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LIFE HISTORY OF *NEMORIA GLAUCOMARGINARIA* (BARNES & McDUNNOUGH) AND LARVAL TAXONOMY OF THE TRIBE NEMORIINI (GEOMETRIDAE: GEOMETRINAE)

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ABSTRACT. Morphology, chaetotaxy, and color pattern of immature *Nemoria glaucomarginaria* (Barnes & McDunnough) are described for the first time. Large dorsolateral projections on the middle abdominal segments provide crypsis on the host plant (*Quercus* spp.), enhanced by a "shaking" behavior while moving. Larval color pattern of *N. darwiniata punctularia* Barnes & McDunnough is also figured, and two new hosts are reported (*Arctostaphylos* sp. and *Ceanothus cordulatus* Kell.). The description of *glaucomarginaria* is used as the basis for recognition of the genus *Nemoria*. A preliminary key to larvae of the four genera in the tribe Nemoriini is presented, based on fourteen species.

Taxonomy of the Geometrinae based on adult genital morphology has been covered in detail by Ferguson (1969, 1985). His studies reveal a remarkable array of parallelisms and convergences in the facies of adults. Individuals from different species groups within genera, or even from different tribes, have routinely been classified as conspecific in major museum collections. For example, *Nemoria glaucomarginaria* (Barnes & McDunnough) of the *bistriaria* group is often found with *N. darwiniata* (Dyar) of the *obliqua* group, and species of *Dichordophora* Prout (Dichordophorini) are often found with *Dichorda* Warren (Nemoriini). Although the taxonomic groupings outlined by Ferguson are well defined, their interrelations remain unknown. Adult characters present numerous problems for phylogenetic reconstruction: the "superficial" characters show many parallelisms, convergences, and plesiomorphies, while the genitalia are so different between tribes and so similar within genera that most phylogenetic information is lost. However, the larvae show remarkable adaptations for crypsis, and may give information of phylogenetic significance not present in the adults.

This paper describes the larva and life history of *Nemoria glaucomarginaria* and uses this information as the basis for the generic recognition of *Nemoria* larvae. It concludes with a preliminary key to the genera of nemoriine larvae.

MATERIALS AND METHODS

Gravid females of *N. glaucomarginaria* and *N. darwiniata punctularia* Barnes & McDunnough were collected at ultraviolet and visible wavelength fluorescent lights from the following California localities in 1984 and 1985: *glaucomarginaria*: Gold Run, Placer Co.; Washington, Nevada Co.; Rubicon River Cyn., 1.5 km N Uncle Tom's Cabin, El Dorado Co.; Barton Flats, San Bernardino Nat. For., San Bernardino Co.; *d. punctularia*: Santa Rosa, Sonoma Co.; Baxter, Placer Co.; Meeks Bay, El Dorado Co.; Carson River Cyn., Alpine Co.; Mill Ck. (Lundy Cyn.), Mono Co. Additional preserved material of *d. punctularia* was examined from Ash Cyn., Huachuca Mts., Cochise Co., Arizona.

Ova were collected from moths confined in inflated, resealable plastic sandwich bags. Larvae were reared on foodplant cuttings in similar containers at 25°C under natural photoperiods throughout spring and summer. Specimens of each stage and instar were preserved in KAAD before transfer to 95% ethyl alcohol. Color photographs were taken of the ultimate instars. Figures were drawn with the aid of a camera lucida, with color patterns added freehand from the color slides. Chaetotaxy follows McGuffin (1964, 1967, 1977).

More than 100 larvae were reared to adults. Five specimens of each stage were examined for morphological details. Colors are described from two specimens of each species exhibiting the most common coloration. Colors should not be relied on for specific identification.

