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CONTENTS

BIOLOGY OF THE MEALY PLUM APHID, HYALOPTERUS PRUNI (GEOFFROY)

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BIOLOGY OF THE MEALY PLUM APHID, *HYALOPTERUS PRUNI* (GEOFFROY)¹

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Hyalopterus pruni (Geoffroy)
Aphis pruni Geoffroy 1762
Aphis arundinis Fabricius 1775
Aphis pruni Fabricius 1775
Aphis amygdali Blanchard 1840
Aphis prunifex Amyot 1847
Aphis calamaphis Amyot 1847
Aphis gracilis Walker 1850
Hyalopterus pruni (Fabr.) 1857
Hyalopterus arundinis (Fabr.) 1857
Aphis phragmitidicola Oestlund 1886
Hyadaphis umbellulariae Davidson 1911

HISTORICAL REVIEW OF THE TAXONOMY OF *HYALOPTERUS PRUNI* (GEOFFROY)

THE SCIENTIFIC NAME of this species has been changed repeatedly; in fact, if each of the following authors is recognized, the status of the name has been changed twenty-one times, in the course of which the species has been described eight times as new. This review of the taxonomy does not include many of the lesser notes of an economic nature, which give *Hyalopterus arundinis* (Fabr.) priority over *H. pruni* (Fabr.) and vice versa.

1737. De Réamur⁽⁵¹⁾ ³ recorded certain observations on an aphid on plum trees in France. This aphid was coated with a white powder. There can be little doubt but that he was dealing with *Hyalopterus pruni* (Geoff.).
1762. *Aphis pruni* Geoffroy. This species was described in an anonymous publication, known to be the work of E. L. Geoffroy. This was the earliest use of a binomial name for this species, according to Hottes.⁽⁵¹⁾

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³ Superscript numbers in parentheses refer to "Literature Cited" at the end of this paper.

1773. *Aphis pruni* Geoffroy was recognized and cited by De Geer⁽¹⁹⁾ in his observations on the life history of this species.
1794. *Aphis arundinis epigejos* Fabricius⁽²⁴⁾ and *Aphis pruni domesticae* Fabricius.⁽²⁴⁾ At this date the two species listed above were described, the former from *Arundinis epigejos* (*Calamagrostis epigeios*) and the latter from *Prunus domestica* L. Hottes and Frison⁽³²⁾ state that Fabricius,⁽²⁸⁾ in 1775 (a work not available to this author), described *arundinis* and *pruni*, and that the former has page priority.
1840. *Aphis amygdali* Blanchard.⁽⁶⁾ Blanchard collected the species on peach near Paris and described it as new.
1847. *Aphis prunifex* Amyot and *Aphis calamaphis* Amyot.⁽¹⁾ At this time Amyot re-named a number of species of *Aphis* by adding the suffix "fex" to many of the existing species. *Aphis prunifex* was derived from *Aphis pruni* Fabr., which was listed as a synonym. In addition, he described the species as new under the name of *A. calamaphis*.
1850. *Aphis pruni* Fabr. Walker⁽⁶²⁾ recognized that *pruni* and *arundinis* of Fabricius were identical and gave the former priority. He also listed *Aphis prunifex* Amyot and *A. calamaphis* Amyot as synonyms.
1860. *Hyalopterus pruni* (Fabr.). Passerini⁽⁴⁶⁾ designated *Aphis pruni* Fabr. as the type of the genus *Hyalopterus* of Koch⁽³⁵⁾ since that author had failed to name a type species. *Aphis arundinis* Fabr. was listed as a synonym of *A. pruni* Fabr.
1879. *Hyalopterus pruni* (Fabr.) and *Hyalopterus arundinis* (Fabr.). Buckton⁽⁴⁰⁾ saw fit to separate these two species which had been united by Walker.⁽⁶²⁾ As synonyms of *H. pruni* (Fabr.) he listed *Aphis pruni* Fabr. and *Aphis pruni prunifex* Amyot. As synonyms of *H. arundinis* (Fabr.) he listed *Aphis arundinis* Fabr., *Aphis calamaphis* Amyot, and *Hyalopterus arundinis* Koch. (Koch, however, did not name a species *arundinis*.) At the same time he listed *Aphis calamaphis* Amyot and *A. prunifex* Amyot as synonyms of *Aphis pruni* Réamur [= *Anuraphis helichrysi* (Kalt.)]
1886. *Aphis phragmitidicola* Oestlund. Oestlund⁽⁴⁸⁾ described the species as new, under this name, although he remarked, "This may be the Linnean species *arundinis*." Linnaeus, however, did not name a species *arundinis*.
1887. *Hyalopterus arundinis* (Fabr.). Oestlund⁽⁴⁴⁾ recognized this name and placed his *Aphis phragmitidicola* Oestl. as a synonym. As additional synonyms he listed *Aphis arundinis* Fabr. and *Hyalopterus arundinis* Koch.
1893. *Hyalopterus pruni* (Fabr.). Osborne and Sirrine⁽⁴⁷⁾ recognized this name and listed *H. arundinis* (Fabr.) as a synonym.
1897. *Hyalopterus pruni* (Fabr.), *Hyalopterus arundinis* (Fabr.), and *Aphis pruni* Fabr. Lowe⁽³⁰⁾ stated that these three species attack the plum and gave notes on each species.
1901. *Hyalopterus arundinis* (Fabr.). Hunter⁽³³⁾ recognized this name, which is obviously a misspelling of *Hyalopterus*. He listed *Aphis pruni* Fabr. and *A. phragmitidicola* Oestl. as synonyms. He also listed *Aphis prunifoliae* Fitch as a synonym although this latter is now known to be a distinct species.
1905. *Hyalopterus*. Kirkaldy⁽³⁴⁾ listed *Hyalopteris* Hunter as a synonym of *Hyalopterus*.
1906. *Hyalopterus arundinis* Fabr. and *Hyalopterus pruni* Fabr. Schoutenden⁽⁵²⁾ considered these two species as distinct, the former on *Arundo phragmites* and the latter on *Prunus* sp. He recognized *Hyalopterus phragmiticola* Oestlund as a

- synonym of *H. arundinis* (Fabr.). This was obviously a misspelling of *phragmitidicola* Oestl.
1907. *Hyalopterus pruni* (Fabr.). Mordwilko⁽⁴¹⁾ gave this species priority over *H. arundinis* (Fabr.).
1910. *Hyalopterus arundinis* (Fabr.). Davis⁽¹⁷⁾ recognized this species and placed *phragmitidicola* Oestl. as a synonym.
1910. *Hyalopterus pruni* (Fabr.) and *Hyalopterus arundinis* (Fabr.). Henrich⁽⁸⁰⁾ considered these species distinct from each other and gave a key for their separation.
1911. *Hyadaphis umbellulariae* Davidson. W. M. Davidson⁽¹⁵⁾ described the species as new from alate females collected on the bay tree, *Umbellularia californica* Nutt.
1911. *Hyalopterus arundinis* (Fabr.). Essig⁽²¹⁾ recognized this name and listed *Aphis pruni* Fabr. and *Aphis phragmitidicola* Oestl. as synonyms.
1914. *Hyalopterus pruni* (Fabr.). Theobald⁽⁵⁹⁾ gave this name priority over *H. arundinis* (Fabr.) and *H. phragmiticola* Oestl. (misspelling of *H. phragmitidicola* Oestl.).
1917. *Hyalopterus pruni* (Fabr.). Van der Goot⁽²⁰⁾ listed as synonyms of this species, the following: *Aphis pruni* Fabr., *A. arundinis* Fabr., *Hyalopterus pruni* Koch, and *Hyalopterus arundinis* Koch.
1917. *Hyalopterus pruni* (Fabr.). Matsumura⁽⁴⁰⁾ gave this name priority over the same names as van der Goot.
1918. *Hyalopterus pruni* (Fabr.). Theobald⁽⁶⁰⁾ placed *H. arundinis* Fabr. and *H. phragmiticola* Oestl. (misspelling of *phragmitidicola* Oestl.) as synonyms of this name.
1918. *Hyalopterus pruni* (Fabr.). Das⁽¹³⁾ gave this name priority over *H. arundinis* Fabr.
1919. *Hyalopterus arundinis* (Fabr.). W. M. Davidson⁽¹⁸⁾ recognized this name, and placed *Aphis arundinis* Fabr., *A. pruni* Fabr., *A. phragmiticola* Oestl. (misspelling of *phragmitidicola* Oestl.) and *Hyadaphis umbellulariae* Davidson as synonyms.
1919. *Hyalopterus arundinis* (Fabr.). Arkhangel'sky⁽²⁾ gave this name priority over *H. pruni* (Fabr.).
1920. *Hyalopterus*. Baker⁽³⁾ placed the genus *Hayhurstia* Del Guercio, 1917, as a synonym of *Hyalopterus* and suggested that *Pergandeidia* Schoutenden may be a synonym, as well.
1921. *Hyalopterus pruni* (Fabr.). Takahashi⁽⁵⁵⁾ gave this name priority over *Aphis pruni* Fabr., *A. arundinis* Fabr., *Hyalopterus pruni* Koch, and *H. arundinis* Koch.
1925. *Hyalopterus arundinis* (Fabr.). Laing⁽⁸⁷⁾ used this name and placed *Aphis gracilis* Walker as a synonym, after examining Walker's type.
1925. *Hyalopterus arundinis* (Fabr.). Davidson⁽¹⁴⁾ listed *H. pruni* (Fabr.) as a synonym of this species.
1927. *Hyalopterus arundinis* (Fabr.). Theobald⁽⁶¹⁾ gave this name priority and placed as synonyms: *Aphis pruni* Fabr., *A. arundinis* Fabr., *A. calamaphis* Amyot, *A. prunifex* Amyot, *A. gracilis* Walker, *Hyalopterus pruni* Koch, *H. phragmiticola* Oestl. (misspelling of *phragmitidicola* Oestl.).
1928. *Hyalopterus pruni* (Fabr.). Opmanis⁽⁴⁸⁾ gave this name priority over *Aphis pruni* Fabr., *A. arundinis* Fabr., *Hyalopterus arundinis* (Fabr.) and *Hyalop-*

terus phragmiticola Oestl. (misspelling of *phragmitidicola* Oestl.). In this same publication he listed *Aphis prunifex* Amyot and *Aphis calamaphis* Amyot, as synonyms of *Brachycaudus helichrysi* Kalt. and cites Buckton as the authority for this change. These two names are now considered to be synonymous with *Hyalopecterus pruni* (Geoffroy), and distinct from *B. helichrysi* Kalt.

1930. *Aphis pruni* Geoffroy. Hottes⁽³¹⁾ called attention to Geoffroy's name *pruni* published anonymously in 1762 but known to be the work of Geoffroy. He pointed out that this use of *pruni* preceded *Aphis pruni* Scopoli 1763, *Aphis pruni* Fabr. 1775, and *Aphis pruni* Koch 1854. He therefore stated that this name should be used instead of *arundinis* Fabr. or *pruni* Fabr.
1931. *Hyalopecterus arundinis* (Fabr.). Börner⁽⁸⁾ placed *Aphis amygdali* Blanchard as a synonym of *Hyalopecterus arundinis* (Fabr.).
1931. *Hyalopecterus arundinis* (Fabr.). Takahashi⁽³⁰⁾ used this name and listed *arundinis* and *pruni* of Fabricius and of Koch as synonyms.
1931. *Hyalopecterus pruni* (Geoffroy). Hottes and Frison⁽³²⁾ referred to the species under this name, and placed Geoffroy's *Aphis pruni* in the genus *Hyalopecterus*. In this work *A. pruni* Fabr. and *A. arundinis* Fabr. are listed as synonyms.
1932. *Hyalopecterus phragmitidicola* Oestl. Börner⁽⁹⁾ suggested that this name be used in place of *H. pruni* (Fabr.) and *H. arundinis* (Fabr.). He pointed out that *Aphis pruni* Scopoli 1763 has precedence over *A. pruni* Fabr. 1775, so that the latter has been listed as a synonym of *A. arundinis* Fabr. Fabricius listed a single host for *Aphis arundinis*, namely, *Arundo epigejos* (= *Calamagrostis epigeios*), which, Börner pointed out, is a hard-leaved sandgrass belonging to the tribe Agrostideae and not at all similar to the known alternate hosts of the plum aphid, *Arundo* and *Phragmites*, which belong to the Festuceae. His investigations led him to the conclusion that the mealy plum aphid does not live on *Calamagrostis epigeios* and that *A. arundinis* Fabr. referred to another species. Consequently, he proposed that the name *phragmitidicola* Oestl. be used.
1932. *Hyalopecterus arundinis* (Fabr.). Gillette and Palmer⁽²⁷⁾ used the above name, and listed *Aphis pruni* Fabr. as a synonym.

Conclusion on Nomenclature.—The very pertinent observations of Börner⁽⁹⁾ indicate that the name *Aphis pruni* Fabr. was preoccupied and that *Aphis arundinis* Fabr. may have referred to some other species than the mealy plum aphid, since it was described on a plant on which this species could not be found. The writer's observations lend support to this view (see discussion under "Host Plants," pp. 201–202). In view of these facts, it is fortunate that Hottes^(31, 32) has called attention to the priority of *Aphis pruni* Geoffroy and placed it in the genus *Hyalopecterus*.

