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Hybridization and Speciation in the Pacific Coast Irises

Lee W. Lenz

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HYBRIDIZATION AND SPECIATION IN THE PACIFIC COAST IRISES

LEE W. LENZ

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INTRODUCTION

A long experience has taught me that Irises
grown from seed vary in a wonderful way . . .

Clusius, 1601

Although the above was written more than three and a half centuries ago we are still studying variation in irises, but today interest is for the most part centered around

the factors which are responsible for the presence of the variation rather than in the variation itself. In the present paper, which is Part II of a general survey of the Pacific Coast irises, an attempt has been made, first, to show that natural hybridization is a common occurrence within the *Californicae*, and, second, to examine some of the factors which may account for its occurrence. Finally, an attempt is made to postulate what effect hybridization may have on the future speciation within the group.

The taxonomic portion of this work has been published previously (Lenz, 1958), and the reader is referred to it for taxonomic descriptions, distribution maps, and illustrations of the species involved.

ACKNOWLEDGMENTS

It is a pleasure for me to acknowledge the help which has so generously been given me during the course of this investigation by many people in many fields of endeavor. Unfortunately it is impossible for me to mention every name. I would like to express my sincere gratitude to Dr. Philip A. Munz, Director of the Rancho Santa Ana Botanic Garden, for his continued interest in, and support of, this work. Thanks are also due E. K. Balls, Steve Tillett, Bill Klein, Cal Dodson, Donald Stryker, and Peg Grey. Finally, I would like to thank my colleague, Verne Grant, for his many helpful suggestions received during the course of this study.

The outline map used in Figure 24 is one of a series published by the University of California Press and is used with their approval. The photograph shown in Figure 3 was taken by Jean G. Witt.

FLOWER BIOLOGY AND SEED DISPERSAL

FLOWER BIOLOGY

The presence of a distinct, though sometimes short, perianth tube above the ovary is the character which separates the genus *Iris* from the closely related African genus *Moraea* in which the perianth segments are free. In the case of *Iris*, the perianth tube is surmounted by a perianth consisting of an inner and an outer whorl, each with three segments. In the members of the series *Californicae*, the sepals or falls which form the lower whorl, are usually marked with conspicuous veins or lines which tend to coalesce on the narrow basal portion of the sepal and form guide lines leading into the flower. In addition to this veining, many of the flowers possess white or brilliant yellow "signal patches" on the sepals which may help to attract insects to the flowers.

The two whorls of perianth segments surround a central style column which branches into three petaloid style branches opposite the three sepals. Each style branch bears on its under surface and near its outer extremity, a triangular (or truncate in one species) stigmatic lip. Beyond the stigmatic lip the style branch splits into two style crests which, in the *Californicae*, vary in form from broadly rounded overlapping structures to long and narrow rabbit ear-like projections. The style branches are slightly arched and somewhat concave on their inner surface and are located over the haft portion of the sepal segments. The stamen is composed of a rather short filament and a relatively long anther which is held against the inner face of the style branch with the outer tip of the anther usually not reaching the stigmatic flap. In *I. bartwegii* the anthers may at times be exerted beyond the stigmatic flap but this is a rather rare occurrence in the *Californicae*. The long slender anthers dehisce on the lower side through two linear slits. The pollen is powdery and in our species varies in color from cream to yellow.

The flowers of the *Californicae* are ideally suited for insect pollination. At the time that the flower opens, the anther slits have started to separate but no pollen has fallen onto the sepal and the stigmatic flap is still held firmly against the underside of the

style branch, its surface well protected from chance contact with an insect visitor. An insect lands on the recurved portion of the sepal and crawls into the flower through a tunnel-like opening between the sepal and the style branch. Nectar is produced in quantity at the base of the perianth segments. On entering a freshly opened flower, the insect brushes its back against the mature anther and through the two movements, that of entering the flower and backing out again, it removes much of the pollen on its back. About twenty-four hours after opening of the flower, the stigmatic flap recurves and forms a short triangular curtain which partially closes the opening across the tunnel-like corridor. An insect visiting such a flower brushes against the pappilose stigmatic flap which removes pollen from the visitor's back. Such a flower arrangement should assure cross pollination. However, this may not always be the case. Many of the *Californicae* produce large numbers of flowers on a single plant and by vegetative reproduction a single clone may cover several square feet of space. Such a colony will have numerous flowers open at one time with new ones opening daily. If an insect visited a fresh flower and then flew directly to another plant and visited a receptive flower, cross pollination would be assured. Very often, however, an insect has been observed to enter a number of flowers on the same plant before moving to another. Some of the flowers visited were fresh and contained pollen, whereas others were receptive. In this case there would appear to be at least some selfing unless the plant possessed an incompatibility system which would prevent this happening.

Controlled pollination experiments on caged plants have shown that all the *Californicae* can be selfed and the resulting seed germinates readily. In some instances there may be a somewhat lowered seed set on selfed flowers, but normally the capsules are plump and well filled. In these irises, pollen is produced in abundance and after an insect visited a number of flowers on different plants its pollen load might well be composed of a mixture of types. If foreign pollen had any selective advantage over self pollen, the flower might be effectively out-crossed even though pollinated with a mixture containing some of its own pollen. Tests are now being conducted to determine if any such selective action can be shown.

Dykes (1913) was of the opinion that large numbers of the *Apogon* irises were self-fertilized without the intervention of insects. In *I. sibirica* L., which has tongue-shaped stigmatic flaps similar to those found in the *Californicae*, he reported that the plants were quite independent of insects for fertilization. According to him, the anthers sometimes actually reached the reflexed tongue of the stigma whereas in other instances the tongue was able to gather the pollen which had fallen onto the haft portion of the sepal. In the work carried on at this Garden, no seed was ever produced on plants of either the *Californicae* or the *Sibiricae* which were protected by insect-proof cages unless the flowers had been hand pollinated. Only a limited number of plants of the *Sibiricae* were available for study and further work needs to be done with them before it can be stated with certainty that autogamy does not occur in that group.

SEED DISPERSAL

A number of species of iris native to moist stream sides or boggy areas possess seeds which are adapted for distribution by water. In some instances the seeds have a thick and spongy or corky seed coat which allows them to float for long periods of time. This is true of the members of the *Hexagonae*: *I. fulva* Ker-Gawl and *I. hexagona* Walt. Members of the *Spuriae* on the other hand usually have seeds with a loose papery outer coat which allows them to float in water. In this case, air is trapped between the papery outer coat and the hard inner seed coat. *Iris laevigata* Fisch. also

has seeds of this type. *Iris foetidissima* L., a woodland species, is unique in the genus in having seeds which remain firmly attached after the capsule has dehisced. The seeds of this species are fleshy and brilliant orange-scarlet in color. According to Ridley (1930) they are distributed by birds. In the case of *I. ruthenica* Ker-Gawl, it has been reported (Ridley, 1930) that ants carry the seeds away after they are on the ground.

A number of years ago a large amount of seed of *I. douglasiana* was broadcast in the Botanic Garden at Claremont in an attempt to establish plants in a new area. Within a few days, large quantities of the seed were found to have been carried by ants to the vicinity of the entrance to their underground tunnels and there the seeds were neatly piled in circles around the entrances themselves. As much as a handful of seed was sometimes found at a single tunnel opening. According to Sernander, quoted by Ridley (1930), ant-distributed seeds usually possess an oil, or oily substance, the Elaisome, which the ants find attractive. Presumably not all the seeds are carried to the areas of storage, but some of them are dropped along the way, probably after the ants have removed the oily Elaisome. Another character which is often correlated with the presence of the Elaisome is that the seed capsules tend to hang toward the ground and the seeds are dropped together in a pile. This characteristic has been noted a number of times in the members of the woodland forms of the *Californicae*. Very often when the capsules are nearly mature they will be found to be hanging toward the ground and later small clusters of seeds will be found on the ground directly under the opened capsule.

Birds have never been seen to feed on the seeds and there is no evidence that they are responsible for their dispersal. Rain may be responsible for transporting some seeds, especially hard summer showers which would find the seeds lying on, or near, the surface of the soil. However, the principal method of seed dispersal for this group may well be ants. The possibility of transfer of seeds in the wool of sheep will be discussed later.

GARDEN HYBRIDS

SERIES *Californicae* × SERIES *Californicae*

Many members of the *Californicae* possess attractive flowers which make the plants desirable garden subjects and at the present time all, or nearly all, of them are being grown in cultivation. The first to be grown was *I. tenax* which was collected by the early plant explorer, David Douglas, in 1825 and was introduced into cultivation in England shortly thereafter. It is also the first of the Pacific Coast irises to be illustrated and it was figured in Edward's *Botanical Register* in 1829 (t. 1218). The next species of this series introduced into gardens was *I. douglasiana* which was grown by the English firm of James Veitch and Sons at least as early as 1873. In the ensuing years other species followed, with *I. fernaldii* and *I. munzii* probably being the last of the group to be grown, the latter only having been introduced into cultivation in 1948.

It is not known who produced the first garden hybrid in this group, nor are the species involved known. During the latter part of the 19th Century, Sir Michael Foster in England initiated the first definite iris breeding and hybridizing program of any consequence and in the years between 1870 and 1895 he brought together a collection representative of nearly every important section in the genus. According to Sir Arthur Hort (1921) Foster did not grow many of the western American species because of conditions prevailing in his garden. The exception was *I. longipetala* which grew well in the chalk soil at Shelford.

It is entirely possible that the first garden hybrids between species of the *Californicae* arose as chance seedlings in Dykes' garden. In 1912 he wrote, "The diverse

and delicate colourings to be found among those irises [the *Californicae*] are endless, and the general rule that multiplication must be by seeds rather than division has its compensation in the surprises to which it gives rise. *Iris bracteata*, which in its typical state has yellow flowers veined with brownish-purple has already given me several forms some of which are approaches to crimson, while one is a delightful colour that may best be described as old rose. A descendant of this second or third generation of what was originally a cross between *I. douglasiana* and *I. macrosiphon* has flowers of pure white, conspicuously veined with violet-purple, and there seems to be no end to the colour forms to which this variable group may give rise."

In more recent years numerous interspecific hybrids involving members of the *Californicae* have been recorded in the literature. Unfortunately there are usually no vouchers preserved and very often the only available information is a brief mention of the hybrid. In 1956 Smith and Clarkson published a valuable list of controlled interspecific hybrids which they had produced in Oregon. Since 1948 numerous controlled hybridizations have also been made at the Rancho Santa Ana Botanic Garden and the results of the work of Smith and Clarkson and that of the author are shown in the crossing diagram (Fig. 1). No attempt has been made to show the direction of the crosses nor are subspecific taxa indicated. In many instances the crosses have been reciprocal and in no instance has a cross been shown to be possible in but one direction.

FIG. 1. Crossing diagram showing known garden interspecific combinations in the *Californicae*. Subspecific entities and direction cross was made not shown. Solid lines indicate fertile hybrids. BRA, *I. bracteata*; CHR, *I. chrysophylla*; DOU, *I. douglasiana*; FER, *I. fernaldii*; HAR, *I. hartwegii*; INN, *I. innominata*; MAC, *I. macrosiphon*; MUN, *I. munzii*; PUR, *I. purdyi*; TEN, *I. tenax*; TMA, *I. tenuissima*.

Vigor of F₁ Hybrids.—In all interspecific hybrids observed by the writer the plants of the F₁ generation have shown as much, or more vigor than the parental species themselves. This is in accord with the findings of Dykes as well as those of Smith and Clarkson (1956) who report that most of the F₁ plants grown by them exhibit hybrid vigor and some are much more vigorous than the parental species. According to these authors the hybrids involving *I. bracteata* and *I. tenuissima* are much more vigorous than either of those species which are somewhat difficult to maintain in the garden. During the course of the horticultural breeding program being conducted with these irises, large number of F₂ and subsequent generations have been grown at this Botanic Garden and many of the present day hybrids represent combinations of three or more species. No deterioration in vigor has been observed in these hybrids. However, it must be noted that the hybrids have been subjected to a strong artificial selection which would have eliminated the less vigorous plants.

Fertility of Hybrids.—Smith and Clarkson (1956) report that highly fertile hybrids are produced whenever any two species belonging to the *Californicae* (*sensu* Clarkson, 1955; Lenz, 1958) are crossed. In the hybrids which they examined these workers reported no cytological irregularities and all their hybrids set abundant seed when open pollinated. They further reported that most of the hybrids produced from 1-5 per cent sterile pollen and this they attributed to other factors than meiotic irregularities. They did not grow many F₂ plants in their studies. In general, the findings of this laboratory are in agreement with those of Smith and Clarkson. However, several hybrid combinations have been produced at this Garden which were not available to them. Notable among them are those involving *I. munzii*, a narrow endemic belonging to the *I. tenax-hartwegii* alliance and known only from Tulare County, California. Table 1 shows pollen fertility of some of the species and hybrids grown at Claremont as determined by staining with cotton blue in lactophenol.

TABLE 1

Species	Pollen grains counted	Percentage stainable pollen
<i>I. bracteata</i>	864	99.5
<i>I. douglasiana</i> (Cañada Hondo)	853	92.0
<i>I. douglasiana</i> (clone 1)	4563	99.7
<i>I. fernaldii</i>	1829	99.8
<i>I. macrosiphon</i>	933	99.5
<i>I. munzii</i> (Kaweah)	3590	99.3
<i>I. munzii</i> (clone 1)	1467	99.9
<i>I. munzii</i> (clone 2)	1666	100.0
<i>I. tenuissima</i>	998	99.2
<i>Hybrids</i>		
<i>I. bracteata</i> × <i>I. munzii</i>	4660	83.6
<i>I. douglasiana</i> × <i>I. innominata</i> (clone 1)	1502	99.6
<i>I. douglasiana</i> × <i>I. innominata</i> (clone 2)	1035	98.9
<i>I. douglasiana</i> × <i>I. innominata</i> (clone 3)	1795	98.8
<i>I. douglasiana</i> × <i>I. innominata</i> (clone 4)	2347	99.7
<i>I. hartwegii</i> × <i>I. munzii</i>	3061	95.2
<i>I. innominata</i> × <i>I. munzii</i>	3725	99.3
<i>I. macrosiphon</i> × <i>I. munzii</i>	3158	97.5
<i>I. munzii</i> × <i>I. innominata</i>	2073	97.5
<i>I. munzii</i> × <i>I. innominata</i> (clone 2)	2908	97.5
<i>I. munzii</i> × <i>I. macrosiphon</i>	1314	98.7

In the list of species shown in Table 1 it will be noted that of the plants of *I. douglasiana* examined, those from Cañada Hondo in Santa Barbara County, California, showed a somewhat lower percentage of stainable pollen than the other plants examined. The Cañada Hondo material is interesting because it is the southernmost colony known of that species and is separated by about 80 miles from the next colony north. The population at Cañada Hondo is small, containing perhaps not over 100 plants, and it has probably been isolated from the rest of the species for a considerable period of time.

Among the hybrids, number 6-046 (*I. bracteata* $\times$ *I. munzii*) has shown the lowest percentage of viable pollen of any hybrid examined with an average of 83.6 percent. Both parental species are narrow endemics with *I. munzii* restricted to the low foothills of the Sierra Nevada in Tulare County, California, and *I. bracteata* to the shady ponderosa pine forests of Josephine County, Oregon, and portions of adjacent Del Norte County, California. Investigations are now under way to determine if possible the cause of the lowered pollen fertility shown by this hybrid. Vegetatively the plants are vigorous and strong growers but very little seed has been set by the plants when left for open pollination, but the seed that did set gave a high percent of germination. No seed was obtained when the plants were selfed.