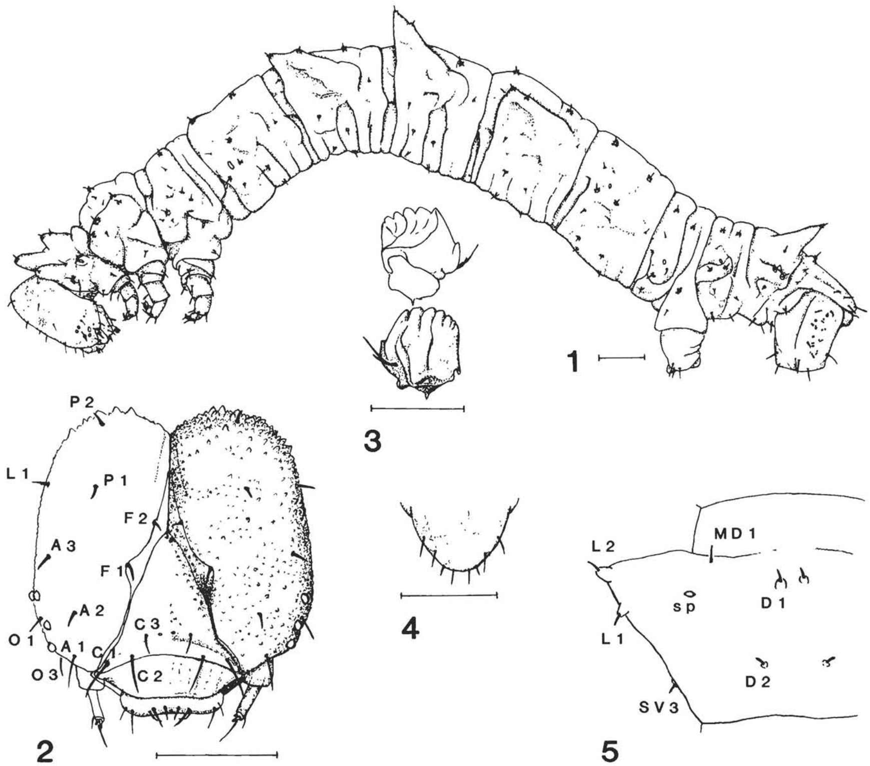
Larvae of additional species used in constructing the key are from personal rearings or from the collection of Noel McFarland. The species examined were *Nemoria pulcherrima* (Barnes & McDunnough), *N. unitaria* (Packard), *N. arizonaria* (Grote), *N. festaria* (Hulst), *Chlorosea margaretaria* Sperry, *C. roseitacta* Prout, *C. banksaria gracearia* Sperry, *Dichorda consequaria* (Hy. Edwards), *D. illustraria* (Hulst), and *Dichordophora phoenix* (Prout). An additional undetermined larva from near Valyermo, Los Angeles Co., California, was also examined; it is probably *N. intensaria* (Pearsall). Specimens used in formulating these descriptions will be deposited in the Bohart Museum (University of California, Davis) and in the McFarland Collection.

Nemoria glaucomarginaria (Barnes & McDunnough)

Egg. Ovate, 0.7 mm long by 0.5 mm wide, with flattened, slightly concave top; vertical sides 0.2–0.3 mm thick, with sharp edge between sides and top; decorated with small ridges in an irregular reticulate hexagonal pattern. Yellow when laid, gradually darkening through orange to dark red over a period of 9–12 days, becoming translucent 2 days before hatch. Larva emerges through hole chewed in side wall at anterior end. A photograph of the related *N. darwiniata punctularia* (Comstock & Henne [1940], as *pistacearia* [Packard]) is representative of *glaucomarginaria*, as well as all *Nemoria* examined to date. Details of microstructure of *glaucomarginaria* eggs were not examined, but seem to agree with those of *N. bistriaria rubromarginaria* (Packard) (Salkeld 1983:153). Clutches of up to 55 eggs were recorded.

First instar. Similar to ultimate instar (Fig. 1), but with dorsolateral projections on A2–4 smaller, thicker, and squared off; setae L1 and L2 at tips. Projections half as wide as segments anteroposteriorly (*Dichorda* are ¾ as wide in the first instar). Color mottled brown, pattern obscure; setae clear and blunt. Head width 0.3 mm, body length 3 mm at hatch. Chaetotaxy not examined.

Second instar. Like first instar, except dorsolateral projections on A2–4 slightly more



FIGS. 1–5. *Nemoria glaucomarginaria*, scale 1 mm, except as indicated. **1,** Morphology of fifth instar, lateral view; **2,** Head of fifth instar. Pattern of larger spicules and darker markings at right, chaetotaxy at left. Setae translucent; **3,** Right mandible. Internal aspect unshaded, external shaded. Scale 0.5 mm; **4,** Anal shield, dorsal view; **5,** A3, dorsal view, showing placement of setae and spiracle.

elongate at L2 than L1. Color mottled brown, gross elements of fifth instar pattern sometimes visible posteriorly and dorsally.

