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ERIOPHYID STUDIES XII *

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Eriophyid Studies XI appeared in the Bulletin of the California Department of Agriculture, Vol. 30, No. 2, p. 192, May 26, 1941. Installment XII is an account of experimental taxonomy illustrating female dimorphism, or alternation of generations, in a Phyllocoptine mite, *Oxypleurites aesculifoliae* K., the buckeye rust mite. This mite serves as an example of the life histories of a limited number of other species on deciduous trees and shrubs, as explained below. Species having two kinds of females are deuterogynous. In the case of *Oxypleurites aesculifoliae*, one female resembles the male and is therefore the primary type on which the taxonomy of the species is based. The other female type is structurally different from the primary type, has no male counterpart, and is therefore the secondary female. Thus the primary female is the *primogyne*; the secondary female the *deutogyne*.

The buckeye rust mite, *Oxypleurites aesculifoliae* K., is common on buckeye leaves in many parts of California, and causes more or less severe rusting of both leaf surfaces. Examination of mite infested buckeye leaves in late May and throughout June usually will reveal a high population of individuals which can be separated into two types. One type is generally flattened, with broad back plates bearing a central ridge and projecting as lateral lobes. This is the typical *Oxypleurites* mite, the genus being characterized by the laterally projecting lobes or points. The other type of mite, while possessing dorsal setae, featherclaws and genitalia, similar to the *Oxypleurites* type, is more cylindrical, lacking the dorsal ridge and lateral lobes, and possessing narrower back plates. This latter type runs to the genus *Phyllocoptes* on conventional taxonomic characters. Thus we apparently have two associated species on the buckeye leaves: an *Oxypleurites* species living with a degenerate Phyllocoptiform species. These two types can be easily distinguished with a binocular magnification of about 30 diameters.

If these mites are examined critically under about 450 diameters the *Oxypleurites* type will be found to consist of males and females, whereas the Phyllocoptiform mites are of females only.

When these two types of mites were taken from the leaves on which they had developed during April and May of 1941, and were isolated in separate cells on clean buckeye leaves, there was no reproduction in the cells containing the Phyllocoptiform mites. On the other hand the *Oxypleurites* individuals reproduced vigorously and many new *Oxypleurites* adults began to appear in the cells in about two weeks or less. Shortly thereafter a check of the *Oxypleurites* cells revealed adult Phyllocoptiform mites appearing in small numbers. This indicated that both kinds are the same species and that the mite exhibits two types of structurally distinct females. Since males only

* A preliminary report on this subject was presented at the American Entomological Society meeting, San Francisco, December 31, 1941.

exist in the *Oxypleurites* form, it constitutes the primary type. The Phyllocoptiform mite is the secondary form or deutogyne.

The buckeye loses its leaves in mid-July.* So in early August when the leaves were gone, examination of the resin covered terminal buds revealed no mites. But on proceeding down the stem 6 inches to a foot or more, many inactive semidesiccated mites were found tucked into bark cracks, old undeveloped buds and cricket egg punctures. Examination of these mites under 450 diameters revealed them to be the deutogynes of the buckeye rust mite. No primogynes were present. Thus the function of the deutogyne is shown to be aestivation followed by hibernation and explains why they will not reproduce the season they are developed.

The problem then remained to reverse the above process and induce the deutogynes to reproduce. Attempts during the summer of 1941 to shock the inactive semidesiccated aestivating deutogynes into activity by refrigeration were unsuccessful. Midwinter examination of deutogynes in the buckeye twig crevices revealed they had recovered from their desiccation and would become active in a warm room.

Small potted buckeye plants were brought indoors in late January and soon began to develop leaves. On February 18, 1942, swelling buckeye buds from outdoor trees were examined and proved to contain active deutogynes under the outer scales. These were placed in cells on buckeye leaves on February 18 and 19. The first egg was observed two days later, and on February 26, eight days after starting the first experiments, the first primary mite appeared.

We have then the following facts on which to base the conclusion that *Oxypleurites aesculifolia* is deuterogynous; 1. The *Oxypleurites* type produced both Phyllocoptiform mites and *Oxypleurites* mites; 2. The Phyllocoptiform mites (deutogynes) do not reproduce the season they develop on the leaves; 3. Only Phyllocoptiform mites can be found hibernating; 4. Phyllocoptiform mites produce *Oxypleurites* mites on the leaves after aestivating and hibernating; 5. Check cells on the leaves open or closed, did not develop any mites; 6. The potted buckeye plants used in these experiments never developed any general infestation during 1941.

