

THE CALIFORNIAN CLOSED CONE PINES
(SUBSECTION *OOCARPAE* LITTLE AND CRITCHFIELD):
A TAXONOMIC HISTORY AND REVIEW

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Summary

Of the seven pines that compose subsection *Oocarpae* (Little and Critchfield) in the genus *Pinus*, only the three Californian species form a coherent group, while the other four differ from each other and from the Californian species. Traits of the Californian species (*Pinus radiata*, *P. muricata*, *P. attenuata*) vary in complex geographic patterns, a situation that has led to nomenclatural confusion. Modern studies of genetic variation clarified some relationships among the taxa and uncovered other new problems. The taxonomic history and present status are reviewed and discussed. Monterey pine has been described as *Pinus californiana*, *P. adunca*, *P. Montereyensis*, *P. monteragensis*, *P. Sinclairii*, *P. tuberculata*, *P. insignis*, and *P. radiata*. Numerous varietal names for the mainland populations were described, then dropped. Current understanding of this species describes pines at Año Nuevo, Monterey, and Cambria as *P. radiata* var. *radiata*, pines on Guadalupe Is. as *P. radiata* var. *binata*, and on Cedros Is. as *P. radiata* var. *cedrosensis*. Complex variation in bishop pine led populations of that species to be called *P. insignis*, *P. Edgariana*, *P. murrayana*, *P. contorta*, and *P. muricata*. Present taxonomy describes central and southern populations as *P. muricata* var. *muricata*, populations north of (and including a few individuals at) Monterey as *P. muricata* var. *borealis*. The status of two cone variants, *P. muricata* var. *stantonii* and *P. remorata* is disputed on the basis of relationships among other traits. The latter appears to be a variant of bishop pine. Knobcone pine has been described as *P. californica*, *P. tuberculata* and *P. attenuata*. Only the latter name is currently used.

Introduction

In his classification of the genus *Pinus*, Shaw (1914) emphasized cone serotiny as a primary systematic trait. Despite heterogeneity among other traits, Shaw placed all 16 species of pines with serotinous or partly serotinous cones in his group *Insignes* (subsection *Pinaster*). Recognizing the diversity among pines in *Insignes*, Duffield (1952) reassessed relationships using terpene chemistry and crossing data, and transferred nine species to other groups. The remaining seven pines composed Duffield's Group XIV, which he felt to be an unsatisfactorily heterogeneous assemblage of species.

Within Duffield's Group XIV, subsequently named *Oocarpae* (Critchfield and Little, 1966), the only truly natural group seems to be the one that comprises three Californian species. They resemble one another in having alpha and beta pinenes in their terpenes (Mirov, 1948), medial resin canals (Critchfield, 1967), armed (with one exception), asymmetric, serotinous cones, and multinodal shoots (Shaw, 1914). The four Latin American species in *Oocarpae* do not form a unified group, although they differ from the Californian closed cone pines in their variable resin canal locations (Critchfield, 1967), symmetrical, unarmed or only slightly armed cones, and tardy cone opening rather than true serotiny (Martinez, 1948). Although in some cases the range of variation in individual phenotypic traits overlaps between the Californian and Latin American species, it is the unique combination of these characteristics that distinguishes the Californian group. Isozyme data from a study of 35 loci further underline the gap between the groups: Whereas the three

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Californian species cluster tightly together, the Latin American species differ greatly from each other and from the Californian species-cluster (Millar et al., 1986).

Patterns of crossability provide especially important evidence for both the unity of the Californian closed cone pines and the distinctness of the Californian and Latin American groups (Duffield, 1952; Critchfield, 1967; Millar and Critchfield, 1986). Crossing data frequently are used to assess relationships among taxa. Although barriers to crossing may arise for many reasons, the ability to interbreed most likely indicates that the taxa are closely related. Thus, it is the absence of barriers that is the most important evidence for phylogeny, since barriers may evolve rapidly even in closely related groups. All combinations among the Californian species have been successfully crossed, with some interspecific combinations as fertile as intraspecific crosses. By contrast, the Californian species are almost completely isolated by crossing barriers from the Latin American species. Only one hybrid combination, represented by a single seedling, has been verified (Critchfield, 1967). Crosses of the Californian closed cone pines to pines of other subsections have failed, with the exception of a single unconfirmed hybrid combination with a species in subsection *Australes* (Critchfield, 1967). One species of the Latin American group has been successfully crossed with two species in *Ponderosae* (Critchfield, 1967).

A classification of the genus *Pinus* based primarily on wood anatomy traits (Burgh, 1973; slightly modified by Burgh and Farjon, 1984) emphasizes the close relationship of the three Californian closed cone pines, although in some cases the classification is not consistent with evidence from other characteristics. In this system, the three Californian species are placed in subsection *Attenuatae* (Burgh) along with two Mexican species. *Oocarpae* (Little and Critchfield emend. Burgh) is modified to include several additional Mexican species. The reasons for separating the two subsections are not clear: in the ten diagnostic wood traits Burgh uses to distinguish subsections in the genus, his *Attenuatae* and *Oocarpae* differ only in two minor and overlapping ways. Furthermore, he does not reconcile confirmed crossing data which indicate that the Mexican species he has placed in the two separate subsections are in fact related. Thus, the two subsections collapse back to *Oocarpae* (Little and Critchfield), with remaining questions focused on the exact number of Mexican species to include.

