

NATURAL HYBRIDS OF TWO SPECIES OF ARCTOSTAPHYLOS IN THE YOSEMITE REGION OF CALIFORNIA

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I. INTRODUCTION

THE purpose of the present note is to record a striking case of natural hybridisation of two species of manzanita bushes, *Arctostaphylos mariposa* Dudley and *A. patula* Greene, in and near Yosemite National Park, California. The weakness of this case, first reported by Epling (1947) is that the available data are derived from field observations in only a fraction of the total distribution area of the species, and are unsupported by experimental evidence. On the other hand, the case is remarkably clear and instructive since the environmental relationships of the parental species and of the hybrids are readily discernible.

2. THE PARENTS AND THE HYBRIDS

A. mariposa and *A. patula* are common and conspicuous members of the preclimax vegetation of the hillslopes in the Transition and in the lower portion of the Canadian life zones of the Sierra Nevada of California. In places they are abundant enough to form dense thickets of tall bushes or small trees on exposed slopes. They do not, however, grow on meadows and become depressed when forest shade develops above them. *A. mariposa* occurs at lower elevations than *A. patula*. According to Hall and Hall (1912) the former species occurs up to the elevation of 6000 feet, and the latter from 4500 to 9000 feet. In the region where the observations reported below have been made, *A. mariposa* extends from about 2500 to 6000 feet; and *A. patula* from approximately 4500 to 8000 feet above sea level. Taken at face value, these figures would indicate that the zone in which both species occur is about 1500 vertical feet. In reality it is usually narrower, because on slopes with southern exposure *A. mariposa* grows higher than on northern exposures. Conversely, the lower limit of *A. patula* extends lower on northern exposures than on southern. The soil drainage likewise influences the altitudinal limits of the species, rocky slopes being more accessible to *A. mariposa* than to *A. patula*. For these reasons, the altitudinal limits of the zone of overlap vary greatly from place to place. Occasionally the replacement of the species occurs without any overlap at all. This has been observed along a trail leading from the Rancheria Mountain to Hetch-Hetchy, in Yosemite Park. This trail first descends a mountain-side with a north-eastern exposure, then emerges on a lower slope

with a southern exposure. Only *A. patula* has been seen on the north-east, only *A. mariposa* on the southern slope.

Morphologically the two species differ so clearly that they can be identified without hesitation even at a distance of one hundred feet or more (Jepson, 1923-25; Epling, 1947). *A. mariposa* has white-glaucous foliage which appears greenish-grey; *A. patula*, bright green glabrous leaves. The former species is generally taller, more erect, and has the branchlets, the inflorescence, and the berries densely covered with glandular pubescence which makes them very sticky to touch. *A. patula* is usually lower, frequently semi-prostrate, and its inflorescence is only minutely pubescent, the berries large, glabrous or nearly so, never sticky. The leaves of *A. mariposa* are on the average smaller (mostly 2 to 4 cm. long) than the *A. patula* (3 to 5 cm. and even more). The stems of *A. patula* form a "burl", i.e. an irregularly globose body, under the soil surface, which crown-sprouts after fire. *A. mariposa* does not have this property.

The hybrid bushes are on the whole intermediate between the parents, but somewhat closer to *A. patula* in the conspicuous traits. Their leaves are bright green, slightly glaucous and therefore not glossy. The leaf size is only slightly smaller than in *A. patula*. The manner of growth approaches that in *A. mariposa* rather than that in *A. patula*. The inflorescence is moderately pubescent but not glandular and not sticky. The berries are almost glabrous, like in *A. patula*. The variation in the hybrids is not any greater than it is in the parental species, and there is no overlapping at all, making the hybrids a morphological array which can be separated without hesitation from those of the parents (Epling, 1947).

