

RECOGNITION OF THE TETRAPLOID,
POLYPODIUM CALIRHIZA (POLYPODIACEAE),
IN WESTERN NORTH AMERICA

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ABSTRACT

Taxonomic study of the *Polypodium californicum*/*glycyrrhiza* complex in California reveals four taxa: a tetraploid, a triploid, and two diploids, *P. californicum* and *P. glycyrrhiza*. The tetraploid, here named *Polypodium calirhiza*, mimics some forms of *P. californicum* in southern California but is readily distinct in northern and central parts of the state. It is probably of allopolyploid origin involving the two diploids, as judged by its morphological intermediacy and chromosome pairing in triploid hybrids with *P. glycyrrhiza*. A principal components analysis also demonstrates this intermediacy. *Polypodium calirhiza* shows a wider tolerance for different habitats and greater range than either of its putative parents.

RESUMEN

El estudio taxonómico del complejo *Polypodium californicum*/*glycyrrhiza* en California revela cuatro taxa: un tetraploide, un triploide, y dos diploides, *P. californicum* y *P. glycyrrhiza*. El tetraploide, aquí nombrado *Polypodium calirhiza*, mimetiza algunas formas de *P. californicum* en el sur de California pero es fácilmente distinguible de los áreas de norte y centro del estado. Probablemente esta nueva especie sea de origen aloploiploide implicando los dos diploides a juzgar por su forma intermedia morfológicamente y su sinapsis cromosómico en híbridos triploides con *P. glycyrrhiza*. Un análisis de los componentes principales también demuestra esta naturaleza intermedia. *Polypodium calirhiza* demuestra una mejor tolerancia a más diversos hábitates y una área de distribución más amplia que cualquiera de sus dos teóricos progenitores.

The *Polypodium vulgare* L. group, comprising perhaps 15 mostly north-temperate species worldwide, is represented in California by six species and several hybrids. Recent cytological and electrophoretic data have provided solid evidence for the relationships among western North American species, and have allowed circumscription of biologically discrete taxa. Such studies also have allowed an assessment of kinship to species from outside western North America.

Perhaps the most difficult problem taxonomically in California has involved *P. californicum* Kaulf. sensu lato (Lloyd 1962; Lloyd and Lang 1964). Hooker and Arnott (1840) distinguished *P. inter-*

medium and implied that their new species was intermediate between *P. californicum* and *P. vulgare* L., the latter based on a European type. The original circumscriptions of *P. californicum* and *P. intermedium*, even though somewhat vague, represented a separation of diploid and tetraploid cytotypes respectively; however, chromosome information would not be forthcoming for more than 100 years. It is now known that the type of *P. californicum* is very likely diploid, whereas the type of *P. intermedium* appears to be tetraploid.

Several authors (Eaton 1877–1879; Fernald 1922; Farwell 1931) subsequently made new combinations with these epithets. Unfortunately, they included both diploids and tetraploids for each taxon in their lists of representative specimens and used these specimens to expand descriptions of the taxa. Munz and Johnston (1922) added to the confusion by recognizing var. *kaulfussii* D. Eaton, a name homotypically synonymous with *P. californicum*, as a distinct entity. More recent treatments in regional and local floras (e.g., Howell et al. 1958; Munz 1973) have followed Abrams (1923) in the recognition of *P. californicum*, the placement of *P. intermedium* in synonymy, and the acceptance of var. *kaulfussii* as a distinct variety.

The first chromosome counts for *P. californicum* s.l. (Manton 1951) were tetraploid, $n = 74$. Lloyd (1962, 1963) discovered that *P. californicum* included both diploid and tetraploid entities. Lloyd and Lang (1964) retained both cytotypes under *P. californicum*, but they hypothesized that the tetraploid was possibly an allopolyploid arising from hybridization between diploids *P. californicum* and *P. glycyrrhiza* (Lloyd 1962; Lloyd and Lang 1964). Lovis (1977), using morphology alone, and Ranker (1982) and Ranker and Mesler (1982), using also guard cell and spore length, suggested both autopolyploid and allopolyploid origins for the tetraploids. By measuring guard cells of plants of known ploidy and using calculations to predict expected guard cell size in diploid parents and polyploid offspring, Barrington et al. (1986) refuted the autopolyploid hypothesis and supported the allopolyploid origin for the tetraploid.

Previous studies using morphological, cytological, karyotypic, chemical (flavonoid), and electrophoretic evidence have revealed that several other tetraploids in *Polypodium* are of allopolyploid origin. These include *P. vulgare* (Manton 1947, 1951, 1958; Shivas 1961a, b) and *P. interjectum* Shivas (Manton 1950; Shivas 1961a, b; Murray 1985) in Europe and *P. hesperium* Maxon (Lang 1965, 1971; Windham 1985) and *P. virginianum* (Manton 1957, 1958; Shivas 1961a; Evans 1970; Bryan and Soltis 1987) in North America. Even though autopolyploid origins have been suggested for several taxa, no autopolyploids have been verified in any of these species. The predominance of allopolyploidy as a speciation mechanism in this group has recently been reemphasized by Haufler and Windham (1991),

who implicate a boreal diploid, *P. sibericum* Siplivinskij, in the formation of two tetraploids, *P. saximontanum* Windham and *P. virginianum*.

It has become clear to us that the most widespread polypody in California is tetraploid. It shows generally additive morphology between two diploids, *P. glycyrrhiza* and *P. californicum*. Although the tetraploid, here named *P. calirhiza*, is of probable hybrid origin, it behaves as a distinct species. It shows no apparent reduction in fertility and has a widespread distribution with distinct habitat and community preferences, indicating a well-established species. Generally it is allopatric with respect to *P. californicum*; in the San Francisco Bay area and the Monterey/Pt. Lobos area the ranges of the two overlap, but field work has shown different habitat preferences. We have not seen the two growing together in the same population.