This paper reviews the taxonomic history and present status of the Californian species of *Oocarpae* (Little and Critchfield). These species are relatively well-known, having been studied by botanists for nearly two centuries. Especially in the last fifty years, major genetic and systematic studies on each species have substantially increased our knowledge of variation and relationships. These studies characterized the Californian closed cone pines as a genetically complex group, with large genetic diversity within species, unusual patterns of variation among populations, inconsistent intergradations among species, crossing barriers within species, and high fertility between some species.

Early taxonomists, attempting to order the complex variation, primarily of cone morphology, in the Californian closed cone pines and following typological species concepts, named many species and varieties, and created confusion with ambiguous designations and multiple names for the same pines. Modern systematists used new information on many traits, and applied evolutionary species concepts to re-evaluate relationships and revise the original nomenclature. The taxonomy of the Californian closed cone pines, however, remains in flux, as the existence of some taxa is questioned, the boundaries of other taxa are debated, and new names continue to be given, often for taxa of unconfirmed status. The historic and contemporary situations make pertinent a review of this genetically complex group. The Latin American species are excluded from this review because their affinities to the Californian species and to other subsections in the genus are unclear, and because they have been little studied.

The Species of the Californian Closed-Cone Pines

The Californian closed-cone pines include a montane, interior species, knobcone pine (*Pinus attenuata* Lemmon), and two maritime, insular species, Monterey (*P. radiata* D.

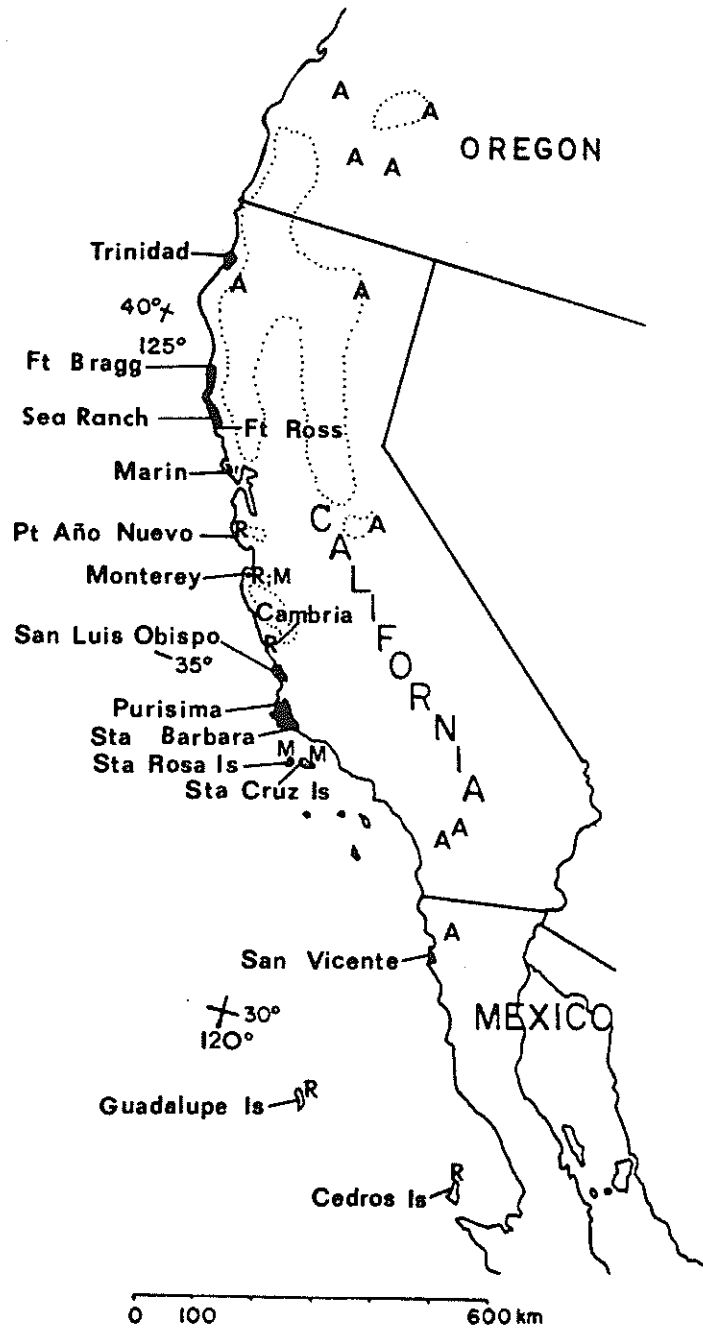


Fig. 1. Distribution of bishop pine (shaded areas and areas marked by "M"), Monterey pine (areas marked by "R"), and knobcone pine (areas marked by dotted lines and "A").

