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REEXAMINATION OF WOOD ANATOMICAL FEATURES IN PINUS KREMPFII (PINACEAE)

by

Stefanie M. Ickert-Bond

Arizona State University, Department of Plant Biology, Box 871601, Tempe, AZ 85287-1601, U.S.A.

SUMMARY

Wood anatomy of *Pinus krempfii* Lecomte, a pine endemic to Vietnam, is described using twig and mature wood collections made in 1995. Characteristics of *Pinus krempfii* wood include axial and radial resin canals with 6–8 thin-walled epithelial cells; latewood tracheids with tangential wall pitting; lignified ray parenchyma with 2–5 pinoid pits per cross-field; and few to no ray tracheids. Longitudinal tracheid diameter and ray height are smaller in the twig wood than in the mature wood. These features, especially the near absence of ray tracheids, suggest a relationship with *Pinus* subgenus *Strobus* section *Parrya* subsection *Balfourianae*, which includes *P. aristata* Engelm. and *P. longaeva* D. Bailey.

Key words: *Pinus krempfii*, *Pinus* section *Parrya*, wood anatomy, ray tracheids, conifers.

INTRODUCTION

Pinus krempfii Lecomte is an unusual pine endemic to the Central Highlands of Vietnam. It occurs in dense, mixed montane evergreen forests mainly on ridgetops at 1800 m elevation in humic soils up to 40 cm deep, these often wet and assuring seedling success. The floristic composition of the forest is very diverse (Kha 1967) with large-trunked conifers, such as *Dacrycarpus imbricatus* (Blume) Laubenfels, *D. pilgeri* Foxw., *Cephalotaxus hainanensis* H.L. Li, occasionally *Pinus kesiya* Royle ex Gordon and *Keteleeria evelyiana* Mast. and several species of evergreen Fagaceae (Ickert-Bond 1997b).

Trees of *P. krempfii* are evergreen and 15–30 m in height, extending high above the general forest canopy (Fig. 1). The trunk is cylindrical, straight, and unbranched for the first 15–20 m and up to 5.5 m diameter at breast height (dbh) (Fig. 2). The crown is sparse and pyramidal in young trees, becoming umbrella-shaped when older. The branching pattern in the crown is almost dichotomizing and unusual for pines. The bark is persistent, reddish brown, very thin, and slightly scaly with shallow longitudinal fissures. Acicular leaves occur in pairs and are arranged in a scissor-like fashion (Rollet 1955; Ickert-Bond 2000). They are oblong-lanceolate, flattened, 4.5–7 cm long and 3.5–4.1 (up to 5) mm wide, with short, slightly twisted petioles (Fig. 3). Key vegetative features that distinguish this pine from other members of the genus

