do not appear to exercise any preference for type of damage inflicted to roots, they do appear to restrict their feeding to the smaller roots. Since there is a wide range in the size of coniferous roots permeating the soil at the depths at which Pleocoma larvae were collected, one would expect all sizes of roots would be equally available to larvae burrowing through the soil in search of food. However, the largest root found known to have been damaged in any way measured 13mm in diameter. Since there were many roots much larger than this present in the soil, one would be inclined to think that larvae avoided the larger roots.

As an example, a fourth or fifth instar P. dubitalis, exhumed

at McDonald Forest, had been burrowing along a root 5mm in diameter for about 5cm with no evidence of the root having been fed on. Upon encountering a smaller branch root, however, the larva began to feed (Figure 24). Two other larvae were unearthed burrowing along through the soil paralleling roots 19mm and 25mm in diameter, respectively. Neither root showed any indication of having been damaged.

The size of roots found in the guts of a given larva are not necessarily an indication of preference for that particular size of root but may be the largest root the larva could physically ingest. The pharynx and oesophagus, like the rest of the alimentary canal, are quite flexible and can stretch considerably to accommodate large pieces of root. However, since the tentorium restricts the expansion of the oesophagus, it will also restrict the diameter of pieces which can pass through the orifice.

The relationship between size of larvae and size of roots or root fragments ingested is shown by the data in Table 14. Almost without exception the larger pieces of roots, both in length and girth, were found in the larger larvae. The ability of larger larvae to ingest larger roots is apparently due to mechanical adaptations of the larger larvae rather than to selective feeding. Although larger larvae can ingest larger roots than can smaller larvae, the range in size of roots, either fragments or intact segments, was usually

Figure 24. Fourth or fifth instar P. dubitalis in soil burrow showing feeding damage (arrow) to small Douglas-fir root which larva had encountered after burrowing along larger root. Notice the three-points of contact the larva has in the burrow; the dorsum of the abdomen, the anal area and the thoracic legs (4X).

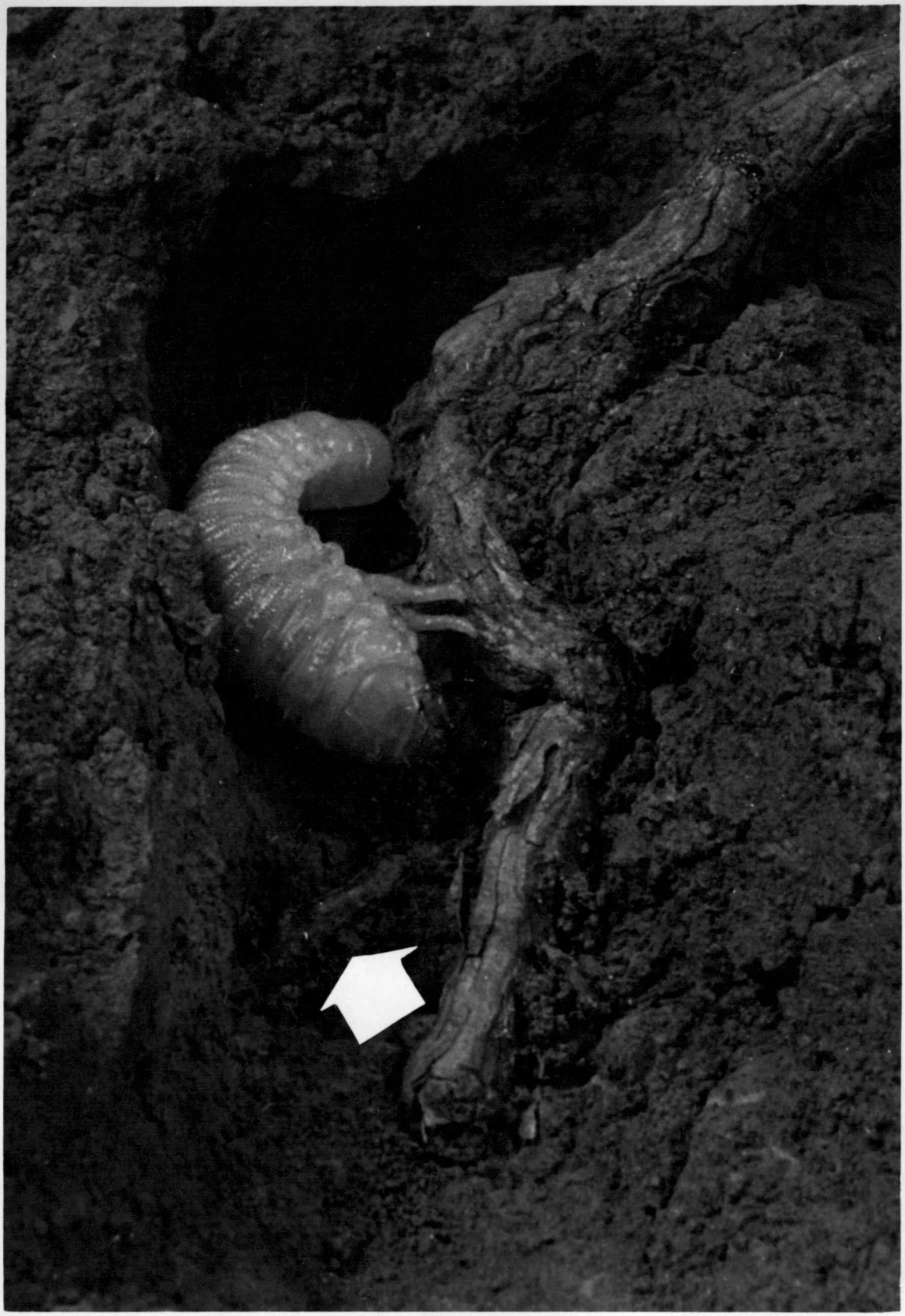


Table 14. Size of roots found in alimentary systems of Pleocoma larvae collected in western Oregon coniferous forest soils in 1960 and 1961

Larvae		Average size of roots or root fragments ingested			
		Intact roots		Root fragments	
Size or instar	No. examined	length (mm)	width (mm)	longest dimension (mm)	narrowest dimension (mm)
		P. dubitalis			
2	34	1.03	0.46	0.91	0.42
3	18	1.46	0.64	1.17	0.49
4	10	1.71	0.78	1.41	0.60
5	12	1.85	0.65	2.04	0.83
6	19	2.35	0.94	2.22	0.84
7	17	2.82	1.02	2.92	1.07
8	9	2.00	1.10	2.93	1.07
9-	14	3.65	1.50	3.83	1.29
		P. simi			
small	33	1.17	0.43	1.19	0.47
medium	47	2.58	0.84	2.29	0.96
large	35	2.98	0.77	3.30	1.31
		P. carinata			
small	7	1.15	0.42	0.92	0.50
medium	9	2.38	1.11	2.24	1.01
large	11	3.91	0.45	2.98	1.19

quite wide. For example, the average width of the smallest roots or root fragments eaten by the biggest larvae was smaller than the average width of the largest roots eaten by the smallest larvae.

Intact root segments in these guts indicated that most of the Pleocoma larvae were confining their feeding to coniferous roots generally smaller than about 2mm in diameter. Fragmented roots were found, however, in many alimentary canals, indicating roots larger than 2mm had been damaged. Since roots of all sizes were equally available, this probably means that Pleocoma larvae preferred to feed on smaller fibrous roots.

Exuvia

During late summer and early fall the most abundant material found in the guts of most Pleocoma larvae was exuviae of previous instars which newly-moulted larvae had consumed following ecdysis.

Most larvae kept in salve tins in the laboratory also consumed their exuvia following ecdysis. Several laboratory-reared second instars had completely consumed their exuvia in six to ten days following the moult.

Pleocoma larvae usually consumed all of the cast skin. Larvae generally fed first on the abdominal and thoracic portions of the exuvia, leaving the harder portions of the cephalic area until last. Even the mandibles of the exuvia were eaten (Figure 25A). When

Figure 25. Alimentary canals of Pleocoma larvae dissected to show exuviae which had been ingested by newly-moulted larvae.

(A) Above--A pair of mandibles, from the exuvia of the second instar, lying exposed in the dissected ventriculus of a third instar P. dubitalis (25X).

(B) Left--The dissected alimentary system of an eighth instar P. dubitalis. Most of the crop (the stomodaeal valve is near the base of the 4th pin down on the right) was filled with what appears to be the remains of fungal hyphae. Cast skin material fills the entire mesenteron. Little of the old exuvia is recognizable but setae can be seen scattered throughout the material (7X).

cast mandibles were found in the guts, they were always intact, having been severed near their bases from the rest of the exuvia. The hardness of the mandibles[16] most likely deterred most larvae from trying to chew them up.

Pleocoma larvae varied in the way they masticated the exuvia, just as they did in how they chewed up the roots. The material exposed in the dissected larval mesenteron shown in Figure 25B is all exuvia. The cast skin is so finely chewed that no portion of the old exuvia is readily recognizable, except setae. In contrast, Figure 26 shows most of the contents of the stomodaeum and ventriculus of a large P. carinata larva. This material is all exuvia consumed by the larva but was not masticated as that shown in Figure 25B. Some structures can be recognized in Figure 26; for example, in upper right center is the distal portion of an antenna, and at far left is the distal portion of a maxillary or labial palp.

All stages of larvae consumed their exuvia, except of course, first instars. First stage larvae did, however, consume the egg chorion. Several first instars were collected in the field with chorion in their guts. Also, most first stage Pleocoma larvae reared in the laboratory consumed the egg chorion shortly after hatching.

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[16] Mandibles of chewing insects have been found, using a scale of mineral hardness, to be harder than tin, copper, zinc, or silver (84, p. 42).

Figure 26. Fragments of cast skin, from the previous instar, removed from the stomodaeum and ventriculus of a large P. carinata larva (6X).

Soil

In addition to feeding on live roots, Pleocoma larvae ingest a certain amount of soil. In an otherwise empty gut it was easy to see soil particles, as their dark color contrasted with the white of the gut epithelium (Figure 27). However, in a gut packed with exuvia (Figure 25B) or roots (Figure 34A), soil particles such as those shown in Figure 27 would have been very difficult as well as time consuming to find.

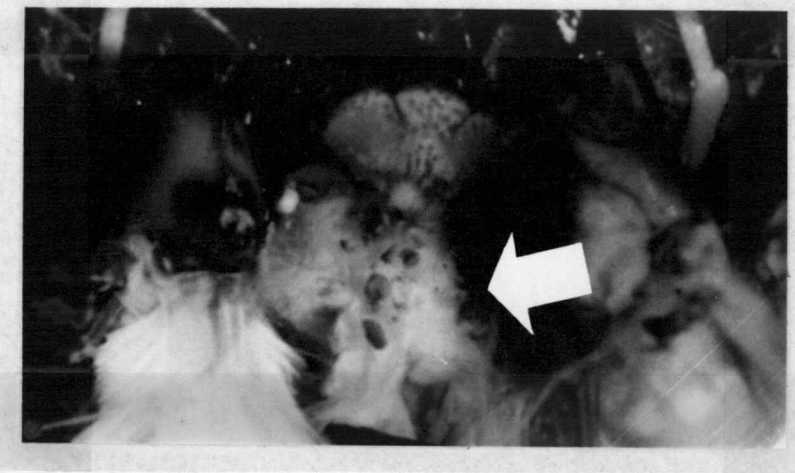

Figure 27. Five small particles (the largest is 170 microns in diameter) of soil (arrow) lying in the dissected pharynx of a third instar P. dubitalis (18X).