3. A SAMPLE TRANSECT

Observations were made on the relative frequencies of the individuals of the two species and of the hybrids in several localities in the Yosemite region. Usually a trail or a road was selected leading from the lower elevations where only *A. mariposa* is found to the higher areas where only *A. patula* is encountered. The bushes on either side of the trail were classified as to species. On two such transects counts were made of the numbers of bushes of the three kinds growing within five metres on either side of the trail. The trail was subdivided into sections 100 paces long, the section boundaries marked, and the bushes counted and recorded. The direction of each section of the trail was determined with the aid of a compass, and a rough map was prepared. The elevation above the sea level of the different parts of the trail was determined with the aid of an aircraft altimeter. Notes were made on the vegetation in each section, as well as on the characteristics of the soil, slope, etc.

One of the transects is reproduced in fig. 1. The individuals of *A. patula* are marked by black circles, *A. mariposa* with white ones,

and hybrids with half black and half white. The trail leads from Mather to the Cottonwood Meadow in the Yosemite Park. The counts were started at the elevation of 4800 feet and finished at 5500 feet. In all, 745 *A. mariposa*, 166 *A. patula*, and 37 hybrids were counted. On this particular transect very few young bushes were found, a majority being mature fruiting individuals. Below 4800 feet many *A. mariposa* and a single hybrid bush were noted, and above 5500 feet numerous *A. patula* and also a single hybrid bush occur along the trail. The part of the trail along which counts were made thus covers the transition between the distribution areas of the two species.

Section 1 of the transect (fig. 1) abuts a flat densely overgrown with young yellow pines (*Pinus ponderosa* Dougl.) and incense cedars (*Libocedrus decurrens* Ferr.). Sections 1-4 climb up a slope of a hill, mostly exposed to the sun, but with few scattered yellow pines. Here are found 192 bushes of *A. mariposa*, no *A. patula*, and 4 hybrids. Sections 5-7 cover fairly flat ground with deeper soil and scattered oaks (*Quercus Kelloggii* Newb.), cedars and pines. There 6 hybrids and 109 *A. mariposa* are found. Sections 8 and 9, elevation 4900 feet, begin to climb up a fairly gentle slope with scattered oaks, pines and cedars. There another eighty hybrids are recorded. Sections 10

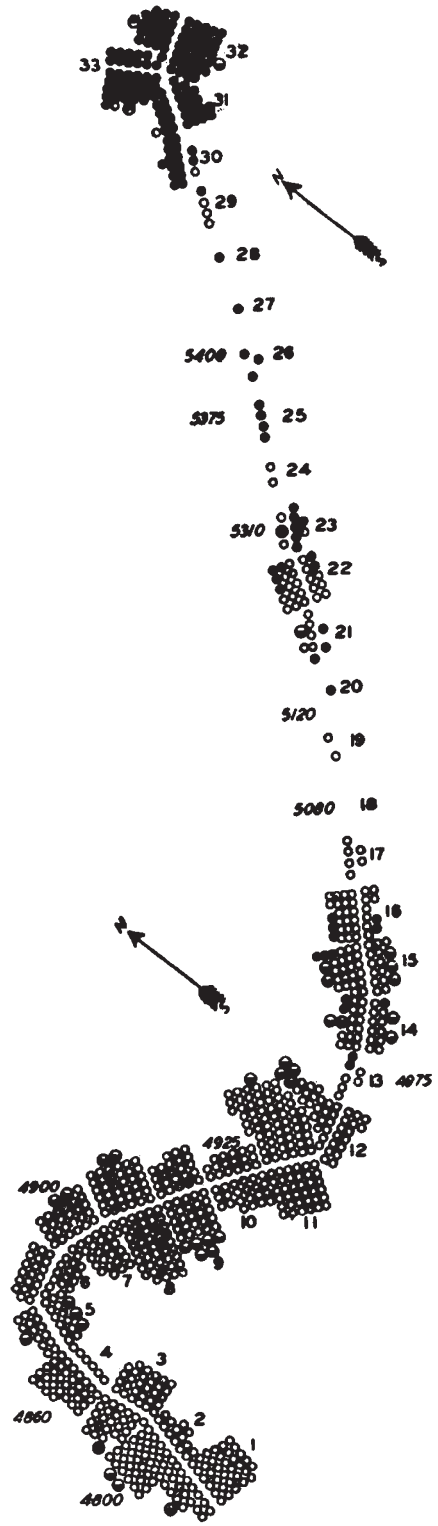


FIG. 1.—A sample transect of the altitudinal zone in which *Arctostaphylos mariposa* (open circles), *A. patula* (solid black circles), and their hybrids (black-and-white circles) occur. The numerals indicate the numbered sections of the transects and the elevations, in feet above the sea level.

