HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOLUME 19 JANUARY, 1950 NUMBER 11

SPITTLE-INSECT VECTORS OF PIERCE'S DISEASE VIRUS

I. CHARACTERS, DISTRIBUTION, AND FOOD PLANTS

DWIGHT M. DELONG and HENRY H. P. SEVERIN

II. LIFE HISTORY AND VIRUS TRANSMISSION

HENRY H. P. SEVERIN

UNIVERSITY OF CALIFORNIA · BERKELEY, CALIFORNIA

In this Issue . . .

SPITTLE-INSECT VECTORS OF PIERCE'S DISEASE VIRUS

SPITTLE-INSECT VECTORS OF PIERCE'S DISEASE VIRUS

II. LIFE HISTORY AND VIRUS TRANSMISSION[1]

HENRY H. P. SEVERIN[2]

INTRODUCTION

EXCEPT FOR A preliminary report (Severin, 1947[3]) on the present investigation, the one reference in the literature to a spittle insect, or froghopper, as a virus vector is that dealing with the meadow spittle insect, *Philaenus leucophthalmus* (Linnaeus), as a possible vector of the peach-yellows virus (Manns, 1939). This spittle insect has shown a greater incidence of infection in limited experimental work here than the plum leafhopper, *Macropsis trimaculata* (Fitch). In the spring of 1936, some of these insects were fed on virulent yellows virus and transferred to large peach trees in hopper-proof cages. All of the trees so treated came down with yellows, while the check trees remained healthy.

In a later paper, Manns (1943) states: "After repeating the work on the meadow froghopper as a possible vector (carrier) of peach viruses, the data show negative results for this insect. These researches on insect vectors of peach viruses in Delaware show that the plum leafhopper, *Macropsis trimaculata,* is the only known vector in this state, its chief host being wild and cultivated plums."

The preliminary note (Severin, 1947) previously mentioned reported the transmission of the virus of Pierce's disease of grapevines by four species and six varieties of spittle insects belonging to three genera.

Several nonvirus diseases have been associated with spittle insects. Among them is a serious disease of sugar cane known as froghopper blight, which occurs in Trinidad. According to Mumford (1926) and a large number of other workers, "there appear to be two main causes of 'blight,' namely, the attacks of the froghopper (*Tomaspis saccharina*) and attacks of root fungi (*Marasmius* and *Odontia*)."

Secrest (1944) reported the damage to jack pine and red pine trees in the Lake states by the Saratoga spittle insect, *Aphrophora saratogensis* (Fitch). Anderson (1947) in coöperation with A. J. Riker and his associates, found the relation of the Saratoga spittle insect and a fungus, *Chilonectria cucurbitula,* to injury of jack pine and red pine trees in Wisconsin.

Garman (1921) reported that the material of spittle balls offers an ideal medium for molds and bacteria which may sometimes be found in large numbers.

[1] Received for publication May 17, 1948.

[2] Entomologist in the Experiment Station.

[3] See "Literature Cited" for data on citations, referred to in the text by author and date.

Doering (1931), however, found none of these organisms in the spittle balls of *Lepyronia quadrangularis* (Say).

Stearns (1923), in his work on the Cercopidae of Connecticut, quotes Kirkaldy (1906) as follows: "It is not alone the exhaustion consequent upon the rapid draining of the plants' juices by the Hemipteron's almost microscopic mouth-setae that is so deleterious; it is the addition of the horde of fungus spores which often subsequently attack the wounded surface, and quickly multiplying, penetrate into the tissues of the plant, causing decay and death." This discussion by Kirkaldy pertains to the hemipterous insects in general and is not confined to the spittle insects of the family Cercopidae.

No spittle insects have been found on grapevines in California up to the present time. Fitch (1856) reported that in New York the four-spotted spittle insect, *Aphrophora 4-notata* Say, and Signoret's spittle insect, *A. signoretii* Fitch, puncture the bark and suck the juices of grapestalks. These two species have not been reported in California. No spittle insects have been found in alfalfa fields in the fog belt of California, where little alfalfa is grown, but nymphs of *Philaenus leucophthalmus* have been taken on volunteer alfalfa (plate 4, *E*) in Strawberry Canyon, Berkeley, Alameda County, as reported in the companion paper (DeLong and Severin, 1950).

Fisher and Allen (1946) reported that alfalfa and clover were severely damaged by the spittle insect, *Philaenus leucophthalmus,* in Wisconsin.

Scholl and Medler (1947) discussed the relation of spittle insects (*Philaenus leucophthalmus*) to alfalfa seed production in Wisconsin.

During an investigation on newly discovered vectors of the California aster-yellows virus, the meadow spittle insect, *Philaenus leucophthalmus,* was tested for virus transmission, and it was observed that the adults excreted a large amount of feces, similar to the sharpshooters (subfamily Tettigoniellidae) demonstrated to be vectors of the virus causing Pierce's disease of grapevines and alfalfa dwarf (Severin, 1949). Three of these leafhopper species have been demonstrated to seek the xylem tissue in the process of feeding (Houston, Esau, and Hewitt, 1947); and probably the spittle insects also feed in the xylem.

In the present investigations, the life histories of four species of spittle insects were studied to determine their natural infectivity on host plants. The efficiency of virus transmission by single adults of the four species, and of five varieties of one species was investigated. Transmission of the virus of Pierce's disease of grapevines from diseased vines to healthy vines and alfalfa, and from alfalfa dwarf to healthy vines and alfalfa was undertaken. Also studied were the latent period of the virus in four varieties of one species of spittle insect, and the retention of the virus in one variety of the same species. Observations were made on leaf curling around the spittle, and the blasting of flowers by one species. Attempts were made to transmit the viruses of curly top and California aster yellows with some of the species of froghoppers.

ANNULATE SPITTLE INSECT, APHROPHORA ANGULATA

Essig (1946) gives the common name annulate spittle bug to *Aphrophora angulata* Ball (plate 1, *A, B, F, G*).

Life History. Van Duzee (1914) reported that the adults of *Aphrophora angulata* were common on willow.

Ball (1915) also captured this species on willow and in low situations where grasses occur in California "but no spittle masses were ever seen, although a careful search was made."

Little is known concerning the life history of the annulate spittle insect, except the food plants of the nymphs (DeLong and Severin, 1949) and a limited number of host plants of the adults. Nymphs have been commonly collected on weeds in the fog belt of California by the writer and on California mugwort (*Artemisia vulgaris*), growing along a creek near Lafayette, Contra Costa County, by J. H. Freitag. Adults were rarely collected on any host plant. A few adults were caught on herbs at San Francisco and on American vetch (*Vicia americana*) at Atherton, San Mateo County. Specimens were occasionally captured in general sweepings. Nymphs of *Aphrophora angulata* and *Philaenus leucophthalmus* were taken in the same spittle mass on goose grass (*Galium aparine*) growing on the Berkeley hills and on yellow melilot (*Melilotus indica*).

The general color of the body, wing pads, and legs of the last instar of *Aphrophora angulata* is brown. The dorsal part of the head and prothorax, and in some the dorsal abdominal segments, have white markings, and the apical segments are black (plate 2, *C*).

The last molted exuvia is gray (plate 3, *A, B, C*).

Natural Infectivity Not Demonstrated. Whenever an adult was collected in the field, it was tested for natural infectivity, by transferring each specimen to a healthy grapevine cutting or alfalfa plant. Twenty-five adults tested singly failed to cause infection. Two lots of 5 nymphs collected on various food plants failed to transmit the virus to 2 healthy vines.

Transmission of Virus. For tests on transmission of the virus from infected to healthy grapevines, nymphs collected on various food plants under natural conditions were reared on healthy alfalfa plants to the adult stage. Each alfalfa plant served as a check or control plant for natural infectivity. The adults were fed on infected grapevines and then each adult was transferred singly to a healthy vine cutting. Ten infections were obtained out of 35 vines inoculated, an incidence of 29 per cent. All alfalfa plants remained healthy.

The transmission of the virus from diseased grapevines to healthy alfalfa was determined with 25 adults, reared during the nymphal stages on healthy alfalfa plants. The adults were fed on diseased grapevine cuttings for one day and then each leafhopper was transferred and kept singly on a healthy alfalfa plant during adult life. One infection was obtained out of 25 alfalfa plants inoculated, an incidence of 4 per cent.

In tests on transmission from alfalfa dwarf to healthy grapevines, 25 adults were caged on infected alfalfa plants for 1 day, and then each froghopper was transferred singly to a healthy grapevine seedling. Three of 25 vines inoculated were infected, or 12 per cent.

Twenty-five adults tested singly, after feeding on infected alfalfa plants for one day, failed to transmit the virus to 25 healthy alfalfa plants. In another trial, 3 adults tested in the same manner transmitted the virus to one alfalfa plant.

WESTERN PINE SPITTLE INSECT, APHROPHORA PERMUTATA

Essig (1946) gives the name "rhubarb spittle insect" to *Aphrophora permutata* Uhler (plate 1, *C, D, E, H, I, J*); but life-history studies here reported indicate that "western pine spittle insect" would be more appropriate.