The life history of the buckeye rust mite is as follows: The Phyllocoptiform mites, i.e., deutogynes become active in late winter, leave their hibernating quarters on the twigs and when the buds swell in February, penetrate beneath the outer scales. There they feed on the green tissue of the inner scales. With the development of the early spring leaves, the deutogynes lay eggs which hatch into nymphs producing primary mites on the leaves. These primaries soon begin active reproduction of additional primary mites. Beginning about the last of April or early May, new deutogynes appear among the primary types and when full fed, these deutogynes travel down the stems 6 inches or more. There they crawl into crevices or other shelters on the previous season's wood. Thus deutogynes are leaving the leaves through May and until leaf drop in the middle of July. The primary mites are confined to the leaves and green tissue and perish with it,

* These observations are based primarily upon park trees in Sacramento. In other parts of California there is considerable variation from the seasonal timing described here. Buckeye trees immediately adjacent to the ocean may hold their leaves a month or six weeks longer than those in the interior of central California. This will of course lengthen the breeding period of the mites.

although reproduction has largely ceased by early July. The mites prefer the underside of the leaves, but usually there is such a high population that both surfaces are inhabited and considerable leaf "rusting" results. Once the deutogynes attain a suitable crevice they become dormant and partially dry out in late summer. However, winter rain and frost reverse this process and recondition the deutogynes for activity the following spring. There is a high mortality among the deutogynes, principally because of crevice limitation.

This account leaves several important considerations unmentioned. The way the mites travel from host to host is presumably usually by wind. Putnam, 1939 (Seventh ann. Rpt. Ent. Soc. Ont. p. 33), working with *Phyllocoptes fockeui* in Canada, has described what is clearly discerned to be a functional deutogyne, and states that both males and females hatch from eggs laid by overwintering females. He considers that these overwintering females (deutogynes) may have been fertilized before hibernation, since he showed that ordinary unfertilized females (primogynes) produce only males. While the spring progeny of the buckeye *Oxypleurites* deutogynes were not critically examined, it was noted that the first series of primary types contained egg-laying females, indicating either predormancy fertilization of the deutogynes or a deuterotokous reproductive capacity. Putnam further noted that the production of "hibernating forms" seemed correlated with foliage hardening, a speculation consistent in the main with observations on the buckeye mite.

The writer first found these buckeye mites in 1938 and named the deutogyne *Phyllocoptes aesculifoliae*, September 7. The primary type was named *Oxypleurites neocarينات* December 23 of the same year; so *aesculifoliae* is the name of the species by priority.

Two other mites belonging to genera related to *Oxypleurites* have been reared long enough to observe the production of deutogynes by primary types. These are: first, the hawthorne rust mite, *Calepitrimerus armatus* (Nal.), and second, the elderberry mite, *Epitrimerus trilobus* Nal.

The rearing of these three species of mites, all noneconomic, is an illustration of how important facts can be learned about pest species by studying similar noninjurious types. Thus, applying the fact of the existence of dimorphic females as shown by the buckeye rust mite, to the pear leaf rust mite, *Epitrimerus pirifoliae* K., immediately clears up the life history of this latter species. The typical rust mite occurs on pear leaves through much of the warmer weather and then disappears. Examination of winter pear twigs reveals many mites tucked into crevices at the base of the current growth and on the apex of the previous season's wood. The mites are rust mite deutogynes and resemble the pear leaf forms only in dorsal setae position, genitalia and featherclaws. The deutogynes of the pear rust mite are not usually observed on the leaves.

The deutogynes of the apple leaf mite, *Calepitrimerus baileyi* K., hibernate around lateral buds on the fruit spurs. These *Calepitrimerus* deutogynes were named *Phyllocoptes aphrastus* by the writer, illustrating again how these secondaries differ structurally from the primaries, and also showing that they are much less diverse than the primary forms.