and 11 are on a much steeper and rocky slope exposed to the south and devoid of shade. Numerous *A. mariposa* grow on this slope, but the single hybrid is found close to the boundary of Section 12, where the conditions change. The absence of hybrids in Sections 10 and 11 is probably significant—they are less well adapted than *A. mariposa* to grow on hot and exposed slopes at this elevation.

Sections 12 to 16 enter the mouth of a canyon, with some large pines, cedars and oaks, particularly to the right of the trail, and with less rocky soil. There 129 *A. mariposa*, 13 hybrids, and the first 13 bushes of *A. patula* have been counted. Both the hybrids and *A. patula* grow in relatively flat, more protected locations with some shade from the larger trees. Sections 17 to 20 are unfavourable for *Arctostaphylos*, being shaded by a dense growth of yellow and sugar pines (*Pinus Lambertiana* Dougl.), cedar, white fir (*Abies concolor* Linde), oak and Douglas fir (*Pseudotsuga taxifolia* Lamb.). The few *A. mariposa* and the single *A. patula* are depressed individuals. Sections 21 to 24 are climbing up along the bottom of a fairly steep-walled canyon with a small impermanent stream at the bottom. The slope to the right (south-east) of the trail is much more densely wooded than that on the left. Almost all *Arctostaphylos* bushes are growing on the left slope of the canyon (although not necessarily to the left of the trail). Both species and hybrids are found, with *A. patula* and the hybrids clearly selecting the less dry and more protected situations.

Sections 25-29 are in the head of the canyon, where the sides are less high and less steep. There is much forest shade, the *Arctostaphylos* bushes being not numerous near the trail but more abundant higher up on the left slope. Examination of these bushes (not entered in fig. 1) discloses that the upper and exposed parts of the slope have chiefly *A. mariposa* and a few hybrids, while along the trail *A. patula* predominates. Finally, Sections 30-33 are on a small plateau at the elevation of approximately 5500 feet. On this plateau, and higher up on the Sierra slope, *A. patula* is clearly the predominant species. Some hybrids, and the last *A. mariposa*, occur, however, on this plateau.

4. OTHER TRANSECTS

Conditions similar to the ones described above have been observed on other transects as well. Within the zone of the overlap, *A. mariposa* grows relatively more frequently in hot, exposed, or rocky situations, while *A. patula* and the hybrids occur in more protected, less arid places, frequently with some shade. And no matter how wide or narrow is the zone of the overlap, always a decided majority of the bushes belong to the two parental species, with hybrids in a minority. Along the road from Mather to Aspen Valley the zone of the overlap extends from the elevation of about 4900 to 6000 feet and for about three miles horizontally. Counts were made of bushes within five metres on either side of the road. *A. patula* was represented by 1051

individuals, *A. mariposa* by 110, and only 27 hybrids were found. The predominance of *A. patula* on this transect is due to the fact that its lower part has too much shade to support numerous *Arctostaphylos*. A few miles away from there, on a margin of Ackerson Meadow which was logged and partly burned in 1946, numerous young bushes are found. Our counts showed that less than 1 per cent. among them are hybrids, and about 80 per cent. are *A. mariposa*. It would be interesting to compare the relative frequencies of the pure species and the hybrids in a decade or a larger time interval, since it is possible that the hybrids may be eliminated at rates greater than the pure species.

