The Leafmining Moths of the Genus *Cameraria* Associated with Fagaceae in California (Lepidoptera: Gracillariidae)

PAUL A. OPLER

and

DONALD R. DAVIS

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The Leafmining Moths of the Genus *Cameraria* Associated with Fagaceae in California (Lepidoptera: Gracillariidae)

*Paul A. Opler*  
*and Donald R. Davis*
ABSTRACT

Opler, Paul A., and Donald R. Davis. The Leafmining Moths of the Genus Cameraria Associated with Fagaceae in California (Lepidoptera: Gracillariidae). Smithsonian Contributions to Zoology, number 333, 58 pages, 131 figures, 2 tables, 9 maps, 1981.—The 17 species of the moth genus Cameraria that feed on Fagaceae in California are treated. A description of the major morphological features and biologies of each species is included, accompanied by appropriate distributional maps and illustrations of diagnostic characters. Fourteen new species are described, including Cameraria anomala, C. diabloensis, C. jacintoensis, C. lobatiella, C. marinensis, C. mendocinensis, C. penteke, C. sadlerianella, C. sempervirensella, C. serpentinensis, C. shenaniganensis, C. temblorensis, C. tildeni, and C. walsinghami.
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The Leafmining Moths of the Genus *Cameraria* Associated with Fagaceae in California (Lepidoptera: Gracillariiidae)

Paul A. Opler
and Donald R. Davis

**Introduction**

The leafmining genus *Cameraria* is believed to be indigenous to the Nearctic region. Before this report, it was represented by 38 species primarily restricted to the eastern deciduous forests of the United States. Intensive field investigations on the Microlepidoptera feeding on the several species of Fagaceae in California (Opler, 1974a, b) have resulted in the discovery of 14 undescribed species. Prior to this field work, only two oak-feeding *Cameraria* were known from California, *C. agrifoliella* (Braun) and *C. mediadorserella* (Braun), while another, *C. wislizeniella* Opler, was described in the course of the above work (Opler, 1971).

This study was partially assisted by a grant from the Smithsonian Research Foundation to D. R. Davis in support of his work on the North American leafmining Lepidoptera. The field investigations were supported by NSF grants GB4014 and GB6813X, with J. A. Powell as principal investigator. In addition to the above assistance, we wish to acknowledge the assistance of Ms. Biruta Akerbergs and Ms. Ann Szymkowicz for preparing the genitalia illustrations. The habitus drawings were by Mr. Vichai Malikul. We wish also to acknowledge the generous assistance of J. A. Powell, University of California, Berkeley, for providing much of the material used in this study. Collection of specimens were by P. A. Opler and/or J. A. Powell unless otherwise stated.

The deposition of specimens has been indicated as follows:

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An understanding of the ecological interactions partaken by the Cameraria species is critical to an understanding of their speciation and evolutionary history. These interactions may be examined in two ways. First, we may examine their role within the communities (or guilds) of leaf-miners to which they belong, and, secondly, we may inspect the ecological similarities and differences between species of Cameraria that feed on different oaks.

**GUILD Ecology.**—The assemblage of miners that feed on a single host has been referred to as a “guild” (Opler, 1974a, b), since these species all utilize the same part of their host in the same way (see Root, 1967). Guilds of leaf-miners are rich on Californian oaks or their relatives, and the number of species found on a given host throughout its distribution ranges from 2 to 18. The number of miners found on a host has been shown to be a function of area of host occupation (Opler, 1974b). Californian oak leaf-miners belong to 15 genera distributed among nine families, and are primarily Lepidoptera. Species belonging to most of these genera feed on Quercus agrifolia, and their life histories have been described in detail (Opler, 1974a). On most hosts, no more than a single species from each genus is present, and in these cases each species fills a generalized niche. For example, the Lithocarpus densiflora miner guild is composed of five species: a Cameraria, a Phyllonorycter (= Lithocolletis of authors), a Caloptilia, a Stigmella, and a Bucculatrix. Cameraria makes an upper epidermal blotch mine, and Phyllonorycter makes a lower epidermal blotch mine. Caloptilia makes a small, lateral, full-depth blotch on very young leaves and then skeletonizes the upper surface from within a folded shelter; Stigmella makes a full-depth serpentine mine; and Bucculatrix makes a small, full-depth, linear mine near the midrib or a lateral vein, later leaving the mine to skeletonize the lower leaf surface. Other genera have analogous stylized feeding patterns, which may have resulted from competition through evolutionary time. The “upper epidermal blotch niche” filled by Cameraria seems to be a basic one in the assembly of leaf-miner guilds, since only the two rarest Californian oaks, Quercus dunnii and Q. tomentella, do not harbor at least one Cameraria (Opler, 1974b), and since Californian oaks with genera represented by more than one species always include Cameraria among their polyspecific genera.

**INTERHOST ADAPTATION.**—The miners, including Cameraria, which feed on evergreen or deciduous Fagaceae in California exhibit two strikingly different adaptive modes (Opler, 1979). It has been shown that, on the average, Cameraria that feed on evergreen Fagaceae are larger, have longer larval feeding periods, have relatively low population densities, and usually have fewer annual generations in comparison to those that feed on deciduous Fagaceae (Table 1; Opler, 1979). In addition to the traits mentioned above there are three additional concomitant contrasts which can be made: the degree of host specificity is greater for Cameraria that feed on evergreen Fagaceae; larval feeding periods encompass the winter months for species with evergreen hosts; and no more than one evergreen-restricted Cameraria is ever found at a single locality, even though several may be found throughout the range of the host (Table 1).

Opler (1979) homologized these two constellations of adaptations with the concepts of r- and K-selection as proposed by MacArthur and Wilson (1967) and as elaborated by Pianka (1970). According to this theory, species which are r-selected are small, have good colonizing ability, have high maximum reproductive rates (r), and have frequent changes in population level, seldom maximizing their resources near carrying capacity (K). In contrast, K-selected species are larger, are poor colonists, but good competitors, have lower
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Table 1.—Host relationships of California _Cameraria_
reproductive rates, and maintain relatively constant population sizes near carrying capacity.

It is hypothesized that evergreen oaks have higher levels of chemical defense and are more predictable resources than are deciduous oaks. In any event, Cameraria that feed on evergreen Fagaceae seem to be K-selected relative to those species that feed on deciduous hosts. A prediction that may be made on the above postulate is that evergreen-feeding Cameraria should oviposit fewer, relatively larger eggs than their deciduous host-associated counterparts (see also Connor et al., 1980).

The observation that more than one evergreen-feeding Cameraria are never found in a single locality is not a necessary correlate of r-K theory and is novel. This implies that the evergreen-feeding Cameraria are relatively strong competitors, and that niche breadths may be broader for these species. In contrast, two or more deciduous-associated Cameraria often occur sympatrically, illustrating a possible lower competitive ability with resultant narrower niche breadths and greater species packing.

Evolution

Biogeographic Considerations.—It has been shown previously that the number of miners found on different Californian Fagaceae is a function of the distributional areas occupied by their hosts (Opler, 1974b). Even when one considers Cameraria alone this regression is still significant \( S = 0.01A^{0.65} \), where \( S \) = number of Cameraria per host, and \( A \) = distributional area occupied by host). As has been discussed previously this correlation is an evolutionary one, but one that is maintained in current ecological time (Opler, 1974b). As was pointed out in the ecological discussion above, the Fagaceae with more than one Cameraria fall into either of two categories. These differing patterns of distributional diversity have been referred to by ecologists as alpha and beta diversity (Whittaker, 1965). Alpha diversity is the relative species richness or diversity at single localities or habitats and may be referred to as within-habitat diversity. On the other hand, beta diversity is the measure of increased species richness or diversity when one considers more than one locality or habitat.

Into one category, alpha diversity, fall those Cameraria that share a single deciduous host. More than one species of these moths often share a single host at a single locality, examples being Cameraria lobatiella and C. mediodorsella at Vacaville, Solano County, on Quercus lobata; and Cameraria lobatiella and C. pentekes near Hanford, Kings County, on Quercus lobata. More than one Cameraria were found on Quercus kelloggii, and the same is expected for Quercus garryana. It is assumed that some difference in seasonal timing or other form of host partitioning has evolved that allows these moths to coexist. In the case of sympatric occurrences on Quercus lobata, one member of the congeneric pair is always Cameraria lobatiella, a moth that frequently forms communal mines.

Some partitioning of host range is seen by Cameraria that feed on Quercus lobata and Q. garryana. The latter, whose range extends over the greatest range of latitude, hosts three Cameraria that never occur together, while the former has two species, C. mediodorsella and C. pentekes, which have not been found sympatrically. Thus some evidence of beta diversity does exist for deciduous oak-associated Cameraria.

A further observation on host-sharing by deciduous oak Cameraria is that, with one exception, all species sharing a host belong to different species groups. For example, the three Cameraria that feed on Quercus lobata belong to the guttifinitella, agrifoliella, and hamadryadella groups. Two of the four Cameraria that feed on Quercus garryana belong to the guttifinitella group, and are therefore an exception, although it should be noted that they do not occur together.

In contrast, all Cameraria that share a single evergreen host never occur sympatrically, and are therefore examples of beta diversity. In addition, all but one such example of host sharing are drawn from the same species group, and some are examples of obvious “sister species.” The pairs of Cameraria that share Lithocarpus densiflora and Quer-
Quercus chrysolepis are the most obvious of such sister species, and speciation has obviously resulted from divergence subsequent to geographic isolation of the same host's populations. In the case of the two Lithocarpus-feeding Cameraria, one is restricted to the host variety echinoides, which is found only in the Siskiyou Mountains, and one of the Quercus chrysolepis-feeding Cameraria is limited to Coast Range and Transverse Range locations, which were isolated islands during the Pliocene, and to which the host variety nana is restricted.

Quercus agrifolia hosts three Cameraria, all belonging to the agrifoliella subgroup. Cameraria wislizeniella and C. anomala also occur widely on a different but closely related host, Q. wislizenii. As has been discussed in the species treatment, the Cameraria wislizeniella populations that feed on Quercus agrifolia exhibit different life history features from those that feed on its more usual host, and may represent a "host race" or weakly differentiated sibling species.

Host Switching.—The events that led to many ultimate speciations of Californian oak Cameraria probably began with sympatric host transfers followed by isolation (Opler, 1974b). This is apparent when one examines the geographic distribution and host composition of several Cameraria species subgroups (Maps 1–9). One case, previously discussed by Opler (1974a), is that of the agrifoliella species group. The moths feed on disparate Fagaceae, Lithocarpus densiflora, Chrysolepis sempervirens, C. chrysophylla, and Quercus agrifolia. In addition other species in the group, Cameraria gaultheriella, C. nemoris, and C. species, feed on Gaultheria shallon, Vaccinium ovatum (both Ericaceae), and Myrica californica (Myricaceae), respectively. The hosts share geographic commonality as all occur in northern coastal California (except Chrysolepis sempervirens) and all probably originated with other mesic elements of the Arcto-tertiary geoflora (Wolfe, 1969). The majority of hosts for members of the mediodorsella species subgroup are most often found in chaparral or similar xeric situations. The group's locus is now in the southern Coast and Transverse Ranges. The lobatiella species subgroup's hosts are centered in the northern Coast Ranges of northern California and southern Oregon.