The decision to recognize the allotetraploid as a distinct species made it necessary to ascertain whether the name *P. californicum* had originally been applied to the diploid or the tetraploid. The original description of *P. californicum* is inconclusive, but probable type material at LE is clearly conspecific with specimens we regard as diploid (Whitmore, ms.). Because there exists no available name at species rank for the tetraploid, we describe it as new and base it on a specimen of known ploidy.

POLYPODIUM CALIRHIZA S. Whitm. & A. R. Smith, sp. nov. (Fig. 1)—TYPE: USA, California, Contra Costa Co., Mount Diablo, arroyo on S slopes, 1.2 miles N of south gate entry to Mount Diablo State Park along South Gate Road, 1 Jan 1982, $2n = 74$ II, *Whitmore 1388* (holotype, UCSB; isotypes, UC, US, RSA, from same rhizome as holotype).

Polypodium intermedium Hook. & Arn. (non Colla, 1836), Bot. Beechey Voy. 405. 1840, a later homonym and hence illegitimate.—*Polypodium californicum* Kaulf. var. *intermedium* D. Eaton, Ferns N. Amer. 1:244, pl. 31. 1878.—*Polypodium vulgare* L. var. *intermedium* (D. Eaton) Fernald, Rhodora 24:139. 1922.—*Goniophlebium cambricum* (L.) Farwell var. *intermedium* (D. Eaton) Farwell, Amer. Midl. Naturalist 12:295. 1931.—TYPE: [USA], California, [San Francisco Co.], San Francisco, *Sinclair s.n.* (holotype, K!, frond on left side of sheet; photo, UC!).

Polypodium vulgare L. var. *intermedium* (D. Eaton) Fernald forma *projectum* Fernald, Rhodora 24:140. 1922.—TYPE: [USA], California, Butte Co., Chico Canyon, *Copeland 2749* (holotype, GH; isotype, POM!).

Polypodium californicum Kaulf. forma *parsonsiaae* C. Morton, Amer. Fern J. 51:75. 1961.—TYPE: greenhouse specimen originally

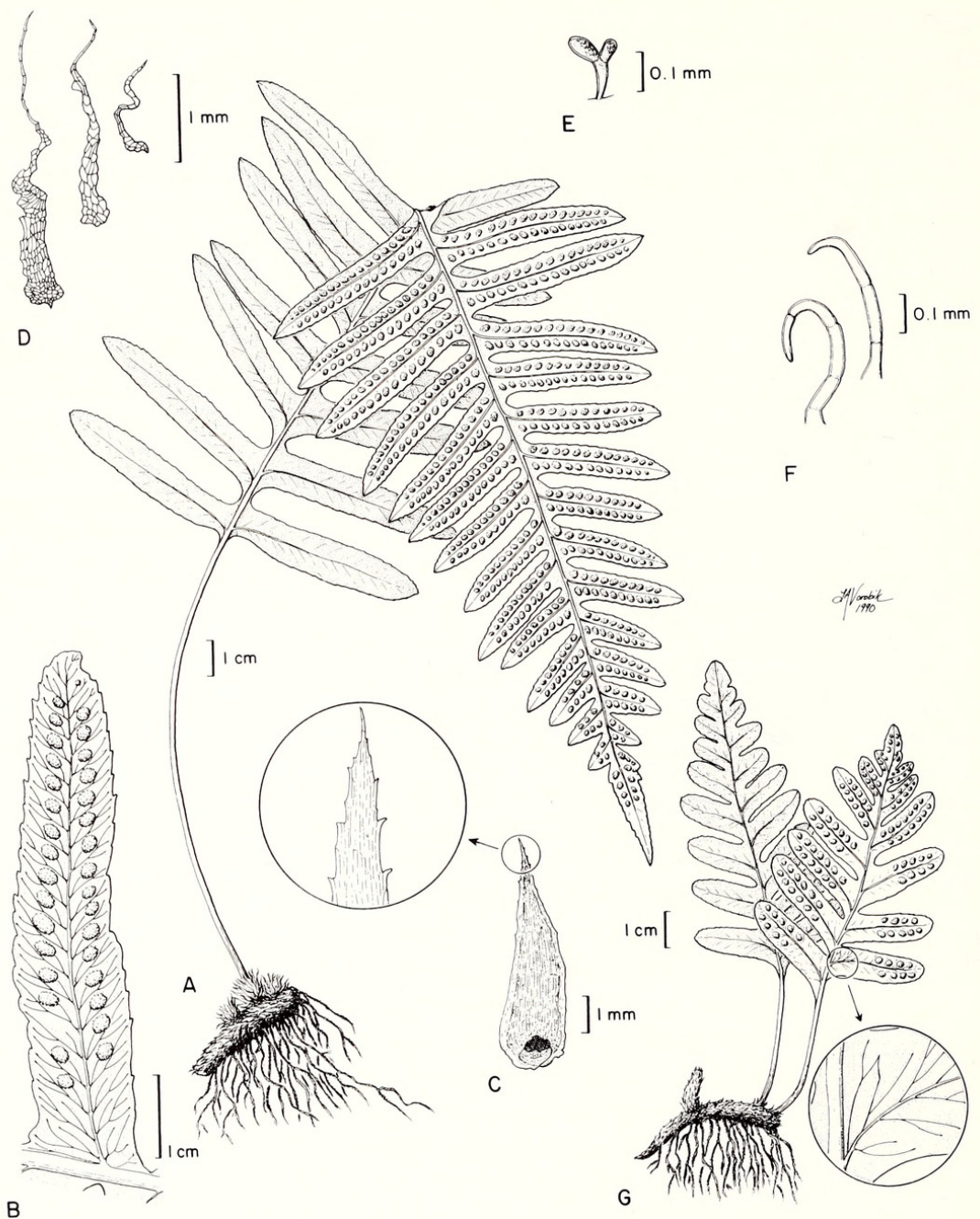


FIG. 1. *Polypodium calirhiza*. A, habit (A–C drawn from *Whitmore 1391*, UC, a topotype). B, pinna. C, rhizome scale. D, stipe and rachis scales (*Whitmore et al. 786*, UCSB). E, glandular trichome from abaxial epidermal surface (*Whitmore 948*, UCSB). F, arcuate, non-glandular trichome from adaxial rachis, typically found on specimens of *P. calirhiza*. G, habit (*Constance 494*, UC).

