

PINACEAE

Review from 1989 of the reproductive morphology of all Pinaceae in relation to all the other conifers

Other morphological features as well as some chemistry are included

Part one

including the pages 247-261 (of 247-305)
of the extremely qualified and informative review
with the for this part misleading title:

THE GENERA OF PINACEAE IN THE SOUTHEASTERN UNITED STATES

by Robert A. Price

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A review of the anatomy of the leaves may be found in

Klaus Napp-Zinn: ANATOMIE DES BLATTES, I GYMNOSPERMEN

1966, Gebrüder Borntraeger · Berlin - Nikolassee

THE GENERA OF PINACEAE IN THE
SOUTHEASTERN UNITED STATES¹ROBERT A. PRICE²

PINACEAE Lindley, Nat. Syst. Bot. ed. 2. 313. 1836, nom. cons.

(PINE FAMILY)

Evergreen [or deciduous], monoecious trees (occasionally shrubs), usually pyramidal in form. Leaves linear to acicular [rarely lanceolate], spirally arranged (often apparently 2-ranked), sessile or short-petiolate; foliage leaves either borne on long-shoots or clustered tightly on short-shoots. Pollen cones (microsporangiate strobili) bearing spirally arranged, bilaterally symmetrical microsporophylls; microsporangia 2 on the abaxial surface of each sporophyll, longitudinally or transversely [or obliquely] dehiscent; pollen grains bisaccate, or less commonly with the saccae reduced to a frill (in *Tsuga* sect. TSUGA) [or nonsaccate in *Larix* and *Pseudotsuga*]; prothallial cells 2. Ovulate cones with

¹Prepared for the Generic Flora of the Southeastern United States, a long-term project made possible through the support of National Science Foundation Grant BSR-8415769 (C. E. Wood, Jr., principal investigator), under which this account was prepared, and BSR-8415637 (N. G. Miller, principal investigator). The 127th in the series, this paper follows the format established in the first one (Jour. Arnold Arb. 39: 296–346. 1958) and continued to the present. The area covered by the Generic Flora includes North and South Carolina, Georgia, Florida, Tennessee, Alabama, Mississippi, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with information about extraregional members of a family or genus in brackets. The references that I have not verified are marked with asterisks.

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The illustrations were drawn by Karen Stoutsenburger in 1977 under the supervision of Carroll Wood, who also made the dissections. Living, liquid-preserved, and some of the dry materials used were variously collected by Walter Judd, Norton Miller, and Carroll Wood. Herbarium materials include an unattributed sheet [A] with mature seeds of *Pinus Strobus* utilized by C. E. Faxon for the illustration in Sargent's *Silva of North America*, as well as specimens collected by Adams & Wherry (2252 [GH]), R. M. Harper (2023, 2027 [GH]), and J. D. Smith (*s.n.*, Aug. 1881 [GH]). The diagrammatic cross sections of leaves of *Pinus* are after J. W. Lanyon's *A Card Key to Pinus Based on Needle Anatomy*. The pollen grain of *P. Strobus* is after a photograph made by Norton Miller.

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spirally arranged, strongly flattened bract-scale complexes; bracts included or exerted, separate from the scales for most of their length; mature ovuliferous scales relatively thin to strongly thickened and woody (in *Pinus*); ovules 2 on the adaxial surface of each scale, the micropyles directed toward the cone axis; archegonia few per ovule, not clustered. Seeds with an elongate terminal wing partially folded around the seed body [wing short or absent in some species of *Pinus*]; embryo straight, cotyledons 2–12[–18]. Chromosome number $2n = 24$ [26 and 44 in one species each]. (Including Abietaceae Walpers; Abietineae Rich.) TYPE GENUS: *Pinus* L.

The largest and most economically important family of conifers, with ten genera and approximately 220 species, the Pinaceae are restricted almost entirely to the Northern Hemisphere³ both at present and as fossils (Florin, 1963). Three small genera are confined to eastern Asia: *Keteleeria* Carr., a genus of perhaps nine species (Cheng & Fu) much in need of further study, and the monotypic *Cathaya* Chun & Kuang (described in 1958 from southern China) and *Pseudolarix* Gordon (golden larch, false larch). *Cedrus* Trew, comprising the true cedars, consists of four closely related species occurring disjunctly in North Africa, the Near East, Cyprus, and the Himalayas and is widely cultivated in temperate areas, including the southeastern United States. All six remaining genera are represented by species native to the United States. Only two of them have no species indigenous to our area: *Larix* Miller, larch, with about ten species in northern North America and Eurasia, and *Pseudotsuga* Carr., Douglas fir, with seven or eight species in western North America and eastern Asia.

The family Pinaceae is a well-defined natural group, distinguished particularly by characters of its ovulate cones. These have well-developed scales that are distinct from the subtending bracts, two inverted ovules per scale, and a prominent terminal seed wing developing from the cone scale. It is supported as a monophyletic group by shared features unique among the gymnosperms, including the pattern of proembryogeny (Doyle, 1963; Singh), protein-type sieve-cell plastids (Behnke), and the absence of biflavonoid compounds (Geiger & Quinn).

On the basis of morphological comparisons (e.g., Eckenwalder; Hart), immunological comparisons of seed-protein extracts (Price & Lowenstein), and phloem polypeptide profiles (Alosi & Park), there is no evidence that the Pinaceae are closely related to any of the other extant families of conifers. Rather, the family has a long fossil history as a distinct lineage, probably dating to the Triassic (Miller, 1977), as is also the case for such other major extant coniferous groups as the Araucariaceae, the Podocarpaceae, and the Cupressaceae-Taxodiaceae lineage. The combination of apparently primitive characters (bisaccate pollen with two prothallial cells, chromosome number $2n = 24$, and lack of bract-scale fusion) and uniquely derived features characteristic of the Pinaceae suggests that its origin should be sought among early conifer groups preceding the extant families (see Florin, 1951). Thus a number of European workers

³One species, *Pinus Merkusii* Jungh & De Vries, is native from Indochina south of the Equator to Sumatra.

(e.g., Emberger; Lebreton & Sartre; Norin) have placed the Pinaceae in the unifamilial order Pinales.

The monotypic *Sciadopitys* Sieb. & Zucc., Japanese umbrella pine (Sciadopityaceae), has sometimes been associated with the Pinaceae on the basis of its unusual "double-needles." These superficially resemble longitudinally fused pairs of *Pinus* needles but in fact differ from them considerably in pattern of development (see Roth). Other morphological and cytological evidence suggests that *Sciadopitys* diverged at an early time from the cupressaceous-taxodiaceous lineage, since *Sciadopitys*—as well as the Cupressaceae *sensu lato* (including Taxodiaceae)—differs from the Pinaceae in having nonsaccate pollen without prothallial cells, substantial fusion of bract and scale in the mature ovulate cone, multiple ovules per scale, and lateral seed wings derived from the seed coat (Florin, 1951; Singh; Sporne). In its proembryogeny *Sciadopitys* appears to be more primitive than either group (Doyle & Brennan; Singh). Immunological comparisons of seed-protein extracts (Price & Lowenstein) and overall patterns of secondary-product chemistry (Hegnauer, 1962, 1986) also indicate that *Sciadopitys* is quite isolated from the Pinaceae.