Evidence of this mode of switching and subsequent speciation is provided by examples of occasional emergence of Cameraria from the "wrong host" at localities where a normal host also occurs. Examples are the one Cameraria lobatiella reared from Quercus douglasii, and Cameraria agrifoliella and C. mediodorsella reared from Quercus suber, introduced cork oak.

The rate of changeover and adaptation is most rapid for moths colonizing deciduous oaks. This can be shown by two kinds of evidence. First, the Cameraria of deciduous oaks are less host specific, the most extreme of which are two California examples, Cameraria lobatiella and C. mediodorsella, which include both Lepidobalanus "white" and Erythrobalanus "red" oaks in their host range. A second kind of evidence is that the only Cameraria with clear affinities external to the Pacific Coast states are species that feed on deciduous oaks, while, in contrast, the most unusual Californian endemic Cameraria are those found on evergreen Fagaceae. Members of the hamadryadella and guttifinitella species groups feed on deciduous oaks, with the exception of Cameraria sadlerianella.

Cameraria Chapman

Cameraria Chapman, 1902:141. [Type of the genus: Lithocolletis guttifinitella Clemens, 1859.]

Diagnosis.—Adults small, 5–12 mm in wing-span, usually red brown to orange (occasionally gray white) with white transverse bands and black patches on forewing; white bands (if distinct) typically dark margined externally. Egg round and flat, transparent, deposited singly (rarely in multiples) on upper leaf surface. Larvae hypermetamorphic, forming blotch mines on the upper surface of host leaves, with one or more creases being formed in the upper epidermis over the mine at maturity. Body form flattened throughout most of larval life, becoming cylindrical at final instar. Pupa without cremaster;
pupation occurring under a flat circular cocoon within the mine. The vast majority of species are restricted to a single host.

**Adult. — Head:** Vestiture of frons consisting of appressed, lustrous white scales; vertex with erect scales, usually white medially and orange brown laterally. Antennae nearly as long as forewing; flagellumeres white basally, black distally; maxillary palpus reduced, less than 0.5 the length of apical segment of labial palpus, 2-segmented, segments only slightly longer than broad, subglobular. Labial palpus moderately long, approximately 1.2X–1.5X diameter of eye; vestiture entirely white, or white anteriorly and black posteriorly.

**Thorax:** Covered with slightly raised scales, dorsum usually white medially, orange brown laterally; tegulae orange brown or white, or orange brown outwardly edged with white inwardly; pleuron and venter covered with appressed, white scales. Forewing (Figure 33) 8-veined; R1 and R4 absent; M1 absent, M2 fused with 3; CuA single branched; dorsal scales non-iridescent, usually orange brown, but occasionally gray (white and black scales intermixed), with transverse white bars or fasciae often edged outwardly with black; venter vestiture black with smaller areas of tan. Hind wing 4-veined, Sc + R1 extremely short, terminating near base of costa; M and CuA each single branched; 1A vestigial; both surfaces pale to dark gray. Foreleg with epiphysis absent; femur white or black, or black dorsally and white ventrally; tibia usually black dorsally, white ventrally; tarsus usually black and white banded; midleg with femur usually white; tibia white with lesser amounts of black, tarsus usually white with narrow black bands; hind leg with femur white, occasionally with a small black patch; tibia predominantly white with black or brown patches; tarsus white with black bands.

**Abdomen:** Dorsum dark gray, paler at posterior (male), pale or dark gray (female), pleuron and venter white. Eighth sternite highly modified in male and usually extending ventrally beneath genitalia (as in *Phyllonorycter*); caudal apex either entire and rounded to subacute, or variously bifid or bilobed.

**Male Genitalia:** Uncus absent. Tegumen partially membranous, reduced to a relatively narrow ring dorsally. Vinculum often relatively well developed, either V- or Y-shaped, typically with a prominent median process (i.e., vincular process) extending posteriorly. Valvae symmetrical, without spines, slender, usually attenuated in western species or with cucullus moderately enlarged. Aedeagus relatively simple, base often flared, gradually tapering to slender apex; cornuti absent although short exogenous spines sometimes present along distal half of shaft.

**Female Genitalia:** Two pairs of apophyses present. Lamella antevaginalis variously developed but usually extended (in western species) posteriorly beyond ostium and with apex either entire or most often bifid. An accessory bursa usually present and arising between middle and posterior fourth of ductus bursae; corpus bursae spherical, with walls membranous except for typically two asymmetrical signa; signa less commonly single or absent.

### Key to the Species of *Cameraria* Chapman

1. Male genitalia with costal margin of valva relatively straight (Figure 34).
   - Female genitalia with signa absent; lamella antevaginalis (seventh sternite) simple, not deeply lobed nor divided (Figure 99). (*guttifinitella* group) .............................................................. 2
2. Male genitalia with costal margin of valva strongly arched or sinuate.
   - Female genitalia with a pair of ovoid signa; lamella antevaginalis deeply lobed (Figure 130) or divided (Figure 105) .................. 4
2. Length of forewing more than 4 mm. Larva on *Quercus sadleriana*
   \[ \text{Cameraria sadlerianella}, \text{ new species} \]
   Length of forewing less than 4 mm. Larva on either *Quercus garryana* or *Q. lobata*
   \[ \text{Cameraria lobatiella}, \text{ new species} \]

3. Forewing relatively narrow; length/width ratio 5.0 or less. Larva on *Quercus lobata*
   \[ \text{Cameraria lobatiella}, \text{ new species} \]
   Forewing relatively broad, length/width ratio greater than 5.0. Larva on *Q. garryana*
   \[ \text{Cameraria mendocinensis}, \text{ new species} \]

4. Ground color mostly white with irregular golden brown bands (Figure 19). Male genitalia with vincular process greatly expanded, 5-pointed (Figure 43). Female genitalia with lamella antevaginalis deeply divided (Figure 105). *(hamadryadella group)*. \[ \text{Cameraria pentekes}, \text{ new species} \]
   Ground color of forewing orange brown to golden brown, banded with white. Male genitalia with vincular process often elongate but not expanded (Figures 47, 51). Female genitalia with a median, sometimes slightly cleft lobe arising from caudal margin of lamella antevaginalis (Figure 130). *(agrifoliella group)* \[ \text{Cameraria pentekes}, \text{ new species} \]

5. Male with eighth sternite approximately as long as broad; caudal lobes slender, reduced in size (Figures 75, 81). Aedeagus sinuate (Figures 76, 82). *(mediadorsella subgroup)*
   \[ \text{Cameraria pentekes}, \text{ new species} \]
   Length of eighth sternite of male more than 1.5X the width; caudal lobes more developed and broad. Aedeagus relatively straight \[ \text{Cameraria pentekes}, \text{ new species} \]

6. Forewing with medial white fascia reduced and incomplete (Figure 28). Male genitalia with vinculum reduced, saccus slender (Figure 80). Caudal lobes of eighth sternite extremely reduced (Figure 81)
   \[ \text{Cameraria serpentinensis}, \text{ new species} \]
   Forewing with medial fascia extending across wing. Male genitalia with vinculum and saccus broad (Figure 74). Caudal lobes of eighth sternite more prominent (Figure 75) \[ \text{Cameraria mediodorsella} \]

7. Larva feeding on deciduous oaks and diapausing as a pupa during winter
   \[ \text{Cameraria mediodorsella} \]
   Larva feeding on evergreen oaks, no pupal diapause
   \[ \text{Cameraria sempervirensella}, \text{ new species} \]

8. Male genitalia with digitate lobe at outer third of valva (Figure 91). Larva feeding on *Chrysolepis*. *(sempervirensella subgroup)* \[ \text{Cameraria sempervirensella}, \text{ new species} \]
   Male genitalia without digitate lobes. Larva on *Quercus* or *Lithocarpus*
   \[ \text{Cameraria sempervirensella}, \text{ new species} \]

9. Dorsum of thorax mostly white. Forewing with basal longitudinal streak; basal fascia absent (Figure 31)
   \[ \text{Cameraria sempervirensella}, \text{ new species} \]
   Dorsum golden brown. Forewing without basal streak; basal fascia present, broken (Figure 32)
   \[ \text{Cameraria tildeni}, \text{ new species} \]

10. Male with eighth sternite possessing a pair of slender caudal lobes turned 90° dorsad (Figure 62); valva with a small, ventral, keel-like lobe at subapex of cucullus (Figure 59)
    \[ \text{Cameraria temblorensis}, \text{ new species} \]
Male with eighth sternite variously modified but not as above; valva without subapical ventral lobe .................................................. 11

11. Male with eighth sternite possessing two pairs of caudal lobes, the largest pair turned 90° dorsal (Figure 50); valva as in Figure 47, with a slightly enlarged setigerous apex .................. **Cameraria agrifoliella**

Male with eighth sternite bilobed, not as above; valva not as in Figure 47 .................................................................................................................. 12

12. Male with eighth sternite possessing a pair of moderately large, rounded, caudal lobes directed dorsal at a 45° angle (Figure 58); valva with a short apical process extending from cucullus as in Figure 55 .......................... **Cameraria wislizeniella**

Male with eighth sternite not as in Figure 58; valva without subapical process ................................................................. 13

13. Male with eighth sternite possessing greatly enlarged caudal lobes separated more than one-third the length of sternite (Figure 54); valva with a large subapical lobe extending more than one-fourth the length of entire valva (Figure 51) .................. **Cameraria anomala**, new species

Male with caudal lobes of eighth sternite separated less than one-fourth the length of sternite; valva without large lobe as in Figure 51 .......................................................... 14

14. Forewings with antemedial fascia completely traversing wing. Male with a broadly rounded, ventral lobe at distal fourth of valva. Lamella antevaginalis (seventh sternite) of female with slender median cleft (Figure 127). *(walsinghami* subgroup) .................................................. 15

Forewings with antemedial fascia incomplete, stopping at middle of wing or less. Male without subapical lobes on valva. Lamella antevaginalis without cleft, instead produced into a median lobe (Figure 115). *(diabloensis* subgroup) .................................................................................................................. 16

15. Eighth sternite of male strongly arched ventrad (Figure 90); valva with apex slightly expanded (Figure 87). Larva feeding on *Lithocarpus densiflora* var. *echinoides* .................. **Cameraria walsinghami**, new species

Eighth sternite not strongly arched (Figure 86); valva with slender apex (Figure 83). Larva feeding on *Lithocarpus densiflora* .......................... **Cameraria marinensis**, new species

16. Costal margin of forewing with white scaling, fascia indistinct (Figure 25). Valva of male with a slight setigerous swelling at outer fourth (Figure 70) .................. **Cameraria shenaniganensis**, new species

Costal margin of forewing same as ground color, golden brown; fascia distinct on costal half of wing (Figure 24). Valva with setigerous swelling at outer third (Figure 63) .......................... **Cameraria diabloensis**, new species

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**The guttifinitella Species Group**

The group of three species centered around *C. lobatiella* is actually a branch of the much larger, predominantly eastern *guttifinitella* species group.

