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# Needle Characteristics of Hybrid Pines

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The forest genetics program of the Institute of Forest Genetics,[2]) Placerville, California, has produced many hybrid pines (genus Pinus), which are being tested in national forests, in various arboreta, and by cooperators elsewhere. Those hybrids which prove of value in silviculture will be planted extensively by foresters. Means of identification, recognition, and verification of hybrids, particularly young plants without cones, are needed. Pine leaves or needles, always present on living plants, have long been useful in identification. Their relatively constant characters generally are correlated with cones and other taxonomic characters. Likewise, needles provide vegetative characters for studying inheritance in hybrid pines at an early age.

The purpose of this article is to present in tabular form the results of studies of gross morphology and microscopic anatomy of leaves or needles of 42 pine hybrids (genus *Pinus)* made at the Institute of Forest Genetics since its establishment in 1925 and growing there by 1957. The tables may be useful in identification of hybrids and in studies of inheritance of characters. Formal botanical descriptions of these hybrids, including twigs, needles, cones, and other characters, and reports of performance will be published elsewhere.

## Review of Literature

Gross characters of the needles of the various species in the genus Pinus are summarized in taxonomic references, such as SHAW (21), PILGER (16), and DALLIMORE and JACKSON (4). Several publications, some with keys, describe and illustrate the anatomy of needle cross sections; for example, COULTER and ROSE (2), SHAW (21), DOI and MORIKAWA (5), HARLOW (10), and SUTHERLAND (24). FERRÉ (8) made a detailed study of the juvenile forms of *Pinus* and related genera and summarized in tables the needle characters of 42 species. HELMERS (11) observed the variation in needle anatomy of *Pinus ponderosa* as related to environment and position on the tree.

A few recent investigations on needle anatomy of hybrid pines have appeared in Silvae Genetica after the studies reported here were made. MERGEN (14, 15) studied number of stomata per unit of needle length as a valid test to identify certain crosses. For the hybrid Pinus peuce X *strobus,* FOWLER and HEIMBURGER (9) analyzed stem and foliage characters including number of needle serrulations. VIDAKOVIĆ (25) and SCHÜTT and HATTEMER (20) investigated the needle anatomy of the hybrid *Pinus nigra* X silvestris.

Examples of the few studies of hybrid pine needles at the Institute of Forest Genetics may be mentioned. Needles were included in formal descriptions of two named hybrids, Pinus X *attenuradiata* STOCKWELL and RIGHTER (19) and P. X *murraybanksiana* RIGHTER and STOCKWELL (22).

STONE and DUFFIELD (23) confirmed by needle characters the hybrid origin of seedlings from difficult crosses made at Institute of Forest Genetics and germinated by embryo culture technique. Seedlings from the two crosses P. *lambertiana* X *armandii* and P. *lambertiana* X koraiensis were without stomata on the dorsal needle surface, as in both pollen parent species.

RICHTER and DUFFIELD (18) observed that 2-year seedlings of P. *ponderosa* X *engelmannii* had longer needles than corresponding non-hybrid seedlings of the first parent. Foliage criteria were included in the study of natural hybrids between P. *coulteri* and P. *jeffreyi* by ZOBEL (27). CALLAHAM (1) found the properties of needle oils in hybrid pines to be intermediate or transgressive and not discriminative for studies of hybridization between the three species analyzed.

## Materials and Methods

The Eddy Arboretum of the Institute of Forest Genetics contains one of the largest collections in the world of different kinds of pine trees (Pinus) — about 70 species and many varieties and hybrids (26). More than 25 artificial pine hybrids growing there have been listed in publications by the research staff *(6,* 7, 17). Thus, abundant material from living plants was available for study.

The two authors worked independently at the Institute of Forest Genetics, KENG in 1953 and LITTLE in 1956 and 1957. While preparing botanical descriptions of the hybrids, the junior author had an opportunity to verify on additional and older plants the observations of the senior author and to examine several newer hybrids not availsble earlier. The tables and text summarize the observation of both authors, while the illustrations were prepared by the first. Both authors are indebted to F. I. RIGHTER, J. W. DUF-

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*Table 1.* — Comparison of needle characters of hybrids of *Pinus lambertiana* with *P. armandii* and *P. koraiensis*.

| Character | *P. armandii* | *P. lambertiana* x *armandii* | *P. lambertiana* | *P. lambertiana* x *koraiensis* | *P. koraiensis* |
|---|---|---|---|---|---|
| Needle | | | | | |
| Number | 5 | 5 | 5 | 5 | 5 |
| Length | 7—13 cm. | 7—11 cm. | 7—11 cm. | 5—7 cm. (small) | 6—12 cm. |
| Stomata | | | | | |
| Dorsal rows | 0 | 0 (A) | 2 | 0 (K) | 0 |
| Ventral rows | 3—8 | 3—5 (I) | 3 | 3—4 (I) | 4—6 |
| Position | Slightly sunken | Slightly or not sunken | Slightly sunken | Not or slightly sunken (I) | Not sunken |
| Hypodermis | | | | | |
| Layers of cells | 1 | 1 (rarely 2) (I) | 1—3 | 1 (K) | 1 |
| Resin canals | | | | | |
| Position | Usually 2 dorsal external and 1 ventral medial, or 1 or both of dorsal medial (or external, external and medial, or medial — SHAW) | 2 dorsal external and sometimes 1 ventral medial (I) | 2 dorsal external and sometimes 1 ventral external or medial | 2 dorsal, both external or 1 external and 1 medial (or often "subexternal"), 1 ventral medial (I) | Medial, 2 dorsal and 1 ventral |
| Number | 3, sometimes 2 | 2, sometimes 3 (L) | 2, sometimes 3 | 3 (K) | 3 |
| Epithelial cells | Thin-walled | Thin-walled, sometimes thick-walled (I) | Thick-walled | Thin-walled sometimes thick-walled (K) | Thin-walled sometimes thick-walled |
| Summary | | 1 A, 4 I, 1 L | | 3 I, 4 K | |

*Table 2.* — Comparison of needle characters of hybrid between *Pinus monticola* and *P. strobiformis*.

| Character | *P. monticola* | *P. monticola* × *strobiformis* | *P. strobiformis* |
|---|---|---|---|
| Needle | | | |
| Number | 5 | 5 | 5 |
| Length | 6—10 cm. | 4—8 cm. (small) | 4—8 cm. |
| Stomata | | | |
| Dorsal rows | 0, sometimes 1—2 | 0—1 | 0, sometimes 1—2 |
| Ventral rows | 3—4 | 2—4 | 3—5 |
| Position | Not to slightly sunken | Slightly sunken | Slightly sunken |
| Hypodermis | | | |
| Layers of cells | 1, sometimes 2 | 1, sometimes 2 | 1 (rarely 2) |
| Resin canals | | | |
| Position | Dorsal, sometimes 1 ventral | Dorsal, sometimes 1 ventral (M) | Dorsal |
| Number | 2, sometimes 3 or 1 | 2, sometimes 3 or 1 (M) | 2 |
| Summary | | 2 M | |

FIELD, N. T. MIROV, W. C. CUMMING, and other members of the staff of the Institute of Forest Genetics for help given while they were working there, and to Professor ADRIANCE S. FOSTER, Department of Botany, University of California at Berkeley, Calif., for reviewing the manuscript.

Needles and twigs were collected from living plants of hybrids and parental species of *Pinus* at the Eddy Arboretum. As the number of individual plants of most categories is large, and as many crosses have been made more than once from parents of different origin, the samples for study were selected at random. Where available, the reciprocal crosses were examined also. Most hybrids were compared with nonhybrid progeny of the same seed parent made also by controlled pollination and usually of the same age.

The senior author generally collected 15-20 needles from each of 4 plants. The junior author usually collected from 2 plants a vigorous lateral twig and examined microscopically the needles of usually 2 to 5 fascicles 1 year old, that is, of the previous year's growth. In a few crosses the samples were limited by small numbers or by young stages of hybrid plants, though generally the progeny were too numerous for individual study.

For examination under a binocular compound microscope, the senior author cut sections midway between ends of needles with a razor. In staining, the sections were transferred from water to 50 percent alcohol, stained in safranin in 50 percent alcohol for 15 minutes, washed in several changes of water, transferred to 50 percent alcohol, then stained in fast green in 50 percent alcohol about 5 minutes, washed in several changes of water, and mounted in lactophenol. The junior author cut sections freehand with razor blades and examined them mounted in water or sometimes in lactophenol.

### Hybrids Examined

In this article the hybrids are designated by formulas with the female or seed parent first and the male or pollen parent second. Reciprocal crosses have been made also, as indicated. Formulas show parentage more clearly than binary names, which seem unnecessary. However, four binary names previously given are listed also as synonyms.

Nomenclature of the native species and varieties of *Pinus* follows the Forest Service Check List (13) with four exceptions. The southwestern white pine of the Mexican border

*Table 3.* — Comparison of needle characters of hybrids of *Pinus monticola*, *P. peuce*, and *P. strobus*, including a trihybrid.

| Character | *P. strobus* | *P. monticola* × *strobus* (and reciprocal cross) | *P. monticola* | *P. monticola* × *peuce* | *P. peuce* | *P. peuce* × *strobus* | *P. monticola* × (*peuce* × *strobus*) (trihybrid) |
|---|---|---|---|---|---|---|---|
| Needle | | | | | | | |
| Number | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| Length | 5—12 cm. | 5—9 cm. (small) | 6—10 cm. | 5—8 cm. (small) | 4—6 (10) cm. (small) | 4—9 cm. (small) | 4—8 cm. (small) |
| Stomata | | | | | | | |
| Dorsal rows | 0 | 0 | 0, sometimes 1—2 | 0 | 0 | 0 | 0 |
| Ventral rows | 2—4 | 3—5 | 3—4 | 3—4 | 2—5 | 3—4 | 3—4 |
| Hypodermis | | | | | | | |
| Layers of cells | 1 | 1 (rarely 2) (I) | 1, sometimes 2 | 1 (rarely 2) (I) | 1 | 1 | 1 (rarely 2) |
| Resin canals | | | | | | | |
| Position | Dorsal | 2 dorsal, sometimes also 1 ventral (M) | 2 dorsal, sometimes also 1 ventral | 2 dorsal, sometimes 1 ventral (M) | Dorsal | Dorsal | Dorsal |
| Number | 2, sometimes 1 or 3 | 2, sometimes 3 | 2, sometimes 1 or 3 | 2, sometimes 3 (M) | 2 | 2, sometimes 1 or 3 (S) | 2 |
| Epithelial cells | Thin-walled | Thin-walled or thick-walled (I) | Thick-walled | Thin-walled to thick-walled (P) | Thin-walled to thick-walled | Thin-walled to thick-walled (P) | Thin-walled to thick-walled (P×S) |
| Summary | | 2 I, 1 M | | 2 M, 1 I, 1 P | | 1 S, 1 P | 1 P×S |

*Table 4.* — Comparison of needle characters of hybrids of *Pinus griffithii* with *P. flexilis*, *P. strobus*, and *P. monticola*.

