

Softwood Anatomy: A Review

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Abstract: Although conifers have very homogeneous wood anatomical structure, some of their features allow differentiation of genera or groups of genera. Softwood anatomy is reviewed and the authors have added contributions, grouping features in five blocks (axial tracheids, axial parenchyma, rays, resin canals and mineral inclusions), with special attention to their diagnostic value at the family, genus or species levels. The discussion addresses, in axial tracheids: growth rings, intercellular spaces, pit arrangement, presence of scalloped tori, torus extensions, notches, warty layer, organic deposits, helical and callitroid thickenings, bars of Sanio and trabeculae; in axial parenchyma: presence or absence, arrangement and type of transverse end walls; in rays: composition, type of horizontal and end walls and cross-field pitting; in resin canals: epithelium and the presence of normal or traumatic resin canals; and in mineral inclusions: presence or absence. Wood structure is characterised at the family level, discussing the main elements that can be used for diagnosis at the genus level or in groups of genera.

Keywords: conifers; Araucariaceae; Cupressaceae; gymnosperms; Pinaceae; Podocarpaceae; Sciadopityaceae; softwoods; Taxaceae; wood anatomy

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1. Gymnosperms

Based on molecular phylogeny, Cole et al. [1] divided the gymnosperms into five orders (Cycadales, Ginkgoales, Gnetales, Pinales and Cupressales) (Figure 1). A total of 669 species, comprising 72 genera in six families (Araucariaceae, Cupressaceae, Pinaceae, Podocarpaceae, Sciadopityaceae and Taxaceae) [2] included in the orders Pinales (Pinaceae) and Cupressales (Araucariaceae, Cupressaceae, Podocarpaceae, Sciadopityaceae and Taxaceae), are known generically by the term conifers (Figure 2) and produce wood in the strict sense (i.e., secondary xylem). The family with the highest number of species is Pinaceae (235), followed by Podocarpaceae (191) and Cupressaceae (170). The most numerous genera by far are *Pinus* (118) and *Podocarpus* (115).

The wood produced in Cycadales (Cycadaceae and Zamiaceae) and Gnetales (Ephedraceae, Welwitschiaceae and Gnetaceae) (Figures 3 and 4) differs from conifer wood.

In Ginkgoales, *Ginkgo* is very similar to *Cycas* in embryology, but in macromorphology and vegetative anatomy it is more similar to the conifers, suggesting that it may occupy an intermediate phylogenetic position between cycads and conifers [3]. It has secondary growth and produces wood similar to conifers, with abundant druse crystal

inclusions in axial parenchyma [4]. Because of its similarity to conifer wood, *Ginkgo* was included in the *IAWA list of microscopic features for softwood identification* [5] (Figure 5).

In the genus *Cycas*, Terrazas [6] confirmed the presence of a first vascular cambium simultaneously active alongside later successive cambia. The secondary xylem of *Cycas* can be described schematically as the presence of rows of tracheids mixed with thin-walled parenchyma cells.

The nine genera of Zamiaceae (*Bowenia* Hook., *Ceratozamia* Brongn., *Dioon* Lindl., *Encephalartos* Lehm., *Lepidozamia* Regel, *Macrozamia* Miq., *Microcycas* (Miq.) A.DC., *Stangeria* T.Moore, *Zamia* L.) have a similar structure to Cycadaceae (monoxylie), with rows of tracheids and abundant parenchyma cells, generally with high starch content.

The genus *Ephedra*, the only one in Ephedraceae, develops wood with features characteristic of conifers and Dicotyledonous Angiosperms, causing Carlquist [7] to question which group it belongs to. Some authors [8,9] considered it to clearly be a Gymnosperm, while others [10] described it as an Angiosperm due to the presence of vessels with scalariform perforation plates. The presence of elements characteristic of both large groups (Angiosperm vessels and conifer tracheids) certainly makes this genus very special from an anatomical and evolutionary perspective (Figure 5).

Welwitschia mirabilis Hook. f. produces in its lifetime only two leaves, whose tips necrose as the plant grows. The plant develops a small trunk, where successive cambia develop, producing xylem and phloem, although not annually. It produces vessel elements and tracheids that are always very narrow, and therefore, all secondary xylem can be considered latewood in character [11,12]. Structurally, it is very different from typical conifer or dicotyledonous angiosperm wood, but its individual elements are characteristic of wood (vessels with simple perforation plates, tracheids, small portions of diffuse axial parenchyma between vessels and tracheids of the secondary xylem and rays with exclusively upright cells).

Gnetum also contains tracheids and vessels with secondary growth similar to *Ephedra*, in tree or bush species, while lianoid species have anomalous cambial growth [13]. The primary cambium quickly ceases activity and successive cambia appear from the outermost secondary phloem towards the inside (Figure 5).

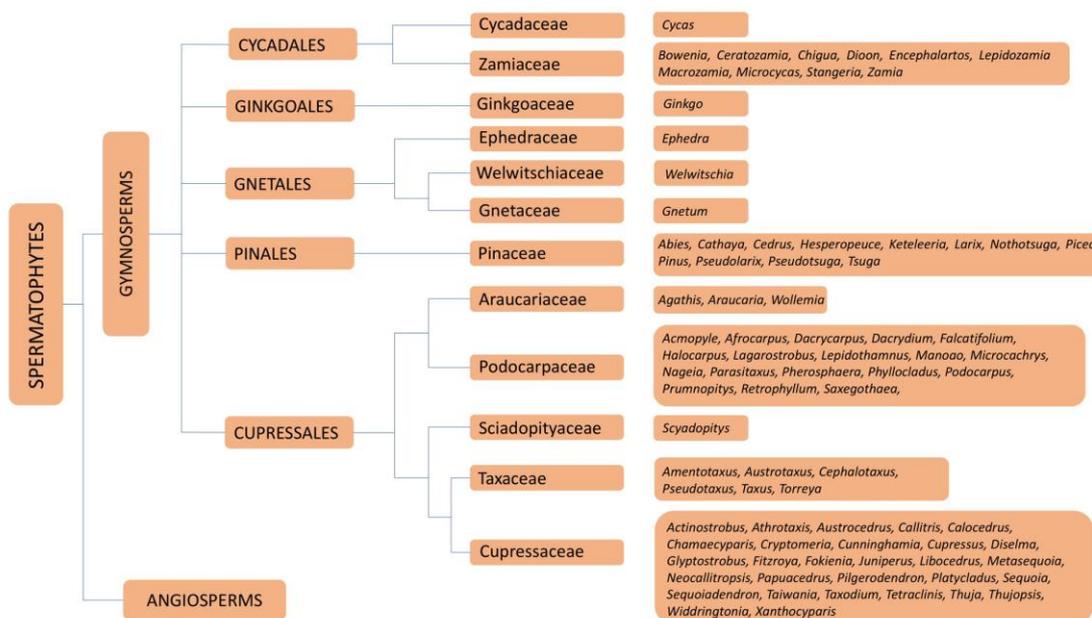


Figure 1. Gymnosperm tree based on molecular phylogeny data of tracheophytes [1].

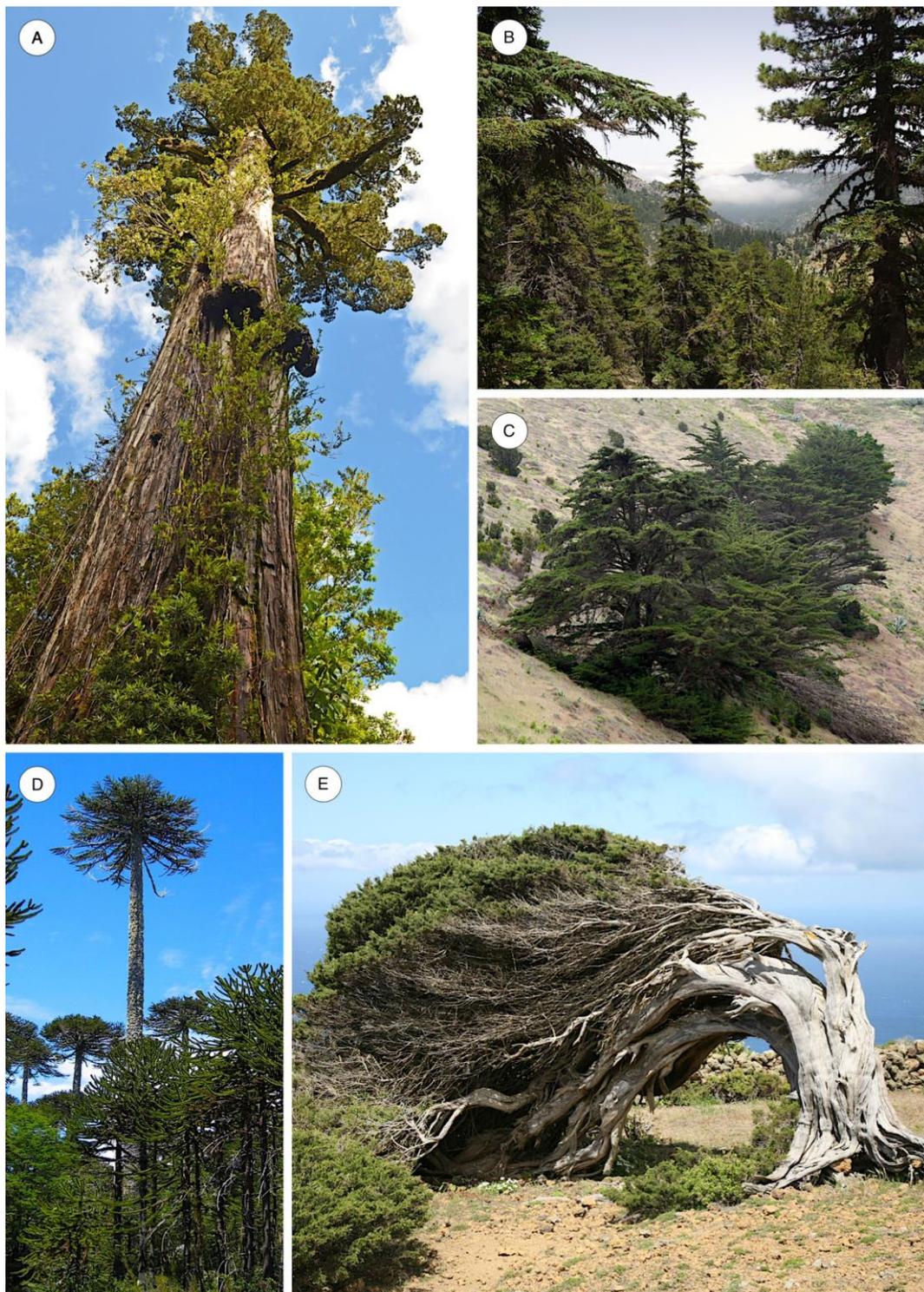


Figure 2. Coniferous gymnosperms. (A) *Fitzroya cupressoides* (Molina) I.M.Johnst.; (B) Mixed conifer forest of *Abies pinsapo* subsp. *marocana* (Trab.) Emb. and Maire, *Cedrus atlantica* (Endl.) Manetti ex Carrière and *Pinus nigra* subsp. *salzmannii* (Dunal) Franco; (C) *Juniperus cedrus*, Webb and Berthel.; (D) *Araucaria araucana* (Molina) K.Koch; (E) *Juniperus canariensis*, Guyot and Mathou.



Figure 3. Non-coniferous gymnosperms. (A) *Cycas revoluta* Thunb.; (B) *Ginkgo biloba* L.; (C) *Zamia* sp.



Figure 4. Non-coniferous gymnosperms. (A) *Ephedra viridis* Coville; (B) *Welwitschia mirabilis* Hook. f.; (C) *Gnetum gnemon* L.

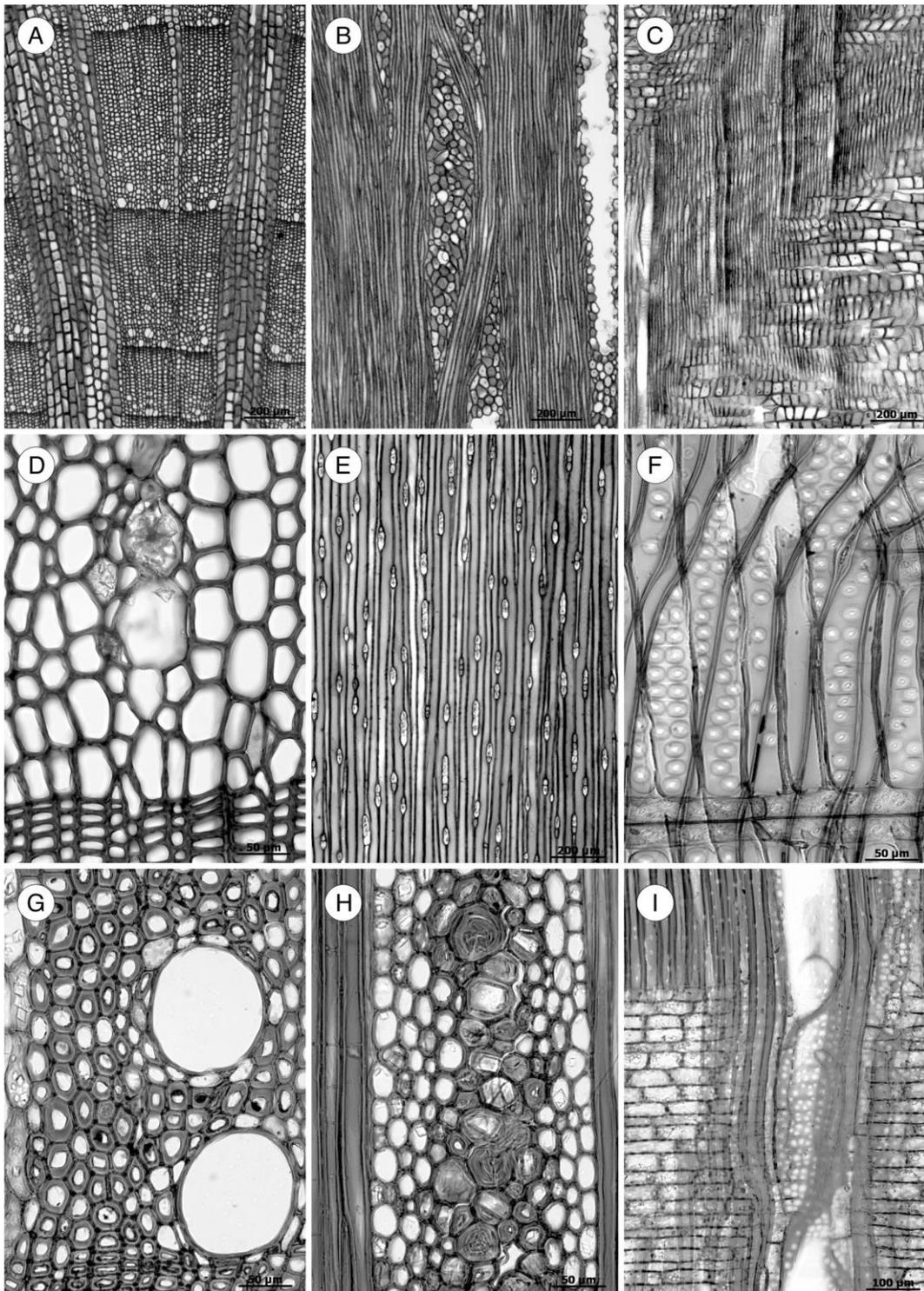


Figure 5. Anatomy of the “wood” of non-coniferous gymnosperms. (A–C) *Ephedra gerardiana* Wall. ex Klotzsch and Garcke; (D–F) *Ginkgo biloba* L.; (G–I) *Gnetum gnemon* L.

The use of molecular phylogeny continues in the production of numerous changes in conifer systematics and taxonomy. However, this does not affect the study of their anatomy unless the aim is to make an association between anatomy and phylogeny, a good way to answer certain questions, such as the place of *Cedrus* in Abietoideae. Unlike the other Abietoideae genera, *Cedrus* is the only genus of this subfamily capable of forming traumatic axial and radial resin canals [14]. Molecular phylogenetic studies indicate that

Cedrus is the only problematic genus of the six genera included in Abietoideae (*Abies-Cedrus-Keteleeria-Nothotsuga-Pseudolarix-Tsuga*) [15].

Nonetheless, taxonomic classification is a dynamic process with the discovery of new genera and species [16], which necessitates ongoing review using both morphological and molecular studies [17].

2. Geographical Distribution of Conifers

Conifers are widely distributed around the world and although they have been on Earth for more than 300 million years, they continue to occupy and dominate extensive areas of vegetation, particularly in the northern hemisphere.

The distribution pattern of conifers differs from north to south. The extensive boreal forest belt around Earth is dominated by a few species. The number of species increases in the south, with a predominant pattern of a more abundant presence of conifers in the principal mountain ranges, e.g., western North America, Mexico and Central America, the Andes, Europe (circum-Mediterranean forest belt from Spain to Greece), North Africa (Atlas Mountains), the Himalaya (extending towards China and Japan), New Guinea and New Zealand. In the eastern United States and southeast China, angiosperm forests predominate. Australia and Malaysia have unexpected occurrences of conifers, and some small islands are rich in conifers, e.g., New Caledonia, Taiwan and Tasmania. Conifers are absent only in Antarctica, the northern Arctic, steppes and deserts, the Amazon Basins, the Congo Basin and West Africa, where tropical forests occur, the Indian subcontinent (where only *Nageia wallichiana* occurs, in the Western Ghats), and most of the Tibetan Plateau. In Africa, in addition to forests in the north (Atlas Mountains from Morocco to Algeria), two other two geographical areas are significant for conifers: the region from Ethiopia to South Africa, and Madagascar [18] (Figure 6).

The families Pinaceae, Sciadopityaceae and Taxaceae are virtually confined to the northern hemisphere, whereas Araucariaceae and Podocarpaceae occur in the southern hemisphere and Cupressaceae occurs in both.

The extensive distribution of *Podocarpus*, *Araucaria* and *Agathis* in the southern hemisphere is thought to be due to the existence of the precursor species before the separation of the continents more than 125 million years ago [19].

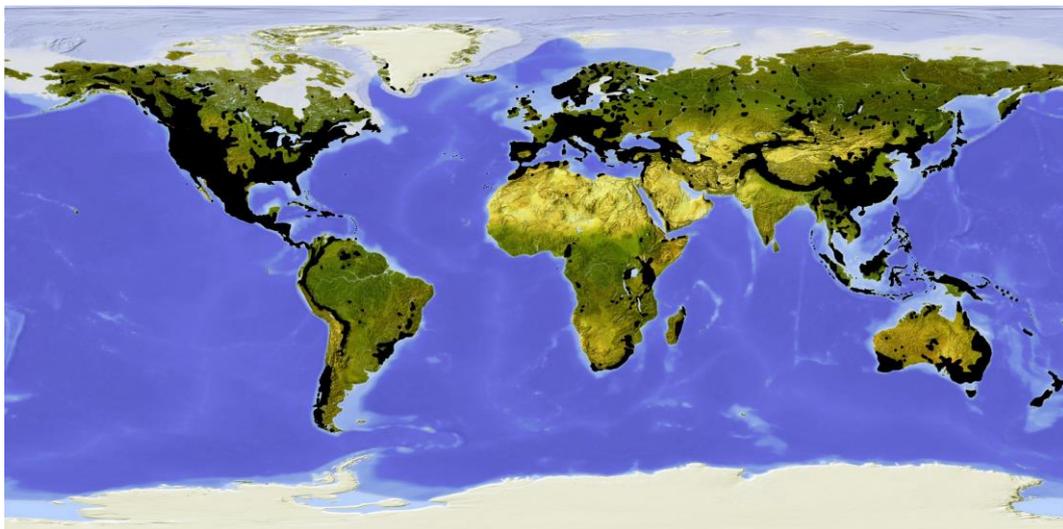


Figure 6. Worldwide distribution of conifers (shown in black) (based on Farjon and Filer [18]).

3. Softwood Structure

3.1. Literature

Conifer wood anatomy has been extensively studied since the second half of the 19th century. Sanio [20,21] described compression wood for the first time, Castellarnau [22] studied the wood of *Abies pinsapo*, Kleeberg [23] studied conifer rays and Penhallow [24] proposed a classification of North American conifers. Further studies in the first half of the 20th century increased knowledge of softwood anatomy, including those by Jeffrey [25] on the comparative anatomy and phylogeny of Coniferales and extending knowledge of the genus *Sequoia*; Bitting [26] on histological differences between *Pinus taeda* and *P. palustris*; Bailey [27] on the wood structure of Pineae; Brooks [28] on the wood of *Podocarpus spinulosus*; Baker and Smith [29] on the pines of Australia; Thompson [30,31] on the origin of rays in conifers and ray tracheids in the genus *Abies*, respectively; Gordon [32] on the ray tracheids of *Sequoia sempervirens*; Holden [33] on ray tracheids in Coniferae; Chrysler [34] on rays in the genus *Cedrus*; Jeffrey [35] on the anatomy of woody plants; Kanehira [36] providing an anatomical description of Formosan woods; Kanehira [37] describing the anatomical features of the most important woods of Japan; Saint-Laurent [38] on the anatomical features of the woods of Algeria; Patton [39] on the anatomy of the Australian conifers; Pool [40] on the wood anatomy of Araucaria; Metcalfe [41] describing the anatomy of *Fokienia hodginsii*; Brown and Panshin [42] in their work “*Commercial timbers of the United States: their structure, identification, properties, and uses*”, extended in the 1940 edition; Brem [43] proposing a method to differentiate *Picea* and *Larix*; Bannan [44] on axial resin canals in Abietineae; Peirce [45–48] describing the xylem of *Pseudolarix* and *Sciadopitys*, the anatomical interrelations in Taxodiaceae, and the systematic anatomy of the wood of Cupressaceae, respectively; Shimakura [49] describing the wood anatomy of Taiwan; Bernath [50] on the conifers of Chile and Covas [51] on the native conifers of Argentina.

The work by Phillips [52], subsequently reprinted without changes (1948, 1959 and 1963), was the first publication about the wood anatomical features of conifers, providing detailed descriptions of their features, with instructions on how to interpret them where necessary, and constituting a seminal work for later studies [5,53–57]. Adopting the approach of the work by Clark [58] on hardwoods, it included a system of multiple-entry-perforated cards. This work can be considered a turning point both in describing conifer wood using terminology that is still used today, and in identifying conifer wood using a multiple-entry system. From its publication until the proposal by the IAWA Committee [5], the number of related works increased (e.g., [53,54,59–88]).

The work by the IAWA Committee [5] is the list of softwood features currently used worldwide, and since 2020, Insidewood [89] includes these features and a search engine for conifer woods.

3.2. Softwood Identification

The work by Phillips [52] “*Identification of coniferous wood by their microscopic structure*” is probably the turning point from which softwood features were grouped. Alongside the use of perforated cards, a qualitative leap occurred in softwood identification based on anatomy. The work described 33 features divided into five groups (general features, tracheids, parenchyma, rays and resin ducts), in a radical shift from traditional dichotomous keys to a multiple-entry key. It did not include biometry, except for the number of resin canal epithelial cells and cross-field pits. Greguss [53] conducted a broad descriptive study in his work “*Identification of living Gymnosperms on the basis of xyloatomy*”, describing 345 species, and added 160 species in 1972 (*Xyloatomy of the living conifers*). Subsequently, Esteban et al. [56] published “*Anatomy and identification of conifers wood as a species*”, proposing a multiple-entry identification key with 81 anatomical features (axial tracheids, 29; axial parenchyma, 8; rays, 37; resin canals, 7), including the geographical distribution and descriptions of 352 species. Rather than addressing the impossible task of identifying

species, the authors aimed to characterise the species they listed. The features proposed were a little different from those addressed by the IAWA Committee [5] “*IAWA list of microscopic features for softwood identification*”, now the main document covering all softwood features available to be used by researchers to describe softwoods. Heinz [57] wrote the doctoral thesis “*Systematische Erfassung und Dokumentation der mikroanatomischen Merkmale der Nadelhölzer aus der Klasse der Pinatae*”, a broad study of softwood anatomy at family, genus and species level.

The use of computer databases, such as DELTA (Descriptive Language for Taxonomy), developed in Australia [90], and the addition of the conifer database to the University of North Carolina’s InsideWood platform in 2020 [89], have provided systems based on interactive multiple-entry keys that are very versatile for softwood identification.

Despite the anatomical homogeneity of softwoods, their structure contains sufficient features for reliable identification on a genus level. The objective of this study was to perform a literature review of softwood anatomy, which, alongside the contributions made by the authors, enables features with diagnostic value to be assigned to family and genus levels.

4. Material and Methods

The material comprised microscope slides of 352 species from the wood collection of the Universidad Politécnica de Madrid (UPMAw) and 420 species used by Heinz [57] in his doctoral thesis. All the samples were either collected by the authors themselves or obtained through exchanges with leading collections from highly recognised institutions dealing in wood anatomy, whose collections have been built up over decades.

Observations and photos were taken with a Leica DFC420 camera and Leica DM2500 light microscope (Leica Microsystems Inc., Buffalo Grove, IL, USA) and a JEOL JSM-6380 scanning electron microscopy (SEM).

For nomenclature and taxonomy at the family, genus and species levels, POWO [2] was used as the database. We also referred to The Gymnosperm Database. <http://www.conifers.org> (accessed on 20 November 2022) [91]. Only three exceptions were made: the genera *Actinostrobus* and *Neocallitropsis* were maintained as distinct from *Callitris*, and *Cupressus* and *Hesperocyparis* were dealt with together.

For geographical distribution, the work of Farjon and Filer [18] was used. The basis for reviewing features was the *IAWA list of microscopic features for softwood identification* [5].

5. Microscopic Features

5.1. Axial Tracheids

One of the most unique features of conifer woods is the homogeneity of their microscopic structure, which is primarily composed of axial tracheids. Because of this, they are known as homoxylous woods.

Modern tracheids appeared in the Early Devonian, while ray tracheids and axial parenchyma have been present since at least the Late Devonian or Early Carboniferous [92].

Tracheids are the most abundant element in present-day conifer wood, comprising 90% of the total xylem volume [93]. The remaining 10% is made up of three elements: axial parenchyma, rays and resin canals. In Araucariaceae, the absence of axial parenchyma and resin canals results in a percentage of axial tracheids as high as 95%. Their typical shape is a long prism, with tips obliquely truncated by planes parallel to a line in the radial section. They are joined longitudinally through these planes, forming alignments parallel to the axis of the trunk [94].

With regard to tracheid length, in the Late Carboniferous some plants contained tracheids several centimetres long (*Medullosa*), although today they are barely more than 1 cm in length. This large size, which is associated with a high number of pits, has led some researchers [95] to suggest, in Carboniferous genera (*Medullosa*, *Callistophyton* and *Lyginopteris*), atypical hydraulic activity linked to warm humid environments with no risk

of embolism caused by frost or drought. Strangely, although conditions were similar in some stages of the Mesozoic, no fossil records have been found with tracheids of that length or as many pits [96].

Tracheid length now varies from 2000 μm in *Taxus baccata* or 3500 μm in *Larix decidua* to 10,000 μm in *Araucaria angustifolia*. It is measured in macerated wood or using microscope slides using methods such as those described by Ladell [97] and Wilkins and Bamber [98], which are less accurate than maceration but provide satisfactory results. In any case, tracheid length must always be measured in mature wood due to the influence of the cambial age on length. The provenance of wood also affects tracheid length, with significant variation depending on whether the sample is from the trunk, branches or roots.

In some taxa with very low or very high tracheid length values, length can aid diagnosis, but in most cases it is of little diagnostic value.

In the transverse section, trees from temperate forests in both hemispheres produce wood with true growth rings, showing differences between earlywood and latewood. Species of Cupressaceae, Pinaceae and Taxaceae in these areas typically produce wood with distinct growth ring boundaries. In tropical and subtropical forests, however, rings correspond to the rainy season and are indistinct or only slightly distinct. In tropical mountain sites, growth rings can be distinct or indistinct. Araucariaceae and Podocarpaceae species are characteristic of these areas. The transition from earlywood to latewood can be abrupt or gradual (Figure 7).

Rings are normally gently curved in their outline, but in some species they are undulating (*Taxus* spp. and *Juniperus* spp.) or very undulating, as in *Pilgerodendron uviferum* (Cupressaceae). Undulations must be differentiated from what is known as hazel growth, characteristic of some species such as *Picea abies* and *Pinus jeffreyi*, an unexplained phenomenon [57]. All these features are associated with differences between earlywood and latewood, growth ring type and transition must be interpreted with caution when identifying species because they are not constant features but depend on the location of the species. The same occurs with the presence of false growth rings, normally produced by a particular phenomenon, or wedging growth rings, which result from partially absent wood formation in the transverse section, due to, among other causes, insufficient supply of reserve metabolites [99,100] (Figure 8).

Although it is typically very laborious to obtain tracheid length, wall thickness is easily determined. The IAWA Committee [5] and Heinz [57] established two groups of wood based on the ratio of the double wall thickness (2WT), always measured in the radial direction, and the lumen diameter (L) in latewood tracheids: thin-walled ($2WT < L$) and thick-walled ($2WT > L$) (Figure 9). Despite the relatively low diagnostic value of wall thickness, some groups of wood have $2WT-L$ ratios that can be used for diagnosis, such as the soft pines (thin-walled) or southern yellow pines, *Larix* spp. and *Pseudotsuga menziesii* (thick-walled).

The transverse section of axial tracheids, associated exclusively with earlywood tracheids, is polygonal in most softwoods but circular in certain species, e.g., some species of the genus *Juniperus*. A third type described by Willebrand [101] in *Agathis* and *Podocarpus*, refers to axial tracheids with polygonal outline and circular lumen (Figure 9).

In some taxa, the transverse section may present intercellular spaces frequently associated with tracheids more or less circular in outline, although they are also associated with polygonal tracheids, e.g., *Agathis alba* and *Pilgerodendron uviferum*. This feature, characteristic of some taxa such as *Juniperus communis*, *J. virginiana* and *Calocedrus formosana* [4], must not be confused with the intercellular spaces generated in compression wood as a result of the circular tracheids generated in this type of wood. It can be easily differentiated by verifying, in any section, the spiral grooves inherent to compression wood (Figure 10). The absence of intercellular spaces cannot not be used for diagnosis.