In California, the *lobatiella* subgroup consists of three sibling species, each limited primarily to a single host *Quercus*, and all with nearly identical maculation. The male genitalia of the three species are also very similar in form and resemble
the genitalia of most of the eastern species of *Cameraria* (including the type of the genus) in possessing relatively simple unmodified valvae and eighth sternites. In this respect, the male genitalia of the *lobatiella* subgroup differ markedly from all other California *Cameraria*, which typically possess sinuate valvae and more modified eighth sternites.

The female genitalia are characteristic in possessing two pairs of abdominal apophyses, a completely membranous corpus bursae with no signa, and the ostium flush with the abdominal wall.

**Cameraria lobatiella**, new species

*Figures 1, 2, 18, 34-36, 98, 99; Map 1*

**Diagnosis.** —The maculation and genital morphology of this species closely resembles that of the other members of the *lobatiella* group, *C. mendocinensis* and *C. sadlerianella*. *Cameraria lobatiella* differs in possessing relatively short, broad wings (see Table 2) as well as in certain biological features. The larvae are gregarious in the mines (solitary in the other two species) and feed on *Quercus lobata*, *Q. douglasii*, and *Q. kelloggii*. Whereas the other two species in this group are single brooded, *Cameraria lobatiella* may undergo as many as three or four broods.

**Male.** —Length of forewing: 2.8–3.8 mm.

*Head:* Labial palpus white. Antenna almost as long as forewing; scape and flagellar segments dark brown dorsally, white ventrally. Front white. Vertex brown anteriorly, white mixed with brown posteriorly.

*Thorax:* Pronotal scaling brown with white laterally and anteriorly; tegula brown and narrow white laterally; pleuron white with some brown; venter white. Prothoracic leg dark brown. Mesothoracic leg with femur white possessing medial black patch; tibia white with black patches; tarsus predominantly white with two black bands. Metathoracic leg with femur white, tibia and tarsus black-and-white banded.

*Forewing:* Ground bronze brown. Two white transverse fasciae edged outwardly with black at 0.33 and 0.67 length from base; small white patch at 0.8 length from base edged outwardly with black extending from inner margin outwardly toward costa, occasionally reaching costa near apex. Outer margin with brown-tipped black scales. Apical tuft brown.

*Hind Wing:* Ground and fringe dark gray.

*Abdomen:* Dorsum dark gray with genital segments white; pleuron and ventrum white.

*Genitalia:* As in Figure 34 (drawn from USNM 17580). Valvae very slender (ca. 0.6 mm long with a maximum width across cucullus of less than 0.08 mm). Apex of eighth sternite entire, broadly rounded.

**Female.** —Length of forewing: 3.2–3.7 mm. As described for male except genitalia as in Figure 98 (drawn from female slide USNM 17581). Ovipositor with both anterior as well as posterior pairs of apophyses present. Ostium flush with sternite, not modified. Accessory bursa and signum absent.

**Type Material.** —Holotype: ♂, Walnut Creek, Contra Costa Co., California, 16 Sep 1967, JP 67J7 (em. 29 Jan 1968), reared *Quercus lobata*, J. A. Powell, deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.


Paratypes: 98 specimens. **California: Butte Co.:** Oroville, 1♂, 1♀, 18–19 Jun 1926, H. H. Keifer, reared *Quercus lobata*. Contra Costa Co.: Lafayette, 1♂, 1♀, 2 Sep 1968, JP 68J6 (em. 19 Sep 1968); 1♀, 21 Sep 1968, JP 68J101 (em. 5 Mar 1969); 1♀, 27 Sep 1968, JP 68J102 (em. 5 Mar 1969); all reared *Quercus lobata*. Orinda, 1 mi

Hosts.—*Quercus lobata* Nee; *Quercus douglasii* Hooker and Arnott (rarely); *Quercus kelloggii* Newberry (rarely).

Mine.—Shape irregular, epidermis opaque, red brown (yellow tan for mine on *Q. douglasii*); mines usually extend across leaf midrib (5 of 7), solitary but may coalesce with more than one adult eclosing; normally two parallel folds present. With respect to leaf axis, dimensions are: longitudinal, 2.23 cm ± 0.87 S.D.; latitudinal, 1.6 cm ± 0.88 S.D.

Life History.—This moth has two or three larval feeding periods and three or four adult emergences each year, depending upon the host and locality. Pupae in mines of the last generation each season overwinter and eclose the following spring after their host’s new leaves have expanded. Eggs resulting from these adults develop directly, and another emergence presumably takes place in early or midsummer. Larvae in mines resulting from oviposition by the summer adults complete their development by September or October. At higher elevations all the resultant pupae enter diapause, but at lower elevations only a portion of the pupae enter diapause, and a third cohort of larvae results from adults that eclose. Some of these larvae may not complete their development before their host leaves senesce and dehisce, but at many locations leaves on

![Figure 1.—Leaf mine of *Cameraria lobatiella*, new species, on *Quercus lobata* Nee (scale = 10 mm).](image-url)
Quercus lobata remain green until December or January. Many mines are communal containing more than one larva (see Figure 2).

**ETYMOLOGY.**—The name of this new species is derived from the specific name of its principal host, *Quercus lobata*.

**Cameraria mendocinensis, new species**

**Figures** 37–39, 100, 101; **Maps** 2, 3

**Diagnosis.**—This species agrees with both *Cameraria lobatiella* and *C. sadlerianella* in maculation and genital morphology. It differs from *C. lobatiella* in possessing more narrow wings (see Table 2) and from *C. sadlerianella* in having shorter wings. The larva is a solitary miner, so far reported only from *Quercus garryana* and *Quercus lobata*.

**Male.**—Length of forewing: 3.5–4 mm. As described for *C. lobatiella*.

**Genitalia:** As in Figure 37 (drawn from DRD 3052).

**Female.**—Length of forewing: 3.8–4 mm. As described for male of *C. lobatiella*.

**Genitalia:** As in Figure 100 (drawn from USNM 21261).

**Type Material.**—Holotype: ♂, 4 mi [6.4 km] W Eel River Ranger Station, Mendocino Co., California, 9 Jun 1972, J. Powell No. 72F1 (em. 27 Jun 1972), reared *Quercus garryana*; J. Powell; deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.

**Allotype:** ♀, same data as holotype. UCB.


**Host.**—*Quercus garryana* Douglas, *Quercus lobata* Nee.

**Mine.**—Not examined.

**Life History.**—The life history of this species is similar to that of *Cameraria lobatiella* in being multivoltine, with the pupa overwintering inside the mine.

**Cameraria sadlerianella, new species**

**Figures** 3, 40–42, 102, 103; **Map** 1

**Diagnosis.**—This species is essentially identical in appearance to the other members of the *lobatiella* group, *C. lobatiella* and *C. mendocinensis*. Morphologically, it differs in possessing longer wings (see Table 1). From *C. lobatiella* it further differs in being single brooded (3 to 4 broods in the former), with the larvae solitary in the mines.

**Male.**—Length of forewing: 4.3–4.9 mm. As described for *C. lobatiella*. 

**Paratypes:** 12 specimens. CALIFORNIA. MENDOCINO CO., same data as holotype except: 6♂, 4 ♀ (em. 27 Jun 1972), reared *Quercus lobata*. Paratypes deposited in BM(NH), CAS, LACM, UCB, UCD, and USNM collections.
**Figure 3.**—Leaf mine of *Cameraria sadleriana*, new species, on *Quercus sadleriana* R. Brown in Campster (scale = 10 mm).

**Genitalia:** As in Figure 40 (drawn from USNM 17582).

**Female.**—Length of forewing: 4.4–4.7 mm. As described for male of *C. lobatiella*.

**Genitalia:** As in Figure 102 (drawn from DRD 3275).

**Type Material.**—**Holotype:** ♂, Siskiyou Spring, 12 mi [19.2 km] S O'Brien, Josephine Co., Oregon, 3 Oct 1968, JP 68K44 (em. 25 Feb 1969), reared *Quercus sadleriana*, P. Opler, collector; deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.

**Allotype:** ♀, same data as holotype except em. 19 Feb 1969. UCB.


**Host.**—*Quercus sadleriana* R. Brown in Campster.

**Mine.**—Shape ovoid to triangular; epidermis opaque, yellow tan; mines usually one side of midrib (11 of 14), with one mine edge oriented adjacent to midrib; solitary, usually one mine per leaf; normally one longitudinal fold; dimensions with respect to leaf axis: longitudinal, 2.51 cm ± 0.43 S.D.; latitudinal, 1.80 cm ± 0.32 S.D.

**Life History.**—*Cameraria sadlerianella* is most likely univoltine. Adults probably emerge in late May or June under field conditions. The larvae complete their development in late fall or early winter, and all resultant pupae enter diapause. Collecting records to date indicate the larvae are solitary in the mines.

**Etymology.**—The name of this new species is derived from the specific name of its host, *Quercus sadleriana*.

**The *hamadryadella* Species Group**

This group consists of a minimum of four North American species, one of which remains undescribed. Only one species, *C. pentekes*, new species, is known to occur in California. The members of the group are characterized by their very similar maculation, arcuate valvae, and well-developed, typically lobed, vincular processes of the male genitalia, and by the deeply excavated, V-shaped cleft of the lamella antevaginalis in the female. The larvae of most species either prefer or are known to feed only on white oaks. The larvae of the eastern *C. hamadryadella* also feed on red and black oaks, as well as *Magnolia* and *Ostrya* (Braun 1908b:330).
Cameraria pentekes, new species
Figures 4, 5, 19, 43-46, 104, 105; Maps 2, 3

Diagnosis.—This species resembles the common eastern Cameraria hamadryadella closely in maculation. Although the color pattern varies in both species, a majority of the specimens examined of C. pentekes were more whitish in appearance and less heavily marked with golden brown scaling. The male genitalia of C. pentekes are characteristic in possessing a greatly enlarged vincular process terminating in five distinct apices. The vinculum in C. hamadryadella possesses only three such processes. The eighth sternite of C. pentekes is also quite distinct in being subtruncate with broadly separated caudal lobes. The female genitalia of C. pentekes differs markedly from that of C. hamadryadella in the form of the lamella antevaginalis, with that of the former being more deeply divided. The biology of the two species differs in that the larvae of C. pentekes is solitary, compared to the sometimes gregarious or solitary habit of C. hamadryadella.

Male.—Length of forewing: 3.5-5 mm.

Head: Labial palpus white dorsally, dark fuscous ventrally. Vertex and frons silvery white. Antenna about 0.9 the length of forewing; scape white, slightly irorated with fuscous dorsally; flagellum mostly white, banded with pale brown dorsally.

Thorax: Dorsum mostly white, lightly speckled with fuscous-tipped scales. Prothoracic leg white ventrally, mostly pale brown dorsally over femur and tibia; tarsal segments darkly ringed with fuscous. Meso- and metathoracic legs mostly white with tarsal segments darkly ringed.

Forewing: Ground color white with typically four brown fasciae more or less distinct and bordered by thin irregular lines of dark fuscous scales; basal fascia poorly developed and usually interrupted medially by white scales; second fascia, at basal third, typically the most complete and well defined; third fascia, at distal third, interrupted medially by a streak of dark-tipped white scales that extends through a very reduced subapical fascia to apex of wing.