Amorphous soil particles were rather easily detected in those stomodaea which had been sectioned and mounted on glass slides, by use of polarized light. Polarization rendered the soil particles bright against a dark background (Figure 28). Some of the root tissues, especially the hard xylem tissue (which stained bright red with Safranin O) also showed up brightly against the dark background under polarized light. Xylem could be distinguished from soil particles by its association and attachment to other root tissues and its definite cellular structure.

Irregular bits of mineral soil particles, such as those visible in Figure 28, were seen in all of the 150 Pleocoma stomodaea examined. Although I did not make a quantitative analysis, I would estimate that the amount of mineral matter ingested by Pleocoma

larvae is considerably less than five percent by volume. Smith and Hadley (70, p. 20) report that guts of Japanese beetle larvae contain about 16 percent mineral matter by volume of the material eaten.

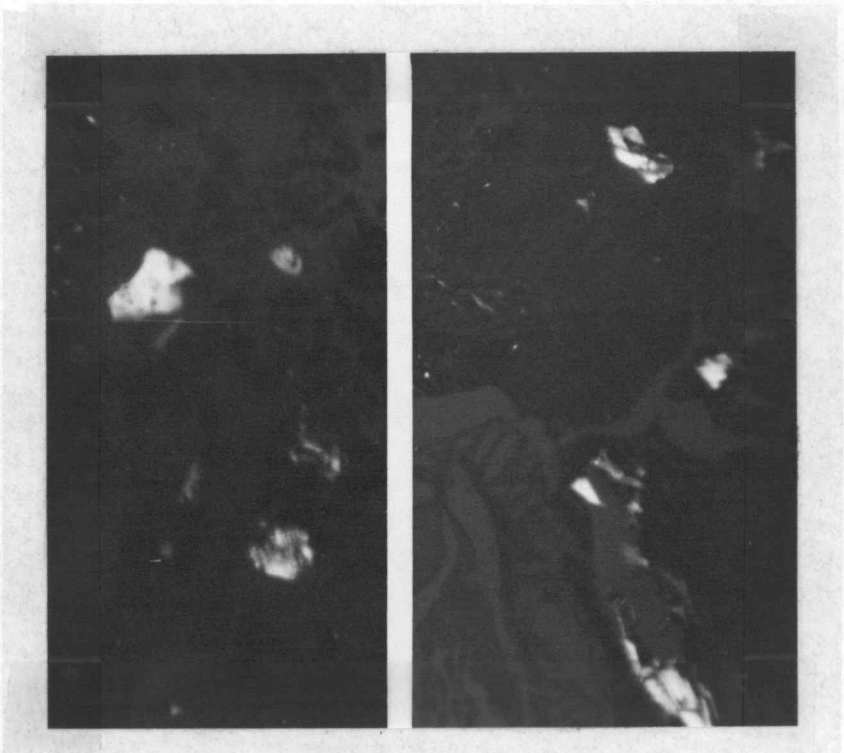

Figure 28. Photomicrographs of portions of two Pleocoma stomodaeal sections taken with polarized light to render mineral particles visible. (Left--Large P. simi larva (205X); Right--Medium-sized P. simi larva (140X)). Mineral particles show up brightly on the dark background. Subdued outline of gut epithelium is visible in lower left of photo on right. Bright material to right of center in bottom of photo at right is xylem tissue of roots.

Other Material

In addition to the three types of material discussed in the foregoing sections, what appears to be at least five other types of material, were found in the guts of many larvae. Most of these

materials have not been identified for certain, although specialists in related fields have provided some tentative identifications. Each type of material is tentatively identified and discussed below.

Remains of Fungal Hyphae. Scattered throughout the alimentary system of many Pleocoma larvae was a fine, fluffy, cottony-like, light to dark brown material. In many stomodaea which were packed with roots this material was interspersed throughout; in other root-packed crops there was little or none. Some crops which were otherwise empty were packed with the same material. This material (Figure 29) has been tentatively identified[17] as the remains of fungal hyphae. The material is probably fairly abundant in the soil and could constitute a considerable component of the diet of Pleocoma larvae.[18]

Hyphae were often seen in guts otherwise filled with exuvia (Figure 25B). It is of interest that hyphae are present in the guts of larvae at a time when most larvae have temporarily ceased feeding

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[17] Personal communication with Dr. M. F. Day, Commonwealth Scientific and Industrial Research Organization, Division of Entomology, Canberra, Australia.

[18] As early as 1890, Rivers (57, p. 24-26) indicated that fungus may form part of the diet of some Pleocoma larvae. After noting that decaying rootlets of shrubs and trees pass through the soil and intermixed with humus in which burrows of P. behrensii larvae are found he says, "The decaying fibres, together with fungoids, appear to be the only possible vegetable food within the reach of this insect in its growing state."

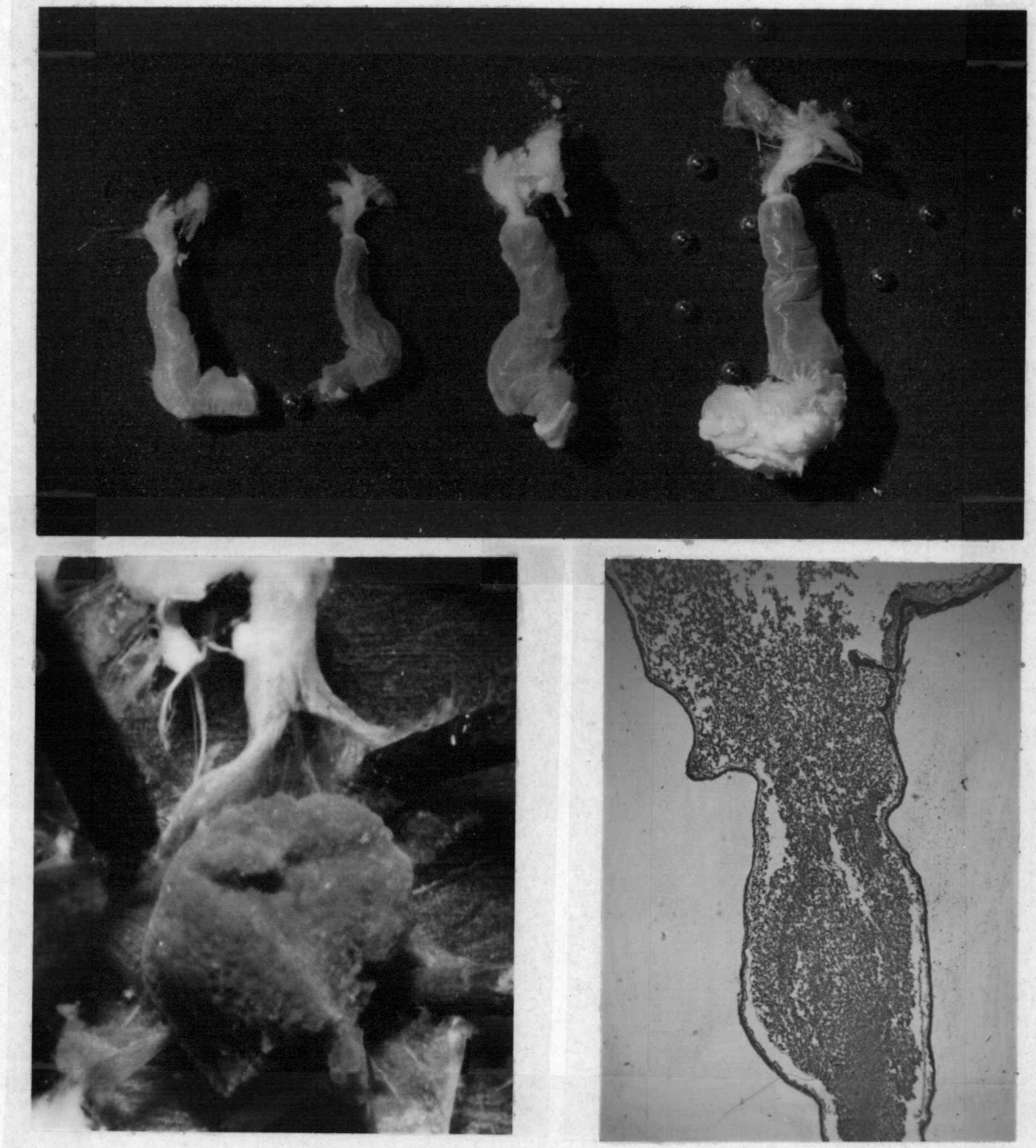

Figure 29. Stomodaea of Pleocoma larvae containing what has been tentatively determined to be the remains of fungal hyphae.

(A) Above--Stomodaea of four P. dubitalis larvae filled with this apparent fungal hyphal material (8.5X).

(B) Below left--A wad of apparent remains of fungal hyphae dissected from the oesophagus of a fifth instar P. dubitalis. The unincised anterior oesophagus is in the upper half of the photo (26X).

(C) Below right--Photomicrograph of anterior crop and oesophagus of an eighth instar P. dubitalis showing what appears to be the remains of fungal hyphae. Stomodaea, such as those shown in in (A), appear as shown here after having been sectioned and stained (33X).

on roots and are feeding only on their exuvia.

Fungal hyphae were found in larvae of all sizes in every month of the year, and in larvae of each species. Oftentimes, when hyphal remains were found fairly well packed in a gut, they appeared to be darker toward the rear (Figure 30).

Figure 30. Contents of portion of crop and ventriculus of a small P. carinata larva collected on 19 July 1961. That portion of the crop shown (above white arrow) is packed with the apparent remains of fungal hyphae but quite light in color. The material in the ventriculus between the white arrow and the upper black arrow is material of the same consistency but much darker in color. The material in the rear part of the ventriculus between the two black arrows (the lower black arrow designates the pyloric valve) is tentatively identified as cast ventricular epithelium. The ileum of this larva was full of roots, the colon and anus empty (10X).

The possibility was considered that there may be some relationship between these hyphae and the fungal hyphae forming the

mantle on mycorrhizal rootlets found in the guts of Pleocoma larvae. At least six different species of mycorrhizal fungi were identified[19] in the guts of many Pleocoma larvae examined. All were associated with mycorrhizal rootlets or mycorrhizal fragments (Figure 31).

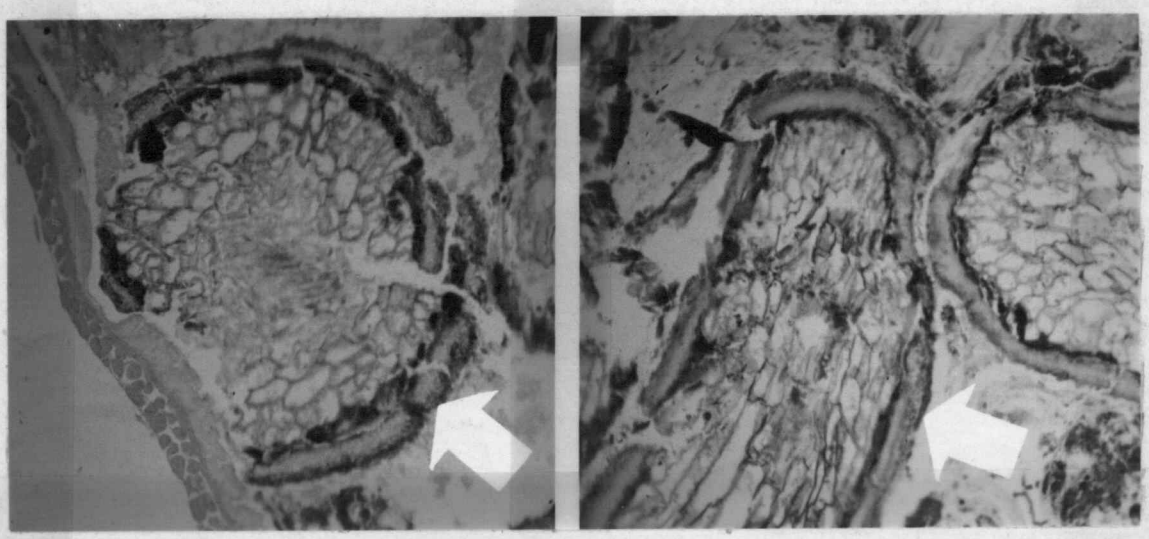

Figure 31. Photomicrographs of portions of stomodaea of two Pleocoma larvae containing mycorrhizal rootlets or mycorrhiza fragments (both photos 90X).

