



**Studies from the Herbarium
California State University, Chico**

-Number 6-

**VIOLACEAE
OF BUTTE COUNTY, CALIFORNIA**

F. Jay Fuller

and

-Number 7-

**CUCURBITACEAE
OF BUTTE COUNTY, CALIFORNIA**

Robert A. Schlising



April 1987

Studies from the Herbarium
California State University, Chico
Chico, CA 95929-0515

ISBN 978-0-9726953-4-3

Scan-to-pdf May 2011

Studies from the Herbarium
California State University, Chico

-- Number 6 --

April 1987

V I O L A C E A E
O F B U T T E C O U N T Y , C A L I F O R N I A

F. Jay Fuller

Meriam Library

California State University, Chico

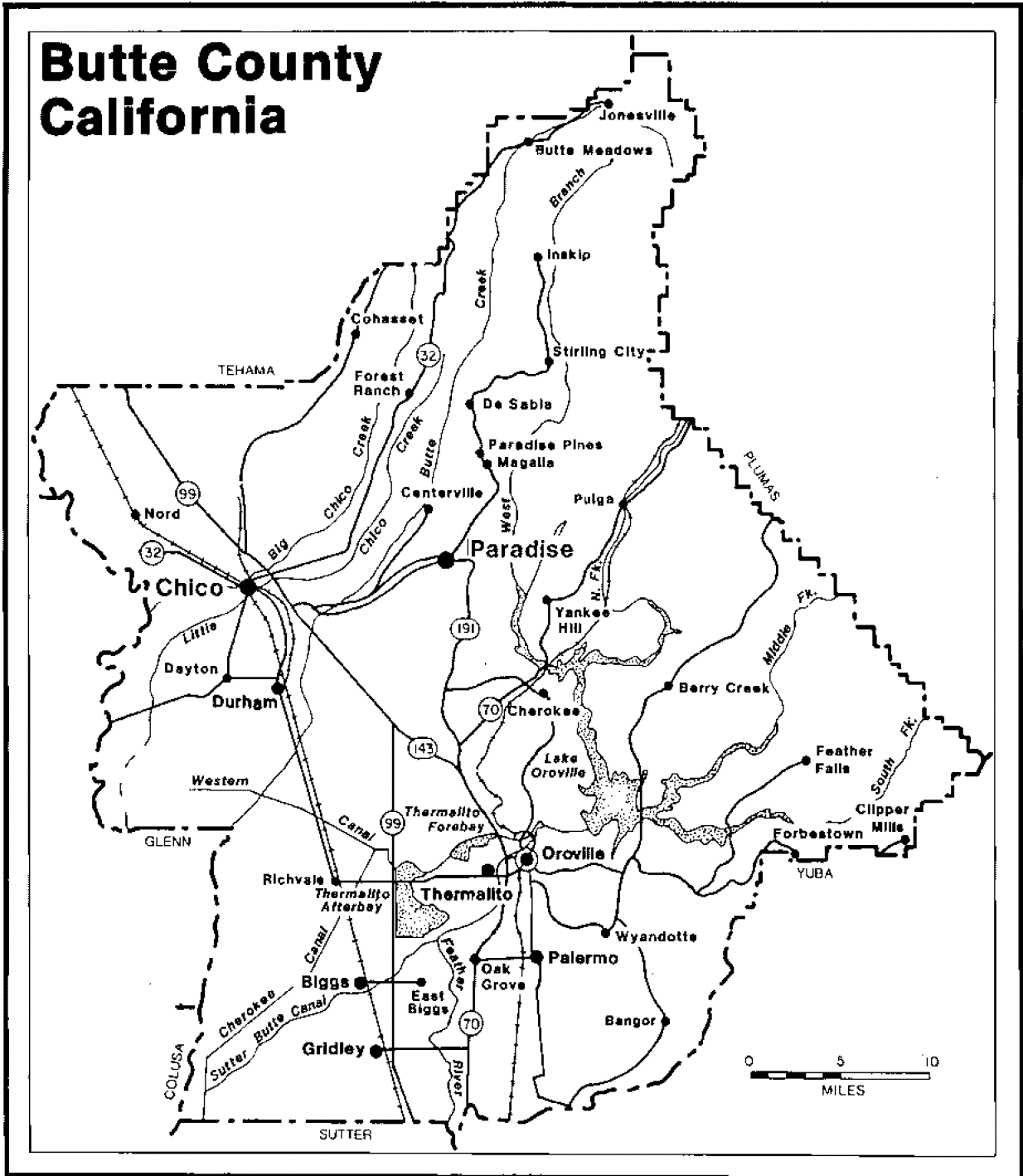
The upper photograph on the cover is of Viola lobata subsp. psychodes (the lower is of Marah watsonii, a member of the Cucurbitaceae).

There are 12 species (with 1 variety and 5 subspecies) of the Violaceae (the violet or pansy family) known to occur without cultivation in Butte County, California. The majority of these 18 taxa are native to the region. They occur in all major plant communities except freshwater marsh, with 8 of the species most common in yellow pine and/or red fir forests, and 4 species most common in valley grassland or foothill woodland. Several of these natives are poorly represented by collections or contemporary sightings, and may be quite rare in the county (e.g., V. bakeri, V. quercetorum, V. sheltonii, and some of the subspecies of V. purpurea). Two of the Butte County violets are introduced weeds (V. odorata and V. tricolor), one of which (V. odorata) has the potential to become inextricably established in and about some of the county's low elevation riparian systems.

The following treatment for all species in the Violaceae is based primarily on field studies in the county 1982-1985. In addition, it is based on specimens from Butte County on file in herbaria of California State University, Chico (CHSC), and the University (UC) and Jepson (JEPS) Herbaria at the University of California, Berkeley. Descriptions and keys are designed mainly for identification and separation of Butte County taxa. Characteristics listed in the keys are occasionally repeated in the descriptions, and the short descriptions are not exhaustive in covering all aspects of each species. Studies of western violets by Baker (1935, 1936, 1940, 1949a,b,c, 1953, 1957 and 1960) and Clausen (1929, 1964) have been primary sources for taxonomic information. The two major floras used in the preparation of this study -- Munz (1968) and Abrams (1951)-- should be consulted for more complete descriptions, for Latin names in synonymy up to these dates, and for illustrations (in Abrams). Common names are based on Abrams (1951), and Niehaus and Ripper (1976).

A feature of this local floristic study is a summary of the literature on reproductive biology for the genus and each species as it pertains to Butte County taxa. Flowering dates in the literature have been modified to agree with observations made during field research. Studies of insect visitors do not reflect research or field observations in Butte County, unless specifically stated. These are included to indicate probabilities as to what may be the case until further research is done.

Dots on the county range maps included for each taxon indicate 1) herbarium specimens studied by the author, 2) sight records made in the field by the author and in some cases, 3) specific locations cited in taxonomic treatments if the identity of the taxon seems certain. The Butte county outline maps (including the location map shown on the next page) have been provided by Charles Nelson, Department of Geography, California



State University, Chico. Plant community boundaries on some of the dot maps are taken from a map prepared by James Nelson in the "Land Use Element of the Butte County, California General Plan" (Nelson, 1979). Plant community names are from Munz (1968).

The VIOLACEAE in Butte County

Perennial herbs related to the garden pansy, and represented only by the genus Viola; leaves alternate or basal, simple, entire, lobed or divided, with stipules; sepals 5, free or united at base, persistent; flowers in most species of 2 kinds: 1) showy, chasmogamous and asymmetric, found at the ends of leafy stems or on stems arising directly from the root-stock, occurring in early flowering season and, 2) inconspicuous and cleistogamous, without petals, located in upper axils of leaves, rarely in axils of underground stems, occurring with or later than showy flowers; petals 5, the lower one large, with a nectar spur projecting backwards, the upper 2 slightly smaller, the lateral 2 smaller still and bearded; stamens 5, alternate with the petals, the lower 2 with appendages projecting into the nectar spur; ovary superior, style club-like, with the entire stigma turned to one side; fruit an ovoid capsule, opening explosively by 3 boat-shaped valves.

Viola is one of the most easily recognized genera of native plants in California and, paradoxically, one of the most difficult taxonomically. No matter the habitat, whether in a dry grassland, in a mountain meadow or on a windblown peak, the flower's shape is so consistent that even a young child recognizes a violet when finding one in the wild. But, this similarity of flower masks a web of complexity which several botanists have devoted a lifetime's work to untangle.

Plants of Viola use a number of reproductive strategies which give them the ability to successfully grow in diverse habitats, and which demonstrate their competitive efficiency and ecological versatility. These strategies are: 1) the use of rooting, vegetative stolons, 2) the production of showy, chasmogamous flowers which, though having the ability to self-pollinate, primarily attract insect visitors for cross-pollination, 3) the ability to hybridize with other members of the genus which are closely related, and 4) the production of cleistogamous flowers which are obligate self-pollinators.

None of the native violets uses vegetative stolons for reproduction. However, Viola odorata and other species use this method quite successfully in many parts of the world and this capacity is one of the reasons that V. odorata may become an established part of the Butte County flora.

Some of California's native violets produce only chasmogamous flowers and use neither vegetative stolons nor

cleistogamy (examined below) as strategies (e.g., V. douglasii, V. pedunculata), though the majority of Butte County plants use both chasmogamy and cleistogamy in reproduction.

Chasmogamous flowers serve a number of reproductive functions. Their primary function is to provide a bank of viable seed for the continuance of the species. This is accomplished, as it is for most angiosperms, through the movement of pollen from one plant to another of the same species by insect visitors. This activity also serves to maintain the genetic fitness of the population through gene exchange, produces new genotypes for colonization of new habitats and increases speciation through hybridization (Beattie 1976).

Violets are especially flexible in their ability to hybridize (Brainerd, 1904, 1906). First, their chasmogamous flowers attract a wide range of insect visitors and pollinators. Beattie (1974) lists the insect genera Andrena, Bombus, Osmia, Bombylius and Rhingia as visiting Viola. To this list, Moldenke (1976) adds Ashmeadiella and Dialictus, while Krombein et al. (1979) lists Chelostomopsis and Proteriades. Gerrit (1976) adds Eristalis to the list and Baker (1935) has observed thrips visiting and pollinating at least one group of violets (Chamaemelanium). Some butterflies are also implicated (Beattie, 1971, Brittnacher et al., 1978). The majority of these insects are generalists and move freely from one species to another in search of nectar or pollen. Second, genetic barriers are lacking between violet species which are closely related (Russel, 1954). Baker (1949a,b,c) and Clausen (1962) have studied the chromosome numbers of North American violets and find that within any group (taxonomic "section") there is a series of plants characterized by multiples of basic chromosome numbers. And third, species which are closely related often have geographic ranges which overlap (e.g., Viola purpurea subspecies and V. pedunculata), allowing the potential for gene exchange between species.

Possibly the violet's most interesting reproductive strategy is the production of cleistogamous flowers. These are flowers which do not have petals and are strictly self-pollinating. They are formed every year, regardless of the plant's age or of environmental conditions which may prevent the production of the showy, chasmogamous flowers. Clausen (1962) states that the majority of the seeds produced by violets are made by the cleistogamous flowers. The advantages to this mode of seed production are, 1) if predators of chasmogamous flowers or seed should build up to critical levels, there is an alternate seed source, and 2) the production of numerous seeds with the same gene combination as the ecologically adapted parent plant maintains the gene combination best suited to the local conditions.

