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HYBRIDIZATION OF *SATURNIA MENDOCINO* AND *S.* *WALTERORUM*, AND PHYLOGENETIC NOTES ON *SATURNIA* AND *AGAPEMA* (SATURNIIDAE)

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ABSTRACT. The taxonomic relationship of *Saturnia walterorum* and *S. mendocino* is discussed in terms of laboratory hybrids, larval morphology, comparative life history, and phenetics of intermediate populations. Results indicate that these moths represent different taxa, but are best described as semispecies. The two taxa freely interbreed in the laboratory. Hybrid F₁ females with *walterorum* as the female parent had normal fertility and fecundity; females from the reciprocal cross were viable but sterile. The two taxa are very similar morphologically and differ mainly in the dimorphic female of *walterorum*. Populations in the southern California Coast Ranges may represent intergrades. A discussion of the phylogeny of the endemic California *Saturnia* and the closely related *Agapema* stresses the coevolution of these moths and their sclerophyllous host plants in response to historic climatic changes.

In the New World, the genus *Saturnia* consists of three species whose distribution is centered in California. The three species, *Saturnia walterorum* Hogue & Johnson, *S. mendocino* Behrens, and *S. albofasciata* (Johnson), exhibit life history characteristics which are adaptations to utilizing sclerophyllous food plants in a Mediterranean climate of winter rains and summer drought. The localized populations of these moths, their rapid and erratic flight, and the rugged terrain they inhabit, make them difficult to collect. As a result, complete and accurate life history descriptions are lacking for all three species. In this paper we examine the taxonomic relationship of *S. walterorum* and *S. mendocino* in terms of laboratory hybrids, comparative life histories, larval and adult phenotypes, and phenetics of

geographically intermediate populations. We extend our discussion to include a proposed phylogenetic scheme which includes the closely related genus *Agapema*, based on biogeographic and geofloral data.

METHODS

In an effort to understand the genetic relationship between *Saturnia walterorum* and *S. mendocino*, we began hybridization studies in 1974. Our *walterorum* stock was from Dictionary Hill, Spring Valley, San Diego Co., Calif., while the *mendocino* used in the study came from Thompson Canyon, near Lake Berryessa, Yolo Co., California. A large series of wild and reared adults from each location was examined, and characters which represent diagnostic differences between the two species were sought. We selected six characters which could be either measured or scored as to presence or absence: forewing length, dorsal forewing and hindwing discal eyespot length, the ratio in length between the forewing and hindwing discal eyespot, the presence or absence in males of a white apical patch of scales on the ventral surface of the forewing, and the presence or absence of a bold submarginal black band on the dorsal forewing surface of females.

Larvae secured during the study were reared outdoors in screen cages after the first instar on fresh branches of *Arctostaphylos* spp. maintained in water. Most larvae pupated by June, and began to emerge the following year during February or March. Cage matings were easily obtained, usually within minutes after the female began "calling." Mated females oviposited readily in paper bags or other containers in the absence of food plant.

The fecundity of each female was determined by measuring the number, size, and batch weight of the eggs. The degree of fertility was based on the number of eggs which hatched within each batch. In the field, males were obtained by means of funnel traps or wire cages each containing a virgin female. In this way we were able to sample populations more efficiently than searching for larvae or adults.

RESULTS

In order to interpret the phenotypes of hybrid specimens we estimated the range of variation in the parental populations. The right forewing length of male *walterorum* averaged just over 11 percent greater than that of male *mendocino*, while that of female *walterorum* was 18 percent greater than female *mendocino* (Table 1). A t-test indicated that the difference in wing length between the two species

TABLE 1. Phenotypic data for *S. walterorum*, *S. mendocino* and their hybrids.

	FEMALES					MALES				
	Eyespot			F-wing length	Sbm. band	Eyespot			F-wing length	Apical spot
	F-wing	H-wing	ratio			F-wing	H-wing	ratio		
a. <i>mendocino</i>	3.70 ¹ 0.40	3.81 0.41	0.97	32.84 1.75	no	2.60 0.30	2.73 0.35	0.95	27.07 1.11	no
b. ♂ F_{1a} hybrid × ♀ <i>mendocino</i>	4.71 0.24	4.82 0.23	0.98	33.11 0.54	no ²	3.78 0.26	3.63 0.24	1.04	28.14 0.54	no
c. ♂ <i>walterorum</i> × ♀ <i>mendocino</i> = F_{1a}	5.33 0.39	5.63 0.31	0.95	37.20 2.42	yes	3.48 0.21	3.75 0.47	0.93	29.43 1.96	no
d. ♂ F_{1a} hybrid × ♀ F_{1a} hybrid	—	—	—	—	—	3.41	3.80	0.90	28.20	no
e. ♂ F_{1b} hybrid × ♀ F_{1b} hybrid	5.33	4.33	1.23	32.00	no ²	3.55	3.00	1.18	27.00	yes
f. ♂ <i>mendocino</i> × ♀ <i>walterorum</i> = F_{1b}	5.55 0.33	5.24 0.25	1.06	34.93	no ²	4.23 0.42	3.81 0.39	1.11	28.18 1.00	no
g. ♂ F_{1a} hybrid × ♀ <i>walterorum</i>	6.23 0.62	6.02 0.32	1.04	37.08	yes	4.17 0.26	3.81 0.31	1.09	28.80 1.92	yes
h. <i>walterorum</i>	7.34 0.55	6.28 0.46	1.17	40.33 1.64	yes	4.25 0.40	4.08 0.44	1.04	30.52 1.27	yes

¹ Measurements in mm with S.D. given below.
² Some females showed a trace of submarginal band.
³ Sex ratio based on undamaged, measured specimens. Complete data for b not available. Hybrid sex ratios do not differ significantly from expected 1:1.

TABLE 2. Fecundity and fertility of *S. walterorum*, *S. mendocino* and their hybrids.

Cross	No. ova laid	Ova length		Avg. ova wt. g	% hatch
		mm	S.D.		
a. ♀ <i>walterorum</i>	114	2.44	0.06	0.0035	97.0
b. ♀ <i>mendocino</i>	83	2.47	0.07	0.0037	96.4
c. ♂ <i>walterorum</i> × ♀ <i>mendocino</i> = F _{1a}	77	2.47	0.07	0.0037	97.5
d. ♂ F _{1a} hybrid × ♀ <i>mendocino</i>	73	2.47	0.07	0.0037	87.8
e. ♂ F _{1a} hybrid × ♀ <i>walterorum</i>	137	2.24	0.07	0.0034	91.5
f. ♂ F _{1a} hybrid × ♀ F _{1a} hybrid	33	1.79	0.69	0.0025	3.3
g. ♂ <i>walterorum</i> × ♀ F _{1a} hybrid	52	1.75	0.68	0.0017	0.0
h. ♂ <i>mendocino</i> × ♀ F _{1a} hybrid	44	1.92	0.18	0.0022	0.0
i. ♂ <i>mendocino</i> × ♀ <i>walterorum</i> = F _{1b}	130	2.47	0.05	0.0036	96.0
j. ♂ F _{1b} hybrid × ♀ F _{1b} hybrid	96	2.14	0.01	0.0036	98.0
k. (♂ F _{1a} hybrid × ♀ <i>walterorum</i>)2	73	2.10	0.09	0.0037	96.7
l. (♂ F _{1a} hybrid × ♀ <i>mendocino</i>)2	75	2.21	0.16	0.0032	0.0