GEOGRAPHICAL DISTRIBUTION

Hyalopecterus pruni (Geoff.) has been frequently reported in many sections of the world, and particularly in the north temperate zone. It has been reported in Africa (Union of South Africa), Australia, Belgium, Canada, China, Denmark, Egypt, England, France, Germany, India, Ireland, Italy, Japan, Java, Latvia, Morocco, New Zealand, Norway,

Palestine, Peru, Portugal, Russia, Scotland, Slavonia, Sweden, and Switzerland. This distribution is indicated on the map in figure 1.

In the United States this species was first reported from the vicinity of Carmel, California, in 1881. It was reported in Minnesota in 1885. At present it is known to occur in California, Colorado, Connecticut, Illinois, Iowa, Kansas, Maine, Minnesota, Nebraska, Nevada, New Jersey, New York, Ohio, South Dakota, and Utah.

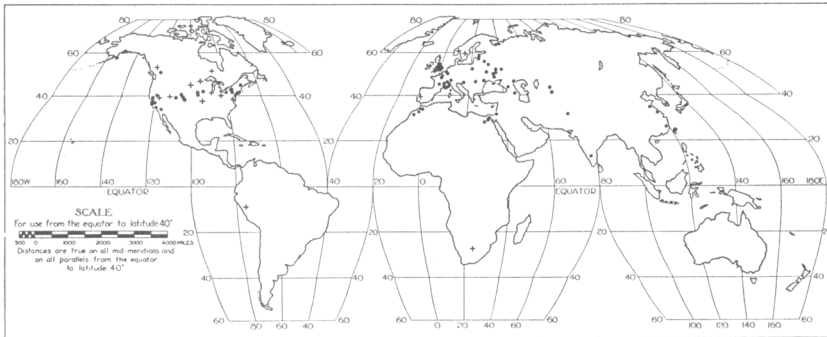


Fig. 1.—Distribution of *Hyalopterus pruni* (Geoff.) in the world. A dot indicates a definite locality; a cross indicates an indefinite locality, as a country or state. (Outline map adapted from Goode's series of base maps and graphs No. 101 HC, by permission of the University of Chicago Press.)

TERMINOLOGY

To avoid cumbersome descriptions, the following terms, taken from various authors, are used in this paper, with the following meanings:

Eggs: deposited on the perennial or *primary* host.

Fundatrices: apterous, parthenogenetic viviparous females which hatch from the overwintered eggs and which normally give birth to:

Fundatrigeniae: apterous, parthenogenetic viviparous females borne by fundatrices or by earlier generations of fundatrigeniae on the primary host.

Migrantes: alate, parthenogenetic viviparous females borne by the fundatrigeniae, which fly to the *secondary*, or summer hosts, where they give birth to:

Alienicolae: apterous, parthenogenetic, viviparous females borne by migrantes or by earlier generations of alienicolae on the secondary hosts.

Gynoparae: alate, parthenogenetic, viviparous females borne by alienicolae on the secondary hosts which fly to the primary host and give birth to oviparous females.

Males: alate sexual males, born on the secondary hosts as brothers of

the gynoparae, which fly to the primary hosts, and copulate with the oviparous females.

Oviparous females: small, apterous, sexual females, borne on the primary hosts by the gynoparae. These mate with the sexual males, and lay eggs.

In certain other species of aphids, for example, *Myzus pseudosolani* Theobald, which exhibit facultative or obligatory polyphagy, the males are apterous, as are the oviparous females, and in this case the winged parthenogenetic females which fly to the primary hosts and give birth to these forms are called "sexuparae." Such a condition does not obtain in *Hyalopterus pruni*, however.

DESCRIPTION OF STAGES IN THE ANNUAL CYCLE

Egg.—The egg is regularly ovoidal and conforms to the usual type of aphid egg. It is black, but covered with a loose, sparse coating of silvery, waxlike rods, which cause it to appear gray to the unaided eye (fig. 2). When magnified about 15 times the egg appears black and sparsely covered with a shining white powder. The newly laid egg is light brilliant green, and is covered with white wax immediately after being laid. It darkens slowly and at the end of two or three days is entirely black.

Length, 0.47 to 0.66 mm; width, 0.22 to 0.35 mm; mean ratio $W : L = 0.47$.

Fundatrix.—First instar: head dark green with darker-green marking extending solidly across the vertex and posteriorly as two broad stripes across the occiput, leaving a narrow, lighter-green stripe in the mid-line and above each eye, not pulverulent; eyes dark reddish brown to black; antennae (fig. 3, *A*) very dark green to black. Thorax and abdomen uniformly dark green, dorsum not pulverulent, venter with a uniform coat of white meal; cornicles visible at moderate magnifications as round black dots, apparently not raised above the surface of the body. Antennae 4-jointed; length: 0.24 to 0.30 mm; mean, 0.26 mm. Length of the meta-tibiae, 0.13 to 0.18 mm; mean, 0.15 mm.

Second instar: same as first instar though coloring generally lighter; antennae 4-jointed; length: 0.32 to 0.40 mm; mean, 0.35 mm. Meta-tibiae length, 0.19 to 0.27 mm; mean, 0.22 mm (based on 60 specimens).

Third instar: same as adult instar, but considerably darker in color; markings and meal as in the adult. Antennae 5-jointed; length: 0.41 to 0.51 mm; mean, 0.46 mm. Meta-tibiae length, 0.28 to 0.40 mm; mean, 0.33 mm (based on 117 specimens).

Fourth instar: coloring and meal similar to adult, lighter in color than preceding instars. Antennae 5-jointed; length: 0.52 to 0.68 mm; mean, 0.61 mm. Meta-tibiae length, 0.42 to 0.56 mm; mean, 0.49 mm (based on 96 specimens).

Adult: apterous; body ovoidal (fig. 4); dorsum rounded or arched, not flattened as in succeeding generations; general color light green, of the same shade as the midrib of the young leaves of the plum, with three longitudinal darker green very irregular stripes, composed of minute irregular pigmented spots, one stripe medio-dorsal and the others dorso-lateral; dorsum not pulverulent; venter covered with a thin, uniform coating of white meal. The mid-dorsal stripe is more distinct than the dorso-lateral stripes, venter concolorous, light greenish white, body segmentation indistinct. Head very pale green; antennae (fig. 3, *B*) colorless, translucent to pale

green, often black-tipped, occasionally with black or dark-gray color shading into the terminal half of the penultimate segment, borne on short frontal tubercles, length about one-third that of the body (for measurements see tables 1 and 2); eyes conspicuous, dark reddish brown to black; proboscis pale green, tip dark gray to black, reaching to meso-coxae. Legs vary from colorless, translucent, to yellowish light green; tibiae sometimes with apices darkened; tarsi dark gray or black. Cornicles

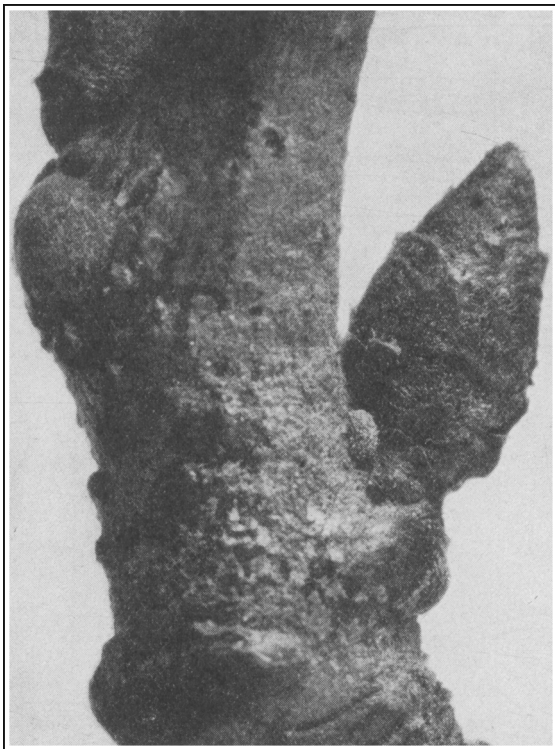


Fig. 2.—Egg of *Hyalopterus pruni* (Geoff.) in its usual position at the base of the bud.

(fig. 3, *L*) dark brown to black, protruding very slightly above the body wall, conical; length, 0.053 mm; width, 0.049 mm. Cauda light yellowish green, or tipped with dark gray or black (fig. 3, *Q*), hairs on each side, 3 to 5 hairs in each row.

Fundatrigenia.—First instar: elongate, body straight, nearly parallel-sided, somewhat carinate, coloration and meal as in adult. Antennae (fig. 3, *C*) 5-jointed; length: 0.40 to 0.54 mm; mean, 0.48 mm. Tibiae, length: 0.24 to 0.35 mm; mean, 0.31 mm (measurements based on 82 individuals of the first generation).

Second instar: similar to the first. Antennae 5-jointed; length: 0.59 to 0.75 mm; mean, 0.68 mm. Tibiae, length: 0.40 to 0.48 mm; mean, 0.44 mm (based on 59 individuals of the first generation).

Third instar: body more rounded and tapering anteriorly than preceding instars;

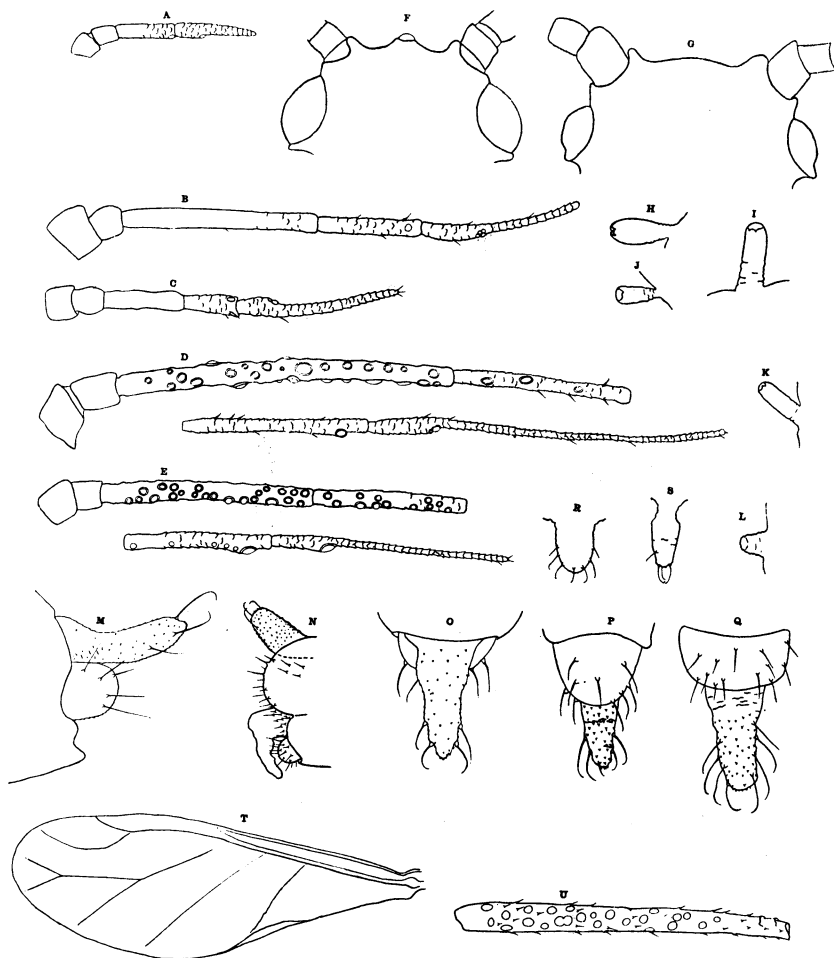


Fig. 3.—Anatomical taxonomic features of *Hyalopterus pruni* (Geoff.):

- | | |
|--|---|
| A, Antenna, first-instar fundatrix. | M, Cauda and anal plate, migrans, lateral view. |
| B, Antenna, adult fundatrix. | N, Cauda and anal plate, male, side view. |
| C, Antenna, first-instar fundatrigenia. | O, Cauda and anal plate, migrans, dorsal view. |
| D, Antenna, adult migrans. | P, Cauda and anal plate, migrans, ventral view. |
| E, Antenna, adult male. | Q, Cauda and anal plate, fundatrix, ventral view. |
| F, Dorsal view of head, migrans. | R, Cauda, oviparous female, dorsal view. |
| G, Dorsal view of head, adult fundatrigenia. | S, Cauda, male, dorsal view. |
| H, Cornicle, migrans. | T, Wing of gynopara. |
| I, Cornicle, fundatrigenia. | U, Meta-tibia, oviparous female. |
| J, Cornicle, male. | |
| K, Cornicle, oviparous female. | |
| L, Cornicle, fundatrix. | |

Camera lucida drawings, all at the same magnification, except T.

coloration and meal as in the adult. Antennae 6-jointed; length: 0.82 to 0.99 mm; mean, 0.90 mm. Tibiae, length: 0.54 to 0.66 mm; mean, 0.60 mm (based on 84 individuals of the first generation).

Fourth instar: similar to adult. Antennae 6-jointed; length: 1.04 to 1.26 mm; mean, 1.16 mm. Meta-tibiae, length: 0.75 to 0.86 mm; mean, 0.81 mm (based on 50 individuals of the first generation).