Third instar. Structurally identical to fifth instar; coloration as in second instar, except pattern elements usually more visible.

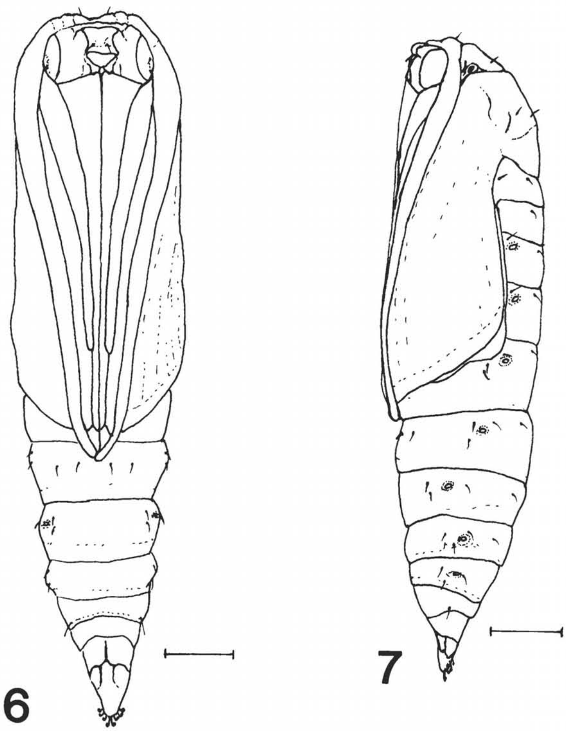
Fourth instar. Identical to fifth instar, except in size.

Fifth instar. The following description is given by segment.

Head (Fig. 2) width 2.1–2.5 mm; tan to brown, mottled with darker pigment as shown; covered with spiculiferous projections containing white pigment spots under a clear cuticle, spicules reaching greatest devlopment on dorsal epicranium. Setae translucent, not black as shown. Clypeus lighter than head, with wrinkles as in *d. darwiniata* (Dyar 1904). Mandibles as illustrated (Fig. 3).

The following descriptions refer to Figs. 1, 8, and 10, except as indicated:

T1 with dorsal conical projections bearing setae XD1 and XD2; caudad another projection bearing setae D1 and D2 together. Another swelling dorsolaterally bears setae L1 and L2; SV2 and SV3 on swelling above leg. L2 long and hairlike, probably acting as a proprioceptor. Pattern as figured, colors light to very dark brown, with whitish markings; addorsal line often dark green. **T2** with large protuberance elevating setae L1–3, SD1, and SV3; SV2 on swelling above leg. SD2 long and thin. Color as in T1. **T3** structure as



FIGS. 6, 7. *Nemoria glaucomarginaria* pupa. **6**, Ventral aspect; **7**, Lateral aspect.

in T2; green, resembling color of foodplant, especially posteriorly, with lighter markings as shown; protuberance light brown, dorsal markings green or brown.

A1 with D1 barely raised, closer to mid-dorsal line than D2. Lateral protuberance small, bearing SD2 only. Spiracle below protuberance, above L2 and L1. Color green with markings as shown; darker green shading below protuberance. Anterior mid-dorsal patch dark. **A2–4** (Fig. 5) with D1 as in A1, except raised more. Spiracle above projection; MD1 thin, anterior to spiracle, probably a proprioceptor. SD setae absent. Dorsolateral projections large, conical, slightly bidentate, bearing L2 at greatest extremity, L1 caudad; projections longer and more pointed on A3. SV4 on line between L3 and SV2 in segments A3 and A4. Pattern as shown; color brown on anterior part of segments and on distal half of projections, green elsewhere. A2 often completely brown as shown, A3 usually mostly green. White markings around anterior mid-dorsal patch, on caudal edge of projections, anterior subdorsal patch, and lateral line, pronounced in intersegmental areas; smaller whitish markings as figured. Adventral line dark, chainlike, often obscure. **A5** with D1 placed further from mid-dorsal line than on A1–4, still closer to mid-line than D2. SD setae absent. Lateral protuberance small, raising L1 and L2. Spiracle above protuberance. Color green, pattern as on A2–4, except anterior mid-dorsal patch obscure. **A6** with D1 and D2 equidistant from mid-dorsal line. SD setae absent. Small swelling below spiracle bearing L1 and L2. Crochets reduced to half length in center, not wholly interrupted. Pattern as shown; anterior green, posterior brown to purplish brown with frosty countershading on leg. **A7** with D1 and D2 equidistant from mid-dorsal line. SD setae absent. Small swelling below spiracle elevating L1 and L2. Pattern as shown; color light brown on swelling to dark brown generally, markings white; brown countershades

