

CYTOTAXONOMIC STUDIES IN IRIS, SECTION APOGON BAKER,
SUBSECTION CALIFORNICAE DIELS

by

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CYTOTAXONOMIC STUDIES IN IRIS, SECTION APOGON BAKER

SUBSECTION CALIFORNICAE DIELS

Introduction

This study was undertaken to investigate species relationships in the subsection Californicae, section Apogon, of the genus Iris. The work was planned to utilize ecological, genetic, cytological, and conventional taxonomic methods in an analysis of those relationships. No attempt has been made to interpret the relationship of the subsection to other subgeneric groups within the genus Iris.

According to Foster (13), the genus Iris can be divided into two major groups, those with bulbous and those with rhizomatous rootstocks. The section Apogon is distinguished from the other six sections of the rhizomatous irises by the absence of multicellular hairs on the sepals. All but two of the species of North American Iris belong to the Apogon Irises. The section is also represented by species in Europe, Asia and Africa.

The subsection Californicae of section Apogon was considered by Foster in 1937 to consist of 12 species and 5 varieties. Since that date he has added 2 new species (14) and 3 species and 2 varieties have been described by Miss Alice Eastwood (10), (11), (12). One of the species included by Foster (I. tenuis Wats.) has been excluded from this study for cytological and morphological reasons which will be discussed in a later section. The remaining 16 species are rhizomatous, clump-forming perennials

characterized by a usually deltoid stigma; D-shaped, cubical, or ovoid seeds; the absence of foliaceous stem leaves; and tough basal leaves which are reddish at base. Dykes (9) and Foster state that few roots are produced by members of the subsection, but this characteristic is not supported by field observations. The roots tend to break easily when pulled from the ground and herbarium specimens often show only a few roots.

General distribution of the subsection is west of the Cascade-Sierra crest from Washington to southern California. However, most of the species are found in southwestern Oregon and northwestern California.

Taxonomically a number of characters have been used for distinguishing the species:

Stigma - The stigma is deltoid and entire in all species except *I. purdyi* Eastw. which has a tongue-shaped and bilobed stigma.

Style - The style branches are petaloid and usually the same color as the perianth. There are variations in length and these have been regarded as significant (1).

Perianth - The petals are usually narrow and about the same length as the sepals. The sepals are linear to spatulate in shape. Color of the perianth is variable, ranging from white, purple, pale yellow, golden yellow, to apricot and maroon. Because color is difficult to measure accurately, it has never been adequately evaluated. It may or may not have taxonomic significance throughout the subsection.

Stamens - The anthers are basifixed, much longer than the filaments, and vary in color from yellow to lavender and purple.

Perianth tube - The perianth tube varies in length from 0.4 to 12 centimeters. Perianth tube length is an important taxonomic character, especially when considered in relation to the length of the pedicel.

Capsule - The capsule is 3-6 angled and loculicidally dehiscent.

Seeds - The seeds are D-shaped, cubical, or ovoid. The surface is reticulate.

Pedicel - The pedicel varies in length approximately inversely with the length of the perianth tube. The relative length of these two characters is taxonomically significant.

Bracts of the inflorescence - The bracts, or spathes, are variable in shape from ovoid to linear; in length from 2 to 15 centimeters; and in position from opposite to 4 centimeters distant.

Stem leaves - The stem leaves are bract-like and short. In some taxa they are inflated and without blades.

Basal leaves - The basal leaves vary in width from 2 to 20 millimeters or more. They are either green, glaucous, green on one surface and glaucous on the other, or (*I. bracteata* Wats.) glossy green on one surface and glaucous on the other.

Rhizome - The rhizome is fairly uniform throughout.

Aside from Baker (3) in 1892 and the works previously cited, no

treatment of the subsection as a whole has been made. Foster's treatment, intended only as a survey, has nonetheless provided a sound basis to begin a cytotaxonomic analysis. Floristic treatments of all or part of the subsection are found in Abrams (1), Peck (20), and Jepson (17).

Cytologically the species have been studied as a group only by Foster and Simonet (21). Chromosome counts of $N = 20$ for I. tenax Dougl. var. australis (Parish) Foster and I. munzii Foster have been reported by Lenz (18). Simonet reported counts of $N = 20$ for I. douglasiana Herbert and I. tenax and $2N = 40$ for I. tenax var. gormanii (Piper) Foster. Foster reported chromosome counts of $2N =$ "apparently 40" for I. bracteata Wats. He confirmed Simonet's count of $2N = 40$ for I. tenax, I. tenax gormanii, and I. douglasiana. Foster also reported $2N = 40$ for I. purdyi Eastw. Foster summarized his and previous findings with the statement that differences of karyotype can be of little use in distinguishing species in the subsection Californicae.

Species in the Californicae have been distinguished almost entirely on quantitative grounds. That is, the differences between species are what have been called differences in degree and not differences in kind. Many of the species have been described from only a few specimens, in some cases only one. The occurrence of plants which seemed to be intermediate between some of the species made further investigation seem necessary. Accordingly, this study was undertaken to investigate species relationships and to evaluate

the nomenclature.

Methods

Three characteristics of the subsection determined the method of analysis: (1) the quantitative nature of the difference between taxa, (2) the suggestion, by Foster and others, that hybridization may have played an important role in the variability present, (3) the similarity in chromosome number and morphology.

A number of different but closely correlated methods were used. In each case the nomenclature of Foster and Eastwood was utilized as a beginning point. All names used are based on their publications unless otherwise indicated.

The first of these methods consisted of the production (by Dr. Frank H. Smith of the Botany Department, Oregon State College) of artificial hybrids of many of the species and the subsequent analysis of chromosome pairing in the pollen mother cells of those F_1 hybrids. For cytological study, young anthers were fixed in McClintock's solution. After several days to a week, they were transferred to 70 percent alcohol. Either from the fixative or from the alcohol, a small segment of an anther was removed, smeared on a slide in a drop of propionic-orcein and heated gently over an alcohol burner. The slides were made permanent by the vapor jar method (4). Observations on growth habits, vigor, and general morphology of the hybrids were made in addition to limited genetic observations. Parent plants were analysed with regard to constancy of taxonomic characters and vigor under cultivation.

Field studies were conducted to search for natural hybrids and to examine variation within species. A series of collections was made wherever two species came together in an attempt to detect possible hybridization beyond the first generation. Wherever there was evidence of variability within a colony, mass collections were made for which specimens were selected to represent the total variation present. Where little variation was evident, only routine herbarium collections were made. In all cases, notes were made on ecological conditions.

In addition to experimental and field studies, a limited amount of herbarium material was examined. Considerations based on herbarium specimens will be discussed where appropriate. Specimens were seen from the herbaria of the following institutions: Oregon State College, University of Oregon, University of California at Davis, Fresno State College, and the State College of Washington. In addition, type specimens were borrowed from the herbarium of the California Academy of Sciences and from the Gray Herbarium of Harvard University.

Analysis of Parent Plants and F_1 Hybrids

Parent plants and hybrids were grown first at the home of Dr. Frank H. Smith, Corvallis, Oregon, and later were transferred to the experimental farm of the Department of Botany and Plant Pathology, Oregon State College. In each case the plants were grown under adverse conditions. At the first site they were crowded into a small area on a heavy clay soil. At the second, the plants were in constant competition with weeds. Despite these conditions, both the F_1 hybrids and the parents produced an abundance of flowers and considerable vegetative growth.

