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EVIDENCE OF NONSPECIFIC TRANSMISSION OF CALIFORNIA ASTER-YELLOWS VIRUS BY LEAFHOPPERS

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CHARACTERS, DISTRIBUTION, AND FOOD PLANTS OF PHLEPSID LEAFHOPPER VECTORS OF CALIFORNIA ASTER-YELLOWS VIRUS¹

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INTRODUCTION

SEVERIN (1934, 1940)⁴ has previously reported that 3 species and 1 physiological race of leafhoppers transmit the California aster-yellows virus. The present paper deals with the characters, distribution, habitat, and food plants of six species of phlepsid leafhopper vectors. A companion paper (Severin, 1945) presents evidence that the transmission of the virus by the 6 species is not specific.

The genus *Phlepsius* was established by Fieber (1866) for a small number of European species. Van Duzee (1892) published the first paper on North American forms and recorded 18 species, including 13 new ones. Later his catalogue (Van Duzee, 1917) recorded 63 species and 1 variety of *Phlepsius*, including 7 species occurring in California. Ball (1918), who recorded the Mexican and Central American species, established 4 new subgenera. Osborn and Lathrop (1923), publishing a synopsis of the genus, discussed 89 North American species and 1 variety of both genera, and recorded 11 species occurring in California. After their paper had appeared, DeLong (1923) discussed the food plants and habitats of some of the North American *Phlepsius*. Ball (1927) discussed the synonymy of North American phlepsids and established 1 new subgenus. A later paper (Ball, 1931) described some new species and varieties of *Phlepsius*. DeLong and Caldwell (1937) in their check list of the Cicadellidae of America, north of Mexico, recorded 69 species and 4 varieties in the genus *Phlepsius*, 5 species occurring in California; and 29 species and 1 variety in the genus *Texananus*, 7 species distributed in California.

DeLong (1938a) described 4 new species of *Texananus* and 3 new species of *Phlepsius*. In the same year (1938b), he described 3 new species of *Texananus*, one of which, *pergradus*, is a vector discussed in this paper.

DeLong also (1938c) studied the male genitalia as distinguishing characters of closely related species, or of species regarded as synonymous with the genus

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⁴ See "Literature Cited" for complete citation, referred to in the text by author and date of publication.

Phlepsius of North America. The ventral segment of the female was illustrated as an aid to be used in identification if the males were not included in the series. Keys were constructed for the species in 3 subgenera, including 46 species and 1 variety of *Phlepsius*, 9 species and 1 variety of *Pendara*, 6 species of *Paraphlepsius*, 1 species of the new subgenus *Josanus*, and 1 species of *Zioninus*, or a total of 63 species and 2 varieties all belonging to the typical *Phlepsius* group.

DeLong (1939) discussed the members of the *majestus* group of *Texananus* and described 4 new species. In the following year (1940) he discussed the species of these 2 genera occurring in Mexico, illustrating the genitalia of all the Mexican species and describing 9 new species. Later (1943) he described 3 more new species of western *Texananus*, 1 of which, *latipex*, is also a vector of the aster-yellows virus. Then, again, in two separate papers (1944a and 1944b) DeLong described 13 more new species of the Mexican fauna of *Phlepsius* and *Texananus*, listing all the species of these 2 genera occurring in Mexico and illustrating the male and female genital structures.

Until 1918, all the leafhoppers with brown ramose pigment lines were placed in *Phlepsius*; the whole group commonly was called the phlepsids. That year, Ball separated the narrow-headed forms, which he named *Texananus*. Because the European-type species is narrow headed, the name *Texananus* is likely to become a synonym of *Phlepsius*, whereas the broad-headed group will probably become *Paraphlepsius*.

GENERAL DISTRIBUTION

The species of *Phlepsius* and *Texananus* reach their greatest known abundance in the temperate regions of North America. Probably the greatest number of species would be found in the lower or central Mississippi Valley. Examining the genus *Phlepsius* proper, one finds that approximately half of the known North American species occur in the southeastern states, whereas about one fourth are northeastern in distribution. When compared with this eastern predominance of species, about 7 per cent occur in the southwestern states, 7 per cent in the plains states, and 13 per cent in the western United States and western Canada.

If the species of *Texananus* are considered in like manner, the predominance is reversed, for these are most abundant in the western and southwestern states. More than 35 per cent of the group are southwestern in distribution, and slightly less than that number are western and northwestern. Only 5 per cent are southeastern, approximately the same number are plains species, and some 15 per cent are northeastern in distribution. Apparently, then, the genus *Phlepsius*, comprising about twice as many species as *Texananus*, is predominantly eastern; *Texananus* is predominantly western. This supposition is borne out by recent work upon the Mexican fauna of this group: the species of *Texananus* are fairly abundant in Mexico; those of *Phlepsius* are rather scarce. Were it not for the fact that the subgenus *Tropicanus*, together with several recently described species, is definitely tropical, the genus *Texananus* would be decidedly predominate in distribution.

Even if the species of *Tropicanus* are included, the genus *Phlepsius* is still represented in Mexico by less than one fourth the number occurring in the

United States, whereas two thirds as many species of *Texananus* have been recorded for Mexico as for this country.

In connection with the western distribution of these two groups, one notes that 5 of the 6 vectors of the aster-yellows virus in California belong to the genus *Texananus*.

HABITAT AND FOOD PLANTS

The habitat may range from bog or marsh to the arid southwestern plains. Most of the species feed upon grass or herbaceous plants and are found under varying conditions. Some occur on the herbaceous growth of the pine woodland floor, and several are abundant in swamp and marsh. Certain of these species are common in the Florida everglades, either on the maiden cane-sawgrass association or in the moist prairies. In the northern fresh-water marsh, several species occur on the *Carex-Phragmites* association or the *Juncus-Eleocharis-Scleria* association. Still others are found in a prairie-grass habitat. A few species occur in the sphagnum-tamarack bog association, whereas others are manzanita species, confined to *Arctostaphylos* and similar types of vegetation.

Though few species live upon trees, one interesting group is the brown-and-white-banded species, all of which feed upon pine. Certain species live upon the southern pines, *Pinus palustris*, *P. caribaea*, and the like; others live upon the northern white pine, *P. Strobus*; and still other northern species on *P. rigida* and *P. virginiana*. Certain phlepsid species, distinct from those in the United States, are found harbored by the Mexican species of pine.

The meadow, upland pasture, and other grazing areas support large populations of several species. *Phlepsius irroratus* (Say) is both the most common and the most widely distributed species of the genus. The character of the meadow may vary to a high degree. The grassy area may be high or rolling and well drained, or it may be a low, wet meadow; in consequence, the kind of plant and the humidity factor may vary decidedly. Such conditions determine largely the occurrence and abundance of different species in the various areas of the United States. Thus each of the species of *Poa*, *Andropogon*, *Aristida*, *Bouteloua*, and other grasses has its specific kinds of phlepsids.

The optimum habitat for several species is found in open woodland areas of the deciduous forest, especially in the mixed mesophytic forest, where the humidity and ground moisture are rather high and there is a rich growth of herbaceous plants. Some species live in more restricted parts of these forests, such as the ground layer of a mixed hemlock-beech woodland. The *Texananus majestus* group occurs only in the more densely shaded woodlands, on the herbaceous ground layer.

IDENTIFICATION AND SEPARATION OF SPECIES

The narrow-headed species, being similar in color and external appearance, cannot be easily distinguished by these characters. The last ventral segment of the female abdomen and the chitinous structures of the genital chamber, particularly the aedeagus, are the most dependable means of separating the species of this group. Illustrations of these genital structures are appended as an aid in identifying or separating these species of *Phlepsius* and *Texananus*.

KEY TO THE SIX SPECIES

1. Head as wide as pronotum.....*Phlepsius apertinus*
 —Head narrower than pronotum..... 2
2. Smaller in size, not exceeding 5.5 mm..... 3
 —Larger in size, 6 mm or more in length..... 4
3. Female segment with a rather broad, rectangular median notch. Male styles tapered, narrow on apical third, the sickle-shaped portion of aedeagus narrow, with a long, slender, basal "handle" and without a thumb at base of curved portion.....
Texananus lathropi
 —Female segment with a short, narrow V-shaped notch at middle of broadly excavated portion. Male styles broad on apical third; the sickle-shaped portion of aedeagus with a short, broad basal "handle" and a long thumb protrusion at base of curved portion extending more than halfway to apex.....*Texananus pergradus*
4. Female segment slightly produced at middle, forming a blunt tooth on either side of median V-shaped notch. Male plates long, tapered to acutely pointed apices, which reach or exceed apices of pygofer.....*Texananus spatulatus*
 —Female segment broadly excavated on posterior margin, not produced at middle. Male plates short, rounded at apex or with blunt tips, not reaching apex of pygofer..... 5
5. Female segment broadly excavated, without a median notch. Male plates broadly rounded, together semicircular in shape. Aedeagus ventral process short, thick, with prominent dorsally and ventrally produced processes at blunt apex. The dorsal portion is a small, sickle-shaped process.....*Texananus oregonus*
 —Female segment broadly excavated, with a short, median V-shaped notch. Male plates short, divergent at apex, and bluntly pointed. Aedeagus ventral process slender, simple, elongate. The dorsal portion is sickle-shaped, with apex bifid.*Texananus latipez*

PHLEPSIUS APERTINUS OSBORN AND LATHROP

(Plate 1)

The head of *Phlepsius apertinus* is a little wider than the pronotum, and the anterior portion of the elytra appears to have a pale band. The length is 6 to 6.5 mm. The vertex is bluntly angled anteriorly and acutely angled, with the front forming a rather definite margin. The length at the middle is less than half the basal width between the eyes. The vertex, pronotum, and scutellum are white, with brown or black irrorations. There is a pale, irregular band in front of the middle of the clavus. There are a few large, whitish areas on the apical portion of the clavus and elytra. The costa is marked with several black spots. The front is black at the base; it is paler, with broken arcs, below.

In the female the last ventral segment slopes on the lateral margins to the rounded posterior angles. The posterior margin is broadly, deeply excavated almost to the base of the segment, the excavation being broadest at the base. The margins of the apex of the excavation are formed by broad, toothlike, pointed projections extending from the posterior margin at either side. The male plates are elongate, broad at the apex, rounded to the outer margins. The styles are long and narrow, extending almost to the apex of the plates, tapered to bluntly pointed apices. The aedeagus is rather short, broadened at the base, and tapered to a pointed apex. In a lateral view it appears barbed, with one barb close to the apex on the posterior margin and another barb more basal on the anterior margin. There is a short process near the base, extending anterio-dorsally. The pygofer bears a long, slender spine on the ventro-caudal margin.

Geographic Range.—*Phlepsius apertinus* is found in Oregon and California.

Distribution and Food Plants in California.—This species of leafhopper is common in fields of alfalfa (*Medicago sativa*) in the Santa Clara, San Joaquin, and Sacramento valleys. The localities in which the food plants grow and the populations were collected are as follows:

Sonoma County: A small number of adults were swept from pasture vegetation at Trinité, on June 4, 1943, by N. W. Frazier.

Santa Clara County: In Gilroy, on May 10, 1943, a few adults were captured in an alfalfa field by J. H. Freitag.

Sacramento County: In a locality known as the "Sacramento Pocket," on September 5, 1941, many adults were taken by H. H. P. Severin and N. W. Frazier, by sweeping cocklebur (*Xanthium canadense*), which grew in the shade of trees. On September 12, 1941, also, Severin found adults in abundant quantity in fields of alfalfa and Ladino clover (*Trifolium repens* L. var. *latum* McCarthy), and wild licorice (*Glycyrrhiza lepidota*).

Merced County: Two females were swept from pasture vegetation by N. W. Frazier on the summit of Pacheco Pass, May 6, 1943.

Madera County: At Madera, on October 9, 1941, a few adults were caught in an alfalfa field by N. W. Frazier.

Fresno County: On October 9, 1941, at Fresno and Selma, a small number of adults were taken in alfalfa fields by N. W. Frazier.

Tulare County: On May 4, 1941, at Woodlake, many adults were collected in an alfalfa field by N. W. Frazier. Later, on June 1 and on July 4, 1944, adults were commonly taken in a grassy Ladino clover field by J. H. Freitag. At Exeter, on October 9, 1943, adults were collected in abundant numbers by N. W. Frazier on bur-clover (*Medicago hispida*), as well as on annual yellow sweetclover (*Melilotus indica*), on common foxtail (*Hordeum murinum*), and on certain grasses.

TEXANANUS LATHROPI BAKER

(Plate 2)

Texananus lathropi is one of the short, broad species of the *ovatus* group. The length is 5.0 to 5.5 mm. The vertex is short and blunt, almost twice as wide between the eyes at the base as the median length; the margin is thick. The vertex, pronotum, scutellum, and inner border of clavus are yellow, with fuscous irrorations. The elytra is whitish and hyaline, marked with dark brown and fuscous. The costal area has darker spots.

The female segment is short and is broadly, shallowly excavated, with a deep quadrangular excavation at the middle.

The male valve is broadly triangular; the plates are strongly convexly rounded to a produced blunt apex on the inner margin. The styles are broad at the base, concavely rounded on the outer margin, and tapered to blunt apices, which are turned outward. The aedeagus is composed of two parts, the lower part being rather long and narrow in lateral view, tapered to a pointed apex, and the dorsal part being sickle-shaped, with a rather long, straight basal portion.

This species was first described as *Phlepsius annulatus* (Osborn and Lathrop, 1923); but Baker (1925), finding that name preoccupied, named the leafhopper *P. lathropi*.

Geographic Range.—One female was reported to have been collected from the base of Mt. Hood, and one male from Alsea Mountain (Oregon) on undergrowth at the edge of a fir forest. The species was taken at Los Angeles, California, by D. W. Coquillett; and in Nevada by C. F. Baker (Baker collection).

Distribution and Food Plants in California.—The localities and food plants of *Texananus lathropi* in California are as follows:

Sonoma County: At Trinita, on June 25, 1939, a mixed population containing 22 specimens of *Texananus lathropi* and *T. latipex* was collected by N. W. Frazier on drying pasture vegetation in a mountainous area at an elevation of 1,800 feet. Later collections in the same locality were made by Frazier as follows: May 29, 1942, when 10 females were captured on bur-clover, wild pea (*Lathyrus Bolanderi*) and *Thermopsis macrophylla*; on June 4, 1943, when 1 female was taken on wild pea; and on June 8, 1944, when 1 male was caught on pasture grasses and weeds.

Alpine Valley: On March 28, 1942, N. W. Frazier collected 8 females on bur-clover.

Marin County: At San Rafael, April 5, 1943, 1 female was collected, probably on wild pea, by N. W. Frazier. At Montara, July 31, 1942, 1 female was captured on tree lupine (*Lupinus arboreus*), by H. H. P. Severin.

Napa County: N. W. Frazier collected 1 female on wild pea at Dry Creek School on April 5, 1943.

Merced County: N. W. Frazier also caught 1 female on pasture vegetation at the entrance to Pacheco Pass on December 19, 1941.