from USA, California, Marin Co., near Kentfield, 14 Sep 1903, *Parsons s.n.* (holotype, US!).

A *Polypodio californico* et *P. glycyrrhiza* combinatione characterum sequentium differt: rhizomatibus parum dulcibus et acerbis; frondibus demissis; paleis stipitum et rhachidum lanceolato-ovatis, 4–8(–12) cellulis in latitudine; laminis oblongo-ovatis, leviter glaucis

abaxialiter; pinnis acutis vel obtusis ad apicem; venis irregularibus, perparce vel plerumque anastomosantibus usque ad 33(–56)%; soris ovalibus, (1.5–)2–4 mm diametro; sporis verrucatis vel tuberculatis, ut videtur normalibus; chromosomatum numero $2n = 74$ II.

Rhizome creeping, 5–10 mm diam., pale brown with an acrid plus slightly sweet taste, covered with acuminate, light brown scales; stipe green to greenish brown; abaxial surface of distal part of stipe and proximal part of rachis and costae sparsely covered with light brown, very narrowly acuminate, caducous scales with slightly erose margins; abaxial surface of the lamina with short, 2–3(–8)-celled, branched or unbranched, glandular trichomes; adaxial surface of the rachis and costae densely to moderately pubescent with arcuate, multicellular (4–8-celled), uniseriate, non-glandular trichomes and with occasional, short, 2–3(–8)-celled, branched or unbranched, glandular trichomes; blade oblong-ovate, normally pinnatifid although occasionally with secondary pinnatifidation of proximal pinnae, herbaceous to chartaceous, stiff, slightly thickened, 10–20(5–40) \times 4–9(3–15) cm; 8–12(6–25) pinna-pairs per frond; pinnae narrowly oblong, proximal 1–3 pairs distinctly shorter than middle pinnae, tips acute to somewhat obtuse with conspicuous serrations, margins serrate to dentate, with the teeth spreading; veins mostly free, anastomosing irregularly and only occasionally near rachis, to anastomosing more frequently between the rachis and the proximal $\frac{1}{3}$ – $\frac{1}{2}$ of pinna, number of anastomosing pairs per pinna 0–several, occasionally many, varying from pinna to pinna on each blade; vein pathways commonly slightly uneven and forming an irregular pattern; sori oval, orange-brown to brown, (1.5–)2–4 \times 1–2 mm, distinctly raised, often increasing in size closer to rachis, sometimes becoming confluent near rachis, lacking soral sporangiasters or paraphyses with sporangial-length stalks; capsule of sporangium without trichomes and with 11–14(8–17) indurated annulus cells; spores bilateral, yellow at maturity with coarsely verrucate to tuberculate surface, 57–86 μ m long (mean = 68 μ m; measurements include tubercles); chromosome number $2n = 74$ II.

The epithet *calirhiza* is derived by combining parts of the names of the putative parents, *P. californicum* and *P. glycyrrhiza*.

Representative specimens.—MEXICO: MEXICO: Munic. Tezcoco, 14 km SE of Tezcoco, 9 km SE of Tequesquinahuac, on Cerro Tlaloc, 22 Feb 1978, *Koch 789* [7809?] (NY). OAXACA: Dist. Ixtlán, S edge of Cuajimoloyas, 23 km N of Dias Ordaz, 2 Oct 1973, *Mickel 7426* (NY, UCSB).

UNITED STATES: CALIFORNIA: Alameda Co., Redwood Ridge, 23 Mar 1932, *Constance 494* (UC); Amador Co., Ione, Dec 1904, *Braunton 1265* (NY, UC); Amador Co., Ione, Dec 1904, *Braunton s.n.* (POM); Butte Co., Feather River, near Yankee Hill,