The ten genera of Pinaceae are clearly delimited, but subfamilial groupings have been controversial. *Pinus*, in recognition of its unusual short-shoots (needle fascicles) and its distinctive, usually highly thickened cone scales, is often placed by itself in subfam. Pinoideae. Vierhapper and a number of later authors (e.g., Florin, 1931, 1963; Krüssmann; Pilger & Melchior) divided the remaining genera into two groups based on presence or absence of strongly condensed vegetative short-shoots that bear the majority of the foliage leaves. The genera with marked shoot dimorphism (*Cedrus*, *Larix*, *Pseudolarix*) have been placed in subfam. Laricoideae Pilger & Melchior, with the remaining genera (long-shoots only) in subfam. Abietoideae Ascherson & Graebner *emend.* Pilger & Melchior or in equivalent groups of lower rank. The relatively recently discovered genus *Cathaya*, which has less-marked shoot dimorphism (see photo in Chun & Kuang, 1958), was placed by Florin (1963) in the Abietoideae. However, other morphological characters show little concordance with shoot dimorphism, so division of the family on this basis alone is highly artificial.

Another subfamilial division, first proposed by Van Tieghem (1891), placed together those genera with resin canals in the primary root adjacent to each protoxylem pole (*Pinus*, *Picea*, *Larix*, *Pseudotsuga* (and *Cathaya*; see Hu & Wang), comprising the Pinées or Epixylocèles of Van Tieghem, here termed the pinoid group) and those with a single central resin canal in the primary root (*Cedrus*, *Tsuga*, *Abies*, *Keteleeria*, and *Pseudolarix*, comprising the Cedrées or Myélocèles of Van Tieghem, here termed the abietoid group). This classification appears to be a natural one, based on the concordance of root anatomy with other morphological features. Each of the pinoid genera regularly exhibits both vertical and horizontal resin canals in the wood and lacks resin vesicles in the seed coat, while the abietoid genera have much more localized resin canals in the wood following wounding ("traumatic resin canals," usually in the vertical system) and have resin vesicles in the seed coat (Jeffrey; Phillips; Price *et al.*). Immunological comparisons of seed-protein extracts have also yielded precisely the abietoid and pinoid groups of Van Tieghem (Prager *et al.*;

Price *et al.*). Thus recognition of two subfamilies, the Pinoideae and the Abietoideae, corresponding to the groups of Van Tieghem—or of three subfamilies, with *Pinus* placed in a monogeneric Pinoideae and the remaining pinoid genera in the Laricoideae—seems to be the most reasonable alternative.

Within the pinoid group, *Larix* and *Pseudotsuga* appear to be closely related sister-genera on the basis of their shared possession of nonsaccate pollen, a highly modified micropylar apparatus at time of pollination, fiber-sclereids in the bark, and similar, relatively asymmetric karyotypes, all of which seem to be derived characters within the family. They also group together in immunological comparisons of seed proteins (Prager *et al.*; Price *et al.*).

Chromosome counts have been obtained for all ten genera and approximately 75 percent of the species of Pinaceae (see particularly Khoshoo, 1961). The number $2n = 24$, which is apparently primitive for the conifers,⁴ has been found in all but two species (*Pseudotsuga Menziesii* (Mirbel) Franco, $2n = 26$, and *Pseudolarix amabilis* (Nelson) Rehder, $2n = 44$). Counts are available for six of the remaining seven species of *Pseudotsuga*; all have $2n = 24$ (Doerksen & Ching; El-Kassaby *et al.*). Karyotypes have been obtained for all genera of the Pinaceae (see particularly Chu & Sun; Khoshoo, 1962; Kuo *et al.*; Sax & Sax; see also Saylor, 1964, 1972, 1983, cited under *Pinus*); they vary from largely symmetrical (11 of 12 chromosomes metacentric or submetacentric in *Pinus*, *Cathaya*, and *Cedrus*; nine of 12 metacentric in *Picea* and *Tsuga*) to extremely asymmetric in *Pseudolarix*. *Pseudotsuga* and *Larix* both have asymmetric karyotypes—six metacentric and six subtolocentric chromosomes, with one metacentric chromosome replaced by a subtolocentric and an additional short telocentric chromosome in *P. Menziesii*. *Pseudolarix amabilis* has a particularly unusual karyotype, with two metacentric and 20 shorter subtolocentric chromosomes (Sax & Sax), implying an aneuploid increase involving fission of ten of the original 12 chromosomes (Ehrendorfer; Khoshoo, 1959). Given their long fossil record, the Pinaceae have shown remarkably little change in chromosome number, a situation shared with the other conifer families except the Podocarpaceae (Ehrendorfer; Khoshoo, 1962), but one differing markedly from most angiosperm groups. Individuals or cells with polyploid chromosome numbers have occasionally been reported in the Pinaceae (Khoshoo, 1959), but polyploid plants apparently seldom survive under natural conditions.

The Pinaceae are characterized by a specialized variant of the coniferous pattern of proembryogeny (Dogra, 1980; Doyle, 1963; Singh). Two free-nuclear mitotic divisions yield four nuclei that come to lie in a more or less planar arrangement. A third mitotic division yields two tiers of four nuclei that rapidly become separated by transverse walls. The Pinaceae differ from the other conifers in that the lower of the two tiers produced by vertical division of the original upper or “open” tier does not elongate to form the suspensor. Instead, the tier of cells below this, produced by vertical division of the lowest original tier, forms the suspensor, while only the lowest of the four tiers forms the embryonal mass. In *Pseudotsuga* (at least in *P. Menziesii*) apparently only the

⁴This number is also found in *Taxus* (Taxaceae), *Cephalotaxus* (Cephalotaxaceae), some Podocarpaceae, and the outgroup *Ginkgo* L. (see discussions in Ehrendorfer, and Khoshoo, 1962).

lower of the original two tiers divides, yielding a three-tiered proembryo (Allen & Owens; Singh).

Although only a single embryo usually matures in each seed, polyembryony is characteristic of many conifers, including all genera of Pinaceae. Simple polyembryony, where embryos are formed in more than one archegonium per ovule, occurs relatively frequently. Cleavage polyembryony, where multiple embryos are formed by the splitting up of the products of a single zygote, is also a regular feature in *Pinus*, *Cathaya*, *Cedrus*, *Tsuga*, and *Keteleeria* (Doyle & Brennan; Wang & Chen). It also occurs in a limited percentage of embryos in some species of *Abies* but has not been found in *Pseudolarix*, *Picea*, *Larix*, or *Pseudotsuga*. In the last two genera, unequal growth rates often cause two of the units to overtop the others (although the four embryonal units do not separate from one another, a situation termed "incipient cleavage" by Doyle & Brennan).

The Pinaceae have the highest average number of cotyledons and the greatest range in this number of any family of seed plants (Butts & Buchholz). The highest numbers are found in *Pinus*, which has the entire range of numbers for the family (2–18, with intraspecific averages ranging from ca. 4 to 14), and in *Cedrus* (5–14, averaging ca. 9 or 10). Detailed discussions of the vascular-bundle patterns in the cotyledons and embryos are presented in Boureau (1939) and Ferré (1952).

Ovulate-cone anatomy in the Pinaceae has been studied by Aase, Miller (1976), Radais, and Van Tieghem (1869), with emphasis on distribution of the vasculature and resin canals. *Pinus* appears to be unusual in having partial fusion of the bract and scale traces at their bases. The arrangement of the resin canals associated with these traces seems to be fairly specific to each genus (Miller, 1976; Radais), with those in the cones of *Pinus* restricted to the area abaxial to the scale trace, perhaps because of the basal fusion of the traces. The axial vascular cylinder of the cone is reduced in thickness and much dissected in the genera with abscising cone scales (*Abies*, *Cedrus*, *Pseudolarix*; Miller, 1976).