and both sexes is significant ($P < .05$). The eyespots on the dorsal forewing and hindwing are about twice as large in *walterorum* as in *mendocino*. In *walterorum*, the forewing eyespot is larger than the hindwing eyespot, while in *mendocino* the opposite is true. Thus the ratio of the forewing to hindwing eyespot is greater than 1 in *walterorum*, and less than 1 in *mendocino*. This character was scored qualitatively and not treated statistically. As with wing length, the larger discal eyespot size of male and female *walterorum* are significantly greater than those of *mendocino* ($P < .05$). Analysis indicated that only 10 percent of the difference in eyespot size is attributed to the difference in wing length between the two species. Considering the few characters available, a hybrid index was not deemed necessary. In terms of qualitative differences, all male *walterorum* have a distinct white apical patch about 2 mm long, on both surfaces of the forewing. Males of *mendocino* may have a similar, but smaller white apical patch on the dorsal surface only, thus the presence or absence of the white apical patch on the ventral surface is diagnostic. Finally, all female *walterorum* have a bold submarginal black band on both the dorsal and ventral surface of the forewing, which is lacking in female *mendocino* (Table 1a, h).

The average egg weight and length of both *walterorum* and *mendocino* is similar (ca. 0.0036 g, 2.46 mm, Table 2). One way analysis of variance combined with a Duncan multiple range was used to compare both egg weight and length. Although no difference was found between *walterorum* and *mendocino* ova, a statistically significant difference in average egg weight and length was found between F_{1a} ova and both parental species ($P < .05$) (Table 2a, b, f, g, h). Female *mendocino* usually deposit 70 to 80 eggs within 5 or 6 hours

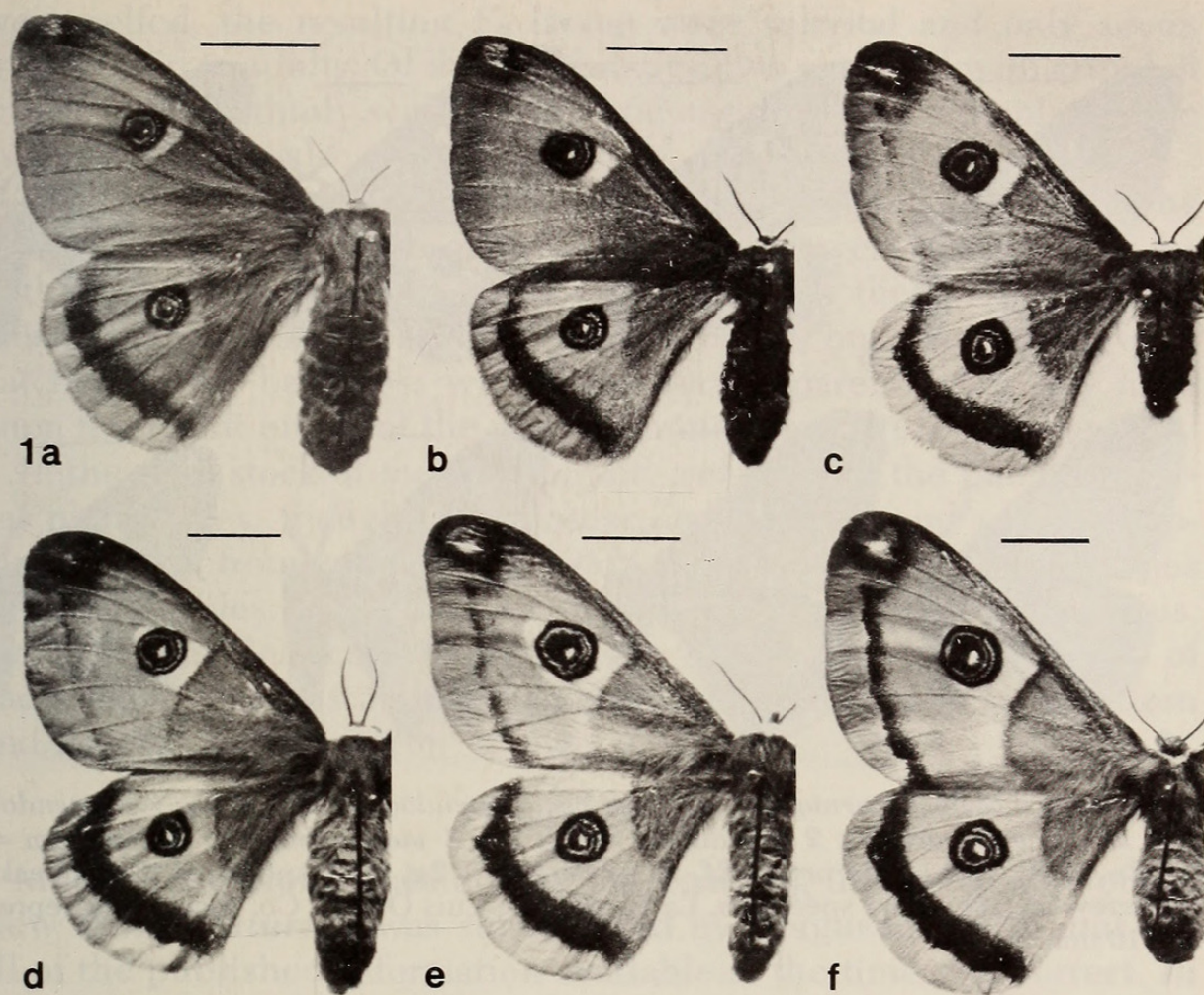


FIG. 1a-f. Female *Saturnia* and hybrids. 1a, *S. mendocino*; 1b, ♂ $F_{1a} \times \text{♀ } \textit{mendocino}$; 1c, ♂ *walterorum* $\times$ ♀ *mendocino* = F_{1a} ; 1d, ♂ *mendocino* $\times$ ♀ *walterorum* = F_{1b} ; 1e, ♂ $F_{1a} \times \text{♀ } \textit{walterorum}$; 1f, *S. walterorum*. Black lines represent 10 mm.

after mating, while *walterorum* females deposit 100 to 140 eggs. The average fertility of each species was near 97 percent.