Life History. Ball (1920) states that all of our local species of Cercopidae have a single generation. According to him, the number of generations produced in a year by Hemiptera is not the result of adjustments to a temporary excess of heat or cold, moisture or dryness, but is rather determined by deep-seated and fixed adaptations developed over many seasons.

In his general discussion on spittle insects, Essig (1946) likewise states that there is a single generation annually; the adults hibernate, and the nymphs appear in spring and early summer.

A study was made of the life history of *Aphrophora permutata* in and near Sharp Park on the ocean in San Mateo County. Two generations occur in this locality. The nymphs of the first generation feed on native plants and introduced weeds, and the nymphs of the second generation feed on Aleppo pine, *Pinus halepensis* (plate 4, *B*), and Monterey pine, *P. radiata.*

One of the preferred weeds of the first-generation nymphs is bristly ox-tongue, *Picris echioides* (plate 4, *A*), growing in vacant fields adjacent to pine trees bordering Sharp Park. In 1947, nymphs were found on bristly ox-tongue as early as February 25, during March, and up to the middle of April. The nymphs first appeared on pines in early May, and became scarce toward the end of July. In 1948 nymphs were taken on bristly ox-tongue on February 26; none were observed on this weed on February 20. Adults were first collected on the two species of pines during April. It is evident that the adults of the first generation develop on native plants and weeds and fly to pine, where the second generation develops. No adults were collected on pine trees during the winter.

All attempts to find where this species of spittle insect deposits its eggs on native plants and introduced weeds have failed. It seemed likely that the females of the second generation deposit their eggs in the twigs of pines, and that the nymphs after hatching drop to the ground, and from there seek a food plant, as in the case of some cicadas (Ball, 1901).

One reference occurs in the literature on egg deposition in a host plant of a cercopid, *Aphrophora salicis* DeGeer, introduced from Europe into eastern

Massachusetts. Metcalf and Barber (1929) reported that the eggs are laid in the terminal twigs of willows, usually quite near the tip, and that the entire portion of the twig dies. As a rule, the egg punctures contained two eggs, although many contained but one.

In an effort to learn whether the western pine spittle bug deposits its eggs in pine twigs or needles, large shallow pans containing water were placed beneath the lower branches of pine trees during February and March, 1947, before and after spittle first appeared on weeds below the trees. (Although all nymphal instars cover themselves with spittle when immersed in water, they drown within a few minutes.) Not a single first-instar nymph was taken in these pans.

Adults and nymphs were abundant in 1947 on Aleppo pine bordering Sharp Park. Branches were broken from the trees on February 20, 1948 (before the spittle appeared on bristly ox-tongue), and placed in 5-gallon crocks in large tanks of water. No drowned nymphs were found. Branches of the same species of pine showing small crusts of pitch, possibly covering egg punctures, were handled in the same manner, but no drowned nymphs were found in the water at the bottom of the tanks.

Dried pine needles were collected by N. W. Stoner and the writer below pine trees and placed on the soil and in contact with alfalfa planted in flower pots, but no nymphs appeared on these plants. Apparently the eggs are not deposited in pine needles.

In order to determine if eggs were deposited in bristly ox-tongue, 36 of these weeds free from spittle were dug in a field adjacent to a row of pine trees bordering Sharp Park on February 25, 1947, when the spittle first appeared on some of these host plants. The soil was washed from the root system, each weed was transplanted to a 6-inch flower pot, and kept in a greenhouse. No spittle appeared on any of the plants. The experiment was repeated on February 20, 1948, before the nymphs hatched, but no froth appeared on any of the 25 weeds. Again on February 26, 1948, 40 bristly ox-tongue plants, this time containing recently hatched nymphs, were dug in the same locality, the nymphs were removed, and the soil was washed from the root system. Again no spittle appeared on any of the plants. Apparently the eggs are not deposited in the tissue of this weed.

In another test, 25 bristly ox-tongue plants in the vicinity of pine trees were dug with the soil adhering to the roots on February 20, 1948, before the nymphs hatched, and were transplanted to flower pots. Spittle appeared on 2 plants.

Lumps of soil adhering to the root system of bristly ox-tongue were broken into small particles and sieved through a coarse and then through fine-meshed sieves. Nymphs were present in the soil, but no food was available, and they were allowed to die. The next day alfalfa plants were placed on the soil, and spittle appeared on two plants. Apparently the eggs are deposited in the soil adjacent to this weed, but no eggs or eggshells were found in the soil.

Ball (1919) suggested that it is probable that the nymphs of *Aphrophora permutata* are subterranean.

Frequently more than one nymph is found in spittle at the base of the stem of bristly ox-tongue (plate 4, *A*) and on a large number of other introduced weeds and native plants. The soil becomes wet from drops of liquid which fall from the frothy material. The common position of the spittle containing the nymphs on most plants is at the base of the stems near the soil in localities exposed to the sunshine, but in moist canyons, along streamways, and under trees, the nymphs may be higher on the plants. The froth on pine trees occurs at the base of a cluster of pine needles (plate 4, *B*). It is not unusual to find the nymphs of *Aphrophora permutata* and *A. angulata* in the same spittle mass, except on pine trees.

Doering (1931) published the general field notes taken by R. H. Beamer, University of Kansas, on the molting of *Aphrophora permutata* observed in Sequoia National Park, California.

A more detailed study was made on the process of molting of the same species of spittle insect reared in the greenhouse. When the nymph is ready to pass through the last molt, it leaves the spittle mass, and crawls about the plant to find a suitable place on the petiole or stem, where it firmly attaches its claws (plate 3, *E*). It telescopes the last abdominal segment back and forth and emits successive droplets of spittle, which cover the lower surface of the abdomen and thorax. When the telescoping of the last abdominal segment ceases, the nymph places the lower surface of the abdomen in contact with the petiole or stem, and then stretches out the front pair of legs, so that the thorax and head form an acute angle with the petiole or stem (plate 3, *E*). The nymph becomes quiescent for a time, allowing the spittle to become viscid and gradually dry, gluing the lower surface of the abdomen firmly to the petiole or stem. It bends the head and prothorax down, and the soft membrane joining the head and the prothorax dorsally becomes swollen.

The old chitinous exoskeleton splits longitudinally along the dorso-median line at the region of the prothorax, and the split increases in length during the process of extrication. After the adult has completely withdrawn itself from the exuvia, the cleft extends from the head region to the end of the thorax (plate 3, *D*).

During the process of ecdysis, the dorsal portion of the prothorax pushes out first from the old integument; next comes the head, followed by the rest of the thorax and finally by a portion of the abdomen. Within 20 minutes after breaking of the exuvia, the head, thorax, and five or six abdominal segments are drawn out of the molted skin. Of the appendages, the antennae are liberated first, followed by the wing pads, proboscis, front, middle, and hind legs.

The adult may remain suspended by the tip of the abdomen within the exuviated integument for half an hour or longer. In this position its head hangs downward, its legs are sprawled apart, its wings held at right angles

to the body, and its elytra kept away from the lower wings. Later it turns around, head upward, and grasps the exuvia or stem with its legs, while the tip of the abdomen is withdrawn from the molted skin. The external genitalia are spread apart.

During the process of molting, the dorsal surface of the head and wings are white, the thorax and abdomen rusty brown, and the sides of the anterior abdominal segments red. The ocelli are conspicuously bright red.

When a nymph in the process of molting is submerged in water and the swollen prothorax is punctured with a needle, numerous bubbles of air arise from the wound. In all probability the pressure of the air, and possibly of the blood in the swollen pouch or cervical ampulla behind the head, rupture the exoskeleton along the dorsal median line of the prothorax.

After the insect has completed its last molt, the spittle begins to dry into a layer of viscid, sticky substance, and later becomes a white, flaky material adhering to the leaves and stem (plate 5, *E*) for a long time.

The early nymphal instars can readily be distinguished by the red abdominal segments. In the fourth instar only the sides of the anterior abdomen are red (plate 2, *E*). In the last instar the abdomen is black (plate 2, *D*), the tylus is white bordered with black and with a basal black band, and the vertex is white between the compound eyes. The prothorax has two anterior pairs of white bands and two posterior white stripes, and there are two short white stripes on the mesothorax. The rest of the prothorax and mesothorax is brownish black. The wing pads, metathorax, and abdomen are black (plate 2, *D*).

Natural Infectivity Not Demonstrated. Up to the present time no virus disease has been reported on pine trees. There was no evidence of natural infectivity of the nymphs and adults collected in the fog belt of California. Each of 25 lots of 5 nymphs collected on pine trees bordering Sharp Park was transferred directly to a healthy grapevine cutting. No infection occurred. In a second test, each of 20 lots of 2 nymphs removed from bristly ox-tongue growing below or adjacent to pine trees at Sharp Park was kept on a grapevine seedling, but no infection was produced. In a third experiment, 20 lots of 2 nymphs each, taken on bristly ox-tongue, growing below pine trees on the campus of the University of California, all failed to transmit the virus to grapevine seedlings. The virus was not transmitted to healthy alfalfa plants by any of 50 lots of 2 or 5 nymphs collected on bristly ox-tongue growing below or near pine trees at Sharp Park, and below pine trees on the campus of the University of California.