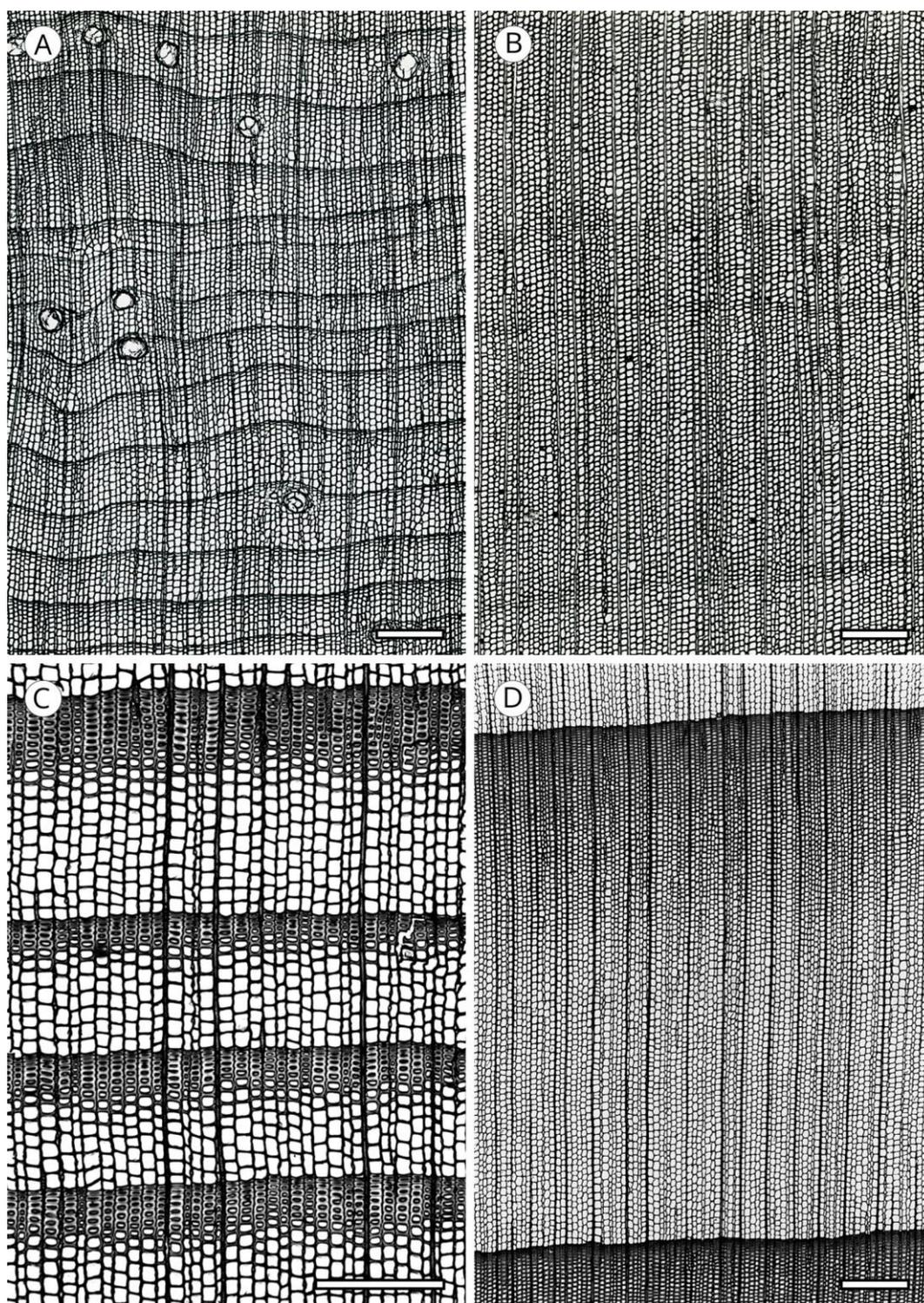


Figure 7. Growth rings. (A) Distinct growth ring boundaries in *Pinus cembra* L.; (B) Indistinct growth ring boundaries in *Afroparpus gracilior* (Pilg.) C.N. Page; (C) Growth rings with abrupt transition in *Abies nordmanniana* subsp. *equi-trojani* (Asch. & Sint. ex Boiss.) Coode and Cullen; (D) Growth rings with gradual transition in *Abies alba* Mill. Scale bars. (A–D) = 500 μ m.

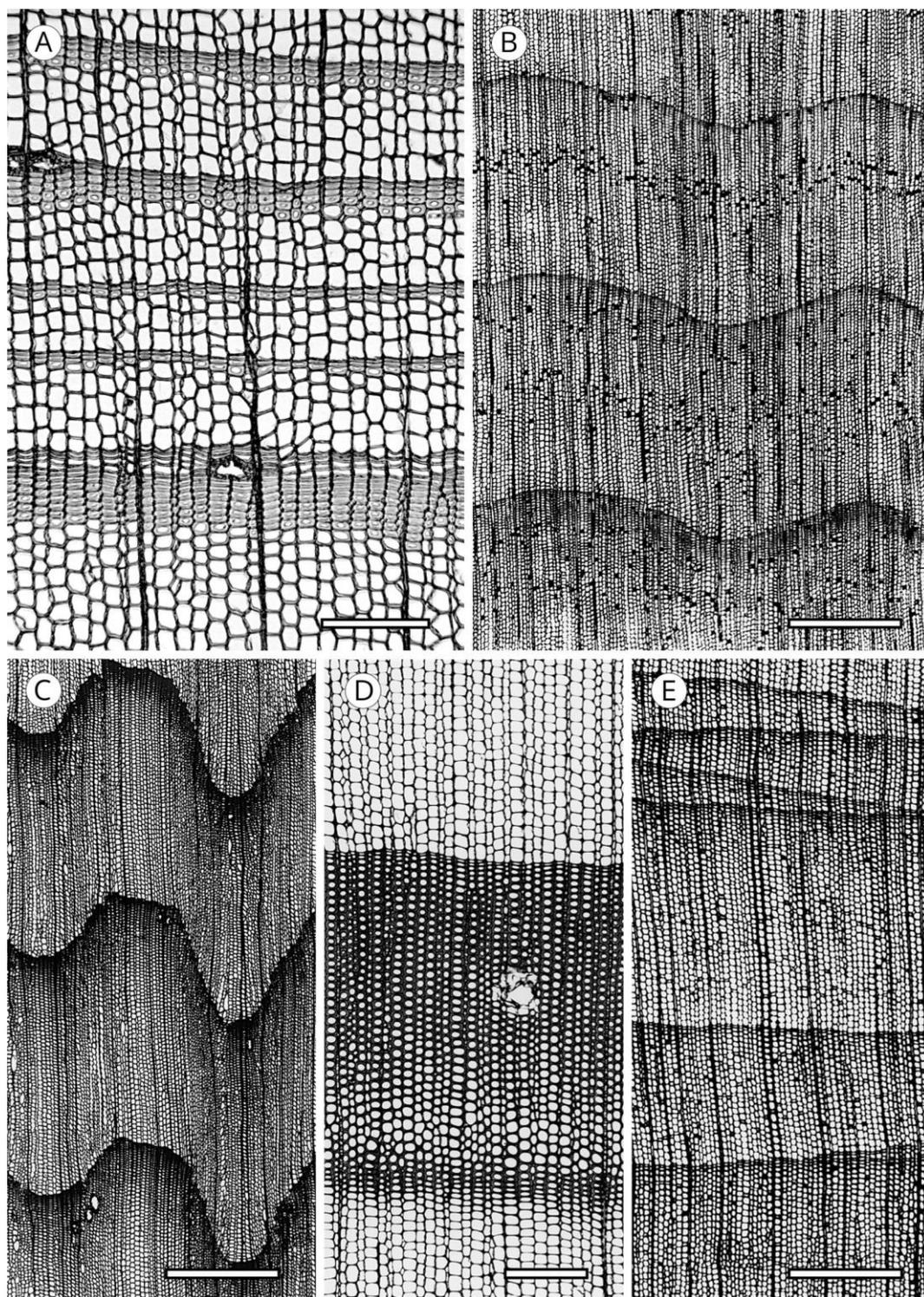


Figure 8. Growth rings. (A) Normal rings in *Larix sibirica* Ledeb.; (B) Undulating rings in *Picegerodendron uviferum* (D.Don) Florin; (C) Hazel growth rings in *Picea abies* (L.) H.Karst.; (D) False growth ring in *Pinus sylvestris* L.; (E) Wedging rings in *Nageia nagi* (Thunb.) Kuntze. Scale bars. (A) = 50 μm ; (B,C,E) = 1 mm; (D) = 250 μm .

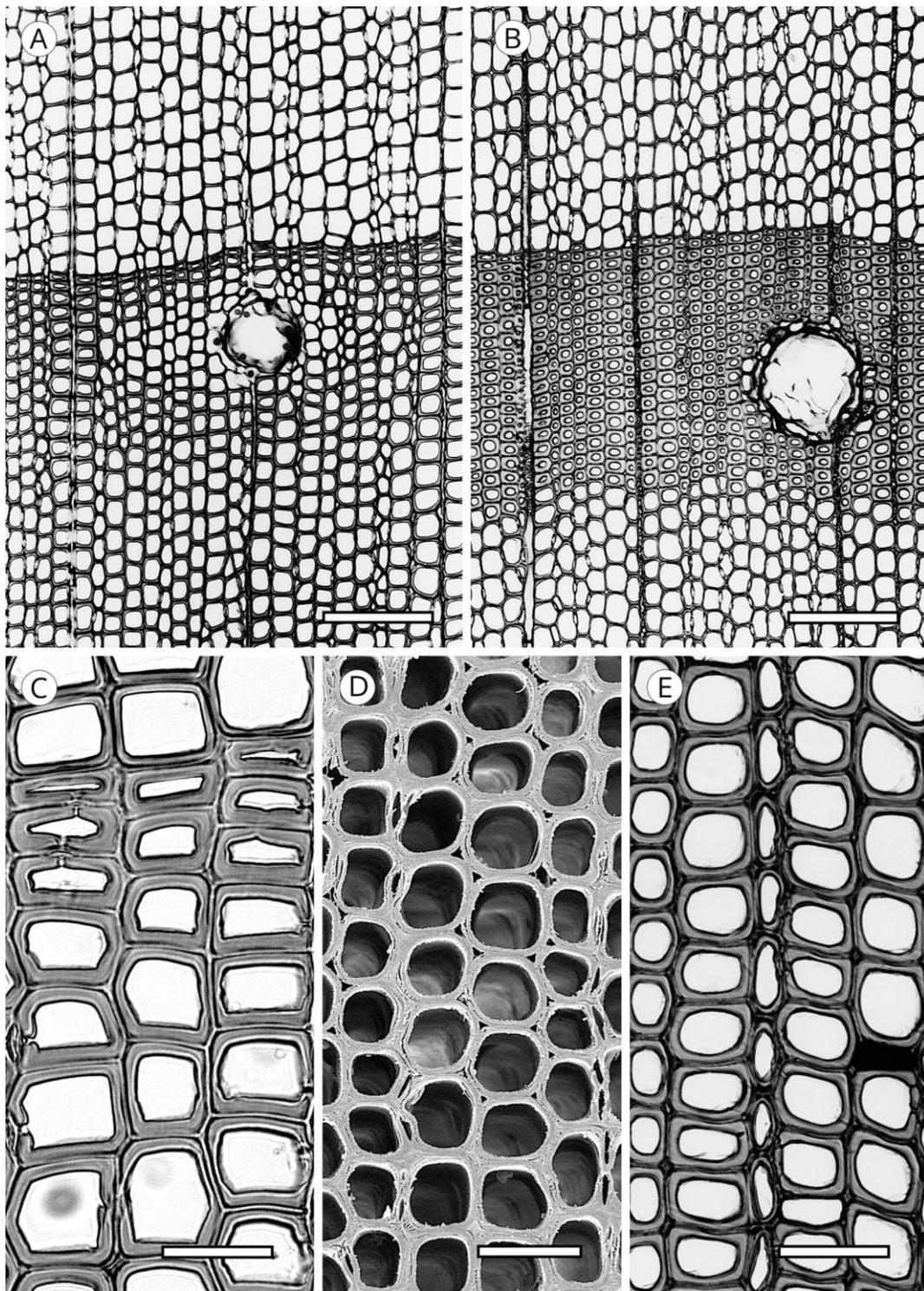


Figure 9. Axial tracheids. (A) Thin-walled in *Pinus strobus* L.; (B) Thick-walled in *Pinus palustris* Mill.; (C) Polygonal tracheids in *Callitropsis nootkatensis* (D.Don) Oerst. (Syn.—*Xanthocyparis nootkatensis* (D.Don) Farjon & Harder); (D) Circular tracheids in *Callitris endlicheri* (Parl.) F.M.Bailey (SEM); (E) Polygonal tracheids with circular lumen in *Falcatifolium falciforme* (Parl.) de Laub. Scale bars. (A,B) = 250 μ m; (C–E) = 50 μ m.

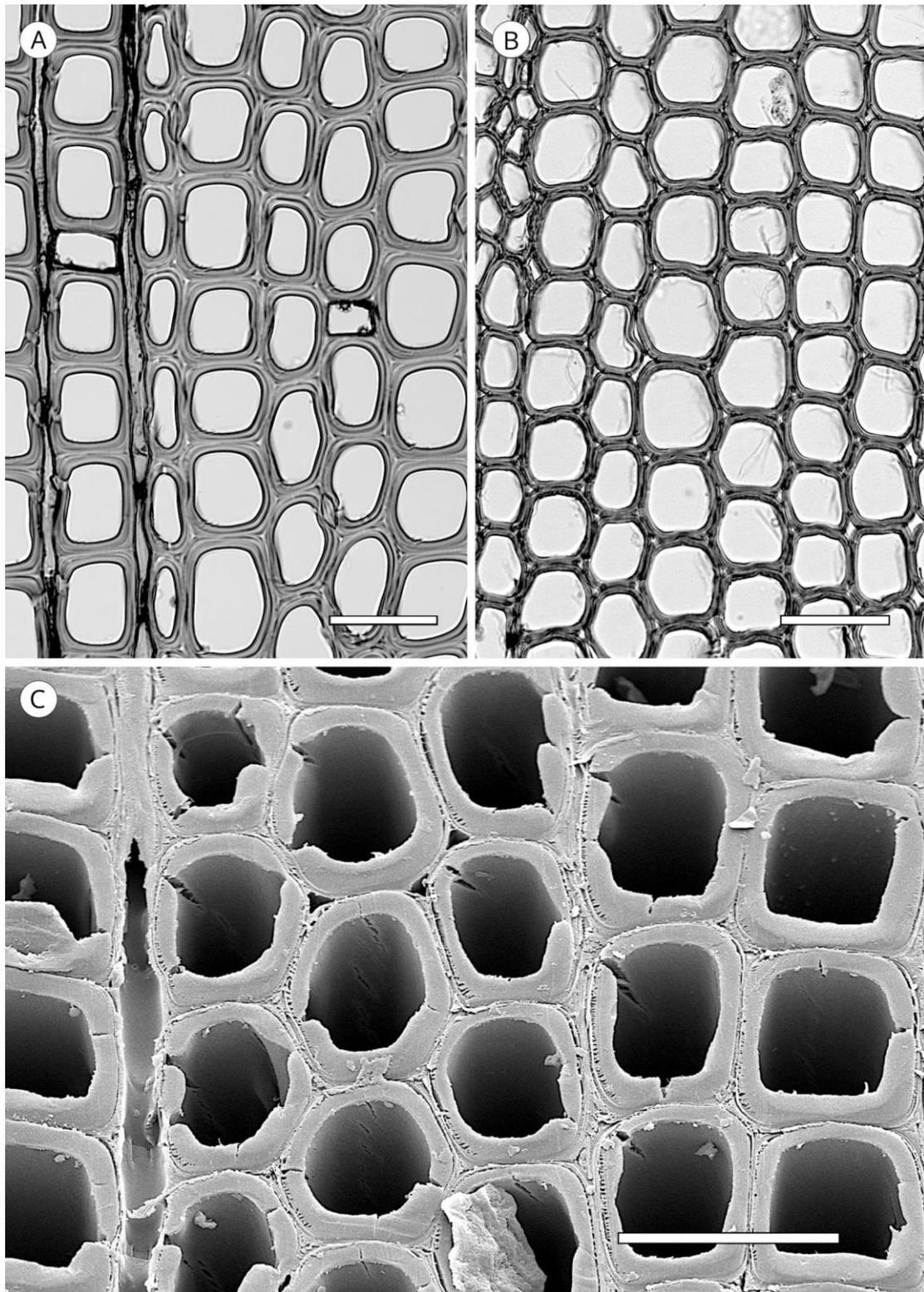


Figure 10. Intercellular spaces. (A) *Agathis alba* (Rumph. ex Hassk.) Foxw.; (B) *Pilgerodendron uviferum* (D.Don); (C) Intercellular spaces and spiral grooves in compression wood in *Taiwania cryptomerioides* Hayata (SEM). Scale bars. (A–C) = 50 μm .

These longitudinal intercellular spaces are connected only with radial intercellular spaces [102]. Intercellular spaces are generally thought to have three functions: for gas exchange, as a conduit for storage of water and nutrients, and as a pathway for diffusing heartwood substances [103].

5.1.1. Tracheid Pits

The first records of tracheid pits are from fossils of the Late Devonian–Early Carboniferous in progymnosperms and spermatophytes [104–106]. Although pits were originally circular, scalariform pits have also been found in tracheids of *Rellimia* and *Protopytis* [104].

The appearance of tracheid pits with a torus may have been one of the most important evolutionary stages in conifers. Their presence has ensured efficient conduction even in sites affected by drought and frost, safeguarding the existence of this type of plant in extreme climates such as tundra, deserts and high mountain sites, nearly always as dwarf trees and shrubs. Tracheid pits occur in all present-day conifers, in Gnetales and Ginkgoales but not in Cycadales [62], and have even been found in ferns of the genus *Botrychium* [107]. The earliest records are from the Middle Triassic [108] and their appearance remains an enigma in plant evolution, although they most likely correspond to the need to optimise conduction safety and efficiency.

Tracheid pits are located in tangential and radial walls, not always occurring in the former but always present in the latter, where they are larger in diameter and more numerous. Tangential wall pits are generally associated with latewood tracheids on the growth ring boundary and their presence appears to correspond to the improved transport at the end of the growing season (Figure 11). Unlike radial wall pits, they have no crassulae thickenings [93]. The greater spacing between tangential pits and their smaller diameter probably make strengthening the periphery of these pits with crassulae thickenings unnecessary.

Tangential pits have no diagnostic value. In a study of 230 species, Willebrand [101] concluded that the presence of this feature could not be assigned to any of them.

Tracheid pitting appears as a thickening of the secondary cell wall, extending over the non-thickened part in a dome shape, normally smooth and occasionally with radial striation, perforated at the vertex (aperture), leaving a space known as a chamber. The middle lamella has a thickening, known as a torus. Under normal conditions, water moves from one tracheid to another through the margo, which is located in the central plane of communication between the two tracheids and allows fluids to pass through it. When conditions are adverse, e.g., embolism due to extreme temperatures, the margo membrane is aspirated against the pit aperture and the torus plugs it, preventing air-seeding. Tracheids are not only efficient conductors, but also ensure a high level of hydraulic safety in adverse conditions. The torus has traditionally been thought of as an impermeable disc that functions as a valve, but in some species the torus is punctured by plasmodesmatal pores with a mean diameter of about 50 nanometres. Although most pores do not extend through the entire torus, there appears to be a relationship between species with a punctured torus and lower resistance to cavitation. However, it seems unlikely that punctured tori are the only cavitation mechanism in conifers, as this feature does not occur in all conifer species [109] (Figure 12).

The arrangement of tracheid pitting must be observed in earlywood tracheids. It is usually uniseriate but is biseriate in some taxa, generally opposite (e.g., *Larix* spp.). In some species of Pinaceae, tracheid pitting has a tendency toward alternate biseriate arrangement (e.g., *Cedrus* spp., *Keteleeria* spp.). Biseriate pitting is common in Araucariaceae, Cupressaceae (e.g., *Widdringtonia*, *Taxodium*), Pinaceae (e.g., *Cedrus*, *Larix*, *Pinus*, *Tsuga*) and Podocarpaceae (e.g., *Phyllocladus*, *Podocarpus*). Opposite multiseriate (three or more) tracheid pitting also occurs in *Sequoia sempervirens*, *Taiwania cryptomerioides* and *Taxodium distichum* [64]. In the three genera of Araucariaceae it is alternate and polygonal in appearance, as described by Phillips [52] in *Araucaria* and *Agathis* and Heady et al. [81] in *Wollemia* (Figure 13). Pit arrangement is a very important feature for wood identification and a key factor in plant evolution. Ancestral gymnosperm pits are thought to have been alternate [84].

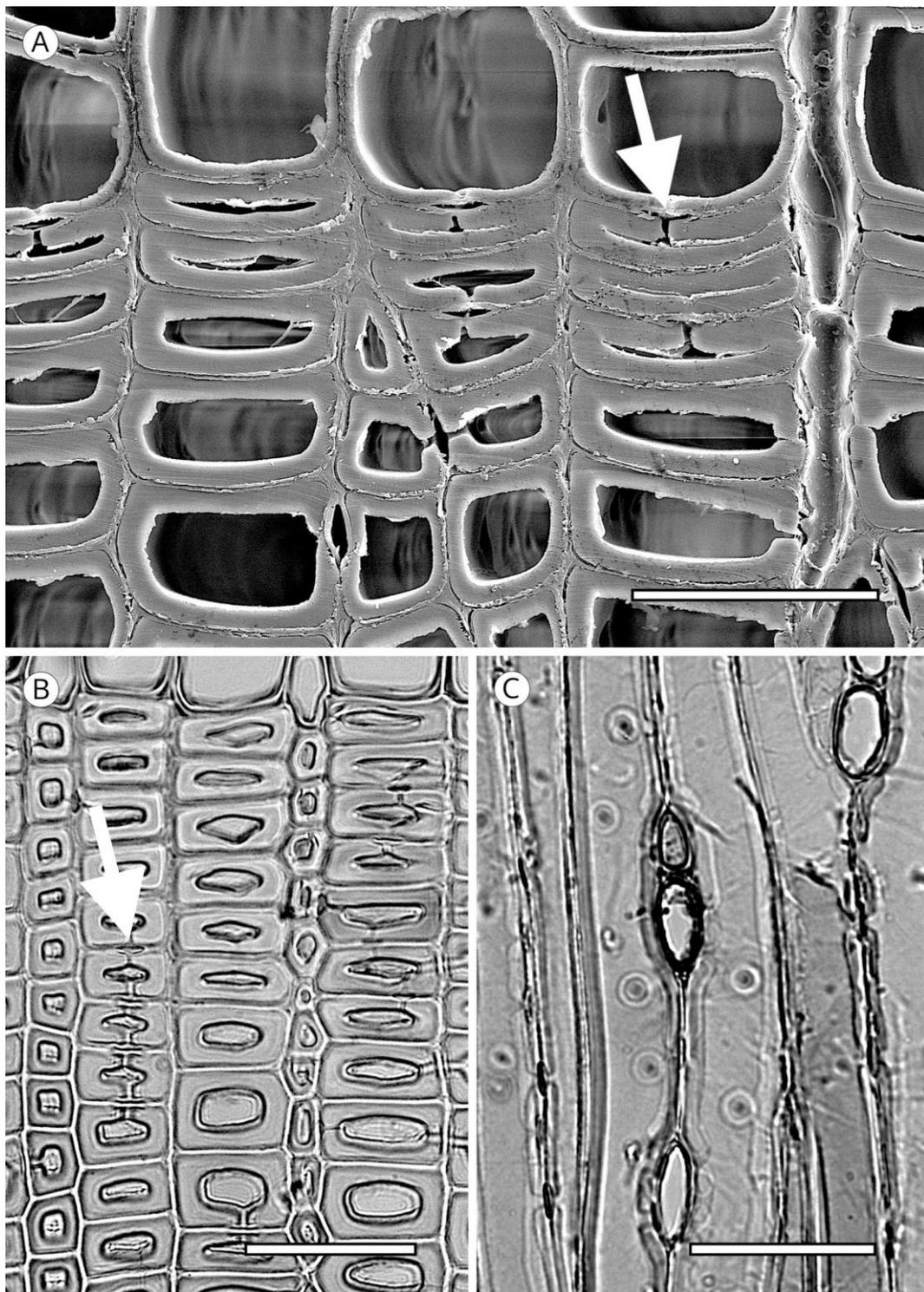


Figure 11. Tangential pits. (A) Tangential pits in transverse section in *Chamaecyparis obtusa* (Siebold & Zucc.) Endl. (SEM); (B) Tangential pits in transverse section in *Athrotaxis selaginoides* D.Don; (C) Tangential pits in tangential section in *Tetraclinis articulata* (Vahl) Mast. Scale bars. (A–C) = 50 μm .

The diameter of radial wall pits usually occupies two thirds of the axial tracheid diameter, although in *Dacrydium* and *Podocarpus* it can be less than half the tracheid diameter. This feature must be used with caution and only as a guideline, due to considerable intra-species variability [57] (Figure 13).

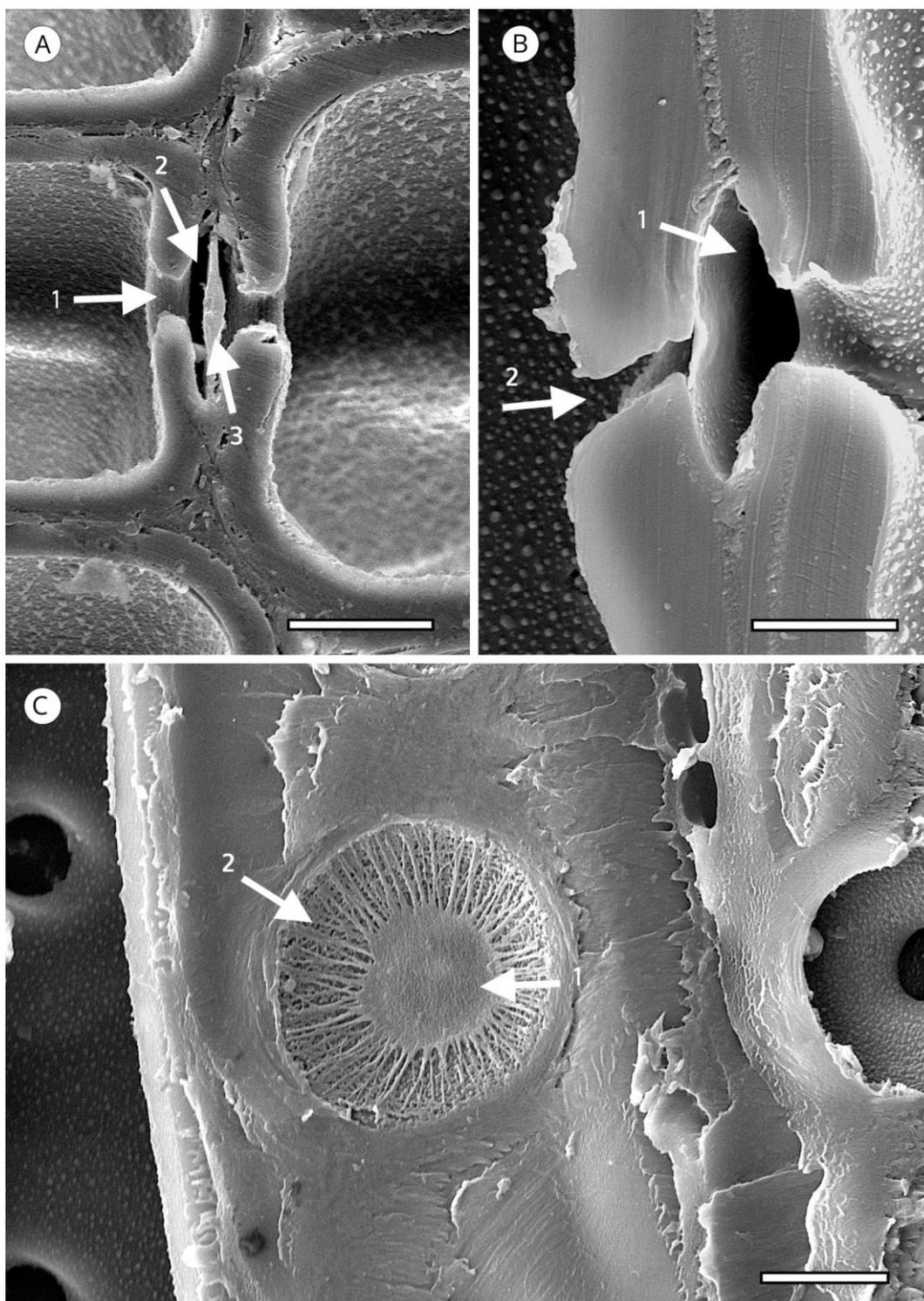


Figure 12. Tracheid pits. (A) *Juniperus barbadensis* L. (SEM), 1. Aperture; 2. Dome or chamber; 3. Torus; (B) *Callitropsis nootkatensis* (D.Don) Oerst. (SEM), 1. Dome or chamber; 2. Aperture; (C) *Hesperocyparis sargentii* (Jeps.) Bartel (Syn.—*Cupressus sargentii* Jeps.) (SEM). 1. Torus; 2. Margo. Scale bars. (A) = 10 μm ; (B,C) = 5 μm .

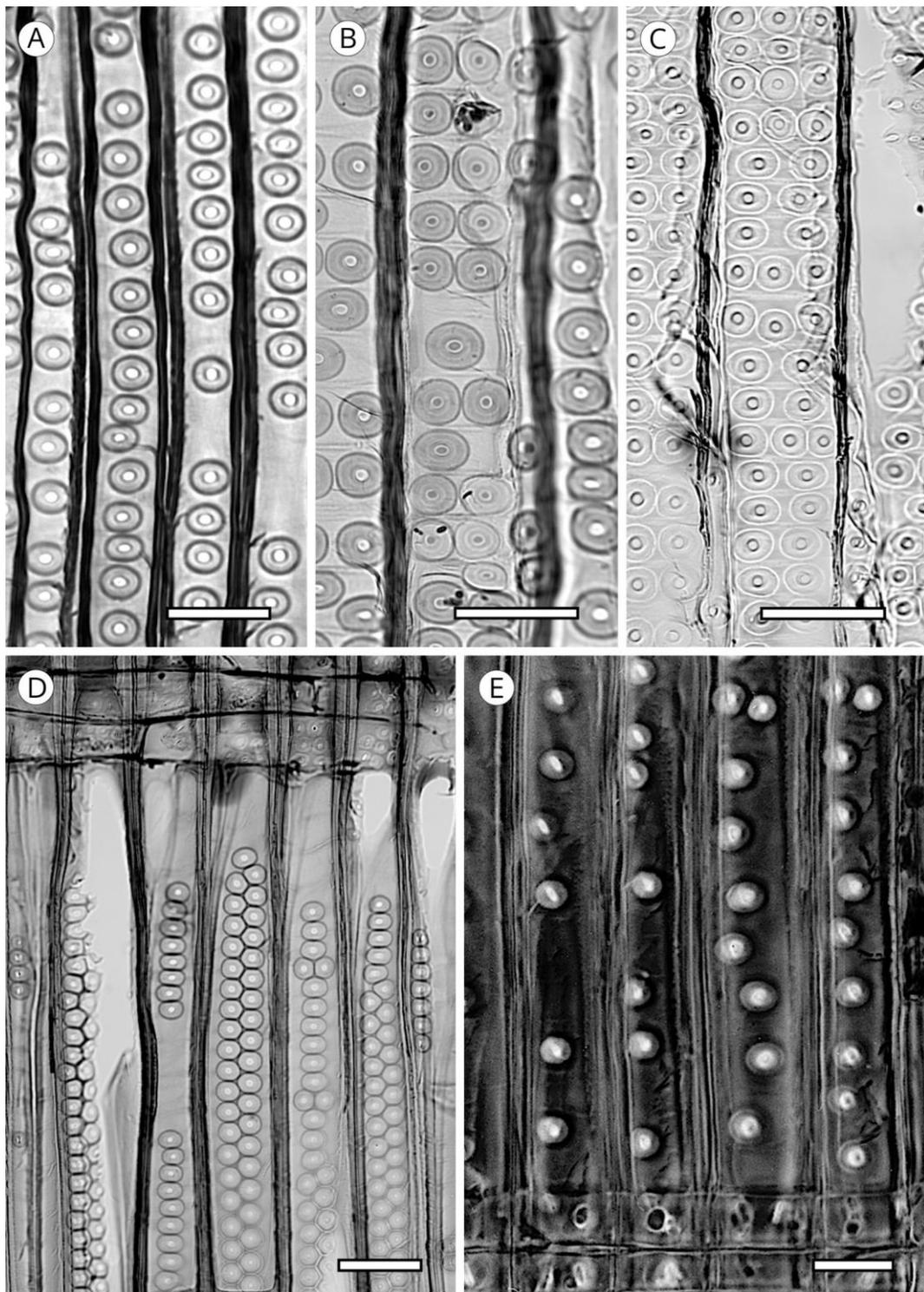


Figure 13. Pit arrangement. (A) Uniseriate in *Abies fraseri* (Pursh) Poir.; (B) Biseriate in opposite arrangement in *Pinus arizonica* Engelm.; (C) Multiseriate in *Taxodium distichum* (L.) Rich.; (D) Biseriate alternate and polygonal in *Araucaria columnaris* (G.Forst.) Hook.; (E) Pits in radial wall less than half tracheid diameter in *Dacrydium elatum* (Roxb.) Wall. ex Hook. Scale bars. (A–D) = 50 μm ; (E) = 25 μm .