Table 1 presents phenotypic data on the hybrids that were produced under controlled conditions. The initial mating of a male *walterorum* to a female *mendocino* produced the F_{1a} hybrids, which were nearer in size to *walterorum* than *mendocino*. Hybrid F_{1a} females also had a distinct submarginal band which was not as well developed as that of typical *walterorum* (Table 1c; Figure 1c). The forewing to hindwing eyespot ratio of these hybrids was <1 as in *mendocino*. The F_{1a} hybrids also resembled *mendocino* in the appearance of the male apical spot (Table 1c). When the F_{1a} male was backcrossed to a female *mendocino*, the resulting adults were almost identical to typical *mendocino*, but the male eyespot ratio was equal to that of *walterorum* even though the eyespot size was greatly reduced relative to *walterorum*. Females lacked the submarginal band, and expressed an eyespot ratio similar to *mendocino*, although the absolute size of the spots

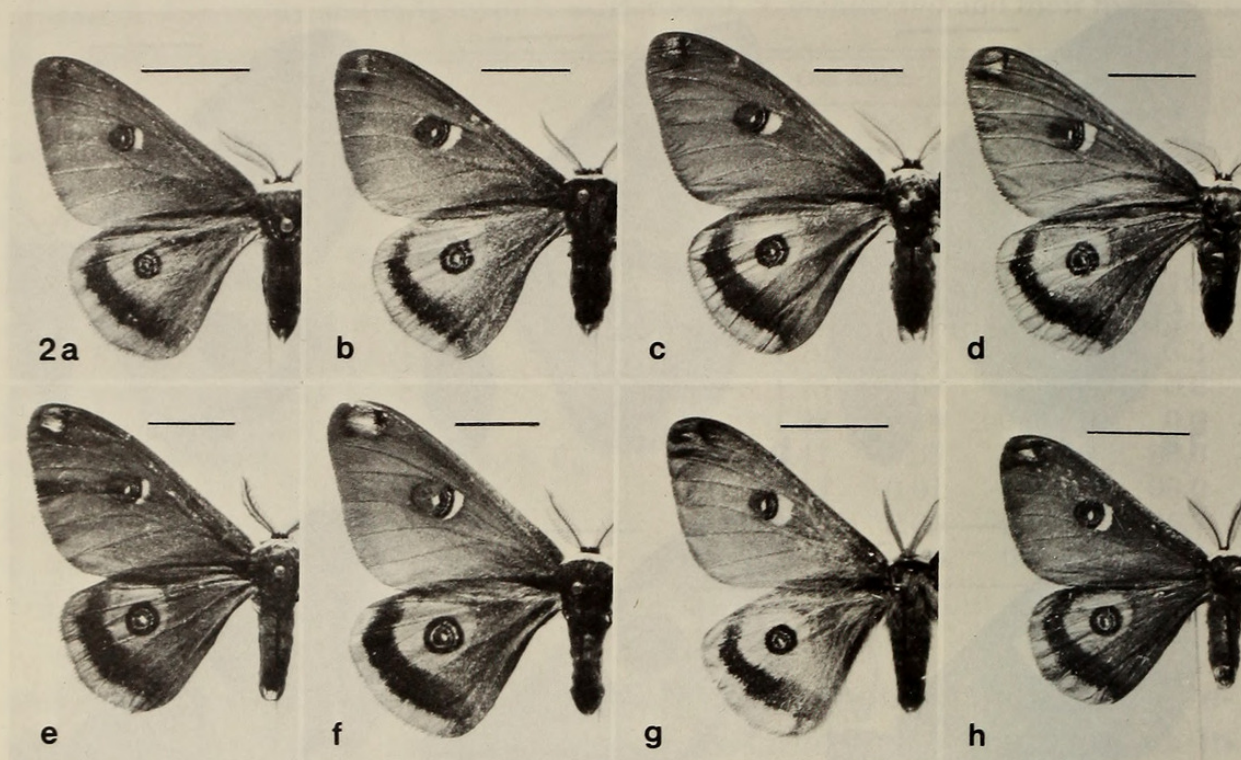


FIG. 2a-h. Male *Saturnia* and hybrids. **2a**, *S. mendocino*; **2b**, ♂ F_{1a} × ♀ *mendocino*; **2c**, ♂ *walterorum* × ♀ *mendocino* = F_{1a} ; **2d**, ♂ *mendocino* × ♀ *walterorum* = F_{1b} ; **2e**, ♂ F_{1a} × ♀ *walterorum*; **2f**, *S. walterorum*; **2g**, Wild specimen, Cone Peak, Monterey Co.; **2h**, Wild specimen, La Panza, San Luis Obispo Co. Black lines represent 10 mm.

were larger. The F_{1a} male backcrossed to a female *walterorum* produced progeny which expressed all of the qualitative characters associated with *walterorum*, while the quantitative characters were intermediate (Table 1e). In both backcrosses of F_{1a} males to the parent species, the fertility was 6 to 9 percent below normal (Table 2d, e).

Unlike F_{1a} males, the F_{1a} females were almost totally sterile, and laid about half the normal number of ova. The eggs which these hybrid females produced were small, and of unusual shape and size, with an average weight of only 50–65 percent of normal (Table 2f, g, h). Dissection revealed some eggs contained dead, partially formed larvae, but the majority of the eggs lacked any observable embryonic development. Of the 96 eggs resulting from backcrosses to male *walterorum* and *mendocino*, none was fertile.

The progeny from the reciprocal cross, ♂ *mendocino* × ♀ *walterorum*, were the F_{1b} hybrids. The F_{1b} adults were similar in size to *mendocino*, and lacked the apical patch in the males, and submarginal bands in females. The eyespot size and ratio was intermediate in the females, while in the males the eyespot ratio was close to that of *walterorum*. Unlike F_{1a} females, F_{1b} females were fertile, producing the normal weight and number of eggs (Table 2j). When the F_{1b} adults

were selfed, the resulting F_2 larvae were subvital and only seven were reared to adults. Of the five females, two emerged with crippled wings, two had thinly scaled wings and one appeared normal; the two males were normal.

The fertility and fecundity of the backcross progeny were tested by selfing (Table 2k, l). The ova size and weight were near normal for both crosses. The percent hatch was normal for the ova laid by the female whose female parent was *walterorum*, but none of the eggs hatched in the backcross with a *mendocino* parent. This may have been the result either of the pair separating prematurely or sterility.

In the pure stock of *mendocino* and *walterorum* the immature larval phenotypes, though very similar, are discrete and non-overlapping. Larvae from any given hybrid cross could express phenotypes of either species, as well as any number of intermediate forms. Thus, there was no clear case of phenotypic dominance. Mature larvae of each species can best be distinguished by differences in setal pattern and length (Tuskes, 1976).