Hind Wing: Uniformly pale gray to white.

Abdomen: Dorsum pale brown; pleuron and venter silvery white.

Genitalia: As in Figure 43 (drawn from slide USNM 17138). Valvae strongly curved dorsally, abruptly narrowing beyond sacculus to form slender elongate cucullus; apex slightly enlarged, setiferous. Vincular process greatly enlarged, expanding caudally to form five pointed lobes, of which the middle three are the largest. Eighth sternite nearly as broad as long, terminating in two acute, widely separated lobes.

Female.—Length of forewing: 3-4.5 mm. As described for male except genitalia as in Figure 104 (drawn from slide USNM 17595). Caudal margin of lamella antevaginalis deeply cleft, forming a deep V-shaped pocket with the sclerotized end of the ostium supported near the middle. An accessory bursa arising from the ductus bursae near its caudal third. A pair of oval signa present, approximately equal in diameter but different in structure; one signa with a minute spine arising from its center.

Type Material.—Holotype: ♀, Oroville, California, 27 Jun 1929, H. H. Keifer, collector, reared Quercus douglasii, deposited in the California Academy of Sciences.

Allotype: ♂, same data as holotype except: 29 Jun 1927. UCB.

HOSTS.—*Quercus douglasii* Hooker and Arnott and *Quercus lobata* Née. *Quercus garryana* Douglas is the presumed host of Washington and British Columbia material, since it is the only *Quercus* occurring naturally in that region.

MINE.—Shape oblong to ovoid; epidermis opaque, green yellow; mines all to one side of midrib on lower half of leaf (10 of 10); mines along leaf margin or midrib and solitary with some leaves supporting more than one mine, usually with many minute parallel folds, occasionally with one or two, more or less pronounced.

ECLOSION usually at upper half of mine; dimensions with respect to leaf axis: longitudinal, 1.44 cm ± 0.23 S.D.; latitudinal, 0.64 cm ± 0.15 S.D.

LIFE HISTORY.—This moth has at least three adult emergences: April, late June–early July, and late August–early September. Three larval cohorts occur: May–June, July–August, and September–October. Pupae undergo diapause through the winter and early spring in fallen leaves. Unlike its either communal-feeding or solitary eastern relative, *C. hamadryadella*, the larva of *C. pentekes* is always solitary.

ETYMOLOGY.—The specific name refers to the diagnostic form of the vincular process of the male and is derived from the Greek *pente* (five) and the suffix -*ekes* (pointed).
The *agrifoliella* Species Group

This is by far the most dominant species group of *Cameraria* in the western United States (i.e., west of the Great Plains). Nearly all of the western *Cameraria* belong to this group, including several species that are restricted to nonfagaceous hosts and that are, therefore, excluded from this paper. Except for *Cameraria conglomeratella* (Zeller) and *C. ulmella* (Chambers), no other eastern species are known to belong to this group.

The main morphological features of the *agrifoliella* group are the sinuate and often slender valvae of the male genitalia and the variously modified eighth sternite of the male with its basically bifid caudal apex. The female genitalia are less diagnostic, but all possess two pairs of abdominal apophyses, a completely membranous accessory bursae, and usually a pair of asymmetrical, oval platelike signa.

On the basis of biological data, host associations, and minor morphological similarities, the *agrifoliella* group can be further subdivided into several subgroups of sister species.

The *agrifoliella* Subgroup

This subgroup, as now defined, represents a rather miscellaneous group of species that may not be monophyletic. The subgroup is characterized largely on the basis of host associations, with most of the species treated feeding on *Quercus agrifolia* or *Q. wislizenii*. The eighth abdominal sternite of the male is somewhat characteristic in having the caudal lobes directed sharply dorsad. The aedeagus is relatively short and straight.

*Cameraria agrifoliella* (Braun)

**Figures 6, 20, 47-50, 106, 107; Map 4**


**Diagnosis.**—This species is most easily recognized by the male genitalia. The valvae are strongly curved and very slender with a slightly enlarged apex. The eighth sternite is particularly diagnostic in possessing a quadrilobed apex.

**Male.**—Length of forewing: 3.8-4.2 mm.

**Head.** Labial palpus white dorsally, black ventrally. Vertex with orange-brown scales laterally and intermixed white and orange-brown scales mesally. Antenna about as long as forewing; scape orange brown dorsally, white ventrally. Flagellum with a few basal segments entirely white, the more distal segments white basally and ringed with black apically.

**Thorax.** Dorsum of prothorax with orange-brown scales; a small patch of white scales anteriorly. Tegula covered with orange-brown scales. Prothoracic leg with femur white, a small black area at base; tibia white with small black patches at middle and apex; tarsus white with two black dorsal patches. Mesothoracic leg with femur black dorsally, white ventrally; tibia black dorsally with a small white spot, completely white ventrally; tarsus white basally, black distally. Metathoracic leg with femur white, a fuscous patch at basal third; tibia white with two large brown patches at distal third; tarsus predominantly white, each segment narrowly ringed with black distally.

**Forewing.** Ground color orange brown; pattern dominated by two white fasciae, 0.2 and 0.5 the distance from base, both broadly edged outwardly with black; a small white or black spot on inner margin at 0.1 the distance from base; a small white bar on costal margin at 0.75 the distance from base; a discontinuous white line extending from inner margin at 0.8 the distance from base to costal margin at 0.9 the distance from base; costal margin edged with black from 0.75 to 0.9 the distance from base; apical portion of wing distal to white line predominantly black, except for brown over posterior 25%; outer margin with dark brown-tipped, pale brown to whitish scales.

**Hind Wing.** Uniformly gray.

**Abdomen.** Dorsum gray brown, mostly white.
over genital segments. Pleuron white with a brownish medium streak. Venter white with a scattered irroration of brownish scales along midline.

*Genitalia:* As in Figure 47 (drawn from slide USNM 17053). Valvae elongate, abruptly narrowing beyond sacculus to form a slender, sinuous cucullus; apical fourth slightly enlarged, setiferous. Eighth sternite elongate, tapering to a relatively narrow quadrilobed apex; dorsolateral pair of lobes the largest and projecting nearly perpendicular from caudal end of sternite.

**FEMALE.**—Length of forewing: 3.9-4.1 mm. As described for male except genitalia as in Figure 106 (drawn from slide USNM 17964). Caudal lobe of lamella antevaginalis well developed, slightly longer than broad, with apex smoothly rounded. Accessory bursa enlarged, elongate, arising midway along ductus bursae. A pair of oval signa present, approximately equal in diameter but different in structure; one signa with a minute spine arising from center.

**TYPE.**—Lectotype, δ (present designation): B218; Mills College, Cal., 6.III.08, G. R. Pilate; type, collection of Annette F. Braun; lectotype, δ, *Lithocolletis agrifoliella* Braun, by Opler and Davis; in the Academy of Natural Sciences, Philadelphia.

**TYPE-LOCALITY.**—Mills College, Alameda County, California.

**Host.**—Quercus agrifolia Née.

**Mine.**—Shape irregular, circular or ovoid; epidermis opaque greenish yellow; mines often cross midrib (12 of 28); mines always solitary; most mines with a single fold (25 of 30), often at angle to midrib, some with two folds (5 of 30); eclosion near fold, but usually not at end; eclosion at either upper or lower half; dimensions with respect to leaf axis: longitudinal, 2.13 cm ± 0.56 S.D.; latitudinal, 1.64 cm ± 0.36 S.D.

**Life History.**—The seasonal timing of *Cameraria agrifoliella’s* life history has been described in detail by Opler (1974a). All stages may be found at any time of year, although the principal adult emergence occurs in spring, resulting from the major larval cohort, which feeds during fall, winter, and early spring. At some times of year larvae require at least 4.5 months to complete development.


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**Figure 6.** Leaf mine of *Cameraria agrifoliella* (Braun) on *Quercus agrifolia* Née (scale = 10 mm).
Cameraria anomala, new species

Figures 21, 51–54, 108, 109; Map 5

Diagnosis.—In maculation, this species closely resembles Cameraria mediodorsella, but differs in having the median white fascia less oblique and always separated by considerable ground color from the subapical costal white spot. The male genitalia are unique in possessing the most irregular valvae among the Cameraria. Similarly, the lobing of the eighth sternite is also the most pronounced. The median caudal lobe of the lamella antevaginalis of the female is minutely cleft. Certain similarities of the genitalia, particularly the unusual form of the valvae, eighth sternite, and cleft median lobe, may indicate some relationship with the walsinghami group.

Male.—Length of forewing: 4–4.8 mm.

Head: Labial palpus white with dark brown scaling ventrally. Antenna nearly as long as forewing; scape silvery white ventrally and golden brown dorsally; flagellum white with brown bands dorsally at apex of each segment. Front silvery white. Vertex white mesally, narrowly margined with brownish scales laterally.

Thorax: Pronotum golden brown with a median streak of white; tegula golden brown; pleuron and venter mostly white, with a slight suffusion of light brown sometimes around coxal joints. Prothoracic leg with coxae mostly white, occasionally with pale brown suffusion dorsally; venter of tibia and femur white, dorsum fuscous; tarsus white with two fuscous bands. Mesothoracic leg mostly white with three dorsal bands of fuscous on tibia; tarsus white with three bands of fuscous. Metathoracic leg mostly white with a suffusion of light brown at apex of coxa and at subapex of femur; tibia with a narrow dorsal band of pale brown near base and a much broader pale brown band near apex; tarsus almost entirely white except for small fuscous dorsal patch near apex of first and second segments. Tibial spurs of all legs white, narrowly banded with fuscous.

Forewing: Ground color golden brown. Basal portion of inner margin narrowly edged with white; an antemedial white fascia extending obliquely from costa nearly halfway; a medial white fascia extending obliquely from costa nearly to middle and separated from a similar bar from inner margin of wing; postmedial fascia reduced to a small white spot which is separated by ground from an elongate, often continuous white line extending from tornus to near apex on costal margin; all fasciae margined externally by black-tipped scales; median fascia terminating in a relatively large, acutely shaped patch of black-tipped scales; a large narrow and slightly sinuate patch of black-tipped scales immediately beyond and bordering apical fascia.

Abdomen: Dorsum pale yellowish brown; venter more white but sometimes heavily suffused with pale yellowish brown.

Genitalia: As in Figure 51 (drawn from slide USNM 21002). Valvae elongate, broad at base, rapidly narrowing to relatively slender but irregularly lobed cucullus; apex slender and slightly curved and acute. Eighth sternite longer than broad, irregular in shape and terminating in a pair of large, prominently divided lobes.

Female.—Length of forewing: 3–4.5 mm. As described for male except genitalia as in Figure 108 (drawn from slide USNM 21258). Caudal lobe of lamella antevaginalis narrow, rather deeply cleft almost the length of the lobe. Accessory bursa well developed, as large or larger than corpus bursae arising from near middle of ductus bursae. A pair of oval signa present, basal signa reduced, apical signa well developed and with a minute, median spine.

Type Material.—Holotype: ♂, 5 mi [8 km] E Lakeside, San Diego County, California, 30 Mar 1977, D. S. Green, coll., J. Powell No. 777C130 (em. 3 May 1977), reared Quercus agrifolia; deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.

