HYBRIDIZATION AND CLASSIFICATION OF THE WHITE PINES (PINUS SECTION STROBUS)

William B. Critchfield

Summary

Many North American and Eurasian white pines retain their ability to hybridize even after long isolation, and about half of all white pine hybrids from controlled pollinations are inter-hemisphere crosses. Within the morphologically homogeneous and otherwise highly crossable core group of white pines, an exception in crossing behavior is Pinus lambertiana of western North America. Although it is an archetypal white pine in its winged seeds and long, unarmed cones that open at maturity, P. lambertiana has not been successfully crossed with any other species in the core group. It has been hybridized only with P. armandii and P. koraiensis, two natives of eastern Asia that do not resemble P. lambertiana or each other in the characteristics used to classify white pines. Both Asian species have seeds without wings, and P. koraiensis has indehiscent cones that retain the seed at maturity. Wingless seeds and seed-retaining cones may have evolved more than once as adaptations to seed dispersal by birds, and their taxonomic value is questionable. Lack of agreement among the kinds of data that bear on relationships of the white pines emphasizes the need for new approaches to their classification.

Introduction

The two largest aggregations of species in the genus Pinus, the white pines of section Strobus and the hard pines of section Pinus (classification of Little and Critchfield, 1969), present remarkable contrasts in crossing behavior. In section Pinus, which includes more than one-half of the species in the genus, the ability to hybridize is closely tied to geography. No verified hybrids have been produced between hard pines native to the Eastern and Western hemispheres; an earlier report of such a cross (P. nigra × P. resinosa: Critchfield, 1963) must be discounted on the basis of isoenzyme data (Morris et al., 1980). And in North America, where the hard pines are most numerous and diverse, even crosses between species native to different parts of the continent are mostly unsuccessful.

The white pines, about one-fifth of the species in the genus, exhibit no such geographic restrictions. Neither their ability to cross with each other nor the ease with which they can be crossed is related to geography. Of all verified white pine hybrids, about one-half are combinations of Eastern and Western hemisphere species (Critchfield, 1975).

Much of the impetus for exploratory hybridization of the white pines has come from efforts to increase resistance to white pine blister rust (caused by the fungus Cronartium ribicola) in three economically important and highly rust-susceptible white pines of North America: P. strobus (eastern white pine), P. monticola (western white pine), and P. lambertiana (sugar pine). In most classifications they are placed in subsection Strobi, one of two or three subsections in section Strobus. Within the subsection, these species and several other North American and Eurasian species form a morphologically coherent group of typical white pines, with five-needled fascicles, elongate, thin-scaled cones that open and shed their seeds at maturity, and winged seeds. Pinus strobus and P. monticola, but not P. lambertiana, are also typical of this group in the ease with which they can be crossed with most other species in the group.

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Within this group, *P. lambertiana* is unique in its crossing behavior. It has not been successfully crossed with any other species in the group, nor has it been crossed with any North American white pine outside the group. Verified hybrids of *P. lambertiana* have been produced with only two other species, both forest trees native to eastern Asia: *P. armandii* and *P. koraiensis*. These two Asian species are among the most resistant of the white pines to blister rust (Bingham, 1972). The rust is also native to Asia, and Bingham (1977) has speculated that the high level of resistance in these pines can be attributed to coevolution of host and rust.

Most classifications of the species in section *Strobus* are based on just two characteristics: the presence or absence of seed wings and the retention or release of seeds at cone maturity. *Pinus koraiensis* and *P. armandii* differ from *P. lambertiana* and each other in one or both characteristics. *Pinus koraiensis* is usually grouped in subsection *Cembrae* with a few other species having wingless seeds and seed-retaining cones. *Pinus armandii* also has wingless seeds but its cones open at maturity. It is variously classified in subsections *Cembrae* or *Strobi* or in a separate subsection (Flexiles).

None of the existing classifications of the white pines has made use of crossing data. This paper updates what is known about crosses among the species in section *Strobus*, including unpublished results from the breeding program of the U.S. Forest Service’s Institute of Forest Genetics (IFG), Placerville, California. Classifications of the white pines are reviewed, and relationships are reevaluated on the basis of contradictory evidence from morphology, biochemistry, and crossing behavior.