(A) Left--Portion of stomodaeum of medium-sized P. carinata larva. The fungus mantle (arrow) surrounds the conifer rootlet shown.

(B) Right--Portion of stomodaeum of a P. simi larva. The fungus mantle (arrow) surrounds the conifer rootlet. Hyphae of the mycorrhizal fungus Cenococcum graniforme (Sow.) Ferd. and Winge, were detected in this stomodaeum.

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[19] Personal correspondence in 1964 with: Dr. Robert G. McMinn, Forest Ecologist, Forest Entomology and Pathology Laboratory, Canada Dept. of Forestry, Victoria, British Columbia; and Dr. James M. Trappe, Pacific Northwest Forest and Range Experiment Station, U. S. Forest Service, Portland, Oregon.

There does not appear, however, to be any relationship between the material tentatively determined to be the remains of fungal hyphae and the mycorrhizal fungi associated with the periphery of conifer rootlets ingested by Pleocoma larvae. Hence, Pleocoma larvae do not appear to be utilizing the mycorrhizal material.

Cast Ventricular Epithelium. There are reports (72, p. 373) that in most holometabolous insects there is probably more or less of a renovation of the stomach ventricular epithelium accompanying each larval moult, although the renovation does not always involve a complete loss of the old cell wall. In some cases the mid-gut epithelium becomes uniformly vacuolated and the entire epithelium is cast off into the lumen (11, p. 282-283).

During the period of the year in which Pleocoma larvae were moulting I often found material in the mid or hind guts which could have been shed ventricular epithelium. The material which fills the lumen of the mid gut in Figure 32A certainly has the appearance of what a complete ventricular epithelium might look like after having been shed into the gut lumen. Moving rearward, this material appears to have become compressed as it moved in the ileum (Figure 32B).

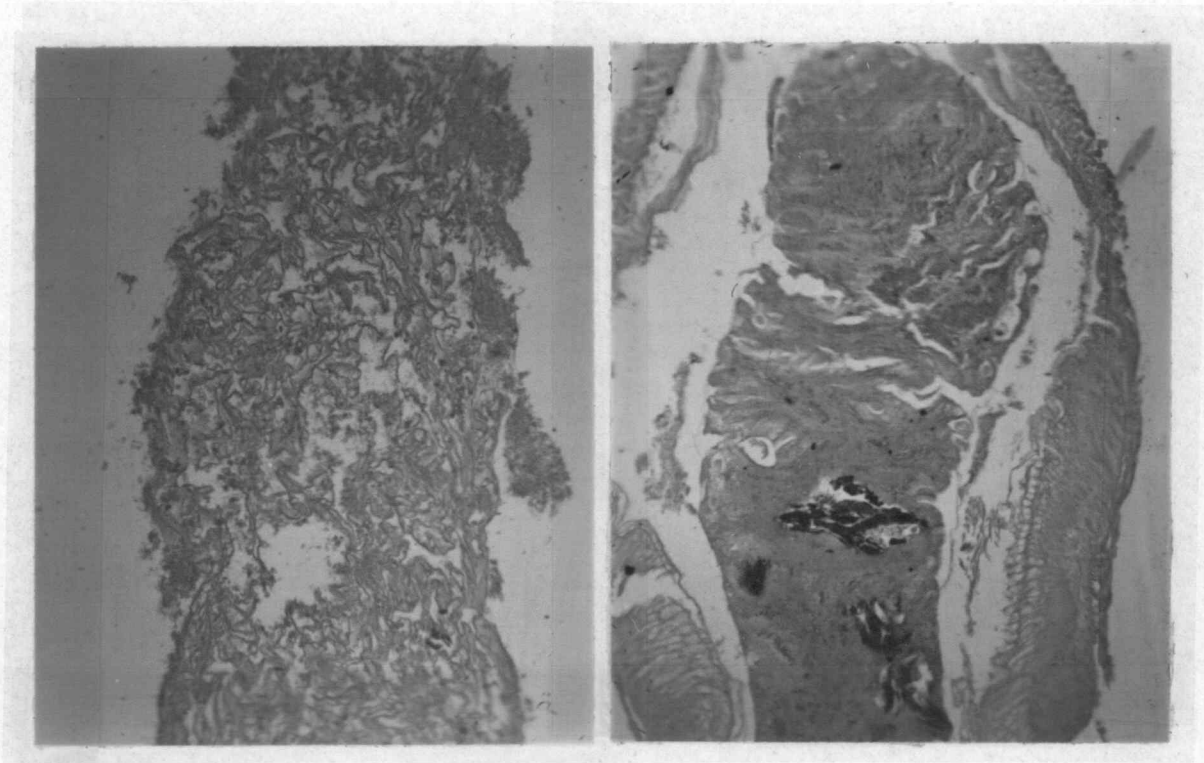

Figure 32. Photomicrographs of portions of the alimentary system of a second instar P. dubitalis, collected 28 July 1961, showing what may be the shed ventricular epithelium lying in the gut lumen.

(A) Left--Anterior portion of the larval midgut showing the material rather loosely distributed (83X).

(B) Right--Anterior portion of the larval hindgut showing the material as it has become compressed. The dark objects shown engulfed in the material are fragments of roots (125X).

As well as becoming more compact, as it moves caudally, this cast ventricular epithelium appears to darken. In some larvae in which this material was compressed in the ileum or colon it was a dark charcoal brown to black in color.

There are three observations which support the contention

that this material is cast ventricular epithelium. (1) The material was found in guts only during the period of the year when larvae were moulting. (2) It was never observed in the stomodaeum. Most often it was found in the mesenteron and less often in the proctodaeum. (3) The larval stages in which this material was found coincide with larval stages in which this physiological process has been found to take place (3, p. 577).

Gregarine Parasites. In many Pleocoma larval guts I observed numerous small (1mm in length), usually light colored bodies, irregular in shape but always smooth-sided and usually flattened. In most cases these bodies were seen in the mesenteron just beneath the peritrophic membrane and completely enveloping the roots in the gut (Figure 33). In other cases the bodies were found in alimentary canals devoid of roots and either empty or containing some other material.

These bodies, either completely enveloping the gut contents as shown in Figure 33, or loose in otherwise empty guts, were observed in Pleocoma larvae throughout the year. They were never observed in stomodaea, at least in the manner completely enveloping the gut contents as shown in Figure 33. In some otherwise empty alimentary canals, a few of these bodies seemed to have drifted forward into the foregut.

Figure 33. Mesenteron of a medium-sized P. carinata larva showing small irregular-shaped bodies lying just within the peritrophic membrane around the roots in the guts. The gut shown in the upper half of the photo has been dissected to expose the roots. That portion of the gut in the lower half of the photo has not been disturbed except the gut epithelium has been removed (9X).

After having examined a photograph, identical to that shown in Figure 33, Dr. M. F. Day (see footnote #17) wrote, "....the only suggestion I can make is that the bodies have some resemblance to gregarine parasites. Admittedly they don't look very much like the classical forms but I have seen many larvae very completely infected

where the organisms have some resemblance to the bodies in your photograph."

Bacteria. After his examination of some of the Pleocoma stomodaeal sections, Dr. Day (see footnote #17) wrote, "We also see quantities of material which appear from your sections to be bacteria. However, the fixation and staining does not seem to be adequate to be certain about this."[20]

Acarina (Mites). Mites were found in the digestive tracts of three larvae. One mite was found among bits of wood in the mesenteron of a third instar P. dubitalis. Another mite was enveloped in woody material in the ileum of a second instar P. dubitalis. A third mite was found in the proctodaeum of a third instar P. dubitalis. The mites were not identified. Similar mites were often found clustered in the integumental folds around the head capsules of many larvae.

Factors Influencing Feeding Habits

Alimentary systems of some larvae were found full or partly full of roots, the guts of some larvae were empty and the guts of others were full of exuvia or other material. Some of the more

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[20] As noted on page 15, all slides were stained with safranin and fast green as recommended for woody material. Therefore, the staining procedures would be inadequate for material other than woody roots.

important factors which influence feeding habits and hence determine why certain materials are present in varying amounts in the guts of Pleocoma larvae during the year are discussed below.

Time of Year

With some exceptions the alimentary canals of most Pleocoma larvae were full of roots throughout most of the year. With with exception of some larvae of pupating stages there is no indication that Pleocoma larvae feed less in the winter.

The physiological process preceding and during moulting appears to be the most important and influential factor responsible for a general cessation of root feeding during late summer. It is not uncommon in Insecta, as the time for moulting approaches, for the organisms to cease feeding and become inactive (20, p. 109), the inactivity often commencing when the cuticula begins to separate from the epidermis (72, p. 64). Except at moulting time, the alimentary canal, especially in larvae, is in many insects often kept full of food (80, p. 12).

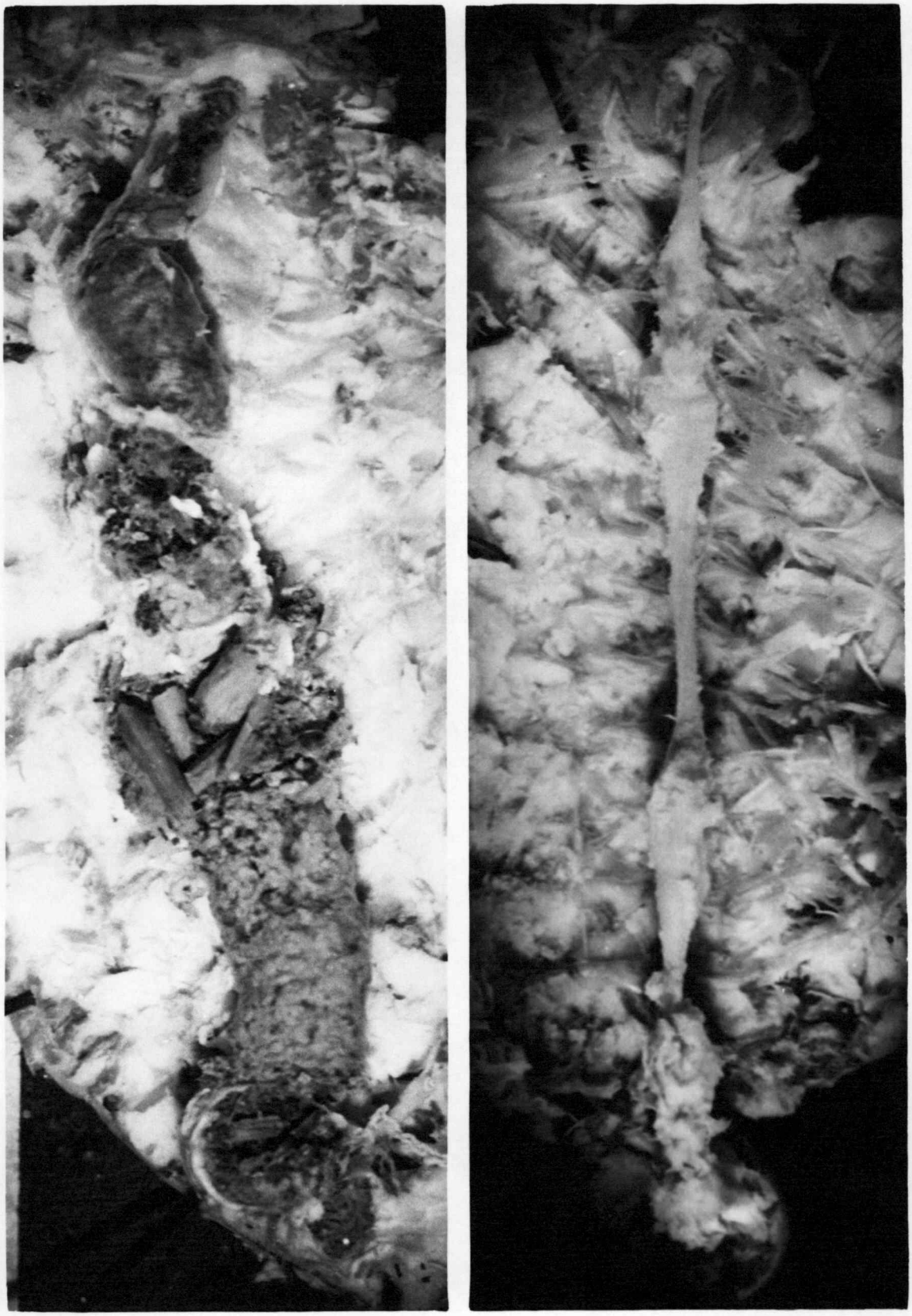
Alimentary systems of larvae heavily feeding appear as that shown in Figure 34A. When feeding ceases, either prior to moulting or prior to pupation the alimentary system is devoid of food and withdrawn as shown in Figure 34B.