Allotype: ♀, same data as holotype. UCB.

Paratypes: 35 specimens. CALIFORNIA MENDOCINO CO.: Hopland Field Station, Kelsey Cab. Orch. area, 2600–2800 ft [793-854 m], 15, 28 Apr.

**HOSTS.**—Quercus agrifolia Nee and Quercus wislizenii A. de Candolle.

**MINE.**—Not observed.

**LIFE HISTORY.**—This moth has been reared from two hosts, Quercus agrifolia and Q. wislizenii. On both hosts it appears to be univoltine, with the adults emerging after new leaf expansion of the hosts (April to June).

**ETYMOLOGY.**—The specific name is derived from the Greek anomalus (uneven, irregular) in reference to the highly irregular margin of the male valvae.

**Cameraria wislizeniella Opler**

**Figures 7, 22, 55–58, 110, 111; Map 5**


**DIAGNOSIS.**—Cameraria wislizeniella closely resembles *C. mediodorsella* in maculation, but differs in having the labial palpi entirely white and the white medial fascia externally edged with black. The male genitalia most resembles that of *C. agrifoliella* and *C. nemoris*, differing primarily in the form of the apices of the valvae. The eighth sternite of *C. wislizeniella* is readily distinguished from the other two species in terminating in two rather large caudal lobes compared to four in *C. agrifoliella* and two rather slender lobes in *C. nemoris*.

**MALE.**—Length of forewing: 3.1–4.7 mm.

**Head:** As described for *C. mediodorsella* except labial palpus white-scaled over entire length. Antenna with flagellum fuscous dorsally, tan ventrally.

**Thorax:** As described for *C. mediodorsella* except prothoracic leg with tarsus black ringed with white. Mesothoracic leg with tibia white. Metathoracic leg with tibia brown orange dorsally, white ventrally; tarsus white and black at base and at junction of first and second segments.

**Forewing:** As described for *C. mediodorsella* except with white medial fascia externally edged with black midway along costa; a small white postmedian costal spot externally edged with black; a broken white line extending from tornus to costal margin near apex; apex of forewing distal to white stripe with black scaling.

**Hind Wing:** Ground color and fringe light gray.

**Abdomen:** As described for *C. mediodorsella*.

**Genitalia:** As in Figure 55 (drawn from DRD 3244). Valvae elongate, slender, strongly arched dorsally; apex relatively simple with a slight subapical swelling; an elongate tuft of setae arising at distal three-fourths. Eighth sternite with a pair of rather large, narrowly separated, and strongly upcurved caudal lobes.

**FEMALE.**—Length of forewing: 2.4 to 4.3 mm. As described for male except genitalia as in Figure 110 (drawn from slide DRD 3277, allotype). Caudal process of lamella antevaginalis well developed, slightly longer than broad, with apex superficially bilobed. Accessory bursa well developed, equalling size of corpus bursae, arising midway along ductus bursae. A pair of signa present, one signum triangular in form, the other oval with a minute, median spine.

**TYPE.**—Holotype δ, deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.

**TYPE-LOCALITY.**—Knight’s Ferry, Stanislaus Co., California.

**HOSTS.**—Quercus wislizenii A. de Candolle, Quercus wislizenii A. de Candolle var. frutescens Engelmann, Quercus agrifolia Nee.

**MINE.**—Shape oblong to ovoid, occasionally circular; epidermis opaque, green yellow; mines usually cross midrib (12 of 24), solitary, usually
only one per leaf; usually with a single fold (12 of 16), occasionally two folds (4 of 12); eclosion adjacent to fold at upper (5 of 12) or lower (7 of 12) half of leaf; dimensions in relation to leaf axis: longitudinal, 1.85 cm ± 0.43 S.D.; latitudinal, 1.31 cm ± 0.30 S.D.

**Life History.**—This moth is found on three different hosts, *Quercus agrifolia*, *Q. wislizenii* var. *frutescens*, and *Q. wislizenii*. On each host the moth has a different seasonal life history. On both *Q. w. var. frutescens* and *Q. wislizenii*, the insect is strictly univoltine. Adults emerge after host leaves, during emergence and expansion (March-April on *Q. wislizenii*, May-June on *Q. w. var. frutescens*). Larvae have a long development period, including at least fall, winter, and early spring. There may be an egg diapause with hatching delayed until late summer or fall. Mines are always solitary on these two hosts.

When found on *Quercus agrifolia* the species is multiple-brooded, and mines are often communal. All stages may be found at all times of the year, although major emergences occur in spring and fall.

Cameraria temblorensis, new species

Figures 8, 23, 59–62, 112, 113; Map 8

Diagnosis.—The maculation of this species is very similar to that of *C. mediodorsella* except that the ground color is darker, and the median fascia is not interrupted with black scaling. The valva of the male is unique in possessing a rather broad, subapical ridge ventrally. The eighth sternite is characteristic in having the paired caudal lobes arising dorsad and perpendicular from the sternite. The lamella antevaginalis of the female is short and typically conical in form.

Male.—Length of forewing: 3.5–4 mm. As described for *C. mediodorsella* except labial palpus white with black on inner base.

Genitalia: As in Figure 59 (described from USNM 17912). Valvae elongate, strongly curved dorsally; apical three-fourths very slender, sinuate, with a slightly swollen setiferous ventral lobe at basal third and keel-like ventral ridge at subapex. Eighth sternite with a pair of divergent, subacute caudal lobes; lobes arising perpendicular and dorsally from sternite.

Female.—Length of forewing: 3–3.7 mm. As described for male except genitalia as in Figure 112 (drawn from USNM 17913). Lamella antevaginalis conical in form, relatively short (length less than width at base); apex rounded. Accessory bursa joined to caudal third of ductus bursae. Signa paired, both oval in form but dissimilar in structure; one with a minute spine near center.

Type Material.—Holotype: δ, Temblor Range, 12 mi [19.2 km] W McKittrick, Kern County, California, 17 Feb 1968, J. Powell No. 68B159 (em. 5 Mar 1968), reared *Q. dumosa* × *engelmanii*. UCB. Allotype: 9, 5 mi [8 km] E San Juan Capistrano, Orange Co., California, 13 Feb 1968, J. Powell No. 68B96 (em. 5 Mar 1968), reared *Q. dumosa* × *engelmanii*. UCB.


Hosts.—*Quercus × alvordiana* Eastwood (*Q.
The diabloensis Subgroup

This is a small but distinctive subgroup consisting of two species, both of which feed on Quercus chrysolepis. The male genitalia are characterized as possessing long sinuate valvae with simple, acute apices. The eighth sternite of both species is elongate with a pair of small dorsal ridges and prominently bilobed caudal apices.

Cameraria diabloensis, new species

Figures 9, 24, 63–66, 114, 115; Map 6

Diagnosis.—The male genitalia of this species most resembles that of C. shenaniganensis, but differs in the shape of the valvae, with the valvae of C. diabloensis narrowing more abruptly from the base. The eighth sternite of the male also differs in form between these two species, with the caudal end being more enlarged in C. diabloensis. The female genitalia differ particularly in the structure of the caudal lobe of the lamella antevaginalis, with that of C. diabloensis lacking the subapical notch present in C. shenaniganensis.

Male.—Length of forewing: 3.3–4.1 mm.

Head: Labial palpus white laterally, black mesally. Antenna equal to forewing in length; scape white; ventral portion of flagellar segments white basally, black distally, dorsum of flagellum white. Vertex white mesally, orange brown laterally.

Thorax: Dorsum white mesally, orange brown laterally. Tegula orange brown. Prothoracic leg with femur white; tibia black and white intermixed; tarsus black basally, black and white banded distally. Mesothoracic leg with femur and tibia white; tarsus white with narrow black bands distally. Metathoracic leg with femur white; tibia white with some black scales distally; tarsus mostly white, banded with black basally.

Forewing: Ground color orange brown; ante-
medial and postmedial white bars on costal margin narrowly edged distally with black scales; a transverse narrow white line extending from tornus to costa near apex; a medial band of black scales extending distally from postmedial white bar to transverse anteterminal white line; apical area with a patch of black-tipped white scales; outer margin with long narrow orange scales with black tips; inner margin with a broad white streak extending two-thirds the distance from base to tornus.

**Hind Wing:** Uniformly light gray.

**Abdomen:** Dorsum black; genital segments white; pleuron and venter white.

**Genitalia:** As in Figure 63 (drawn from DRD 3307). Valvae abruptly narrowing beyond sacculus to form long, slender, sinuate cucullus; a slight setiferous swelling present midway along cucullus. Eighth sternite narrowing caudally to a slightly enlarged, bilobed apex; a pair of low dorsal ridges present at caudal third.

**FEMALE.**—Length of forewing: 3.6–4.3 mm. As described for male except forewing with white scaling more extensive on costa.

**Genitalia:** As in Figure 114 (drawn from USNM 17586). Caudal lobe of lamella antevaginalis elongate, nearly 2× as long as wide, with a superficially bilobed apex. Accessory bursa enlarged, joined to ductus bursae midway along its length. A pair of large oval signa present, dissimilar in structure with a small spine arising from center of one signum.

**TYPE MATERIAL.**—**Holotype:** δ, Mt. Diablo, 3849 ft [1173 m], Contra Costa County, California, 13 Apr 1969, J. Powell No. 69D16 (em. 27 Apr 1969), reared *Q. chrysolepis*, δ genitalia DRD 3307, P. A. Opler; deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.

**Allotype:** Same data as holotype. UCB.


**Host.**—*Quercus chrysolepis* Liebmnan var. nana Jepson.

**MINE.**—Shape ovoid to quadrate; epidermis opaque yellow tan; all mines cross midrib (29 of 29), and consume 60%–95% (normally 75%–80%) of leaf surface; mines solitary; mines normally with two parallel folds (20 of 29), occasionally one (5 of 29) or three (4 of 29); eclosion between folds on upper half of mine; dimensions with respect to leaf axis: longitudinal, 2.0 cm ± 0.24 S.D.; latitudinal, 1.42 cm ± 0.18 S.D.

**LIFE HISTORY.**—*Cameraria diabloensis* is univoltine. Adult emergence occurs in early summer...
after its host's leaves have expanded. Larval feeding occurs during late fall, winter, and spring. An egg diapause may occur through late summer and early fall.

**Etymology.**—The specific name is derived from the type-locality (Mt. Diablo) and the Latin suffix -ensis (denoting place, locality).

**Remarks.**—Excluded from the type series but possibly representing this species are 11 adults collected by D. Frack from Hathaway Creek, San Bernardino Mountains, California. These were reared 6-11 Aug 1975 reportedly from *Quercus wislizenii*, a questionable host. The male genitalia (Figures 67-69) most resemble that of *Cameraria diabloensis*. The host record, however, requires confirmation.

**Cameraria shenaniganensis**, new species

**Figures** 10, 25, 70-73, 116, 117; **Map** 6

**Diagnosis.**—This species appears most related to *C. diabloensis*, but may be easily distinguished on characters of the male and female genitalia. In *C. shenaniganensis* the valvae taper gradually from the base, and the setose swelling is located nearer to the apex of the cucullus. The apical lobes of the eighth sternite are not set off caudally by a subapical constriction (as in *C. diabloensis*), and the paired dorsal ridges are located more basally in *C. shenaniganensis*. The female genitalia of this species may be distinguished by the subapical dorsal notch in the caudal lobe of the lamella antevaginalis, which is lacking in *C. diabloensis*.