Tulare County: At Exeter, October 10, 1939, 1 male and 3 females were taken on puncture vine (*Tribulus Terrestris*) by H. H. P. Severin.

This leafhopper occurs in the fog belt and in the interior regions of California. The dates of collection indicate that it overwinters in the adult stage.

TEXANANUS PERGRADUS DeLONG

(Plate 3)

This is a small species of the *ovatus* group. The length is 4.5 to 5.5 mm. The vertex is bluntly angled, about $1\frac{1}{2}$ times as wide between the eyes at the base as the median length. The color is variable. In darker specimens a brown spot occurs on either side of the apex, and a broken brown band between the eyes on the disc. The scutellum has four brown spots on the anterior margin. The elytra is pale, with dark-brown ramose pigment lines. There are three pale, distinct spots along the commissure.

The female last ventral segment is rather strongly, broadly excavated, with a short V-shaped notch at the apex of the excavation.

The male valve is produced and triangular. The plates are short, broad, strongly, convexly rounded, together appearing semicircular. The styles are elongated, narrowed except at the base. The apex is bluntly angled. The aedeagus in lateral view shows a slender, delicate, ventral process and a broader sickle-shaped dorsal process, which has a long prominent thumb at the base of the curved portion.

Geographic Range.—The states in which *Texananus pergradus* was collected include Oregon, California, Utah, Colorado, Arizona, New Mexico, Texas, and Mexico.

Distribution and Food Plants in California.—As determined by N. W. Frazier, the localities and food plants of this leafhopper in California are as follows:

San Luis Obispo County: Two males and 1 female were caught in pasture and abandoned vineyards at Santa Maria on June 12, 1942.

Ventura County: On June 11, 1942, at Cavin Station, 3 miles east of Fillmore, 27 males and 24 females were collected on annual yellow sweetclover and annual burweed (*Franseria acanthicarpa*), growing in the Santa Clara river bottom.

Orange County: On June 5, 1942, at Anaheim, 2 males and 1 female were swept from annual burweed growing in the Santa Ana river bottom.

Riverside County: At Banning, June 5, 1942, 3 males and 12 females were collected on annual burweed.

San Diego County: At Boulevard, 5 males and 5 females were taken on *Franseria* sp. on June 7, 1942.

San Bernardino County: On June 5, 1942, at the entrance to Cajon Pass, 1 male and 2 females were captured on *Lotus* sp.

Tulare County: On pasture vegetation along a riverbank at Woodlake on May 4, 1940, 12 males and 14 females were collected.

San Joaquin County: At Byron, November 12, 1942, 1 male was swept from Bermuda grass.

TEXANANUS SPATULATUS VAN DUZEE

(Plate 4)

This is the largest and most common species of the genus in the southwestern United States and Mexico. The length is 6.5 to 7.0 mm. The vertex is produced and bluntly angled, almost twice as wide between the eyes at the base as the median length. The margin is thick and rounded. The color is brown. The vertex has a mottled transverse band between the eyes, anterior to which are two triangular mottled spots.

The female last ventral segment is short, with broadly rounded lateral angles. The posterior margin is slightly produced at the center and bears a V-shaped notch extending about one fourth the distance to the base. The posterior margin is broadly, shallowly excavated on either side, between the lateral angles and the produced tooth on each side of the median notch.

The male valve is short and triangular. The plates are long, tapered to acutely pointed tips, which extend to the apex of the pygofers. The styles, broad at the base, are rapidly narrowed to slender apical portions, which are pointed on the outer apical margins. The aedeagus has a pair of long, slender ventral processes and a dorsal process that arises at the base, is bent caudad, and forms a ventral and dorsal branch at about half its length. The ventral branch is long, slender, and acutely pointed.

Geographic Range.—The distribution of this species includes California, Colorado, Kansas, Texas, and Mexico.

Distribution and Food Plants in California.—The localities and food plants of this leafhopper in the San Joaquin Valley were as follows:

Merced County: At the summit of Pacheco Pass, May 6, 1942, 136 adults were collected on pasture vegetation by N. W. Frazier.

Tulare County: On October 10, 1941, at Ivanhoe, 4 males and 8 females were collected on rough pigweed (*Amaranthus retroflexus*), by H. H. P. Severin, N. W. Frazier, and J. H. Freitag. At Exeter, on October 10, 1941, 1 male was captured on puncture vine, by H. H. P. Severin; on April 1, 1942, 5 males and 5 females were taken on redstem filaree (*Erodium cicutarium*), by N. W. Frazier; and at Woodlake, on January 8, 1942, he collected 3 males, 3 females, and 28 nymphs from redstem filaree, and from whitestem filaree, (*E. moschatum*).

Kern County: At Delano, October 10, 1941, 2 males and 1 female were caught in an alfalfa field by H. H. P. Severin. On December 21, 1941, at Arvin, 62 males and 68 females were taken below leaves of nettle-leaf goosefoot (*Chenopodium murale*), and also on grass under leaves in grape vineyards, by N. W. Frazier and J. H. Freitag.

Evidently this leafhopper overwinters in the nymphal and adult stages and undergoes an incomplete hibernation.

TEXANANUS OREGONUS BALL

(Plate 5)

Texananus oregonus is a rather robust species, 6.5 mm. in length. The vertex, produced and bluntly angled, is about two thirds as wide between the eyes as the median length. It is pale brown, with black markings at the ends of the claval veins along the posterior margin of the elytra. Although it resembles *superbus* and other species of the genus, the genital structures will easily distinguish it from allied species.

The female last ventral segment is short and broad. The lateral margins slope to rounded posterior angles. The posterior margin is broadly, shallowly excavated, and brown-margined.

The male valve is short and triangular, with a blunt apex. The plates are short, broadly rounded from base to apex. Together they appear semicircular. The pygofer is a little longer than the plates. The styles are broad on the basal two thirds; the apical third is abruptly narrowed and produced as a narrow portion on its inner margin. The aedeagus is bifid at the apex, with a dorsal process arising near the base, which is sickle-shaped on the apical portion. The aedeagus proper is rather short, in lateral view broadened at the apex, with a dorsally directed and a ventrally directed pointed process. The apex is truncate.

Geographic Range.—This leafhopper has been recorded from Washington, Oregon, California, and Mexico.

Distribution and Food Plants in California.—As determined by N. W. Frazier, the localities and food plants of populations collected in California, are as follows:

Sonoma County: At Trinit, on May 12, 1940, 10 males and 12 females were taken on bur-clover and wild pea. On March 28, 1942, 1 male and 5 females were taken on wild pea. On February 13, 1943, 2 males and 1 nymph (a female after the last molt) were captured on an annual species of *Lotus* and on wild honeysuckle (*Lonicera hispidula* Dougl. var. *californica* Jepson). On April 7, 1943, 1 female was swept from wild pea. On June 8, 1944, 2 nymphs (1 male

and 1 female after the last molt) were caught on pasture grasses and weeds. At Alpine Valley, on March 28, 1942, 4 females were collected on bur-clover.

Napa County: Two females were taken on wild pea at Dry Creek School, February 13, 1943.

The collection data show that the adults winter over.

TEXANANUS LATIPEX DeLONG

(Plate 6)

This is one of the short, broad phlepsids of the *ovatus* group. The length is 6 mm. The vertex is bluntly angled, almost twice as wide between the eyes at the base as the median length. The vertex, pronotum, and scutellum are yellowish, marked with brown ramose pigment. The basal angles of the scutellum have dark-brown spots. The elytra are more heavily marked with brown pigment, with three distinct commissural spots.

The female last ventral segment is short, with rather prominent lateral angles, between which the posterior margin is rather deeply, broadly excavated, with a slight median V-shaped notch.

The male valve is triangular. The plates are short, convexly rounded to bluntly pointed, produced, diverging apices. The styles are elongated, concavely curved, and tapered to narrow blunt apices. The aedeagus is composed of an upper and a lower portion. In lateral view the ventral portion is rather long, narrow, and tapered to an acute tip. The dorsal portion is broad, strongly curved, sickle-shaped, broadened apically, and bifid at the apex, forming two stout teeth.

Geographic Range.—*Texananus latipex* occurs in British Columbia, Washington, Montana, North Dakota, Oregon, Idaho, Wyoming, California, Nevada, Utah, Colorado, Arizona, New Mexico, Texas, and Mexico.

Distribution and Food Plants in California.—The localities in which this leafhopper was collected in California and its food plants are as follows:

Sonoma County: At Trinité, on June 25, 1939, a mixed population of *Texananus latipex* and *T. lathropi* was collected on drying pasture vegetation in a mountainous area at an elevation of 1,800 feet. One female was taken on pasture vegetation July 14, 1943, in the same locality. At Alpine Valley, March 28, 1942, 1 female was captured on bur-clover by N. W. Frazier.

San Mateo County: On September 19, 1941, at Half Moon Bay, 1 female and 1 nymph (a female, after the last molt) were taken on spiny clothbur (*Xanthium spinosum*) by H. H. P. Severin.

Santa Clara County: At Milpitas, February 19, 1943, 3 females were caught in a depleted, grassy alfalfa field by J. H. Freitag. He also collected 1 female in an alfalfa field at San Jose on March 4, 1942; and 1 female on grasses in a bog at Gilroy on August 11, 1942.

Alameda County: At Pleasanton, June 30, 1943, 1 female was captured in an alfalfa field by J. H. Freitag.

Madera County: On October 9, 1941, at Madera, 1 female was taken in an alfalfa field by H. H. P. Severin. At Chowchilla, December 19, 1941, 4 females and 2 males were collected on pasture vegetation by N. W. Frazier.

Fresno County: At Fresno, November 17, 1941, 4 females and 2 males were

caught on redstem filaree, and 2 females were collected on Bermuda grass (*Cynodon Dactylon*), on April 22, 1942. At Raisin City, on December 22, 1941, 1 female was taken on grass by N. W. Frazier.

Tulare County: At Exeter, on October 9, 1941, H. H. P. Severin captured 1 female in an alfalfa field and 2 females on puncture vine. At Visalia, June 18, 1942, 1 female was caught on inland saltgrass (*Distichlis stricta*), and at Ivanhoe-Elderwood, April 29, 1943 was collected 1 female on pasture vegetation by N. W. Frazier.

Kern County: On October 10, 1941, at Delano, 1 female was collected in an alfalfa field by H. H. P. Severin.

Evidently *Texomanus latipex* occurs in the fog belt, in the San Joaquin Valley, and in the mountains of Sonoma County. This insect overwinters in the adult stage.

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PLATES

PLATES

1. *Phlepsioides apertinus* Osborn and Lathrop
2. *Texananus lathropi* Baker
3. *Texananus pergradus* DeLong
4. *Texananus spatulatus* Van Duzee
5. *Texananus oregonus* Ball
6. *Texananus latipex* DeLong

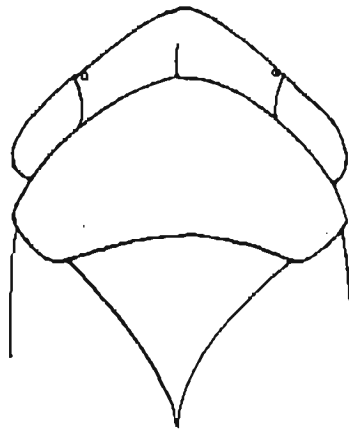
KEY TO FIGURES ON PLATES

- A—Dorsal view of head, pronotum, and scutellum
B—Ventral view of male genitalia
C—Lateral view of male genitalia
D—Ventral view of female last ventral segment

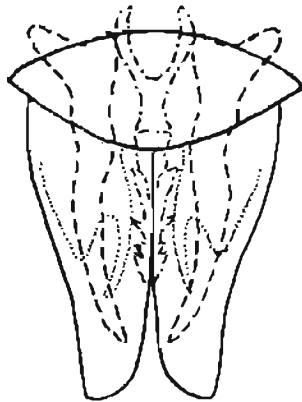
KEY TO FIGURE DETAIL OUTLINES

- style
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..... dorsal spine of pygofer

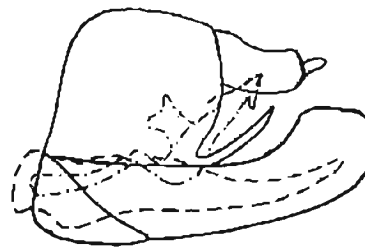
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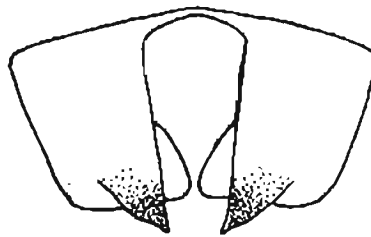
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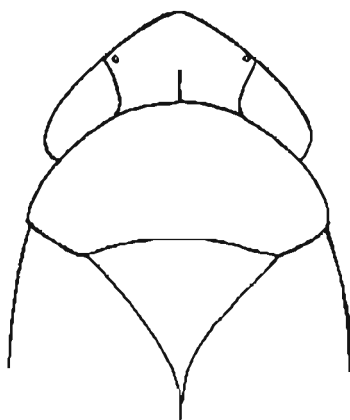
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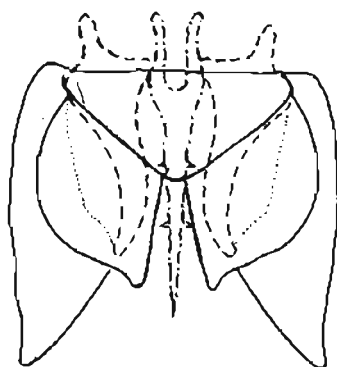
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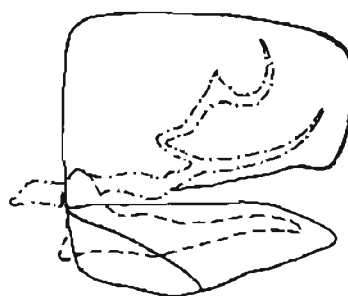
TEXANANUS LATHROPI



