Article

Comparative Wood Anatomy in Pinaceae with Reference to Its Systematic Position

Luis García Esteban , Paloma de Palacios , Alberto García-Iruela , Francisco García-Fernández ,
Lydia García-Esteban and David González de Vega

Departamento de Sistemas y Recursos Naturales, Escuela Técnica Superior de Ingeniería de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid, Ciudad Universitaria, s/n, 28040 Madrid, Spain; paloma.depalcios@upm.es (P.d.P.); agiruela17@gmail.com (A.G.-I.); francisco.garcia@upm.es (F.G.-F.); lydia.garcia@upm.es (L.G.-E.); dm.gonzalezdevega@alumnos.upm.es (D.G.d.V.)

* Correspondence: luis.garcia@upm.es; Tel.: +34-91-067-1751

Abstract: The wood anatomy of 132 species of the genera *Abies*, *Cathaya*, *Cedrus*, *Keteleeria*, *Larix*, *Nothotsuga*, *Picea*, *Pinus*, *Pseudolarix*, *Pseudotsuga* and *Tsuga* was studied to determine the elements that characterise the xylem of each genus and discuss possible groupings by wood anatomy for comparison with clades established by molecular phylogeny. The presence of resin canals and ray tracheids supports the family Pinaceae, although the absence of ray tracheids in *Keteleeria* and their occasional presence in *Abies* and *Pseudolarix* weakens it. Based on wood structure, Pinaceae clearly supports division into two groups, coinciding with molecular phylogeny: Pinoideae (*Cathaya-Larix-Picea-Pinus-Pseudotsuga*) and Abietoideae (*Abies-Cedrus-Keteleeria-Nothotsuga-Pseudolarix-Tsuga*). Although differences between genera are slight in Pinoideae, the Abietoideae group presents problems such as the presence of only axial resin canals in *Keteleeria* and *Nothotsuga*, absence of ray tracheids in *Keteleeria* and presence of traumatic radial resin canals in *Cedrus*. However, other features such as pitted horizontal walls and nodular end walls of ray parenchyma cells, indentures, scarce marginal axial parenchyma and presence of crystals in ray parenchyma strengthen the Abietoideae group.

Keywords: Abietoideae; anatomy; Laricoideae; phylogeny; Piceoideae; Pinaceae; Pinoideae; wood

Citation: García Esteban, L.; de Palacios, P.; García-Iruela, A.; García-Fernández, F.; García-Esteban, L.; González de Vega, D. Comparative Wood Anatomy in Pinaceae with Reference to Its Systematic Position. *Forests* **2021**, *12*, 1706. <https://doi.org/10.3390/f12121706>

Academic Editor: Cristina Nabais

Received: 10 November 2021

Accepted: 3 December 2021

Published: 5 December 2021

Publisher's Note: MDPI stays neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Copyright: © 2021 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

1. Introduction

The family Pinaceae, consisting of 11 genera and 236 species, is the largest conifer family [1]. Traditional botanical classifications, such as that by Frankis [2] and Farjon [3] based on the morphological structure of vegetative and reproductive organs, include four subfamilies: Pinoideae (*Pinus* L.), Piceoideae (*Picea* A.Dietr.), Laricoideae (*Cathaya* Chun & Kuang, *Larix* Mill., *Pseudotsuga* Carrière) and Abietoideae (*Abies* Mill., *Cedrus* Mill., *Keteleeria* Carrière, *Nothotsuga* Hu ex C.N.Page, *Pseudolarix* Gordon, *Tsuga* Carrière).

Using the comparative anatomy of the canals in leaves, bark and wood, Wu and Hu [4] subsequently divided Pinaceae into three groups: *Cathaya*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga*, with normal resin canals; *Abies*, *Cedrus*, *Pseudolarix* and *Tsuga* without normal resin canals; and *Keteleeria*, with or without normal resin canals. Lin et al. [5], after confirming the constant presence of axial resin canals in mature wood of *Keteleeria* and the arrangement of traumatic resin canals in this genus, proposed a classification of Pinaceae in three groups, more in line with the wood anatomy of the family: *Cathaya*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga* with radial and axial resin canals; *Keteleeria* and *Nothotsuga* with only axial resin canals; and *Abies*, *Cedrus*, *Pseudolarix* and *Tsuga*, without resin canals.

The wood structure of Pinaceae has been widely studied both at the genus and species level (e.g., [5–15]). Comparative anatomy studies of the wood of this family have dealt with the presence/absence of resin canals (both normal and traumatic) and their arrangement, and elements of the rays (horizontal and end walls of ray parenchyma

cells, cross-field pitting, ray tracheids), axial parenchyma typology (presence/absence, arrangement, smooth/nodular transverse end wall), axial tracheids (presence/absence of helical thickenings, organic deposits in tracheids, warty layer) and the presence of crystals [4,5,8,16–20].

Molecular phylogenetic studies have demonstrated the existence of clades among these genera [21,22] which either agree or disagree with groupings established by wood anatomy.

New studies of this type can reveal new relations between clades constructed based on molecular phylogeny and common anatomical features at genus level.

The objective of this study was to compare the wood anatomy of the family Pinaceae and discuss possible groupings of genera based on their anatomical features using the samples studied and with reference to the numerous studies on conifer anatomy, in order to compare these groupings with the clades established by molecular phylogeny.

2. Materials and Methods

The material used in this study came from the wood collections of ten research centres. A study was made of the wood anatomy of 132 taxa: *Abies* (35 spp. + 1 subsp. + 3 var.), *Cathaya* (1 spp.), *Cedrus* (4 spp.), *Keteleeria* (3 spp.), *Larix* (7 spp.), *Nothotsuga* (1 spp.), *Picea* (13 spp. + 1 var.), *Pinus* (48 spp. + 1 subsp. + 2 var.), *Pseudolarix* (1 spp.), *Pseudotsuga* (2 spp. + 1 var.) and *Tsuga* (8 spp.). Appendix A lists the species with references to the collections from which the samples were obtained [23].

Microscopic slides were prepared in accordance with accepted methods of softening, microtome cutting to a thickness of 10–15 µm, staining and mounting. Samples were observed before and after staining with safranin and Sudan 4 to make the resin red [24]. The descriptions follow the recommendations of the IAWA Committee [25]. Samples were observed using light microscopy and scanning electron microscopy (SEM), model JEOL JSM-6380.

3. Results and Discussion

Summary of features by genus of Pinaceae based on the species studied is given in Table 1. Appendix B Table A1 shows the 132 taxa analysed with their particular features.

3.1. Resin Canals

The presence of resin canals in conifers is restricted to Pinaceae. *Cathaya*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga* have both axial and radial resin canals (Figure 1A,B). *Keteleeria*, according to Lin et al. [5], has only axial resin canals, which generally have associated subsidiary tissue (Figure 1C). Normal axial resin canals have been recorded in *Nothotsuga* by other authors [11], although none were observed in the sample studied, probably because the wood was juvenile and this type of wood has very few resin canals. *Abies*, *Cedrus*, *Pseudolarix* and *Tsuga* do not have normal resin canals (Figure 1D).

Although in *Pinus* only thin-walled epithelial cells were observed (Figure 1E), resin canals in *Cathaya*, *Keteleeria*, *Larix*, *Picea* and *Pseudotsuga* had thick-walled epithelial cells (Figure 1F). Jin-Xing et al. [11] also reported thick epithelial in *Nothotsuga*. Moreover, axial resin canals in *Pinus* were usually larger and more numerous than in the other taxa.

Traumatic axial resin canals were observed in all genera studied except in the samples of *Pseudolarix* and *Nothotsuga*, although they were cited by Wu and Hu [4] as a response to wounding. In all cases, the traumatic resin canals were arranged in tangential rows and their diameter was greater than in normal resin canals.

Table 1. Summary of features by genus based on the species studied. + Present, – Absent, (+) Occasional.