The period of the year when larvae cease feeding on roots

Figure 34. Alimentary canals of two Pleocoma larvae, one empty and one packed with roots.

(A) Left--The entire alimentary canal of a ninth-larger instar P. dubitalis packed with roots. (The gastric caeca were removed from the crop.) The mid-ventriculus has been opened to show the size of pieces of root which have been ingested. These pieces of root xylem, visible near the center of the photograph, have been split lengthwise before they were ingested (5X).

(B) Right--A completely empty alimentary system of a large P. simi larva. Note the absence of gastric caeca on the crop and at the proventriculus, 6cm from top of photo (5X).



during moulting was generally the same for each species studied, however, there appear to be some minor interspecific differences.

Pleocoma dubitalis larvae generally feed quite heavily on roots from October through June. Toward the first part of July root feeding seems to be slowing down and the non-root feeding period extends at least through mid-September. Toward late August and on into late September most larvae are feeding on their exuviae. By mid-October most larvae have resumed root feeding. However, some P. dubitalis larvae were still feeding on exuviae as late as 21 November in 1961 (Table 15).

Though collections of P. simi and P. carinata were made less frequently, their feeding habits seemed to follow the same general pattern as those of P. dubitalis. Larvae of both species were generally feeding on roots during the winter and spring but sometime during late June to early July begin a non-root feeding period (Table 15). The non-root feeding period extended through July and August, when larvae were either not feeding or were consuming their exuviae. Since few fall collections were made for these two species, the exact period in the fall when root feeding resumes is not known. Larvae of these two species probably resume root feeding sometime between mid-September and mid-October.

Data from three collections of P. minor and P. crinita in June and September, 1960, indicate that larvae of both species also

Table 15. Contents of the alimentary systems of three species of Pleocoma larvae collected during 1960 and 1961 at several sites in western Oregon coniferous forests.

Larvae collected			Contents of the alimentary system				
			Roots				
No.	Date	Site	Full	Partly full	Trace	Empty	Exuvia
			P. dubitalis				
15	28 I 1961	32	8			7	
18	25 II 1961	32	16			2	
20	18 III 1961	32	12	5		3	
7	31 III 1961	32	6			1	
14	24 IV 1961	32	12		1	1	
8	7 V 1961	32	6			2	
7	13 V 1961	32	6	1			
14	29 V 1961	32	12			2	
7	28 VI 1961	32	4		1	2	
7	8 VII 1961	32		1		6	
14	28 VII 1961	32		1	6	6	1
5	15 VIII 1961	32			3	2	
6	25 VIII 1961	32				5	1
7	13 IX 1961	32				2	5
14	21 X 1961	32	8			4	2
13	21 XI 1961	32	9			1	3
13	22 XII 1961	32	12			1	
			P. simi				
6	7 I 1961	14	5			1	
46	22 III 1961	19	36	1	4	5	
1	19 V 1960	10	1				
32	26 V 1961	19	30	1		1	
21	16 VI 1960	21	18	2		1	
4	19 VII 1960	14		2	1	1	
1	26 VIII 1960	11					1
7	26 VIII 1960	16			2	1	4
5	1 IX 1960	10			2		3
3	14 X 1960	14				3	
16	7 XII 1961	19	5	6		5	
			P. carinata				
5	3 I 1961	3	4			1	
7	28 III 1961	8	3	2	1	1	
1	11 V 1961	3	1				
2	12 V 1961	2	2				
12	21 V 1960	2	12				
6	19 VII 1961	2		2	1	3	
12	2 IX 1960	2				2	10
1	27 X 1961	8	1				

cease feeding on roots during the moulting period in late summer.

It appears that P. minor begins a period of non-root feeding earlier in the summer than any of the other species. Of 12 P. minor larvae collected on 14 June 1960, the guts of nine were either empty or only partially full of roots. Since no exuviae was found in any of the guts, these larvae were probably preparing to moult. This would agree well with prior observations (15, p. 27) that P. minor larvae begin moulting near 12 June.

This earlier period of reduction in root feeding by P. minor larvae was the only major interspecific difference between the five species of Pleocoma larvae in their feeding habits throughout the year.

The period of the year when Pleocoma larvae are feeding most extensively is the period when some other root feeding scarabaeids, especially Phyllophaga spp., are not causing much damage. In forest tree nurseries and plantations in the South, Phyllophaga grubs are relatively inactive during the winter but resume feeding in the spring and damage trees throughout the summer and fall (73, p. 149).

Stages of Larvae

Besides the cessation of root feeding during the moulting period each year, there are at least two other periods in the life of

Pleocoma larvae when they are not feeding on roots: (1) during the first stage and early part of the second stage and (2) during the entire stage prior to pupation. The known feeding habits of larvae during these two periods are discussed below.

First-Second Stage Larvae. In the laboratory, first instar P. dubitalis and P. carinata spent approximately half of the first stage feeding on the chorion of their eggs. Some first stage Pleocoma larvae fed on chorion in the field. After they had stopped feeding on the chorion all first instars reared from eggs in the laboratory were provided with tiny rootlets. None, however, fed at all on the rootlets provided. Furthermore, no roots were found in the alimentary systems of any first instars collected in the field.

Second stage P. dubitalis larvae began feeding on roots not long after they moulted from first instars and moved away from the egg niches about mid-November. Gut contents of second instars collected between mid-November and late summer indicate that they feed on roots throughout that period until the general cessation of feeding prior to moulting to third instars.

Last Stage Larvae. From the time they begin feeding on roots in the fall as second instars, Pleocoma larvae generally are feeding on roots, with the exception of the moulting period each year, until they reach the final instar. Contents of the alimentary canals of nearly 60 seventh instar and older P. dubitalis larvae indicate

that last stage larvae pass the entire stadium without feeding on roots. Some of these larvae will, however, ingest and pass exuvia of the penultimate instar.

Furthermore, last stage larvae confine themselves to cells constructed in the soil somewhat less than 20 inches in depth. The generalization can be made that seventh instar or larger P. dubitalis larvae collected at any time of the year shallower than 20 inches in the soil at McDonald Forest, or perhaps in a similar soil type elsewhere, will not be feeding on tree roots.

Though data on P. simi and P. carinata are fewer, they do indicate that feeding habits of last stage larvae of these species are similar to those of P. dubitalis. Contents of the alimentary canals of P. simi and P. carinata larvae collected throughout the year at several sites indicate that regardless of soil type, large larvae preparing to pupate burrowed to the shallower depths and ceased feeding.

These observations on non-feeding last instar Pleocoma larvae support some earlier studies on changes in the digestive tract of older larvae. It has been found (3, p. 563) that both sets of gastric caeca degenerate in late instar Pleocoma larvae, accompanied by a shortening of the mid gut and a lengthening of the fore and hind guts. These two conditions plus the degeneration of the mid-gut epithelial cells led to the suggestion (3, p. 575) that late

instar Pleocoma larvae cease feeding or change their feeding habits.

The non-feeding last stage larvae collected at the shallower depths usually were without gastric caecae and had relatively short mid guts. The alimentary canal illustrated in Figure 34B is typical of this condition. The reduced length of the midgut is obvious when compared to the length of midgut in a feeding larva (Figure 34A). It should be noted, however, that the gastric caecae do not degenerate nor does the midgut shorten in all later Pleocoma instars, but only those terminal instars preparing for pupation. For example, Figure 34A is a photograph of the gut of a very large ninth or larger instar P. dubitalis, which was obviously not preparing to pupate. It was collected on 29 May 1961 at a depth of 34 inches in the soil.

Soil Type and Depth of Larvae

Soil type affects the feeding habits of Pleocoma larvae only indirectly through its influence on tree roots and the vertical distribution of larvae.

Regardless of soil type, depth of larvae did not appear to influence larval feeding habits, either at the time of year when larvae were predominantly feeding on roots or when they were not feeding or feeding on exuvia. The only exception to the relationship between depth of larvae and feeding habits is the selection of shallower depths in the soil by last stage larvae, discussed in the foregoing section.

Otherwise, larvae were generally feeding on roots throughout the range in depths over which they were collected.

Movement of Food Through the Gut

Method of Movement

The pharyngeal intima of Pleocoma larvae is covered with spines protruding inwardly and caudally, a feature observed previously with Pleocoma larvae (3, p. 564) and common in many insects (72, p. 350). These spines apparently function through peristaltic action to move roots and other material through the pharynx and on into the oesophagus. The position of these spines relative to roots passing through the pharynx shows (Figure 35A) how the roots are forced rearward but also prevented from migrating anteriorly.