A



B



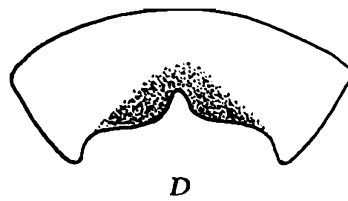
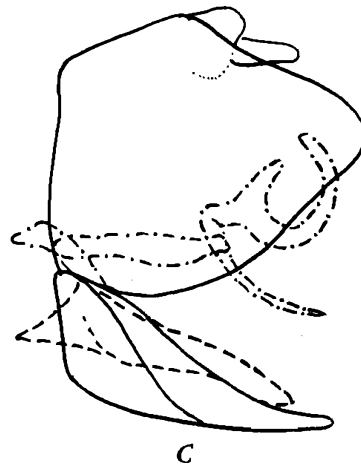
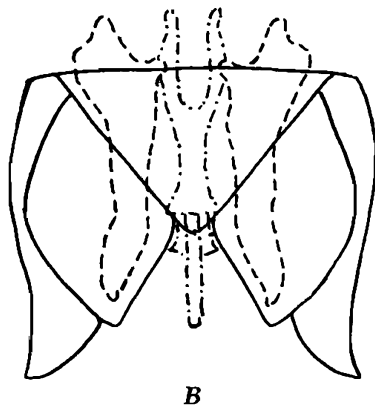
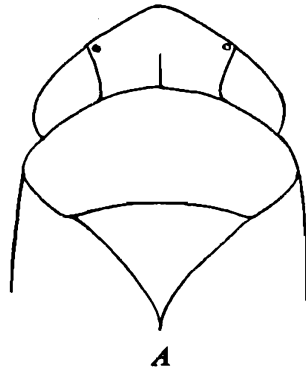
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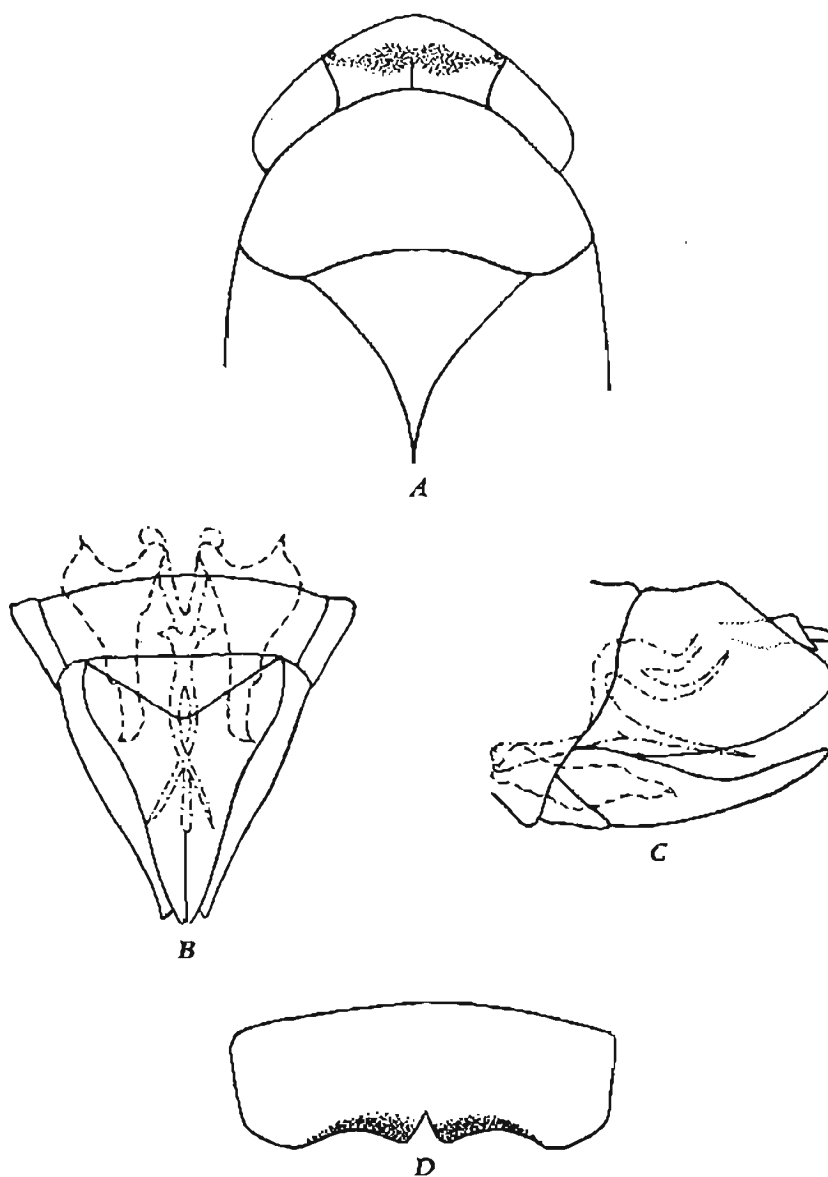
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TEXANANUS PERGRADUS



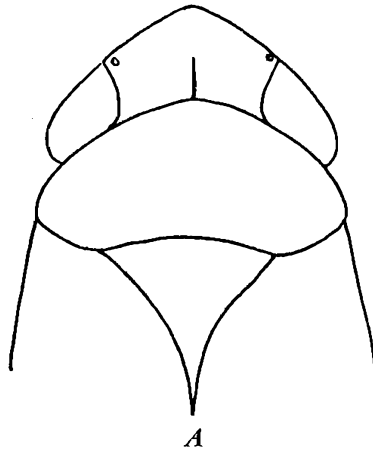
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TEXANANUS SPATULATUS

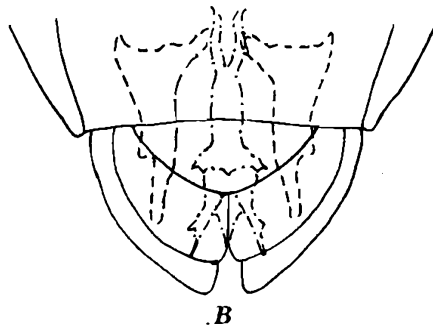


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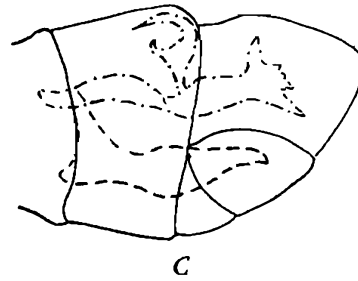
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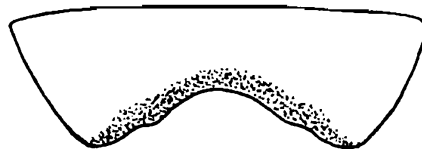
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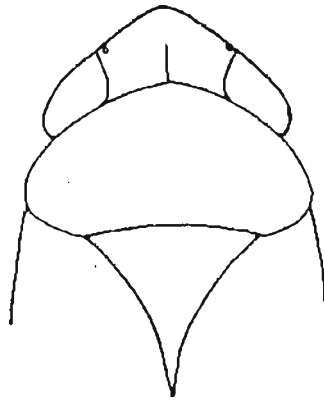
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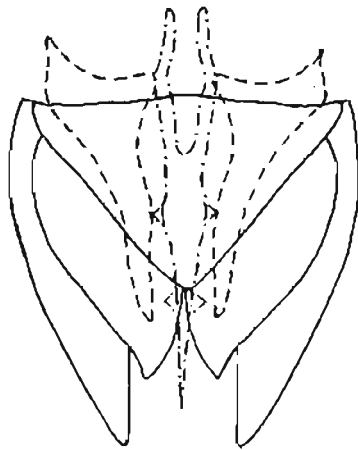
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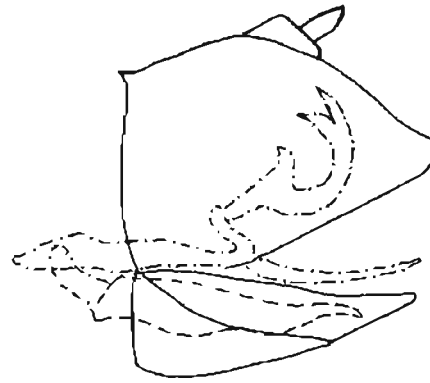
TEXANANUS LATIPEX



A



B



C



D

(For explanation of plate see page 14.)

EVIDENCE OF NONSPECIFIC TRANSMISSION OF
CALIFORNIA ASTER-YELLOWS VIRUS
BY LEAFHOPPERS

HENRY H. P. SEVERIN

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EVIDENCE OF NONSPECIFIC TRANSMISSION OF CALIFORNIA ASTER-YELLOWS VIRUS BY LEAFHOPPERS¹

HENRY H. P. SEVERIN²

INTRODUCTION

IT MAY BE NECESSARY to define two terms before proceeding with this paper. Specificity is the transmission of a particular virus by one or two closely related species of vectors. "When a virus can be transmitted only by one or two closely related insects and cannot be transmitted artificially (except by grafting) the insect transmission is considered obligatory" (Leach, 1940).³

Formerly it was assumed that a specific relation existed between each plant virus and its aphid vector. Among the viruses transmitted by aphids, specificity is now regarded as exceptional rather than common.

In the opinion of Smith (1937), a rather strong point in favor of a specific relationship between leafhopper and virus lies in the fact that certain plant viruses can be transmitted by only one species. Heretofore it has been assumed that the aster-yellows virus could be disseminated only by the aster leafhopper, *Macrostelus divisus* (Uhl.) = [*Cicadula sexnotata* (Foll.)], and by no other means except grafting and budding of the plant.

According to Kunkel (1926), the intimate and specific relation existing between the aster-yellows virus and its insect vector is important evidence that the causative entity is biological rather than chemical. Leach (1940) emphasizes the biological, obligatory, and highly specific transmission of viruses by leafhoppers.

There may be some viruses which can be transmitted by only one species of leafhopper. During the past thirty years many species of leafhoppers collected in sugar-beet fields were tested by the author for the transmission of the curly-top virus, but up to the present time no other vector is known except the beet leafhopper, *Eutettix tenellus* (Baker). According to DeLong (1942), the North American fauna of leafhoppers, north of Mexico, consists of 2,000 species belonging to about 150 genera. No other species of the genus *Eutettix* has been tested up to the present time. It is naturally assumed that closely related species in the same genus should be tested; on the other hand, species in genera belonging to different subfamilies may be vectors. The sugar beet is an introduced plant, and it may be possible that if leafhoppers are collected on native host plants of the virus, other vectors may be discovered. As will be discussed with aster yellows in this paper, host plants highly susceptible to the virus should be used instead of the sugar beet.

Herewith is presented evidence that the transmission of the aster-yellows virus by six species of phlepsid leafhoppers is not specific. The characters, distribution, and food plants of these six vectors are discussed in a companion paper (DeLong and Severin, 1945). It is evident in the following review of literature that the prevailing concept has in general favored specificity.

¹ Received for publication November 8, 1944.

² Entomologist in the Experiment Station.

³ See "Literature Cited" for complete citation, referred to in the text by author and date of publication.

REVIEW OF LITERATURE ON LEAFHOPPER-TRANSMITTED VIRUSES

Aster Yellows.—Severin (1929) reported the transmission of the California aster-yellows virus to celery, lettuce, and ornamental flowering plants by the short-winged aster leafhopper. Severin and Haasis (1934) showed that potato could be experimentally infected with the virus by means of the short-winged aster leafhopper. The virus was not recovered by previously noninfective leafhoppers from infected potato plants, nor from potato tubers obtained from plants showing symptoms of aster yellows. Severin (1940) proved that potato was naturally infected; also that the virus was recovered and transferred to healthy asters by the long-winged aster leafhopper, a race of the same species. Severin (1934) reported the transmission of the California aster-yellows virus by the mountain leafhopper, *Colladonus montanus* (V.D.) = (*Thamnotettix montanus* V. D.), and by the geminate leafhopper, *Idiodonus geminatus* (V. D.) = (*T. geminatus* V. D.). In a recent paper, Severin (1942) stated that the mountain and geminate leafhoppers are the most important vectors of the virus to delphinium, and that both species breed on this plant under natural conditions. Delphinium is an unfavorable food plant of the short-winged and long-winged aster leafhoppers; some of the insects feeding on the plant died within 4 to 6 hours, and most of them within 24.

Sugar-Beet Curly Top.—Ball (1906) associated the abundance of the beet leafhopper with curly top in the beet fields. Considerable controversy appears in the literature as to whether he was the first to prove that curly top was induced by this insect. He caged 14 beets in the field, introduced beet leafhoppers into 7 cages, and used 7 as controls (Ball, 1909). Cages 1 to 3 were failures; the insects escaped. Ball stated "Temperature and moisture could not be controlled and no curly top was produced in the remaining cages." In another experiment, 12 leafhoppers and their eggs stopped the growth of a beet in less than 2 weeks; and they together with their progeny killed it in less than 2 weeks more. A footnote reports the occurrence of curly top in cages arranged by T. G. Titus in joint investigations with Ball. Shaw (1910) demonstrated that the beet leafhopper caused curly top of sugar beets in cages in the field. The leafhopper occurs in British Columbia (Davis, 1927), western United States (Severin, 1933), Lower California (Severin and Henderson, 1928), and western Mexico as far south as Guasave, Sinaloa (California Agricultural Experiment Station, 1928).

Fawcett (1927) reported a similar curly-top disease of sugar beets in Argentina—a different strain of the virus, transmitted by the leafhopper *Agallia ensigera* Oman. This leafhopper was first determined as *Agallia sanguinolenta* (Prov.) by McAtee in 1928 and later (during the same year) as *A. sticticollis* Stal by Osborn and Ball. *A. sticticollis* is the species referred to by Fawcett (1925, 1927) and by Severin and Henderson (1928); but Oman (1934), examining numerous specimens from Fawcett and Henderson, failed to find Stal's species in any of the material. There seems to be at present no reason to believe that *A. sticticollis* occurs in the sugar-beet-growing regions of the Argentine Republic.

Pierce's Disease of Grapevine and Alfalfa Dwarf.—Hewitt, Frazier, and Houston (1942) reported that two undetermined species of leafhoppers in the genera *Draeculacephala* and *Carneocephala* transmitted the virus of Pierce's disease of grapevine. In a later paper Hewitt, Frazier, Jacobs, and Freitag (1942) named, as vectors of the virus, the green sharpshooter, *D. minerva* Ball; the redheaded sharpshooter, *C. fulgida* Nott.; and the blue-green sharpshooter, *Neokolla circellata* (Baker) = [*Cicadella circellata* (Baker)]. Frazier (1945) lists the following 6 additional species of leafhoppers as vectors: *Carneocephala triguttata* Nott., *Heliochara delta* Oman, *Neokolla gothica* (Sign.), *N. confluens* (Uhler), *N. heiroglyphica* (Sat.), and *Cuerna occidentalis* Oman & Beamer. All are species of the subfamily Amblycephalinae=(Cicadellinae), according to Medler (1942).

Alfalfa Witches'-Broom.—Menzies (1944) has presented evidence that the leafhopper *Platymoides acutus* Say is the vector of the virus of alfalfa witches'-broom. This disease occurs in Washington.

False Blossom of Cranberry.—Dobrosky (1929, 1931) demonstrated that the virus of false blossom of cranberries is transmitted by the blunt-nosed leafhopper, *Euscelis striatulus* Fall. The disease occurs wherever cranberries are grown in the United States.

Peach Yellows.—Kunkel (1933) proved that the vector of peach-yellows virus is the plum leafhopper, *Macropsis trimaculata* (Fitch). The dissemination of the virus in nature had defied the efforts of plant pathologists for forty-five years. Peach yellows is limited in its distribution to the eastern United States.

Potato Yellow Dwarf.—Black (1937) has proved that virus of potato yellow dwarf is transmitted by the clover leafhopper, *Acertatagallia sanguinolenta* (Prov.); and his findings were confirmed by Walker and Larson (1938). In a later paper Black (1941) reported that *A. sanguinolenta* carried a strain of virus from New York and that *Agallia constricta* V. D. transmitted a strain of virus from New Jersey. According to him, "the results indicate that there exists a high degree of specificity, perhaps an absolute specificity, in the relationship between the two varieties of virus and the two related leafhoppers."