SERIES *Californicae* $\times$ SERIES *Sibiricae*

The closest allies of the North American *Californicae* are the Eurasian *Sibiricae* (Dykes, 1913; R. C. Foster, 1937; Lenz, 1958), a group of about eight species distributed from central Europe eastward to the Himalayas, China and Japan. Cytologically they can be separated into two groups: *I. orientalis* Thunb. and *I. sibirica* L. with $2n=28$, and *I. bulleyana* Dykes, *I. chrysographes* Dykes, *I. clarkei* Baker, *I. delavayii* Mich., *I. forrestii* Dykes, and *I. wilsonii* C. H. Wright, all with $2n=40$. The majority of the 40-chromosome group are of Chinese origin, the exception being *I. clarkei* which comes from the Himalayas. The 28-chromosome group is more widely distributed, extending all the way from central and eastern Europe to Japan. Most of the members of the 40-chromosome group were introduced into cultivation during the late 1890's and the early years of this century, and hybrids between them and the *Californicae* were reported by Dykes beginning about 1912. Since that time a number of these hybrids have been recorded by other workers. The known hybrid combinations between these two series are shown in the crossing diagram (Fig. 2). Numerous interspecific hybrids have been produced between the various members of the *Sibiricae* but these are not shown. Figure 3 shows a flower of *I. chrysophylla* $\times$ *I. forrestii* which was produced by Joseph A. Witt at the University of Washington Arboretum. The two parental species are also shown in the figure. The early *Californicae* $\times$ *Sibiricae* hybrids were all between the 40-chromosome *Californicae* and the 40-chromosome *Sibiricae*, and hybrids involving the *Californicae* and the 28-chromosome *Sibiricae* were first reported by Lenz (1956).

Vigor of Hybrids.—From my own limited experience, and from information available in the literature it would appear that the F_1 hybrids which have been produced between these two related series are vigorous and many of them have been very floriferous and of considerable horticultural merit. In 1927 the British Dykes' Medal was awarded to 'Margot Holmes,' which was raised from a cross between *I. douglasiana* and *I. chrysographes*. An exception to the rule of floriferousness is the hybrids so far produced between the *Californicae* and the 28-chromosome group of Siberians; these plants, while vigorous, have been very reluctant bloomers at Claremont.

Fertility of Hybrids.—In all known instances hybrids between the *Californicae* and the *Sibiricae* have proven to be completely sterile regardless of the chromosome group involved.

NATURAL HYBRIDIZATION: POPULATION ANALYSIS

The person who first detected natural hybridization in the *Californicae* is not known. Dykes was an astute and careful observer of these plants but in his monograph of the genus (1913) he does not mention the possibility of natural hybridization taking place within the group. He was aware that it was possible to cross the species in the garden and in his monograph he mentioned hybrids which appeared in his garden between *I. bracteata* and possibly *I. douglasiana* or *I. tenax* since both species were growing near by. The next student of the group was R. C. Foster who fully recognized the fact that natural hybridization was occurring in the group and he detected and correctly annotated many of the hybrids which he found in herbaria. Clarkson (1955), working with the Oregon species, was able to show that natural hybridization was prevalent among the Oregon species. The present author's interest has been an attempt to determine the extent of hybridization within the group today and to determine if possible its role in the past and future speciation of the group. Figure 4 shows the naturally occurring interspecific hybrids which are known at the present time.

The concept of introgressive hybridization was first formulated by Anderson and Hubricht in 1938 and it was later admirably presented by Anderson in his *Introgressive Hybridization* (1949) and in subsequent papers (1951, 1953, 1954). The entire subject of natural hybridization and introgressive hybridization was reviewed by Heiser (1949). With the development of the concept of the pictorialized scatter diagram, workers in the field of experimental taxonomy and plant breeding were given a new tool which has proven to be of the utmost importance in the study of natural hybridization and introgression in many groups of organisms.

MATERIALS AND METHODS

In order to facilitate work, scoring sheets were prepared, mimeographed, and assembled in looseleaf notebooks for use in the field. Fourteen standard characters were measured or scored for each flower or flower stalk. In addition, depending upon the morphological characters present in a particular species, as many as six other characters were recorded; thus at times as many as 20 characters were scored for a particular plant. Two characters which have proven to be very useful are the perianth tube length and the maximum width of the outer spathe valve. In all the scatter diagrams in this paper, the perianth tube length has been used as the ordinate and the spathe valve width the abscissa, both measured in millimeters. The list of morphological characters recorded and the method used for scoring them have been given in an earlier paper (Lenz, 1958).

Wherever possible, 25 plants were measured from each population studied. Care was taken to secure only one flower stalk from a single plant or clone. Many of the *Californicae* have 2-3-flowered inflorescences (on unbranched flower stalks) and in order to assure as much uniformity as possible in selecting specimens for scoring, only the first flower in the inflorescence to open was used and, wherever possible, only a freshly opened but mature flower was taken. In most cases the scoring was done on the spot before the plant had a chance to wilt, but collections made late in the day were sometimes placed in containers of water in the refrigerator of the collecting truck and saved for scoring that night. A mass collection was made for the herbarium at the same time that the collection was made for scoring. In all types of measuring and scoring there is a personal element and the scores of two individuals working with identical material may be somewhat different. In order to reduce the personal element to the minimum all scoring in connection with this work was done by the author.

FIG. 2. Crossing diagram showing known garden hybrids between species belonging to the *Californicae* and the *Sibiricae*. Subspecific entities and direction cross was made not shown. Broken lines indicate sterile hybrids. Solid line circles indicate $2n=40$ chromosome species; broken line circles indicate $2n=28$ chromosome species. *Californicae*: BRA, *I. bracteata*; CHR, *I. chrysophylla*; DOU, *I. douglasiana*; FER, *I. fernaldii*; HAR, *I. bartwegii*; INN, *I. innominata*; MAC, *I. macrosiphon*; MUN, *I. munzii*; PUR, *I. purdyi*; TEN, *I. tenax*; TMA, *I. tenuissima*. *Sibiricae*: BUL, *I. bulleyana*; CLA, *I. clarkei*; CRS, *I. chrysographes*; DEL, *I. delavayii*; FOR, *I. forrestii*; ORI, *I. orientalis*; SIB, *I. sibirica*; WIL, *I. wilsonii*.

In connection with the use of the pictorialized scatter diagrams in studying natural hybridization, there is one factor which must be kept in mind. When a population of flowering plants is studied on a particular day and the flowers measured or scored and a scatter diagram prepared, the results tell us certain things about the population in bloom at the time that the study was made. A similar study made a week before or a week later may or may not give an identical picture. In the case of hybrids where there is even a slight difference in the date of peak of bloom of the parental species, the differences shown by the plants in a single population studied at different times may be considerable. In the California irises there is a difference in the date of peak of bloom in many of the species. In some of the populations studied the plants resembling one species would already be in early seed while those more like the second species were in peak bloom. Thus the scatter diagram would show the population as a

FIG. 3. F_1 hybrid between *I. chrysophylla* (Californicae) and *I. forrestii* (Sibiricae), center; *I. chrysophylla*, left; *I. forrestii*, right.

whole tending more toward the second species because it was impossible to score the plants which were past flowering. This in no way invalidates the system used but only skews, one way or the other, the population as plotted in the scatter diagram.

In the discussion of hybrids which follows, the specific names will be listed alphabetically in accordance with the rules of botanical nomenclature. No attempt will be made to discuss, or even to list, all localities where hybrids have been found. The known locations have been listed previously (Lenz, 1958), and future field work will undoubtedly turn up many new ones.

In some instances the hybrid populations have been given code names for ease in discussing the plants. These names are usually geographic and taken from a nearby

landmark and they should not necessarily be taken to mean the exact location where the population was found.

NATURALLY OCCURRING INTERSPECIFIC HYBRIDS

Iris douglasiana $\times$ *I. purdyi*.

Eel River Series.—One of the major drainage systems in north coastal California is that of the Eel River with its many branches and tributaries. The river flows in a northwesterly direction from its sources north of Clear Lake and west of the Yolly Bolly Mts. through the Coast Ranges and empties into the Pacific Ocean a few miles south of Humboldt Bay. In May, 1951, a study was made of the irises growing along the river from near its mouth to a point on the south fork of the river five miles south

FIG. 4. Known naturally occurring interspecific hybrids in the *Californicae*: BRA, *I. bracteata*; CHR, *I. chrysophylla*; DOU, *I. douglasiana*; FER, *I. fernaldii*; HAR, *I. hartwegii*; INN, *I. innominata*; MAC, *I. macrosiphon*; MUN, *I. munzii*; PUR, *I. purdyi*; TEN, *I. tenax*; TMA, *I. tenuissima*.

of Richardson Grove in northern Mendocino County, a distance of about 80 miles. Five stops were made along the highway (U.S. 101) which runs through this area and mass collections of irises were made and the plants scored. The area around the southern end of Humboldt Bay and inland about as far as Fernbridge is low and rather level with much of it in pasturage at the present time. Beyond Fernbridge the river enters, at first, a rather broad canyon which originally contained a typical redwood forest; farther along, the canyon narrows and in many places it is narrow and rocky. *Iris douglasiana* is abundant in many places in the Fortuna-Rio Dell area and the first mass collection of the species was made near Scotia about 15 miles inland

from the coast (Fig. 5-2). The second collection was made near Dyerville (Fig. 5-3), and the third stop was made near the top of the grade at Nelson's Grove (Fig. 5-4). The fourth collection came from an area on the inland side of the slope near Miranda (Fig. 5-5), south of the Nelson Grove collection. The final collection in this series (Fig. 5-6) came from five miles south of Richardson Grove in Mendocino County. These locations are shown on the map (Fig. 6).

Iris douglasiana is typically a coastal plant with broad dark green shining leaves and flower stems which are usually, but not always, branched. The flower stalks may bear 1-several cauline leaves but these are never inflated and they are free for most of their length. The inflorescence is normally 3-flowered and the stigmatic flap is triangular to tongue-shaped. *Iris purdyi*, on the other hand, is a native of the North Coastal Coniferous Forest,¹ the Mixed Evergreen Forest, and the Redwood Forest where it grows in areas of light to moderate shade at the edge of the forest or in somewhat open areas within the forest. The leaves are dark green to gray-green above and lighter beneath. They are both narrower and shorter than those of *I. douglasiana*. The flower stalks are never branched and, in the typical form of the species, are covered with short inflated or overlapping cauline leaves which only have their tips free. In this species the stigmatic flap is truncate or even bilobed and in this respect the species is unique in the *Californicae*. The morphological characters separating these two species are tabulated in Table 2.

TABLE 2

<i>Iris douglasiana</i>	<i>Iris purdyi</i>
1. Flower stem usually branched	Flower stem never branched
2. Stigmatic flap triangular or tongue-shaped	Stigmatic flap truncate or bi-lobed
3. Few cauline leaves and these never inflated or overlapping	Cauline leaves short, free only at their tips, overlapping and inflated
4. Capsule triangular in cross section, nipple-like projection at tip	Capsule more or less circular in cross section
5. Flower mostly lavender to purplish	Flowers on typical form a soft yellow

A study of the scatter diagrams for this series (Fig. 5-2-6) will show that as you proceed inland along U.S. 101, the plants which at Scotia appear to be typical of the maritime *I. douglasiana* give way to populations which show combinations of characters of both *I. douglasiana* and *I. purdyi*, and finally the Richardson Grove material would, on a taxonomic basis, appear to be more or less "good" *I. purdyi*. This population will, however, be discussed again later. The population of *I. douglasiana* studied at Scotia was small and so another population, one from near Orick (Fig. 5-1), is included for comparison. The Orick material was collected near the coast about midway between Eureka and Crescent City and is believed to be typical of the northern California form of that species.

The Eel River series, excluding the two species, *I. douglasiana* and *I. purdyi*, represents strictly roadside populations. The Eel River highway has in some places been cut through steep canyons and in other places through dense redwood forest and an examination of the surrounding areas shows that irises are rare or entirely absent

¹The plant community classification used is that worked out by P. A. Munz and D. D. Keck, *California Plant Communities*, El Aliso 2: 87-105, 199-202. 1949-1950.

FIG. 5-1

FIG. 5-2

FIG. 5-3

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 251.

FIG. 5-4

FIG. 5-5

FIG. 5-6

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 251.

except for those along the banks of the roadway where they may occur in great abundance. In much of the forested area on either side of the road, timber is so dense and the ground so covered with ferns and shade-tolerant associates that it would be impossible for the irises to either invade the area or to maintain themselves if they were initially successful in becoming established.

Mattole River Hybrids.—The Mattole River is a relatively small river which lies to the west and southwest of the Eel River and for much of its length runs in a north-westerly direction almost parallel with the Pacific Ocean. It lies inland from the beach from four to seven miles and is separated from the ocean part of the way by the Cooksie Ridge. The river empties into the Pacific about 2½ miles south of Punto Gordo in Humboldt County.

One of the finest hybrid swarms encountered in this study was discovered in flower in May, 1955, on a slope above the Mattole River between Petrolia and Upper Mattole (see Fig. 7). These plants were studied again in June, 1958, when they were in fruiting condition. The original forest cover in this area consisted of North Coastal Coniferous Forest which occupies an area between the Redwood Forest and the ocean. Here are found *Pseudotsuga*, *Umbellularia*, *Thuja*, and *Picea*. The Mattole Valley has been subjected to heavy logging and more recently to frequent burning in order to maintain grazing land for stock (see Fig. 8). Today many sheep ranchers occupy areas in the valley. *Iris douglasiana* is common along the immediate coast and inland along the lower stretches of the river. *Iris purdyi* is abundant farther inland, growing in the North Coastal Coniferous Forest and even more abundantly in the somewhat drier Mixed Evergreen Forest. The area studied consisted of a cutover hillside which still had growing on it a number of small groups of medium sized trees separated by broad areas of sunny slope. The irises were abundant in the area and a collection was made and scored (Fig. 9-2). Figure 9-3 shows plants of *I. purdyi* which were collected farther inland along Wilder Ridge, about seven miles from the Mattole River

SHORT CAULINE LEAVES

Present

Intermediate

Absent

SPATHE VALVES

50-73 mm.

74-97 mm.

98-121 mm.

STIGMAS

Truncate

Intermediate

Triangular

NUMBER OF FLOWERS

Two

Three

BRANCHING

Unbranched

Branched

Explanation for symbols used in Figs. 5, 1-6

hybrids. These locations are shown in Figure 6. The *I. purdyi* plants here were growing in abundance in lightly shaded areas in the Mixed Evergreen Forest and along the boundaries between the forest and the North Coastal Prairie which covers large areas within the forest (Fig. 10). The plants shown in the scatter diagram (Fig. 9-2) do

FIG. 6

not, however, give an entirely accurate picture of the population growing on the slope, the reason being that here *I. purdyi* blooms slightly earlier than does *I. douglasiana* and at the time that the collection was made the more *purdyi*-like plants were in early fruit and not available for scoring.

The hybrid nature of this population was clearly evident from the first but it was interesting to note that the more *douglasiana*-like plants were usually found in the open or unshaded areas whereas the more *purdyi*-like forms were in the more shaded

FIG. 7. Mattole River Valley looking upstream. The *I. douglasiana* $\times$ *I. purdyi* hybrids shown in Fig. 9-2 were growing just above bend in river left of center in picture.

FIG. 8. Near Honeydew showing cutover and grazed timber land.

FIG. 9-1

FIG. 9-2

FIG. 9-3

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 255.

FIG. 10. Mixed Evergreen Forest and North Coastal Prairie. *Iris purdyi* is abundant in the lightly shaded forest and on the boundaries between the forest and the prairie.

areas. In making the mass collection, care was taken to obtain a fair sample of the flowering plants of the entire area.

In June, 1958, the area was again visited and this time the plants were in fruit and

---

SPATHE VALVES	● 50-73 mm.	● 74-97 mm.	● 98-121 mm.
STIGMAS	● Triangular	● Intermediate	● Truncate
SHORT CAULINE LEAVES	● Absent	● Intermediate	● Present
BRANCHING	● Unbranched		● Branched
NUMBER OF FLOWERS	● Two		● Three

Explanation of symbols used in Figs. 9, 1-3.

FIG. 11. Maturing seed capsules of *I. purdyi* (top), *I. douglasiana* $\times$ *I. purdyi* from Mattole River (center), *I. douglasiana* (bottom).

a collection of the stalks with the maturing capsules was made for photographing (Fig. 11). The capsules of *I. purdyi* which are shown were gathered on Van Schoiack Ridge a few miles away. Since 1955, the locality where the hybrids were studied has been used as a sheep bedding ground because of the shade produced by the trees and the size of the capsules in the hybrid population may be partially due to the addition of fertilizer to the area.