Rate of Movement

A few observations were made on the passage of exuvia through the gut of some Pleocoma larvae. Five newly-moulted second instar P. dubitalis, confined with their exuvia, were dissected and examined at intervals after completely consuming the exuvia. The alimentary systems of three of these larvae, examined 12, 24, and 48 hours, respectively, after feeding, were all packed with

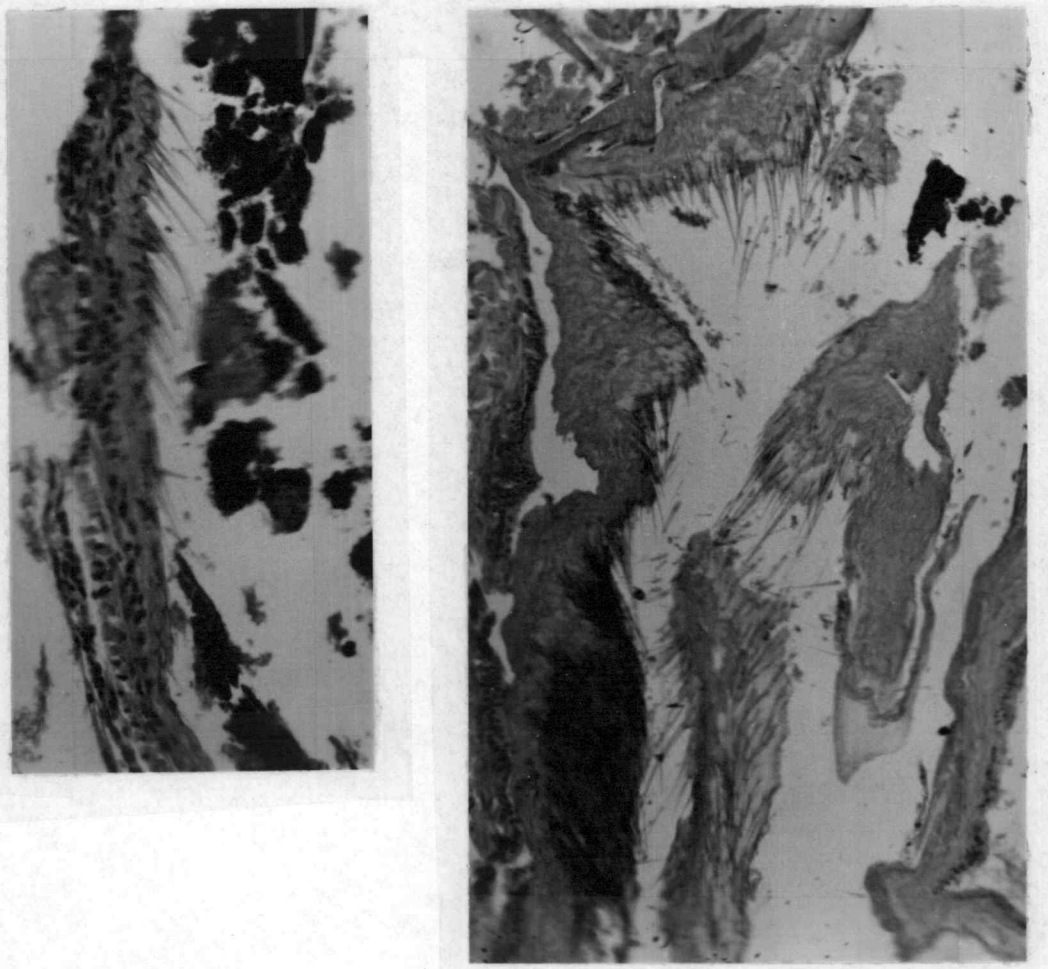


Figure 35. Photomicrographs of the pharyngeal epithelium and intima of two P. dubitalis larvae showing the long backward-projected spines arising on the intima. Buccal cavity is out of view beyond the top of the photographs.

(A) Left--Sagittal section of portion of pharynx of a third instar. The dark objects immediately to the right of the spines are root fragments (220X).

(B) Right--Parasagittal section of portion of pharynx of seventh-eighth instar. Only one small root fragment (the dark object in upper right of photo) is visible in this pharynx (190X).

exuvia from anterior crop through the colon. One larva examined after three days had exuvia in the colon only, and the fifth larva, after seven days had a trace of exuvia in the crop and the colon was packed full. One seventh instar, examined 19 days after feeding, still had a few setae in the posterior ventriculus and in the ileum and colon.

The length of time exuvia was retained by these Pleocoma larvae can be compared to egestion time in some other insects: 25 to 80 minutes in stored grain insects (69, p. 204); 16 to 31 hours in the American roach (12, p. 303); two to three hours in silkworms (37, p. 79); and 1.6mm/ hour in adult earwigs and 50-75mm/ hour in blowfly larvae (80, p. 3-4).

Mastication of Roots

In many species of insects, the mouthparts and the proventriculus, often provided with numerous chitinized plates or spines, break up food particles to dimensions suitable for the action of digestive secretions (12, p. 305).

There are no special structures such as teeth, pads, or spines in the proventricular area of Pleocoma larvae (3, p. 564). Hence any reduction in the size of material to be passed through the system must be done by the mandibles. Pleocoma larvae often masticate some roots into rather small pieces while others are left

in fairly large chunks (Figure 36).

Figure 36. Stomodaeum of a ninth-larger instar P. dubitalis showing spatial arrangement of roots as they pass through the system. Some roots were chewed into quite small pieces by the mandibles, others remain as relatively large fragments. The epithelium has been removed from this stomodaeum; the translucent intima still holds the roots in place (8X).

Once having been masticated by the mandibles, there appears to be little or no change in the size of intact roots or root fragments as they pass through the alimentary system. Root fragments dissected from the hindguts of many Pleocoma larvae appeared to be no different in size from root fragments removed from the oesophagus

of respective larvae (Figure 37). Two relatively large root fragments embedded in a frass pellet are shown in Figure 38A.

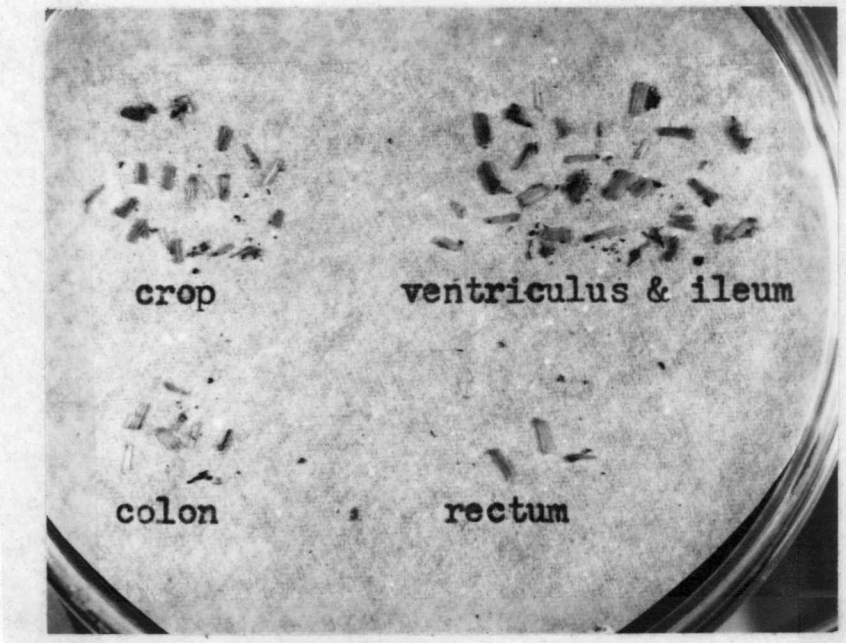


Figure 37. Roots taken from the alimentary canal of a P. simi larva show that there is little or no change in size of root fragments as they move caudally in the alimentary canal (1.2X).

Although there appears to be no change in the size of roots with alimentation, just what nutrients, if any, are extracted from these roots, and how they are extracted is not known. Some plant-feeding insects with the proper digestive enzymes utilize cellulose in their diets. However, "In the vast majority of species cellulose is quite unaffected by passage through the intestinal canal; those plant cells that are not ruptured...." by the mandibles, "....pass through the gut with their walls intact, although their contents may

be digested" (83, p. 50).

On the other hand, many insects have a rich fauna of bacteria or protozoa in the gut. For example, "Some lamellicorn beetle larvae that feed on pine needles and such like, ingest with their food those microorganisms which ordinarily ferment cellulose in nature" (83, p. 50). Bacteria have been, with some reservation, identified in the guts of Pleocoma larvae. If they are normally present, they may be involved in the utilization of coniferous roots by Pleocoma larvae.

The passage of large fragments of roots through the alimentary system of Pleocoma larvae may indicate that they are similar to other phytophagous insects in that they ".... eat to satisfy their requirements for essential nutrients and in doing so destroy enormous amounts of food and fiber (19, p. 70). This habit may be brought about by the fact that as a rule, "Phytophagous larvae are inefficient in converting food into body tissues...." (19, p. 58). Two genera of Cerambycidae, for example, must ingest huge quantities of their food material in order to extract from it the carbohydrates sufficient for their growth (40, p. 253).

Excretion

Though many root fragments passed through the guts of Pleocoma larvae with no evidence of having been compressed or

mechanically triturated in any way, the contents of some frass pellets, either found in the larval burrow or dissected from the rectum, seemed to have been compressed into fairly compact balls of excrement (Figures 38B and 38D).

Material passing through the alimentary canals of Pleocoma larvae showed no indication of becoming compacted until it reached the colon. One or more of at least three factors probably contributed to the compaction, as follows: (1) The well developed circular muscles of this section of the gut (3, p. 570); (2) Some phase of digestion. It is reported (83, p. 51) that the greater part of digestion in wood-eating lamellicorns (Lamellicornia = Scarabaeoidea) takes place in the hindgut; (3) Water conservation, a function of the hindgut, especially in conjunction with constriction by circular muscles. Fecal material dissected from the larvae was always well compacted and dry. Several frass pellets are shown in Figure 38.

Figure 38. Frass of Pleocoma larvae.

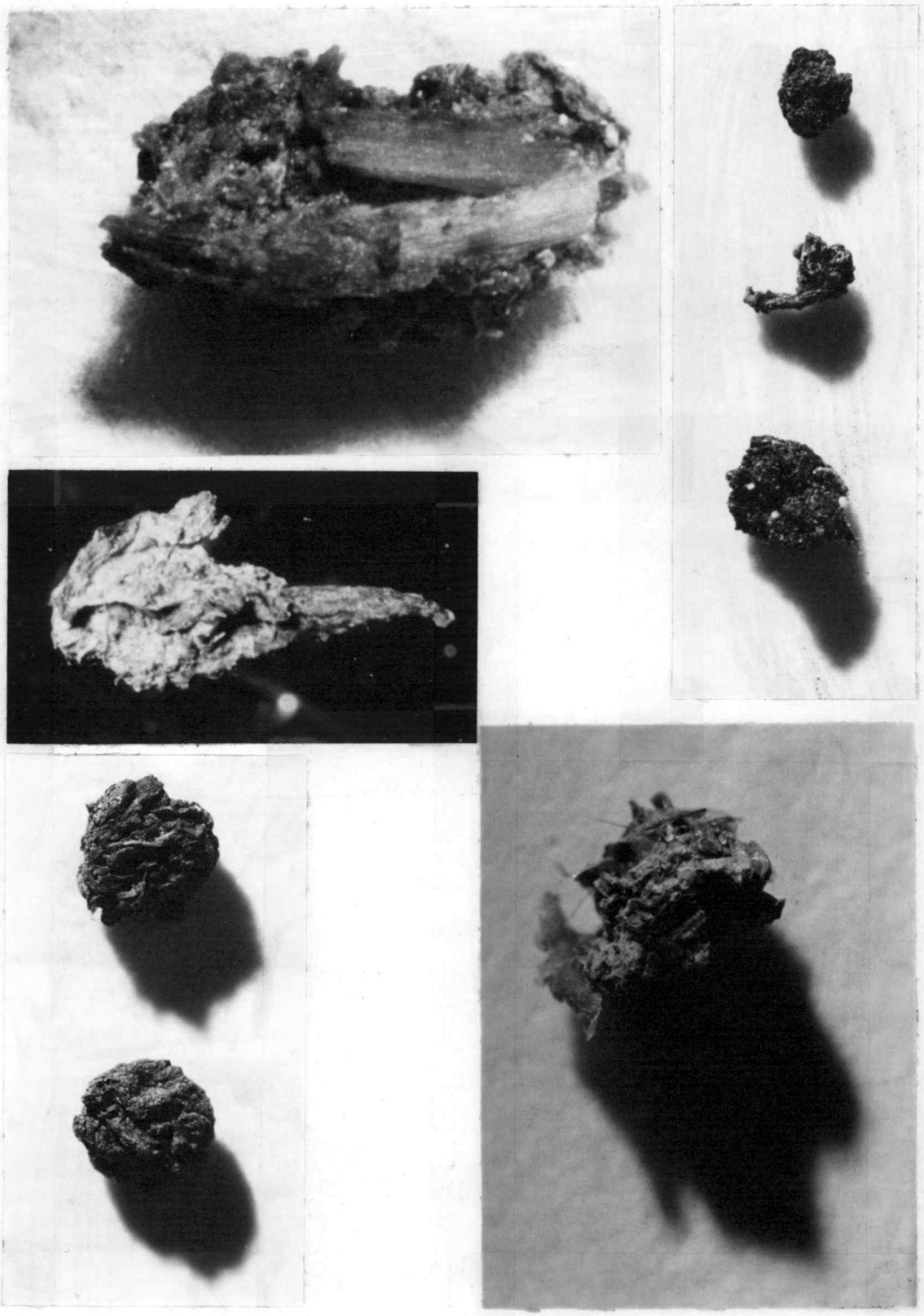
(A) Upper left--Pellet from medium-sized P. simi larva. Two fairly large root fragments are embedded in the material. These two pieces show no evidence of having been mechanically triturated as they passed through the system (23X).