Pollen grains are bisaccate in the Pinaceae, except in *Larix* and *Pseudotsuga*, where they are spheroidal and nonsaccate, and *Tsuga* sect. TSUGA, where the saccae are reduced to a subequatorial frill (G. Erdtman, 1957, 1965; Ueno). Saccate pollen is evidently the primitive state both in the Pinaceae and among the conifers generally (see Florin, 1951; Millay & Taylor), but the saccae have been lost in all other extant coniferous groups except the Podocarpaceae, where pollen may be bi-, tri-, or nonsaccate.

The Pinaceae are wind pollinated, as are the other conifers, and often release huge volumes of pollen. Specific mechanisms of pollination have been reviewed by Dogra (1964), Doyle (1945), and Singh and have recently been elegantly demonstrated through scanning electron, as well as light, microscopy for a number of western North American taxa by Owens and coworkers (Allen & Owens; Owens & Molder; and additional references cited under the individual genera). A pollination-drop mechanism has been substantiated only in *Pinus* and *Picea* and is lacking in the other genera examined to date (*Cathaya*, *Keteleeria*, and *Pseudolarix* are unstudied in this regard). It is found in most other

gymnosperms and is presumably the primitive state for the Pinaceae (see Doyle, 1945; Singh).

In *Pinus* and *Picea*, pollen is caught on a sticky film on the inner surfaces of the two integumentary arms and, when contacted by the pollination drop, is then drawn into the micropylar canal, after which it floats or is pulled up to the nucellus (Owens *et al.*, 1981, 1987, cited under *Pinus* and *Picea*, respectively). *Pseudotsuga* and *Larix* have a highly specialized mechanism in which the unwinged pollen is caught between hairs on the highly expanded outer-integument lip and then drawn into the micropylar canal by collapse of the surface of the lip (Allen & Owens; Owens & Molder). In *Cedrus* and *Abies*, pollen is caught on the inner surface of the funnel-shaped integumentary area around the micropyle, and the nucellus grows out to the pollen (Doyle, 1945; Owens & Molder, 1977, cited under *Abies*). In *Tsuga Mertensiana* (Bong.) Carr., of sect. HESPEROPEUCE, the situation is similar, but the integument tip is very asymmetric; in sect. TSUGA the pollen lands primarily on the bract surfaces rather than the ovule tip, and then the pollen tubes grow over to the nucellus (Doyle & O'Leary). This unusual situation is otherwise seen only in the Araucariaceae and in *Saxegothaea* Lindley (Podocarpaceae), which also have unwinged pollen (Doyle, 1945). Doyle (1945) related the pollination mechanisms of Pinaceae to the groupings of Van Tieghem (1891) in an evolutionary diagram, showing series leading from *Pinus* and *Picea* to *Larix* and *Pseudotsuga* on the one hand, and *Cedrus*, *Abies*, and *Tsuga* on the other. *Cathaya* might be expected to have a mechanism similar to that of *Pinus* and *Picea*, and *Keteleeria* and *Pseudolarix* to have ones similar to those of the other abietoid genera.

A characteristic feature of the Pinaceae is the formation of ectomycorrhizal associations with a variety of fungi, including a number of basidiomycetes, such as *Armillaria matsutake* and *Boletus edulis*, that are highly sought for their edible mushrooms. The presence of mycorrhizae appears to help buffer the plants against various types of environmental stress, and thus mycorrhizal associations have been much investigated in regard to commercial tree production.

Because of the economic importance of the Pinaceae, numerous studies of the chemical composition of the leaves, wood, and bark have been made on many species (see reviews by Hegnauer, 1962, 1986; Norin; Squillace; Von Rudloff), with particular emphasis on *Pinus*, *Picea*, *Abies*, and *Pseudotsuga*. The chemistry of *Cedrus* has recently been reviewed by Agrawal & Rastogi. Significant gaps remain in our knowledge of the chemosystematics of even the best-known genera, however.

The Pinaceae contain a diversity of terpenoid compounds in the bark, wood, leaves, and cones, particularly in the characteristic oleoresins of the resin canals or vesicles. The bulk of the volatile portion of the stem and leaf oleoresins is usually a complex mixture of monoterpenes. These impart much of the characteristic fragrance associated with Pinaceae. Terpenoid and hydrocarbon profiles of the oleoresins or turpentine (the steam-distillable portion thereof) often show significant differences among species and have been widely used in chemosystematics of the Pinaceae (see particularly the reviews by Squillace and

Von Rudloff and the papers by Mirov, Von Rudloff, Zavarin, and their co-workers cited under the individual genera).

Sesquiterpenoid compounds have received much less attention than monoterpenoids, although the former may also be of considerable chemosystematic utility. *Cedrus* is particularly notable for its array of unusual structural types including the atlantones, himachalenes, and allohimachalenes (Agrawal & Rastogi; Norin).

Diterpene resin acids are major constituents of the "rosin" remaining after removal of the volatile components of pinaceous oleoresin by steam distillation (Hegnauer, 1962, 1986; Norin). Resin acids of the abietane and pimarane types have been reported from woods of *Pinus*, *Picea*, *Larix*, *Pseudotsuga*, and *Abies* (H. Erdtman, 1963; Norin) and from the cone oleoresins of *Cedrus* (Norin). These compounds are to be expected in the other genera if appropriate oleoresins are examined. Both pimarane and abietane terpenoids occur widely in the conifers (Hegnauer, 1986), although the abietane type was once thought to be specific to the Pinaceae (H. Erdtman, 1963). Several other types of diterpenoids have also been found in the Pinaceae, including labdane terpenoids in various species of *Pinus*, *Picea*, *Larix*, and *Abies*, and macrocyclic compounds of the thunbergene type in *Pinus*, *Picea*, *Larix*, and *Pseudotsuga* (Norin). Pseudolaric acids, a very unusual structural class of diterpenes, have been isolated from the roots of *Pseudolarix amabilis*; these constitute the active components of antifungal medicines in traditional use in China (Zhou *et al.*).

Serratene triterpenoids are characteristic bark components of *Pinus* and *Picea* (Hegnauer, 1962, 1986; Norin) and the morphologically similar *Cathaya* (He *et al.*) but have not been found in the other genera. Unusual lanostane triterpenoids have been isolated from the bark or needles of a few species of *Abies* (Hegnauer, 1962, 1986; Norin), while other tetracyclic triterpenes have been found in *Larix*, *Pseudotsuga*, *Pinus*, and *Picea*.

Alkaloids do not occur frequently in the Pinaceae but have been detected in some species of *Pinus*, *Picea*, and *Keteleeria* (Hegnauer, 1962; Willaman & Schubert). The pyridine alkaloids pinidine and α -pipecoline have been isolated from needles of several species of *Pinus* but are apparently absent in many others.

The Pinaceae are unusual in their almost total lack of biflavonoid compounds, otherwise ubiquitous among the conifers and *Ginkgo* (Geiger & Quinn). A single biflavonoid compound, abiesin, has recently been reported to occur in low concentration in the needles of *Abies spectabilis* (D. Don) Spach (Hegnauer, 1986).

Anthocyanins (3-glucosides of cyanidin (red) and delphinidin (blue), either singly or in combination) are important in the coloration of the young pollen and seed cones of the Pinaceae (Santamour, 1966). They are also involved in the transient spring coloration of *Picea* needles (Santamour, 1967).

Cyclitols (sugar 5-methyl ethers) such as sequoyitol and pinitol occur widely among the conifers, including the Pinaceae, and are of interest in that pinitol is the sugary substance exuded from the trunk of sugar pine (*P. Lambertiana* Douglas) and the related *P. Ayacahuite* Ehrenberg (Hegnauer, 1962). The related compound D-1-O-methylmucoinositol occurs widely in the leaves of the

other families of conifers but is apparently absent in those of the Pinaceae (Dittrich *et al.*).