In addition to the Eel and Mattole river series, hybrids between *I. douglasiana* and *I. purdyi* have been collected in a number of other areas (Lenz, 1958). The north coastal ranges in Mendocino and Humboldt counties have been the scene of great logging activity dating back to the middle of the last century and hybrids between these two species may be encountered in many places where human activity has altered the habitat sufficiently to allow the species to come together. In this hybrid combination an alteration in the amount of light has probably been one of the major ecological factors involved.

Iris douglasiana × *I. innominata*.

Rogue River Series.—Along the California-Oregon border is a complex and irregular group of mountains known collectively as the Klamath Mountains. Included within the system are a number of conspicuous ranges, the Rogue, Siskiyou, Scott, and Trinity, whose long axes tend more or less in an east-west direction, and the Salmon River Range whose axis tends to be north and south and at right angles to the other ranges. The Klamath Mountains are believed to be much older than either the Oregon Coast Range lying to the north, or the Coast Ranges of California to the south. Geologically their history is more complex than that of the Coast Range systems.

The Rogue River Range extends from its western terminus, which abuts on the Pacific Ocean, eastward across southwestern Oregon. The Rogue River which drains much of the area has in places cut narrow and steep gorges through the mountains on its way to the Pacific where it empties into the ocean near the town of Gold Beach in Curry County.

Iris innominata is a native of the Klamath Mountain System and is extremely abundant in places especially in the area of the Rogue itself, but also extending into other areas even as far south as northern California. The species was first discovered in the late 1920's and because of the extreme ruggedness of much of the terrain, even today the exact limits of the species are not known and avid horticultural collectors are yearly reporting new stations for the species. Essentially, it is a species of the inland area and according to Riddle (1948), except for one small area, the species is not found within sight of the Pacific Ocean. *Iris innominata* is one of the most delightful species in the *Californicae* with its narrow, deep green, grass-like foliage and relatively large attractive flowers which are usually some shade of yellow veined a darker color. At one time it was generally believed that the flowers of this species were never any color other than yellow. Partially on this basis, certain lavender forms found farther south have been called *I. thompsonii*. It is known today that this species does contain both yellow and lavender forms (Lenz, 1958).

The plants of this species are generally found in rather open places in fir and pine forests, in sunny meadows and on lightly shaded slopes. In favorable areas the plants become quite large and often produce several dozen flowers at a time on a single plant. Plants may, however, occasionally be found in somewhat more shady areas and there they remain relatively small and produce few flowers. If the timber is removed and the shade decreased, the plants within a short period of time increase greatly in size and floriferousness as well as in numbers. In general, the area where this species is

found has rocky porous soil which is well drained. The winter climate is cold with snow and the summers are hot and dry. In places the iris is associated with *Rhododendron macrophyllum*, *R. occidentale*, and *Xerophyllum tenax*.

Morphologically, *I. innominata* differs from *I. douglasiana* in a number of characteristics. These are tabulated in Table 3.

TABLE 3		
<i>Iris douglasiana</i>		<i>Iris innominata</i>
1. Stems usually branched		Stems never branched
2. Spathe valves lanceolate-acuminate, aver. 92 mm. long and 9.6 mm. wide		Spathe valves broadly lanceolate to ovate, aver. 45 mm. long and 5.5 mm. wide
3. Inflorescences 2- 3-flowered, usually 3-flowered		Inflorescences 1- 2-flowered
4. Flowers usually some form of blue or purple, yellow forms rare		Flowers usually some form of yellow, occasionally blue or purple
5. Capsule with distinct nipple-like tip		Capsule without nipple-like tip
6. Capsule distinctly triangular in cross section		Capsule not triangular in cross section
7. Leaves broad, as much as 2 cm. wide and 1 m. long		Leaves narrow and usually rather grass-like
8. Maritime species		Woodland species

Iris douglasiana is very abundant along the coast in Curry County and extends up the Rogue River for a distance of several miles where it is found in low-lying sunny pastures or meadows, or in lightly shaded woods if found at higher elevations in the hills.

In May, 1951, a trip was made to the Rogue River to study these irises and since that time the area has been visited rather regularly during the blooming season or early seed stage. One of the collections made in 1951 (Fig. 12-2) came from Squaw

OVARY LENGTH	 11-21 mm.	 22-31 mm.	 32-41 mm.
PEDICEL LENGTH	 7-22 mm.	 23-37 mm.	 38-52 mm.
NUMBER OF FLOWERS	 One	 Two	 Three
SPATHE VALVES	 33-52 mm.	 53-81 mm.	 82-120 mm.
BRANCHING	 Unbranched		 Branched

Explanation of symbols used in Figs. 12, 1-9.

FIG. 12-1

FIG. 12-2

FIG. 12-3

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 258.

FIG. 12-4

FIG. 12-5

FIG. 12-6

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 258.

FIG. 12-7

FIG. 12-8

FIG. 12-9

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 258.

Valley about 6-8 miles inland from the mouth of the Rogue and on the north side of the river. Here the plants were growing on a hillside in full sun. The plants were large with many flower stems and all the flowers were some shade of yellow with varying amounts of darker veining. According to a local informant, the irises which

FIG. 13

bloomed earliest were somewhat smaller in size and had narrower leaves than the ones then in flower. Figure 12-1 shows a population of *I. innominata* made at Iron Mt. some 30 miles away and used here for comparison with the Squaw Valley population. The area where these populations were studied is shown on the map (Fig. 13).

At the crest of the ridge, and several hundred yards from the *I. innominata* were several large clumps of what appeared to be typical *I. douglasiana* but these plants were not then in flower and according to the local guide the yellow-flowered irises would be gone before the purple ones came into bloom. It is interesting that here the *I. douglasiana* plants were growing in light shade rather than in full sun. Also in light shade, and only a short distance away from the *I. douglasiana* clumps, a number of plants were just coming into bloom and these showed indications of being of hybrid origin; the leaves were intermediate in width between the two and the flower color varied from yellow through light lavender to reddish-violet. The stems were all unbranched and each bore only a single flower in the inflorescence, a characteristic of the *I. innominata* plants in that area. For many years this region has been used for sheep grazing and the pastured hills are often enclosed by old stone fences. The owner, who had lived on the ranch for over thirty years, informed me that the yellow irises, i.e., *I. innominata*, formerly were rare in areas along the lower Rogue where they are common today.

The Doyle Ranch series (Fig. 12, 3-5) was collected from one large mountainside with Doyle #1 being located near the top of the ridge and at about 1000-foot elevation. Doyle #2 was collected half way down the slope, and #3 came from near the bottom and directly above a pasture. The pasture extended along the bottom of the canyon for about one mile to the river. *Iris douglasiana* is common here in the bottom-lands along the river.

The Doyle #1 material was growing on a rock-strewn hillside in a peculiar red soil. This particular population possessed the widest range of flower colors seen in the area and the fields of flowers resembled the experimental fields at Claremont as far as the color range was concerned. There were yellow, bronze, raspberry, mahogany, and violet-colored flowers in abundance. The population of Doyle #2 contained fewer flower colors, being mainly lavender, violet, cream and yellow whereas those of Doyle #3 near the bottom of the mountain side were all violet and blue-violet. In plant form and size these three populations favored *I. innominata*. They were mainly rather short-stemmed with narrow leaves and the stems were unbranched. This mountain side is nearly devoid of trees and shrubs as well as grass and the hills are marked by long stone fences built many years ago. According to the present owner, the ranch has been held continuously by his family since 1876 and during all these years it has been pastured regularly.

On the opposite side of the Rogue, i.e., the south side, a large population of plants were studied at Saunders Creek (Fig. 12-6) about three miles inland from the beach. The area here is lower-lying than the Doyle ranch and occupies a somewhat wooded area along the creek, with Douglas Fir, Umbellularia, etc. alternating with grassy slopes. The area was logged at one time. In this area the irises tend to be found in light shade to full sun, growing in soil relatively rich in humus. The population here is intermediate between *I. douglasiana* and *I. innominata*, the leaves varied from short and narrow to long and very broad; the flowers are nearly all lavender or bluish-lavender, and only a single yellow flower was seen. Large clumps of what was taken to be *I. douglasiana* were common in the area but they had not yet come into bloom. Many of the plants at both Saunders Creek and Doyle #3 would be similar to R. C. Foster's *I. thompsonii*.

Figure 12-8 shows a population studied near Carpenterville a few miles south of the Rogue River. This population was growing in a large pasture and some of the individual plants were as much as six feet in diameter. The flower color was light to medium lavender and no yellow-flowered forms were seen.

As in the case of the Louisiana irises where the fields of multi-colored hybrids became favorite localities for horticultural collectors, so too have the fields of hybrids in the lower Rogue River area become favored spots for collecting, and because of the destructive methods employed by a few persons, the finest hybrid populations in the area have been almost completely destroyed.

The most unusual feature of the situation along the lower Rogue is the fact that where *I. douglasiana* is found on the hillsides and slopes above the river, it is very often found in light shade. In the pasture lands near the mouth of the river it occurs in full sun where it normally grows. The reason for its restriction to the shade of trees on the hillsides here is believed to be edaphic. Many of the hills in this area have a very thin covering of soil which is of a red color. The open hillsides are not the result of logging but they were originally treeless. In the area where there are trees, and often plants of *I. douglasiana*, the soil is deeper and contains considerable humus.

Iris bracteata × (*I. ×thompsonii*)

Smith River Series.—The Smith River of Del Norte County, California, is a relatively short stream which drains much of the area of the south side of the Siskiyou Mountains. In general it flows in an east-west direction emptying into the ocean a few miles north of Crescent City and only a short distance south of the California-Oregon border. The canyon of the Smith River is one of the most picturesque in northern California and U.S. 199 follows it for a number of miles between Crescent City, California, and Grants Pass, Oregon. The road crosses the crest of the Siskiyou at Hazelview Summit (2435-feet elevation). Shortly after 1850, the northwestern corner of California, now Del Norte County, was the scene of great mining activity and large numbers of prospectors entered the area, at first in search of gold but later other minerals were also mined. Mining activity continues on a limited scale even today. The entire region is marked by the remains of old prospecting holes, mines, and ghost towns. The first road to be built between Crescent City and Waldo, Oregon, was completed in 1860. The bulk of the mining activity was gone by the 1880's, and for many years the road between the two towns was closed because of the cost of keeping it in repair.

Iris bracteata is native to the north slope of the Siskiyou and the type was collected at Waldo by T. Howell in 1884. The species is almost endemic to Josephine County, only getting over into Del Norte County, California, in a few places. This species is one of the most distinctive of all the Pacific Coast irises with large attractive flowers usually marked with reddish-brown lines. The plants produce relatively few leaves in each fan but they are unique in being stiff and a dark glossy green above and yellowish-green on the underside. The flower stems have short, more or less inflated, bract-like leaves and the flower stalks and leaf bases are colored a brilliant pink or red. Ecologically, *I. bracteata* is a plant of shady areas in the ponderosa pine forests, or if growing in cutover woodland it is usually found in the shade of bracken ferns and large shrubs. This species is one of the few in the *Californicae* for which no color is known except yellow.

Iris ×thompsonii was described by R. C. Foster (1937) from plants gathered near Douglas Park in Del Norte County and according to Foster, it is most closely related to the yellow-flowered *I. innominata* found farther north. Clarkson (1955) came to the conclusion that this taxon was possibly the result of hybridization between *I. douglasiana* and *I. innominata* with the characters which he associated with the species having become fixed by backcrossing of the hybrids to *I. innominata*. I have come to somewhat the same conclusion (see Lenz, 1958), but I also recognize certain purple-flowered plants in the Siskiyou Mountains as colored forms of *I. innominata* and not

of hybrid origin and I do not believe that the hybrids between *I. douglasiana* and *I. innominata* here represent a stabilized population which can now be given specific status.

The population shown in Figure 14-1 was growing in the Smith River Canyon where Myrtle Creek empties into the river. The population, in bloom at the time that the study was made, appeared to be quite "good" colored *I. innominata*. Again, large clumps of *I. douglasiana* were seen about two miles away and toward the ocean but they were not in bloom at the time that study was made. The population shown in Figure 14-2 came from an area nearly midway between Gasquet and Patricks creeks whereas those of Figure 14-3 were collected near Idlewilde still farther on. The *I. bracteata* plants shown in Figure 14-4 were collected at the state border about two to three miles north of the summit of the range. (See map, Figure 15, for the location of these stations.) As one travels up the Smith River Canyon, flower color changes are quite conspicuous with the flowers becoming increasingly more yellow as one approaches the Oregon border while at the same time the plants become more shade tolerant. Clarkson (1955) also studied the plants in this same area and I agree with him, "The transition between the two species is gradual. . . ." The plants shown in Figure 14-5 came from the type locality of *I. bracteata*, a few miles from those at the state line. A study of the population from Waldo and those from the state line will show that there are slight differences between the two. It would appear that those from the state line population, although they would pass as *I. bracteata* on a taxonomic basis, actually show some introgression. Figure 14-6 shows the means for the populations from the Smith River Canyon and the area as far as Waldo.

Iris douglasiana $\times$ *I. tenax*.

Langlois Hybrids.—*Iris douglasiana* reaches its northern limit along the coast south of Coos Bay, Coos County, Oregon. *Iris tenax* on the other hand is principally an inland species which reaches its southern limit somewhere in southwestern Oregon and is reported from both Coos and Curry counties. It is common in unshaded or lightly shaded areas, on hillsides, etc., and is very abundant in the Willamette and Umpqua Valleys. According to Clarkson (1955) it is not a species of the coniferous forests unless they have been logged and roads constructed.

Morphologically, *I. douglasiana* and *I. tenax* are quite different. In *I. tenax* the spathe valves are quite narrow and are separated, compared with the relatively broad and usually opposite ones found in *I. douglasiana*. In *I. tenax*, the perianth tube is much shorter than that found in *I. douglasiana*, the flower stem is never branched, and the inflorescences are very often one-flowered compared with the 2- 3-flowered ones in *I. douglasiana*. The capsules of *I. tenax* are not triangular in cross section and they do not possess the nipple-like tip of *I. douglasiana*. The leaves of *I. tenax* are narrow and slender and the plants deciduous. These differences are summarized in Table 4.

For the most part the ranges of these two species are allopatric and relatively few specimens have been seen which are considered to be of hybrid origin. The only hybrid population studied in the field was one found on the ridge above Langlois (see Fig. 16, 17) in extreme northern Curry County and about 14 miles from Bandon Beach, the locality of certain hybrid forms seen in the University of Washington Herbarium (Lenz, 1958). The population shown in Figure 18-2 was of obvious hybrid origin. Figure 18-1 shows a population of *I. tenax* collected near Veronia whereas that of *I. douglasiana* (Fig. 18-3) came from near Orick, California. The blooming season for the two species is somewhat different, with *I. tenax* here blooming earlier than *I. douglasiana*. At the time that the study was made, many of the

FIG. 14-1

FIG. 14-2

FIG. 14-3

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 268.

FIG. 14-4

FIG. 14-5

FIG. 14-6

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 268.

more *tenax*-like plants were already in early fruit and consequently the scatter diagram does not give a true picture of the population as a whole. This population was kindly shown me by Donald Stryker who told me that he knew of no other nearby area where *I. tenax* might be found. The history of this region is one of logging and grazing and this particular population came from a large sheep pasture.

TABLE 4

<i>Iris douglasiana</i>	<i>Iris tenax</i>
1. Spathe valves usually opposite, aver. 9.6 mm. in width	Spathe valves separated and divergent, aver. 4.1 mm. in width
2. Perianth tube 15-28 mm. long, aver. 22 mm.	Perianth tube 6-10 mm. long, aver. 8 mm.
3. Capsule triangular in cross section, nipple-like projection at tip	Capsule nearly circular in cross section, never with a nipple-like tip
4. Flower stem usually branched	Flower stem never branched
5. Inflorescences 2- 3-flowered, usually 3	Inflorescences 1- 2-flowered, never 3
6. Leaves rather broad, as much as 2 cm. wide, evergreen	Leaves quite narrow, 3-5 mm. wide, deciduous

Iris macrosiphon × *I. purdyi*.

