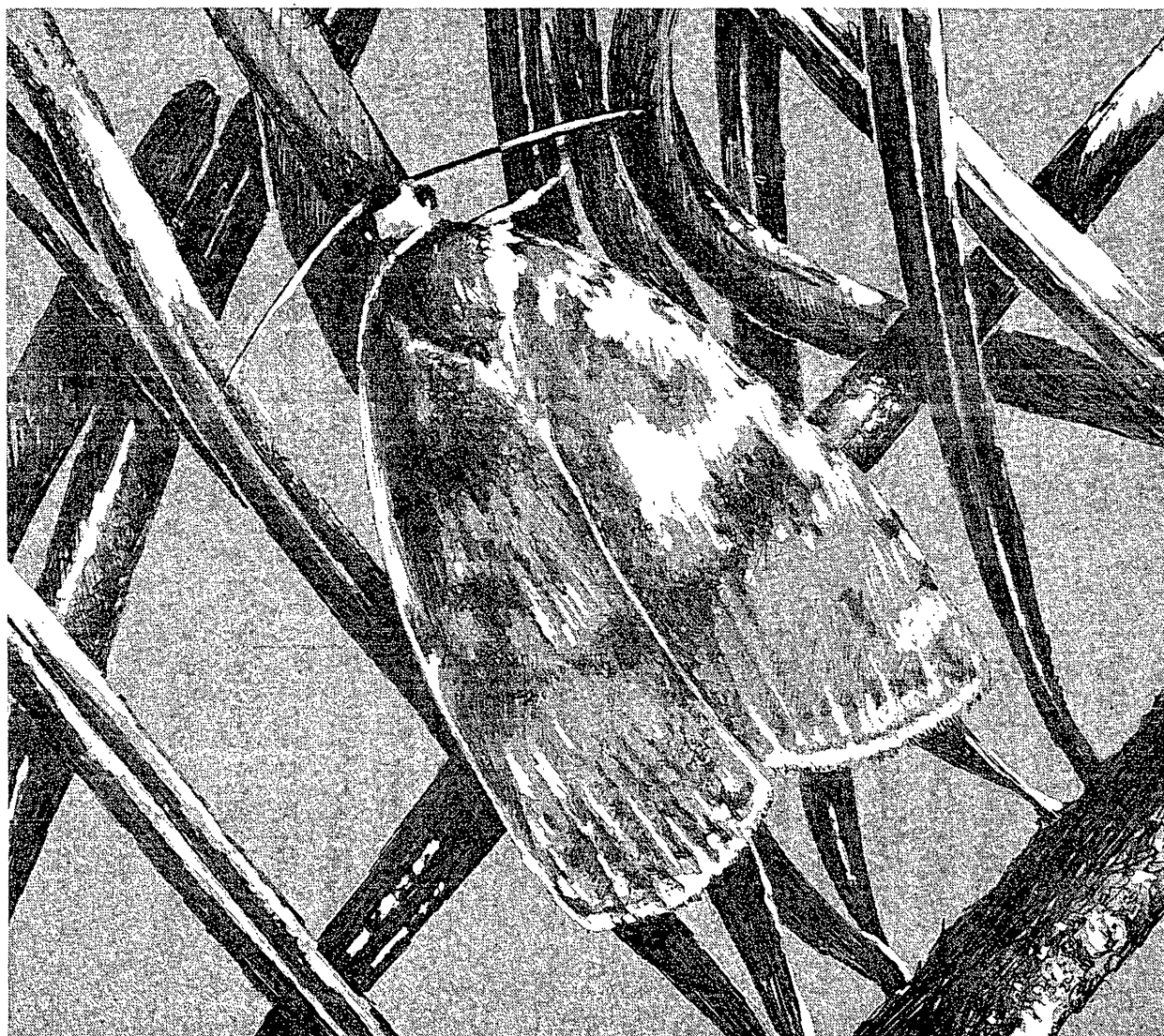


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# Nomenclature of Nearctic Conifer-Feeding *Choristoneura* (Lepidoptera: Tortricidae): HISTORICAL REVIEW AND PRESENT STATUS

Jerry A. Powell

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## ABSTRACT

There have been 18 species-group names proposed for Nearctic conifer-feeding moths in the genus Choristoneura. Of these, houstonana (Grote) and its synonym, retana (Walsingham), apply to Cupressaceae-feeding populations now assigned to Cudonigera Obraztsov & Powell. The remaining species are Pinaceae-feeders, mostly members of two series: (1) the Fumiferana complex, associated with spruces and firs (subfamily Abietoideae) and considered to consist of 5 allopatric species (with three synonyms); and (2) the Lambertiana complex, feeding on pines (subfamily Pinoideae) and consisting of two allopatric species, the western C. lambertiana (Busck) with three subspecies and the eastern C. pinus Freeman with two subspecies. A third group, the Carnana complex, is believed to be associated with Douglas-fir (Pseudotsuga). Its populations occur in California, with two named races, sympatric with elements of both the Abietoideae- and Pinoideae-feeding complexes. One named entity, spaldingiana Obraztsov, in Utah, is of unknown affinities.

Keywords: Nomenclature (insect), Choristoneura.

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I thank USDA Forest Service researchers V. M. Carolin Jr., G. E. Daterman, R. E. Stevens, and T. R. Torgersen; and W. J. A. Volney, University of California, Berkeley, for review of a draft of the manuscript. Although not all my nomenclatural decisions are necessarily endorsed by any one reviewer, their comments and criticisms were helpful in clarifying the discussion and in developing the conclusions. Field travel during 1966-70 and study at the British Museum in 1971 were in part funded by National Science Foundation grants GB-4014 and **GB-6813X**. USDA Forest Service personnel allowed me to use facilities in the Modoc and Shasta National Forests in 1970-74 and provided field collections from the 1974 pilot study of the effects of Dylox.