The IAWA Committee [5] divided the coniferous taxa into two large groups based on the torus in transverse section. In one group the torus is well defined, with a dense central area of the pit membrane with microfibril deposits in circular or radial orientation [110], often including incrustations with amorphous substances. In this group, the torus

has a disc shape, visible in earlywood, a convex lens shape in latewood, or a flat transition from torus to margo. The other group comprises taxa without a defined torus, as in some species of *Thuja* and *Thujopsis* (Figure 14). The torus normally has a well-defined regular and smooth outline, but some taxa present variations that can be used to identify genus, e.g., *Cedrus* spp.

Cedrus spp. has scalloped tori (Figure 15), a feature characteristic of this genus. Despite reports of similar forms in *Fitzroya* [72] and transitional forms in *Pseudolarix* [101] and Cupressaceae [5], scalloped tori occur regularly only in all species of *Cedrus*, and therefore, this feature has diagnostic value. It is not known why *Cedrus* has this form of torus, but it could be associated with a strengthening of the margo for greater efficiency in situations of water stress. Liese [111] explained it as an accumulation of an irregularly dissolved matrix on the edge of the torus.

Cedrus has unique behaviour within Pinaceae, specifically in Abietoideae. According to Germandt et al. [15], molecular evidence supports the genus *Cedrus* as a sister group to the other Pinaceae and should occupy a basal or root position in the family such that the subfamily Abietoideae can be considered paraphyletic. In addition to this special feature of *Cedrus*, the genus forms both axial and radial traumatic resin canals but lacks normal resin canals [14].

Another unique feature of the torus is torus extensions, or margo straps. These are radial thickenings from the torus to the margo periphery (Figure 15) made up of agglomerations of cellulose microfibrils. Like scalloped tori, they may correspond to the strengthening of the torus to improve the response to cavitation. Torus extensions occur regularly in *Tsuga*, *Widdringtonia* and *Lagarostrobos franklinii* [5], and more sporadically in *Abies* [112], *Actinostrobus*, *Fitzroya*, *Juniperus*, *Pilgerodendron* and *Thujopsis* [101]. In *Abies*, Heinz [57] confirmed the presence of extensions in 34 of the 48 species studied, while Esteban et al. [113] examined 33 species of *Abies*, one subspecies and four varieties, and confirmed the presence of extensions in 22 of them. Heinz [57] reported similar structures in *Austrocedrus chilensis*, *Cupressus dupreziana* and *Juniperus* spp., but the samples observed showed signs of degradation caused by fungi and/or bacteria, and therefore, this finding must be treated with caution.

In some species, the periphery of the pit has notched borders that can be used for diagnosis, particularly to separate almost identical taxa, such as *Sequoia* and *Sequoiadendron*, or even species of the same genus, as in the case of *Juniperus* [85]. They have been reported in *Athrotaxis cupressoides*, *A. selaginoides*, *Chamaecyparis pisifera*, *Cryptomeria*, *Cupressus dupreziana*, *Juniperus thurifera*, *Papuacedrus papuana*, *Sequoia*, *Taiwania*, *Thuja occidentalis*, *Torreya californica*, *T. nucifera*, *T. taxifolia* [101] and *Juniperus brevifolia* [85]. Heinz [57] recorded less pronounced notched borders in *Athrotaxis* spp., *Juniperus foetidissima*, *Sequoiadendron*, *Thuja plicata*, *T. standishii* and *Thujopsis* (Figure 16).

The presence of any of these three features associated with torus (scalloped tori, extensions and notched borders) therefore has significant diagnostic value.

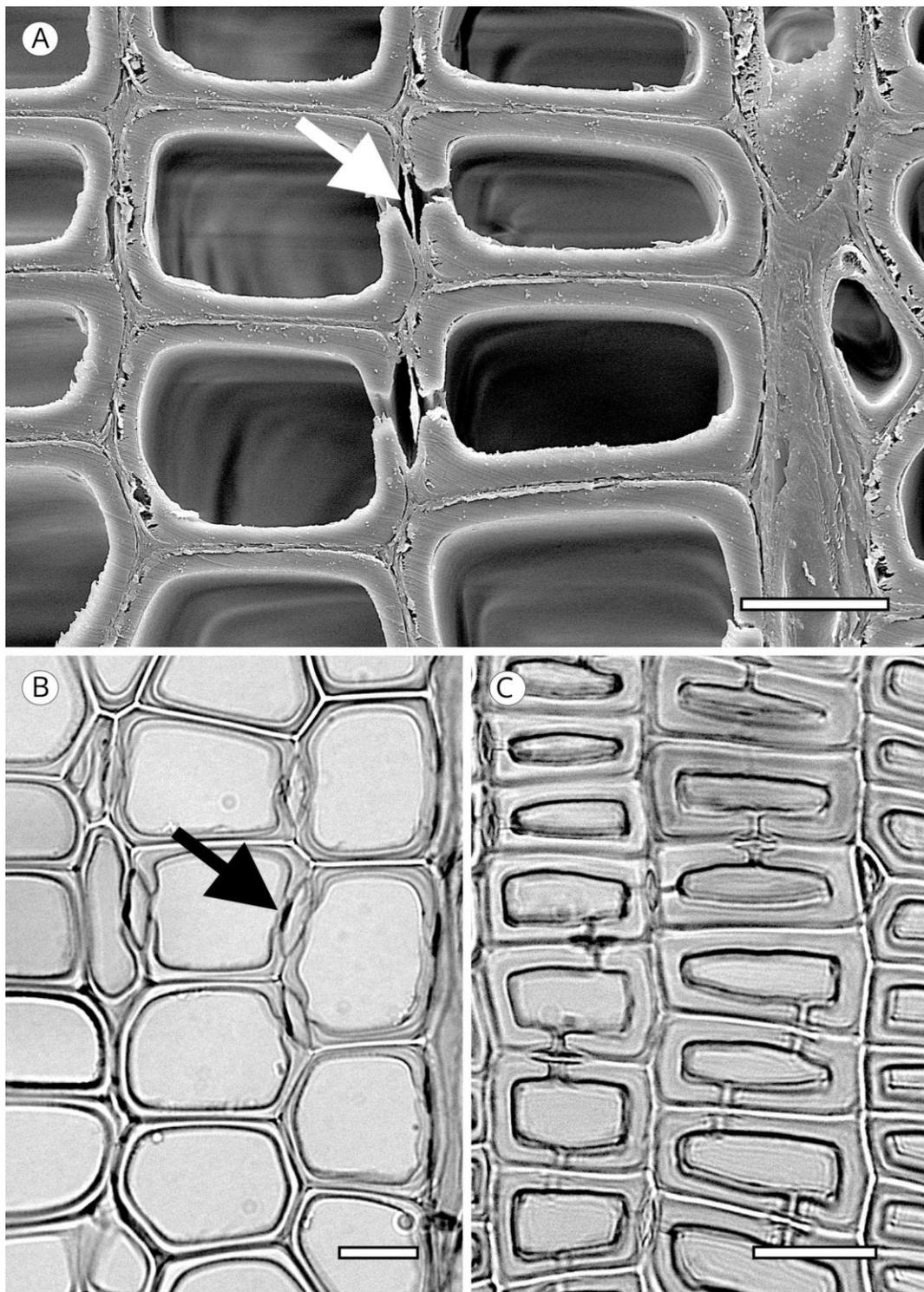


Figure 14. Torus. (A) Torus defined in *Chamaecyparis formosensis* Matsum. (SEM); (B) Torus defined in *Cupressus cashmeriana* Royle ex Carrière; (C) Torus not defined in *Thuja plicata* Donn ex D.Don. Scale bars. (A–C) = 25 μ m.

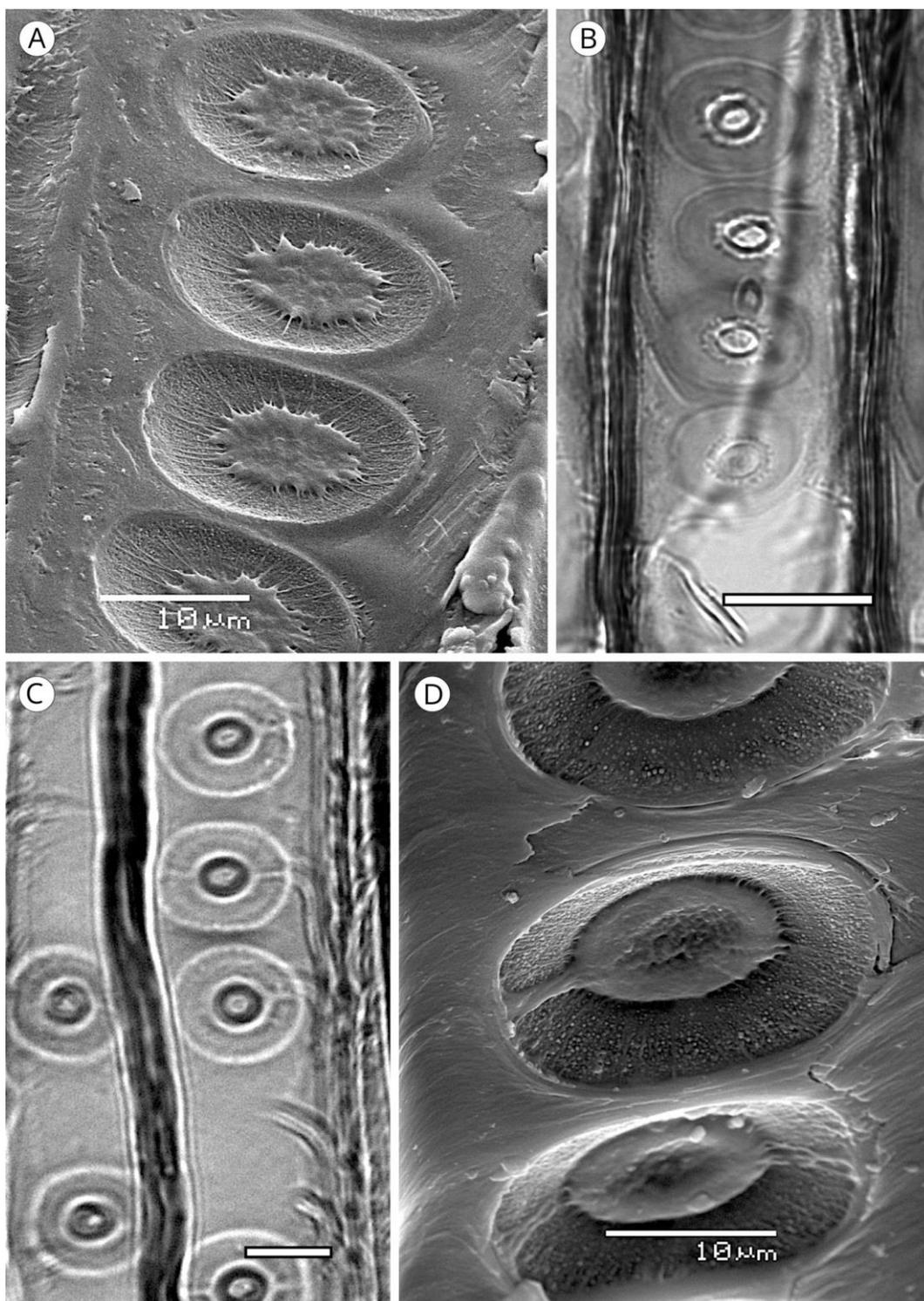


Figure 15. Scalloped torus and extensions. (A) Scalloped torus in *Cedrus atlantica* (Endl.) Manetti ex Carrière (SEM); (B) Scalloped torus in *Cedrus atlantica* (Endl.) Manetti ex Carrière; (C) Torus extensions in *Abies magnifica* A.Murray bis; (D) Torus extensions in *Abies pinsapo* Boiss. (SEM). Scale bars. (B,C) = 25 μm.

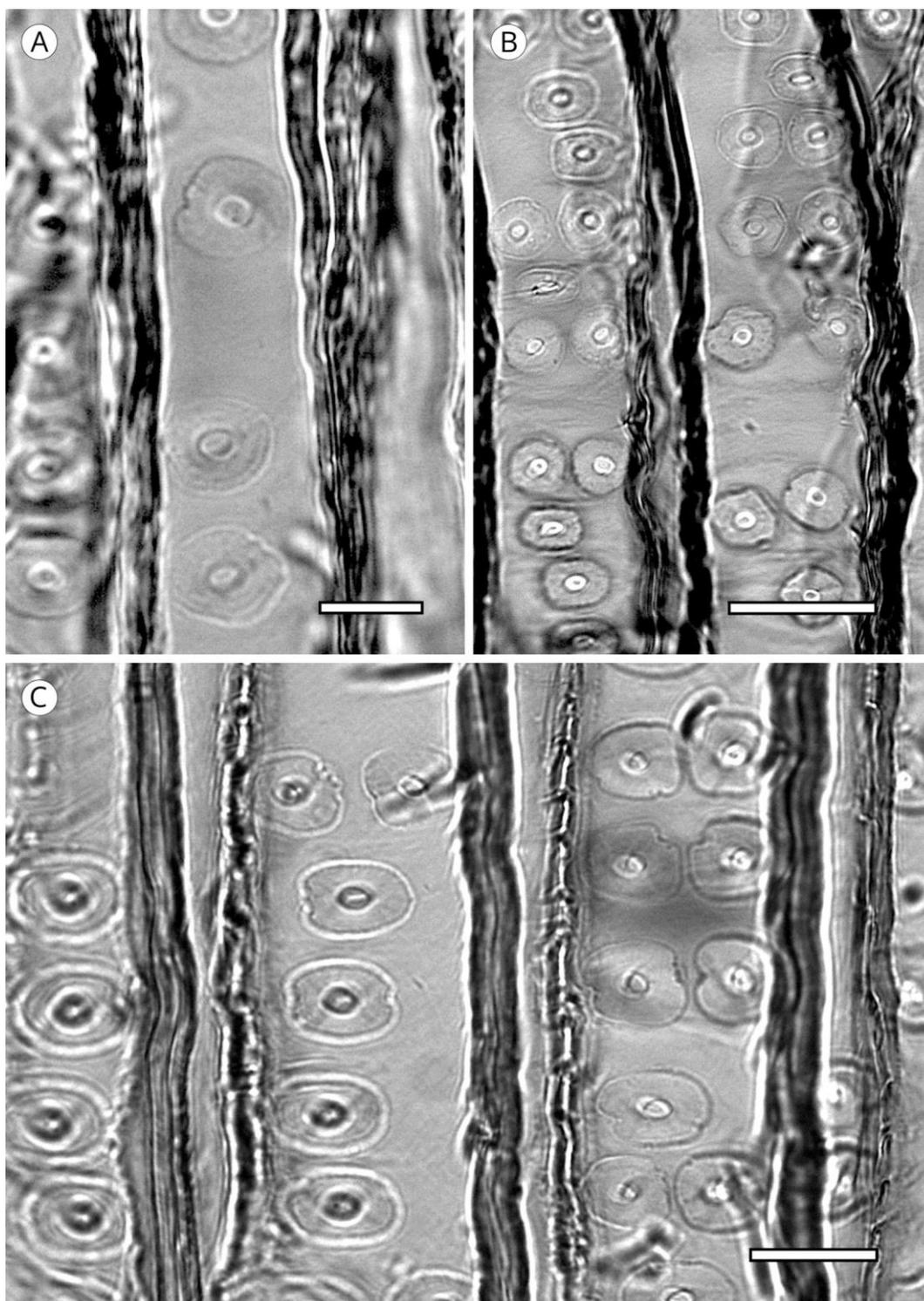


Figure 16. Notched borders. (A) *Calocedrus decurrens* (Torr.) Florin; (B) *Athrotaxis cupressoides* D.Don; (C) *Taiwaniana cryptomerioides* Hayata. Scale bars. (A–C) = 25 μ m.

5.1.2. Warty Layer

On the inner layer of tracheids (S3 or tertiary wall), some taxa present small wart-like thickenings 100 to 500 nm in diameter, rarely reaching 1 μ m, and 500 nm to 1 μ m in height, made up of lignin and hemicellulose and known as a warty layer. Liese [114] determined that the size, distribution and frequency of warts varies between taxa. Some authors have used this feature to compare genera and species, e.g., Heady and Evans [115] in

Actinostrobus, and Esteban et al. [116] in *Tetraclinis*. The presence of a warty layer is a feature of significant diagnostic value.

Jansen et al. [117] reported that a warty layer is present in most conifer wood, but Harada et al. [110] noted its absence in *Taxus cuspidata*, *Taxus floridana*, *Torreya nucifera* (Taxaceae), *Cephalotaxus harringtonia* var. *harringtonia*, *Nageia nagi* and *Podocarpus macrophyllus* (Podocarpaceae). However, as Heinz [57] indicated, these observations are based on electron microscopy and few species have warts that are large enough or grouped densely enough to allow observation with light microscopy.

In some genera (*Abies*, *Actinostrobus*, *Juniperus* and *Callitris*) the warty layer can be observed without difficulty under light microscopy (Figure 17), but scanning electron microscopy (SEM) is recommended for biometry and morphology (Figure 18). Warts have been reported in numerous genera of Cupressaceae (*Athrotaxis*, *Chamaecyparis*, *Cryptomeria*, *Cupressus*, *Fitzroya*, *Sequoia*, *Sequoiadendron*, *Tetraclinis*, *Thuja*, *Thujopsis* and *Widdringtonia*), in *Pinus* (*P. bungeana*, *P. massoniana*) and some *Podocarpus* [5]. Heinz [57] reported them in *Diselma*, *Fokienia* and *Platycladus* (Cupressaceae) and in *Pinus gerardiana*, *P. monophylla* and *P. quadrifolia* (Pinaceae), and Esteban and de Palacios [14] in the subfamily Abietoideae (Pinaceae) (*Abies*, *Cedrus*, *Tsuga*).

Based on the hypothesis of Zimmermann [118], Heady and Evans [115] proposed that the small warts of slightly more than 1 μm in height in *Actinostrobus* are responsible for catching the air bubbles produced in recently thawed tracheid water to prevent them from coalescing and forming large bubbles that could create a risk of blockage in tracheids. Such bubbles have the potential to block the tracheids by expanding as xylem pressure decreases and transpiration restarts [115]. The three species of *Actinostrobus* have thin barks that are probably insufficient to counter the effect of extreme temperatures (especially frost) where they grow, and they frequently develop frost rings in their wood. Frost rings have been observed in other Cupressaceae, e.g., *Diselma*, which, strangely enough, has somewhat smaller warts. Other genera of Cupressaceae, characteristic of drier sites, such as *Tetraclinis*, also contain the same type of warts, probably to prevent cavitation by water stress, but the question remains as to why other conifers in the same or similar sites have no warty layer in their tracheids. The warty layer could, therefore, be a defence mechanism against cavitation in species subjected to extreme temperatures, but this can be confirmed only by physiological studies.

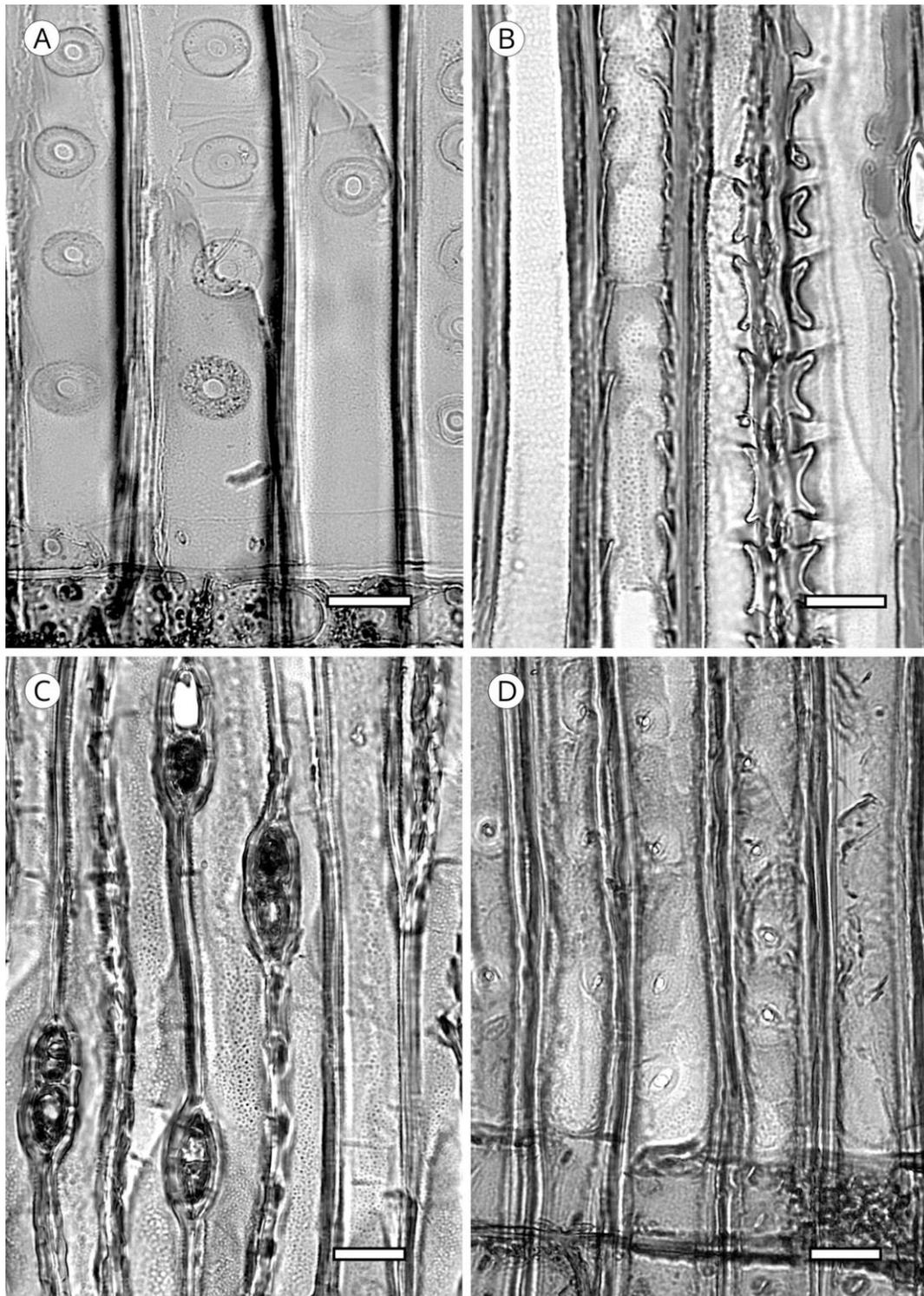


Figure 17. Warty layer (light microscopy). (A) *Abies spectabilis* (D.Don) Mirb.; (B) *Callitris endlicheri* (Parl.) F.M.Bailey; (C) *Juniperus californica* Carrière; (D) *Tetraclinis articulata* (Vahl) Mast. Scale bars. (A–D) = 25 μ m.

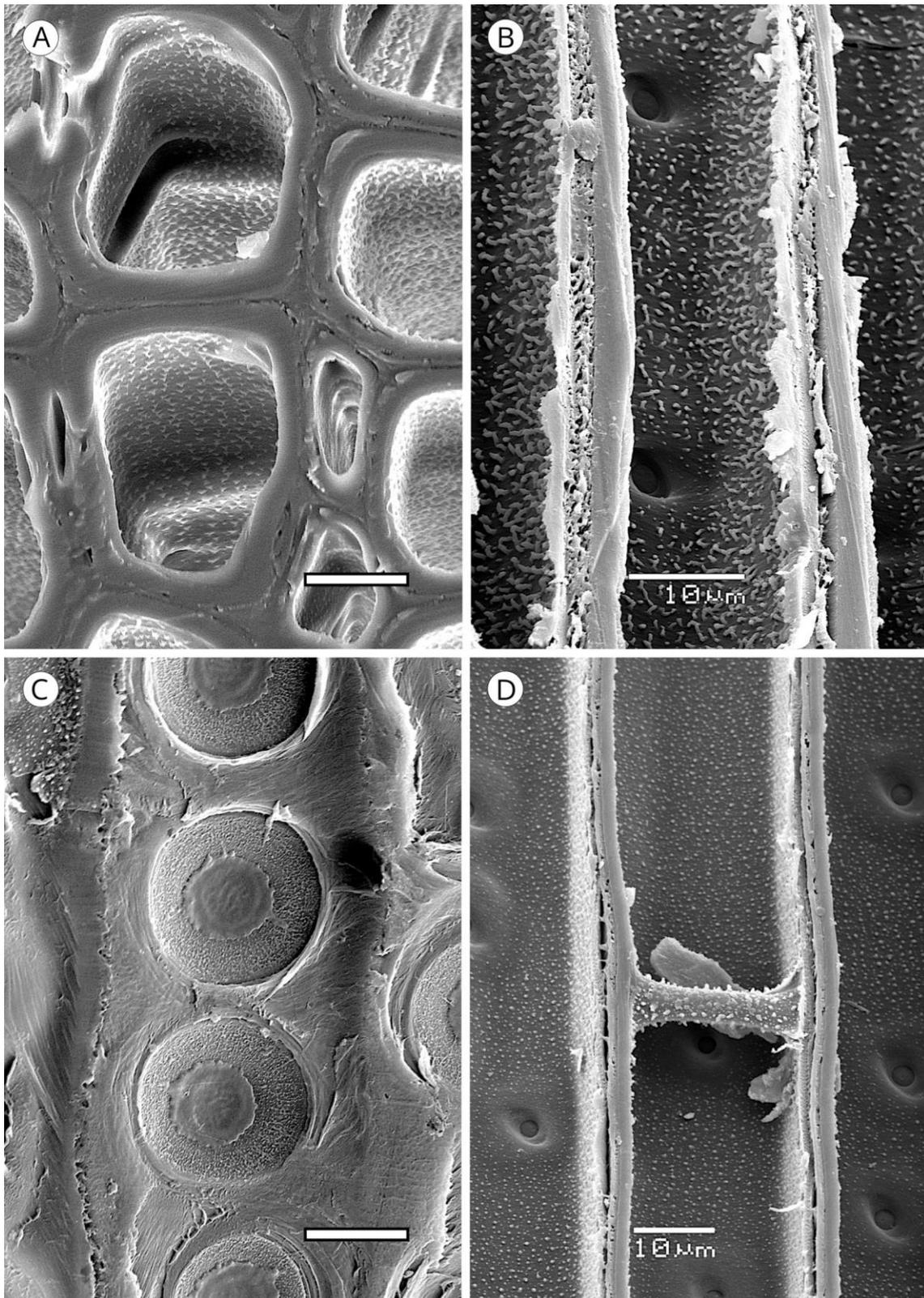


Figure 18. Warty layer (SEM). (A) *Callitris drummondii* (Parl.) Benth. and Hook.f. ex F.Muell.; (B) *Callitris acuminata* (Parl.) F.Muell.; (C) *Callitris oblonga* Rich.; (D) *Diselma archeri* Hook.f. Scale bars. (A,C) = 25 µm.

5.1.3. Organic Deposits

Some species develop organic deposits in heartwood tracheids (Figure 19). They are mentioned in the scientific literature as resin plugs, resin spools or resin plates, and although they are visible in the transverse section, they are more readily observed in longitudinal sections. They are normally located near the rays and are dark-coloured, occupying all or part of the cell lumen. Because of their unique features, their presence is of significant diagnostic value. Without naming them as such, Peraza [119] described organic deposits in the resinous wood of *Pinus canariensis*. They have been reported in axial tracheids in *Abies pinsapo* [120] and *Halocarpus biformis* [57], and described in *Agathis* and *Araucaria*, normally more abundant in the former.

Deposits in parenchyma cells have been described in *Callitris glauca*, *Calocedrus* spp., *Cupressus* spp., *Fitzroya cupressoides*, *Juniperus procera*, *J. virginiana*, *Thuja plicata*, *T. standishii*, *Widdringtonia* spp., *Dacrydium elatum*, *Podocarpus totara*, *P. ferrugineus* and *Saxegothaea conspicua* [55].

The presence of organic deposits in tracheids seems to be associated with the mechanisms of heartwood formation as a tree defence against attacks by xylophagous agents. When a tracheid cell lumen is plugged, hyphae progression is prevented. The occurrence of organic deposits in tracheids in wood without normal resin canals, e.g., *Abies*, *Agathis* and *Araucaria*, indicates that tracheid plugging cannot be explained solely by the presence of resin canals. The blockage of axial tracheids can be explained only by a metabolic pathway, such as that described by Hillis [121] for impregnating axial tracheids with resin in *Pinus radiata* through cross-field pits from the ray parenchyma cells.

It should be noted that when preparing microscope slides, particularly during the dehydration stage, organic solvents may dissolve the content of deposits and cause the loss of this diagnostic feature. Additionally, tracheids in archaeological wood can resemble organic deposits due to encrusted extraneous substances such as paint, resin, tar, oil or iron oxide [57].