Key to the species of VIOLACEAE in Butte County

- A Flowers yellow, at least at bases of petals and on the nectar spur; spur as wide as long; access to spur cavity blocked by style
 - B Stipules 3-lobed, almost as large as leaves
 - 1. VIOLA TRICOLOR
 - BB Stipules lanceolate, much smaller and very different from leaves
 - C Leaves deeply lobed or divided; leaf margins without serration or dentation
 - D Leaf blades palmately 3-7 lobed, the lobes broad and not further dissected
 - 2. VIOLA LOBATA
 - DD Leaf blades cut into distinct narrow divisions, each division again parted 3-5 times
 - E Plants of granitic or basaltic slopes; leaves broader than long, palmately 3-divided, each division palmately 3-parted into oblong segments; cleistogamous flowers present in axils of underground stems
 - 3. VIOLA SHELTONII
 - EE Plants of valley grassland; leaves as long or longer than broad, bipinnately 3-5 divided, each division linearly parted into 3-5 cleft segments; cleistogamous flowers absent
 - 4. VIOLA DOUGLASII
 - CC Leaves not lobed or divided; leaf margins toothed or entire
 - F Upper petals yellow on back, though whole corolla may darken somewhat with age; plants strictly erect
 - G Leaves heart-shaped, with glabrous, toothed margins; petals deep yellow, the lateral and lower with purple veins; sepals 5-7 mm long; plants of shaded stream banks and wet meadows
 - 5. VIOLA GLABELLA

- GG Leaves lanceolate, with entire, pubescent margins; petals light yellow, the lateral and lower with brown veins; sepals 4-5 mm long; plants of dry red fir forest
6. VIOLA BAKERI
- FF Upper petals brown or purple on back, the entire corolla retaining color with age; plants erect to prostrate
- H Plants of rocky outcrops in valley grassland; cleistogamous flowers absent
7. VIOLA PEDUNCULATA
- HH Plants of foothill woodland or conifer forest; cleistogamous flowers present in axils of upper leaves
- I All leaves triangular in outline with leaf margins entire to regularly toothed; leaves and flowers crowded at tops of stems
2. VIOLA LOBATA
- II Basal leaves ovate, upper leaves lanceolate with leaf margins entire to irregularly toothed; leaves and flowers scattered along the stems
- J Leaves with fine hairs, gray-green on both sides; plants of chaparral and foothill woodland
8. VIOLA QUERCETORUM
- JJ Leaves somewhat succulent, often with a distinct purple tint to the dorsal side; plants of conifer forests
9. VIOLA PURPUREA
- AA Flowers white, blue or purple, without yellow on petals or nectar spur; spur longer than wide; access to spur cavity not blocked by style
- K Plants of cultivated lawns, riparian systems and waste areas below 2500 feet elevation; leafy stolons present; flowers purple, very fragrant
10. VIOLA ODORATA
- KK Plants of meadows and damp banks above 2500 feet elevation; stolons absent; flowers white or blue, lacking fragrance

- L Petals white; leaves and flowering stems arising directly from the root-stock
11. VIOLA MACLOSKEYI

- LL Petals blue; leaves and flowers scattered along the stems
12. VIOLA ADUNCA

1. VIOLA TRICOLOR L.
Wild Pansy

MAP 1

Description Short lived perennial; leaves heart-shaped, 1-2 cm wide, regularly serrate, peduncles surpassing the leaves; sepals 6-10 mm long, glabrous; petals 12-16 mm long, the lower purple, the upper 2 yellow, and the lateral 2 yellow, often white.

Reproductive biology Flowers February to September. Viola tricolor is regularly visited by domestic honeybees and native Bombylius species.

Distribution and habitat This species is an ephemeral garden escape which has, on occasion, established itself in waste areas close to human habitation below 1000 feet elevation. Field observation has not discovered a population without cultivation which has survived for over two years.

2. VIOLA LOBATA Benth.
Yellow Wood Violet, Pine Violet

Viola lobata has been divided into two subspecies and one variety. Two of these, subspecies psychodes and variety integrifolia, occur in Butte County. There is the possibility that V. lobata subsp. lobata may also exist within the county near its SE corner, where it comes into contact with Plumas and Yuba counties. Subspecies lobata, which is not included in the key, looks very much like subsp. psychodes, but is visibly pubescent throughout, especially on the upper surfaces of the leaves and along the veins of each leaf's lower side.

Key to the subspecies of Viola lobata in Butte County

- A Leaves glabrous, wedge- or kidney-shaped in outline, with the margins having lobes of more or less equal length
2a. VIOLA LOBATA subsp. PSYCHODES

- AA Leaves minutely pubescent, triangular in outline, with the margins deeply toothed to entire; if toothed, the central tooth distinctly longer than the others
2b. VIOLA LOBATA var. INTEGRIFOLIA

2a. VIOLA LOBATA Benth. subsp. PSYCHODES (Greene) Munz
[V. psychodes Greene] MAP 2

Description Glabrous perennial; leaves ovate to wedge-shaped in outline, 2.5-8 cm wide, palmately 3-7 lobed, the glaucous lobes of essentially equal size; peduncle tending to surpass the leaves; sepals 6-8 mm long, glabrous; petals 8-12 mm long, deep yellow, all or lower 3 purple-brown veined at base, upper 2 purple on back, lateral 2 yellow-bearded; cleistogamous flowers present in axils of upper leaves.

Reproductive biology Flowers April to October. This violet is visited by Bombylius species. Cleistogamous flowers develop in July and have been observed by the author to persist on the plants until the first snowfall in November.

Distribution and habitat V. lobata subsp. psychodes has been found in Butte County from the lower limits of the yellow pine forest (ca 1800 feet elevation) to 5500 feet. Often it can be located in close proximity to V. purpurea subsp. purpurea, the latter being found in open woods, while V. lobata subsp. psychodes will be found under the surrounding shrubs. Baker (1960) states that several of the collections he examined were made on serpentine areas and noted the possibility that it might be restricted to that substrate; however, no collections or sightings of this subspecies have been made on the county's extensive serpentine outcrops.

2b. VIOLA LOBATA Benth. var. INTEGRIFOLIA Wats.
[V. deltoidea Greene] MAP 3

Description Glabrous perennial; leaves heart-shaped to triangular in outline, 4-10 cm wide, entire to deeply toothed, the teeth acute at apex and central tooth longer than others; peduncles tending to surpass the leaves; sepals 6-9 mm long, glabrous; petals 8-14 mm long, deep yellow, all or lower 3 purple-brown veined at base, upper 2 purple on back, lateral 2 yellow-bearded; cleistogamous flowers present in axils of upper leaves.

Reproductive biology Flowers April to July. This variety is visited by Bombylius species. Like the above subspecies, it develops cleistogamous flowers in July.

Distribution and habitat Field observations for V. lobata var. integrifolia have located only scattered populations south of the Middle Fork of the Feather River. These have tended to be at lower elevations than subspecies psychodes (1165 to 2550 feet) and in more open habitats. It seems to do particularly well where the yellow pine forest and foothill woodland intergrade. Munz (1968) notes that this variety in NW California and adjacent Oregon supplants subspecies lobata. Though Butte County is geographically removed from this location, environmental conditions may be such that variety

integrifolia has filled the ecological niche in Butte County where subspecies lobata is usually found; hence, the reason why subspecies lobata is conspicuously absent.

3. VIOLA SHELTONII Torr.
Shelton's Violet

MAP 4

Description Glabrous perennial; leaves wedge-shaped in outline, 3-7 cm wide, broader than long, palmately 3-divided, each division again 3-parted into oblong segments; peduncles 8-15 mm long, somewhat surpassing the leaves; sepals 6-8 mm long, with fine hairs; petals 10-13 mm long, deep lemon-yellow, the lower 3 purple-brown veined, the upper 2 purple-brown on back, the lateral 2 with club-like hairs; cleistogamous flowers present in upper axils of underground stems.

Reproductive biology Flowers from April to June. Insect visitors have not been observed in the field nor can specific information be found in the existing literature. It is possible that some species of Bombylius and Osmia may act as pollinators of the showy flowers. Viola sheltonii probably does quite well without pollinators, since it not only produces cleistogamous flowers with an abundance of fertile seed, but because those flowers are located in the axils of underground stems, it plants its progeny when sowing its seed!

Distribution and habitat This violet is restricted in Butte County to granitic areas near the Middle Fork [F. J. Fuller, 0108 (CHSC) and V. Oswald, 1122, personal herbarium] and North Fork [R. A. Schlising, 3999 (CHSC)] of the Feather River between 1600 and 2250 feet elevation, and on the Lovejoy basalt formation of Lumpkin Ridge at 4400 feet elevation.