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Possibly no species of Lepidoptera has been more intensively studied during the past quarter century than the spruce budworm in North America, yet the nomenclature of the Choristoneura fumiferana group has continued to be confusing. Although some problems are traceable to premature or careless taxonomic work, the principal source of turmoil lies in the complexity of variation among populations. An array of inter-relationships exists: sympatric populations exhibit varying degrees of reproductive isolation, and allopatric populations show geographical variations in size and color of adults, larvae, and pupae and in preferences for host plants. There are both polymorphic and continuously variable features, and characters conventionally used by taxonomists in defining species in moths are not sufficiently differentiated in this group to provide reliable morphological indicators of genetic and behavioral compatibility among populations.

An increase in research on the Nearctic conifer-feeding Choristoneura as a result of the Canada/U.S. Spruce Budworms Program, launched in 1977, has broadened interest in and the need for better communication about these insects. Despite considerable funding and intricate organizational planning, disagreement exists concerning the number, level of taxonomic distinctness, and geographical distributions of species and races, as well as the names applied to them. Thus, an updated summary of nomenclature in this species group and agreement among researchers about correct application of names seem essential.

Moreover, a revised checklist of North American Lepidoptera, which has been several years in preparation by a team of specialists, is nearly completed--the first updated list in 40 years (Hodges et al., in press). Acceptance of the nomenclature in this list by the U.S. Department of Agriculture and the Entomological Society of America (and therefore the E.S.A. common names list--Sutherland et al. 1978) is anticipated. This should provide a considerably stronger base for stabilization of names of all North American Lepidoptera. I have contributed the text for the Tortricidae, aided by reviews and contributions from several contemporary specialists, including R. W. Brown, R. W. Hodges, and W. E. Miller. Table I lists valid and synonymous names applied to conifer-feeding Choristoneura and Cudonigera as they will be treated in Hodges' (in press) checklist.

In general, the checklist is not envisioned as a vehicle for revising taxonomic work, but there will be many nomenclatural changes. Names formerly applied in many taxa have become obsolete as a result of taxonomic study of Nearctic or other faunas, particularly the Palearctic. Authors have been expected to incorporate nomenclatural changes where firsthand taxonomic expertise enables generic reassignments and synonymies. Therefore, many new combinations and new synonymies will be published in the checklist without explanations. In most instances, explanations would be of interest only to specialists, but in a few cases the importance of the insects in agricultural entomology or other applied fields is such that

# CHRONOLOGICAL HISTORY OF THE SPECIES GROUP NAMES

published interpretation is warranted. Because the Canada/U.S. Spruce Budworms Program is in its early phases, the spruce budworm complex is such a case.

Table 1--Checklist of valid and synonymous names used for North American conifer-feeding Choristoneura and Cudonigera (synonyms underlined)<sup>1/</sup>

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Choristoneura Lederer, 1859  
fumiferana (Clemens, 1865)  
nigridia (Robinson, 1869)  
retiniana (Walsingham, 1879)  
lindseyana Obraztsov, 1962  
viridis Freeman, 1967  
occidentalis Freeman, 1967  
biennis Freeman, 1967  
orae Freeman, 1967  
carnana (Barnes & Busck, 1920)  
c. californica Powell, 1964  
lambertiana (Busck, 1915)  
1. ponderosana Obraztsov, 1962  
1. subretiniana Obraztsov, 1962  
pinus Freeman, 1953  
p. maritima Freeman, 1967  
spaldingiana Obraztsov, 1962  
Cudonigera Obraztsov & Powell, 1977  
houstonana (Grote, 1873)  
retana (Walsingham, 1879)

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<sup>1/</sup>After Powell in Hodges et al. (in press).

fumiferana Clemens, 1865, Proc. Entomol. Soc. Phila. 5:129 (Tortrix)

The earliest name applied to any North American conifer-feeding Choristoneura is fumiferana, described from "Virginia." A lectotype was designated by Darlington (1947), who indicated there are no data associated with the specimen, as is true of Clemens' material generally (see Miller (1973) for a review of the history and status of Clemens' types and associated catalog numbers). Thus, the accuracy or any restriction of the type locality cannot be determined. Treated in Tortrix or Harmologa, a New Zealand genus, in early literature, the species later was placed in Archips (= Cacoecia) until Freeman (1947) assigned fumiferana to the Palearctic genus Choristoneura.

nigridia Robinson, 1869, Trans. Am. Entomol. Soc. 2:268 (Tortrix)

Described from "Ohio, Pa., and Mass.," this is the only synonymous name proposed for the widespread spruce budworm of eastern Nearctic boreal forests. Darlington (1947) mentioned a cotype at the Academy of Natural Sciences, Philadelphia; but apparently no formal designation of a lectotype and restriction of the type locality has been made. Representative specimens of type material of nigridia and fumiferana were examined by Fernald in the 1870's (Darlington 1947, p. 86), who concluded the two are synonyms (Fernald 1881, p. 63).