Transmission of Virus. The efficiency of this vector in transmitting the virus from infected to healthy grapevines was determined with 50 males and 50 females in single-insect tests. The adults were collected on pine trees. The insects were fed on diseased vines for 1 or 2 days, and then each was kept on a healthy grapevine seedling during adult life. If a grapevine seedling died during the test, another seedling was substituted. The males infected 25 of 50 vines, or 50 per cent; and the females 23 of 50 vines, or 48 per cent.

In another test, 23 lots of 3 or 5 adults were caged on diseased grapevines from 1 to 8 days and then each lot was kept on a healthy grapevine cutting during adult life. Twelve infections were obtained, an incidence of 52 per cent.

Grapevines are unfavorable food plants for this insect; single adults lived from 1 to 6 days on grapevine seedlings and from 4 to 15 days on vine cuttings. On the other hand, nymphs acquired the winged stage on alfalfa, and the adults lived a long time on this food plant.

The transmission of the virus from diseased grapevines to healthy alfalfa was determined with 10 lots of 3 adults. Each lot was fed on diseased grapevines for 1 day and then was transferred to and kept on healthy alfalfa until they died. Two of the 10 alfalfa plants, or 20 per cent, developed infections.

In tests on transmission from alfalfa dwarf to healthy grapevines, 10 lots of 2 adults were caged on infected alfalfa for 2 days, and then each lot was transferred to healthy grapevine cuttings. Six of the 10 vines were infected, or 60 per cent.

Fifteen lots of 3 adults each, after feeding on diseased alfalfa for 1 day, failed to transmit the virus to 15 healthy alfalfa plants.

Attempt to Transmit Curly-Top Virus. Ten lots of 3 adults, after being caged on curly-top beets for 1 or 2 days, failed to transmit the virus to 10 healthy sugar beets.

CLASTOPTERA BRUNNEA

Life History. In San Mateo County, California, the first generation of *Clastoptera brunnea* Ball (plate 2, *A, B*) completes the nymphal stages during May and June on coyote brush or chaparral broom, *Baccharis pilularis* (plate 5, *A*). No nymphs were taken on any of these plants during the middle of July, but adults were abundant. No adults of the first generation were captured on this host plant during August. The adults had flown to some other food plant, apparently California mugwort, *Artemisia californica,* where the second generation of nymphs developed during July and August. The earliest record of second-generation nymphs on this host plant was July 19, and they were more abundant on July 23, 1946. The first adults of the second generation were collected on August 29, on California mugwort; none were captured during November and December.

During this study we found many fluffy, cottony, gall-like structures (plate 5, *D*), resembling somewhat the spittle masses of *Clastoptera brunnea,* on California mugwort. A. E. Pritchard identified this gall fly (Cecidomyidae) as *Diarthronomyia floccosa* Felt.

The first generation of *Clastoptera brunnea* also completed the nymphal stages during May and June, 1946, on coyote brush or chaparral broom on Mare Island, Marin County, and enormous numbers of spittle masses occurred on the tips of the branches. By the middle of July no nymphs were found on this host plant. Adults were abundant during most of July, but were scarce toward the end of this month, having flown to other host plants.

The host plants of the second generation of *Clastoptera brunnea* on Mare Island in Marin County are different from those so far discovered in San Mateo County. Recently hatched nymphs of the second generation appeared on mule fat, *Baccharis viminea,* and on gum plant, *Grindelia camporum.* Eggs were deposited beneath the epidermis of the stems of both host plants. During July and August great numbers of spittle masses occurred on these two plants (plate 5, *A, B*), and in September high populations of second-generation adults were captured on them; but during October adults were scarce on mule fat, which was mostly dry except for the green tips of the stems. No adult froghoppers were taken on any host plant during November and December.

Clastoptera brunnea overwinters in the egg stage. During the spring nymphs were reared from eggs deposited in the stems of California mugwort, collected in Pacheco Pass, in the northern San Joaquin Valley. Enormous numbers of nymphs hatched from eggs deposited in the dried stems of mule fat taken on Mare Island during the spring. Egg punctures through which the nymphs emerged were extremely abundant in the stems of this host plant. In localities on Mare Island where mule fat did not occur, nymphs hatched from eggs deposited in the stems of coyote brush, or chaparral broom.

The general color of the last-instar nymph of *Clastoptera brunnea* is black and yellow. The tylus is black, and a gray area between the compound eyes extends through the prothorax. The remainder of the thorax, the dorsal portion of the last three abdominal segments, and the apical end of the abdomen are black; the rest of the abdomen is yellow (plate 2, *F*).

The last nymphal instar leaves the spittle mass before molting, and the exuviae were abundant on the midribs of the leaves of mule fat (plate 6, *E*).

Natural Infectivity Not Demonstrated. During 1945 and 1946 nymphs of *Clastoptera brunnea* were tested for natural infectivity. The stems with the spittle masses were cut from many plants of the four host species: coyote brush or chaparral broom, *Baccharis pilularis;* California mugwort, *Artemisia californica;* mule fat, *Baccharis viminea;* and gum plant, *Grindelia camporum.*

Two thousand nymphs from these plants were transferred in lots of 10 to 100 healthy grapevines and 100 healthy alfalfa plants. Not a single infection occurred.

Transmission of Virus. The efficiency of this insect in transmitting the virus from diseased to healthy grapevines was determined with 50 males and 50 females. The adults were fed on diseased grapevines for one day and then each adult was transferred singly to a healthy vine seedling. Twelve infections resulted, six from males, six from females.

Ten lots of 5 adults each, fed 1 day on diseased grapevines, transmitted the virus to 2 of 10 vines, or 20 per cent; and 8 lots of 10 adults each infected 3 of 8 vines, or 37 per cent. Evidently the number of spittle insects in each lot is important in the transmission of this virus to grapevines.

No infections were obtained with 25 females kept on diseased grapevines for one day and transferred singly to healthy alfalfa plants.

Ten lots of 10 adults each, after feeding one day on diseased vines, caused no infection in 10 alfalfa plants.

Twenty-five adults tested singly, after feeding on diseased alfalfa for one day, failed to transmit the virus to 25 healthy vines.

Ten lots of 10 adults, after feeding one day on infected alfalfa, failed to transmit the virus to 10 grapevines.

Large populations of last-instar nymphs were caged on diseased alfalfa plants. After passing through the last molt, the adults were transferred to healthy vines. One lot of 10 adults, which had fed on infected alfalfa from 1 to 4 days during the last nymphal stage, caused infection of one grapevine. Two other lots of 10 adults reared during the last nymphal stage on diseased alfalfa failed to transmit the virus.

Twenty-five adults were caged on infected alfalfa for one day, and then transferred singly to a healthy alfalfa plant. One plant of the 25 was infected, or 4 per cent.

Ten lots of 10 adults fed one day on diseased alfalfa failed to transmit the virus to 10 healthy alfalfa plants.

These investigations of *Clastoptera brunnea* have been limited to the fog belt of California and the entrance of Pacheco Pass in the northern San Joaquin Valley. Grapevines and alfalfa were unfavorable food plants for the nymphs and adults, and they only lived a few days on these host plants.

Attempts to Transmit Viruses of Curly Top and California Aster Yellows. Because of the interest in two other prevalent viruses, attempts were made to transmit sugar-beet-curly-top and California aster-yellows viruses by means of *Clastoptera brunnea*. Ten lots of 10 adults after feeding one day on curly-top beets were transferred to 10 healthy beets, but all remained healthy. No infection of celery occurred with 10 lots of 10 adults fed for 7 days on celery infected with the California aster-yellows virus and then moved to 10 healthy celery plants.

MEADOW SPITTLE INSECT, PHILAENUS LEUCOPHTHALMUS

Life History. The observations on the meadow spittle insect, *Philaenus leucophthalmus* (Linnaeus) (Muesebeck, 1946), agree for the most part with the life history of a grass-feeding spittle insect, *P. lineatus* Linnaeus, in Connecticut, as reported by Garman (1921).

One generation of the meadow spittle insect occurs on herbs as food and breeding plants in San Francisco. In 1946 the spittle containing the nymphs first appeared in early April, and became extremely abundant during May and June and less abundant in July. Adults were first collected in May, appeared in enormous numbers during the summer, and became less numerous during the autumn. In a few hours of sweeping on herbs, 6 males and 19 females were taken on November 19. This species overwinters in the egg stage.

While kept on Sacramento barley, *Hordeum vulgare,* in the greenhouse, the females occasionally deposited eggs. The eggs are laid diagonally in packets and firmly attached to the stem (plate 6, *D*). Though some adults lived for a long time on alfalfa plants, no egg masses were found on this food plant. On the other hand, when such alfalfa plants were kept over winter in a greenhouse, a few spittle masses containing the nymphs appeared in the spring (plate 4, *D*). Under natural conditions no egg masses have been found on three species of herbs in San Francisco. One grower cut off rosemary plants, *Rosmarinus officinalis,* and piled them up along the roadside. During the spring spittle containing the nymphs appeared on those plants which were still green. It is evident that the egg masses were deposited on this herb, but an intensive search by several investigators failed to find them.