DISCUSSION

Much of the biological information regarding the life history of the New World *Saturnia* was summarized by Ferguson (1972), but not all of the published information available at the time was correct. In describing *mendocino*, Behrens (1896) gave the type locality as "the forests of Sequoia Sempervirens, of the Coast range of Mendocino County, Cal." Thus, Ferguson (1972) contrasted the "moist coniferous forest" inhabited by *mendocino*, to the arid chaparral habitat of *walterorum* in southern California, and implied that this ecological distinction might be diagnostic. In fact, *mendocino* occurs in the arid Oak-Digger Pine woodland, and chaparral plant communities, where it feeds on manzanita, *Arctostaphylos* spp. (Ericaceae). Though these plant communities may occur adjacent to coastal or canyon redwood forests, the ecological and climatological differences are severe (Bakker, 1971; Major, 1977). In addition to manzanita, there is one report (Tilden, 1945) of *mendocino* larvae feeding on Madrone, *Arbutus menziesii* Pursh (Ericaceae), which on occasion is found in drier areas along the border of the redwood community, and opens the possibility that *mendocino* may occur there.

Saturnia mendocino occurs in the western foothills of the Sierra Nevada, from Tulare Co., north into the Cascade range of Siskiyou Co. (Fig. 3). One specimen has been collected just north of the California border in Jackson Co., Oregon (Tuskes, 1976), and marks the northern limit of well defined chaparral communities; whether *mendocino* occurs farther north on *Arctostaphylos* or possibly *Arbutus*

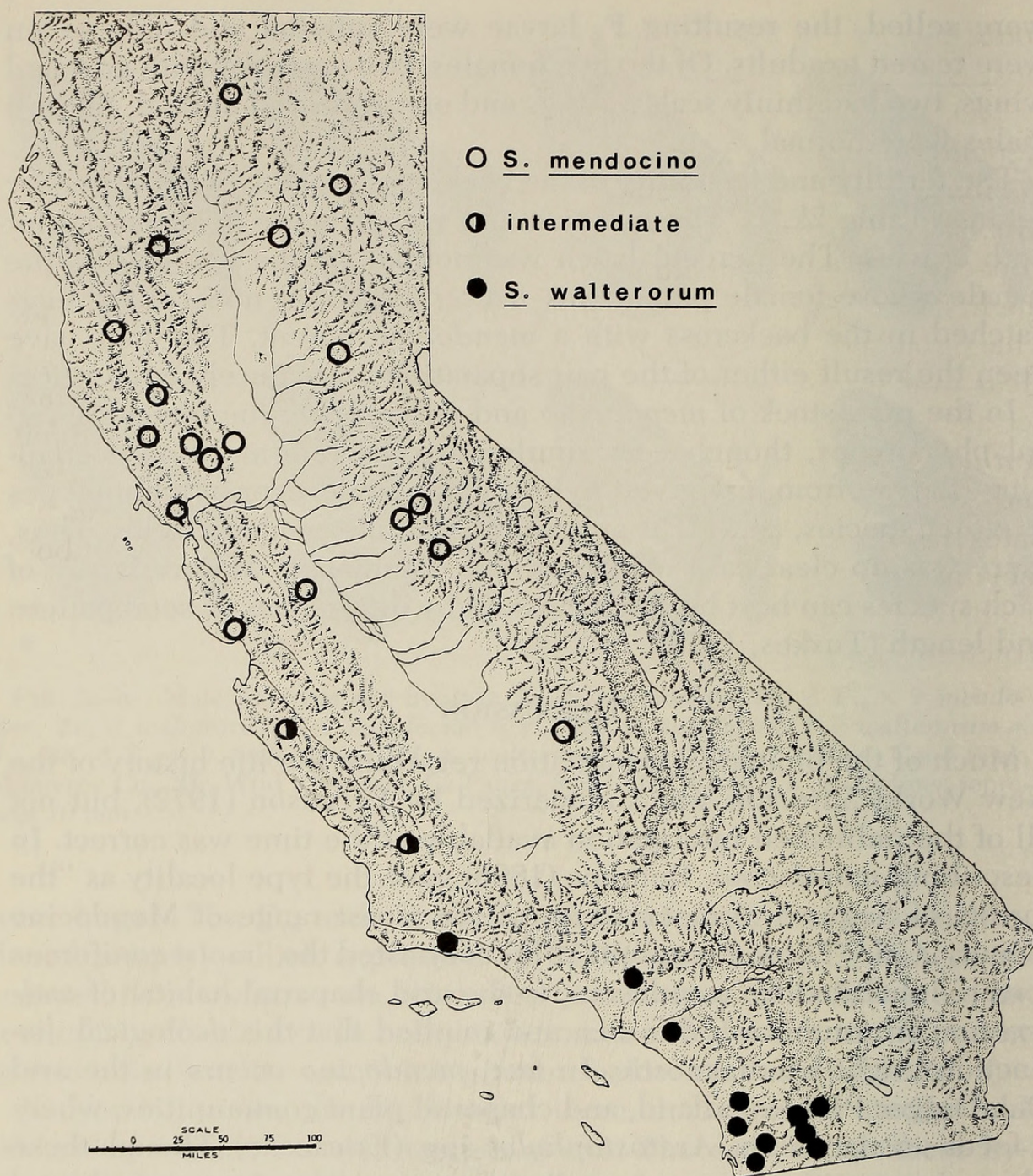


FIG. 3. The known distribution of *S. walterorum* and *S. mendocino* in California.

remains to be determined. The southern limits of *mendocino* in the Coast Range have not been adequately determined. Specimens with intermediate phenotypes have been collected in Monterey and San Luis Obispo Counties, and will be discussed later. *Saturnia walterorum* is found from Santa Barbara Co. south to San Diego Co. and undoubtedly occurs in Baja California. Though *walterorum* is not reported from Riverside or San Bernardino Counties, suitable habitat for it occurs in both counties. In the coastal chaparral community, *walterorum* is associated with *Rhus laurina* Nutt. and *Rhus integri-*

folia Benth. & Hook. (Anacardiaceae) while above 1300 m the larval host is *Arctostaphylos* (Tuskes, 1974).

The flight time for both species is generally from February to April, depending on altitude and seasonal differences. Populations of *mendocino* in the Cascade Range, of those of *walterorum* in the Laguna Mts. at 2600 m may not emerge until April or early June. The emergence of adults appears to be highly synchronized, and occurs during the first few days of warm weather following a protracted cool period. The pupae of both *walterorum* and *mendocino* possess a patch of clear integument over the brain which suggests that daylength may act as a cue controlling development as has been demonstrated in *Antheraea polyphemus* and *A. pernyi* (Williams & Adkisson, 1964) and *Actias* (Miyata, 1974). Whether this mechanism in *Saturnia* initiates development in the spring or controls summer diapause, or both remains to be determined.

Sala & Hogue (1958) mention the development of definable adult structures, such as wings and legs in the pupa during early autumn and state further that no *walterorum* pupae remained viable longer than one year. We have not found the development of the pupa to be different from other North American saturniids. In addition, we found that both *mendocino* and *walterorum* are capable of surviving at least two years in the pupal stage. Differences in pupal development and the ability to survive more than a year in the pupal stage may be the result of different rearing conditions.