The parent plants were gathered from the sources shown in table 1 and were selected as typical representatives of the species. The morphological characteristics of the plants remained constant upon transplanting. For at least five years, there has been no indication of temporal variation for any of the taxonomic characteristics used to distinguish taxa within the subsection. If the F_1 offspring of any cross demonstrated much variability, both the hybrids and the parents were discarded to prevent possible use of natural hybrids as parents. This practice gives greater validity to cytological generalizations but it reduces the genetic variation available for analysis.

The F_1 hybrids produced are listed in table 2. All the hybrids were produced without difficulty, in most cases only a single artificial pollination was required. There was no indication of

Table 1

Species used as parents for the production of F_1 hybrids.
 All locations are in Oregon unless otherwise indicated.
 Voucher specimens have been filed at the Oregon State
 College herbarium.

Species	Location
bracteata	Josephine County
chrysophylla	Lane County
douglasiana	Curry County
hartwegii	Butte County, California
innominata	Curry County
macrosiphon	Mendocino County, California
purdyi	Humboldt County, California
tenax	Benton County
tenax australis	San Bernardino County, California
tenax gormanii	Washington County
tenuissima	Shasta County, California
thompsonii	Curry County

Table 2

F₁ hybrids produced and grown at Oregon State College.
 Voucher specimens have been filed at the Oregon State
 College herbarium.

chrysophylla x bracteata	purdyi x tenuissima
chrysophylla x douglasiana	purdyi x thompsonii
chrysophylla x macrosiphon	tenax x bracteata
chrysophylla x tenax	tenax x chrysophylla
chrysophylla x tenax australis	tenax x douglasiana
chrysophylla x tenax gormanii	tenax x hartwegii
chrysophylla x thompsonii	tenax x innominata
douglasiana x bracteata	tenax x macrosiphon
douglasiana x chrysophylla	tenax x purdyi
douglasiana x douglasiana	tenax x tenax
douglasiana x hartwegii	tenax x tenax australis
douglasiana x innominata	tenax x tenax gormanii
douglasiana x macrosiphon	tenax x thompsonii
douglasiana x tenax	tenax australis x bracteata
douglasiana x tenax australis	tenax australis x macrosiphon
douglasiana x tenax gormanii	tenax gormanii x purdyi
douglasiana x tenuissima	tenax gormanii x tenax
douglasiana x thompsonii	tenuissima x chrysophylla
innominata x bracteata	tenuissima x macrosiphon
innominata x chrysophylla	tenuissima x tenax
innominata x douglasiana	tenuissima x tenax gormanii
innominata x hartwegii	tenuissima x thompsonii
innominata x tenax	thompsonii x bracteata
innominata x tenax gormanii	thompsonii x chrysophylla
purdyi x bracteata	thompsonii x douglasiana
purdyi x chrysophylla	thompsonii x innominata
purdyi x douglasiana	thompsonii x macrosiphon
purdyi x innominata	thompsonii x tenax
purdyi x macrosiphon	thompsonii x tenax gormanii

aborted seed in the parent plants following pollination and germination was as high as from open pollinated flowers of the parents. A limited number of F_2 hybrids were grown and seem vigorous and healthy.

Genetically, the artificial hybrids cannot be expected to compare with natural hybrids in all details. The deliberate selection away from variation in choosing parent plants tends to reduce the opportunity of producing exactly comparable individuals. Also, the few plants used as parents for each cross cannot compare with the large numbers available in nature. In addition, the artificial hybrids are of the F_1 generation while natural hybrids undoubtedly represent all degrees of hybridization. The possibilities for recombination and segregation available in nature cannot be duplicated artificially. Nonetheless, the known hybrids are of considerable value in understanding and interpreting natural hybrids.

The F_1 hybrids of any given cross are uniform with respect to all traits with the exception of color. This indicates that the parent plants are relatively homozygous for the major taxonomic traits. The artificial hybrids are intermediate between the parents for most traits which indicates quantitative inheritance. Since most taxonomical characteristics of these Iris are inherited in this way, natural hybrids can be expected to be intermediate between their parents.

The inheritance of flower color is complex and has been inadequately studied. If white-flowered I. tenax is crossed with white-flowered I. douglasiana the offspring are purple-flowered.

This indicates that at least two factors are necessary for the production of purple flower color and that of these a different factor is missing in each of the parents. However, crosses between yellow-flowered forms and purple-flowered forms result in offspring with maroon, or greyish-lavender flowers. This situation is discussed by Sinnot, Dunn and Dobzhansky (23). Red, blue and related colors are due to anthocyanin pigments while the yellow colors are due to anthoxanthins. There are genes which control the presence or absence of each pigment and other genes which control the amount of each pigment developed. Color inheritance in hybrids between yellow and purple-flowered forms cannot be easily interpreted without extensive experimental work. In crosses between yellow-flowered forms, golden yellow appears to have some dominance over pale yellow and the F_1 hybrids of such a cross have golden yellow flowers.

Cytological Results

Chromosomes in metaphase of the first division of meiosis were examined from the following F_1 hybrids:

- I. chrysophylla x I. douglasiana
- I. douglasiana x I. harwegii
- I. douglasiana x I. purdyi
- I. douglasiana x I. tenax
- I. douglasiana x I. tenuissima
- I. douglasiana x I. thompsonii
- I. innominata x I. chrysophylla
- I. innominata x I. douglasiana
- I. innominata x I. tenax
- I. tenuissima x I. tenax
- I. thompsonii x I. innominata

One F_2 hybrid (I. innominata x I. douglasiana) was also examined in the first division. Metaphase figures of these hybrids are illustrated in figures 1 to 12. All drawings were made with the aid of a camera lucida at about 1800X magnification.

In addition to the first division figures, anaphase I counts were made in the following F_1 hybrids:

- I. douglasiana x I. douglasiana
- I. purdyi x I. macrosiphon
- I. tenax x I. bracteata
- I. tenuissima x I. chrysophylla

No irregularities have been found in any of the hybrids studied. Pairing appears to be constant for all the pairs, and no univalents have been observed. The chromosomes are distributed regularly in both divisions. The chromosome number is $N = 20$ for all the material examined. During the preparation of slides for cytological study, many mature pollen grains were examined. Although no particular study of this stage of development was made, no indication of sterile pollen was observed and pollen production in all the hybrids is high. The data demonstrate the absence of cytological barriers to hybridization between the species studied. Because of the consistent karyotype reported for the subsection, it seems reasonable to assume that there are no cytological barriers between the other species. Insufficient second generation hybrids have been studied to determine fertility of later generations. This will be considered in connection with field studies.

In addition to the cytological study of chromosome pairing, seeds of the hybrids have been examined for two consecutive years. While the examination was made prior to full development, there was no indication of defective seed. All the capsules are well filled by the first of June and the seeds are plump and regular.

Figures 1 - 4. Metaphase in pollen mother cells of known hybrids. All are F_1 hybrids unless otherwise indicated. About 1800X.

1. I. innominata x I. tenax
2. I. douglasiana x I. purdyi
3. I. chrysophylla x I. douglasiana
4. I. innominata x I. douglasiana (F_2)



Figure 1.