(B) Upper right--Three pellets collected in larval burrow with a fourth-fifth instar P. dubitalis. The center pellet has a small piece of root protruding from the main body of the pellet (26X).

(C) Center left--Pellet removed from rectum of medium-sized P. simi larva. When removed from the larva, the root, seen projecting to right of main body of pellet, was protruding up into the colon (21X).

(D) Lower left--Two balls of excrement collected in a burrow behind a P. dubitalis larva (13X).

(E) Lower right--Fecal pellet removed from rectum of a medium-sized P. simi larva. This pellet is composed entirely of cast skin material; two setae can be seen protruding from the left side of the pellet (18X).



DISTRIBUTION

Although a study of the distribution of Pleocoma in Oregon was not a major objective of the present work, many new sites were discovered from which Pleocoma, especially P. simi and P. carinata, were not known prior to 1960. The new sites are incorporated into a geographic distribution map (Appendix Figure 1) on which are located all the sites where Pleocoma adults are known to have been collected, as of April 1962.

Pleocoma larvae were collected at eleven of the sites numbered in Appendix Figure 1. P. dubitalis larvae were collected at two sites, P. simi at six sites[21] and P. carinata at three sites (Appendix Table 1). P. crinita and P. minor were collected at several sites in forested areas adjacent to Pleocoma-infested orchards in the Hood River Valley. These sites are not numbered but lie within the area encircled for these two species in Appendix Figure 1. Photographs of eight of the sites where larvae were collected are shown in Appendix Figures 2 to 6. Four sites are also illustrated where no larval collections were made but where adults were collected in flight.

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[21] Eight sites were visited in search of P. simi larvae; larvae were found at only six of them.

GENERAL EVALUATION--THE ROLE OF *PLEOCOMA* IN THE FOREST

This study indicates a very close relationship between soil-inhabiting *Pleocoma* larvae and many old-growth coniferous forests in western Oregon, since tree roots appear to form the major part of the larval diet. However, *Pleocoma* larvae do not seem to be serious pests in these old-growth forests. The relatively light impact of this root feeding by *Pleocoma* larvae on old-growth and advanced second-growth (Saplings and Poles) in western Oregon coniferous forests is determined by at least three aspects of the biology, feeding habits and distribution of the larvae.

1. Most *Pleocoma* larvae in forest soils are feeding on the smaller roots, generally those smaller than 2mm in diameter. The largest root known to have been damaged in any manner measured only 13mm in diameter and it had been merely scored--only the phloem and outer bark eaten away from part of the root. The largest root found to have been severed was only 6mm in diameter.

This type of damage contrasts with the damage done by *Pleocoma* larvae in orchards. "Fibrous roots, main roots, and underground portions of the trunk of bearing and non-bearing trees are destroyed or scored by the grubs" (15, p. 8). In severe cases, ".... most of the root surface and underground part of the trunk...." are scoured out by the strong mandibles of the voracious *Pleocoma*

grubs. This scouring, which may be shallow or relatively deep, ".... occurs in irregular patches and winding bands which often girdle the roots especially on roots of smaller diameter" (56, p. 41).

2. Pleocoma larvae are not feeding on roots during the larval moulting period which extends from mid-summer through early fall. Thus, trees are not being attacked during periods of active growth or high transpiration stress.

3. Populations of Pleocoma larvae in the forest are widely scattered and erratic. Even where existent, populations per unit area are much lower than larval populations in orchards where Pleocoma larvae are destructive. It is conceivable that if larval populations in the forests were to increase, even in localized areas, to the numbers now found in some orchards, that larval damage symptoms similar to those exhibited in the orchards might begin to show up. Such symptoms would probably be manifested in the form of a subtle and slow steady decline in the vigor and general appearance of the trees. In the forested area, six miles north of Oakland, where the densest populations were found (5.1 larvae per square foot), larvae must have consumed considerable portions of the fibrous root systems of the trees. Trees at this site (Appendix Figure 3B), however, showed no above-ground symptoms of excessive root damage and there was no evidence, either from larval gut examinations or from roots examined in sample holes, that root

feeding was not confined to fibrous roots and rootlets. Ellertson and Ritcher concluded (15, p. 9) that in the Hood River Valley orchards ".... these grubs are not serious pests unless present in large numbers, whereupon destruction of the fibrous root system results in a slow decline of the tree."

Though not causing any apparent serious damage at this time in old-growth and second-growth sapling and pole-sized stands, larval populations of serious proportions could build up in localized areas and effect some damage.

In western Oregon, as well as in many other areas in the West, old-growth forests are gradually being cut and the forest economy is being geared to a younger age-class of timber. On the Umpqua Forest in Oregon, for example, "Old-growth mixed-species forests of varying density...." stretch ".... almost unbroken for miles in all directions" (74, p. 135). On the Umpqua, as on many other National Forests in the West, these great expanses of forest are being dotted with more and more openings, clearcut blocks (Appendix Figure 3A) where the old-growth has been completely removed and new forests are being seeded or planted, artificially or naturally.

As these older trees are removed and their roots die and disintegrate, it will be interesting to see what plants Pleocoma larvae will use for food. In at least one case Pleocoma larvae fed on the

roots of one- and two-year-old conifer seedlings growing in a seedbed located in the middle of a recently logged area (74, p. 134). This may be an indication that seedlings established in the ever-increasing number of clearcut blocks of forest land will be subject to damage by Pleocoma larvae, if they happen to be located in an infested area. In any given area, the amount of damage to forest tree seedlings caused by Pleocoma larvae feeding on roots in seedbeds, in clear cuts, planted or seeded naturally or artificially, or in afforested areas will depend on the following:

1. The type of soil in which the seedlings are growing could be influential. In soils with silicate clay hardpans the larvae will tend to congregate at shallower depths in the same strata as the roots of seedlings. In soils without a silicate clay layer, many of the larvae will be at depths lower than even the lowermost roots of the young seedlings, especially during summer months. Regardless of the soil type, however, Pleocoma larvae are generally not feeding on roots at depths shallower than six to eight inches.[22]

2. The presence of locally abundant larval populations will be necessary to effect any amount of damage. Larval populations

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[22] Although the six P. simi larvae he found in his seedbeds were at depths between 9.1 and 17.7 inches, Stein (74, p. 138) found P. simi larvae to have severed the taproot of 31 one- and two-year-old conifer seedlings between the ground line and 10.2 inches in depth. One one-year-old ponderosa pine seedling was cut so near the soil surface that it fell over.

encountered during this study were widely scattered and many areas of the forests have no larvae in the soil at all. Larval movement, however, will allow them to travel through the soil in search of food so the colonies are not static.

3. The kind and amount of food available will be important. Though the major portion of the diet of larvae studied was conifer roots, other species of roots were found in the guts in those areas where angiosperms and ferns were growing. The general absence of undergrowth in many of the old-growth stands where larvae were collected may explain why conifer roots were most often found in the guts. The oligophagus feeding habits of the genus indicate its adaptability in feeding on a variety of plants as well as inhabiting many sites and soil types. In many clearcuts an abundance of brush is often growing, the roots of which could satisfy the needs of Pleocoma larvae, minimizing damage to conifer roots. Furthermore, the species of conifer available could have some influence on the damage caused.

In the Lake States, a definite correlation was found between grub damage and the extent of denuded land in any locality. One particular forest made up of predominantly denuded land suffered the most severe damage. Other forests, diversified both as to soil type and forest cover suffered least (21, p. 266).

4. The age of a seedling, and its rooting characteristics

could be significant. The older seedlings with a more luxuriant root system could certainly withstand more damage than a one-year-old seedling with a limited root system. An interesting example of these relationships is provided by another conifer-feeding scarab. Phyllophaga prunonculina (Burn.) larvae, in damaging pine seedlings during summer and early fall shortly after transplanting, concentrated their feeding in the top six to eight inches of soil. Hence, shallow-rooted loblolly pine was most severely damaged while deeper rooted slash and longleaf pine were less severely damaged (81, p. 711). Furthermore, damage to a newly transplanted seedling would be more serious than damage to one once it had become established. In Wisconsin, more red pine died during the season following the year of planting, as a result of Phyllophaga feeding on the roots, than in subsequent years (65, p. 651).

5. The type of damage done to the roots will be important. Stripping of the phloem and outer bark from the xylem is not usually fatal unless roots are girdled. Whether roots are girdled or completely severed may be of no consequence since in either case that portion of the root distad of the damage is killed. Whether a seedling is killed by severance of the main taproot will depend on just where the taproot is severed and on how many roots are left to sustain the tree. Stein (74, p. 136, 138-139) found many seedlings to be alive following drastic curtailment of their root system by feeding P. simi

larvae.

6. Moisture and weather conditions might be one of the most critical factors in determining if Pleocoma-damaged seedlings will live or die. On a dry site, seedlings damaged may not recover, or may recover slower than seedlings with equivalent damage on a moister site. Seedlings with a root system curtailed by Pleocoma larval feeding have survived when moisture stresses were low (74, p. 138). Even though Pleocoma larvae are not generally feeding on roots during the summer, seedlings damaged during the winter have been known to fade rapidly under the added stress of dry summer weather (74, p. 136).

Notwithstanding the conditions discussed above, Pleocoma larvae are a potential insect pest of forest regeneration, not only in clearcut forested areas where new tiny seedlings are replacing old-growth timber, but also in land being afforested or denuded land where forests are being established for the first time. Because they are feeding underground where they are not readily apparent, they may at this time be causing damage of which we are unaware, a type of damage which, "....would merge with all the other influences that mold composition and succession in developing forest stands" (74, p. 140).

As mature forests are being cut, and the land transformed from the production of old-growth often overmature stands to the

support of young trees, it may be expected that typical plantation insects, which cause relatively minor damage to the virgin forest, will flourish under the impetus of tree farming and extensive plantations and inevitably present increasing control problems. In many areas in both this country and Canada the accelerated plantation and reforestation programs already have been accompanied by serious insect problems; in some areas planting programs have been curtailed because of insect pests of forest regeneration.

Since there are numerous difficulties involved in the establishment of a new forest, any agent, insect or otherwise, which interferes with the successful growth of the young trees is important. In this respect, Pleocoma larvae are a potential insect pest of forest regeneration in western Oregon.