| Character | *P. flexilis* | *P. flexilis* × *griffithii* | *P. griffithii* | *P. strobus* × *griffithii* | *P. strobus* | *P. monticola* × *griffithii* | *P. monticola* |
|---|---|---|---|---|---|---|---|
| Needle | | | | | | | |
| Number | 5 | 5 | 5 | 5 | 5 | 5 | 5 |
| Length | 3.5—6 cm. | 7—10 cm. (I) | 10—14 cm. | 8—12 cm. (I) | 5—12 cm. | 5—12 cm. (I) | 6—10 cm. |
| Position | Straight | Spreading (I) | Slightly drooping | Spreading (I) | Straight | Spreading (I) | Straight |
| Margin | Usually entire | Serrulate (G) | Serrulate | Serrulate | Serrulate | Serrulate | Serrulate |
| Stomata | | | | | | | |
| Dorsal rows | 2 | 0 (rarely 1) (I) | 0 | 0 | 0 | 0 (G) | 0, sometimes 1—2 |
| Ventral rows | 2—5 | 4—6 (I) | 5—6 | 3—6 (I) | 2—4 | 4—6 (I) | 3—4 |
| Hypodermis | | | | | | | |
| Layers of cells | 1, sometimes 2 | 1 | 1 | 1 | 1 | 1 | 1, sometimes 2 |
| Resin canals | | | | | | | |
| Position | Dorsal | Dorsal | Dorsal, sometimes also ventral | Dorsal | Dorsal | Dorsal | Dorsal, sometimes also 1 ventral |
| Number | 2, sometimes 3 | 2, sometimes 1 | 2, sometimes 1 or 3 | 2 | 2, sometimes 1 or 3 | 2, sometimes 1 or 3 | 2, sometimes 1 or 3 |
| Epithelial cells | Slightly thick-walled | Thin-walled or slightly thick-walled (I) | Thin-walled | Thin-walled | Thin-walled | Thick-walled or thin-walled (I) | Thick-walled |
| Summary | | 5 I, 1 G | | 3 I | | 1 G, 4 I | |

is designated as a separate species *P. strobiformis* ENGELM., instead of *P. flexilis* var. *reflexa* ENGELM. Two varieties of *P. contorta* DOUGL. used in crosses are distinguished, largely after CRITCHFIELD (3). *P. contorta* var. *contorta* is the low scrubby shore pine of the Pacific coast, and *P. contorta* var. *murrayana* (GREV. & BALF.) ENGELM. is the taller, inland lodgepole pine of the California Sierra. The Rocky Mountain variation of ponderosa pine is distinguished here as a variety, *P. ponderosa* var. *scopulorum* ENGELM. *P. muricata* D. DON, Bishop pine, of the Check List and this article includes the form separated by some authors as *P. remorata* MASON.

The hybrids, like the species, may be grouped under the two subgenera, the soft or white pines, *Pinus* subgenus *Haploxylon* KOEHNE, and the hard or yellow pines, *Pinus* subgenus *Pinus* (*Diploxylon* KOEHNE). (Under the International Code of Botanical Nomenclature, 1956 edition, Article 22, the subgenus including the type species repeats the generic name. Thus, as *P. sylvestris* L. is the lectotype of *Pinus*, the subgenus is designated *Pinus* subgenus *Pinus*.)

In the following list, the table number of each hybrid is given. The 42 hybrids from a total of 30 species may be summarized as follows: 35 first generation interspecific hybrids ($F_1$), not counting 6 reciprocal crosses but counting 6 crosses of another variety of 1 parent species; 2 trihybrids or 3-species hybrids; 3 backcrosses of $F_1$ hybrids; and 2 intraspecific or varietal hybrids. All except 1 natural hybrid are artificial hybrids made by controlled pollination.

*Table 5.* — Comparison of needle characters of hybrid between *Pinus canariensis* and *P. roxburghii*.

| Character | *P. canariensis* | *P. canariensis* × *roxburghii* | *P. roxburghii* |
|---|---|---|---|
| Needle | | | |
| Number | 3 | 3 | 3 |
| Length | 11—20 (30) cm. | (9) 13—21 cm. | 11—23 (30) cm. |
| Width | 1— mm. | 1— mm. (C) | 1— to 1+ mm. |
| Position | Sometimes spreading to drooping | Straight (R) | Straight |
| Stomata | | | |
| Dorsal rows | 2—4 | (2) 3—5 (I) | 5—6 (7) |
| Ventral rows | 2—3 | 3—4 | 2—3 |
| Hypodermis | | | |
| Layers of cells | 3—5 | 3—5, sometimes 2 (I) | 2—4 |
| Inner border | Angled or curved | Angled or curved (C) | Curved |
| Resin canals | | | |
| Position | External, sometimes septal | External, sometimes septal (C) | External |
| Number | 2, sometimes 3—4 | 2, often 3 | 2, sometimes 3—6 |
| Side of needle | 2 dorsal | 2 dorsal, often also 1 ventral (I) | Dorsal, dorsal and ventral, or ventral |
| Endodermis | | | |
| Cell walls | Thin-walled | Thin-walled (C) | Outer walls thick (sometimes thin-walled in small plants) |
| Transfusion tissue | | | |
| Thick-walled cells | Scattered | Scattered (C) | Outside phloem, outside xylem, between vascular bundles |
| Summary | | 5 C, 2 I, 1 R | |

### *Soft Pine Hybrids, Pinus subgenus Haploxylon*

The 10 following hybrids from 9 species include 9 first generation interspecific hybrids (also reciprocal cross of 1) and 1 trihybrid.

*P. lambertiana* Dougl. × *P. armandii* Franch., *Table 1.*

*P. lambertiana* Dougl. × *P. koraiensis* Sieb. & Zucc., *Table 1.*

*P. monticola* Dougl. × *P. strobiformis* Engelm., *Table 2.*

*P. monticola* Dougl. × *P. strobus* L. and reciprocal cross, *Table 3.*

*P. monticola* Dougl. × *P. peuce* Griseb., *Table 3.*

*P. peuce* Griseb. × *P. strobus* L., *Table 3.* (This hybrid was received from C. C. Heimburger, Canada, as scions, which were grafted here.)

*P. monticola* Dougl. × *P. (peuce* × *strobus),* trihybrid, *Table 3.*

*P. flexilis* James × *P. griffithii* McClelland, *Table 4.*

*P. strobus* L. × *P. griffithii* McClelland, *P.* × *schwerinii* Fitschen, *Table 4.*

*P. monticola* Dougl. × *P. griffithii* McClelland, *Table 4.*

### *Hard Pine Hybrids, Pinus subgenus Pinus (Diploxylon)*

The 32 following hybrids from 21 species (1 with 2 varieties and 1 with 3 varieties) may be grouped as follows: 19 first generation interspecific hybrids (also reciprocal crosses of 5), 6 additional interspecific hybrids involving another variety of 1 parent species (also reciprocal cross of 1), 1 natural interspecific hybrid, 1 trihybrid with reciprocal cross, 3 backcrosses of $F_1$ hybrids, and 2 intraspecific or varietal hybrids.

*P. canariensis* Sm. × *P. roxburghii* Sarg., *Table 5.*

*P. elliottii* Engelm. × *P. palustris* Mill. and reciprocal cross, *Table 6.*

*P. elliottii* Engelm. × *P. taeda* L. and reciprocal cross, *Table 6.*

*P. palustris* Mill. × *P. taeda* L., *P.* × *sondereggeri* H. H. Chapm., natural hybrid, *Table 6.*

*Table 6.* — Comparison of needle characters of hybrids of *Pinus elliottii, P. palustris,* and *P. taeda.*

| Character | *P. palustris* | *P. palustris* × *elliottii* (and reciprocal cross) | *P. elliottii* | *P. elliottii* × *taeda* (and reciprocal cross) | *P. taeda* | *P. palustris* × *taeda; P. sondereggeri* (natural hybrid) |
|---|---|---|---|---|---|---|
| Needle | | | | | | |
| Number | 3 | 3 and 2 (E) | 3 and 2 | 3 and 2 (E) | 3 | 3 |
| Length | 20—45 cm. | 15—30 cm. (I) | 15—25 (30) cm. | 10—19 cm. (I) | 10—17 cm. | 12—22 cm. (I) |
| Position | Curved to straight or drooping | Straight to curved or drooping (I) | Straight | Straight | Straight | Straight |
| Hypodermis | | | | | | |
| Layers of cells | 3—6 | 2—4 (I) | 2, sometimes 3—4 | 2, sometimes 3 (E) | 2—4 | 2, sometimes 3—4 (T) |
| Inner border | Curved | Curved or straight (I) | Straight, sometimes curved | Straight | Straight, curved or angled | Straight or curved (I) |
| Resin canals | | | | | | |
| Position | Internal (rarely internal and medial) | Internal and medial, or internal (E) | Internal, or internal and medial, or partly subinternal | Medial, internal and medial, or partly subinternal (I) | Medial, or internal and medial | Medial and internal, or partly subinternal (I) |
| Number | 3—7 (rarely 2) | 2, sometimes 3—4 | 2—6 | 2—7 | 2—7 | 2—6 |
| Endodermis | | | | | | |
| Casparian dots | | | Not prominent | Prominent (T) | Prominent | |
| Summary | | 4 I, 2 E | | 2 E, 2 I, 1 T | | 3 I, 1 T |

*Table 7.* — Comparison of needle characters of hybrids of *Pinus echinata* with *P. elliottii* and *P. taeda*.

| Character | *P. elliottii* | *P. echinata* × *elliottii* | *P. echinata* | *P. echinata* × *taeda* | *P. taeda* |
|---|---|---|---|---|---|
| Needle | | | | | |
| Number | 3 and 2 | 2, sometimes 3 | 2, sometimes 3 | 3, sometimes 3 and 2 (I) | 3 |
| Length | 11—25 (30) cm. | 11—20 cm. (I) | 4—8 (12) cm. | 7—12 cm (I) | 10—17 cm. |
| Hypodermis | | | | | |
| Layers of cells | 2—3, sometimes 4 | 2, sometimes 3 (rarely 4) (I) | 1—2 (rarely 3) | 2, sometimes 1 (rarely 3) (I) | 2—4 |
| Inner border | Straight, sometimes curved | Straight | Straight | Straight (EC) | Straight, curved, or angled |
| Resin canals | | | | | |
| Position | Internal and medial, or internal | Medial, or medial and internal (EC) | Medial, sometimes medial and internal | Medial, sometimes medial and internal | Medial, sometimes medial and internal |
| Endodermis | | | | | |
| Casparian dots | Not prominent | Prominent (EC) | Prominent | | Prominent |
| Summary | | 2 I, 2 EC | | 1 EC, 3 I | |

*Table 8.* — Comparison of needle characters of hybrids of *Pinus rigida* with *P. taeda* and *P. serotina*.

| Character | *P. taeda* | *P. rigida* × *taeda* | *P. rigida* | *P. rigida* × *serotina* (3-year seedlings) | *P. serotina* |
|---|---|---|---|---|---|
| Needle | | | | | |
| Number | 3 | 3 | 3 | 3 | 3 |
| Length | 10—22 cm. | 10—20 cm. (I) | 6—14 cm. | 7—14 (R) | 12—20 cm. |
| Hypodermis | | | | | |
| Layers of cells | 2—4 | 2—5 | 2—5 | 2 (rarely 3) (R) | 3—5 |
| Resin canals | | | | | |
| Position | Medial, or medial and internal | Medial (rarely also internal) | Medial, or medial and internal | Medial | Medial, or medial and internal |
| Number | 2—7 | 2 (rarely 3) | 2—6 (11) | 2 (R) | 3—6 |
| Summary | | 1 I | | 3 R | |