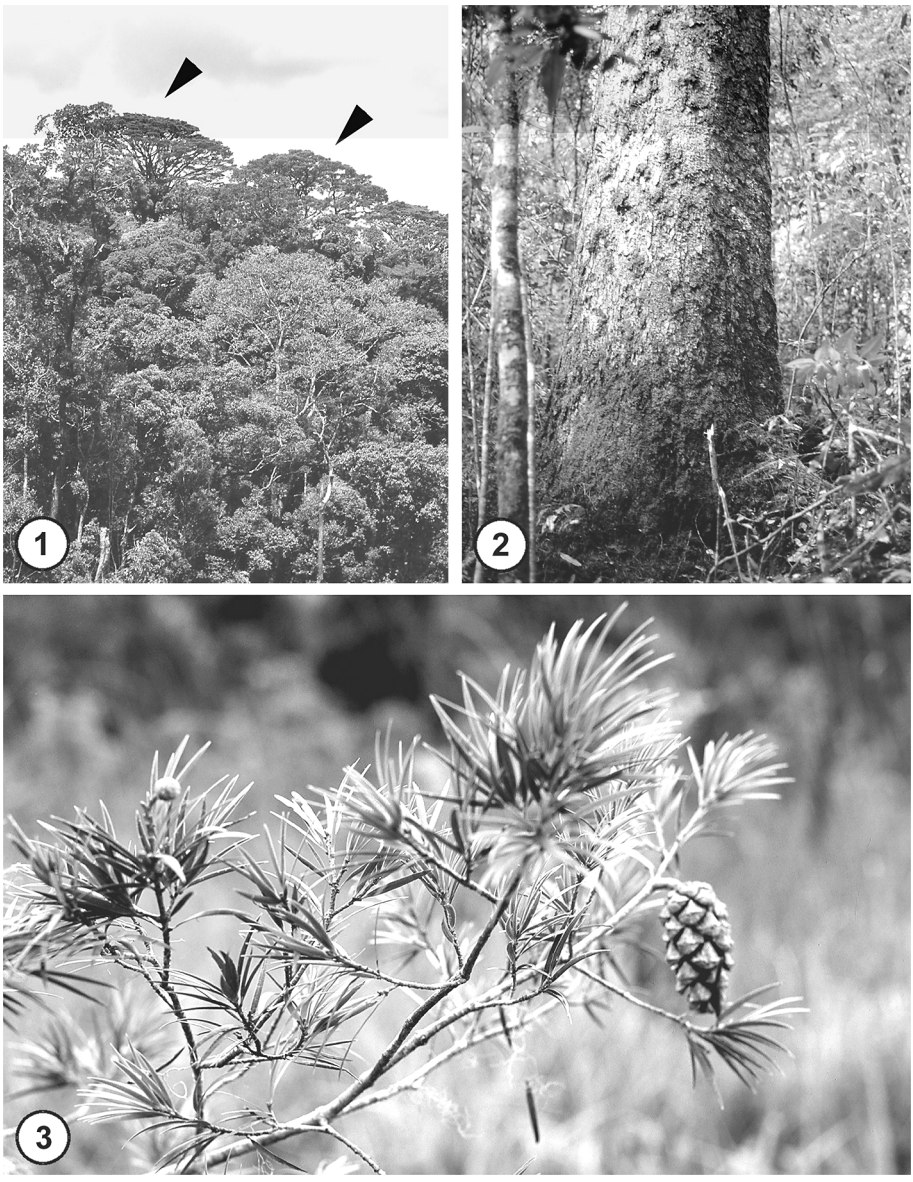

Fig. 1–3. Habit of *Pinus krempfii*. – 1: Stands with large umbrella-shaped crowns ranging high above the general forest canopy (arrows). – 2: Mature trunk. – 3: Branching pattern with broad needles and ovulate cone (at right). Photographs by Richard Bond.

Pinus include the characteristic falcate flat needles, crescent-shaped cross section of the needle, early-deciduous fascicle sheaths, dimorphic mesophyll and the occurrence of dimorphic leaves (Ickert-Bond & Pigg 1996; Ickert-Bond 1997a, 1997b, 2000).

Taxonomically, *Pinus krempfii* has been the subject of much debate. It has been placed in *Pinus* subgenus *Strobus* as monotypic in subsection *Krempfianae* Little & Critchfield (Little & Critchfield 1969; Klaus 1980; Farjon 1984; Price et al. 1998), or in subsection *Balfourianae* Engelm. (Van der Burgh 1973), or in subgenus *Ducampopinus* A. Chev. (Ferré 1948). It has even been elevated to a monotypic generic rank (Chevalier 1944; Hudson 1983; Landry 1994) as *Ducampopinus krempfii* (Lecomte) A. Chev.

While most morphological features are undisputed, there is conflicting information about characters of the wood anatomy (Buchholz 1951; Budkevich 1958; Greguss 1962; Hudson 1983). Part of the variation reported may be related to differences in age of material studied, as some authors have looked at mature stem wood (Budkevich 1958; Hudson 1983) and others at small twigs (Buchholz 1951). Among the differences observed are the presence (Greguss 1962) or absence of ray tracheids (Buchholz 1951; Budkevich 1958; Hudson 1983), the unusual presence (Budkevich 1958) or, more commonly, the absence of axial parenchyma (Greguss 1962), and according to Budkevich (1958) and Hudson (1983) the occurrence of a taxodioid cross-field pit type unique within *Pinus*. These characters are important in understanding pine evolution and assigning pines in a classification system. In order to clarify its structure and variation, this paper describes mature and twig wood anatomy of *Pinus krempfii* based on new collections from Vietnam. Results suggest that *P. krempfii* shares ancestral features with pines in section *Parrya* and related genera of the Pinaceae.

MATERIALS AND METHODS

Collections were made of *Pinus krempfii* on May 5–12, 1995, from Lam Dong Province near Cong Troi, Vietnam. Wood anatomy is described based on both wood from a mature trunk and 16 twigs. A large block (20 cm high and 7 cm wide) of mature wood was obtained from Dr. Tiep of Dalat University, Vietnam, from a tree measuring 5 m dbh. He collected it from a population near BiDoup, Langbian Mountains, Vietnam. The block consists mainly of fine-grained heartwood. Twig wood of 2 cm in diameter was collected from three different populations near Cong Troi, Langbian Mountains (Table 1). The trees varied from 1–3 m dbh. Three twigs per population sample were examined for a total of nine measured wood samples. Additional slides of *Pinus krempfii* twig wood were available in the Bailey-Wetmore Wood Collection of Harvard University (Table 1). Wood material was rehydrated in water and sectioned on a sliding microtome at 20 μm and subsequently stained with safranin (following Johansen 1940); staining for lignin was accomplished with phloroglucinol (Ruzin 1999). Voucher specimens and wood blocks are deposited in the wood collection housed in the Fossil Plant Collections, Arizona State University Herbarium, Tempe, Arizona (ASU) (Table 1). Measurements of tracheid diameter and ray height were taken from tangential sections, while ray parenchyma diameter was obtained from radial sections. For each of these characters, means, maximum and minimum values were determined. These values were based on 25 measurements per slide.