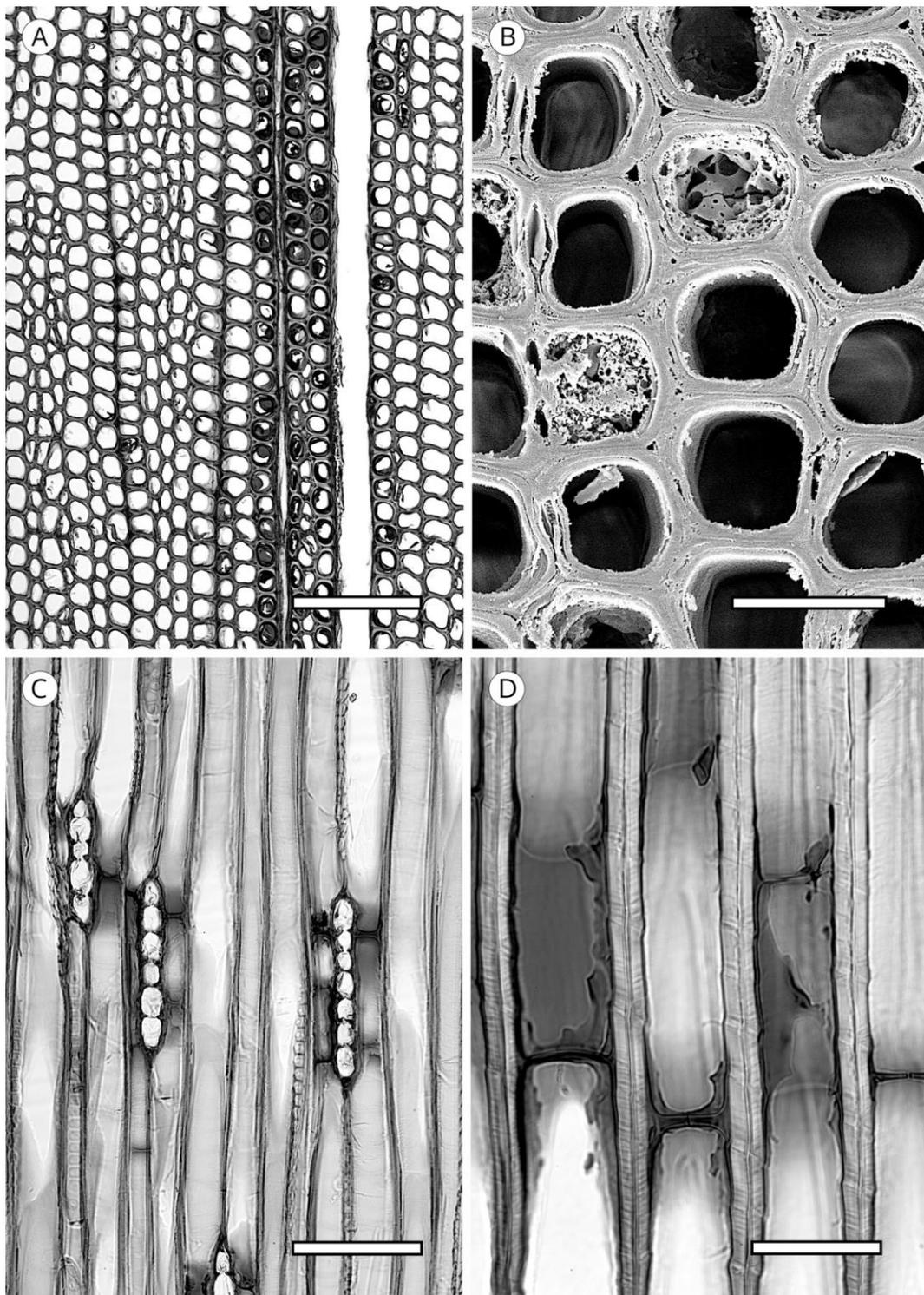


Figure 19. Organic deposits. (A,C,D) *Araucaria columnaris* (G.Forst.) Hook.; (B) *Callitris endlicheri* (Parl.) F.M.Bailey (SEM). Scale bars. (A) = 250 μm ; (B,D) = 50 μm ; (C) = 150 μm .

5.1.4. Helical Thickenings

Some species always have thickenings in the form of ridges that occur as helicoids on the inner face of tracheids (Figure 20). Helical thickenings are true deposits inside tracheids.

These ridges are produced during the final stage of secondary wall formation through cortical microtubules obliquely oriented to the axis of the cell [122].

They have been reported in all genera of Taxaceae (*Amentotaxus*, *Pseudotaxus*, *Taxus*, *Torreya* and *Cephalotaxus*) except in *Austrotaxus* [56]; in *Cathaya*, in earlywood and latewood [123–128]; in *Pseudotsuga* [56,125], in *Pseudotsuga sinensis* and *P. menziesii* in earlywood and latewood, although in the latter they are sometimes present only in latewood; in some species of *Larix*, only in latewood tracheids (*L. decidua*, *L. griffithii*, *L. occidentalis*, *L. potaninii*); in *Picea spinulosa*, well-developed in earlywood and latewood, and in *Picea abies*, *P. brachytyla*, *P. glauca*, *P. glehnii*, *P. jezoensis*, *P. koraiensis*, *P. mariana*, *P. sitchensis* and *P. torano*, only in latewood [129]. For other authors [60,130] they are regularly present in earlywood and latewood in *Picea brachytyla*, *P. maximowiczii*, *P. morrisonicola*, *P. purpurea*, *P. schrenkiana*, *P. smithiana* and *P. spinulosa*, later confirmed by Heinz [57]. Helical thickenings are most easily seen in earlywood because in wood with particularly narrow rings, they are either overlooked or simply not visible.

The grouping of helical thickenings (single, double or triple), spacing, inclination angle, thickness, branching and connection to the inner cell wall vary among taxa. Some parameters can be quantified, but others are highly variable and difficult to measure. In *Taxus* and *Pseudotsuga*, helical thickenings are normally single (Figure 20), whereas in *Amentotaxus* and *Torreya* they are double (Figure 20) or even triple in *Torreya*. In *Cephalotaxus* they can be grouped or not grouped in the same wood [57]. The inclination angle and thickness of spirals are correlated with spacing. *Pseudotsuga* and some taxa of *Picea* have very thin spirals with little spacing, forming an angle of 80° to 90° with the tracheid axis, while in *Amentotaxus*, *Cephalotaxus*, *Taxus* and *Torreya* they are typically thicker and have a steeper angle. The spacing between helical thickenings is considered narrow when there are typically more than 120 spirals per axial mm, e.g., *Pseudotsuga* (120–180) and *Picea smithiana* (150–200), and wide when there are typically less than 120 spirals per axial mm, e.g., in *Torreya*, with 80–100 (40–50 pairs), and *Taxus* (40–80). *Cephalotaxus* has 80–140, and may be included in either category depending on the species and/or sample [5]. Some authors [78] observed differences in taxa with helical thickenings in the connection of spirals to the S3 layer. For example, in *Taxus*, *Torreya* and *Cephalotaxus*, helical thickenings have a narrow base loosely connected to the inner layer of the secondary wall (S3) (Figure 21B), while in *Pseudotsuga*, they have a wider base, as if the spirals were more securely fastened to the S3 layer by connecting microfibrils (Figure 21A). Moreover, in some species of *Picea*, *Torreya* and *Cephalotaxus*, helical thickenings can be present in branches but absent in the trunk [131].

Spiral grooves found in compression wood must not be confused with helical thickenings. Spiral grooves are normally at steep angles of around 45° and appear as cracks in the cell wall (Figure 21C,D). The same can occur in archaeological wood, where the enzymatic activity of soft-rot fungi produces cavities resembling spiral grooves in compression wood [132] (Figure 21C,D).

The mechanical effects of helical thickenings on the cell wall are unknown. It appears that these ridges, with a small diameter relative to cell wall thickness, have little influence on the mechanical properties of the wood that contains them, although they may affect water conduction in the cell lumen [133].

The presence of helical thickenings and their grouping (single or in pairs or triplets) have significant diagnostic value.

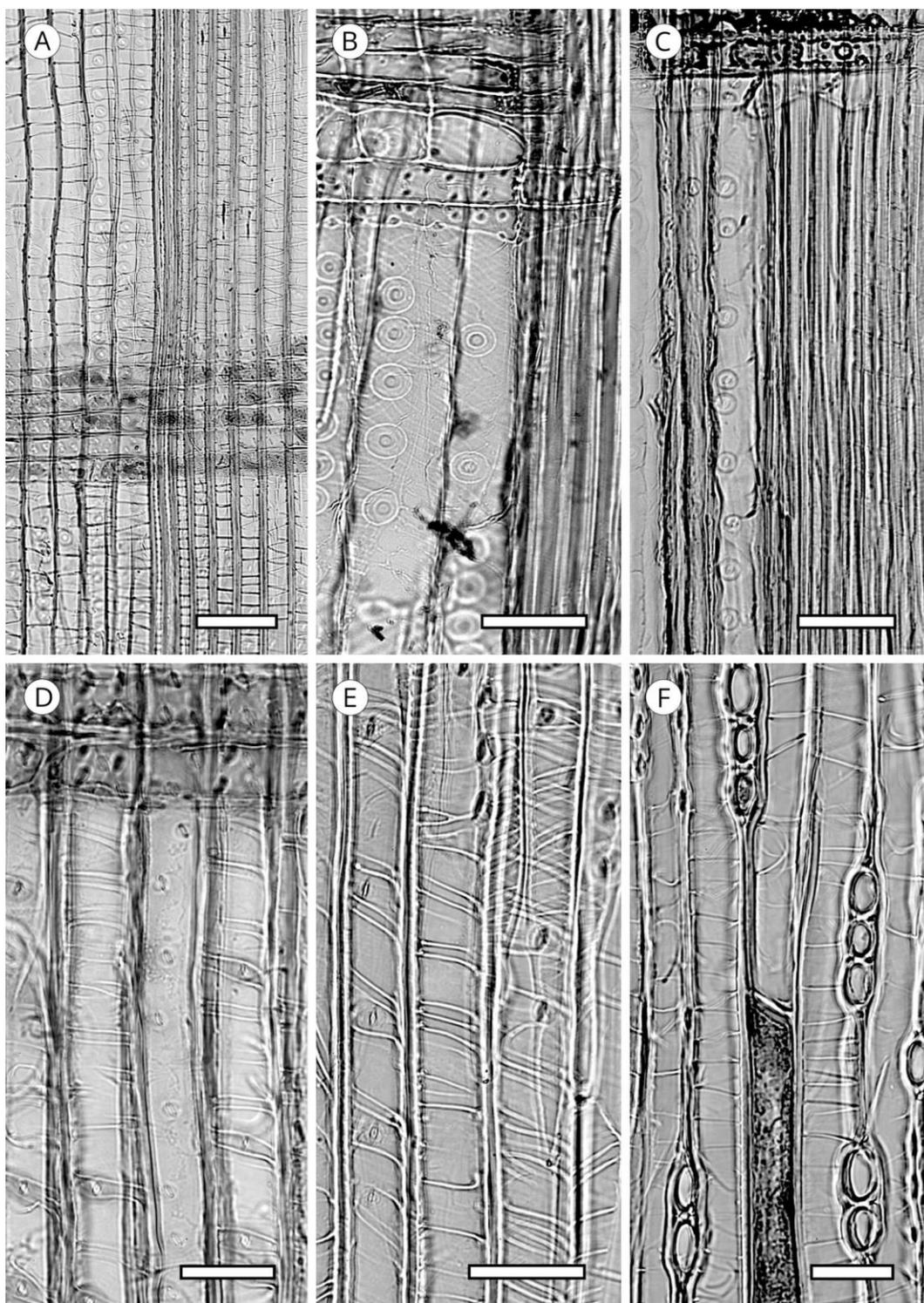


Figure 20. Helical thickenings. (A) Single in *Taxus baccata* L.; (B) In earlywood of *Pseudotsuga menziesii* (Mirb.) Franco; (C) In latewood of *Larix decidua* Mill.; (D) Grouped in pairs in *Amentotaxus argotaenia* (Hance) Pilg.; (E) Grouped in pairs and triplets in *Torreya nucifera* (L.) Siebold and Zucc.; (F) Single in *Cephalotaxus harringtonia* (Knight ex J.Forbes) K.Koch. Scale bars. (A) = 100 μm ; (B–F) = 50 μm .

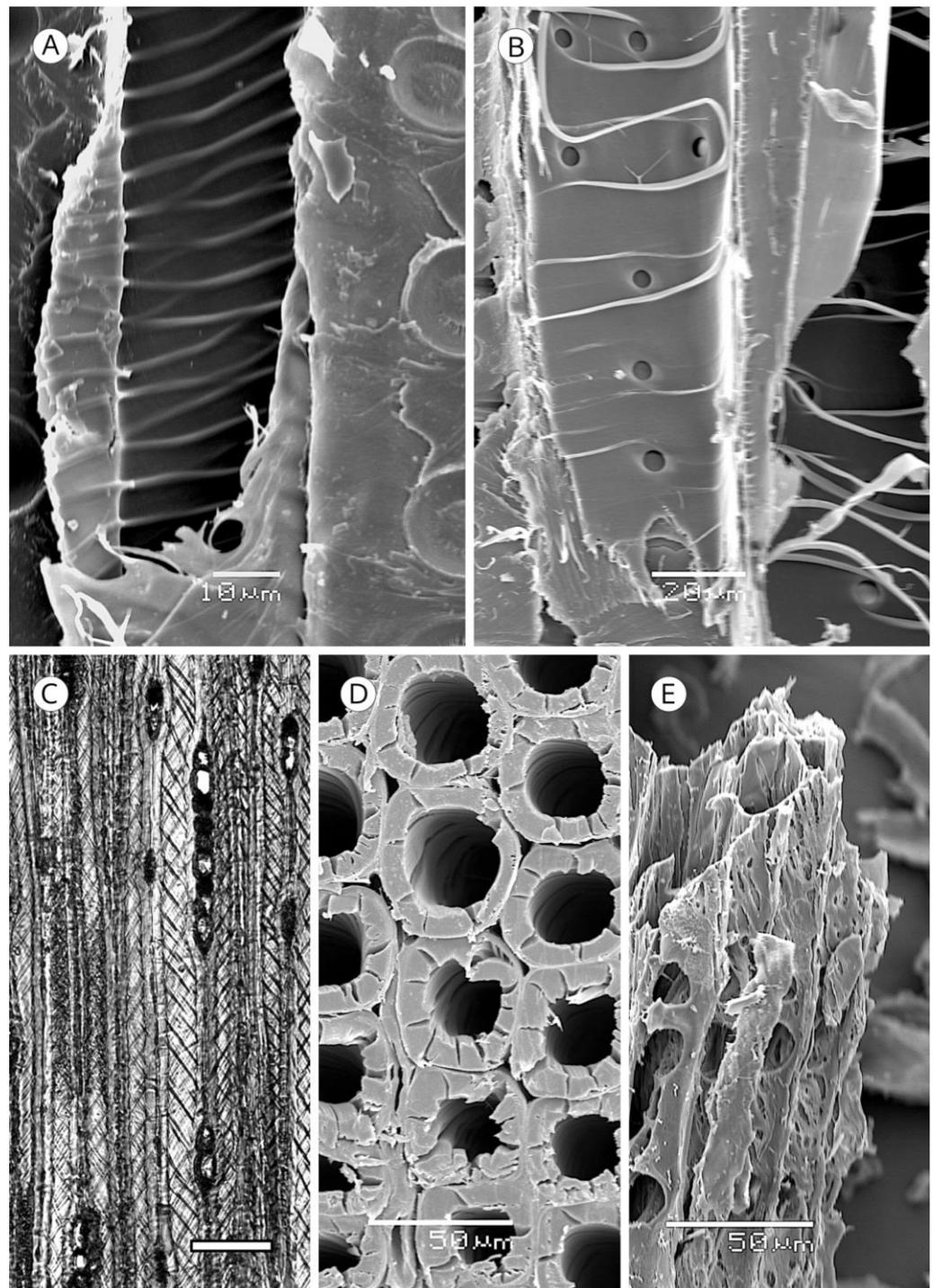


Figure 21. Helical thickenings and spiral grooves. (A) Helical thickenings in *Pseudotsuga sinensis* Dode. (SEM); (B) Helical thickenings in *Torreya nucifera* (L.) Siebold and Zucc. (SEM); (C) Spiral grooves in *Neocallitropsis pancheri* (Carrière) de Laub.; (D) Spiral grooves in *Pinus roxburghii* Sarg. (SEM); (E) Cavities caused by soft-rot in *Pinus sylvestris* L. resembling spiral grooves (SEM). Scale bars. (C) = 150 μm .

5.1.5. Callitroid Thickenings

Another type of thickening present in the secondary wall of longitudinal tracheids is the callitroid thickening. It occurs in all species of *Callitris* and in the latewood of the three species of *Actinostrobus* [115], although it has also been reported in other taxa, e.g., Phillips [132] noted its presence in *Pseudolarix* and *Juniperus*, Howard and Manwiller [134] in some species of the southern pine group, Meylan and Butterfield [135] in *Dacrydium cupressinum*

and Schweingruber [71] in *Tetraclinis*. However, according to Phillips [52], these observations should be considered “rare and inconspicuous”. This type of thickening must, therefore, be reserved as a feature exclusive to *Actinostrobus* and *Callitris*, and thus, its presence has significant diagnostic value.

Callitroid thickening appears as two parallel ridges above and below the pit aperture, resembling an awning in the tangential section. Heady and Evans [80] also recorded the presence of this thickening in cross-field pits (Figures 22 and 23).

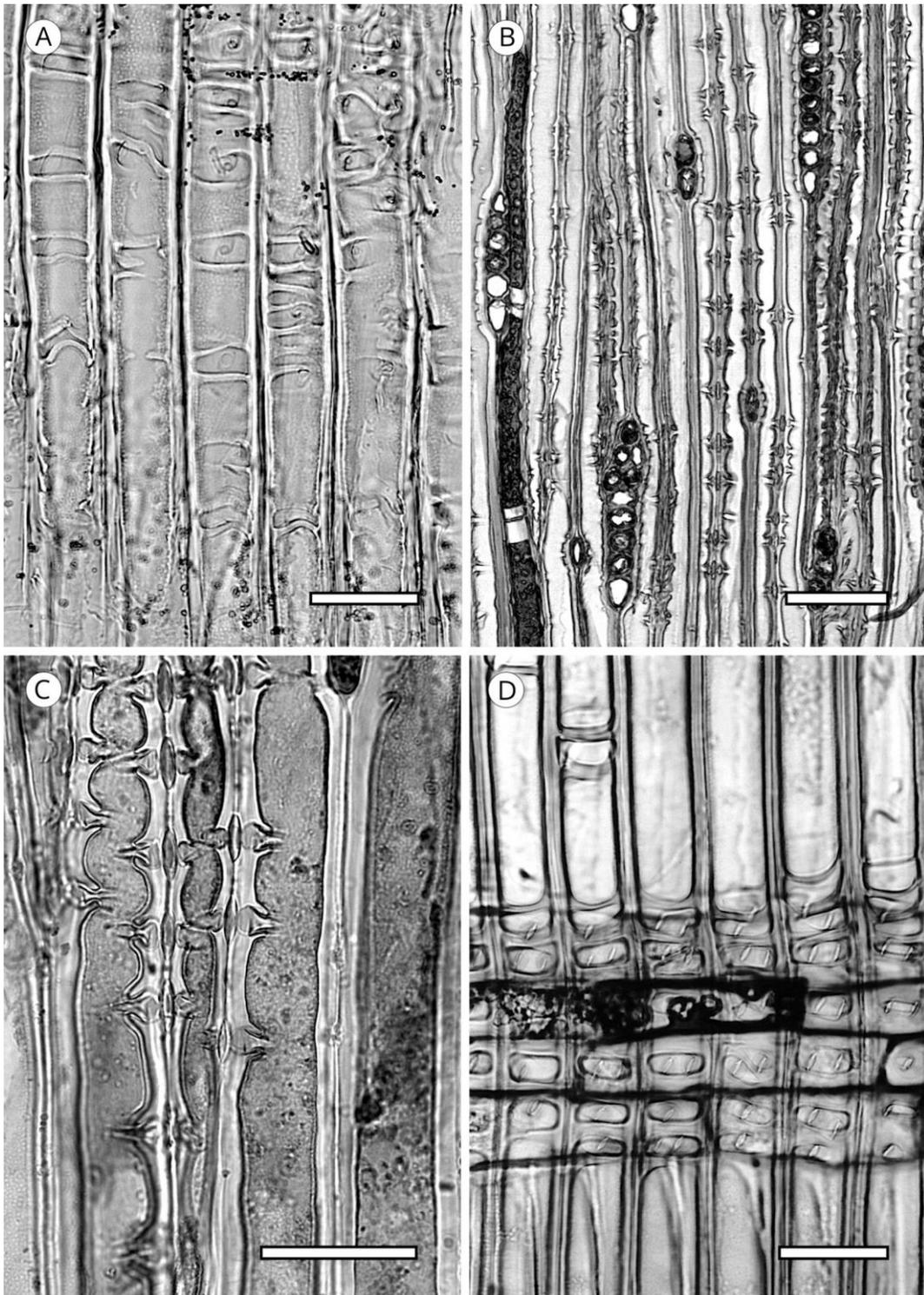


Figure 22. Callitroid thickenings. (A) In axial tracheids (radial section) in *Callitris columellaris* F.Muell.; (B,C) In axial tracheids (tangential section) in *Callitris endlicheri* (Parl.) F.M.Bailey; (D) In

cross-fields (radial section) in *Callitris columellaris* F.Muell. Scale bars. (A,C,D) = 50 μm ; (B) = 100 μm .

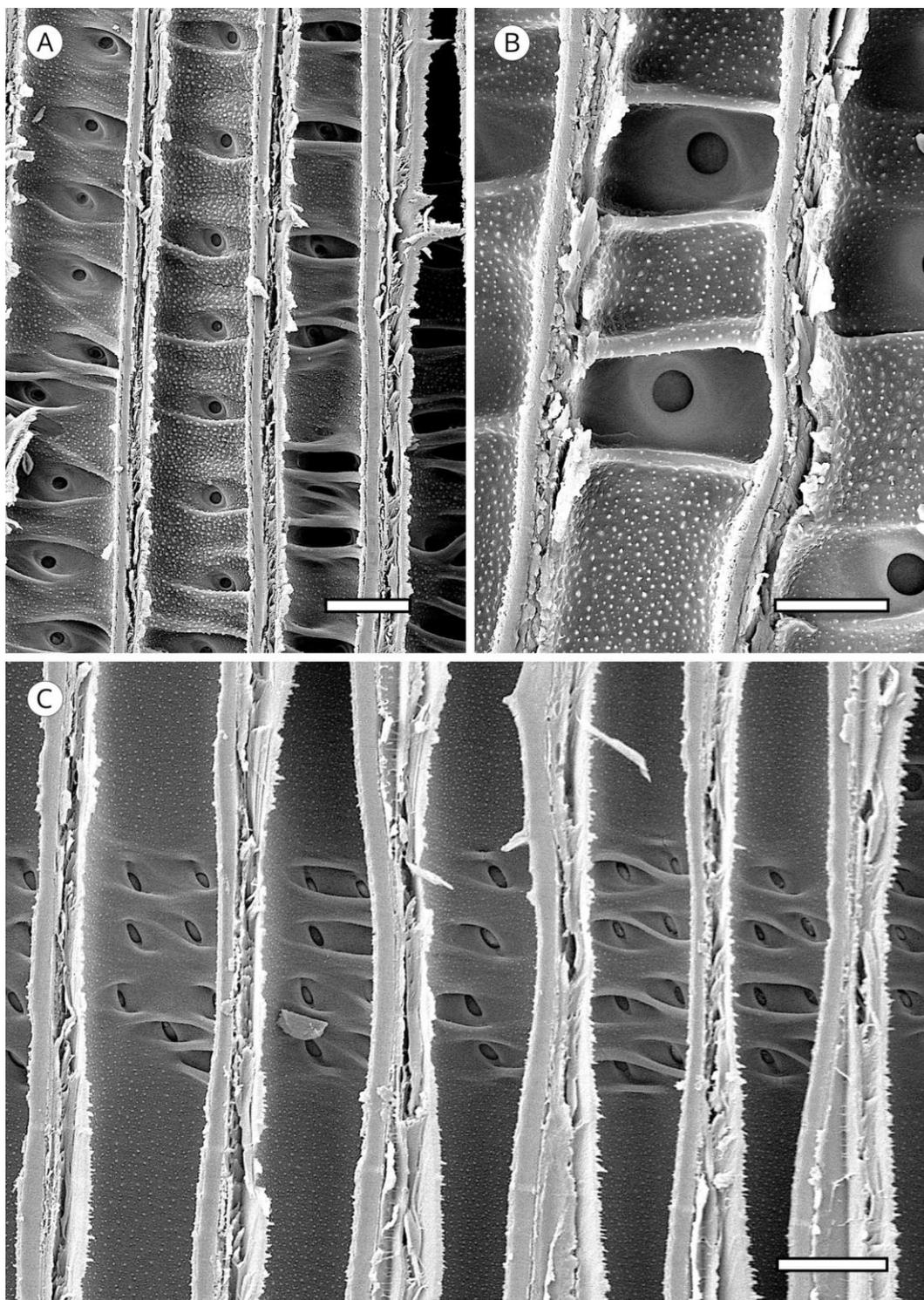


Figure 23. Callitroid thickenings (SEM). (A) In axial tracheids (radial section) in *Callitris verrucosa* (A.Cunn. ex Endl.) F.Muell.; (B) In axial tracheids (radial section) in *Callitris endlicheri* (Parl.) F.M.Bailey; (C) In cross-field pits (radial section) in *Callitris verrucosa* (A.Cunn. ex Endl.) F.Muell. Scale bars. (A,C) = 25 μm ; (B) = 10 μm .

Heady and Evans [80] showed that the frequency of thickening is higher (>85%) in species of *Callitris* from dry sites in Australia (*C. canescens*, *C. endlicheri*, *C. glaucophylla*, *C. tuberculata* and *C. verrucosa*) than in humid sites with high precipitation (<10%) (*C. macleayana*, *C. neocaledonica*, *C. oblonga* and *C. sulcata*), and that in species with higher frequency of callitroid thickening, the thickening occurs in tracheids with a smaller diameter. Because of this, these authors suggested that the transverse bars on each side of the pit aperture, the region of the dome where the cell wall is weakest, could be regarded as reinforcement or supporting braces for the pit to prevent collapse.

5.1.6. Bars of Sanio

Bars of Sanio, or crassulae thickenings, are present in all conifer wood except Araucariaceae, where their absence was confirmed by Brown et al. [93] in *Araucaria* and *Agathis* and Heady et al. [81] in *Wollemia*. They have no diagnostic value. They are formed by a thickening of the middle lamella and the primary wall on the outside of both uniseriate and multiseriate pits and their mission seems to be to strengthen the cell wall on the periphery of the pits (Figure 24) [93]. This feature is not exclusive to conifers, as it has also been reported in *Centaurodendron dracaenoides* [136].

5.1.7. Trabeculae

Trabeculae occur occasionally in the axial tracheids of some conifers. They can occur in all conifer wood and have also been observed in hardwoods. They have no diagnostic value. They are cylindrical bars that extend through the tracheid lumen from wall to wall (Figure 25). Bars are usually wider where they join with the wall, and in species that have a warty layer, the warts extend through the bar of the trabecula. In earlywood trabeculae, they are usually thin, but in latewood they are shorter and wider. When trabeculae are present they do not usually appear in only one tracheid, but in several adjacent tracheids from the same cambial cell and at the same height. Because of this arrangement, [93] considered that trabeculae developed from the cambial cell. McElhanney et al. [137] attributed the formation of trabeculae to an accumulation of cell wall material on the hyphae of cambial fungi. Troncoso and Greslebin [87] demonstrated that trabeculae the formation in *Austrocedrus chilensis* wood is clearly associated with invasion by *Phytophthora austrocedri*.

Although Grosser [138] suggested that trabeculae act as bracing elements in tracheids to prevent collapse, this is unlikely in view of the scarcity and irregularity of their presence when they occur.

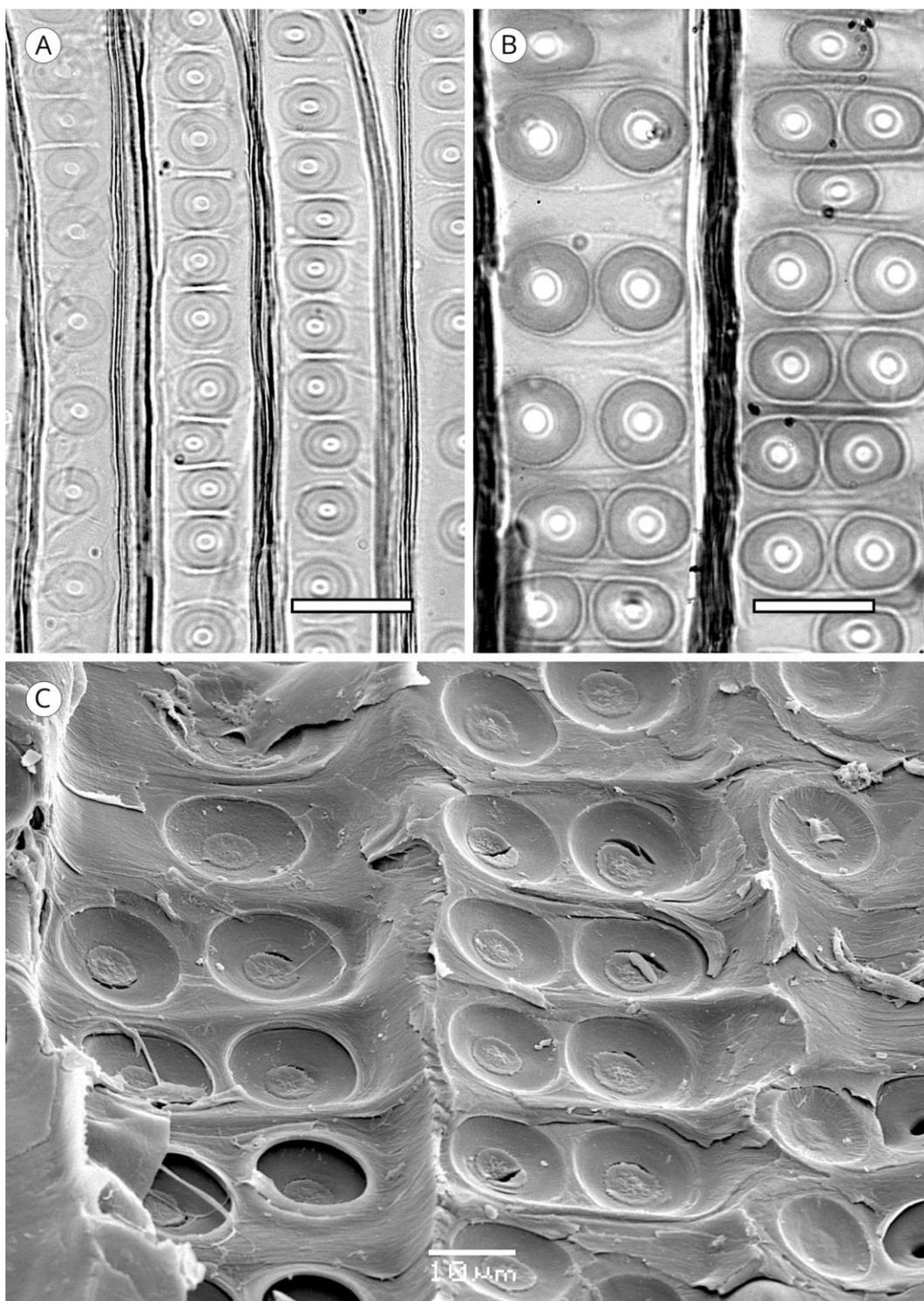


Figure 24. Bars of Sanio. (A) In uniseriate pits of *Pinus elliottii* Engelm.; (B) In biseriate pits in opposite arrangement in *Pinus montezumae* Lamb.; (C) In biseriate pits in opposite arrangement in *Neocallitropsis pancheri* (Carrière) de Laub. (SEM). Scale bars. (A,C) = 25 μm ; (B) = 10 μm .