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houstonana Grote, 1873, Bull. Buffalo Soc. Nat. Sci. :15 (Tortrix)

The next oldest name used for a conifer-feeding moth formerly considered a member of Choristoneura is houstonana Grote, which was based on a specimen from "Texas." The type specimen is believed to be no longer extant. A synonym, retana Walsingham, is available, but the species is distinctive, and Grote's description seems unequivocal so that neither suppression of it as a nomen dubium nor designation of a neotype seems necessary. This species was included in Choristoneura (Freeman 1958, Powell 1964); but recently Cudonigera Obraztsov and Powell was proposed for houstonana, primarily on the basis of morphological features of the adult which differ markedly from all other Choristoneura (Powell and Obraztsov 1977). Cudonigera houstonana feeds exclusively on Juniperus (Cupressaceae) (Powell 1964, Heinrichs and Thompson 1968); all other Nearctic conifer-feeding Choristoneura are restricted to Pinaceae (Stehr 1967).

retana Walsingham, 1879, illus. Lepid. Het. Br. Mus. 4:13 (Lozotaenia)

This name was recognized by Grote (1881, p. 9) as synonymous with houstonana, a conclusion accepted by subsequent workers. The type locality, cited as "Texas," is Bosque County, Texas, according to data on the lectotype (Powell and Obraztsov 1977).

retiniana Walsingham, 1879, illus. Lepid. Het. Br. Mus. 4:12 (Lozotaenia)

The earliest name applied to any western budworm is retiniana Walsingham, described from one specimen collected at Mount Shasta, California, in 1871. Failure to recognize its status by most subsequent taxonomists precluded use of this name in literature on budworms. Generally, it was listed in the genus Archips by earlier workers, but Freeman (1958) transferred retiniana to Choristoneura, suggesting that it might be related to the pine-feeding species. Freeman illustrated a specimen from Mono County, California, as representing retiniana.

Obraztsov (1962) recognized that Freeman's assumption was based on a misidentification of moths now called subretiniana Obraztsov, a pine-feeder. Obraztsov illustrated structural features of the holotype of retiniana and presented photographs of specimens from Oregon and New Mexico which he supposed to be conspecific. Powell (1964) applied the concept of fumiferana Clemens broadly, to include all fir- and spruce-feeding populations, and recognized retiniana as a synonym because pale specimens of Abies-feeding populations in Modoc County (about 150 km--90 miles--east of Mount Shasta) resemble Walsingham's description and illustration of retiniana.

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lambertiana Busck, 1915, Proc. Entomol. Soc. Wash. 17:86 (Tortrix)

The earliest name proposed for any pine-feeding population in Nearctic Choristoneura is lambertiana Busck, described from Ashland, in southern Oregon (Jackson County). The locality was originally 'given as "Oakland," Oregon, but the type series is from Ashland according to the labels and Hopkins' data. Some of the labels are printed by machine, and some are handwritten; the latter were evidently misread by Busck. The species was assigned to Choristoneura by Freeman (1958), who listed the species also from California and New Mexico without specific data. The concept of lambertiana was broadened by Obraztsov (1962) to include populations in Idaho, Montana, Wyoming, and New Mexico.

carnana Barnes and Busck, 1920, Contr. Nat. Hist. Lepid. N.A. 4(3):214 (Tortrix)

This distinctive, rust- and white-colored moth was described on the basis of specimens labeled "Camp Baldy, San Bernardino Mountains, California." The type locality presumably is at or near the place now known as Mount Baldy Post Office (designated as Camp Baldy on roadmaps as recently as 1947), which is situated at about 1 300-m (4,250-foot) elevation near the Los Angeles-San Bernardino County line in the San Gabriel Mountains. There have been no verified records from the San Bernardino Mountains. The species was recognized as a Choristoneura related to fumiferana by Freeman (1958), and subsequently carnana was treated as a subspecies of lambertiana (Powell 1964).

pinus Freeman, 1953, Can. Entomol. 85:122 (Choristoneura)

This name was provided by Freeman for pine-feeding populations of eastern Canada, following extensive studies by several researchers on differences in biology, phenology, immature stages, parasites, and isolating mechanisms between this and the sympatric Choristoneura fumiferana. The type locality is Beausejour, Manitoba.

spaldingiana Obraztsov, 1962, Am. Mus. Novit. 2101:6 (Choristoneura)

This species was described from Provo, Utah, on the basis/of a single male specimen.

~~sub~~retiniana Obraztsov, 1962, Am. Mus. Novit. 2101:9 (Choristoneura)

Using specimens from "Monachee," Tulare County, California, 8,000 feet (2 450 m), Obraztsov described subretiniana. Presumably this is the site now called Monache Meadows, situated near the headwaters of the south fork of the Kern River, west of Olancho Pass in the southern Sierra Nevada.. This race was treated as a subspecies of lambertiana by Powell (1964) on the basis of phenotypic similarity of adults in populations of the central and northern Sierra Nevada and the pine-feeding population of Warner Mountains, Modoc County, and because of the allopatric occurrence of these populations in relation to lambertiana s. str. and californica Powell west of the Sierran crest.

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ponderosana Obraztsov, 1962, *Am. Mus. Novit.* 2101:14 (Choristoneura)

In broadening the concept of lambertiana, Obraztsov recognized similarity of moths in Colorado to those of the northern Rockies which he treated as lambertiana, and he designated a series reared from ponderosa pine at Sugar Loaf, Boulder County, as ponderosana.

lindseyana Obraztsov, 1962, *Am. Mus. Novit.* 2101:16 (Choristoneura)

A collection of Choristoneura was made by A. W. Lindsey in the Davis Creek area of the Warner Mountains, Modoc County, California, in 1922. Included were nearly 100 specimens representing each of two populations now known to be fir-feeding and pine-feeding species and referred to as retiniana and subretiniana, respectively. A portion of the polymorphic Abies-feeding population there consists of individuals with pale tan forewings without dark markings, and this form was selected by Obraztsov to name. He supposed this to be a subspecies of lambertiana, despite the fact that specimens phenotypically similar to subretiniana had been collected by Lindsey in the Warner Mountains, and others had been reared by USDA Forest Service researchers from lodgepole pine in 1952-53 (Powell 1964, p. 183). In treating fumiferana broadly, I relegated lindseyana to synonymy, recognizing the tan form as a polymorphic phase in samples reared from Abies (Powell 1964, p. 175).