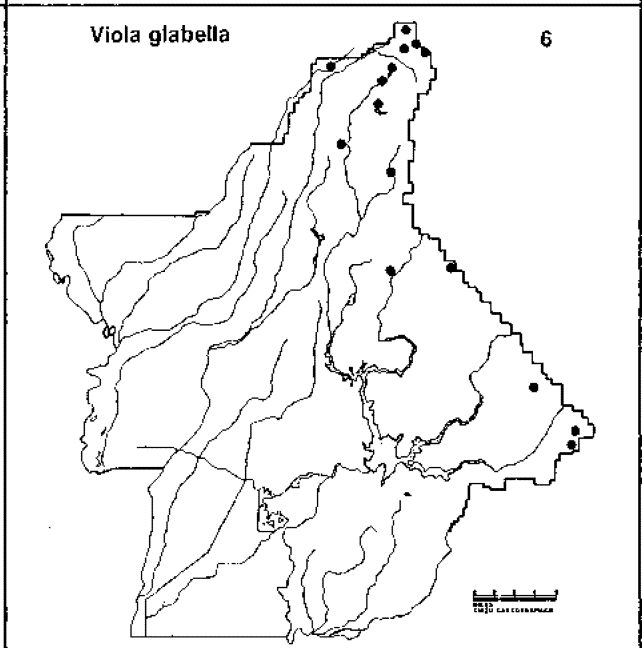
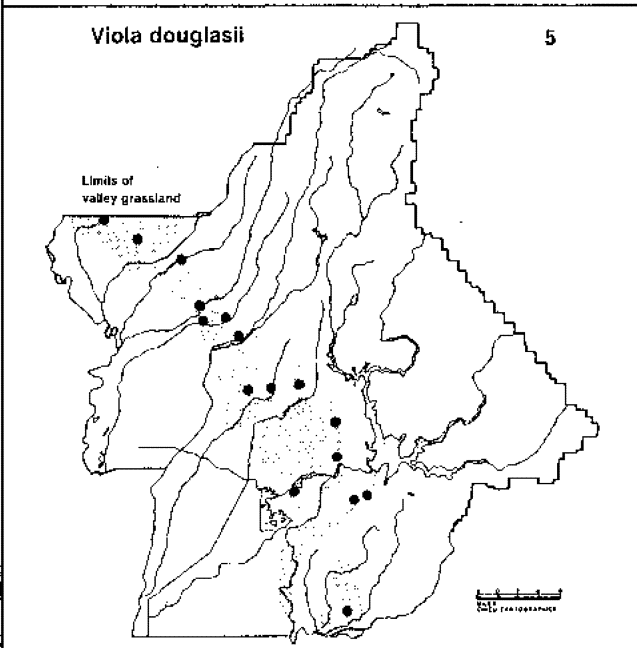
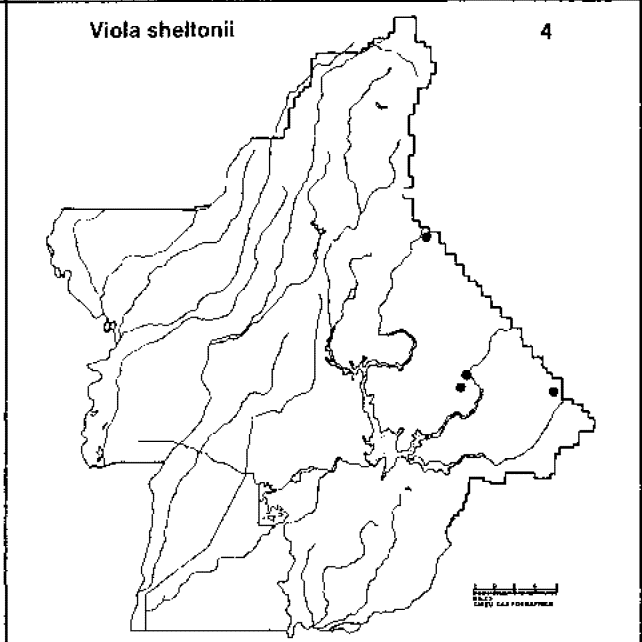
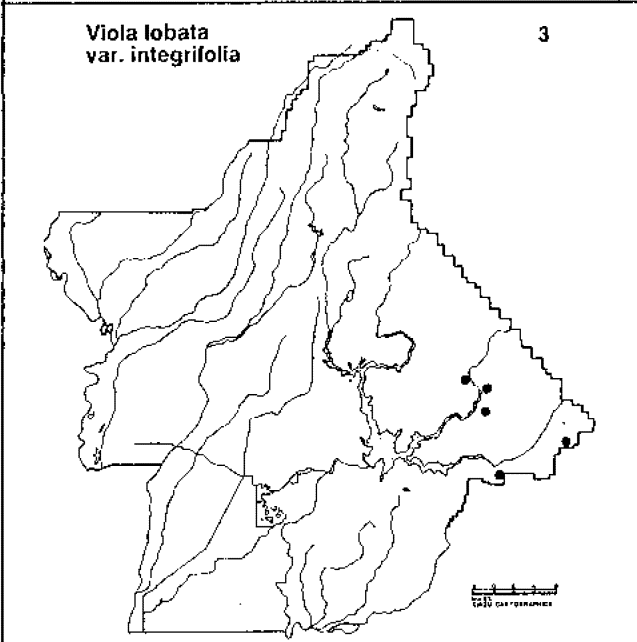
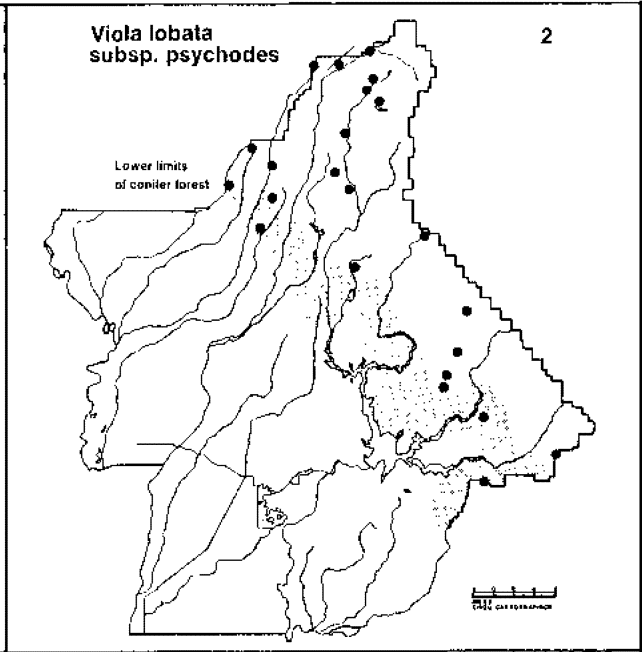
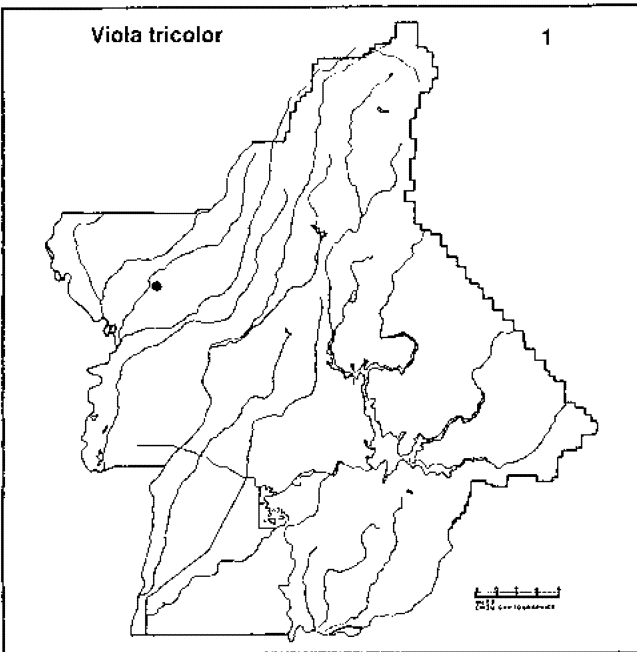
4. VIOLA DOUGLASII Steud.
[V. chrysantha Hook. not Schrad.]
California Golden Violet

MAP 5

Description Pubescent perennial; leaves ovate in outline, 2-5 cm long, longer than broad, bipinnately 3-5 parted into 3-5 cleft linear or oblong segments; peduncles 2.5-12 cm long, usually surpassing the leaves; sepals 6-10 mm long, with fine hairs; petals 8-15 mm long, light golden-yellow with dark veins, the upper 2 petals light to rich brown on back, the lateral 2 yellow-bearded; cleistogamous flowers not produced.

Reproductive biology Flowers from February to May. Insect visitors have not been observed in the field, though Bombylius, Bombus and Osmia species may possibly act as pollinators.

Distribution and habitat This violet is restricted to valley grassland from 150 feet to 2300 feet elevation. Populations are widely distributed and consist of numerous individuals.



5. VIOLA GLABELLA Nutt.

Stream Violet, Smooth Yellow Violet, Wood Violet MAP 6

Description Glabrous to finely pubescent perennial; basal leaves heart to kidney-shaped, 2.5-7 cm wide, usually wider than long; stem leaves ovate to heart-shaped, smaller than basal leaves, found only where stem and peduncle meet; peduncles 2-5 cm long; sepals 5-7 mm long, glabrous to finely pubescent; petals 6-12 mm long, deep yellow, the lower 3 with purple veins, the lateral 2 bearded; cleistogamous flowers present in upper axils of stem leaves.

Reproductive biology Flowers March to August. In spite of this violet's preferred habitat of shade, when direct sunlight becomes present numerous insect visitors have been recorded. Beattie (1971), in a study of this violet in the coastal redwoods, has observed flies of the families Bibionidae, Muscidae, Calliphoridae, and Tachinidae, crane flies of the Tipulidae and Trichoceridae, all on the foliage, while sawflies (Tenthredinidae), hoverflies (Sypidae: Sphegina infuscata, Sphegina armatipes, Xylota rainerei), small bees (Andrenidae: Andrena spp. and Halictidae: Lasioglossum spp.), and occasional butterflies (unspecified) visited the flowers. Also observed in the general vicinity of the plants were a few parasitic species such as Ichneumonids, Conopids and solitary wasps (unspecified).

Distribution and habitat This violet has been found between 3020 and 6690 feet elevation in Butte County. Viola glabella prefers moist habitats such as stream banks and wet meadows, particularly where abundant shade is produced by stands of large shrubs such as Salix spp. and Prunus spp. Often close inspection of the bases of these shrubs at proper elevations will uncover otherwise hidden populations.

6. VIOLA BAKERI Greene

Baker's Violet

MAP 7

Description Minutely pubescent perennial; leaves lanceolate to narrow ovate, 2.5-6 cm long, entire, almost smooth to short-pubescent on margins and veins; peduncles slender, equal to or shorter than leaves; sepals 4-5 mm long; petals 8-10 mm long, light yellow, the lower 3 with brownish-red veins, the lateral 2 scaly-pubescent at base; cleistogamous flowers present in upper axils of leaves.

Reproductive biology Flowers late June through August. Insect visitors to this violet are unknown.

Distribution and habitat Viola bakeri is possibly the rarest member of the genus in Butte County. It has been collected in a few locations by Willow Creek, 6420 feet elevation, [F. J. Fuller, 0087 (CHSC)] and by the Carr Mine, 5600 feet, [R. A. Schlising, 4441 (CHSC)] at points near the lower limits of the

red fir forest. These small populations consist of a few widely scattered individuals. A verbal report has been made of this violet possibly occurring in Coon Hollow (5600 feet) below Snow Mountain, though this sighting has yet to be confirmed by the author or by an herbarium specimen.

7. VIOLA PEDUNCULATA T. & G.
Johnny jump-up, Wild Pansy

MAP 8

Description Almost smooth to slightly hairy perennial; leaves triangular-ovate, 2-5.5 cm long, about as wide, coarsely but shallowly serrate; peduncles up to 15 cm long, much exceeding the leaves; sepals 6-8 mm long, puberulent; petals 10-16 mm long, orange-yellow, the lower 3 with reddish-brown veins, the upper 2 red-brown on back, the lateral 2 bearded; cleistogamous flowers not produced.

Reproductive biology Flowers February to April. Krombein et al. (1979) report the polylectic leaf-cutter bee Chelostomopsis rubifloris as using the pollen of V. pedunculata. No insect visitor has been observed in the field by the author.

Distribution and habitat In Butte County, V. pedunculata has been collected and observed exclusively on Table Mountain, a volcanic mesa (1000 feet to 1580 feet elevation) just north of Oroville. The mesa's vegetation consists mainly of valley grassland species, with the stout rootstocks of V. pedunculata embedded in the basaltic outcrops and cobbles which litter the mesa's upper surface (Jokerst, 1983). The plants are unusually large and robust, and have generated some debate among local botanists as to their exact nature. Some have attributed their size to optimal growing conditions, while others think that the violets listed under this heading are hybrids of unknown lineage. Cytological investigations should help clarify this plant's relationship to others in the genus. Until such studies are conducted, it appears from the gross morphology that these plants are V. pedunculata.

8. VIOLA QUERCETORUM Baker & Clausen

MAP 9

Viola quercetorum is a tetraploid species (N=12) which, because of its obvious physical similarity to both V. pedunculata (N=6) and to two of the subspecies of V. purpurea (both N=6), has given rise to an interesting disagreement concerning its evolutionary history. Stebbins et al. (1963) claim that V. purpurea subsp. purpurea and subsp. mohavensis were the parent taxa. Their argument is based on morphology (leaf pubescence, anther appendages, etc.), geographical distribution and chromatographic evidence. Clausen (1964) thinks that V. pedunculata and V. purpurea subsp. purpurea crossed to produce V. quercetorum. His theory rests on the fact that V. quercetorum

"occupies an ecological zone that became available after the rise of the Coast Ranges and after the development of the oak woodlands between the coast and the coniferous forests of the lower Sierra Nevada. Before that time V. pedunculata must have found congenial habitats over a considerably larger territory than now because the coastal influence reached farther inland." He partially concedes that V. purpurea subsp. mohavensis may have been involved in the process, but that it became involved only because "V. pedunculata probably was contiguous to V. purpurea ssp. purpurea in Pliocene central California and to relatives of ssp. mohavensis in Pliocene southern California." However, that does not mean that the two subspecies of V. purpurea crossed with each other, but that "it is possible that V. quercetorum may have arisen more than once, from crossings between V. pedunculata and the two subspecies of V. purpurea" (pp. 186-187).