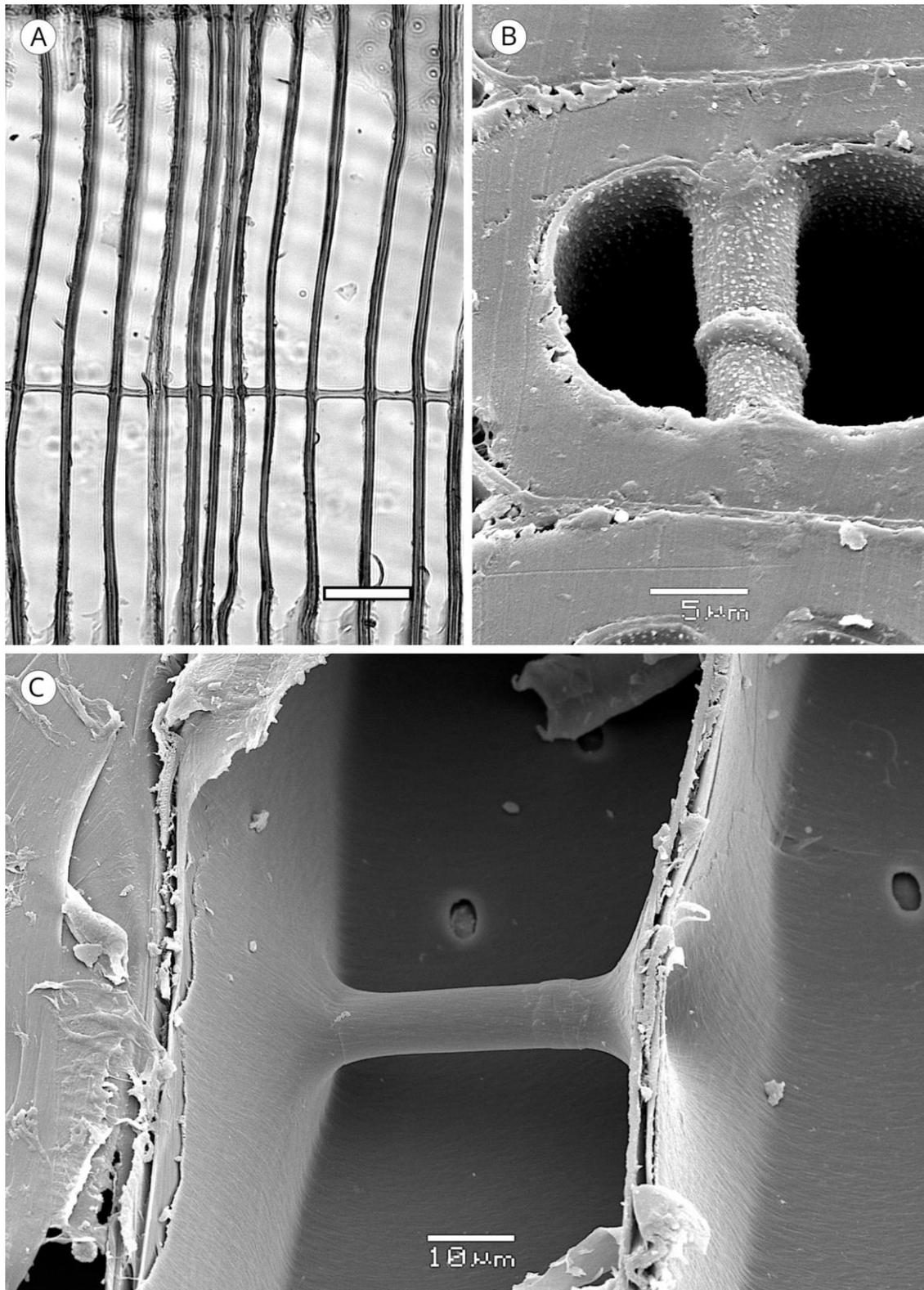


Figure 25. Trabeculae. (A) *Widdringtonia nodiflora* (L.) Powrie; (B) *Actinostrobus pyramidalis* Miq. (SEM); (C) *Metasequoia glyptostroboides* Hu and W.C.Cheng (SEM). Scale bars. (A) = 50 μm.

5.2. Axial Parenchyma

Axial parenchyma is less abundant in softwoods than in hardwoods. It appears in strands of more or less rectangular cells, generally with simple pits, that are responsible for storing metabolites. Its presence must be confirmed in longitudinal sections. It is rare or absent in Araucariaceae, Phyllocladaceae and Sciadopityaceae. Ghimire et al. [139] recorded it in *Amentotaxus* and *Austrotaxus* and it is common in *Cephalotaxus* and most Podocarpaceae [5]. In Cupressaceae it is present in all genera.

When axial parenchyma cells are cut transversely, they are very similar to the adjacent axial tracheids, but have thinner walls and frequently include dark contents [93]. The arrangement of axial parenchyma in the transverse section can be used for identification. It must be observed at low magnification, viewing as many growth rings as possible because in some taxa with regular presence of axial parenchyma it can be scarce or absent in a single ring. Three patterns of arrangement can be distinguished (Figure 26). Diffuse: axial parenchyma cells single or in pairs distributed evenly along growth rings (*Cephalotaxus* and Podocarpaceae); tangentially zonate: parenchyma cells distributed in lines of different lengths parallel or oblique to the growth ring, occurring most frequently in the earlywood/latewood transition zone and in latewood, e.g., in Cupressaceae s.l. [19], conspicuous in the genera *Callitris*, *Calocedrus*, *Chamaecyparis*, *Cryptomeria*, *Cupressus*, *Juniperus*, *Taiwania*, *Taxodium* and *Thuja* [5]; and marginal: single axial parenchyma cells distributed along the growth ring boundary in the last row of latewood and/or first row of earlywood, e.g., in all genera of Abietoideae [14]. In addition, a single species can present all three arrangements.

The transverse end walls of axial parenchyma cells, observable in longitudinal sections, can be smooth, irregularly thickened, or nodular (Figure 27); in the latter case is generally more conspicuous in the tangential section. Although the morphology of the transverse end walls is used as a diagnostic feature in conifers, in Cupressaceae it must be interpreted with caution, as both smooth and irregular walls appear in some taxa, e.g., *Glyptostrobus* [83], *Fitzroya* [140], *Sequoiadendron*, *Cryptomeria*, *Diselma* and *Fokienia* [56], as well as *Tetraclinis* [116]. In Cupressaceae, moreover, the nodular appearance of transverse end walls is caused by the thickening of the primary wall rather than pitting in the strict sense, while in *Abies*, *Cathaya*, *Keteleeria*, *Larix*, *Picea*, *Pseudotsuga* and *Tsuga*, nodules have a similar appearance but exist due to the true pitting of the secondary wall [52]. In any case, this feature must be observed in mature wood, as its appearance can differ in juvenile wood.

End walls are smooth in *Callitris*, *Callitropsis nootkatensis*. (Syn. — *Xanthocyparis nootkatensis* (D. Don) Farjon and Harder), *Tetraclinis articulata*, *Thuja occidentalis*, *Widdringtonia* spp. (Cupressaceae), *Dacrydium cupressinum* and *Podocarpus* spp. (Podocarpaceae). Irregularly thickened walls occur in *Chamaecyparis thyoides* and *Cryptomeria japonica*. Markedly nodular walls are observed in *Taxodium distichum*, *Calocedrus decurrens* and *C. formosana*, *Chamaecyparis obtusa* and *C. pisifera*, some species of *Juniperus*, *Thuja standishii*, and *Thujopsis dolabrata* (Cupressaceae), and *Abies*, *Cedrus*, *Keteleeria*, *Pseudolarix*, *Pseudotsuga* and *Tsuga* (Pinaceae) [5].

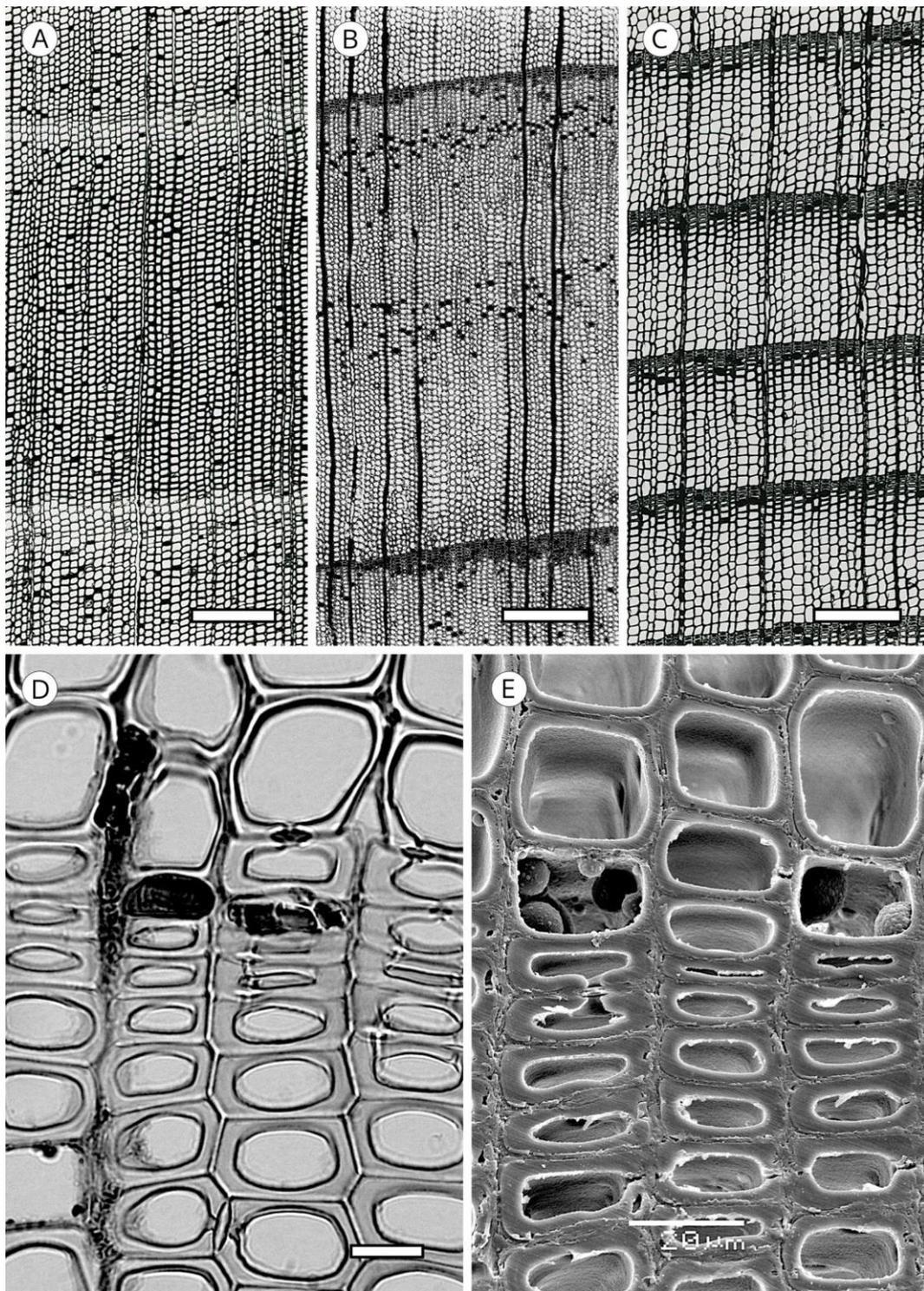


Figure 26. Arrangement of axial parenchyma. (A) Diffuse in *Dacrydium elatum* (Roxb.) Wall. ex Hook.; (B) Tangentially zonate in *Juniperus excelsa* M.Bieb.; (C) Marginal in *Fitzroya cupressoides* (Molina) I.M.Johnst.; (D) Marginal in *Hesperocyparis macrocarpa* (Hartw.) Bartel (Syn. — *Cupressus macrocarpa* Hartw.); (E) Marginal in *Juniperus chinensis* L. (SEM). Scale bars. (A) = 350 μm ; (B) = 600 μm ; (C) = 400 μm ; (D) = 25 μm .

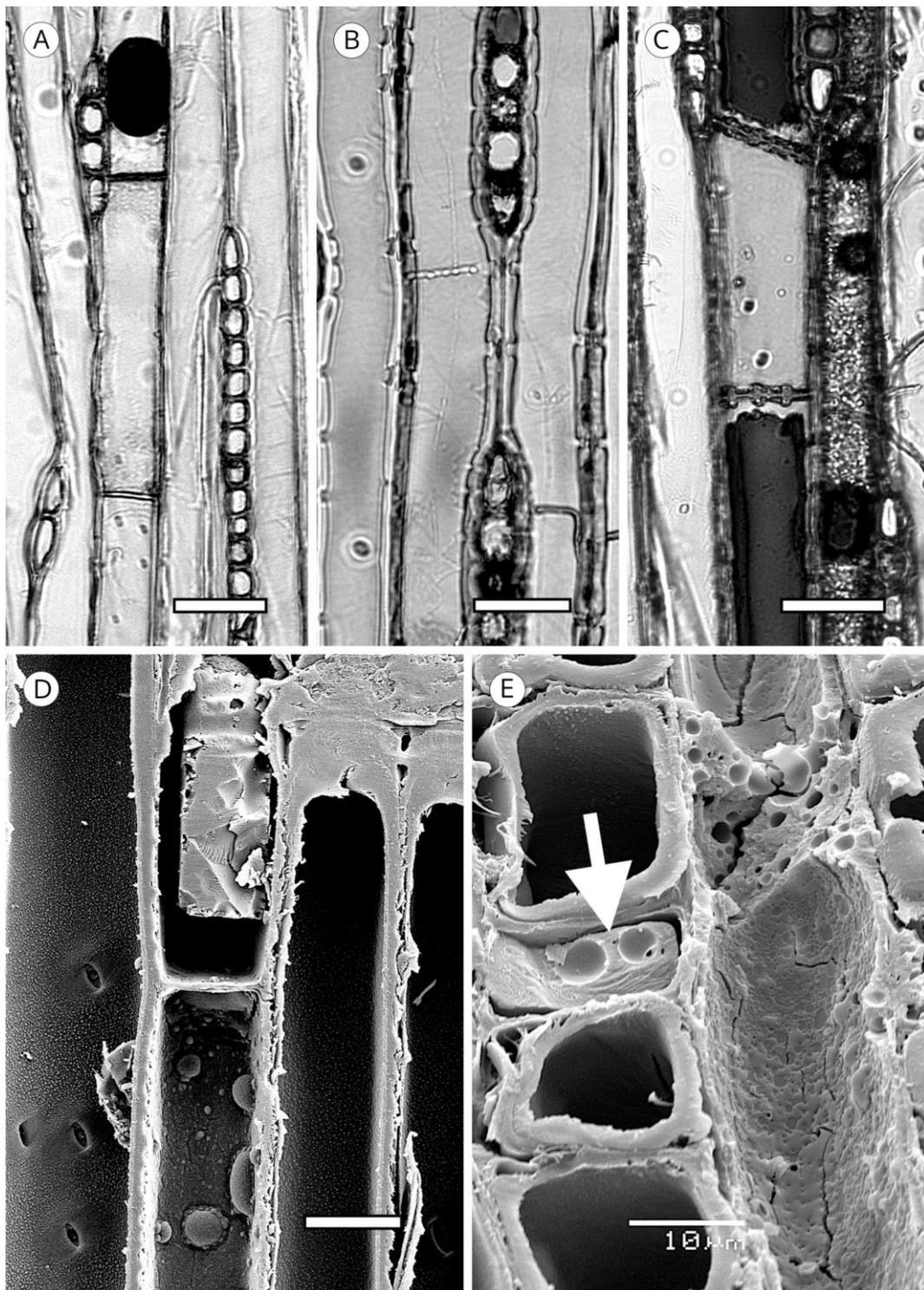


Figure 27. Transverse end walls of axial parenchyma. (A) Smooth in *Cunninghamia konishii* Hayata; (B) Irregularly thickened in *Juniperus canariensis* Guyot and Mathou; (C) Nodular in *Taxodium distichum* (L.) Rich.; (D) Smooth in *Callitris robusta* (SEM); (E) Nodular in *Juniperus brevifolia* (SEM). Scale bars. (A) = 50 μm ; (B) = 35 μm ; (C) = 50 μm ; (D) = 25 μm .

5.3. Rays

One of the unique wood features of today's conifers is that their rays are uniseriate and occasionally biseriate in some species (Figure 28) [56]. However, the term biseriate is attributed to a sample only when at least 10% of all larger rays are biseriate over nearly the full height [5]. Only the presence of radial resin canals in taxa with longitudinal axial

resin canals (*Cathaya*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga*) causes the presence of thickened fusiform rays around the canal (Figure 28). In some species of the genus *Pinus*, particularly in section *Strobus* (e.g., *P. cembra*, *P. koraiensis*, *P. lambertiana*, *P. monticola* and *P. strobus*), the uniseriate extensions at both ends of the ray may be very high, and this must be taken into account when measuring ray height, ensuring the entire ray is included in the total measurement [5].

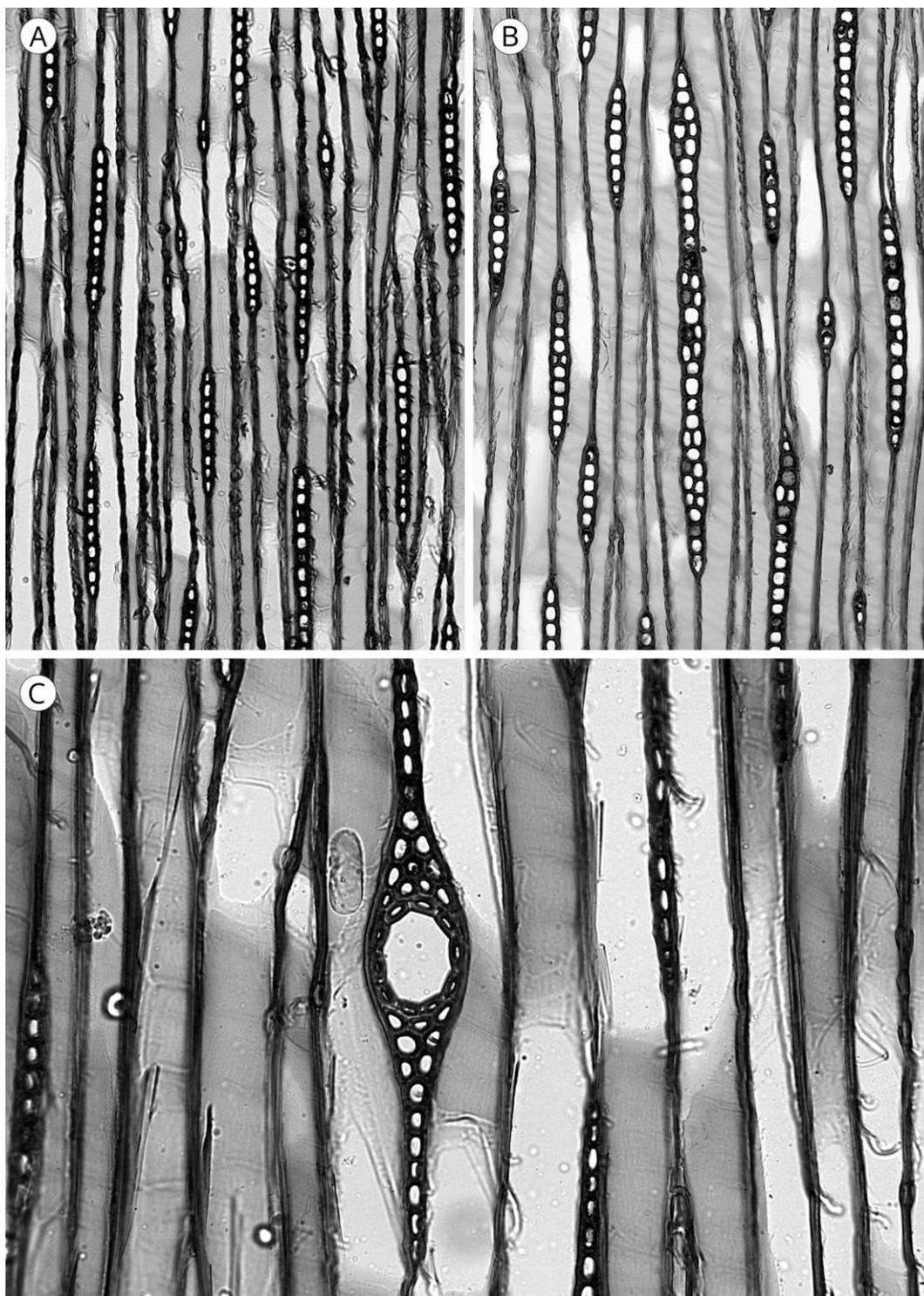


Figure 28. Ray width. (A) Uniseriate in *Abies numidica* de Lannoy ex Carrière; (B) Biseriate in *Cedrus atlantica* (Endl.) Manetti ex Carrière; (C) Fusiform in *Picea alcoquiana* (H.J.Veitch ex Lindl.) Carrière. Scale bars. (A–C) = 100 μ m.

With regard to ray height, fossil records from the Carboniferous have demonstrated the coexistence of wood with uniseriate rays one or two cells high, as in the genus *Biliginea*, and wood with multiseriate rays up to 100 cells high in *Calamopitys* and *Pitus* [92,141,142].

Ray height is a good diagnostic feature in conifer wood. In *Abies* it is used, among other features, to separate the genus from other genera and even to differentiate groups of species in the genus [113,143]. Ray height is expressed in number of cells or in μm . Esteban et al. [56] and the IAWA Committee [5] proposed very similar thresholds for number of cells. The first authors proposed three categories (1 to 15, 16 to 30 and more than 30), while the IAWA Committee [5] proposed a fourth range in the lowest heights: up to 4 cells, 5 to 15, 16 to 30 and more than 30. In any case, ray height in number of cells can be a feature common to a group of softwoods in taxonomic terms, e.g., in Cupressaceae [93].

Ray height must always be measured in mature wood because of the differences between mature and juvenile wood, as it is lower in juvenile wood.

5.3.1. Ray Tracheids

A softwood ray in its most complex composition is made up of ray tracheids, ray parenchyma cells and resin canal epithelial cells. When it is composed of ray tracheids and parenchyma cells, it is termed heterocellular. In contrast, when it comprises only ray parenchyma cells, it is termed homocellular [94] (Figure 29). Although the position of tracheids in the ray has no diagnostic value, they may be above or below the ray, i.e., in marginal rows, e.g., *Larix*, *Picea* and *Pinus*, or in alternate rows, both marginal and inside the ray [64] (Figure 29). In some taxa, rays can be composed solely of tracheids, as in species of southern yellow pine and very rarely in species of *Picea* and *Larix* [65,131]. Ray tracheids have the same characteristics as axial tracheids, but differ slightly in morphology and pit size. Ray tracheids are usually more irregularly shaped, with less tapered end walls, especially in marginal arrangement, and ray tracheid pits are always smaller in diameter than pits in the radial walls of longitudinal tracheids [56].

In Pinaceae, ray tracheids are found only in taxa with normal resin canals, except for *Tsuga*, which lacks resin canals.

In Abietoideae, *Tsuga* invariably has ray tracheids, *Cedrus* frequently has them, *Abies*, *Nothotsuga* and *Pseudolarix* rarely have them and they are absent in *Keteleeria*. The absence of ray tracheids in *Keteleeria* has diagnostic value because it separates it from *Nothotsuga*, as they are the only two genera of all the conifers that have only normal axial resin canals [14].

Other non-Pinaceae species have ray tracheids, particularly Cupressaceae, e.g., *Cupressus arizonica*, *Sequoia* and *Thujopsis dolabrata* [52], and *Callitropsis nootkatensis*, which has some rays formed solely of tracheids and others solely of parenchyma cells [5] (Figure 29).

Hudson [144] proposed a classification of ray tracheids in *Pinus* with 14 groups based on degree of dentation, from very slight horizontal wall thickenings in *P. cembra* to reticulate in *P. ponderosa*, *taeda* and *palustris*.

The IAWA Committee [5] and Heinz [57] established **three types** of degree of dentation in ray tracheids: **smooth**, e.g., the “soft pines” group (*Pinus*, section *Strobus*: e.g., *P. cembra*, *P. koraiensis*, *P. lambertiana*, *P. monticola* and *P. strobus*); **dentate**, with dentations of variable thickness arranged as protrusions from the upper and lower cell wall of ray tracheids, very prominent in *Pinus*, e.g., sections *Sylvestris* (e.g., *P. densiflora*, *P. nigra*, *P. resinosa* and *P. sylvestris*) and *Ponderosa* (e.g., *P. contorta*, *P. patula*, *P. pinaster*, *P. ponderosa* and *P. radiata*); less prominent and with typically sinuous tracheid walls, e.g., in *Pinus*, sections *Sula* (*P. canariensis*, *P. halepensis*, *P. leucodermis*, *P. longifolia*) and *Khasya* (*P. khasya*); inconspicuous, as in some species of *Picea* [52]; and **reticulate**, when thickenings are thin-walled, very numerous, narrow, with tooth-like protrusions from the top to the bottom of the tracheid, resulting in a characteristic reticulate appearance, e.g., *Pinus*, section *Taeda* (including, i.a., *P. banksiana*, *P. palustris*, and *P. taeda*) (Figure 30). Some authors [119,145]

studied the morphology of tracheid dentations in an attempt to differentiate very closely related species, e.g., *Pinus nigra* and *P. sylvestris*, but the results obtained were not conclusive.

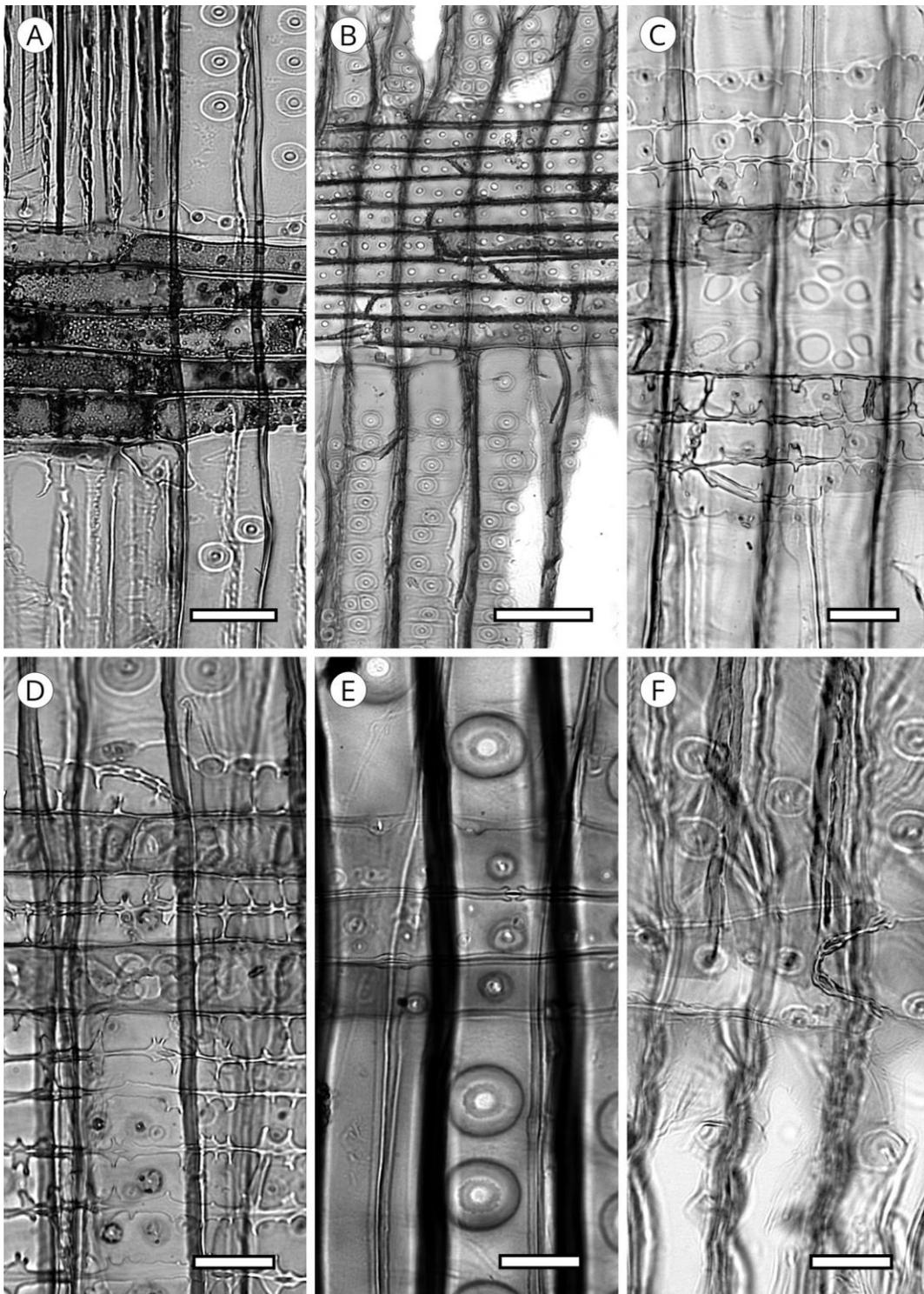


Figure 29. Ray composition. (A) Heterocellular ray composed of internal rows of ray parenchyma cells and marginal tracheids in *Nothotsuga longibracteata* (W.C.Cheng) H.H.Hu ex C.N.Page; (B) Homocellular ray composed solely of parenchyma cells in *Keteleeria davidiana* (C.E.Bertrand) Beissn.; (C) Heterocellular ray composed of ray tracheids in marginal rows in *Pinus arizonica* Engelm.; (D) Heterocellular ray composed of ray tracheids in alternate rows, both marginal and inside the ray in *Pinus arizonica* Engelm.; (E) Homocellular ray composed solely of ray tracheids in *Pinus armandii*

Franch.; (F) Homocellular ray composed solely of compound ray tracheids in *Callitropsis nootkatensis* (D.Don) Oerst. Scale bars. (A,B) = 50 μm ; (C–F) = 25 μm .