I pointed out that Obraztsov's lindseyana types had been extracted

from a series of Choristoneura "fumiferana" (= retiniana) and these matched specimens reared from Abies in the Warner Mountains during 1950-57 (Powell 1964, p. 176).

californica Powell, 1964, *Univ. Calif. Publ. Entomol.* 32:179 (Choristoneura)

This name was applied to populations in the North Coast Range (type locality: Anderson Springs, Lake County), southern Cascade Range, and west slope of the Sierra Nevada. Although none had been reared, larvae of these populations were assumed to be pine-feeding, and californica was associated with lambertiana as a subspecies on the basis of the allopatry with lambertiana in the strict sense to the north, subretiniana to the east, and carnana in southern California.

~~biennis~~ Freeman, 1967, *Can. Entomol.* 99:451 (Choristoneura)

This species was distinguished primarily on the basis of the larger average size and darker coloration of adults and the fact that 2 years are required to complete the life cycle. The type locality is 8 miles (13 km) south of Cherryville (in the Monashee Mountains near Vernon) in southern British Columbia, where specimens were reared from spruce (Picea sp.) and fir (Abies lasiocarpa).

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occidentalis Freeman, 1967, Can. Entomol. 99:451 (Choristoneura)

Considered to be the most widespread, dominant conifer-feeding Choristoneura in the western Nearctic, occidentalis was described from Klickitat County, Washington, reared from Pseudotsuga. Populations believed to be conspecific were recorded from New Mexico through the northern Rocky Mountain States to British Columbia and in northern California (Freeman 1967).

orae Freeman, 1967, Can. Entomol. 99:452 (Choristoneura)

This name was applied to a population at Kitimat in north coastal British Columbia. Choristoneura orae consists of small individuals which are phenotypically similar to fumiferana. The type series was reared from Abies and Picea. Differences in polymorph phases (Stehr 1964) and characteristic physiological data (Harvey 1967) appear to be the primary distinguishing features of the population.

viridis Freeman, 1967, Can. Entomol. 99:452 (Choristoneura)

On the basis of collections from Bidwell Creek, Modoc County, California, Freeman renamed the fir-feeding population of the Warner Mountains viridis, disregarding the nomenclatural priority of lindseyana for that population. Despite biological information documenting the status of lindseyana as the pale form of the fir-feeding Choristoneura and the occurrence of a sympatric pine-feeding species (Powell 1964),

Freeman (1967, p. 453) listed lindseyana among several forms thought to be pine-feeders.

maritima Freeman, 1967, Can. Entomol. 99:455 (Choristoneura)

This name was proposed as a subspecies of Choristoneura pinus, to include populations from Massachusetts south to Kentucky. The type locality is Blain (Perry County), in the Allegheny Mountains of south central Pennsylvania. Known hosts include pines of the subsections Australes and Contortae.

## CURRENT STATUS OF NAMED FORMS

There are two series of populations among North American Pinaceae-feeding Choristoneura, one feeding primarily on spruces and firs of the genera Picea, Abies, and Pseudotsuga (subfamily Abietoideae; Ferre 1952), and the other almost exclusively on Pinus (subfamily Pinoideae). For convenience, these are referred to here as the Fumiferana complex and Lambertiana complex, respectively. In each there are parallel patterns of geographical distribution, with resultant widespread sympatric pairs, one Abietoideae-feeding and one Pinoideae-feeding, in eastern and western portions of the Nearctic.

There do not seem to be documented instances of sympatric species within either the Fumiferana complex or Lambertiana complex. There is a third group of populations, however, here called the Carnana complex, for which insufficient data are available to precisely define relationships. Formerly, these were thought to be members of the Lambertiana complex, based on allopatric distributions in relation to known pine-feeding populations (Powell 1964). Recent evidence, however, indicates that the Carnana complex consists of populations feeding on Pseudotsuga, which are parapatric (Mount Shasta) or sympatric (west slope of Sierra Nevada, San Gabriel Mountains) with Abies-feeding populations of the Fumiferana complex.

Instances of larvae feeding on other than the normal Abietoideae or Pinoideae host are occasionally observed but usually only in mixed stands of conifer genera. For example, in 1974 we reared a large number of Choristoneura retiniana from late

instar samples collected on Abies concolor in the Warner Mountains, California.<sup>1/</sup> These included all larvae thought to differ from the typical green budworm in preliminary sorting, as well as random subsamples of green budworm from each collection. Of 5,368 moths reared, about 3,200 (60 percent) were C. retiniana and only about 5 (<1 percent) C. lambertiana subretiniana, which sometimes causes visible defoliation of lodgepole pine at the same localities (Pierce and Hall 1974). Stehr (1967), who attributes most such records to dispersal of young larvae in autumn or spring, states that there are no known records of oviposition on the reciprocal host leading to successful establishment of larvae. Probably some published records or data on labels of the "wrong" host are the result of misidentification of larvae or reared adults. In general, the ecological subdivision appears to be remarkably distinct.

In the Fumiferana and Lambertiana complexes, the parallel situation exists wherein each is represented in the eastern half of the continent by a widespread species that is relatively constant in biological and phenotypic characteristics, but in the western portion is more complicated. Entomologists agree that Choristoneura fumiferana is a monotypic form occurring from the McKenzie River near

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<sup>1/</sup>Powell, J. A., and V. Donahue. 1974. Monitoring the effects of Dylox on microlepidopterous larvae. USDA For. Serv., Coop. Agreement Final Rep., 17 p.