The third American species in this genus, *S. albofasciata*, is unique when compared to the other two. The adults of this species exhibit strong sexual dimorphism, and fly during October and November, rather than the spring. Male *albofasciata* fly and mate in the late afternoon, while females oviposit within a few hours after sunset. The larvae feed on *Ceanothus* (Rhamnaceae) and *Cercocarpus* (Rosaceae). *Saturnia albofasciata* occurs in both the Coast Range and the foothills of the Sierra Nevada from Lake Co. south to Los Angeles Co. (Ferguson, 1972). Recently specimens have been taken near Julian and Campo in San Diego Co., and this species probably occurs in northern Baja California. Additional details regarding this moth are given by Johnson (1938, 1940) and Hogue et al. (1965).

Comparison of Larvae

The larvae of *walterorum* and *mendocino* are very similar but can be distinguished at all stages of development. Color polymorphism occurs in both species, and the larvae of *mendocino* are especially variable. The first and last instars of *walterorum* have been described (Sala & Hogue, 1958) and all the developmental stages of *mendocino*

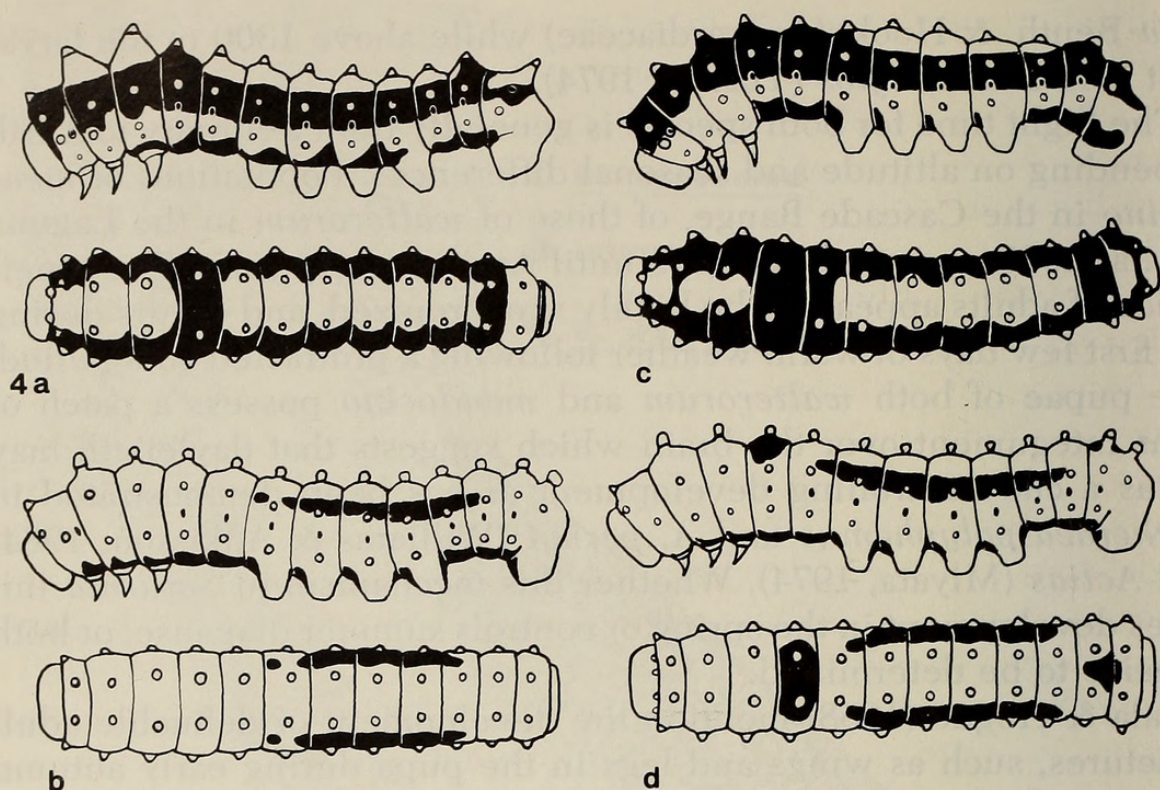


FIG. 4a-d. Dorsal and lateral view of *Saturnia* larvae. Second (4a) and third instar (4b) larvae of *S. walterorum*; second (4c) and third instar (4d) larvae of *S. mendocino*.

were described by Comstock (1960), although he did not recognize the fourth instar as the final larval stage due to the loss of the brood. We provide here a more complete description of variation, and list diagnostic characters for both species.

Figure 4 illustrates the dorsal and lateral view of the second and third instar larvae of *walterorum* and *mendocino*. The setae were omitted to emphasize pattern differences. In second instar *walterorum*, the dorsal scoli of abdominal segments I and VIII are enclosed in posterior and anterior dorsal black bands, while in *mendocino* these two dorsal bands enclose the dorsal scoli of the meso- and metathoracic segments as well as those of abdominal segments I, II, VIII and IX. The meso- and metathoracic dorsal scoli of *mendocino* are also smaller than those of *walterorum*.

In the third instar, *walterorum* lacks the posterior and anterior dorsal bands of abdominal segments I and VIII, which are present in *mendocino*. The length of the lateral stripe is variable in *mendocino*, and may be as illustrated, or may connect with the thoracic transverse band; in extreme cases a connection also exists with the caudal band, forming a rectangle, enclosing the dorsal abdominal scoli. Upon molting into the third instar, the ground color of *mendocino* is yellowish pink dorsally and dull, salmon pink laterally. The day after ecdysis a

rapid color change occurs; some larvae become lemon yellow, others turn light green, while a smaller number are a salmon pink with a yellow tinge. The green phase of both species is probably the most common. A similar polymorphism occurs in *walterorum* except that the yellow phase usually has an orange tint.

The mature larvae of *walterorum* and *mendocino* are very similar and can be reliably separated only by the greater number of dark proleg setae in *mendocino* (Tuskes, 1976). Ferguson (1972) noted that the description by Sala & Hogue (1958) of the mature *walterorum* larvae made no mention of a prominent yellow lateral line seen in *mendocino* and inferred that this was a means to distinguish the two species. This line does exist in *walterorum*, and extends from the caudal area to the metathoracic segment, passing just below the spiracles. Donahue (1979) illustrated in color a mature *walterorum* larva photographed by one of the authors. We have also found that unlike *mendocino* larvae, which pass through only four instars, approximately 62 percent of the *walterorum* have five instars, the remainder matured in four. Furthermore, about 80 percent of the larvae with five instars developed into females. Fourth and fifth instar larvae are identical in color and pattern and as in the third instar, the green color phase is the most common. In *mendocino*, lemon yellow larvae often have a greenish tint, while *walterorum* larvae in this phase are yellowish-orange. The third color form is more difficult to describe but has been called mauve by Comstock (1960) and salmon by Sala & Hogue (1958). We have noted Yolo Co. *mendocino* in this phase are a salmon-pink with a yellowish cast. Infrequently a variation occurs which is a richer color, close to a reddish-brown. Williams (1905) recorded the green form and this brownish phase of *mendocino* from Mt. Shasta, and Tilden (1945) collected this color form in Santa Cruz Co. Interestingly, the color of the third instar larva cannot be used to predict the color phase of the mature larva.