Table 1. *Pinus krempfii* material examined.

Voucher	Slide numbers	Type of material	Locality in Vietnam	Herbarium
Ickert-Bond 268	268-96-1, 268-96-2, 268-96-3	Twig wood	Dalat Flower Garden	ASU
Ickert-Bond 278	278-96-1, 278-96-2, 278-96-3, 278-96-4, 278-96-5, 278-96-6	Twig wood	Công` Trôi, Dalat	ASU
Ickert-Bond 300	300-96-1, 300-96-2, 300-96-3	Twig wood	Công` Trôi, Dalat	ASU
Truong Van Len s. n.	A, B	Twig wood	Boungia / Dalat	GH
Tiep s. n.	T-96-1, T-96-2, T-96-3, T-96-4, T-96-5	Mature wood	BiDoup, Lang Bian	ASU

RESULTS

Macroscopic features

Heartwood has a reddish brown color. The transition from earlywood to latewood is gradual (Fig. 4). Growth increments are narrow and up to 29 have been counted in the large mature block over 1 cm, whereas twig wood only had 18 growth rings over a 1 cm radius.

Microscopic features

Axial resin canals are common in the secondary xylem, particularly in the earlywood, and are surrounded by 6–8 thin-walled epithelial cells (Fig. 4 & 5). Maximum axial resin canal diameter in the large block is 90 μm, and 60 μm in the twig wood. Resin canals of the twig wood are surrounded by axial parenchyma (Fig. 5). Both mature and twig wood have tracheids with radial walls that show uniseriate and biseriate circular-bordered pits (Fig. 7 & 8). Tangential walls of latewood tracheids show numerous circular-bordered pits, typical of soft pines (Fig. 8) (Hudson 1960; Van der Burgh 1973). Tracheids are 32 μm (22–45) in tangential diameter in the twig wood, 51 μm (39–77) in the mature wood. Uniseriate rays are 2–16 cells and 142–224 μm high (twig wood 77–220 μm, mature wood 154–418 μm). Fusiform rays are 6–18 cells and 173–407 μm high (twig wood 110–264 μm, mature wood 198–638 μm). Fusiform rays are bi- or triseriate throughout the central portion with a single transverse resin canal, and taper above and below to uniseriate margins (Fig. 6). Uni-