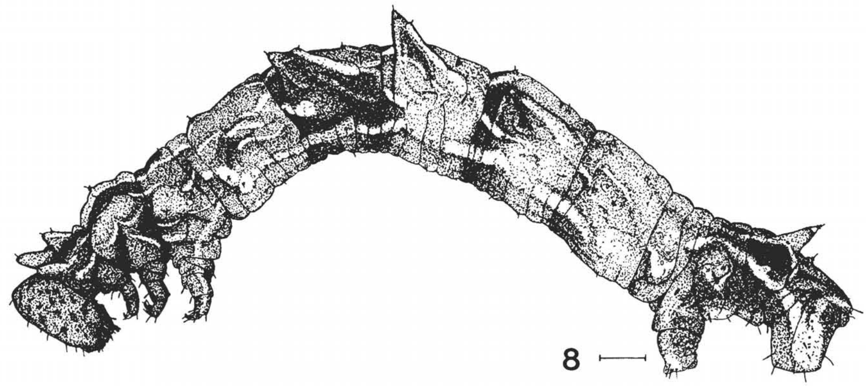


FIG. 8. *Nemoria glaucomarginaria*. Lateral aspect showing pattern of markings on fifth instar. Refer to text for color description. Scale 1 mm.

to whitish ventrally. **A8** with D1 raised dorsally on high conical projection directed caudally. Pattern as shown; projection light brown with whitish tip, dark chestnut brown on patch below this. Purplish brown below white subdorsal line, fading to whitish ventrally. **A9** with D1 on large chalaza; other setae as shown. **A10** with anal plate as shown (Fig. 4). Sclerotized shield of proleg marked with darkly pigmented indentations of various sizes (Figs. 1, 10), slightly variable in placement. An additional seta, herein named LG4, present on the anteroventral corner of shield (also present in all other *Nemoria* examined). Pattern as shown; markings white to buff on brown background. Crochets wholly interrupted in center by fleshy pad.

Entire surface of larva covered with spicules, each usually with white spot of pigment inside. They reach greatest size dorsally and on projections and protuberances, approaching length of blunt setae. Spicules smaller below, giving rugose, granular or velvety appearance; most without white pigment on segments A6–10. Most setae (except MD1) raised on chalazae (Fig. 10), which often accumulate spicules, especially dorsally.

A loose cocoon is spun on the foodplant along a twig, incorporating pieces cut from nearby leaves, or from cage material (such as cloth or paper).

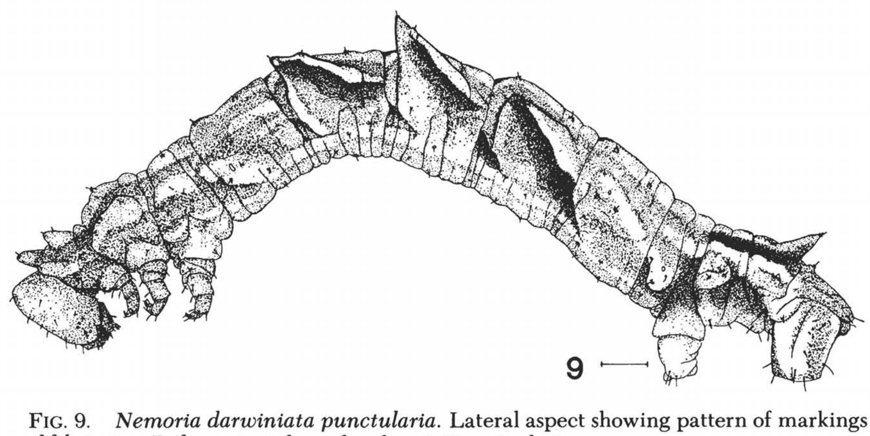


FIG. 9. *Nemoria darwiniata punctularia*. Lateral aspect showing pattern of markings on fifth instar. Refer to text for color description. Scale 1 mm.