Description Finely hairy perennial; leaves of 2 kinds, the lowest erect, rounded to ovate, with wedge to heart-shaped base, 2-5 cm long, 2-3 cm wide, irregularly round-toothed, the upper leaves smaller, lanceolate, more acute; peduncles 4-13 cm long, usually exceeding the leaves; sepals 6-8 mm long, hairy; petals 10-12 mm long, yellow, the upper 2 somewhat darkened on back, the lateral 2 club-bearded; cleistogamous flowers present in the axils of upper leaves.

Reproductive biology Flowers March to June. Specific insect visitor information is lacking in the literature, but it can be hypothesized, considering the morphological similarity of V. quercetorum with its suggested parent species, that leaf-cutter bees like Chelostomopsis rubifloris, Proteriades rufina, and Osmia spp. are responsible for pollination of the chasmogamous flowers.

Distribution and habitat This plant is poorly represented in herbarium collections at CHSC, often mistakenly identified as V. purpurea and occupying the same sheet [P. Delaplane, 71 (CHSC)]. Collections at other herbaria (UC, JEPS) do not include specimens from Butte County. There have been only two positive sightings in the field (one on Highway 32 between Chico and Forest Ranch, the other on Table Mountain).

9. VIOLA PURPUREA Kell., not Stev.
Mountain Violet, Yellow Pine Violet

V. purpurea has been taxonomically divided into a series of ten closely related subspecies which occur in the western United States and northwestern Mexico (Clausen, 1964). Seven of the subspecies are found in California (Munz, 1968); six of these are in Butte County (subsp. purpurea, mesophyta, atriplicifolia, integrifolia, dimorpha and geophyta).

Baker (1949c) and Clausen (1964) suggest that these subspecies are ecotypes, each adjusted to a specific climatic zone and edaphically distinct habitat, which retain their

morphological character, even though some hybridization occurs where these taxa come into contact.

The Butte County plants reflect this hypothesis quite well. Usually, plants found which fit the key are located in a distinct habitat, and leave little doubt as to their character in relation to the other subspecies; however, occasions have arisen where, even after close and repeated inspection, the subspecific character of the material is not ascertainable.

Line drawings (after Baker, 1949c) are included in the key to help in identifying material. These are included with the kind permission of the California Botanical Society.

Key to the subspecies of Viola purpurea in Butte County

A Basal leaves wedge-shaped at base

B Upper leaves triangular, with toothed margins; plants of ponderosa pine forest
9a. VIOLA PURPUREA subsp. PURPUREA



BB Upper leaves lanceolate, with more or less entire margins; plants of jeffery pine forest
9b. V. PURPUREA subsp. MESOPHYTA



AA Basal leaves truncate to heart-shaped at base

C Basal leaves pointed at apex, deeply toothed, almost lobed
9c. V. PURPUREA subsp. ATRIPLICIFOLIA



CC Basal leaves rounded at apex

D Foliage green; plants of red fir forest

E Margins of all leaves entire; stems scarcely developed above ground
9d. V. PURPUREA subsp. INTEGRIFOLIA



Basal Upper
(life-size)

EE Margins of upper leaves
toothed; stems well
developed above ground
9e. V. PURPUREA subsp. DIMORPHA



DD Foliage grayish; plants of open
areas in red fir forest, with
stems buried in volcanic ash
9f. V. PURPUREA subsp. GEOPHYTA



Basal Upper

9a. VIOLA PURPUREA Kell., not Stev. subsp. PURPUREA MAP 10
[V. purpurea Kell., not Stev. subsp. pinetorum Greene]

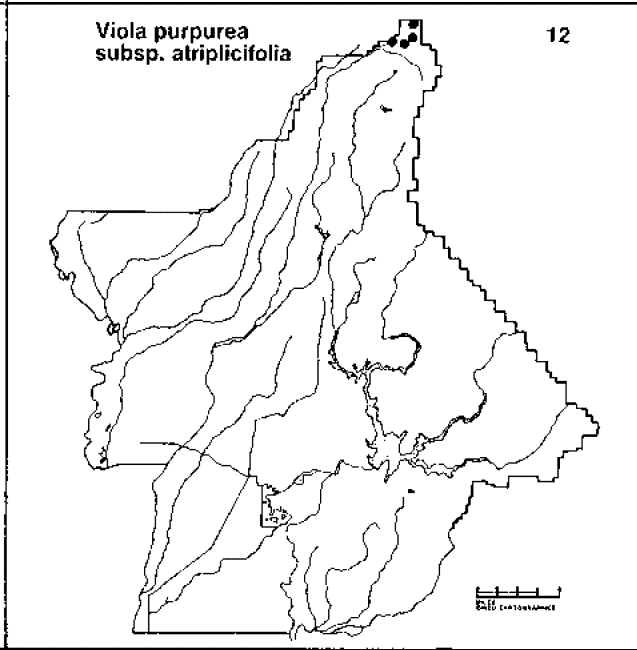
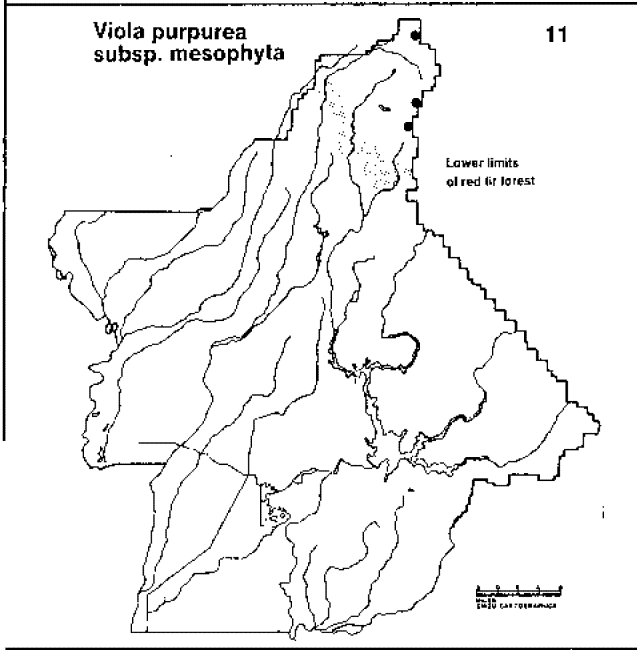
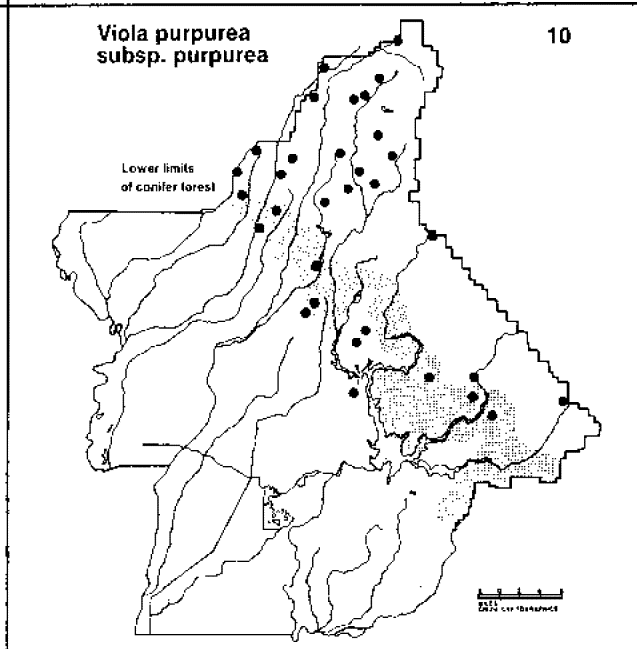
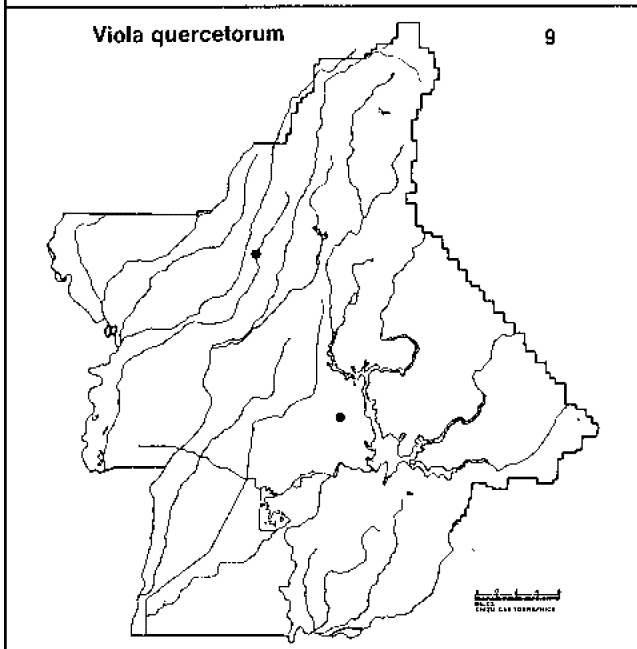
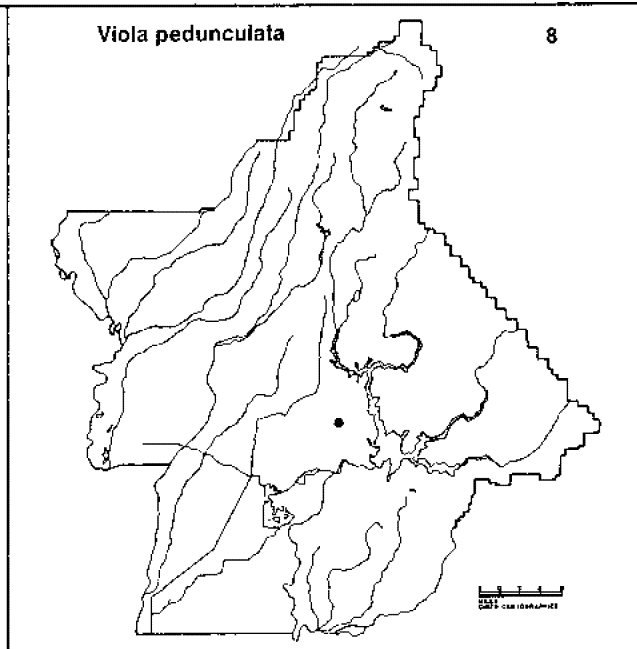
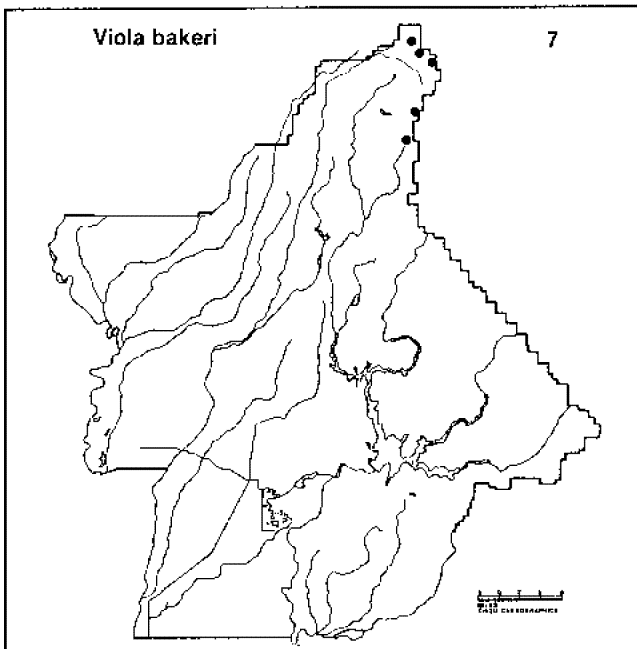
Description Somewhat succulent perennial; basal leaves ovate, wedge-shaped at base, 1.5-3 cm wide, 1.8-3.5 cm long, irregularly sinuate-dentate, with purple tint to dorsal side; upper leaves broadly lanceolate, regularly crenate-serrate; peduncles 3-10 cm long, exceeding the leaves; sepals 4-6 mm long; petals 8-10 mm long, deep lemon-yellow, the lower 3 with purplish-brown veins, the upper 2 purple on back, the lateral 2 bearded; cleistogamous flowers present in axils of upper leaves.