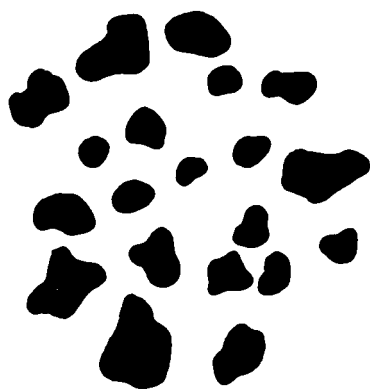


Figure 2.

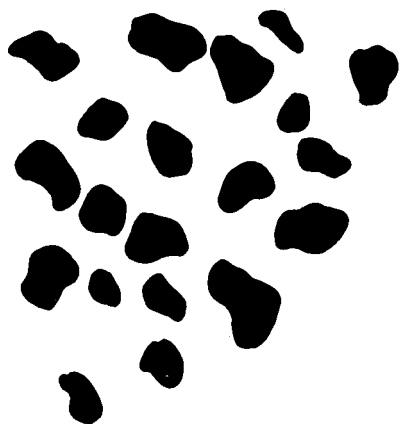


Figure 3.

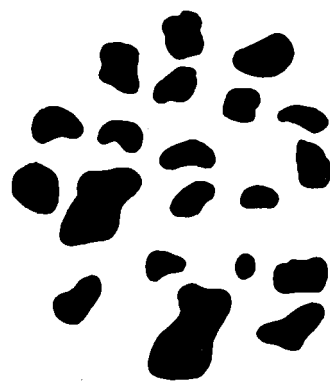


Figure 4.

Figures 5 - 8. Metaphase in pollen mother cells of known F_1 hybrids. About 1800X.

5. I. douglasiana x I. tenax
6. I. douglasiana x I. tenuissima
7. I. douglasiana x I. thompsonii
8. I. thompsonii x I. innominata

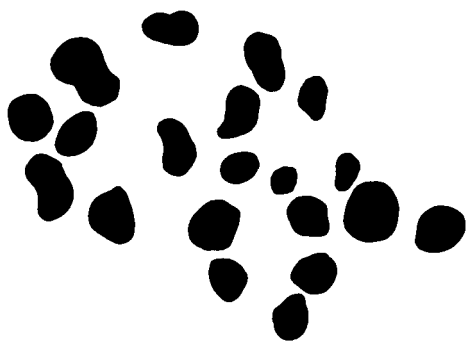


Figure 5.

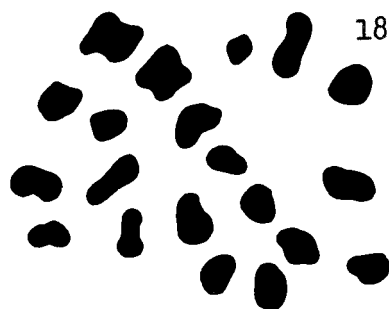


Figure 6.

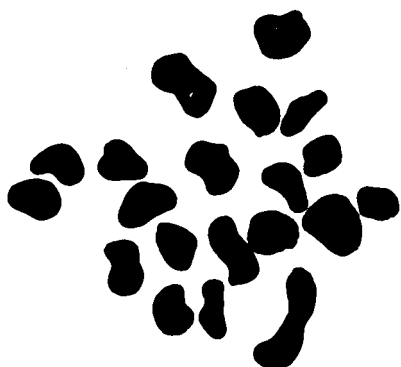


Figure 7.



Figure 8.

Figures 9 - 12. Metaphase in pollen mother cells of known F_1 hybrids. About 1800X.

- 9. I. tenuissima x I. tenax
- 10. I. douglasiana x I. hartwegii
- 11. I. innominata x I. chrysophylla
- 12. I. innominata x I. douglasiana

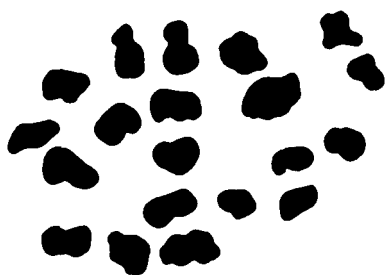


Figure 9.



Figure 10.



Figure 11.



Figure 12.

Field Studies

Despite the fact that differences between species are probably quantitative, inadequate knowledge of the distribution of species and of the variation within species made it necessary to conduct field studies on a qualitative basis. For these reasons such comparative terms as lanceolate, ovoid, broad, and narrow are used to describe differences which would be expressed quantitatively had a reliable sample been possible. Also, a detailed quantitative study of the morphological and ecological characteristics of any of the hybrid colonies in the following discussion is a major study in itself. Such a study is not within the scope of this problem.

Constancy of the characteristics of each species has been studied in the field and on specimens from the herbaria cited. Specimens have been collected as vouchers of the new information presented in the following discussion of natural hybrids. Most of these voucher specimens are mass collections and are filed as a special series under the genus Iris at the Oregon State College herbarium. A duplicate set of specimens are filed at the State College of Washington. Other specimens collected for this study are deposited at the Oregon State College herbarium but will not be retained in a special series.

I. tenax - I. chrysophylla hybrids.

I. tenax is characterized by narrow, distant bracts; a perianth tube from 4 to 9 millimeters in length and by lavender to purple

flowers with broad spatulate sepals. The plants are tall with definite stems. Though the species is typically purple flowered, two yellow-flowered populations have been found. One of these is along Scoggin's Creek in Washington County, Oregon. It has been treated as I. gormanii Piper and more recently as I. tenax var. gormanii (Piper) Foster. The second yellow-flowered population is on Monument Peak, Linn County, Oregon. This local population is apparently not well known and has not been cited in the literature of the subsection. Neither of these populations can be distinguished from the typical phase of I. tenax by any trait other than color.

General range of the species is from the central part of western Washington to southern Oregon. Ecologically it is a species of unshaded conditions and is abundant on the oak-covered hills of the Willamette and Umpqua valleys. It does not extend into coniferous areas unless trees are cut, roads built, or conditions otherwise disturbed in such a way that shading is reduced. Within the general range there seem to be no soil or moisture factors limiting its distribution. Factors controlling the northern and southern limits of the species range are probably climatic in nature.

I. chrysophylla is characterized by lanceolate, opposite bracts; a perianth tube 5 to 9 (occasionally to 12) centimeters in length; a pedicel less than 1 centimeter in length; and by pale yellow flowers with narrow perianth parts. In southwestern Oregon, where the species is most abundant, well marked stems are produced.

In the Cascade mountains of northern Oregon, the plants are often nearly stemless. Plants at two previously unreported stations of the species, Mill Creek, Polk County, Oregon, and Prairie Mountain, Benton County, Oregon, are of the Cascade type.

Ecologically I. chrysophylla is a species of open coniferous forests. It grows best on drier soils and will tolerate more shade than I. tenax. It is a characteristic species of the ponderosa pine and ponderosa pine - Douglas fir communities of southwestern Oregon. Excessive moisture seems to be the limiting factor in the distribution of I. chrysophylla.

Distinctive hybrids between I. tenax and I. chrysophylla have been found at three locations: (1) $4\frac{1}{2}$ miles up Mill Creek from the Dallas - Wallace Bridge highway, Polk County, Oregon. (2) $13\frac{1}{4}$ miles southwest of Roseburg, Douglas County, Oregon, along Oregon State highway number 42. (3) Steep hills along the first tributary of the North Santiam River west of the Detroit Dam, Marion County, Oregon. These locations are shown on figure 13. In all three locations conditions have been disturbed at the limits of the range of I. chrysophylla.