This principle of deutero-gyny can not be applied at the present to any Phyllocoptine mites on evergreen trees or shrubs, or on herbs. Examples of such mites known to the writer have not been found to have two female forms. Thus one of the causes for this deutero-gyny in leaf-surface inhabiting Phyllocoptines seems to be correlated with the deciduous nature of their host trees and shrubs. Further observations will be necessary to either explain this or disprove it. A clearer reason for deutero-gyny is based on the frail and almost sedentary condition of Eriophyid nymphs, causing them to develop to the adult as quickly as possible, and indicating that specialized dimorphism for dissemination and hibernating purposes must bear directly on the adult stage. (In Tyroglyphid mites the *Hypopus* is a nymph specialized for wandering.)

Phyllocoptine deutogynes probably have a phylogenetic significance. With the exception of *Rhyncaphytoptus* deutogynes, which have the large beak of that genus, these secondaries are very similar to one another, whereas the primary types are diverse. The primary mites have heavy back plates and thinner sternites, but the deutogynes are less differentiated dorso-ventrally, appearing tougher throughout. The following synopses will serve to indicate the similarities and differences among these mites. Obviously these synopses are only suitable for the purpose of this article and are subject to amplification.

ERIOPHYINAE

Cephalothoracic shield never overhanging beak anteriorly, beak usually moderate in size or small; abdomen wormlike with no dorso-ventral differentiation, at least anteriorly. No species known to be structurally or functionally deutero-gynous, though possibly polymorphic in some cases. Principal genus *Eriophyes*.

PHYLLOCOPTINAE

Cephalothoracic shield nearly always bearing an anterior lobe over beak, or beak large and set at right angles to body; abdomen usually more robust and flattened, with broad back plates; a minority of species wormlike. Certain inhabitants of deciduous trees and shrubs showing deutero-gyny, the deutogynes more wormlike. The known deutero-gynous species fall into the following genera.

- I. Abdomen divided laterally into tergal and sternal areas, the tergum often ridged or furrowed, abdomen often flattened, microtubercles clearly present, at least on sternites; these mites usually more spindleform or angular when viewed from above ----- Primary Types
- II. Abdomen with tergites more resembling sternites by the narrowing of the tergites and increase in their number; tergites always evenly arched; microtubercles weakly developed or absent ----- Gall formers and Deutogynes

PRIMARY TYPES

- a. Beak large, set at right angles to body; (abdomen often wormlike; cephalothoracic shield not always overhanging beak) ----- (Diptilomiopini) *Rhyncaphytoptus*
- a. Beak usually small, projecting obliquely down ----- (Phyllocoptini) b.
- b. Tergites evenly or nearly evenly arched in cross section ----- *Phyllocoptes*
- b. Tergites formed into longitudinal abdominal ridges, furrows, or lateral projections ----- (Epitrimeri) c.
- c. Tergites broader, with lateral teeth or lobes, central ridge present or absent ----- *Oxypleurites* d.
- c. Tergites narrower, no lateral teeth, central ridge ----- d.
- d. Central ridge gradually fading posteriorly evenly with lateral ridges ----- *Epitrimerus*
- d. Central ridge ending abruptly in broad dorsal trough before end of body ----- *Calepitrimerus*

GALL FORMERS AND DEUTOGYNES

- a. Beak large, set at right angles to body: (microtubercles absent) -----
- a. Beak small, projecting obliquely downward ----- (Diptilomiopini) *Rhyncaphytoptus deutogynes*
- b. Microtubercles faint but present ----- (Phyllocoptini) b.
- b. Microtubercles absent ----- c.
- (Epitrimeri) d.

- c. Gall formers (those structurally similar to deutogynes)-----**Phyllocoptes** *
 c. Correlated with mites living on open leaf surfaces-----**Phyllocoptes deutogynes**
 d. Two to four sternites springing laterally from each tergite throughout most of
 body length-----**Oxypleurites deutogynes**
 d. Most tergites covering only one sternite, a minority giving off two or three sternites
 -----**Deutogynes of Epirimerus and Calepitrimerus**

The hibernation position on the host twigs of various species and types of mites is characteristic and important. Thus the Eriophine mites are usually found in or near terminal buds. The pear leaf blister mite (*Eriophyes pyri* Pgst.) for example, spends the winter in a semiactive state in the terminal buds, carrying on both feeding and breeding activities when temperature permits. In contrast to this, the pear leaf rust mite, as has been mentioned above, hibernates as the deutogyne in a dormant condition in crevices and suppressed buds on the previous season's wood. On peach twigs which bear both peach silver mite and the big beaked plum mite, the silver mite may be found in and around buds along the apical 8-12 inches. Below this these mites drop out and the big beaked plum mite may be found.