Jamieson & Reid surveyed the fatty acids of conifer leaves, including representatives of seven genera of the Pinaceae. These uniformly exhibited a series of 18-carbon polyunsaturated acids that were absent in the other conifers examined.

Many species of Pinaceae are of great economic importance, with the family supplying over half of the world's timber (Sporne). *Pinus*, *Pseudotsuga*, *Picea*, *Larix*, *Abies*, *Tsuga*, and *Cedrus* are all of major significance in this regard. These genera are important sources of ornamental trees, and numerous horticultural varieties have been developed (L. H. Bailey; Dallimore & Jackson; Den Ouden & Boom; Krüssmann). The attractive golden larch (*Pseudolarix amabilis*), grown as an ornamental in China, is suitable to much of our region. Species of *Abies* (e.g., *A. balsamea* and *A. Fraseri*), *Picea*, and *Pinus* are frequently used as Christmas trees. The Pinaceae, particularly *Pinus*, are also economically important as the source of turpentine, pitch, and rosin used in shipbuilding (often termed "naval stores"), as well as in other industries. In addition, the leaf and stem resins of several genera have been used by native peoples of the United States and Canada in treating respiratory ailments and aiding wound healing, as well as for other medicinal purposes (Arnason *et al.*; Krochmal & Krochmal).

REFERENCES:

- AASE, H. C. Vascular anatomy of the megasporophylls of conifers. *Bot. Gaz.* **60**: 277–313. 1915.
- AGRAWAL, P. K., & R. P. RASTOGI. Chemistry of true cedars. *Biochem. Syst. Ecol.* **12**: 133–144. 1984. [*Cedrus*.]
- ALLEN, G. S., & J. N. OWENS. The life history of Douglas fir. x + 139 pp. Ottawa, Canada. 1972. [*Pseudotsuga Menziesii*; numerous illustrations, including seven color plates.]
- ALOSI, M. C., & R. B. PARK. A survey of phloem polypeptides in conifers. *Curr. Topics Pl. Biochem. Physiol.* **2**: 250. 1983.
- ARNASON, T., R. J. HEBDA, & T. JOHNS. Use of plants for food and medicine by native peoples of eastern Canada. *Canad. Jour. Bot.* **59**: 2189–2325. 1981. [Pinaceae, 2202, 2216, 2315–2317.]
- BAILEY, I. W. The structure of wood in the Pineae. *Bot. Gaz.* **48**: 47–55. *pl. 5*. 1909.
- BAILEY, L. H. The cultivated conifers in North America. ix + 404 pp. *158 pls.* New York. 1933.
- BAILLON, H. Conifères. *Hist. Pl.* **12**: 1–45. 1894. [Pinaceae, 16–22, 27–29, 44.]
- BANNAN, M. W. Vertical resin ducts in the secondary wood of the Abietineae. *New Phytol.* **35**: 11–46. *pl. 1*. 1936. [Results of experimental wounding on resin-canal distribution in Pinaceae; response is greater in pinoid than in abietoid genera.]
- BARNER, H., & H. CHRISTIANSEN. The formation of pollen, the pollination mechanism, and the determination of the most favorable time for controlled pollinations in *Larix*. *Silvae Genet.* **9**: 1–11. 1960.
- BEAN, W. J. Trees and shrubs hardy in the British Isles. ed. 8. 4 vols. London. 1970–1980. [*Abies*, **1**: 143–169; *Picea*, **3**: 176–199; *Pinus*, **3**: 209–248; *Tsuga*, **4**: 622–630.]
- BEHNKE, H.-D. Sieve element plastids of Gymnospermae: their ultrastructure in relation to systematics. *Pl. Syst. Evol.* **123**: 1–12. 1974. [Protein-type plastids seen only in Pinaceae.]
- BENTHAM, G., & J. D. HOOKER. Abietineae. *Gen. Pl.* **3**(1): 438–442. 1880. [Pinaceae.]

- BOBROV, E. G. On intergeneric hybridization in the family Pinaceae. (In Russian; English summary.) Bot. Zhur. **68**: 857–865. 1983. [Forestry Abstr. **48**: 564. 1987; suggests origins of pinaceous taxa—e.g., portions of *Larix*, *Picea*, and *Tsuga*—by this mechanism; needs independent experimental verification.]
- BOUREAU, E. Recherches anatomiques et expérimentales sur l'ontogénie des plantules des Pinacées et ses rapports avec la phylogénie. Ann. Sci. Nat. Bot. XI. **1**: 1–219. 1939.
- BUCHHOLZ, J. T. Polyembryony among Abietineae. Bot. Gaz. **69**: 153–167. 1920. [See also Am. Jour. Bot. **7**: 125–145. 1920.]
- . The pine embryo and the embryos of related genera. Trans. Illinois Acad. Sci. **23**: 117–125. 1931.
- . A comparison of the embryogeny of *Picea* and *Abies*. Madroño **6**: 156–167. 1942.
- . Generic and subgeneric distribution of the Coniferales. Bot. Gaz. **110**: 80–91. 1948.
- BUTTS, D., & J. T. BUCHHOLZ. Cotyledon number in conifers. Trans. Illinois Acad. Sci. **33**: 58–62. 1940. [Data from population samples; literature review.]
- CAMPO, M. VAN, & J. SIVAK. Structure alvéolaire des pollens à ballonets des Abiétacées. Pollen Spores **14**: 115–141. 1972. [Alveolar structure of pollen saccae in the Pinaceae.]
- CAMPO-DUPLAN, M. VAN. Recherches sur la phylogénie des Abiétinées d'après leurs grains de pollen. Trav. Lab. Forest. Toulouse, Tome II, Sect. I, Vol. IV, Art. I: 1–186. 1950.
- CARRIÈRE, E. A. Traité général des conifères. ed. 2. xii + 910 pp. Paris. 1867. [Pinaceae, 239–589; first treatment to use the nine known genera with their modern circumscriptions; *Tsuga* raised to rank of genus in ed. 1 (1855).]
- CHAMBERLAIN, C. J. Gymnosperms: structure and evolution. xi + 484 pp. Chicago. 1935.
- CHANG, Y.-P. Bark structure of North American conifers. U. S. Dep. Agr. Tech. Bull. **1095**. ii + 86 pp. 1954. [Pinaceae, 12–48, figs. 3–28; detailed anatomical comparisons for six genera; numerous photomicrographs; keys to genera.]
- CHENG, W.-C., & L.-K. FU, eds. Gymnospermae. (In Chinese; nomenclatural portions primarily in English and Latin.) Fl. Reipubl. Pop. Sinicae **7**. xiv + 544 pp. 1978. [Pinaceae, 32–281; significant new treatments of the Chinese species, including *Keteleeria* (9 species) and *Tsuga* (5 species); many useful illustrations of little-known taxa.]
- CHOWDHURY, C. R. The morphology and embryology of *Cedrus Deodara* (Roxb.) Loud. Phytomorphology **11**: 283–304. 1961.
- . The embryogeny of conifers: a review. *Ibid.* **12**: 313–338. 1962.
- CHOWDHURY, K. A. *Abies* and *Picea*: morphological studies. Council of Sci. and Industr. Res., Bot. Monogr. **9**. viii + 46 pp. New Delhi. 1974. [Critical review, Phytomorphology **25**: 124. 1974.]
- CHRISTIANSEN, H. The formation of pollen, the pollination mechanism, and the determination of the most favorable time for controlled pollination in *Pseudotsuga Menziesii*. Silvae Genet. **11**: 89–124. 1962. [See also *Ibid.* **18**: 97–104. 1969, which contains the unusual claim that the male gametes are unique among conifers in being ciliated and rapidly motile; needs verification.]
- CHU, C. A brief introduction to the Chinese species of the genus *Pseudotsuga*. Davidsonia **12**: 15–17. 1981. [Key, map, and distributional information; five species recognized for China and eight worldwide.]
- CHU, C.-C., & C.-S. SUN. Chromosome numbers and morphology in *Cathaya*. (In Chinese; English summary.) Acta Phytotax. Sinica **19**: 444–446. 1981. [$2n = 24$.]
- CHUN, W.-Y., & K.-Z. KUANG. A new genus of Pinaceae—*Cathaya* Chun et Kuang, *gen. nov.*, from southern and western China. (In Russian and Latin; English summary.) Bot. Zhur. **43**: 461–476. 1958. [Extensive illustrations; see also the later

