FOODPLANT SPECIFICITY IN THE *PLEBEJUS* (*ICARICIA*) *ACMON* GROUP (LYCAENIDAE)

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The *Plebejus acmon* group is composed of three closely related butterfly species: *P. acmon* (Westwood & Hewitson), *P. lupini* (Boisduval), and *P. neurona* (Skinner) (Goodpasture, 1973). These species comprise the *Eriogonum* (Polygonaceae)—feeding members of the subgenus *Icaricia. Plebejus acmon* ranges widely in western North America from the Pacific Coast west to the Great Plains, *P. lupini* occurs primarily in mountains of the Pacific Coast states, and *P. neurona* is restricted to elevations above about 5,000 ft. in central and southern California. Two subspecies of *P. lupini* are recognized; *l. lupini* occurring north of approximately 37° latitude, and *l. monticola* (Clemence) in southern and Baja California. Three subspecies of *P. acmon* are recognized; *a. acmon* in the southwestern region of the distribution of the species, *a. lutzi* dos Passos in the north, and *a. texanus* Goodpasture in the south. In California, where the distributions of the three species overlap, *P. acmon* is extensively sympatric with *P. lupini*, but *P. neurona*, tending to occur at higher elevations is only marginally sympatric with *P. lupini*.

The purpose of this investigation was to determine the relative degree of foodplant specificity among members of the *P. acmon* group. Data suggesting possible biological interactions between foodplant and both larval and adult butterflies are discussed.

Subspecific differences and interspecific variation in foodplant use were determined by direct observation in the field. The procedure established by Shields et al. (1970) for collecting and accurately reporting foodplant records was followed closely. Observations of larval feeding and adult oviposition are recorded in detail in an unpublished M.S. thesis (Goodpasture, 1971). Only a brief summary of foodplant records is given.

RESULTS

Larval foodplants of P. neurona. Comstock & Dammers (1933) briefly described the early stages of *P. neurona* and stated that this insect is found in association with *Eriogonum wrightii* Torr. Immature stages they described were reared on *E. fasciculatum* Benth. from, "Eggs secured from captive females taken at Blue Ridge, above Wrightwood, San Bernardino County on June 8, 1932" (Comstock & Dammers, 1933).

Subsequent oviposition records and field observations have confirmed this association and indicate a definite preference for leaves as oviposition sites. Laboratory rearing of adults has been carried out on *E. w.* var. *subscaposum* (Wats.) from eggs and first instar larvae found on leaves of this plant.

Foodplant acceptance tests have shown that *P. neurona* cannot complete development on legume plant species that are acceptable to larvae of *P. acmon acmon* (Goodpasture, 1971).

Evidence of foodplant specificity was obtained from field observations made near Mt. Hillyer, Angeles National Forest, Los Angeles Co., California, elev. 6,000 ft. At this locality, a number of plants of several abundant *Eriogonum* species were found within a radius of 100 feet. *Plebejus neurona* was the only abundant[1] *Icaricia* species encountered here during June and July 1969 and 1970 when a systematic search was made of the following *Eriogonum* species at this locality: *wrightii* var. *subscaposum*, *nudum* var. *publiflorum* Benth., *davidsonii* Greene, and *umbellatum* Torr. ssp. A total of 17 eggs, microscopically identical to eggs obtained from captive female *P. neurona*, were found on *E. wrightii* var. *subscaposum*, while none were located on the other species of *Eriogonum.*

Two often sympatric varieties of *E. wrightii* occur throughout the range of *P. neurona*: *E. w. subscaposum* in the San Bernardino Mountains north into the Sierra Nevada, and *E. w. trachygonum* (Torr. ex Benth.) from northern Los Angeles County to the base of the Sierra Nevada (Munz, 1968). Foodplant records and field observations indicate that *P. neurona* is restricted to these low, matted shrubs in montane coniferous forest associations.