Clover Club-Leaf.—In a recent paper, Black (1944) reported that *Agalliopsis novella* (Say) collected near Washington, D. C., transmitted two viruses to crimson clover; but in nature the diseases are unknown.

Dwarf or Stunt Disease of Rice.—The relation of leafhoppers to the dwarf disease of rice was first experimentally proved by Hatsuzo Hashimota, a local grower of Shiga prefecture, in 1884, according to Ishikawa (1928) on the authority of Katsura (1936). Takata (1895-96) concluded that among several leafhoppers investigated, *Deltocephalus dorsalis* Motsch. was not the vector of the virus causing dwarf disease of rice; but in his further investigations in 1900 Takata reported that only the rice leafhopper, *Nephotettix apicalis* Motsch. var. *cincticeps* Uhl., was capable of transmitting the virus. According to Fukushi (1937), Japanese plant pathologists have generally regarded the rice leafhopper as the sole agent that transmits the virus. In his studies on the relation of several species of leafhoppers to the transmission of the virus, *D. dorsalis* proved to be another vector. Dwarf of rice has been a serious disease in Japan for many years.

Agati, Sison, and Abolis (1941) demonstrated that the rice leafhopper, *Nephotettix bipunctatus cincticeps*, is also the vector of the virus of dwarf disease of rice in central Luzon.

Streak of Corn (Maize).—Storey (1925a, 1928) reported the transmission of the virus of corn by the maize leafhopper, *Cicadulina mbila* (China) = (*Balclutha mbila* Naude). Later he found that two other closely related species, *C. zeal* China and *C. storeyi* China, carry the virus (Storey, 1937). The most efficient vector is *C. mbila*. Evidently, 3 species of leafhoppers belonging to one genus transmit the virus. Streak of corn is a destructive disease in South Africa.

Mottle of Corn (Maize).—Storey (1937) discussed the transmission of the virus of mottle of corn by 3 species of leafhoppers—*Cicadulina mbila* Naude, *C. zeal* China, and *C. storeyi* China. He suggests that the mottle and streak viruses may be regarded as two strains of one virus. In his text and summary, however, he states: "The mottle virus is regarded as a new one, unrelated to that of streak disease." This is the first example of 2 viruses being transmitted by the same 3 species of leafhoppers. An insect already carrying one virus may also take up and transmit the other. The disease has been found in Tanganyika Territory.

Streak Disease of Sugar Cane.—Storey (1925b) reported that the virus of streak of sugar cane is spread only by the maize leafhopper, *Cicadulina mbila*. By feeding the leafhoppers on the tip of a single leaf of diseased sugar cane and then transferring them to the tip of a single leaf of healthy cane, he caused 5 to 19 plants to develop streak. The virus from corn caused only a transitory infection of sugar cane, from which the plant subsequently recovered. The virus from sugar cane produced in corn a permanent but mild form of streak disease. Storey and McClean (1930) concluded that the virus of corn streak and the virus of cane streak are not identical. Evidently, *C. mbila* transmits 3 viruses.

According to Storey (1926), attenuation of the virus of cane streak occurred in passage from sugar cane to corn by use of the maize leafhopper, *Cicadulina mbila*. The transfer of the virus to corn streak to cane caused only a few chlorotic stripes, and the foliage was healthy thereafter. The cane plants were therefore thought to have been infected by the virus from maize, but to have recovered from it.

Sugar-Cane Mosaic.—No leafhopper is known to transmit a mosaic virus up to the present time. Kunkel (1944) in a review of Bawden's (1943) book called attention to the fact that the virus of sugar-cane mosaic is disseminated by aphids, but is not known to be transmitted by any species of leafhopper. Brandes (1920), Ingram and Summers (1936), Ingram (1937), Ingram, Haley, and Charpentier (1939) reported that *Draeculacephala portola* Ball = [*D. mollipes* (Say) Abbott and Ingram (1942)], failed to transmit the virus of sugar-cane mosaic. The following species of aphids are vectors of the virus: corn aphid, *Aphis maidis* Fitch, reported by Brandes (1920), Kunkel (1922), and Chardon and Veve (1922); rusty plum aphid, *Hysteroneura setariae* (Thomas), reported by Ingram and Summers (1936), Ingram (1937), and Ingram, Haley, and Charpentier (1939); spring grain aphid, *Toxoptera graminum* Rond., reported by Ingram (1937), Ingram and Summers (1938),

and Ingram, Haley, and Charpentier (1939); and *Carolinaia cyperi* Ainslie, Tate, and Vanderberg (1939).

Chlorotic Streak of Sugar Cane.—Abbott and Ingram (1942) offer proof that the leafhopper *Draeculacephala portola* is a vector of the virus of chlorotic streak of sugar cane. The disease occurs in the Gulf states.

Yellow Dwarf of Tobacco.—According to Hill (1941), the leafhopper *Thamnotettix argentea* (Evans) is the vector of the virus of tobacco yellow dwarf in Australia.

Wallaby Ear Disease of Corn (Maize).—Schindler (1942) concluded that the leafhopper *Cicadula bimaculata* Evans is responsible for the wallaby ear disease, which is probably caused by a virus. He reported transmission to corn in 2 cages containing *C. bimaculata*; and in 4 of 5 cages containing *C. bimaculata* and the corn leafhopper (fulgorid) *Peregrinus maidis* Ash. In 1 cage containing *P. maidis*, the disease failed to develop.

Big Bud of Tomato.—Hill (1937, 1943) reported that the virus of big bud of tomato and tobacco yellow dwarf was transmitted by the leafhopper *Thamnotettix argentea* (Evans). The list of additional economic plants experimentally infected by *T. argentea* includes eggplant, pepper, sugar beet, white and red clover, also ornamental flowering plants and weeds, a total of 23 species of plants of 13 families. Evidently this leafhopper transmits two viruses. Big bud of tomato occurs in all the Australian states.

Ryjkoff (1935) and Ryjkoff and Karatchevsky (1935) consider tomato woodiness, virescence of tobacco flowers, belladonna, and weeds in the Crimea and Ukraine to be identical with big bud of tomato. They suggest that the leafhopper *Agallia sinuata* is responsible for its spread in the field.

Little-leaf of Eggplant.—Thomas and Krishnaswami (1939) reported that 2 species of leafhoppers disseminate a virus to eggplants. The virus was transmitted from diseased eggplants to 19 of 59 healthy plants by *Eutettix phycitis* Dis.; to 1 of 9 healthy plants by *Empoasca devastans* Dis. The disease causes considerable damage to the crop in south India, resulting in dwarfed leaves and sterility. Hill (1943) considers little-leaf of eggplant to be either the same as big bud of tomato or a closely related disease.

VIRUS TRANSMISSION EXPERIMENTS AND BIOLOGY OF *TEXANANUS LATHROPI* BAKER AND *T. LATIPEX* DELONG

A species of *Texananus* was collected on July 31, 1934, in miscellaneous sweepings on weeds, grasses, and ornamental flowering plants in South Canyon Nursery, near Montara, San Mateo County. A population was reared on celery infected with the California aster-yellows virus, but during the winter the leafhoppers died. This species proved to be *T. latipex* DeLong, described by DeLong (1943). Five years later 22 adults were collected by N. W. Frazier, on drying pasture vegetation in a mountainous area at an elevation of 1,800 feet near Trinité, Sonoma County, on April 25, 1939. A large population was reared on diseased celery. Adults were sent to P. M. Oman, Division of Insect Identification, Bureau of Plant Quarantine, Washington, D. C. Oman⁴ found a mixed population containing *T. lathropi* Baker and a new species. Before

⁴ P. M. Oman in a letter to the author, dated May 6, 1941.

he could publish a description of the latter, he joined the United States Army. He sent the leafhoppers to R. H. Beamer, University of Kansas, Lawrence, Kansas, for determination. Beamer forwarded the specimens to DeLong, who described the new species as *T. latipex*. Etherized females of the two species were separated from a mixed population by means of a binocular microscope, and the investigations were resumed.

A study was undertaken with the two species of leafhoppers to determine the efficiency of the vectors in transmitting the virus by single males and females, each kept on a healthy celery plant until symptoms of the disease developed, or for 2 months if no symptoms appeared. Varying numbers of adults were kept for different periods on healthy celery and asters and upon successive asters. Attempts were made to determine the latent period of the virus and the retention of the virus in the adults. The ability of the two leafhopper species to transmit the viruses of curly top and Pierce's disease of grapevine was also investigated. Life histories of the two phlepsid species were studied.

METHODS AND EQUIPMENT USED WITH THE TWO VECTORS

Etherized adult males and females of both species were segregated under a binocular microscope. The cages used and the method of transferring leafhoppers in a dark chamber have already been described (Severin, 1930, 1931). Repeated capturing of the leafhoppers results in a mortality and was therefore avoided in all experiments. During transfers of the adults to successive healthy celery plants, the clay pot on which the cage rested was jarred on the table in a dark chamber, and a breath of air was blown between the petioles to free the plant from leafhoppers.

TRANSMISSION OF CALIFORNIA ASTER-YELLOWS VIRUS

To Celery by Single Males and Females.—An experiment was conducted on the transmission of the virus by 150 males and 150 females of *Texananus lathropi*, each kept singly on a healthy celery plant. The males and females had completed the nymphal stages on diseased celery, requiring an average of 59.5 and 66.4 days, respectively, during January and February (table 10). Whenever an infected celery plant became unfavorable as food, the nymphs were transferred to a second diseased celery plant. A total of 300 adults were kept singly on healthy celery. The males infected 28 of 150 plants inoculated or 18.7 per cent and the females 24 of 150 plants or 16.0 per cent.

A similar test was made with 100 males and 100 females of *Texananus latipex*, each kept singly on a healthy celery plant. The males and females completed the nymphal stages on diseased celery, requiring an average of 52.6 days and 56.3 days, respectively, during February and March (table 10). The males infected 18 of 100 plants inoculated and the females 32 of 100 plants.

To Celery Alternating with Asters in Daily and Weekly Inoculations.—The transmission of the virus to successive celery and asters by each species of leafhopper was compared. Lots of 40 recently molted males or females, which had completed the nymphal stages on diseased celery, were transferred daily for 42 to 46 days to healthy celery alternating with asters. In a similar experi-

ment weekly inoculations were made alternately on celery and asters. Table 1 indicates the results.

As this table shows, when the males and females of *Texanonus lathropi* were transferred daily to celery alternating with asters, the males infected 20.2 and the females 11.4 per cent of the celery, respectively. When transferred weekly to celery alternating with asters, the males infected 50.0 and the females 45.8 per cent of the celery. Under the same conditions, transmission by *T. latipex* was as follows: daily transfers to celery, males 25.0 per cent and females 22.5; weekly transfers to celery, males 44.4 per cent and females 58.3. Evidently

TABLE 1

TRANSMISSION OF VIRUS TO CELERY ALTERNATING WITH ASTERS IN DAILY AND WEEKLY INOCULATIONS, BY ADULT *Texanonus lathropi* AND *T. latipex*

Number of lots	Species and number of adults in each lot	Celery			Asters			Adults alive at end of 6 weeks
		Plants inoculated	Plants infected	Per cent infected	Plants inoculated	Plants infected	Per cent infected	
Daily inoculations								
8	<i>T. lathropi</i> , 40 males.....	168	34	20.2	168	2	1.2	20-35
8	<i>T. lathropi</i> , 40 females.....	184	21	11.4	179	2	1.1	21-33
5	<i>T. latipex</i> , 40 males.....	116	29	25.0	113	4	3.5	18-33
6	<i>T. latipex</i> , 40 females.....	138	31	22.5	135	14	10.4	16-35
Weekly inoculations								
8	<i>T. lathropi</i> , 40 males.....	24	12	50.0	24	0	0.0	18-38
8	<i>T. lathropi</i> , 40 females.....	24	11	45.8	24	0	0.0	26-37
4	<i>T. latipex</i> , 40 males.....	18	8	44.4	18	2	22.2	35-39
4	<i>T. latipex</i> , 40 females.....	12	7	58.3	12	0	0.0	18-21

the period of exposure of healthy celery to the leafhoppers is important in the virus transmission.

A total of 347 asters were inoculated by lots of 40 males or females of *Texanonus lathropi* in daily transfers, and 4, or 1.2 per cent, were infected; but of 48 asters inoculated in weekly transfers, none showed any effect. In daily transfers, lots of 40 males or females of *T. latipex* inoculated 248 asters, infected 18 or 7.3 per cent in daily transfers. They infected 2 of 30 asters, or 6.7 per cent in weekly transfers.

To Asters Alternating with Celery in Daily and Weekly Inoculations.—The retention of the virus by single males and females of the two species of leafhoppers, to be discussed later, indicates that many leafhoppers cause only 1 infection apiece during adult life. For this reason, lots of 40 males and 40 females were transferred daily and weekly during a period of 6 weeks to asters alternating with celery, instead of celery alternating with asters as in the previous experiment. The results appear in table 2: lower percentages of infection were obtained in asters and celery in daily than in weekly transfers with both species of leafhoppers.

To Successive Celery Alternating with Asters, by Varying Numbers of Adults Reared on Infected Celery.—A study was made of the transmission of the virus by single males and by lots of 5, 10, and 20 males of *Texanonus latipex* reared on diseased celery and transferred to celery alternating with asters.

TABLE 2

TRANSMISSION OF VIRUS TO ASTERS ALTERNATING WITH CELERY IN DAILY AND WEEKLY INOCULATIONS, BY ADULT *Texanonus lathropi* AND *T. latipex*

Number of lots	Species and number of adults in each lot	Asters			Celery			Adults alive at end of 6 weeks
		Plants inoculated	Plants infected	Per cent infected	Plants inoculated	Plants infected	Per cent infected	
Daily inoculations								
4	<i>T. lathropi</i> , 40 males	84	9	10.7	84	28	33.3	20-23
5	<i>T. lathropi</i> , 40 females	105	5	4.8	105	29	27.6	21-30
12	<i>T. latipez</i> , 40 males	252	16	6.3	252	69	27.4	21-32
Weekly inoculations								
8	<i>T. lathropi</i> , 40 males	24	3	12.5	24	14	58.3	25-40
9	<i>T. lathropi</i> , 40 females	24	2	8.3	24	7	29.2	25-36
11	<i>T. latipez</i> , 40 males	27	4	14.8	27	16	59.3	20-36
8	<i>T. latipez</i> , 40 females	24	8	33.3	24	12	50.0	24-35

TABLE 3

TRANSMISSION OF VIRUS TO SUCCESSIVE CELERY ALTERNATING WITH ASTERS, BY VARYING NUMBERS OF ADULT *Texanonus latipex* REARED ON INFECTED CELERY

Number of lots	Number of males in each lot	Plants inoculated	Plants infected	Per cent infected	Plants inoculated	Plants infected	Per cent infected
100 50 50 50	1 5 10 20	First set of celery			First set of asters		
		100	11	11.0	100	1	1.0
		50	12	24.0	50	2	4.0
		50	37	74.0	50	18	36.0
		50	40	80.0	50	12	12.0
100 50 50 50	1 5 10 20	Second set of celery			Second set of asters		
	
		50	4	8.0	50	0	0.0
		50	17	34.0	50	5	10.0
		50	11	22.0	50	4	8.0

Each of the 100 males was kept on a healthy celery plant for 4 weeks and then was transferred to a healthy aster and kept there during adult life. Lots of 5, 10, and 20 males were changed weekly during a period of 4 weeks to successive celery plants alternating with asters. Table 3 shows the results.