Adult (fig. 5): body somewhat fusiform, rounded at the ends, with the greatest transverse diameter slightly posterior to the middle, dorsum convex, but not as highly arched as in the fundatrix; general color light green with three darker-green

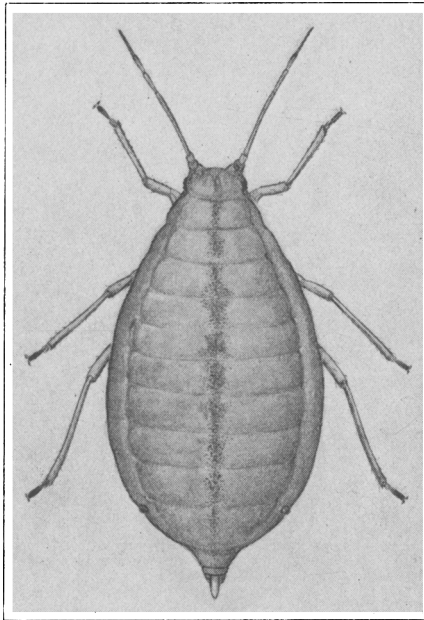


Fig. 4.—Fundatrix. The body is rounded and the antennae and legs are relatively short.

Figures 4 to 8 are at the same magnification.

stripes situated as in the fundatrix, but lighter in color; white meal arranged in four longitudinal bands on the dorsum of thorax and abdomen, each band composed of a circumscribed area on each body segment; venter of thorax and abdomen uniformly covered with white meal. Head light green, uniformly pulverulent; eyes dark reddish brown to black; antennae 6-segmented, about two-thirds as long as the body (for measurements see tables 1 and 2), borne on short frontal tubercles (fig. 3, *G*), translucent light yellowish green, with VI dark gray or black, V often dark in the distal half; proboscis hyaline, pale green, apex dark gray or black, extending to meso-coxae. Legs yellowish or greenish white, translucent, tips of tibiae and tarsi dark gray or black. Cornicles straight-sided or rarely somewhat fusiform (fig. 3, *I*), apex without flange, slightly imbricated; length, 0.116 mm; width, 0.040 mm; dark

gray or black. Cauda pale green or tipped with dark gray or black, a row of inward-curved hairs on each side, 2 to 3 hairs in each row.

Migrans.—First and second instars: identical to those of fundatrigenia, antennae 5-jointed.

Third instar: like the second, but with slight swellings on the thorax, the first indication of wing-pads, antennae 6-jointed.

Fourth instar (pupa): thorax twice as broad as apterous form; wing pads pale green, dark gray along the margins; otherwise color and pulverulence as in the adult.

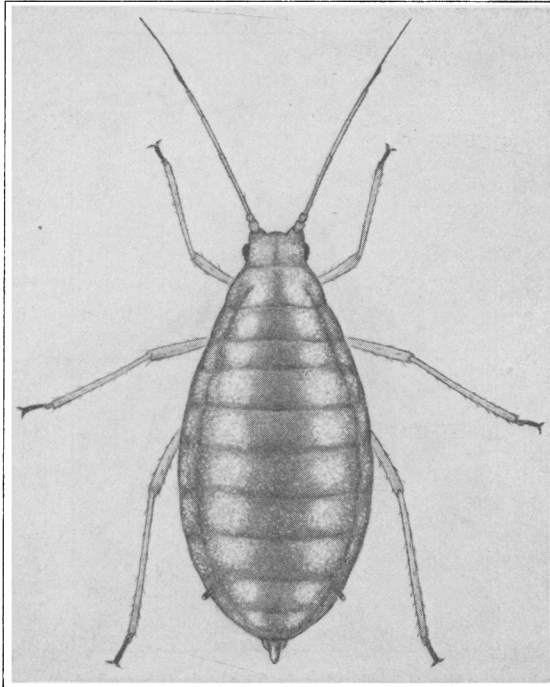


Fig. 5.—Fundatrigenia. The body is elongated and the antennae and legs are relatively long.

Antennae 6-jointed; length: 1.04 to 1.34 mm; mean, 1.19 mm. Tibiae, length: 0.51 to 0.85 mm; mean, 0.68 mm (based on 138 specimens).

Adult (fig. 6): head and thorax dark brownish or grayish black to black; abdomen light green; the whole body pulverulent, hairs sparse and small. Eyes very dark reddish brown to black. Antennae (fig. 3, *D*), about two-thirds as long as the body, borne on very short frontal tubercles (fig. 3, *F*), 6-jointed (see tables 1 and 2 for length of segments), very dark brown or black throughout, or with the base of III light brown or pale yellow; secondary sensoria circular, membrane convex, arranged in a row on IV; III with 18–30 sensoria; IV with 3–8; V with 0–2. Proboscis light yellowish green to dark green with tip light gray to black, extends to midway between the pro- and meso-coxae. Prothorax dark gray or black or with the posterior margin green; mesothorax, lobes very dark brown to black, pleural sclerites and venter dark

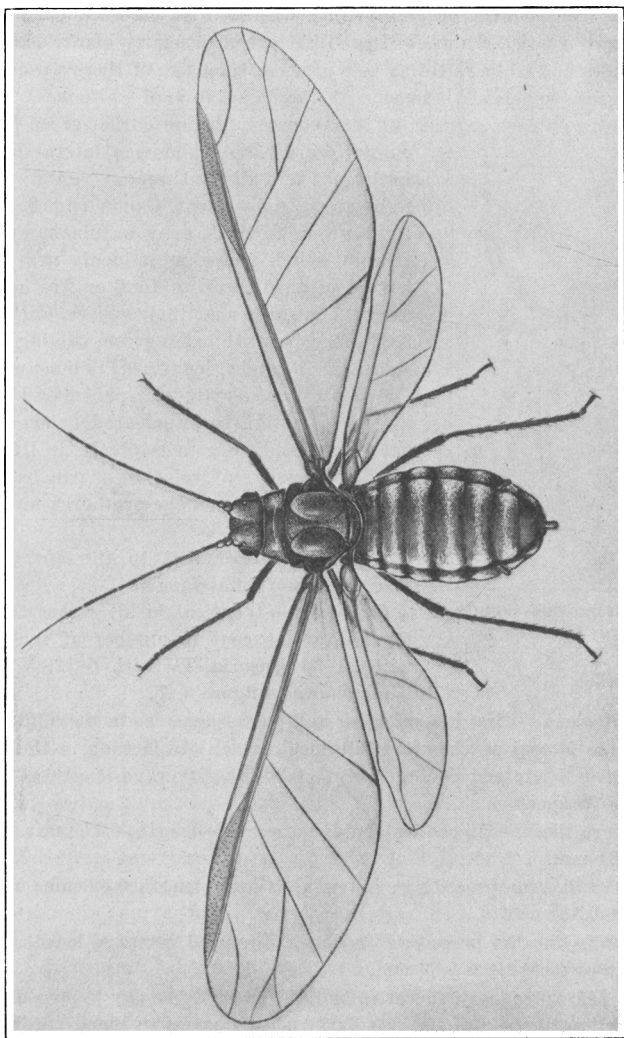


Fig. 6.—Migrans. Gynoparae are identical in appearance to this form.

brown to black, integument between pleural sclerites dark green, thorax uniformly pulverulent. Wings transparent, without markings, iridescent; veins light reddish brown except the heavy subcosta, which is light green; point of attachment of hamuli to fore wing, brown; stigma green with brownish borders; wing insertions light green; media twice-branched. Legs light green to nearly black, darker at the apexes of femora and tibiae, shading into green at the bases of these segments; tarsi black; coxae green to black. Abdomen with two dorsal rows of white mealy spots, one spot for each row on each segment of the abdomen, median darker-green line broad-

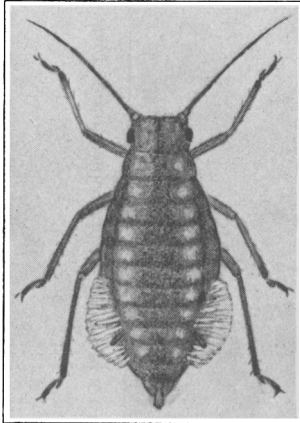


Fig. 7.—Oviparous female, showing lateral tufts of wax-like rods which serve to camouflage the egg.

ening toward base of abdomen, lateral darker lines indistinct and discontinuous; venter uniformly light green, pulverulent. Cauda (fig. 3, *M*, *O*, *P*), light green to dark gray or black, cylindrical, straight-sided, widening suddenly near the base, curved upward, bearing four or five hairs which are bent inwards near their apexes. Cornicles (fig. 3, *H*) black or with bases green, shining, glabrous, shorter than cauda; length, 0.113 mm; width 0.042 mm; club-shaped-cylindrical, not flared or flanged at the tip; slightly imbricated or smooth; held nearly perpendicular to the body, in life. Lateral papillae transparent, colorless or pale brown, hemispherical; one pair on the prothorax and each abdominal segment.

Alienicola.—Identical to the corresponding stages of the fundatrigenia.

Gynopara.—Identical in all stages to those of the migrans, except in number of sensoria: III with 21–34 sensoria, IV with 6–12, V with 0–2. Wing shown in figure 3, *T*.

Oviparous Female.—First instar: color and pulverulence as in the adult, with the exception of the lateral patches of white meal, which are lacking in the immature stages. Antennae 5-jointed; average length 0.36 mm. Average length of tibia 0.17 mm (based on 39 specimens).

Second instar: like the preceding; antenna, average length, 0.41 mm; tibia average length 0.21 mm.

Third instar: like the preceding; antenna, average length 0.52 mm; meta-tibia, average length 0.33 mm.

Fourth instar: like the preceding; antenna 5-jointed, average length 0.62 mm; average length of meta-tibia 0.39 mm.

Adult (fig. 7): apterous; general color light green to smoky yellow. Head light green, light yellow, or pale pink; eyes dark reddish brown to black; proboscis pale green, tip dark gray to black; antenna 6-jointed, often with III and IV fused, basal portion light green, distal portion of V and tip of IV dark gray to black. Thorax yellowish green, rarely pale pink, pulverulent pattern continuous with that of abdomen. Legs pale green with darker green or gray shading on the apexes of femora and tibia; tarsi black; color of meta-legs darker than pro-legs, meta-tibiae (fig. 3, *U*) slightly swollen throughout their length, bearing from 33 to 58 small circular sensoria. Abdomen with two large elliptical patches of white on each side, extending from about segment 4 to 8 inclusive, composed of silvery, reflective rods, sometimes

as long as the distance between the antennae, projecting postero-laterally as conspicuous tufts; a darker-green stripe extends along the mid-dorsal line of the thorax and abdomen, widening in the middle of the body; on either side of this a pulverulent line, simulating a light-gray stripe; on either side of these gray stripes a somewhat darker-green lateral stripe; venter uniformly pale yellowish green, lateral mealy patches conspicuous, extending one-third of the distance to the mid-ventral line

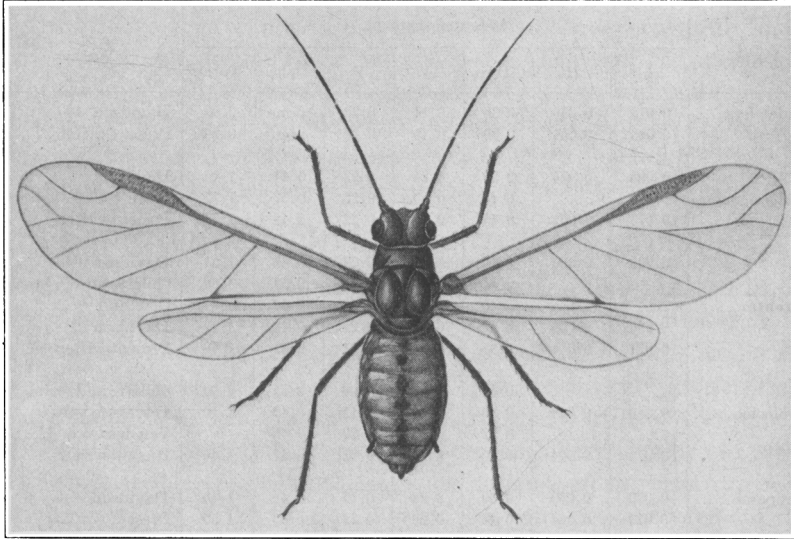


Fig. 8.—Male.

(and about as far onto the dorsum). Cornicles (fig. 3, *K*) black or dark brown, sometimes with base green; often partially imbedded in lateral mealy tufts; slightly or not at all imbricated; length, 0.067 mm; width, 0.028 mm; held perpendicular to body and diverging from each other at an angle of 30°. Cauda and sometimes last abdominal segment light green to dark gray or black, cauda (fig. 3, *R*) usually dark.

Male.—Fourth instar (pupa): coincident with pupae of gynoparae but easily distinguished by general body color. Body pale yellowish brown, rarely pale green, pulverulence as in fourth-instar gynoparae; eyes dark brown to black; antennae, segments I and II pale brown, III–VI inclusive dark brown to black; proboscis yellow, tip black; legs hyaline, tarsi dark gray; wing-pads brown with dark brown around the margins; venter of abdomen with pulverulence delimited by segments.