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66 N, southeastward in a broad arc through southern Canada and adjacent parts of the United States, to the Maritime Provinces and Newfoundland. Choristoneura pinus is sympatric along the southern part of this range in the Great Lakes region, extending farther south than does fumiferana, in the northern Plains States, and in the Allegheny–Appalachian region, where populations are referred to as the subspecies E. pinus maritima.

West of the continental divide, populations of the Fumiferana and Lambertiana complexes are also sympatric in many areas, but there is considerably greater variability. Among western components of both the Abietoideae– and Pinoideae–feeding groups, a great deal of polytypic (interpopulational) variation exists, not only in adult and larval morphologies, but in degree of genetic polymorphism, physiological traits, and preferences for host plants. Part of the complexity can be attributed to a relatively fragmentary status of sampling compared with eastern areas. In general, however, the situation reflects real biological phenomena: the intermingling of forest tree species, small-scale patterning of pure stands, and geographical complexity of western forest regions (Eyre 1954, p. 9; Stehr 1967). The isolation or semi-isolation of populations by the islandlike distribution of mountain ranges and host tree types presumably has led to divergence and changes in mechanisms that isolate species. Probably the biological instability corresponds generally to the more recent, postglacial colonizing of these areas and the consequent reestablishment of contact between floras and

faunas which were isolated during glacial advances.

## Western Components of the Fumiferana Complex

Present taxonomic concepts consider this array to comprise four mainly allopatric species, the names of which have been applied through historical chance. The oldest name was given to the only representative available a century ago (Walsingham 1879); more recent names were proposed for samples of sporadically collected adults (Obraztsov 1962) or were applied to the populations which were best known through laboratory studies a decade ago (Freeman 1967).

Choristoneura retiniana (Wlsm.).-- Clarification of the status of retiniana is pivotal to nomenclatural assignments. Surveys were conducted in northern California and southern Oregon in 1966–70, toward this goal.<sup>2/</sup> Only sporadic rearing records were obtained, but sufficient population samples of moths taken at lights were accumulated to assess variation. I compared representative specimens with the holotype of retiniana at the British Museum in 1971 and established its identity with samples from McBride Springs on Mount Shasta and Donner Summit (Placer County), California (reared from Abies concolor). Obraztsov's (1962) description of the

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<sup>2/</sup>Powell, J. A. 1970. Taxonomic and biological investigations on California microlepidoptera. Univ. Calif. Agric. Exp. Stn. proj. 2063. Prog. Rep. 1970, 3 P.

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retiniana type specimen as "badly denuded and damaged" is in error. The specimen is in good condition.

T. D. Eichlin of the California State Department of Food and Agriculture and I carried out further surveys in the Modoc-Siskiyou area in 1974, partly in collaboration with the USDA Forest Service, which provided samples of larvae from nine sites in Modoc County from a pilot control project of Dylox on the Modoc budworm (see footnote 1). Larval collections from Abies on Mount Shasta produced moths confirming similarities in phenotype, polymorphic variation, and the weak sclerotization of larval and pupal integument (source of the common name "green budworm") among populations there and in Modoc County. Therefore, I believe the name retiniana applies to Abies-feeding populations in the southern Cascade Range, at Mount Shasta, and in the Warner Mountains. If, in the future, the Warner Mountains population is deemed sufficiently distinguishable to warrant nomenclatural recognition, the name lindseyana Obraztsov, 1962, has priority over viridis Freeman, 1967.

Southward, in the Sierra Nevada, Tehachapi Range, and mountains of southern California, there are populations of Choristoneura that exhibit similar genetic polymorphism, having a morph with pale tan, unmarked forewings. Though the adult phenotype is much less variable than that of retiniana in Modoc County, these populations appear to be a counterpart of retiniana. Their distribution is entirely in association with Abies, and larvae reared in 1979 from Abies in El Dorado County were of the green, unmarked form. In the San

Gabriel Mountains and at lower elevations (below 1 700.m--5,500 feet) in the Sierra Nevada, these retiniana-like Choristoneura are sympatric with the monomorphic, Pseudotsuga-feeding C. carnana, and at higher elevations, near the Sierran crest (e.g., Lake Tahoe), with Pinus-feeding C. lambertiana subretiniana.

Northward, C. retiniana is replaced by occidentalis, either abruptly, in northern Oregon as indicated by Freeman (1967) and Stehr (1967), or gradually in a series of blend zone populations. V. M. Carolin (personal communication) states that a Choristoneura with green larvae identical to retiniana of Modoc County, California, occurs in the King Mountain area near Burns, in east-central Oregon, whereas a fir-feeding form in south-central Oregon west of Lakeview is heterogeneous, showing a gradation between retiniana and occidentalis morphs in both larvae and adults. Currently under investigation by W. J. A. Volney and W. E. Waters, University of California, Berkeley, populations in this region are critical to a more thorough understanding of the systematic and biological relationships of C. retiniana, C. carnana californica, and C. occidentalis.