- treatment in *Acta Bot. Sinica* **10**: 245, 246. *pls. 1–3*. 1962, in which one of the two original species is placed in synonymy.]
- COKER, W. C., & H. R. TOTTEN. *Trees of the southeastern states*. ed. 3. viii + 419 pp. Chapel Hill, North Carolina. 1945. [Pinaceae, 15–42.]
- COULTER, J. M., & C. J. CHAMBERLAIN. *Morphology of gymnosperms*. ed. 2. xi + 466 pp. Chicago. 1917.
- CRITCHFIELD, W. B. Impact of the Pleistocene on the genetic structure of North American conifers. Pp. 70–118 in R. M. LANNER, ed., *Proceedings of the Eighth North American Forest Biology Workshop*. Logan, Utah. 1984. [Reviews variation in electrophoretic alleles, terpenoids, and morphology for selected species of *Picea*, *Abies*, *Pinus*, and *Pseudotsuga*.]
- DALLIMORE, W., & A. B. JACKSON. *A handbook of Coniferae and Ginkgoaceae*. ed. 4 (revised by S. G. HARRISON). xix + 729 pp. 46 *pls.* London. 1966.
- DEN OUDEN, P., & B. K. BOOM. *Manual of cultivated conifers*. x + 2 unnumbered + 526 pp. The Hague. 1965.
- DICKINSON, T., P. KNOWLES, & W. H. PARKER. Data set congruence in northern Ontario tamarack (*Larix laricina*, Pinaceae). *Syst. Bot.* **13**: 442–455. 1988. [Compares morphometric and isozyme data.]
- DITTRICH, P., M. GIETL, & O. KANDLER. D-1-O-methyl-mucoinositol in higher plants. *Phytochemistry* **11**: 245–250. 1971. [Absent from the leaves of Pinaceae.]
- DOERKSEN, A. H., & K. K. CHING. Karyotypes in the genus *Pseudotsuga*. *Forest Sci.* **18**: 66–69. [$2n = 24$ in five Asian species.]
- DOGRA, P. D. Pollination mechanisms in gymnosperms. Pp. 142–175 in P. K. K. NAIR, ed., *Advances in palynology*. Lucknow. 1964. [General review relying heavily on work of DOYLE.]
- . Embryogeny of gymnosperms and taxonomy—an assessment. *Glimpses in Plant Research* **5**: 114–128. 1980.
- DOYLE, J. Developmental lines in pollination mechanisms in the Coniferales. *Sci. Proc. Roy. Dublin Soc.* **24**: 43–62. 1945. [Evolutionary interpretation of pollination mechanisms in Pinaceae.]
- . Proembryogeny in *Pinus* in relation to that in other conifers—a survey. *Proc. Irish Acad. B.* **62**: 181–216. 1963.
- & M. BRENNAN. Cleavage polyembryony in conifers and taxads—a survey II. Cupressaceae, Pinaceae and conclusions. *Sci. Proc. Roy. Dublin Soc. A.* **4**: 137–158. 1972.
- & A. KANE. Pollination in *Tsuga Pattoniana* and in species of *Abies* and *Picea*. *Sci. Proc. Roy. Dublin Soc. II.* **23**: 57–70. *pls. 2, 3*. 1943. [*T. Pattoniana* = *T. Mertensiana* (Bong.) Carr.]
- & M. O'LEARY. Pollination in *Tsuga*, *Cedrus*, *Pseudotsuga* and *Larix*. *Sci. Proc. Roy. Dublin Soc. II.* **21**: 191–204. *pls. 4, 5*. 1935.
- ECKENWALDER, J. E. Re-evaluation of Cupressaceae and Taxodiaceae: a proposed merger. *Madroño* **23**: 237–256. 1976. [Comparisons among the families of conifers.]
- EHRENDORFER, F. Evolutionary significance of chromosomal differentiation patterns in gymnosperms and primitive angiosperms. Pp. 220–240 in C. B. BECK, ed., *Origin and early evolution of angiosperms*. New York. 1976.
- EICHLER, A. W. Coniferae. In: A. ENGLER & K. PRANTL, *Nat. Pflanzenfam. II.* **1**: 28–116. 1889. [With contributions by ENGLER and PRANTL.]
- EL-KASSABY, Y. A., A. M. COLANGELLI, & O. SZIKLAI. A numerical analysis of karyotypes in the genus *Pseudotsuga*. *Canad. Jour. Bot.* **61**: 536–544. 1983. [Compares karyotypes of all species except *P. brevifolia* Cheng & Fu.]
- & E. E. WHITE. Isozymes and forest trees: an annotated bibliography. *Canad. Forest Serv. Pacific Forest Res. Ctr. Info. Rep.* **BC-X-267**. 1985.*
- EMBERGER, L. Gymnospermes. *Traité de botanique systématique* **2(1)**: 383–459. 1960. [Pinaceae placed in a monofamilial Pinales.]
- ERDTMAN, G. Pollen and spore morphology/plant taxonomy. Vol. 2. Gymnospermae,