**Morphology and Classification of Section Strobus**

In his classic monograph of *Pinus*, Shaw (1914) segregated the white pines of this section into three groups (Table 1): *Cembrae*, with indehiscent (seed-retaining) cones and wingless seeds; *Flexiles*, also with wingless seeds but having cones that release their seeds at maturity; and *Strobi*, also with seed-releasing cones but having conspicuously winged seeds. Shaw later (1924) discarded *Flexiles*, adding its two species (*P. flexilis* and *P. armandii*) to *Strobi*.

Shaw’s *Cembrae* has been retained intact in most modern classifications of the white pines (Rehder, 1940; Little and Critchfield, 1969; Landry, 1977). It includes *P. cembra* of Europe and *P. sibirica* of northern Eurasia (taxa that he treated as conspecific), *P. koraiensis* and *P. pumila* of eastern Asia, and *P. albicaulis* of western North America.

Shaw’s amended group *Strobi* includes all other species in section *Strobus* (Table 1). All have cones that open and release the seed, most have elongate cones with thin scales, and most have winged seeds. In addition to *P. strobus*, *P. monticola*, and *P. lambertiana*, his enlarged *Strobi* includes several other species that have been used in species crossing: *P. griffithii*, *P. parviflora*, and *P. armandii* of southern and eastern Asia; *P. peuce* of southeastern Europe; and the *P. ayacahuite*–*P. strobiformis*–*P. flexilis* complex of western North America. No crosses have been reported with several species of restricted distribution in warm-temperate and subtropical parts of Asia and North America.

The distinction between *Cembrae* and *Strobi* is based on the “indehiscent” cone of the former. The distally thickened cone scales of *Cembrae* have less vascular tissue and sclerenchyma than the scales of *Strobi* and other pines, and are structurally incapable of relaxing sufficiently to release the seed (Shaw, 1914). Unlike the serotinous cone of hard pines, however, the indehiscent cone does not necessarily remain tightly closed at maturity. Detailed information is sparse and contradictory, chiefly because most maturing cones of *Cembrae* pines are destroyed by seed-eating birds and small mammals. But it is certain that the cone scales of *P. albicaulis* sometimes separate at maturity (D. F. Tomback, personal communication, 1980; Lanner, 1982b), and scale separation is apparently usual in *P. koraiensis* (Shaw, 1914) and *P. pumila* (Wilson, 1916; Pivnik, 1957).

In his amended classification of the white pines, Shaw (1924) also contrasted the wingless seeds of *Cembrae* with the seeds of *Strobi*, which he described as having adnate wings.
Table 1. Classifications of white pines. Boxes enclose taxa that are grouped together in all classifications.

<table>
<thead>
<tr>
<th></th>
<th>Engelmann, 1880</th>
<th>Shaw, 1914</th>
<th>Shaw, 1924</th>
<th>Pilger, 1926</th>
<th>Gaussen, 1960</th>
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<tr>
<td><strong>CEMBRAE</strong>¹</td>
<td><strong>CEMBRAE</strong></td>
<td><strong>CEMBRAE</strong></td>
<td><strong>CEMBRA</strong></td>
<td><strong>ARMANDIOIDES</strong></td>
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<td>pumila</td>
<td>pumila</td>
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<td>stibirica</td>
<td>albicaulis</td>
<td>albicaulis</td>
<td>albicaulis</td>
<td>parviflora</td>
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<tr>
<td><strong>FLEXILES</strong></td>
<td>flexilis</td>
<td>strobiformis</td>
<td>(part)</td>
<td>flexilis</td>
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<tr>
<td>armandii</td>
<td>parviflora</td>
<td>strobiformis</td>
<td>armandii</td>
<td>parviflora</td>
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<tr>
<td><strong>EUSTROBI</strong></td>
<td>strobiformis</td>
<td>(part)</td>
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<td>parviflora</td>
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<td>flexilis</td>
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<td>parviflora</td>
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¹ Capitalized names are sections (Pilger, 1926; Gaussen, 1960), subsections (Engelmann, 1880), or groups (Shaw, 1914, 1924). Other nomenclature follows Little and Critchfield (1969).