Reproductive biology Flowers April to July. Krombein et al. (1979) do not segregate insect visitors to V. purpurea by subspecies, but list the following leaf-cutter bees under the heading V. purpurea: Chelostomopsis rubifloris, Proteriades rufina, Osmia exigua, and Osmia albolateralis visenda. Bombylius spp. are listed by Moldenke (1976) and have been observed in the field by the author.

Distribution and habitat This subspecies is the most common violet in Butte County, ranging from the lower limits of the yellow pine forest (ca 1800 feet elevation) to the lower limits of the red fir Forest (ca 6000 feet). It is found where the forest canopy is open and the floor relatively clear. In many locations, it is in such abundance as to be one of the major contributors to the vegetative understory, sharing that distinction with Iris macrosiphon and Ceanothus prostratus.

9b. VIOLA PURPUREA Kell., not Stev. subsp. MESOPHYTA MAP 11
Baker & Clausen
[V. purpurea Kell., not Stev. var. mesophyta Peck.]

Description Much like subsp. purpurea; basal leaves longer than broad; upper leaves lanceolate with more or less entire margins, 2-5 cm long.



Reproductive biology Flowers May to August. Insect visitors may be the same as for subspecies purpurea.

Distribution and habitat Subspecies mesophyta is most readily separated subspecies purpurea by habitat. Whereas subspecies purpurea occurs below the red fir forest and in the company of Pinus ponderosa and Quercus kelloggii, subspecies mesophyta is found where Pinus jefferyi replaces P. ponderosa and Quercus vaccinifolia replaces Q. kelloggii. This area is a small corner of NE Butte County from near Humboldt Peak (ca 7100 feet elevation) to just east of Crane Valley (ca 5500 feet).

9c. VIOLA PURPUREA Kell., not Stev. subsp. ATRIPLICIFOLIA
(Greene) Baker & Clausen MAP 12
[V. purpurea Kell., not Stev. var. atriplicifolia Peck.]

Description Much like subsp. purpurea; basal leaves about as wide as long, evenly 5-7 toothed, almost lobed; upper leaves only slightly toothed.

Reproductive biology Flowers May to August. Insect visitors may be the same as for the subspecies purpurea.

Distribution and habitat This subspecies is, again, most readily separated from the other subspecies known to occur in Butte County by habitat. Subspecies atriplicifolia grows in close association with Abies magnifica (red fir) where the trees are well spaced and the floor litter is scant or absent. It has been found from just above Jonesville (ca 5250 feet elevation) to very near the top and just east of Humboldt Peak (7087 feet elevation).

9d. VIOLA PURPUREA Kell., not Stev. subsp. INTEGRIFOLIA
Baker & Clausen MAP 13

Description Much like subsp. purpurea; margins entire on all leaves, without any dentation at all.

Reproductive biology Flowers June to August. Insect visitors may be the same as for subspecies purpurea.

Distribution and habitat Subspecies integrifolia tends to grow in the dense shade beneath young red and white firs. It seems especially prevalent on the east side of the county, often near subspecies mesophyta, where Abies magnifica are interspersed with Pinus jefferyi.

9e. VIOLA PURPUREA Kell., not Stev. subsp. DIMORPHA
Baker & Clausen MAP 14

Description Stems more robust and of upright structure than subsp. purpurea; margins of upper leaves toothed.

Reproductive biology Flowers June to September. Insect visitors may be the same as for the subspecies purpurea.

Distribution and habitat This subspecies has been found just east of Humboldt Peak (7087 feet elevation) and just south of Humberg Summit (6000 feet) in open red fir forest. One collection was mentioned by Clausen (1964) [Keck & Clausen, 3770], and that presumed population has been observed by the author. The area is an opening in the red fir forest with clumps of Arctostaphylos nevadensis scattered at regular intervals.

9f. VIOLA PURPUREA Kell., not Stev. subsp. GEOPHYTA
Baker & Clausen

MAP 15

Description Stems deeply buried in volcanic ash; leaves covered with short, gray hairs.

Reproductive biology Probable flowering time is May to August. Insect visitors are unknown, but are probably much the same as for subspecies purpurea.

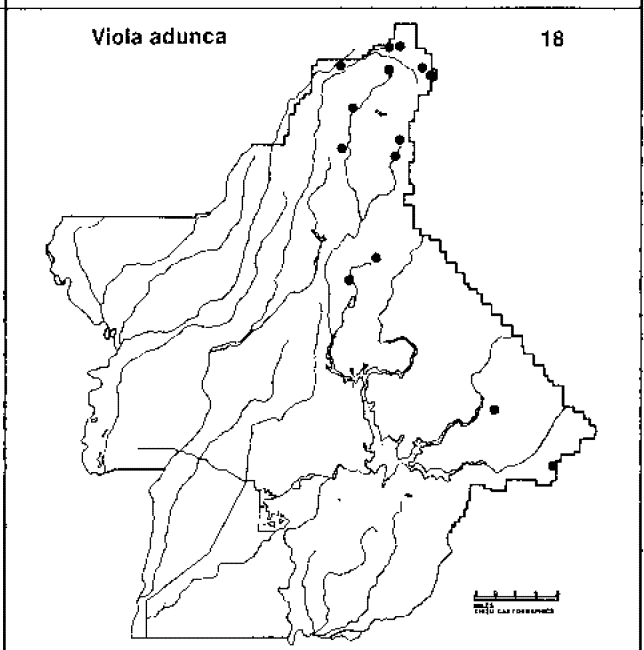
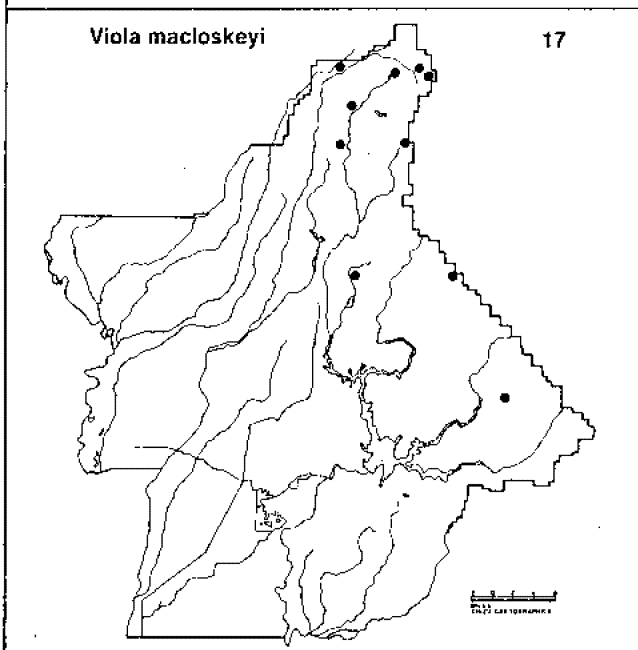
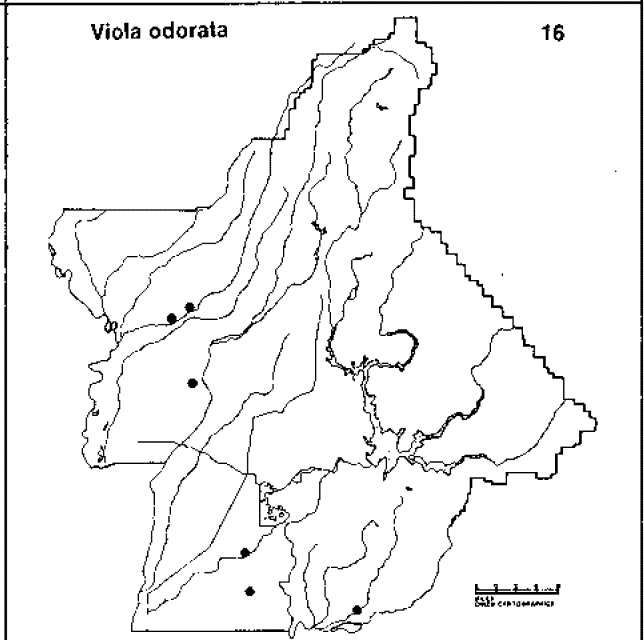
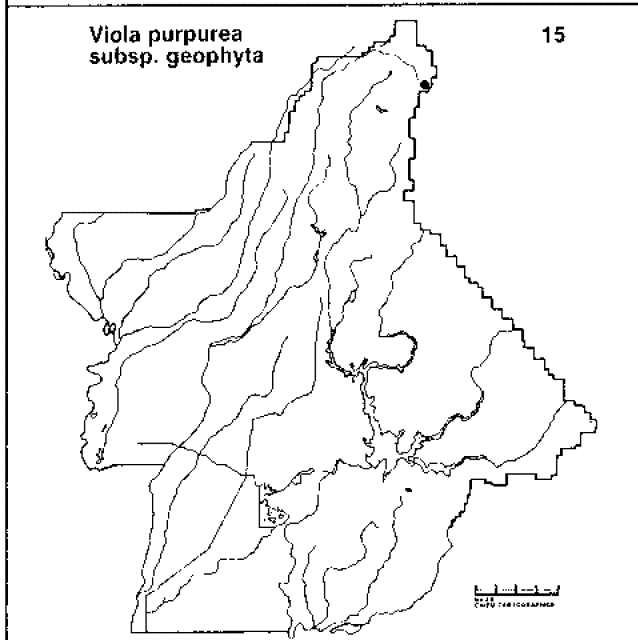
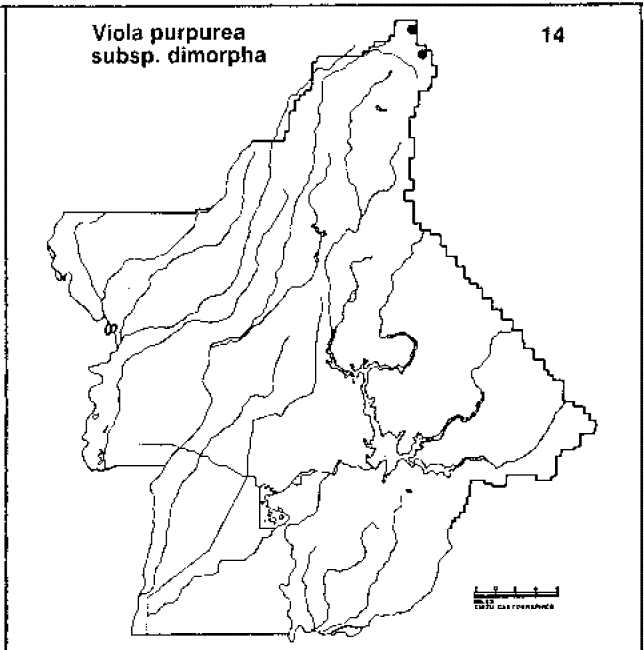
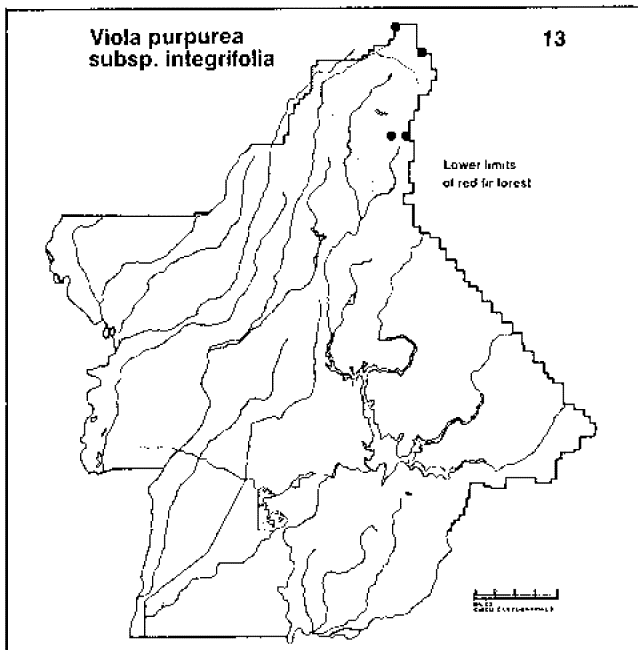
Distribution and habitat This violet has been found only on Snow Mountain (6900 feet elevation), south of Snag Lake. This is an old volcanic cauldery whose southwestern rim is composed of volcanic ash and populated with Abies magnifica (red fir).