Examination of Eriophyid literature reveals very little about these dimorphic Phyllocoptine females. Nalepa, 1924, (*Marcellia* Vol. 20, p. 87), in an article entitled, "Polymorphic Eriophyids" did little more than hint that there might be a closer relationship between certain *Epirimerus-Phyllocoptes* associations, than their conventional generic characters would indicate. This whole problem seems to have been little understood.

The following is an annotated list of mite species occurring in California that are known to be deuterogynous.

Rhyncaphytoptus megarostris K.

Keifer—Bul. Cal. Dept. Agr., Vol. 27, p. 305, 1938

The above reference refers only to the primary type. The deutero-gyne has not been characterized but differs mainly from the primogyne in lacking microtubercles. The host is valley white oak, *Quercus lobata* Nee.

Rhyncaphytoptus salicifoliae K.

Keifer—Bul. Cal. Dept. Agr., Vol. 28, p. 230, 1939

Phyllocoptes cornutus Banks

Keifer—Bul. Cal. Dept. Agr., Vol. 30, p. 208, May 26, 1941

Phyllocoptes advens K.

Keifer—Bul. Cal. Dept. Agr., Vol. 27, p. 192, June 22, 1938

This mite was described from lemon, locality Pomona Heights. This is seen now to be a deutogyne of a *Phyllocoptes* species, and in order to correctly characterize the species it will have to be correlated with its primary type.

* For a figure of a gall forming *Phyllocoptes*, see Keifer, Bul. Cal. Dept. Agr. Vol. 27, pp. 192 and 205, June 22, 1938. This is *P. laevigatae* Hassan. The gall forming *P. toxicophagus* Ewing, figured in same article, will run to the key for Primary types because of its dorso-ventral differentiation and strong microtuberculation.

Epitrimerus trilobus (Nal.)

Plates 168, 169

Nalepa—Anz. Akad. Wiss. Wien., Vol. 27, p. 2, 1890 as *Cecidophyes trilobus*.

This mite occurs on elderberry, *Sambucus glauca* Nutt., at Davis, California, and elsewhere in California. It causes silvering of the leaves and some edge curling. The deutogyne is presumably *Phyllocoptes trilobus* Nal. It differs from the primogyne not only in lacking the subdorsal furrows but also in lacking the longitudinal wax bands possessed by the primary form. A cell into which 20 primary mites were placed on September 22, 1941, contained several eggs the following day, numerous nymphs on the 29th, several new primary adults on October 3, and one new deutogyne on October 13. Another cell into which nine primaries were placed on September 22 had produced one deutogyne October 20. The eggs of this species are nearly globular. The plates are of the primary types and deutogyne.

Epitrimerus pirifoliae K.

Plate 167

Keifer—Bul. Cal. Dept. Agr., Vol. 27, p. 309, 1938

The above reference refers to the description of the primogyne and male. The plate included with this article is of the deutogyne.

Calepitrimerus anatis K.

Keifer—Bul. Cal. Dept. Agr., Vol. 29, p. 31, 1940

This description refers to the primary type. The deutogyne has not been characterized. The host is *Amelanchier alnifoliae* Nutt.

Calepitrimerus armatus (Can.)Canestrini—Atti. Soc. Venet.—Trent. Vol. 12, p. 23, 1890 as *Phyllocoptes armatus* (the deutogyne?)Nalepa—Denkschr. Akad. Wiss. Wien., Vol. 77, p. 143, 1904, as *Epitrimerus armatus*.

This mite occurs on Crataegus at San Mateo and Burlingame, California. A leaf cell with six primary type mites placed therein May 25, 1941, produced one deutogyne June 7. Another cell innoculated June 3 with several primary mites contained 13 nymphs, 24 primary adults and six deutogynes on June 23. Three cells innoculated with deutogynes produced nothing. Two check cells failed to produce any mites.

Calepitrimerus baileyi K.

Keifer—Bul. Cal. Dept. Agr., Vol. 27, p. 310, 1938, description of the primary type.