29 Mar 1919, *Heller 13090* (CAS); Contra Costa Co., Mount Diablo State Park, ridge above Devil's Elbow Trail, 19 Nov 1981, *Smith & Lemieux 828* (UC); Humboldt Co., Ocean Beach at Samoa, opposite Eureka, 27 Jan 1901, *Tracy 985* (UC); Kern Co., Tehachapi Mountains, El Paso Canyon, Tejon Ranch, 23 May 1961, *Twisselmann 6162* (CAS); Lake Co., Mount Konocti, 7 Mar 1923, *Blankinship s.n.* (CAS); Marin Co., Mt. Tamalpais, Jun 1874, *McLean s.n.* (UC); Marin Co., near Stinson Beach School, 3 Mar 1962, *Penalosa 2244* (CAS); Marin Co., Point Reyes National Seashore, along Sky Trail, 31 Dec 1981, *Smith 835* (UC); Mariposa Co., Yosemite National Park, above Tunnel View on Fresno Road, 20 Dec 1981, *Parris & Croxall 9654* (K); Mendocino Co., Russian Gulch State Park, 29 Jul 1961, *Lloyd 502* (RSA); Napa Co., St. Helena Creek, near Patten's, 21 Mar 1926, *Howell 1729* (CAS); Nevada Co., Sierra Nevada Mountains, South Yuba River, Excelsior Ditch, Feb 1966, *Mott s.n.* (CAS); Plumas Co., canyon of the North Fork of the Feather River, granite near mouth of Chambers Creek, 22 Jun 1967, *Howell 42658* (CAS); San Benito Co., Pinnacles National Monument, along Bear Gulch Trail, Dec 1981, *Smith 831* (UC); San Francisco Co., San Francisco, gully S of Stanley Drive, E of Lake Merced, 4 Nov 1956, *Rubtzoff 3054* (CAS, RSA); San Mateo Co., San Bruno Mountain, 9 Mar 1963, *Penalosa 2700* (CAS); Santa Clara Co., foothills W of Los Gatos, 5 Mar 1904, *Heller 7255* (NY, UC); Sierra Co., Sierra Nevada, Sierra Valley, E of Downieville and Sierra City, NE of Yuba Pass, along Highway 49, 1880, *Lemmon s.n.* (POM); Siskiyou Co., Klamath National Forest, Indian Creek, 4 ml N of Happy Camp, 13 Aug 1934, *Lee 1056* (UC); Solano Co., Vaca Mountains, N of Fairfield, 16 Jan 1954, *Raven 6376* (CAS); Sonoma Co., Adobe Canyon, Mar 1892, *Michener & Bioletti s.n.* (UC); Sutter Co., S part of Marysville Buttes [Sutter Buttes], 7 Apr 1928, *Vortriede s.n.* (CAS); Tulare Co., southern Sierra Nevada, Tule River Canyon, Soda Creek, 27 Jul 1963, *Kiefer 647* (LA); Tuolumne Co., Italian Bar, 5 Jun 1915, *Jepson 6365* (JEPS, UC). OREGON: Lincoln Co., near ocean shore S of Newport, 18 May 1918, *Lawrence 1484* (UC).

Distribution (Fig. 2).—*Polypodium calirhiza* occurs throughout the coast ranges of northern and central California to Anastasia Canyon, Monterey Co., through the interior foothills of the Sierra Nevada from the Feather River, Plumas Co., south to the Tehachapi Mountains in Kern Co. It is slightly disjunct in the coast ranges at Newport, Oregon, and greatly disjunct in the states of Mexico and Oaxaca (Mickel and Beitel 1988) in southern Mexico.

Habitat.—The distribution of *P. calirhiza* includes a wide diversity of habitats and vegetation types ranging from coastal headlands to the drier interior foothill regions. In the central California coast ranges it is found in mixed evergreen forest, oak savanna, riparian

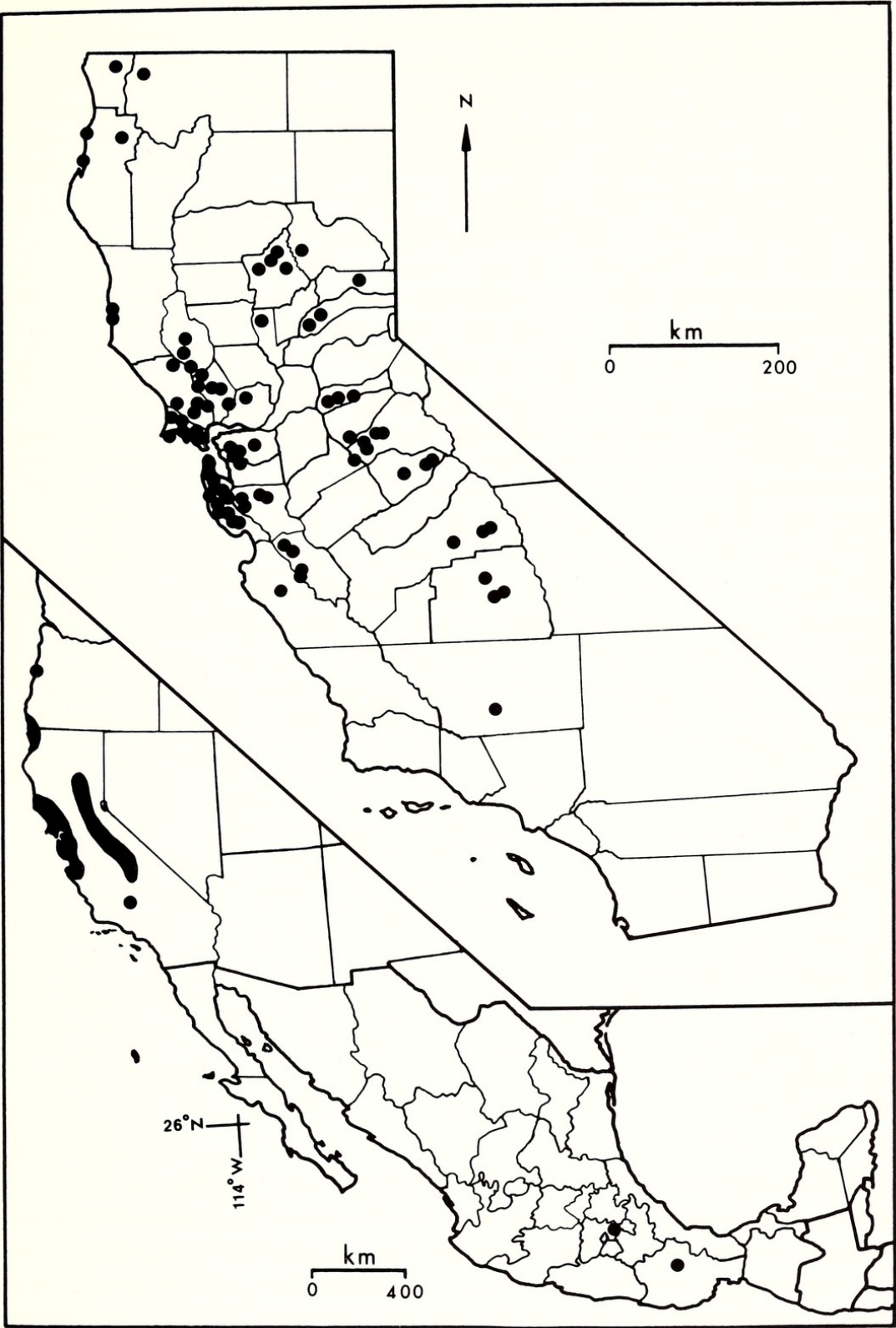


FIG. 2. Distribution of *Polypodium calirhiza*. Each dot represents one or more collections at single site, or two or more at adjacent sites.