Hybridization Studies

We have directed the results of our hybridization studies toward three areas of investigation: a functional measure of genetic incompatibility between *walterorum* and *mendocino* through all stages of development; an evaluation of potential barriers to interspecific mating; and a comparison of hybrid phenotypes to specimens from geographically intermediate populations.

The results indicate a certain degree of genetic compatibility between *walterorum* and *mendocino*. The successful production of F_1 adults, using either species as the female parent, indicates that the mode of gene expression throughout development is compatible in

the two species, and indirectly implies a great deal of allelic homology. By contrast, developmental incompatibility has been demonstrated in hybrids of closely related species of *Callosamia* (Peigler, 1977) and *Phyciodes* (Oliver, 1978). During the formation of gametes in the F_1 progeny, the once equal representation of chromosomes from each parental species is randomly assorted in meiosis. Dissimilarities in chromosomes can cause aborted gonad or gamete formation especially in the heterogametic sex (Dobzhansky, 1970). Thus, sterile hybrid females are common in studies with *Hyalophora* (Sweadner, 1937; Collins, 1973), and European *Saturnia* (Standfuss, 1900, 1901a, b). Yet in this study fertile F_1 hybrid females were produced when the female parent was *walterorum*, while the reciprocal cross produced sterile females which possessed about half of the normal number of ova. These results suggest that perhaps the observed nonreciprocal sterility is somehow linked to the genetic basis of sexual dimorphism, which is strongly expressed in *walterorum* but less so in *mendocino*. In Lepidoptera ZW represents the heterogametic female sex chromosome combination, and ZZ denotes the male sex chromosomes. Perhaps the action in hybrid females of the Z chromosome from *walterorum* is incompatible with that part of the W chromosome from *mendocino* which affects gametogenesis. In male hybrids of various combinations the eyespot size is close to *walterorum*, while in female hybrids the eyespots grade from small to large, depending on the parentage of the cross (Table 1, Fig. 1). This is additional circumstantial evidence of disruptive effects caused by the Z chromosome of *walterorum*. Further, it appears that at least some of the sexual dimorphism observed in female *walterorum* (ground color and submarginal forewing band) is sex limited and is not carried by alleles on the W chromosome. Though none of these characters are expressed by male *walterorum*, they are transmitted by the male to the F_1 female progeny when mated to a female *mendocino*. In addition, it would also appear that discal eyespot size and ground color are polygenic and not expressed as simple dominant or recessive traits.

Although F_{1a} females were sterile, F_{1b} females backcrossed to the parent species had nearly normal fertility and fecundity. In backcrosses, partial genome integrity is preserved via the non-hybrid parent. By contrast, F_2 females were sterile. High mortality in the F_2 generation may be ascribed to hybrid breakdown, the disruption of highly integrated parts of the genome (Dobzhansky, 1970, 1977).

Analysis of Intermediate Populations

Populations of *Saturnia* exhibiting intermediate characters were found in the central Coast Range (Fig. 3). Three male *Saturnia* were

trapped, using an F_1 female as bait, near Cone Peak, Santa Lucia Mountains, Monterey Co. These specimens are the size of *mendocino* but possess 26 percent larger hindwing eyespots (Fig. 2g). The ventral apical mark appears as a trace, similar to many F_1 male specimens. Ferguson (1972) and Tuskes (1974) cite Tilden's capture of three male *walterorum* in the La Panza Range, San Luis Obispo Co. but upon examining these specimens we found that they are not typical *walterorum*. We collected three additional males which were attracted to a female *mendocino* near La Panza Summit. The La Panza males have larger eyespots than the Cone Peak specimens and exhibit the white apical mark of *walterorum*. They resemble *mendocino* in size and in having a larger hindwing eyespot than forewing eyespot, as do the Cone Peak males (Fig. 2). If the eyespot size relative to forewing length of these intermediate specimens is compared to the Santa Barbara *walterorum*, we find that the hindwing eyespot of the Cone Peak males, and fore- and hindwing eyespots of La Panza males are proportionately larger. As mentioned in Results, difference in overall size accounts for only 10 percent of the difference in eyespot size between typical *mendocino* and *walterorum*. Thus, both the Cone Peak and La Panza *Saturnia* appear like *mendocino* in overall size and in having an eyespot ratio less than one, but have prominent apical marks and larger eyespots; the *walterorum* characters are more pronounced in the more southern La Panza population.

One of the La Panza males was mated to the female *mendocino* and the resulting larvae exhibited mixed larval phenotypes. Five females and one male were reared to maturity; the females were the size of *mendocino* and lacked any trace of a submarginal black forewing band, but showed the ground color of *walterorum*, much like the laboratory F_1 hybrids.

We can offer only tentative conclusions about the taxonomic status of the *Saturnia* in the Santa Lucia and La Panza mountains. A larger sample needs to be collected, especially of the more diagnostic females. However, the available phenotypic evidence, combined with the demonstrated lack of reproductive barriers, and high degree of genetic compatibility in hybrids, suggests that at some time in the past the *Saturnia* in the central California Coast Range could have undergone a period of hybridization and introgression between *mendocino*-like and *walterorum*-like populations. We theorize below that this event may have been secondary to the divergence of these taxa, perhaps during the post Pleistocene xerothermic event.

In summary, *Saturnia mendocino* and *S. walterorum* can best be classified as semispecies, as exemplified by *Drosophila paulistorum*

(Dobzhansky et al., 1977). Morphological differences between the two taxa are slight; mature larvae, cocoons, pupae, and adult males are very similar, while immature larvae and adult females are distinct. No prezygotic barriers to reproduction exist under laboratory conditions. Postzygotic mechanisms act to reduce reproductive fitness in certain primary crosses, but backcrosses can be fertile in both sexes. The F_2 adults are sterile and frequently malformed. The historic isolation between *mendocino* and *walterorum* in the southern Coast Range has probably been topographic. Between the southern Sierra Nevada and the Coast Range there are expanses of desert and numerous small mountain ranges which lack host plants of either species. In the central Coast Range, *Arctostaphylos* chaparral is discontinuous, separated by other types of vegetation and intervening lowlands (Hanes, 1977). Such discontinuities appear to exist in northern Santa Barbara and southern San Luis Obispo counties, and may represent the boundary between the two species.

Phylogeny of *Saturnia* and *Agapema*

Recent phylogenies of Lepidoptera have combined morphological and biogeographical data with a comparative knowledge of foodplant preferences (Ehrlich and Raven, 1965), based on the general finding that host plant choices are taxonomically specific and evolutionarily conservative. Conversely, evolutionary radiation is often accompanied by new host plant associations. Such insect-plant relationships are thought to represent coevolution at the community level (Whittaker & Feeny, 1971; Feeny, 1973).