Keifer—Bul. Cal. Dept. Agr., Vol. 29, p. 29, 1940, description of deutogyne as *Phyllocoptes aphrastus*.

The deutogynes of this mite are clustered around the lateral bud on fruit spurs during the winter.

Calepitrimerus vitis (Nal.)Nalepa—Anz. Akad. Wiss. Wien., Vol. 42, p. 268, 1905, as *Epitrimerus*

This mite has been taken on wine grape leaves at Ontario, California, and on native grape near Sacramento.

Oxypleurites cornifoliae K.

Keifer—Bul. Cal. Dept. Agr., Vol. 28, p. 235, 1939

The description refers to the primary type. The deutogyne has not been characterized. The host is *Cornus californicus* C.A.

Oxypleurites aesculifoliae K.

Fig. 10, 11; Plates 165, 166

Keifer—Bul. Cal. Dept. Agr., Vol. 27, p. 307, 1938—description of the deutogyne as *Phyllocoptes aesculifoliae*.

Keifer—Bul. Cal. Dept. Agr., Vol. 28, p. 11, 1939—description of the primary types as *Oxypleurites neocarinatus*.

The egg is a thin surface section of a sphere, flattened below, evenly curved above, about 55-60 μ * in diameter. There are two nymphal stages preceding the adult, though no definite means of distinguishing these by measurement was found. The beak is about as large in the first nymph as in the adult. These nymphal stages have the genital setae, but the genitalia are not present externally. The nymphal abdomen is Eriophyiform, not showing the adult structures. The first nymph is about 65 μ long shortly after hatching, whitish. The second nymph is about 128 μ long when first formed, yellowish-white. The adult primary type is 170-180 μ long, varying from yellow to light orange; the deutogyne is slightly larger and more orange.

The usual position of the adult and nymphal dorsal setae on the cephalothoracic shield on the buckeye rust mite is on the rear shield margin, the setae pointing dorso-caudad in most nymphs. The nymphal illustration on plate 166-NIDA, upper right, illustrates an unusual position of these dorsal setae noted on a few first stage *aesculifoliae* nymphs. This is similar to the dorsal setae of a number of *Oxypleurites* species, but no buckeye rust mite adult has ever been observed to deviate from the usual arrangement.

The shortest period noted from adult to adult through egg, and two nymphs was eight days. The length of life of the primary type adults was not ascertained. They are attached to the green tissue and the buckeye only remains in leaf four months. The deutogynes, on the other hand, if able to survive the summer and winter, live nearly a year.

Table I indicates sample results of experiments designed to induce primary types to produce secondaries. The mites were placed in celluloid rings, "cells," held on the leaves by paraffin. After the mites had been placed in position a coverslip was fastened over the top by melting the paraffin. All mites starting the experiments shown in Table I were removed from leaves or green flower stalks. The term "primaries" is used in preference to "primogynes" since males and females could not be distinguished. The symbols are: P—primary; N—nymph; E—egg; D—deutogyne; double symbols indicate plurals.

Table II shows sample experiments with deutogynes. The first two 1941 cells listed are of secondaries taken from the leaves where they developed. The third 1941 lot is of secondaries taken from aestivation positions on the buckeye twig. The 1942 experiments were started with deutogynes removed from swelling buckeye buds. These 1942

* For μ read μ .

Table 1. Examples of experiments with Primogynes
(For explanation, see text)

May 12, 1941 5 primaries	May 17 EE NN	May 21 Over 22 mites including NN	May 23 11 PP	May 28 Many P, N, E	June 4 5 D Many P, N, E	June 7 Many mites including DD	June 10 Approx. 19 D	June 26 Leaf dying
May 12, 1941 7 primaries	May 17 EE NN	May 19 Many E, N	May 21 2 new P 1 D Many N	May 28 34 P 1 D EE, NN	June 2 2 D Many P, N	June 4 Leaf dying		
May 13, 1941 14 primaries	May 17 EE	May 19 2 N	May 21 14 N	June 26 3 D 57 E, E, N	July 9 Leaf dead			
May 13, 1941 1 primary	May 17 EE	May 19 7 N	May 21 EE 7 N	May 23 Old P dead 10 N, EE, 1 P	May 28 12 P 9 N	June 1 Leaf dead		
May 15, 1941 7 primaries	May 17 EE	May 21 EE 1 N	May 23 NN	May 28 Many N Many P	June 2 Many N Many P	June 4 1 D Many P N, E	June 13 Leaf dead	
May 29, 1941 17 primaries	June 4 EE NN	June 7 Many N	June 10 New PP	June 26 Many P, N, E, D	July 9 Leaf dead			
May 29, 1941 21 primaries	June 6 25 N	June 10 2 D NN, PP	June 16 10 D NN, PP	July 9 Leaf dead				