The wing of a pine seed originates from the uppermost layers of the cone scale, and is continuous with the spermoderm, or outermost layer of the seed coat. Seeds of Cembrae pines lack any trace of a wing but are highly variable in spermoderm development: *P. koraiensis* seeds are unique in having a nearly continuous spermoderm, and *P. albicaulis* seeds are unusual in lacking spermoderm.

All species of Strobi, as Shaw (1914) first defined the group, have seeds with conspicuous membranous wings. More difficult to interpret are the seeds of *P. flexilis* and *P. armandii*, which he added to the group a decade later. They have a well-developed spermoderm forming a marginal ridge or flange that may project as much as 1 mm (*P. armandii*) or 2 mm (*P. flexilis*) at the end of the seed opposite the micropyle. This extension is not at all membranous and wing-like, but occasionally *P. flexilis* seeds do have true membranous wings a few mm long. When Shaw (1914) created a separate group (*Flexiles*) for these problem species, he described their seeds as wingless but with “the spermoderm forming a narrow border with a rudimentary prolongation.” When he later discarded the group, he observed of their seeds that “The seed-wing, though very short, is nevertheless obvious” (Shaw, 1924). One reason Shaw combined *Flexiles* with *Strobi* was the similarity of seed variations in *P. flexilis* and its southern replacement, *P. strobiformis*. Another reason was the apparent relationship of the latter with *P. ayacahuite*, a typical white pine of the Strobi group native to Mexico and Central America. Shaw’s *Flexiles*, despite its artificial character, has been retained in some classifications (e.g. Landry, 1977). More commonly, *P. armandii* and *P. flexilis* are included in either *Strobi* (Shaw, 1924) or *Cembra* (Pilger, 1926) (Table 1).

Classifications of the white pines based on characters other than cone opening and presence or absence of seed wings correlate poorly with Shaw’s *Cembra* and *Strobi*. In an earlier monograph of *Pinus*, Engelmann (1880) used the position of the principal resin canals in the needles to separate the pines of section *Strobus* into two subsections, *Cembrae* and *Eustrobi* (Table 1). The two principal canals in a pine needle are located in the angles formed by the adaxial and abaxial faces of the needle. They are often larger than other (accessory) canals, and are more constant in presence and position. In Engelmann’s *Cembrae*, the principal canals are medial (surrounded by mesophyll parenchyma). This group
includes *P. cembra*, *P. sibirica*, and *P. koraiensis*, but not *P. pumila* or *P. albicaulis*. *Pinus armandii* was not described until a few years later, but Engelmann would presumably have also placed it in *Cembrae*; this species is unique among the white pines in having its principal resin canals in both medial and external locations. All species in Engelmann's *Eustrobi* group, including *P. pumila* and *P. albicaulis*, have external principal canals, adjacent to the dermal tissues of the needle.

The only modern classification utilizing vegetative characteristics, that of Gaussen (1960), is based partly on an informal regrouping of the Eurasian white pines by de Ferre (1960). A nonbeliever in the rules of plant nomenclature, Gaussen gave his groups invalid names, but the groups themselves are more coherent morphologically and geographically than other classifications of section *Strobus*. A Eurasian group, defined by central resin canals and wingless seeds, approximates Engelmann's *Cembrae*: *P. cembra*, *P. sibirica*, *P. koraiensis*, and *P. armandii* (Table 1). *Pinus pumila* is grouped with *P. parviflora* and its relatives, following de Ferre (1960). The largest group, and the only one with species in both hemispheres, is equivalent to Shaw's (1914) *Strobi minus P. parviflora*. A novel feature of Gaussen's classification is his fourth group, which associates *P. albicaulis* with *P. flexilis*-*P. strobiformis*. This North American group is based on vegetative similarities that were recognized by Engelmann in the 19th century but neglected in later classifications.