*Table 9.* — Comparison of needle characters of hybrids among varieties of *Pinus ponderosa*.

| Character | *P. ponderosa* var. *scopulorum* | *P. ponderosa* var. *ponderosa* × var. *scopulorum* | *P. ponderosa* var. *ponderosa* | *P. ponderosa* var. *ponderosa* × var. *arizonica* | *P. ponderosa* var. *arizonica* |
|---|---|---|---|---|---|
| Needle | | | | | |
| Number | 3 or 2 | 3 (rarely 2) (PP) | 3, sometimes 2 | 4 or 5, sometimes 3 (I) | 5, sometimes 4 (rarely 3) |
| Length | 7—15 cm. | 10—25 cm. (I) | 12—25 cm. | 11—22 cm. (I) | 10—21 cm. |
| Stomata | | | | | |
| Dorsal rows | 10—14 | 8—11 (PS) | 11—15 | 4—9 (I) | 3—5 |
| Ventral rows | 6—9 | 3—6 (PP) | 4—8 | 3—6 (I) | 2—5 |
| Hypodermis | | | | | |
| Cell walls | Biform | Biform (PS) | Biform or multiform | Biform (PA) | Biform |
| Endodermis | | | | | |
| Outline | Elliptic | Elliptic | Elliptic | Elliptic, sometimes circular (PA) | Elliptic, sometimes circular or triangular |
| Summary | | 2 PS, 1 I, 2 PP | | 4 I, 2 PA | |

*P. echinata* Mill. × *P. elliottii* Engelm., *Table 7.*
*P. echinata* Mill. × *P. taeda* L. *Table 7.*
*P. rigida* Mill. × *P. taeda* L., *Table 8.*
*P. rigida* Mill. × *P. serotina* Michx., *Table 8.*
*P. ponderosa* Laws. var. *ponderosa* × var. *arizonica* (Engelm.) Shaw, *Table 9.*
*P. ponderosa* Laws. var. *ponderosa* × var. *scopulorum* Engelm., *Table 9.*
*P. ponderosa* Laws. var. *ponderosa* × *P. montezumae* Lamb., *Table 10.*
*P. ponderosa* var. *scopulorum* Engelm. × *P. montezumae* Lamb., *Table 10.*
*P. engelmannii* Carr. × *P. (jeffreyi* × *ponderosa)* and reciprocal cross, trihybrid, *Table 10.*
*P. engelmannii* Carr. × *P. montezumae* Lamb., *Table 11.*
*P. jeffreyi* Grev. & Balf. × *P. montezumae* Lamb., *Table 11.*
*P. engelmannii* Carr. × *P. ponderosa* Laws. var. *ponderosa* and reciprocal cross, *Table 12.*
*P. engelmannii* Carr. × *P. ponderosa* var. *arizonica* (Engelm.) Shaw, *Table 12.*
*P. engelmannii* Carr. × *P. ponderosa* var. *scopulorum* Engelm. and reciprocal cross, *Table 12.*
*P. jeffreyi* Grev. & Balf. × *P. ponderosa* Laws. var. *ponderosa* and reciprocal cross, *Table 13.*

*Table 10.* — Comparison of needle characters of hybrids of *Pinus montezumae* with *P. ponderosa* var. *ponderosa* and var. *scopulorum*.

| Character | *P. ponderosa* var. *ponderosa* | *P. ponderosa* var. *ponderosa* × *montezumae* | *P. montezumae* | *P. ponderosa* var. *scopulorum* × *montezumae* | *P. ponderosa* var. *scopulorum* |
|---|---|---|---|---|---|
| Needle | | | | | |
| Number | 3, sometimes 2 | 4, sometimes 3 or 5 (I) | 5, sometimes 4 | 3—4, sometimes 5 (I) | 3 or 2 |
| Length | 12—25 cm. | 14—27 cm. (I) | 20—27 cm. | 10—20 cm. (I) | 7—15 cm. |
| Width | 1+ mm. | 1+ mm. (PP) | 1— mm. | 1+ mm. (PS) | 1+ mm. |
| Position | Straight | Drooping or curved (M) | Drooping or curved | Curved and spreading (I) | Straight |
| Stomata | | | | | |
| Dorsal rows | 11—15 | 5—12 (I) | 4—6 | 6—10 (I) | 10—14 |
| Ventral rows | 4—8 | 3—5 (M) | 3—5 | 3—5 (M) | 6—9 |
| Position | Slightly to deeply sunken | Slightly sunken (I) | Not sunken | Slightly sunken (PS) | Slightly sunken |
| Hypodermis | | | | | |
| Cell walls | Biform or multiform | Multiform, sometimes biform | Multiform, sometimes biform | Multiform, sometimes biform (M) | Biform |
| Endodermis | | | | | |
| Outline | Elliptic | Elliptic, sometimes circular (I) | Circular, sometimes elliptic | Elliptic (PS) | Elliptic |
| Casparian dots | Prominent | Prominent (PP) | Not prominent | Prominent (PS) | Prominent |
| Summary | | 2 PP, 5 I, 2 M | | 2 M, 4 I, 4 PS | |

*Table 11.* — Comparison of needle characters of hybrid of *Pinus montezumae* with *P. engelmannii* and *P. jeffreyi* and trihybrid between *P. engelmannii* and *P. jeffreyi* × *ponderosa*.

| Character | *P. engelmannii* | *P. engelmannii* × *montezumae* | *P. montezumae* | *P. jeffreyi* × *montezumae* | *P. jeffreyi* | *P. engelmannii* × (*jeffreyi* × *ponderosa*) (and reciprocal cross) | *P. jeffreyi* × *ponderosa* var. *ponderosa* |
|---|---|---|---|---|---|---|---|
| Needle | | | | | | | |
| Number | 3 (rarely 2, 4, or 5) | 3, often 4, sometimes 5 (I) | 5 (sometimes 4) | 3 (I) | 3, sometimes 2 | 3 (rarely 2 or 4) (I) | 3 (rarely 2) |
| Length | 15—35 cm. | 19—29 cm. | 20—27 cm. | 14—25 cm. (I) | 12—21 cm. | 17—27 cm. (I) | 14—25 cm. |
| Width | 1.5 mm. | 1+ mm. (I) | 1— mm. | About 1 mm. (I) | 1+ mm. | 1+ mm. | 1+ mm. |
| Position | Spreading | Spreading to drooping (M) | Spreading to drooping | Erect to spreading (I) | Erect | Erectly to slightly spreading (I) | Erect |
| Color | Green | Green | Green | Green (M) | Gray green | Green | Green |
| Stomata | | | | | | | |
| Dorsal rows | 8—14 | 5—10 (I) | 4—6 | 5—8 (I) | 8—11 | 7—12 | 8—12 |
| Ventral rows | 5—7 | 3—4 (M) | 3—5 | 2—5 | 3—5 | 3—7 | 3—7 |
| Position | Deeply sunken | Slightly sunken (I) | Not sunken | Slightly sunken (I) | Deeply sunken | Deeply sunken | Deeply sunken |
| Hypodermis | | | | | | | |
| Cell walls | Biform | Biform or multiform (M) | Multiform or biform | Multiform, sometimes biform | Multiform, sometimes biform | Biform or multiform (JXP) | Multiform or biform |
| Layers of cells | 3—6 | 2—4 (M) | 2—4 | 2—4 | 2—5 | 2—5 (JXP) | 2—5 (7) |
| Inner border | Angled | Straight or curved (M) | Curved | Curved | Curved, sometimes straight | Angled, sometimes slightly curved (I) | Curved |
| Resin canals | | | | | | | |
| Number | 3—9 | 2, sometimes 3—4 (I) | 2—3 (6) | 2—6 | 2—4 (6) | 2, sometimes 3 or 4 (JXP) | 2—5 (7) |
| Endodermis | | | | | | | |
| Outline | Elliptic | Elliptic, sometimes nearly circular (I) | Nearly circular, sometimes elliptic | Elliptic (J) | Elliptic | Elliptic | Elliptic |
| Cell walls | Thin or outer wall thick | Thin or outer wall thick (E) | Outer wall thick | Outer wall thick | Outer wall thick, sometimes thin | Outer wall slightly thick | Outer wall thick |
| Summary | | 1 E, 6 I, 5 M | | 1 M, 5 I, 2 J | | 4 I, 3 JXP | |

*P. jeffreyi* Grev. & Balf. × *ponderosa* var. *scopulorum* Engelm., *Table 13.*

*P. (jeffreyi* × *ponderosa)* × *P. jeffreyi* Grev. & Balf., backcross, *Table 13.*

*P. (jeffreyi* × *ponderosa)* × *P. ponderosa* Laws. var. *ponderosa* backcross, *Table 13.*

*P. jeffreyi* Grev. & Balf. × *P. washoensis* Mason & Stockwell, *Table 14.*

*Table 12.* — Comparison of needle characters of hybrids of *Pinus engelmannii* with varieties of *P. ponderosa*.

| Character | *P. engelmannii* | *P. engelmannii* × *ponderosa* var. *ponderosa* (and reciprocal cross) | *P. ponderosa* var. *ponderosa* | *P. engelmannii* × *ponderosa* var. *arizonica* | *P. ponderosa* var. *arizonica* | *P. engelmannii* × *ponderosa* var. *scopulorum* (and reciprocal cross) | *P. ponderosa* var. *scopulorum* |
|---|---|---|---|---|---|---|---|
| Needle | | | | | | | |
| Number | 3 (rarely 2, 4, or 5) | 3 (rarely 4 or 5) | 3, sometimes 2 | 4-3, sometimes 5 (I) | 5, sometimes 4 (rarely 3) | 3, sometimes 2 (I) | 3 or 2 |
| Length | 15-35 cm. | 17-30 cm. (I) | 12-25 cm. | 15-28 cm. (I) | 10-21 cm. | 14-23 cm. (I) | 7-15 cm. |
| Stomata | | | | | | | |
| Dorsal rows | 8-14 | 10-15 (I) | 11-15 | 7-11 (I) | 3-5 | 9-12 (I) | 10-14 |
| Ventral rows | 5-7 | 4-8 (PP) | 4-8 | 3-6 (I) | 2-5 | 3-6 (E) | 6-9 |
| Position | Deeply sunken | Slightly to deeply sunken (PP) | Slightly to deeply sunken | Slightly to deeply sunken (I) | Slightly sunken | Deeply sunken (E) | Slightly sunken |
| Hypodermis | | | | | | | |
| Cell walls | Biform | Biform, sometimes multiform (I) | Biform or multiform | Biform, often multiform (D) | Biform | Biform | Biform |
| Layers of cells | 3-6 | 2-5 (I) | 2-4 | 2-5 (I) | 2-4 | 2-5, sometimes 6 (I) | 2-5 |
| Inner border | Angled | Curved, sometimes angled (I) | Curved | Angled (E) | Curved | Curved, sometimes angled (I) | Curved |
| Resin canals | | | | | | | |
| Number | 3-9 | 2, sometimes 3 (rarely 4-7) (PP) | 2, sometimes 3 or more (10) | 2, sometimes 3-5 (I) | 2, sometimes 3 or 4 | 2-4 (rarely 6) (I) | 2 (rarely 3-4) |
| Endodermis | | | | | | | |
| Outline | Elliptic | Elliptic | Elliptic | Elliptic, sometimes circular (I) | Elliptic, sometimes circular or triangular | Elliptic | Elliptic |
| Summary | | 5 I, 3 PP | | 1 E, 8 I, 1 D | | 2 E, 6 I | |