TABLE 1. CHROMOSOME COUNT VOUCHERS FOR *POLYPODIUM CALIRHIZA*. ALL COUNTS ARE $2N = 74$ II OR CA. 74 II. VOUCHERS ARE IN UCSB UNLESS OTHERWISE INDICATED.

USA: California: Alameda Co.: Redwood Regional Park, 14 Mar 1981, *Smith* 811 (UC). Contra Costa Co.: Mt. Diablo St. Park, N slope of Mt. Diablo, 19 Nov 1981, *Smith* (& *Lemieux*) 826 (UC), above Devil's Elbow Trail, *Smith* (& *Lemieux*) 828 (UC); Mt. Diablo, S slopes, along South Gate Road, 1 Jan 1982, *Whitmore* 1388. Marin Co.: Pt. Reyes Nat. Seashore, Pt. Reyes, 6 Feb 1979, *Whitmore et al.* 433; San Anselmo, Sir Francis Drake Blvd., 16 Nov 1979, *Whitmore* 692; San Anselmo, Sir Francis Drake Blvd., 6 Feb 1980, *Whitmore* (& *Smith*) 786; Lucas Valley Road, 15 Dec 1980, *Whitmore* (& *Smith*) 948; Panoramic Hwy., E of Stinson Beach, 16 Dec 1980, *Whitmore* 975; Hwy. 1, near Marshall, 17 Dec 1980, *Whitmore* 1006; Pt. Reyes Nat. Seashore, along Bear Valley Trail, 10 Dec 1981, *Whitmore* (& *Smith*) 1311; Pt. Reyes Nat. Seashore, along Sky Trail, 31 Dec 1981, *Smith* 836 (UC); Pt. Reyes Nat. Seashore, along Bear Valley Trail, 31 Dec 1981, *Smith* (& *Whitmore*) 838 (UC); end of Lagunitas Rd., trail to Phoenix Lake, 15 Dec 1978, *Smith* 714 (UC). Mendocino Co.: 1 mi N of Ten Mile River along Hwy 1, *Lemieux s.n.* (UC). Plumas Co.: Feather River, collected from greenhouse plant (SBBG 76-128), 14 Dec 1979, *Whitmore* 762. San Benito Co.: Pinnacles Nat. Monument, along loop of Juniper Canyon Trail, 28 Dec 1981, *Smith* 830 (UC), along Bear Gulch Trail, *Smith* 831 (UC), along Old Pinnacles Trail, *Smith* 832 (UC). San Mateo Co.: Skyline Blvd., N of jct. with Hwy 84, 10 Feb 1980, *Whitmore* 883; King's Mt. Rd., E of Skyline Blvd., 8 Jan 1981, *Whitmore* 1051. Santa Cruz Co.: Ben Lomond, along San Lorenzo River, 2 Apr 1978, *Whitmore* 291. Sonoma Co.: Bodega, base of E cliffs, 7 Feb 1980, *Whitmore* 894.

woodland, and sometimes coastal redwood forest up to 1220 m; in the Sierra Nevada it occurs in oak savanna and foothill chaparral up to 1370 m; in the Tehachapis it occurs in oak savanna/riparian woodland. *Polypodium calirhiza* most commonly grows in disturbed habitats such as roadcuts and landslide areas, rocky cliffs with unstable surfaces, and rocky outcrops in grazed pastures. It also may be found in relatively undisturbed habitats: crevices of rocks, rocky cliffs, rocks or rocky outcrops in grasslands, and creek banks. Proliferation around rocky outcrops is particularly common in the warmer or drier habitats. *Polypodium calirhiza* can occur in shady or sunny situations in all of the above habitats. It also grows on old stumps, or at the bases of trees, or even high on tree trunks of *Acer macrophyllum* or *Umbellularia californica* in particular.

Cytology. — *Polypodium calirhiza* usually has 74 bivalents at meiosis (base number 37); occasionally ca. 72 bivalents and 2–4 significantly smaller chromosome configurations have been seen (see Table 1 for localities). The triploid hybrid frequently growing in association with this tetraploid has ca. $37 \text{ II} + 37 \text{ I}$ during meiosis. The occurrence of regular bivalent formation in the tetraploid and a genomic number of bivalents and univalents in the triploid hybrid suggest allosyndetic pairing of chromosomes in both the tetraploid and triploid hybrid. As indicated by Lovis (1977), further evidence for the allopolyploid origin of *P. calirhiza* might obtain from the dis-

covery of equal numbers of bivalents and univalents in the other (as yet unknown) backcross triploid.

We have found no diploid hybrids between *P. californicum* and *P. glycyrrhiza* in their area of sympatry or in the range of *P. calirhiza*. Cytological examination of plants that are morphologically intermediate between *P. californicum* and *P. glycyrrhiza* has not revealed any of the following kinds of evidence of hybridity: univalents and bivalents in meiosis I; lagging chromosomes at the metaphase plate; or a significant percentage of malformed spores. All such plants have proven to be assignable to either *P. calirhiza* or to variant forms of *P. californicum* or *P. glycyrrhiza*. This absence of diploid hybrids is typical of *Polypodium* in North America and Europe (Lang 1965, 1971).