At all three sites individuals have been found which are intermediate between the parent species and which cannot be assigned to either species. Parent species and hybrids from the Douglas County location are shown in figure 15. Bracts of the hybrids are broader than is characteristic of I. tenax but not so broad as those of I. chrysophylla, and are opposite; flower color is maroon

Figure 13. Locations of natural hybrids.

- △ I. tenax - I. chrysophylla hybrids
- + I. bracteata - I. thompsonii hybrids
- I. innominata - I. douglasiana hybrids

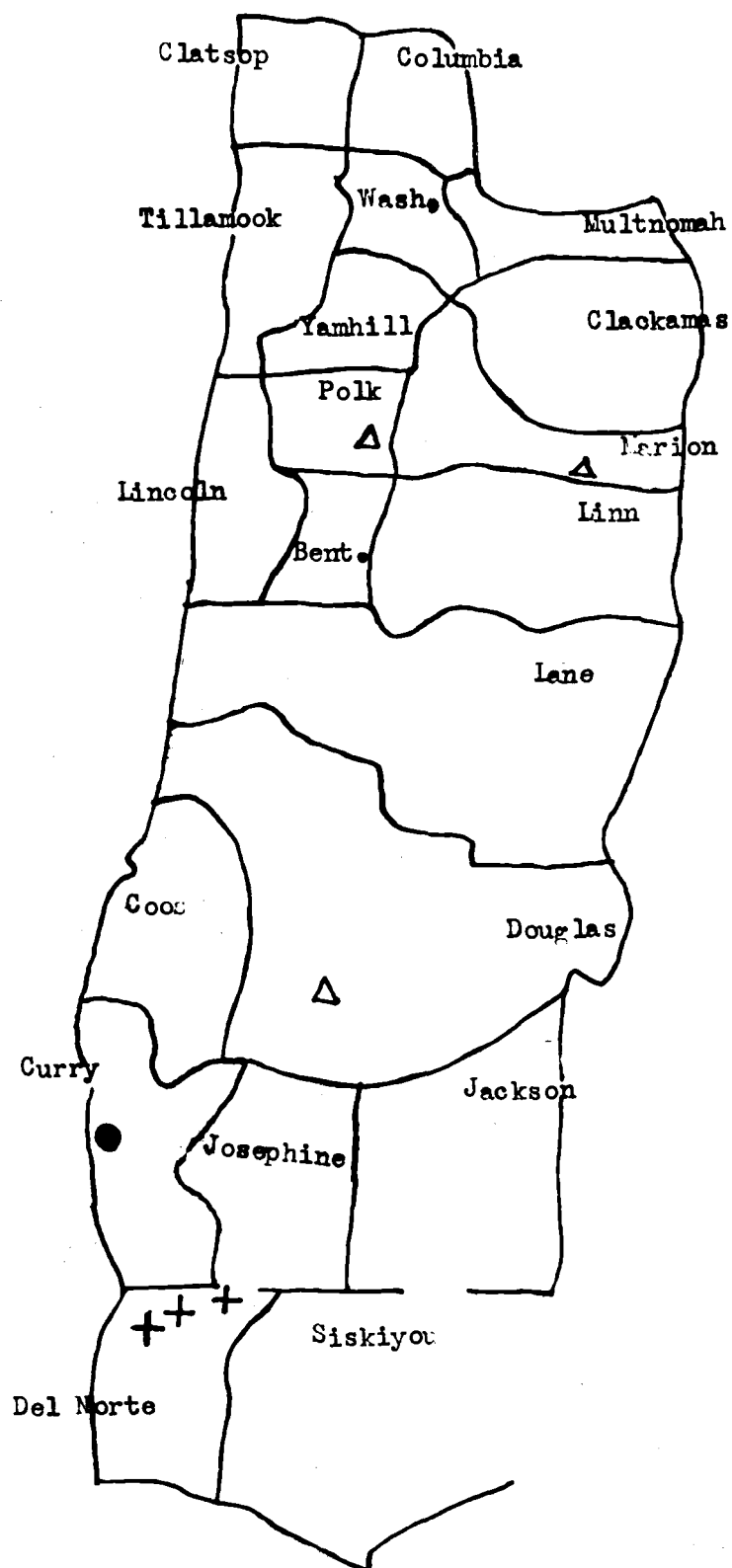


Figure 13.

Figure 14. Type specimen of I. thompsonii Foster.

Figure 15. I. tenax, I. chrysophylla, and hybrid forms.
Plants from 13 $\frac{1}{2}$ miles southwest of Roseburg,
Douglas County, Oregon.

- A. Typical I. tenax.
- B. Probable backcross hybrid.
- C. Intermediate form which is possibly an F_1 hybrid.
- D. Intermediate form which is possibly an F_1 hybrid.
- E. Typical I. chrysophylla.

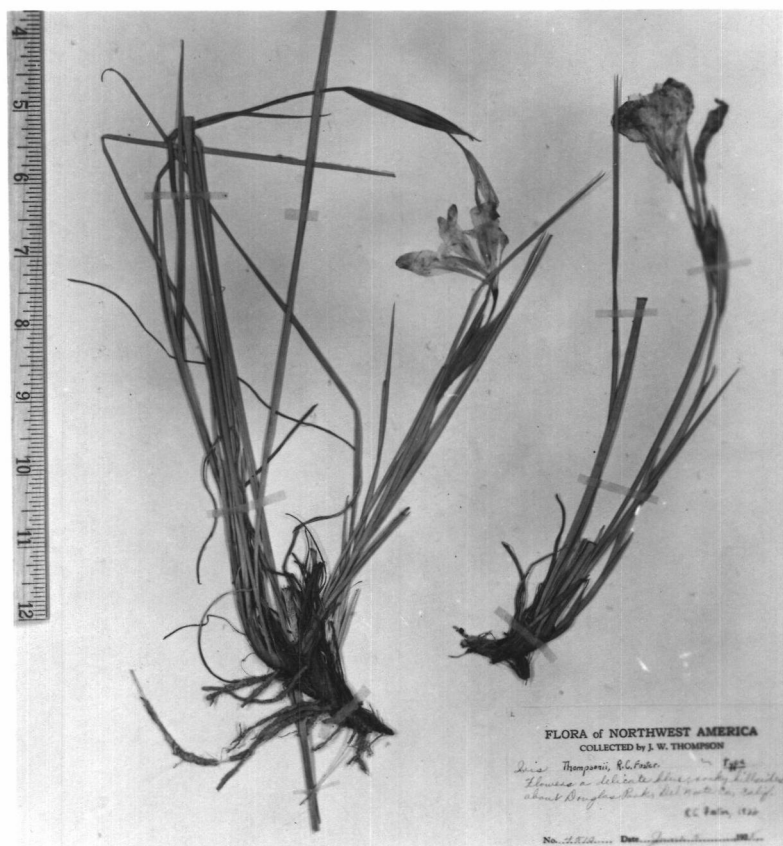


Figure 14.