Larval foodplants of P. acmon acmon. Documented records indicate that *P. acmon acmon* feeds on more species of plants than any other group member and that it is the only subspecies to utilize legumes as well as plants of the family Polygonaceae.

Localities where observation of utilization of more than one plant family as foodplant and or oviposition site have been made are: Monticello Dam, Napa Co. [*Lotus scoparius* (Nutt.) Ottley, *L. purshianus* (Benth.), and *Erigonum nudum* (Dougl. ex Benth.)], Frazier Park, Kern Co. [*L. procumbens* (Greene) Greene, and *Eriogonum* sp. (probably *nudum* or *elongatum* Benth.)], and Laguna Grade, San Diego Co. [*Lotus* sp. and *E. wrightii* var. *membranaceum* Stokes ex Jeps]. At localities near Davis, Yolo Co., several foodplants such as *L. purshianus* and

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[1] *Plebejus* (*Icaricia*) *icarioides* (Bdv.) and *P. acmon acmon* were common at localities within at least 1 mi. of the Mt. Hillyer locality, yet none were taken here during the course of this study probably due to the absence of appropriate legume foodplants in the immediate Mt. Hillyer area.

Polygonum aviculae L., an introduced weed, co-occur with *P. acmon acmon* and are probably utilized simultaneously. At all other localities records are available for only one plant species and it is not known if these populations are actually or potentially polyphagous.

At localities such as Monticello Dam where adult flight period extends from spring to late summer, suitable foodplants appear to be used sequentially according to their seasonal availability. Records from the central Coast Ranges in California for *Lotus scoparius*: 7 March–9 May; *E. latifolium-nudum*: 19 February–15 May (leaves), 3–15 August (flowers); and *L. purshianus*: 21 May–6 September, coincide with seasonal availability of these plants. Gorelick (1969) has suggested sequential utilization of *E. latifolium* Sm. in Rees. in the San Bruno Mountains, San Mateo Co., with the larvae feeding on leaves in spring prior to early summer die-back, and on flowers as they become available to successive generations during later months. At Monticello Dam, larvae were found to move from drying flower heads of *E. nudum* during late summer to overwintering sites in leaf litter at the base of these plants. At other localities, only a single suitable plant species may occur as at Putah Creek, U.C.D. campus, Yolo Co., where the only foodplant is the annual *L. purshianus*. *Plebejus acmon acmon* adults are not found at this locality until June (based on two years observation and museum specimens), when plants are well established. Seed germination of *L. purshianus* begins very early in winter, with the result that by March there are numerous new shoots about four inches long growing under dense winter annual vegetation. Progeny of females collected at Monticello Dam from March through August and at Putah Creek from June through mid-September do not enter diapause when reared under laboratory conditions of constant temperature and naturally occurring daylength. It is assumed that both populations are multivoltine. Individuals from these two populations respond similarly to decreasing photoperiod and enter diapause in late summer as early instar larvae (Goodpasture, 1973). Seasonal flight data indicate that these populations differ markedly in response to conditions initiating breaking of diapause. Termination of diapause in winter at Putah Creek would seem disadvantageous if foodplant is available only in summer months. Termination of diapause in winter (December?) at Monticello Dam would allow earlier activity of adults and might be advantageous where a polyphagous population feeds on plants available at different times of the year.

A number of plants not known to be fed upon by wild *P. acmon* larvae have been found to be acceptable as laboratory foodplants. These plants are *Lotus corniculatus* L., *Lupinis albifrons* Benth., *Eriogonum fascicu-*

latum, and *E. umbellatum* (Goodpasture, 1971). In addition, flowers of *Trifolium obtusiflorum* Hook. were reported by Gorelick (1969) to be acceptable as larval foodplant. These plants are available to females of *P. acmon acmon* at various localities but are apparently not selected for oviposition and are probably not utilized as food. *Eriogonum fasciculatum*, for example, is coextensive with *P. acmon acmon* in southern California, but appears not to be used as food.