Iris macrosiphon is a variable species widely distributed on the eastern slopes of the North Coast Ranges of California and in the low foothills of the western slopes of the Sierra Nevada as far south as Mariposa County. On the western side of the state it occurs as far south as Mt. Hamilton in Santa Clara County. Ecologically it is a species of sunny grassy hills, edges of woods, or even in lightly shaded spots within the woodland areas, and it is especially abundant in the Foothill Woodland, Northern Oak Woodland, and somewhat less common in the Mixed Evergreen Forest plant communities. This species possesses forms with distinct flower stems which

Explanation of symbols used in Figs. 14, 1-6.

may be up to 14 inches tall and others with stems so short that the flowers appear to be borne on the ground. Flower color is equally variable, the most common color being a blue-lavender or purple, but in central California around Lake Pillsbury and Clear Lake, yellow-flowered forms are common.

Iris purdyi has already been described. Geographically, the range of this species lies between *I. macrosiphon* on the east and *I. douglasiana* in the west. As mentioned previously, it is a species of the North Coastal Coniferous Forest and Redwood Forest

FIG. 15

where it grows in areas of light to moderate shade. The two species are well separated morphologically and the differences are tabulated in Table 5.

TABLE 5

<i>Iris macrosiphon</i>	<i>Iris purdyi</i>
1. Stigmatic flaps triangular or tongue-shaped	Stigmatic flaps truncate to bilobed
2. Spathe valves moderately broad, aver. 6.2 mm., never flushed with color	Spathe valves broad, aver. 10 mm., slightly inflated and often flushed with red
3. Flower stem with few cauline leaves and these free for about 1/2 their length, never inflated	Flower stem with several short, overlapping and inflated cauline leaves which are free only at their tips
4. Leaf bases usually colorless	Leaf bases usually pink or purple
5. Flower color usually bluish, purple, yellow known in Clear Lake area	Flower color pale yellow with conspicuous veining on falls, or whitish with pale pinkish lavender on falls
6. Sepals 39-68 mm. long, aver. 53 mm.	Sepals 55-88 mm. long, aver. 63 mm.

The morphological characters of *I. purdyi* listed in Table 5 are for the most part those of the type description. The illustration in Dykes monograph (Plate II), and that of Figure 30 in Part I of this study (Lenz, 1958) also belong here. When field work was begun in the spring of 1949 a special effort was made to collect *I. purdyi* because of its potential importance for horticultural work. Field trips into the areas where the species occurs usually ended in failure as far as finding plants which fit the original description. Later, plants were found which did match the description but the vast majority of the plants found in much of the area occupied by this species show certain morphological differences. Many of them do not possess the large attractive flowers associated with *I. purdyi* but rather they are pale creamy-yellow with a light pinkish-lavender wash on the falls; occasionally they are cream or creamy-yellow, again with a lavender wash, and the flowers are usually somewhat smaller than those of the yellow-flowered forms. The conspicuous inflated cauline leaves were usually lacking or, if present, were often separated rather than overlapping and only slightly inflated. For the most part, the stigmatic lobes were truncate or flattened across the top. The leaves and leaf bases were usually colored very much like the ones in the yellow-flowered forms. In recent work, the large yellow forms have usually been referred to as "typical" or "good" *purdyi*. The scatter diagrams (Fig. 19, 1-6) show two populations of *I. macrosiphon*, one from Willits (Fig. 19-1) in Mendocino County, and one from near Middletown (Fig. 19-2) in Sonoma County. One population of "good" *I. purdyi* is shown in Figure 19-6 from Honeydew in Humboldt County. The scatter diagrams of the "lavender" forms of *I. purdyi* are from near Xenia (Fig. 19-3) and Harris (Fig. 19-4), both in southern Humboldt County and from south of Richardson Grove in Mendocino County (Fig. 19-5). (See map, Figure 20, for the locations of these populations.) It will be noted that the main difference between the lavender series and the "good" *I. purdyi*, as shown in the scatter diagrams, is that the lavender forms tend to have narrower spathe valves and longer perianth tubes than do the yellow ones. From study of the plants in the field, as well as from the scatter diagrams, it would appear that the colored forms of *I. purdyi* shown here all show introgression of genes of *I. macrosiphon* into that species. Geographical distributions of the two species as well as ecological requirements of the two would

FIG. 16. Hills behind Langlois, Curry County, Oregon. *Iris douglasiana* $\times$ *I. tenax* hybrids in foreground.

FIG. 17. Another view of same area shown in Fig. 16. Iris in foreground.

support such an hypothesis. Garden studies have shown conclusively that hybrids between plants having pale yellow flowers and those with lavender or bluish-lavender flowers, do, in the F_2 and subsequent generations, show forms which are nearly white but with a faint lavender or pinkish-lavender wash over the surface of the falls. The ground color, whether pale creamy-yellow or nearly white, as well as the amount of overlying anthocyanin pigment is determined by the amounts of anthocyanin in the one parent and the depth of the yellow color in the other.

In 1939, Alice Eastwood described *I. landsdaleana* from an area south of Richardson Grove. In describing the species, she said that it approached *I. purdyi*, differing in the color of the flowers, in the obtuse segments of the perianth, and in the scale of the stigma. I have studied the plants in this area for several years and one population is shown in Figure 19-5. In general, they are quite similar to the other populations of the lavender *I. purdyi* except that a few showed stigmatic flaps which more nearly approached those of *I. macrosiphon* than did those from Xenia (Fig. 19-3) or Harris (Fig. 19-4). The cauline leaves were scored as being similar to *I. purdyi* but they were not as extreme as those of the large yellow-flowered forms of that species which were studied later. It is my opinion that *I. landsdaleana* represents an introgression of *I. macrosiphon* into *I. purdyi*.

Iris purdyi $\times$ *I. tenuissima*.

Willow Creek Hybrids.—*Iris purdyi*, which has been described in detail earlier, reaches the northeastern limit of its distribution in the mountains west of Willow Creek and east of Blue Lake in Humboldt County, California. *Iris tenuissima*, on the other hand, reaches its western limits in eastern Humboldt County, extending eastward to Shasta County and south to Butte County on the western slopes of the Cascades. *Iris tenuissima* is a distinctive species which in the past has for the most part been poorly understood and it has generally been included with the better known *I. macrosiphon* although there are good morphological features which separate the two. As pointed out earlier (Lenz, 1958), this species is actually more closely related to *I. chrysophylla* than to *I. macrosiphon*. In *I. tenuissima* the perianth segments are usually very narrow and widespreading and they are usually distinctly crisped. It is one of the most difficult of the *Californicae* when it comes to making herbarium specimens because the slender flower parts break so easily. The basic flower color is generally a creamy-white with very distinct dark markings on the sepals. This is one species of the *Californicae* in which little flower color variation is known. As in many of the other species, forms are known which have a distinct flower stem whereas

SPATHE VALVE LENGTH

●
50-73 mm.

●
74-97 mm.

●
98-121 mm.

NUMBER OF FLOWERS

●
One

●
Two

●
Three

BRANCHING

●
Unbranched

●
Branched

Explanation of symbols used in Figs. 18, 1-3.

FIG. 18-1

FIG. 18-2

FIG. 18-3

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 272.

FIG. 19-1

FIG. 19-2

FIG. 19-3

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 276.

FIG. 19-4

FIG. 19-5

FIG. 19-6

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 276.

others bear the flowers nearly at ground level. Ecologically it is a species of the dry, lightly shaded woods around the northern end of the Sacramento Valley. The principal morphological differences between *I. purdyi* and *I. tenuissima* are shown in Table 6.

TABLE 6

<i>Iris purdyi</i>	<i>Iris tenuissima</i>
1. Stigmatic flaps truncate or bilobed	Stigmatic flaps sharply triangular to tongue-shaped
2. Flower stems with short, inflated, overlapping leaves, free only at their tips	Flower stems with 1-3 leaves, but these not overlapping nor inflated and free for about 1/2 their length
3. Style crests narrowly ovate, not approaching the length of the style branch	Style crests linear, often nearly equal to the length of the style branch
4. Flowers usually fairly large, sepals 55-84 mm. long, flower parts not crisped	Flowers spreading, fragile, sepals narrowly lanceolate, 47-75 mm. long, flower parts crisped

The plants of *I. tenuissima* shown in the scatter diagram (Figure 21-1) were collected in dry sunny woods near Dedrich in Trinity County; those of *I. purdyi* (Fig. 21-3) came from near Honeydew in Humboldt County. The hybrids shown in Fig. 21-2 were collected in rather shady places just west of Willow Creek along Highway 299 in Humboldt County. *Iris tenuissima* is common in the woods all along the Trinity River as far east as Weaverville but as one leaves the river near Willow Creek and starts up the east slope of the Coast Range the vegetation soon becomes more dense and very shortly, *I. tenuissima* is left behind. Farther along, especially near the summit of the range, *I. purdyi* becomes very common. The hybrids shown in Fig. 21-2 came from near the bottom of the Coast Range but they were growing in a situation quite different from that normally occupied by *I. tenuissima*.

Iris bracteata × *I. chrysophylla*.

For the most part the distribution of these two species is allopatric but there is an overlap in southwestern Oregon where the two are both found growing within close proximity of one another. Where the two species are found in the same general area, those of *I. chrysophylla* will usually be found in full sun or very light shade whereas those of *I. bracteata* are usually found in shade. After studying the plants growing in

Explanation of symbols used in Figs. 19, 1-6.

FIG. 20

Josephine County, Oregon, Clarkson (1955) was of the opinion that distinct hybrids between these two species could not be clearly demonstrated and he reported that but one individual had been found which he pronounced to be of an intermediate nature.

After having studied the hybridization occurring between certain other species in the *Californicae*, I was impressed by the lack of hybrids between *I. bracteata* and *I. chrysophylla*. In the area between Cave Junction and Selma in Josephine County, populations of the two species will be found growing within perhaps a few hundred yards of one another, but I have never been able actually to find the two species growing intermixed and neither have I ever found what appeared to be a hybrid between the two. The only ecological factor which I was able to detect as being different is possibly the amount of sun which the plants received. However, the possibility of edaphic differences cannot be ruled out. The area is one which has been greatly disturbed by human activities and it is now difficult to tell whether the present distributions of the two species are not a recent development. These species were also found in close association along the Sanger Lake Road in Del Norte County, California, but again no evidence of hybridization was noted. Here the two species appeared to be restricted in their altitudinal range with *I. bracteata* being found as high as 3100 feet elevation with *I. chrysophylla* above it reaching at least 3700 feet. The season was too early to tell how much higher the species might go.

The form of *I. bracteata* found in the area between Kerby and Selma differs somewhat from the form of the species common near Waldo a few miles away in that it is a much smaller plant than those found at the latter locality. Originally it was thought that these plants might be of hybrid origin, but plants grown from seed collected from the small form have shown no segregation or variation when grown in the experimental garden where they have retained their small stature. In all respects except size, these plants appear identical with the rest of the species. After studying these same plants, Clarkson (1955) was of the opinion that they were of hybrid origin and he noted that they exhibited the narrow perianth parts of *I. chrysophylla* and that *I. chrysophylla* in the same area showed more yellow coloring than it did elsewhere. The length of the perianth tube is a very sensitive indicator for the detection of hybridity between species possessing long perianth tubes and those with short tubes. These two species approach the two extremes to be found in the *Californicae* with respect to perianth tube length, *Iris bracteata* having perianth tubes varying from 5-10 mm. in length, whereas those of *I. chrysophylla* are from 43-120 mm. long. The tube length in the small form of *I. bracteata* varied between 5-9 mm. and those of the large-flowered form between 8-10 mm.; those of *I. chrysophylla* growing near

---

STIGMAS

●	●	●
Truncate	Intermediate	Triangular

CAULINE LEAVES

●	●	●
Absent	Intermediate	Present

STYLE CRESTS

●	●	●
Narrow Ovale	Intermediate	Linear

Explanation of symbols used in Figs. 21, 1-3.

FIG. 21-1

FIG. 21-2

FIG. 21-3

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 278.

the small-flowered *I. bracteata* varied from 52-72 mm. in length compared with 55-73 mm. for the same species from near Jacksonville in Jackson County, an area well removed from any known locality for *I. bracteata*.

From the work of Clarkson, as well as my own work, it would appear that hybridization between these two species does occur at times but it is rare and no hybrid swarms have been discovered. The possible reasons for the absence of hybridization between these two species will be found in the general discussion of hybridization in the *Californicae*. Further investigations are needed to determine if possible the origin of the small form of *I. bracteata*.

Iris chrysophylla $\times$ *I. tenax*.

These two species tend to be sympatric in their ranges but with *I. tenax* extending farther north than *I. chrysophylla*. Ecologically, however, they inhabit quite different habitats, with *I. tenax*, a plant of unshaded areas, being especially abundant on the oak-covered hills of the Willamette and Umpqua Valleys (Clarkson, 1955). According to this same author, it does not enter the coniferous areas unless the region has been logged or roads built.

Iris chrysophylla, on the other hand, is an inhabitant of the open coniferous forests, being especially abundant in southern Oregon. Morphologically, the two species are well separated and these differences are shown in Table 7.

TABLE 7

<i>Iris chrysophylla</i>	<i>Iris tenax</i>
1. Perianth tube long and slender, 43-120 mm. long, aver. 57 mm.	Perianth tube short, funnel-form, 6-10 mm. long, aver. 8 mm.
2. Spathe valves 6-10 mm. wide, opposite, connivent	Spathe valves narrow, 3-5 mm. wide, separated and divergent
3. Flowers usually with rather narrow perianth segments	Flowers usually with rather broad flower parts
4. Flowers usually pale creamy-yellow to nearly white, distinctly veined	Flowers usually lavender, bluish, or purple, but yellows are known
5. Style crests much longer than broad, nearly entire	Style crests rounded, edges incised or dentate

Clarkson made a careful study of these species and he reports that hybrids between the two were found in several counties. I was able to study hybrids in the field at only two locations, both in Douglas County, Oregon. Near Brockway, one obvious hybrid was found which might have been an F_1 hybrid. The flower had a lavender wash over a cream-colored background and had the dark veining characteristic of *I. chrysophylla*. Spathe valves were opposite, as in *I. chrysophylla*, but somewhat divergent as in *I. tenax*. In *I. chrysophylla* the ovary gradually tapers into the perianth tube. In *I. tenax* there is an abrupt break between the two. The hybrid was quite intermediate between the two. This plant is shown in the scatter diagram (Fig. 22-1) along with populations of the two species collected in the same general area. In the scatter diagram, except for the perianth tube length and spathe valve width, the plant appears to favor *I. chrysophylla*. Actually this was not true, but according to the measurements used, it falls within the limits set for that species. However, in both the ratio of the style crest to the style branch and in sepal width, the hybrid was at the extreme of the range of *I. chrysophylla*. In the scatter diagram (Fig. 22-1), the means for the two species, *I. chrysophylla* and *I. tenax*, are shown as open circles. In the case of the former species it will be noted that the population at Brockway tends somewhat

toward *I. tenax*. This might indicate that there has been some introgression of genes of *I. tenax* into the population. In the case of *I. tenax* the population is so small that conclusions cannot be drawn regarding the possibility of introgression. Clarkson who has done the most intensive work on this hybrid combination reports that hybridization appears to be introgressive toward *I. tenax* and that plants of that species showed

FIG. 22-1

SPATHE VALVES

Separated

Opposite

RATIO: $\frac{\text{STYLE CREST}}{\text{STYLE BRANCH}}$

1-50

51-100

SEPAL WIDTH

20-30mm.

15-20mm.

Explanation of symbols used in Fig 22-1. ORDINATE: perianth tube length;
Abscissa: spathe valve width.

definite traces of *I. chrysophylla* for at least ten miles from typical *I. chrysophylla*. On the other hand, *I. chrysophylla* remained constant and no individuals were found which exhibited *I. tenax* characteristics. Clarkson concluded that this introgression has resulted in a considerable increase in the variability of *I. tenax* while *I. chrysophylla* has remained constant. It is interesting to note here, and perhaps significant, that in the case of the perianth tube length we are again dealing with near extremes in the *Californicae*. This same perianth tube relationship was pointed out earlier in connection with *I. bracteata* and *I. chrysophylla*.