- Pteridophyta and Bryophyta (illustrations). *Frontisp.* + iv + 151 pp. 5 pls. Stockholm. 1957. [Pinaceae, 6, 7, 10, 11, 13, 27, 28, 32–36, 39, 40, 43, 44.] Vol. 3. Gymnospermae, Bryophyta (text). 191 pp. 24 pls. Stockholm. 1965. [Pinaceae, 11, 13, 14, 22–25, 45–48, 54–60, 69–71, 78–80; pls. 1, 8–19, 21.]
- ERDTMAN, H. Conifer chemistry and taxonomy of conifers. Pp. 1–27 in K. KRATZL & G. BILLEK, eds., Proceedings of the Fourth International Congress of Biochemistry, Vienna, 1958. Vol. 2. New York. 1959. [Pinaceae, 2–12.]
- . Some aspects of chemotaxonomy. Pp. 88–125 in T. SWAIN, ed., Chemical plant taxonomy. London. 1963. [See particularly pp. 106–112.]
- FERRÉ, Y. DE. Les formes de jeunesse des Abiétacées. Trav. Lab. Forest. Toulouse, Tome II, Sect. I, Vol. III, Art. I: 1–284. 1952. [Morphology of cotyledons and primary and secondary leaves compared.]
- & H. GAUSSEN. Le rameau phylétique: *Pinus*, *Pseudolarix*, *Keteleeria*. Bull. Soc. Hist. Nat. Toulouse 80: 108–118. 1945. [Reprinted as Trav. Lab. Forest. Toulouse, Tome I, Vol. IV, Art. VIII: 1–11. 1945.]
- FITSCHEN, J. Handbuch der Nadelholzkunde. xv + 765 pp. Berlin. 1930. [Revised 3rd ed. of BEISSNER's Handbuch der Nadelholzkunde.]
- FLORIN, R. Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales. Sv. Vet.-akad. Handl. III. 10: 1–588. pls. 1–58. 1931. [Classic treatment of vegetative anatomy of the conifers; Pinaceae, 93–111, 306–347, pls. 34–39; generic relationships and classification of the Pinaceae, 476–483.]
- . Evolution in cordaites and conifers. Acta Horti Berg. 15: 285–388. 1951. [Classic study of the evolution of the coniferous ovulate cone; see also Biol. Rev. 19: 367–389. 1954.]
- . The systematics of the gymnosperms. Pp. 323–403 in E. L. KESSEL, ed., A century of progress in the natural sciences, 1853–1953. San Francisco. 1955. [Historical review, mostly of morphology.]
- . The distribution of conifer and taxad genera in time and space. Acta Horti Berg. 20(4): 121–312. 1963.
- FLOUS, F. Classification et évolution d'une groupe d'Abiétinées. Trav. Lab. Forest. Toulouse, Tome I, Vol. II, Art. XVII: 1–286. 1936. [Classification, with useful historical discussion; putative evolutionary relationships in the Pinaceae; see also *Ibid.*, Tome I, Vol. III, Art. I: 1–16. 1938.]
- FOWELLS, H. A., compiler & reviser. Silvics of forest trees of the United States. U. S. Dep. Agr. Agr. Handb. 271. vi + 762 pp. 1965. [Maps by E. L. LITTLE, JR.]
- GAUSSEN, H. Abiétacées. In: Les gymnospermes: actuelles et fossiles. Trav. Lab. Forest. Toulouse, Tome II, Sect. I, Vol. I, Chap. XI: 1–716. 1960–1967. [*Pinus* (fasc. VI), 1–272. 1960; *Pinus* (suite), *Cedrus*, *Abies* (fasc. VII), 273–480. 1964; *Pseudolarix*, *Keteleeria*, *Larix*, *Pseudotsuga*, *Pityites*, *Picea*, *Cathaya*, *Tsuga* (fasc. VIII), 481–672. 1966; Additions et corrections (fasc. IX), 673–716. 1967; Bibliographie, Tome II, Vol. I, Partie III: 1–180. 1979 (bibliography for the entire work).]
- GEIGER, H., & C. QUINN. Biflavonoids. Pp. 692–742 in J. B. HARBORNE, T. J. MABRY, & H. MABRY, eds., The flavonoids, pt. 2. London. 1975. [Pinaceae unique among conifers in lacking biflavonoids.]
- GIANNASI, D. E., & D. J. CRAWFORD. Biochemical systematics II. A reprise. Evol. Biol. 26: 25–248. 1986. [Terpenoids in Pinaceae, pp. 66–71.]
- GREGUSS, P. Identification of living gymnosperms on the basis of xylotomy. 263 pp. 350 pls., 8 tables. Budapest. 1955. [Pinaceae, 183–249, pls. 196–345.]
- . Xylotomy of the living conifers. 172 + 329 pp. Budapest. 1972. [Pinaceae, 109–159, pls. 10, 115–165, figs. 95–145; an extension of GREGUSS, 1955.]
- HAMRICK, J. L., J. B. MITTON, & Y. B. LINHART. Levels of genetic variation in trees: influence of life history characters. Pp. 35–41 in M. T. CONKLE, tech. coord., Proceedings of the Symposium on Isozymes of North American Forest Trees and Forest Insects. U. S. Dep. Agr. Gen. Tech. Rep. PSW-48. 1981. [Compares isozyme variability in *Abies*, *Picea*, *Pinus*, and *Pseudotsuga*.]

- HARDIN, J. W. Studies of the southeastern United States flora. II. The gymnosperms. Jour. Elisha Mitchell Sci. Soc. **87**: 43–50. 1971. [Keys; valuable commentary on Pinaceae.]
- HART, J. A. A cladistic analysis of conifers: preliminary results. Jour. Arnold Arb. **68**: 269–307. 1987. [Both intergeneric and interfamilial cladograms; character states tabulated for all genera of Pinaceae.]
- HE, G.-F., Z.-W. MA, W.-F. YIN, & M.-L. CHENG. On serratene components in relation to the systematic position of *Cathaya* (Pinaceae). Acta Phytotax. Sinica **19**: 440–443. 1981. [Found in bark of *Cathaya*, *Pinus*, and *Picea*.]
- HEGNAUER, R. Chemotaxonomie der Pflanzen. Band 1. Thallophyten, Bryophyten, Pteridophyten und Gymnospermen. 517 pp. Basel and Stuttgart. 1962. [Pinaceae, 373–410, 480, 481.] Band 7. Nachträge zu Band 1 und Band 2. xii + 804 pp. 1986. [Pinaceae, 504–523, 801; extensive literature review.]
- HICKEL, R. Graines et plantules des conifères. Bull. Soc. Dendrol. France **19**: 13–115; **20**: 134–204. 1911. [Pinaceae, 52–115 (seeds), 163–204 (seedlings).]
- HILL, T. G., & E. DE FRAINE. On the seedling structure of gymnosperms. II. Ann. Bot. **23**: 189–227. pl. XV. 1909.
- HO, R.-H., & O. SZIKLAI. On the pollen morphology of *Picea* and *Tsuga* species. Grana Palynol. **12**: 31–40. 1972. [Emphasizes morphology of *T. Mertensiana* in comparison to that of other taxa.]
- HU, Y. S., & F. H. WANG. Anatomical studies of *Cathaya* (Pinaceae). Am. Jour. Bot. **71**: 727–735. 1984. [Thorough treatment of vegetative features and comparison with other genera.]
- & B. J. YAO. Transfusion tissue of gymnosperm leaves. Bot. Jour. Linn. Soc. **83**: 263–272. 1981.
- HUNTLEY, B., & H. J. B. BIRKS. An atlas of past and present pollen maps for Europe: 0–13000 years ago. xiv + 667 pp. Cambridge, England. 1983. [*Abies*, 22, 73–89; *Larix*, 35, 253–263; *Picea*, 39, 285–305; *Pinus*, 41, 42, 306–336.]
- JAMIESON, G. R., & E. H. REID. The leaf lipids of some conifer species. Phytochemistry **11**: 269–275. 1972. [Includes seven genera of Pinaceae.]
- JEFFREY, E. C. The comparative anatomy and phylogeny of the Coniferales. Part 2. The Abietineae. Mem. Boston Soc. Nat. Hist. **6**: 1–37. 1905. [Wood anatomy of Pinaceae supports the groupings of VAN TIEGHEM; groups treated as tribes Abieteeae and Pineae.]
- KHOSHOO, T. N. Polyploidy in gymnosperms. Evolution **13**: 24–39. 1959. [A very rare intraspecific phenomenon in Pinaceae.]
- . Chromosome numbers in gymnosperms. Silvae Genet. **10**: 1–9. 1961. [Comprehensive summary of the literature.]
- . Cytogenetical evolution in the gymnosperms—karyotype. Pp. 119–135 in P. MAHESHWARI, B. M. JOHRI, & I. K. VASIL, eds., Proceedings of the Summer School of Botany, Darjeeling. New Delhi. 1962.
- KONAR, R. N., & R. NAGMANI. Female gametophyte and embryogeny in *Picea Smithiana* and *Abies Pindrow* (Pinaceae). Bot. Jahrb. **101**: 267–297. 1980.
- & Y. P. OBEROI. Recent work on reproductive structures of living conifers and taxads—a review. Bot. Rev. **35**: 89–116. 1969. [Pinaceae, 90–95.]
- KROCHMAL, A., & C. KROCHMAL. A field guide to medicinal plants. vii + 274 pp. New York. 1984.
- KRÜSSMANN, G. Handbuch der Nadelgehölze. ed. 2 (revised by H.-D. WARDA). 6 unnumbered + 396 pp. 160 pls. Berlin and Hamburg. 1983. [Also published in English as Manual of cultivated conifers (M. E. EPP, translator). 361 pp. 160 pls. Portland, Oregon. 1985.]
- KUO, S. R., T. T. WANG, & T. C. HUANG. Karyotype analysis of some Formosan gymnosperms. Taiwania **17**: 66–80. 1972. [Includes *Keteleeria*, *Tsuga*, *Pseudotsuga*, *Picea*, and *Pinus*.]