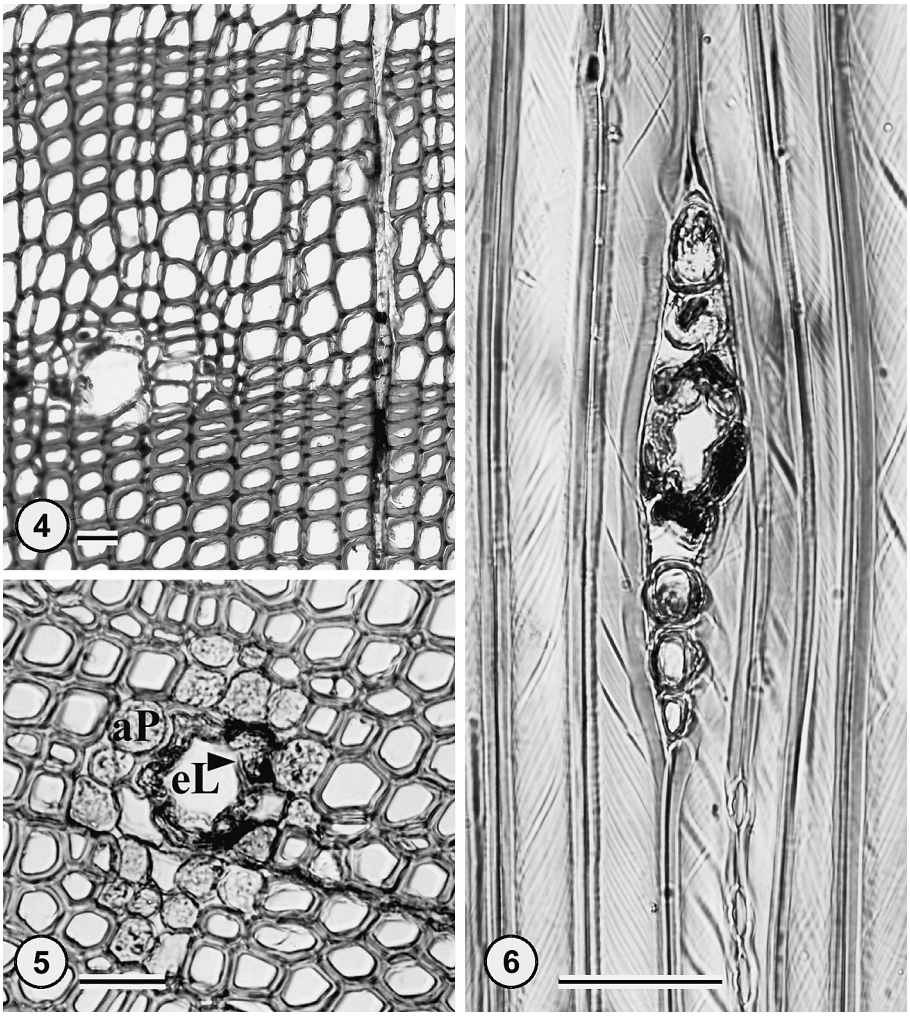

Fig. 4–6. *Pinus krempfii* wood. – 4 & 5. Cross sections. – 4: Growth rings with gradual transition from earlywood (middle) to latewood (top); note resin canal located in the earlywood. – 5: Resin canal with 7–12 epithelial cells with thin lining (eL) and associated axial parenchyma (aP). – 6: Tangential section showing fusiform ray. — Scale bars = 50 μm.

seriate rays are usually homocellular, composed only of parenchyma cells; ray tracheids are nearly always absent (Fig. 7). In more than 400 rays of juvenile and mature wood studied, only two ray tracheids were observed (Fig. 11). Ray parenchyma cells have 1 to 5 pinoid (*sensu* Greguss 1955) cross-field pits (Fig. 9 & 10). The cell walls are lignified as they stain deeply red with phloroglucinol.