10. VIOLA ODORATA L.

English Violet, Marsh Violet, Sweet Violet MAP 16

Description Slightly hairy, stemless perennial; leaves broadly ovate to heart-shaped, 2-5 cm wide, margins slightly toothed; peduncles 10-15 mm long, equal to or slightly exceeding the leaves; sepals 5-7 mm long, blunt, with hairs; petals 14-16 mm long, deep violet, with some white at base; cleistogamous flowers present in leaf axils.

Reproductive biology Flowers December to June. This violet has received a great deal of research attention in other parts of the world (e.g., Britain). Recently in America, an extensive comparative study of V. odorata's chasmogamous and cleistogamous flower development has been conducted by Mayers and Lord (1983a, 1983b, 1984). This violet is a prodigious producer of cleistogamous flowers, which contributes to its weedy nature in our Mediterranean climate. One of its most interesting reproductive strategies is the development of food-bodies (elaiosomes) on its seeds. After the seeds have been dispersed by ballistic projection (Beattie and Lyons, 1975), the food-bodies attract certain species of ants which further scatter some of the seeds by taking them to their nests to use as food. When the elaiosome has been eaten away, the seed is dumped into the refuse pile outside the nest where it germinates (Beattie, 1985). Many of our native western violets may produce such food-bodies, though research along these lines has not been conducted. It is known that some parts of this violet are toxic to all Speyeria species of Butterfly (Brittnacher et al., 1978).



Distribution and habitat Viola odorata is a garden escape, but unlike V. tricolor, its potential for becoming a permanent member of the Butte County flora is somewhat assured. Many communities have parks with streams which do not dry during the summer months (e.g., Bidwell Park in Chico). Add to this the cities' watering practices, which attempt to keep a luxuriant grass carpet available to the public, and V. odorata's weedy nature, and this moisture loving violet will spread and prosper. Many of the collections in Chico State's herbarium have been made in the stream bed of Big Chico creek [P. Moyer, 89 (CHSC)] or in moist areas on private range land [L. Ahart, s.n. (CHSC)].

11. VIOLA MACLOSKEYI Lloyd
[V. blanda auth., not Willd.] MAP 17
Macloskey's Violet, White Violet

Description Glabrous, stemless perennial; leaves round to kidney-shaped, 1-2.5 cm long, margins entire to roundly toothed; peduncles 2-5 cm long, surpassing the leaves; sepals 3-4 mm long, ovate to lanceolate, glabrous; petals 6-9 mm long, white; the lower 3 with purple veins, the lateral occasionally bearded; cleistogamous flowers present in leaf axils.

Reproductive biology Flowers May to August. Insect visitors are unknown through the literature or through observation.

Distribution and habitat Viola macloskeyi has been found throughout the county between elevations of 2200 and 6200 feet, in meadows and on damp banks. It is quite inconspicuous and takes a good deal of searching to spot, even though it grows relatively in the open. This violet often occurs in close association with V. adunca.

12. VIOLA ADUNCA Sm.
[V. filipes Greene] MAP 18
Western Blue Violet, Western Dog Violet

Description Pubescent perennial; leaves round-ovate, somewhat heart-shaped at base, obtuse at apex, 1-4 cm long, obscurely toothed; peduncles varying from shorter to longer than leaves; sepals 4.5-5.5 mm long, lance-linear; petals 8-13 mm long, deep blue to violet, the lower 3 white at base and purple veined, the lateral white-bearded; cleistogamous flowers present in axils of upper leaves.

Reproductive biology Flowers May to September. Insect visitors of V. adunca in the west are unknown through the literature or through observation.

Distribution and habitat Viola adunca has been found in much the same habitat and has the same distribution as V. macloskeyi, though it has been found at slightly higher elevations (6330 feet) without V. macloskeyi being present. It tends to be in

areas which are somewhat more dry than V. macloskeyi, but not completely without moisture at flowering time.

REFERENCES CITED

- Abrams, L. 1951. Illustrated flora of the Pacific States, vol. 3. Stanford University Press, Stanford, Calif.
- Baker, M. S. 1935. Studies in Western Violets, I. Madrono 3: 51-57.
- Baker, M. S. 1936. Studies in Western Violets, II. Madrono 3: 232-239.
- Baker, M. S. 1940. Studies in Western Violets, III. Madrono 5: 218-231.
- Baker, M. S. 1949a. Studies in Western Violets, IV. Leaflets of Western Botany 5: 141-147.
- Baker, M. S. 1949b. Studies in Western Violets, V. Leaflets of Western Botany 5: 173-177.
- Baker, M. S. 1949c. Studies in Western Violets, VI. Madrono 10: 110-128.
- Baker, M. S. 1953. Studies in Western Violets, VII. Madrono 12: 8-16.
- Baker, M. S. 1957. Studies in Western Violets, VIII. Brittonia 9: 217-230.
- Baker, M. S. 1960. Studies in Western Violets, IX. Madrono 15: 199-204.
- Beattie, A. J. 1971. Itinerant pollinators in a forest. Madrono 21: 120-124.
- Beattie, A. J. 1974. Floral evolution in Viola. Annals of the Missouri Botanical Garden 61: 781-793.
- Beattie, A. J. 1976. Plant dispersion, pollination, and gene flow in Viola. Oecologia 25: 291-300.
- Beattie, A. J. 1985. The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, New York.
- Beattie, A. J., and N. Lyons. 1975. Seed dispersal in Viola: adaptations and strategies. American Journal of Botany 62: 714-722.

- Brainerd, E. 1904. Hybridism in the Genus Viola, II. Rhodora 6: 213-223.
- Brainerd, E. 1906. Hybridism in the Genus Viola, III. Rhodora 8: 49-61.
- Brittnacher, J. G., S. R. Sims, and F. J. Ayala. 1978. Genetic differentiation between species of the genus Speyeria (Lepidoptera: Nymphalidae). Evolution 32: 199-210.
- Clausen, J. 1926. Genetical and cytological investigations on Viola tricolor L. and V. arvensis Murr. Hereditas 8: 1-156.
- Clausen, J. 1929. Chromosome number and the relationship of some North American species of Viola. Annals of Botany 43: 741-764.
- Clausen, J. 1962. Stages in the evolution of plant species. Hafner Publishing Co., New York.
- Clausen, J. 1964. Cytotaxonomy and distributional ecology of Western North American violets. Madrono 17: 173-197.
- Gerrit, D. 1976. A study of some intermountain violets (Viola sect. Chamaemelianum). Madrono 23: 274-283.
- Jokerst, J. D. 1983. The vascular flora of Table Mountain, Butte County, California. Madrono 30 (suppl.): 1-18.
- Krombein, K. V., P. D. Hurd, Jr., D. R. Smith, and B. D. Binks. 1979. Catalog of Hymenoptera in America north of Mexico, vol. 2. Smithsonian Institutional Press, Washington, DC.
- Mayers, A. M., and E. L. Lord. 1983a. Comparative flower development in the cleistogamous species Viola odorata: I. A growth rate study. American Journal of Botany 70: 1548-1555.
- Mayers, A. M., and E. L. Lord. 1983b. Comparative flower development in the cleistogamous species Viola odorata: II. An organographic study. American Journal of Botany 70: 1556-1563.
- Mayers, A. M., and E. L. Lord. 1984. Comparative flower development in the cleistogamous species Viola odorata: III. A histological study. Botanical Gazette 145: 83-91.
- Moldenke, A. R. 1976. California pollination ecology and vegetation types. Phytologia 34: 305-361.
- Munz, P. A. 1968. A California flora and supplement. University of California Press, Berkeley, Calif.

Nelson, J. R. 1979. The assessment and protection of rare and endangered plants of Butte County, California. M. A. thesis, California State University, Chico, Calif.

Niehaus, T. F., and C. L. Ripper. 1976. A field guide to Pacific States wildflowers. Houghton Mifflin Co., Boston, Massachusetts.

Russel, N. J. 1954. Three field studies of hybridization in stemless white violets. American Journal of Botany 41: 679-686.

Stebbins, G. L., B. L. Harvey, E. L. Cox, J. N. Rutger, G. Jelencovic, and E. Yagil. 1963. Identification of the ancestry of an amphiploid Viola with the aid of paper chromatography. American Journal of Botany 50: 830-839.

I wish to thank the many people who assisted with this project. Bob Banchemo, Rob Preston, Kirsten Tarp and Pauline Broyles for their companionship in the field. The California Botanical Society for kindly giving their permission to reproduce the line drawings of the Viola purpurea subspecies. Bob Ediger, Lawrence Janeway, Vern Oswald and Paula Woods for reviewing the manuscript and offering helpful comments. And, especially Rob Schlising, who has been a constant source of inspiration, guidance and support in both the field and in the herbarium, and who suggested that I get my hands dirty in botany by working with violets.

Studies from the Herbarium
California State University, Chico

-- Number 7 --

April 1987

CUCURBITACEAE
OF BUTTE COUNTY, CALIFORNIA

Robert A. Schlising
Department of Biological Sciences
California State University, Chico

The lower photograph on the cover is of Marah watsonii (the upper is of Viola lobata subsp. psychodes, a member of the Violaceae).

This report on the Cucurbitaceae (the cucurbit, squash or gourd family) for Butte County, California, includes three native species. One of these (Cucurbita foetidissima) was probably brought to agricultural Butte County from farther south (e.g., from the San Joaquin Valley) during relatively recent times. Several common garden plants of this family occasionally "volunteer" in Butte County (Oswald, 1986), but are not described in this report since it is doubtful whether they can persist or spread without cultivation. These include Citrullus lanatus (Thunb.) Mansf. [=Citrullus vulgaris L.], the watermelon, and Cucumis melo L., the muskmelon.