One hundred males tested singly on celery and then on asters infected 11 celery plants and only 1 aster. Fifty lots of 5 males caused 24.0 per cent infec-

tions of celery; 50 lots of 10 males, 74 per cent; and 50 lots of 20 males, 80 per cent. Again the period of exposure of healthy celery to leafhoppers influenced virus transmission.

The percentages of infections with the second set of celery, the first and second sets of asters, show no progressive increase with lots of 5, 10, and 20 males; but lower percentages were obtained with lots of 5 than with lots of 10 and 20 males.

To Successive Asters Alternating with Celery, by Varying Numbers of Adults Reared on Infected Asters.—In the previous experiment the percentages of infection showed no progressive increase with varying numbers of

TABLE 4
TRANSMISSION OF VIRUS TO SUCCESSIVE ASTERS ALTERNATING WITH CELERY, BY VARYING
NUMBERS OF ADULT *Texananus latipex* REARED ON INFECTED ASTERS

Number of lots	Number of males in each lot	Plants inoculated	Plants infected	Per cent infected	Plants inoculated	Plants infected	Per cent infected
		First set of asters			First set of celery		
100	1	100	4	4.0	100	10	10.0
100	5	100	4	4.0	100	5	5.0
50	10	50	2	4.0	50	8	16.0
50	20	50	8	16.0	50	20	40.0
6	40	6	1	16.7	6	5	83.5
		Second set of asters			Second set of celery		
100	1
100	5	50	0	0.0	50	3	6.0
50	10	50	2	4.0	50	7	14.0
50	20	50	4	8.0	50	8	16.0
6	40	6	0	0.0	6	4	66.7

leafhoppers reared on infected celery; hence another experiment was conducted with males of *Texananus latipex* reared on diseased asters. Table 4 gives the results.

One hundred males each tested singly on healthy celery for 4 weeks, infected 10 celery plants, as compared with 11 plants in the previous experiment. In the first and second sets of celery there was a progressive increase in the percentages of infections obtained with lots of 5, 10, 20, and 40 males transferred weekly. Again there was no progressive increase in the percentages of infections with lots of varying numbers of adults in the first and second sets of asters. The number of leafhoppers, however, plays an important role in the transmission of virus to celery.

To Successive Asters by Adults Reared on Infected Asters.—In the experiment on the transmission of the virus to celery alternating with asters, no asters became infected by lots of 40 males or females of *Texananus latipex*, or by females of *T. latipex* in weekly inoculations (table 2). In the experiment on transmission to asters alternating with celery, the percentages of infections by both species of leafhoppers in weekly inoculations varied considerably. For this reason another experiment was inaugurated in which the period

of exposure on each successive aster was increased to 3 weeks with lots of 40 males or females of *T. latipex* reared on diseased asters. The results are indicated in table 5.

A total of 56 asters were inoculated by 10 lots of 40 males each, and 24 asters or 42.9 per cent were infected; and 27 of 55 asters or 49.1 per cent were infected by lots of 40 females (table 5). With both males and females, the highest percentages of infections were obtained with the first set of asters. As the results show, the period of exposure of healthy asters to infective adults affects the percentages of infections obtained.

TABLE 5
TRANSMISSION OF VIRUS TO SUCCESSIVE SETS OF ASTERS INOCULATED FOR THREE WEEKS,
BY ADULT *Texanonus latipex* REARED ON INFECTED ASTERS

Number of lots	Number of adults in each lot*	Plants inoculated	Plants infected	Per cent infected	Plants inoculated	Plants infected	Per cent infected
		First set of asters			Second set of asters		
10	40 males.....	10	10	100.0	10	4	40.0
10	40 females.....	10	8	80.0	10	6	60.0
		Third set of asters			Fourth set of asters		
10	40 males.....	10	5	50.0	10	3	30.0
10	40 females.....	10	4	40.0	10	4	40.0
		Fifth set of asters			Sixth set of asters		
10	40 males.....	9	0	0.0	7	2	28.6
10	40 females.....	8	1	12.5	7	4	57.1
		Total of all sets					
10	40 males.....	56	24	42.9			
10	40 females.....	55	27	49.1			

* Adults alive at the end of 12 to 18 weeks: males, 11-28; females, 15-35.

LATENT PERIOD OF VIRUS IN ADULTS

The literature on the so-called virus-incubation period in leafhoppers may be briefly reviewed. Smith and Bonquet (1915) were first to use the term "incubation period of the inciting agent of curly leaf" in connection with the beet leafhopper. Severin (1921) mentioned the "incubation period of the causative agent of curly leaf" in the same insect and later (1931) spoke of the "virus-incubation period." As pointed out by Bawden (1943), the term "incubation period" implies a fixed time during which the virus develops or multiplies. Storey (1939) wrote of "a delay in the development of infective ability," termed by other workers the "latent," "waiting," or "incubation period," and he coupled it with the retention of the virus by the vectors. Leach (1940) employs the term "latent period" in his textbook.

The latent period of the virus in the two species of leafhoppers was deter-

mined by using lots of 80 previously noninfective males or females, which were kept on diseased celery for 1 day. Daily transfers were made to successive healthy celery during a period of 41 days. The mortality of the adults by the end of 42 days was recorded. The results appear in table 6.

The minimum latent period of the virus in *Texananus lathropi*, using 80 males or females, was 7 and 8 days, respectively; in *T. latipex*, with 1 lot of 80 males, it was 8 days (table 6). The maximum latent period in *T. lathropi* was 33 days with 80 females; in *T. latipex*, 37 days with 80 males. Four lots of 80 adults of *T. lathropi* and 3 lots of *T. latipex* failed to transmit the virus.

TABLE 6
LATENT PERIOD OF VIRUS IN ADULTS OF TWO SPECIES OF PHLEPSIDS,
ON DISEASED CELERY

Days on infected celery	Successive plants inoculated	Plants infected	Per cent infected	Days after transfer on which successive infections occurred, including initial day on infected celery	Adults alive at end of 42 days
Two lots of 80 males each, <i>Texananus lathropi</i>					
1	41	15	36.6	7, 10, 13, 14, 16, 17, 20, 21, 22, 23, 25, 28, 30, 31, 42.	38
1	41	6	14.6	9, 13, 19, 20, 30, 35.	37
Four lots of 80 females each, <i>Texananus lathropi</i>					
1	41	8	19.5	8, 13, 14, 16, 19, 24, 30, 42.	28
1	41	3	7.3	11, 12, 14.	54
1	41	3	7.3	33, 37, 42.	25
1	41	2	4.9	14, 17.	58
Two lots of 80 males each, <i>Texananus latipex</i>					
1	41	17	41.5	8, 9, 12, 15, 16, 20, 22, 24, 26, 27, 29, 32, 36, 37, 39, 40, 41.	41
1	41	2	4.9	37, 39.	32

RETENTION OF VIRUS

By Varying Numbers of Adults.—To determine whether a longer period of exposure on diseased celery to varying numbers of adults is a factor in transmission of the virus, lots of 40, 20, and 10 males or females were kept on diseased celery for 8 days, and then each lot was transferred daily to healthy celery during 34 days (table 7).

As table 7 shows, two lots of 40 males and 1 lot of 20 males of *Texananus lathropi* produced 3 infections and 1 lot of 40 males caused 2 infections. Single infections occurred with 13 lots of 40, 20, and 10 adults of *T. lathropi* and 4 lots of 40 males of *T. latipex*. Evidently the number of leafhoppers kept on diseased celery for 8 days, and then transferred daily to healthy celery during a period of 34 days, determines the number of infections obtained. Seven lots of 40, 9 lots of 20, and 11 lots of 10 adults of *T. lathropi* and 6 lots of 40 and 4 lots of 20 males of *T. latipex* failed to cause infection.

Since 7 lots of 80 adults of *Texananus lathropi* produced 2 to 15 infections

TABLE 7

RETENTION OF VIRUS BY VARYING NUMBERS OF ADULT *Texananus lathropi* AND *T. latipex*

Days on infected celery	Successive plants inoculated	Plants infected	Per cent infected	Days after transfer on which successive infections occurred including 8 days on infected celery	Adults alive at end of 42 days
Five lots of 40 males each, <i>Texananus lathropi</i>					
8	34	3	8.8	10, 13, 31.....	35
8	34	3	8.8	21, 26, 31.....	18
8	34	2	5.9	39, 42.....	19
8	34	1	2.9	16.....	19
8	34	1	2.9	20.....	30
Four lots of 40 females each, <i>Texananus lathropi</i>					
8	34	1	2.9	15.....	14
8	34	1	2.9	20.....	28
8	34	1	2.9	30.....	33
8	34	1	2.9	36.....	28
Three lots of 20 males each, <i>Texananus lathropi</i>					
8	34	3	8.8	36, 41, 42.....	13
8	34	1	2.9	38.....	16
8	34	1	2.9	42.....	10
Two lots of 20 females each, <i>Texananus lathropi</i>					
8	34	1	2.9	35.....	17
8	34	1	2.9	41.....	15
Two lots of 10 males each, <i>Texananus lathropi</i>					
8	34	1	2.9	26.....	9
8	34	1	2.9	40.....	6
One lot of 10 females, <i>Texananus lathropi</i>					
8	34	1	2.9	34.....	6
Three lots of 40 males each, <i>Texananus latipex</i>					
8	34	1	2.9	13.....	29
8	34	1	2.9	34.....	20
8	34	1	2.9	40.....	26
One lot of 20 males, <i>Texananus latipex</i>					
8	34	1	2.9	17.....	16

(table 6) or an average of 5.3, in determining the latent period of the virus, it seemed desirable to increase the time spent on diseased celery. Two lots of 80 female *T. lathropi*, after completing the nymphal stages on infected celery, an average of 66.4 days (table 10), were provided with healthy celery for 41 days. Each of the 2 lots caused 23 infections, or 56.1 per cent. Again it is evident that the amount of virus obtained by the nymphs in a long period on diseased celery, and the number of adults used, influences the number of infections produced.

By Single Adults.—The retention of the virus was determined by single males and females of both species of leafhoppers, all of which completed the nymphal stages on infected celery. Each leafhopper was confined in a cage enclosing a healthy celery plant until symptoms developed and then was transferred daily to successive healthy celery plants during adult life. The results are indicated in table 8.

The virus was retained 5 to 77 days (males) or 62 days (females) by *Texananus lathropi*; 22 to 39 days (males) and 1 to 42 days (females) by *T. latipex*. Two adults of *T. lathropi* and 10 of *T. latipex* caused only 1 infection each. The period on the first plant is not included in the retention of the virus, since the adults were able to acquire the virus again.

ATTEMPTS TO TRANSMIT VIRUSES OF CURLY TOP AND PIERCE'S DISEASE OF GRAPEVINE

Because of the interest in two other prevalent viruses, attempts were made to transmit these by means of the two species of leafhoppers.

Fifty noninfective female *Texananus lathropi* and 50 noninfective male *T. latipex* were kept on curly-top beets for 2 days after which each lot was transferred to 10 successive healthy sugar beets. All beets remained healthy. At the end of 12 days, 43 females of *T. lathropi* and 40 males of *T. latipex* were alive.

Texananus lathropi failed to transmit the virus of Pierce's disease of grapevine to 10 healthy grapevines and 10 plants of common or Chilean alfalfa, *Medicago sativa* L.; and from alfalfa dwarf to 10 healthy grapevines and 10 alfalfa plants. *T. latipex* also failed to transmit that same virus to 5 healthy grapevines and 5 alfalfa plants and from alfalfa dwarf to 10 healthy grapevines and 5 alfalfa plants.

BIOLOGY OF TEXANANUS LATHROPI AND T. LATIPEX

DeLong and Severin (1945) have described the characters of the male and female *Texananus lathropi* and *T. latipex*. These closely related species can be readily distinguished by the U-shaped excavation (plate 1, A) which extends halfway through the last ventral segment of the female *T. lathropi* and by the V-shaped indentation (plate 1, B) of the posterior margin of the last sternite of *T. latipex*.

According to Osborn and Lathrop (1923), very few species of *Phlepsius* have been studied for life history; there is an opportunity for careful work in determining detail of habits, life history, and ecology.

Oviposition.—The eggs of *Texananus lathropi* are deposited in two rows in the petioles of celery (plate 1, C) or in the stems of aster plants. One egg of

TABLE 8
RETENTION OF VIRUS BY SINGLE ADULTS OF TWO SPECIES OF PHLEPSIDS
WITH CELERY AS THE HOST PLANT

Days on first plant before symptoms developed	Plants inoculated after first infection	Plants infected after first infection	Per cent infected after first infection	Days after first infection on which successive infections occurred	Longevity of adults, days
Six lots of single males, <i>Tezananus lathropi</i>					
28	77	12	15.6	37, 39, 41, 44, 47, 53, 55, 57, 58, 58, 68, 72, 77.....	105
29	24	6	25.0	4, 5, 6, 16, 17, 21.....	53
28	11	2	1.8	4, 5.....	39
29	80	1	1.2	72.....	109
29	86	1	1.2	10.....	115
28	79	0	0.0	0.....	107
Two lots of single females, <i>Tezananus lathropi</i>					
28	56	1	1.8	62.....	82
34	95	0	0.0	0.....	129
Eleven lots of single males, <i>Tezananus latipex</i>					
30	98	5	5.1	26, 27, 28, 36, 39.....	128
24	34	4	11.8	14, 32, 33, 34.....	58
28	28	1	3.6	28.....	58
23	76	1	1.3	22.....	99
30	80	0	0.0	0.....	110
30	59	0	0.0	0.....	89
40	57	0	0.0	0.....	27
24	41	0	0.0	0.....	65
28	41	0	0.0	0.....	69
30	19	0	0.0	0.....	49
26	15	0	0.0	0.....	41
Nine lots of single females, <i>Tezananus latipex</i>					
25	44	8	18.2	8, 10, 14, 23, 25, 29, 33, 37.....	69
32	103	7	9.8	2, 5, 19, 20, 30, 40, 42.....	135
36	29	1	3.4	29.....	65
33	28	1	3.6	14.....	61
45	2	1	50.0	2.....	47
21	1	1	100.0	1.....	22
44	70	0	0.0	0.....	114
42	51	0	0.0	0.....	93
42	51	0	0.0	0.....	93

one row is deposited between two eggs of the opposite row (plate 1, *D*). The petiole sometimes cracks when long rows of eggs are deposited. After inserting the egg in the petiole, the female secretes a liquid (which becomes white when dry) in the form of a papilla over each egg puncture. Sometimes the papilla terminates in a hairlike structure. The papillae covering two eggs in opposite rows are arranged in V shape. In hatching, the nymph often pushes off the papilla. After all the nymphs have emerged from two rows of eggs, the zigzag

arrangement of the openings of the egg punctures can readily be seen with a binocular microscope. The papilla is a secretion from the accessory glands and probably protects the eggs from parasites.