Iris hartwegii $\times$ *I. macrosiphon*.

Iris hartwegii is a distinctive little plant native to the Yellow Pine Forest in the Sierra Nevada where it occurs at altitudes of from about 2000 feet in the north to 5000-6500 feet in the south. In this species, flower color may vary from a rather light lavender color to deep bright yellow, a similar range to that shown by at least four other species in the *Californicae*. *Iris macrosiphon*, as pointed out earlier, is a widespread and variable species occurring in the foothills and lower mountains on both sides of the Great Valley of California. On the east side of the Valley it ranges from Mariposa County north to Butte County. Here it is found in the low foothills of the Sierra Nevada where the plants are usually found in the Foothill Woodland plant community at altitudes of from near 1000 feet to as much as 2500 feet near Nevada City, always at an altitude lower than where *I. hartwegii* is found although, as will be mentioned later, the two approach one another in cutover woods in some areas. Occasionally this species will be found in a mixture of Chaparral and Foothill Woodland, but it is seldom if ever found growing in pure Chaparral.

Morphologically, these two species are readily distinguished. The major differences are shown in Table 8.

TABLE 8

<i>Iris hartwegii</i>	<i>Iris macrosiphon</i>
1. Spathe valves separated and divergent	Spathe valves opposite and connivent
2. Perianth tube short, aver. 7.8 mm., thick	Perianth tube long, aver. 53 mm., slender
3. Pedicel variable but usually quite long, aver. 47 mm.	Pedicel variable but usually quite short, aver. 9 mm.
4. Flower color usually soft yellow but lavender forms are common in some areas, deep yellow forms rare	Flower color of forms on east side of Valley never other than lavender, sometimes quite pale

During the course of this investigation, the Sierran area has been studied intensively over a period of years but I have never seen a plant which I considered to be a distinct hybrid intermediate between these two species. However, I have seen three herbarium sheets with plants which were undoubtedly of hybrid origin. These plants had been collected in El Dorado and Placer counties. One specimen had been gathered by G. T. Benson one mile north of Camino in El Dorado County. This specimen, deposited in the Dudley Herbarium, shows a plant which would appear to be, possibly, a first generation hybrid. The second plant was collected by C. F. Stone in 1891 at Auburn in Placer County. Morphologically, this specimen appears to be more closely related to *I. macrosiphon* than to *I. hartwegii*, and it may represent a back cross to the former species. A third specimen collected by W. S. Shockley at Georgetown appears to be more like *I. hartwegii*.

The area around Placerville, formerly known as Hangtown, has been the scene of

great mining and lumbering activity ever since gold was discovered in 1848 at Sutter's Mill (now Coloma), a short distance from Placerville. Since 1849, the entire region has been disturbed time and again, and today much of the area consists of the remains of cutover woodlands, some of it with second and third growth trees. Interspersed throughout the area are numerous small farms and orchards. It is in this region that *I. hartwegii* and *I. macrosiphon* are found within close proximity of one another, *Iris hartwegii* in light shade and *I. macrosiphon* on the sunny road banks and hillsides, or even occasionally in light shade as it is along the roadsides between Placerville and Coloma. Figure 23-2 shows one population of *I. hartwegii* studied between Placerville and Camino and probably only two or 2½ miles from where Benson collected his hybrid specimen previously referred to. A photograph of the area where these plants were growing is shown in an earlier paper (Lenz, 1958; Fig. 15). For comparison is a population of the same species from near Colfax (Fig. 23-1). The *I. macrosiphon* populations shown were collected at Nevada City (Fig. 23-3), and in Mariposa County (Fig. 23-4).

The population of *I. hartwegii* collected between Placerville and Camino is unique in two respects: seven out of the 24 plants had opposite spathe valves and the average perianth tube length was 10.3 mm. with one plant having a tube 17 mm. long. The average tube length of this population is greater than any other population of the species which has been studied. While the evidence presented is certainly not conclusive, it does suggest the possibility of an introgression of genes of *I. macrosiphon* into *I. hartwegii* in this particular population. As has been brought out before, in crosses between plants with long perianth tubes and those with very short ones, tube length is a very sensitive indicator of hybridity. At least two of the plants from the Placerville collection show perianth tubes longer than those found in any of the other plants of this species which have been scored. The opposite spathe valves are also unusual for *I. hartwegii* and it is a character which could have been derived from *I. macrosiphon*.

If it is assumed that there has been an introgression of genes of *I. macrosiphon* into *I. hartwegii* at least locally in the Placerville area, the question arises of whether there are any indications of the reverse process, i.e., introgression of *I. hartwegii* into *I. macrosiphon*. Evidence for this occurring is perhaps even less conclusive and is almost entirely dependent upon differences in perianth tube length and pedicel length in populations of *I. macrosiphon* growing on the east side of the Valley compared with those growing on the west side. In the species with long perianth tubes, *I. macrosiphon*, *I. tenuissima*, and *I. chrysophylla*, what appears to be natural variation in tube length is greater than in those species with very short perianth tubes where the variation is not very great. Scatter diagram (Fig. 23-5) shows a population of *I. macrosiphon* from near Middletown and Fig. 23-6 one from Clear Lake Park, both from the west side of the Valley and both believed to represent "pure" *I. macrosiphon*. Figure 23-3 and Figure 23-4 are two populations already referred to from the east side of the Valley. As will be seen, the major difference between the two groups is in the length of the tube. Average for all populations studied of *I. macrosiphon* from the west side was 52.4 mm. for tube length and 9.3 mm. for pedicel length. For the east side it was 38.2 mm. for tube length and 16.8 mm. for pedicel length. It should be pointed out that in general in natural populations, tube length and pedicel length vary inversely. However, in garden studies it has been shown that these characters can vary independently and many plants have been grown which had short perianth tubes and short pedicels. The flowers of such plants very often fail to open properly because the perianth segments are held firmly together by the spathe valves. In nature, such plants would set little or no seed because they could not be pollinated and this

FIG. 23-1

FIG. 23-2

FIG. 23-3

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 286.

FIG. 23-4

FIG. 23-5

FIG. 23-6

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 286.

genotype would eventually be eliminated from the population. Plants with very long perianth tubes and very long pedicels have not been observed either in the field or in the experimental garden.

Iris fernaldii × *I. macrosiphon*.

Although these two species are closely related and, until R. C. Foster's study of the group both had been included under *I. macrosiphon*, there are distinct differences between them. These differences are tabulated in Table 9.

TABLE 9

<i>Iris fernaldii</i>	<i>Iris macrosiphon</i>
1. Leaves 7-8 mm. wide, up to 4 dm. long; peculiar gray-green color which is retained on drying, leaf bases usually colored	Leaves up to 5 mm. wide, green or glaucous, leaf bases usually colorless
2. Upper portion of perianth tube usually (but not always) enlarged to form a distinct throat	Upper portion of tube bowl-like, never with a dilated throat
3. Flower color pale creamy-yellow with darker veining	Flower color extremely variable, purple to bright yellow
4. Plants growing in light to moderate shade in mixed woods	Plants of sunny and grassy slopes, seldom in shade

Flower color in general is not a dependable character in the majority of the *Californicae*, but in the case of *I. fernaldii* no color is known except a soft creamy-yellow. *Iris macrosiphon*, on the other hand, is a species with a wide range of colors, all the way from deep purplish-blue through lavender to yellow. In the type locality, plants of *I. fernaldii* show large amounts of anthocyanin pigments on the leaf bases and usually on the spathe valves as well. *Iris macrosiphon* normally has colorless leaf bases and there is never any color on the spathes.

Ecologically, *I fernaldii* grows in areas of greater shade than does *I. macrosiphon*, but it is now difficult or impossible to assign either species to distinctive plant communities in the Sonoma-Lake-Napa counties area because of the long and continued disturbance to the area by human occupation.

Distinctive hybrids between these two species, while somewhat more difficult to detect than many other hybrid combinations, have, however, been found in several areas. One such hybrid population was studied in an area eight miles south of the Lake-Napa County line, in Napa County along California state highway #29. The plants here were growing in shade on dry wooded slopes in what now appears to be a yellow pine forest. Flower color in this population showed a range of colors similar to an F₂ population produced in the experimental garden between a lavender *I. macrosiphon* and the pale yellow *I. fernaldii*. Yellow color tends to be dominant to anthocyanin and the population studied showed a wide range of creamy-yellow flowers

PEDICEL LENGTH

●
41-60mm.

●
21-40mm.

●
0-20mm.

SPATHE VALVES

●
Separated

●
Opposite

Explanation of symbols used in Figs. 23, 1-6.

as well as those of creamy-yellow with lavender veining or lavender wash over the falls. A few were very similar in color to a light form of *I. macrosiphon*. Most of the plants had the distinctive perianth tube associated with *I. fernaldii* and the leaves, although somewhat narrow for that species were of the gray-green color found in *I. fernaldii*. There was basal leaf coloring on the plants here but it was not as intense as that found in *I. fernaldii* from the Petrified Forest area only a few miles away.

A second hybrid population between these species was observed near Mt. St. Helena in Sonoma County. In this area the plants were growing on very steep slopes in a mixture of Chaparral and Yellow Pine Forest and in appearance these plants were similar to those studied earlier.

In addition to the two hybrid populations reported here, many other populations have been studied in the Sonoma-Napa-Lake counties area which would appear to be hybrids between these two species. Taxonomically it is impossible to assign them to either species and because of their prevalence in the area it was thought for a time that *I. fernaldii* only represented one facies of the more prevalent and better known *I. macrosiphon*. However, after seeing *I. fernaldii* in what is believed to be a rather "pure" form in the area of the Petrified Forest the intermediate character of many of the other forms became evident. According to Sweeney (1956), this entire area has been subjected to repeated burning over a period of many years with the result that the original vegetation has been either destroyed or greatly altered. As this author points out, one of the major changes brought about by a fire is the increase in the amount of light reaching the ground. Since amount of light is one, if not the most, important factor governing the distribution of these two species, it might be argued that original distribution of these plants may have been quite different from what it is today. The role of fire as a factor in natural hybridization of these irises will be discussed later.

The Santa Cruz Irises.—One of the most difficult groups of irises studied during the course of this investigation was of those native to the Santa Cruz Mountains and nearby areas.²

The region is today one of high population density and the land has been subjected to intensive logging, clearing, burning, planting, and urban development, with the result that little remains of the original vegetation. Within this general area there are three species of Iris: *I. douglasiana* along the coast and inland for short distances, and farther inland, *I. fernaldii* and *I. macrosiphon*. Figures 24, 1-3 and 24-6 show four populations studied within the general area. Figures 24-5 and 24-4 show populations of *I. macrosiphon* from near Boonville, Mendocino County, and *I. fernaldii* from near Calistoga. These are included as being representative of what is believed to be "pure" forms of these species. One of the most distinctive differences between many of the *fernalddii*-like plants from the Santa Cruz area and those from the type locality is the lack of any color at the base of the leaves in the former. Very few of the plants found in the Santa Cruz area show any coloring, but in other respects they are typical of the species, possessing the peculiar leaf color and dilated throat of *I. fernaldii*. The population of *I. douglasiana* shown in Figure 24-6 was collected along Coyote Creek about 4½ miles inland from the beach between San Gregorio and La Honda in San Mateo County. These plants appeared to be more or less typical of the species with the exception that one of them has a dilated throat which is not characteristic of *I. douglasiana*, and a number of the plants lacked stem branching. The latter

²The term, Santa Cruz Mt. area, is here used in the sense of that of the Division of Forestry, State of California, and includes the area from Half Moon Bay south along the coast to the vicinity of Watsonville and on the inland side from San Mateo south to Gilroy.

FIG. 24-1

FIG. 24-2

FIG. 24-3

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 290.

FIG. 24-4

FIG. 24-5

FIG. 24-6

ORDINATE: perianth tube length; ABSCISSA: spathe valve width. Explanation of symbols, page 290.

character, although very frequently found in this species, may be absent in some populations. The Boulder Creek population (Fig. 24-1) was collected about four miles out of Boulder Creek on the road to Big Basin Redwood State Park. These plants all possessed creamy-yellow flowers with varying amounts of lavender veining or lavender wash on the falls. There was no anthocyanin pigment on the vegetative portions of the plants and a few of the flowers lacked the *I. fernaldii* throat. This population appeared to be a roadside group and no plants were observed more than a short distance back from the roadway. The area is quite heavily wooded and the light relationship may be an important factor here in the distribution of the plants. This area was at one time probably redwood forest. Today there are scattered redwood trees, *Quercus chrysolepis*, and madrone.

The Eagle Rock population (Fig. 24-2) was unique in several respects. Looking over the population as a whole, the flower colors were similar to a large F_2 population of a cross between a pale yellow and a medium dark lavender flower. The individual plants were very large and scattered over several acres of sunny to lightly shaded ground. The leaves in general were too broad for either *I. macrosiphon* or *I. fernaldii*. One of the most interesting things about this population was the presence of stem branching in a few of the plants and the occurrence of three flowers in an inflorescence in others. So far as is known, neither of these characters could have come from any species in the area except *I. douglasiana*. The broadness of the leaves likewise could have come from this same source. As can be seen in the scatter diagram (Fig. 24-2), the spathe valve width tends toward *I. douglasiana*. Most of the plants had the *I. fernaldii* throat but in a few it was somewhat intermediate. None of the plants had any basal coloration. The exact area where this population was collected was one mile east of Eagle Rock Lookout which is at 2250-foot elevation and inland about eight miles from the beach.

It is my opinion that many of the irises found today in the Santa Cruz area are hybrids between two or more of the three species which are known to occur in the area. In populations such as the one of *I. douglasiana* from La Honda, it is impossible to say whether the lack of stem branching in a few of the plants, or the occurrence of two-flowered inflorescences represents introgression of genes of one of the other two species into *I. douglasiana*, or whether they are characters inherent to that population. The presence or absence of color at the base of the leaves is a character that in several of the members of the *Californicae* can only be said to be generally present or gen-

Explanation of symbols used in Figs. 24, 1-6.

erally absent. In *I. macrosiphon* it is generally absent; in *I. fernaldii*, from the type locality, it is generally present as it is in the case of *I. douglasiana*.

SPECIATION

The family Iridaceae is undoubtedly of Old World origin and the family is very highly developed in Africa. The large genus, *Iris*, which is widespread throughout the northern hemisphere, finds its greatest development in Europe and Asia with a lesser representation of species in North America. According to Lawrence's (1953) reclassification of the major units within the genus, the *Californicae* constitute one series of the subsection *Apogon*, of the beardless and rhizotamous irises (sect. *Spathula*). Within the *Apogon* subsection there are thirteen series. Of these, the New World *Californicae* appear to be more closely related to the Old World *Sibiricae* than they are to any other group. The latter have a distribution extending from France westward to China and Japan. The *Californicae* on the other hand are restricted to the three west coast states: California, Oregon, and Washington. It would appear that the prototypes of the present day *Californicae* probably reached the west coast of America by way of the Bering Strait and then spread southward reaching their present position, perhaps after the beginning of the formation of the Sierra Nevada-Cascade axis since they are completely unknown from any area to the east of these ranges. Within the youthful and extremely varied terrain of the Pacific Coast, with its large number of distinctive ecological niches, the irises became adapted to specific habitats and later became reproductively isolated populations within the various plant communities. Speciation of this type, i.e., ecological isolation of sympatric species, is rather common in plants and it has played an important role in several other Western American genera, among them *Ceanothus*, *Diplacus*, *Aquilegia*, and *Quercus*.