Both Engelmann and Gaussen excluded from *Cembrae* the two species that are chiefly responsible for the heterogeneous character of the group as Shaw defined it: *P. pumila* and *P. albicaulis*. *Pinus pumila* has traditionally been grouped with *P. cembra* and *P. sibirica*, and Shaw lumped all three taxa. Evidence to the contrary was summarized by de Ferre (1960, 1966), who pointed out the similarities of *P. pumila* to the *P. parviflora* group. She also drew attention to an unusual aspect of needle structure in which *P. cembra* and *P. sibirica* differ not only from *P. pumila*, but from all other pines. The walls of their mesophyll parenchyma are nearly devoid of the folds or ridges that give the pine mesophyll cell its characteristic lobed appearance.
*Pinus albicaulis* is unique among American white pines in its seed-retaining cones. It closely resembles *P. flexilis* in other respects, and early in its taxonomic history it was classified as a subspecies of *P. flexilis* (Engelmann, 1880). The two species are sympatric in parts of western North America, and the difficulty of distinguishing them is illustrated by repeated, unsuccessful attempts to find consistent differences between them in number and placement of accessory resin canals in the needles (Ericson, 1964; Brayshaw, 1965; Kalgutkar, 1973).

*Pinus albicaulis* and *P. flexilis* share several vegetative characteristics that are sometimes present in other western American species but absent in Eurasian white pines:

1. They differ from all other members of section *Strobus* in having needles that are nearly or entirely lacking in marginal teeth. Most pines in the group have closely spaced teeth, but they are sometimes sparse or obscure in *P. pumila* (Wilson, 1916), *P. strobiformis* (Steinhoff and Andresen, 1971), *P. lambertiana*, and *P. monticola*.

2. Both species and *P. lambertiana* have many stomata widely distributed on the abaxial (rounded) face of the needle. This is also true to varying degrees of *P. strobiformis* (Steinhoff and Andresen, 1971) and *P. monticola*. Abaxial stomata are uncommon to rare in all other pines of section *Strobus*.

3. Both species share with *P. monticola* and *P. ayacahuite* an unusual pattern of vascular organization in a minority of their seedlings (de Ferre, 1965). The transition between root and stem in the arrangement of vascular tissues is completed at the base of the hypocotyl, and the resin canals of the root terminate in the same region. This pattern is represented in one other western American white pine, *P. aristata* (subsection *Balfourianae*, section *Parrya*, Little and Critchfield, 1969). In all other pines that have been studied (including most of the species in section *Strobus*), reorganization of the vascular tissue takes place higher in the hypocotyl or at the level of the cotyledons, and the root canals terminate in the same regions.

**Interspecific Hybridization**

Crossovers within section *Strobus* were summarized most recently by Bingham et al. (1972). Figure 1 is modified from their tabulation of successful combinations. A recent addition is *P. sibirica* × *cembra*, produced in Siberia (Titov, 1977). The same author also reported a failed cross between *P. sibirica* and *P. peuce*, which produced cones and hollow seeds.

The core group within subsection *Strobi* accounts for most successful combinations: *P. monticola*, *P. strobiformis*, *P. griffithii*, *P. parviflora*, and *P. peuce*. Degree of success can be measured by crossability: yield of sound seeds per cone from interspecific crosses expressed as a percentage of the yield of sound seeds per cone in the maternal-parent species. Crossabilities in the group are high; the range was estimated at 10 to 50 percent by Wright (1976), and the crossability of Idaho *P. monticola* in combination with the other four species was 2 to 40 percent (data of Bingham et al., 1972).

The *P. flexilis*–*P. strobiformis*–*P. ayacahuite* complex occupies an uncertain position in relation to this group of crossable white pines. *Pinus ayacahuite* is usually considered part of the core group (e.g. Wright, 1976), but most or all combinations involving this species were made with a tree of uncertain identity growing near Philadelphia (Wright, 1959; Patton, 1966; Steinhoff, 1972). The crossability of *P. flexilis* and *P. strobiformis* with other white pines is mostly low or undocumented. A well-studied example is *P. strobos* × *P. flexilis*, which yields few sound seeds (Patton, 1966; Wright, 1959; Kriebel, 1972). An apparent exception to this low crossability is *P. monticola* × *P. flexilis*, which produces large numbers of sound seeds per cone (Bingham et al., 1972).

More information is available for several species combinations listed as Uncertain by Bingham et al. (1972):

1. Failures: *Pinus monticola* × *P. albicaulis*—young seedlings showed no obvious differences from *P. monticola* (R. J. Steinhoff, personal communication, 1980). *Pinus armandii* × *P. koraiensis*—a cone-bearing graft growing at IFG, from the original cross by A. G. Johnson (Wright, 1959), is not a hybrid. It is identical to *P. armandii* in several features distinguishing that species from *P. koraiensis*.
(Shaw, 1914): glabrous twigs, dehiscent cones with long (3-cm) peduncles, apophyses that are not long and reflexed, a well-defined spermoderm confined to the dorsal (upper) face of the seed, and a poorly defined hilum.