*Table 13.* — Comparison of needle characters of hybrids of *Pinus jeffreyi* with varieties of *P. ponderosa* and backcrosses.

| Character | *P. ponderosa* var. *ponderosa* | *P. jeffreyi* × *ponderosa* var. *ponderosa* (and reciprocal cross) | *P. jeffreyi* | *P. jeffreyi* × *ponderosa* var. *scopulorum* | *P. ponderosa* var. *scopulorum* | *P. (jeffreyi* × *p.* var. *ponderosa)* × *p.* var. *ponderosa* (backcross) | *P. (jeffreyi* × *p.* var. *ponderosa)* × *jeffreyi* (backcross) |
|---|---|---|---|---|---|---|---|
| Needle | | | | | | | |
| Number | 3, sometimes 2 | 3 (rarely 2) | 3, sometimes 2 | 3, sometimes 2 | 3 or 2 | 3 (rarely 2) | 3 (rarely 2) |
| Length | 12—25 cm. | 14—25 cm. (PP) | 12—21 cm. | 11—15 cm. (I) | 7—15 cm. | 14—24 cm. (PP) | 16—26 cm. (PP) |
| Color | Green | Green (PP) | Gray green | Green (PS) | Green | Green (PP) | Gray green (J) |
| Stomata | | | | | | | |
| Dorsal rows | 11—15 | 8—12 (J) | 8—11 | 7—11 (J) | 10—14 | 9—12 | 8—13 |
| Ventral rows | 4—8 | 3—7 (I) | 3—5 | 4—6 (I) | 6—9 | 4—7 (PP) | 4—5 |
| Position | Slightly to deeply sunken | Deeply sunken (J) | Deeply sunken | Deeply sunken (J) | Slightly sunken | Slightly to deeply sunken (PP) | Deeply sunken (J) |
| Hypodermis | | | | | | | |
| Cell walls | Biform or multiform | Multiform or biform | Multiform, sometimes biform | Multiform, sometimes biform (J) | Biform | Multiform or biform | Multiform, sometimes biform |
| Resin canals | | | | | | | |
| Number | 2, sometimes 3 or more (10) | 2—5 (7) | 2—4 (6) | 2, sometimes 3 (I) | 2 (rarely 3—4) | 2, sometimes 3 | 2 |
| Summary | | 2 PP, 1 I, 2 J | | 3 J, 3 I, 1 PS | | 4 PP | 1 PP, 2 J |

*P. ponderosa* Laws. var. *ponderosa* × *P. washoensis* Mason & Stockwell and reciprocal cross, *Table 14.*

*P. washoensis* Mason & Stockwell × *P. ponderosa* var. *scopulorum* Engelm., *Table 14.*

*P. jeffreyi* Grev. & Balf. × *P. coulteri* D. Don, *Table 15.*

*P. jeffreyi* Grev. & Balf. × *P. (jeffreyi* × *coulteri),* backcrosses of artificial and natural hybrids, *Table 15.*

*P. contorta* Dougl. var. *contorta* × *P. banksiana* Lamb., *Table 16.*

*P. contorta* var. *murrayana* (Grev. & Balf.) Engelm. × *P. banksiana* Lamb., *P.* × *murraybanksiana* Righter & Stockwell, *Table 16.*

*P. virginiana* Mill. × *P. clausa* (Chapm.) Vasey, *Table 17.*

*P. attenuata* Lemm. × *P. muricata* D. Don (*P. remorata* Mason), *Table 18.*

*P. attenuata* Lemm. × *P. radiata* D. Don, *P.* × *attenuradiata* Stockwell & Righter, *Table 18.*

### Tables

Comparisons of needle characters of these 42 hybrids and their parents are summarized in *Tables 1—18.* Two or three crosses generally have been placed together in same table for ready comparison and to save space of repetition of parental characters. 8 reciprocal crosses are mentioned

*Table 14.* — Comparison of needle characters of hybrids of *Pinus washoensis* with *P. jeffreyi* and varieties of *P. ponderosa*.

| Character | *P. jeffreyi* | *P. jeffreyi* × *washoensis* | *P. washoensis* | *P. ponderosa* var. *ponderosa* × *washoensis* (and reciprocal cross) | *P. ponderosa* var. *ponderosa* | *P. washoensis* × *ponderosa* var. *scopulorum* | *P. ponderosa* var. *scopulorum* |
|---|---|---|---|---|---|---|---|
| Needle | | | | | | | |
| Number | 3, sometimes 2 | 3 (rarely 2) | 3 (rarely 2) | 3 (rarely 2) | 3, sometimes 2 | 3 (W) | 3 or 2 |
| Length | 12—21 cm. | 10—20 cm. | 10—22 cm. | 11—23 cm. | 12—25 cm. | 10—15 cm. (I) | 7—15 cm. |
| Color | Gray green | Green (D) | Slightly gray green | Green (PP) | Green | Green (PS) | Green |
| Stomata | | | | | | | |
| Dorsal rows | 8—11 | 8—12 | 8—15 | 8—13 | 11—15 | 8—11 | 10—14 |
| Ventral rows | 3—5 | 3—5 (J) | 4—8 | 4—6 | 4—8 | 3—5 (W) | 6—9 |
| Position | Deeply sunken | Slightly sunken (W) | Slightly sunken | Slightly sunken | Slightly to deeply sunken | Slightly sunken | Slightly sunken |
| Hypodermis | | | | | | | |
| Cell walls | Multiform, sometimes biform | Multiform, sometimes biform (J) | Biform | Biform or multiform (PP) | Biform or multiform | Biform | Biform |
| Resin canals | | | | | | | |
| Number | 2—4 (6) | 2—3 (J) | 2—8 (10) | 2, sometimes 3 (PP) | 2, sometimes 3 or more (10) | 2, sometimes 3 (PS) | 2 (rarely 3—4) |
| Summary | | 3 J, 1 D, 1 W | | 3 PP | | 2 W, 1 I, 2 PS | |

*Table 15.* — Comparison of needle characters of hybrid of between *Pinus coulteri* and *P. jeffreyi* and backcrosses of artificial and natural hybrids.

| Character | *P. coulteri* | *P. jeffreyi* × *coulteri* | *P. jeffreyi* | *P. jeffreyi* × (*jeffreyi* × *coulteri*); backcross of artificial hybrid | *P. jeffreyi* × (*jeffreyi* × *coulteri*); backcross of natural hybrid [1] | *P. jeffreyi* × (*jeffreyi* × *coulteri*); backcross of natural hybrid [2] |
|---|---|---|---|---|---|---|
| Needle | | | | | | |
| Number | 3 | 3 | 3 (rarely 2) | 3 | 3 | 3 |
| Length | 15—30 cm. | 16—25 cm. (I) | 12—21 cm. | 12—25 cm. (I) | 17—24 cm. (I) | 17—25 cm. (I) |
| Color | Gray green | Gray green | Gray green | Gray green | Gray green | Gray green |
| Stomata | | | | | | |
| Surface view | Larger white squares | Minute white dots (J) | Minute white dots | Minute white dots (J) | Minute white dots (j) | Minute white dots (j) |
| Position | In large V-shaped notch | In U-shaped notch (J) | In U-shaped notch | In U-shaped notch (J) | In U-shaped notch (J) | In U-shaped notch (J) |
| Dorsal rows | 8—12 | 7—10 | 8—11 | 8—12 | 9—11 | 6—9 |
| Ventral rows | 3—5 | 3—5 | 3—5 | 4—6 | 4—5 | 3—5 |
| Hypodermis | | | | | | |
| Cell walls | Multiform | Multiform (C) | Multiform sometimes biform | Multiform, sometimes biform (J) | Multiform (C) | Multiform (C) |
| Layers of cells | 4—5 sometimes 3 | 3—5 | 2—3 | 3—5 | 2—4 sometimes 5 | 3—4 |
| Inner border | Angled, sometimes curved | Curved (I) | Curved, sometimes straight | Curved, sometimes straight (j) | Curved (I) | Curved, sometimes straight (J) |
| Endodermis | | | | | | |
| Cell walls | Thin | Thin (C) | Outer wall thick | Outer wall usually thick (J) | Outer wall thick (J) | Thin (C) |
| Casparian dots | Not prominent | Prominent (J) | Prominent | | | |
| Summary | | 2 C, 2 I, 3 J | | 1 I, 5 J | 1 C, 2 I, 3 J | 2 C, 1 I, 3 J |

[1]) Backcross of natural hybrid tree from Brauns, Calif.
[2]) Backcross of natural hybrid tree from San Benito, Calif.

in the tables but not listed separately since the progeny appeared to be identical.

In each table the parents and hybrids are compared in needle characters by which the parents differ, though needle number and length are listed for all. Most characters common to parents and progeny are omitted. Where crosses are combined in a table, some parents and hybrids may not differ for certain listed characters. In the hybrids, characters are indicated as intermediate (I), like one parent by the first letter of the epithet of that parent, and rarely as different (D). These characters are summarized for each hybrid at the bottom of the tables.

### External Characters

The main external characters of gross morphology by which needles of parent species and hybrids were compared are: number of needles in a fascicle; needle length; needle color; needle margin; and position and rows of stomata.

*Table 16.* — Comparison of needle characters of hybrids of *Pinus banksiana* with varieties of *P. contorta*.

| Character | *P. contorta* var. *contorta* | *P. contorta* var. *contorta* × *banksiana* | *P. banksiana* | *P. contorta* var. *murrayana* × *banksiana*; *P.* × *murray-banksiana* | *P. contorta* var. *murrayana* |
|---|---|---|---|---|---|
| Needle | | | | | |
| Number | 2 | 2 | 2 | 2 | 2 |
| Length | 4—6 cm. | 4—6.5 cm. (CC) | 3—5 cm. | 3—5 cm. (B) | 4—6 cm. |
| Position | Slightly divergent | Slightly divergent (CC) | Divergent | Slightly divergent (CM) | Slightly divergent |
| Epidermis | | | | | |
| Shape of cells in cross section | Some nearly square | Some nearly square (CC) | Rectangular | Some nearly square (CM) | Some nearly square |
| Hypodermis | | | | | |
| Cell walls | Biform, sometimes uniform | Biform (B) | Biform | Biform | Biform |
| Layers of cells | 2, sometimes 1 | 2, sometimes 3 (B) | 2, sometimes 3 | 2, sometimes 3 | 2, sometimes 3 (or 4) |
| Resin canals | | | | | |
| Position | Absent | Medial or absent (I) | Medial | Medial | Medial |
| Number | 0 | 1, 2, or 0 (I) | 2, sometimes 1 or 0 | 2 (sometimes 3) | 2 |
| Endodermis | | | | | |
| Outline | Elliptic, sometimes constricted | Elliptic, often constricted | Elliptic, often constricted | Elliptic, usually constricted | Elliptic, often constricted |
| Cell walls | Thin | Thin (CC) | Thin, or sometimes outer wall thick | Outer wall usually thick (CM) | Outer wall often thick |
| Summary | | 4 CC, 2 I, 2 B | | 1 B, 3 CM | |

### *Number of Needles in a Fascicle*

All the soft pines *(Pinus* subgenus *Haploxylon)* studied and their hybrids have needles uniformly 5 in a fascicle. Most species of hard or yellow pines *(Pinus* subgenus *Pinus)* crossed have 3 needles or both 3 and 2. However, *P. montezumae* and *P. ponderosa* var. *arizonica* have needles in fascicles of 5, sometimes 4 (rarely also 3 in the latter).