Figure 15.

to greyish lavender; and the perianth parts are slender. The plants are smaller than typical I. tenax but have a definite stem. Perianth tube length in the natural hybrids averages 2.2 centimeters and the pedicel averages 1.4 centimeters. Comparative measurements in the known hybrids are 1.8 and 2.5. This indicates that the hybrids are possibly of the F_1 generation. For other characters the natural hybrids compare closely with the known hybrids.

The area of overlapping ranges is, in all three cases, small. At Mill Creek and along the North Santiam highway, a transect of less than 100 yards extends through the area occupied by both species. At the site southwest of Roseburg, a similar transect extends less than one-half mile.

Hybridization between these two species appears to be introgressive toward I. tenax. Individuals of I. tenax show definite I. chrysophylla characteristics for at least ten miles from typical I. chrysophylla. These individuals exhibit a change in color toward a pale purple; a reduction in size; and a tendency toward broader and less distant bracts. These modifications in I. tenax are what might be expected as a result of hybridization with I. chrysophylla. The intermediates previously discussed are found in the areas where the two species occur together but I. chrysophylla remains constant and no individuals of that species have been found which exhibit I. tenax characteristics.

Introgressive hybridization between these two species is a close parallel of a situation described by Anderson (2) in which

hybridization is followed by backcrossing and selection of backcross types. Apparently, in this case, only the offspring of the intermediate - I. tenax backcross are selected. The factors of the ecology and of the genetics of the organisms which bring about this selection are not known. The introgression, however, has resulted in a considerable increase in the variability of I. tenax while I. chrysophylla has remained constant.

The occurrence of I. chrysophylla at two locations in the Coast Range of Oregon was not unexpected. The presence of individuals of I. tenax in the Coast Range west of Corvallis, Oregon, with lanceolate, opposite bracts suggested possible hybridization with I. chrysophylla. At the Mill Creek location in Polk County, Oregon, the two species are in contact at the present time, as was previously mentioned. At Prairie Mountain, Benton County, Oregon, there is no present day contact on the north and probably not on the south. I. chrysophylla is abundant on a broad, well-drained meadow, along a south-facing slope near the summit of Prairie Mountain at an elevation of about 3200 feet. I. tenax is not now in contact on the north presumably because of the dense growth of Douglas fir on that side. The south side of the mountain is more open and the two species may come together though no intermediates have been found. I. tenax specimens collected at Horton, Lane County, eight miles to the south, have a narrower and more pale perianth which suggests hybridization with I. chrysophylla.

Thirty miles north of Prairie Mountain are individuals of

I. tenax with linear-lanceolate, opposite bracts, and narrow, pale purple perianth parts. These plants are probably the result of introgression from I. chrysophylla to I. tenax. These hybrid forms indicate either that I. chrysophylla is more abundant in the Coast Range than is now known or that it was more abundant in the past and has survived only on the more favorable sites. Either hypothesis may be true in part, but it seems unlikely that these forms are the result of recent hybridization. I. chrysophylla has not been found in the Coast Range between Prairie Mountain and Mill Creek, and distances are probably too great for plants at those locations to be involved as parents. The most probable explanation is that I. chrysophylla was more abundant in the Coast Range of northern Oregon in the past and has remained only at the dry, open sites such as Mill Creek and Prairie Mountain. The occurrence of a warm, dry period in postglacial times, followed by general cooling and increase in moisture (15) makes this a reasonable assumption. Whether I. chrysophylla was distributed throughout the general area of northwestern Oregon in the past or only on the higher peaks, is a question which cannot be answered. In either case, abundant opportunities for hybridization could have existed. Introgression, such as occurs today, could have given greater adaptive value to I. tenax while I. chrysophylla remained more constant and more subject to environmental change.

There is, however, no reason to suppose that the yellow-flowered forms of I. tenax on Monument Peak and in Washington County, Oregon,

are of hybrid origin. All the hybrids between these two species, including the artificial hybrids produced for this study, exhibit a tendency toward the lanceolate, opposite bracts of I. chrysophylla. The purple flower color is reduced to greyish lavender in the known F_1 hybrids, and none of the hybrids found in nature have yellow flowers. An independent origin for this color trait is not improbable. I. hartwegii, which is closely related to I. tenax, has yellow flowers, and there are yellow-flowered forms in I. macrosiphon which is otherwise purple-flowered.

I. douglasiana - I. innominata hybrids.

I. douglasiana is a tall species averaging about 60 centimeters in height and is characterized by leaves about a centimeter wide; a branching stem; lanceolate, opposite bracts; large, pale purple to white flowers; and a perianth tube 1 to 2 centimeters in length. Two or three flowers per branch are produced. Distribution of the species in Oregon is limited chiefly to a narrow, open coastal strip from Coquille, Coos County, south. The species normally extends inland only along river valleys. It has not been seen in dense shade.

I. innominata is a low species averaging about 35 centimeters in height and is characterized by narrow leaves which are about 4 centimeters wide; simple stems; ovate, opposite bracts; small, golden yellow flowers; and a perianth tube 1 to 2.5 centimeters in length. Distribution of the species is limited to the open meadows

and hills of southern Douglas, Coos, and Curry counties, Oregon.

Hybrid colonies of about 100 plants each of the I. douglasiana - I. innominata cross have been found along Saunder's Creek, Curry County, Oregon. The sites are $1\frac{1}{2}$ and $2\frac{1}{2}$ miles from the Rogue River, 3 miles upriver from Gold Beach, along the south side. The approximate location of these colonies is shown in figure 13. The colonies are found in cut-over forest land with most of the plants completely exposed to the sun, though a few are found in the shade of Umbellularia californica. No red or maroon colors such as are found in the artificial hybrids have been seen in nature. Aside from color, some of the individuals are similar to the known hybrids grown for cytological study. Perianth size and plant size appear to be intermediate between the parent species and the bracts are shorter and more ovoid than are those of I. douglasiana but are longer and narrower than those of I. innominata. These individuals may be F₁ hybrids. Other plants appear to be the result of backcrossing and segregation.

The taxonomic significance of the hybrids is considerable, aside from the demonstration of genetic continuity between species. Figure 13 shows individuals from one of the hybrid colonies in comparison with individuals referred to I. thompsonii Foster. There is a strong suggestion of the hybrid origin of that taxon. The type specimen of I. thompsonii is shown in figure 14. I. thompsonii has been collected along the Rogue River and along U.S. highway number 101 from Carpenterville to Brookings, Curry County, Oregon.

Figure 16. I. innominata, I. douglasiana and hybrid forms from Saunder's Creek, Curry County, Oregon.

- A. Typical I. innominata
- B. - E. Hybrid individuals
- F. Typical I. douglasiana



Figure 16.

In California it has been collected along Smith River, northeast of Crescent City, Del Norte County. The species can be distinguished from I. innominata by the more lanceolate bracts and by the pale purple to lavender flower color. It also seems to be taller, averaging about 45 centimeters. These are characteristics which could be fixed by backcrossing of the I. douglasiana - I. innominata hybrids to I. innominata.

A similar hypothesis can be erected to explain those specimens with more ovate bracts and lavender-gray flowers referred by Foster (13) to a new variety, I. douglasiana var. oregonensis. Backcrossing of the intermediate hybrids of the I. douglasiana - I. innominata cross to I. douglasiana could result in the fixing of these I. innominata traits in otherwise typical I. douglasiana.