At many localities the shrub-like *E. fasciculatum* occurs and other, usually herbaceous species of *Eriogonum* and/or legumes are used as foodplants. For example, at Del Puerto Canyon, Stanislaus Co., and Frazier Park, *E. nudum* is the only known foodplant. Field observations of foodplant utilization, and adult flight period, and *Eriogonum* ecology, show that at these localities *E. fasciculatum* is potentially available to larvae and ovipositing females from March or April through June. At other localities such as Switzer's Camp, Los Angeles Co., and Laguna Grade, adult flight season extends from June through September or October when *E. fasciculatum* is probably not suitable as larval foodplant due to cessation of vegetative growth of this plant during summer drought.

Preference for oviposition on certain plant parts may exist in some populations. At some localities, oviposition has been observed on all plant parts (*Lotus*, Switzer's Camp and Putah Creek), exclusively on leaves (*Eriogonum wrightii*, Laguna Grade), or exclusively on flowers (*E. elongatum*, Hidden Valley and Lake Sherwood, Ventura Co.). Where *Eriogonum* species are utilized as foodplant, eggs might be placed on floral or leaf structures depending on seasonal availability or suitability of plant material.

In conclusion, the foodplants of *P. acmon acmon* in California are plants of the families Leguminosae and Polygonaceae. As can be seen in Fig. 1, the perennial herbaceous *Eriogonum* species *latifolium*, *nudum*, and *elongatum*, as well as certain legumes (*Lotus scoparius* and *L. purshianus*), are the most frequently encountered foodplants. In southern California, *Lotus* species may serve as the primary food source, with several additional *Eriogonum* species of rather limited distribution (e.g. *E. parvifolium* Sm. in Rees. and *E. plumatella* Dur. & Hilg.) as occasional foodplants.

Larval foodplants of P. acmon lutzi and P. acmon texanus. Foodplants of *P. acmon* occurring outside of California are poorly known. Available records are primarily associational and indicate that various *Eriogonum* species are utilized as foodplants.

Association of adults of *P. acmon lutzi* with *E. marifolium* T. & G. and

E. pyroliifolium Hook at Mt. Bachelor, Oregon suggests use of these plants. Adults of *P. a. lutzi* form *spangelatus* have been reared from larvae collected on an unidentified *Eriogonum* species, Olympic Mountains National Park, Washington (J. Pelham, pers. comm.). Foodplant records for Wyoming include *E. flavum* Nutt. and *E. umbellatum* (C. D. Ferris, pers. comm.).

Observations of oviposition and co-occurrence of adults and plants suggest that *P. acmon texanus* feeds on *E. wrightii* var. *wrightii* at localities in Arizona, New Mexico, and Texas, and that *E. corymbosum* var. *velututinum* Reveal & Brotherson is a foodplant near Cerrillos, New Mexico. Oviposition records, as well as associational data, indicate that *E. effusum* Nutt. and *E. racemosum* Nutt. are utilized at several Colorado localities.

Larval foodplants of P. lupini lupini. Several shrub-like *Eriogonum* species are documented as larval foodplants of *P. lupini lupini.* In California, *E. umbellatum* and *E. ovalifolium* Nutt. are the only known foodplants. Emmel & Emmel (1962), and Garth & Tilden (1963) have noted adult association with *Eriogonum* at Donner Pass and in Yosemite National Park. It appears from available records, that *E. umbellatum* is the primary food source in the Sierra Nevada and the north Coast Ranges at least in California. In Nevada, a wider variety of *Eriogonum* species may be utilized. Records from mountainous areas in central Nevada indicate use of *E. kearneyi* Tidestr., *E. ovalifolium*, *E. palmerianum* Reveal, and *E. umbellatum.* Statements that *Lupinus* spp. are utilized (Boisduval, 1869, ". . . dans le sud de la Californie."; Jones, 1951, Washington) are without supporting data.