		Pinoideae	Piceoideae	Laricoideae			Abietoideae					
		<i>Pinus</i>	<i>Picea</i>	<i>Cathaya</i>	<i>Larix</i>	<i>Pseudotsuga</i>	<i>Abies</i>	<i>Cedrus</i>	<i>Keteleeria</i>	<i>Nothotsuga</i>	<i>Pseudolarix</i>	<i>Tsuga</i>
Tracheids	Organic deposits in heartwood tracheids	(+) ¹	—	—	—	—	(+) ¹	—	(+) ¹	—	—	—
	Helical thickenings	—	(+) ¹	+	(+) ¹	(+) ¹	—	—	—	—	—	—
	Torus scalloped	—	—	—	—	—	—	+	—	—	—	—
	Warty layer	—	—	—	—	—	+	+	—	+	—	+
Axial parenchyma	Present (marginal)	—	+	+	+	+	+	+	+	+	+	+
	Transverse end walls nodular	—	+	+	+	+	+	+	+	+	+	+
Rays	Permanent ray tracheids present	+	+	+	+	+	—	+	—	+	—	+
	Smooth ray tracheids	+	+	+	+	+	(+)	+	—	+	(+)	+
	Dentate ray tracheids	+	—	—	—	—	—	—	—	—	—	—
	Reticulate ray tracheids	+	—	—	—	—	—	—	—	—	—	—
	Helical thickenings in ray tracheids	—	(+) ¹	+	—	(+) ¹	—	—	—	—	—	—
	Horizontal walls of ray parenchyma cells pitted	(+) ¹	+	+	+	+	+	+	+	+	+	+
	End walls of ray parenchyma cells pitted	(+) ¹	+	+	+	+	+	+	+	+	+	+
	Pinoid	+	—	—	—	—	—	—	—	—	—	—
	Window-like	+	—	—	—	—	—	—	—	—	—	—
	Piceoid	—	+	+	+	+	+	+	+	—	+	+
	Cupressoid	—	—	—	—	—	—	—	+	+	—	+
	Taxodioid	—	—	—	—	—	+	+	+	+	+	—
Intercellular canals	Axial resin canals	+	+	+	+	+	—	—	+	+ ²	—	—
	Radial resin canals	+	+	+	+	+	—	—	—	—	—	—
	Thick-walled epithelial cells	—	+	+	+	+	—	—	+	+ ²	—	—

Table 1. Cont.

		Pinoideae	Piceoideae	Laricoideae				Abietoideae				
		<i>Pinus</i>	<i>Picea</i>	<i>Cathaya</i>	<i>Larix</i>	<i>Pseudotsuga</i>	<i>Abies</i>	<i>Cedrus</i>	<i>Keteleeria</i>	<i>Nothotsuga</i>	<i>Pseudolarix</i>	<i>Tsuga</i>
	Thin-walled epithelial cells	+	—	—	—	—	—	—	—	—	—	—
	Traumatic axial resin canals	+	+	+	+	+	+	+	+	+ ³	+ ³	+
	Traumatic radial resin canals	+	+	+	+	+	—	+	—	—	—	—
Mineral inclusions	Crystals	+	—	—	—	—	+	+	+	+	+	+

¹ see species in Appendix B Table A1, ² reported by Jin-Xing et al. [11]; ³ reported by Wu and Hu [4].

Figure 1. Resin canals. (A) Axial resin canals *Picea koraiensis*. (B) Radial canals *Picea koraiensis*. (C) Axial resin canals *Keteleeria davidiana*. (D) Without resin canals *Tsuga diversifolia*. (E) Axial resin canals with thin-walled epithelial cells *Pinus resinosa*. (F) Axial resin canal with thick-walled epithelial cells *Larix kaempferi*. (G) Traumatic axial resin canals *Picea abies*. (H) Traumatic radial resin canal *Picea abies*. (I–K) Traumatic axial resin canals. (I) *Keteleeria fortunei*. (J) *Abies nephrolepis*. (K) *Cedrus brevifolia*. (L) Traumatic radial resin canal *Cedrus brevifolia*. Scale bars: in (F) = 100 μm , in (C,G,L) = 150 μm , in (A,B,D,E,H–K) = 250 μm .

Cathaya, *Larix*, *Picea*, *Pinus* and *Pseudotsuga* had both axial and radial traumatic resin canals (Figure 1G,H). In *Keteleeria* and *Nothotsuga* traumatic resin canals were only axial and appeared randomly and in tangential rows (Figure 1I), differentiating this genus from the others, in which traumatic resin canals were always arranged in tangential rows (Figure 1J). Jin-Xing et al. [11] suggested that *Keteleeria* and *Nothotsuga* have a high level of affinity due to the presence of axial resin canals in latewood and resin cavities in the bark. *Cedrus* follows a different pattern from the other genera without normal resin canals, as it is the only genus capable of forming both traumatic axial (Figure 1K) and radial (Figure 1L) resin canals. Molecular phylogenetic studies have shown that of the six Abietoideae genera, only *Cedrus* is difficult to include in the clade [22].

The presence of normal resin canals, therefore, allows three groups to be established: *Cathaya-Larix-Picea-Pinus-Pseudotsuga*, with axial and radial resin canals; *Keteleeria-Nothotsuga*, with only axial resin canals; and *Abies-Cedrus-Pseudolarix-Tsuga*, without resin canals. The groups established by the presence of traumatic axial resin canals are: *Cathaya-Larix-Picea-Pinus-Pseudotsuga*, with both normal and traumatic axial and radial resin canals; *Keteleeria-Nothotsuga*, in which traumatic resin canals are only axial, in conjunction with

normal resin canals, similarly only axial; *Abies-Pseudolarix-Tsuga*, with only traumatic axial resin canals and no normal resin canals; and *Cedrus*, with traumatic axial and radial resin canals but without normal resin canals.

3.2. Rays

Ray cell composition has been used as an essential element for classifying conifer families [26]. Ray tracheids always occurred in Pinoideae (*Pinus*) (Figure 2A), Piceoideae (*Picea*) (Figure 2B) and Laricoideae (*Cathaya*, *Larix*, *Pseudotsuga*) (Figure 2C). In Abietoideae ray tracheids are present in *Cedrus* (Figure 2D), *Nothotsuga* (Figure 2E) and *Tsuga* (Figure 2F), while in *Abies* and *Pseudolarix* they are rarely present. Only *Keteleeria* has no ray tracheids, which was confirmed in the samples studied (Figure 2G).

Figure 2. Rays. (A–I) Ray tracheids. (A) *Pinus echinata*. (B) *Picea alcoquiana*. (C) *Larix occidentalis*. (D) *Cedrus atlantica*. (E) *Nothotsuga longibracteata*. (F) *Tsuga diversifolia*. (G) Ray tracheids absent *Keteleeria davidiana*. (H) Dentate ray tracheids *Pinus resinosa*. (I) Smooth ray tracheids *Pinus wallichiana* var. *wallichiana*. (J) Irregularly shaped marginal ray cells *Cedrus libani*. (K) Helical thickenings in ray tracheids *Pseudotsuga sinensis*. (L–N) Ray parenchyma. (L) Pitted horizontal walls *Abies nephrolepis*. (M) Nodular end walls *Abies nordmanniana* subsp. *equi-trojani*. (N) Indenture *Abies vejari*. Scale bars: in (A–C,F,H,I,K–N) = 50 µm, in (D,E,G) = 100 µm, in (J) = 150 µm.

Three types of ray tracheids have been differentiated in *Pinus*: smooth (*P. armandii*, *P. ayacahuite*, *P. brutia*, *P. cembra*, *P. cembroides*, *P. gerardiana*, *P. griffithii*, *P. halepensis*, *P. hartwegii*, *P. koraiensis*, *P. merkusii*, *P. monophylla*, *P. morrisonicola*, *P. parviflora*, *P. peuce*, *P. pinea*, *P. quadrifolia*, *P. strobus*, *P. wallichiana*) (Figure 2I), dentate (*P. arizonica*, *P. banksiana*, *P. brutia*, *P. canariensis*, *P. caribaea*, *P. cembroides*, *P. contorta*, *P. densiflora*, *P. devoniana*, *P. douglasiana*, *P. elliotii*, *P. gerardiana*, *P. griffithii*, *P. halepensis*, *P. hartwegii*, *P. heldreichii*, *P. jeffreyi*, *P. kesiya*, *P. lawsonii*, *P. leiophylla*, *P. massoniana*, *P. maximinoi*, *P. merkusii*, *P. monophylla*, *P. montezumae*, *P. mugo*, *P. nigra*, *P. palustris*, *P. pinaster*, *P. pinea*, *P. ponderosa*, *P. pseudostrobus*, *P. quadrifolia*, *P. radiata*, *P. resinosa*, *P. rigida*, *P. sylvestris*, *P. tabuliformis*, *P. taeda*, *P. tecunumanii*, *P. teocote*, *P. thunbergii*, *P. tropicalis*) (Figure 2H) and reticulate (*P. arizonica*, *P. banksiana*, *P. caribaea*, *P. contorta*, *P. devoniana*, *P. douglasiana*, *P. elliotii*, *P. heldreichii*, *P. jeffreyi*, *P. maximinoi*, *P. palustris*, *P. ponderosa*, *P. rigida*, *P. taeda*, *P. tecunumanii*). Due to variability within the genus, this feature does not allow intergeneric groupings to be established in Pinaceae, but it has been used by other authors [27] to establish groups in *Pinus*.