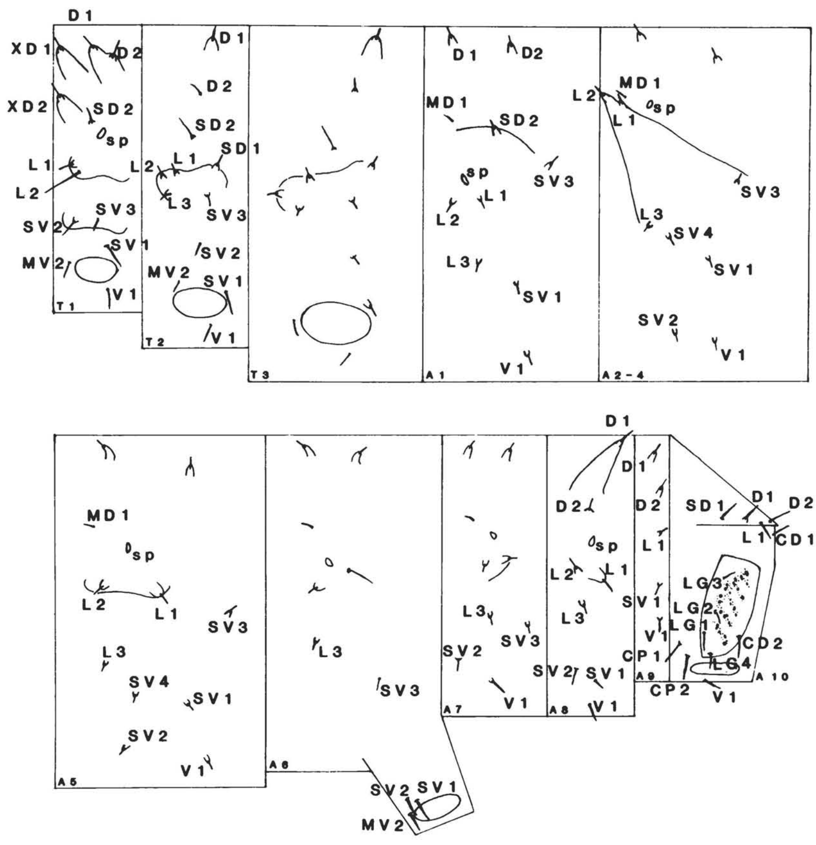


FIG. 10. Setal map of *Nemoria glaucomarginaria*.

Prepupa essentially a stout, compacted fifth instar larva. Dorsolateral projections gradually absorbed during 3- to 4-day prepupal period.

Pupa (Figs. 6, 7) unadorned except for light sculpturing about face and antennal bases. Wing cases extend to middle of A5; antennae and T3 legs often extend just beyond. Figs. 6 and 7 show range of observed variation in relative lengths of wing and antennal cases. Faint venation visible on wing cases. Single setae at bases of antennae, between antennae and eyes, on T1 anterior to spiracle and dorsally; 2 setae on T2; seta on each abdominal segment in a single dorsal row and spiracular group of 3; a pair on A6 ventrally. Cremaster usually with 8 hooks, longest distally; 7 or 6 in some individuals. Yellow at molt, coloring to tan; black markings dorsal to spiracles, surrounding prespiracular setae, and dotted on wing veins. Mid-dorsal line dark. Eyes darken after 6–8 days, wings color to green with lines visible in 10–15 days; abdominal spots visible 12–24 h before eclosion. Emergence at dawn or dusk; pupal duration 12–18 days, with males emerging first (protandry). Winter diapause probably occurs as pupa, but this has not been verified, and at least some Nemoriini and Synchlorini diapause in third instar.

Pattern markings on larvae remarkably constant, although degree of pattern expression varied slightly, and coloration varied considerably. Larvae reared during summer on *Quercus suber* L. (Fagaceae), a Mediterranean species with grayish foliage, showed little pattern, resulting in mostly gray-green larvae. Those reared in spring on *Q. lobata* Nee., a native species, showed greatest contrast, resulting in green and brown mottled larvae. Whether this effect is genetic, seasonal, or a reaction to foodplant is unknown.