Ball (1928) states that all genera but *Monecphora bicincta* Say crawl out of the spittle mass to make their transformation to adults. Doering (1931) disagrees with Ball and reports that *Lepyronia quadrangularis* (Say) passes the last molt in the spittle.

Philaenus leucophthalmus usually crawls out of the spittle to undergo the last molt, but an occasional adult with the exuvia was observed in the froth. The bubbles of air in the spittle had disappeared and the surface was dry.

More than one nymph may be found in the spittle; a half dozen or more is not unusual. Sometimes a nymph of *Aphrophora angulata* or *A. permutata* and one or more nymphs of *Philaenus leucophthalmus* may be associated in the same froth.

The general color of the last-instar nymph of *Philaenus leucophthalmus* is green and yellow. The tylus and a portion of the head posterior to the tylus is green, the thorax and wing pads are yellow, and the abdomen is green except for the tip of the apical segment, which is yellow (plate 2, *G*).

Efficiency of Virus Transmission by Five Varieties of Philaenus leucophthalmus. To determine the efficiency of virus transmission by five varieties of *Philaenus leucophthalmus* collected in the field, males and females were kept on diseased grapevines for one week and then were transferred singly to healthy vines grown from seeds. Each spittle insect was kept on a healthy seedling during adult life. The results obtained are shown in table 1.

The variety *leucophthalmus* proved to be an efficient vector of the virus, averaging 65 per cent infections for the males and females. The variety *fabricii* averaged 52 per cent, the variety *pallidus* 45 per cent, and the variety *marginellus* 40 per cent (table 1). The variety *impressus* is an inefficient vector of the virus, averaging 15.5 per cent infections for both sexes.

Transmission of the Virus by Multiple Lots. In the preliminary work with the meadow spittle insect, *Philaenus leucophthalmus,* one lot of 35 adults, after feeding 2 days on diseased grapevines, was transferred at intervals of 2 to 10 days to 13 successive healthy Emperor grapevines; 11 vines developed typical symptoms of the disease. Some of the adults were still alive 83 days after the last transfer.

TABLE 1
TRANSMISSION OF VIRUS OF PIERCE'S GRAPEVINE DISEASE TO HEALTHY VINE SEEDLINGS BY SINGLE ADULTS OF FIVE VARIETIES OF *PHILAENUS LEUCOPHTHALMUS*

Scientific name of variety of *Philaenus leucophthalmus*	Adults tested	Plants inoculated	Plants infected	Per cent infected	Adults tested	Plants inoculated	Plants infected	Per cent infected
	Males				Females			
Philaenus leucophthalmus var. *leucophthalmus*	50	50	32	64	50	50	33	66
Philaenus leucophthalmus var. *pallidus*	50	50	24	48	45	45	19	42
Philaenus leucophthalmus var. *fabricii*	50	50	26	52	50	50	26	52
Philaenus leucophthalmus var. *marginellus*	2	2	0	0	8	8	4	50
Philaenus leucophthalmus var. *impressus*	21	21	7	33	50	50	4	8

A comparison was made of the number of infections produced by varying numbers of adults of four varieties of *Philaenus leucophthalmus* transferred to successive healthy grapevine cuttings. Each lot of adults was kept on a healthy vine for one week to determine natural infectivity. Results are shown in table 3. A high mortality of the spittle insects occurred on grapevines in an advanced stage of the disease, and hence a constant number of adults of each variety could not be used, but a low death rate occurred on healthy vines

TABLE 2
TRANSMISSION OF VIRUS FROM PIERCE'S DISEASE OF GRAPEVINES BY VARYING NUMBERS OF ADULTS OF THREE VARIETIES OF *PHILAENUS LEUCOPHTHALMUS* TO SUCCESSIVE HEALTHY ALFALFA PLANTS

Number of adults in each lot	Days on diseased grapevines	First set of healthy alfalfa plants		Adults alive	Second set of healthy alfalfa plants		Adults alive	Third set of healthy alfalfa plants	
		Plants inoculated	Plants infected		Plants inoculated	Plants infected		Plants inoculated	Plants infected
Philaenus leucophthalmus var. *leucophthalmus*									
20	9	1	1	18	1	0	18	1	0
20	3	1	0	17	1	1	17	1	0
Philaenus leucophthalmus var. *pallidus*									
20	5	1	0	20	1	0	19	1	1
20	3	1	0	16	1	0	16	1	1
Philaenus leucophthalmus var. *impressus*									
20	3	1	1	20	1	1	20	1	0
20	3	1	0	20	1	0	20	1	1
20	2	1	0	20	1	0	20	1	1
20	2	1	0	18	1	0	17	1	1

TABLE 3

TRANSMISSION OF VIRUS OF PIERCE'S DISEASE OF GRAPEVINES BY VARYING NUMBERS OF ADULTS OF FOUR VARIETIES OF *PHILAENUS LEUCOPHTHALMUS* TO SUCCESSIVE HEALTHY VINES

Number of adults in each lot	Days on diseased grapevines	First set of healthy vines		Adults alive	Second set of healthy vines		Adults alive	Third set of healthy vines	
		Plants inoculated	Plants infected		Plants inoculated	Plants infected		Plants inoculated	Plants infected
Philaenus leucophthalmus var. *leucophthalmus*									
35	8	1	1	35	1	1	32	1	1
33	7	1	1	32	1	1	30	1	1
22	7	1	1	19	1	1	18	1	1
19	3	1	1	19	1	1	18	1	1
8	7	1	1	8	1	1	..	1	1
Philaenus leucophthalmus var. *pallidus*									
22	7	1	1	20	1	1	..	..	..
20	6	1	0	18	1	1	17	1	1
19	7	1	1	19	1	1	17	1	1
15	7	1	1	13	1	1	10	1	1
12	7	1	1	7	1	1	6	1	1
11	7	1	1	11	1	1	7	1	1
9	..	1	1	..	1	1	..	..	..
5	7	1	1	4	1	1	..	..	..
Philaenus leucophthalmus var. *fabricii*									
20	9	1	1	18	1	1	14	1	1
11	7	1	1	5	1	1	3	1	1
10	6	1	*	10	1	1	6	1	1
Philaenus leucophthalmus var. *impressus*									
26	7	1	1	22	1	1	20	1	1
20	11	1	1	20	1	1	11	1	0
20	9	1	1	17	1	*	18	1	0
20	9	1	0	17	1	*	14	1	0
20	7	1	1	20	1	1	20	1	*
20	7	1	1	20	1	1	9	1	*
20	7	1	1	20	1	*	17	1	*
17	7	1	1	11	1	1	11	1	1
14	7	1	1	13	1	1	11	1	1
13	7	1	1	13	1	1	13	1	1
13	7	1	1	13	1	1	12	1	1

* Grapevine cutting died.

(table 3). After feeding on diseased vines the adults were kept on successive healthy vines for periods varying from 3 to 11 days.

One lot of the *Philaenus leucophthalmus* var. *pallidus* kept on a diseased grapevine for 6 days failed to infect the first vine, on which they had fed for 5 days. One lot of the var. *impressus* did not transmit the virus to the first and third sets of vines and two lots failed to infect the third set of vines. Two

lots of the var. *fabricii* and one lot of the var. *impressus* (not tabulated) did not pick up the virus. Including the nontabulated tests, a total of 87 vines were inoculated by the four varieties of spittle insects, and 66 infections were

TABLE 4

TRANSMISSION OF VIRUS FROM ALFALFA DWARF BY VARYING NUMBERS OF ADULTS OF THREE VARIETIES OF *PHILAENUS LEUCOPHTHALMUS* TO SUCCESSIVE HEALTHY GRAPEVINES

Number of adults in each lot	Days on alfalfa dwarf	First set of healthy vines		Adults alive	Second set of healthy vines		Adults alive	Third set of healthy vines	
		Plants inoculated	Plants infected		Plants inoculated	Plants infected		Plants inoculated	Plants infected
Philaenus leucophthalmus var. *leucophthalmus*									
35	13	1	1	32	1	1	..	..	..
35	15	1	1	34	..	..	..	..	..
35	14	1	1	35	..	..	..	..	..
35	14	1	1	35	..	..	..	..	..
35	13	1	1	35	..	..	..	..	..
35	13	1	1	35	..	..	..	..	..
20	9	1	1	19	1	1	17	1	1
20	8	1	1	20	1	1	7	1	1
15	11	1	1	14	1	1	13	1	1
Philaenus leucophthalmus var. *pallidus*									
35	13	1	1	19	1	0	..	..	..
35	14	1	1	35	..	..	..	..	..
22	7	1	1	20	1	1	20	..	..
20	11	1	1	18	1	1	9	1	1
20	11	1	1	17	1	1	10	1	0
20	8	1	0	10	1	0	3	1	1
Philaenus leucophthalmus var. *impressus*									
35	14	1	1	35	..	..	..	..	..
25	10	1	1	25	1	0	9	1	1
20	11	1	1	19	1	1	11	1	1
20	7	1	1	20	1	1	14	1	1
20	7	1	1	20	1	0	18	1	1
20	8	1	0	20	1	0	15	1	1
20	9	1	1	20	1	*	10	1	0
20	9	1	1	20	1	*	10	1	*
10	7	1	1	10	..	..	..	..	..