Some authors explained the presence of ray tracheids associated with wounding [7,28], as occurs with the presence of traumatic resin canals, although Holden [26] reported the presence of traumatic axial canals and the absence of ray tracheids as a response to wounding in *Keteleeria*. This absence of ray tracheids in *Keteleeria* disagrees with the clade proposed in the molecular phylogenetic study by Wang et al. [29], who concluded that the clade *Abies-Keteleeria-Pseudolarix-Tsuga* was well resolved.

Ray tracheids normally occur in marginal arrangement in one row (*Abies*, *Cathaya*, *Cedrus*, *Nothotsuga*, *Pseudolarix*, *Pseudotsuga*, *Tsuga*), in two or three rows (*Larix*, *Picea*), or in several marginal cell rows and occasionally in alternate rows (*Pinus*).

In *Cedrus*, especially in marginal rows, irregularly shaped cells have been observed (Figure 2J), described by Chrysler [30] as degenerated cells, although they are actually irregularly shaped ray parenchyma cells.

Helical thickenings in ray tracheids have been observed only in *Cathaya*, *Picea spinulosa*, *P. torano* and *Pseudotsuga sinensis* (Figure 2K).

Taking into account the presence of ray tracheids and their characteristics, a single group can, therefore, be established of the genera in which ray tracheids are always present *Cathaya-Cedrus-Larix-Nothotsuga-Pinus-Picea-Pseudotsuga-Tsuga*, in addition to *Abies-Pseudolarix*, where they are occasionally present. *Keteleeria* is the only genus remaining outside this group and its inclusion is, therefore, unresolved.

Pitted horizontal (Figure 2L) and distinctly nodular ray parenchyma end walls (Figure 2M) are present in all genera of Pinaceae, although some species of *Pinus* do not conform (see Appendix B).

Indentures were also found in all genera, although they presented different degrees of development. In *Abies* (Figure 2N), they were well developed but in *Cedrus*, *Keteleeria*, *Nothotsuga* and *Pinus*, they were only slightly developed.

Lastly, cross-field pitting did not show a common pattern and cannot be used to establish groups, as variation in this feature is not only intergeneric but also intrageneric: *Abies* (piceoid, taxodioid), *Cathaya* (piceoid), *Cedrus* (piceoid, taxodioid), *Keteleeria* (cupressoid, taxodioid), *Larix* (piceoid), *Nothotsuga* (cupressoid, taxodioid), *Picea* (piceoid), *Pinus* (pinoid, window-like), *Pseudolarix* (piceoid), *Pseudotsuga* (piceoid) and *Tsuga* (piceoid).

3.3. Axial Tracheids

One of the most significant features of the axial tracheids of Pinaceae is the presence of helical thickenings: in *Cathaya* well developed in early and latewood; in some species of *Larix* only in latewood tracheids (*L. decidua*, *L. griffithii*, *L. occidentalis*); in *Picea spinulosa* well developed in early and latewood; in *Picea abies*, *P. brachytyla*, *P. glauca*, *P. glehnii*, *P. jezoensis*, *P. koraiensis*, *P. mariana*, *P. sitchensis*, *P. torano* only in latewood; in *Pseudotsuga sinensis* in early and latewood and in *P. menziesii* only in latewood (Figure 3A). The other genera of Pinaceae do not have helical thickenings in axial tracheids. Therefore, this can

be used as a distinguishing feature to establish groups in Pinaceae, specific to Pinoideae (*Cathaya-Larix-Picea-Pseudotsuga*) with the exception of *Pinus*.

Figure 3. Axial tracheids, axial parenchyma and crystals. (A–G) Axial tracheids. (A) Helical thickenings *Pseudotsuga sinensis*. (B) SEM, scalloped tori *Cedrus atlantica*. (C) Biseriate tracheid pitting *Larix occidentalis*. (D) Organic deposits in tracheids *Abies pinsapo*. (E) Tracheid pitting in tangential walls *Keteleeria evelyniana*. (F) Tracheid pitting in tangential walls on the growth ring boundary *Abies nordmanniana*. (G) SEM, warty layer *Abies pinsapo*. (H–I) Axial parenchyma. (H) Marginal parenchyma *Tsuga mertensiana*. (I) Nodular transverse end wall *Pseudolarix amabilis*. (J) Crystals in ray parenchyma cells *Abies procera*. Scale bars: in (B) = 2 μ m, in (G) = 10 μ m, in (F,J) = 50 μ m, in (A,C) = 100 μ m, in (D,E,H,I) = 150 μ m.

Cedrus had scalloped tori (Figure 3B), a feature not observed in other Pinaceae, present in all samples studied [7,25]. Although Willebrand [31] described intermediate forms of scalloped tori in *Pseudolarix*, they were not found in the present study. Therefore, this feature does not support grouping of genera and, as with the presence of traumatic axial and radial resin canals, *Cedrus* seems to differ from the other genera.

When biseriate tracheid pitting was present in earlywood, it was in opposite arrangement in all genera (Figure 3C) and very rarely in alternate arrangement.

Organic deposits in tracheids were found only in *A. pinsapo*, agreeing with Esteban et al. [32], *Abies guatemalensis* and *Pinus canariensis* (Figure 3D), but should not be regarded as characteristic of the genus, as they are in *Agathis* and *Araucaria* [33,34]. Organic deposits in tracheids have also been cited in *Picea sitchensis* [10].

All the genera of Abietoideae studied presented tracheid pitting in tangential walls (Figure 3E) in the vicinity of the growth ring, generally in the first rows of latewood (Figure 3F). Tracheid pitting was very scarce in the other genera. A warty layer was

observed only in *Abies*, *Cedrus*, *Nothotsuga* and *Tsuga* (Figure 3G), although it has also been recorded in *Pinus* [25].

3.4. Axial Parenchyma

Although very scarce, axial parenchyma was observed in all genera of Pinaceae except *Pinus*. It was limited to the growth ring boundary, both in earlywood and latewood (Figure 3H). Transverse end walls were nodular in all genera studied (Figure 3I). The presence of this feature supports a single group for all genera except *Pinus*.

3.5. Crystals

The presence of crystals is a frequent feature in all genera of Abietoideae [35] and crystals also occur in some non-Abietoideae taxa. In this work, crystals were observed in many taxa of *Abies* (see Appendix B) and are a feature of this genus [18], all species of *Cedrus* and *Keteleeria*, *Nothotsuga longibracteata*, *Pinus brutia*, *P. cembroides*, *P. contorta*, *P. halepensis*, *P. heldreichii*, *P. monophylla*, *Pseudolarix amabilis* and all species of *Tsuga* except *T. dumosa*. They are usually located in marginal and submarginal rows of the ray parenchyma and in irregularly shaped marginal ray cells (Figure 3J).

The presence of crystals has even been used to differentiate very close species in *Pinus* [36,37]. Crystal inclusions have also been recorded in subsidiary tissue of resin canals, e.g., in *Abies pinsapo* [32]. In this study, they were observed only in traumatic resin canals of *Abies*.

These considerations indicate that the presence of crystals must be interpreted as a feature allowing the formation of a single group in Pinaceae.

3.6. Anatomy and Phylogeny

Irrespective of their typology and arrangement, resin canals allow a well-resolved group to be formed in Pinaceae as they occur in all genera, either normal and traumatic or only traumatic. Although some non-Pinaceae genera, specifically Cupressaceae, can have traumatic canals, their presence is occasional, as reported by Bailey and Faull [38] in *Sequoia sempervirens*, Jeffrey [39] in *Sequoiadendron*, Benkova and Schweingruber [40] in *Microbiota* and Esteban et al. [41] in *Tetraclinis articulata*.

The presence of ray tracheids also supports the grouping of the family Pinaceae. Although this feature is also found in non-Pinaceae conifers (*Cupressus* L., *Sequoia* Endl. and *Thujopsis* Siebold & Zucc.) [7], it occurs in these species very rarely. However, the absence of ray tracheids in *Keteleeria* and their occasional presence in *Abies* and *Pseudolarix* weakens the group.