Morphology.—Table 2 summarizes selected morphological characters of *P. calirhiza*, its putative diploid parents, and the triploid hybrid. Numerical data are means or ranges of measurements of specimens that have been determined by chromosome count, or in some cases by spore length measurements. Spore surface terminology follows Tryon and Tryon (1982).

Polypodium calirhiza displays morphological characteristics of both putative diploid parents, *P. californicum* and *P. glycyrrhiza*, supporting the hypothesis that it is of allopolyploid origin. It also has characters found exclusively in only one parent: the epiphytic habit of *P. glycyrrhiza* and the tuberculate verrucae of the spores and anastomosing venation of typical *P. californicum*. The triploid, *P. calirhiza* × *glycyrrhiza*, is morphologically intermediate between *P. calirhiza* and *P. glycyrrhiza* but perhaps generally closer to *P. glycyrrhiza*, suggesting that it is a hybrid between those two taxa rather than between *P. californicum* and *P. calirhiza*.

Polypodium calirhiza differs from *P. glycyrrhiza* by the venation pattern: *P. glycyrrhiza* has veins that are free with vein pathways even and regular, whereas *P. calirhiza* has at least one set of vein endings anastomosing per frond and more commonly, 1–2 (up to about half) of the vein sets anastomosing per pinna. Separating *P. calirhiza* from type material of *P. californicum* and from specimens of *P. californicum* from the central coast of California is relatively straightforward using the following characters of *P. californicum*: a bland, or very slightly sweet rhizome, pinnae having mostly anastomosing veins forming a row of oblique areoles with the anastomosing points usually several mm from the margin, a rachis that is almost glabrous adaxially or sometimes with scattered to moderate pubescence, and a succulent blade. Spore or guard cell measurements or chromosome number are more definitive but usually unnecessary.

It can be quite difficult to distinguish *P. calirhiza* from some specimens of *P. californicum* from southern California. The most

TABLE 2. COMPARISON OF TAXA IN THE *POLYPODIUM CALIFORNICUM*/*GLYCYRRHIZA* COMPLEX WITH SELECTED CHARACTERS.

Character	<i>Polypodium californicum</i> 2n = 37 II	<i>Polypodium calirhiza</i> 2n = 74 II	<i>Polypodium calirhiza</i> × <i>glycyrrhiza</i> 2n = 37 II + 37 I, or variable: 2n = ca. 35- 37 II + 35-37 I + multivalents	<i>Polypodium glycyrrhiza</i> 2n = 37 II; rarely 2n = 36 II + 2 I
Chromosome number	2n = 37 II	2n = 74 II	2n = 37 II + 37 I, or variable: 2n = ca. 35- 37 II + 35-37 I + multivalents	2n = 37 II; rarely 2n = 36 II + 2 I
Rhizome taste	Acrid or bland	Sweet plus acrid	Sweet plus ± acrid	Intensely sweet, and ± bitter aftertaste
Blade shape	Deltate to ovate	Oblong-ovate	Oblong-ovate	Lanceolate-ovate
Frond aspect	Upright	± drooping	Drooping	Drooping, arching
Stipe/rachis scales and number of cells wide	Deltate-ovate, 12-18(- 20)	Lanceolate-ovate, 4-8(- 12)	Lanceolate, 3-6(-8)	Lanceolate, 3-6(-8)
Abaxial surface of blade	Not noticeably glaucous	Slightly glaucous	Glaucous	Glaucous
Pinna tip shape	Widely obtuse to acute	Acute to obtuse	Acute to ± obtuse	Attenuate to acute
Percent of veins anasto- mosing/pinna	100-5.0%	0-33(-53.6)%	0-12.5%	0%
Venation pattern	Highly irregular	Irregular	Irreg to ± regular	Regular, even
Sorus shape and size	Elongate-oval-round; (1.5-)2-3(-3.5) mm	Oval, raised; (1.5-)2-4 mm	Round to ± oval; 1.3- 2.5(-3) mm	Round, rarely ± oval; raised; 1.0-2.5 mm
Number of indurated annulus cells	(10-)11-17(-27!)	(8-)11-14(-17)	(9-)11-13(-17)	(9-)12-13(-16)
Spore surface	Tuberculate	Verrucate to tuberculate	Rugose to ± verrucate	Rugose to ± verrucate
Spores % malformed	Mostly normal; <10% malformed	Mostly normal; <10% malformed	Mostly malformed; >40% malformed	Mostly normal; <10% malformed
Habitat	Epipetric, terrestrial	Epipetric, epiphytic	Epipetric, epiphytic	Epipetric, epiphytic
Geographic range	Ore. to Baja California	C. Ore. to C. Calif. and S. Mexico	S. Ore. to C. Calif.	Alaska to C. Calif.

reliable method is to count chromosomes or measure spore lengths or guard cells. More subtle characters that can be useful are the regular blade outline, the commonly ovate blade shape, and the more evergreen fronds (with frequent summer rain or watering) of *P. calirhiza* relative to the "sloppy", slightly irregular blade and pinna outline, the frequently deltate blade, and the summer-deciduous fronds of *P. californicum*.