Hybrids from species differing in needle number generally are intermediate between the parents. For example, *P. muricata (P. remorata)* has needles in 2's, *P. attenuata* in 3's, and their hybrid in both 3's, and 2's. *P. echinata* has 2, sometimes 3, needles in a fascicle, *P. taeda* 3, and their hybrid 3 or sometimes 3 and 2. In 5 crosses between a pine with 3 needles and another with 3 and 2 needles, the hybrid is nearer one parent in needle number.

In three crosses of *P. montezumae* (5, sometimes 4 in a fascicle) with pines having 3 or sometimes also 2 needles in a fascicle, the progeny are intermediate with usually 3 and 4, sometimes 5. However, in another hybrid with *P. jeffreyi* (3, sometimes 2), only 3 needles were observed. Two crosses of *P. ponderosa* var. *arizonica* (5, sometimes 4, rarely 3) with pines having 3 (or sometimes also 2) needles in a fascicle resulted in intermediate progeny having 4, 3, and 5 needles.

### *Needle Length*

Needle length varies considerably both within a species and within an individual. The differences result from the interacting factors of genotype, environment, age, and vigor. Within a tree, needles produced on vigorous shoots or in more favorable seasons may be longer than average. In 21 of the 42 crosses the 2 parents overlap in needle length; in 16 the needle length of 1 parent is within the range of the other; and in 5 the maximum of 1 parent is less than the minimum of the second. In general, the hybrids are intermediate between the parents.

*Needle length, soft pine hybrids.* — Except on small plants, the soft pine hybrids are intermediate in needle length. Some young hybrid plants only 2 to 3 feet tall when studied had needles shorter than both parents. *P. griffithii* has needles longer than the other species and slightly drooping, while its three interspecific hybrids have needles intermediate in length and spreading to slightly drooping.

*Needle length, hard pine hybrids.* — Nearly all hard pine hybrids studied have needle length intermediate in range between that of the parents. However, in the small popula-

*Table 17.* — Comparison of needle characters of hybrid (2-year seedlings) between *Pinus virginiana* and *P. clausa*

| Character | *P. virginiana* | *P. virginiana* × *clausa* (2-year seedlings) | *P. clausa* |
|---|---|---|---|
| Needle | | | |
| Number (seedlings) | 2, sometimes 3 | 2, sometimes 3 | 2, sometimes 3 |
| Length | 4—9 cm. | 6—8 cm. | 4—9 cm. |
| Width | 1— to 1+ mm. | 1+ mm. (V) | 1— mm. |
| Shape in cross section | Semicircular, sometimes flattened | Semicircular, sometimes flattened (V) | Semicircular |
| Stomata | | | |
| Dorsal rows | 11—13 | 10—14 (V) | 8—10 |
| Ventral rows | 8—11 | 7—10 (V) | 5—7 |
| Epidermis | | | |
| Outer cell wall | Not arched | Slightly arched (I) | Conspicuously arched |
| Hypodermis | | | |
| Cell walls | Biform, sometimes uniform | Uniform (C) | Uniform (rarely biform) |
| Layers of cells | 1—2 | 1 (C) | 1 (rarely 2) |
| Endodermis | | | |
| Outline | Elliptic and usually constricted | Elliptic (C) | Elliptic |
| Vascular bundles | | | |
| Position | Widely separated | Widely separated (V) | Separated by less than bundle width (widely separated in seedlings) |
| Summary | | 5 V, 1 I, 3 C | |

*Table 18.* — Comparison of needle characters of hybrids of *Pinus attenuata* with *P. radiata* and *P. muricata (P. remorata).*

| Character | *P. radiata* | *P. attenuata* × *radiata*; *P.* × *attenuradiata* | *P. attenuata* | *P. attenuata* × *muricata* | *P. muricata (P. remorata)* |
|---|---|---|---|---|---|
| Needle | | | | | |
| Number | 3, sometimes 2 | 3 (A) | 3 | 3 and 2 (I) | 2 |
| Length | 9—13 cm. | 8—12 (18) cm. | 9—17 cm | 10—16 (18) cm. (A) | 9—12 cm. |
| Width | Narrow | Intermediate (I) | Broad | Broad | Broad |
| Epidermis | | | | | |
| Walls arched over stomatal court | Present | Present (R) | Absent | Absent | Absent |
| Resin canals | | | | | |
| Position | Medial, sometimes medial and internal | Medial | Medial, sometimes also internal | Medial, or medial and internal (or subinternal) | Medial and internal sometimes medial only |
| Number | Usually 2, sometimes 1, 0, 3 or 4 | Usually 2, sometimes 1 or 0 (R) | 2—3, sometimes 4—5 | 3—7 (M) | 3—7 |
| Transfusion tissue | | | | | |
| Thick-walled cells | Line outside phloem or absent | Line outside phloem or absent (R) | Absent | Absent or sometimes line outside phloem (I) | Line outside phloem or absent |
| Summary | | 1 A, 1 I, 3 R | | 1 A, 2 I, 1 M | |

tions examined, 5 exceptions were noted. The hybrid *P. rigida* × *serotina* has short needles more like the first parent, while the hybrid *P. ponderosa* var. *scopulorum* × var. *ponderosa* has long needles like the second parent. In 3 interspecific crosses the maximum needle length of the $F_1$ exceeded slightly by 0.5—1 cm. the maximum of the parent with longer needles.

### *Needle Color*

Usually the needle color of related species and their hybrids is approximately the same shade of green. However, *P. jeffreyi* and *P. washoensis* have gray green needles, and their hybrids with *P. ponderosa* have the green color of the latter. Also, the hybrid *P. jeffreyi* × *montezumae* has green needles.

### *Needle Margin*

All the soft pines crossed have serrulate needles except *P. flexilis*, which has usually entire needles. The only hybrid of this species, *P. flexilis* × *griffithii*, has serrulate needles. In hard pines the needles uniformly are serrulate.

### *Position and Rows of Stomata*

The surface of pine needles bear longitudinal whitish lines which are rows of stomata. Stomata are absent from the abaxial (dorsal) surface of needles in the soft pines except the following: *P. flexilis* and *P. lambertiana* both with 2 rows of dorsal stomata, and *P. monticola* and *P. strobiformis* with no or sometimes 1 or 2 rows. First generation soft pine hybrids lack dorsal stomata with 2 exceptions. One row of dorsal stomata is rarely present in needles of the cross *P. flexilis* × *griffithii*, and no or 1 row present in the cross *P. monticola* × *strobiformis*. Thus, absence of dorsal stomata apparently is dominant in these crosses.

In the hard pines, stomata are present on all needle surfaces, dorsal as well as ventral. Though recorded for each species and hybrid studied, the number of stomatal rows generally is without taxonomic significance. The dorsal surface has more rows than each of the two ventral surfaces of the same needle. Number of stomatal rows is greater on wider needles, including those fewer in a fascicle. When species with sightly different numbers of stomatal rows are crossed, the offspring usually are intermediate.

## Internal Characters

The main internal characters by which needles of parent species and hybrids were compared are: epidermis, including stomata; hypodermis; resin canals, position and number; endodermis; vascular bundles; and transfusion tissue.

### *Epidermis*

The epidermis or outermost layer of pine needles has epidermal cells generally uniform and more or less rectangular in shape as seen in cross section. However, in *P. contorta*, including both var. *contorta* and var. *murrayana*, some epidermal cells are nearly square in cross section. When either variety is crossed with *P. banksiana*, the first generation hybrid also has these squarrish cells. *P. clausa* has the outer epidermal cell walls conspicuously arched, not straight as in most pines. Hybrids with *P. virginiana* have these cell walls slightly arched and intermediate. *P. attenuata* has epidermal cell walls arched conspicuously over the stomatal court, and its hybrid with *P. radiata* retains this distinctive feature.

### *Stomata*

In some species the stomata are not or only slightly sunken below the needle epidermis, but in others they are deeply sunken two or sometimes more layers of cells below the surface. Generally, hybrids between species with extremes have stomata intermediate in position, or slightly sunken. However, the hybrids between *P. jeffreyi* and *P. ponderosa* have the deeply sunken stomata of the former.

*P. coulteri* has distinctive stomata deeply sunken in large V-shaped notches, deeper and broader than the U-shaped cavities of the other species studies. Also, under a hand lens the stomata appear as large white squares, instead of minute white dots. However the hybrid with *P. jeffreyi* possesses instead the stomata of the latter in smaller U-shaped notches.

### *Hypodermis*

This tissue, also called hypoderm, is under or next within the leaf epidermis. The hypodermis varies among the pine species both in number of layers of cells and in thickness of cell walls and contributes characters of minor

taxonomic value. In the species studied the range in layers of cells is from 1 to 6, with some variation within a needle.

Based upon the relative thickness of cell walls in the different layers, the hypodermis may be uniform, biform, or multiform. The uniform hypodermis, composed of cells with walls of equal thickness, either thin or thick, is characteristic of the soft pines *(fig. 1A)*. The biform hypodermis, with a layer of thin-walled cells adjacent to the epidermis and one to a few layers of thick-walled cells beneath, is common in species of hard pines *(fig. 2A, 4C, 5C)*. In the multiform hypodermis there is a gradation from thin-walled cells next to the epidermis to successively thicker-walled cells internally, for example, in *P. coulteri*. These kinds of hypodermis intergrade, and two, such as uniform and biform, or biform and multiform, may often be found in the same needle.

*Hypodermis in soft pine hybrids.* — The soft pines crossed have 1 layer of cells in the hypodermis, except *P. lambertiana* with 1—3 layers, *P. monticola* and *P. flexilis* with 1 or sometimes 2 layers, and *P. strobiformis* with 1 or rarely 2 layers. First generation hybrids have 1 layer except sometimes also 2 layers in *P. monticola* × *strobiformis* and rarely also 2 layers in 3 other crosses. The hypodermis is uniform and of slightly thick-walled cells in all soft pines crossed and in their first generation hybrids, with these exceptions: *P. peuce* has thin-walled cells in hypodermis, *P. strobus* has thin-walled to slightly thick-walled cells, and their hybrid is like the latter.

*Hypodermis in hard pine hybrids.* — The hypodermis in the hard pine species studied has commonly 2 to 5 layers of cells, sometimes 1 to 6, being thickest in the angles and midway between stomata. Offspring from parental species differing in average thickness of this layer generally are intermediate.