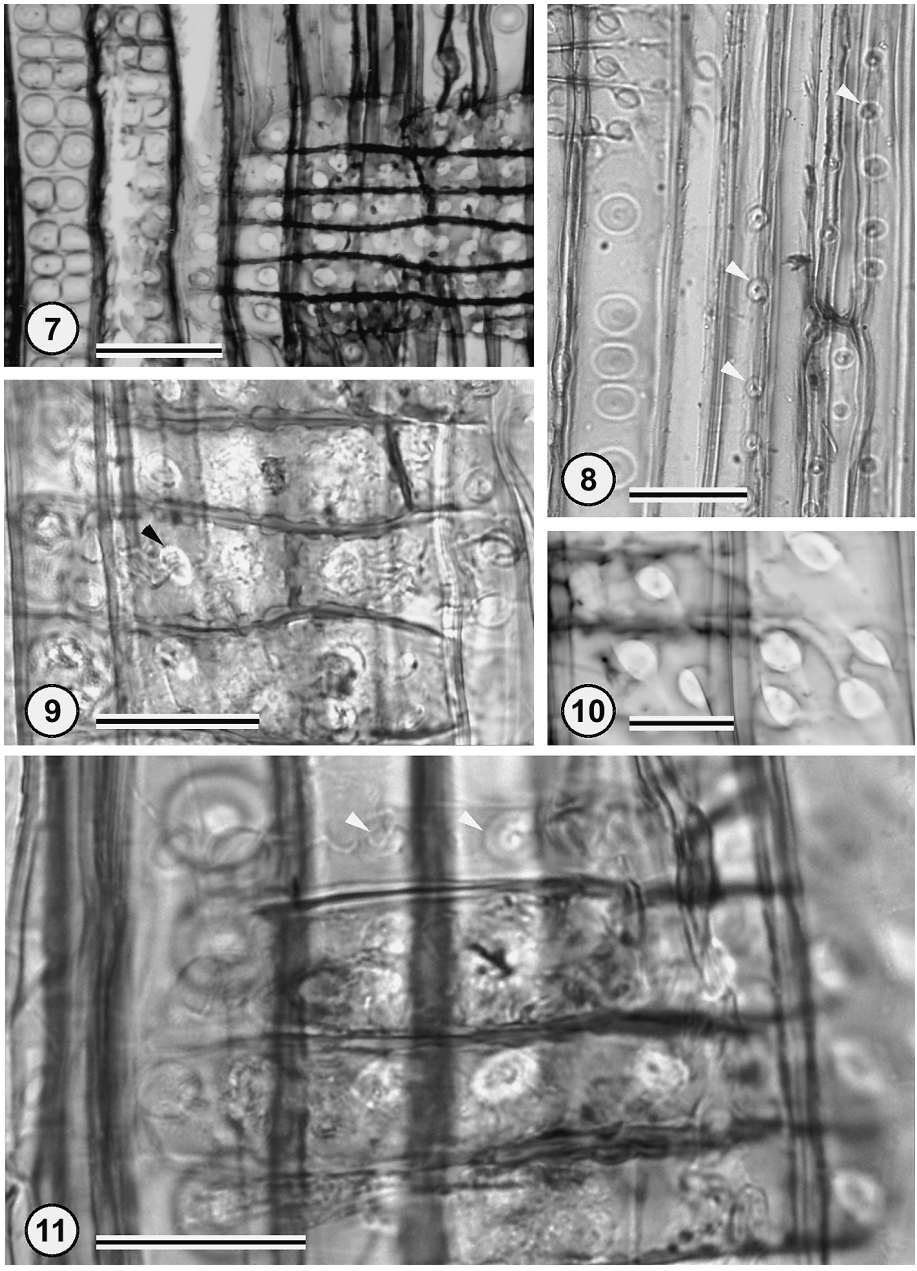

Fig. 7–11. Radial sections of *Pinus krempfii* wood. – 7: Biseriate intertracheary pits (at left), and a ray six cells high, composed of only ray parenchyma cells. – 8: Circular bordered pits on radial walls (at left) and also on tangential wall (arrows) of latewood. – 9: Ray parenchyma cells showing nature of wall and cross-field pits (at arrow). – 10: Cross-fields with 2–4 pinoid pits. – 11: Uniseriate intertracheary pits (at left) and ray composed of ray parenchyma and ray tracheid on top (arrows). — Scale bars = 100 μm for 7; 50 μm for 8 & 9; 30 μm for 10 & 11.

DISCUSSION

Main characteristics of the typical wood of *Pinus* include: 1) Epithelial cells of the resin canals thin-walled (e.g., Esau 1965), 2) Absence of axial parenchyma (Jane 1956), 3) Cross-field pits pinoid, piceoid or fenestriform (Greguss 1955; Hudson 1960), 4) Typical presence of ray tracheids (Panshin & De Zeeuw 1980). Other genera in the Pinaceae differ from this combination of characters. For example, ray tracheids are absent from *Abies*, *Keteleeria* and *Pseudolarix* (Esau 1965) but are present in *Cathaya* (Hu & Wang 1984), *Larix*, *Picea*, *Cedrus*, *Tsuga* and *Pseudotsuga* (Panshin & De Zeeuw 1980). The absence of resin canals further separates those genera with ray tracheids. Normal resin canals are absent from *Cedrus* and *Tsuga* wood, while *Cathaya*, *Larix*, *Picea* and *Pseudotsuga* have normal resin canals, but are distinguished from *Pinus* by having thick-walled rather than thin-walled epithelial cells.

Taxonomic value of anatomical wood characters

Within the genus *Pinus*, a binary taxonomic division is generally accepted and can be substantiated by characters of the wood anatomy. The dentations of the walls of the ray tracheids (Bailey 1910; Phillips 1941; Hudson 1960) can be used to distinguish between the two subgenera *Strobus* and *Pinus*. Ray tracheids have smooth walls to occasionally slightly dentate walls in subgenus *Strobus* and dentate to heavily dentate walls in subgenus *Pinus*. In a survey of the wood anatomy of numerous species Hudson (1960) described a scale of 10 different dentation types that are correlated with subgenera. Types 1– 4 correlate with smooth to slightly dentate walls of the ray tracheids and are restricted to subgenus *Strobus*, while Types 5 –10, with increasingly pronounced dentations, define subgenus *Pinus*. In the present study the few ray tracheids that were observed showed smooth walls of Type 1 similar to those in *P. cembra* (Hudson 1960) or *P. aristata* (Süss 1989) of subgenus *Strobus* (Table 2).

Other characters that are frequently used in assigning species to sections within *Pinus* include cross-field pitting (Greguss 1962; Van der Burgh 1973), circular bordered pits on tangential walls of latewood (Hudson 1960; Van der Burgh 1973), and lignification of ray parenchyma cells (Van der Burgh 1973).