Other features such as pitted horizontal walls and nodular end walls in ray parenchyma cells, cross-field pitting and indentures do not support the grouping, as they occur in non-Pinaceae families. These considerations are supported by phylogeny studies by Gugerli et al. [42], who used the second intron in the mitochondrial gene *nad1* to show that two clearly distinct clades can be established within the conifers: Pinaceae and non-Pinaceae.

Based on wood anatomy, other subgroups can be established in the family Pinaceae that differ from the subfamilies proposed by Frankis [2] and Farjon [3] but agree with the classification by Lin et al. [5]. However, this classification differs from molecular phylogenetic studies by other authors.

Wang et al. [29] established the existence of two distinct clades within Pinaceae: *Cathaya-Larix-Picea-Pinus-Pseudotsuga* and *Abies-Keteleeria-Nothotsuga-Pseudolarix-Tsuga*. Germandt et al. [22] confirmed this division by phylogenetic analysis of chloroplast DNA (*matK* and *rbcL*) and concluded that Pinaceae supports two clearly distinct monophyletic groups: Abietoideae and Pinoideae, corresponding with the general structure of the family in the two subfamilies.

Moreover, Wang et al. [29], in their study of intergeneric relations of Pinaceae using sequences of the chloroplast *matK*, mitochondrial *nad5* and nuclear 4CL genes, established a

three-genome phylogeny consisting of the clade *Larix-Picea-Pinus-Pseudotsuga* similar to the phenogram established by Hart [43] based on cladistic analysis and to the clade established by Price et al. [44] through immunological comparison. The four genera of this clade have normal resin canals, both axial and radial, as does *Cathaya*.

Although some authors consider that the only species of the genus *Cathaya* (*C. argyrophylla*) belongs to the genus *Pseudotsuga* [45–47], using PCR-RFLP analysis of the chloroplast gene *trnK*, concluded that *Cathaya* is a separate genus and must be treated outside of *Pseudotsuga*. The presence of axial and radial resin canals with thick-walled epithelial cells supports the clade *Cathaya-Larix-Picea-Pseudotsuga*, but excludes the genus *Pinus*, which has thin-walled epithelial cells.

Despite the obvious differences in the anatomy of the secondary xylem between *Keteleeria* and *Nothotsuga* and the other Abietoideae genera (presence of axial resin canals, arrangement of traumatic resin canals and absence of ray tracheids in *Keteleeria*), the two genera appear to form a well-resolved clade with *Abies-Pseudolarix-Tsuga* [47]. Liston et al. [21] also confirmed that *Nothotsuga-Pseudolarix-Tsuga* form a sister clade to *Abies-Keteleeria*, with only *Cedrus* remaining unresolved.

However, molecular evidence supports the genus *Cedrus* as a sister group to the other Pinaceae and reinforces the idea that it should occupy a basic or root position in the family, to the extent that the subfamily Abietoideae can be considered paraphyletic [22]. This coincides with the peculiar behaviour observed in two features of *Cedrus*: it is the only genus with scalloped tori and has traumatic radial resin canals even though it has no normal resin canals. These features, particularly the latter, constitute different behaviour in *Cedrus* from the clade *Abies-Keteleeria-Nothotsuga-Pseudolarix-Tsuga*, as these genera do not have tori or traumatic radial resin canals.

Despite these distinctive features of *Cedrus*, the genera in Abietoideae form a homogeneous group in terms of wood structure, except for the resin canals in *Keteleeria* and *Nothotsuga* and the absence of ray tracheids in *Keteleeria*, which supports the clade *Abies-Cedrus-Keteleeria-Nothotsuga-Pseudolarix-Tsuga*, as all of these species have ray parenchyma with pitted horizontal walls and nodular end walls, indentures, scarce axial parenchyma on the growth ring boundary and crystals in ray parenchyma [35].

4. Conclusions

Wood anatomy and molecular phylogeny agree that Pinaceae is clearly differentiated from the other conifers by the presence of two features in its wood structure exclusive to the family—resin canals and ray tracheids—which are only very rarely present as exceptions in non-Pinaceae conifers.

Based on wood structure, Pinaceae clearly supports division into two groups: Pinoideae (*Cathaya-Larix-Picea-Pinus-Pseudotsuga*) and Abietoideae (*Abies-Cedrus-Keteleeria-Nothotsuga-Pseudolarix-Tsuga*), although within Abietoideae two subgroups can be considered based on resin canals: with normal axial resin canals (*Keteleeria-Nothotsuga*) and without (*Abies-Cedrus-Pseudolarix-Tsuga*).

Although division into two groups (Pinoideae and Abietoideae) is clearly supported by molecular phylogeny, the subgroups within Abietoideae differ from molecular phylogenetic studies that include *Keteleeria* and *Nothotsuga* with no exceptions and exclude *Cedrus*. However, the exclusion of *Cedrus* agrees with the differences in its wood structure compared to the anatomy of other genera.

Author Contributions: Conceptualization, L.G.E. and P.d.P.; Data curation, A.G.-I. and F.G.-F.; Formal analysis, A.G.-I. and F.G.-F.; Investigation, L.G.E., P.d.P., A.G.-I., F.G.-F., L.G.-E. and D.G.d.V.; Methodology, L.G.E., P.d.P., A.G.-I., F.G.-F., L.G.-E. and D.G.d.V.; Project administration, L.G.E. and P.d.P.; Resources, L.G.E., P.d.P., A.G.-I., F.G.-F., L.G.-E. and D.G.d.V.; Supervision, L.G.E.; Validation, L.G.E., P.d.P. and F.G.-F.; Visualization, L.G.E., P.d.P. and A.G.-I.; Writing—original draft, L.G.E. and P.d.P.; Writing—review and editing, L.G.E., P.d.P., A.G.-I., F.G.-F., L.G.-E. and D.G.d.V. All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Data Availability Statement: Not Applicable.

Conflicts of Interest: The authors declare no conflict of interest.

Appendix A

List of the species, subspecies and varieties studied, with references to the collections from which the samples were obtained and list of the features observed. + Present, – Absent, (+) Occasional. For wood sample acronyms see [23].