Field observations made at Echo Lake, El Dorado Co., suggest that flowers of *E. umbellatum* var. *umbellatum* are preferred as an ovipositional site. Seven females seen ovipositing at this locality (13–19 July 1970) laid a total of 17 eggs, 15 on flowers and two on leaves. Females were not seen to oviposit on other *Eriogonum* species (*nudum*, *incanum* Torr. & Gray, *lobii* Torr. & Gray, and *wrightii*) also present at this locality.

Plebejus lupini appears most similar to *P. neurona* in terms of larval acceptance and the nutritional adequacy of several plants, as well as in preferences inferred from field data. Larvae of these two species accept flowers of *Lotus corniculatus* but develop poorly and suffer high mortality, whereas *P. acmon acmon* larvae show no mortality on this plant (Goodpasture, 1971).

Larval foodplants of P. lupini monticola. Foodplant records from eight localities suggest that *P. lupini monticola* is restricted to *E. fasciculatum*

Foodplant	P. neurona	P. acmon acmon	P. acmon lutzi	P. acmon texanus	P. lupini lupini	P. lupini monticola
POLYGONACEAE						
Polygonum aviculae		D2				
Eriogonum corymbosum			S1			
effusum				D2		
elongatum		D2				
fasciculatum						D7
kearneyi					D1	
latifolium & nudum		D9				
marifolium & pyroliifolium			S1			
ovalifolium					D1	
palmerianum					D1	
parvifolium		D1				
plumatella		D1				
racemosum				D1		
umbellatum			D1		D6	
umbellatum ssp.						D1
wrightii wrightii				D,S 4		
w. subscaposum & w. trachygonum	D5					
LEGUMINOSAE						
Lotus & Astragalus		D13				

Fig. 1. Summary of foodplant records for the *Plebejus acmon* group. Documented records (D) = larval rearing to adult, oviposition observed. Suspected foodplants (S) = adults collected in association with plant, pre-oviposition behavior observed. Numerals refer to number of localities (more than 10 miles apart) where observations of foodplant use have been made.

in most of its range throughout chapparral communities in the southern half of California. Utilization of more than one species of *Eriogonum* may occur at Laguna Grade, where females have been observed to oviposit on *E. wrightii* var. *membranaceum* as well as on *E. f.* var. *polifolium* (Benth.). At this locality, near the upper altitudinal limit of *E. fasciculatum*, *E. w.* var. *membranaceum* is the more common plant,