**Male.**—Length of forewing: 4.4-4.2 mm. As described for *C. diabloensis* except:

*Head:* Labial palpus entirely white. Vertex with white scales, bordered by a few orange-brown scales laterally.

*Thorax:* Prothoracic leg with tibia white, irrorated with fuscous dorsally; tarsus banded with black and white. Mesothoracic leg with femur and tibia entirely white; tarsus with black and white bands. Metathoracic leg white; tarsus with black and white bands.

*Forewing:* Costal and inner margins broadly marked with white; black-tipped scaling in apical area more extensive than in *C. diabloensis*; antemedial white bar completely masked; the postmedial bar nearly so.

**Genitalia:** As in Figure 70 (drawn from USNM 17587). Valvae gradually narrowing beyond sacculus to form long, slender, sinuate cucullus; a slight setiferous swelling present at distal fourth of cucullus. Eighth sternite gradually narrowing caudally to a bilobed apex, the latter is not enlarged nor constricted; a pair of low dorsal ridges present at anterior third.

**Female.**—Length of forewing: 3.1-4 mm. As described for male except genitalia as in Figure 116 (drawn from DRD 3278). Caudal lobe of lamella antevaginalis elongate, nearly 2X as long as wide; apex round, with a subapical pair of small lateral indentations (viewed ventrally) or (when viewed laterally) a single, relatively large, subapical dorsal notch. Accessory bursa enlarged, arising midway along ductus bursae. A pair of oval signa present, similar to those in *C. diabloensis* but with reticulated signum reduced in diameter.

**Type Material.**—*Holotype:* $, Shenanigan Flat, Sierra Co., California, 19 Apr 1968, J. Powell No. 68 D 148 (em. 12 May 1968), reared *Q. chrysolepis*, $ genitalia slide PAO 297, P. A. Opler; deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.

*Allotype:* Same data as holotype, $ genitalia slide DRD no. 3278. UCB.


**Host.**—*Quercus chrysolepis* Liebmann.

**Mine.**—Shape irregular, oblong to quadrate; epidermis opaque, yellow green; all mines cross midrib (4 of 4), and consume 50%-90% (normally 60% of leaf surface); mines solitary; all mines with two parallel folds (4 of 4); eclosion between folds, normally at upper half of mine (3 of 4); all mines on spinose margined leaves and all strongly upward bowed; dimensions with respect to leaf axis:
**Cameraria mediodorsella (Braun)**

*Figures 11, 26, 74–76, 118, 119; Map 7*


**Cameraria mediodorsella** (Braun).—Ely, 1917:52.

**Diagnosis.**—Morphologically this species, for all practical purposes, is inseparable from *Cameraria jacintoensis*. The male genitalia of the two are essentially identical, within the normal range of variation. The eighth sternite varies slightly with that of *C. mediodorsella* being relatively shorter (see Figure 75). The two species differ most markedly in their biologies, with the larvae of *C. mediodorsella* feeding on deciduous oaks and undergoing a pupal diapause in the winter. The larvae of *C. jacintoensis* are restricted to evergreen oaks with perhaps no diapause in any stage.

**Male.**—Length of forewing: 2.8–4.3 mm.

- **Head:** Labial palpus white with black tip. Antenna almost as long as forewing; scape and flagellar segments dark brown dorsally, white ventrally. Front white. Vertex white mesally, narrowly margined with brownish orange laterally.

- **Thorax:** Pronotal scaling white mesally, orange brown laterally; tegula orange brown; pleuron white; venter white. Prothoracic leg with femur and tibia black dorsally, white ventrally; tarsus predominantly black with some white scaling. Mesothoracic leg with femur white; tibia and tarsus black and white dorsally, white ventrally. Metathoracic leg with femur white; tibia with basal half white, distal half brown; tarsus white with two narrow black bands.

- **Forewing:** Ground bronzy orange brown. Basal portion of inner margin narrowly edged with white; an antemedial white bar along costa; a medial transverse white fascia; a postmedial white spot on costal margin; a broken white line extending outwardly from tornus to near apex on costal margin; a medial patch of black scaling extending from and interrupting medial fascia.

- **Hind Wing:** Ground and fringe light gray.
**Abdomen:** Dorsum dark gray with genital segments white scaled; pleuron and venter white.

**Genitalia:** As in Figure 74 (drawn from slide USNM 18015). Valvae elongate, broad at base, gradually narrowing to slender, sinuate cucullus; apex curved sharply ventrad at a nearly 90° angle. Eighth sternite broader than long, with a bilobed caudal apex; lobes reduced in size, widely separated by a distance exceeding their length.

**Female.**—Length of forewing: 2.5–4.1 mm. As described for male except genitalia as in Figure 118 (drawn from slide USNM 18015). Caudal lobe of lamella antevaginalis relatively depressed, with a minutely bilobed apex; length of caudal lobe approximately equal to width. Accessory bursa enlarged, elongate, arising midway along ductus bursae. A pair of oval signa present, approximately equal in size but different in structure; one signum with a minute spine arising from center.

**Type.**—Lectotype, ♂ (present designation); 576; Sonoma Co., Cal.; oak; ♂ genitalia slide USNM 21189; type no. 12006; lectotype, *Cameraria mediodorsella* Braun, by Opler and Davis; *Lithocolletis mediodorsella* Braun, ms, type. Deposited in the National Museum of Natural History, Smithsonian Institution.

**Type-locality.**—Sonoma Co., California.

**Hosts.**—*Quercus garryana* Douglas, *Quercus lobata* Nee, *Quercus kelloggii* Newberry, *Quercus suber* L. [exotic host].

**Mine.**—Shape oblong to quadrate; epidermis opaque, yellow tan (*Q. garryana*); mines in lobe (5 of 12) or at base adjacent to midrib (6 of 12), none crossing midrib; mines solitary, with two parallel folds (7 of 14) or one longitudinal fold (7 of 14); dimensions with respect to leaf axis: longitudinal, 1.24 cm ± 0.20 S.D.; latitudinal, 0.83 cm ± 0.12 S.D.;

**Life History.**—*Cameraria mediodorsella* has at least two larval feeding periods and at least two adult emergences each year. Adults emerge in fall and in spring from diapaused pupae. Whether eggs laid by spring females enter diapause or develop directly to produce a midsummer emergence is unknown.

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Cameraria jacintoensis, new species

Figures 12, 27, 77–79, 120, 121; Map 8

Diagnosis.—This species is morphologically very similar to C. mediodorsella. The eighth sternite of the male varies slightly, with that of C. jacintoensis being relatively longer (see Figure 78). As discussed under C. mediodorsella, the two species differ most strikingly in their biologies, with the larvae of C. jacintoensis feeding on evergreen oaks. Furthermore, in contrast to the pupal diapause experienced by C. mediodorsella, C. jacintoensis may not diapause in any stage.

Male.—Length of forewing: 3.2–4.4 mm. As described for C. mediodorsella.

Genitalia: As in Figure 77 (drawn from USNM 17598).

Female.—Length of forewing: 2.8–4.5 mm. As described for male of C. mediodorsella.

Genitalia: As in Figure 120 (drawn from DRD 3249).

Type Material.—Holotype: ♂, Mt. San Jacinto, 14 mi [22.4 km] E Hemet, Riverside Co., California, 29 Mar 1968 (em. 27 Apr 1968). J. Powell No. 68C85, reared Quercus dumosa, P. A. Opler, collector; deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.

Allotype: ♀, same data as holotype except (em. 15 Apr 1968), ♀ genitalia on slide 3249. UCB.


Hosts.—Quercus dumosa Nuttall, Quercus dumosa × turbinella ssp. californica.

Mine.—Shape ovoid, epidermis opaque, green tan; mines normally cross midrib (8 of 11) and consume 25%–100% of leaf surface; mines solitary, normally with two parallel folds (9 of 11), rarely one or three; eclosion between folds, often at middle or upper half (6 of 8); dimensions with respect to leaf axis: longitudinal, 1.88 cm ± 0.52 S.D.; latitudinal, 1.01 cm ± 0.24 S.D.

Life History.—Cameraria jacintoensis is bivoltine. Adult emergences occur in late spring and fall, while the two larval cohorts feed in the summer-early fall and winter-early spring, respec-
It is presumed that diapause is lacking in all stages.

Etymology.—The specific name is derived from the type-locality (Mt. San Jacinto) and the Latin suffix -ensis (denoting place, locality).

Cameraria serpentinensis, new species

Figures 13, 28, 80-82, 122, 123; Map 8

Diagnosis.—The maculation of this species is very similar to that of C. mediodorsella, except less heavily marked. The male genitalia of C. serpentinensis are readily recognized by the unique form and curvature of the valvae and by the greatly reduced, bifurcate caudal lobes of the eighth sternite. The female genitalia are unique in having the lamella antevaginalis greatly extended into a prominent lobe bearing a shallow apical cleft.

Male.—Length of forewing: 3.2–4.2 mm.

Head and Thorax: As described for C. mediodorsella except labial palpus mostly white, sometimes with a slight suffusion of darker scales.

Forewing: As described for C. mediodorsella except pattern generally reduced; entire length of inner margin edged with white; antemedial and medial white bars present on costal margin, both narrowly edged outwardly with black; postmedial white spot absent; anteterminal white slash extending inwardly from costal margin.

Hind Wing and Abdomen: As described for C. mediodorsella.

Genitalia: As in Figure 80 (drawn from USNM 17596). Valvae with a slightly swollen, setiferous area at middle; distal half of valva very slender and evenly curved. Eighth sternite subquadrate; caudal lobes greatly reduced, spindelike.

Female.—Length of forewing: 3.6–4 mm. As described for male except genitalia as in Figure 122 (drawn from USNM 17597). Lamella antevaginalis greatly lengthened and relatively slender (length more than 2.3X greatest width); caudal apex minutely bifid. Accessory bursa joined to caudal third of ductus bursae. Signa paired, both oval in form but dissimilar in structure; one with a minute spine near center.

Type Material.—Holotype: ♂, Cedar Mtn., Alameda County, California; 3 Mar 1968, J. Powell No. 6801 (em. 23 Mar 1968), reared Quercus durata, P. A. Opler; deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.

Allootypes: ♀, same data as holotype except (em. 26 Mar 1968), ♀ genitalia slide DRD 3251. UCB.