Abies alba Mill. (UPMAw-X1530); *A. amabilis* Douglas ex J. Forbes (UPMAw-X1216); *A. balsamea* (L.) Mill. (MADRw2173); *A. borisii-regis* Mattf. (MADw17846); *A. bracteata* (D. Don) Poit. (MADw18347); *A. cephalonica* Loudon (RBHw7079; MADRw1592; MADw1784); *A. cilicica* (Antoine & Kotschy) Carrière (RBHw14036; MADRw2084; MADw17376; Uw362); *A. concolor* Lindl. ex Hildebr. (MADRw1577; MADRw1594); *A. delavayi* Franch. (K-Jw18361); *A. durangensis* Martínez (USw32800); *A. firma* Siebold & Zucc. (CTFw11458ch); *A. fraseri* (Pursh) Poir. (RBHw5552; MADw771; USw14814); *A. grandis* (Douglas ex D. Don) Lindl. (UPMAw-X1526); *A. guatemalensis* Rehder (MADRw1593); *A. hickelii* Flous & Gaussen (SJRw37237); *A. holophylla* Maxim. (UPMAw-X1155); *A. homolepis* Siebold & Zucc. (MADw4428; TWTw1348; TWTw9276; TWTw11943; TWTw18725; USw23684); *A. kawakamii* (Hayata) T. Itô (RBHw 7243; MADw2006; USw21248); *A. koreana* E.H. Wilson (MADRw2171); *A. lasiocarpa* (Hook.) Nutt. (RBHw12097; RBHw11392; MADw25431; USw14492); *A. lasiocarpa* var. *arizonica* (Merriam) Lemmon (RBHw11383; MADRw1576); *A. magnifica* A. Murray bis (MADw6307; USw14485); *A. mariesii* Mast. (RBHw9103; RBHw7230; MADw20334; TWTw598; TWTw9347; TWTw18156; TWTw18691; TWTw20555; TWTw21799; USw24492); *A. nephrolepis* (Trautv. ex Maxim.) Maxim. (CTFw22366ch); *A. nordmanniana* (Steven) Spach (MADw10536; MADw39459; Uw314); *A. nordmanniana* Spach ssp. *equi-trojani* (Asch. & Sint. ex Boiss.) Coode & Cullen (RBHw14031; RBHw14034; MADw49056); *A. numidica* de Lannoy ex Carrière (K-Jw18393; Uw192); *A. pindrow* (Royle ex D. Don) Royle (K-Jw18394); *A. pinsapo* Boiss. (UPMAw-X2175; UPMAw-X2176; UPMAw-X2177); *A. pinsapo* Boiss. var. *tazaotana* (S. Cózar ex Villar) Pourtet (UPMAw-X2267); *A. pinsapo* Boiss. var. *marocana* (Trab.) Ceballos & Martín Bol. (UPMAw-X2268); *A. procera* Rehder (RBHw11428; MADw44891; USw19149); *A. recurvata* Mast. (SJRw23054-085); *A. religiosa* (Kunth) Schltdl. & Cham. (CTFw1218); *A. sachalinensis* Mast. (CTFw11459ch); *A. sibirica* Ledeb. (K-Jw18406); *A. spectabilis* Spach (K-Jw18417); *A. veitchii* Lindl. (K-Jw18422); *A. vejarii* Martínez (MADw25208; USw32803); *Cathaya argyrophylla* Chun & Kuang (UPMAw-X1732); *Cedrus atlantica* Manetti (K-Jw18423); *C. brevifolia* Elwes & Henry (UPMAw-X0952); *C. deodara* (Roxb. ex Lambert) G. Don (K-Jw70743); *C. libani* A. Rich. (K-Jw18453); *Keteleeria davidiana* Beissn. (USw18469); *K. evelyniana* Mast. (MADw42042); *K. fortunei* Carrière (K-Jw18462); *Larix decidua* Mill. DC. (UPMAw-X0227; UPMAw-X0955); *L. gmelini* (Rupr.) Kuzen (UPMAw-X1450; UPMAw-X1595); *L. griffithii* Hook. f. (K-Jw18509); *L. laricina* (Du Roi) K. Koch (UPMAw-X0955); *L. kaempferi* (Lamb.) Carrière (CTFw11460; CTFw19334); *L. occidentalis* Nutt. (UPMAw-X0956; UPMAw-X1223); *L. sibirica* Ledeb. (MADRw1732); *Nothotsuga longibracteata* (W.C. Cheng) H.H. Hu ex C.N. Page (MADw32679); *Picea abies* (L.) H. Karst. (UPMAw-X0957); *P. alcoquiana* (Veitch ex Lindl.) Carrière (K-Jw18566 W2); *P. brachytyla* (Franch.) E. Pritz. (UPMAw-X0958); *P. glauca* (Moench.) Voss. (UPMAw-X0960; UPMAw-X1224); *P. glehnii* (F. Schmidt) Mast. (K-Jw18589); *P. jezoensis* (Siebold & Zucc.) Carrière (UPMAw-X0375; UPMAw-X1453); *P. koraiensis* Nakai (CTFw22363; CTFw26171); *P. mariana* (Mill.) Britton et al. (MADRw1590); *P. omorika* (Pancic) Purk. (UPMAw-X0119); *P. rubens* Sarg. (MADRw-P1588); *P. sitchensis* (Bong.) Carrière (UPMAw-X0961); *P. spinulosa* (Griff.) Beissn. (K-Jw18642); *P. torano* (Siebold. Ex K. Koch) Koehne (UPMAw-P1264); *Pinus arizonica* Engelm. var. *cooperi* (C. E. Blanco) Farjon (UPMAw-X1227); *P. armandii* Franch. (K-Jw18649); *P. ayacahuite* Ehrenb. ex Schltdl. (CTFw15135; CTFw15439; CTFw15129); *P. banksiana* Lamb. (UPMAw-X0962; UPMAw-X1521); *P. brutia* Ten. (UPMAw-P1272); *P. canariensis* C. Sm. (UPMAw-X2141); *P. caribaea* Morelet var. *caribaea* Barret & Golfari (UPMAw-X2297); *P. cembra* L. (UPMAw-X0966; UPMAw-

X1488); *P. cembroides* Zucc. (MADRw1574); *P. contorta* Douglas ex Loudon (UPMAw-X0967; UPMAw-X1525); *P. densiflora* Siebold. & Zucc. (UPMAw-X0376); *P. devoniana* Lindl. (UPMAw-X1230); *P. douglasiana* Martinez (UPMAw-P1279); *P. elliottii* Engelm. (UPMAw-X0968; UPMAw-X1517); *P. gerardiana* Wall ex D. Dom in Lambert (K-Jw18728); *P. halepensis* Mill. (UPMAw-X0970; UPMAw-X1563); *P. hartwegii* Lindl. (UPMAw-X1229); *P. heldreichii* D. H. Christ. (UPMAw-X2038); *P. jeffreyi* Balf. in Murray (MADRw1586); *P. kesiya* Royle ex Gordon (UPMAw-X0971; UPMAw-X1478); *P. koraiensis* Siebold. & Zucc. (CTFw22356; CTFw26174; CTFw31572); *P. lawsonii* Roezl. ex Gordon (UPMAw-X1228); *P. leiophylla* Schlecht & Cham. (CTFw11323; CTFw25752; CTFw28882); *P. massoniana* Lambert (UPMAw-P1628); *P. maximinoi* H.E. Moore (UPMAw-X2292); *P. merkusii* Jungh & de Vriese (K-Jw18762; CTFw3340; CTFw3353; CTFw7712); *P. monophylla* Torr. & Frém. (UPMAw-X1730); *P. montezumae* Lamb. (CTFw11318; CTFw28949); *P. morisonicola* Hayata (K-Jw18911); *P. mugo* Turra subsp. *uncinata* (Ramond ex DC.) Domin (UPMAw-X2338); *P. nigra* J. F. Arnold (UPMAw-X2298); *P. palustris* Mill. (UPMAw-X0973; UPMAw-X1476); *P. parviflora* Siebold. & Zucc. (CTFw11464; CTFw19338; CTFw22357); *P. peuce* Griseb. (UPMAw-X0974; UPMAw-X1729); *P. pinaster* Aiton (UPMAw-P1302); *P. pinea* L. (UPMAw-X0973; UPMAw-X1476; UPMAw-X1787); *P. ponderosa* Douglas ex C. Lawson (UPMAw-X0976; UPMAw-X1232; UPMAw-X1480); *P. pseudostrobus* Lindl. (UPMAw-X2293); *P. quadrifolia* Parl. ex Sudw. (UPMAw-X1481); *P. radiata* D. Don (UPMAw-X0008; UPMAw-X0977; UPMAw-X1477); *P. resinosa* Aiton (UPMAw-X0978; UPMAw-X1233; UPMAw-X1482); *P. rigida* Mill. (UPMAw-X1483); *P. strobus* L. (UPMAw-X0979; UPMAw-X1234; UPMAw-X1484); *P. sylvestris* L. (UPMAw-X2317); *P. tabuliformis* Carrière (CTFw28176); *P. taeda* L. (UPMAw-P1314); *P. tecunumanii* Eguiluz & J. P. Perry (K-Jw18790); *P. teocote* Schiede & Schlecht. (K-Jw18902); *P. thunbergii* Parl. (K-Jw18900); *P. tropicalis* Morelet (UPMAw-X2269); *P. wallichiana* A. B. Jacks. var. *wallichiana* (UPMAw-X0969; UPMAw-X1508); *Pseudolarix amabilis* Rehder (K-Jw18924); *Pseudotsuga menziesii* (Mirb.) Franco (UPMAw-X0983; UPMAw-X1518); *P. sinensis* Dode (K-Jw18940); *P. menziesii* (Mirb.) Franco var. *menziesii* (UPMAw-X0234; UPMAw-X0984; UPMAw-X1237); *Tsuga canadensis* Carrière (UPMAw-X1515); *T. caroliniana* Engelm. (K-Jw18950); *T. chinensis* (Franch.) Pritz in Diels (CTFw26180 ch); *T. diversifolia* (Maxim.) Mast. (RBHw621; RBHw7081; RBHw9112; MADw48033; MADw26122; TWTw593; TWTw11949; TWTw18088; TWTw18152; TWTw18665; TWTw20551); *T. dumosa* Eichl. (K-Jw18953); *T. heterophylla* Sarg. (UPMAw-X1239); *T. mertensiana* (Bong.) Carrière (MADRw1397); *T. sieboldii* Carrière (KYOw0382).

Appendix B

Table A1. Features observed in the species studied. + Present, – Absent, (+).