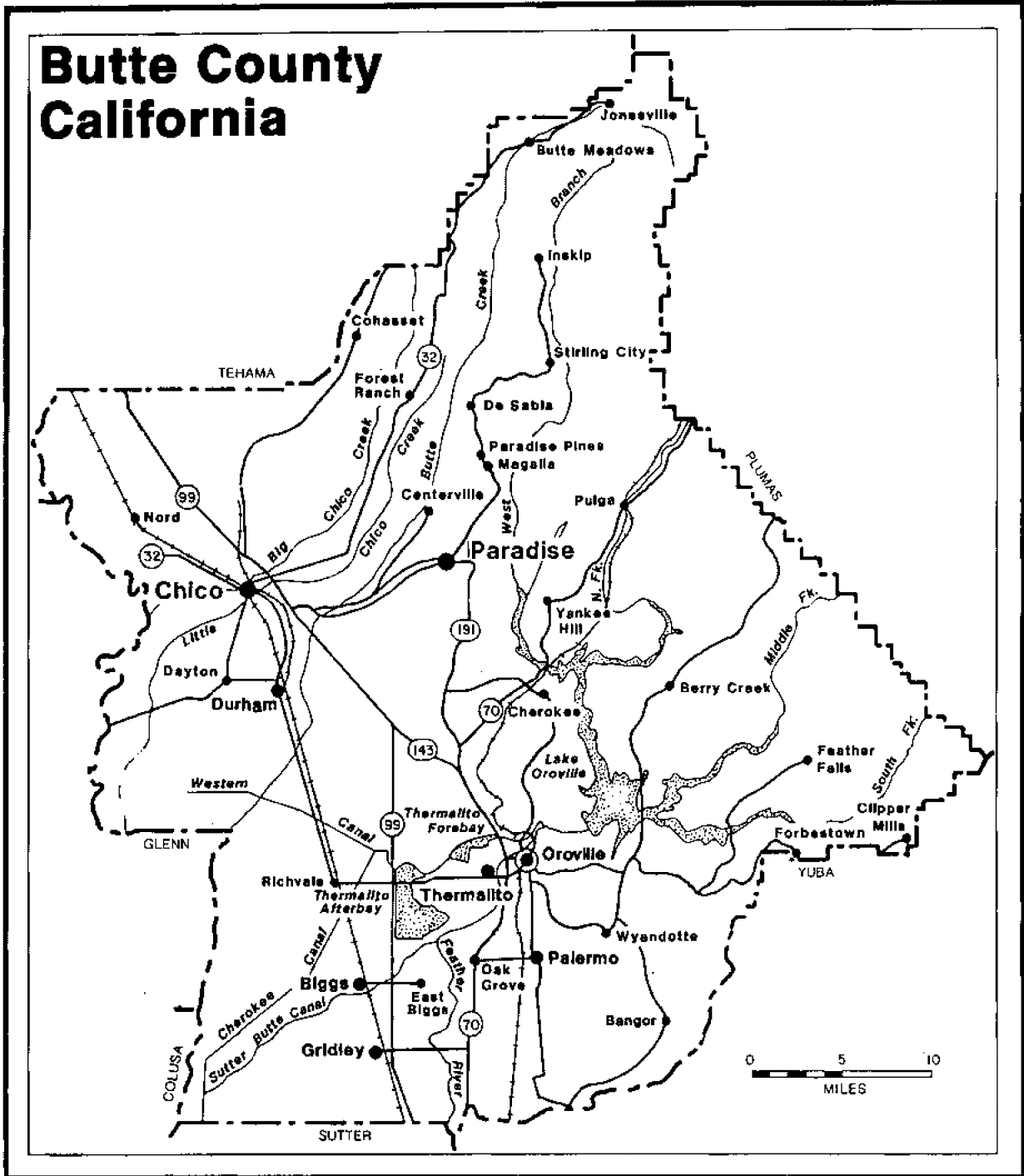
This treatment for Butte County cucurbits is based on field study 1980-1986, and on specimens in herbaria of California State University, Chico; California Academy of Sciences, San Francisco; and in the University and the Jepson Herbaria at the University of California, Berkeley. Descriptions and keys are based on Butte County plants. Munz (1968), Abrams and Ferris (1960), Bailey (1943), and Stocking (1955) give more complete descriptions. The Abrams and Ferris work has illustrations for the Butte County taxa, and lists names in synonymy up to 1960. The most recent synonyms are included within brackets in the present report.

The county range maps show dots based on 1) herbarium specimens and 2) sight records made in the field by the author. The Butte County outline maps (including the location map shown on the next page) were provided by Charles Nelson, Department of Geography, California State University, Chico. Plant community boundaries shown on dot maps are from a map prepared by James Nelson (1979) for the "Land Use Element of the Butte County, California General Plan."

The author thanks Pauleen Broyles for reviewing this manuscript.

The CUCURBITACEAE in Butte County

Perennials with trailing or climbing stems (vines), annually dying back to the massive root or tuber; leaves alternate, palmately veined, lance-shaped or rounded and lobed, with tendrils opposite them; plants monoecious, with the staminate and pistillate flowers not always present at the same time; calyx 5-lobed or sometimes apparently lacking; corolla lobed, usually of 5 fused petals; stamens usually appearing as 3 due to complex fusions and contortions during development; pistillate flower with inferior ovary and large stigma; fruit an indehiscent gourd, or a capsule dehiscing irregularly when dry.



Key to the genera of CUCURBITACEAE in Butte County

Leaves lance-shaped, blades of the older usually well over 10 cm long; flowers yellow, over 5 cm wide, both staminate and pistillate solitary at nodes; fruit a smooth-surfaced gourd
CUCURBITA

Leaves rounded or kidney-shaped, shallowly lobed, the blades mostly less than 10 cm long; flowers cream-colored or white, 1.5 cm or less wide, the staminate in clusters, the pistillate solitary; fruit a capsule, with few to numerous soft prickles
MARAH

CUCURBITA L.

Squash, Gourd

Reference: Bailey (1943)

1. CUCURBITA FOETIDISSIMA HBK NO MAP
Calabazilla, Chili Coyote, Coyote Melon

Description Large-rooted perennial, with coarse, foul-smelling vines up to 4 m long; leaves lance-shaped or triangular, erect, on petioles 5-15 cm long; flowers solitary at nodes, up to 10 cm long; calyx deeply lobed; corolla bell-shaped, yellow; stigmas deeply lobed; fruit a rounded, indehiscent pepo, 5-10 cm wide, green with whitish stripes and blotches when immature, yellow when mature; seeds numerous, flat, whitish, about 12 mm long.

Reproductive biology Collected once, in fruit, on 20 September; probably flowers June through August in Butte County. Moldenke (1976) lists California plants of this genus as self-incompatible. Each flower lasts but a single day, and they wilt and close most quickly on the days with the highest air temperatures (Hurd and Linsley, 1964). Both the annual, domestic (garden) cucurbitas (squashes, pumpkins and gourds) and the perennial, wild species (including Cucurbita foetidissima), have been well studied in relation to bee flower-visitors. Moldenke (1976) notes that flowers of wild Californian species are heavily visited and produce full seed set. The following summary is based on studies mainly outside Butte County (Hurd and Linsley, 1964, 1967, 1970) but pertains to C. foetidissima here.

In Cucurbita foetidissima, as well as in the other wild and domestic cucurbitas, pollen is produced very early in the morning, permitting its exploitation by two groups of native bees that collect pollen preceding or just after sunrise. These include the species in two anthophorid genera, Peponapis and Xenoglossa, in which the females take pollen exclusively from species of Cucurbita for provisioning their nests. For example, Peponapis pruinosa uses pollen only from Cucurbita foetidissima and the domestic cucurbitas; this species has been recorded taking pollen from garden cucurbitas, near both Chico and Gridley in Butte County. Hurd and Linsley maintain that

P. pruinosa and several other of these highly specialized "squash and gourd bees" have been able to extend their geographic ranges away (e.g., in this case, northward) from their required wild pollen plants by substituting pollen of the more recently introduced domestic cucurbitas. These authors report that each of the wild cucurbitas has its own species of squash and gourd bees that utilize it. They list (1970) two species of Peponapis and four of Xenoglossa that use Cucurbita foetidissima pollen to provision their nests. Bees of Peponapis and Xenoglossa--particularly the males--frequently spend the nights and parts of hot days inside the wilted flowers of C. foetidissima or other cucurbitas. These squash and gourd bees also utilize nectar from Cucurbita flowers, but many also visit flowers on other plants for nectar.

Flower visitors of C. foetidissima, in addition to Peponapis and Xenoglossa, are listed in Krombein et al. (1979): bees that collect pollen from many sources, including C. foetidissima, are Melissodes tessellata, Anthophora curta curta, Xylocopa californica diamesa and X. varipuncta. Some of these species, and yet additional species, use C. foetidissima flowers for nectar. Moldenke (1976) adds Agapostemon as another genus of bees that visit wild Cucurbita flowers.

In addition to effective seed production via flowers, C. foetidissima has an effective method of vegetative reproduction. This species easily develops roots from nodes of the vines trailing on the ground (Jepson, 1936).

Distribution and habitat This species has been collected once "in the wild" in Butte County, along Richvale West Road, 4.3 mi W of the RR crossing in Richvale; it grows with Convolvulus arvensis in a heavily disturbed roadside [R. A. Schlising, 4194, 20 September 1981, in California State University, Chico, Herbarium]. In addition, Cucurbita foetidissima is known to have two sites in the city of Chico, in both cases apparently unattended and prospering for several years. South of Butte County this species is found commonly in the San Joaquin Valley and southward, and thence eastward over a large region of North America. In California it has apparently been moving northward through the activity of people, for Hurd and Linsley (1967) have noted that in their search for squash and gourd bees they have seen Cucurbita foetidissima growing along a railroad siding as far north of the San Joaquin Valley as Anderson, in Shasta County.

MARAH Kellogg

Wild Cucumber, Manroot, Bigroot

References: Stocking (1955), Schlising (1966)

Description Tuberous perennials with nearly hairless stems, climbing by means of tendrils; leaves palmately 3 to 7-lobed,

on long petioles; staminate flowers on long-stalked racemes or somewhat brached inflorescences (less commonly, single) in leaf axils; pistillate flowers usually single and in leaf axil below the staminate raceme; sepals small or lacking; corolla usually 5-lobed; fruit a capsule which dehisces irregularly; seeds 1-4, large, rounded or egg-shaped.

Reproductive biology Considerable information exists on the reproductive biology of plants in this genus (Schlising, 1966, 1969; Stocking, 1955). Although most details were obtained from studies outside Butte County, and particularly on Marah oreganus (which does not occur in the county), the following paragraphs based mainly on these studies probably pertain to the Butte County species (Marah fabaceus and M. watsonii).

Self-incompatibility has been demonstrated only for M. oreganus, but almost certainly obtains in the two Butte County species (Schlising, 1966; Moldenke, 1976). All species of Marah are monoecious, and a distinct flowering sequence occurs on the plants. Very early in the flowering season, it is common for there to be a raceme of staminate flowers, or simply a single staminate flower, in the axil of a new leaf. During most of the flowering season, a raceme of staminate flowers occurs in a leaf axil, along with a single pistillate flower at the same node. Late in the season, each node may bear only a single pistillate flower. In Butte County Marah fabaceus shows this sequence more faithfully than the fewer-flowered and shorter-vined M. watsonii. Moldenke (1976) believes that flowers of Marah are seldom visited by insects and produce very low seed set.

For Marah in general, Moldenke (1976) lists bumblebees, Andrena bees, and gnats as pollinators (i.e., flower visitors). Insects recorded (Schlising, 1966) taking pollen and/or nectar from flowers of Marah oreganus in Contra Costa County are likely to visit Marah flowers in Butte County as well. These include, as most frequent or important, the bees Ceratina acantha, C. nanula, and Apis mellifera, and as less frequent or important, the bees Bombus vosnesenskii, Halictus tripartitus, Lasioglossum sp., Dufourea versatilis, and species of Osmia. Occasional ants, small beetles, and syrphid and bombyliid flies have also been seen at flowers. Stocking (1955) also lists small black ants, honeybees and small beetles as flower visitors to Marah plants.