The hypodermis is not continuous, being interrupted by the stomata and their chambers, and varies in the shape of its innermost border as seen in cross section. The inner border of the hypodermis commonly is straight or nearly so where this tissue is thin, such as only 1 or 2 or sometimes 3 layers of cells in thickness. A thick hypodermis, such as 3 to 6 layers of cells, has an inner border usually curved between 2 stomata, or wavy in cross section, being thinnest adjacent to the stomata, or angled or ridged between 2 stomata and appearing in cross section as if pointed or toothed. Examples of these three types of inner border of hypodermis are: *P. banksiana (fig. 5C)*, straight; *P. ponderosa (fig. 4A)*, curved or wavy; and *P. engelmannii (fig. 4C)*, angled. These characters associated with thickness of hypodermis may be of some use in identification, though intergrading. The angled type is least common and most distinctive.

In the few crosses where one parent species has the hypodermis with angled inner border, the progeny often has this character also or is intermediate. For example, *P. canariensis* has the inner border angled or curved, *P. roxburghii* curved, and their hybrid angled or curved. *P. engelmannii* has the inner border angled, the three varieties of *P. ponderosa* curved, and the three hybrids have the inner border at least sometimes angled. However, this character was not found in small hybrid plants between *P. engelmannii* and *P. montezumae*, which species has the inner border curved. Also, the hybrid *P. echinata* × *taeda* has the straight-bordered hypodermis of the first parent, though the hypodermis of the second may be straight, curved, or angled.

### *Mesophyll and Resin Canals*

The mesophyll, located between the hypodermis and the endodermis toward the interior of the pine needle, is composed of uniform cells, green and containing chloroplasts. The mesophyll lacks taxonomic importance. Within or bordering the mesophyll are the resin canals or resin ducts, which secrete resin and are bordered by usually 1 or 2 layers of thin-walled or thick-walled cells. Rarely, resin canals are absent, as in *P. contorta* var. *contorta (fig. 5A)* and sometimes in *P. radiata*. Though variable within a species, the position and number of resin canals are useful diagnostic characters.

*Resin canals, position.* — The four positions of resin canals, as defined by SHAW (21) and others, are: (1) external, or against the hypodermis, as in *P. lambertiana (fig. 1A)*; (2) medial, or within the mesophyll or green tissue and touching neither hypodermis nor endodermis, as in *P. koraiensis (fig. 1C)*; (3) internal, or against the endodermis, as often in *P. elliottii (fig. 2A)*; and (4) septal, or connecting both hypodermis and endodermis to form a septum, sometimes present in *P. canariensis*.

*Resin canals, position in soft pine hybrids.* — The soft pines and first generation hybrids in this study have external resin canals except as noted here. *P. koraiensis* has medial resin canals. *P. armandii* has the resin canals external and medial (usually 2 dorsal external and 1 ventral medial or 1 or both of the dorsal medial) or all medial or according to SHAW (21) also all external. Medial resin canals as well as external were recorded for *P. griffithii* and *P. lambertiana* by SHAW.

The hybrid *P. lambertiana* × *koraiensis (fig. 1B* and *D)* has the 2 dorsal canals external or 1 external and 1 medial (or often subexternal) and also 1 ventral medial. By "subexternal" is meant an intermediate position in the mesophyll almost surrounded by green cells but connected with the hypodermis by 1 or sometimes more thick-walled non-green cells. In *P. lambertiana* × *armandii* sometimes 1 ventral medial canal is present, as in *P. armandii*, in addition to 2 dorsal external canals. Thus, medial canals are expressed in progeny or indicated by the intermediate almost external or subexternal canals.

As to side of needle, resin canals in the soft pines studied are dorsal except as noted. One ventral external resin canal of the needle sometimes is present in *P. lambertiana, P. monticola, P. griffithii*, and in the following hybrids: *P. monticola* × *strobiformis, P. monticola* × *peuce*, and *P. monticola* × *strobus* (also reciprocal cross). In *P. armandii* 1 ventral medial resin canal usually is present, but in *P. koraiensis* there are usually 3 medial, 1 in each corner. One ventral canal is present in the hybrid *P. lambertiana* × *koraiensis* and sometimes also in *P. lambertiana* × *armandii*. Thus, the ventral canal of a parent species is usually present in the first generation hybrid.

*Resin canals, position in hard pine hybrids.* — In the hard pines studied, the commonest position of the resin canals is medial, while the arrangement of both internal and medial together also is common. Hybrids generally are intermediate.

*P. elliottii (fig. 2A)* has resin canals internal or medial or both or sometimes with 1 or more intermediate or "subinternal", that is, in the mesophyll but joined to the endodermis by 1 or a few thick-walled non-green cells. Subinternal resin canals were observed in the following hybrids: *P. taeda* × *elliottii (fig. 2B), P. taeda* × *palustris*, and *P. attenuata* × *muricata*.

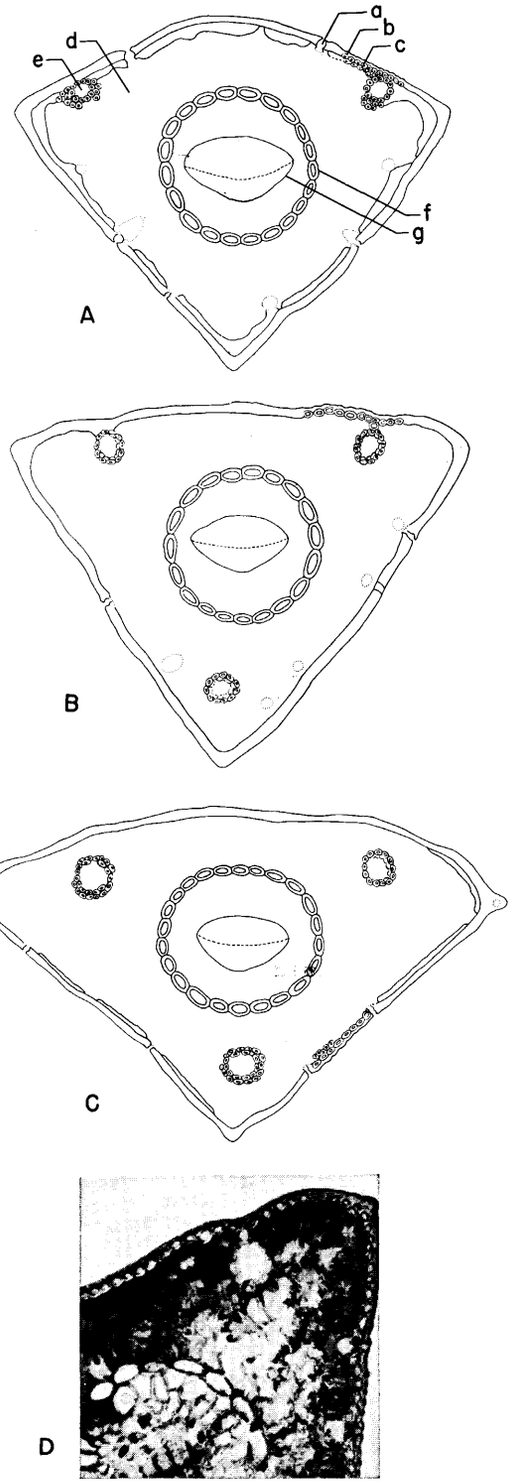


*Figure 1.* — Needle cross sections illustrating inheritance of position of resin canals and stomata in the soft pine hybrid between *Pinus lambertiana* and *P. koraiensis*. — *A:* — *P. lambertiana* has 2 dorsal external resin canals and 2 dorsal rows of stomata. Parts of a needle: *a*, stoma; *b*, epidermis; *c*, hypodermis; *d*, mesophyll; *e*, resin canal; *f*, endodermis; *g*, vascular bundle. — *B and D:* — The hybrid, *P. lambertiana* × *koraiensis*, has 3 resin canals including 2 dorsal subexternal and 1 ventral medial and no dorsal stomata. — *C:* — *P. koraiensis* has 3 medial resin canals, 2 dorsal and 1 ventral, and no dorsal stomata.

*P. canariensis* has resin canals external, sometimes septal, as does the hybrid *P. canariensis* × *roxburghii*. In *P. roxburghii* the resin canals are external.

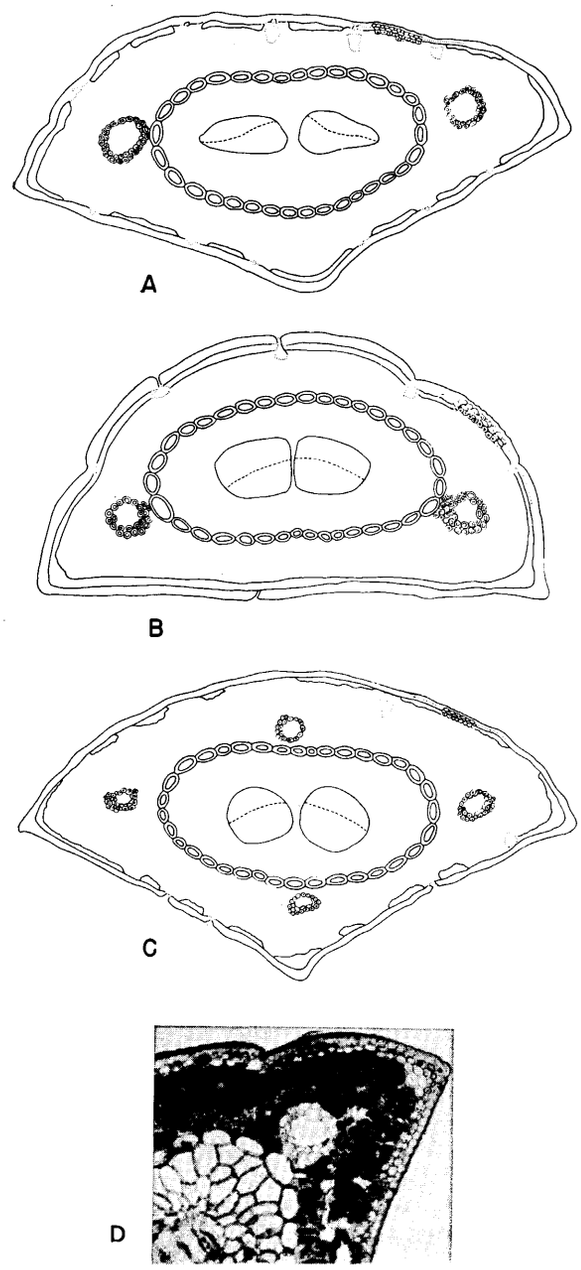


*Figure 2.* — Needle cross sections showing inheritance of position of resin canals in the hybrid between *P. elliottii* and *P. taeda*. — *A:* — This needle of *P. elliottii* has 1 medial resin canal and 1 internal. — *B and D:* — The hybrid *P. elliottii* × *taeda* has 1 internal resin canal and 1 subinternal. — *C:* — This needle of *P. taeda* has 4 medial resin canals.

*Number of resin canals.* — The number of resin canals in a needle cross section varies but often is constant within a species or hybrid. In the soft pine species and hybrids, resin canals are commonly 2 and dorsal, less frequently 3 or 1. However, 3 is the usual number in *P. armandii*, *P. koraiensis*, and *P. lambertiana* × *koraiensis*, while *P. lambertiana* × *armandii* has 2 or 3. Thus, hybrids are similar to parents or intermediate.