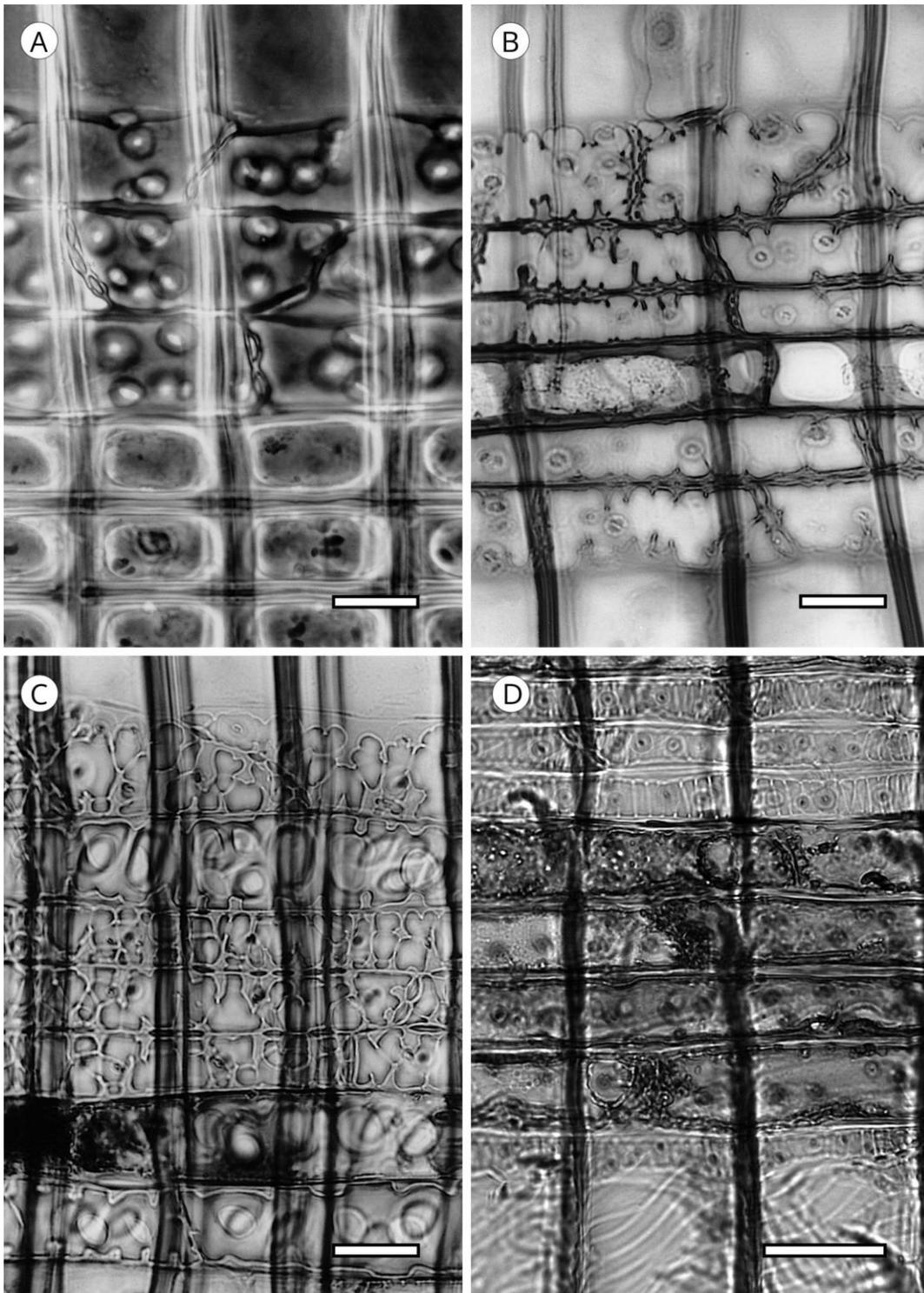


Figure 30. Ray tracheid walls. (A) Smooth in *Pinus strobus* L.; (B) Dentate in *Pinus sylvestris* L.; (C) Reticulate in *Pinus pungens* Lamb; (D) With helical thickenings in *Pseudotsuga sinensis* Dode. Scale bars. (A–D) = 25 μm .

Esteban et al. [129], following the classification of the **three types** of dentations, included the following species of *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* and *P. wallichiana*), **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* and *P. tropicalis*), 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* and *P. tecunumanii*).

In the ray tracheids of some species, helical thickenings develop with the same characteristics as thickenings in axial tracheids (Figure 30), e.g., *Cathaya argyrophylla* [128], *Pseudotsuga sinensis* [129], some species of *Larix* (*L. potaninii* var. *himalaica* [69] *L. sibirica* [57], and *Picea* (*P. polita*) [60], *P. spinulosa* and *P. torano* [129]. In other species, e.g., *Pseudotsuga menziesii* and *Larix kaempferi*, helical thickenings rarely occur [5] and have no diagnostic value due to their variable occurrence [57].

In the radial section, Bartholin [66] studied the morphology of the aperture in ray tracheid pit borders in *Picea*, distinguishing two types: pits that are thickened by small lumps, giving the aperture the appearance of a narrow canal (*Picea*-1 type), and thickenings resembling small horns on the edge of the pit aperture (*Picea*-2 type). This anatomical peculiarity enables differentiation between *Picea* and *Larix*, as the latter has ray tracheid pits with larger apertures [66,130] (Figure 31).

5.3.2. Ray Parenchyma

Most conifer wood has horizontal walls of ray parenchyma cells that are thin and have no pitting. Species with pitted horizontal walls are limited to all genera of Pinaceae (*Abies* (Figure 32B,C), *Cathaya*, *Cedrus*, *Keteleeria*, *Larix*, *Nothotsuga*, *Picea*, *Pseudotsuga* and *Tsuga*), although numerous species of *Pinus* do not conform to this [5,57,129]; pitted horizontal walls are inconspicuous in *Pseudolarix* [14]. Heinz [57] described intermediary situations with the presence of smooth to slightly pitted horizontal walls in *Calocedrus*, *Cryptomeria*, *Cupressus*, *Juniperus*, *Metasequoia*, *Platycladus*, *Taxodium* (Figure 32A), *Thuja* (Cupressaceae), *Taxus* and *Torreya* (Taxaceae).

Like the horizontal walls, end walls in most conifer woods are thin, with little or no pitting. Nodular end walls are limited to the genera of Pinaceae (absent in some species of *Pinus*, slightly nodular in *Pinus* section *Strobus* (e.g., *P. cembra*, *P. koraiensis*, *P. lambertiana*, *P. monticola* and *P. strobus*) [5] and Cupressaceae. In *Abies* they are present in all species [113]. They are considered characteristic of this genus [52,53,146] and can be used to differentiate *Abies* from the other conifer genera, except for those in Abietoideae, as the presence of nodules in end walls is common to the whole subfamily [14]. In Cupressaceae, nodular end walls are different in appearance, occurring in *Calocedrus*, *Cunninghamia* (normally smooth), *Cupressus*, *Diselma*, *Fitzroya*, *Juniperus* and *Xanthocyparis* [86] (Figure 33). From our observations in the two species of *Cunninghamia* we cannot confirm that they are mostly smooth. A review of the literature shows that most authors report smooth end walls, whereas we observed both smooth and distinctly nodular end walls. Moreover, some genera, especially *Juniperus* and *Cupressus*, have smooth and nodular end walls in a single species and many transitional forms can be found, and therefore, this feature should be used with caution.

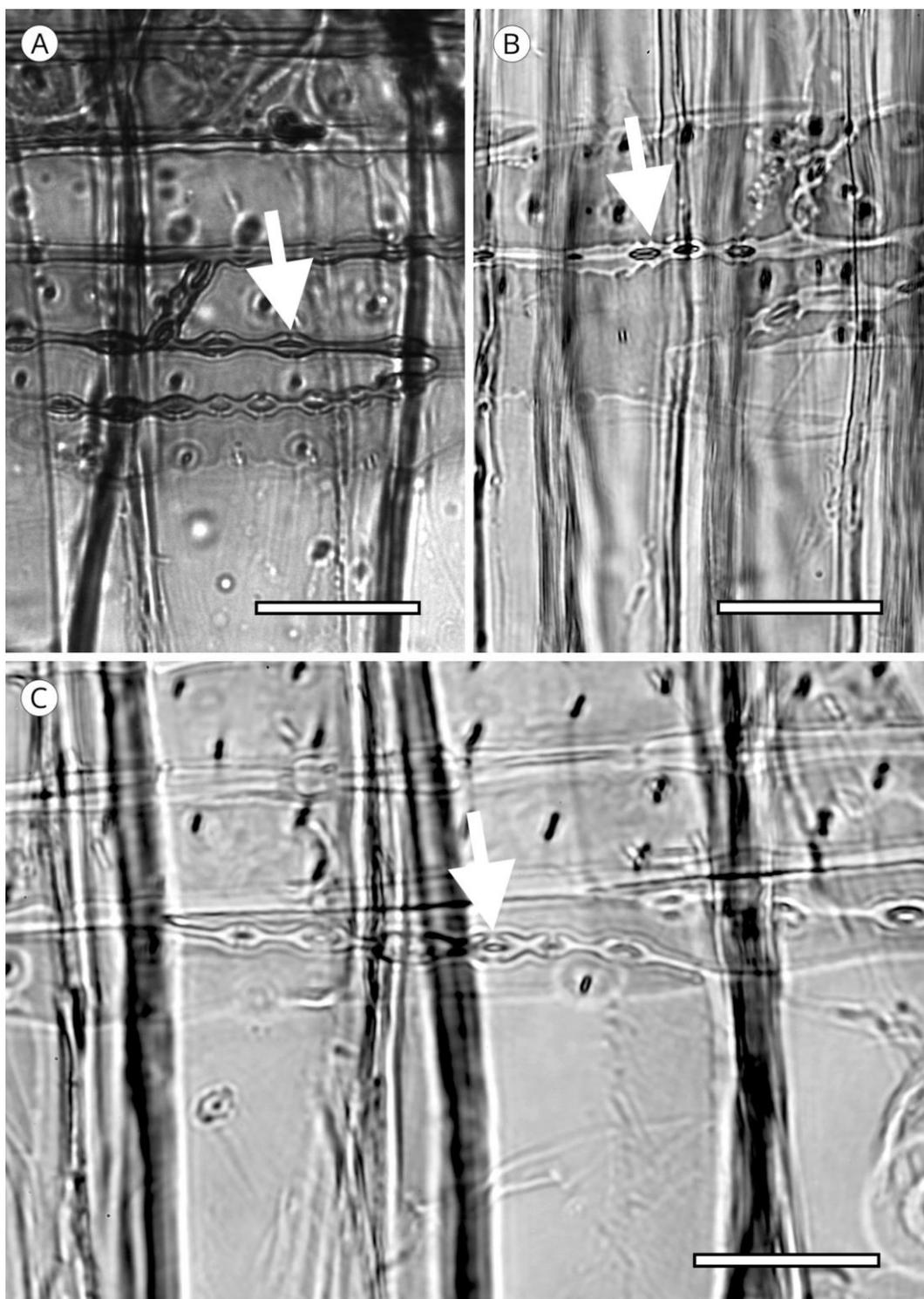


Figure 31. Pit borders of ray tracheids. (A) Pit apertures narrow in *Picea alcoquiana* (H.J.Veitch ex Lindl.) Carrière; (B) Pit borders with dentate thickenings in *Picea abies* (L.) H.Karst.; (C) Pits with wide apertures in *Larix laricina* (Du Roi) K.Koch. Scale bars. (A–C) = 25 μ m.

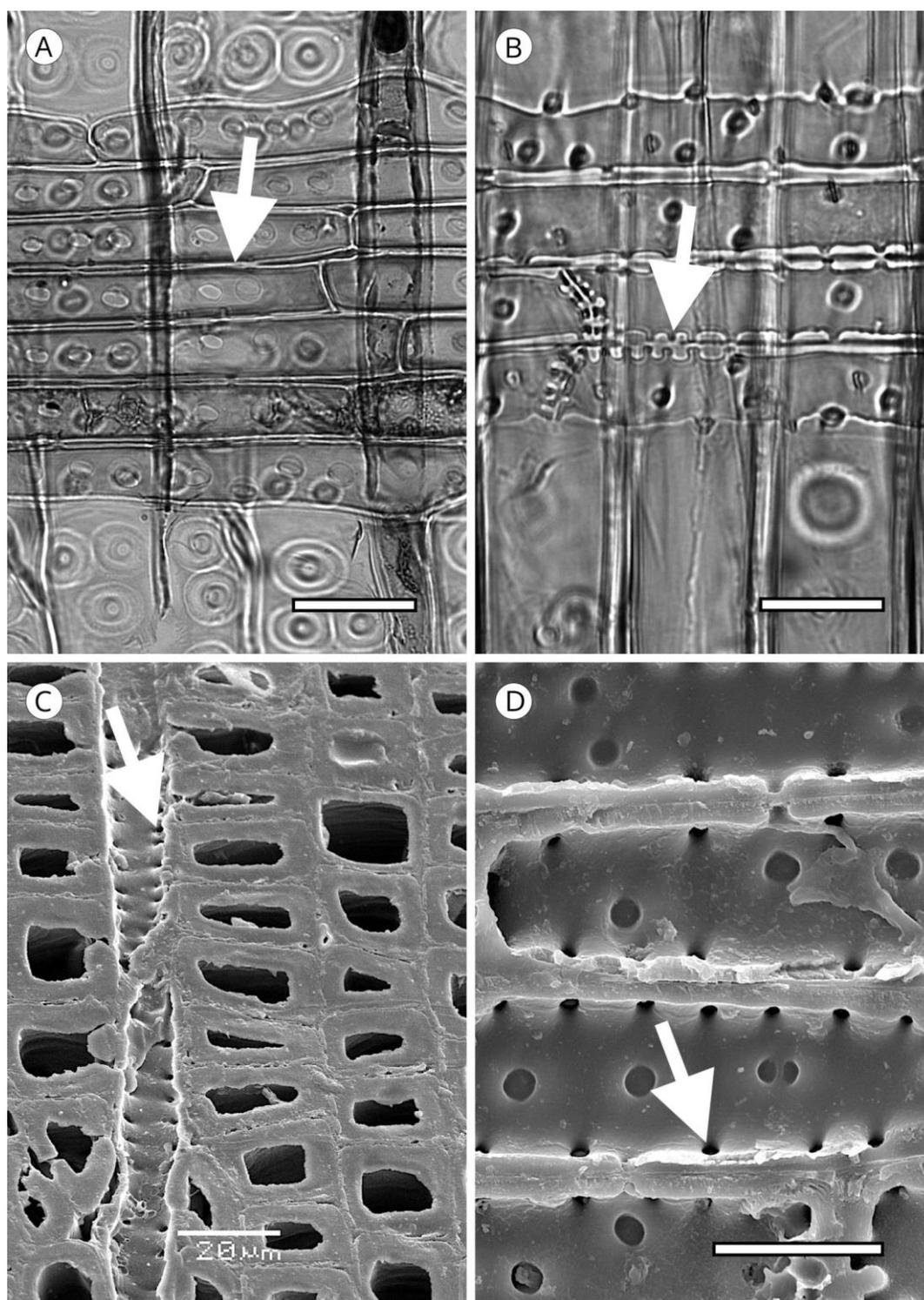


Figure 32. Horizontal walls of ray parenchyma cells. (A) Smooth in *Taxodium distichum* (L.) Rich.; (B) Pitted in *Abies procera* Rehder; (C) Pitted in *Abies veitchii* Lindl. (SEM); (D) Pitted in *Abies cilicica* (Antoine & Kotschy) Carrière (SEM). Scale bars. (A,B) = 50 µm; (D) = 25 µm.

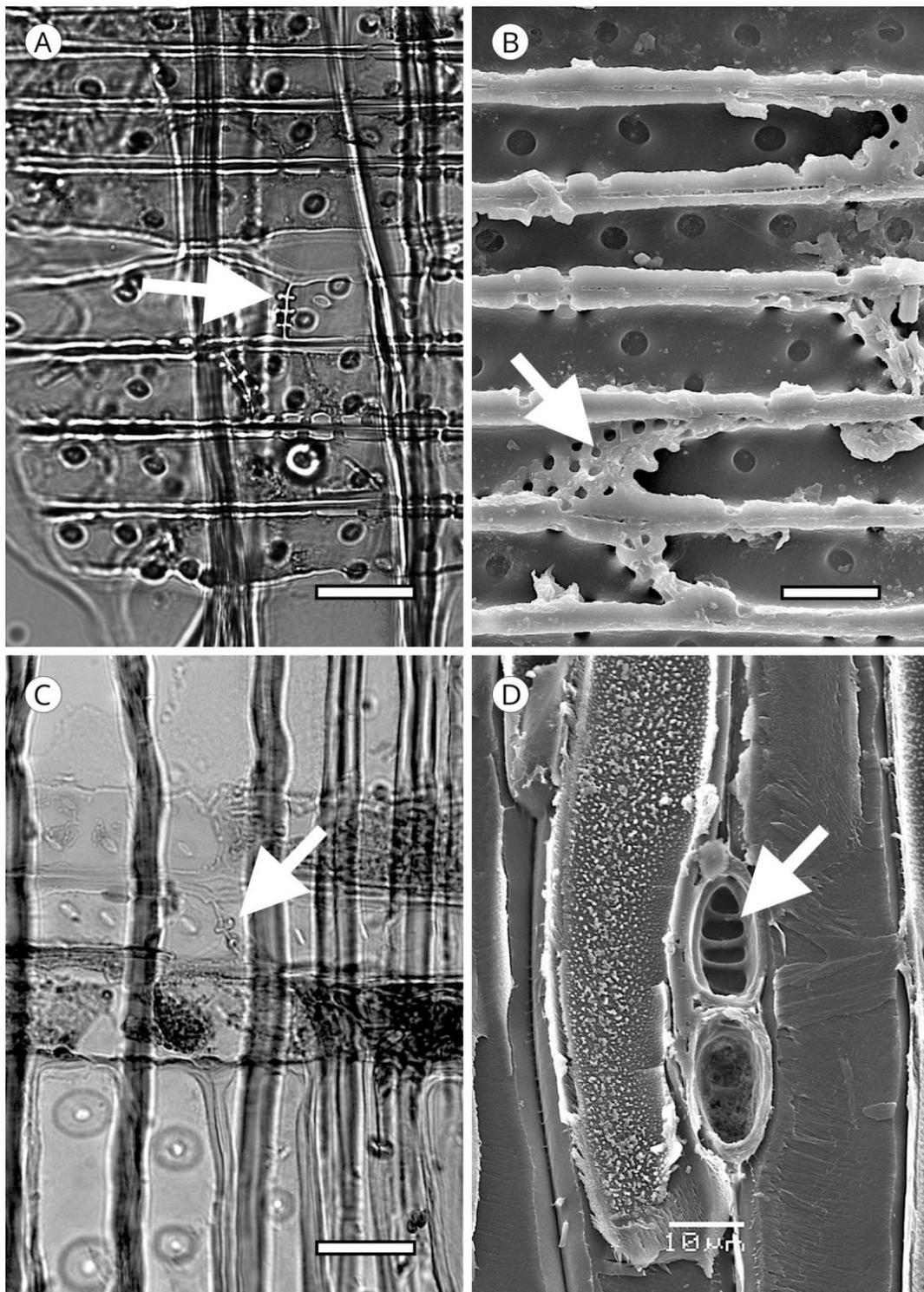


Figure 33. Nodular end walls of ray parenchyma cells. (A) *Abies alba* Mill.; (B) *Abies cilicica* (Antoine & Kotschy) Carrière (SEM); (C) *Fitzroya cupressoides* (Molina) I.M.Johnst.; (D) *Juniperus californica* Carrière (SEM). Scale bars. (A–C) = 25 μ m.

At the junction of end walls with horizontal walls of ray parenchyma cells, depressions can appear. Peirce [47] first named them **indentures**, reporting them as particularly common in the genera *Cunninghamia* and *Taiwania* (Cupressaceae). According to Phillips [52], indentures occur in all conifer families except Araucariaceae; in Podocarpaceae they are present only in *Podocarpus salignus* and *Dacrycarpus* (*Podocarpus dacrydioides*), and in *Cedrus*, *Keteleeria* and *Pinus* (Pinaceae) they are only poorly developed. However, Esteban

and de Palacios [14] reported that they are clearly visible in all genera of Abietoideae (*Abies*, *Cedrus*, *Keteleeria*, *Nothotsuga*, *Pseudolarix* and *Tsuga*). Yatsenko-Khmelevsky [131] stated that in *Cedrus*, *Keteleeria* and *Pinus* they are poorly developed or absent, while according to Farjon [19], they must be considered a feature of diagnostic value in Cupressaceae s.l. In fact, Román-Jordán [86] recorded them in *Austrocedrus*, *Calocedrus*, *Cryptomeria*, *Cunninghamia*, *Fokienia*, *Glyptostrobus*, *Pilgerodendron*, *Sequoia*, *Taxodium* and *Xanthocyparis* (Figure 34). To avoid misidentification, this feature should be used with caution and not in wood with poorly defined and rare indentures [5].

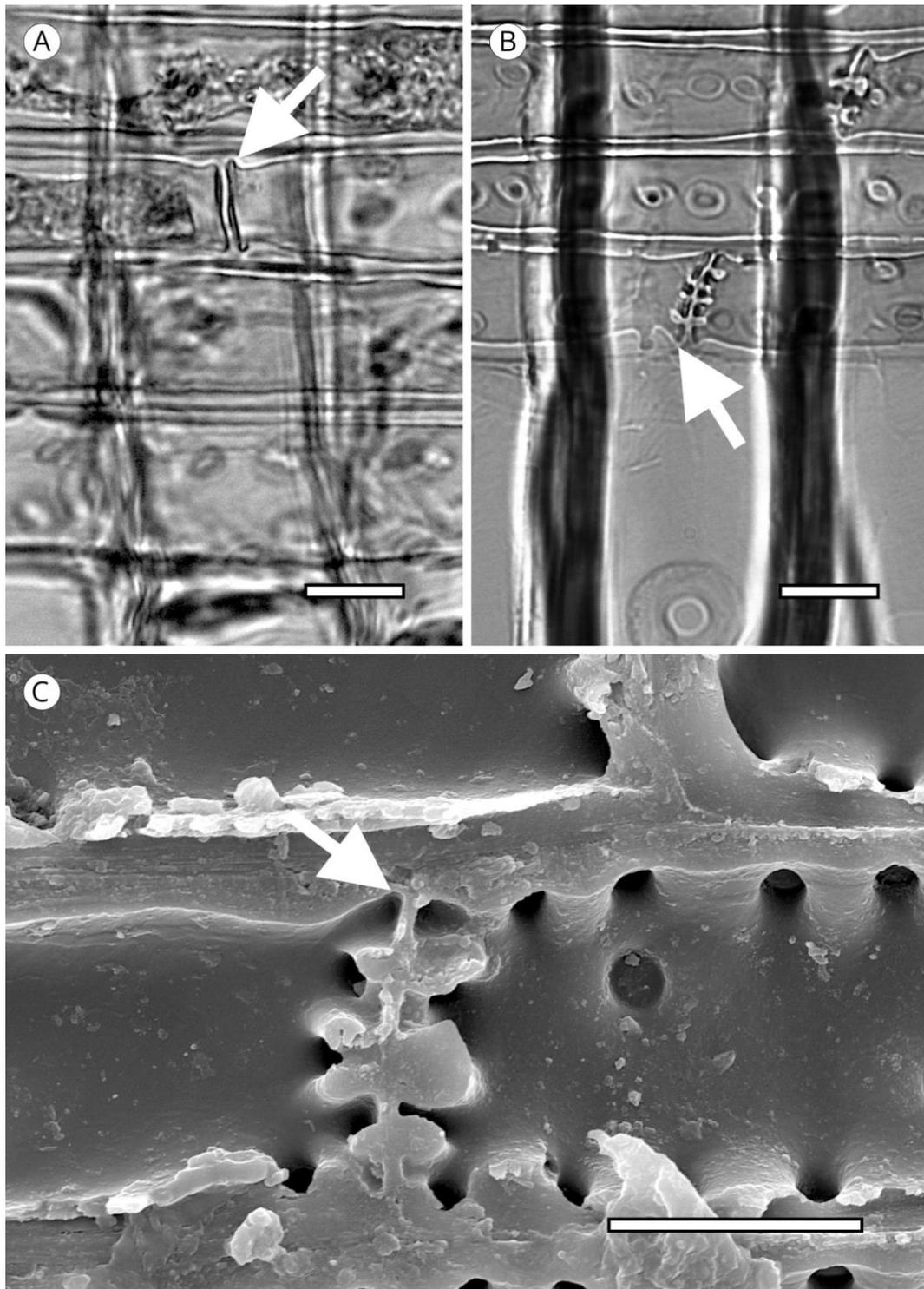


Figure 34. Indentures. (A) *Calocedrus decurrens* (Torr.) Florin; (B) *Abies cilicica* (Antoine & Kotschy) Carrière; (C) *Abies lasiocarpa* (Hook.) Nutt. (SEM). Scale bars. (A–C) = 25 μ m.

In nearly all species of *Abies* [113] and in *Cedrus* [34], irregularly shaped parenchyma cells that are easily distinguishable from other cells frequently appear in the marginal rows of the rays (Figure 35). This feature can be used to differentiate *Abies* and *Cedrus* from the other genera.

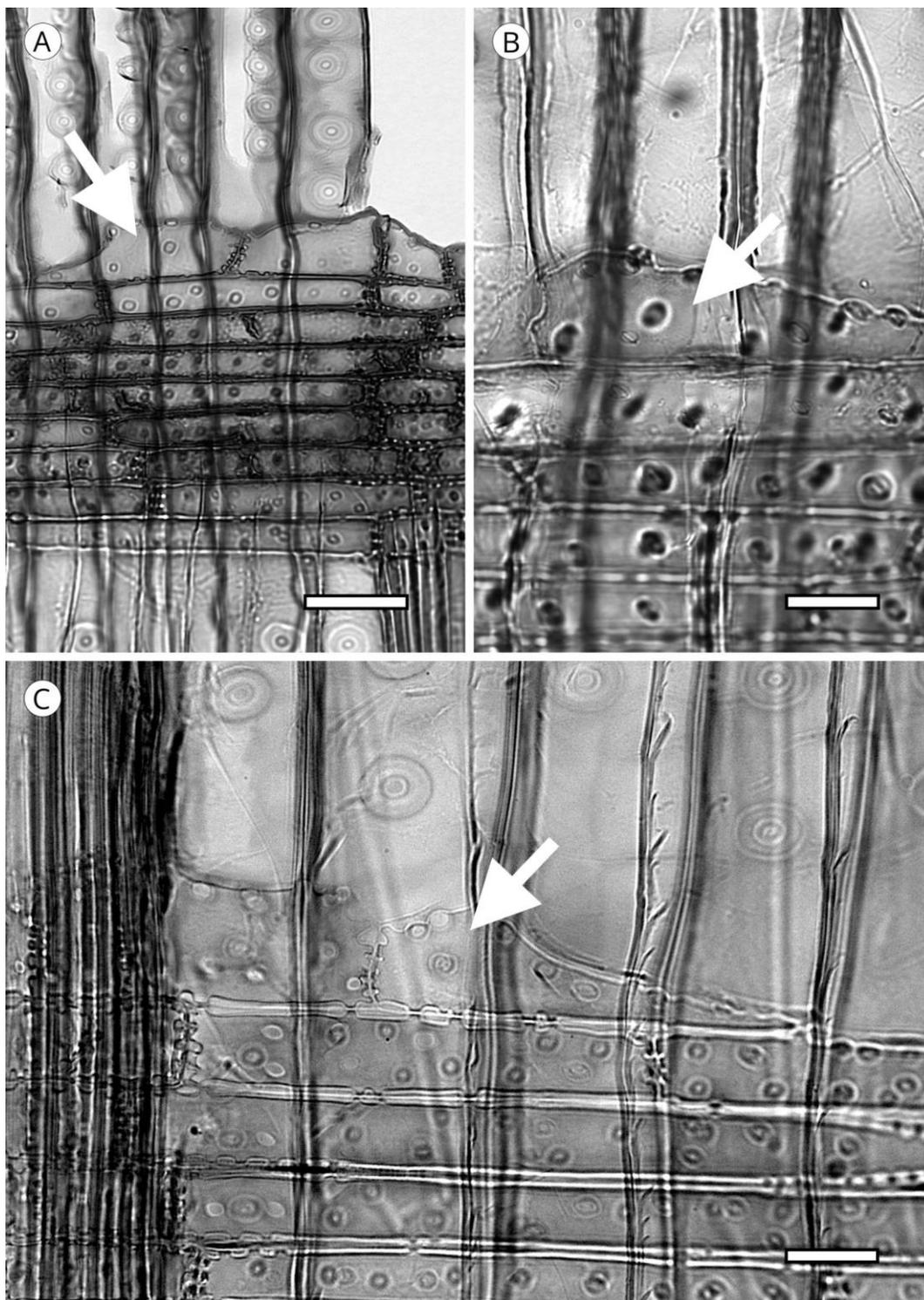


Figure 35. Irregular parenchyma cells in the marginal rows of the rays. (A) *Abies fraseri* (Pursh) Poir.; (B) *Abies hickelii* Flous and Gausсен; (C) *Abies nephrolepis* (Trautv.) Maxim. Scale bars. (A) = 50 μm ; (B,C) = 25 μm .

5.3.3. Cross-Field Pitting

Cross-field pitting is undoubtedly one of the most valuable analytical features for softwood identification. Pits are located in the area of contact between the intersecting walls of a single longitudinal tracheid and a single ray parenchyma cell as seen in radial section. The cross-field pit features analysed are the frequency, arrangement, form, size and/or position of the aperture relative to the border of the pits.

Cross-field pit types are based on the classification established by Phillips [52] to which the IAWA Committee [5] added the araucarioid type used by Barefoot and Hankins [55] and re-evaluated by Vogel [73] (Figures 36 and 37):

Window-like. Pits occupy nearly the entire cross-field. They are square or rectangular and there are usually one or two per cross-field. They have almost no borders and are exclusive to the genus *Pinus* (sections *Strobus* and *Sylvestris*) (Pinaceae) IAWA Committee [5], *Lagarostrobos*, *Phyllocladus*, *Sundacarpus amarus* (Podocarpaceae) and *Sciadopitys* (Sciadopityaceae) (Phillips, 1941) [52]. According to Rol [147], *Pinus kesiyi* and *P. merkusii* should be included as examples of taxa that present these types of pits with more than two pits per cross-field [5].