(2) Unverifiable: *Pinus monticola × P. cembra, P. monticola × P. koraiensis*—seedlings died from blister rust or unknown causes before hybrid verification (R. J. Steinhoff, personal communication, 1978).

(3) Unverifiable (Possible Successes): *Pinus cembra × P. albicaulis*—seedlings died from blister rust (L. Zsuffa, personal communication, 1980), but some were intermediate in needle serrations and number and extent of stomatal rows (C. Heimburger, personal communication to R. J. Steinhoff, 1967). *Pinus albicaulis × P. pumila*—seedlings died before hybrid verification (unpublished data, IFG). Early germination of the seeds (2 to 3 weeks, compared to 1 month or more for *P. albicaulis*) suggests they may have been authentic hybrids. *Pinus albicaulis × P. cembra*, listed by Bingham et al. (1972: Table 2), is a duplicate listing of *P. albicaulis × P. pumila*.

Several species combinations have received additional study at the IFG:

(1) *Pinus albicaulis × P. flexilis*: Putative hybrids were listed by Bingham et al. (1972) as Uncertain, and the evidence concerning their identity is still conflicting. *Pinus albicaulis* is difficult to use as a female parent; conelet abortion is heavy, maturing cones must be protected from destruction by Clark's nutcracker (*Nucifraga columbiana*), and seed germination is low and tardy compared with *P. flexilis*. Only 7 of 14 crosses with *P. flexilis* have produced mature cones, but 4 of the 7 yielded sound seeds. In two seasons, the seeds were intermediate in speed and amount of germination, differing significantly from both parent species. In growth rate, the putative hybrid seedlings resembled their much slower growing *P. albicaulis* siblings. The parent species are so similar in most other vegetative characters that further verification of hybrid identity may be impossible before the trees produce cones.

(2) *Pinus lambertiana × P. strobus*: This combination was reported as a success by F. I. Righter of the IFG staff (in Wright, 1959), and then listed as a failure (Bingham et al., 1972). The pollen parent was named as *P. ayacahuite* in both reports, and later identified as *P. strobus*. A 20-year-old putative hybrid resembled its maternal parent in its longer needles, scattered leaf serrations, and abaxial stomata extending nearly to the needle base. (The *P. strobus* parent had few serrations except near the needle tip, and abaxial stomata were restricted to the upper third of the needle.) This tree is probably not a hybrid, but its identity can be determined more reliably when it produces cones.

(3) *Pinus monticola × P. lambertiana*: All attempts on *P. lambertiana* females failed, but offspring were produced in 4 of 19 attempts on *P. monticola*. All four progenies were evaluated at an early age and considered to be nonhybrid on the basis of gross differences in early height growth. *Pinus monticola* seedlings of California origins are extremely slow growing, and *P. lambertiana* seedlings were 2.7 to 4.4 times as tall as *P. monticola* and putative hybrid seedlings after one or two growing seasons. Two 12-year-old trees were probably not hybrids. They resembled their maternal parent in their short needles (6.1 cm, compared with 8.2 cm for the *P. lambertiana* parent), and unlike the latter they lacked stomata over much of the abaxial face of the needle.

(4) *Pinus lambertiana × P. albicaulis*: This unsuccessful combination, first noted by Righter and Duffield (1951) as attempted at the IFG, and included in the most recent summary by Bingham et al. (1972), must have been listed in error. The IFG has no record of any attempts to make this cross in either direction.