In the hard pine species studied, 2 and 3 are the commonest numbers of resin canals, but the range sometimes is from 2 to 6 or 7, rarely to 10 or 11. One is infrequent, and none, as noted above, is rare. Hybrids are intermediate in number of resin canals or like the parent with lower number. However, the low number in hybrids may be associated

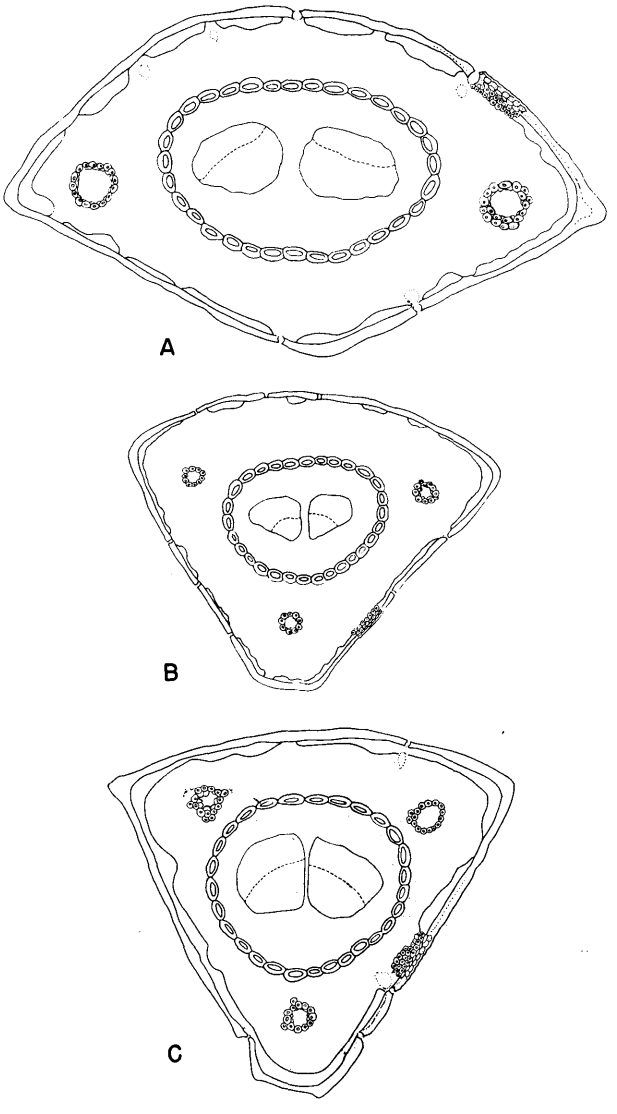


*Figure 3.* — Needle cross sections illustrating inheritance of needle number with change in shape of needle cross section and of endodermis in the hybrid between *P. ponderosa* var. *ponderosa* and *P. montezumae*. — *A:* — *P. ponderosa* var. *ponderosa*, a broad needle from a fascicle of 3 and with elliptic endodermis. — *C:* — *P. montezumae*, a very narrow needle from a fascicle of 5 and with circular endodermis. — *B:* — *P. ponderosa* × *montezumae*, a narrow needle from a fascicle of 4 and with slightly elliptic endodermis.

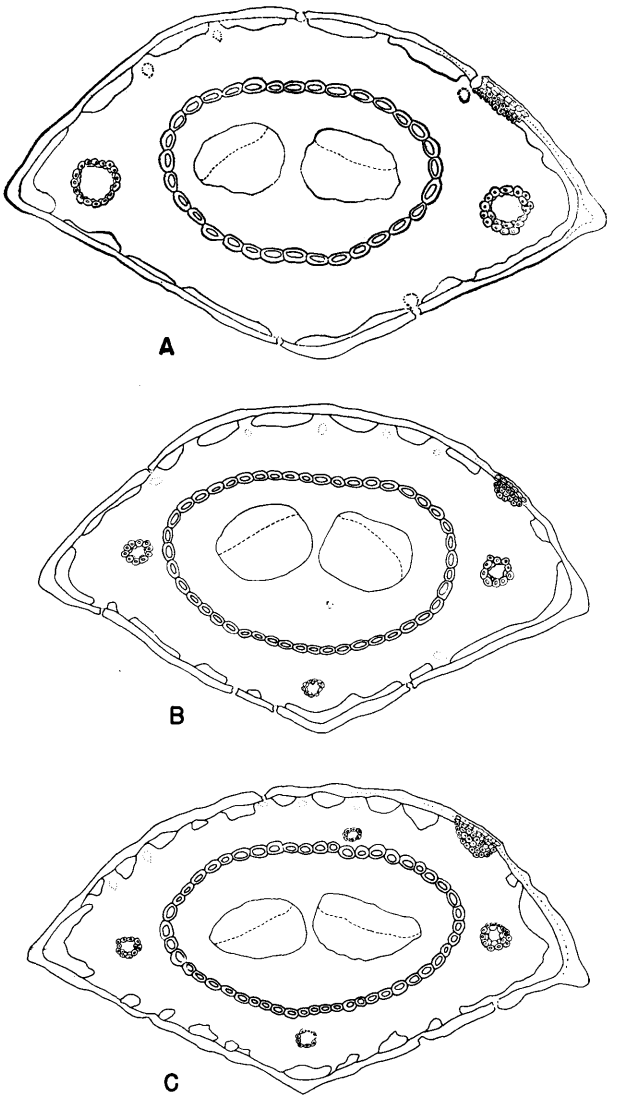


*Figure 4.* — Needle cross sections showing inheritance in hypodermis in the hybrid between *P. ponderosa* var. *ponderosa* and *P. engelmannii*. — *A:* — *P. ponderosa* var. *ponderosa* has slightly thick hypodermis with curved or wavy inner border in needle cross section. — *B:* — *P. engelmannii* × *ponderosa* var. *ponderosa* has slightly thickened hypodermis with inner border curved in this needle cross section though sometimes also angled. — *C:* — *P. engelmannii* has thick hypodermis with inner border angled in needle cross section.

with the small size and age of the young progeny in a few species.

*Resin canals, diameter.* — Some variation was noted in the size of resin canals, as measured in diameter of cavity, but most differences apparently are not significant. The commonest diameter is 40—60 microns, but the size 40 microns was observed in all these species and hybrids, and the range of variation is about 20—90 microns.

*Resin canals, epithelial cells.* — Epithelial cells lining the resin canals are thin-walled in some species and slightly thick-walled in others, though often variable and perhaps limited in taxonomic value. Hybrids of parents differing in this character usually are intermediate.

### *Endodermis*

The endodermis is a layer of cells between the outer, green mesophyll and the inner, stelar region. In cross section it appears as a ring of cells, circular in needles that are 5 in a fascicle *(figs. 1A, 3C)* and usually elliptic in needles that are 2 or 3 in a fascicle *(figs. 3A, 5A)*. A few pines with needles in 2's, such as *P. banksiana (fig. 5C)* and *P. contorta* var. *murrayana* and their hybrid, have the elliptic endodermis often slightly constricted in the shorter dimension.

The cells of the endodermis usually are alike but infrequently, as in *P. engelmannii (fig. 4C)*, of both large and small size. The cell walls may be uniform and usually thin or sometimes thick, or the outer cell walls may be thickened. When a species having the outer endodermal cell walls thickened, such as *P. jeffreyi*, is crossed with another with thin endodermal cell walls, such as *P. coulteri*, the hybrid usually has thin endodermal cell walls.

Casparian strips are prominent on walls between adjacent endodermal cells in some species and are made clearer by safranin stain. In crosses between a species with Casparian strips prominent and another not prominent, the hybrid was observed to have prominent strips. *P. ponderosa*,

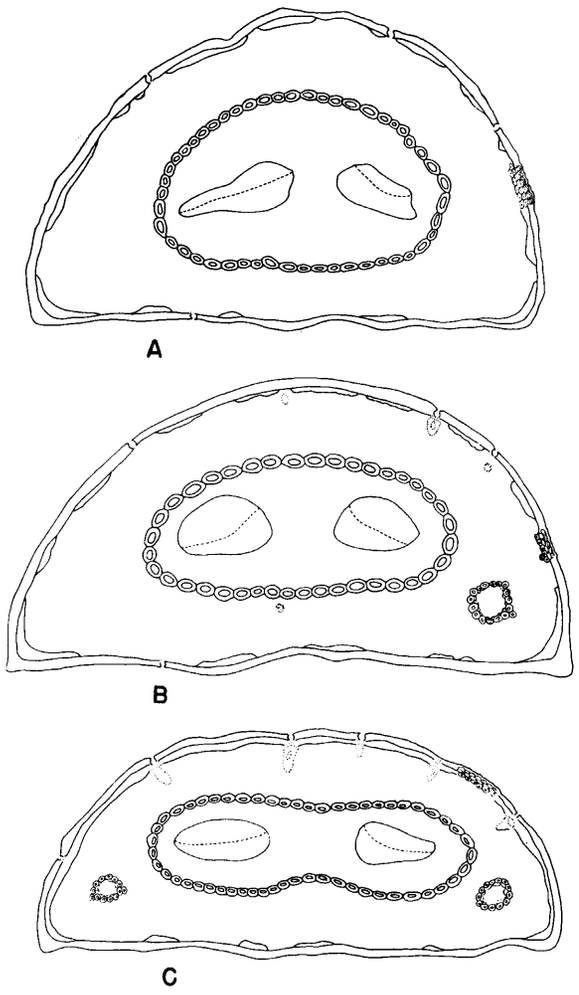


*Figure 5.* — Needle cross sections illustrating inheritance of resin canals and endodermis in the hybrid between *P. contorta* var. *contorta* and *P. banksiana*. — *A:* — *P. contorta* var. *contorta* lacks resin canals and has elliptic endodermis with cell walls of uniform thickness. — *B:* — The hybrid *P. contorta* var. *contorta* × *banksiana* is intermediate with 1 resin canal and like the former parent in elliptic endodermis with cell walls of uniform thickness. — *C:* — *P. banksiana* has 2 resin canals and constricted endodermis with outer cell walls thickened.

*P. echinata*, and *P. taeda* have prominent Casparian strips, as do the hybrids *P. ponderosa* × *montezumae*, *P. echinata* × *elliottii*, and *P. elliottii* × *taeda*.

### *Vascular Bundles*

In the central part of the stelar region there are 2 vascular bundles in the hard pines, rarely united as 1, or 1 in the soft pines. This fundamental character was employed by KOEHNE (12, pp. 28—30) in distinguishing his 2 sections of the genus *Pinus*, *Diploxylon* and *Haploxylon*, afterwards raised to subgenera by REHDER. The two bundles are close together in most species but widely separated by more than the bundle width in a few. In the cross between *P. virginiana* having widely separated vascular bundles and *P. clausa* not, the progeny seedlings were like the former. The 2 vascular bundles sometimes are united in the hybrid *P. ponderosa* var. *ponderosa* × *washoensis*.