Pinoid. These pits are simple or have almost no border. They are irregularly shaped and highly variable in number, with up to six pits per field, normally with three or more. Pinoid pits are exclusive to the species of the genus *Pinus* that do not have window-like pits.

Piceoid. Pits have borders and the apertures, in this case, are long, narrow, typically oval and extend beyond the borders. These are the smallest of all the pit types. This type of pitting occurs in Pinaceae in *Cathaya* [128], *Larix*, *Picea* and *Pseudotsuga* [5] and all the genera of Abietoideae except *Nothotsuga* [14].

Cupressoid. Pits have borders and the oval apertures are contained entirely within them. This type of cross-field pitting is characteristic of Cupressaceae, except for the genus *Thuja*, where pitting is taxodioid. It is also present in Podocarpaceae and Taxaceae.

Taxodioid. These are large pits, oval to circular, with apertures of the same shape. The aperture exceeds the width of the border at its widest point. These pits occur in most of the former family Taxodiaceae (now Cupressaceae), e.g., *Cunninghamia*, *Sequoia*, and *Taxodium*, although they have also been reported in *Thuja* (Cupressaceae), in some species of Podocarpaceae [5] and in Abietoideae (*Abies*, *Cedrus*, *Nothotsuga* and *Pseudolarix*) [14]. However, taxodioid pits in the subfamily Abietoideae are considerably smaller and similar in size to piceoid pits, with included apertures within the limits of the pit border (contrary to the often extended piceoid pits). In the literature they are also referred to as “abietoid” pits [53]. In some Cupressaceae genera, in particular *Sequoia* and *Taxodium*, pits are usually arranged in rows of two or three per cross-field except in marginal cells [5]. Many transitional forms between cupressoid and taxodioid cross-field pitting occur, and therefore, both types should be taken into account for identification if necessary.

Araucarioid. Restricted to Araucariaceae (*Agathis*, *Araucaria* and *Wollemia*). These are cupressoid pits but with a different grouping, with a tendency to crowd, which gives pit perimeters the appearance of alternate polygonal pits (honeycomb-like) similar to those in axial tracheids in Araucariaceae.

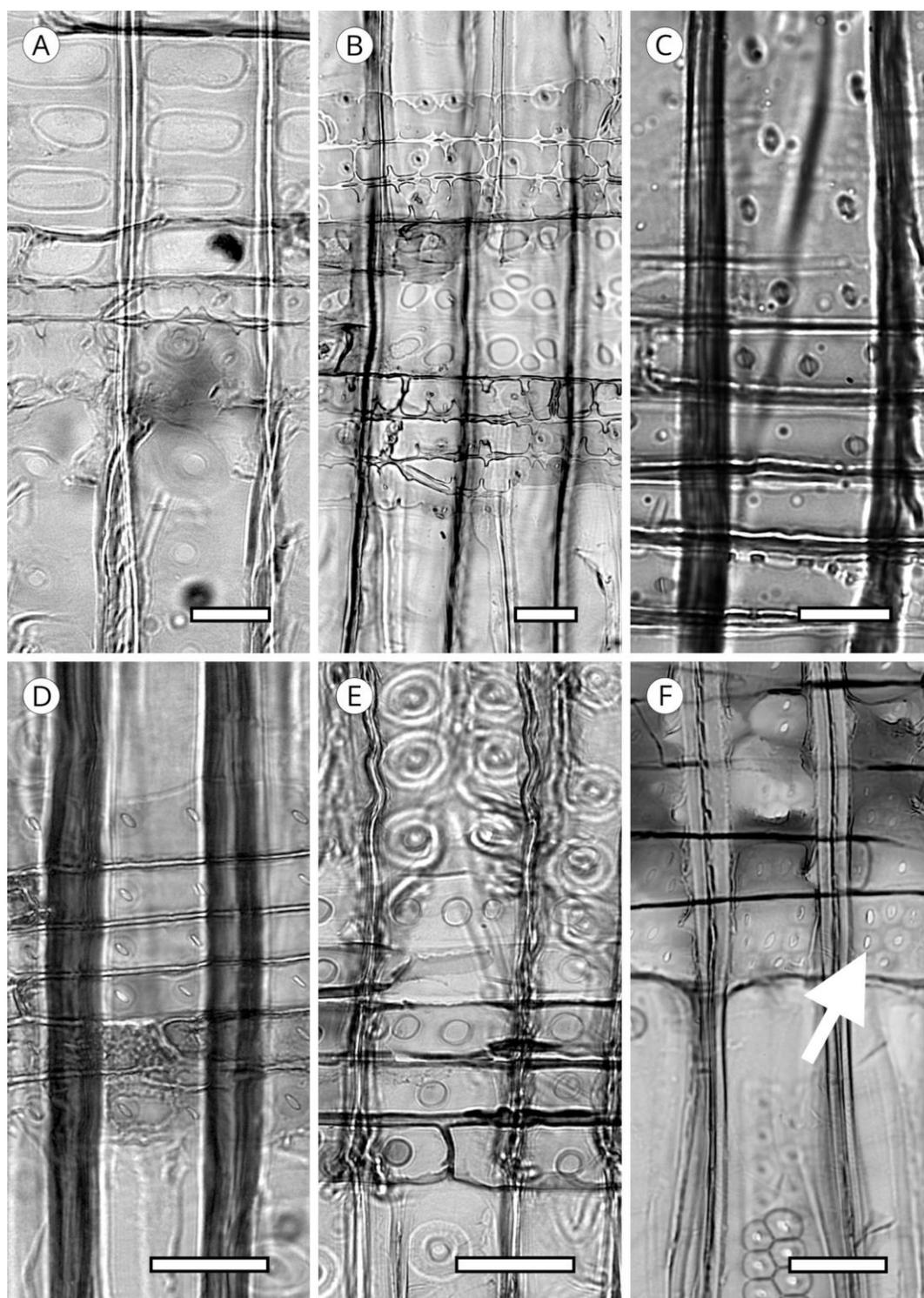


Figure 36. Cross-field pitting. (A) Window-like in *Pinus resinosa* Aiton; (B) Pinoid in *Pinus arizonica* Engelm.; (C) Piceoid in *Abies cilicica* (Antoine & Kotschy) Carrière; (D) Cupressoid in *Juniperus canariensis*, Guyot and Mathou; (E) Taxodioid in *Metasequoia glyptostroboides*, Hu and W.C.Cheng; (F) Araucarioid in *Araucaria columnaris* (G.Forst.) Hook. Scale bars. (A–F) = 25 μ m.

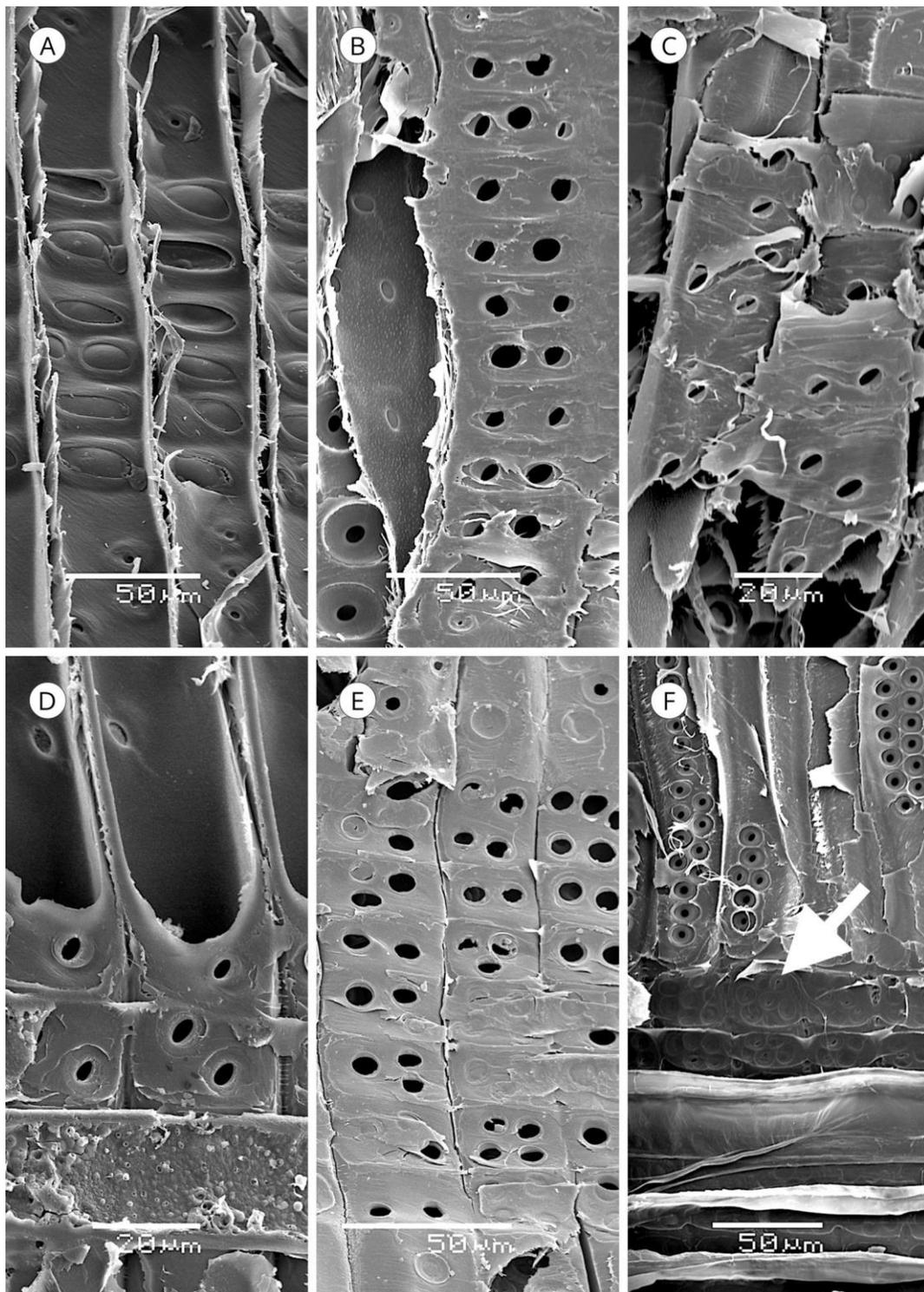


Figure 37. Cross-field pitting (SEM). (A) Window-like in *Sciadopitys verticillata* (Thunb.) Siebold and Zucc.; (B) Pinoid in *Pinus pinea* L.; (C) Piceoid in *Cedrus atlantica* (Endl.) Manetti ex Carrière; (D) Cupressoid in *Juniperus chinensis* L.; (E) Taxodioid in *Glyptostrobus pensilis* (Staunton ex D.Don) K.Koch; (F) Araucarioid in *Araucaria cunninghamii* Mudie.

5.4. Resin Canals

Resin canals are postcambial tubular structures formed by the separation of groups of contiguous cells (schizogenesis) [93]. The cells lining the tubular cavity are derived from fusiform cells in the cambium that have undergone mitotic divisions [67,148,149] from the same type of cells that form axial tracheids. However, rather than maturing into tracheids,

they remain as parenchyma cells, producing transverse walls [93]. The cells enclosing the whole tube constitute the epithelium of the sheath of the resin canal.

In Pinaceae, some taxa have subsidiary cells around the canals (e.g., *Pinus canariensis*) [120], and although some authors called them axial parenchyma cells (e.g., Kibblewhite and Thompson [148] in *Pinus elliottii*, LaPasha and Wheeler [70] in *Pinus taeda*, Howard and Manwiller [134] in the southern yellow pines, Fahn [150] in *Pinus densiflora*, Ickert-Bond [151] in *Pinus krempfii*), Wiedenhoeft and Miller [82] unified the terminology of resin canals, defining the canal as the intercellular space itself and the epithelium as the single layer of cells lining the canal, reserving the term subsidiary cells for the cells outside the epithelium, which can be subsidiary parenchyma and/or strand tracheids. Unlike normal axial tracheids, strand tracheids are shorter and divided by transverse walls containing normal tracheid pits. Some authors considered them to be transitional elements between axial tracheids and epithelial cells or axial parenchyma cells [93], although they based this solely on the association of strand tracheids with one cell type or another (Figure 38).

In *Cathaya*, *Larix*, *Picea* and *Pseudotsuga*, the resin canal is composed solely of the canal itself and the epithelium. However, some authors have reported subsidiary cells in some species of these genera, e.g., Takahara et al. [152] in *Picea abies* and Sato and Ishida [153] in *Larix kaempferi*. In *Pinus* the presence of more than one layer of cells is very frequent [82].

Radial resin canals have similar ontogeny. The canal cavity is also formed by schizogenesis, but in this case, cells with transverse walls are not divided from long cells into shorter units. Some ray cells, rather than becoming ray parenchyma or ray tracheids, are directly converted into epithelial cells [93].

Epithelial cells, which can be thin- or thick-walled, are where the resin released into the canal is produced.

Resin canals are a key feature for the taxonomic position of conifers [44,53,123,150,154–156]. The presence of normal resin canals in Pinaceae has led to various classifications of the family.

Jeffrey [157] made two divisions in Pinaceae: the presence of resin canals in seeds supported the monophyly of *Abies*, *Cedrus*, *Keteleeria*, *Pseudolarix*, *Tsuga*, and resin canals in secondary xylem and leaves with endodermis having thickened Casparian strips supported the monophyly of *Cathaya*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga*. Wu and Hu [155] divided Pinaceae into three groups: with normal resin canals (*Cathaya*, *Pinus*, *Larix*, *Pseudotsuga* and *Picea*); without normal resin canals (*Abies*, *Pseudolarix*, *Cedrus* and *Tsuga*); and normal resin canals absent or present in *Keteleeria*. After confirming the permanent presence of axial resin canals in mature wood in all species of *Keteleeria* and the pattern of traumatic resin canals, Lin et al. [156] proposed a classification of Pinaceae in three groups: with radial and axial resin canals (*Cathaya*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga*); with only axial resin canals (*Keteleeria* and *Nothotsuga*) and without resin canals (*Abies*, *Pseudolarix*, *Cedrus* and *Tsuga*). Esteban and de Palacios [14] confirmed this classification, based on the resin canals and other features of the secondary xylem. Lin et al. [158] suggested that on the basis of the presence of axial resin canals in latewood and resin cavities in their bark, *Nothotsuga* and *Keteleeria* have a high number of similarities. Therefore, based on the presence of resin canals, Abietoideae supports two clearly distinct groups: *Abies*, *Cedrus*, *Pseudolarix* and *Tsuga* without resin canals, and *Keteleeria* and *Nothotsuga* with only axial resin canals.

Various authors have classified the anatomy of resin canals based on the presence of thick- or thin-walled epithelial cells [64,146,149,159–162], while others have attempted to establish the number of epithelial cells surrounding the canals in taxa with thick-walled cells as a distinguishing feature [55,56,60,63]. There is definitely some discrepancy in the intervals proposed, and therefore, the IAWA Committee [5] did not include this feature. Moreover, the IAWA Committee [5] indicated that at times it is difficult to establish a division between thin- and thick-walled epithelial cells, e.g., in *Larix* and *Picea*, because the two types can be mixed. Nonetheless, overall, two large groups of softwood with resin

canals can be distinguished based on the epithelial cells: thick-walled (*Cathaya*, *Keteleeria*, *Larix*, *Nothotsuga*, *Picea* and *Pseudotsuga*) and thin-walled (*Pinus*).

Both axial and radial resin canals can be normal or of traumatic origin [94]. Normal resin canals occur only in some genera of Pinaceae. *Cathaya*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga* have axial and radial resin canals, while *Keteleeria* [52,79,146,156,163] and *Nothotsuga* [158] have only axial resin canals. The absence of resin canals in some descriptions of *Nothotsuga* [154,155,157] is probably because the wood analysed was juvenile or from branches. No conifer taxon contains only normal radial resin canals (Figures 39 and 40).

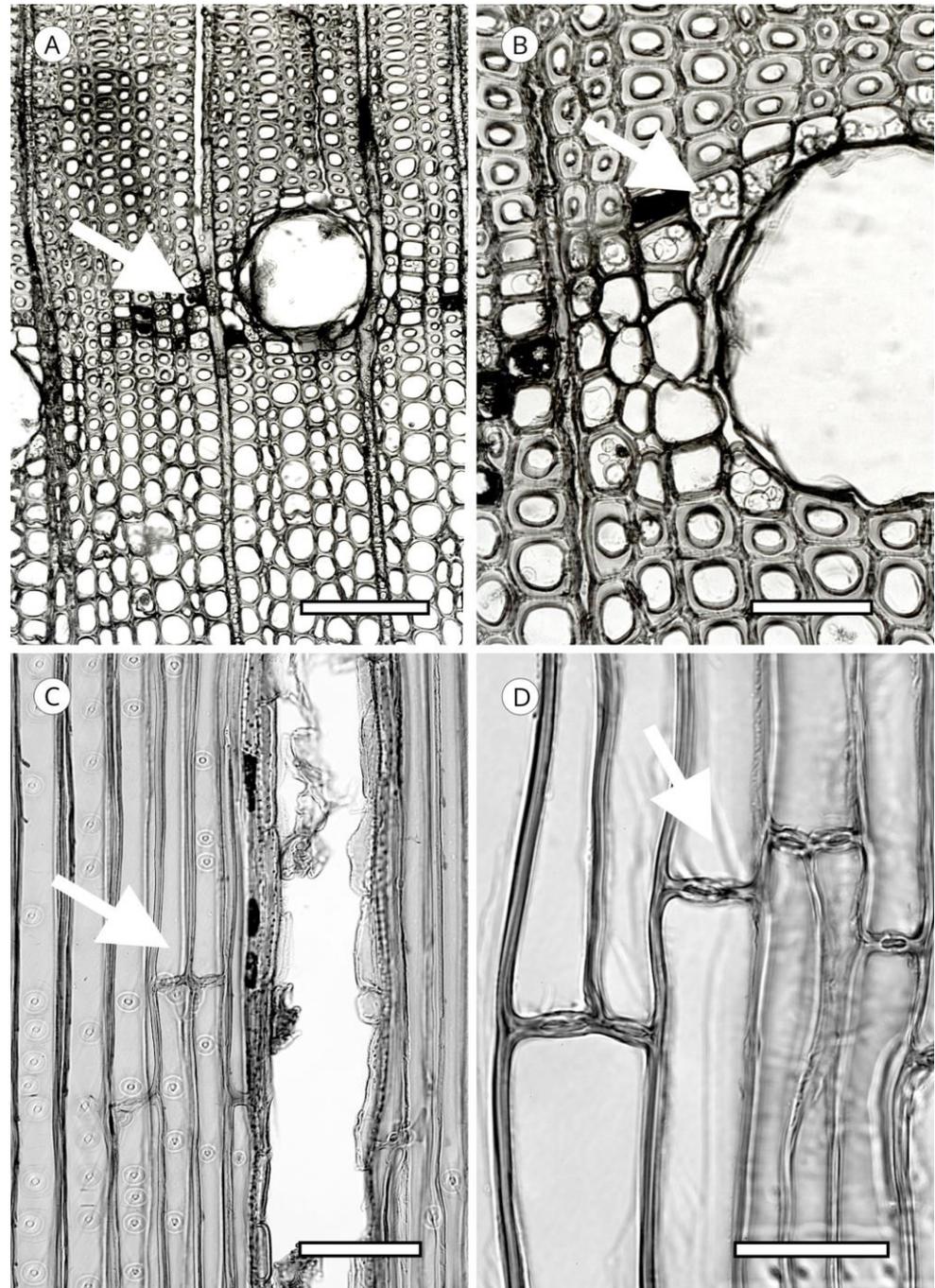


Figure 38. Resin canal subsidiary cells. (A,B) Parenchyma cells with starch content in *Pinus canariensis* C.Sm. ex DC.; (C,D) Strand tracheids in *Picea glehnii* (F.Schmidt) Mast. Scale bars. (A) = 350 μ m; (B–D) = 100 μ m.

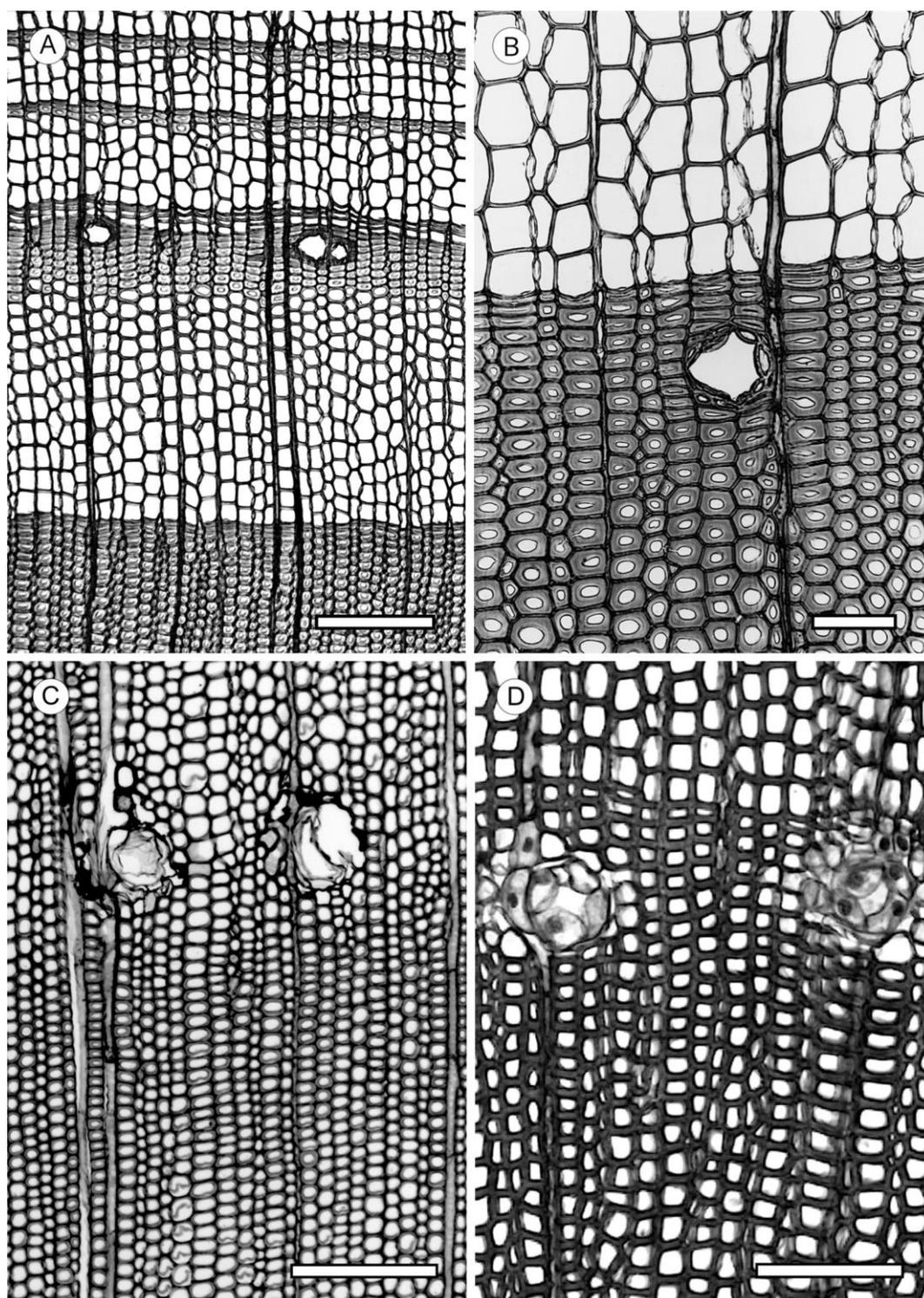


Figure 39. Normal axial resin canals. (A,B) Thick-walled epithelial cells in axial resin canals of *Larix decidua* Mill.; (C) Thin-walled epithelial cells in axial resin canals of *Pinus radiata* D.Don. and (D) Thin-walled epithelial cells in axial resin canals of *Pinus sylvestris* L. Scale bars. (A) = 500 μm ; (B) = 100 μm ; (C) = 200 μm , (D) = 100 μm .

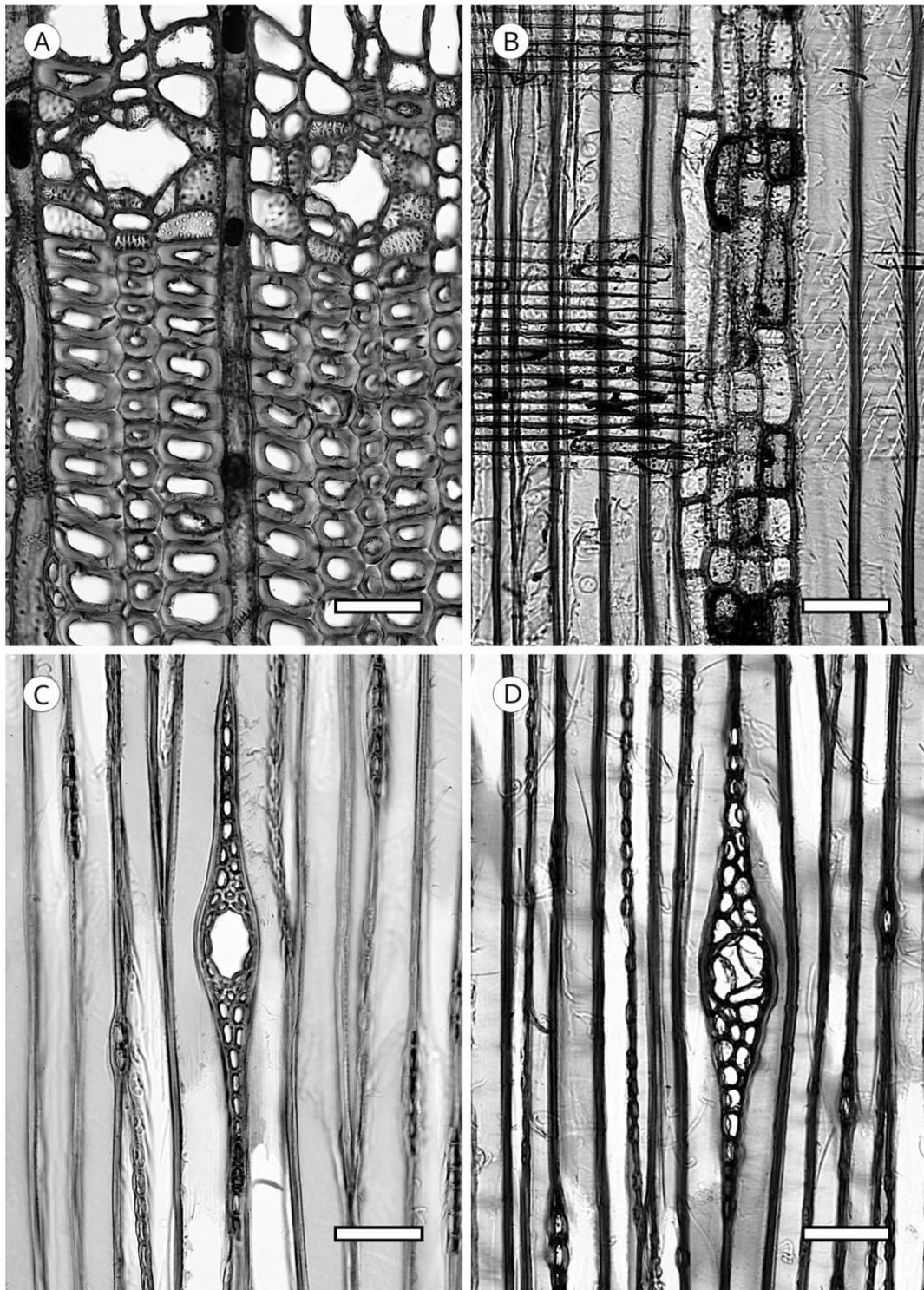


Figure 40. Normal axial and radial resin canals. (A,B) Axial resin canals in *Keteleeria davidiana* (C.E.Bertrand) Beissn.; (C) Thick-walled epithelial cells in radial resin canals of *Picea glehnii* (F.Schmidt) Mast.; (D) Thin-walled epithelial cells in radial resin canals of *Pinus armandi* Franch. Scale bars. (A–D) = 50 μ m.

Traumatic resin canals are formed in response to wounding in Pinaceae, both in genera with normal resin canals (*Cathaya*, *Keteleeria*, *Larix*, *Nothotsuga*, *Picea*, *Pinus* and *Pseudotsuga*) and in genera without them (*Abies*, *Cedrus*, *Nothotsuga*, *Pseudolarix* and *Tsuga*) (Figure 41). In non-Pinaceae genera, they have been reported in *Sequoia sempervirens* [164], *Sequoiadendron* [25], *Microbiota* [165] and *Tetraclinis* [116].

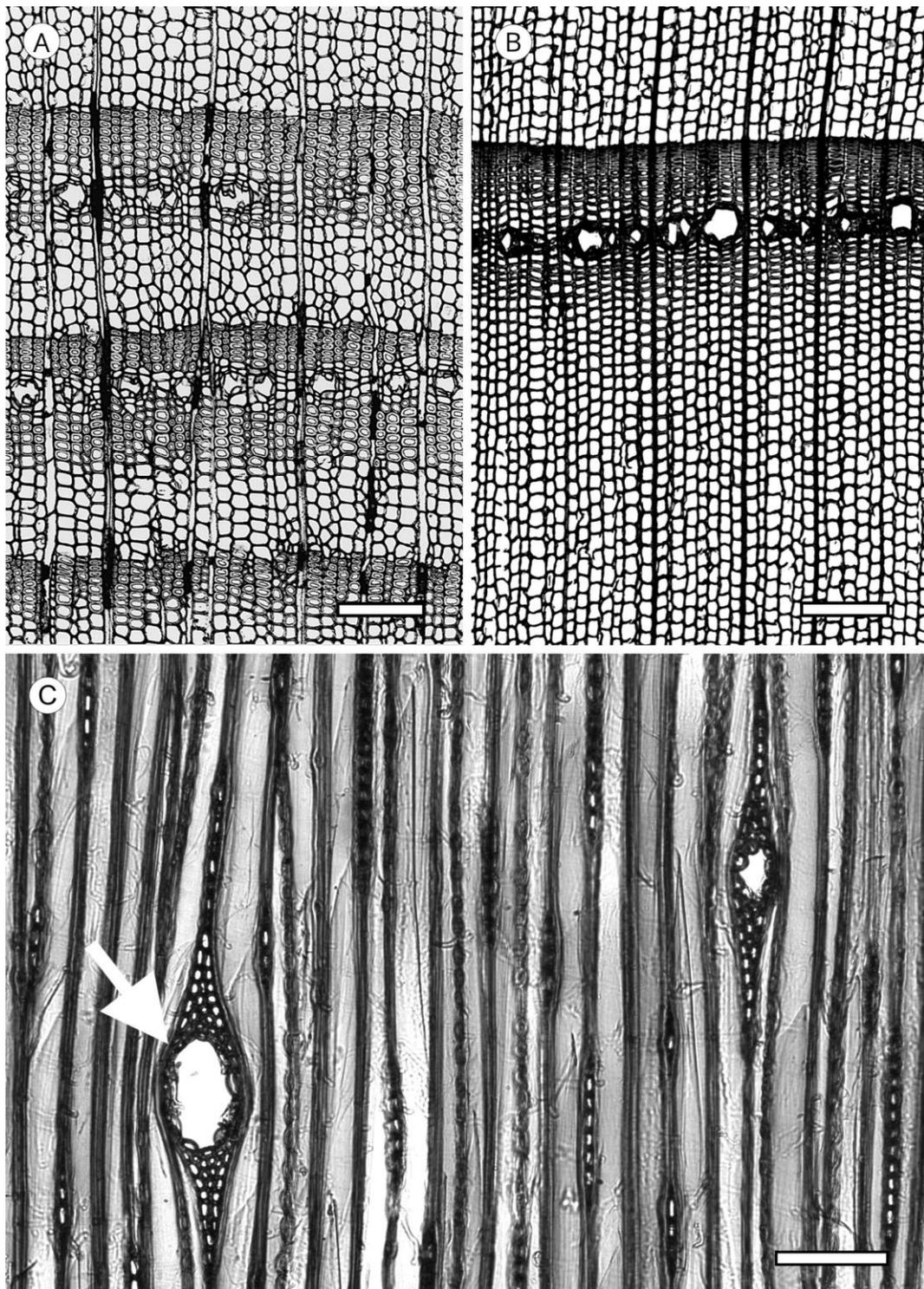


Figure 41. Traumatic axial and radial resin canals. (A) Traumatic resin canals in tangential rows in *Keteleeria davidiana* (C.E.Bertrand) Beissn.; (B) Traumatic resin canals in tangential rows in *Abies nephrolepis* (Trautv.) Maxim.; (C) Radial traumatic resin canals in *Picea abies* (L.) H.Karst. Scale bars. (A,B) = 300 μ m; (C) = 150 μ m.