deutogynes collected in February had been reactivated by the previous winter conditions and had already penetrated beneath the loosening bud scales. In the case of the last listed experiment two new deutogynes appeared on March 12. As the new primogynes had begun egg laying about March 4, and as no deutogyne in the other cells reproduced anything but primogynes, the conclusion is that these new deutogynes are from the primaries. Thus we apparently find the first generation of primogynes reproducing a certain percentage of deutogynes. Symbols for Table II are the same as for Table I.

DESIGNATIONS ON PLATES

AP1	Internal female genitalia
CD	Cross section outline of deutogyne
CP	Cross section outline of primary type
D	Dorsal view of mite
DA	Dorsal view of anterior part
ES	Structure of side skin
F	Featherclaw
GF	Female genitalia
GFD	External genitalia of deutogyne
GFP	External female genitalia of primary type
GF1	Female genitalia and coxae
GM1	Male genitalia and coxae
L	Left legs
L1, L2	Front and rear legs
N1	Side view of first stage nymph
N1DA	Anterior dorsal view of first stage nymph
N1VA	Anterior ventral view of first stage nymph
N2	Side view of second stage nymph
O	Egg
S	Side view of mite
SA	Side of anterior part of mite
SD	Side view of deutogyne
SP	Side view of primary male

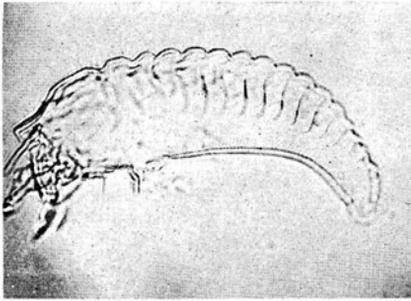