Host plants. No wild collected larvae are known. All larvae were reared on new shoots of *Quercus* spp. available in Davis, California. *Quercus agrifolia* Nee., *Q. lobata,* and *Q. suber* were readily accepted. I often collected adults in association with *Q. kelloggi* Newb. in numerous localities in the Sierra Nevada and San Bernardino Mts. Material from Los Molinos, Tehama Co., in the northern Central Valley, probably fed on *Q. lobata,* the only oak species native to that area (Griffin & Critchfield 1976). Those collected at Norden, Nevada Co., California probably use *Q. vaccinifolia* Kell., the only oak in that area (A. M. Shapiro, pers. comm.). Those from coastal Orange and San Diego counties must have fed on *Q. agrifolia,* or on an ornamental species, for the same reason (Griffin & Critchfield 1976, Munz & Keck 1968). Five larvae fed *Salix hindsiana* Benth. (Salicaceae; a species acceptable to *darwiniata*) died in third instar.

Behavior. All instars exhibited the often described "shaking" behavior, imitating a piece of dried plant material in a light breeze. This behavior is common to all Nemoriini and Synchlorini reared to date, but is apparently absent in the Hemitheini. First and second instars were observed with bits of food and fecal material attached to the body, a common behavior of the Synchlorini. Closer examination revealed that this adhered due to high humidity in the rearing containers, and not by silken threads as in the Synchlorini. The larvae did not replace removed material, and larvae reared in drier containers showed no attached materials. Young larvae, and to some extent even mature larvae, showed a marked tendency to remain feeding in the same place even if the food began to deteriorate. This behavior appears to be adaptive; dead plant material is typically associated with caterpillar herbivory, and larvae may enhance crypsis by remaining at the feeding site.

Distribution. Records are scattered throughout California west of the Great Basin (Fig. 11). The species is also distributed northward through the Coast Ranges and Cascades to British Columbia (Ferguson 1985). The dense cluster of points in S California, the San Francisco Bay area, and in the Sierra Nevada from El Dorado to Plumas counties are no doubt attributable to differences in collecting intensity. I am responsible for much of the cluster W of Lake Tahoe. The only dubious record shown is of two specimens in the Bohart Museum from Alturas, Modoc Co., California, in the NE corner of the state. These were part of a large light trap sample at the Agricultural Inspection Station (J. S. Buckett, pers. comm.). There are no native oak species within 60 km of that locality (Griffin & Critchfield 1976), implying that the specimens were probably either carried in on a vehicle or mislabelled.

Phenology. *Glaucomarginaria* has 2 generations annually in northern California at low to mid elevations, one flying in mid-May and one in early July. These dates are variable depending on elevation and season. Ferguson (1985) reports slightly earlier dates in southern California. Adults of the spring brood may be collected when the leaves of the foodplant begin to unfurl. I have only encountered one generation at Norden, Nevada Co., elevation 2,140 m.

Nemoria darwiniata punctularia Barnes & McDunnough

Color pattern of the mature larva of *N. darwiniata punctularia* Barnes & McDunnough is shown in Fig. 9. This species has been figured (Comstock & Henne 1940, as *pistacearia*), but the reproduction lacks details for specific identification. *Nemoria darwiniata punctularia* is usually paler than *glaucomarginaria,* typically yellowish green, with medium brown markings and whitish lines. The body is slightly stouter, and projections correspondingly shorter. The spicules tend to be smaller and more even in size, giving a more velvety appearance than *glaucomarginaria.* The differences, however, are so slight that I use a tracing of Fig. 1 (*glaucomarginaria*) to illustrate the *d. punctularia* pattern. Fig. 9 also agrees with Dyar's (1904) written description of *d. darwiniata* (Dyar) from British Columbia. The third instar has the same pattern of markings, but is brown from the lateral line dorsally to beneath the protuberances, giving the aspect of a serrate brown line on the side of the body.