### *Transfusion Tissue*

The transfusion tissue surrounding the vascular bundles in pine needles consists of two different kinds of cells: living parenchyma cells with nonlignified walls and thin-walled but lignified tracheids with bordered pits. The sclerenchyma cells often form a line outside the phloem, often also a line outside the xylem, sometimes between the vascular bundles, or they may be scattered. However, as their presence and amount are variable, these thick-walled cells have only limited value for identification of species and hybrids. Most soft pines studied and their hybrids lack these sclerenchyma cells.

## Discussion

*Pinus* is a difficult genus for studies of hybrids and inheritance, because vegetative characters are similar among the various species; sharply contrasting vegetative characters are few. All these species of pine have leaves of similar, needle shape, though varying in length and slightly in width. Though the genus has its peculiar spur shoot with fascicled needles, the variation in needle number is limited from 1 to 5 (rarely more) and commonly to 2, 3, or 5.

Obviously, most related species of pines, including those probably crossable, differ only slightly from one another in needle characters. Some of these characters are quantitative, variable, and overlapping and thus of only limited value in identification. Fortunately, the needle characters including microscopic needle anatomy are sufficiently constant for identification of most wild pine trees in the absence of cones.

It follows that hybrids between closely related species differ even less slightly from the parents in needle characters and are less easily recognized. Where parent species are scarcely separable by needle anatomy, the hybrids likewise probably are not distinguishable.

At the Institute of Forest Genetics, all the numerous hybrid progeny examined from the many controlled closed pollinations with repeated crosses and backcrosses seem authentic. Nearly all these successful hybrids are from closely related species which may be expected to be readily crossable, as classified by DUFFIELD (6). The many additional failures need not be mentioned here.

### *Identification of Hybrids*

In the identification of wild or planted pines, reproductive characters, such as those of cones and seeds, are more conclusive than vegetative characters alone and should be examined whenever present.

When neither parent species of a putative hybrid pine without cones is known, the first step in identification should be to use a key for identification of species of pines by needles, such as that by HARLOW (10). The key should eliminate all but a few species. Then, for the species and hybrids within this article, the specimen may be compared with the appropriate examples from *Tables 1—18* for further identification.

For recognition of certain hybrids, particularly young plants without cones, the tables may be helpful in showing what characters to look for in the $F_1$ generation. Also, in verification of hybrid origin, as in intergrading wild populations and in plantations from mass open pollinations, the tables may suggest which plants probably are hybrids and which not.

Naturally, the hybrids most easily recognized are those with dissimilar parents. It may not be possible to identify positively from needle characters alone the hybrids between certain closely related species. The following examples

illustrate hybrids scarcely distinguishable in needle anatomy from their parents: *P. monticola* × *strobiformis*, *P. monticola* × *strobus*, *P. peuce* × *strobus*, and *P. rigida* × *taeda*.

### *Methods of Inheritance*

A few additional observations on inheritance of needle characters in these hybrid pines may be mentioned, though preliminary, limited to only one generation, and lacking statistical analysis. A count was made of the characters in the 35 interspecific hybrids in *Tables 1—18*. Needle characters by which parents differ average 5.7, of which the first generation hybrid is intermediate in 2.6 and more like one parent or the other in 3.1, sometimes in overlapping characters. In progeny as well as parents, many of these characters are slight and variable and possibly may be less pronounced in large populations. Thus, the first generation interspecific hybrids are intermediate in nearly half the needle characters but approach each parent in roughly a fourth.

In many quantitative characters the hybrids usually are intermediate between the parents. Examples are needle number, needle length, and number of layers of cells in the hypodermis.. In other characters involving position of parts, such as position of resin canals and depth of stomata, the hybrids commonly are intermediate. However, the hybrids are nearer to one parent in some characters.

Relatively few distinctive qualitative characters were observed. In these there appears to be some dominance, though perhaps mostly more complex than single pairs of genes. To analyze the manner of inheritance of the various characters, studies of large numbers of progeny, successive generations, and backcrosses would be necessary.

### *Different Characters*

Only 2 examples were found where the first generation hybrid of interspecific crosses differed in needle characters from both parent species and was not intermediate. These 2 examples out of the 200 pairs of contrasting characters in the 35 interspecific hybrids in *Tables 1—18* are designated by (D). The hybrid *P. jeffreyi* × *washoensis* was described as having green needle color, not gray green as in the former parent nor slightly gray green as in the latter. In the hybrid *P. engelmannii* × *ponderosa* var. *arizonica*, the hypodermis was observed to be biform, often multiform, not constantly biform as in both parents. Also, as mentioned above though not in a table, the 2 vascular bundles sometimes are united in the hybrid *P. ponderosa* var. *ponderosa* × *washoensis* though not in the parents.

### *Hybrid Vigor*

Hybrid vigor, or heterosis, was conspicuously absent among the needle characters of the 35 interspecific hybrids and others summarized in *Tables 1—18*. However, hybrid vigor would be shown in other characters than needles, such as height and rate of growth. As noted above, in 3 interspecific crosses the maximum needle length of the $F_1$ exceeded slightly by 0.5—1.0 cm. the maximum of the parent with longer needles. These slight differences may not be significant. Also, in a few small young hybrids the needles were short.

### *Backcrosses*

The three backcrosses studied are: *P. jeffreyi* × *(jeffreyi* × *coulteri) (Table 15); P. (jeffreyi* × *ponderosa* var. *ponderosa)* × *ponderosa* var. *ponderosa;* and *P. (jeffreyi* × *ponderosa* var. *ponderosa)* × *jeffreyi (Table 13).* Though intermediate, the progeny show a greater resemblance to the backcrossed parent, as expected. In the hybrids between *P. jeffreyi* and *P. ponderosa* var. *ponderosa*, the characteristic gray green needle color of *P. jeffreyi* was present only in the backcross, but the deeply sunken stomata appeared also in the first generation hybrid.

### *Trihybrids*

The two trihybrids or triple hybrids studied are: *P. monticola* × *(peuce* × *strobus) (Table 3) and P. engelmannii* × *(jeffreyi* × *ponderosa) (Table 11),* also the reciprocal of the latter. In the former, the three closely related parental species and progeny all are similar and scarcely distinguishable in needle anatomy. In the latter, the progeny are intermediate in several characters.

### *Reciprocal Crosses*

Of the 42 hybrids studied, reciprocal crosses of 8 were examined. As expected, the hybrid progeny from the same two parent species are identical with either species as seed parent or pollen parent. Thus, inheritance is normal and without irregularities such as parthenogenesis.


### Summary

Gross morphology and microscopic anatomy of leaves or needles of 42 pine hybrids (genus *Pinus)* growing at Institute of Forest Genetics, Placerville, Calif., were studied by the authors in 1953, 1956, and 1957. These include 35 first generation interspecific hybrids from 30 species counting 6 crosses of another variety of 1 parent species, also 2 trihybrids, 3 backcrosses, and 2 intraspecific or varietal hybrids. All but one are artificial hybrids.

The 18 tables in which these hybrids are compared in needle characters with their parents may be used in the identification of hybrid plants, particularly young plants without cones. However, it may not be possible to identify positively from needle characters alone the hybrids between certain closely related species.

Preliminary observations on inheritance of needle characters indicate that the first generation interspecific hybrids are intermediate between the parent species in nearly half the contrasting needle characters, especially quantitative characters, and more like one parent or the other in other characters, though some differences are slight.



### Zusammenfassung

Titel der Arbeit: *Nadel-Eigenschaften bei Kiefernbastarden.*

Morphologie und mikroskopische Anatomie der Nadeln von 42 Kiefernbastarden des Instituts für Forstgenetik in Placerville/Californien wurden von den Autoren 1953, 1956 und 1957 untersucht. Dabei waren 35 $F_1$-Artbastarde aus 30 Arten und 6 Kreuzungen von Varietäten einer Elternart, ferner 2 Trihybriden, 3 Rückkreuzungen und 2 Innerart- oder Varietätenhybriden. Alle Bastarde außer einem sind künstlich hergestellt.

Die 18 Tabellen der Arbeit, in denen diese Bastarde in den Nadel-Eigenschaften mit ihren Eltern verglichen werden, können für die Identifizierung von Bastardpflanzen benutzt werden, besonders bei jungen Pflanzen ohne Zapfen. Es ist jedoch nicht möglich, nach den Nadel-Merkmalen allein Bastarde zwischen nahe verwandten Arten eindeutig zu identifizieren.

Vorläufige Beobachtungen über die Vererbung von Nadel-Eigenschaften zeigen, daß $F_1$-Artbastarde sich intermediär verhalten zwischen den Elternarten. Besonders bei quantitativen Merkmalen liegen sie bei der $F_1$ etwa in der Mitte zwischen den beiden sich unterscheidenden Nadeleigenschaften; bei anderen Eigenschaften können sie dem einen oder dem anderen Elter ähnlicher sein, obgleich auch da einige Unterschiede nur gering sind.


### Résumé

Titre de l'article: *Caractéristiques des aiguilles des pins hybrides.*

Les auteurs ont étudiés en 1953, 1956 et 1957 la morphologie et l'anatomie des aiguilles de 42 pins hybrides poussant à l'Institut de Génétique forestière de Placerville (Californie). Ces pins hybrides comprennent 35 hybrides interspécifiques de première génération de 30 espèces, 2 trihybrides, 3 croisements en retour et deux hybrides intraspécifiques ou variétaux. Tous sauf un sont des hybrides artificiels.

Les 18 tableaux dans lesquels ces hybrides sont comparés à leurs parents d'après les caractéristiques des aiguilles peuvent être utilisés pour l'identification des plants hybrides en particulier les jeunes plants sans cônes. Il n'est cependant pas toujours possible d'identifier de façon certaine, d'après les seuls caractères des aiguilles, des hybrides entre quelques espèces très voisines.

Les premières observations sur la transmission héréditaire des caractères des aiguilles montrent que les hybrides interspécifiques de première génération sont intermédiaires entre les parents pour à peu près la moitié des caractères nettement différenciés, en particulier les caractères quantitatifs, et pour le reste des caractères, ressemblent plus à l'un ou à l'autre parent, bien que certaines différences soient assez faibles.


### Literature Cited


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# Microsporogenesis in Abies[1])


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### Introduction

The genus *Abies* contains more than 40 species, and members of the genus are found in the northern hemisphere in a band that circumscribes our planet. On the American Continent its southern range extends into the mountains of Guatemala, and in Africa it occupies certain sites in Algeria. Many species are exploited commercially in forestry and planted trees are effectively used as ornamentals. Despite their wide distribution and commercial importance, members of this genus have received a minimum of attention from forest scientists. Little is known about the phylogenetic relationships within this genus, and past hybridization attempts have been sporadic and on too limited a scale to be of great help. There are, however, reports on natural hybrids, and several species have yielded hybrids from artificial crosses. Because of the neglect of this genus, there are good opportunities to contribute basic knowledge on reproductive habits, normal and abnormal cytology, as well as on variation patterns in individual species and hybrids. Various aspects of the genetics of *Abies* are currently being investigated, such as crossing patterns, karyotypes, and responses to mutagens. Results from treatment with colchicine have been prepared (Mergen and Lester, 1961).

There is no complete description of the phenolgy of flowering in *Abies* in either forestry or botany literature, but there have been reports on some of the later stages


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