FIG. 10—Photograph of Buckeye Rust Mite primogyne

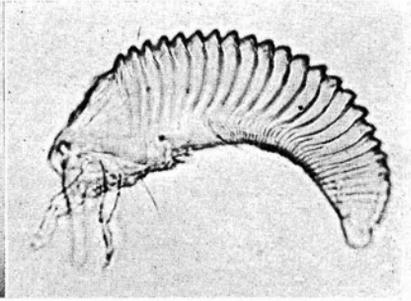


FIG. 11—Photograph of Buckeye Rust Mite deutogyne

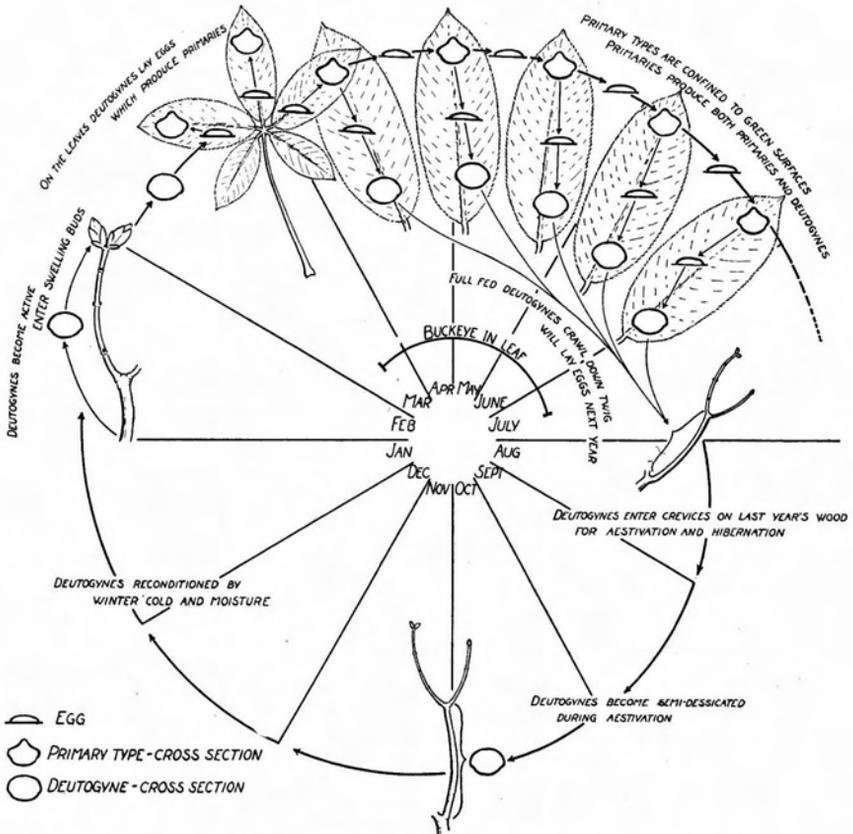


PLATE 165—Buckeye Rust Mite annual life cycle in central California

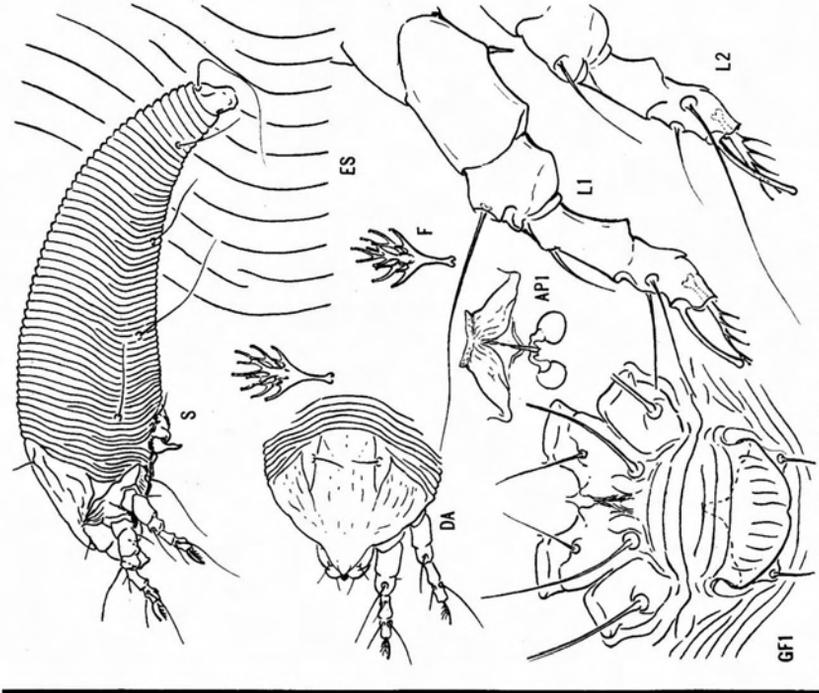


PLATE 167—*Epirimerus pirifoliae* K. deutogyne

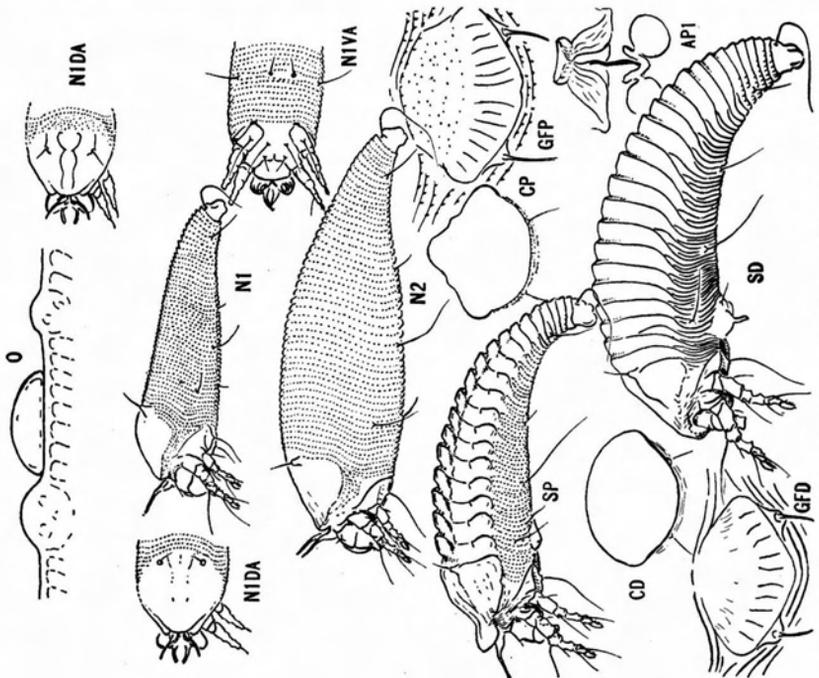


PLATE 166—*Oxypleurites aesculifoliae* K. illustrating all stages

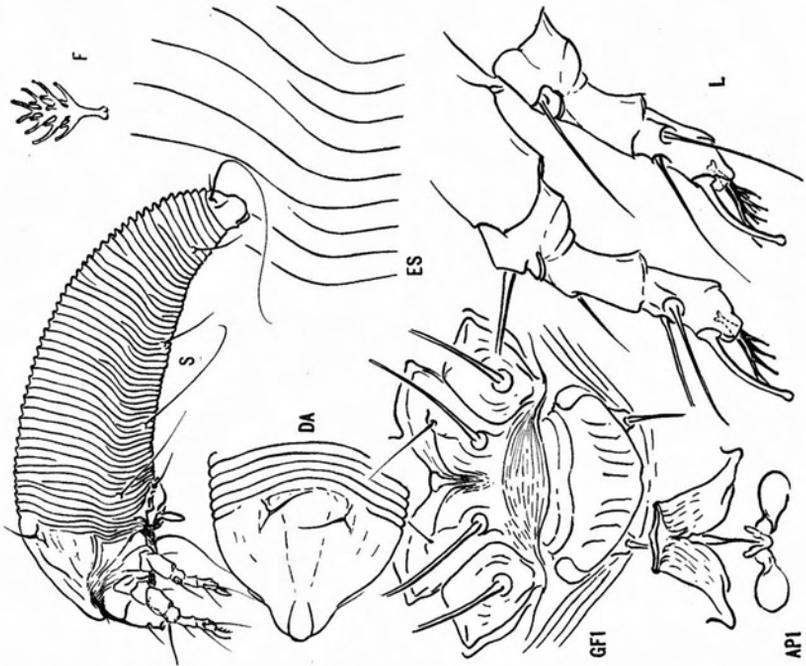


PLATE 169.—*Epiptimerus trilobus* Na. deutogyne

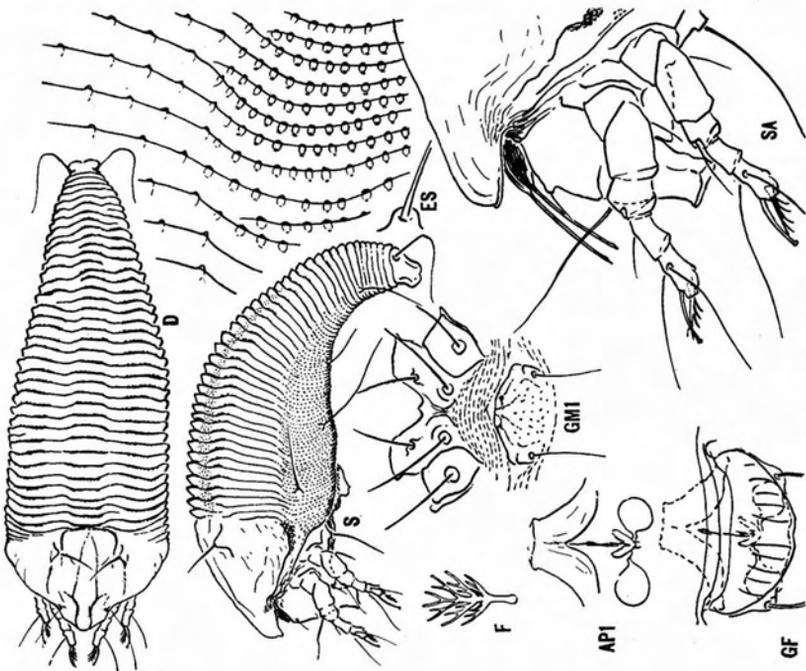


PLATE 168.—*Epiptimerus trilobus* Na. primaries