* Grapevine cutting died.

obtained, an incidence of 76 per cent. Thirty lots of the four varieties of spittle insects were tested; three lots failed to pick up the virus, or 90 per cent produced infections.

The virus of Pierce's disease of grapevines was not often transmitted by three varieties of *Philaenus leucophthalmus* to healthy alfalfa, as is shown in table 2. None of the lots transmitted the virus to three successive alfalfa

plants; and only 1 lot infected two successive plants. A total of 24 alfalfa plants were inoculated by the three varieties of spittle insects, and 9 infections were obtained, or 38 per cent. Eight of 24 lots of three varieties of spittle insects picked up the virus, or 33 per cent.

TABLE 5

TRANSMISSION OF VIRUS FROM DISEASED ALFALFA DWARF BY VARYING NUMBERS OF THREE VARIETIES OF *PHILAENUS LEUCOPHTHALMUS* TO SUCCESSIVE HEALTHY ALFALFA PLANTS

Number of adults in each lot	Days on alfalfa dwarf	First set of healthy alfalfa plants		Adults alive	Second set of healthy alfalfa plants		Adults alive	Third set of healthy alfalfa plants	
		Plants inoculated	Plants infected		Plants inoculated	Plants infected		Plants inoculated	Plants infected
Philaenus leucophthalmus var. *leucophthalmus*									
20	2	1	0	19	1	1	19	1	0
20	4	1	0	16	1	0	15	1	1
Philaenus leucophthalmus var. *fabricii*									
20	7	1	1	20	1	0	19	1	0
Philaenus leucophthalmus var. *impressus*									
20	7	1	1	20	1	0	20	1	0
20	2	1	0	15	1	1	15	1	1
20	8	1	0	20	1	1	20	1	0
20	2	1	0	15	1	1	15	1	0
20	2	1	0	20	1	0	20	1	1
20	3	1	0	19	1	0	19	1	1
20	3	1	0	18	1	0	16	1	1
14	8	1	0	13	1	0	11	1	1

Table 4 shows the transmission of the virus from alfalfa to successive healthy grapevines by varying numbers of three varieties of *Philaenus leucophthalmus*. A total of 53 vines were inoculated; 41 were infected, or 77 per cent.

The virus causing alfalfa dwarf was not often transmitted to healthy alfalfa plants by three varieties of *Philaenus leucophthalmus*. A total of 186 alfalfa plants were inoculated by 54 lots of 10 or 20 adults on the first plants, and only 12 infections occurred, or 6 per cent. Of 54 lots, only 11 lots produced infections, or 20.4 per cent. Table 5 shows the results obtained with these 11 lots; lots on which all results were negative are not tabulated.

Natural Infectivity. Grapevines used as check or control plants on which varieties of adult *Philaenus leucophthalmus* collected in the field were fed sometimes became diseased. The adults of six varieties used in the experimental work were captured in enormous numbers on the following herbs:

sweet marjoram (*Majorana hortensis*), rosemary (*Rosmarinus officinalis*), and narrow-leaf sage (*Salvia officinalis*). Four lots of 20 adults each, of the variety *leucophthalmus* and two lots of the variety *spumarius* were demonstrated to be naturally infected. Nymphs taken on spearmint (*Mentha spicata*) and on Australian tea tree (*Leptospermum laevigatum*) also caused infection. No symptoms of the disease could be detected on any of these food plants. Whenever a check or control plant became infected, the data of that lot of adults were discarded.

Whenever high populations of nymphs occur on certain plants, many nymphs wander to other food plants. Hence first-instar nymphs were further tested for natural infectivity. Thirty lots of 5 nymphs were transferred from sweet marjoram, rosemary, narrow-leaf sage, and wild marjoram, *Origanum vulgare,* to healthy grapevine cuttings, but no infections occurred.

Grapevine cuttings and alfalfa are favorable food plants of the nymphs and adults. Although this spittle insect has been reported to be a serious pest of alfalfa and clover in Wisconsin, in California the nymphs have been taken only on volunteer alfalfa in the fog belt. No intensive investigations were made in alfalfa fields in the interior regions of the state.

An interesting observation was made on two occasions of known vectors of the virus of Pierce's disease of grapevines feeding on the same food plant with nymphs of *Philaenus leucophthalmus.* Nymphs of the meadow spittle insect were abundant on California mugwort growing in Niles Canyon. Adults of the blue-green sharpshooter, *Neokolla circellata* (Baker), the most efficient vector of the virus to grapevines, were taken on the same plants on which the nymphs were feeding. Again, nymphs of *P. leucophthalmus* were abundant on California mugwort growing in Strawberry Canyon, Berkeley, and adults of *Pagaronia confusa* Oman and the blue-green sharpshooter were commonly taken on the same plants.

LATENT PERIOD IN ADULTS

The latent period of the virus of Pierce's disease of grapevines was determined with four varieties of *Philaenus leucophthalmus.* The adults were collected on sweet marjoram, rosemary, and narrow-leaf sage. The four varieties were sorted out, and then lots of 20 males or females were kept for one week on healthy grapevines, which served as check or control plants to determine whether the spittle insects were naturally infective. Each lot, usually containing 20 males or 20 females, was fasted for 1 or 2 hours, then was kept on diseased grapevines for 1, 2, 3, or 4 hours, and finally was transferred hourly to 6 or 7 successive healthy vines.

The minimum virus latent period in the variety *leucophthalmus* varied from 3 to 7 hours, in the variety *pallidus* from 2 to 6 hours, in the variety *spumarius* 6 hours, and in the variety *impressus* from 3 to 5 hours (table 6). The highest number of infections was produced when the adults of the variety *leucophthalmus* were kept on diseased grapevines for a period of 4 hours.

Some lots of the four varieties of *Philaenus leucophthalmus* (not tabulated) after feeding 1 hour on diseased grapevines failed to transmit the virus to any of the successive healthy vines. After each lot of adults was transferred to 6 or 7 healthy vines, the surviving insects were kept permanently

TABLE 6

LATENT PERIOD OF VIRUS CAUSING PIERCE'S DISEASE OF GRAPEVINES IN ADULTS OF FOUR VARIETIES OF *PHILAENUS LEUCOPHTHALMUS* WITH GRAPEVINE CUTTINGS AS A HOST PLANT

Lot no.	Adults in each lot	Hours on infected grapevines	Successive plants inoculated	Plants infected	Hours on which successive infections occurred, including period on infected plants	Latent period, hours	Adults alive at the end of 7 hours
				Philaenus leucophthalmus var. *leucophthalmus*			
1	20	1	6	3	3, 4, 6	3	20
2	20	1	6	2	3, 4	3	15
3	20	1	6	2	3, 7	3	18
4	5	1	6	1	7	7	5
5	20	2	7	2	4, 7	4	20
6	20	2	7	2	6, 7	6	18
7	20	2	7	1	6	6	19
8	20	3	6	1	4	4	17
9	20	3	6	3	5, 8, 9	5	20
10	20	4	6	6	4, 5, 6, 7, 8, 9	4	19
11	20	4	6	5	5, 6, 7, 8, 9	5	17
12	20	4	6	3	5, 6, 7	5	20
				Philaenus leucophthalmus var. *pallidus*			
13	20	1	6	4	2, 3, 4, 5	2	20
14	20	1	6	1	2	2	18
15	20	1	6	3	4, 5, 6	4	18
16	20	1	6	1	6	6	19
17	20	1	6	1	6	6	18
				Philaenus leucophthalmus var. *spumarius*			
18	20	1	6	2	6, 7	6	17
				Philaenus leucophthalmus var. *impressus*			
19	20	1	6	2	3, 6	3	18
20	20	1	6	1	3	3	20
21	20	1	6	1	5	5	20

on a healthy vine during adult life. In addition to those tabulated, two lots of 20 adults of the variety *leucophthalmus,* three lots of the variety *spumarius,* two lots of the variety *impressus,* and one lot of the variety *fabricii* failed to pick up the virus. One lot of 20 adults of the variety *fabricii* failed to infect any of the six successive healthy vines in hourly transfers, but did produce an infection when kept permanently on a healthy vine during adult life.

RETENTION OF VIRUS

The retention of the virus was determined with single males of *Philaenus leucophthalmus* var. *leucophthalmus,* which had completed the last nymphal stages on diseased grapevines. The combined feeding time of the nymphs and adults which had molted on diseased vines was 30 days. Each adult was transferred daily to successive healthy grapevine seedlings. The results are shown in table 7.