Adult (fig. 8): alate; head and thorax dark brown to black; eyes reddish brown; proboscis light greenish yellow, tip dark brown. Antennae (fig. 3, *E*) dark brown, lighter toward the tip, secondary sensoria circular; III, 32 to 48 sensoria; mean, 39.7; IV, 13 to 25 sensoria; mean, 19.8; V, 5 to 18; mean, 10.3 (for measurements of antennal segments see table 1). Prothorax dark brown with anterior and posterior margins dark green, lobes dark brown to black, integument between sclerites of pleurae yellow; venter of thorax dark brown; head and thorax glabrous to very slightly pulverulent. Abdomen, basic color yellow with a green spot on each segment simulating a discontinuous median and two lateral lines; dorsum glabrous; venter

thinly powdered. Cornicles (fig. 3, *J*) somewhat claviform, short; length, 0.071 mm; width, 0.028 mm; dark brown. Cauda, anal plate, and accessory lobes (fig. 3, *N, S*), dark brown to black.

TABLE 1
LENGTHS IN MILLIMETERS OF ANTENNAL SEGMENTS OF VARIOUS ADULT FORMS
IN THE YEARLY CYCLE

Form	Antennal segment							Author
	I	II	III	IV	V	VI	Total	
Fundatrices.....	0.075	0.060	0.30	0.14	0.22	none	0.80	Davidson ⁽¹⁶⁾
	0.063	0.054	0.30	0.15	0.22	none	0.79	Present writer
Fundatrigeniae.....	0.085	0.075	0.39	0.24	0.22	0.44	1.45	Davidson ⁽¹⁶⁾
	0.45	0.30	0.25	0.57	1.77	Lowe ⁽³⁹⁾
	0.073	0.067	0.43	0.27	0.22	0.48	1.54	Present writer
Migrantes.....	0.090	0.060	0.39	0.26	0.23	0.48	1.51	Davidson ⁽¹⁶⁾
	0.41	0.27	0.23	0.53	1.60	Gillette and Palmer ⁽²⁷⁾
	0.40	0.25	0.20	0.50	Oestlund ⁽⁴⁴⁾
	0.080	0.060	0.40	0.26	0.21	0.48	1.49	Davidson ⁽¹⁶⁾
	0.071	0.061	0.33	0.24	0.21	0.49	1.40	Present writer
Alienicolae.....	0.51	0.37	0.29	0.53	2.00	Gillette and Palmer ⁽²⁷⁾
	0.080	0.045	0.26	0.16	0.15	0.40	1.10	Davidson ⁽¹⁶⁾
	0.37	0.27	0.22	0.48*	Van der Goot ⁽²⁹⁾
	0.073	0.064	0.40	0.24	0.21	0.47	1.46	Present writer
Gynoparae.....	0.070	0.060	0.39	0.23	0.17	0.48	1.40	Davidson ⁽¹⁶⁾
	0.073	0.064	0.42	0.29	0.22	0.52	1.59	Present writer
Males.....	0.080	0.070	0.38	0.25	0.23	0.46	1.47	Davidson ⁽¹⁶⁾
	0.064	0.058	0.35	0.23	0.22	0.46	1.38	Present writer
Oviparous females.....	0.05	0.23	0.05	0.22	0.72	Lowe ⁽³⁹⁾
	0.060	0.035	0.14	0.06	0.08	0.24	0.62	Davidson ⁽¹⁶⁾
	0.051	0.045	0.17	0.10	0.12	0.30	0.79	Present writer

* Van der Goot gave ratios, so 0.480 was arbitrarily selected as a basis.

TABLE 2
RATIOS OF THE LENGTHS OF ANTENNAL SEGMENTS

Form	Antennal segment					
	I	II	III	IV	V	VI
Fundatrices.....	1.2	1.0	5.3	2.6	3.9	...
Fundatrigeniae.....	1.1	1.0	5.9	3.8	3.3	7.0
Migrantes.....	1.3	1.0	6.5	4.3	3.6	8.3
Alienicolae.....	1.4	1.0	7.1	4.8	4.0	8.5
Gynoparae.....	1.2	1.0	6.6	4.2	3.2	8.2
Males.....	1.1	1.0	5.7	3.8	3.5	7.2
Oviparous females*.....	1.4	1.0	3.9	2.0	2.6	6.9

* Exclusive of the measurements by Lowe, ⁽³⁹⁾ which are obviously incorrect.

Several authors have recorded the length of the segments of the antennae of the various stages, either in taxonomic or biological observations on this species. These figures have been converted into millimeters, and are presented in table 1, together with measurements made by the present writer.

The figures presented in table 1 indicate a great variation in the length of the various segments of the antennae of the several adult forms of the mealy plum aphid. These differences are the result of variation in size of the aphids in response to environmental factors, and to differences in technique of preparing and measuring specimens. In view of the variability of the measurements, ratios seem to be more dependable. In table 2 are presented ratios based on a summation of table 1.

LIFE HISTORIES AND YEARLY CYCLE IN CALIFORNIA

The eggs (fig. 2), deposited in the late fall, are usually placed in the axils of lateral buds. When three or four buds occur in a cluster, as on the tip of a fruit spur, the eggs are usually wedged into the cavity enclosed by the bases of these buds. Such eggs are entirely hidden from view. Small cracks or crevasses in the bark are also utilized for oviposition. Eggs are never found exposed on the smooth bark of year-old wood. As a result of their position, the eggs are submerged in water during a considerable part of the winter. Water from rain, dew, and fog collects on the twigs and runs down to the lateral buds where the force of surface tension causes it to be retained between the bud and the twig. The eggs are often submerged, in this manner, to a depth of 1 or 2 millimeters. This fact bears an important relation to commercial spraying for control.

During the spring of 1932, the rate of hatching of the eggs was recorded. The eggs on twigs were kept in a lath-house at San Jose. This condition was presumed to simulate the alternate light and shade produced by the higher limbs of a tree upon the lower. Each day during the hatching period the twigs were shaken over a large sheet of white paper. A few moments after shaking, all dirt and debris could be blown from the paper without dislodging any of the newly hatched aphids. They were then easily counted, for they contrasted with the white background. These data are presented in table 3. A thermograph in a standard Weather Bureau kiosk, about 50 yards away, supplied the temperature records.

Although the eggs are usually laid during two months or more in the fall, they all hatch in about ten days in the spring. This indicates that the elapsed time from deposition to hatching is not constant. The cumulative percentage hatched is presented graphically in figure 9, together

with the temperatures for this period and for the preceding three weeks. This graph suggests that when the mean daily temperature approached 14° C, hatching was initiated. Roughly 6 to 10 days later 50 per cent of the eggs had hatched.

The various species and varieties of *Prunus* which serve as primary hosts for the mealy plum aphid, are in various stages of development during the hatching period. In California, the common hosts, prunes and European plums, generally have the white petals visible beyond the

TABLE 3
HATCHING OF EGGS AT SAN JOSE, 1932

Date, March, 1932	Mean temperature, °C	Number hatched	Per cent hatched	Summation of per cent hatched	Date, March, 1932	Mean temperature, °C	Number hatched	Per cent hatched	Summation of per cent hatched
6	8.9	52	10.6	10.6	14	13.5	0	0.0	90.5
7	6.5	108	22.0	32.6	15	11.5	6	1.2	91.7
8	7.8	16	3.3	35.9	16	13.4	17	3.5	95.2
9	7.9	38	7.8	43.7	17	11.4	16	3.3	98.5
10	7.0	36	7.3	51.0	18	13.0	6	1.2	99.7
11	7.5	64	13.1	64.1	19	14.5	1	0.2	99.9
12	9.2	65	13.3	77.4	20	14.1	1	0.2	100.1
13	9.9	64	13.1	90.5					

green sepals by the time hatching is well started. This is commonly known as the "popcorn stage," or the "white-bud stage." By the time 5 or 10 per cent of the flowers have reached full bloom, approximately 90 to 95 per cent of the eggs have hatched. The survival of this species depends upon delaying hatching until the buds have opened, so that suitable feeding places will be available; but hatching cannot be delayed too long since a large percentage of the eggs are glued to the scales of the dormant buds, and they would fall from the trees with these scales, as the latter loosen and are blown away.

A few young fundatrices may emerge from the egg at the time the dormant fruit buds are just beginning to swell. As the buds elongate, the white bases of the scales become visible. The early aphids settle on this white tissue and apparently feed there. The majority of the newly hatched fundatrices, however, make their appearance about the time that the green sepals of the flower buds appear. They establish themselves on the sepals, usually with head towards the peduncle. In the Agen (French) prune, Grand Duke plum, and other species in which two or more flower buds arise from a single dormant bud, the aphids force their way between the appressed flower buds, and into the cup formed by the loosened dormant bud scales, wherein they establish themselves on the peduncles of the future flowers.

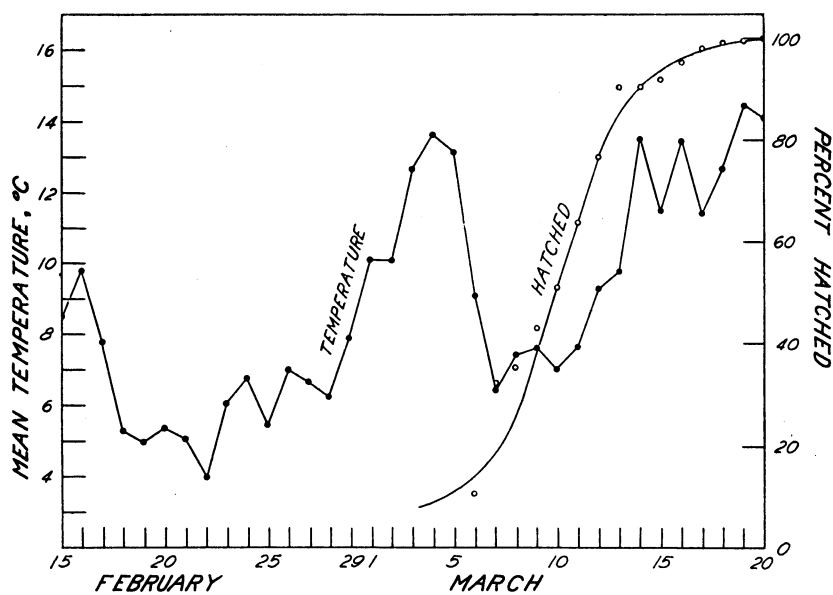


Fig. 9.—Hatching of eggs in the field, and concurrent temperatures, San Jose, 1932.

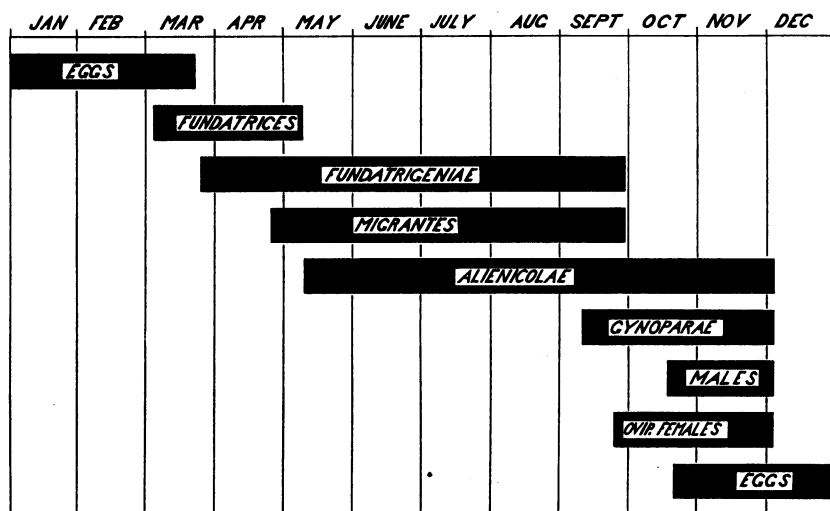


Fig. 10.—Seasonal occurrence of the various stages in the annual cycle, in California. (Data from table 4.)

At the time of full bloom, all of the eggs have hatched, and many second- and third-instar fundatrices can be found. In full bloom, the sepals of the flowers curl backwards, often forming a complete circle as they touch the calyx cup. The majority of aphids then take their positions on the inside of the recurved sepals.

When the calyx cup, or "jacket" as this portion of the perigynous flower of *Prunus* is commonly called, begins to dry and lose its succulence, the aphids move onto the lower surface of the young leaves. At about this time some of the fundatrices mature and give birth, parthenogenetically, to the first fundatrigeniae.

The dates of earliest and latest seasonal observations of the various stages, in several localities and on various hosts, are recorded in table 4. These data are represented graphically in figure 10.

The newly born fundatrigeniae settle in close proximity to the fundatrix, always on the lower surface of the developing leaves. When mature, they give birth parthenogenetically to another identical generation of fundatrigeniae and this is repeated until from three to ten generations of fundatrigeniae have been completed.

These aphids always attempt to establish themselves on the lower surfaces of the leaves, and are found on the upper surfaces or on petioles or twigs only under very unusual conditions. Gregariousness is a conspicuous trait of the fundatrigeniae and, in fact, of other stages of this species. The fundatrigeniae congregate in dense clusters on certain leaves, while other leaves in the immediate vicinity may be completely uninfested. This habit of gregariousness endows the aphids with the ability to curl the leaves of the plum. An early spring colony, consisting of a fundatrix surrounded by thirty or forty fundatrigeniae is capable of curling a young leaf. The curling does not partake of any of the characteristics of structures produced by typically gallicolous aphids. It consists of a simple rolling of the margins of the leaf toward the midrib, together with an arching or high convexity of the dorsal surface of the leaf, as seen in lateral view.