Thicker textured forms of both *P. calirhiza* and *P. californicum* in coastal California are sometimes confused with *P. scouleri*, which is restricted to the fog-belt from Baja California to British Columbia. *Polypodium calirhiza* can be distinguished from *P. scouleri* Hook. & Grev. by its abundant arcuate trichomes along the adaxial rachis, thinner lamina, and verrucate spores (vs. nearly smooth under the light microscope in *P. scouleri*). The spore differences alone strongly suggest to us that *P. scouleri* is not involved in the parentage of *P. calirhiza*. From species of the *P. vulgare* complex in Europe, *P. virginianum* in eastern North America, and the *P. amorphum* Suksdorf/*P. hesperium* group in central and western North America, *P. calirhiza* differs by its abundant pubescence of arcuate, non-glandular trichomes along the adaxial rachis and lack of sporangiasters. Production of mostly normal spores (less than 10% malformed) separates *P. calirhiza* from triploid *Polypodium* hybrids in western North America.

Polypodium calirhiza is exceedingly variable possibly as a result of several factors: an increase in heterozygosity because of genome contributions from two parents differing in phenotypic expression and habitat preference; and increased abnormality and variability in morphology because of reduced genetic control (Wagner 1962). It may also be polyphyletic as a result of more than one hybridization event between the diploid progenitors, as has been documented in allopolyploid species of *Asplenium* (Werth et al. 1985). A result of this morphological diversity is the more extensive distribution of the tetraploid vis-à-vis the two diploids.

Statistical analysis.—A principal components analysis (PCA) was performed using a program by Kovach (M.V.S.P.: A multivariate statistical package for the IBM PC and compatibles, 1986) to evaluate the distances of specimens within and between taxa. Specimens collected from natural populations were primarily used; some specimens were greenhouse- or lathhouse-grown. Ploidy of most specimens was determined by chromosome count or occasionally by spore length, which is generally correlated with ploidy in *Polypodium* (Evans 1970; Kott and Britton 1982) and in other pteridophytes (Barrington et al. 1986). Characters used in the PCA were selected from those more useful or reliable in identification. An effort was made to choose characters that are more variable among taxa than within a taxon.

TABLE 3. CHARACTERS AND CHARACTER STATES SCORED FOR THE PRINCIPAL COMPONENTS ANALYSIS OF THE TAXA IN THE *POLYPODIUM CALIFORNICUM*/*GLYCYRRHIZA* COMPLEX. Factor loadings for the first two principal components.

Character/character states	PC I	PC II
1. Ratio of pinna length (mm) to pinna width (mm)	-0.22	-0.61
2. Regularity of vein patterns (1 = regular, 2 = slightly irregular, 3 = very irregular)	0.33	-0.28
3. Pinna thickness (mm)	0.07	-0.00
4. Shape of pinna tip (1 = attenuate, 2 = acute, 3 = broadly acute, 4 = obtuse, 5 = broadly obtuse, 6 = rounded)	0.52	0.49
5. Number of anastomosing points per vein pair per pinna	0.42	-0.52
6. Location of anastomosing points relative to pinna margin (qualitative: 1-4)	0.08	-0.13
7. Distance (mm) from pinna margin to anastomosing point	0.15	-0.13
8. Ratio of distance (mm) from pinna margin to anastomosing point to distance (mm) from pinna margin to costal vein	-0.00	-0.02
9. Sorus length (mm)	0.18	-0.06
10. Sorus shape (1 = round, 2 = slightly oval, 3 = oval, 4 = elongate-oval)	0.57	-0.05
11. Number of indurated annulus cells in sporangium	0.03	-0.05
Eigenvalue	3.688	1.050
Percent of total variance	57.94	16.49

From the original 20 characters or ratios, 11 were selected for use in the PCA; seven are quantitative and four are qualitative (Table 3). Generally four or five measurements were made per specimen for each character, except that 20-25 sporangia were used to count the indurated annulus cells. Cytological or related data (spore or guard cell length) were not used in the PCA, to avoid overpowering the morphological data with the very distinct ploidal-level categories. Data were log-transformed, and a centered correlation matrix was used (Neff and Marcus 1980).

The first and second principal components of the resulting analysis (Table 3) have similar character loadings. Characters that load heavily on both the first and second principal components are: shape of pinna tip, number of anastomosing points per pinna, and vein patterns, with two other characters, pinna length/width ratio and sorus size, contributing to a lesser degree. Two exceptions here are sorus shape, which contributes heavily to the first component and very little to the second, and pinna length/width ratio, which loads heavily