- LEBRETON, P., & J. SARTRE. Les pinales, considérées d'un point de vue chimiotaxinomique. *Canad. Jour. Forest Res.* **13**: 145–154. 1983. [Flavonoids in representatives of nine genera of Pinaceae.]
- LI, H. L. Present distribution and habitats of the conifers and taxads. *Evolution* **7**: 245–261. 1953.
- LITTLE, E. L., JR. Atlas of United States trees. Vol. 1. Conifers and important hardwoods. U. S. Dep. Agr. Forest Serv. Misc. Publ. **1146**. v + 9 pp. 2 base maps, 200 species maps, 9 overlay maps. 1971. [Detailed range maps for all American species of Pinaceae.]
- . Checklist of United States trees (native and naturalized). U. S. Dep. Agr. Forest Serv. Agr. Handb. **531**. iv + 375 pp. 1979.
- . The Audubon Society field guide to North American trees. Eastern region. 714 pp. New York. 1980.
- LOTOVA, L. I. On the correlation of the anatomical features of the wood and phloem in the Pinaceae. (In Russian.) *Vestn. Moskov. Univ. Biol.* **6**: 1: 41–51. 1975.
- MAHESHWARI, P., & H. SINGH. The female gametophyte of gymnosperms. *Biol. Rev.* **42**: 88–130. 1967.
- MEHRA, P. N., & T. N. KHOSHOO. Cytology of conifers. I. *Jour. Genet.* **54**: 165–180. pl. 5. 1956. [Chromosome counts and karyotypes in *Pinus*, *Cedrus*, *Picea*, and *Abies*; all $n = 12$.]
- MERGEN, F. Microsporogenesis and macrosporogenesis in *Pseudolarix amabilis*. *Silvae Genet.* **25**: 183–188. 1976.
- MILLAY, M. A., & T. N. TAYLOR. Evolutionary trends in fossil gymnosperm pollen. *Rev. Palaeobot. Palynol.* **21**: 65–91. 1976.
- MILLER, C. N., JR. Early evolution in the Pinaceae. *Rev. Palaeobot. Palynol.* **21**: 101–117. 1976. [Compares ovulate-cone anatomy of extant and fossil genera.]
- . Mesozoic conifers. *Bot. Rev.* **43**: 217–280. 1977.
- . Current status of Paleozoic and Mesozoic conifers. *Rev. Palaeobot. Palynol.* **37**: 99–114. 1982. [Preliminary phylogenetic comparisons of fossil and extant genera based on ovulate-cone characters alone.]
- . *Pityostrobus pubescens*, a new species of pinaceous cones from the Late Cretaceous of New Jersey. *Am. Jour. Bot.* **72**: 520–529. 1985. [Includes anatomical comparisons of the extant genera of Pinaceae.]
- MIRANDA, V., & M. CHAPEKHAR. SEM study of the inner periclinal surface of leaf cuticles in the family Pinaceae. *Bot. Jour. Linn. Soc.* **81**: 61–78. 1980.
- NIEMANN, G. J., & H. H. VAN GENDEREN. Chemical relationships between Pinaceae. *Biochem. Syst. Ecol.* **8**: 237–240. 1980. [Compares flavonoid “fingerprints” of species in nine genera.]
- NORIN, T. Some aspects of the chemistry of the order Pinales. *Phytochemistry* **11**: 1231–1242. 1972. [Valuable review emphasizing wood-extractive chemistry of the Pinaceae.]
- OWENS, J. N., & M. MOLDER. Sexual reproduction of *Larix occidentalis*. *Canad. Jour. Bot.* **57**: 2673–2690. 1979.
- & S. SIMPSON. Pollen from conifers native to British Columbia. *Canad. Jour. Forest Res.* **16**: 955–967. 1986. [SEM and LM photographs and descriptions; includes *Abies*, *Tsuga*, *Pseudotsuga*, *Larix*, *Picea*, and *Pinus*.]
- PANT, D. D., & N. BASU. A comparative study of the leaves of *Cathaya argyrophylla* Chun & Kuang and three species of *Keteleeria* Carrière. *Bot. Jour. Linn. Soc.* **75**: 271–282. 1977.
- PARLATORE, P. Coniferae. *DC. Prodr.* **16**(2): 361–521. 1868. [Pinaceae, 364, 365, 377–431.]
- PHILLIPS, E. W. J. Identification of softwoods by their microscopic structure. *Dep. Sci. Industr. Res. London Forest Prod. Res. Bull.* **22**. iii + 56 pp. 3 pls. 1948. [Excellent comparative treatment of wood anatomy for all genera except *Cathaya*; a similar account in *Jour. Linn. Soc. Bot.* **52**: 259–320. 1941.]