The males retained the virus from 29 to 76 days (table 7). The number of infections produced by the five adults varied from 6 to 15 per cent, and averaged 18 per cent. Three males each caused an infection on the last day of adult

TABLE 7

RETENTION OF VIRUS BY SINGLE ADULT *PHILAENUS LEUCOPHTHALMUS* VAR. *LEUCOPHTHALMUS*

Lot no.	Plants inoculated	Plants infected		Days on which successive infections occurred	Longevity of adults, days
		Number	Per cent		
1	80	15	19	11, 14, 22, 23, 25, 28, 31, 32, 40, 46, 59, 69, 71, 74, 76	80
2	64	10	16	15, 20, 24, 28, 30, 31, 34, 58, 62, 64	64
3	51	6	12	12, 17, 22, 44, 47, 51	51
4	32	9	28	10, 12, 19, 20, 21, 28, 29, 31, 32	32
5	31	6	19	5, 9, 22, 23, 27, 29	31
Average	*52*	*9*	*18*		*52*

life. The longest period between two successive infections with each of the other two males was 13 days, and the period between the last infection and death of the adults was 2 and 4 days. It is evident that the virus was retained during the entire adult life of these five males with grapevine seedlings as a host plant. On the other hand, under natural conditions, the virus may not be retained during the entire adult life, since life-history studies show that the spittle insects normally live longer.

STUNTING, LEAF CURLING, AND BLASTING OF FLOWERS

Osborn (1916) reported that the meadow spittle insect, *Philaenus spumarius,* caused shriveled, blasted flowers on buttercup and clover, which failed to produce seeds.

Secrest (1944) suggested that the injury to jack pine and red pine by the Saratoga spittle insect, *Aphrophora saratogensis,* was caused primarily by the removal of sap by the insects and the girdling effect produced by the infiltration of resin into the tissues surrounding feeding punctures. The latter effect blocked the conducting tissue of the phloem and xylem.

Fisher and Allen (1946) caged adult spittle insects, *Philaenus leucophthalmus,* on alfalfa, and observed dwarfing, rosetting, blossom blasting, and necrosis of the foliage after approximately one month of feeding. The damage

in cages was not so great as that caused by feeding of the nymphs which had been observed in the field earlier.

Scholl and Medler (1947) showed that the feeding of the nymphs and adults of *Philaenus leucophthalmus* caused a characteristic bunchy-top condition of alfalfa plants. The feeding of the adults on immature seed pods also may be a factor in alfalfa seed production, since it results in shriveled seed.

In California the feeding of the nymphs of *Philaenus leucophthalmus* causes leaf curling around the spittle on celery (plate 6, *A*). An enormous population of nymphs occurred on sweet marjoram, many of which left this food plant, probably at night, and crawled into an adjacent celery field. When the spittle insects were removed and the celery plants were transplanted into flower pots, the newly developing leaves were normal.

Leaf curling around the spittle masses of *Philaenus leucophthalmus,* and dwarfing of the apical leaves was found to be common among ornamental flowering plants (plate 6, *B*). It was frequently observed on many species of weeds that leaves curl around the spittle mass, particularly on California mugwort, *Artemisia vulgaris* (plate 5, *F*). Nymphs feeding on goose grass, *Galium aparine,* caused an upward curling of the whorl of leaves around the spittle mass (plate 6, *C*) and a blasting of the flowers.

Although no studies were conducted on the effect of the extraction of food materials by the meadow spittle insects, or the interference of food translocation resulting from the mouthparts-puncture injuries, probably these aspects also were of importance. A local or systemic toxic salivary secretion may also play a part in the rolling of the leaves around the spittle masses and blasting of the flowers.

LITERATURE CITED

ANDERSON, R. F.
1947. Saratoga spittlebug injury to pine. Jour. Econ. Ent. **40**:26–33.

BALL, E. D.
1901. The food habits of some *Aphrophora* larvae. Ohio Naturalist **1**:122–24.
1915. Adaptations to arid conditions in Cercopidae and Membracidae. Ent. Soc. Amer. Ann. **8**(4):365–68.
1919. Notes on the Cercopidae with descriptions of some new species. Iowa Acad. Sci. Proc. **26**:143–50.
1920. The life cycle in Hemiptera (excl. aphids and coccids). Ent. Soc. Amer. Ann. **13**: 142–55.
1928. Notes on the Cercopidae of America north of Mexico (Homoptera). Ent. News **39**(2):47–49.

DELONG, D. M., and H. H. P. SEVERIN.
1950. Spittle-insect vectors of Pierce's disease virus. I. Characters, distribution, and food plants. Hilgardia **19**(11):339–56.

DOERING, K. C.
1922. Biology and morphology of *Lepyronia quadrangularis* (Say)—Homoptera, Cercopidae. Kansas Univ. Sci. Bul. **14**:515–87.
1931. Some biological notes on the Cercopidae north of Mexico (Homoptera). Kansas Ent. Soc. Jour. **4**:48–51.

ESSIG, E. O.
1926. Insects of western North America. 1035 p. The Macmillan Company, New York.
[FISHER, E. H., and T. C. ALLEN.]
1946. Alfalfa and clover severely damaged by spittle bugs. *In:* What's New in Farm Science. Wisconsin Agr. Exp. Sta. Bul. **469**:15–16.
FITCH, A.
1856. Third report of the noxious and other insects of the State of New York. New York State Agr. Soc. Ann. Rept. p. 315–490.
GARMAN, P.
1921. The grass-feeding frog-hopper or spittle-bug. Connecticut [New Haven] Agr. Exp. Sta. Bul. **230**:327–34.
HOUSTON, B. R., K. ESAU, and W. B. HEWITT.
1947. The mode of vector feeding and the tissues involved in the transmission of Pierce's disease virus. Phytopathology **37**:247–53.
KIRKALDY, G. W.
1906. Leaf-hoppers and their natural enemies. Hawaii. Sugar Planters' Assoc. Ent. Bul. **1** (pt. 9):271–479.
MANNS, T. F.
1939. Yellows and little peach; the cause, means of dissemination, and control. *In:* Delaware Agricultural Experiment Station Annual Report. Delaware Agr. Exp. Sta. Bul. **220**:1–43.
1943. Peach yellows and little peach. *In:* Delaware Agricultural Experiment Station Annual Report. Delaware Agr. Exp. Sta. Bul. **244**:1–44.
METCALF, Z. P., and G. W. BARBER.
1929. Notes on *Aphrophora salicis* DeGeer in America. Psyche **36**:51–57.
MUESEBECK, C. F. W.
1946. Common names of insects approved by the American Association of Economic Entomologists. Jour. Econ. Ent. **39**:427–48.
MUMFORD, T. P.
1926. Notes on the froghopper blight of sugar-cane in Trinidad. Bul. Ent. Research **17**(2):139–50.
OSBORN, H.
1916. Studies of life histories of froghoppers of Maine. Maine Agr. Exp. Sta. Bul. **254**: 268–88.
SCHOLL, J. M., and J. T. MEDLER.
1947. Spittle bugs in relation to alfalfa seed production in Wisconsin. Jour. Econ. Ent. **40**(3):446–48.
SECREST, H. C.
1944. Damage to red pine and jack pine in the Lake states by the Saratoga spittle bug. Jour. Econ. Ent. **37**:447–48.
SEVERIN, H. H. P.
1947. Transmission of virus of Pierce's disease of grapevines by spittle insects. Phytopathology **37**(5):364.
1949. Transmission of the virus of Pierce's disease of grapevines by leafhoppers. Hilgardia **19**(6):190–206.
STEARNS, L. A.
1923. Family Cercopidae. *In:* Britton, W. E. Guide to the insects of Connecticut. Part IV. State of Connecticut State Geol. and Nat. Hist. Sur. Bul. **34**:206–38.
VAN DUZEE, E. P.
1914. A preliminary list of the Hemiptera of San Diego County, California. San Diego Soc. Nat. Hist. Trans. **2**:1–57.