5. CONCLUSIONS

A. mariposa and *A. patula* are two Mendelian populations which are adapted to occupy related but distinctly different adaptive niches. The former is superior under the more arid conditions of the lower, and the latter under the less arid ones of the intermediate elevations, in the Sierra Nevada of California. The two populations must clearly be regarded as specifically rather than only racially distinct. This is because the gene exchange between them is clearly not effective enough to erase the barriers to further gene flow. Their genetic systems are almost completely closed. This fact is reflected on the morphological surface to permit classifying the individuals observed in three discrete arrays—that of *A. mariposa*, of *A. patula*, and that of the hybrids. The first two arrays are much larger than the third one, even in the zone of the geographic and environmental overlap where the hybrids occur.

It should be stressed that the hybrids do not seem to be sterile. At any rate, the hybrid bushes produce crops of berries just as abundantly as do the parental species. The seeds are visibly normal, but no germination experiments have been made. This raises the question of what prevents the spread of the hybrids and the swamping of the species boundary, at least in the zone of the distributional overlap, which would degrade the species to races. A great majority of the hybrids are, as stated above, a discrete array which is not noticeably more variable than the parental species. This suggests that they are the F_1 hybrid generation, although one cannot exclude the possibility that a small minority of them may be F_2 or backcross products. Bushes which, on morphological grounds, appear to be backcross individuals are rare, although they are found. In the part of the Yosemite region in which the observations were made, eight bushes have been noted which, with varying degrees of assurance, can be described as intermediates between the F_1 hybrids and the parents. Of these, six suggest backcrosses to *A. mariposa* and two to *A. patula*. Four are fairly large, and they have been observed to produce berries in several successive seasons.

Efforts have been made to detect the possible introgression of

the genes of *A. mariposa* into *A. patula*, and vice versa, particularly in the zone of the overlap. Although the writer does not claim an "ability to spot introgression in the field, sometimes almost instantly and frequently in organisms with which one was unfamiliar" (Anderson, 1951), the populations of both species were inspected within and outside the zone of the overlap. Such inspection shows, to an increasing degree as one becomes more familiar with the plants, the existence of local, intercolonial variations in all sorts of traits. How much of this variation, is genotypic and how much purely environmental is, of course, impossible to tell. What is important for our purpose is that no indication was observed of mutual approximation of the species in the zone of the overlap, except, possibly, that *A. patula* tends to be more erect than it is further up the Sierran slope. The erectness is a trait characteristic of *A. mariposa*.

It is quite possible that a narrow channel for gene exchange between the species is preserved. Morphological observation could not exclude this possibility entirely, especially since backcrosses of the hybrids to *A. patula* might produce progenies that would be difficult to recognise. The important fact is that the gene exchange, if it occurs, does not furnish in the *Arctostaphylos* case genetic building blocks for adaptive modification of local populations. Since both *A. mariposa* and *A. patula* come up most abundantly on disturbed soils after burning or logging the forest, human activities have doubtless increased the sizes of the populations of both species as well as opportunities for species crosses. It is, however, unlikely that no hybrids at all were found until men came. If so, the absence of clear introgression effects suggests that the two species are coherent genetic systems which form a reasonably fit F_1 hybrid, but which suffer a breakdown in F_2 and in backcrosses, with natural selection eliminating most or all recombination products. Formation of some viable and fertile hybrids between species in nature does not necessarily erase the reproductive isolation which keeps their genetic systems separate.

6. SUMMARY

Two species of manzanita bushes, *Arctostaphylos mariposa* and *A. patula*, form some natural hybrids. The former species occurs at lower elevations and in drier and more exposed sites than the latter, but in a fairly narrow altitudinal belt the two occur together. The hybrids, which are mostly F_1 and much less often F_2 or backcross products, never form more than 10 per cent. of the population of the region in or near which both parental species also occur (*cf.* fig. 1). In that region, the parental species and the hybrids tend to occupy somewhat different habitats. There are no indications of extensive introgression of genes of *A. mariposa* into *A. patula* or vice versa. It is suggested that an important isolating mechanism which keeps the

gene pools of these species closed systems is adaptive inferiority of most products of gene recombination.

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