The eggs of *Texananus latipex* are deposited singly or in one short row. A quantity of accessory gland secretion covers the egg puncture and may be flattened against the petiole; or the papilla may be upright or vertical, terminating in a hair.

TABLE 9
DURATION OF EGG PERIODS AND DAILY EMERGENCE OF NYMPHS OF TWO
SPECIES OF PHELEPSIDS

Days from oviposition to hatching	Eggs deposited January 16-22; temperature: 72.8°-78.9°; mean 68.4° F		Eggs deposited February 15-19; temperature: 68.6°-77.1°; mean 60.5° F		Eggs deposited March 16-20; temperature: 67.6°-76.6°; mean 59° F		Eggs deposited April 16-19; temperature: 69.7°-79.7°; mean 60° F	
	Nymphs hatched	Percent-age of total hatched	Nymphs hatched	Percent-age of total hatched	Nymphs hatched	Percent-age of total hatched	Nymphs hatched	Percent-age of total hatched
<i>Texananus lathropi</i>								
19.....	65	5.2	34	19.0	1	2.3
20.....	4	1.7	360	29.0	71	39.7	5	11.6
21.....	68	29.3	375	30.0	45	25.1	17	39.5
22.....	62	26.7	241	19.4	24	13.4	13	30.2
23.....	60	25.9	163	12.3	4	2.2	7	16.3
24.....	22	9.5	35	2.8	1	0.6
25.....	13	5.6	8	0.6
26.....	3	1.3	3	0.2
Total.....	232		1,240		179		43	
<i>Texananus latipex</i>								
19.....	29	27.4
20.....	3	13.0	17	31.5	41	38.7	2	11.1
21.....	3	13.0	25	46.3	22	20.8	11	61.1
22.....	7	30.0	11	20.4	9	8.5	3	16.7
23.....	8	34.8	1	1.9	5	4.7	2	11.1
24.....	1	4.3
25.....	1	4.3
Total.....	23		54		106		18	

Egg.—The average length of eggs deposited by the two species of leafhoppers is 1.05 mm; the average width 0.28 mm. The eggs are translucent when first deposited. They are elongated and are narrower at one end than at the other. Near the hatching period, the compound eyes of the embryo become visible.

Egg Periods.—The egg periods of each species of leafhopper were determined from eggs deposited during 4 months from January to April, inclusive. Females of each species were confined in cages enclosing potted celery plants and were transferred daily to successive plants during a period of 3 to 7 days. The plants in which the eggs were deposited were covered with cages and ob-

TABLE 10
DURATION OF PERIODS BETWEEN MOLTS OF TWO SPECIES OF PHELEPSIDS

Sex and date hatched	Duration of stadia, days					
	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Total
<i>Texananus lathropi</i>						
Males:						
January 20.....	11	8	9	11	20	59
January 30.....	13	7	8	9	19	56
January 30.....	12	9	9	11	21	62
February 1.....	11	8	9	11	22	61
Average.....	11.7	8.0	8.7	10.6	20.6	59.6
Females:						
February 1.....	11	9	9	12	22	63
February 10.....	12	9	9	14	20	64
February 10.....	9	10	10	14	21	65
February 10.....	12	11	12	13	20	68
February 10.....	14	10	12	15	21	72
Average.....	11.6	9.8	10.4	13.6	20.8	66.4
<i>Texananus latipex</i>						
Males:						
February 4.....	10	9	8	10	19	56
February 11.....	13	9	11	12	14	59
March 5.....	15	10	6	8	13	52
March 6.....	12	9	6	7	13	47
March 7.....	12	10	7	8	12	49
Average.....	12.4	9.4	7.6	9.0	14.2	53.6
Females:						
February 4.....	10	9	8	10	19	56
February 4.....	10	11	9	11	15	56
February 4.....	11	10	10	12	17	60
February 7.....	12	12	11	15	23	73
February 9.....	12	9	9	12	18	60
February 11.....	13	9	11	12	14	59
February 11.....	12	9	10	13	17	61
March 4.....	7	11	13	9	14	54
March 5.....	10	8	10	9	17	54
March 5.....	13	12	6	12	15	58
March 6.....	12	9	6	8	15	50
March 7.....	9	10	7	8	11	45
March 7.....	10	10	7	9	13	49
Average.....	10.1	9.9	9.0	13.0	16.0	56.8

served daily for the hatching of nymphs. Eggs deposited during one day usually hatched over a period of several days. In an effort to measure the egg periods more accurately, a daily count of the nymphs hatched in each cage was taken, and the results of each monthly test were summed up and tabulated. The egg periods, with the number and percentage of nymphs that hatched, are indicated in table 9.

As this table shows, the egg periods of *Texananus lathropi* were longer with

eggs deposited in January and February than with those laid in March and April. In *T. latipex* the periods were longer with eggs deposited in January than with those dating from February, March, and April. *T. lathropi* produced more eggs than *T. latipex*, though approximately equal numbers of females were used. Conceivably, a higher percentage of the *T. lathropi* may have been at the egg-laying stage.

Period between Molts.—The interval or period between molts (stages or stadia) and the total duration of the nymphal stages of both species of leaf-

TABLE 11
AVERAGE MEASUREMENTS IN MILLIMETERS OF TWO SPECIES OF PHLEPSIDS
AFTER EACH MOLT

Nymphs and adults	Diameter, head across compound eyes		Length, head, thorax, and abdomen		Length, head to end of wings	
	Range	Mean	Range	Mean	Range	Mean
<i>Texananus lathropi</i>						
First instar.....	0.40-0.43	0.41	1.15-1.32	1.24
Second instar.....	0.53-0.57	0.55	1.62-2.16	1.81
Third instar.....	0.73-0.76	0.75	2.43-2.80	2.60
Fourth instar.....	0.94-1.03	0.99	2.97-3.40	3.16
Fifth instar.....	1.27-1.36	1.31	3.73-4.34	4.03
Adult male.....	1.39-1.44	1.42	4.43-5.41	5.02	4.59-5.20	4.97
Adult female.....	1.46-1.55	1.51	4.94-5.99	5.43	5.08-5.48	5.26
<i>Texananus latipex</i>						
First instar.....	0.39-0.40	0.40	1.15-1.38	1.25
Second instar.....	0.53-0.55	0.54	1.59-1.89	1.73
Third instar.....	0.66-0.71	0.69	1.89-2.48	2.21
Fourth instar.....	0.89-0.96	0.92	2.67-3.32	2.84
Fifth instar.....	1.17-1.31	1.24	3.43-4.10	3.80
Adult male.....	1.34-1.49	1.40	3.89-5.18	4.68	4.37-5.02	4.79
Adult female.....	1.35-1.51	1.45	4.43-5.55	4.99	4.78-5.35	5.00

hoppers is given in table 10. The males of *Texananus lathropi* required 56 to 62 days, an average of 59.5, to complete the nymphal stages; the females 63 to 72 days, an average of 66.4. To reach the adult stage, the males of *T. latipex* required 47 to 59 days, an average of 52.6; the females 45 to 73 days, an average of 56.3. With both species of leafhoppers, the total duration of the nymphal stages is shorter for males than for females.

Measurements.—Table 11 gives the average measurements for various parts of the body of ten specimens one day after each molt, together with measurements for the adults of both leafhopper species. As shown by the mean measurements, the nymphal instars, males, and females of *Texananus lathropi* are larger than those of *T. latipex*. The males of the two species are smaller than the females. The instars can be determined accurately from the measurements of the head across the compound eyes.

Color of Nymphal Instars.—Recently hatched nymphs of both species are white with pink compound eyes. A few hours after hatching, the nymphs of

both species become dark brown or black, with light areas of brown, yellow, and white that give them a mottled appearance (plate 2, *A* to *F*). The color patterns of the five instars of both species are almost identical; but, in general, the nymphs of *Texananus latipex* are darker than those of *T. lathropi*.

Color of Adults.—Adults of *Texananus lathropi* have a slight rosaceous tinge, a little more distinct on the elytrae than on the head and pronotum. Osborn and Lathrop (1923), who described the species, discuss the color pattern in detail. Two patterns occur with the males and females of *T. latipex*—dark-brown and light-brown forms, mottled with white and black (plate 2, *G, H, I, J*); details are given by DeLong (1943).

Mating.—An attempt was made to mate female *Texananus lathropi* with male *P. latipex* after the last molt, and female *T. latipex* with male *T. lathropi*. The experiment was repeated with 10 females of each species. Coition did not occur. Though eggs were deposited by some females, not a single nymph hatched. Evidently the two species will not cross or interbreed.

Preoviposition Period.—The period from the time the female reached the winged stage after the last molt until egg laying began was determined with each species. The preoviposition period of 2 females of *Tenananus lathropi* that passed through the last molt on January 17 and 20, was 40 and 44 days respectively. Two females that reached the winged stage on April 16 required 20 and 34 days. The preoviposition period of *T. latipex* that passed through the last molt on May 2 was 34 days; May 4, 16 days; and May 6, 23 days.

Egg-laying Capacity.—To determine how many eggs a single female of *Texananus lathropi* deposits during her adult life, 1 female and 1 to 5 males after the last molt were confined in each cage enclosing a large healthy celery plant. When the celery became unfavorable as food, the female and males were transferred to a second plant—sometimes to a third. The eggs were allowed to hatch; and the total number of nymphs removed from each cage would equal the egg-laying capacity, provided all the eggs hatched. The nymphs were removed twice a month from each cage. The numbers that hatched from eggs deposited by each of 5 females were as follows: 229, 231, 345, 369, and 395, or an average of 341. The numbers that hatched from eggs deposited by each of 4 female *T. latipex* were as follows: 140, 171, 180, and 208, or an average of 175.

VIRUS TRANSMISSION EXPERIMENTS WITH *TEXANANUS SPATULATUS* VAN DUZEE (Plate 3, *C, D*)

A study was undertaken on the possibility of transmitting the virus during the nymphal stages. To determine the efficiency of the vector, virus-transmission experiments were conducted with single males and females; varying numbers of adults were tested on healthy celery and asters, and upon successive asters. Attempts were made to determine the latent period of the virus in the adults, and the ability of this insect to transmit the viruses of curly top and Pierce's disease of grapevine.

The characters, distribution, and food plants of *Texananus spatulatus* have already been discussed by DeLong and Severin (1945).

EXPERIMENTAL METHODS

In the transmission studies of the California aster-yellows virus, adults were used that had completed the nymphal stages on infected celery, and sometimes on asters. If leafhoppers were not reared, then the adults were fed on diseased celery for 10 days or longer to complete the latent period of the virus. Noninfective *Texanonus spatulatus* were obtained by allowing females

TABLE 12
TRANSMISSION OF VIRUS TO CELERY BY VARYING NUMBERS OF NYMPHS OF
Texanonus spatulatus

Number of lots	Number of nymphs in each lot	Days on infected celery	Days on healthy celery	Celery		
				Plants inoculated	Plants infected	Per cent infected
Stadium I						
3	5	3	3	3	0	0.0
2	5	4	4	2	0	0.0
3	10	3	3	3	0	0.0
2	10	4	4	2	0	0.0
Stadium II						
2	5	11	6	2	2	0.0
3	5	12	7	3	3	0.0
2	10	11	6	2	2	100.0
3	10	12	7	3	3	100.0
2	20	10	8	2	2	100.0
3	20	11	7	3	3	100.0
4	20	12	8	4	4	100.0
Stadium III						
2	5	20	10	2	2	100.0
3	10	20	10	3	3	100.0
2	20	20	10	2	2	100.0
Stadium IV						
2	5	30	30	2	2	100.0
1	10	30	30	1	1	100.0
1	20	30	30	1	1	100.0

to oviposit in healthy sugar beets, immune to aster yellows; and the nymphs that hatched were transferred to healthy celery. Because sugar beets are not a favorable food plant of this insect, many nymphs failed to reach the adult stage.

TRANSMISSION OF VIRUS TO CELERY

By Varying Numbers of Nymphal Instars.—An experiment was conducted to determine whether each nymphal instar could transmit the virus. Lots consisting of varying numbers of each instar were fed during varying periods

on infected and healthy celery. As the results show (table 12), the first instar was not able to transmit the virus, whereas each lot of the second (with 2 exceptions), third, and fourth instars infected healthy plants.

By Single Males and Females.—A comparison was made of the transmission of the virus by single male and female leafhoppers. After the adults had remained on diseased celery for 30 days, each leafhopper was fed on healthy celery until the plant manifested symptoms or until the insect died. As table 13 shows, 34 of 100 males and 29 of 100 females transmitted the virus to healthy plants.

By Varying Numbers of Adults.—A comparison was made of the infections produced by 5 males and 5 females that had completed the nymphal stages on diseased celery. Each lot of adults was transferred to a healthy celery

TABLE 13
TRANSMISSION OF VIRUS TO CELERY BY VARYING NUMBERS OF ADULT
Texananus spatulatus

Number of lots	Number of adults in in each lot	First set of celery			Second set of celery		
		Plants inoculated	Plants infected	Per cent infected	Plants inoculated	Plants infected	Per cent infected
100	1 male.....	100	34	34.0
100	1 female.....	100	29	29.0
25	5 males.....	25	22	88.0	15	6	40.0
25	5 females.....	25	18	72.0	8	4	50.0

plant and kept there until symptoms developed; then the surviving adults were transferred to a second healthy celery plant.

Table 13 shows the results obtained. The virus was transmitted to the first set of healthy celery by 22 of 25 lots of 5 males, or 88.0 per cent; and to 6 of 15 of the second set of plants, or 40 per cent. It was transmitted to the first set of celery by 18 of 25 lots of 5 females, or 72.0 per cent; and to 4 of 8 plants of the second set, or 50.0 per cent.

TRANSMISSION OF VIRUS TO ASTERS ALTERNATING WITH CELERY

A comparison was made of the transmission of the virus to healthy asters and celery. Five lots of 40 males and 5 lots of 40 females, which had completed the nymphal stages on infected celery, were transferred daily or weekly to successive healthy asters alternating with celery (table 14).

The percentages of celery plants infected were as follows: daily, by males 28.7 per cent, by females 17.3 per cent; weekly, by males 80.0 per cent, by females 23.1 per cent. Since lower percentages of infections were obtained in daily than in weekly transfers, evidently the period of exposure of the leafhoppers on healthy celery is a factor in virus transmission. In daily and weekly transfers of the males and females, only 1 aster was infected, and that was by daily transfers of the males (table 14).