4½*m*-1,'50(B5463)

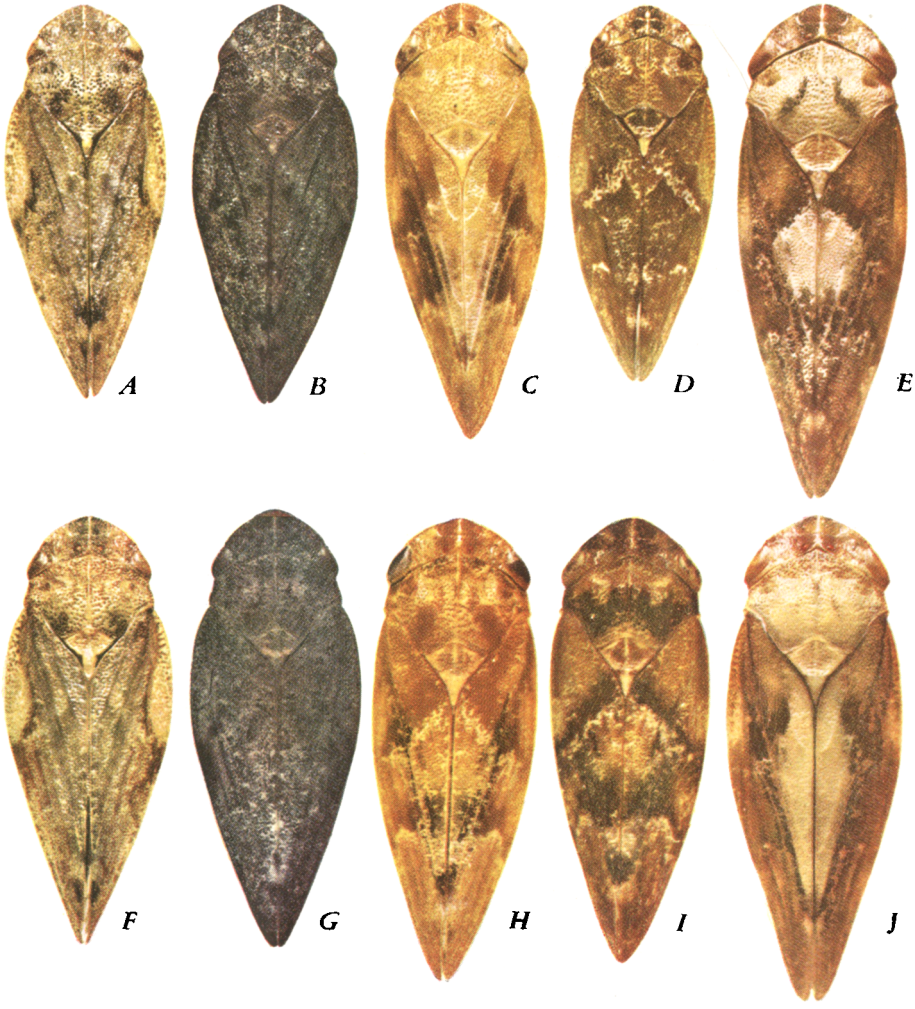


Plate 1. Color variations of adults of two species of spittle insects, vectors of virus of Pierce's disease of grapevines and alfalfa dwarf: *A*, *B*, males, *F*, *G*, females of annulate spittle insect, *Aphrophora angulata* Ball; *C*, *D*, *E*, males; *H*, *I*, *J*, females of western pine spittle insect, *Aphrophora permutata* Uhler.

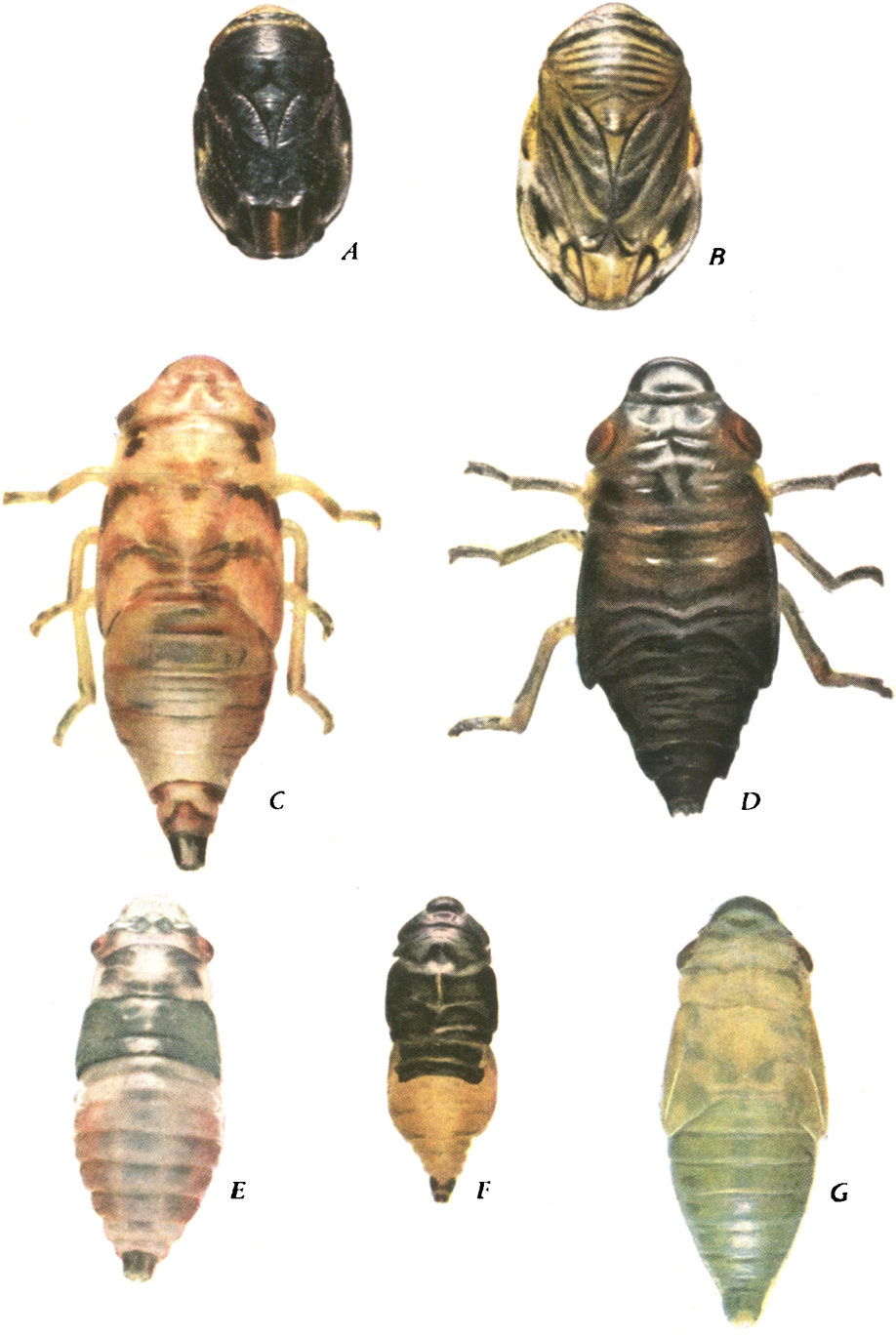


Plate 2. *A*, male, *B*, female *Clastophora brunnea* Ball; *C*, color pattern of last-instar nymph of annulate spittle insect, *Aphrophora angulata*; *D*, of western pine spittle last-instar nymph, *A. permutata*; *E*, fourth instar of *A. permutata* showing red sides on the abdomen; *F*, color pattern of last-instar nymph of *C. brunnea*; *G*, last-instar nymph of meadow spittle insect, *Philaenus leucophthalmus* (Linnaeus).

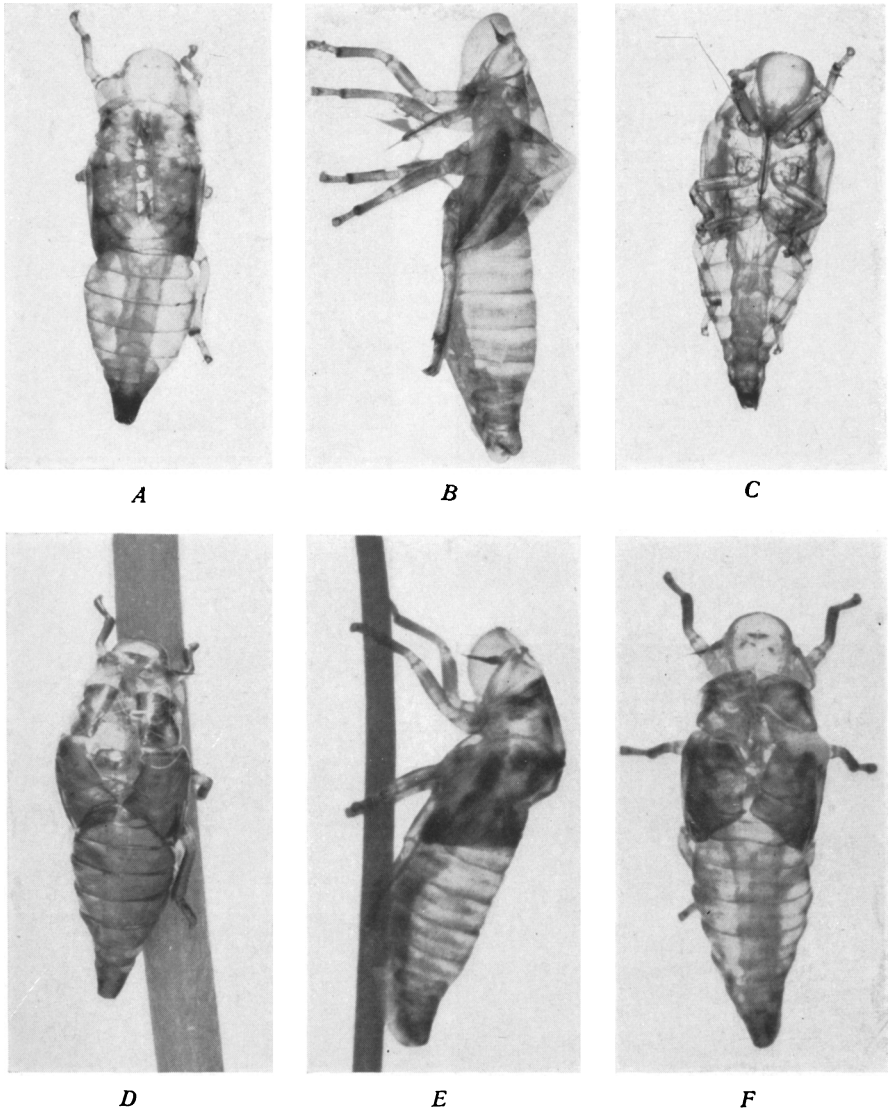
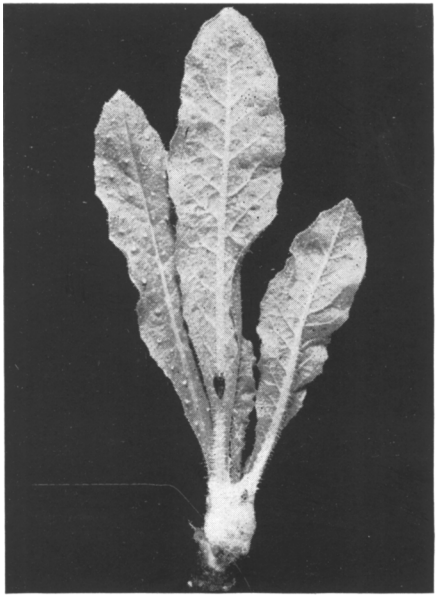
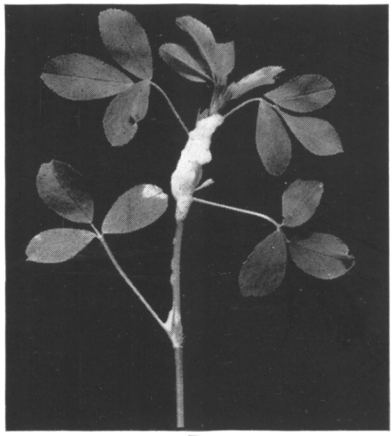