	Axial Tracheids				Axial Parenchyma	Rays										Intercellular Canals											
	Organic Deposits in Heartwood Tracheids																										
	Helical Thickenings	Tori Scalloped	Warty Layer	Present (Marginal)	Transverse end Walls Nodular	Ray Tracheids Present	Ray Tracheids Smooth	Ray Tracheids Dentate	Ray Tracheids Reticulate	Helical Thickenings in Ray Tracheids	Horizontal End Walls of Ray Parenchyma Smooth	Horizontal Walls of Ray Parenchyma Cells Pitted	End Walls of Ray Parenchyma Cells Smooth	End Walls of Ray Parenchyma Cells Nodular	Pinoid	Window-Like	Piceoid	Cupressoid	Taxodioid	Axial Resin Canals	Thick-Walled Epithelial Cells	Thin-Walled Epithelial Cells	Traumatic Axial Resin canals	Radial Resin Canals	Traumatic Radial Resin Canals	Crystals. Mineral Inclusions	
<i>Abies alba</i> Mill.	—	—	—	—	+	+	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	—	—	—	+	
<i>A. amabilis</i> Douglas ex J.Forbes	—	—	—	—	+	+	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	—	—	—	+	
<i>A. balsamea</i> (L.) Mill.	—	—	—	—	+	+	+	+	—	—	—	+	—	+	—	—	—	—	+	—	—	—	—	—	—	—	
<i>A. borisii-regis</i> Mattf.	—	—	—	+	+	+	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	—	—	—	+	
<i>A. bracteata</i> (D. Don) Poit.	—	—	—	+	+	+	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	+	—	—	—	
<i>A. cephalonica</i> Loudon	—	—	—	—	+	+	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	—	—	—	—	
<i>A. cilicica</i> (Antoine & Kotschy) Carrière	—	—	—	—	+	+	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	—	—	—	+	
<i>A. concolor</i> Lindl. ex Hildebr.	—	—	—	—	+	+	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	—	—	—	+	
<i>A. delavayi</i> Franch.	—	—	—	+	+	+	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	—	—	—	+	
<i>A. durangensis</i> Martínez	—	—	—	—	+	+	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	—	—	—	+	

Table A1. Cont.

<i>A. firma</i> Siebold & Zucc.	–	–	–	+	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. fraseri</i> (Pursh) Poir.	–	–	–	+	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. grandis</i> (Douglas ex D.Don) Lindl.	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	–
<i>A. guatemalensis</i> Rehder	+	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	+	–	–	+
<i>A. hickelii</i> Flous & Gaussen	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	–
<i>A. holophylla</i> Maxim.	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. homolepis</i> Siebold & Zucc.	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. kawakamii</i> (Hayata) T.Itô	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	+	–	–	–
<i>A. koreana</i> E.H.Wilson	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	–
<i>A. lasiocarpa</i> (Hook.) Nutt.	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. lasiocarpa</i> var. <i>arizonica</i> (Merriam) Lemmon	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	–
<i>A. magnifica</i> A.Murray bis	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. mariesii</i> Mast.	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. nephrolepis</i> (Trautv. ex Maxim.) Maxim.	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	+	–	–	–
<i>A. nordmanniana</i> (Steven) Spach	–	–	–	+	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	+	–	–	+
<i>A. nordmanniana</i> Spach ssp. <i>equi-trojani</i> (Asch. & Sint. ex Boiss.)	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. numidica</i> de Lannoy ex Carrière	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. pindrow</i> (Royle ex.D. Don) Royle	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. pinsapo</i> Boiss.	+	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. pinsapo</i> Boiss. var. <i>tazaotana</i> (S.Cózar ex Villar) Pourtet	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. pinsapo</i> Boiss. var. <i>marocana</i> (Trab.) Ceballos & Martín Bol.	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. procera</i> Rehder	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	+
<i>A. recurvata</i> Mast.	–	–	–	–	+	+	–	–	–	–	–	–	+	–	+	–	–	–	–	+	–	–	–	–	–	–	–

Table A1. *Cont.*

<i>A. religiosa</i> (Kunth) Schltdl. & Cham.	—	—	—	—	+	+	—	—	—	—	—	—	+	—	+	—	—	—	—	—	—	—	—	—	+
<i>A. sachalinensis</i> Mast.	—	—	—	—	+	+	—	—	—	—	—	—	+	—	+	—	—	—	—	—	—	—	—	—	—
<i>A. sibirica</i> Ledeb.	—	—	—	—	+	+	—	—	—	—	—	—	+	—	+	—	—	—	—	—	—	—	—	—	—
<i>A. spectabilis</i> Spach	—	—	—	+	+	+	—	—	—	—	—	—	+	—	+	—	—	—	—	—	—	—	—	—	—
<i>A. veitchii</i> Lindl.	—	—	—	—	+	+	—	—	—	—	—	—	+	—	+	—	—	—	—	—	—	+	—	—	—
<i>A. vejarii</i> Martínez	—	—	—	—	+	+	—	—	—	—	—	—	+	—	+	—	—	—	—	—	—	—	—	—	—
<i>Cathaya argyrophylla</i> Chun & Kuang	—	+	—	—	+	+	+	+	—	—	+	—	+	—	+	—	—	+	—	—	+	+	—	+	+
<i>Cedrus atlantica</i> Manetti	—	—	+	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	—	+
<i>C. brevifolia</i> Elwes & Henry	—	—	+	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	+	—	—	+	—	+
<i>C. deodara</i> (Roxb. ex Lambert) G.Don	—	—	+	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	—	+
<i>C. libani</i> A.Rich.	—	—	+	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	+	—	—	—	—	+
<i>Keteleeria davidiana</i> Beissn.	—	—	—	—	+	+	—	—	—	—	—	—	+	—	+	—	—	—	+	—	+	+	—	—	+
<i>K. evelyniana</i> Mast.	—	—	—	—	+	+	—	—	—	—	—	—	+	—	+	—	—	—	—	+	+	+	—	—	+
<i>K. fortunei</i> Carrière	—	—	—	—	+	+	—	—	—	—	—	—	+	—	+	—	—	—	+	+	+	+	—	+	+
<i>Larix decidua</i> Mill. DC.	—	+ ¹	—	—	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	+	+
<i>L. gmelini</i> (Rupr.) Kuzen	—	—	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	—
<i>L. griffithii</i> Hook. f.	—	+ ¹	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	—
<i>L. laricina</i> (Du Roi) K. Koch	—	—	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	—
<i>L. kaempferi</i> (Lamb.) Carriere	—	—	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	—
<i>L. occidentalis</i> Nutt.	—	+ ¹	—	—	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	+	+
<i>L. sibirica</i> Ledeb.	—	—	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	—
<i>Nothotsuga longibracteata</i> (W.C.Cheng) H.H.Hu ex C.N.Page	—	—	—	+	+	+	+	+	—	—	—	—	+	—	+	—	—	—	+	+	+ ²	+ ²	—	—	—
<i>Picea abies</i> (L.) H. Karst.	—	+ ¹	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	+	+
<i>P. alcoquiana</i> (Veitch ex Lindl.) Carrière	—	—	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	—
<i>P. brachytyla</i> (Franch.) E. Pritz.	—	+ ¹	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	—
<i>P. glauca</i> (Moench.) Voss.	—	+ ¹	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	—

Table A1. Cont.

<i>P. glehnii</i> (F. Schmidt) Mast.	—	+ ¹	—	—	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—
<i>P. jezoensis</i> (Siebold. & Zucc.) Carrière	—	+ ¹	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—
<i>P. koraiensis</i> Nakai	—	+ ¹	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—
<i>P. mariana</i> (Mill.) Britton et al.	—	+ ¹	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—
<i>P. omorika</i> (Pancic) Purk.	—	—	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—
<i>P. rubens</i> Sarg.	—	—	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—
<i>P. sitchensis</i> (Bong.) Carrière	—	+ ¹	—	—	—	—	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—
<i>P. spinulosa</i> (Griff.) Beissn.	—	+	—	—	+	+	+	+	—	—	+	—	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—
<i>P. torano</i> (Siebold. Ex K. Koch) Koehne	—	+ ¹	—	—	—	—	+	+	—	—	+	—	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—
<i>Pinus arizonica</i> Engelm. var. <i>cooperi</i> (C. E. Blanco) Farjon	—	—	—	—	—	—	+	—	+	+	—	+	—	+	—	+	—	—	—	—	+	—	+	+	+	+	—
<i>P. armandii</i> Franch.	—	—	—	—	—	—	+	+	—	—	—	—	+	+	+	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. ayacahuite</i> Ehrenb.ex Schltdl.	—	—	—	—	—	—	+	+	—	—	—	+	—	+	+	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. banksiana</i> Lamb.	—	—	—	—	—	—	+	—	+	+	—	+	—	+	—	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. brutia</i> Ten.	—	—	—	—	—	—	+	+	+	—	—	—	+	—	+	+	—	—	—	—	+	—	+	—	+	—	+
<i>P. canariensis</i> C. Sm.	+	—	—	—	—	—	+	—	+	—	—	—	+	+	—	+	—	—	—	—	+	—	+	+	+	+	—
<i>P. caribaea</i> Morelet var. <i>caribaea</i> Barret & Golfari	—	—	—	—	—	—	+	—	+	+	—	+	—	+	—	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. cembra</i> L.	—	—	—	—	—	—	+	+	—	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. cembroides</i> Zucc.	—	—	—	—	—	—	+	+	—	—	—	+	—	+	—	+	—	—	—	—	+	—	+	—	+	—	+
<i>P. contorta</i> Douglas ex Loudon	—	—	—	—	—	—	+	—	+	+	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	+
<i>P. densiflora</i> Siebold. & Zucc.	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. devoniana</i> Lindl.	—	—	—	—	—	—	+	—	+	+	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. douglasiana</i> Martinez	—	—	—	—	—	—	+	—	+	+	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. elliotii</i> Engelm.	—	—	—	—	—	—	+	—	+	+	—	+	—	+	—	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. gerardiana</i> Wall ex D.Dom in Lambert	—	—	—	—	—	—	+	+	+	—	—	—	+	—	+	+	—	—	—	—	+	—	+	—	+	—	+

Table A1. Cont.