**Biochemical Characteristics**

Most pines differ in the composition of the volatile portion of the xylem resin (Mirov, 1967). Although this resin system has not proved to be a widely useful indicator of relationships between species, the distributions of three compounds in section *Strobus* could be significant. The sesquiterpene 6-cadinene is present in the resin of *P. albicaulis, P. flexilis,* and *P. parviflora*; its alcohol, 6-cadinol, is present in *P. albicaulis, P. armandii, P. sibirica,* the *P. parviflora* group, and probably *P. lambertiana* (Mirov, 1967). Cembrene, a diterpene hydrocarbon, occurs in the resin of *P. albicaulis, P. koraiensis, P. armandii,* the *P. parviflora* group, *P. peuce,* and probably *P. flexilis.*

The presence or absence of a dozen phenolic constituents of heartwood broadly characterizes the major subdivisions of the genus *Pinus* (summary in Erdtman, 1963), but...

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differences within section Strobus (Erdtman, 1963; Hata and Sogo, 1954) correlate poorly with groupings based on other characteristics. Most species differ in at least two to five phenols (presence or absence of some compounds is questionable). Pinus lambertiana, P. armandii, and P. koraiensis all differ by five or six constituents. Pinus lambertiana and P. armandii are the most distinctive species analyzed, differing from nearly all others in a minimum of three to seven compounds. They are most like P. peuce and P. parviflora, respectively, although in other respects they have no special affinity with those species. One group with nearly identical heartwood constituents includes most of the Cembrae pines (P. koraiensis, P. cembra, and P. albicaulis, but not P. pumila), together with elements of Strobi with seed wings (P. ayacahuite) and without wings (P. flexilis). This group seems to be of phylogenetic significance, but it is not readily compatible with any other proposed scheme of white pine relationships.

Relationships

The lack of congruence between morphological, crossability, and other data has two principal foci in section Strobus: (a) P. lambertiana, and (b) those species with wingless seeds that may or may not be retained in the mature cone. The first of these, the genetic isolation of P. lambertiana from its supposed closest relatives, has been interpreted by Wright (1962, 1976) in two different ways. A suggestion that this species might be misclassified in Shaw's (1914) original Strobi group (Wright, 1962, p. 163) is not supported by other data. P. lambertiana differs from the Eurasian species of Strobi in such needle characters as abaxial stomata and sparse serrations, but these features are shared with other white pines of western North America, including western white pine. And all available evidence, including crossing data, firmly anchors P. monticola in the core group of Strobi.

An alternative hypothesis advanced by Wright (1962, 1976) is that the reproductive isolation of P. lambertiana may have arisen by selection against hybridization with P. monticola. Most pines in section Strobus have allopatric distributions, but P. lambertiana and P. monticola are occasionally sympatric near the upper elevational limits of the former. "Apparently as a result of occupying the same range, genetic barriers to crossability have been formed, not only between sugar and western white pines but between sugar and nearly all other white pines . . ." (Wright, 1976, p. 323).

Unless selection acted unilaterally in some unexplained way to produce barriers to interbreeding only in P. lambertiana, the crossing behavior of P. monticola should provide a partial test of this hypothesis. Distinct races of P. monticola are present in the Pacific Northwest and in California (Steinhoff et al., 1983), but only the California race is sympatric with P. lambertiana. Pinus monticola has a long fossil history in the Pacific Northwest and other parts of western North America (Bingham et al., 1972; Axelrod, 1976). The fossil record of P. lambertiana is nearly as long, extending back to the Miocene, but it is confined to California and adjacent Nevada (Axelrod, 1976).

If selection acted on both species, the Pacific Northwest race of P. monticola should cross more easily with other white pines than the California race, since the former presumably lacks a long history of contact with P. lambertiana, whereas the latter may have been sympatric with P. lambertiana for millions of years. The crossability of the Pacific Northwest (Idaho) race with four other species can be estimated from the data of Bingham et al. (1972, Table 3). It crosses most readily with P. parviflora, followed in decreasing order by P. strobus, P. peuce, and P. griffithii. The crossability of California P. monticola decreases in this order: P. strobus, P. peuce, P. parviflora, and P. griffithii (IFG, unpublished data). When the two sets of estimates are compared, the California race is more crossable with P. griffithii, about the same as the Idaho race with P. strobus, and less crossable with P. parviflora and P. peuce. Although these are crude estimates, they offer no support for the view that reproductive barriers evolved in the California race of P. monticola as a consequence of its sympatric distribution with P. lambertiana. And Wright's (1976) hy-
pohesis supplies no mechanism by which P. lambertiana could have unilaterally evolved a set of barriers that isolate it not only from both races of P. monticola but from nearly all other white pines.