While both assumptions are largely hypothetical, they are lent support by the occurrence of these variants in an area where the two species come together and hybridize. The only barriers seem to be ecological, though exact factors cannot be stated. The removal of the forest trees with the accompanying reduction in shade has apparently removed the barrier to hybridization in the case discussed here, but elevation and soil factors may be important in other locations. However, hybrids probably will be found wherever the hills of Coos and Curry Counties are near the ocean and conditions are disturbed or where I. douglasiana extends inland along river valleys. In these areas, at least, the two species can be expected to occur together.

I. bracteata - I. thompsonii hybrids.

I. bracteata is a tall species averaging about 50 centimeters in height with a thick perianth tube 0.5 to 1.0 centimeter in length, a pedicel 3 to 6 centimeters long, and golden yellow flowers. Typically the leaves are a glossy green on the upper surface and glaucous on the lower. The species has been seen only in southwestern Josephine County, Oregon, and northeastern Del Norte County, California. Ecologically it is restricted to shaded places. The species is found in greatest abundance within ponderosa pine communities, but it is sometimes found on cut-over forest land under a cover of bracken fern.

I. thompsonii has been discussed as a possible hybrid segregate of the I. douglasiana - I. innominata cross. Colonies are best developed along the lower Smith River, from 12 to 15 miles northeast of Crescent City, California. In this location, the colonies are well established on open rocky hillsides, and have not been seen in the shade.

Proceeding northeastward from Jedediah Smith State Park in Del Norte County, over the Siskiyou mountains into Oregon, the colonies become more shade tolerant. Color changes gradually from predominantly pale purple flowers to predominantly yellow flowers in the colony, though a few white-flowered plants are present. Bract characteristics appear to be intermediate between the two species, changing gradually from ovoid and 5 centimeters long, to narrower and 7 centimeters long. Height of the plant also becomes

progressively greater as colonies near typical I. bracteata are examined. Three miles north of the summit of the Siskiyou mountains only typical I. bracteata has been seen. Specimens representing three colonies are shown in figure 17 to illustrate the transition.

No individuals that compare with the F_1 hybrids have been found. The transition between the two species is gradual, probably because of ecological requirements which permit more hybridization and survival of most of the hybrid offspring.

I. bracteata - I. chrysophylla hybrids.

Distinct hybrids between these two species have not yet been clearly demonstrated. Despite the pronounced morphological differences between the two, only one individual has been secured which can be considered intermediate. The relationship of the perianth tube to the pedicel is reversed in these two species. I. chrysophylla has a perianth tube 5 to 6 times longer than the pedicel. In I. bracteata the pedicel is 5 to 6 times longer than the perianth tube. In the intermediate specimen cited above, the pedicel is twice the length of the perianth tube, clearly not characteristic of either I. chrysophylla or I. bracteata. This specimen was collected near Bridgeview, Josephine County, Oregon, where the two species occupy the same general area.

Complementing this admittedly limited evidence, field examination reveals hybrid characteristics which are not readily demonstrable with pressed specimens. Near Cave Junction, Josephine County,

Figure 17. I. thompsonii, I. bracteata and hybrid form.

- A. I. thompsonii.
- B. Hybrid form.
- C. I. bracteata.

Figure 18. Two specimens of I. thompsonii from Carpenterville, Curry County, Oregon, and two hybrid plants from the I. innominata - I. douglasiana cross, Saunder's Creek, Curry County, Oregon.

- A-B. I. thompsonii.
- C-D. Hybrid forms.



Figure 17.

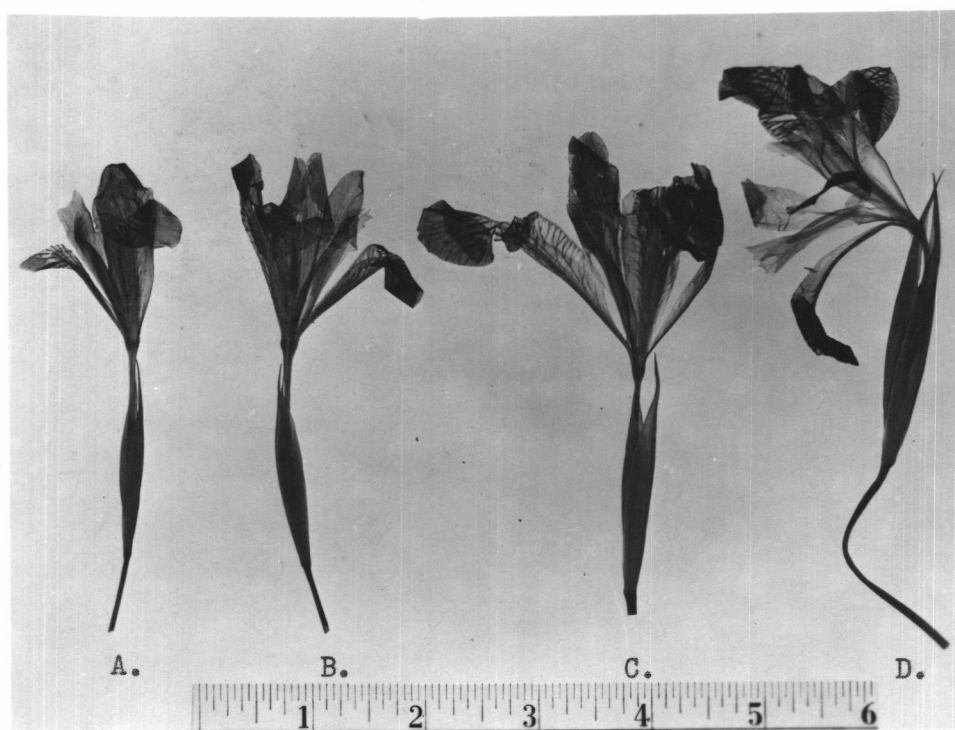


Figure 18.

there are individuals of I. bracteata with narrow perianth segments characteristic of I. chrysophylla. The hybrid origin of these individuals is supported by the fact that all the known hybrids involving I. chrysophylla as a parent exhibit the narrow perianth of that species. There are also specimens, in the Cave Junction area, of I. chrysophylla with perianth color similar to the golden yellow of I. bracteata. The known I. bracteata x I. chrysophylla hybrid has golden yellow flowers and all other crosses involving golden yellow and pale yellow-flowered parents show the flower color of the golden yellow parent.

Taxonomy

Species concept.

The following species concept is based on the work of Stebbins (25), Dobzhansky (8), Mayr (19), Simpson (22), Huxley (16), Clausen, Keck and Hiesey (5) (6) (7), and others. In addition, numerous discussions with colleagues have aided in clarifying the ideas expressed by those authors. The species concept has been developed around two principles: The nomenclature should reflect the biology of the organisms, and it should be as objective as possible.

A species is considered to be a population or series of inter-fertile populations which are reproductively isolated from other such groups. The term population is used in a general sense to refer to small or large numbers of individuals which freely inter-breed. To use this definition, the individual specimen must be viewed not as a unit in itself but as a representative of the population of which it is a member.

While this definition is an attempt to attain complete objectivity in nomenclature, such an end is impossible of attainment because of the varying degrees of intersterility between populations. Except in rare cases, sterility develops over a period of many years and at any one point it may be necessary to set arbitrary limits to a species. Reproductive isolation is developed by the accumulation of genetic differences between

populations to the extent that hybrid offspring either do not survive or do not reproduce. Complete isolation is not abruptly developed and not all the hybrids between two populations will have the same degree of genetic imbalance.