THE SHORT PERIANTH TUBE COMPLEX

Within the *Californicae* there are species groups which may be clearly recognized on a morphological basis. The most clearcut of these is the *I. tenax-hartwegii-munzii* complex which is separated from the remaining *Californicae* by the presence of separated and divergent spathe valves as opposed to the opposite and connivent spathe valves in the other species. This group is characterized also by the presence of very short but relatively broad perianth tubes. The only other member of the *Californicae* having a short perianth tube is *I. bracteata* which appears to have no special affinity with any of the other members of the series. *Iris tenax* and *I. hartwegii* are allopatric species, the former native to western Oregon and north to west central Washington whereas the latter is a species of the western slopes of the Sierra Nevada in California. Morphologically the two are quite distinct. *Iris tenax* has narrower spathe valves than *I. hartwegii* and it is usually caespitose with light green leaves which are of a softer texture than those of *I. hartwegii*. The latter is seldom caespitose and the leaves are often quite glaucous and somewhat harsh to the touch. The flower form of the two species is quite different, *I. tenax* usually having broader perianth segments than *I. hartwegii*. The seeds of the two species are also somewhat different. Ecologically, the two grow in very different types of habitats. *Iris tenax* is found in sunny open situations. According to Clarkson (1955), it does not extend into the coniferous forests unless the trees are cut and light admitted. *Iris hartwegii* on the other hand is native to the yellow pine forests of the Sierra Nevada where it occurs at middle altitudes of from 2000 feet in the north to about 6500 feet in the south. It is usually found growing in light shade although if the forest is cut it will continue to persist on rather sunny slopes. Both species are deciduous and both possess an array of flower color from lavender to purple to yellow. In the past, certain yellow-flowered forms

of *I. tenax* have been given specific or varietal status and have been known as *I. gormanii* or *I. tenax* var. *gormanii*. In the latest treatments of the group (Clarkson, 1955; Lenz, 1958), they are included within the limits of the species itself.

Iris hartwegii subsp. *australis* occurs mainly in the San Bernardino Mts. of southern California where it grows in a habitat similar to that of the species. It has also been reported in the San Gabriel Mts. and the San Jacinto Mts., but its presence in the latter range is doubtful. The taxonomic disposition of these plants has been the subject of greater disagreement than any other taxon in this series. R. C. Foster (1937) considered the plants as a variety of *I. tenax*, but in doing so he overlooked certain consistent morphological differences as well as the differences in their ecological habitats. On the other hand, *I. hartwegii* and *I. hartwegii* subsp. *australis* are certainly very much alike and their ecological habitats are the same. Geographically they are separated by a distance of about 125 miles. The San Bernardino Range where *australis* is so abundant is a vast fault block about 80 miles long and 30 miles wide which extends in a southwesterly direction across southern California. The block is cut off on all sides by faults and is partially surrounded by the Mojave Desert. According to geologists, the surface represents an old worn-down landscape which has been elevated to its present position by faulting. Chaparral covers the lower slopes of the range with vast areas of yellow pine forest above. It is in the yellow pine forest that *australis* is found. Morphologically these plants differ from *I. hartwegii* in having spathe valves which average 7.9 mm. in width compared with 5.2 mm. for the species. Pedicel length, although variable, averages 47 mm. for *I. hartwegii* and 28 mm. for *australis*. The flower color of *australis* is a deeper purple than any known form of *I. hartwegii*. In general, there is less plant to plant variation within *australis* than there is in *I. hartwegii* or indeed less than in many of the *Californicae*. Certainly *I. hartwegii* and *I. hartwegii* subsp. *australis* are very similar and the present *australis* probably represents what was once the southernmost extension of a more or less continuous distribution of the species. When the San Bernardino fault block was lifted, these plants became isolated and the slight differences existing today between *I. hartwegii* and the subspecies probably developed since that time.

Iris munzii is a large and distinctive species which is endemic to Tulare County where it is found in the foothills of the Sierra Nevada. This species clearly belongs to the *I. tenax-hartwegii* complex and in plant size it is the largest of all the *Californicae* with flower stems as much as a meter tall and leaves often almost as long and up to 2 cm. wide. The leaves of this species are a distinctive blue-green color and the flowers vary in color from light lavender to medium reddish-purple. Another distinctive character of this species is that the unbranched inflorescence has three or even four flowers compared with one or at the most two for all the other members of the complex (*I. hartwegii* subsp. *columbiana*, an exception, will be described later). Ecologically, this species is found in lightly to moderately shaded and fairly moist areas on hillsides and near stream bottoms within the Foothill Woodland plant community along with such plants as Digger Pine (*Pinus sabiniana*), Blue Oak (*Quercus douglasii*), California Buckeye (*Aesculus californica*), and Redbud (*Cercis occidentalis*). The altitude here does not exceed 2600 feet and the climate is relatively mild and wet during the winter and hot and dry during the summer. Citrus groves are common in the area only a short distance away and at a slightly lower elevation. In cultivation *I. munzii* appears to be the least cold tolerant of the *Californicae*. In the Tule River area, the Foothill Woodland is separated from the Yellow Pine Forest, the habitat of *I. hartwegii*, by a band of Chaparral. The two species occur within perhaps three miles of one another but in different plant communities separated by still

a third community and one in which irises are not ordinarily found. Within the range of its distribution in Tulare County, *I. munzii* is found in the same narrow altitudinal range on all three forks of the Tule River as well as on Bear Creek, a tributary of the north fork. The total altitudinal range of this species is probably not more than 1200 feet. It is also known to occur on the Kaweah River, also in Tulare County, and the first major drainage system north of the Tule. The natural occurrence of the species in this watershed is open to question since it is known that seeds of the species were distributed along the Kaweah a number of years ago (Lenz, 1958). From its known distributional range and ecological requirements, it would appear that *I. munzii* today represents a relictual species which was perhaps more widely distributed at an early and more mesic period and as the interior of California became progressively drier, the species became more restricted and today it is found in only a few spots where it has suitable conditions for growth. Within the present populations seedlings are found but there is no evidence that the species is extending its range at the present time. In cultivation, *I. munzii* has proven to be a very vigorous species and is being widely used in the horticultural breeding program at the Rancho Santa Ana Botanic Garden.

Growing in a small area high above the south fork of the Stanislaus River in Tuolumne County, California, is a group of plants obviously belonging to the *I. tenax-hartwegii-munzii* complex and in many ways quite intermediate between *I. hartwegii* and *I. munzii*. These plants, so far as is known, are confined to an area of not more than two or three miles in extent between Five Mile Creek and Italian Bar. This area is well known to botanists but apparently the irises have only been collected a few times. The only herbarium material which I have seen is two collections in the Jepson Herbarium made in 1915 and 1916 (Lenz, 1958). In 1956 I visited the area and studied the plants while they were in bloom and in 1958 the area was again visited for the purpose of collecting seed. These plants were subsequently described as *I. hartwegii* subsp. *columbiana* (Lenz, 1958), the subspecific epithet being taken from one of the historic Mother Lode mining towns near where the plants were found. Morphologically, the plants of *columbiana* are remarkably similar to a population of hybrids grown in the experimental garden from a cross between *I. hartwegii* (♂) and *I. munzii* (♀). In this cross the pale yellow flower color of *I. hartwegii* is dominant to the relatively pale lavender of *I. munzii* and the 3-flowered inflorescence of *I. munzii* is nearly completely dominant to the 1-2-flowered inflorescences of *I. hartwegii*. In *columbiana* the flowers are pale yellow and for the most part have 3-flowered inflorescences. There is, however, some variation in the population in this respect. The foliage of *columbiana* more nearly approximates that of *I. hartwegii*, especially vigorous forms of that species.

As has already been pointed out, *I. munzii* and *I. hartwegii* are well isolated ecologically and no evidence of hybridization or introgression has heretofore been detected between the two species. Geographically, *I. hartwegii* and *I. hartwegii* subsp. *columbiana* are found in the same general area, although *columbiana* is found at 2000-foot elevation, an altitude somewhat lower than where *I. hartwegii* may be expected, especially in an area as far south as Tuolumne County. The area nearest the Five Mile Creek-Italian Bar locality where I have seen *I. hartwegii* is in the vicinity of Twain Harte and Long Barn where the elevations are approximately 4000 feet and 4900 feet respectively. This area is about seven to ten miles from Italian Bar. The terrain here is extremely rugged with deep, steep-sided canyons, and populations of *I. hartwegii* may well occur closer to *columbiana* than this. *Iris munzii*, on the other hand, is much farther removed from the Italian Bar plants and the nearest populations today are about 140 miles away.

No two members of the *Californicae* are more specific in their ecological requirements than are *I. hartwegii* and *I. munzii*, being restricted to the Yellow Pine Forest and Foothill Woodland plant communities respectively. If *columbiana* arose as a hybrid between those two species, as seems probable, then it might be expected to occur in an intermediate habitat, and that is exactly where it is found. The hillsides between Five Mile Creek and Italian Bar are composed of a mixture of Foothill Woodland and Yellow Pine Forest. About a century ago, this area was the scene of great mining activity and Columbia, about five miles away, was at one time the largest mining camp in California. Italian Bar was one of the many smaller communities scattered around the central town itself and the present narrow mountain road leading into the area may well follow the same route used during mining days. Today no trace remains of the buildings that once marked the location of Italian Bar, and the village of Columbia, because of its historical significance, has been set aside as a state park. The entire Sonora-Columbia landscape was altered by mining operations and a recent author (Rensch and Hoover, 1933) had the following to say: "From an area of three hundred acres on the outskirts of the town, millions of dollars in gold were washed out, leaving a vast expanse of fantastic, ghost-like rocks partially hidden today by small trees and bushes which have grown up among them."

If *columbiana* does represent the results of an earlier hybridization between *I. munzii* and *I. hartwegii*, there are two possible alternatives in explaining how this hybridization could have taken place, one explanation being that *I. munzii* was at one time native to the Columbia area but has since disappeared, the other being that seeds or plants of *I. munzii* were carried to the area either intentionally or unintentionally. From what is known today of the spotty distribution of that species, it is not unfeasible that it might in the past have had a distribution farther to the north. Ecologically there would appear to be many areas along the foothills of the Sierras where it might have found suitable habitats. If the area along the Tule River where it is found today, had been the scene of as much mining activity as has the Columbia region, it is quite possible that the species would have disappeared from there. The second alternative, that of the species having been carried to the Columbia region within historic times, cannot now be proven or disproven. It is known that there was much travel all along the foothills of the Sierras during the latter half of the past century and seeds might well have been accidentally carried along. The possibility of the intentional introduction of the species cannot however be ruled out. *Iris munzii* is a large-flowered and attractive iris and we do know that there was an intentional attempt to introduce the species into the Kaweah River system. Another possibility is that *columbiana* represents an ancestral type from which *I. hartwegii* and *I. munzii* have evolved. If this were true, then the habitat of *columbiana* might be considered ancestral and to have given rise to yellow pine forest on the one hand and foothill woodland on the other. There is no evidence that this has occurred and the mixed habitat can best be explained as having arisen as a response to disturbance by mining operations.

Iris hartwegii subsp. *pinetorum* was originally described as *I. pinetorum* by Alice Eastwood from plants collected at Forest Lodge near Greenville in Plumas County, California. During the past few years this area has been visited a number of times and the plants have been studied at the type locality as well as in other nearby areas, all, however, within the Greenville-Lake Almanor region. These plants were found to bear a striking resemblance to both *I. hartwegii* and *I. tenuissima*. In her original description, Eastwood noted its similarity to *I. tenuissima* but considered that it was perhaps nearer *I. californica* (= *I. macrosiphon*). R. C. Foster was able to examine only the type specimen but he noted the narrow, divergent, and separated spathe valves which were similar to those of *I. hartwegii*. He also noted, however, its similar-

ity to *I. tenuissima* and he further postulated a possible hybrid origin for the plant. After several years of study of the plants, I am of the same opinion as Foster on its possible origin through hybridization between *I. hartwegii* and *I. tenuissima*. In the character of the spathe valves it is similar to *I. hartwegii*; the perianth tube is intermediate between the two but nearer that of *I. hartwegii* in length; in the character

FIG. 25. Map showing county distribution records for *I. hartwegii* (open circles), *I. tenuissima* (dark circles), *I. hartwegii* subsp. *pinetorum* (circle with dot).

of the dilated throat it is nearer *I. tenuissima*. The flower color is very much like the common form of *I. hartwegii*, i.e., pale creamy-yellow and unlike *I. tenuissima* in the absence of dark veining on the falls which is so characteristic of that species. In seed characteristics, it is nearer *I. tenuissima*. There is some plant to plant variation in *pinetorum* but the populations are relatively uniform. One peculiarity of this plant not possessed by either presumed parental species, nor for that matter by any other member of the *Californicae*, is that both flowers in the 2-flowered inflorescence may be open at the same time. In all the others, the two or more flowers open consecutively.

Iris hartwegii reaches its northern known limit in Plumas County a few miles south of where *pinetorum* is found. *Iris tenuissima*, on the other hand, reaches its eastern and southern limit in Butte County (see map, Fig. 25) with *pinetorum* occurring to

the north and east of the two species. The same general area marks the boundaries between the Sierra Nevada and the Cascade ranges, *Iris hartwegii* being native to the Sierra Nevada, whereas *I. tenuissima* belongs in the Cascade-Klamath mountain system.

Ecologically, all three taxa are here members of the Yellow Pine Forest community and all grow in some shade. In places in Butte County where *I. hartwegii* and *I. tenuissima* occur in the same general area, the latter will be found at an altitude above *I. hartwegii*. The two have never been found growing together and no presumed hybrids or hybrid swarms have been located. The ecological factor, or factors, responsible for maintaining these two species at their respective altitudes is not known. It is possible that it may be one of temperature relationships. Butte County is an interesting area because not only do *I. hartwegii* and *I. tenuissima* reach the limits of their distribution here, but also it is the northern limit on the east side of the Valley for *I. macrosiphon*. The latter, however, is found in another plant community, the Foothill Woodland, and at a lower elevation. As one proceeds from Paradise to Butte Meadows, one goes through first a zone with *I. macrosiphon*, then one with *I. hartwegii*, and finally near Butte Meadows, *I. tenuissima* is encountered. I know of no place else where three species of the *Californicae* occur above one another in such a manner.

Iris tenax subsp. *klamathensis* is a distinctive little endemic which appears to have the center of its very limited distribution near the village of Orleans in eastern Humboldt County, California. Here it is found in quite shaded places along the hillsides above the Klamath River, growing in Mixed Evergreen Forest with such species as Douglas Fir (*Pseudotsuga taxifolia*), *Umbellularia californica*, Madrone (*Arbutus menziesii*), and the large-leaved maple (*Acer macrophyllum*). So far as is now known, it does not extend north of the junction of the Klamath and Salmon rivers nor south of Crawford Creek, and it is completely surrounded by *I. tenuissima*. Morphologically, it is well separated from the latter species, *klamathensis* having very narrow (aver. 4.3 mm.) spathe valves which are separated and divergent as opposed to the relatively broad (aver. 7.5 mm.) opposite and connivent ones of *I. tenuissima*. The perianth tubes of the two are also very distinctive in shape as well as in length, those of *klamathensis* being 11-20 mm. long compared with 30-58 mm. for *I. tenuissima*. In the latter species the perianth tube is relatively narrow except the dilated throat. In *klamathensis* the tube is relatively thick. Ecologically, *I. tenuissima* may occur in Yellow Pine Forest, Mixed Evergreen Forest, Northern Oak Woodland, and Foothill Woodland plant communities, but it is never found in as much shade as where *klamathensis* grows.

Iris tenax subsp. *klamathensis* is obviously a member of the *I. tenax-hartwegii-munzii* complex and morphologically it is nearest *I. tenax*. However, it does have a longer perianth tube than that species or any member of that complex, with 11-20 mm. for *klamathensis* compared with 5-10 mm. of the others. There is also a slight indication of a dilated throat in some of the specimens. The flower color is a pale buff-yellow with conspicuous deep maroon or brown lines. This same flower color has been noted in other members of the *Californicae* but the ground color is darker than any known form of *I. tenuissima* although the veining is similar to what is found in that species. In respect to color, the plants are not unique since *I. bracteata* and *I. innominata* both show conspicuous maroon or brown veining on the sepals in at least some of the plants. Near Crawford Creek a few plants were found which appeared to be hybrids between *klamathensis* and *I. tenuissima*.