- PILGER, R. Pinaceae. *In*: A. ENGLER, Nat. Pflanzenfam. ed. 2. **13**: 271–342. 1926. [Definitive separation of Pinaceae from Taxodiaceae and Cupressaceae; introduction of the modern system of families.]
- & H. MELCHIOR. Gymnospermae. *In*: H. MELCHIOR, Engler's Syllabus Pflanzenfam. ed. 12. **1**: 312–344. 1954. [Pinaceae, 329–332, *figs.* 132, 133.]
- PRAGER, E. M., D. P. FOWLER, & A. C. WILSON. Rates of evolution in conifers (Pinaceae). *Evolution* **30**: 637–649. 1976. [Immunological comparison and electrophoretic characterization of seed proteins.]
- PRICE, R. A., & J. M. LOWENSTEIN. An immunological comparison of the Sciadopityaceae, Taxodiaceae, and Cupressaceae. *Syst. Bot.* (in press). [Seed-protein extracts compared by radioimmunoassay; *Sciadopitys* relatively isolated and not close to Pinaceae.]
- , J. OLSEN-STOJKOVICH, & J. M. LOWENSTEIN. Relationships among the genera of Pinaceae: an immunological comparison. *Syst. Bot.* **12**: 91–97. 1987. [Immunological comparison of seed proteins supports the classification of VAN TIEGHEM (1891).]
- RADAIS, M. L. Anatomie comparée du fruit des conifères. *Ann. Sci. Nat. Bot.* **VII**. **19**: 165–368. *pls.* 1–15. 1894. [Emphasizes vascular anatomy of the ovulate cone.]
- RADFORD, A. E., H. E. AHLES, & C. R. BELL. Manual of the vascular flora of the Carolinas. lxi + 1183 pp. Chapel Hill, North Carolina. 1968. [Pinaceae, 34–40; dot maps, illustrations.]
- REHDER, A. Manual of cultivated trees and shrubs hardy in North America, exclusive of the subtropical and warmer temperate regions. ed. 2. xxx + 996 pp. New York. 1940. [Pinaceae, 8–47.]
- . Bibliography of cultivated trees and shrubs hardy in the cooler temperate regions of the Northern Hemisphere. xl + 825 pp. Jamaica Plain, Massachusetts. 1949. [Detailed nomenclatural treatment; Pinaceae, 6–41.]
- ROTH, I. Histogenese und morphologische Deutung der Doppelnadeln von *Sciadopitys*. *Flora* **152**: 1–23. 1962. [“Double-needles” of *Sciadopitys* are not comparable to a fused pair of needles.]
- SANTAMOUR, F. S., JR. New chromosome counts in *Pinus* and *Picea*. *Silvae Genet.* **9**: 87, 88. 1960. [*Picea* (15 species) and *Pinus* (12 species), all $n = 12$.]
- . Anthocyanins of conelets in the Pinaceae. *Forest Sci.* **12**: 429–431. 1966.
- . Anthocyanins in spruce foliage. *Bull. Morris Arb.* **18**: 41, 42. 1967.
- SARGENT, C. S. *Silva of North America*. Vol. 11. *Pinus*. vii + 163 pp. *pls.* 538–592. Boston and New York. 1897 [1898]. Vol. 12. Abietineae after *Pinus*. vii + 144 pp. *pls.* 593–620. Boston and New York. 1898 [1899]. [Excellent illustrations of *Abies*, *Picea*, *Pinus*, *Tsuga*, *Pseudotsuga*, and *Larix*; much useful information about utilization of the genera.]
- SAX, K., & H. J. SAX. Chromosome number and morphology in the conifers. *Jour. Arnold Arb.* **14**: 356–374. *pl.* 75. 1933. [Chromosome numbers and karyotypes for most genera of Pinaceae.]
- SCHOPF, J. M. The embryology of *Larix*. *Illinois Biol. Monogr.* **19**(4): 1–97. 1943.
- SEITZ, F. W. Chromosomenzahlenverhältnisse bei Holzpflanzen. *Silvae Genet.* **1**: 22–32. 1951. [Review of chromosome counts, mainly from the literature; includes a few otherwise-unpublished counts by the author for *Abies* and *Picea* (all $n = 12$).]
- SIMAK, M. Karyotype analysis of *Larix Griffithiana* Carr. *Hereditas* **56**: 137–141. 1966. [See also *Stud. Forest. Suecica* **17**: 1–15. 1964.]
- SINGH, H. Embryology of gymnosperms. Band 10, Teil 2 *in* K. LINSBAUER, *Handbuch der Pflanzenanatomie*. ed. 2. xii + 302 pp. Berlin. 1978. [Male and female gametophytes; pollination mechanisms; embryogeny; extensive bibliography.]
- SIVAK, J. Les caractères de diagnose des graines de pollen à ballonets. *Pollen Spores* **17**: 349–421. 1975. [Extensive scanning electron microscopic comparisons of pinaceous pollen.]

- SMALL, J. K. Manual of the southeastern flora. xxii + 1554 pp. New York. 1933. [Pinaceae, 3–8.]
- SNAJBERK, K., & E. ZAVARIN. Mono- and sesqui-terpenoid differentiation of *Pseudotsuga* of the United States and Canada. *Biochem. Syst. Ecol.* **4**: 159–163. 1976. [Cortical oleoresin composition of *P. macrocarpa* and *P. Menziesii*.]
- SPORNE, K. R. The morphology of gymnosperms. ed. 2. 216 pp. London. 1974.
- SQUILLACE, A. E. Analysis of monoterpenes of conifers by gas-liquid chromatography. Pp. 126–157 in J. P. MIKSCH, ed., *Modern methods in forest genetics*. Berlin. 1976. [Extensive bibliography cross referenced by taxa.]
- SRIVASTAVA, L. M. Secondary phloem in the Pinaceae. *Univ. Calif. Publ. Bot.* **36**: 1–142. 1963. [35 plates of micrographs; compares development and anatomy of species in six genera; emphasis on western North America.]
- STAIRS, G. R. Monoterpene composition in *Larix*. *Silvae Genet.* **17**: 182–184. 1967.
- STERLING, C. Structure of the male gametophyte in gymnosperms. *Biol. Rev.* **38**: 167–203. 1963.
- TAYLOR, R. J. The relationship and origin of *Tsuga heterophylla* and *Tsuga Mertensiana* based on phytochemical and morphological interpretations. *Am. Jour. Bot.* **59**: 149–157. 1972. [Leaf phenolics of *Tsuga* and *Picea* species.]
- TEOH, S. B., & H. REES. Nuclear DNA amounts in populations of *Picea* and *Pinus* species. *Heredity* **36**: 123–137. 1976.
- TIEGHAM, P. VAN. Anatomie comparée de la fleur femelle et du fruit des Cycadées, des Conifères et des Gnetacées. *Ann. Sci. Nat. Bot.* V. **10**: 269–304. 1869. [Important early contribution on ovulate-cone anatomy of the Pinaceae, with emphasis on vasculature.]
- . Structure et affinités des *Abies* et des genres les plus voisins. *Bull. Soc. Bot. France* **38**: 406–415. 1891. [Defines subfamilial groups based on resin-canal position in the primary root; provides synopsis of *Abies* species based on leaf anatomy.]
- UENO, J. Some palynological observations of Pinaceae. *Jour. Inst. Polytech. Osaka Univ. ser. D.* **9**: 163–177. pls. 1–3. 1958. [All genera except *Cathaya* compared.]
- VIERHAPPER, F. Entwurf eines neuen Systemes der Coniferen. *Abh. Zool.-Bot. Ges. Wien* **5**(4): 1–56. 1910. [Classification of Pinaceae emphasizing shoot dimorphism.]
- VON RUDLOFF, E. Volatile leaf oil analysis in chemosystematic studies of North American conifers. *Biochem. Syst. Ecol.* **2**: 131–167. 1975a. [Important review paper; includes comparisons of species of *Abies*, *Tsuga*, *Pseudotsuga*, *Picea*, and *Pinus*.]
- WANG, F.-H. Life history of *Keteleeria*. I. Strobili, development of the gametophytes and fertilization in *Keteleeria Evelyniana*. *Am. Jour. Bot.* **35**: 21–27. 1948.
- & T.-S. CHEN. The embryogeny of *Cathaya* (Pinaceae). (In Chinese; English summary.) *Acta Bot. Sinica* **16**: 64–69. pls. 1–3. 1974. [Similar to that of *Pinus*.]
- WATTS, W. A. Vegetational history of the eastern United States 25,000 to 10,000 years ago. Pp. 294–310 in H. E. WRIGHT, ed., *Late-Quaternary environments of the United States*. Vol. 1. The Late Pleistocene (S. C. PORTER, ed.). Minneapolis. 1983. [Discusses current vegetation and Quaternary distribution of *Abies*, *Larix*, *Picea*, *Pinus*, and *Tsuga*.]
- WILLAMAN, J. J., & B. G. SCHUBERT. Alkaloid-bearing plants and their contained alkaloids. U. S. Dep. Agr. Agr. Res. Serv. Tech. Bull. **1234**. 287 pp. 1961. [See also WILLAMAN, J. J., & H. L. LI, *Lloydia* **33**(Suppl.). 286 pp. 1970.]
- WODEHOUSE, R. P. Pollen grains. xv + 574 pp. New York. 1935. [Pinaceae, 256–268, fig. 78, pls. 2, 3.]
- ZHOU, B.-N., B.-P. YING, G.-Q. SONG, Z.-X. CHEN, J. HAN, & Y.-F. YAN. Pseudolaric acids from *Pseudolarix Kaempferi*. *Pl. Med.* **47**: 35–38. 1983. [Structures of anti-fungal agents from bark of *P. amabilis* (*P. Kaempferi*) characterized.]

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