Plate 3. *A, B, C,* dorsal, lateral, and ventral views of last molted exuviae of annulate spittle insect, *Aphrophora angulata* Ball; *C, D, E,* same views of last molted exoskeleton of western pine spittle insect, *Aphrophora permutata* Ball.



A

B

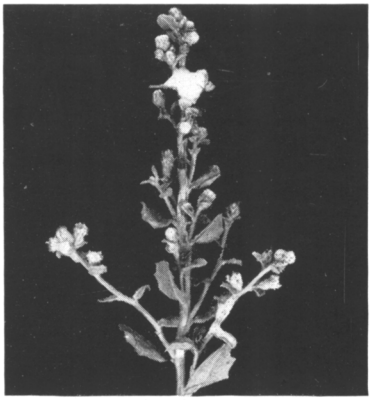


D

C

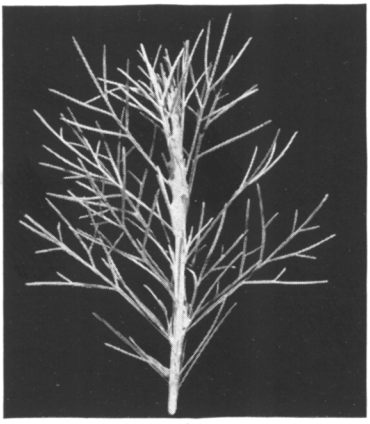
E

Plate 4. Spittle masses on various host plants: *A*, western pine spittle nymphs, *Aphrophora permutata*, of first generation in froth at base of bristly ox-tongue, *Picris echioides*; one nymph crawled out of the spittle during photographing; *B*, nymphs of second generation in froth on Aleppo pine, *Pinus halepensis*; *C*, spittle masses of *Philaenus leucophthalmus* on narrow-leaf sage, *Salvia officinalis*; *D*, froth of the same species on volunteer alfalfa, *Medicago sativa*; and *E*, on rose, *Rosa* sp.

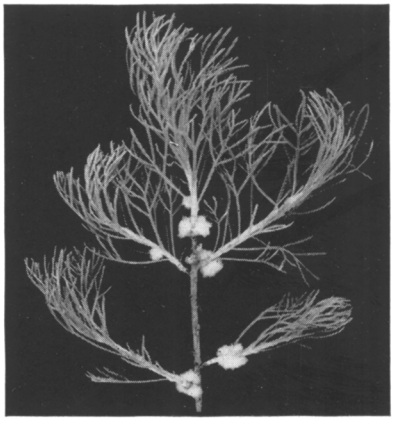


A

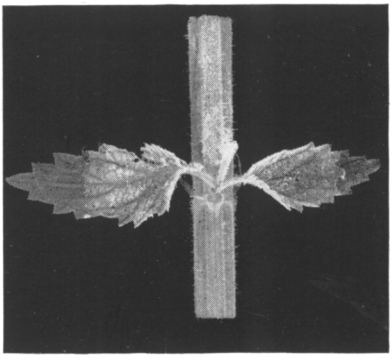
B



C



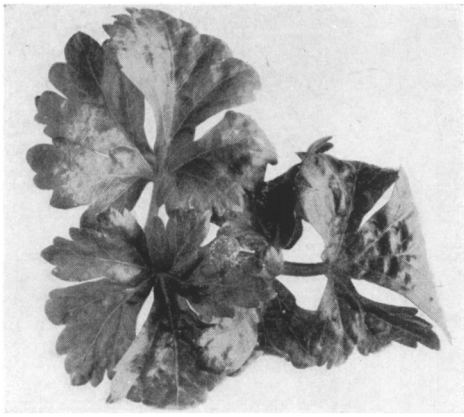
D



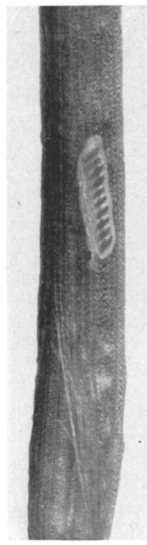
E

F

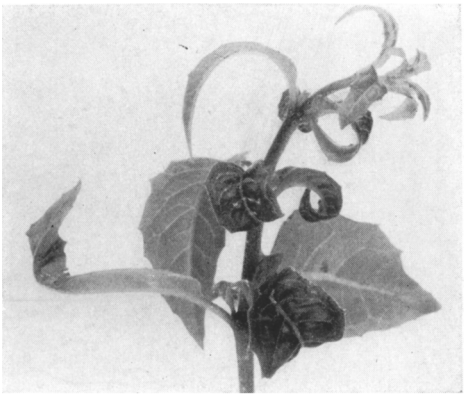
Plate 5. *A*, Twig of coyote brush or chaparral broom, *Baccharis pilularis*, showing spittle containing first generation nymphs of *Clastophora brunnea; B*, apical twigs of gum plant, *Grindelia camporum*, showing froth containing second generation nymphs of *C. brunnea; C*, branch of California mugwort, *Artemisia californica*, showing spittle containing second generation nymphs of *C. brunnea; D*, fluffy, cottony, gall-like structures of *Diarthronomyia floccosa* Felt, resembling somewhat spittle of *C. brunnea* on California mugwort; *E*, stem and leaves of coast nettle, *Urtica californica*, showing dried, white, flaky spittle which adheres to the plant for a long time after the nymphs of *Aphrophora permutata* leave the froth and pass through the last molt; *F*, apical shoot of California mugwort, *Artemisia vulgaris*, showing spittle of *Philaenus leucophthalmus*, balled leaf (lower right), and dwarfed apical leaves.



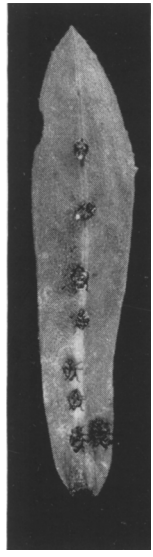
A



D



B



E

C

Plate 6. *A*, Leaf curling of celery leaflets (*Apium graveolens* var. *dulce*) around froth caused by the feeding of the meadow spittle insect, *Philaenus leucophthalmus; B*, leaf curling around the spittle masses of meadow spittle insect and dwarfing of the leaves of *Fuchsia triphylla; C*, goose grass, *Galium aparine*, showing whorl of leaves curled upward on spittle of meadow spittle insect; *D*, packets of eggs of meadow spittle insect, laid diagonally and firmly attached to the stem of Sacramento barley, *Hordeum vulgare; E*, exuviae of last nymphal instars of *Clastophora brunnea* on the midrib of mule fat, *Baccharis viminea*.

The journal *Hilgardia* is published at irregular intervals, in volumes of about 600 pages. The number of issues per volume varies.

Subscriptions are not sold. The periodical is sent as published only to libraries, or to institutions in foreign countries having publications to offer in exchange.

You may obtain a single copy of any issue free, as long as the supply lasts; please request by volume and issue number from:

Publications Office
College of Agriculture
Berkeley 4, California

The limit to nonresidents of California is 10 separate issues on a single order. A list of the issues still available will be sent on request.