<i>P. griffithii</i> McClell	—	—	—	—	—	—	+	+	+	—	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. halepensis</i> Mill.	—	—	—	—	—	—	+	+	+	—	—	+	—	+	+	+	—	—	—	—	+	—	+	+	+	+	+
<i>P. hartwegii</i> Lindl.	—	—	—	—	—	—	+	+	+	—	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. heldreichii</i> D. H. Christ.	—	—	—	—	—	—	+	—	+	+	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	+
<i>P. jeffreyi</i> Balf. in Murray	—	—	—	—	—	—	+	—	+	+	—	+	—	+	—	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. kesiya</i> Royle ex Gordon	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. koraiensis</i> Siebold. & Zucc.	—	—	—	—	—	—	+	+	—	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. lawsonii</i> Roez. ex Gordon	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. leiophylla</i> Schlecht & Cham.	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. massoniana</i> Lambert	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. maximinoi</i> H.E. Moore	—	—	—	—	—	—	+	—	+	+	—	+	—	+	—	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. merkusii</i> Jung. & de Vriese	—	—	—	—	—	—	+	+	+	—	—	+	—	+	—	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. monophylla</i> Torr. & Frém.	—	—	—	—	—	—	+	+	+	—	—	—	+	—	+	+	—	—	—	—	+	—	+	—	+	—	+
<i>P. montezumae</i> Lamb.	—	—	—	—	—	—	+	—	+	—	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. morrisonicola</i> Hayata	—	—	—	—	—	—	+	+	—	—	—	+	—	+	+	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. mugo</i> Turra subsp. <i>uncinata</i> (Ramond ex DC.) Domin	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. nigra</i> J. F. Arnold	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	+	—	—	—	+	—	+	+	+	+	—
<i>P. palustris</i> Mill.	—	—	—	—	—	—	+	—	+	+	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. parviflora</i> Siebold. & Zucc.	—	—	—	—	—	—	+	+	—	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. peuce</i> Griseb.	—	—	—	—	—	—	+	+	—	—	—	+	—	+	+	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. pinaster</i> Aiton	—	—	—	—	—	—	+	—	+	—	—	+	—	+	+	+	—	—	—	—	+	—	+	+	+	+	—
<i>P. pinea</i> L.	—	—	—	—	—	—	+	+	+	—	—	—	+	—	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. ponderosa</i> Douglas ex C. Lawson	—	—	—	—	—	—	+	—	+	+	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. pseudostrobus</i> Lindl.	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. quadrifolia</i> Parl. ex Sudw.	—	—	—	—	—	—	+	+	+	—	—	—	+	—	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. radiata</i> D. Don	—	—	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. resinosa</i> Aiton	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. rigida</i> Mill.	—	—	—	—	—	—	+	—	+	+	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	—

Table A1. Cont.

<i>P. strobus</i> L.	—	—	—	—	—	—	+	+	—	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. sylvestris</i> L.	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. tabuliformis</i> Carrière	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. taeda</i> L.	—	—	—	—	—	—	+	—	+	+	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. tecunumanii</i> Eguiluz & J. P. Perry	—	—	—	—	—	—	+	—	+	+	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. teocote</i> Schiede & Schlecht.	—	—	—	—	—	—	+	—	+	—	—	+	—	+	+	+	—	—	—	—	+	—	+	—	+	—	—
<i>P. thunbergii</i> Parl.	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. tropicalis</i> Morelet	—	—	—	—	—	—	+	—	+	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>P. wallichiana</i> A. B. Jacks. var. <i>wallichiana</i>	—	—	—	—	—	—	+	+	—	—	—	+	—	+	—	—	+	—	—	—	+	—	+	—	+	—	—
<i>Pseudolarix amabilis</i> Rehder	—	—	—	—	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	—	—	—	—	—	+	+
<i>Pseudotsuga menziesii</i> (Mirb.) Franco	—	+	—	—	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	+	+	+	—
<i>P. menziesii</i> (Mirb.) Franco var. <i>menziesii</i>	—	+	—	—	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—
<i>P. sinensis</i> Dode	—	+	—	—	+	+	+	+	—	—	+	—	+	—	+	—	—	+	—	—	+	+	—	—	+	—	—
<i>Tsuga canadensis</i> Carrière	—	—	—	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	—	—	—	+	—	—	+
<i>T. caroliniana</i> Engelm.	—	—	—	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	—	—	—	—	—	—	+
<i>T. chinensis</i> (Franch.) Pritzel in Diels	—	—	—	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	—	—	—	—	—	—	+
<i>T. diversifolia</i> (Maxim.) Mast.	—	—	—	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	—	—	—	—	—	—	+
<i>T. dumosa</i> Eichl.	—	—	—	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	—	—	—	—	—	—	—
<i>T. heterophylla</i> Sarg.	—	—	—	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	—	—	—	—	—	—	+
<i>T. mertensiana</i> (Bong.) Carrière	—	—	—	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	—	—	—	—	—	—	+
<i>T. sieboldii</i> Carrière	—	—	—	+	+	+	+	+	—	—	—	—	+	—	+	—	—	+	—	—	—	—	—	—	—	—	+

¹ only in latewood; ² reported by Jin-Xing et al. [11]; ³ reported by Wu and Hu [4].