The American *Saturnia* and the closely related genus *Agapema* seem to represent examples of organisms coevolving with the sclerophyllous members of the Madro-Tertiary flora in western North America. While fossils of these moths are lacking, fossil records of their present day host plants do exist, and knowledge of floral distribution through time provides a framework for a phylogenetic discussion. We must assume that the present day host plants of *Saturnia* and *Agapema* reflect ancient associations, at least at the family level. Before reviewing the fossil flora evidence, we discuss our reasons for including *Agapema* in the discussion and briefly compare the host plants of Eurasian *Saturnia* and their allies with their North American relatives.

The genus *Agapema* is morphologically distinct from *Saturnia* but is closely related to it; Ferguson (1972) separates these genera but Michener (1952) treated *Agapema* as a subgenus of *Saturnia*. Many European and Asian *Saturnia*, as well as related genera such as *Dityoploca* and *Caligula* are similar to *Agapema* in pattern and color-

ation and are also sexually monomorphic nocturnal fliers. The larvae of *Dictyoploca* and *Caligula* are adorned with long hairs and bear a resemblance to the larvae of *Agapema* in this respect. As noted by Hogue et al. (1965) the nocturnal female of *S. albofasciata* somewhat resembles the nocturnal gray-colored adults of *Agapema*. *Saturnia albofasciata* also resembles the European *S. pavonia* in flight rhythm and sexual dimorphism, and an ancestral link between these two species has been suggested by Hogue et al. (1965). Yet, Ferguson (1972) notes the genitalia of *Agapema* are more primitive and quite similar to *S. pavonia*, while the three American *Saturnia*, especially *albofasciata*, are more specialized and divergent from the European *Saturnia*. Lemaire (1979) also stresses the uniqueness of the American *Saturnia* (which he places in the subgenus *Calosaturnia*) and within this group he further recognizes *S. albofasciata* as the most divergent member, even though this species resembles Old World species in retaining the aedeagus, which is lost in *S. walterorum* and *S. mendocino*. Thus the similarities between *S. pavonia* and *S. albofasciata* may be parallelisms; such phenotypic and phenological flexibility is characteristic of Saturniidae in general.

The Old World *Saturnia*, as well as the related Eurasian genera *Caligula*, *Cricula*, and *Dictyoploca*, tend to be polyphagous; important host plant families include Ericaceae, Rosaceae, Salicaceae, and Fagaceae, but not, apparently, Rhamnaceae. Several trends are apparent in comparisons of New and Old World host plants. The ericaceous preference of *S. pavonia* is seen in *S. walterorum* and *S. mendocino*, but not in the superficially similar *S. albofasciata*, thus further substantiating a more derived rather than ancestral status for this species. *Saturnia albofasciata* does retain a widespread Old World preference for rosaceous plants in its inclusion of *Cercocarpus* as a host plant, although it is possible this plant merely resembles Rhamnaceae biochemically and that this is the basis for its utilization by the moth. Rhamnaceae may be a new host plant group acquired during the New World evolution of *Saturnia* and *Agapema*. The larvae of *A. homogena* feed on *Rhamnus* in Arizona (Mr. Kenneth Hansen, pers. comm.) and are said to refuse *Arctostaphylos* in captivity. Other species of *Agapema* feed principally on *Condalia* and related Rhamnaceae. As mentioned above, *S. albofasciata* feeds on *Ceanothus* (Rhamnaceae). Thus, morphological similarity establishes a tie between *Agapema* and Eurasian *Saturnia* and related genera, and general morphology and host plant selection provides a link between *Agapema* and American *Saturnia*, especially *albofasciata*. *Rhus laurina* and *R. integrifolia* are food plants only of *walterorum* and may be associated with this species' divergence from *mendocino*, as dis-

TABLE 3. Fossil records of present day *Saturnia*-*Agapema* host plant genera.

MIOCENE	PLIOCENE
Techachapi; Southern Calif. (Axelrod, 1939): <i>Arctostaphylos glandulosa</i> <i>Cercocarpus betuloides</i> <i>Rhamnus californica</i> <i>Rhus integrifolia</i> <i>Ceanothus cuneatus</i>	Anaverde, Mt. Eden, Piru George; Southern Calif. (Axelrod, 1950): <i>Arctostaphylos</i> <i>Cercocarpus</i> <i>Rhamnus</i> <i>Rhus laurina</i>
Aldrich-Fallon-Middlegate; Interior Nevada (Axelrod, 1956): <i>Arbutus</i> <i>Ceanothus</i> <i>Cercocarpus</i>	Table Mountain, Remington Hills, Chalk Hills; Cent. Calif. (Chaney, 1944): <i>Arbutus</i> <i>Ceanothus cuneatus</i> <i>Cercocarpus</i> <i>Arctostaphylos</i> <i>Rhamnus</i>
Mint Canyon; Southern Calif. (Axelrod, 1940): <i>Ceanothus cuneatus</i> <i>Cercocarpus betuloides</i> <i>Rhamnus crocea</i>	Mulholland; Coastal Central Calif. (Axelrod, 1944): <i>Ceanothus</i> <i>Cercocarpus</i> <i>Rhamnus</i> <i>Arbutus</i> <i>Rhus laurina</i>

cussed below. In summary, no American species in either genus possesses both primitive Old World genitalic structure and host plant preferences. It is our thesis that these New World genera became specialized by coevolving with their host plants as climate and topography changed during the late Tertiary and Quaternary.

The evolution of sclerophyllous plants, as part of the Madro-Tertiary flora, with which the *Saturnia* are closely associated, has been dealt with in detail by Axelrod and others (Table 3). Axelrod (1977) presents a summary discussion and we cite other original papers. His thesis rests on the premise that ancient climates can be deduced from the species composition of geofloras, whose leaf shapes and structures are clues to their ecological requirements. In many cases these ancient species closely resemble living forms. As climates and topography changed, the distribution of plant species shifted accordingly. Those groups preadapted to xeric conditions underwent rapid speciation (e.g., *Ceanothus*, *Arctostaphylos*, *Quercus*), while plants dependent on summer rain were displaced as the climate became cooler and drier. Thus, during the Miocene-Pliocene there was a general coastward movement of Madro-Tertiary flora.

The Madro-Tertiary flora in the early Tertiary developed as more

xeric tolerant elements of a very generalized, diverse woodland, including deciduous species, which enjoyed a moderate climate of summer rains and mild winters. Due to the lack of major topographic relief and the widespread floras, it is possible that in the Miocene the *Saturnia-Agapema* ancestral stock existed as one or a few distinct species, having arrived from Asia via a land bridge during Eocene-Oligocene times. Yet, modern host plant relationships could have evolved at this time.