TRANSMISSION OF VIRUS TO ASTERS

In the experiment on the transmission of the virus to asters alternating with celery in daily and weekly transfers, only 1 aster was infected of 188 inoculated (table 14). For this reason, the period of exposure on each aster was increased. Fifty lots of 5 males or 5 females that had completed the

TABLE 14
TRANSMISSION OF VIRUS TO ASTERS ALTERNATING WITH CELERY, BY ADULT
Texananus spatulatus

Number of lots	Number of adults in each lot	Asters			Celery		
		Plants inoculated	Plants infected	Per cent infected	Plants inoculated	Plants infected	Per cent infected
Daily inoculations							
5	40 males.....	79	1	1.3	80	23	28.7
5	40 females.....	81	0	0.0	81	14	17.3
Weekly inoculations							
5	40 males.....	15	0	0.0	15	12	80.0
5	40 females.....	13	0	0.0	13	3	23.1

TABLE 15
TRANSMISSION OF VIRUS TO ASTERS BY VARYING NUMBERS OF ADULT
Texananus spatulatus

Number of lots	Number of adults in each lot	Plants inoculated	Plants infected	Per cent infected
50	1 male.....	50	0	0.0
50	1 female.....	50	0	0.0
25	5 males.....	25	2	8.0
25	5 females.....	25	3	12.0
5	40 males.....	59	1	1.7
5	40 females.....	150	1	0.7

nymphal stages on diseased celery were transferred and kept on healthy aster until they died. Two of 25 asters, or 8.0 per cent, were infected by lots of 5 males; 3 of 25 asters, or 12 per cent, by lots of 5 females (table 15). Possibly if the adult life on asters had been longer, a higher percentage of infection would have resulted.

It was decided to rear the leafhoppers on diseased asters instead of celery. Ten lots of 40 males or females were transferred daily to successive healthy asters during adult life. One of 59 asters, or 1.7 per cent, was infected by the males; and 1 of 150 asters, or 0.7 per cent, by the females (table 15).

Fifty recently molted males and 50 females reared on infected asters were transferred singly to healthy asters. No aster yellows developed.

LATENT PERIOD OF VIRUS IN ADULTS

The latent period of the virus was determined with lots of 40 males or females. After 1 day on infected celery, the adults were transferred daily to successive healthy celery plants throughout a period of 41 days. The mortality of the adults at the end of 42 days was recorded (table 16). The minimum latent period of the virus was 6 days; the maximum, 35 days. Only 18 of the 410 celery plants inoculated, or 4.4 per cent, became infected. This low percentage can be explained by the fact that each healthy plant was exposed to the adults for 1 day. One lot of males and 1 lot of females failed to transmit the virus.

TABLE 16
LATENT PERIOD OF VIRUS IN ADULTS OF *Texananus spatulatus* WITH CELERY
AS THE HOST PLANT

Days on infected celery	Successive plants inoculated	Plants infected	Per cent infected	Days after transfer on which successive infections occurred, including initial day on infected celery	Adults alive at end of 42 days
Four lots of 40 males each					
1	41	3	7.3	6, 19, 35.....	29
1	41	3	7.3	12, 14, 15.....	16
1	41	1	2.4	33.....	21
1	41	1	2.4	35.....	37
Four lots of 40 females each					
1	41	3	7.3	17, 18, 29.....	22
1	41	3	7.3	23, 41, 42.....	26
1	41	2	4.9	16, 19.....	30
1	41	2	4.9	18, 27.....	11

RETENTION OF VIRUS

By Varying Numbers of Adults.—To determine whether a longer period of exposure on diseased celery is a factor in transmission of the virus by varying numbers of leafhoppers, lots of 20, 10, and 5 adults were kept on infected celery for 8 days and then were transferred daily to healthy celery for 34 days (table 17). Nine lots of 20 males and females infected 23 of 306 plants inoculated, or 7.5 per cent; 9 lots of 10 males and females infected 39 of 306 plants, or 12.4 per cent; and 4 lots of 5 males infected 4 of 136 plants, or 2.9 per cent. The latent period of the virus with lots of 20, 10, and 5 adults cannot be determined accurately; since the insects were kept on diseased celery for 8 days, it is not known whether they picked up the virus on the first day or later.

By Single Adults.—The retention of the virus was determined by use of single males and females, each of which had completed the nymphal stages on diseased celery. Each leafhopper was kept on a healthy celery plant until the latter showed symptoms; then the insect was transferred daily to successive healthy celery plants throughout its adult life. Table 18 shows the results.

One male retained the virus for 84 days, and 1 female for 99 days. Seven males and 6 females produced only 1 infection. The first infection is not included in the retention of the virus, since the adults were able to pick up the virus again.

TABLE 17

RETENTION OF VIRUS BY VARYING NUMBERS OF ADULT *Texanonus spatulatus*

Number of adults in each lot	Days on infected celery	Successive plants inoculated	Plants infected	Per cent infected	Days after transfer on which successive infections occurred, including initial day on infected celery	Adults alive at end of 42 days
Five lots of 20 males each						
20	8	34	5	14.7	37, 39, 40, 41, 42.....	14
20	8	34	3	8.8	9, 11, 15.....	6
20	8	34	1	3.0	13.....	9
20	8	34	1	3.0	25.....	7
20	8	34	1	3.0	39.....	9
Four lots of 20 females each						
20	8	34	6	17.6	16, 24, 28, 32, 34, 36.....	9
20	8	34	3	8.8	11, 12, 15.....	5
20	8	34	2	5.9	12, 41.....	17
20	8	34	1	3.0	31.....	13
Five lots of 10 males each						
10	8	34	12	35.3	10, 11, 17, 23, 24, 29, 30, 33, 34, 37, 39, 42...	8
10	8	34	7	20.6	14, 30, 31, 32, 34, 38, 40.....	10
10	8	34	5	14.7	9, 10, 38, 40, 41.....	8
10	8	34	4	11.8	22, 23, 33, 35.....	4
10	8	34	3	8.8	25, 28, 35.....	6
Four lots of 10 females each						
10	8	34	4	11.8	28, 35, 38, 40.....	9
10	8	34	2	5.9	31, 41.....	6
10	8	34	1	3.0	38.....	6
10	8	34	1	3.0	39.....	5
Four lots of 5 males each						
5	8	34	1	3.0	9.....	4
5	8	34	1	3.0	30.....	3
5	8	34	1	3.0	32.....	3
5	8	34	1	3.0	39.....	5

ATTEMPTS TO TRANSMIT VIRUSES OF CURLY TOP AND PIERCE'S DISEASES OF GRAPEVINE

An attempt was made to transmit the curly-top virus by means of *Texanonus spatulatus*. Fifteen lots of 5 to 20 males or females reared during the nymphal stages on nettleleaf goosefoot (sowbane), *Chenopodium murale*, were exposed to curly-top beets for periods varying from 2 to 14 days; and then each lot was transferred to a healthy beet. All beets remained healthy.

An attempt was made to transmit and recover the curly-top virus from susceptible host plants on which *Texananus spatulatus* were collected in the field. Noninfective leafhoppers after feeding on 2 nettleleaf goosefoot plants and 2 rough pigweeds, *Amaranthus retroflexus*, inoculated by infective beet leafhoppers, failed to recover the virus and transmit it to healthy sugar beets.

In another test 135 adults collected on pasture vegetation on the summit of Pacheco Pass on May 5, 1942, were distributed on 3 curly-top beets and kept

TABLE 18
RETENTION OF VIRUS BY SINGLE ADULTS OF *Texananus spatulatus* WITH
CELERY AS THE HOST PLANT

Days on first plant before symptoms developed	Plants inoculated after first infection	Plants infected after first infection	Per cent infected after first infection	Days after first infection on which successive infections occurred	Longevity of adults, days
Ten lots of single males					
39	105	0	5.7	14, 17, 30, 37, 38, 39.....	144
46	95	4	4.2	26, 54, 63, 84.....	141
46	36	2	5.6	14, 27.....	82
34	98	0	0.0	132
39	21	0	0.0	60
26	14	0	0.0	40
41	12	0	0.0	53
27	50	0	0.0	77
31	4	0	0.0	35
23	2	0	0.0	25
Eight lots of single females					
31	169	4	2.3	45, 62, 79, 99.....	200
36	95	3	3.2	26, 35, 60.....	130
28	131	0	0.0	158
45	102	0	0.0	147
37	35	0	0.0	72
31	12	0	0.0	43
34	4	0	0.0	38
27	1	0	0.0	28

there for 2 days; then each lot was transferred to a healthy sugar beet. All beets remained healthy.

Lots of 20 adults of *Texananus spatulatus*, after feeding on Pierce's disease of grapevines, failed to transmit the virus to 6 healthy grapevines and 5 common or Chilean alfalfa plants, and from alfalfa dwarf to 5 healthy grapevines and to 5 alfalfa plants.

There was no evidence to show that the beet leafhopper, *Eutettix tenellus* (Bakers), could transmit the curly-top virus to healthy grapevines. Severin (1928) demonstrated that Hairy Peruvian alfalfa, *Medicago sativa* L., was naturally and has been experimentally infected with curly top. The beet leafhopper failed to transmit the virus of Pierce's disease of grapevine to healthy grapevines and alfalfa.

TEXANANUS PERGRADUS DeLONG AS A VECTOR(Plate 3, *E, F*)

This phlepsid leafhopper has been collected on a variety of food plants, as shown by DeLong and Severin (1945). It has been reared on celery infected with aster yellows, but few nymphs reached the adult stage.

Adults that completed the nymphal stages on infected celery were transferred singly to healthy celery. If symptoms of the disease developed, the insects were fed on one or more additional plants. Single males and females each transferred to one or more healthy celery plants transmitted the virus to 5 of 14 and 11 of 22 plants respectively (table 19). In other tests, adults collected in the field were kept on infected celery for 10 days or longer to complete the latent period of the virus, before transferring to healthy plants. Lots of 2 to 10 adults infected 12 of 31 plants inoculated as shown in table 19.

TABLE 19
TRANSMISSION OF VIRUS TO CELERY BY VARYING NUMBERS OF ADULT
Texananus oregonus

Males					Females				
Number of lots	Number of adults in each lot	Plants inoculated	Plants infected	Per cent infected	Number of lots	Number of adults in each lot	Plants inoculated	Plants infected	Per cent infected
8	1	14	5	35.7	11	1	22	11	50.0
1	2	7	1	14.3	1	2	12	2	16.7
1	3	1	1	100.0	2	3	2	1	50.0
4	10	4	4	100.0	2	5	4	2	50.0
..	1	10	1	1	100.0

TEXANANUS PERGRADUS DeLONG AS A VECTOR(Plate 3, *G, H*)

This leafhopper was reared on celery infected with aster yellows from 12 males and 14 females collected on May 4, 1940, on pasture vegetation along a riverbank at Woodlake, Tulare County. The characters, distribution, and food plants are reported by DeLong and Severin (1945).

Fifty males and 50 females tested singly on healthy celery failed to cause infection, but 1 aster was infected by 1 of 50 males as is shown in table 20. Twelve lots of 10, 25 lots of 20, and 5 lots of 40 males produced 1, 5, and 1 infections as indicated in table 20.

PHLEPSIUS APERTINUS OSBORN AND LATHROP AS A VECTOR(Plate 3, *A, B*)

This leafhopper is common in alfalfa fields. The characters, distribution, and food plants have been discussed by DeLong and Severin (1945). The insect has not been reared on any host plant up to the present time.

Adults collected in the field were kept on diseased celery for 10 days or

TABLE 20
TRANSMISSION OF VIRUS TO CELERY AND ASTERS BY VARYING NUMBERS OF ADULT
Texanonus pergradus

Males					Females				
Number of lots	Number of adults in each lot	Plants inoculated	Plants infected	Per cent infected	Number of lots	Number of adults in each lot	Plants inoculated	Plants infected	Per cent infected
Celery									
50	1	50	0	0.0	50	1	50	0	0.0
12	5	12	0	0.0	2	5	2	0	0.0
12	10	12	1	8.3	1	10	1	0	0.0
25	20	25	5	20.0	3	20	3	0	0.0
5	40	48	1	2.1	5	40	45	0	0.0
Asters									
2	40	50	1	2.0	2	40	50	0	0.0

TABLE 21
TRANSMISSION OF VIRUS TO CELERY BY VARYING NUMBERS OF ADULT
Phlepsiis apertinus

Males					Females				
Number of lots	Number of adults in each lot	Plants inoculated	Plants infected	Per cent infected	Number of lots	Number of adults in each lot	Plants inoculated	Plants infected	Per cent infected
9	1	13	7	53.8	10	1	14	8	57.1
1	2	1	0	0.0	1	5	2	0	0.0
1	5	1	0	0.0	1	8	2	1	50.0
1	9	1	1	100.0	9	20	12	5	41.7
1	10	1	1	100.0	1	25	5	1	20.0
1	12	2	2	100.0	1	30	1	1	100.0
1	13	2	0	0.0
1	14	3	2	66.7
1	15	1	0	0.0
3	20	3	0	0.0

longer to complete the latent period of the virus. Males and females tested singly on healthy celery plants transmitted the virus to 7 of 13, and 8 of 14 plants respectively. Lots of 2 to 30 adults produced 14 infections as shown in table 21.

SUMMARY

Six newly demonstrated vectors of the California aster-yellows virus are reported in this paper; this proves that the virus is not transmitted by a specific leafhopper.

Texananus lathropi and *T. latipex*: The infections produced by 150 males and 150 females of *T. lathropi*, each kept singly on a healthy celery plant, was 18.7 and 16.0 per cent respectively, and by 100 males and 100 females of *T. latipex* was 18.0 and 32 per cent respectively.

Lots of 40 males or females of both leafhopper species, placed on celery alternating with asters, caused lower percentages of infections in celery in daily than in weekly transfers, a fact indicating that the period of exposure of healthy celery to the leafhoppers affects virus transmission. Lower percentages of infections occurred with asters than with celery; and, with one exception, lower percentages of asters were infected in daily than in weekly transfers. Higher percentages of infections occurred with 6 successive asters inoculated by *Texananus latipex* every 3 weeks than in daily inoculations or, with one exception, weekly inoculations—a fact again demonstrating that the period of exposure of asters to leafhoppers influences virus transmission.

Since there was an increase in the percentages of infections in celery with lots of 5, 10, and 20 adults, apparently the number of leafhoppers play a role in virus transmission.

The minimum latent period of the virus in the males and females of *Texananus lathropi* was 7 and 8 days respectively; in *T. latipex* with 1 lot of 80 males it was 8 days. The maximum latent period in *T. lathropi* was 33 days; in *T. latipex*, 37 days.

The virus was retained by single adults of *Texananus lathropi* from 5 to 77 days and by *T. latipex* from 1 to 42 days after the first infection was produced. Many of the leafhoppers of both species caused only 1 infection each.

Attempts to transmit the viruses of curly top and Pierce's disease of grape-vine by means of the two species of leafhoppers were failures.

Life history studies were made of the egg periods, egg-laying capacity, and duration of the nymphal instars.