References

1. POWO. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Available online: <http://www.plantsoftheworldonline.org/> (accessed on 14 July 2021).
2. Frankis, M.P. Generic inter-relationships in Pinaceae. *Notes R. Bot. Gard. Edinb.* **1989**, *45*, 527–548.
3. Farjon, A. *Pinaceae: Drawings and Descriptions of the Genera Abies, Cedrus, Pseudolarix, Keteleeria, Nothotsuga, Tsuga, Cathaya, Pseudotsuga, Larix and Picea*; Koeltz Scientific Books: Königstein, Germany, 1900; p. 330.
4. Wu, H.; Hu, Z.H. Comparative anatomy of resin ducts of the Pinaceae. *Trees Struct. Funct.* **1997**, *11*, 135–143. [\[CrossRef\]](#)
5. Lin, J.X.; Liang, E.Y.; Farjon, A. The occurrence of vertical resin canals in *Keteleeria*, with reference to its systematic position in Pinaceae. *Bot. J. Linn. Soc.* **2000**, *134*, 567–574. [\[CrossRef\]](#)
6. Bailey, I.W. Anatomical characters in the evolution of *Pinus*. *Am. Nat.* **1910**, *44*, 284–293. [\[CrossRef\]](#)
7. Phillips, E.W.J. *Identification of Softwoods by their Microscopic Structure*; Forest Products Research Bulletin No. 22; HMSO: London, UK, 1948; p. 55.
8. Greguss, P. *Identification of Living Gymnosperms on the Basis of Xylotomy*; Akadémiai Kiadó: Budapest, Hungary, 1955; p. 263.
9. Jacquot, C. *Atlas D'anatomie des Bois des Conifères*; Institut National du Bois: Paris, France, 1955; p. 134.
10. Kukachka, B.F. Identification of coniferous woods. *Tappi* **1960**, *43*, 887–896.
11. Jin-Xing, L.; Yu-Shi, H.; Wang, F.H. Wood and Bark Anatomy of *Nothotsuga* (Pinaceae). *Ann. Mo. Bot. Gard.* **1995**, *82*, 603–609. [\[CrossRef\]](#)
12. Esteban, L.G.; de Palacios, P.; Guindeo, A.; García, L.; Lázaro, I.; González, L.; Rodríguez, Y.; García, F.; Bobadilla, I.; Camacho, A. *Anatomy and Identification of Conifers Wood as a Species*; Fundación Conde del Valle de Salazar-Mundi Prensa: Madrid, Spain, 2002; p. 421.
13. Esteban, L.G.; de Palacios, P.; García Fernández, F.; Martín, J.A. Wood anatomical relationships within *Abies* spp. from the Mediterranean area: A phyletic approach. *Investig. Agrar. Sist. Recur. For.* **2009**, *18*, 213–225. [\[CrossRef\]](#)
14. Esteban, L.G.; de Palacios, P.; García Fernández, F.; Moreno, R. Wood anatomy of the genus *Abies*: A review. *IAWA J.* **2009**, *30*, 231–245. [\[CrossRef\]](#)
15. Heinz, I. *Systematische Erfassung und Dokumentation der Mikroanatomischen Merkmale der Nadelhölzer aus der Klasse der Pinatae*; Technische Universität München: Munich, Germany, 2004; p. 209.
16. Bannan, M.W. Vertical resin ducts in the secondary wood of the Abietineae. *New Phytol.* **1936**, *35*, 11–46. [\[CrossRef\]](#)
17. Xie, F.H. *Wood Structure and Taxonomical Position of Cathaya (Abstract)*. *Symposium on the Exploitation of Tropical Resources in South China*; Forestry Press: Beijing, China, 1957.
18. Kennedy, R.W.; Sastry, C.B.R.; Barton, G.M.; Ellis, E.L. Crystals in wood of genus *Abies* indigenous to Canada and United States. *Can. J. Bot.* **1968**, *46*, 1221–1228. [\[CrossRef\]](#)
19. Jain, K.K. Evolution of wood structure in Pinaceae. *Isr. J. Bot.* **1976**, *25*, 28–33.
20. Fahn, A. *Secretory Tissues in Plants*; Academic Press: London, UK, 1979; p. 302.
21. Liston, A.; Gernandt, D.S.; Vining, T.F.; Campbell, C.S.; Piñero, D. Molecular phylogeny of Pinaceae and *Pinus*. *Acta Hort.* **2003**, *615*, 107–114. [\[CrossRef\]](#)
22. Gernandt, D.S.; Magallón, S.; López, G.G.; Flores, O.Z.; Willyard, A.; Liston, A. Use of simultaneous analyses to guide fossil-based calibrations of Pinaceae phylogeny. *Int. J. Plant Sci.* **2008**, *169*, 1086–1099. [\[CrossRef\]](#)
23. Lynch, A.H.; Gasson, P.; Lens, F. Index Xylariorum 4.1. Institutional Wood Collections of the World. *IAWA J.* **2016**. Available online: <https://www.iawa-website.org/uploads/soft/Abstracts/Index%20Xylariorum%204.1.pdf> (accessed on 14 July 2021).
24. Jane, F.W. *The Structure of Wood*, 2nd ed.; Adam & Charles Black: London, UK, 1970; p. 478.
25. Richter, H.G.; Grosser, D.; Heinz, I.; Gasson, P.E. IAWA COMMITTEE. IAWA List of microscopic features for softwood identification. *IAWA J.* **2004**, *25*, 1–70. [\[CrossRef\]](#)
26. Holden, R. Ray tracheids in the Coniferales. *Bot. Gaz.* **1913**, *55*, 56–65. [\[CrossRef\]](#)
27. Hudson, R.H. The anatomy of the genus *Pinus* in relation to its classification. *J. Inst. Wood Sci.* **1960**, *6*, 26–46.
28. Chamberlain, C.J. *Gymnosperms. Structure and Evolution*; University of Chicago Press: Chicago, IL, USA, 1935; p. 484.
29. Wang, X.Q.; Tank, D.C.; Sang, T. Phylogeny and divergence times in Pinaceae: Evidence from three genomes. *Mol. Biol. Evol.* **2000**, *17*, 773–781. [\[CrossRef\]](#)
30. Chrysler, M.A. The medullary ray of *Cedrus*. *Bot. Gaz.* **1915**, *59*, 387–396. [\[CrossRef\]](#)
31. Willebrand, G. Untersuchung von ausgewählten mikroanatomische Merkmalen zur Bestimmung von Nadelhölzern. Ph.D. Thesis, Fachhochschule Rosenheim, Rosenheim, Germany, 1995.
32. Esteban, L.G.; de Palacios, P.; Guindeo, A.; Fernandez, F.G. Comparative anatomy of the wood of *Abies pinsapo* and its two Moroccan varieties. *IAWA J.* **2007**, *28*, 285–299. [\[CrossRef\]](#)
33. Esteban, L.G.; Guindeo, A.; de Palacios, P. *Maderas de Coníferas. Anatomía de Géneros*; Fundación Conde del Valle de Salazar: Madrid, Spain, 1996; p. 336.
34. Esteban, L.G.; Gasson, P.; Climent, J.M.; de Palacios, P.; Guindeo, A. The wood of *Pinus canariensis* and its resinous heartwood. *IAWA J.* **2005**, *26*, 69–77. [\[CrossRef\]](#)

35. Esteban, L.G.; de Palacios, P. Comparative wood anatomy in Abietoideae (Pinaceae). *Bot. J. Linn. Soc.* **2009**, *160*, 184–196. [[CrossRef](#)]
36. Kellogg, R.M.; Rowe, S.; Koeppen, R.C.; Miller, R.B. Identification of the wood of the soft pines of Western North-America. *IAWA Bull.* **1982**, *3*, 95–101. [[CrossRef](#)]
37. Wiedenhoef, A.C.; Miller, R.B.; Theim, T.J. Analysis of three microscopic characters for separating the wood of *Pinus contorta* and *P. ponderosa*. *IAWA J.* **2003**, *24*, 257–267. [[CrossRef](#)]
38. Bailey, I.W.; Faull, A.F. The cambium and its derivative tissues. IX. Structural variability in the redwood, *Sequoia sempervirens*, and its significance in the identification of fossil woods. *J. Arnold Arbor.* **1934**, *15*, 233–254. [[CrossRef](#)]
39. Jeffrey, E.C. The comparative anatomy and phylogeny of the Coniferales. Part 1. The genus *Sequoia*. *Mem. Boston Soc. Nat. Hist.* **1903**, *5*, 441–459.
40. Benkova, V.E.; Schweingruber, F.H. *Anatomy of Russian Woods. An Atlas for the Identification of Trees, Shrubs, Dwarf Shrubs and Woody Lianas from Russia*; Haupt Verlag: Bern, Switzerland, 2004; p. 456.
41. Esteban, L.G.; de Palacios, P.; García-Iruela, A.; Román-Jordán, E.; García-Fernández, F.; Díaz Fernández, S.; Conde, M. Wood anatomy of *Tetraclinis articulata* from its natural distribution area in southeast Spain. *IAWA J.* **2015**, *36*, 22–35. [[CrossRef](#)]
42. Gugerli, F.; Sperisen, C.; Buchler, U.; Brunner, L.; Brodbeck, S.; Palmer, J.D.; Qiu, Y.L. The evolutionary split of Pinaceae from other conifers: Evidence from an intron loss and a multigene phylogeny. *Mol. Phylogenet. Evol.* **2001**, *21*, 167–175. [[CrossRef](#)] [[PubMed](#)]
43. Hart, J.A. A cladistic analysis of conifers: Preliminary results. *J. Arnold Arbor.* **1987**, *68*, 269–307. [[CrossRef](#)]
44. Price, R.A.; Olsen-Stojkovich, J.; Lowenstein, J.M. Relationships among the genera of Pinaceae: An immunological comparison. *Syst. Bot.* **1987**, *12*, 91–97. [[CrossRef](#)]
45. Greguss, P. Similar xylotomy and leaf-epidermis of the *Pseudotsuga* and new genus *Cathaya*. *Bot. Közlemények* **1970**, *57*, 51–55.
46. Greguss, P. *Xylotomy of the Living Conifers*; Akadémiai Kiadó: Budapest, Hungary, 1972; p. 379.
47. Wang, X.Q.; Han, Y.; Hong, D.Y. PCR-RFLP analysis of the chloroplast gene *trnK* in the Pinaceae, with special reference to the systematic position of *Cathaya*. *Isr. J. Plant Sci.* **1998**, *46*, 265–271. [[CrossRef](#)]