Don) and bishop (*P. muricata* D. Don) pines (Fig. 1; Griffin and Critchfield, 1976). Knobcone pine most often grows in small, disjunct populations on dry rocky sites that are prone to fire. It extends from southern Oregon to northern Baja California in the coast ranges and on the west slope of the Sierra Nevada. Knobcone pine usually forms pure stands,

although it may mix with ponderosa (*P. ponderosa* Laws.) and sugar (*P. lambertiana* Dougl.) pines, or grow in oak/chaparral woodlands. The highly discontinuous mainland populations of bishop and Monterey pines extend from northern California to Baja California on coastal terraces and slopes within 10 km of the ocean, and on sites where fog is common. Both species usually grow in pure stands, but may occur mixed with coast redwood (*Sequoia sempervirens* (D. Don) Endl.) or Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco). Insular closed cone pine populations occur on Santa Cruz and Santa Rosa Islands in California, and on Guadalupe and Cedros Islands in Mexico. The only areas of sympatry between species are at Pt. Año Nuevo, where knobcone and Monterey pines grow together in a small area, and on the Monterey peninsula, where the small bishop pine population is surrounded by Monterey pine. A 640 km gap in Mexico separates the Californian closed-cone pines from the Latin American species of *Oocarpae*.

Monterey Pine

1. *Early taxonomy.*—The 19th century taxonomy of Monterey pine was complex due not only to poor communication among pine botanists and hence redundant naming, but also to the prevailing typological species concepts, whereby even slight phenotypic variants (especially cone) were considered separate species. Loiseleur des Longchamps (1812) was the first to publish a description of a maritime pine from California that most likely was a closed cone pine. He recorded the collection of seed in 1787 at Monterey, California by the gardener Colladon (elsewhere Collignon) of the La Pérouse voyage to America from France. Colladon sent seeds to the Museum of Natural History in Paris the same year, and the seeds were planted in the Jardin des Plantes. Loiseleur named this pine *Pinus californiana*, distinguished by leaves in two's and three's, with cones resembling maritime pine, *P. pinaster*, but one-third larger, and bearing seeds like *P. cembra* that were good to eat.

Although the description of the leaves, cone, and location adequately specify present-day Monterey pine, the seeds described by Loiseleur certainly do not, and probably came from another collection that was accidentally mixed with the cone and leaves from the Monterey pine specimens. Despite the confusion in Loiseleur's description, the plants that derived from seeds planted in the Jardin des Plantes clearly were Monterey pine (Lemmon, 1893).

The name *Pinus californiana* Loise. (sometimes *P. californica* Loise., e.g., Hooker and Arnott, 1841; Lemmon, 1893) was used by many prominent botanists for one of many closed cone pines described from California during the 19th century (e.g., Loudon, 1838; Lemmon, 1892a, 1893). At the same time, other botanists (e.g., Endlicher, 1847; Engelmann, 1880a, b) largely ignored the name, considering it inadequately described and the tree poorly identified.

Several other names that appeared in the early literature and vaguely described a pine from Monterey include *P. adunca* Boscawen ex Poiré (1816), *P. Montereyensis* Godefroy (elsewhere ascribed to Rauch), and *P. montheragensis* Godefroy (Loudon, 1838). These names were considered to be synonyms for *P. californiana*, having been used to refer to trees growing in the French Horticultural Society Garden, and deriving from seeds sent by Godefroy in 1829 of the same pine as *P. californiana* (Loudon, 1838).

Another name was used during this part of the century for a maritime pine that probably was Monterey pine. Hooker and Arnott (1841), in reporting the botanical collections of Captain Beechey's voyages in 1825–1828, described *P. Sinclairii* as a two- and three-leaved pine that covered the hills from "Monterey to Carmelo and to Punta Pinos." The single cone they had, however, was obviously from a different species (probably *P. montezumae*, Bannister, 1954), for their description and figure show a cone 30 cm long and 13 cm wide unattached to any foliage, with scales widely reflexed and devoid of seed. They concluded that this may be the same pine as *P. californiana* Loise. (which they later claim in the same volume, however, to be a "very dubious species"). Later botanists, realizing the mix-up

of foliage and cone, ignored *P. Sinclairii*, considering it a "factitious species" (Engelmann, 1880a, b).

On the basis of a few cones collected by Coulter on the coast of the Monterey Peninsula, the British taxonomist David Don described Monterey pine as *P. radiata* in a paper he presented in 1835 to the Linnaean Society of London (Don, 1837). Although he had no foliage, Don assumed that *P. radiata* had three leaves per bundle. In the same place, and again based only on cone specimens, Don (1837) described another maritime pine from Monterey, *P. tuberculata*, distinguished from the former by the form of its cones. This pine undoubtedly also was Monterey pine.

In 1838, Loudon listed four maritime species growing on the Monterey Peninsula that refer to present-day Monterey pine: *P. californiana* Loise. (and synonyms above), *P. radiata* Don, *P. tuberculata* Don, and a new species, *P. insignis*. Loudon credited collection in 1831 of the latter to Douglas, and based his descriptions on specimens in the British Horticultural Society collection. Loudon's description of *P. insignis*, the first complete description of Monterey pine, characterizes cones, needles, buds, growth, and tree form.

Probably owing to the completeness of Loudon's description of *P. insignis*, and the wide circulation of his book, this name became widely used for the pine from Monterey. Lemmon (1888) named two new varieties at Monterey in addition to typical *P. insignis*, *P. insignis* var. *radiata* (large coned variant meant to be the specimens Don described as *P. radiata*), and *P. insignis* var. *laevigata* (smooth coned variant). Other botanists agreed with Loudon's implications that *P. radiata* and *P. tuberculata* were independent species that grew with *P. insignis* at Monterey (Gordon, 1858; Engelmann, 1880b).