The fundatrigeniae increase in numbers in the Sacramento and San Joaquin valleys until the approach of very warm weather in the latter part of June or early part of July. At this time they occur in maximum numbers, and subsequently decrease rapidly. At the time of maximum infestation, plum orchards with a normally heavy infestation present a striking appearance. The mealy plum aphid produces copious sticky excrement, or honeydew, which coats the upper surfaces of the leaves below the colony and resembles varnish. At times, a black smut fungus grows in the excrement and causes the trees to appear blackened as

TABLE 4
EARLIEST AND LATEST SEASONAL OCCURRENCE OF THE VARIOUS STAGES
IN THE ANNUAL CYCLE

Form	Occurrence	Date	Host	Locality	Abundance
Eggs.....	{ Earliest.....	10/29/28	Plum	Davis	Rare
		10/18/29	Plum	Penryn	Rare
		11/ 3/30	Plum	Linden	Common
		10/21/32	Plum	Linden	Rare
	{ Latest.....	3/ 8/29	Plum	Davis	Rare
		3/13/31	Plum	Penryn	Rare
		3/20/32	Plum	San Jose	Absent
Fundatrices.....	{ Earliest.....	3/ 5/29	Plum	Penryn	Rare
		3/11/29	Plum	Newcastle	Common
	{ Latest.....	5/10/32	Plum	San Jose	Absent
Fundatrigeniae.....	{ Earliest.....	3/20/29	Plum	Penryn	Rare
	{ Latest.....	9/ 1/28	Plum	Penryn	Absent
		9/ 1/30	Plum	Penryn	Absent
Migrantes.....	{ Earliest.....	9/30/30	Plum*	San Jose	Rare
		5/ 6/29	Plum	Davis	Rare
		5/ 7/29	Plum	Penryn	Rare
		4/21/31	Plum	Penryn	Rare
		4/22/31	Plum	Linden	Common
		5/ 2/31	Plum	San Jose	Common
		5/21/29	Cattail	Penryn	Rare
		5/30/29	Reed	Antioch	Common
		5/ 6/31	Cattail	Penryn	Common
		5/16/32	Cattail	Penryn	Common
	{ Latest.....	7/13/29	Plum	San Jose	Rare
		8/13/29	Plum	Penryn	Rare
		9/ 1/30	Plum	Penryn	Absent
		9/ 4/28	Cattail	Penryn	Absent
		10/ 3/29	Cattail	Penryn	Rare
		9/ 1/30	Cattail	Penryn	Rare
		9/29/31	Reed	Stockton	Rare
Alienicolae.....	{ Earliest.....	5/13/29	Cattail	Penryn	Common
		5/16/32	Cattail	Penryn	Common
	{ Latest.....	12/ 3/29	Cattail	Penryn	Rare
		11/17/32	Reed	Stockton	Common
Gynoparae.....	{ Earliest.....	10/ 5/28	Cattail	Penryn	Common
		10/ 2/29	Cattail	Penryn	Rare
		10/ 6/30	Cattail	Penryn	Rare
		9/10/31	Cattail	Penryn	Rare
		9/ 8/32	Cattail	Penryn	Rare
		10/16/28	Plum	Penryn	Rare
		10/22/31	Plum	Penryn	Rare
		9/26/32	Plum	San Jose	Rare
	{ Latest.....	12/ 3/29	Cattail	Penryn	Rare
		11/17/32	Cattail	Penryn	Rare
		11/17/32	Reed	Stockton	Common

* Plum is used in this table to include "prune."

TABLE 4—(Concluded)

Form	Occurrence	Date	Host	Locality	Abundance
Males	{ Earliest	{ 11/ 8/28	Cattail	Penryn	Common
		{ 10/18/29	Cattail	Penryn	Rare
		{ 10/21/32	Plum	Linden	Rare
		{ 10/28/32	Cattail	Penryn	Common
	{ Latest	{ 12/ 3/29	Cattail	Penryn	Rare
		{ 11/17/32	Reed	Stockton	Common
		{ 11/17/32	Cattail	Penryn	Common
Oviparous females	{ Earliest	{ 10/16/28	Plum	Penryn	Common
		{ 10/29/28	Plum	Davis	Rare
		{ 10/18/29	Plum	Penryn	Rare
		{ 10/25/29	Plum	Davis	Common
		{ 9/26/30	Plum	San Jose	Rare
		{ 11/ 3/30	Plum	Linden	Common
		{ 10/22/31	Plum	Penryn	Rare
		{ 12/ 3/32	Plum	San Jose	Rare
	{ Latest				

though covered with soot. In heavy infestations the white molted skins stick in the excrement until the trees may appear light gray.

With the approach of warm summer weather, the fundatrigeniae give birth to young which develop into migrantes. As the summer advances the fundatrigeniae abandon the older leaves and congregate on the new, succulent growth at the tips of the branches. The young migrantes do not move in this manner, so that they are frequently found almost unmixed with fundatrigeniae on the older, lower leaves.

The fundatrigeniae are unable to endure the high midsummer temperatures of the Sacramento and San Joaquin valleys. They escape destruction for a time by releasing their hold on the lower surfaces of the leaves and allowing their bodies to hang vertically downward, suspended by the proboscis and one or both pro-tarsi. On hot days all of the aphids assume this position and remain thus throughout the middle of the day. But even this expediency proves insufficient in the interior valleys, and all of the fundatrigeniae are killed by the high temperatures. After the first period of unusually warm weather, myriads of dead fundatrigeniae can be found suspended to the lower surfaces of the exposed leaves, while a few survivors may be found in the coolest, shady portion of the tree. These few stragglers are killed by predators, or recurrent warm weather, so that orchards in the Sacramento and San Joaquin valleys are normally quite free from aphids by the middle of August.

In the Santa Clara and Sonoma valleys a few of the fundatrigeniae are able to withstand the hottest days of summer. In these cooler coastal

valleys, either a large percentage of the aphids are killed by the heat, or the fundatrigeniae are influenced to produce exclusively migrantes. However, a few escape and continue the line of fundatrigeniae. During July these survivors are very rare, but with the advent of cool fall weather they give rise to colonies. These colonies may persist until the leaves drop from the trees. They have misled many observers and have initiated the idea that this species was able to live on the trees year after year without the intervention of an alternate host. While it is true that in the coastal valleys the aphids or their eggs may be found on the trees at any time of the year, it is not true that they can survive a year on the trees in the absence of an alternate host. In the Santa Clara Valley the writer has frequently seen colonies of fundatrigeniae which persisted on the trees in considerable numbers until the arrival of gynoparae from secondary hosts. The gynoparae soon gave rise to oviparous females, so that the colonies often contained fundatrigeniae, migrantes, gynoparae, oviparous females, and males.

In northern California, the egg alone possesses ability to endure the winter. The ability to produce eggs is restricted to the oviparous females; and the ability to bear oviparous females is restricted to gynoparae. The spring forms on the primary hosts, that is, the fundatrigeniae and migrantes, cannot give rise to forms capable of depositing eggs. The writer has closely observed field colonies of fundatrigeniae on experimental trees in a lath-house at San Jose during the fall of 1930 and of 1932. They persisted until all the leaves fell from the trees in the early winter, but at no time were other forms than fundatrigeniae and migrantes produced.

Migrantes are produced by the fundatrigeniae over a long period of spring and summer, as indicated in table 4. They occur in maximum numbers on the trees during the latter part of June and early part of July. As the fourth-instar nymphs, or "pupae" molt to the adult stadium, they shed their pulverulent patches with the exuvium and appear glabrous.

Blakey⁽⁶⁾ misinterpreted this phenomenon as follows: "There is a certain proportion of the winged forms about the third generation that divest themselves of their mealy covering, no doubt in preparation for migration." On the contrary, newly molted, glabrous specimens do not leave the primary host but remain there for several hours or even one or two days, until fully hardened and a conspicuous pulverulence has appeared.

The presence of migrantes on the trees has led to the popular misconception that these alate forms are responsible for the spread of this

species from tree to tree and from orchard to orchard. A number of publications record this idea as a fact. Banks⁽⁴⁾ states "Winged specimens are occasionally developed which migrate to other trees." Blakey⁽⁵⁾ states: "In August winged females are produced [which] only travel from place to place on the same tree." Theobald⁽⁶⁸⁾ states: Migrants "fly from tree to tree." Theobald,⁽⁶¹⁾ referring to migrants, states: "These alatae fly away, some to settle on other plums. . . ." Willcocks⁽⁶⁴⁾ states that sum-

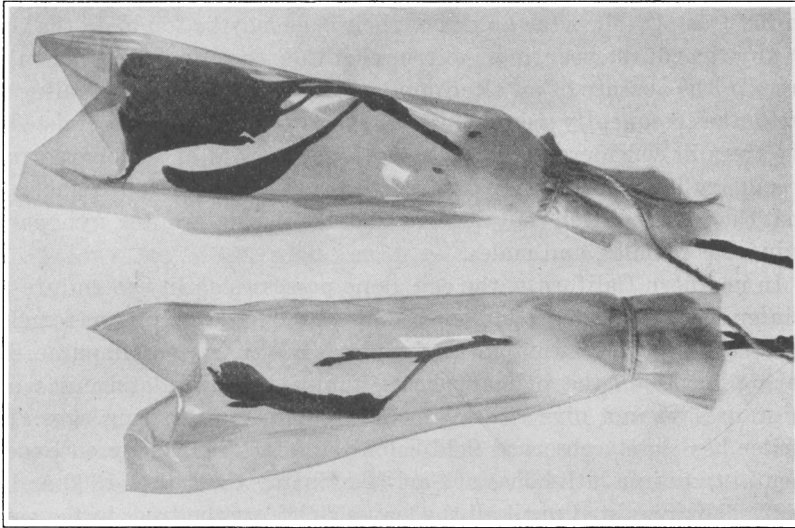


Fig. 11.—Cellophane bags used to cage aphids on trees in the field.

mer migrants "fly off to other apricot or peach trees. . . ." In addition, all taxonomists who saw fit to describe the aphids from the primary hosts as a distinct species, denied the fact of alternation of host plants, and implied that migrants moved only to other primary hosts.

The question of the spread of this species in the orchards by the medium of the migrants is of primary importance to fruit growers concerned. In order to shed additional light on this point, the writer during the seasons of 1929–1932 repeatedly caged migrants on plum and prune trees. Transparent paper bags, described by Smith⁽⁵⁴⁾ and shown in figure 11, and cloth cages out of doors and in a lath-house were used. Both types of cages were shown to be successful when used to confine any particular form on its proper host. Migrants when confined to plum or prune, failed to settle on the leaves, but walked or flew about the cage. At the expiration of 3 to 5 days, all migrants became moribund, shrunken as though from starvation, and soon died. In no case were

young borne by migrantes on plum or prune. Apparently some peculiar change occurs in the migrans at the time of the fourth molt, which prevents the adult from obtaining nourishment from the plant which constituted the pabulum of the nymphal instars. Consequently, removal to secondary hosts is obligatory in the case of the migrantes, not facultative, as recorded by the above observers; and this alate form *does not* serve to distribute the species from tree to tree or directly from orchard to orchard.

Migrantes do not fly during the warmest part of the day, nor at times of considerable air movement. Their main flight period occurs from 4 to 7 in the evening, on clear, warm, still days. At such times in the latter part of June or early part of July in heavily infested areas the "air becomes full" of flying aphids. While driving 7 miles through a plum-raising section on such an occasion an average of 743 migrantes per square foot struck the windshield of the car.

On several occasions a flight of large numbers of migrantes was observed in the morning. Such a flight was observed at 10 o'clock in the morning on June 14 and 15, 1932, near San Jose. Hundreds of migrantes could be seen in the air, in all directions. The sky was completely overcast on both days, and there was little air drift. The temperature was 60° F on both mornings and the relative humidity 56 and 66 per cent, respectively.

The flight of the aphids is very weak, yet field evidence indicates that migration normally occurs over a distance of some miles. In 1928, all of the secondary hosts were removed for a radius of 4 miles around Davis. The following year the plums there suffered from an unusually heavy infestation of the mealy plum aphid. This indicates that migratory forms easily complete a flight greater than 4 miles.

Large stands of common reed, *Phragmites communis*, occur along the banks of drainage canals in the delta west of Stockton. Multitudes of migrantes arrive on these plants each year, although the nearest plum trees are 20 to 25 miles distant. The migratory tendency is strong in this species, as is shown by the fact that secondary host plants growing in heavily infested orchards, are frequently found to be less infested than hosts several miles distant from a source of migrantes. According to field evidence, this species normally migrates from 10 to 30 miles, and considerably greater distances may be possible. Under favorable conditions of climate and host plants, the mealy plum aphid would extend its range, naturally, at the rate of 60 miles a year: 30 miles would be covered by the migrantes and another 30 miles by the gynoparae and males.