Both Hudson (1960) and Van der Burgh (1973) showed in their surveys of wood anatomy of numerous pine species that the frequency of circular bordered pits on tangential walls of the latewood corresponds to the binary division of the genus *Pinus*. In subgenus *Strobus*, namely section *Strobi* and section *Parrya*, numerous circular bordered pits occur in the latewood tangential walls, while in subgenus *Pinus* relatively few pits occur in the latewood tangential walls. An exception is found in subsection *Lumholtzii* of subgenus *Pinus,* in which numerous circular bordered pits occur in the latewood. In the present study, numerous circular bordered pits were found on the tangential walls of the latewood of *P. krempfii*, affiliating the wood with subgenus *Strobus*. Van der Burgh (1973) assumes the directionality for this character to be from numerous to few circular bordered pits as realized in all sections of subgenus *Pinus*.

Van der Burgh (1973), in his survey of the wood anatomy of 67 pine species, distinguished between two general types of cross-field pitting: (‘Type a’) those with 1– 3

Table 2. Comparison of selected character states of *Pinus* wood anatomy between subgenus *Pinus*, subgenus *Strobus* (subsections *Strobi* and *Parrya*), and *Pinus krempfii*.

Characters	Subgenus *Pinus* Section *Pinus* All subsections	Subgenus *Strobus* Section *Strobi* Subsection *Strobi*	Subgenus *Strobus* Section *Parrya* Subsection *Balfourianae*	*Pinus krempfii*
Walls of the ray tracheids	Heavily dentate (H. sc. 7–11)	Smooth to slightly dentate (H. sc. 1–4)	Smooth to slightly dentate (H. sc. 1–6)	Smooth, if present (H. sc. 2)
Cross-field pitting / cross-field	1–3 large fenestriform pits	1–3 large fenestriform pits	3–5 small pinoid pits	1–4 small pinoid pits
Circular bordered pits on tangential walls of latewood	None or few	Numerous	Numerous	Numerous
Ray parenchyma cells	Non-lignified	Lignified	Lignified	Lignified
Presence of ray tracheids	Frequent	Frequent	Infrequent	Very rare to absent

H. sc. = Hudson scale.

large fenestriform pits and ('Type b') those with numerous small pinoid pits per cross-field. 'Type a' occurs in both section *Strobi* (subgenus *Strobus*) and section *Pinus* (subgenus *Pinus*), while all other sections are characterized by numerous small pinoid pits per cross-field of 'Type b'. Specimens of *P. krempfii* showed 2–5 pinoid pits per cross-field pit; in subgenus *Strobus* this character state is confined to section *Parrya*. Süss (1989) showed 3–5 small "pinoid or piceoid" pits for 25-year-old branch wood of *P. aristata,* which is also of section *Parrya*. Van der Burgh (1973) hypothesized that the ancestral state is that of section *Parrya* because this character state is also found in all branch wood of other sections of *Pinus*; and other genera of the Pinaceae show numerous small well developed "pinoid or piceoid" cross-field pits as well.

The lignification of ray parenchyma cells has also been used by Bailey (1910) and later by Van der Burgh (1973) to distinguish among sections of the genus *Pinus*. Two categories are recognized, one with lignified ray parenchyma cell walls as in sections *Strobus*, *Parrya*, *Pinea* and *Sula*, the other with either unlignified and heavily lignified walls occurs in all other sections. Ray parenchyma cells in *Pinus krempfii* are lignified as in sections *Strobus* and *Parrya*.

Position of P. krempfii within the genus Pinus

In summary, the wood of *P. krempfii* has characteristics typical of the genus *Pinus*, including thin-walled epithelial cells, axial parenchyma restricted to near the resin canals, and both vertical and horizontal resin canals. Affinity with the soft pines (*Pinus* subgenus *Strobus* and, in particular, section *Parrya*) is indicated by the occurrence of

numerous circular-bordered pits on tangential walls of latewood tracheids (Hudson 1960; Van der Burgh 1973; Table 2), lignified ray parenchyma cells, and pinoid cross-field pitting. These features occur within subgenus *Strobus* section *Parrya*, in such species as *Pinus gerardiana* Wall., *P. bungeana* Zucc. (Van der Burgh 1973), and *P. longaeva* (Baas et al. 1986; Süss 1989) and in some species of subgenus *Pinus* section *Pinus* subsection *Sylvestres*. Pinoid pits also occur in wood of section *Pinaster* subsection *Australes* of subgenus *Pinus*, e.g., *Pinus pungens* Lamb. ex Michx. and *P. rigida* Mill. (Hudson 1960).