By the 1880's, Monterey pine populations at Año Nuevo (Engelmann, 1880b; Lemmon, 1888) and Cambria (Hartweg, 1848) were ascribed to *P. insignis*. Hartweg (1848) first described the Monterey pines at Cambria as a "variety of *P. insignis* with larger cones than those about Monterey." Gordon (1858) used *P. insignis macrocarpa* Hartweg as a synonym of *P. radiata* Don, and Carrière (1867) used the same name, giving *P. radiata* as its synonym.

Monterey pine populations on the islands off the California and Baja California coasts were first mentioned by Watson (1876), who reported but did not name a two-leaved variety of *P. insignis* collected by E. Palmer in 1875 on Guadalupe Island. Engelmann mentioned, in his description of *P. insignis* in 1880, a variety "*binata*, collected by Dr. Palmer on Guadalupe Island, with the normal cones of *P. insignis* but leaves in pairs" (Engelmann, 1880b). Eight years later, Lemmon also mentioned "an outlying variety (?) [sic] *binata* on the Island of Guadalupe" (Lemmon, 1888, 1895). The Monterey pine population on Cedros Island was originally ascribed to bishop pine, and its affinity to Monterey pine has been acknowledged only recently (see below). Some authors incorrectly described the bishop pines on Santa Cruz and Santa Rosa Islands as *P. insignis* var. *binata* (Greene, 1887; Brandegee, 1888, 1890).

Lemmon argued in several places over the priority of names for Monterey pine. Initially (1892a, b), he defended Loiseleur's *P. californiana* (or *P. californica*) as the proper original name, but later conceded that Loiseleur's description was sufficiently vague as to refer to "any three-leaved maritime pine the La Pérouse expedition might have collected" (Lemmon, 1893). At roughly the same time, but in different places, he argued for Don's priority with *P. radiata* (Lemmon, 1888, 1893). In 1895, he officially discarded the name *P. insignis* and recognized the name *P. radiata*, which he applied to the mainland Californian populations at Año Nuevo, Monterey, and Cambria as well as the varieties (Lemmon, 1888, 1893, 1895). By 1895, however, Lemmon apparently ignored several varietal names he had previously used, and listed only two varietes of *P. radiata*, namely, var. *binata*, which included "a few trees on the islands of Santa Cruz and Guadalupe," and var. *tuberculata*, a small-coned pine from Monterey that Don had originally called *P. tuberculata*. In subsequent literature, the recognition of the name *P. radiata* seems to have been accepted, and it became widely used.

2. *Modern studies.*—Modern nomenclature of Monterey pine, based on studies of variation and evolutionary species concepts, includes the three mainland populations (Año Nuevo, Monterey, and Cambria), variety *binata* on Guadalupe Island, and variety *cedrosensis* on Cedros Island. An old idea that two species, *P. radiata* and *P. insignis* grow together at Monterey was again suggested by Todd (1934) and considered by Jepsen (1934), but is clearly refuted by genetic studies. Despite variability among the mainland populations of Monterey pine in growth and form (Forde, 1964; Fielding, 1961a; Burdon and Bannister, 1973; Guinon et al., 1982), cone (Bannister, 1954; Forde, 1953, 1964; Axelrod, 1980) and needle traits (Forde, 1964), terpenes (Bannister et al., 1962), disease and cold resistance (Cobb and Libby, 1968; Hood and Libby, 1980), and seed proteins and isozymes (Murphy, 1981; Plessas and Strauss, 1986) the differences in most traits are relatively small, and the three populations compose a distinct unit.

Relationships among the three mainland populations are unclear because patterns of resemblances differ among traits. Fielding (1961a) suggested that the Cambria population differed enough to warrant varietal designation, and he encouraged the transfer of *P. insignis macrocarpa* Hartweg ex Carrière to *P. radiata*. Later evidence, however (Forde, 1964; Bannister et al., 1962), did not uphold Cambria's distinctiveness, and isozyme (Plessas and Strauss, 1986), disease resistance (Old et al., 1985), and terpene data (Bannister et al., 1962) indicate that Año Nuevo is distinct, and Monterey and Cambria are similar. In light of the low magnitude of differences among the mainland populations and the lack of overall distinctness of any population, I do not recommend using a varietal designation for Cambria or any of the mainland populations.

By contrast to the low divergence among the mainland populations, the Guadalupe and Cedros Island populations differ distinctly from one another and from the three mainland populations. During the first half of the 20th century, several names based primarily on cone variation were used for the two-leaved pines on Guadalupe Island: *P. muricata*, *P. radiata*, *P. radiata* var. *binata* (Mason, 1932), *P. remorata* (McMinn and Maino, 1935; Mason, 1949), *P. radiata* forma *binata*, and *P. radiata* forma *guadalupensis* (Howell, 1941). Later genetic studies confirmed the affinity of Guadalupe Island pine to mainland *P. radiata* in terpenes (Bannister et al., 1962; Bannister and McDonald, 1983), growth (Crowley, 1974), phenology and crossing behavior (Libby, pers. comm.), and seed proteins (Murphy, 1981). Despite these similarities, differences between Guadalupe Island pine and the mainland populations in needle number, growth, stem form (Crowley, 1974), disease resistance (Libby et al., 1968; Power and Dodd, 1984), seed proteins (Murphy, 1981), resin canal number (Bannister, 1958a; Newcomb, 1959), terpenes (Bannister and McDonald, 1983) and isozymes (Brown and Moran, 1979) are large relative to the magnitude of differences among the mainland populations. This population commonly is referred to as *P. radiata* var. *binata*.