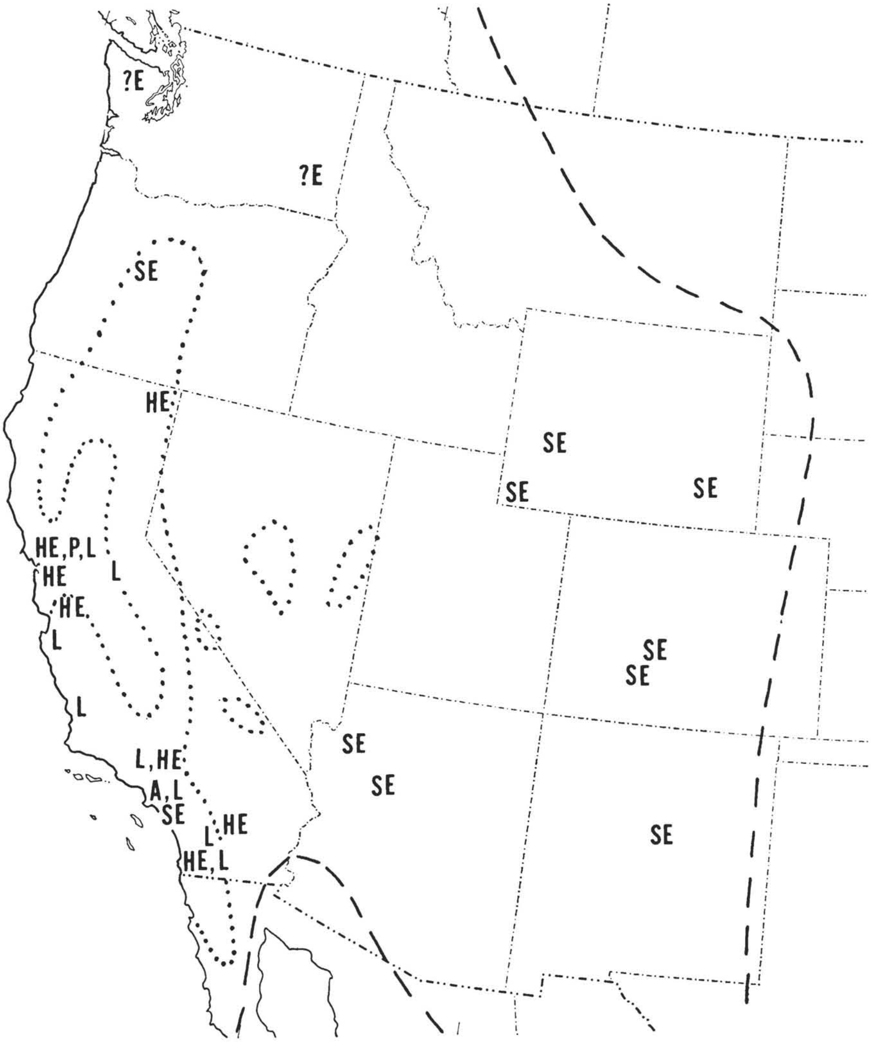

Fig. 2. Geographical distribution of foodplant specificity in *Plebejus acmon*. Dashed line represents approximate known distribution of *P. acmon*. Dotted line represents distribution of *P. lupini* and area of *P. acmon–P. lupini* sympatry. *P. lupini* foodplants are shrub-like *Eriogonum* species throughout its range. A = *Astragalus*, L = *Lupinus*, P = *Polygonum*, HE = herbaceous *Eriogonum*, SE = shrub-like *Eriogonum* species. Herbaceous *Eriogonum* species include *elongatum*, *latifolium*, and *nudum*. Other species of *Eriogonum* mentioned in the text are considered shrub-like (Munz, 1968).

and appears to be the principal foodplant. Oviposition by a single female has been observed on *E. umbellatum* subsp. at Horse Thief Springs, San Bernardino Co. Other *Eriogonum* species present at this locality include *fasciculatum*, *wrightii*, and *heermannii* Dur. & Hilg. (A. O. Shields, pers. comm.) and may also be utilized by *P. lupini monticola*.

Observations of oviposition behavior and placement of field collected eggs indicate that floral structures are preferred over leaves as oviposition sites when both are available (Goodpasture, 1971).

Geographical distribution of foodplant specificity. Fig. 1 illustrates that members of the *Plebejus acmon* group tend to have mutually exclusive diets. This is especially evident in California where distributions of four of these entities overlap. *Plebejus neurona*, *P. lupini monticola*, and *P. lupini lupini* have no foodplants in common at the varietal level and are narrowly oligophagous, feeding predominantly on a single species or subspecies of *Eriogonum*. Outside of California, at least in central Nevada, *P. lupini* apparently utilizes a much wider variety of *Eriogonum* foodplants. As can be seen in Fig. 2, polyphagy in *P. acmon* shows some correlation with geography and distribution of *P. lupini*. Thus, *P. acmon* feeds on *Astragalus* (A), *Lotus* (L), *Polygonum* (P), herbaceous (HE), and shrub-like *Eriogonum* (SE) species only in California where it is broadly sympatric with *P. lupini*. Outside of California, *P. acmon* is known to utilize only shrub-like *Eriogonum* species.