After arriving on the secondary hosts, the migrantes do not imme-

TABLE 5
MODIFICATION OF FALL SEX RATIO ON SECONDARY HOSTS

Colony No.	Locality	Host	Date	Gynoparae		Males	
				Number	Per cent	Number	Per cent
1	Penryn	Cattail.....	10/ 5/28	54	100	0	0
2	Penryn	Cattail.....	10/ 5/28	15	100	0	0
3	Penryn	Cattail.....	{ 11/16/29 11/22/29	7 5	20 10	28 43	82 90
4	Penryn	Cattail.....	{ 10/ 7/30 10/29/30	28 47	93 55	2 39	7 45
5	Stockton	Reed.....	{ 10/ 9/30 10/29/30	7 24	100 63	0 14	0 37
6	Penryn	Cattail.....	{ 10/27/32 10/28/32 10/30/32	5 3 4	71 75 44	2 1 5	29 25 56
			{ 11/ 4/32 11/ 7/32 11/12/32	10 29 0	16 74 0	54 10 7	84 26 100
			{ 11/ 1/32 11/ 4/32	202 149	60 59	133 104	40 41
			{ 11/ 6/32 11/11/32 11/14/32 11/17/32	33 3 13 2	45 12 32 5	41 23 28 37	55 88 68 95
			{ 11/ 1/32 11/ 4/32	35 33	25 15	105 186	75 85
			{ 11/ 6/32 11/11/32 11/14/32 11/17/32	8 3 3 7	13 6 6 12	55 49 47 52	87 94 94 88
8	Penryn	Cattail.....	{ 11/ 1/32 11/ 4/32 11/ 6/32 11/11/32 11/14/32 11/17/32	35 33 8 3 3 7	25 15 13 6 6 12	105 186 55 49 47 52	75 85 87 94 94 88
9	Stockton	Reed.....	{ 10/21/32 10/30/32	160 55	86 70	25 24	14 30
10	Stockton	Reed.....	{ 11/ 1/32 11/ 4/32 11/ 6/32	246 556 25	78 76 26	68 175 73	22 24 74
			{ 11/ 1/32 11/ 4/32 11/ 6/32	61 272 48	85 76 48	11 87 53	15 24 52
			{ 11/ 1/32 11/ 4/32 11/ 6/32	62 285 31	78 76 60	17 89 21	22 24 40
12	Stockton	Reed.....	{ 11/ 1/32 11/ 4/32 11/ 6/32	62 285 31	78 76 60	17 89 21	22 24 40
			{ 11/ 8/32 11/11/32 11/14/32 11/17/32	39 26 23 5	53 39 29 5	35 41 56 103	47 61 71 95
			{ 11/ 8/32 11/11/32 11/14/32 11/17/32	29 40 19 20	40 51 40 20	44 38 28 82	60 49 60 80
			{ 11/ 8/32 11/11/32 11/14/32 11/17/32	44 36 43 116	45 34 37 32	53 71 74 246	55 66 63 68
13	Stockton	Reed.....	{ 11/ 8/32 11/11/32 11/14/32 11/17/32	39 26 23 5	53 39 29 5	35 41 56 103	47 61 71 95
14	Stockton	Reed.....	{ 11/ 8/32 11/11/32 11/14/32 11/17/32	29 40 19 20	40 51 40 20	44 38 28 82	60 49 60 80
15	Stockton	Reed.....	{ 11/ 8/32 11/11/32 11/14/32 11/17/32	44 36 43 116	45 34 37 32	53 71 74 246	55 66 63 68

diately settle down, but rather walk about until they encounter other migrantes resting on the leaves, then settle in the immediate vicinity. As a result of this gregarious tendency, migrantes are generally found in compact colonies on the secondary hosts and appear to have been developed there. A typical colony on a cattail blade on June 11, 1929, extended for 15 inches (on one side of the leaf only) and was composed of 148 migrantes.

TABLE 6
SUMMARY OF SEX RATIOS, 1932

Date, 1932	Penryn, on cattails		Stockton, on reeds	
	Total aphids	Per cent males	Total aphids	Per cent males
October 21.....	185	13.1
October 27.....	7	28.6
October 28.....	4	25.0
October 30.....	9	55.6	79	30.4
November 1.....	475	50.1	465	20.6
November 4.....	536	64.2	1,464	24.0
November 6.....	137	70.1	151	58.6
November 7.....	39	25.6
November 8.....	244	54.1
November 11.....	78	92.3	252	59.5
November 14.....	91	82.4	243	65.0
November 17.....	98	90.8	572	75.3

When space permits, the migrantes, after becoming established on a secondary host, move their bodies around in a circle with the proboscis as center. As a result a circle of white powder is deposited on the leaf. The radius of this circle is roughly equal to the length of the body of the migrant. Curiously, this rotation of the body does not twist and break the inserted stylets of the proboscis.

On the first or second day of their existence on the secondary host, the migrantes begin the parthenogenetic viviparous production of alienicolae (plate 1, A). These are apterous parthenogenetic viviparous females identical in appearance to the fundatrigeniae. The first alienicolae give rise to other alienicolae and this cycle is repeated for about three to ten generations. On common cattail, *Typha latifolia*, the alienicolae are almost always found packed in dense colonies on the inner, or flat, surface of the leaf. They seek shade and are usually found on that portion of the blade which receives the maximum of shade during the day. They are never found crowded between the leaf base and the stem, as is the case with the majority of other aphids found on the cattail.

On *Phragmites communis* they prefer the lower surfaces of the leaves,

although large colonies are sometimes found on the dorsal surfaces of the leaves. On both of these hosts, but more particularly on the latter, the alienicolae at times produce a drying and killing of the leaf tissue.

Throughout the fall (see table 4 for dates) the alienicolae sporadically produce gynoparae, interspersed with other alienicolae. Shortly after the appearance of gynoparae in large numbers, a few alate males are found. These are apparently likewise produced by unmodified alieni-

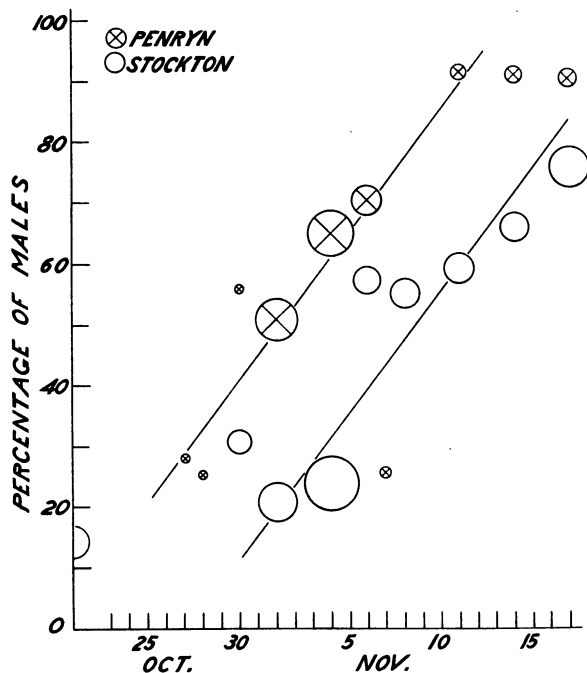


Fig. 12.—Trend in the sex ratio on secondary hosts. Areas of circles are proportionate to number of aphids in each count. Straight lines fitted by eye. (Data from table 6.)

colae. As winter approaches the number of males produced increases while the number of gynoparae produced decreases, as shown in table 5. The data presented in table 5 consist of counts made on specimens newly collected in the field or reared a few days later from material brought to the laboratory. Adults were identified as male or female by mounting on slides in euparal and examining genitalia and number of sensoria on antennal segment V. Later, counts were made by liberating living specimens on a window. The transmitted light accentuated their color differences, so that color, general size, and shape were used to classify them. These counts were checked periodically by microscopical examination.

For purposes of clarification and generalization the data obtained in 1932 have been summarized in table 6, and presented graphically in figure 12. The relative areas of the circles roughly represent the proportions of aphids used in determining each percentage. The straight lines representing the rate of increase of percentage of males on cattails at Penryn and on reeds at Stockton, have been fitted by eye. If the posi-

TABLE 7
RATE OF PRODUCTION OF OVIPAROUS FEMALES BY GYNOPARAE

Gyno-para No.	Day after arrival on primary host										Total young	Total life of gynoparae on plum, days
	1	2	3	4	5	6	7	8	9	10		
	Number of young born											
1	1	0	3	5	0	1	0	0	0	0	10	29
2	5	3	1	0	1	1	0	0	0	0	11	17
3	4	3	1	0	1	1	1	0	0	1	12	35
4	3	2	1	1	1	1	0	0	0	0	9	35
5	7	1	0	2	0	0	0	0	0	0	10	10
6	7	1	1	1	0	0	0	0	0	0	10	26
7	3	3	1	1	1	1	0	0	0	0	10	39
8	0	0	4	1	2	0	0	1	0	0	8	36
9	6	1	0	1	1	1	0	0	0	0	10	34
10	2	1	3	0	1	0	0	1	0	1	9	34
11	0	3	0	5	0	0	2	0	0	0	10	26
12	4	1	0	1	2	0	1	0	0	0	9	13
13	5	1	0	1	0	0	2	0	0	0	9	23
Totals	47	20	15	19	10	6	6	2	0	2	127	357
Averages	3.6	1.5	1.2	1.5	0.8	0.5	0.5	0.2	0.0	0.2	9.8	27.5

tion of the two straight lines is assumed to be correct, this graph indicates that the season at Penryn is about 7 days in advance of the season at Stockton.

The gynoparae are similar in most respects to the migrantes. The newly molted adults remain 1 or 2 days on the secondary hosts, then fly back to the plum and prune trees. They reach maximum numbers on the trees about the middle of November.

When gynoparae were confined on secondary hosts, they, like the migrantes confined on primary hosts, produced no young. However, when gynoparae were confined on plum or prune they immediately produced young, as shown in table 7.

As indicated in table 7, the gynoparae deposit their complement of young soon after arriving on the primary host, but may live for a considerable time thereafter. Two factors have no doubt fixed this habit of rapid deposition of the oviparous females. These are: firstly, the males

follow soon after the gynoparae, and often arrive on the trees before the oviparous females have matured; and secondly, normal leaf fall is usually initiated during the maturation of the oviparous females, and many of them fall to the ground on the abscised leaves.

The return flight of the gynoparae and males to the primary hosts is of importance to orchardists, since it is at this time only that the orchard receives an infestation. It has previously been shown that the migrantes do not directly distribute this species in the orchards. Certain phenomena, connected with the flight of the gynoparae, have led to much confusion in the interpretation of distribution and occurrence of this species. Numerous observers, particularly growers, have noted that heavy infestations occurred year after year on the same orchards, or on the same part of an orchard, while each year another portion of the orchard repeatedly remained free from aphid attack. As a matter of fact, this phenomenon is the rule, rather than the exception. It has led to the widespread conviction among growers that these aphids live the year round on the trees. The writer has had opportunity to observe on many occasions that trees which yearly showed a heavy infestation were in the immediate vicinity of a windbreak. The flight of the gynoparae is usually nondirective; it consists of a simple fluttering which does little more than maintain the aphid in mid-air. Horizontal movement is achieved by the aid of air currents. When the flying gynoparae enter the sheltered area near a windbreak they cease horizontal movement and after a period of fluttering, alight. Their repeated deposition on these trees is a process similar to "settling out" and is occasioned by the production of a body of stagnant air in the vicinity of a windbreak.

The gynoparae establish themselves on the lower surfaces of the leaves of the plum tree. They likewise manifest gregarious tendencies upon their arrival, but soon settle and generally remain fixed throughout the remainder of their lives.

The immature oviparous females are always found on the lower surfaces of the leaves, usually in close proximity to the gynopara which produced them (plate 1, *B*). At the fourth (last) molt, small circular sensoria-like organs appear on the meta-tibiae of the oviparous females. These structures are believed to serve the purpose of exuding an odorous material to attract the male. The males are certainly attracted to the females in some efficient manner, as is indicated by the following observation: In the fall of 1929, the mealy plum aphid occurred in greatly reduced numbers in Placer County. Only one gynopara, with her young could be found on about 1,000 leaves. Ten colonies were located after considerable search, and observed daily. They varied from 1 to 10 ovip-

arous females. Males may be assumed to have been no more numerous than the gynoparae which preceded them (table 6); yet each colony was visited by a male at least once.

Observations on the sexual cycle in cages, at Penryn in 1929 and at San Jose in 1932, have established the following points: (1) Oviparous females will not deposit eggs prior to copulation. In the absence of males these females remain stationary on the leaves. Such virgin females had lived for over 1 month, at which time death resulted from starvation since the leaves became detached from the twig. (2) A single copulation lasts from 5 to 30 minutes. (3) Males and females may both copulate repeatedly, and at intervals of 15 or more minutes. (4) A single copulation suffices to enable a female to deposit her full complement of eggs, although this process may require several days. (5) Oviposition usually occurs a few hours after copulation. (6) Males often combat for females. (7) Copulation and oviposition occur during the warmer part of the day. (8) Males which matured on secondary hosts at the same time as certain gynoparae, can maintain themselves on plum leaves until these gynoparae have given birth to young, and the young have reached maturity. Such old males successfully copulate and give rise to fertile eggs. Thus the changing sex ratio (fig. 12) is not absolutely essential to the survival of this species. (9) The maximum length of life of an oviparous female, from birth to death, was 49 days.