The pines on Cedros Island, originally described as a population of *P. muricata* and later as *P. muricata* var. *Anthonyi* (Abrams, 1923), *P. remorata* (Mason, 1930, 1949; Axelrod, 1967), and *P. radiata* var. *binata* (Axelrod, 1967), were formally named *P. muricata* var. *cedrosensis* (Howell, 1941). Like Guadalupe Island pine, pines on Cedros Island have been shown to resemble mainland Monterey pine more than bishop pine in phenology, growth, cone morphology, resin canal number (Newcomb, 1959; Fielding, 1961b), crossing behavior (Brown, 1966), terpene composition (Bannister and McDonald, 1983), and seed proteins (Murphy, 1981). As in the Guadalupe Island pine, the degree of differences that distinguishes the Cedros Island population from the other Monterey pine populations is greater than that among the mainland populations. Axelrod (1980) acknowledged the affinities and differences when he transferred the varietal name to Monterey pine, *P. radiata* var. *cedrosensis*.

Bishop Pine

1. *Early taxonomy.*—On the basis of cones collected by Coulter near San Luis Obispo, Don described in 1835 another maritime pine, *P. muricata* (Don, 1837). Since he again

had no leaves to examine, Don (wrongly) assumed, "it is probable that, like the greater part of American pines, [the leaves] grow in threes." Eleven years later, Hartweg (1848) described a similar pine growing in a small area on the Monterey peninsula surrounded by Monterey pine (then called *P. insignis*), and also south of San Luis Obispo at Purisima, as *P. Edgariana*. Although Hartweg noted that leaves of *P. Edgariana* grew in pairs, Gordon (1858) seems to have been the first to correctly describe bishop pine as having adult leaves primarily in two's.

Hartweg's name was little used, and Don's priority was widely recognized for *P. muricata* at Monterey, Purisima, and San Luis Obispo. Pine populations at Mendocino (on and off the "pygmy forests") and Pt. Reyes were also soon ascribed to *P. muricata* (Gordon, 1858; Bolander, 1866; Engelmann, 1880b) and the small mainland population near San Vicente was described as var. *Anthonyi* for its small cones (Lemmon, 1895). Bishop pine at Trinidad was not discovered until 1915 (Metcalf, 1921). Bishop pines growing on Santa Cruz and Santa Rosa Islands were originally referred to *P. insignis* (Greene, 1887; Brandegee, 1888, 1890), later *P. radiata* (Lemmon, 1895; Sudworth, 1908), and not considered *P. muricata* until the early 20th century (Abrams, 1923; Mason, 1930). A brief and errant reference to bishop pine as *P. murrayana*, growing at 2500 m in the Siskiyou Mtns. of northern California, occurred in Gordon (1858), and Bolander (1866) seems to have mistaken the bishop pines at Tomales Pt. for *P. contorta*.

2. *Modern studies.* — Modern studies on bishop pine have documented genetic structuring in bishop pine that was not recognized earlier, or that was confused with variation in other species. A major divergence in bishop pine has been described that occurs between northern populations and populations in central and southern California and Baja California (Duffield, 1951). Duffield first reported an abrupt transition in several traits within continuous pine stands in Sonoma County (northern California). North of a narrow (2–3 km) zone at Sea Ranch (Fig. 1), pines differ qualitatively from bishop pines south of Sea Ranch in stomatal anatomy and waxiness (Duffield, 1951), monoterpene compositions (Mirov et al., 1966), allozymes, and flowering phenology (Millar, 1983). The population south of Sea Ranch extends uniformly 30 km to Ft. Ross, where a major geographical discontinuity occurs between Ft. Ross and the Pt. Reyes population. Populations north and south of the Sea Ranch zone do not differ with respect to other traits, including growth, bark characteristics, stem form, cone abundance, cone serotiny, resin canal number, and coefficients of variation. Variation in these traits, however, distinguishes all populations north of Ft. Ross from populations south of Monterey, with the Pt. Reyes and Monterey populations having intermediate characteristics (Duffield, 1951; Fielding, 1961a; Doran, 1974; Everard and Fourt, 1974; Shelbourne et al., 1982).

Recognizing these differences, Duffield (1951) proposed but did not publish the name "*P. muricata* var. *borealis*," which unclearly referred either to all populations north of Ft. Ross, or only to those populations north of the abrupt transition at Sea Ranch. In the forestry literature, the populations north and south of the Sea Ranch transition are called blue and green bishop pine (referring to the stomatal trait). Duffield left the Pt. Reyes and Monterey populations in an undetermined status (not var. "*borealis*," or var. *muricata*), because, depending on trait, the variation was either unique to one or both populations, resembled northern populations, resembled southern populations, or was intermediate. The reports (Critchfield, 1967; Millar and Critchfield, 1986) of complete crossing barriers between bishop pines from northern California (Mendocino Co.) and southern California (several locations) suggested that at least some northern populations are genetically isolated from southern populations, and may warrant independent species status. The cause for the evolution of this unusual crossing barrier among obviously related pines is unclear. To date no taxonomic revisions have been proposed on the basis of these data.