Study of chromosome pairing and distribution in hybrids is one method of evaluating the genetic differences between populations. While pairing and distribution may be regular and the organism still be sterile, or pairing and distribution be irregular and some fertility still be present (24), cytological studies correlated with pollen and seed condition give a reliable estimate of hybrid fertility.

In this subsection, apparently the only factors which keep the populations distinct are environmental. Ecological isolation almost axiomatically indicates genetic differences between populations. If these genetic differences continue to develop, internal barriers can occur and the species of this definition evolve. However, the absence of internal barriers does not mean that a group as complex as this subsection should be combined into a single nomenclatural category. There remains the question of delimiting interspecific entities. For that reason, the nomenclature of the subsection Californicae will be revised only where field study is thought sufficient to indicate the limits of the various taxa.

Oregon species.

I. tenuis Wats. clearly does not belong in the subsection with

the other members of the Californicae. The species differs morphologically and also in chromosome number ($2N = 28$). Hybrids between this species and other members of the Californicae could not be produced and have not been observed in the field.

The species is distinguished by its wide, pale green, ensiform leaves; slender, branched stems; small, scarious bracts; and narrow white flowers. In most of these characters it resembles the eastern I. cristata Ait. While such a relationship is not impossible from the viewpoint of geography, there are pronounced cytological differences between I. tenuis and I. cristata. I. cristata has a diploid chromosome number of $2N = 32$ according to both Foster and Simonet. However, Foster cites a report by Longley of $N = 12$. Whichever count is accepted, there is a difference of 4 chromosomes between I. tenuis and I. cristata which must be accounted for. The loss, or gain, of chromosomes is not impossible but it cannot be assumed without study. One method of analysis which might establish the relationships of I. tenuis is the detailed analysis of the chromosome morphology of I. tenuis and its suspected allies. In the meantime, no disposition of the species is proposed.

Nomenclatural revision will be proposed for the remainder of the Oregon species. Because there are no apparent cytological barriers there is good reason to suppose that hybrids will be found wherever two of the taxa occur together. A key to the Oregon taxa retained is given below. Complete descriptions and citations are not given because they are readily available in Foster. Though

there are hybrid forms which will not fit the key, descriptions have not been emended to include these individuals because that would result in a taxonomic category so broad as to obscure relationships and make recognition of distinct populations difficult. Subspecies, rather than variety, is used as a nomenclatural category to emphasize the ecological and geographical isolation present in these forms. I. tenax Dougl. is the oldest valid name in this group and in the subsection and must be retained as the binomial combination.

Key to the Oregon Subspecies

- A. Bracts distant, perianth tube 1 cm. or less long.
 - 1. I. tenax ssp. tenax
- AA. Bracts opposite.
 - B. Perianth tube at least 5 cm. long.
 - 2. I. tenax ssp. chrysophylla.
 - BB. Perianth tube not more than 4 cm. long.
 - C. Bracts lanceolate.
 - D. Flower golden yellow.
 - 3. I. tenax ssp. bracteata.
 - DD. Flowers dark to pale purple or sometimes white.
 - 4. I. tenax ssp. douglasiana.
 - CC. Bracts ovate.
 - D. Flowers golden yellow.
 - 5. I. tenax ssp. innominata.
 - DD. Flowers pale purple.
 - 6. I. tenax ssp. thompsonii.

1. I. tenax Dougl. subspecies tenax (I. tenax Douglas ex Lindley, Bot. Reg. xv. t. 1218, 1829). This subspecies includes the typical form which has been discussed previously in this paper as I. tenax. Also included, without nomenclatural distinction is the yellow-flowered I. tenax var. gormanii. The yellow-flowered form from Monument Peak, Linn County, Oregon, will be included within I. tenax gormanii and therefore within I. tenax tenax without nomenclatural distinction.

2. I. tenax subspecies chrysophylla (Howell) (I. chrysophylla Howell, Fl. N.W. America i 633, 1902). No type specimen was designated for Howell's I. chrysophylla. However, filed with the type specimen collection at the herbarium of the University of Oregon is a specimen labeled "type specimen" in the distinctive handwriting of Thomas Howell. This specimen, collected at Grants Pass, Josephine County, Oregon, in May 1887, must be considered the type specimen for Howell's species and therefore for the proposed subspecies.

3. I. tenax subspecies bracteata (Watson) (I. bracteata Watson, Proc. Amer. Acad. xx. 375, 1885). This subspecies includes the species as described by Watson.

4. I. tenax subspecies douglasiana (Herbert) (I. douglasiana Herbert, Bot. Beech. Voy. 395, 1841). Included in I. tenax douglasiana without nomenclatural distinction is I. douglasiana var. oregonensis Foster. So long as it is understood that Foster's variety is probably of hybrid origin, there is no need to distinguish

a form which obviously belongs to what has been described as I. douglasiana. Since this subspecies is found in California as well as Oregon, this new combination must necessarily include the California plants. This does not mean that the California plants of this taxon should be ignored in any further study. There is undoubtedly considerable variation present that is not included in the Oregon representatives.

5. I. tenax subspecies innominata (Henderson) (I. innominata Henderson, Rhodora xxxii 23, 1930). This subspecies has been retained as originally described except for the reduction in rank.

6. I. tenax subspecies thompsonii (Foster) (I. thompsonii Foster, Rhodora xxxviii 199, 1936). The only real difference between this proposed new subspecies and I. tenax innominata is in the purple flower color of I. tenax thompsonii. Since it has been suggested that I. tenax thompsonii may be of hybrid origin with I. tenax innominata as one parent, a close morphological relationship is to be expected. The two taxa differ slightly in distribution, I. tenax thompsonii is a species of elevations between 400 and 1000 feet while I. tenax innominata is usually at sites over 1500 feet. For that reason and because I. tenax thompsonii does form distinct colonies, it is retained.

California species.

Nomenclatural revision of the California species of the subsection will not be undertaken until adequate field studies can

be made because the complexity present in this group cannot be sufficiently analyzed by an examination of herbarium material. Field work with the Oregon species has demonstrated the inadequacy of herbarium specimens to represent the sometimes great variation present within a small colony. A discussion of the California taxa follows.

I. hartwegii Baker.

This species has been recognized (13) as a close relative of I. tenax tenax. It differs only in being smaller and having yellow flowers. Since yellow flowers are present in typical I. tenax and herbarium material is often inadequate in representing size, there seems to be no good reason to retain I. hartwegii as a separate species. However, pending field study it will not be reduced in nomenclatural rank.

I. tenax Dougl. var. australis (Parish) Foster

The only taxonomic question regarding this variety in recent years is concerned with whether it should be retained as a variety of I. hartwegii or of I. tenax. Since it has been suggested that I. hartwegii is closely related to I. tenax, there is no good reason why this variety should not be included within I. tenax. Further work is necessary before a decision can be made regarding whether this variety should be retained or be included within I. tenax subspecies tenax.

I. munzii Foster

This species is known only from Tulare County, California. In appearance it resembles I. tenax but is much larger, with lanceolate bracts, and has leaves nearly a centimeter wide. In his original description (14) Foster cited five specimens, of which the type has been seen.