Oviposition is accompanied by a procedure rarely encountered in the Aphididae. The female backs into the axil of a bud, or occasionally into a depression in the bark. The pale green egg is then extruded slowly over a period of about 2 minutes. Then while standing over the egg, the female scrapes the waxlike rods from the pleurae and venter of the abdomen by means of the meta-tibiae, and applies them to the egg. This process is repeated over and over, slowly, for about 20 minutes and at the end of this period the egg has a uniform coat of white rods (fig. 2) which cause it to appear light gray to the unaided eye.

Several authors^(22, 26, 28, 53) have described the egg as "black and shiny." When a female is removed artificially, immediately after depositing an egg and before the mealy covering has been applied, the egg finally appears black and shining. Such an interruption of the normal process rarely occurs in nature, and the author has not found black and shining eggs occurring naturally.

To gather further information on oviposition, seven cages were used, containing respectively 1, 2, 3, 3, 8, 9, and 37 oviparous females. These females were isolated from males for a few days after maturity, and no eggs were deposited. Males were introduced and egg deposition began a

few hours later. The eggs were counted daily with a hand lens, and the numbers of oviparous females surviving recorded. These data are summarized in table 8.

The total number of eggs is based on a count made with a binocular microscope at the end of the test. One isolated female laid 5 eggs, although the average was 3.3 eggs per female. This table indicates that a large percentage of the eggs are deposited within the first four days after mating.

TABLE 8
RATE OF OVIPOSITION

Day after mating	Number of females	Number of eggs laid	Eggs per female	Mean temp., °C
1.....	37*	22	0.59	11.7
2.....	60	35	.58	17.2
3.....	57	37	.65	18.6
4.....	49	31	.63	16.9
5.....	47	2	.04	15.0
6.....	45	12	.27	9.7
7.....	42	6	.14	9.7
8.....	38	11	.29	15.6
9.....	32	11	.34	12.2
10.....	31	3	.10	16.4
11.....	29	3	.10	17.2
12.....	27	1	0.04	17.2
Total.....	60	196†	3.3	

* Data not recorded for the smaller cages on the first day.

† Microscopic count at end of test.

The average number of eggs which would be deposited on a tree following the arrival of a single gynopara may be computed from tables 7 and 8. This number would be the product of the average number of oviparous females produced by one gynopara, and the average number of eggs laid by one oviparous female, and amounts to 32.3 eggs. Field experience has shown that the arrival of a single gynopara (and one or more males) is sufficient to produce a severe infestation over the entire tree the following spring.

HOST PLANTS

In California the plum aphid is generally limited to three hosts, namely, plum, *Prunus domestica* Linn.; common reed, *Phragmites communis* Trin.; and cattail, *Typha latifolia* Linn. Of these, the two latter are secondary hosts.

In this state plums are usually grown for prune making. The total acreage planted to plums for table fruit and canning is much less than that planted to plums for drying. The four leading varieties used for

prunes, all of which belong to *Prunus domestica*, are Agen (French), Sugar, Sergeant (Robe de Sergeant), and Imperial. The writer has seen all of these heavily infested with *Hyalopterus pruni*.

In the Sierra foothills on the eastern side of the Sacramento Valley, many varieties of plums are grown for table fruit. In this area many blocks of Japanese plums, *Prunus salicina* Lindl. are grown contiguously with common garden plums, *Prunus domestica*. The varieties of

TABLE 9
HOSTS ACCEPTABLE TO NEWLY HATCHED FUNDATRICES
(Ten aphids per cage)

Cage	Date hatched, 1932	Trial host	Observations on aphids			
			March 17	March 21	March 27	April 11
1	March 6	Grand Duke plum.....	normal	normal	normal	about 200 aphids
3	March 12	Santa Rosa plum.....	normal	normal	normal	all dead
2	March 11	J. H. Hale peach.....	abnormal	all dead
6	March 12	Mayflower peach.....	abnormal	all dead
4	March 12	Mission fig.....	abnormal	all dead
5	March 12	Bing cherry.....	abnormal	abnormal	all dead
7	March 13	Bosc pear.....	normal	normal	normal	all dead
8	March 13	Comice pear.....	normal	normal	normal	all dead

Prunus domestica have nearly all been found to be infested by mealy plum aphid but not a single specimen of this species has been found on any of the varieties of *Prunus salicina*. It may be concluded that under California conditions, and probably elsewhere, Japanese varieties and most, if not all, Japanese hybrid varieties, are immune to plum-aphid attack.

Although *Hyalopterus pruni* has been recorded from many other species of *Prunus* in various parts of the world, there are but two reports of any other *Prunus* host in California. These reports^(12, 22) pertained to slight infestations on apricot (*Prunus armeniaca* Linn.). The writer has at no time found *Hyalopterus pruni* occurring naturally on apricot. During the spring of 1931 large numbers of fundatrigeniae were transferred from plum to apricot and peach trees in cages like those shown in figure 11. No young were born on the peach and the aphids were all dead within a few days after transfer. Young were born on the apricot and a strong colony developed.

In order to avoid the possible complicating factor of individual adaptation of plum prior to transfer, or of adaptation of the parthenogenetic line, hosts were tested during the spring of 1932, using newly hatched fundatrices. The results are shown in table 9.

The results presented in table 9 are in harmony with field observations. The Santa Rosa plum is a variety of *Prunus salicina*, the Japanese plum, and is not a host under field conditions.

Immunity under field conditions might be the result of selection on the part of gynoparae. To test this hypothesis, ten gynoparae and ten males were confined on each of several hosts with the results indicated in table 10.

TABLE 10
HOSTS ACCEPTABLE TO GYNOPARAE AND MALES
(Ten each per cage)

Trial host	Number of oviparous females born at end of 9 days	Alates surviving after 9 days	Trial host	Number of oviparous females born at end of 9 days	Alates surviving after 9 days
Moorpark apricot.....	70	17	<i>Prunus americana</i>		
Moorpark apricot.....	0	20	(wild).....	71	7
<i>Prunus armeniaca</i>			Purple leaf myro-		
(wild).....	0	0	balan.....	48	6
Mayflower peach.....	30	4	Bing cherry.....	0	0
J. H. Hale peach.....	0	0	Bartlett pear.....	0	0
Grand Duke plum....	72	19	Delicious apple.....	0	3
Wickson plum.....	4	15	Black fig.....	0	0

In this test several partial failures can be traced to the fact that the leaves abscised early and the aphids died of starvation. This was the case with Mayflower peach, J. H. Hale peach, *Prunus armeniaca* (wild) and the second cage on Moorpark apricot. The Wickson plum is a hybrid, probably *P. salicina* × *P. domestica*.

According to this test, the common garden plum, *Prunus domestica*; peach, *Prunus persica* Sieb. and Zucc.; and apricot, *Prunus armeniaca*, are capable of supporting gynoparae, males, and oviparous females. Field evidence indicates, however, that the alates do not seek the two latter species, under California conditions.

The favorite secondary host of *Hyalopterus pruni* is the common reed, *Phragmites communis*. This is a perennial graminaceous plant belonging to the tribe Festuceae. It is hydrophytic and grows equally well in fresh and brackish marshes. The erect culms generally attain a height of 8 or 10 feet, and carry alternate, lanceolate, flat leaves which are often 2 inches wide at the point of greatest width. Culms arise from submerged stolons which may attain a length of several feet. The aerial portions of this plant are killed by frost each winter, in northern California, and new culms arise each spring. Hence there is no opportunity for *Hyalopterus pruni* to survive the winter on this host. In the latter part of the summer the reed produces a large, loose, terminal panicle which persists

after fruition until after the death of the culm. The panicle becomes silvery white and generally droops slightly to one side. It serves as a ready indicator of this species, as it towers above all other marsh plants. The common reed is widely distributed in California and is particularly abundant along canal and river banks in the deltas of the Sacramento and San Joaquin rivers.

The only other secondary hosts in California, known to the writer, are the common cattail, *Typha latifolia*, and rarely *Typha angustifolia* Linn. The cattail (Typhaceae) is a hydrophytic plant found in shallow, lenitic and lotic fresh-water environments. The radical leaves, 3 to 6 feet tall, are usually flat on the inner surface and slightly convex on the outer. Internally they show a peculiar, porous structure. A few cauline leaves arise from the simple, nonsegmented culm. In this monoecious plant, the staminate flowers are borne in a loose spike immediately above the compact, smooth, velvety, brown cylindrical spike of pistillate flowers.

The aerial portions of this plant likewise are killed by winter frosts. The plants occur in dense colonies, and spread by means of stout, submerged rhizomes. The species is widely distributed in California.

Typha angustifolia is characterized by having the staminate portion of the spike removed an inch or two from the pistillate portion, whereas in *T. latifolia* these portions are contiguous. In Placer County these two species are sometimes found in mixed stands. In such cases, although *T. latifolia* is heavily infested, *T. angustifolia* may support but an occasional small colony.

In Placer County *Typha* is the only secondary host, since *Phragmites* does not occur there. In San Joaquin County, however, *Phragmites communis* and *Typha latifolia* frequently occur in mixed stands, and although *Phragmites* may be heavily infested with alienicolae, no colonies whatsoever have been found on *Typha*. It seems likely that the aphids in Placer County are adapted to cattail, and those in San Joaquin County to reed.

Arundo donax Linn., a host in other parts of the world, is not a host in California. Several stands of this plant have been examined in Placer, San Joaquin, and Santa Clara counties and no plum aphids found on them. Migrants were placed on *Arundo* at San Jose, in cages, but bore no young, and soon died.

Large numbers of diverse plants have been recorded as hosts of the mealy plum aphid in the literature. Many of these plants have been subjected to cage tests at San Jose, and a considerable number have been found unsuited to this aphid. The list on pages 200-201 separates the known host plant species from those which are not hosts.

I. Authenticated hosts of the mealy plum aphid :

NAME GIVEN IN LITERATURE	PRESENT ACCEPTED NAME
<i>Arundo</i> <i>Arundo donax</i> Linn. (giant reed)
<i>Arundo donax</i>	
<i>Arundo phragmites</i>	
<i>Typha latifolia</i> <i>Typha latifolia</i> Linn., common cattail
Cattails	
<i>Typha angustifolia</i> Linn. <i>Typha angustifolia</i> Linn.
<i>Phragmites communis</i> <i>Phragmites communis</i> Trin., common reed
Reed grass	
<i>Phragmites</i>	
<i>Phragmites phragmites</i>	
<i>Phragmites vulgaris</i>	
<i>Phragmites arundo</i> <i>Phragmites karka</i>
<i>Phragmites kirki</i>	
<i>Phragmites kiski</i> <i>Prunus domestica</i> Linn., common garden plum
Plum and prune	
<i>Prunus domestica</i>	
<i>Prunus</i> sp.	
European plum	
Pershores	
American plum	
Greengages	
Violet Gage plum	
Gages	
Czar plum	
Victoria <i>P. domestica</i> var. <i>insilitia</i> Bailey (Damsons, Bullaces, Mirabelles, St. Juliens)
Monarch	
<i>Prunus insilitia</i> <i>Prunus spinosa</i> Linn., blackthorn or European sloe
Damson	
<i>Prunus spinosa</i> <i>Prunus persica</i> Sieb. & Zucc., peach
Sloe	
Blackthorn <i>Prunus communis</i> Fritsch, almond
Peach	
<i>Prunus persicae</i>	
<i>Prunus communis</i> <i>Prunus armeniaca</i> Linn., common apricot
Almond	
<i>Prunus amygdalis</i> <i>Prunus americana</i> Marshall, American wild plum
<i>Amygdalus communis</i>	
Apricot <i>Prunus persica</i> var. <i>nucipersica</i> Schneid., nectarine
<i>Prunus armeniaca</i>	
<i>Prunus americanus</i>	
Nectarine	

II. Species formerly listed as hosts which are not hosts:

NAME GIVEN IN LITERATURE	PRESENT ACCEPTED NAME
<i>Calamagrostis arenarius</i>	} <i>Calamagrostis epigeios</i> Linn.
<i>Arundo epigeios</i>	
<i>Arundo erigyros</i>	
<i>Calamagrostis littorea</i>	
<i>Juncus</i> sp.	<i>Juncus</i> sp., rushes
Tules	<i>Scirpus acutus</i> Muhl., common tule
<i>Scirpus lacustris</i>	<i>Scirpus lacustris</i> Vahl., great bulrush
<i>Scirpus caespitosus</i>	<i>Scirpus caespitosus</i> Linn.
<i>Amophila arundinacea</i>	<i>Ammophila arenaria</i> Link, beach grass
<i>Salix</i>	<i>Salix</i> sp., willow
<i>Salsola kali</i>	<i>Salsola kali</i> Linn., Russian thistle
<i>Umbellularia californica</i> Nutt.	<i>Umbellularia californica</i> Nutt., California laurel
Grape	<i>Vitis</i> sp., grape
<i>Pyrus malus</i>	} <i>Pyrus malus</i> Linn., apple
Apple	

III. Doubtful hosts species:

NAME GIVEN IN LITERATURE	PRESENT ACCEPTED NAME
<i>Poa annua</i>	<i>Poa annua</i> Linn., * common blue grass
<i>Elymus arenarius</i>	<i>Elymus arenarius</i> Kinn., * sea lyme-grass
<i>Phalaris arundinacea</i>	<i>Phalaris arundinacea</i> Linn., * reed canary grass
<i>Dactylis glomerata</i>	<i>Dactylis glomerata</i> Linn., * or- chard grass
<i>Chenopodium album</i>	<i>Chenopodium album</i> Linn., * white pigweed
<i>Phaseolus vulgaris</i>	<i>Phaseolus vulgaris</i> Linn., * bean
<i>Buddleia madagascariensis</i>	<i>Buddleia madagascariensis</i> Lam.
<i>Prunus serotina</i>	<i>Prunus serotina</i> Ehrh., wild black cherry
<i>Prunus pissardi</i>	<i>Prunus cerasifera</i> var. <i>pissardii</i> Koehne
Choke cherry	<i>Prunus virginiana</i> Linn., choke cherry

* Probably not a host.