Axelrod (1983) published Duffield's name *P. muricata* var. *borealis* to describe a pine with distinct cone shape. Since he distinguished the variety by cone morphology, he did not reconcile other genetic variants and discontinuities within this proposed taxon. Thus, he did not apply the name either to blue bishop pine (north of Sea Ranch) or to all

populations north of Ft. Ross, but rather extended the variety southward to include the entire Pt. Reyes population and a few "relict trees on Huckleberry Hill, Monterey." Thus, the variety as now defined is unsatisfactorily heterogeneous, since it comprises not only the relatively homogeneous populations north of the Sea Ranch transition, but also the diverse Sonoma, Pt. Reyes, and some members of the Monterey populations. Axelrod's description implies that *P. muricata* var. *borealis* is sympatric with var. *muricata* at Monterey, a biologically improbable situation.

The bishop pine populations on the southern mainland (San Luis Obispo, Santa Barbara, and Baja California) are, despite heterogeneity among some traits (resin canal number, cone morphology) and large within-population variation, relatively coherent in monoterpene composition (Forde and Blight, 1964; Mirov et al., 1966), growth, stem form (Duffield, 1951; Fielding, 1961a; Doran, 1974; Shelbourne et al., 1982), cone habit (Duffield, 1951), and crossing compatibility (Critchfield, 1967). These populations, which include the type locality at Coon Cr. near San Luis Obispo, are commonly accepted as typical *P. muricata*. Lemmon's (1895) designation of *P. muricata* var. *Anthonyi* for the Baja population, although retained by some authors (Abrams, 1923; Mason, 1932), has more commonly been rejected. Genetic studies refute this designation.

The nomenclature of bishop pine populations on Santa Cruz and Santa Rosa Islands has changed considerably since the early 20th century. Originally named *P. insignis* var. *binata*, then *P. radiata* var. *binata* (retained by Abrams, 1923; Sargent, 1947), genetic studies have shown closer affinities of these pines to southern populations of bishop pine (Forde and Blight, 1964; Crowley, 1974; Shelbourne et al., 1982) than to Monterey pine. In growth, stem form, resin canal number, phenology, and crossing behavior, the Channel Island pines most resemble the southern California bishop pine populations. Several characteristics, however, distinguish them from these and other bishop pine populations. Monoterpene composition (Forde and Blight, 1964; Mirov et al., 1966), phenology (Libby, pers. comm.), cone morphology (Mason, 1930), and allozyme frequencies (Millar et al., 1986) on the two islands differ in varying degrees from the mainland bishop pine populations.

One difference between mainland and island populations that has received considerable attention is the frequency of trees with thin-scaled, symmetric cones. On the islands, the frequency of this cone type in most stands is high (Mason, 1930; Howell, 1941; Linhart et al., 1967; Linhart, 1978; Axelrod, 1983). On the mainland, frequency varies by population: from Sonoma Co. northward, this cone type is rare or absent, whereas in central and southern populations it is present in variable frequencies. Five disjunct stands within these populations are unusual in having high frequencies of trees with thin-scaled, symmetric cones (Axelrod, 1983).

Mason (1930) seemed to rely on typological species concepts and ascribed considerable importance to cone morphology as a taxonomic trait: He described two taxa on Santa Cruz Island, trees with thick-scaled, asymmetric cones, *P. muricata*, and trees with thin-scaled, symmetric cones, which he named *P. remorata*. Mason further distinguished *P. remorata* from bishop pine as having more resin canals (6-12), and stouter, darker-green foliage. At the time, Mason either was unaware of, or excluded from *P. remorata*, single trees and stands on the mainland with similar cone types. Duffield (1951) demoted cone shape to a polymorphic trait within the species, and described all pines on Santa Cruz and Santa Rosa Islands as a single taxon, *P. muricata* var. *remorata*, a widely used but not formally published name.

Mason (1930, 1932, 1949) proposed that *P. remorata* has been a distinct evolutionary lineage since the late Tertiary, and that hybridization and introgression from the currently more fit *P. muricata* accounted for the extant cone variation on the Channel Islands and adjacent mainland. Axelrod (1980, 1983), the chief proponent of Mason's views, argued that *P. remorata* has a separate fossil history, that the fossil record shows no indication of the range of intermediate cone types presently found, and that the extant species occurs

extensively on the mainland and Channel Islands in drier, more sterile sites than bishop pine. Axelrod (1980) supported and extended Mason's hypotheses that the present variation in cone types in central and southern populations resulted from post-glacial hybridization and introgression of *P. remorata* and *P. muricata*, with the spread of *P. remorata* genes favored by selection for drought-adaptedness.

Other investigators, taking into account variation in all studied traits, have concurred with Duffield's (1951) assessment that *P. remorata* is not a distinct species. In a thorough comparative study of the Channel Island pines, Linhart et al. (1967) found no correlations among cone type, needle stoutness, and resin canal number. Terpene compositions varied among their samples of island pines, with differences related to stand of origin and not to cone type. They concluded that "*P. remorata* is primarily a name given to a particular cone type in a variable species."