Texananus spatulatus: The aster-yellows virus was not transmitted by the first nymphal instar; probably the latent period of the virus was not completed. All other nymphal instars transmitted the virus.

Single males infected 34 per cent of the celery, and single females 29 per cent. Lots of 5 males transmitted the virus to 88.00 per cent and lots of 5 females to 72.0 per cent of the first set of celery and to 40.0 and 50.0 per cent of the second set respectively.

Lots of 40 males and 40 females infected 28.7 and 17.3 per cent respectively in daily transfers to successive celery plants, and 80.0 and 23.1 per cent in weekly transfers. Only 0.6 per cent of the asters were infected in daily transfers and none in weekly transfers to successive asters.

Lots of 5 males and 5 females kept on asters during adult life infected 8.0 and 12.0 per cent of the asters respectively. Lots of 40 males and 40 females reared on diseased asters infected 1.7 and 0.7 per cent, respectively, in daily transfers to successive asters.

The latent period of the virus in the adults was 6 to 42 days.

One male retained the virus for 84 days, and one female 99 days. Most adults caused one infection and then apparently lost the infective dose.

All attempts to transmit the curly-top virus by means of *Texananus spatulatus* were failures. The leafhopper did not recover the virus from susceptible host plants on which they were collected in the field, such as *Chenopodium murale* and *Amaranthus retroflexus*, and transmit it to healthy sugar beets. This leafhopper failed to transmit the virus of Pierce's disease of grapevine and alfalfa dwarf to healthy grapevine seedlings and alfalfa.

There was no evidence that the beet leafhopper could transmit the curly-top virus to healthy grapevine seedlings or the virus of Pierce's disease of grapevine to healthy grapevines and alfalfa.

Texananus oregonus: Males and females tested singly on healthy celery infected 5 of 14 plants and 11 of 22 plants respectively. Lots of 2 to 10 adults infected 18 to 34 plants inoculated.

Texananus pergradus: 100 males and females kept singly on healthy celery caused no infections, but 1 aster was infected by 1 of 50 males. Twelve lots of 10, 25 lots of 20, and 5 lots of 40 males produced 1, 5, and 1 infection.

Phlepsius apertinus: With this species, 13 males and 12 females infected 7 of 13 and 8 of 14 celery plants respectively. Lots of 2 to 30 adults produced 14 infections.

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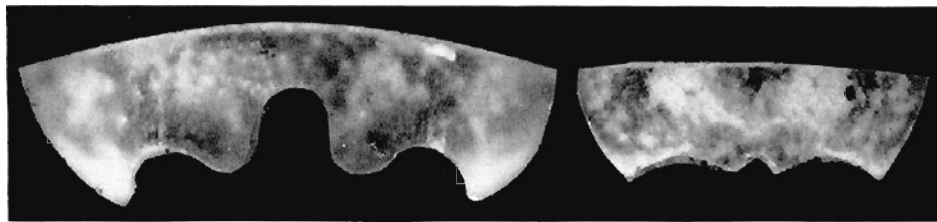
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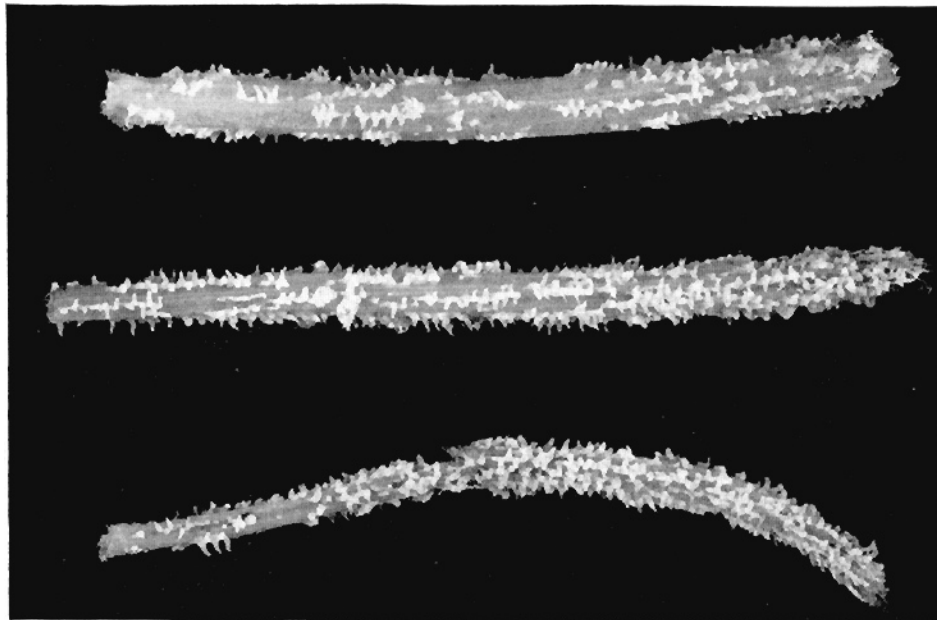
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PLATES

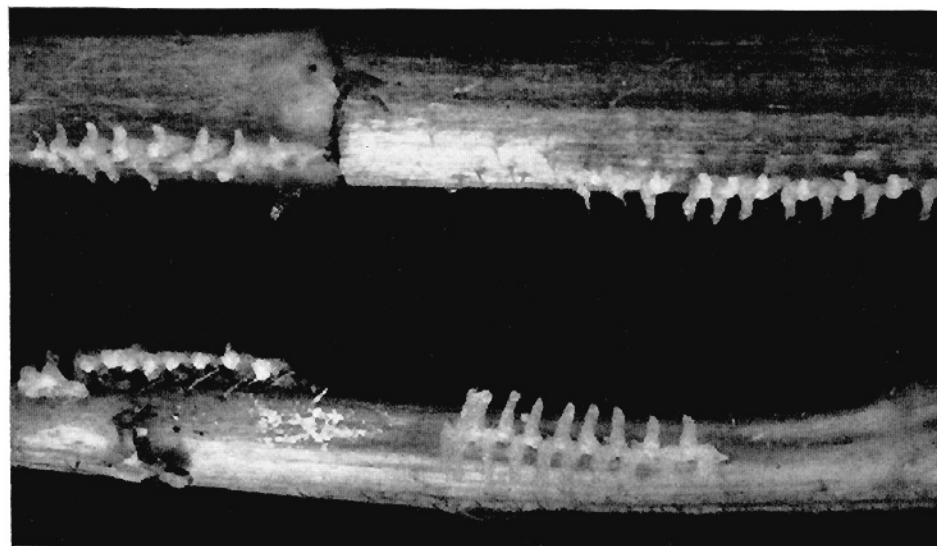


A

B



C



D

Plate 1.—A, Last sternite of female *Texanonus lathropi* Baker, showing U-shaped indentation that extends halfway through the last ventral segment; B, last sternite of female *T. latipex* DeLong, showing V-shaped indentation of the posterior margin of the last ventral segment; C, white papillae covering the egg punctures of *T. lathropi* in the petioles of celyery; D, papillae (enlarged) covering alternating egg punctures in two opposite rows.

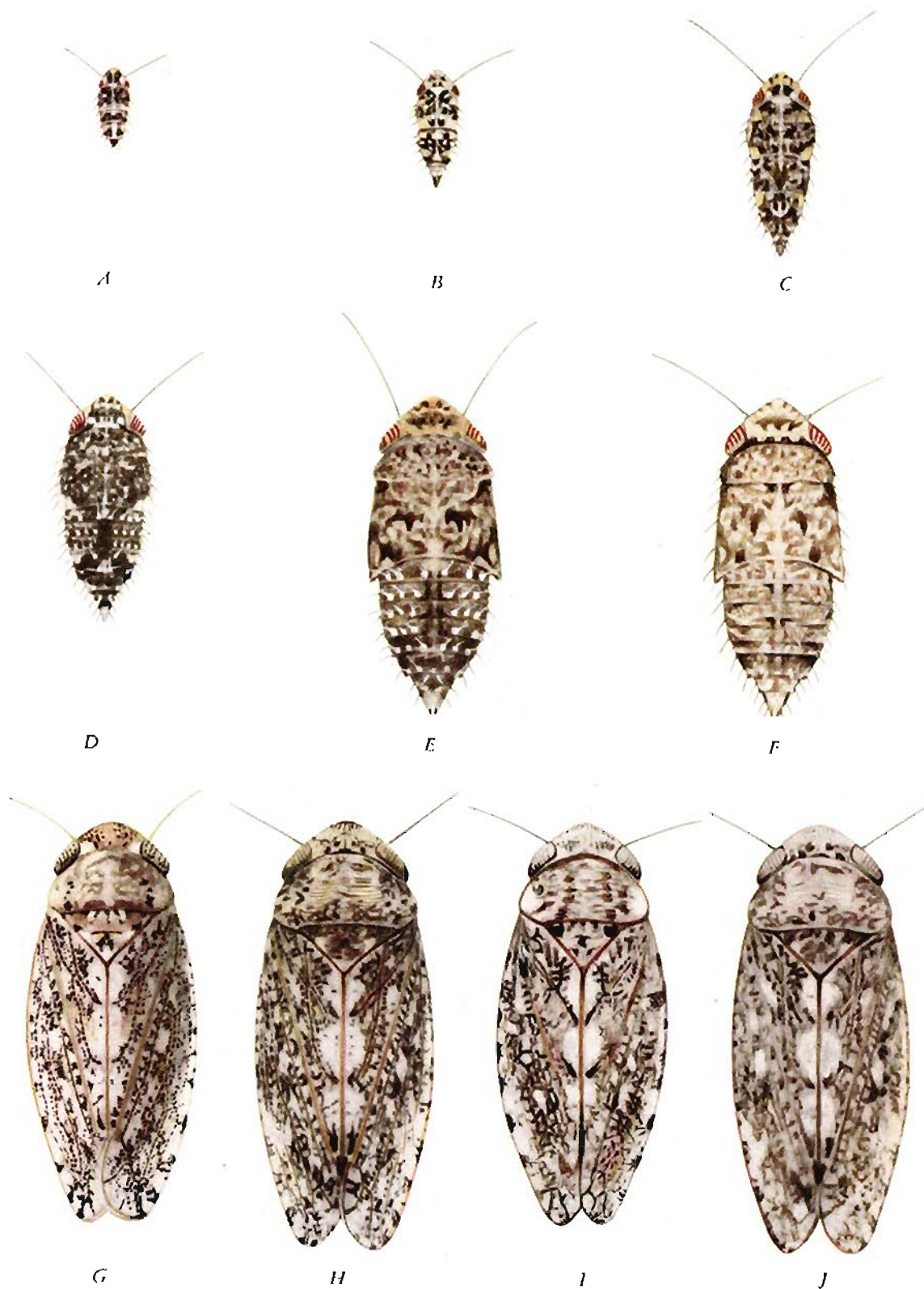


Plate 2.—Color patterns of nymphal instars and adults of *Texanonus latipex* DeLong: A, B, C, D, E, first to fifth nymphal instars; F, brown fifth instar, paler than fifth instar E; G, male, H, female, dark forms; I, male, J, female, hyaline forms.

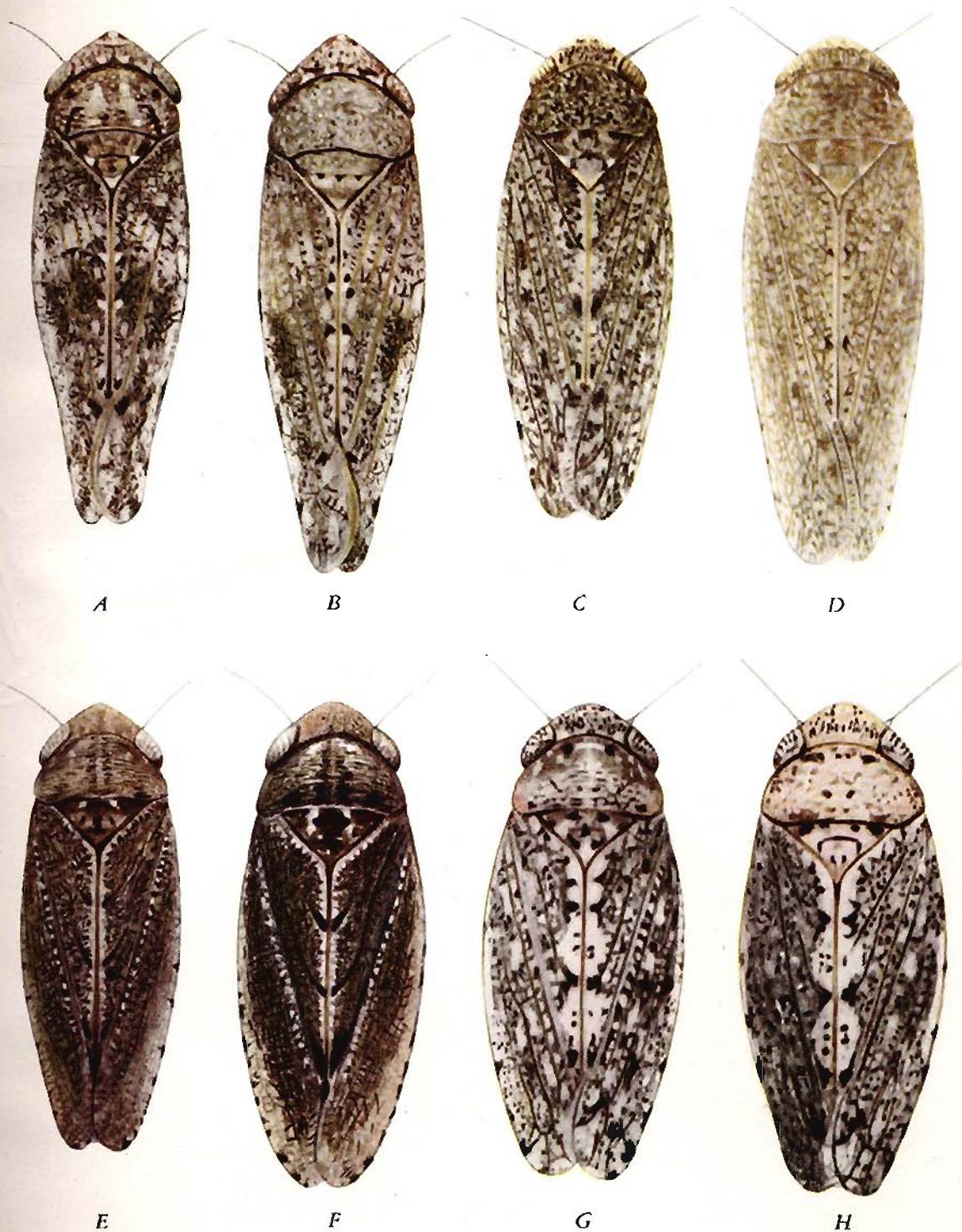


Plate 3.—A, Male, B, female *Phlepsius apertinus* Osborn and Lathrop; C, male, D, female *Texananus spatulatus* Van Duzee; E, male, F, female *Texananus oregonus* Ball; G, male, H, female *Texananus pergradus* DeLong.