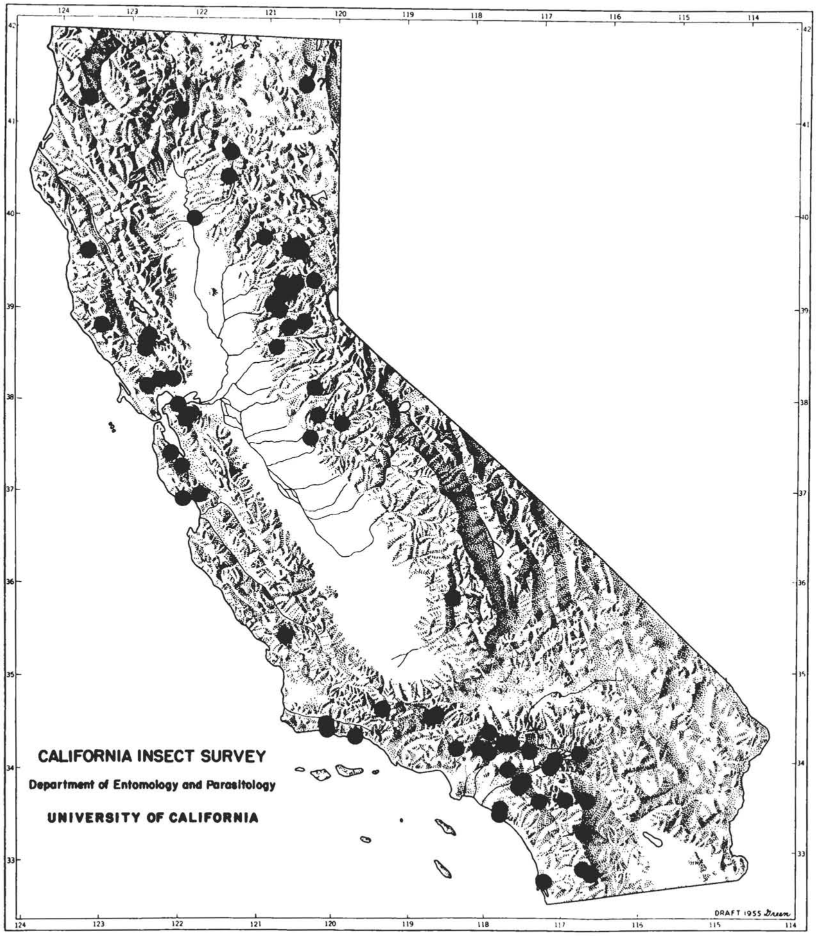


FIG. 11. Distribution of *Nemoria glaucomarginaria* records in California.

These two species are most distinguishable by pattern. In general, the anterior of each abdominal segment is most contrasting in *glaucomarginaria*, while the posterior of each segment is most contrasting in *darwiniata*. *Glaucomarginaria* larvae appear to be indistinguishable in color pattern and morphology from *Nemoria festaria* from the mountains of S Arizona to Texas. Female genitalia are also very similar between these two species (Ferguson 1985). *Darwiniata* is apparently at least oligophagous, being reared from *Salix* (Salicaceae) (Dyar 1904, pers. obs.), *Quercus* (Fagaceae) (Comstock & Henne 1940), and *Arctostaphylos* (Ericaceae) (N. McFarland notes in Los Angeles Co. Museum of Natural History) in the laboratory. I have also recorded it in the field from *Ceanothus cordulatus* Kell. (Rhamnaceae) at Alpine Meadows, Placer Co., California (subsequently reared *ex ova* on this host in the laboratory).

Most larvae of the genus *Nemoria* examined agree in detail with the setal map of Fig. 10, although size and shape of projections and protuberances differ in minor details. Thus, the above morphological description of *N. glaucomarginaria* serves as a working description for the genus. The only exceptions known are discussed in the key below.

DISCUSSION

Ferguson (1985) published the most accurate figure of a *Nemoria* larva to date. A clear figure of *Dichorda* was given by Comstock (1960). No figures of *Chlorosea* and *Phrudocentra* Warren (Nemoriini), or *Dichordophora* (Dichordophorini) have been published.

Nemoriine larval descriptions in most early publications focus on the bizarre morphological adaptations for crypsis and are of little value for taxonomic purposes at the species level. Moreover, because of the difficulties in identifying adults before Ferguson's (1969) revision, descriptions for most taxa need to be verified, and host records confirmed. As early workers did not have a broad range of species for comparative purposes, early figures such as those of Dammers are often misleading, as for example, his figure of *N. leptalea* (=*delicataria* Dyar) compared to the photograph in the same publication (Comstock 1960). His figure of *N. pulcherrima* (=*naidaria* Swett) is stylized as well (Comstock & Dammers 1937). Dethier (1942) figured the ultimate instar of *N. rubrifrontaria* (Packard) with long primary setae (of which some appear to be missing), a condition common to the Synchlorini, but unknown elsewhere in the Nemoriini. Rindge (1949) used Dethier's description as a basis of comparison for a preliminary generic description of *Chlorosea* which is correspondingly inaccurate.