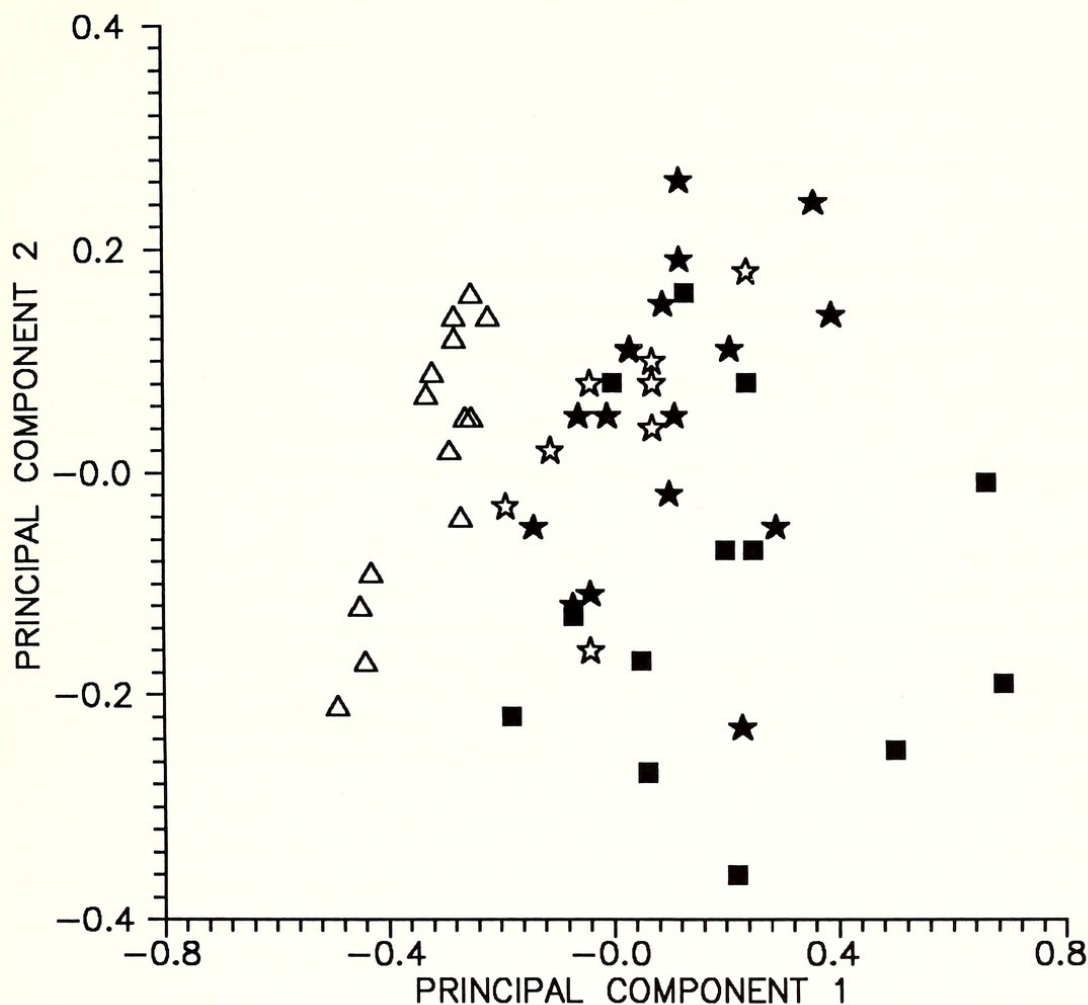


FIG. 3. Ordination of scores of the first and second principal components from a PCA using 11 morphological characters or ratios. The first and second principal components account for 57.9% and 16.5% of the variance respectively (total for the two equals 74.4% of the variance). Ploidal level of most specimens was determined by chromosome count, that of some specimens was determined by measurement of spore length. Taxa include: *Polypodium calirhiza* (solid stars); *P. glycyrrhiza* (triangles); *P. calirhiza* \times *glycyrrhiza* (open stars); and *P. californicum* (squares).

on the second component and only moderately on the first. Although the first component is usually a linear combination of size characters (Reyment et al. 1984), three of the five size or dimension characters load only moderately on the first component and the remaining two size characters do not contribute much at all.

A plot of the first two principal components from the PCA (Fig. 3) shows a clear separation of the two putative parents, *P. glycyrrhiza* and *P. californicum*, with *P. calirhiza* generally intermediate between them. The triploid hybrid appears to be similarly intermediate with a somewhat closer affinity to *P. glycyrrhiza*. These point distributions reflect the morphological variability of natural populations of *Polypodium* and emphasize the difficulty frequently encountered in distinguishing the taxa. The conspicuous variability in the distribution

of graph points for *P. californicum* correlates to some extent with the extremes seen in that species: the five points at the central- and lower right represent specimens similar to type material for *P. californicum*, while many of the *P. californicum* data points in the central region of the graph represent southern California specimens closer to the other end of the gradient.

Ecology. — The ecological behavior of these taxa correlates somewhat with the morphological differences. All four taxa are generally sympatric in the central coastal California region, yet they have distinct habitat preferences. *Polypodium californicum* grows on coastal bluffs and wind-swept grassy headlands while *P. calirhiza* grows in more protected ravines or further inland. *Polypodium calirhiza* is frequently found on roadcuts associated with the triploid hybrid, *P. calirhiza* × *glycyrrhiza*. If the habitat has enough moisture and shade, and has not been disturbed too much, then *P. glycyrrhiza* may also occur with them.

KEY TO TAXA

The following key will separate most specimens of the complex in California. *Polypodium scouleri* is also included because of occasional confusion and sympatry with the other species. Specimens with 50% or more shriveled or malformed spores are most likely hybrids, the commonest being *P. calirhiza* × *glycyrrhiza*. Such hybrids may key to any of the taxa marked with an asterisk.

- a. Veins all free, usually pellucid, vein pathways regular; lamina thin; sori usually round, sometimes oval, conspicuously raised, usually 1–2(–3) mm diam. *P. glycyrrhiza**
- a'. Veins sparingly (1–2 pairs per frond, rarely 0) to commonly anastomosing, not pellucid, vein pathways uneven, irregular, or if regular, lamina coriaceous to leathery; sori oval to round, flat to conspicuously raised.
 - b. Rhizome pruinose; fronds leathery and stiff, or chartaceous and brittle (living fronds and pinnae snapping easily when bent); pinnae with crenate, cartilaginous margins; sori 2–5 (usually over 3) mm long. *P. scouleri* and hybrids
 - b'. Rhizome dull or sometimes slightly glaucous; fronds membranaceous to chartaceous but not leathery, usually not brittle when living; pinnae with serrate margins; sori 1.5–3(–4) mm long.
 - c. Lamina oblong-ovate, regular in outline, proximal 1–3 pinna pairs shorter than those above; sori oval, prominent, frequently becoming confluent near rachis; spores 57–86 μ m long (mean: 68 μ m, including tubercles). *P. calirhiza**
 - c'. Lamina deltate to oblong to ovate, often somewhat irregular in outline; proximal 1–3 pinna pairs as long as or longer than those above; sori round to oval, relatively flat to raised; spores 42–67 μ m long (mean: 52 μ m, including tubercles). *P. californicum**

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