Choristoneura occidentalis (Freeman).--As presently conceived, this name applied to all Abietoideae-feeding populations from northern Oregon, Washington, southern British Columbia, and the Rocky Mountain States south to New Mexico and eastern Arizona (fig. 1). Freeman (1967) also listed California in the range of occidentalis; and Stehr (1967), in his figure 1, showed a symbol for occidentalis in the vicinity of Lake Tahoe, both without indication as to

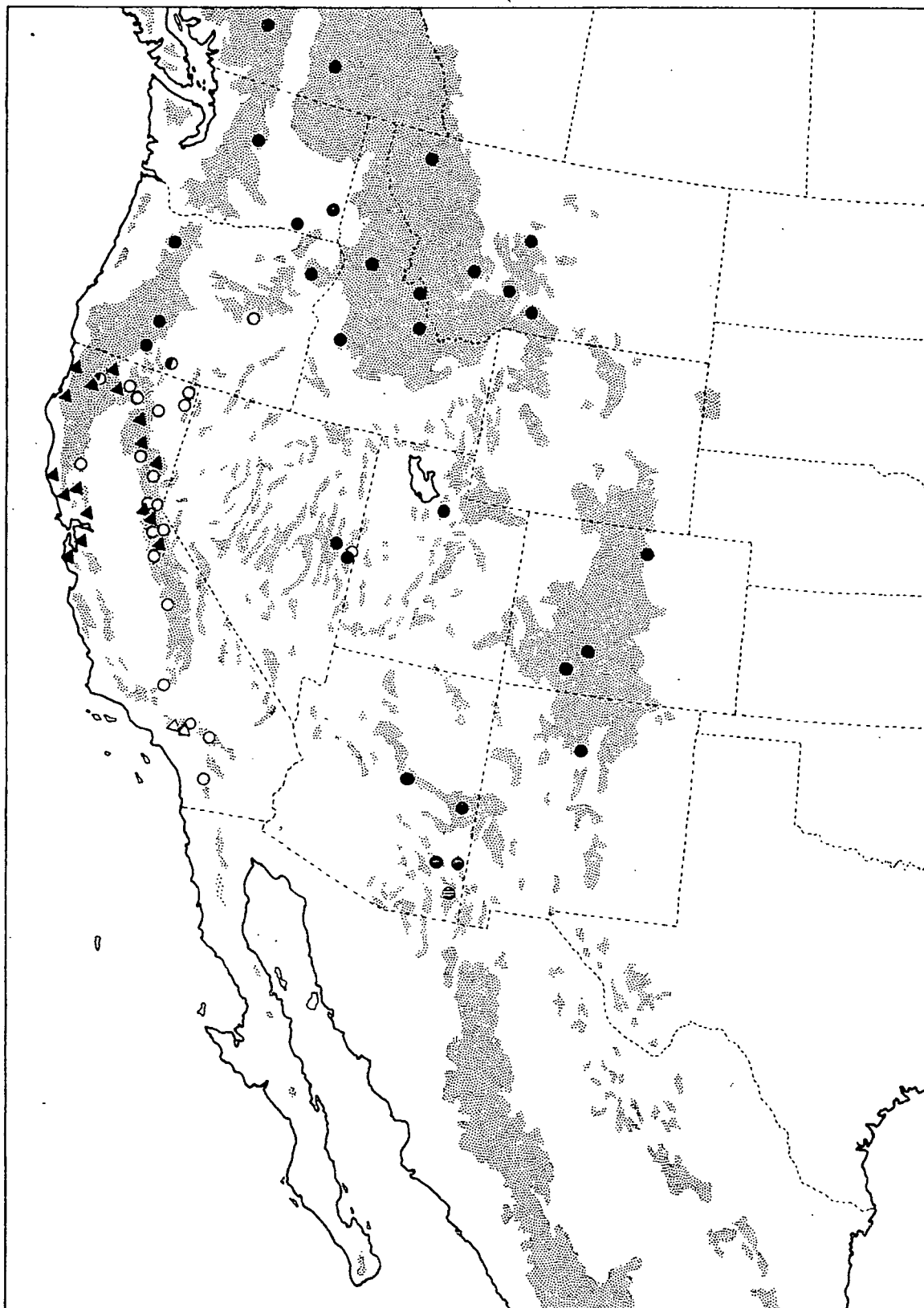


Figure 1.--Distribution of Western United States members of the Abietotoideae-feeding Fumiferana and Carnana complexes: *Choristoneura occidentalis* Freeman (closed circles), *C. retiniana* (wlsn.) (open circles), *C. carnana carnana* (B. & Bsk.) (open triangles), and *C. carnana californica* Powell (closed triangles). Half-closed circles in southern Oregon and northern California indicate localities with possible hybrid populations. (Data from Stehr (1967) and specimens examined.)

the basis of the record. If occidentalis and, retiniana were sympatric in northern California, it would not be possible to morphologically differentiate them except by degree of integumental sclerotization in the larva and pupa. Probably the record for occidentalis in California refers to a population discussed here under C. carnana californica.

'Over the broad range of occidentalis there is considerable interpopulational variation in ecological and geographical features (such as host preferences and phenology), as well as in phenotype of the adults, particularly in existence and frequencies of **poly-**morphic phases. Thus, many populations could be described in which the adults differ from typical occidentalis of eastern Washington.

Choristoneura biennis Freeman.-- The 2-year life cycle **form** replaces C. occidentalis in interior British Columbia and northward. Freeman (1967) and Stehr (1967) listed two Picea species and Abies lasiocarpa as host plants, not specifying which are used in various parts of the range-- reported to include mountains of western Alberta and southwestern Yukon Territory.

Choristoneura orae Freeman.-- Apparently, there have been no further data on the geographical range of this species or its relationship with occidentalis to the south and biennis in the interior of British Columbia at the same latitude.