The following key will serve to rectify some of these errors. It is of course preliminary in that it is not based on all the species, but it will serve to sort out some of the characters for a future phylogenetic analysis of the group.

Preliminary Key to Genera of Nemoriine Larvae

1. Dorsolateral projections on A2–6 wide, rectangular, and lamellate; setae on the outer corners (L1 & L2) and another (SD2) on the anterior edge of each plate .... *Dichorda*

1′. Dorsolateral projections on A2–6 conical, not wide and platelike as above 2

2. Dorsolateral projections on A2–4 tridentate, bearing three setae (SD2, L1, L2); the middle seta (L2) extending farthest from the body .... *Phrudocentra**

* Based on the description of *Phrudocentra* in Ferguson (1985), as I have not seen larvae of this genus. *Dichordophora* (Dichordophorini) also keys out here. These two genera may be separated by locality if adults are not available:

2'. Dorsolateral projections bidentate, bearing two setae 3
3. Dorsolateral projections on A2–4 with posterior seta (L1) extending farthest from body; mid-dorsal projections well developed, bearing both D1 setae .. *Chlorosea***
3'. Dorsolateral projections on A2–4 with anterior seta (L2) extending farthest from body; mid-dorsal projections usually poorly developed of lacking .... *Nemoria****

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Dichordophora is a denizen of the desert areas of Mexico and SW United States, while *Phrudocentra* is from American subtropical and tropical regions.

** *Nemoria pulcherrima* also keys out here. The adult shows affinities to both *Chlorosea* and *Nemoria*, as well as some unique morphological and phenological characters (Ferguson 1985). I leave it here until more data pertaining to its taxonomic status can be gathered.

*** The single undetermined *Nemoria* larva mentioned earlier has a well developed mid-dorsal protuberance, in contrast to all other *Nemoria* examined (except *pulcherrima*). This may prove a phylogenetically useful character when more larvae have been described.

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GENERAL NOTE

MASS EMERGENCES OF THE PINE WHITE, *NEOPHASIA MENAPIA MENAPIA* (FELDER & FELDER), IN COLORADO (PIERIDAE)

Ferris and Brown (1981, Butterflies of the Rocky Mountain states, University of Oklahoma Press, Norman, 442 pp.) cite *Neophasia menapia menapia* (Felder & Felder) as an occasional economic pest in western montane forests, primarily of ponderosa pine (*Pinus ponderosa* Laws.) and lodgepole pine (*P. contorta* var. *latifolia* Engelmann). I observed mass emergences of this species in 1983 and 1984 in the pinon-juniper forest of western Colorado. The location was Eagle Co., White River National Forest, Frying Pan River Valley, 8.85 km E Basalt, ca. 2,196 m elev. In both years the emergence lasted 3 days; 13–15 August 1983 and 3–5 August 1984. The emergences were sudden, synchronized, truly massive in nature, and all the adults disappeared as abruptly as they appeared.

Earliest flight on calm, sunny mornings was recorded ca. 0745 h, and it was that of males typically searching for females around the high outer branch tips of mature pinon pine. Not until ca. 0900–0930 h did flight get fully underway, giving one the sense of the forest being alive with butterflies.

Feeding was never observed in spite of special efforts to confirm Ferris and Brown's observation of early morning nectaring at flowers, which were abundantly available throughout the area. The pinon-juniper association showed no evidence of damage by larvae, densities of which can only be imagined. Both tree species were growing vigorously, and the pinon were filled with developing green cones. Considering their apparent three-day life span and the lack of feeding, it seems possible that these adults are non-feeders.

Male-to-female ratio of specimens collected was 5:1 (n = 58 in 1983, 72 in 1984), though I believe that to be distorted by my efforts to locate the rare females. A ratio of 50:1 is probably closer to the true situation. Females collected were so heavily gravid they struggled to fly.

In the 10 years I lived at this locality (1976–85) this population explosion of *N. m. menapia* occurred only during the aforementioned 2 years.

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