Seeds are shed from the fruits in 8 to 10 weeks after flowers are pollinated. Fruits in Marah usually burst open irregularly (at the end away from the fruit-stalk) while they are still green and moist. The large seeds from fruits hanging on vines drop to the ground, and these, along with seeds from fruits opening on the ground, are likely to be eaten and/or dispersed by assorted mammals. These seeds are remarkably large and heavy in all species of Marah (Schlising, 1966; Baker, 1972; Harper et al., 1970), and are doubtless the heaviest seeds of native herbaceous plants in California. Mean seed weights range from 0.83 g per seed (the lowest weight for the genus, in M. watsonii from Butte County) to 3.08 g per seed (the highest

weight for the genus, in M. horridus from Mariposa County). In these seeds, the cotyledons fill nearly the entire space within the seed coat, and their small cells are packed with stored food granules of proteins, lipids and starch (at least in the studied M. oreganus and M. macrocarpus). Common animals attracted to these food stores in Contra Costa County (and potentially in Butte County as well), that are the most likely to disperse seeds away from parent plants include: voles (Microtus spp.), wood rats (Neotoma fuscipes), deer mice (Peromyscus spp.), harvest mice (Reithrodontomys megalotis), ground squirrels (Spermophilus, especially S. beecheyi), and pocket gophers (Thomomys bottae). Stocking (1955) mentions Citellus (Spermophilus) beecheyi as eating, indeed competing for, seeds of Marah. Other comments from published literature on rodent eaters/dispersers are briefly reviewed in Schlising (1966).

An occasional seed, buried and neglected by a rodent, germinates after cool temperatures and fall/winter rains have conditioned the soil. The large food stores in a Marah seed then function in permitting extensive underground growth of the seedling during the winter. Instead of a primary root emerging first from the seed at germination, the embryonic root and shoot are carried far out of the seed, down into the soil, by the elongating bases of the cotyledons. These cotyledon bases, or petioles, are fused, and as they elongate they form a "sinker" -- a hollow tube that bears the embryonic axis at the extreme tip. The cotyledon petiole tube stops elongating during the winter when anywhere from 2 or 3 to 20 or 25 cm long, depending on the habitat and species. Then, from the sinker's tip the root grows downward and the shoot upward (often partway up the hollow tube of the sinker). The shoot reaches the soil surface when the season of frosts is basically past, completes its first season of growth, and dries up when the dry summer season begins. Even before the shoot grows up out of the petiole tube and above ground, the seedling begins to form a tuber. The fleshy cotyledon blades remain in the seed coat below ground, and some food reserves from the blades are transferred to the tuber that will produce the vines in the following seasons.

This pattern of germination and seedling establishment is now known for species of Marah and for a very few other dicotyledonous plants, all of them growing mainly in areas of hot and dry habitat referred to as having Mediterranean climate (Schlising, 1969). This below-ground elongation of the fused cotyledons is considered a complex adaptation in dicots that helps ensure fast and successful seedling establishment.

Key the to species of MARAH in Butte County

Corolla cream-colored or whitish, shallow saucer-shaped; ovary of pistillate flower (and fruit) unstriped, with numerous fine prickles; seeds 2-4 per fruit; stem and leaves smooth, but not at all glaucous with a powdery film

1. MARAH FABACEUS var. AGRESTIS

Corolla white, deeply cup-shaped; ovary of pistillate flower (and fruit) usually with several dark green stripes, and with, at most, a few broad-based prickles; seeds 1-2 per fruit; stem and at least lower surfaces of leaves glaucous with a powdery blue film

2. MARAH WATSONII

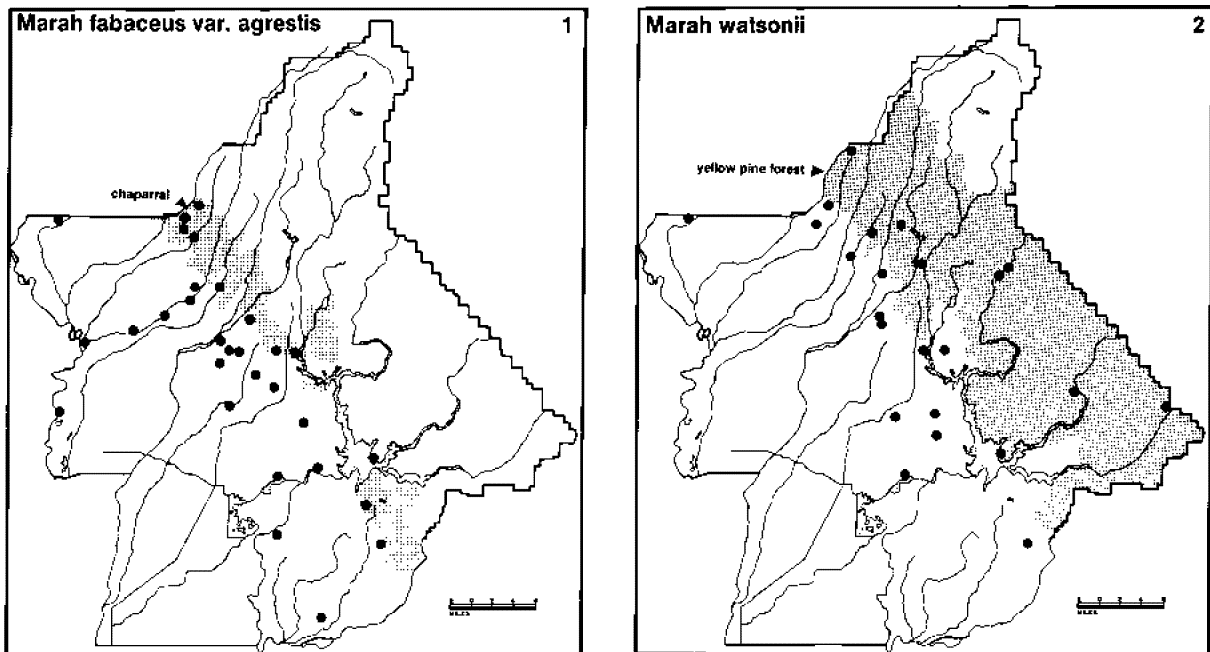
1. MARAH FABACEUS (Naudin) Greene var. AGRESTIS MAP 1
(Greene) Stocking
[Echinocystis fabacea Naudin var. agrestis Congdon]
Valley manroot

Description Stems 3-6 m long; leaves 5-11 cm wide, with lobes less than half the length of blade; staminate flowers 6-35 in a raceme; corolla with unequal lobes, about 10 mm wide in staminate flower, 12-15 mm wide in pistillate; fruit rounded near base, often pointed at tip, covered with soft prickles up to 6 or 8 mm long; seeds 1-4, most commonly 2-3, egg-shaped or rounded, up to 22 mm long.

Marah plants are often observed (or collected) when in early flower. Leaf widths and staminate flower numbers listed refer to fully developed, older plants and may not pertain to young specimens. See the section on reproductive biology, under the genus description, for comments on the sequence in which staminate and pistillate flowers appear.

Reproductive biology Flowers mid February through April.

Distribution and habitat This species is common the length of Butte County in riparian woodland, savanna, and chaparral. It is commonest at low elevations (generally under 1500 feet) at streamsides, and is uncommon at the lowermost reaches of yellow pine forest (e.g., along Cohasset Hwy in Cohasset at about 2000 feet). Lack of dots in the SW portion of Butte County in MAP 1 may be misleading, in that Marah fabaceus var. agrestis probably still occurs at some streamsides in this densely agricultural area that is less visited by botanists.



2. MARAH WATSONII (Congdon) Greene MAP 2
[Echinocystis watsonii Congdon, E. muricata Kellogg]
Taw Manroot

Description Usually smaller than M. fabaceus, with stems 1-3 m long; leaves 3-9 cm wide, quite rounded in outline, 5 to 7-cleft with deep lobes; staminate flowers 3-12 in a raceme; corolla white or greenish, about 5-7 mm wide in staminate flower, 8-12 mm wide in pistillate; fruit rounded, striped with dark green, without prickles or with several prickles with broad bases; seeds 1 or 2, round, 11-14 mm wide.

This description refers to mature vines, and does not necessarily pertain to vines just beginning to flower. See the section on reproductive biology, under the genus description, for comments on the sequence in which staminate and pistillate flowers appear.

Reproductive biology Flowers late March through mid May.

Distribution and habitat Marah watsonii occurs the length of Butte County in a broad NW to SE band that overlaps, but is mainly higher than, the range of M. fabaceus var. agrestis. Marah watsonii occasionally occurs in grassland (e.g., along Pine Creek in extreme NW Butte County, and at the Thermalito Forebay). It is more common in savanna, and especially in chaparral and yellow pine forest (as high as 3600 feet elevation in forest above Cohasset and at 4100 feet on Lumpkin Ridge in E Butte County. Populations of this species usually consist of very few individuals.

REFERENCES CITED

- Abrams, L., and R. S. Ferris. 1960. Illustrated flora of the Pacific States, vol. 4. Stanford University Press, Stanford, Calif.
- Bailey, L. H. 1943. Species of Cucurbita. Gentes Herbarum 6: 267-322.
- Baker, H. G. 1972. Seed weight in relation to environmental conditions in California. Ecology 53: 997-1010.
- Harper, J. L., P. H. Lovell, and K. G. Moore. 1970. The shapes and sizes of seeds. Annual Review of Ecology and Systematics 1: 327-356.
- Hurd, P. D., Jr., and E. G. Linsley. 1964. The squash and gourd bees--genera Peponapis Robertson and Xenoglossa Smith--inhabiting America north of Mexico (Hymenoptera: Apoidea). Hilgardia 35: 375-477.
- Hurd, P. D., Jr., and E. G. Linsley. 1967. Squash and gourd bees of the genus Xenoglossa (Hymenoptera: Apoidea). Annals of the Entomological Society of America 60: 988-1007.
- Hurd, P. D., Jr., and E. G. Linsley. 1970. A classification of the squash and gourd bees Peponapis and Xenoglossa (Hymenoptera: Apoidea). University of California Publications in Entomology 62: 1-39.
- Jepson, W. L. 1936. A flora of California, vol. 2. Associated Students Store, University of California, Berkeley, Calif.
- Krombein, K. V., P. D. Hurd, Jr., D. R. Smith, and B. D. Binks. 1979. Catalog of Hymenoptera in America north of Mexico, vol. 2. Smithsonian Institution Press, Washington, D. C.
- Moldenke, A. R. 1976. California pollination ecology and vegetation types. Phytologia 34: 305-361.
- Munz, P. A. 1968. A California flora and supplement. University of California Press, Berkeley, Calif.
- Nelson, J. R. 1979. The assessment and protection of rare and endangered plants of Butte County, California. M. A. thesis, California State University, Chico, Calif.
- Oswald, V. H. 1986. Vascular plants of Upper Bidwell Park, Chico, California. Studies from the Herbarium, California State University, Chico 3.

Schlising, R. A. 1966. Reproductive ecology of plants in the genus Marah (Cucurbitaceae). Ph. D. dissertation, University of California, Berkeley, Calif.

Schlising, R. A. 1969. Seedling morphology in Marah (Cucurbitaceae) related to the Californian Mediterranean climate. American Journal of Botany 56: 552-561.

Stocking, K. M. 1955. Some taxonomic and ecological considerations of the genus Marah (Cucurbitaceae). Madrono 13: 113-137.