Paratypes: 40 specimens. CALIFORNIA. Same data as holotype except: 1♂ (em. 20 Mar 1968); 13♀, 2♂ (em. 23 Mar 1968); 2♂, 2♀ (em. 26 Mar 1968).
1968); 2♂ (em. 1 Apr 1968); 5♀ (em. 2 Apr 1968). Kern co.: Mill Potrero, 1♂, 29 Apr 1968 (em. 20 May 1968), reared Quercus × alvordiana. Los Angeles co.: Sta. Monica Hills, 1♂, 17 Mar 1969 (em. 31 Mar 1969), reared Quercus dumosa. Westwood Hills, 3♂, 4♀, Mar 1941, 1♂, Apr 1941, in live oak, R. M. Bohart. 2 mi [3.2 km] E Valvermo, 1♂, 2 May 1968 (em. by 11 Feb 1969); 1♀, 2 May 1968 (em. 2 May 1968); reared Quercus dumosa. Orange co.: County Park, 1♂, Apr 1941, R. M. Bohart. Paratypes deposited in BM(NH), CAS, GD, LACM, UCB, UCD, and USNM collections.

Hosts.—Quercus durata Jepson; Q. dumosa Nuttall; Q × alvordiana Eastwood (Q. douglasii × turbinella ssp. Californica).

Mine.—Shape ovoid; epidermis opaque, brown; all mines cross midrib (8 of 8) and consume 60%–90% (normally 80%) of leaf surface; mines solitary, normally with two folds (7 of 8), rarely one (1 of 8); folds not necessarily parallel; three mines with folds more or less perpendicular; leaf bowed up with sunken area at middle of leaf; eclosion normally at upper half of mine (6 of 8); dimensions with respect to leaf axis are: longitudinal, 2.14 cm ± 0.29 S.D.; latitudinal, 1.55 cm ± 0.19 S.D.

Life History.—Cameraria serpentinensis is univoltine. Adults emerge in late spring or early summer after their hosts have leafed out. Following oviposition an egg diapause presumably occurs through the remainder of summer and fall. Larval feeding occurs during winter and spring.

Etymology.—The name of this new species is derived from the type of soil (i.e., serpentine) on which one of its host occurs.

The walsinghami Subgroup

The only two known members of this subgroup are restricted to Lithocarpus. One species (Cameraria marinensis) feeds on the typical species, L. densiflora, and the other (C. walsinghami) feeds on a variety (echinoides) of L. densiflora.

The male genitalia of the two species closely resemble one another (Figures 83, 87). The eighth sternite is characteristic in being strongly attenuated to a broadly bilobed apex. The lamella antevaginalis of the female is diagnostic in possessing a narrow, fissure-like cleft.

Cameraria marinensis, new species

Figures 14, 29, 83–86, 124, 125; Map 9

Lithocolletis agrifoliella Braun, 1939:284 [misidentification, not Braun, 1908].

Diagnosis.—The maculation of this species closely resembles that of C. sempervirensella and C. walsinghami. The male genitalia are sufficiently distinct from both, however, to distinguish C. marinensis easily. In C. marinensis the valvae lack the digitate ventral lobe present in C. sempervirensella. The valvae are most similar to that of C. walsinghami except that the sacculus is less well
developed, and the sinuous cucullus is more narrow, with the subapical swellings more reduced.

**Male.**—Length of forewing: 4.7–5.5 mm.

**Head:** As described for *C. sempervirenella* except dorsal surface of scape white.

**Thorax:** As described for *C. sempervirenella* except lateral portions of pronotum and tegula brown, not golden brown. Prothoracic leg with tarsus white, banded with black. Mesothoracic leg with femur white, tipped with black distally; tibia white with three black anterior patches; tarsus black with white bands. Metathoracic tibia white with two dark brown bands; tarsus black and white banded.

**Forewing:** Ground color brown with three white transverse fasciae—an antemedian, postmedian, and anteterminal—all outwardly edged with black; basal half of inner margin edged with white; a small subapical white line on costal margin connected to medial portion of anteterminal white fascia; apical area with patch of black-tipped white scales.

**Hind Wing and Abdomen:** As described for *C. agrifoliella*.

**Genitalia:** As in Figure 83 (drawn from USNM 17589). Valvae elongate, slightly sinuate with a small subapical swelling situated at distal fourth; sacculus reduced but broad, distinctly smaller than in *C. walsinghami*. Eighth sternite strongly narrowing to a relatively broad, bilobed caudal apex.

**Female.**—Length of forewing 4.5–5 mm. As described for male except genitalia as in Figure 124 (drawn from USNM 17590). Lamella antevaginalis with a median, deeply cleft projection; depth of cleft equaling length of median process. Accessory bursa arising from ductus bursae near middle. Signa paired, relatively large, both oval in form but dissimilar in structure, or with a minute spine near center.

**Type Material.**—**Holotype:** ♂, Alpine Lake, Marin Co., California; 2 Aug 1969, J. Powell No. 6943 (em. 12 Aug 1969), reared *Lithocarpus densiflora*; ♂ genitalia slide PAO 166, P. Opler; deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.

**Allotype:** ♀, same data as holotype except (em. 22 Aug 1969). UCB.

**Paratypes:** 6 specimens. **CALIFORNIA.** Same data as holotype except: 1♂ (em. 8 Aug 1969); 1♂ (em. 11 Aug 1969); 1♂ (em. 18 Aug 1969); 1♀ (em. 21 Aug 1969); 1♀ (em. 22 Aug 1969). **MARIPOSA CO.:** Yosemite Valley, 1♂, 25 May 1965, J. Powell at light. UCB.

**Host:** *Lithocarpus densiflora* (Hooker and Arnott) Rehder.

**Mine.**—Shape oblong, epidermis opaque yellow tan; mines usually to one side of midrib, parallel to it (6 of 9), or mines overlap midrib at apex (3 of 9); mines solitary; mines with one (7 of 9) or two (2 of 9) short folds, about half length;
eclosion near end of fold, usually on upper half of mine (6 of 8); dimensions with respect to leaf axis: longitudinal, 4.69 cm ± 0.34 S.D.; latitudinal, 2.22 cm ± 0.46 S.D.

Life History.—Cameraria marinensis is univoltine. Adult emergence occurs in late summer and early fall (late July–early September). Larval feeding begins in late fall (late October) and continues through July or August of the following year.

Etymology.—The specific name is derived from the type-locality (Marin County) and the Latin suffix -ensis (denoting place, locality).

Cameraria walsinghami, new species

Figures 15, 30, 87-90, 126, 127; Map 9

Diagnosis.—This species is closest to C. marinensis, but differs in possessing more white scaling over the forewings. The two species may also be separated by the male genitalia, with the valvae of C. walsinghami possessing a larger sacculus and a larger subapical swelling at the distal fourth of the cucullus. The lamella antevaginalis is very similar in both species, with an unusual median cleft present in the caudal process; the process in C. walsinghami may be less extended occasionally.

Male.—Forewing length: 4.8–5.5 mm. As described for C. marinensis except as follows:

Forewing: Ground color lustrous golden tan; basic pattern identical to C. marinensis, but often infused and obliterated by extensive white scaling, especially along costal and inner margins and occasionally connecting fasciae so that forewing assumes a “checkerboard” appearance.

Genitalia: As in Figure 87 (drawn from DRD 3296). Valvae elongate, sinuate, with subapical swelling at distal fourth moderately enlarged; sacculus larger than that of C. marinensis, with outer margin more convex. Eighth sternite strongly narrowing to a slightly enlarged, bilobed, caudal apex.

Female.—Length of forewing: 4.5–5.2 mm. As described for male except genitalia as in Figure 126 (drawn from DRD 3040). Lamella antevaginalis very similar to that of C. marinensis, except with caudal process slightly shortened. Accessory bursa arising from ductus bursae near caudal two-fifths.

Type Material.—Holotype: δ, 5 mi [8 km] SW Mt. Shasta City, Siskiyou Co., California; 22 Jul 1969, J. Powell No. 69 G35 (em. 5 Aug 1969), reared Lithocarpus densiflora var. echinoides, P. Opler; δ genitalia slide DRD 3296; deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.

Allosotype: δ, same data as holotype except (em. 13 Aug 1969), δ genitalia slide DRD 3040. UCB.


Paratypes deposited in BM (NH), CAS, GD, LACM, UCB, UCD, and USNM collections.

Host.—Lithocarpus densiflora var. echinoides (R. Brown) Abrams.

Mine.—Shape oblong, epidermis opaque yellow tan; mines usually on both sides of midrib (14 of 17) or, rarely, to one side of midrib on larger leaves (3 of 17); mines always solitary (N = 39), with one (37 of 39) or two (2 of 39) short longitudinal folds, always at edge of leaf; eclosion near end of fold, usually on lower or central part of mine (7 of 10); dimensions with respect to leaf axis: longitudinal, 4.36 cm ± 0.62 S.D.; latitudinal, 2.12 cm ± 0.39 S.D.

Life History.—The seasonal timing of this moth's single-brooded life stages is nearly identical to that of Cameraria marinensis. Emergence of adults occurs in August and September, while larval feeding extends from late fall through late summer of the ensuing year, a period encompassing about ten months.

Etymology.—This species is named in honor of Lord Walsingham (Thomas de Grey), a pioneer
The male genitalia are distinctive in possessing a unique digitate lobe arising from the outer third of the valva.

**Cameraria sempervirensella**, new species

*Figures* 16, 31, 91–94, 128, 129; *Map* 9

**Diagnosis.**—This species exhibits closest affinities to *C. tildeni* as evidenced by the great similarities with regard to their genital morphology and biology. The two species differ most noticeably in adult maculation, with the thorax of *C. sempervirensella* possessing a white dorsum compared to the golden brown dorsum of *C. tildeni*. The forewings of *C. sempervirensella* possess a prominent basal streak (absent in *C. tildeni*) and three rather well-defined transverse striae, which are very irregular or broken in *C. tildeni*. The male genitalia of both species are unique among *Cameraria* in possessing a prominent, digitate process from the outer third of the valvae. In *C. sempervirensella* the sacculus appears broader than in *C. tildeni*.

**Male.**—Length of forewing: 3.5–4.7 mm.

*Head:* Labial palpus white dorsally, black ventrally. Antennae almost as long as forewing; scape orange brown dorsally, white ventrally; flagellomeres white ventrally, white dorsally with black distad. Front white; vertex white medially, orange brown laterally.

*Thorax:* Dorsum white medially, golden brown laterally; tegula golden brown. Pleuron and venter white. Prothoracic leg with femur and tibia black dorsally, white ventrally; tarsus black with some white basally. Mesothoracic leg with femur white, tibia white with two small black spots on ventral surface; tarsus black basally, white distally. Metathoracic leg with femur and tibia white with one black spot ventrally; tarsus white with black scaling distally.

*Forewing:* Ground color golden brown, with a short longitudinal white streak from body; three white transverse fasciae across antemedian, median, and postmedian; the antemedian and median fasciae narrowly edged outwardly with black

**The sempervirensella Subgroup**

Only two species, biologically similar, are presently known for this subgroup. Both are restricted to *Chrysolepis*, with one (*Cameraria sempervirensella*) feeding on *Chrysolepis sempervirens*, and the other (*Cameraria tildeni*) on *Chrysolepis chrysophylla*.

microlepidopterist who had collected extensively in the general areas of the type-locality during 1871–1872.
scales; the antemedian also edged sometimes with black near costa; the postmedian fasciae more acute and edged with black immediately beneath middle; a narrow white subapical fascia extending from costal margin to tornus; a subapical patch of black-tipped white scales immediately distad to subapical fascia.