SUMMARY

White grubs (Coleoptera: Scarabaeidae) are considered as some of the more important forest pests in certain parts of the world. They are especially destructive in forest nurseries and young plantations. In western United States they have not been particularly troublesome since many western forests are old-growth or advanced second-growth. There have been reports, however, of white grubs, usually Polyphylla sp., damaging nursery trees or plantations in Washington and Oregon. In early 1960, larvae of the genus Pleocoma (subfamily Pleocominae) were discovered feeding on roots of forest tree seedlings in western Oregon. This was the first confirmed record of Pleocoma larvae feeding on roots of forest trees. Prior to that time, there were only scattered and unconfirmed reports of Pleocoma larvae feeding on conifer roots elsewhere in the west. Pleocoma larvae, when present in large numbers severely injure the roots of orchard trees causing serious decline in vigor. Since little or nothing was known of the ecology of Pleocoma larvae in forest soils, and since they appeared to be a potential forest pest, a study of the feeding habits and biology of Pleocoma larvae in the forest environment was initiated in late 1960.

Pleocoma larvae were collected in various forested areas in western Oregon. Some larvae were reared in the laboratory and

observations made on their biology, life history, and movement through the soil. Other larvae were preserved and a detailed qualitative analysis was made of their gut contents.

First instar Pleocoma hatch in late summer, the peak occurring in early September. First stage larvae moult to second instars about 30 days after hatching from eggs. Second and subsequent instars moult annually between mid-summer and early fall about the time that first instars are hatching. Some larvae appear to develop through more than nine instars before pupating; others pupate after the seventh or eighth instar. Pupation usually takes place in mid-summer in the upper 20 inches of soil. Male larvae outnumber females by about 30 percent.

A fungus disease, Beauvaria sp. killed from 5 to 22 percent of the Pleocoma larvae at one site. Predaceous Diptera larvae may also be responsible for some larval mortality.

Larvae move through soil primarily by use of the mandibles, some larvae moving more than four inches a day. First stage larvae do not move away from egg niches and second instars do not begin movement until late November. Between early August and late October, especially during September, there is a general period of larval inactivity when larvae are moulting or pupating.

Larval populations varied from none to 4.4 larvae per square foot and were distributed between two and 44 inches in depth. Soil

temperatures and soil moisture influenced most larvae at some sites to leave the upper 16 inches of soil during summer. At other sites, however, a shallow silicate clay hardpan influenced larvae to remain at shallow depths throughout the year.

The major part of the larval diet throughout the feeding period is made up of coniferous roots. Of more than 150 Pleocoma larvae examined, 86 percent were feeding on coniferous roots. Thirty percent of the coniferous roots in the guts were definitely identified as Douglas-fir, the predominant conifer at the sites of collections. Larvae appeared to prefer the smaller roots, mostly smaller than 2mm, many of them mycorrhizal rootlets.

In feeding on roots, most larvae severed and consumed the entire root. Larvae either severed and ingested intact root segments or gnawed on root ends masticating them into very fine pieces before ingestion. A few larvae merely girdled roots, stripping the bark leaving the xylem in the soil. There appeared to be no change in the size of roots as they passed through the larval alimentary system.

With the exception of last instar larvae, usually at shallower depths, and first stage larvae, neither of which appeared to feed on roots, all other larval stages at all depths were feeding on roots throughout the year, except during the moulting period. The cessation of root feeding extended over about a four-month moulting

period from June to September, inclusive. The moulting period varied somewhat between species.

During the moulting period when root feeding had temporarily ceased, most larvae were feeding on their exuvia. With the exception of first stage larvae, which ate their chorion, all stages of larvae consumed their exuvia. Some soil, probably less than five percent by volume, was also ingested by Pleocoma larvae.

In addition to roots, exuvia and soil, at least five other types of material were found in the guts of many larvae. Scattered throughout the alimentary system of many larvae was a fine, fluffy, cottony-like light to dark brown material tentatively identified as remains of fungal hyphae. During the period of the year when Pleocoma larvae were moulting, material was found in the mid and hind guts which appeared to be cast ventricular epithelium. Numerous small usually light colored bodies often found in the mesenteron just beneath the peritrophic membrane and completely enveloping roots in the gut were tentatively determined to be gregarine parasites. Many of the guts appeared to harbor bacteria, and mites were found in the digestive tracts of three larvae.

Pleocoma larvae do not appear to be serious forest pests in old-growth and advanced second-growth coniferous forests in western Oregon because: populations of Pleocoma larvae are widely scattered and erratic, larvae are restricting their feeding to

smaller fibrous roots, and there is little or no root feeding from mid-summer through early fall.

In newly-established forests Pleocoma larvae are potential pests as one or two feeding larvae can kill a tree. In any given area, however, the amount of damage to forest tree seedlings caused by Pleocoma larvae feeding on roots will depend on several things, among them: the type of soil in which seedlings are growing, the abundance of larvae, the kind and amount of food available, the age of trees and their rooting characteristics, the type of damage done to the roots, and moisture and weather conditions.

Only further studies in regenerated areas will determine the role of Pleocoma larvae in the re-establishment of forests on cut-over land.

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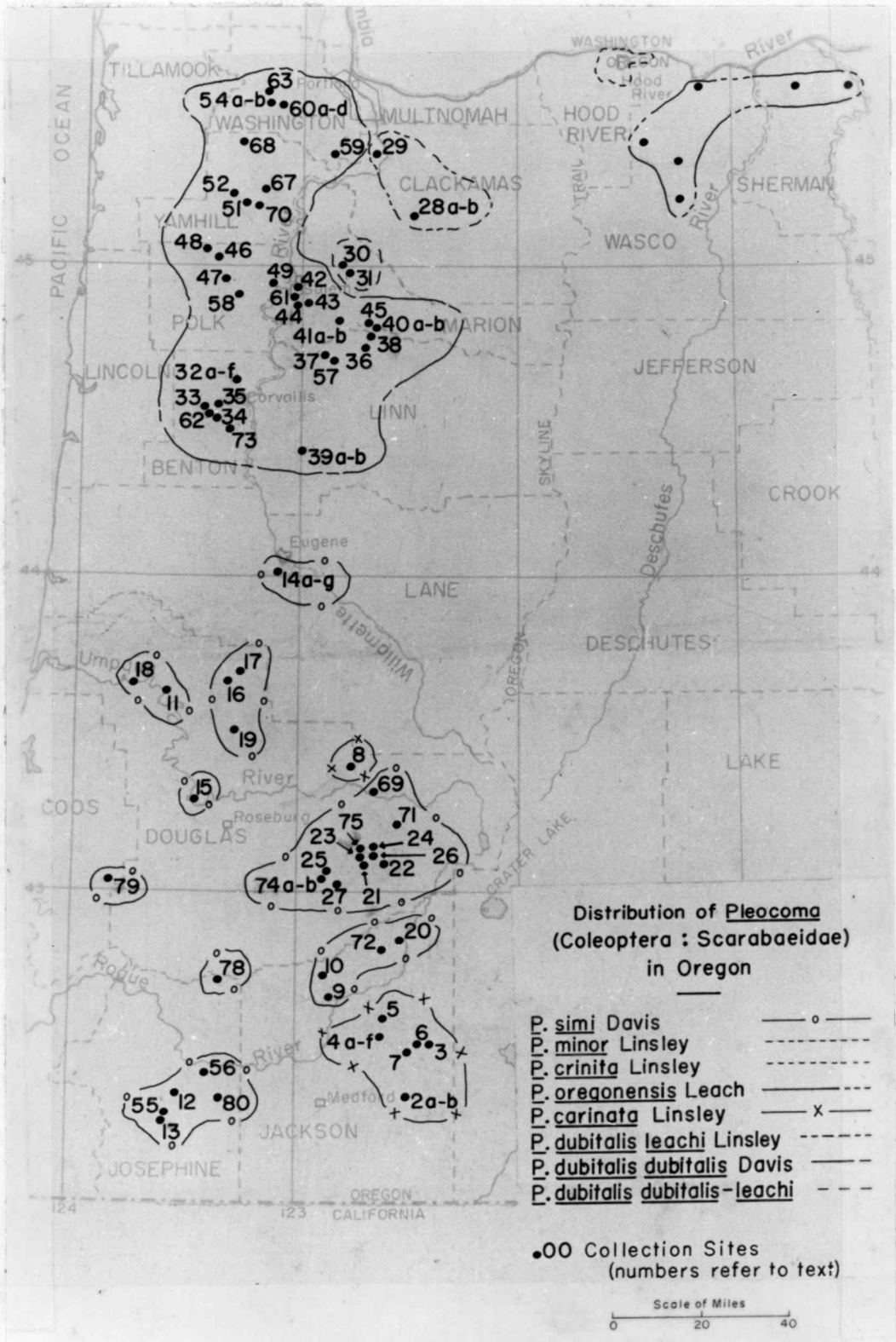
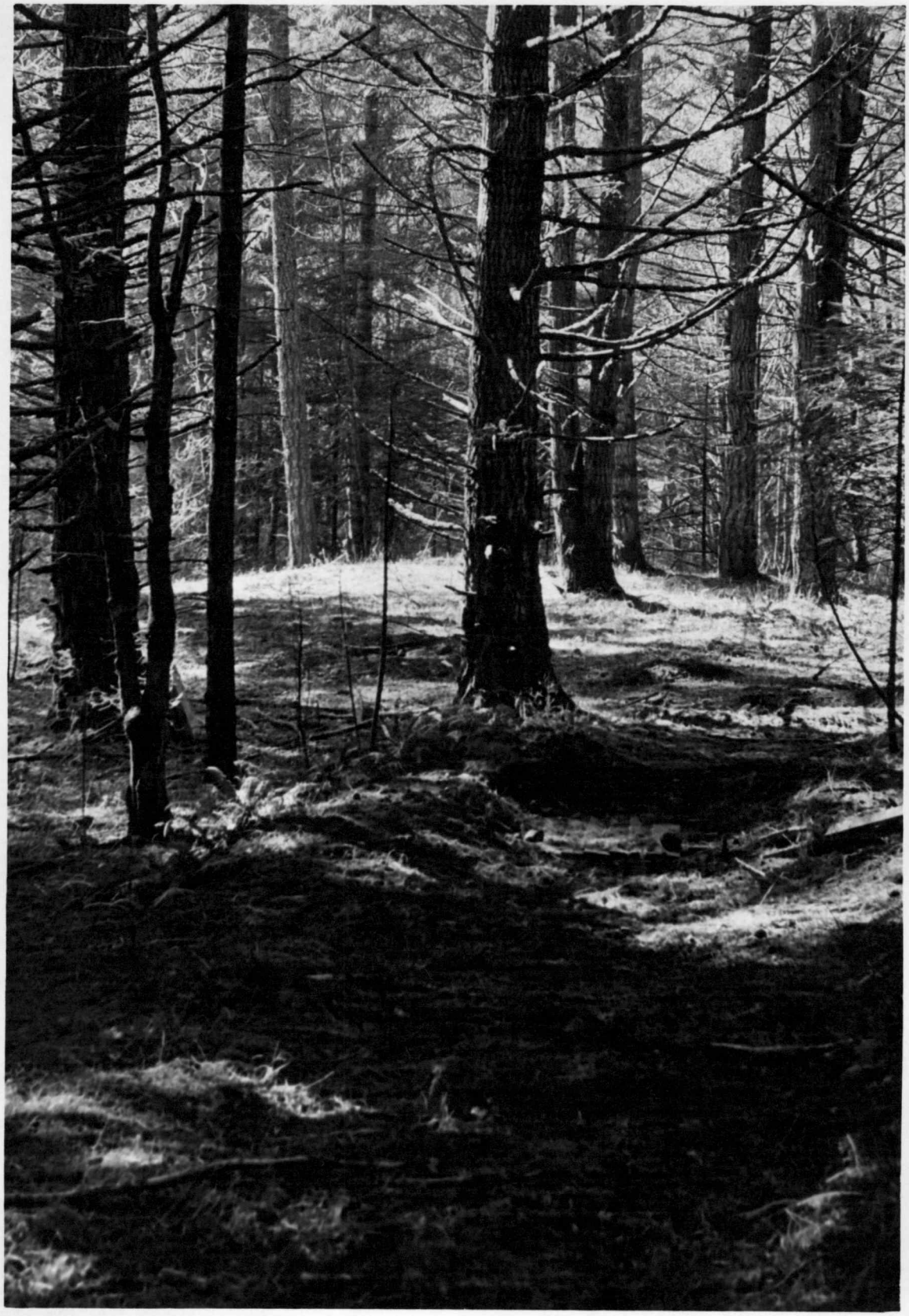
APPENDIX

Appendix Figure 1. Distribution of Pleocoma (Coleoptera:Scarabaeidae) in Oregon as of April 1962. (This map will be updated and presented in a paper, on the distribution of Pleocoma in Oregon, being prepared for publication by the writer and Dr. P. O. Ritcher, head of the Department of Entomology at Oregon State University.)