## Carnana Complex

Choristoneura carnana (Barnes and Busck).--The typical form of this species is known in the literature on from the type series and from one specimen collected at Mount Lowe in the San Gabriel Mountains (Powell 1964, p 184). Recently it has been collected in the Mount Baldy area in association with Pseudotsuga macrocarpa. To the north, along the west slope of the Sierra Nevada, there are populations exhibiting a similar, monomorphic phenotype, but individuals have more extensive, darker rust-orange forewing markings and darker hindwings. Several collections of the latter have been made since my summary of the distribution (Powell 1964: map 9), and its occurrence appears to be restricted to elevations below 1700 m (5,500 feet), corresponding to the range of Pseudotsuga menziesii. Larvae were collected and reared from that host in El Dorado County in 1979.

Choristoneura carnana californica Powell.--The Coast Range populations, northern California were considered along with carnana to be probable pine-feeders because of their allopatric displacement of C. lambertiana and subretiniana (Powell 1964). Subsequently, however, C. carnana californica has been reared from

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Pseudotsuga menziesii in Napa and Lake Counties, near the type locality. Larvae of these and the El Dorado County populations are heavily marked, brick red, similar to certain forms described for C. occidentalis (Harvey and Stehr 1967), contrasting markedly with the green Abies-feeding larvae of retiniana. The Choristoneura recorded as californica from lower elevations around Mount Shasta (Powell 1964, p. 181) has been reared from Pseudotsuga in the Salmon River area of the Siskiyou Mountains by Carolin, Volney, and Waters.

These records, together with the Pseudotsuga-associated distribution of the Sierran west slope populations and carnana carnana, indicate this complex is primarily associated with Abietoideae, not Pinoideae as was previously supposed. This is the first known instance of two sympatric species using Abietoideae. C. carnana (in the broad sense) occurs within a few kilometers of Abies-feeding retiniana at Mount Shasta City (about 600 m--2,000 feet--lower in elevation), and the two species fly together at the same sites in mixed Pseudotsuga-Abies forests on the west slope of the Sierra Nevada (e.g., El Dorado County at 1 300 m--4,250 feet) and in the San Gabriel Mountains (fig.1).

## Western Components of the Lambertiana Complex

Choristoneura lambertiana lambertiana (Busck).--Other than the original series, reared from sugar pine in the vicinity of Ashland, Oregon, the typical race of this species is known only from one collection, from Pinus lambertiana in adjacent Siskiyou County, California. Freeman (1958, p. 36) listed lambertiana from California and New Mexico and cited Juniperus (Cupressaceae) as a food plant, without specific data--the last probably based on misidentified specimens of Cudonigera houstonana. Stehr (1967, p. 461) mentioned a form with pale, washed out forewings within populations of this species (e.g., Obraztsov 1962: figs. 7 and 8) but equated this pale form with ponderosana, populations of which consist entirely of a more extreme washed out phenotype (Obraztsov 1962: figs. 30-31) .

Northern Rocky Mountain moths are somewhat intermediate, exhibiting a mixture of color pattern features of typical lambertiana, subretiniana of eastern Oregon, and ponderosana in Colorado. The concept of lambertiana was expanded to include these populations in Idaho, Montana, and Wyoming by Obraztsov (1962) and Stehr (1967), and some Montana and Wyoming populations were included in C. 1. ponderosana by Stevens et al. (1977). There appears to be clinal change in phenotype in a broad arc through the northern Rocky Mountain States (fig. 2).