At the time of the Pliocene the various genera of food plants utilized by *Saturnia* and *Agapema* were all members of a single community which extended as a more or less continuous flora throughout the present day Great Basin and Southwest. Border redwood, redwood, and chaparral communities occurred to the north in the Sierra, then only 1000–1300 m in elevation. The middle Pliocene was probably the last period when central and southern California coastal floras were intermixed (Chaney, 1944). We can surmise that *Saturnia* had not necessarily diverged into the precursor populations of *mendocino* and *walterorum* since the distribution of *Arctostaphylos* was so widespread. Perhaps the more northern populations also fed on *Arbutus* as members of a tan oak-madrone-canyon oak community, while southern populations extended their ecological tolerance into a warmer coastal community containing *Rhus*.

Climatic and geological factors in the late Pliocene and Pleistocene caused segregation of separate plant communities from more generalized communities. More extreme seasonal fluctuations developed and in general the climate was becoming cooler and drier. The continuing rise of the Sierra Nevada and the subsequent uplift of the Santa Ana and San Gabriel Mountains as well as the Coast Ranges occurred at this time. These altitudinal changes and the accompanying rain shadows produced dramatic environmental clines. Chaparral as a distinct and widespread community type probably first appeared in the Pleistocene as an altitudinal segregate on the lower slopes of uplifting mountains. The final disappearance of summer rains gave rise to a Mediterranean climate along the coast but the interior penetration of the moderating coastal climate was eliminated as mountain building occurred. We can hypothesize that as the southern California *Rhus-Arctostaphylos* association began to separate into montane and coastal communities the moths expanded their distribution accordingly. Northern California populations diverged into *mendocino* on manzanita in the Coast Range and in the Sierras, separated by an increasingly inhospitable valley. A northern bridge of *Arctostaphylos* and perhaps *Arbutus* in the Sierra-Cascades provided genetic continuity to this wide ranging species.

Saturnia albofasciata probably arose as a separate entity in southern California in association with the more xeric-adapted *Ceanothus cuneatus* and *Cercocarpus betuloides*. Its appearance in the Coast Ranges would then be one of invasion as *C. cuneatus* and *C. betuloides* spread on the uplifting coastal mountains. Thus, the sympatry of *mendocino* and *albofasciata* may be rather recent.

The rain shadow of the Sierras and southern California mountains produced an intervening desert which isolated the Arizona derivatives of *Saturnia*. *Agapema homogena* may be a relict species as it now inhabits montane areas of summer rains (Colorado, Arizona, New Mexico, west Texas and portions of northern Mexico) and emerges in early summer. The desert species of *Agapema* probably appeared at this time although it is possible that they speciated earlier in Mexico and subsequently invaded the developing American deserts to the north.

The phenomenon of the xerothermic period may explain the apparently intermediate populations of *Saturnia* in the Santa Lucia and La Panza mountains. The xerothermic of 3000 to 8500 years ago was a sudden warming period between the last glaciation and the more recent cooling period (Axelrod, 1966). This change in climate appears to have forced chaparral species such as *Arctostaphylos glauca* Lindl. north into the Coast Ranges such that relict populations now exist as far north as Mt. Hamilton. Similarly, *Rhus laurina* and *R. integrifolia* have an oddly disjunct population near Cayucos, 130 km N of their normal range. The northern movement of all these plants during a brief period of warmth may have produced a temporary event of hybridization and introgression between *S. mendocino* and *S. walterorum*.

We can hypothesize that the *Saturnia* responded to the same environmental changes as their host plants and evolved phenological and developmental adaptations. The highly synchronized spring adult emergence and facultative egg development of *mendocino* and *walterorum* allow the larvae to exploit the early growth of their food plants. The egg of *albofasciata* represents an alternative modification, allowing the larva to overwinter and emerge in the early spring to feed on new growth. Perhaps the fall flight of this species is a direct result of this adaptation. The genetic potential for this adaptation may well be ancestral; an overwintering egg occurs in the Asian *Caligula* and *Dictyoploca*, and in Arizona populations of *Agapema galbina*. The pupae of *walterorum* and *mendocino* pass through the hot dry summer months, as well as the winter. The open mesh cocoon construction is especially well developed in the desert species of *Agapema*, and much less so in the montane *A. homogena*. The loose mesh cocoon may aid in ventilation, keeping the pupa cooler.

Hogue et al. (1965) proposed that both *mendocino-walterorum* and the genus *Agapema* arose sympatrically from an *albofasciata*-like ancestor by means of dual mutations affecting coloration and flight times, such that dull colored night flying mutant males would encounter more similarly colored nocturnal females, and brightly colored mutant diurnal females would encounter normal brightly colored diurnal males. In this way arose the brightly colored diurnal *walterorum-mendocino* line, which resembles male *albofasciata*, and the dull colored nocturnal *Agapema*, which are similar to the female of *albofasciata*. It should be pointed out that female flight occurs only after mating, and that pheromones, not chance encounters in flight, control mating response. Furthermore, Saturniidae are poor candidates for sympatric speciation as judged by the criteria of current models (Wilson et al., 1975). They are present in large mobile, more or less randomly mating populations, in which the uniting of rare mutants is unlikely. Since the pheromone system controls mating, mutants with allochronic mating behavior would be severely selected against. Rather, we feel that the *Saturnia*-*Agapema* phylogeny is one of coevolution with Madro-Tertiary flora in which moths and their sclerophyllous host plants adapted to changing climate, primarily by altering developmental phenomena. The continual lateral and altitudinal redistribution of plant communities, especially during the Pliocene-Pleistocene, provided ample opportunity for allopatric speciation to occur. In this context the West Coast *Saturnia* are important examples of endemic species which evolved in response to the appearance of a Mediterranean climate.

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RECENT ADDITIONS TO THE COLLECTION OF THE AMERICAN MUSEUM OF NATURAL HISTORY

Dr. Cyril F. dos Passos has donated his collection of 65,382 butterflies to the American Museum of Natural History. Of this total, 64,052 specimens are mounted and identified; 57,870 are from North America and 6182 are from Europe; 1330 are unmounted or unidentified. Included in the collection are 464 paratypes (no holotypes or allotypes) and 617 slides (124 venation, 493 genitalia). Dr. dos Passos started building his collection in 1929; it undoubtedly represents the single largest and most complete one of North American butterflies ever made by one individual. It far surpasses the two previous large collections of butterflies (no moths) received by the Department of Entomology, namely those of J. D. Gunder (27,000 North American specimens, received in 1937) and V. G. L. van Someren (23,000 African specimens, received in 1970). The addition of this collection gives the American Museum of Natural History an unrivaled collection of North American butterflies.

The museum has also received the collection of the late Bernard Heineman, consisting of 7075 mounted butterflies and moths. Of these, 2857 were from Jamaica, with the great majority being butterflies. This is the largest private collection of Jamaican butterflies ever made, and it served as the starting point for the 1972 book entitled, "Jamaica and its butterflies" by F. Martin Brown and Bernard Heineman. The other 4218 specimens represent a world-wide collection made by Mr. and Mrs. Heineman on their various trips throughout the world.

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