The occurrence of this very distinct little plant growing in an area of only a few

square miles and completely surrounded by another species morphologically very different, is hard to explain. It is true that the two do occupy different ecological habitats with shade tolerance perhaps being one critical factor. In this respect, *klamathensis* differs from *I. tenax* which is a sun-loving species. As in the case of *I. hartwegii* subsp. *columbiana*, the center of distribution of *klamathensis*, Orleans, was also the scene of great mining activity a little over a century ago. The town, then known as Orleans Bar, was one of the thriving communities along the Klamath River and between 1855 and 1875 it served as the county seat of the now dissolved Klamath County.

Morphologically, *klamathensis* differs from the other members of this complex mainly in having longer perianth tubes and in showing a slight indication of a broadened throat in some specimens. Both of these differences are in the direction of *I. tenuissima* and it would seem possible that they could represent introgression of genes from that species into *klamathensis*. The occurrence of distinct hybrids between the two along Crawford Creek would seem to indicate that such an explanation was possible.

THE LONG PERIANTH TUBE COMPLEX

A second species complex within the *Californicae* are the long tubed irises, i.e., those with perianth tubes 30-120 mm. long. Included here are *I. chrysophylla*, *I. tenuissima*, *I. macrosiphon*, and *I. fernaldii*. *Iris purdyi* might also be placed here, although it would appear to be somewhat farther removed from the rest of the complex. Certainly the first four of these species are more closely related to one another than they are to the other members of the *Californicae*, but at the same time they are all morphologically quite distinct. Geographically, *I. chrysophylla* occurs farthest north and is quite abundant in southern Oregon, extending onto the northern slopes of the Siskiyou Range and into the Cascades. According to Clarkson (1955), and from my own observations, it appears that *I. chrysophylla* is a species of open and rather dry coniferous forests, especially in the ponderosa pine and ponderosa pine-Douglas fir forests, and Clarkson is of the opinion that excessive moisture is the limiting factor in its distribution.

Iris tenuissima is an inhabitant of the forest of the southern slopes of the Siskiyou and southern Cascades, both areas lying south of the California-Oregon border. *Iris tenuissima* occurs in habitats similar to those of *I. chrysophylla*. According to Detling's (1948) classification of the vegetation areas of the Pacific Northwest, *I. chrysophylla*, in southern Oregon, is found in the Rogue and South Cascade areas whereas *I. tenuissima* is found in the Siskiyou and Sierra areas. It should be noted that Detling's use of the term, southern Cascades, in connection with a vegetation area is somewhat different from that used by geographers. According to Detling's usage, the term, Sierra Area, comprises the region south of the California-Oregon border which according to geographers would include the southern portion of the Cascades and the northern portion of the Sierra Nevada. In discussing the South Cascade and Sierra areas, Detling says, "An environmental break at the Pitt and Klamath rivers makes the transition from the flora of the South Cascade to that of the Sierra Area." Of the Siskiyou and Rogue areas, he says, "... the Siskiyou Area is ... marked by a high extreme of precipitation and low extreme of summer and winter temperatures and of growing season ..." and "... the Rogue Area [lying just to the north] ... is one of relatively low rainfall, high summer temperatures, moderate winter temperatures and long growing season." Morphologically, these species both possess long slender style branches with style crests sometimes nearly as long as the branch itself. They also both have somewhat narrow perianth segments. Flower color is usually a pale creamy-white to creamy-yellow with the sepals showing distinct dark veining.

In these three respects, they differ from *I. macrosiphon*. The most conspicuous difference between *I. chrysophylla* and *I. tenuissima* lies in the structure of the perianth tube itself. In *I. tenuissima* the upper portion of the tube is dilated to form a conspicuous throat sometimes nearly one-third the length of the tube itself. In *I. chrysophylla* the upper portion of the tube usually has a short bowl-like enlargement just below the union of the perianth segments.

In the Feather River Canyon in Plumas County, California, and near the present community of Tobin, there is found a most unusual iris which was described by R. C. Foster (1937) as *I. tenuissima* var. *purdyiformis*. Foster had seen only three herbarium specimens, two of which had originally been labelled as *I. purdyi*, a species unknown to the Sierras or any area on the east side of the Sacramento Valley. In describing the plant Foster said: "In the coloring and shape of the cauline leaves, the short stems, pink-tipped and margined spathes, and the one-sidedly glaucous leaves, this plant does have a deceptive resemblance to *I. Purdyi*. Nevertheless, an examination of the rather poorly preserved flowers shows the petals and sepals to be much smaller and more delicate than those of *I. Purdyi*, or, indeed, than in most specimens seen of *I. tenuissima*. As in that species, however, the style-crests are narrowly linear. On the whole, the floral parts are quite unlike those of *I. Purdyi*. That species has a truncately rounded or flattened stigma, while that of *I. tenuissima* is so acuminate as to be nearly tongue-shaped. In this new variety the stigma is not tongue-shaped, but is apparently more rounded than is the case with *I. Purdyi*, nor does it seem bilobed, as is sometimes true of that species."

Foster was tempted to postulate a hybrid origin for this taxon but he questioned whether living plants would show as great a resemblance to *I. purdyi* as the dried specimens did and he further noted that *I. purdyi* was confined to the coast redwood area and had never been reported so far to the east. The area where this taxon occurs has been studied now for a number of years but nowhere have the plants been found to be common and in the Feather River Canyon where I have seen it, it does not occupy an area of more than a few square miles. Figure 35 of Part I of this work (Lenz, 1958) shows the typical form of this subspecies. As noted by Foster, the cauline leaves are unique and the stem below the inflorescence looks very much like some lavender-flowered forms of *I. purdyi* which have been discussed in detail earlier. In typical or "pure" *I. purdyi*, the cauline leaves are usually overlapping rather than separated and even more inflated than they are here. In *purdyiformis* the spathe valves are somewhat inflated and quite broad as they also tend to be in *I. purdyi*, but they are also somewhat shorter than in that species. Indeed they tend to be shorter on the average than either *I. purdyi* or *I. tenuissima*. As noted by Foster, the flower parts are quite un-*purdyi*-like although not as spidery as many forms of *I. tenuissima* and the style crests are shorter than those of *I. tenuissima*, but the style branch and crest are both very narrow and similar to that species. The dilated throat of *I. tenuissima* is also present in *purdyiformis* although at times it is fairly indistinct. The stigmas are variable and range from strictly triangular to rounded and even nearly truncate (see Fig. 26). In *I. purdyi*, which is the only member of the *Californicae* which has truncate or bilobed stigmatic flaps, the flap is always very short and would only be about $\frac{1}{4}$ - $\frac{1}{3}$ of the length of the one shown at the right in the figure.

Geographically, *I. tenuissima* subsp. *purdyiformis* lies at the extreme southeastern edge of the range of *I. tenuissima* and well away from the present range of *I. purdyi*. Ecologically, it occurs in rather shady places within the Yellow Pine Forest community at about 2000 feet elevation whereas *I. purdyi* is found in the Redwood Forest, North Coastal Coniferous Forest, or Mixed Evergreen Forest plant communities.

After careful field study of *I. tenuissima*, *I. purdyi*, and the subspecies, it is difficult not to postulate a hybrid origin for this taxon. *Iris purdyi* and *I. tenuissima* are known to hybridize where their ranges overlap as they do in both Humboldt and Trinity counties. However, the plants in the hybrid swarms which I have studied have in general been somewhat different from *purdyiformis*. The principal difference is usually that the spathe valves are somewhat shorter in the subspecies than they are in the two species themselves or in the hybrid swarms. If a hybrid origin is accepted for *purdyiformis* the problem arises of explaining how this could have taken place with the present distribution of *I. purdyi* on the opposite side of the Sacramento Valley. The Feather River Canyon is a very interesting area in that it comes close to marking

FIG. 26. Variations in stigmatic flap in *I. tenuissima* subsp. *purdyiformis*.

the separation between the Sierra Nevada which was formed from a single huge fault block uptilted toward the west and the Cascade Mts. which are largely volcanic in origin. Within this same drainage system, but farther toward the headwaters of the river, is found the peculiar little endemic, *I. bartwegii* subsp. *pinetorum* to which reference has already been made.

Iris macrosiphon, the third member of the long-tubed series, is found south of the range of *I. tenuissima* and it is common today on both sides of the Sacramento Valley but it does not extend around the north end of the Valley itself. Thus at the present time it has a disjunct distribution. *Iris macrosiphon* extends south as far as Mt. Hamilton in the west and Tuolumne County in the east. It is an extremely polymorphic species in which it has not been possible to separate out distinct subspecific taxa. Morphologically, it is well separated from *I. tenuissima* (see Lenz, 1958), although many earlier workers failed to note the differences and both concepts have been included under the name of *I. macrosiphon* (Jepson, 1923; Abrams, 1940). Ecologically, *I. macrosiphon* is an inhabitant of open sunny slopes and hillsides, or the edges of woods, and occasionally it is found in light shade. It apparently tolerates less shade than does *I. tenuissima* and where its requirements are met it may be encountered in the Foothill Woodland, Northern Oak Woodland, or Mixed Evergreen plant communities. On the inner slopes of the North Coast Ranges it has been found in Yellow Pine islands surrounded by Chaparral. The occurrence of a species on both sides of the Sacramento Valley is a common distributional pattern in the California flora, but in the majority of instances the species is also found around the end of the Valley. In the case of *I. macrosiphon*, which is replaced by another species in the north, it might be hypothesized that as *I. macrosiphon* migrated from the north it followed the lower hills both to the east and west of the basin which today is the Sacramento Valley. Later, *I. tenuissima* also migrated from the north and displaced *I. macrosiphon* at the end of the Valley, leaving the species with its present disjunct distribution.

Iris fernaldii was the last of the long-tubed species to be described and was first recognized as being distinct by R. C. Foster in 1938. This species possesses leaves which are an unusual gray-green color, it has spathe valves which are somewhat

broader than those of *I. macrosiphon* and the upper portion of the perianth tube is enlarged as it is in *I. tenuissima*, but it lacks the long slender style crests and narrow perianth segments of that species. Other differences between *I. fernaldii* and *I. macrosiphon* are given elsewhere (Lenz, 1958). The distribution of *I. fernaldii* appears to be centered in the San Francisco Bay counties where it is very often found growing in light to moderate shade in the Mixed Evergreen Forest community although it is also known in other plant communities. The exact ecological requirements of this species, as well as its original distribution, are now difficult to determine because of the disturbance of the entire area by human activities during the past century.

Iris purdyi, the last of the long-tubed species, has already been discussed in detail in an earlier section of this paper. Except for the fact that it generally possesses a rather long perianth tube, this species might well be considered as standing by itself as far as relationships with the other members of the *Californicae* are concerned. Among the entire group it is unique in having a truncate or bilobed stigma whereas all the others have triangular or tongue-shaped stigmatic flaps. This species along with *I. bracteata* is the only one with short overlapping cauline leaves, and both normally have yellow flowers. Except for these similarities, the two species do not appear to be closely related.

MISCELLANEOUS SPECIES

The remaining three species of this series, *I. douglasiana*, *I. innominata*, and *I. bracteata*, do not appear to show any special affinities with one another or with either of the two species complexes previously discussed.

Iris douglasiana is unique in the *Californicae* in being the only species that is restricted to the coastal area where it is especially common on the open exposed bluffs above the beaches and on the grassy hillsides along the coast. It also extends inland along the river valleys so long as there is an abundance of sunlight. This species is very aggressive and quickly spreads into areas which are logged or burned, and it even gets into heavy woodland areas by following road cuts. In some coastal areas, grazing appears to favor its spread and in places it has become a weed in pasture lands where only a few years ago the plant was unknown. Geographically, this species has the greatest distribution of any species in the series, extending from near Coos Bay in Oregon south to Santa Barbara County, California. The population at Cañada Hondo in Santa Barbara County is small and today it appears to be barely maintaining itself. The next known population is located some distance to the north and in San Luis Obispo County just south of the Monterey County line. From Monterey County north, the species is common. In general, the distribution of this species (except for the Cañada Hondo population) follows rather closely that of the redwood (*Sequoia sempervirens*) although the two do not normally grow together except in areas of disturbance. Morphologically, *I. douglasiana* is unique in the *Californicae* in several respects: it is the only species which may have branched stalks, it is also unique in having seed capsules which are distinctly triangular in cross section and in having a nipple-like tip. The seeds are also different from those of the other members of the series in being somewhat rounded or pyriform in shape, dark brown, and finely reticulate compared with the more or less cubical or D-shaped seeds of the other species.

Iris innominata approaches *I. douglasiana* in length of perianth tube and both in flower size and color range. Both species are quite variable in respect to these characters. In plant size the two species are quite distinct and the leaf characters are very different. Ecologically, *I. douglasiana* is a maritime species, whereas *I. innominata* is a woodland species. In places the latter species grows associated with *Rhododendron*

macrophyllum and *R. occidentalis* and when the three species are in flower at the same time it forms one of the most delightful sights to be seen in the Klamath area.

Iris bracteata is also quite distinct and shows no relationship with any of the other members of the series except in the characters mentioned in connection with *I. purdyi*. In flower form *I. bracteata* is also unlike any other species in the series and its leaves are unique in being very thick, stiff, and distinctly two-sided. Geographically, it appears to be a narrow endemic known almost entirely from one county in Oregon. In this respect, it is like *I. munzii*, another very distinct species which is endemic to a single county in California.

NATURAL HYBRIDIZATION: GENERAL DISCUSSION

From the facts presented it is evident that in general, natural hybridization is a common occurrence between certain sympatric species of the *Californicae* native to the three west coast states. In some respects, the situation in the *Californicae* is similar to that obtaining in the *Hexagonae* where two sympatric species, *I. fulva* and *I. hexagona* var. *giganti-caerulea*, occurring in the Gulf Coast area, have been shown to hybridize extensively in areas where the ecologically isolating barriers have been altered and new habitats have been made available for genotypes resulting from this interspecific hybridization. In the case of the Louisiana irises, which have been carefully studied by several investigators (Viosca 1935; Riley 1938), it has been shown that in addition to the ecological barriers there was also partial sterility in the hybrids. In the *Californicae*, high hybrid fertility is the rule and the principal barriers to gene flow between sympatric species are the differences in the ecological requirements of the species themselves. Further investigations, however, may show that there are other barriers, or partial barriers, operating between certain of the species, especially in the case of those plants possessing very long perianth tubes and those with very short tubes. The exact amount of natural hybridization occurring between sympatric species of the *Californicae* varies from very little, as for example between *I. macrosiphon* and *I. bartwegii*, to the very extensive hybridizing taking place between *I. douglasiana* and certain other species such as *I. innominata* and *I. purdyi*.

Iris douglasiana is a very widespread and distinct species and is the only maritime species in this series. In its distribution it is restricted to a long narrow area extending along the Pacific Coast for over 500 miles between Coos Bay, Oregon, and Santa Barbara County, California. Along the length of its distribution it comes into contact on the east with five other species. Starting with *I. tenax* in the north, they are next, *I. innominata*, *I. purdyi*, *I. macrosiphon*, and finally *I. fernaldii*. Wherever *I. douglasiana* and one of the other species come into contact, interspecific hybrids are known to occur. Indeed, *I. douglasiana* hybrids are among the most common to be found in the *Californicae*.

There are several reasons for this, one of them being the widespread distribution of the species, another being that *I. douglasiana* is perhaps the most vigorous and aggressive species in the entire series and will quickly invade any coastal area where logging or agricultural operations open up the area so that there is a great deal of sunlight reaching the ground. In this way the species has been able to invade territory to the east and inland normally occupied by other species which are restricted to woodland areas. The exception to this statement is in the case of *I. tenax* which likewise is an inhabitant of sunny open areas, for the most part to the north and inland from *I. douglasiana*. In this instance, logging and agricultural pursuits have provided *I. tenax* with favorable areas for territorial expansion and the two species come into contact in at least a few sunny logged and pastured lands in southwestern Oregon.

Here a few large hybrid swarms have developed. There also appears to have been introgression of *I. tenax* into *I. douglasiana* in areas around Myrtle Point and Bandon Beach in Coos County. R. C. Foster's *I. douglasiana* variety *oregonensis* is most likely representative of such introgression.