**Hind Wing:** Uniformly pale whitish gray.

**Abdomen:** Pale brownish-white to gray dorsally and laterally; mostly silvery white ventrally with small lateral streaks of orange brown.

**Genitalia:** As in Figure 91 (drawn from USNM 17918). Valvae with sacculus moderately broad, then narrowing to a slender cucullus bearing a prominent digitate process from outer third. Eighth sternite elongate and tapering to a relatively large, bilobed caudal apex.

**Female.**—Length of forewing: 4–5 mm. As described for male except genitalia as in Figure 128 (drawn from DRD 3013). Lamella antevagnalis only moderately developed, with a shallow median cleft. Accessory bursa joined to middle of ductus bursae. Signa paired, both oval in form but dissimilar in structure; one signa with a minute median spine.

**Type Material.**—Holotype: ♂, Blodgett Forest, 13 mi [20.8 km] E Georgetown, El Dorado Co., California; 18 May 1968, J. Powell No 68E29 (em. 27 May 1968), reared from *Chrysolepis sempervirens*, J. Bringuel, coll.; deposited in the California Academy of Sciences on indefinite loan from the University of California, Berkeley.

Allotype: ♀, same data as holotype except: (em. 30 May 1966), ♀ slide DRD 3015. UCB.


Host.—*Chrysolepis sempervirens* (Kellogg) Hjelmquist.
MINE.—Shape ovoid; epidermis opaque, tan; all mines cross midrib (9 of 9) and consume 70%-95% (normally 80%-90%) of leaf surface; mines solitary, usually with two folds (5 of 8), but often with one (3 of 8); eclosion always at end of longitudinal fold, usually at upper half of leaf (4 of 6); dimensions with respect to leaf axis are: longitudinal, 2.97 cm ± 0.29 S.D.; latitudinal, 1.47 cm ± 0.18 S.D.

LIFE HISTORY.—Adults of this univoltine moth emerge in June or July each year, while larval feeding extends from at least September through late May and early June of the following year.

ETYMOLOGY.—The name of this new species is derived from the specific name of its principle host, *Chrysolepis sempervirens* (Kellogg) Hjelmquist.

**Cameraria tildeni, new species**

**Figures 17, 32, 95-97, 130, 131; Map 9**

**Diagnosis.**—This species resembles *C. sempervirensella* closely in genital morphology and biology, but differs markedly in adult maculation. In *C. tildeni* the dorsum of the thorax is golden brown (versus white in *C. sempervirensella*), and the white transverse fasciae of the forewings are more irregular and discontinuous than those of *C. sempervirensella*. The male genitalia of the two species appear to differ slightly, with the sacculus being more reduced in *C. tildeni*.

**Male.**—Length of forewing: 4.2 mm.

*Head:* As described for *C. sempervirensella* except labial palpus with black more extensive. Vertex with orange-brown scales anteriorly and white scales posteriorly.

*Thorax:* Dorsum bronzzy golden brown; tegula golden brown with some white scaling posteriorly.

*Forewing:* Ground bronzzy golden brown; four irregular, partially broken, transverse fasciae present at base, antemedian, median, and postmedian positions; all four fasciae white, distally edged by a thin line of dark scales, and partially invaded basally by ground color; median fascia the most acute; postmedian fascia incomplete, broken at middle with costal portion confluent with crescent-shaped subapical white streak; a subapical patch of black-tipped white scales immediately distad to postmedian fascia.

*Hind Wing and Abdomen:* As described for *C. sempervirensella*.

*Genitalia:* As in Figure 95 (drawn from PAO 176). Valvae with sacculus reduced, gradually tapering to long, narrow, and slightly curved cucullus; a prominent digitate lobe arising from outer third of valvae. Eighth sternite with caudal lobes less rounded than in *C. sempervirensella*.

**Female.**—Length of forewing: 3.8-4.2 mm. As described for male except genitalia as in Figure 130 (drawn from DRD 3014). Genitalia as described for *C. sempervirensella*.

**Type Material.**—*Holotype:* ♀, King Mt., San Mateo Co., California; 26 mar 1946, J.W. Tilden, ♀ slide PAO 176; deposited in the California

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**Figure 17.**—Leaf mine of *Cameraria tildeni*, new species, on *Chrysolepis chrysophylla* (Douglas ex Hooker) Hjelmquist (scale = 10 mm).
Academy of Sciences on indefinite loan from the University of California, Berkeley.

**Allotype:** ♀, same data as holotype except: 13 Apr 1946 (em. 19 Apr 1946), reared *Castanopsis* (= *Chrysolepis chrysophylla*). UCB.

**Paratype:** 1 specimen. Same data as holotype except: 1♀, 13 Apr 1946 (em. 24 Apr 1946), reared *Castanopsis*, ♀ slide DRD 3014. UCB.

**Host.**—*Chrysolepis chrysophylla* (Douglas ex Hooker) Hjelmquist.

**Mine.**—Shape oblong-ovoid; epidermis opaque, yellow green; most mines cross midrib (4 of 6); only mature mine with a single fold; dimensions with respect to leaf axis are: longitudinal, 2.88 cm; latitudinal, 1.80 cm.

**Life History.**—The seasonal timing of *Cameraria tildenii*’s life cycle is unknown, but is presumed to be very similar to that of *Cameraria sempervirensella*, whose host is congeneric with that of *C. tildenii*.

**Etymology.**—This new species is named in honor of Dr. J. W. Tilden of San Jose, California, who has been the only entomologist to collect this insect thus far.
Barnes, W., and J. McDunnough

Braun, A. F.

Brown, L. R., and C. O. Eads

Chapman, T. A.

Clemens, B.

Connor, E. F., S. H. Faeth, D. Simberoff, and P. A. Opler

Ely, C. R.

Essig, E. O.

Keen, F. P.


McDunnough, J.

Meyrick, E.

Opler, P. A.


Pianka, E. R.

Root, R. B.

Whittaker, R. H.

Wolfe, J. A.
Figures 18–131
Figures 26–32.—Adult moths: 26, Cameraria mediodorsella (Braun), ♂; 27, C. jacintoensis, new species, ♂; 28, C. serpentimensis, new species, ♂; 29, C. marinensis, new species, ♂; 30, C. walsinghami, new species, ♂; 31, C. sempervirensella, new species, ♂; 32, C. tildeni, new species, ♂. (Scale = 1 mm.)
Figures 33–46.—Wing venation and male genitalia. 33, Cameraria guttifinitella (Clemens). C. lobatiella, new species: 34, ventral view; 35, eighth sternite; 36, aedeagus. Cameraria mendocinensis, new species: 37, ventral view; 38, eighth sternite; 39, aedeagus. Cameraria sadlerianella, new species: 40, ventral view; 41, eighth sternite; 42, aedeagus. Cameraria pentekesi, new species: 43, ventral view; 44, lateral view; 45, eighth sternite; 46, aedeagus. (Scale = 0.5 mm.)
FIGURES 47-62.—Male genitalia. *Cameraria agrifoliella* (Braun): 47, ventral view; 48, aedeagus; 49, eighth sternite, dorsal view; 50, lateral view. *Cameraria anomala*, new species: 51, ventral view; 52, aedeagus; 53, eighth sternite, dorsal view; 54, lateral view. *Cameraria usitizensiella* Opler: 55, ventral view; 56, aedeagus; 57, eighth sternite, dorsal view; 58, lateral view. *Cameraria temblorensis*, new species: 59, ventral view; 60, aedeagus; 61, eighth sternite, dorsal view; 62, lateral view. (Scale = 0.5 mm.)
FIGURES 63–76.—Male genitalia. *Cameraria diabloensis*, new species: 63, ventral view; 64, aedeagus; 65, eighth sternite, dorsal view; 66, lateral view. *Cameraria* species (near *diabloensis*): 67, ventral view, Hathaway Creek, San Bernardino Mts., Calif.; 68, aedeagus; 69, eighth sternite, dorsal view. *Cameraria shenaniganensis*, new species: 70, ventral view; 71, aedeagus; 72, eighth sternite, dorsal view; 73, lateral view. *Cameraria mediodorsella* (Braun): 74, ventral view; 75, eighth sternite, dorsal view; 76, aedeagus. (Scale = 0.5 mm.)
FIGURES 77-90.—Male genitalia. *Cameraria jacintoensis*, new species: 77, ventral view; 78, eighth sternite, dorsal view; 79, aedeagus. *Cameraria serpentinensis*, new species: 80, ventral view; 81, eighth sternite, dorsal view; 82, aedeagus. *Cameraria marinensis*, new species: 83, ventral view; 84, aedeagus; 85, eighth sternite, dorsal view; 86, lateral view. *Cameraria walsinghami*, new species: 87, ventral view; 88, aedeagus; 89, eighth sternite, dorsal view; 90, lateral view. (Scale = 0.5 mm.)
Figures 91-101.—Male and female genitalia. *Cameraria sempervirensella*, new species: 91, ventral view; 92, aedeagus; 93, eighth sternite, dorsal view; 94, lateral view. *Cameraria tildeni*, new species: 95, right valva; 96, eighth sternite, dorsal view; 97, lateral view. *Cameraria lobatiella*, new species: 98, lateral view; 99, ventral view. *Cameraria mendocinensis*, new species: 100, lateral view; 101, ventral view. (Scale = 0.5 mm.)
FIGURES 110–115.—Female genitalia. *Cameraria wislizeniella* Opler: 110, lateral view; 111, ventral view. *Cameraria temblorensis*, new species: 112, lateral view; 113, ventral view. *Cameraria diabloensis*, new species: 114, lateral view; 115, ventral view. (Scale = 0.5 mm.)
FIGURES 116-123.—Female genitalia. *Cameraria shenaniganensis*, new species: 116, lateral view; 117, ventral view. *Cameraria mediiodorsella* (Braun): 118, lateral view; 119, ventral view. *Cameraria jacintoensis*, new species: 120, lateral view; 121, ventral view. *Cameraria serpentinensis*, new species: 122, lateral view; 123, ventral view. (Scale = 0.5 mm.)
Maps 1–9
Map 1.—Distribution of Cameraria lobatiella and C. sadlerianella in relation to different hosts.
* C. mendocinensis (on Q. garryana)
● C. pentekes (on Q. douglasii)
▲ C. pentekes (on Q. lobata)

Q. douglasii
Q. garryana
Q. lobata

Map. 2.—Distribution of Cameraria mendocinensis and C. pentekes in relation to different hosts.
Map 3.—Distribution of Cameraria mendocinensis and C. pentekes in relation to Quercus garryana.
Map 4.—Distribution of Cameraria agrifoliella in relation to Quercus agrifolia.
MAP 5.—Distribution of *Cameraria anomala* and *C. wislizeniella* in relation to different hosts.
MAP 6.—Distribution of *Cameraria diabloensis* and *C. shenaniganensis* in relation to *Quercus chrysolepis*.
MAP 7.—Distribution of *Cameraria mediodorsella* in relation to different hosts.
Map 8.—Distribution of Cameraria jacintoensis, C. serpentinensis, and C. temblorens is in relation to different hosts.
Map 9.—Distribution of Cameraria marinensis, C. walsinghami, C. tildeni, and C. sempervirensella in relation to Lithocarpus and Chrysolepis.
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