DISCUSSION

Larval choice of foodplant in Lepidoptera may be requisite for survival in species with a larval dispersal stage or with larvae defoliating part of their available food supply (Dethier, 1959; Cook, 1961). Larval ability to select proper plant species may also play a role in foodplant relationships in this *Plebejus* group where larvae overwinter as early instars. For example, *P. acmon acmon* terminating diapause in May at Putah Creek must locate early season growth of the annual *Lotus purshianus*. Larvae terminating diapause at localities where annual foodplants are utilized may encounter and accept plant species other than those upon which eggs were laid during the previous growing season. The probability of larvae encountering foodplants of the same species as chosen by females of the final summer generation may depend on such factors as success of seedling establishment in annual plants or the number of acceptable alternative plants growing in close proximity to overwintering larvae.

Larval acceptance tests have demonstrated that larvae from several populations of several subspecies of the *P. acmon* group accept many plant species not known to be utilized in nature. While these potential foodplants elicit and sustain, or at least do not deter, larval feeding, full suitability[2] remains uncertain because fertility of reared adults has not been tested. It is assumed from larval acceptance of various plants, as well as from knowledge of plant distributions, that a large number of *Eriogonum* species are available and suitable to many populations of all group entities. At least some populations of *P. lupini* and *P. neurona* feed on only one of several species of *Eriogonum* growing at one locality. A similar pattern of food resource utilization may exist throughout the *Icaricia.* It has been shown that larvae of *P. icarioides* will feed on any species of *Lupinus* in captivity, but wild populations normally utilize only a few of the possible range of *Lupinus* species growing locally (Downey & Fuller, 1961; Downey, 1962).

Rigid specificity encountered in nature in most members of this group seems to be due primarily to the precision with which females lay their eggs on certain plants, as has been stressed by Merz (1959) for several other Lepidoptera. In field studies, both *P. neurona* and *P. lupini lupini* were found to display a high degree of foodplant specificity. Presumably, females respond to specific plant stimuli in selecting a single *Eriogonum* species for oviposition from among several available at a single locality.

Many populations of the *P. acmon* group differ in both plant species and complement of species utilized for food. Although this may be the result of coincidence of plant distribution, larvae and ovipositing females may have different preferences at different localities. It should be noted that the extent to which differences in foodplant use reflect differences in foodplant preference is unknown in this group.

Failure of *P. acmon* members to utilize certain potential foodplant species during certain times of the year, e.g. *E. fasciculatum* by *P. acmon acmon* during summer months, may be due to unsuitability caused by drying and hardening of leaves and flowers. Although females of at least some *P. acmon acmon* populations will lay eggs on *E. fasciculatum* var. *foliolosum* in captivity, larvae are not able to survive on this plant when hatching from eggs laid during and after June (Goodpasture, 1971). Cole (1967) has shown that shoot growth of several *Eriogonum* species, including *E. fasciculatum*, ceases in May in the Santa Monica Mountains and that dramatic changes in leaf physiology accompany soil drought in summer months.

Differences in feeding preferences within and between closely related species may provide information on evolutionary mechanisms that can

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[2] Remington & Pease (1955) define the test of full suitability of a plant in terms of larval rearing to adult solely on that plant with the production of adults which, when induced to mate, lay eggs which then hatch.

account for changes between polyphagy and monophagy (Dethier, 1954). For example, within this group spatial and temporal differences in foodplant utilization may have evolved independently in isolation or as a result of competition resulting in ecological character displacement. The data available do not allow distinction between these alternatives. However, evidence seemingly in support of competitive displacement is: (1) different sympatric subspecies of this group tend to have mutually exclusive foodplants; (2) *P. acmon* does not utilize shrub-like *Eriogonum* species where it is sympatric with *P. lupini*, and feeds on a wide variety of shrub-like *Eriogonum* species where it is widely allopatric to *P. lupini*; and (3) *P. acmon* is morphologically distinct from *P. lupini* where these two species are sympatric, and convergent to *P. lupini* where it occurs in states widely allopatric to the distribution of *P. lupini* (Goodpasture, 1973).