My findings of the near absence of ray tracheids in wood of *Pinus krempfii* concordant with results from several authors (Buchholz 1951; Budkevich 1958; Hudson 1983) are in contrast to Greguss' (1962) reports that ray tracheids are commonly present. This plesiomorphic character state is shared with pines of subgenus *Strobus* section *Parrya* subsection *Balfourianae*, e.g., *P. aristata* and *P. longaeva* (Van der Burgh 1973; Baas et al. 1986; Süss 1989) and by the Abietoideae. Van der Burgh (1973) documented that all species of subgenus *Strobus* section *Strobi* and section *Parrya* lack ray tracheids in the first three growth rings. Slow-growing branches can lack them for up to eight years. Baas et al. (1986) showed that *P. longaeva* of section *Parrya* lacks ray tracheids even in some mature stem wood. Additionally, Süss (1989) remarked on the rare occurrence of ray tracheids in a 25-year-old branch sample of *P. aristata* of section *Parrya*. In contrast, all species of subgenus *Pinus* show well-developed ray tracheids in the latewood of the first growth ring and in the following growth rings in both earlywood and latewood (Van der Burgh 1973). Based on wood anatomy Mirov (1967) also concluded that *P. krempfii, P. aristata* and *P. longaeva* and Cretaceous pine fossils are more basal within *Pinus*, linking them to other genera within the Pinaceae.

Other fossil woods with *Picea*- and *Pinus*-affinity have been reported to lack ray tracheids (Kräusel 1919, 1949; Watari 1941). Outgroup comparison of *Pinus* with the genera *Abies*, *Keteleeria* and *Pseudolarix* also establishes the plesiomorphic condition of this character state (Hart 1987; Wang & Szmidt 1993; Price et al. 1998; Liston et al. 1999; Wang et al. 1999). In addition to wood anatomical features, a combination of characters, including ovulate cone morphology, biogeography, paleobotany and molecular systematics support a basal position for *Pinus* section *Parrya* (Bailey 1910; Van der Burgh 1973; Klaus 1980; Millar 1998; Wang et al. 1999, 2000). The present study of *Pinus krempfii* wood thus clarifies the character states as conforming with subgenus *Strobus* section *Parrya*, a section believed to be basal within the genus as supported by recent molecular data (Wang et al. 1999, 2000).

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REFERENCES

Baas, P., R. Schmid & B.J. van Heuven. 1986. Wood anatomy of Pinus longaeva (bristlecone pine) and the sustained length-on-age increase of its tracheids. IAWA Bull. n.s. 7: 221–228.

Bailey, I.W. 1910. Anatomical characters in the evolution of Pinus. Am. Midl. Nat. 44: 284–293.

Buchholz, J.T. 1951. A flat-leaved pine from Annam, Indo-China. Amer. J. Bot. 38: 245–252.

Budkevich, E.V. 1958. Anatomical structure of the wood of Ducampopinus krempfii (Lecomte) A. Chevalier. Bot. Zhurn. 43: 1156–1160.

Chevalier, A. 1944. Notes sur les conifères de l'Indochine. Rev. Int. Bot. Appl. Agric. Trop. 24: 7–34.

Esau, K. 1965. Plant anatomy. Wiley, New York.

Farjon, A. 1984. Pines: drawings and descriptions of the genus. Brill, Leiden.

Ferré, Y. 1948. Quelques particularités anatomiques d'un pin indochinois: Pinus krempfii. Trav. Lab. For. Toulouse 83: 1–6.

Greguss, P. 1955. Xylotomische Bestimmung der heute lebenden Gymnospermen. Akad. Kiado, Budapest.

Greguss, P. 1962. Le genre Ducampopinus est-il valable en vertu de sa xylotomie? Trav. Lab. For. Toulouse 6: 1–6.

Hart, J.A. 1987. A cladistic analysis of conifers: preliminary results. J. Arnold Arbor. 68: 269–307.

Hudson, R.H. 1960. The anatomy of the genus Pinus in relation to its classification. J. Inst. Wood Sci. 6: 26–46.

Hudson, R.H. 1983. The evidence from wood anatomy for the taxonomic status of Ducampopinus. J. Inst. Wood Sci. 9: 224–227.

Hu, Y.S. & F.H. Wang. 1984. Anatomical studies of Cathaya (Pinaceae). Amer. J. Bot. 71: 727–735.

Ickert-Bond, S.M. 1997a. Pinus krempfii Lec. – a Vietnamese conifer with problematic affinities. Amer. J. Bot. 84: 203 (Abstract).

Ickert-Bond, S.M. 1997b. Biosystematics of Pinus krempfii Lecomte. Unpublished MSc. thesis, Arizona State University, Tempe, Arizona.

Ickert-Bond, S.M. 2000. Cuticle micromorphology of Pinus krempfii Lecomte (Pinaceae) and additional species from South-East Asia. Intern. J. Plant Sci. 161: 301–317.