The several kinds of evidence assembled in this paper, although they are highly discordant among themselves as indicators of relationships among the white pines, mostly fail to support Shaw's widely accepted division of section Strobus into Cembrae and Strobi. His classification was based on the belief that the indehiscent cone and wingless seed are ancestral conditions within the genus (Shaw, 1914, p. 20). This view was never widely accepted, and is not supported by the earliest fossil records of Pinus. Most carefully studied Cretaceous pine fossils have been identified as hard pines of section Pinus (Miller, 1977). One exception is P. magothenensis, described from well preserved cones found in the State of Delaware, and assigned to section Strobus (Penny, 1947). The cone looks like a typical white pine cone, partly or fully open, and the cone scales bear two seeds with wings.

Shaw's view of the indehiscent cone and wingless seed as primitive has increasingly been supplanted by the interpretation of these features as adaptations to seed dispersal by birds of the crow family (Corvidae) (Turček and Kelso, 1968; Goodwin, 1976; Lanner, 1982a). The wingless-seeded pines in section Strobus are now thought to be primarily dependent for seed dispersal on the two species of Nucifraga (nutcrackers). The ranges of the nutcrackers, one in Eurasia and the other in western North America, encompass but extend beyond the ranges of white pines with wingless seeds, with some races of the variable Eurasian species exploiting other primary food resources (spruce seed, hazelnuts) (Goodwin, 1976).

The absence of seed wings, if it is interpreted as an adaptation to dispersal by nutcrackers and other Corvidae, must have originated independently in several pine lineages (Lanner, 1982a). In addition to species in Shaw's Cembrae and Strobi, seed wings are absent in all of the pinyon pines (subsection Cembroides, section Parrya (Little and Critchfield, 1969)).

In Shaw's revised (1924) classification of the white pines, the single definitive feature of his Cembrae group is seed retention in the cone. It is implicit in his classification that this is a monophyletic trait, an assumption that was articulated and endorsed by Lanner (1982a). This assumption has been undermined, however, by accumulating evidence that two seed-retaining species, P. pumila and P. albicaulis, are most closely related to open-cone species outside Shaw's Cembrae group. The evidence that P. pumila is most closely allied to the P. parviflora group was presented by de Ferré (1966). The evidence assembled in this paper suggests that P. albicaulis is most closely related to P. flexilis–P. strobiformis. This conclusion is contrary to the widely held view that P. albicaulis is an American offshoot of a Eurasian lineage with seed-retaining cones. A novel variation of this view was outlined by Forcella and Rumely (1977) and Forcella (1978). These authors speculated that humans carried with them seeds of P. sibirica in their emigration to the Western Hemisphere by way of Beringia, and P. albicaulis evolved after their arrival in North America. The logistic, ecological, and evolutionary arguments against this notion are overwhelming, but the authors promised future documentation.

I propose that the seed-retaining cone, a less widespread and more specialized adaptation to animal seed dispersal than the wingless seed, has evolved independently at least twice in Eurasia (P. pumila; P. cembra–P. sibirica–P. koraiensis) and once in North America (P. albicaulis). The series P. parviflora–P. pumila and P. strobiformis–P. flexilis–P. albicaulis are interpreted as contemporary approximations of these evolutionary events. If this interpretation is correct, classifications based on seed retention in the cone and the absence of seed wings fail to provide a coherent taxonomy of the white pines because they group together the end-products of convergent evolution in two or more independent lineages.

The contradictions between reproductive characters, vegetative morphology, crossing data, and biochemical variations appear to be irreconcilable, and to undermine most classifications of the species within section Strobus. Perhaps the closest approach to a
workable taxonomy is provided by a vegetative character remote from coevolutionary adaptations of cone and seed: the location of the principal resin canals in the needles. Only four species in section Strobus (and subgenus Strobus) have these canals centrally placed and surrounded by chlorenchyma: P. cembra, P. sibirica, P. koraiensis, and P. armandii. These species also share Eurasian distributions and wingless seeds, and all but P. armandii have indehiscent cones. This informal group, together with a group defined by external resin canals, provide a working hypothesis of white pine relationships that can be tested by new data, including isozyme polymorphisms and variation in nucleotide sequences.

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