During this study, Pleocoma larvae were collected at 11 of the numbered sites shown on this map. The exact location of each of these 11 sites is described in Appendix Table 1. Eight of the sites are illustrated in Appendix Figures 2-6.


TILLAMOOK
OCEAN
PACIFIC
WASHINGTON
MULTNOMAH
CLACKAMAS
HOOD RIVER
SHERMAN
WASCO
YAMHILL
POLK
MARION
LINCOLN
JEFFERSON
LINN
BENTON
CROOK
Corvallis
Eugene
LANE
DESCHUTES
Deschutes
SKYLINE
LAKE
COOS
DOUGLAS
Roseburg
CRATER LAKE
Rogue
Medford
JACKSON
JOSEPHINE
OREGON
CALIFORNIA
Distribution of Pleocoma
(Coleoptera : Scarabaeidae)
in Oregon
P. simi Davis
P. minor Linsley
P. crinita Linsley
P. oregonensis Leach
P. carinata Linsley
P. dubitalis leachi Linsley
P. dubitalis dubitalis Davis
P. dubitalis dubitalis-leachi
•00 Collection Sites
(numbers refer to text)
Scale of Miles
0 20 40

Appendix Figure 2. The Study area at McDonald Forest (Site #32) five miles north of Corvallis, Oregon.



Appendix Figure 3. Sites where Pleocoma simi larvae were collected and/or where adults were taken in flight. (Site numbers refer to Appendix Figure 1.)

(A) Above--Site #27, Oregon, Douglas County, 10 miles northeast of Tiller, T29S, R1W, nw1/4 section 36. Site is clearcut shown in lower right of photo. (Note the other clearcut blocks in left center of photo where old-growth timber has been cut.) The view in the photograph is looking northeastward up the South Fork of the Umpqua River. P. simi adults were collected at seven other sites in the forested area to the upper right center of the photograph.

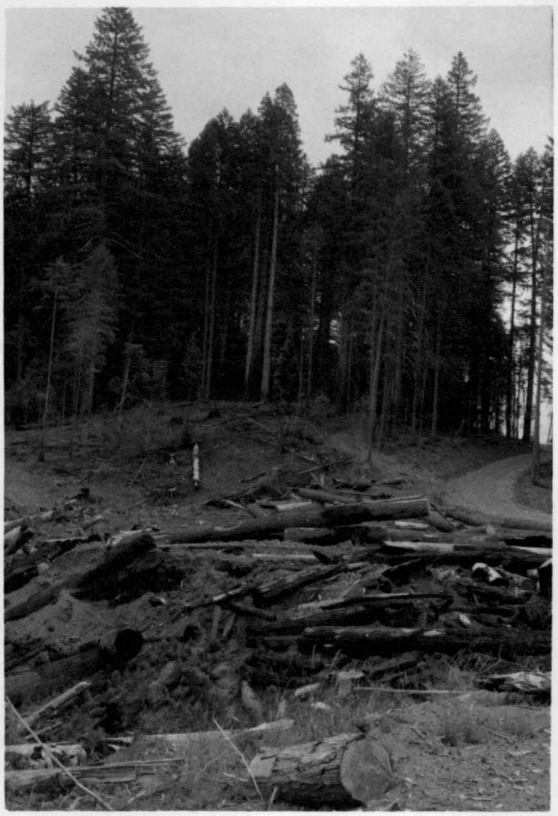
(B) Below--Site #19, Oregon, Douglas County, six miles north of Oakland, T24S, R5W, section 5. Highway #99 paralleled by Union Pacific railroad is shown in photograph. The arrow points to a group of Douglas-fir second-growth, just above railroad signals, where three larval collections were made.

Appendix Figure 4. Sites where Pleocoma simi and P. carinata larvae were collected and where adults were taken in flight. (Site numbers refer to Appendix Figure 1.)

(A) Above left--P. simi site #21, Oregon, Douglas County, 17 miles northwest of Union Creek, T29S, R1E, nw1/4sw1/4 section 3.

(B) Above right--P. carinata site #8, Oregon, Douglas County, 14 miles northeast of Idleyld Park, T25S, R1W, se1/4ne1/4 section 13.

(C) Below--P. carinata site #3, Oregon, Jackson County, 13 miles east of Butte Falls, T35S, R4E, ne1/4ne1/4 section 35. (This site is known as Camp 2.) The photo was taken looking southeastward. Mt. McLoughlin, elevation 9495 ft. is in the background.

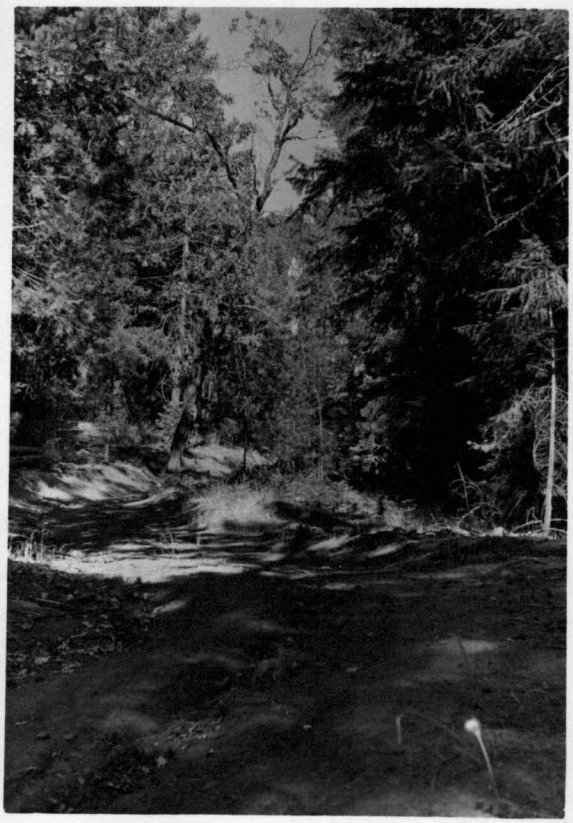


Appendix Figure 5. Sites where Pleocoma larvae were collected and/or where adults were taken in flight. (Site numbers refer to Appendix Figure 1.)

(A) Above left--P. simi site #69, Oregon, Douglas County, 22 miles east of Idleyld Park, T26S, R2E, section 15.

(B) Above right--P. carinata site #2, Oregon, Jackson County, 20 miles east of Medford, T37N, R3E, section 22. This site is near Dead Indian Soda Springs.

(C) Below--P. dubitalis site #39, Oregon, Linn County, 3 miles north of Brownsville, T13S, R2W, section 18. This is the only site, other than site #32, where P. dubitalis larvae were collected.

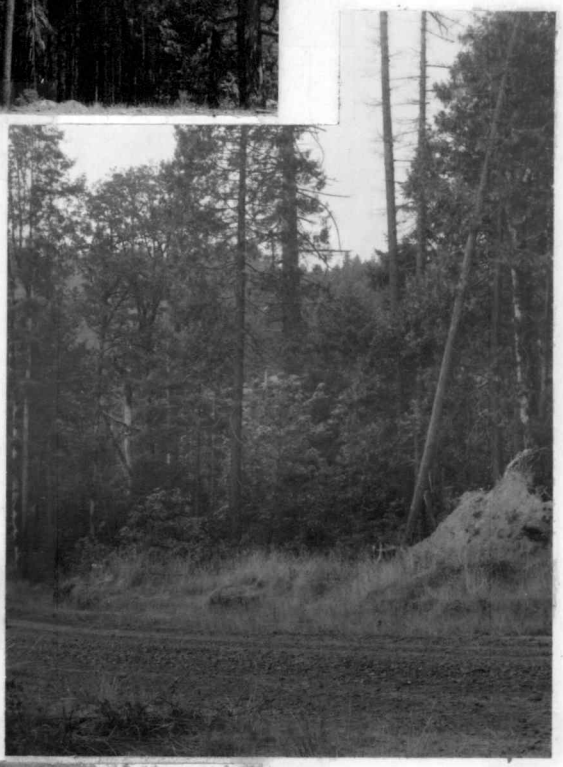


Appendix Figure 6. Sites where Pleocoma carinata adults were collected and where the remains of P. simi adults and/or larvae were collected. (Site numbers refer to Appendix Figure 1.)

(A) Above--P. carinata site #6, Oregon, Jackson County, 11 miles southeast of Butte Falls, T36S, R4E, nw1/4sw1/4 section 18. Mt. McLoughlin, elevation 9495 ft., is seen in upper left of photo.

(B) Center--P. simi site #16, Oregon, Douglas County, 2 miles northwest of Drain, T22S, R6W, section 1. This site is in Hardscrabble Creek.

(C) Below--P. simi site #78, Oregon, Josephine County, 3 miles north of Wolf Creek on U. S. Highway #99 near Stage Road Pass.



Appendix Table 1. Descriptions of sites where Pleocoma larvae were collected in western Oregon coniferous forests in 1960 and 1961.

Site No.[a]	Description of site	Photo of site See:
	P. dubitalis	
32	Benton County, McDonald Forest, five miles north of Corvallis	Appendix Figure 2
39	Linn County, 3 miles north of Brownsville T13S R2W section 18	Appendix Figure 5C
	P. carinata	
2	Jackson County, 20 miles east of Medford, Dead Indian Soda Springs T37N R3E section 22	Appendix Figure 5B
3	Jackson County, 13 miles east of Butte Falls T35S R4E ne1/4ne1/4 section 35	Appendix Figure 4C
8	Douglas County, 14 miles northeast of Idleyld Park T25S R1W se1/4ne1/4 section 13	Appendix Figure 4B
	P. simi	
10	Jackson County, 7 miles north of Trail T33S R1W section 6	Not Illustrated
11	Douglas County, 5 miles west of Elkton	Not Illustrated
14	Lane County, Spencer Butte, 5 miles south of Eugene	Not Illustrated
16	Douglas County, 2 miles northwest of Drain T22S R6W section 1	Appendix Figure 6B
19	Douglas County, 6 miles north of Oakland T24S R5W section 5	Appendix Figure 3B
21	Douglas County, 17 miles northwest of Union Creek T29S R1E section 3	Appendix Figure 4A
	P. crinita and P. minor	
--[b]	Hood River County, larvae were collected at several sites in forested areas adjacent to Pleocoma-infested orchards south of the city of Hood River.	Not Illustrated

[a] Site numbers refer to Appendix Figure 1.

[b] Though the site is not numbered, the area where P. minor and P. crinita are found is shown in Appendix Figure 1.