Ickert-Bond, S.M. & K.B. Pigg. 1996. Reinvestigation of Pinus krempfii Lecomte: an endemic pine from Viet Nam. Fifth Quadrennial Conference of the International Organisation of Palaeobotany, Santa Barbara, California: 48 (Abstract).

Jane, F.W. 1956. The structure of wood. MacMillan Co., New York.

Johansen, D.A. 1940. Plant microtechnique. McGraw-Hill Inc., New York

Kha, N. 1967. The forests of Pinus khasya and Pinus merkusii of central Vietnam. Commonwealth Forestry Institute, Oxford.

Klaus, W. 1980. Neue Beobachtungen zur Morphologie des Zapfens von Pinus und ihre Bedeutung für die Systematik, Fossilbestimmung, Arealgestaltung und Evolution der Gattung. Pl. Syst. Evol. 134: 137–171.

Kräusel, R. 1919. Die fossilen Koniferenhölzer (unter Ausschluß von Araucarioxylon Kraus). Versuch einer monographischen Darstellung. Paleontographica 62: 185–284.

Kräusel, R. 1949. Die fossilen Koniferenhölzer (unter Ausschluß von Araucarioxylon Kraus). Paleontographica, B, 89: 83–203.

Landry, P. 1994. A revised synopsis of the pines. 5: The subgenera of Pinus, and their morphology and behavior. Phytologia 76: 73–79.

Liston, A., W.A. Robinson, D. Pinero & E.R. Alvarez-Buylla. 1999. Phylogenetics of pines (Pinaceae) based on nuclear ribosomal DNA internal transcribed spacer region sequences. Mol. Phylog. Evol. 11: 95–109.

Little, E.L. & W.B. Critchfield. 1969. Subdivisions of the genus Pinus (pines). USDA miscellaneous publication 1144. USDA Forest Service, Washington, D.C.

Millar, C.I. 1998. Early evolution of pines. In: D.M. Richardson (ed.), Ecology and biogeography of Pinus: 69–91. Cambridge University Press, Cambridge.

Mirov, N.T. 1967. The genus Pinus. McMillan Publ., New York.

Panshin, A.J. & C. de Zeeuw. 1980. Textbook of wood technology. McGraw-Hill Book Company, New York.

Phillips, E.W.J. 1941. The identification of coniferous woods by their microscopic structure. J. Linn. Soc. London, Bot. 52: 259–320.

Price R.A., A. Liston & S.H. Strauss. 1998. Phylogeny and systematics of Pinus. In: D.M. Richardson (ed.), Ecology and biogeography of Pinus: 49–68. Cambridge University Press, Cambridge.

Rollet, B. 1955. Pinus krempfii H. Lecomte. Vietnam Cent. Nat. Rech. Sci. Techn. Bull. 3-4: 26–29.

Ruzin, S.E. 1999. Plant microtechnique and microscopy. Oxford University Press, New York.

Süss, H. 1989. Beitrag zur Holzanatomie der Pinaceae am Beispiel des Astholzes der Borstenkiefer, Pinus aristata Engelm. Feddes Repertorium 100: 617–624.

Van der Burgh, J. 1973. Hölzer der Niederrheinischen Braunkohlenformation. 2. Hölzer der Braunkohlengruben 'Maria Theresia' zu Herzogenrath, 'Zukunft West' zu Eschweiler und 'Victor'(Zülpich Mitte) zu Zülpich. Nebst einer systematisch-anatomischen Bearbeitung der Gattung Pinus L. Rev. Palaeobot. Palynol. 15: 73–275.

Wang, X.-R. & A.E. Szmidt. 1993. Chloroplast DNA-based phylogeny of Asian Pinus species (Pinaceae). Plant Syst. Evol. 188: 197–211.

Wang, X.-R., A.E. Szmidt & H.N. Nguyen. 2000. The phylogenetic position of the endemic flat-needle pine Pinus krempfii (Pinaceae) from Vietnam, based on PCR-RFLP analysis of the chloroplast DNA. Plant Syst. Evol. 220: 21–26.

Wang, X.-R., Y. Tsumura, H. Yoshimaru, K. Nagasaka & A.E. Szmidt. 1999. Phylogenetic relationships of Eurasian pines (Pinus, Pinaceae) based on chloroplast rbcL, matK, RPL20-rps18 spacer, and trnV intron sequences. Amer. J. Bot. 86: 1742–1753.

Watari, S. 1941. Studies on the fossil woods from the Tertiary of Japan. II. Fossil woods from the river Nesori, Namiuti Village and the river Hiranuka, Kozuya Village, Ninohe district, Iwate prefecture. Jap. J. Bot. 11: 417–438.