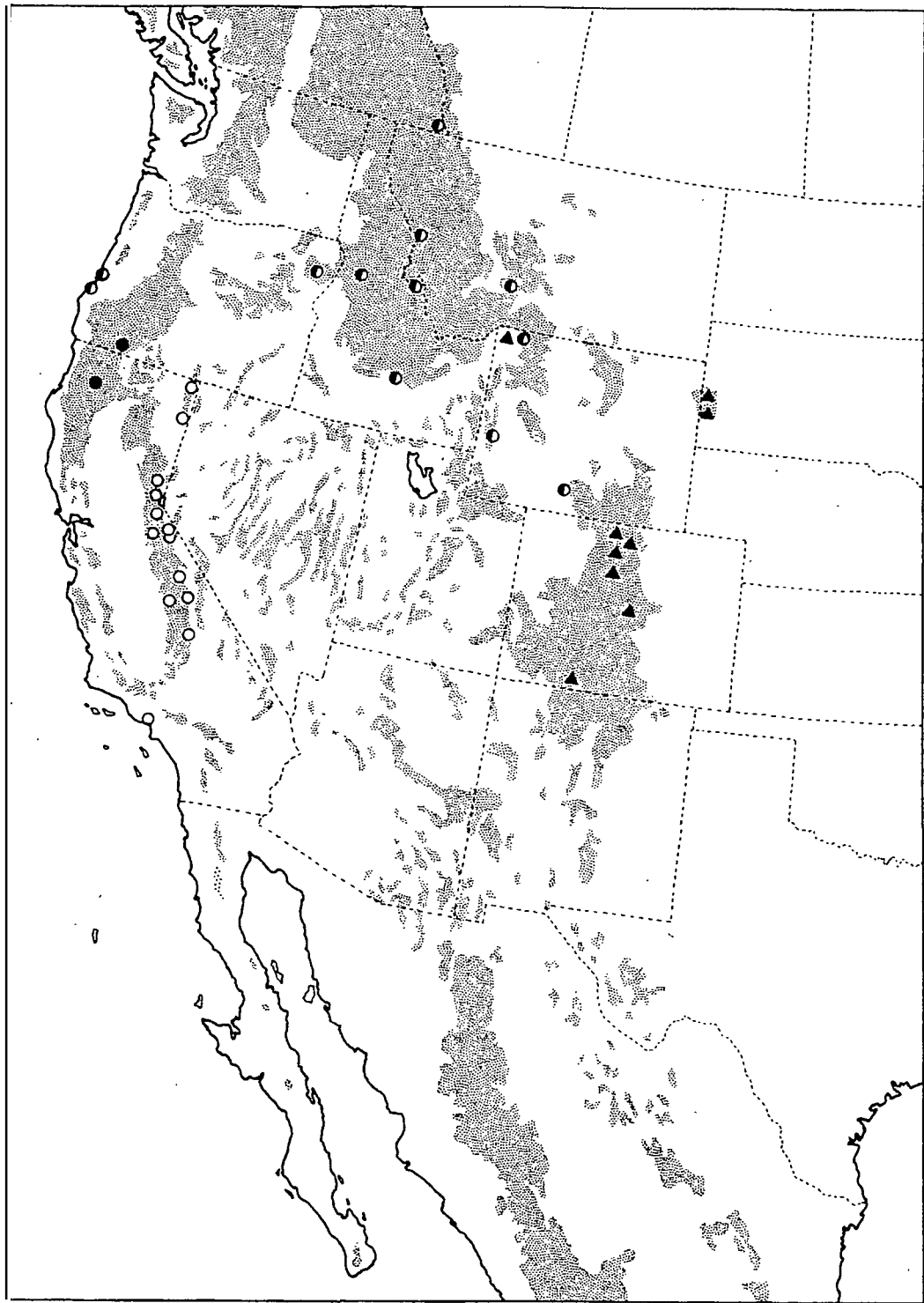


Figure 2.--Distribution of western Nearctic members of the Pinoideae-feeding Lambertiana complex: *Choristoneura lambertiana lambertiana* (Bsk.) (closed circles), *C. lambertiana subretiniana* Obr. (open circles), *C. lambertiana ponderosana* Obr. (triangles). Half-closed circles indicate populations referred to *lambertiana* s.str. by Obraztsov (1962) or Stehr (1967) and/or represented by more recent material of uncertain relationships. (Additional data are from Stevens et al. (1977) and specimens examined.)

Shaded areas on figures 1 and 2 depict major topographic features; areas above 5,000 feet (1530 m) are shaded for all but the central coastal area of California (2,000 ft--600 m) and Great Basin region (7,000 ft--2150 m), matching fairly well the distribution of coniferous woodland.

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Choristoneura lambertiana subretiniana Obraztsov.--This race occurs in eastern Sierra Nevada lodgepole pine forests from Tulare County north to Plumas County, in the Warner Mountains, and, in a slightly different phenotype, in Harney County of eastern Oregon (fig. 2). It has been reared from lodgepole pine in Nevada County (Stark and Borden 1965) and Warner Mountains (Powell 1964, p. 183; Pierce and Hall 1974). Northward from the California border, the phenotype loses the gray color, especially on the forewing interstices between the rust-red banding, and begins to resemble the form prevalent in Idaho and Montana. Harvey and Stehr (1967), who followed Obraztsov in treating subretiniana as a species, cited six larval collections, including three from pine (Pinus contorta, p. jeffreyi, and p. washoensis) and one from Abies concolor, apparently all from the area of Lake Tahoe.

Choristoneura lambertiana ponderosana Obraztsov.--This distinctive race, in which the forewings have no rust or reddish markings, has been recorded at numerous sites along the eastern flank of the Rocky Mountains in Colorado, in extreme southern Colorado near Durango, as well as in Montana, South Dakota, and Wyoming (Stevens et al. 1977). Pinus ponderosa is the host in each recorded instance except in Montana, where Pinus flexilis is used in the same area from which Stehr (1967: fig.1) assigned populations to lambertiana s.str. (fig. 2).

## Uncertain Status

Choristoneura spaldingiana Obraztsov.--This form is too poorly known to associate with any of the above defined complexes. Described from Provo, Utah, at the western edge of the Wasatch Range, data are too sketchy to indicate a probable host. A typical phenotype of C. occidentalis occurs at higher elevations in the Wasatch Range, but no population of the Lambertiana complex is recorded there. Adults which are phenotypically similar to spaldingiana have been collected in the Schell Creek Range of eastern Nevada. The moths were taken in a pure stand of Abies concolor, which suggests the possibility that the name spaldingiana represents a pallid form of the Fumiferana complex in the foothills or dry ranges of the Great Basin.

## CONCLUSIONS

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It is important to understand that names applied to both Abietoideae- and Pinoideae-feeding Choristoneura, particularly in western North America, are little more than signs posted at irregular intervals on mosaics of differing populations. Any attempt to define species as reproductively isolated entities of comparable rank or genetic integrity on the basis of present knowledge will be artificial. Adults vary phenotypically between populations in average size, color, extent and kind of wing markings; larvae and pupae vary in intensity of integumental color; populations differ in whether or not genetic polymorphism is expressed and, if so, in the proportions of the polymorph phases. Physiological and behavioral traits also vary in response to ecological and geographical factors, so that host preferences, seasonal timing of stages, cold-hardiness, and other features differ from place to place independently of the phenotype.

Entomologists should realize that there is every reason to expect that a given population of either the Fumiferana complex or Lambertiana complex will differ in some respects from typical populations representing available species names. For example, many populations assigned to C. occidentalis, especially those of the far north, Great Basin ranges, and southern Rocky Mountains, vary phenotypically to a degree comparable with that to which named "species" differ from typical occidentalis and from one another. Thus, nomenclatural recognition could have been given to many additional populations had there been physiological and genetic studies or were there a need for communication about them. Taxonomists should agree that application of any further names to this complex at our present state of knowledge would be absurd.

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