Dethier (1954) has also suggested that polyphagy is the more primitive condition in phytophagous insects. This may also apply to the *P. acmon* group. Oligophagy and *Eriogonum* feeding as exemplified by the narrow feeding habits of *P. neurona* may have been derived from a polyphagous ancestor with food habits similar to those of *P. acmon acmon*.

SUMMARY

Data on foodplants use by members of the *Plebejus acmon* group are summarized in Fig. 1. *Plebejus acmon acmon* is the only polyphagous group member, feeding on the legumes *Lotus* and *Astragalus* as well as the Polygonaceae *Eriogonum* and *Polygonum*. All other group members are oligophagous and restricted to feeding on one or a few species of *Eriogonum*. Members of this group tend to have mutually exclusive diets.

Differences in foodplant use between species and subspecies of this group are discussed in terms of foodplant ecology, geographical distribution of foodplant specificity, and possible larval feeding and adult oviposition preferences.

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LITERATURE CITED

BOISDUVAL, J. A. 1869. Lepidopteres de la Californie. Ann. Soc. Entomol. Belg. 12: 8–94.

COLE, N. H. A. 1967. Comparative physiological ecology of the genus *Eriogonum* in the Santa Monica Mountains, Southern California. Ecol. Monogr. 37: 1–24.

COMSTOCK, J. A. & C. M. DAMMERS. 1933. Notes on the life histories of four Californian Lepidopterous insects. Bull. So. Calif. Acad. Sci. 32: 77–83.

COOK, L. M. 1961. Foodplant specialization in the moth *Panaxia dominula* L. Evolution 15: 478–485.

DETHIER, V. G. 1954. Evolution of feeding preferences in phytophagous insects. Evolution 8: 33–54.

———. 1959. Foodplant distribution and density and larval dispersal as factors affecting insect populations. Can. Entomol. 91: 581–596.

DOWNEY, J. C. 1962. Hostplant relations as data for butterfly classification. Syst. Zool. 11: 150–159.

———. & W. C. FULLER. 1961. Variation in *Plebejus icarioides* (Lycaenidae). I. Foodplant specificity. J. Lepid. Soc. 15: 34–42.

EMMEL, T. C. & J. F. EMMEL. 1962. Ecological studies of Rhopalocera in a high Sierran community—Donner Pass, California. I. Butterfly associations and distributional factors. J. Lepid. Soc. 16: 23–44.

GARTH, J. S. & J. W. TILDEN. 1963. Yosemite butterflies. J. Res. Lepid. 2: 1–96.

GOODPASTURE, C. E. 1971. Biology and systematics of the *Plebejus* (*Icaricia*) *acmon* group. Unpub. M.S. thesis, Univ. Calif., Davis.

———. 1973. Biology and systematics of the *Plebejus* (*Icaricia*) *acmon* group. I. Review of the group. J. Kansas Entomol. Soc. 46: 468–485.

GORELICK, G. A. 1969. Notes on larval host acceptance in a California population of *Plebejus acmon*. J. Lepid. Soc. 23: 31–32.

JONES, J. R. J. L. 1951. An annotated check list of the Macrolepidoptera of British Columbia. Entomol. Soc. B.C., Occ. Paper No. 1: 1–148.

MERZ, E. 1959. Pflanzen und Raupen. Uber einige Prinzipien der Futterwahl bei Goss-schmetterlingsraupen. Biol. Zentr. 78: 152–188.

MUNZ, P. A. 1968. Supplement to a California flora. Univ. Calif. Press, Berkeley and Los Angeles, 224 p.

REMINGTON, C. L. & R. W. PEASE, JR. 1955. Studies in foodplant specificity. I. The suitability of Swamp White Cedar for *Mitoura gryneus* (Lycaenidae). Lepid. News 9: 4–6.

SHIELDS, O., J. F. EMMEL & D. E. BREEDLOVE. 1970. Butterfly larval foodplant records and a procedure for reporting foodplants. J. Res. Lepid. 8: 21–36.