Three specimens of I. hartwegii borrowed from the herbarium of Fresno State College seem to be transitional between I. hartwegii and I. munzii. The bracts are quite broad and long and the flowers are larger than is typical of I. hartwegii. These specimens are all from Fresno County, California, and bear the following Fresno State College accession numbers: 5676, 6079, 6472.

Comparison of the type specimen of I. munzii with the known hybrids grown at Oregon State College shows a close morphological relationship between I. munzii and the I. hartwegii x I. douglasiana hybrids. However, I. douglasiana has never been reported from the Sierra habitat of I. hartwegii.

I. douglasiana Herbert

This taxon has been discussed with the Oregon species. One variety (I. douglasiana var. mendocinensis Eastw.) is probably a hybrid between I. douglasiana and I. macrosiphon, but it will be included within I. tenax douglasiana of this thesis until better known. Its hybrid origin is indicated by the narrow perianth segments, narrow bracts, and slender perianth tube of the type specimen.

I. fernaldii Foster

This species is known only from the type specimen cited by Foster in his original description (14). It is similar to I. macrosiphon and is probably best included in that complex species until additional material is studied.

I. macrosiphon Torr.

This species is variable with purple and yellow-flowered forms present. It has been seen in the field in the Redwood forest of northern California, on chaparral-covered hills near Ukiah, California and on the east side of the Sacramento valley near Chico, California. It is probable that hybridization with other species is contributing to the diverse ecological and morphological characteristics of this species.

I. macrosiphon Torr. var. elata Eastw.

This variety was described by Miss Eastwood (11) from a specimen collected at Clear Lake Park, Lake County, California. The variety is distinguished from the typical form of the species by its greater height. The original description states that the variety and the typical form are found growing together. In a complex species, it is doubtful if such minor variants should be accorded nomenclatural status.

I. citrina Eastw.

This species was considered by Miss Eastwood (12) to be allied

to I. macrosiphon. Examination of the type specimen indicates that this species should be included in I. macrosiphon as a basis for further study.

I. humboldtiana Eastw.

This species was described from Humboldt County, California. The species is clearly allied to I. macrosiphon and was so considered by Miss Eastwood (11). This species should also be included within I. macrosiphon as a basis for planning further study. The type specimen has been seen.

I. lamsdaleana Eastw.

In the course of field work for this study, specimens of I. lamsdaleana were collected at the type area, Richardson's Grove, Mendocino County, California. These specimens are similar to the type specimen cited in the original description (10). An early flowering species, I. lamsdaleana has been collected in flower in early March and April. Specimens seen suggest a close relationship between I. purdyi Eastw. and I. lamsdaleana.

I. purdyi Eastw.

The inflated stem leaves and comparatively short perianth tube on the type specimen suggest that I. purdyi may be of hybrid origin, with I. bracteata as one parent. The perianth tube is nearly intermediate in length between that of I. bracteata and I. macrosiphon. However, the truncate, lobed stigma would seem to

make this species quite distinct from all others in the Californicae. The reliability of this characteristic must be evaluated in the field because of difficulty in studying the stigma on pressed plants.

I. tenuissima Dykes var. purdyiformis Foster

Foster suggested the possibility of this variety being a hybrid between I. tenuissima and I. purdyi. Examination of a photograph of the type specimen indicates that this suggestion is not improbable.

I. tenuissima Dykes

This species was placed by Foster in the same complex as I. chrysophylla. The limited material seen for this study indicates a close relationship between I. chrysophylla and I. tenuissima. Superficially, the only difference lies in the shorter, more ovoid bracts of I. tenuissima. I. tenuissima, a species of the mountains of northern California, may occur within the range of I. chrysophylla.

I. pinetorum Eastw.

Known only from the type specimen, this species is probably a hybrid between I. hartwegii and I. tenuissima. The bracts are distant suggesting a close relationship with I. hartwegii, but the perianth tube is longer than is found in I. hartwegii.

Summary and Conclusions

The chromosomes of eleven F_1 hybrids (I. chrysophylla x I. douglasiana, I. douglasiana x I. hartwegii, I. douglasiana x I. purdyi, I. douglasiana x I. tenax, I. douglasiana x I. tenuissima, I. douglasiana x I. thompsonii, I. innominata x I. chrysophylla, I. innominata x I. douglasiana, I. innominata x I. tenax, I. tenuissima x I. tenax, I. thompsonii x I. innominata) and one F_2 hybrid (I. innominata x I. douglasiana) have been examined in metaphase of the first division of meiosis. Anaphase I and second division figures have been examined in these four other hybrid combinations. All these hybrids show regular pairing and distribution of chromosomes and all have the same chromosome number ($N = 20$). The same number has been reported for all the other species of the subsection Californicae which have been studied. Because of these data, the absence of cytological barriers to hybridization is assumed. Pollen production in the hybrids is high and the pollen seems normal. The hybrids were produced without difficulty and are vigorous plants. The hybrids, and their parents, are stable upon transplanting and show no annual variation. For the major taxonomic traits, the hybrids are intermediate between their parents.

Field studies were conducted during which natural hybrids were found between I. tenax and I. chrysophylla; I. innominata and I. douglasiana; I. bracteata and I. thompsonii; and I. bracteata and I. chrysophylla. The origin of I. thompsonii as a hybrid

segregate of the I. innominata - I. douglasiana cross is suggested.

Because there are no apparent cytological barriers to hybridization between the six Oregon species named above, and natural hybridization does occur, reduction in nomenclatural rank to subspecies is proposed for all six species. I. tenax is retained as the binomial.

Further work is needed to clarify certain problems. The work presented in this thesis has been conducted on a qualitative and observational basis. Quantitative work can now be done to evaluate ecological relationships between species. This can be done at the locations where natural hybrids occur and can be correlated with a quantitative analysis of morphological changes in the plants due to hybridization. Sufficient information is available so that reliable sampling can be planned. Further cytological work is also needed to provide evidence for some of the conclusions which have been assumed as reasonable. Additional field work is also needed to aid in clarifying the taxonomy of the California species of the subsection.

The Oregon subspecies of the subsection Californicae are not easily placed in groups. I. tenax innominata and I. tenax thompsonii are distinguishable only on a color basis. Since a hybrid origin for I. t. thompsonii has been proposed, a close relationship is reasonable. The gradual transition between I. t. bracteata and I. t. thompsonii suggests a close relationship between those subspecies. I. t. tenax and I. tenax chrysophylla appear to be quite

distinct morphologically and ecologically. Hybrids between the two do occur, but the apparent introgression toward I. t. tenax indicates the presence of at least partial barriers. The exact nature of those barriers will probably require detailed ecological study.

Since all the members of the subsection Californicae appear to be closely related cytologically, a further study must be made before complexes within the subsection can be understood. However, I. tenax tenax, I. tenax var. australis, I. hartwegii, and I. munzii all exhibit narrow, distant bracts and a perianth tube less than one centimeter long and are apparently closely related. I. t. chrysophylla and I. tenuissima, because of long perianth tubes and narrow perianth, appear to be closely related. They also appear to be more closely related to I. macrosiphon than to other taxa. I. t. douglasiana does not appear to belong to any group of taxa, remaining distinct because of the branching stem. I. purdyi and I. bracteata appear to be closely related because of inflated stem leaves and similar perianth tube lengths. Material available for other species is insufficient to suggest relationships.

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