The other reported distinctions of *P. remorata* may be questioned also. Of the hundreds of fossil cones resembling bishop pine that have been recovered from Quaternary deposits, only about 25 have been the smooth cone type. Although the disproportionate number of cones may be a bias of the fossil record, with *P. remorata* poorly represented because it grew on upland dry sites (Axelrod, 1980, 1983), the fossil record may, by contrast, accurately reflect the situation in southern Quaternary forests. The smooth cone type may have been in low frequency then, just as it is in central and southern extant mainland populations.

Fossil cones in the Museum of Paleontology, University of California, Berkeley, led me to question the reported lack of intermediate shapes in the fossil record. Of 104 cones labeled *Pinus "borealis"* from Axelrod's (1980) collections (fossil deposits at Carpenteria and Pt. Sal), I interpreted 20 as having cone types intermediate between the smooth-scaled and heavily armed types.

The reported ecotypic difference of extant smooth-coned pine stands has also been questioned (Vogl et al., 1977). The habitat of the pure stands of the smooth-cone type is well within the broad range of sites occupied by bishop pine. Furthermore, there are many stands in which trees with smooth cones seem to be mixed at random with trees with intermediate-shaped cones and trees with armed cones, with no pattern to the ecological preference of individual trees within these stands.

Finally, if the cone polymorphism in modern populations resulted from recent hybridization and introgression between two species (*P. remorata* and *P. muricata*), we would expect to see correlated patterns of variation in other traits. These patterns are, in fact, not found (Duffield, 1951; Linhart et al., 1967; unpubl. data). Rather, trees with smooth cones resemble the other bishop pines of the populations to which they belong more than they resemble each other over the range of the ensemble. This is expected if cone shape is just one polymorphic trait among many within the species. The only other explanation is that geographic variation in *P. remorata* fortuitously parallels variation in bishop pine. This surely must be rejected, because in all other characteristics studied, the variation of trees with smooth cones goes hand-in-hand with the variation of other trees that grow with them.

In sum, the smooth-scaled cone of the Channel Islands and central and southern mainland stands of bishop pine probably represents one extreme within a continuum of cone variation of a quantitatively varying trait in the species. Alternatively, Bannister (pers. comm.) suggests that there may be relatively simple but primary genotypic control of armed, asymmetric cones versus unarmed, symmetric cones; the wide variation in the armed cones is ascribed to minor genetic control superimposed on the first. Cone variation has existed within bishop pine populations for a long time and over a wide geographic range. Similar cone variation, although of a lesser magnitude, occurs in mainland Monterey pine, in the pines of Guadalupe Island (Lemmon, 1888; Howell, 1941; Bannister, 1954; Forde, 1964), and also in knobcone pine (Newcomb, 1962). In Monterey pine, Bannister (1954) found that cone characteristics vary continuously between two distinct extremes with intermediate

forms most common, as expected of a typical quantitatively varying trait. The important factor here for taxonomy is that all variable traits are considered and reconciled. If the nomenclature of the Channel Island populations of bishop pine were revised, it would be best to consider the cluster of traits that distinguishes the island populations, rather than defining taxa solely or primarily by cone morphology.

Recently, Axelrod (1983) described another taxon on Santa Cruz Island, *P. muricata* var. *stantonii*, sympatric with *P. remorata* and *P. muricata* var. *muricata*, and distinguished by the "broadly triangular apophyses that often are directed outward . . . and cones [that] have fewer scales than the associated cones of *P. muricata* var. *muricata*." The cones of this variety are similar in shape to fossil cones recovered from a Quaternary deposit at Sea Cliff (southern California). No genetic studies, however, have verified its distinctness.

Knobcone Pine

1. *Early taxonomy.*—Knobcone pine, the only interior pine in this group, was discovered in 1846 and named *P. californica* (not *P. californica* of Hooker and Arnott or Lemmon) by Hartweg (1847), who believed it was the "doubtful and little known" tree of Loiseleur. The pine he found, however, was 20 miles north and inland of Monterey in the Santa Cruz Mountains, and from his description was obviously distinct from any pine yet described. This name was little used, and two years later Gordon described the same pine at length, but used Don's name *P. tuberculata* and discredited Hartweg's name (Gordon, 1849). Gordon apparently thought that *P. tuberculata* grew close to the beach at Monterey intermixed with *P. radiata* (Don's description) and also north of Monterey in the Santa Cruz Mtns. In 1842, Lambert published Don's description and location of *P. tuberculata*. His figure, however, shows two views of a cone that matched Hartweg's description, but that differed obviously from cones of Monterey pine. Although Don, Lambert, and Gordon were misled in thinking that knobcone pine grew near the Monterey coast, the name *P. tuberculata* was widely used for the montane, interior closed-cone pine. By 1865, pine populations at Santa Cruz, Ukiah, Oakland, Forest Hill, and Eureka were considered *P. tuberculata* Don (Bolander, 1866). Bolander (1866) abandoned Don's (and Gordon's) original Monterey location for this species, indicating that he recognized that knobcone pine was a different species. Nevertheless, Bolander questioned whether *P. tuberculata* as described by Gordon and *P. insignis* were one or two species.