In the above list a number of recorded hosts have been discredited for the following reasons:

Calamagrostis epigeios: Börner⁶⁹ after examining this plant repeatedly, failed to discover *Hyalopterus pruni* on it. From this and the nature of the plant, he concluded that it was not a host.

Juncus sp.: The only authority for this host is Walker.⁽⁶²⁾ His observations throughout indicate a lack of familiarity with *Hyalopterus pruni*. Since no other observer has recorded *H. pruni* on *Juncus*, this host may be rejected.

Phragmites kirki and *P. kiski*: These names were originated by van der Goot⁽²⁹⁾ and Theobald.⁽⁶¹⁾ A. S. Hitchcock⁴ writes: "There is no *Phragmites kirki* (nor *kiski*). It may be a misspelling for *P. karka*, a species of eastern Asia."

Scirpus acutus, *S. lacustris*, *S. caespitosus*: The writer has repeatedly examined several species of *Scirpus* in the field and at no time found *Hyalopterus pruni* on them. In addition attempts were made to colonize them on *Scirpus acutus*, in cages, without success.

Ammophila arenaria: The leaves of this species are hard and involuted to form a smooth rod. It occurs in exposed situations in shifting sand dunes. It bears no resemblance to the known hosts of the plum aphid. Cage tests at San Jose demonstrated that the aphid cannot survive on it.

Salix: This host was cited only by Walker⁽⁶²⁾ and has been discredited by Theobald.⁽⁶¹⁾

Salsola kali: This plant was recorded as a host by Walker,⁽⁶²⁾ and cited by Patch.⁽⁵⁰⁾ Walker's observations indicate that he was not dealing with the plum aphid, since he recorded a wingless male. Cage tests at San Jose indicated that the plum aphid cannot survive on *Salsola kali*.

Umbellularia californica: W. M. Davidson⁽¹⁵⁾ collected migrantes on this plant, during their normal movement to secondary hosts. They were transients.

Vitis: The plum aphid was cited on grape by Scopoli, according to Theobald.⁽⁶¹⁾ Other investigators have sought the species in vain on this plant.

Pyrus malus: Tavares⁽⁵⁷⁾ is the only authority for the occurrence of the mealy plum aphid on apple. In view of the abundance of both apples and mealy plum aphids, more records would be expected if apple is actually a host. Cage tests at San Jose (see also table 8) indicated that the plum aphid cannot survive on apple.

From a study of the literature the following generalization can be drawn: (1) In the colder regions of the temperate zones *Hyalopterus pruni* attacks plums chiefly or exclusively, and *Phragmites communis* is the usual secondary host. (2) In the warmer temperate and tropical regions *H. pruni* attacks chiefly peach, apricot, and almond, while *Arundo donax* and *Phragmites communis* serve as secondary hosts. This peculiar host specificity, related to climate, is no doubt the result of the

⁴ Personal communication, 1932.

importation of the normally plum-feeding aphid into the warmer regions where plums are rare, and finally into the tropics where plums are absent, with the result that the aphid became adapted to peach, apricot, and almond.

PARASITES AND PREDATORS

Although Gillette and Taylor⁽²⁸⁾ stated that the mealy plum aphid "seems to have few natural enemies . . .," the majority of observers are of the opinion that such enemies are numerous. The writer has seen the plum aphid reduced nearly to extinction by predators, in wide areas of California.

Fundatrices appeared in enormous numbers on the opening buds of plum in the Linden area, early in the spring of 1930. Their abundance predicted an abnormally heavy infestation later in the spring. However, at about the time the fundatrices were establishing colonies of fundatrigeniae, several species of *Podabrus* occurred in large numbers. They reduced the aphid population so effectively that many orchards were virtually free from attack that year.

At the peak of the occurrence of fundatrigeniae, they are found to be heavily attacked in all infested areas of California, chiefly by coccinellids, several species of *Podabrus*, and several species of syrphids. Hemerobiids, chrysopids, and the internal parasite *Praon simulans* (Prov.) are present, but not important factors in reducing the numbers of aphids. Dobrovliansky⁽²⁹⁾ reared a hyperparasite, *Lygocerus* sp., from *Praon flavinode* Hal. in Russia. This hyperparasite has not been reared by the writer in California. It may be present, however, and may account for the lack of efficiency of *Praon simulans* in reducing the plum aphid more effectively.

The same species which feed on the plum aphid in the orchards in California, likewise attack it on secondary hosts. On cattails in Placer County, syrphid larvae have predominated during the last five years. On reeds in San Joaquin County, coccinellids and larvae of *Leucopis* have been most abundant.

During the fall of 1932 at San Jose, an unidentified species of *Geocoris* occurred on trees infested with plum aphids. Both nymphs and adults of *Geocoris* frequently impale plum aphids on their probosces after the manner of *Orius*. But the struggles of the impaled aphids apparently frightened these pseudo-predators, so that they usually withdrew. Occasionally, however, an aphid was eaten.

The total number of species which feed on the mealy plum aphid is, no doubt, very great. No serious attempt has yet been made to discover

and identify them. A number of investigators have, however listed occasional parasites and predators which have come to their attention. These are grouped phylogenetically in table 11.

TABLE 11
PARASITES AND PREDATORS WHICH FEED ON MEALY PLUM APHID

Order and family or species	Country	Authority*
Neuroptera		
Hemerobiidae, various species	U.S.A.	(16)
<i>Chrysopa cognata</i>	Japan	(45)
<i>Chrysopa californica</i>	U.S.A.	(63)
<i>Chrysopa</i> sp.	Morocco	(38)
Chrysopidae, various species	U.S.A.	(16)
Hemiptera		
<i>Triphleps (Orius)</i> sp.	U.S.A.	(16)
<i>Geocoris</i> sp.	U.S.A.	(writer)
Coleoptera		
<i>Hippodamia convergens</i> Guerin	U.S.A.	(16, 26)
<i>Coccinella septempunctata</i>	Morocco	(38)
<i>Scymnus subvillosus</i> var. <i>pubescens</i>	Morocco	(38)
<i>Scymnus suturalis</i>	Morocco	(38)
<i>Donacia clavipes</i>	England	(42)
<i>Cantharis fusca</i> L.	Russia	(36)
<i>Cantharis obscura</i> L.	Russia	(36)
<i>Podabrus comes</i> Le C.	U.S.A.	(16)
<i>Podabrus binotatus</i> Le C.	U.S.A.	(16)
<i>Podabrus pruinosis</i> Le C.	U.S.A.	(writer)
<i>Telephorus divisis</i> Le C.	U.S.A.	(16)
Diptera		
Syrphidae, various species	{ U.S.A. France Russia	(16) (48) (20)
<i>Catabomba pyrastris</i> Lin.	U.S.A.	(11, 16)
<i>Syrphus albomaculatus</i>	Morocco	(38)
<i>Syrphus americanus</i> Wied.	U.S.A.	(11)
<i>Eupeodes volucris</i> O. S.	U.S.A.	(26)
<i>Leucopis</i> sp.	U.S.A.	(16)
<i>Leucopis annulipes</i> Zett.	Germany	(7)
<i>Bremia</i> sp.	Russia	(20)
<i>Aphidoletes meridionalis</i>	U.S.A.	(18)
Hymenoptera		
Hymenopteran, undetermined	Morocco	(38)
<i>Praon flavinode</i> Hal.	Russia	(20)
<i>Praon simulans</i> (Prov.)	U.S.A.	(writer)

* Numbers in parentheses refer to "Literature Cited," at the end of the paper.

SUMMARY

The proper name for the mealy plum aphid is *Hyalopterus pruni* (Geoff.).

The mealy plum aphid is widely distributed in the world: it is reported from 27 countries, and from 15 states in the United States.

The stages in the annual cycle are: egg, fundatrix, fundatrigenia, migrans, alienicola, gynopara, alate male, and oviparous female. Each instar of these forms is described.

Minute differences exist between the two alate stages, migrantes (named *Hyalopterus pruni* by Fabricius) and gynoparae (named *H. arundinis* by Fabricius).

The hatching period is about two weeks in length.

The seasonal occurrence of each form is given.

Migrantes cannot survive on plum, after the fourth molt, and do not serve to distribute the aphids from tree to tree. They can survive only on the secondary hosts. Distribution of this species in the orchards is achieved only in the fall during the return flight of the gynoparae. Each migration may cover 30 miles, which makes possible natural spread at the rate of 60 miles a year.

The percentage of males on the secondary hosts increases throughout the fall and approximates 100 per cent late in November.

Each gynopara produces an average of 9.8 oviparous females.

Oviparous females deposit an average of 3.3 eggs each.

The primary hosts of the mealy plum aphid in California consist only of varieties of *Prunus domestica* Linn. The secondary host in Placer County is the cattail, *Typha latifolia* Linn.; in San Joaquin County the secondary host is the common reed, *Phragmites communis* Trin.

Many hosts cited in the literature have been tested experimentally and found not to be acceptable to the plum aphid.

Numerous species of parasites and predators attack the plum aphid. Syrphid larvae predominate in Placer County, coccinellids and *Leucopis* in San Joaquin County.

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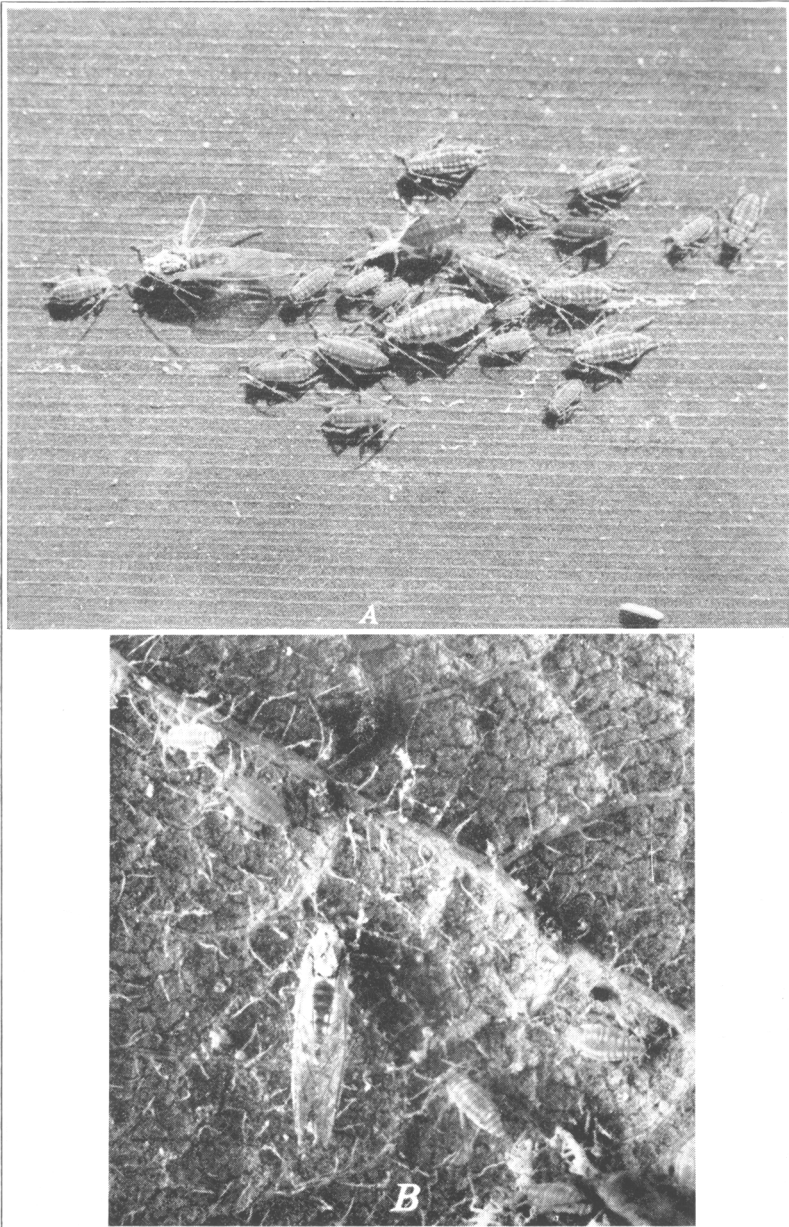


Plate 1.—A, Young colony on leaf of cattail. The migrans (alate) has given birth to a number of alienicolae. One of these (largest apterous specimen) is mature and has borne a few young, which are located directly in rear of the alienicola. Note specimen molting, newly molted specimen without mealy covering, and shell of syrphid egg at lower right.

B, Gynopara and young oviparous females on plum leaf.