To the south of *I. tenax*, *I. douglasiana* comes into contact with *I. innominata* which is in general an inhabitant of sunny to lightly shaded areas in the Klamath Mts., inland from *I. douglasiana*. Again, logging and agricultural pursuits have favored the spread of *I. douglasiana* farther inland than it would otherwise have been found, and in places where it comes into contact with *I. innominata* large and very striking hybrid populations have been developed. In flower color and horticultural importance, these hybrids rival the well known Louisiana Irises and their destruction in many places has been almost as complete as it has been in many areas in Louisiana. There is also some evidence here that *I. innominata* has spread in historic times and perhaps through grazing operations has reached new areas nearer the coast than those it occupied before human occupation of the land began about 100 years ago. Besides the obvious hybrid swarms known here, there has been through back crossing an introgression of genes into the two parental species so that at the present time there is a blurring of the specific differences between the two species along the line of contact. R. C. Foster's *I. thompsonii* is believed to represent, for the most part, hybrids between these two species.

Both *I. douglasiana* and *I. innominata* are more sun loving than are many of the *Californicae* and near the coast in the Brookings area of southern Oregon, hybrids between the two species are often found in areas which have been logged and burned. However, very soon after either burning or logging, the ground becomes covered with a fairly low and dense cover of brush consisting of ceanothus, salal, two species of rhododendron, vaccinium, and bracken fern, and it is doubtful whether the irises can maintain their position here as the growth of the shrubs produces an increasing amount of shade.

Farther south *I. douglasiana* comes into contact with the woodland *I. purdyi* and hybrids between these two species are extremely common over large areas. Here *I. douglasiana* has penetrated far into the forest in places by following roadways as well as logged areas. Hybrid swarms are common but there has also been what appears to be an introgression of genes of *I. douglasiana* into *I. purdyi* for some distance inland. *Iris purdyi* has a relatively long perianth tube and a yellow flower as well as short, inflated, overlapping cauline leaves. Many of the "*purdyi*" plants in the western portion of its distribution show varying amounts of lavender color on the sepals superimposed over the basic yellow color. These plants often have somewhat shorter perianth tubes than the yellow-flowered forms and the cauline leaves which are separated and only slightly inflated. These plants, I believe, show introgression of genes of *I. douglasiana* into *I. purdyi*.

One of the possible results following extensive interspecific hybridization is that of swamping of one or both of the parental species. In the *Californicae* this possibility appears greatest in the case of *I. purdyi*. This species is native to an extremely valuable forest area (Redwood Forest and North Coastal Coniferous Forest) in which harvesting operations have been going on almost continuously for well over 100 years with much of the region being disturbed two or more times. *Iris purdyi* is surrounded on all sides by other species of iris: *I. douglasiana* to the west, *I. tenuissima* to the north and east, *I. macrosiphon* to the east and south. All of these species grow in sunnier habitats than does *I. purdyi* with the result that as the forests have been cleared, the other species have spread into areas which they could not have invaded earlier. Wherever this has happened, hybridization has occurred. Today many of the

forms of *I. purdyi* encountered throughout much of the area evidently contain genes from these other species. The large yellow-flowered plants with short, inflated, overlapping cauline leaves are still found in some places, but in many areas they have been replaced by forms with smaller flowers, usually of a pale cream color or nearly white overlaid with a lavender wash on the falls and with cauline leaves still quite short but usually separated and slightly if at all inflated.

One of the few trihybrids discovered in this group was a population in which *I. douglasiana*, *I. macrosiphon*, and *I. purdyi* had all entered into its composition. This population was found in a locality which was being logged for at least the second time, and in addition it is a region of grazing operations and has been under the influence of human development for over 100 years.

Farther south, *I. douglasiana* comes into contact with both *I. macrosiphon* and *I. fernaldii* and hybrids are known. The most obvious effects of hybridization appear to be the blurring of specific differences near the points of contact between the species.

Iris innominata is a second species which is surrounded on all sides by other species: to the west by *I. douglasiana*, to the north and east by *I. tenax*, to the east by *I. chrysophylla*, and to the south by *I. bracteata*. In this case, many hybrids have also been found, but the overall effect on the species has not been so notable as in the case of *I. purdyi* and the species is still found in quantity in many localities in what would appear to be an uncontaminated state. The reasons for this are several: much of the area occupied by *I. innominata* is extremely rugged and many areas still exist in which no roads have been made and no logging has been done. Scattered homesteads are found in some of the remote regions and a certain amount of grazing has been carried on there for some time. There is some evidence that *I. innominata* has spread toward the coast in historic times, perhaps by seeds being carried in the wool of sheep. It is in this general area where *I. innominata* was unknown, or at least less abundant than it is now, that many of the spectacular hybrids with *I. douglasiana* are found.

Hybrids between *I. chrysophylla* and *I. innominata* have been recorded by Clarkson but I have seen no plants in the field that I would interpret as representing this combination. However, more detailed study of the general area of contact between these species might show that they are hybridizing to a greater extent than is now known.

With the more or less general occurrence of hybrids between members of the *Californicae* wherever their distributions overlap and the ecological habitats in which they occur have been altered, the occasional lack of extensive hybridization between species in disturbed areas is of special interest. During the course of this study, two such instances have been noted. No hybrid swarms have been found between *I. hartwegii* and *I. macrosiphon* or between *I. bracteata* and *I. chrysophylla* even though they may be found growing within a few hundred yards of one another. Individual plants of apparent hybrid origin are known for both of these species combinations but such occurrences appear to be rare. Both of these species pairs represent a combination of one species with a very long perianth tube (*I. chrysophylla*, aver. 57 mm.; *I. macrosiphon*, aver. 53 mm.), and one with a very short tube (*I. bracteata*, aver. 9 mm.; *I. hartwegii*, aver. 8 mm.). In the case of *I. hartwegii* and *I. macrosiphon*, the species occupy adjacent habitats for several hundred miles along the Sierra Nevada and a special effort has been made to find hybrids or hybrid swarms of this combination. I have found no plant in the field that I would take to be such a hybrid although I have seen a few specimens in herbaria which would appear to be of this combination. In another portion of this paper (Page 284, Fig. 23-2), a scatter diagram is shown of one population which, however, might be interpreted as showing introgression of *I. macrosiphon* into *I. hartwegii*.

The second species pair for which I have no evidence of hybridization is that of *I. bracteata* and *I. chrysophylla*. These plants were discussed in detail in another section of this paper (Page 276).

In addition to the two combinations just mentioned, there is another in Oregon which has been studied extensively by Clarkson. Here the ranges of *I. chrysophylla* and *I. tenax* overlap in a few places and Clarkson was able to find hybrids intermediate between the species in three places. According to him, the F_1 hybrids have back crossed to the *I. tenax* parent and in this way there has been an introgression of genes of *I. chrysophylla* into *I. tenax*, thus increasing the variability of *I. tenax* while *I. chrysophylla* has remained constant. Here again the perianth tube relationship between these species is the same as in the two earlier examples. *Iris chrysophylla* has a tube averaging 57 mm. in length compared with an average of 8 mm. for *I. tenax*.

In the three cases mentioned above, F_1 hybrids and hybrid swarms are rare or non-existent despite the fact that the original habitats of the species have been greatly altered by human activity and intermediate sites have apparently been available for the establishment of introgressants. This suggests that some other isolating barrier besides ecological isolation must have been operating between the species. It will be recalled that the isolated species pair consists in each case of one member with a long perianth tube and the other with a short tube. Perhaps the type of pollinating agent and pollination mechanism contributes to species isolation in these cases. The occasional breakdown of such a barrier might permit a limited flow of genes from the long-tubed into the short-tubed species. Work is continuing on this problem.

FACTORS RESPONSIBLE FOR THE BREAKDOWN OF THE ECOLOGICAL BARRIERS SEPARATING THE SPECIES

From my observations there appear to be at least six factors which have been, or are, of major significance in the breakdown of the ecological barriers separating the species in the *Californicae*. These are: (1) logging, (2) road construction, (3) power line construction, (4) grazing, (5) mining, and (6) fire. Of these, logging operations have probably been the greatest single factor and the effects on plant communities of timber harvest as carried on in the great coniferous forests of northern California and Oregon are almost without parallel. Not only are the trees removed, thus greatly altering the light-shade relationships, but also the destruction of much of the accumulated forest soil changes the edaphic conditions, and herbs and undershrubs may either be destroyed entirely or greatly altered in numbers. As a result there is set up an entirely new ecological succession. In northern California and in Oregon the very vigorous and aggressive *I. douglasiana* has thus been able to invade territory far removed from its original maritime habitat due mainly to logging. Also *I. tenax*, an inhabitant of rather open situations, has been able to penetrate into coniferous forests where it was unknown prior to logging. The effects of timber harvest on the woodland species themselves has probably not been, in every case, entirely deleterious. Many of the species are found in areas of light to moderate shade within the forests themselves and with the removal of the heavy shade-producing timber the irises have been able to increase in numbers within the limits of their natural distribution and many of the largest and most floriferous plants have often been found in areas only recently logged (see Fig. 27, 28). It is doubtful if these increased numbers would remain over a very long period of time, especially in areas where dense undergrowth of shrubs would soon increase the amount of shade to the point where the irises would no longer be able to grow.

Perhaps the second most important factor is the construction of the vast road system throughout the West. Here again, species have been able to gain access to otherwise

FIG. 27. Typical scene of timber harvest as carried on in northern California and Oregon.

FIG. 28. Another scene in same area as shown above. Note irises toward lower center of figure.

inaccessible areas by following roadways. This is well exemplified by the occurrence of hybrids along highways and the absence sometimes of any iris more than a few hundred feet from the road itself. The *I. douglasiana*-*I. purdyi* series studied along U.S. Hwy. 101 in the Eel River Canyon is a good example. Here *I. douglasiana* has been able to penetrate far into *I. purdyi* territory by following the highway which cuts through the redwood forest. *I. ×thompsonii*-*I. bracteata* hybrids along U.S. Hwy. 199 between Douglas Park and Hazelview Summit are also another good example. The clearing of rights of way for electric power lines has had much the same effect on the vegetation as has road construction (Fig. 29).

FIG. 29. Powerline right of way clearing showing destruction of timber. Such clearings allow species to migrate into areas where otherwise they would not be found.

Grazing has been of importance in at least some areas. It is believed that *I. inno-minata* has been able to extend its distribution in recent years by seeds being carried in the wool of sheep. In the case of other species some of the finest hybrid populations studied during the course of this investigation were those found in pastures and pastured lands (see Mattole River hybrids and Doyle Ranch series). In these instances the results were similar in many ways to those reported in the pasture lands and wood lots of southern Louisiana. Grazing has also probably played a role in the distribution of *I. douglasiana* and perhaps other species since cattle prefer the grasses to the iris leaves, many of which contain a bitter after-taste. In areas along the Mendocino coast, *I. douglasiana* has now assumed the importance of a noxious weed in some pastures and attempts are being made to eradicate it by sprays. In some of the infested pastures the plants were unknown until recent years. It appears probable that the iris was able to become established in these pastures because the sod of grasses and sedges was broken by the cattles' hooves thus giving the iris a chance to become established.

Mining operations, especially placer mining, like those of lumbering, have been responsible for the destruction of vast acreages of land in many places in California, especially in the Mother Lode country of the Sierra Nevada foothills, along the Klamath River, and in the area around Selma and Waldo in Oregon, as well as elsewhere. Of the four subspecies recognized in the latest taxonomic treatment of this series, three of them, whose origins are postulated as having been through hybridization, are native to areas of extensive past mining operations as well as lumbering. The fourth, whose origin is obscure, is likewise native to an area subjected to intensive mining about 100 years ago.

The last factor involved in the breakdown of the ecological barriers, and perhaps the least important one, is that of fire. In some regions, as for example in the Mattole River area, fire has been used to control the heavy undergrowth which appears in many places within a few years after logging operations and this burning may well help to maintain habitats which are open enough for the survival of the irises. There are indications that in the area around Brookings, Oregon, where the undergrowth has not been burned, the irises which invaded the areas immediately after logging may, within a relatively short period of time, be eliminated due to the heavy shade produced by the growth of undershrubs such as salal, vaccinium, ceanothus, arctostaphylos, and bracken. Sweeney (1956) reports that irises which I have identified as *I. macrosiphon* and *I. fernaldii*, and their hybrids, have appeared in a number of places following chaparral fires.

CONCLUSIONS

From present available evidence it would appear that primary speciation in the *Californicae* has taken place principally, though perhaps not exclusively, through ecological isolation of sympatric forms and there has been little or no chromosomal re-patterning within the group. As a result, the species possess the potential of producing vigorous and fertile hybrids when any breakdown occurs in the ecological barriers separating the species. When this does happen, one of the possible results is the merging of separate species into a single interbreeding population providing that the isolating barriers are altered sufficiently. The general process of the merging of separate species into a single species, Grant (1957) has termed secondary speciation, defining it as "that stage of the evolutionary process at which two or more reproductively isolated populations become combined into one interbreeding population." As he points out, the process is a gradual one. Opposed to the mass fusion of two species into a single interbreeding population is the mere trickle of genes across an inter-specific barrier which is manifest in the production of an occasional hybrid. In the latter instance, the hybridizing entities still remain good species in the taxonomic sense and are only slightly contaminated in the biological sense. Between the two extremes there can be every intermediate stage.

The merging of species may proceed at a rapid rate and go to completion, or it may remain more or less indefinitely in an intermediate phase thus giving rise to serious difficulties in attempting to delimit the species involved. In the *Californicae* it is possible to demonstrate both extremes as well as intermediate stages. *Iris purdyi* is the one species which would appear to be undergoing the most rapid secondary speciation at the present time. This is due in part to the drastic alterations which are taking place in the woodland community where the species occurs. Few wooded areas have been subjected to more concentrated harvest during the past hundred years than have the redwood forest and mixed evergreen forests of northern California. At the present time, *I. purdyi* is hybridizing extensively with three other species, *I. douglasiana*, *I. macrosiphon*, and *I. tenuissima*, all of which are capable of spreading into *I. purdyi*

territory as the forest covering is removed, roads built, and power line rights of way cut through the area.

The other extreme, that of a limited amount of gene flow, can best be demonstrated in the case of *I. bartwegii* and *I. macrosiphon* which are sympatric for a long distance along the Sierra Nevada in California, yet each remains distinct from the other although hybridization is known to occur very occasionally and perhaps there has been a slight introgression of genes of *I. macrosiphon* into *I. bartwegii* in a few areas.

FIG. 29. All the species of the *Californicae* with the exception of *I. munzii* are today linked together through hybridization and may thus be considered as belonging to a single syngameon. The amount of natural hybridization occurring between various species varies from slight (broken lines) to moderate (thin solid line) to extensive (thick solid line). BRA, *I. bracteata*; CHR, *I. chrysophylla*; DOU, *I. douglasiana*; FER, *I. fernaldii*; MAC, *I. macrosiphon*; MUN, *I. munzii*; PUR, *I. purdyi*; TEN, *I. tenax*; TMA, *I. tenuissima*; XTH, *I. Xthompsonii*.

Iris bracteata and *I. chrysophylla*, and *I. chrysophylla* and *I. tenax* also appear to be species pairs between which there is a limited amount of gene flow at the present time. The other hybrid combinations cited earlier would fall between these two extremes.

The evolutionary pattern within the *Californicae* might be likened to that found in the *Gilia tenuiflora* group and described by Grant and Grant (1956). There they believed that four species, *G. tenuiflora*, *G. latiflora*, *G. leptantha*, and *G. cana*, went through a stage of barely completed primary speciation which was followed by extensive hybridization in various combinations. In order to find a convenient means of designating these hybridizing species complexes, V. Grant went back to the term,

syngameon, which had first been used by Lotsy in 1925. Grant then re-defined the term as "the sum total of species or semispecies linked by frequent or occasional hybridization in nature; a hybridizing group of species, the most inclusive interbreeding populations."

According to this same author, in a syngameon the original biological species may either persist as discrete entities within the syngameon to which they belong, or they may come to occupy a subordinate position. In the latter case the species as a biological unit is found in varying degrees of dissolution. Thus, according to this concept, all the members of the *Californicae* with the exception of *I. munzii* would, at the present time, be members of a single syngameon since they are all linked by natural hybridization (Fig. 30).

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