In later publications, Gordon's name was appended to *P. tuberculata*, apparently in recognition that he had described a different pine from Don. Gordon (1880), however, in a later edition of his book, still credited Don as the author of the species. By 1880, the published range of *P. tuberculata* had been extended to include populations in the coast ranges from San Bernardino and the Santa Lucia Mtns., to the Shasta region and southern Oregon, and in scattered populations along the foothills of the Sierra Nevada (Engelmann, 1880b). The only varietal name for the species, var. *acuta*, was given by Mayr (1890). He used this name to describe pines from a southern California population that had short cones with umbos topped by stiff spines, and with angular apophyses in cross section.

The legitimacy of the name *P. tuberculata* was questioned due to the mix-up of Don's original use of the name for a pine that really was Monterey pine and Gordon's use of the same name for Hartweg's pine. Engelmann's (1880a) solution was to defend *P. tuberculata* Gordon (not Don), retaining the specific epithet because of wide use, despite the errancy of Don's description. In 1892, Lemmon argued against the use of a name that had previously described a different species. Claiming that the name *P. tuberculata* was unavailable for knobcone pine, Lemmon proposed *P. attenuata*, a name suggesting the "tapering character of the cones [and the] slender habit of the tree" (Lemmon, 1892a, b). The name *P. attenuata* Lemmon was subsequently used by most botanists.

2. *Modern studies.*—Fewer studies have investigated variation in knobcone pine than in the maritime species (Bannister, 1958b; Newcomb, 1962). Several authors have noted the

lack of distinct variation in knobcone pine by comparison to the maritime pines (Lemmon, 1888; Mirov et al., 1966). After a species-wide analysis of cone morphology, needle morphology, seed weight, germination, and seedling growth traits, Newcomb (1962) concluded that two basic patterns of variation exist in knobcone pine: traits that differ among northern populations (Sierra/Cascade and north coast ranges) vary clinally, whereas traits that differ among southern California and Baja California populations vary discontinuously. Newcomb recommended using the names *P. attenuata* var. *acuta* (from Mayr's (1890) *P. tuberculata* var. *acuta*) for the southern group (characterized by smooth small cones and divergent needle and growth traits), and *P. attenuata* var. *attenuata* for all northern populations. The transfer of var. *acuta* to *P. attenuata* has not been published, although the populations seem quite distinct.

Recently Axelrod (1983) suggested that knobcone pines near the California coast may actually be *P. linguiformis* Mason, a fossil species that differs from *P. attenuata* only in having cone scales that are "more slender and tongue-shaped and are not so well developed distally." Without further evidence, however, these pines should all be considered *P. attenuata*.

Conclusions

The Californian closed-cone pines are a distinct and coherent group in the otherwise heterogeneous subsection *Oocarpae* (Little and Critchfield). Within this group, however, complex patterns of variation have challenged taxonomists since the discovery of the pines by European botanists in the late 18th century. Three Californian taxa are widely recognized as established species, although there is disagreement over the limits of the species and their intra-specific structures (especially in *P. muricata*):

NAME	LOCATION
<i>P. attenuata</i> Lemmon, knobcone pine	southern Oregon, California, northern Baja California
<i>P. radiata</i> var. <i>radiata</i> Don, Monterey pine	California: Año Nuevo, Monterey, Cambria
var. <i>binata</i> Lemmon	Guadalupe Island, Mexico
var. <i>cedrosensis</i> (Howell) Axelrod	Cedros Island, Mexico
<i>P. muricata</i> var. <i>muricata</i> Don, bishop pine	California: Monterey, San Luis Obispo, Santa Barbara; Santa Cruz and Santa Rosa Islands.
	Baja California: San Vicente
var. <i>borealis</i> Axelrod	California: Humboldt, Mendocino, Sonoma, Marin, and Monterey Cos.
var. <i>stantonii</i> Axelrod	Santa Cruz Island

Several designations for these pines either are unconfirmed by genetic studies, or are contested (*P. muricata* var. *stantonii*, *P. remorata*, and the geographic distribution of *P. muricata* var. *borealis*).

Genetic studies at present indicate that the two widely recognized maritime species, Monterey and bishop pines, have complex patterns of variation within and among the disjunct populations. Some infraspecific taxonomic designations in these pines are misleading, since they imply either a uniformity among members that in fact does not exist, the existence of taxa for which there is little supporting evidence, or, in the case of multiple sympatric varieties, an unlikely biological situation. Although some infraspecific names describe clearly distinct taxa and probably should be retained (e.g., *P. radiata* var. *binata*, and *P. radiata* var. *cedrosensis*), in general, I agree with those who have recommended that the number of species and varietal names in the Californian closed cone pines be minimized. In the maritime pines, distinct geographic populations or particular variant types can be identified by place or descriptive names (e.g., the Santa Cruz Island pine, or blue bishop pine) without formal designation, thus avoiding the confusions discussed above.

Of the many taxonomic uncertainties remaining for the Californian closed cone pines, several stand out as warranting further research. In the mainland populations of bishop pine, a study of the relationship of cone morphology, especially the thin-scaled, symmetric cone, to other traits would clarify the significance of cone characteristics as indicators of genetic divergence. Further investigations are needed on crossing relations among populations of bishop pine, and on the significance of crossability when considered in conjunction with other attributes in bishop pine. In knobcone pine, genetic studies of morphological and biochemical variation within and between populations would significantly add to our knowledge of that species. Finally, a broader based genetic study, encompassing all three Californian species with as many populations represented as possible, would give insight into phylogenetic relationships among populations and species.

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