In *Abies* [146,166–168], *Tsuga* [5] and *Pseudolarix* [155], only axial traumatic resin canals occur, while in *Cedrus*, both axial and radial traumatic canals can be present [14,169]. This is the only genus without normal resin canals in which both types of traumatic resin canals occur simultaneously. *Cedrus* is, therefore, the only genus of Pinaceae (Abietoideae) capable of forming both axial and radial traumatic resin canals as a response to wounding,

and consequently, some authors have considered it an intermediary stage between *Pinus* and *Abies* [167]. According to Gernandt et al. [15], molecular evidence supports the genus *Cedrus* as a sister group to the other Pinaceae and should occupy a basic or root position in the family, such that the subfamily Abietoideae can be considered paraphyletic.

Some authors reported the presence of normal resin canals in *Abies*, e.g., Penhallow [170] in *A. concolor*, *A. bracteata*, *A. nobilis* and *A. firma* and Vierhapper [171] in *A. concolor*, *A. nobilis* and *A. bracteata*, but *Abies*, *Cedrus*, *Tsuga* and *Pseudolarix* lack normal resin canals and form canals only in response to wounding. The four genera have features characteristic of traumatic resin canals, with an irregular perimeter and all appearing in tangential rows.

Although traumatic resin canals were not observed in *Pseudolarix*, in this study, they were reported in the genus as a response to wounding by Wu and Hu [155].

With regard to wood that has only normal axial resin canals, both *Keteleeria* and *Nothotsuga* form traumatic axial resin canals in response to wounding, distributed randomly in single arrangement and/or tangential rows [156]. This arrangement differs from the arrangement in traumatic resin canals in *Abies*, *Tsuga*, *Pseudolarix* [44,167] and *Cedrus* [155], where they are invariably in tangential rows.

For resin canal biometry, one of the main problems in reviewing the literature with regard to size is the lack of indications about the method used. This makes it difficult to compare the results obtained by different authors. The three methods established by the IAWA Committee [5] will undoubtedly solve this problem.

Method A. The tangential diameter of the resin canal, including the epithelial cells, is measured at the widest part of the opening. This is the most frequently used method.

Method B. The tangential diameter of the entire resin canal complex is measured at the widest point, taking in all components of the axial resin canal to the point of differentiation from the axial tracheids.

Method C. The radial diameter of the whole canal complex, including the epithelial cells, is measured at the widest point.

Some authors [53,64,67,93,161] considered that the resin canal size can be used as a diagnostic feature. Others, however, [52,54,172] did not consider it a diagnostic method.

This divergence of criteria is probably due to which of these three methods explained by the IAWA Committee [5] is used, as the choice of method could depend on the species. For example, Wiedenhoeff et al. [173] considered that method A [5] does not allow separation of *Pinus contorta* from *P. ponderosa*, whereas method B, which measures the tangential width of the entire resin canal complex [5], is more reliable.

5.5. Mineral inclusions

The presence of calcium oxalate crystals is not very common in coniferous woods (Figure 42). They have been reported in several species of *Abies* [59,113] in all the genera of Abietoideae [14], in *Picea*, in the form of prismatic crystals, and in *Pinus flexilis* as small styloid crystals. Their regular presence has considerable diagnostic value [5]. In addition, crystals in conifers appear to be located in a single cell type in a given taxon. For example, crystals are arranged in marginal and submarginal rows of ray parenchyma in all genera of Abietoideae [14] and in some species of *Picea* [5]. They have also been observed in the epithelium of axial and radial resin canals in the form of styloids in *Pinus bungeana* [57], *Pinus flexilis* [77], *Pinus aristata*, *P. balfouriana*, *P. longaeva* [68] and *Pinus contorta* [173]. Organic crystalline deposits have been reported in axial tracheids in *Tsuga heterophylla* [174], *Callitris endlicheri* [74] and *Torreya yunnanensis* [75].

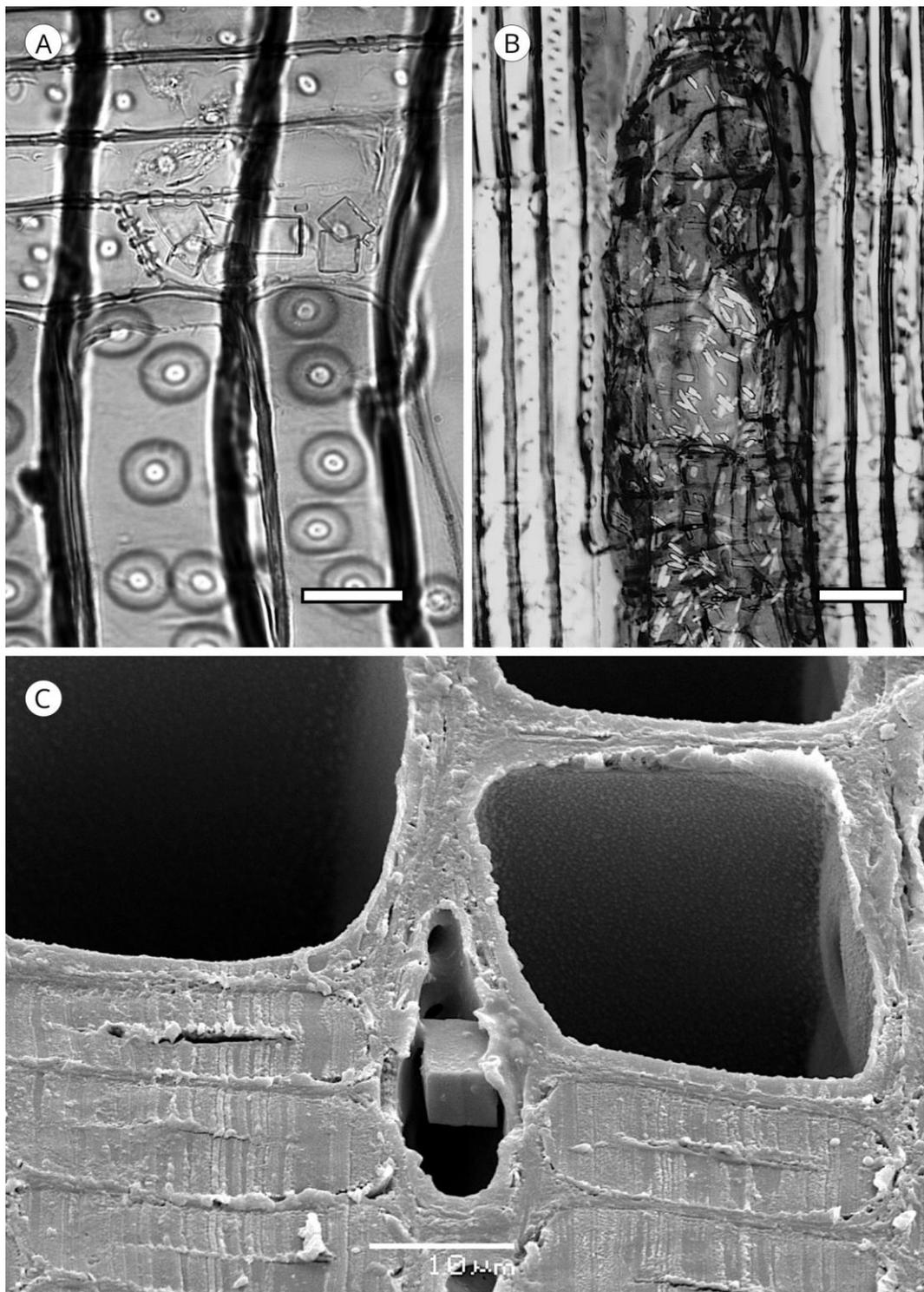


Figure 42. Crystals. (A) Crystals in ray parenchyma of *Abies firma* Siebold and Zucc.; (B) Cubic and styloid crystals in epithelial cells of axial resin canal in *Pinus bungeana* Zucc. ex Endl.; (C) Crystals in ray parenchyma of *Abies nordmanniana* subsp. *equi-trojani* (Asch. & Sint. ex Boiss.) Coode and Cullen. Scale bars. (A) = 25 μm ; (B) = 100 μm .

6. Families and Genera

Araucariaceae Henkel and W.Hochst.—three genera: *Araucaria* Juss. (20 species), *Agathis* Salisb. (17), *Wollemia* W.G.Jones, K.D.Hill and J.M.Allen (1). **Axial tracheids**—intercellular spaces occasional. Tracheid pits in radial walls uniseriate and/or biseriate, also multiseriate, all polygonal in appearance; biseriate/multiseriate pits in alternate

arrangement. Torus defined. Axial tracheids with organic content, often forming groups close to the rays. Additionally, in spools, trabeculae-like. Helical thickenings absent. Callitroid thickenings absent. **Axial parenchyma**—rare or absent. **Rays**—ray tracheids absent. Smooth horizontal and end walls. Cross-field pitting araucarioid. **Resin canals**—absent. **Mineral inclusions**—not observed.

Cupressaceae Gray—thirty two genera: *Actinostrobus* Miq. (3 species), *Athrotaxis* D.Don (3), *Austrocedrus* Florin and Boutelje (1), *Callitris* Vent. (20), *Callitropsis* Oerst. (1), *Calocedrus* Kurz (4), *Chamaecyparis* Spach (5), *Cryptomeria* D.Don (1), *Cunninghamia* R.Br. (2), *Cupressus* L. (14), *Diselma* Hook.f. (1), *Fitzroya* Lindl. (1), *Fokienia* A.Henry and H.H.Thomas (1), *Glyptostrobus* Endl. (1), *Hesperocyparis* Bartel and R.A.Price (17), *Juniperus* L. (68), *Libocedrus* Endl. (5), *Metasequoia* Hu and W.C.Cheng (1), *Microbiota* Kom. (1), *Neocallitropsis* Florin (1), *Papuacedrus* H.L.Li (1), *Pilgerodendron* Florin (1), *Platycladus* Spach (1), *Sequoia* Endl. (1), *Sequoiadendron* J.Buchholz (1), *Taiwania* Hayata (1), *Taxodium* Rich. (1), *Tetraclinis* Mast. (1), *Thuja* L. (5), *Thujopsis* Siebold and Zucc. ex Endl. (1), *Widdringtonia* Endl. (4), *Xanthocyparis* Farjon and T.H.Nguyên (1). **Axial tracheids**—frequent presence of intercellular spaces in *Cupressus* and *Juniperus*. We also observed them in *Calocedrus formosana*, *Chamaecyparis lawsoniana*, *Pilgerodendron* and some species of *Callitris* (*C. columellaris*, *C. endlicheri* and *C. neocaledonica*). Tracheid pitting in radial walls uniseriate and/or biseriate. Biseriate normally in *Sequoia* and *Sequoiadendron*, up to triseriate in *Taxodium*. Torus defined, except in some species of *Thuja* and *Thujopsis*. Torus extensions were present in *Actinostrobus*, *Athrotaxis*, *Austrocedrus*, *Cupressus dupreziana*, *C. funebris*, *Diselma*, *Fitzroya*, *Juniperus brevifolia*, *J. californica*, *J. deppeana*, *J. monosperma*, *J. monticola*, *J. osteosperma*, *J. pinchotii*, *J. scopulorum*, *J. standleyi*, *Pilgerodendron* and *Widdringtonia*. Pits with notched borders were present in *Athrotaxis*, *Calocedrus decurrens*, *Chamaecyparis pisifera*, *Cryptomeria*, *Cunninghamia*, *Cupressus dupreziana*, *Juniperus brevifolia*, *J. thurifera*, *Papuacedrus*, *Sequoia*, *Taiwania*, *Thuja occidentalis*, *Thujopsis* and *Callitropsis nootkatensis*. This feature is used to differentiate *Sequoia* (notched borders present) from *Sequoiadendron* (notched borders absent) [101]. It was also used by de Palacios et al. [85] to differentiate Macaronesian species of *Juniperus*. Habitual presence of warty layer in the family, although we did not observe it in *Libocedrus*, *Neocallitropsis* or *Papuacedrus*, less conspicuous in *Athrotaxis*, *Austrocedrus*, *Calocedrus*, *Cryptomeria*, *Cunninghamia*, *Fokienia*, *Metasequoia*, *Sciadopitys*, *Sequoia*, *Sequoiadendron*, *Taiwania*, *Thujopsis*, *Xanthocyparis* and some species of *Chamaecyparis* and *Juniperus*. Very clear in *Callitris*, *Actinostrobus*, *Tetraclinis* and some species of *Juniperus*. Organic deposits regularly occur in some Cupressaceae genera. They have been reported in *Callitris columellaris*, *Calocedrus decurrens*, *Cupressus*, *Fitzroya*, *Juniperus procera*, *J. virginiana*, *Libocedrus bidwillii*, *Pilgerodendron*, *Thuja plicata* and *T. standishii* [55,175,176]. We observed them in *Widdringtonia* and some species of *Callitris* (*C. endlicheri*, *C. preissii* and *C. rhomboidea*). Helical thickenings were absent. Callitroid thickenings were present in *Actinostrobus* and *Callitris*, occasionally in *Neocallitropsis*. **Axial parenchyma**—regularly present in all genera. Simultaneous occurrence of arrangements (diffuse, tangential and marginal) is common, e.g., in *Actinostrobus pyramidalis*, *Calocedrus decurrens*, *C. macrolepis*, *Chamaecyparis pisifera*, *Hesperocyparis sargentii* (Syn.—*Cupressus sargentii* Jeps.), *Cupressus sempervirens*, *Glyptostrobus pensilis*, *Juniperus barbadensis*, *J. chinensis*, *J. deppeana*, *J. excelsa*, *J. oxycedrus* and *Tetraclinis articulata*). Transverse end walls smooth, irregular or nodular or even transitional; also simultaneous occurrence of types, particularly in *Cupressus* and *Juniperus*. We observed smooth walls or smooth and occasionally irregular walls in *Actinostrobus*, *Athrotaxis*, *Austrocedrus*, *Callitris* and *Cunninghamia*, most *Cupressus*, *Juniperus bermudiana*, *J. oxycedrus*, *J. procera*, *J. standleyi*, *J. taxifolia*, *Libocedrus*, *Metasequoia*, *Microbiota*, *Papuacedrus*, *Taiwania*, *Tetraclinis* and *Widdringtonia*. Transverse end walls nodular or occasionally irregular and nodular in *Calocedrus*, *Hesperocyparis bakeri* (Syn.—*Cupressus bakeri* Jeps.), *H. macnabiana* (Syn.—*Cupressus macnabiana* A.Murray bis), *Glyptostrobus*, most *Juniperus*, *Platycladus*, *Taxodium distichum* and *Thujopsis*. Simultaneous occurrence of smooth, irregular and nodular transverse end walls in *Chamaecyparis*, *Cryptomeria*, *Hesperocyparis goveniana* (Syn.—*Cupressus goveniana* Gordon), *H. macrocarpa* (Syn.—

Cupressus macrocarpa Hartw.), *Diselma*, *Fokienia*, some species of *Juniperus*, *Pilgerodendron*, *Sequoia* and *Sequoiadendron*. Very few genera have exclusively nodular transverse end walls: *Calocedrus*, *Platyclusus* and *Thujopsis*. **Rays**—regular presence of ray tracheids in *Callitropsis nootkatensis*. Horizontal walls of ray parenchyma cells smooth (e.g., *Diselma* and *Fitzroya*), at times lightly pitted. End walls smooth and/or nodular, or even transitional forms. Cross-field pitting cupressoid (*Cupressus* and *Juniperus*), taxodioid (*Athrotaxis*, *Cryptomeria*, *Cunninghamia*, *Fokienia*, *Metasequoia*, *Papuacedrus*, *Sequoia* and *Sequoiadendron*), at times cupressoid and partially taxodioid (e.g., *Austrocedrus*, *Calocedrus*, *Chamaecyparis*, *Fitzroya*, *Libocedrus*, *Pilgerodendron*, *Taiwania*, *Taxodium*, *Thuja*, *Thujopsis* and *Xanthocyparis*). **Resin canals**—absent. In the samples studied, traumatic axial resin canals were observed in *Diselma*, *Sequoia* and *Tetraclinis*. They have also been described in *Actinostrobus pyramidalis* [29], *Callitris drummondii* [126], *Chamaecyparis obtusa* [177], *Cunninghamia lanceolata* [178], *Cupressus funebris* [179], *Cryptomeria* [180], *Hesperocyparis arizonica* (Syn.—*Cupressus arizonica* Greene) [170], *Metasequoia* [181], *Microbiota* [165], *Sequoia* [57] and *Sequoiadendron* [55]. **Mineral inclusions**—not observed.

Pinaceae Spreng. ex F.Rudolphi.—eleven genera: *Abies* Mill. (47 species), *Cathaya* Chun and Kuang (1), *Cedrus* Trew (3), *Keteleeria* Carrière (3), *Larix* Mill. (10), *Nothotsuga* H.H.Hu ex C.N.Page (1), *Picea* A.Dietr. (37), *Pinus* L. (118), *Pseudolarix* Gordon and Glend. (1), *Pseudotsuga* Carrière (4), *Tsuga* (Endl.) Carrière (10). **Axial tracheids**—tracheid pitting in radial walls uniseriate and/or biseriate, normally in opposite arrangement. Torus defined. Scalloped tori in *Cedrus*. Regular torus extensions in *Abies* and *Tsuga*. Regular presence of warty layer in *Abies*, *Cedrus* and *Tsuga*. Occasional organic deposits in *Abies* (*A. pinsapo*) and *Pinus* (*Pinus canariensis*). Helical thickenings present in *Cathaya*, *Pseudotsuga* (*P. sinensis* and *P. menziesii*), some species of *Larix* (*L. decidua*, *L. griffithii*, *L. occidentalis*, *L. potaninii*), and *Picea* (*P. abies*, *P. acoquiana*, *P. brachytyla*, *P. breweriana*, *P. glauca*, *P. glehnii*, *P. jezoensis*, *P. koraiensis*, *P. mariana*, *P. maximowiczii*, *P. morrisonicola*, *P. purpurea*, *P. schrenkiana*, *P. sitchensis*, *P. smithiana*, *P. spinulosa* and *P. torano*). Callitroid thickenings absent. **Axial parenchyma**—present in the whole family, but very scarce, mostly restricted to single cells in marginal arrangement in the last rows of latewood. More abundant in Abietoideae genera (*Abies*, *Cedrus*, *Keteleeria*, *Nothotsuga*, *Pseudolarix* and *Tsuga*). Transverse end walls irregular to nodular. **Rays**—presence of ray tracheids in all genera of the family except *Keteleeria*. Always present in *Cathaya*, *Larix*, *Picea*, *Pinus*, *Pseudotsuga* and *Tsuga*, frequent in *Cedrus* and rare in *Abies*, *Nothotsuga* and *Pseudolarix*. In *Pinus*, ray tracheid walls are smooth, dentate or reticulate. Ray tracheids with helical thickenings in *Cathaya* and some species of *Larix*, *Picea* and *Pseudotsuga*. Horizontal walls of ray parenchyma cells pitted, although many species of *Pinus* do not conform. The same occurs with the end walls of ray parenchyma cells, which are nodular in all genera except in some species of *Pinus*, and slightly nodular in *Pinus* section *Strobis* (e.g., *P. cembra*, *P. koraiensis*, *P. lambertiana*, *P. monticola* and *P. strobus*). At family level, cross-field pitting does not follow a common pattern—*Abies* (piceoid, taxodioid), *Cathaya* (piceoid), *Cedrus* (piceoid and taxodioid), *Keteleeria* (cupressoid and taxodioid), *Larix* (piceoid), *Nothotsuga* (cupressoid and taxodioid), *Picea* (piceoid), *Pinus* (pinoid and window-like), *Pseudolarix* (piceoid and taxodioid), *Pseudotsuga* (piceoid) and *Tsuga* (piceoid)—but at genus level it can be used to establish groups, e.g., in *Pinus*. **Resin canals**—presence of axial and radial resin canals in all non-Abietoideae genera. In *Cathaya*, *Larix*, *Picea* and *Pseudotsuga*, epithelial cells are thick-walled, and in *Pinus*, they are thin-walled. In Abietoideae genera, *Keteleeria* and *Nothotsuga* have only axial resin canals with thick-walled epithelial cells and *Abies*, *Cedrus*, *Pseudolarix* and *Tsuga* lack normal resin canals. However, all genera in Pinaceae form traumatic resin canals, both axial and radial in non-Abietoideae genera, and in Abietoideae only traumatic axial resin canals are formed, except in *Cedrus*, which lacks normal axial and radial resin canals but forms traumatic axial and radial canals. The arrangement of traumatic resin canals is normally in tangential rows, except in *Keteleeria* and *Nothotsuga*, where they can also be in solitary arrangement. **Mineral inclusions**—crystals are frequent

in marginal and submarginal cells of ray parenchyma in all genera of Abietoideae and occasional in *Pinus* and *Picea*.

Podocarpaceae Endl.—nineteen genera: *Acropyle* Pilg. (2 species), *Afroparpus* (Buchholz & N.E.Gray) C.N.Page (5), *Dacrycarpus* (Endl.) de Laub. (9), *Dacrydium* Sol. ex G.Forst. (22), *Falcatifolium* de Laub. (6), *Halocarpus* C.J.Quinn (3), *Lagarostrobos* Quinn (1), *Lepidothamnus* Phil. (3), *Manoao* Molloy (1), *Microcachrys* Hook.f. (1) *Nageia* Gaertn. (5), *Parasitaxus* de Laub. (1), *Pherosphaera* W.Archer bis (2), *Phyllocladus* Rich. ex Mirb. (4), *Podocarpus* L'Hér. ex Pers. (115), *Prumnopitys* Phil. (3), *Retrophyllum* C.N.Page (6) *Saxegothaea* Lindl. (1), *Sundacarpus* (J.Buchholz & N.E.Gray) C.N.Page (1). **Axial tracheids**—tracheid pitting in radial walls normally uniseriate. When it is biseriate, arrangement is opposite. Torus defined. Extensions do not occur regularly, but were observed in *Lagarostrobos*. Notched borders were not observed. The warty layer was not visible. Organic deposits were absent. Helical and callitroid thickenings were absent. **Axial parenchyma**—present in most genera, in diffuse arrangement, transverse end walls smooth. Absent in *Halocarpus*, *Lagarostrobos*, *Lepidothamnus*, *Manoao*, *Microcachrys* and *Sundacarpus*. **Rays**—ray tracheids were absent. Horizontal and end walls of ray parenchyma cells were smooth. Cross-field pitting is normally cupressoid and taxodioid, although the genera *Lagarostrobos*, *Manoao*, *Microstrobos*, *Microcachrys*, *Phyllocladus*, *Prumnopitys* (*P. andina*) and *Sundacarpus* have window-like pitting in addition to taxodioid. **Resin canals**—absent. **Mineral inclusions**—not observed.

Sciadopityaceae Luer—one genus: *Sciadopitys* Siebold and Zucc. (1 species) **Axial tracheids**—tracheid pitting in radial walls uniseriate. Torus was defined. Torus extensions and notched borders were absent. The warty layer was difficult to observe, even with electron microscopy. The deposits were absent; helical and callitroid thickenings were absent. **Axial parenchyma**—very scarce, virtually absent and transverse end walls were smooth. **Rays**—ray tracheids were absent. Horizontal and end walls of ray parenchyma cells were smooth. Cross-field pitting window-like. **Resin canals**—absent. **Mineral inclusions**—not observed.

Taxaceae Gray—six genera: *Amentotaxus* Pilg. (6), *Austrotaxus* Compton (1), *Cephalotaxus* Siebold and Zucc. ex Endl. (8), *Pseudotaxus* W.C.Cheng (1), *Taxus* L. (12), *Torreya* Arn. (6). **Axial tracheids**—tracheid pitting in radial walls uniseriate. The torus was defined. Torus extensions and notched borders were absent. The warty layer was not visible. Organic deposits absent. All genera except *Austrotaxus* have helical thickenings. In *Pseudotaxus* and *Taxus*, they are normally single; in *Amentotaxus*, *Cephalotaxus* and *Torreya*, they are single or double; in *Torreya*, they can be triple. Callitroid thickenings were absent. **Axial parenchyma**—present regularly in diffuse arrangement in *Cephalotaxus*, *Amentotaxus* and *Torreya*. They were present occasionally in *Austrotaxus* and rare or absent in *Taxus* and *Pseudotaxus*. The transverse end walls were smooth; in *Cephalotaxus* smooth to irregularly thickened. **Rays**—ray tracheids were absent. Horizontal and end walls of ray parenchyma cells were smooth. Cross-field pitting cupressoid. **Resin canals**—absent. **Mineral inclusions**—not observed.

7. Conclusions

Axial tracheids—The presence of intercellular spaces is frequent in *Agathis*, *Cupressus*, *Juniperus* and *Pilgerodendron*. The arrangement of pitting is normally uniseriate and when it is biseriate it is generally opposite, except in the three genera of Araucariaceae (*Araucaria*, *Agathis* and *Wollemia*), where pits are closely packed, alternate and hexagonal in appearance. Triseriate arrangement is common in *Keteleeria*, *Sequoia sempervirens*, *Taiwania cryptomerioides* and *Taxodium distichum*. All conifer wood tracheid pits have a defined torus except for some species of *Thuja* and *Thujopsis*. Only *Cedrus* regularly has scalloped tori. Some decaying wood can show apparently scalloped tori. The presence of torus extensions is frequent in *Abies*, *Actinostrobus*, *Fitzroya*, *Juniperus*, *Lagarostrobos*, *Pilgerodendron*, *Tsuga*, *Thujopsis* and *Widdringtonia*. Notched borders in pits allow for the differentiation of *Sequoia* (with notched borders) and *Sequoiadendron* (without). A warty layer

is visible under light microscopy in some genera (e.g., *Abies*, *Actinostrobus*, *Juniperus*, *Callitris* and *Tetraclinis*) and can be used as a distinguishing feature. Organic deposits can also be used for diagnosis, and are habitual in *Araucaria* and *Agathis*. Helical thickenings in axial tracheids are present in all genera of Taxaceae (except *Austrotaxus*), in *Cathaya*, *Pseudotsuga* and in some species of *Picea* and *Larix*. Callitroid thickenings, although reported in other genera, can be used for diagnosis in *Actinostrobus* and *Callitris*.

Axial parenchyma—the presence of axial parenchyma permits the exclusion of the families Araucariaceae and Sciadopityaceae and the genera *Taxus* and *Pseudotaxus* in Taxaceae, *Neocallitropsis*, *Thuja* and *Xanthocyparis* in Cupressaceae, and *Halocarpus*, *Lagarostrobos*, *Lepidothamnus*, *Manoao*, *Microcachrys*, *Phyllocladus* and *Sundacarpus* in Podocarpaceae. With regard to arrangement, diffuse, tangentially zonate and marginal, even simultaneously, are characteristic of Cupressaceae, while in Podocarpaceae it is diffuse.

Rays—ray composition has high diagnostic value. The presence of ray tracheids is exclusive to the genera of Pinaceae that possess normal resin canals, with the exception, outside this group, of *Tsuga* and *Callitropsis nootkatensis*. *Tsuga* always has ray tracheids, in *Cedrus* they are frequent, in *Abies*, *Nothotsuga* and *Pseudolarix* they are rare, and in *Keteleeria* they are absent. The absence of ray tracheids in *Keteleeria* allows it to be differentiated from *Nothotsuga*. Other non-Pinaceae species have ray tracheids, particularly in Cupressaceae, e.g., *Cupressus arizonica*, *Sequoia* and *Thujopsis*. The degree of dentation also allows differentiation of groups in the genus *Pinus*. Helical thickenings in ray tracheids distinguish *Cathaya argyrophylla*, *Pseudotsuga sinensis*, *Larix potaninii* var. *himalaica*, *Picea polita*, *P. spinulosa* and *P. torano* from the rest of the conifers. Distinctly pitted horizontal walls of radial cells distinguish all the genera of Pinaceae from the other conifer genera, although some species of *Pinus* do not conform to this, and in *Pseudolarix* they are less distinct. Nodular end walls are limited to the Pinaceae (absent in some species of *Pinus*) and Cupressaceae. Cross-field pitting has high diagnostic value, although in some genera more than one type can occur simultaneously, particularly in Cupressaceae.

Resin canals—The presence of normal axial and radial resin canals with thick-walled epithelial cells indicates the group *Cathaya*, *Larix*, *Picea* and *Pseudotsuga* (*Cathaya* is distinct from the others because its axial and radial tracheids have helical thickenings); canals with thin-walled epithelial cells are indicative of *Pinus*. The presence of normal axial resin canals but no radial canals is exclusive to *Keteleeria* and *Nothotsuga*. Traumatic axial resin canals are characteristic of Pinaceae and occasionally occur in some Cupressaceae genera (e.g., *Microbiota*, *Sequoia*, *Sequoiadendron* and *Tetraclinis*). *Cathaya*, *Larix*, *Picea*, *Pinus* and *Pseudotsuga* form traumatic axial and radial resin canals. *Keteleeria* and *Nothotsuga* form only traumatic axial canals. *Abies*, *Cedrus*, *Nothotsuga*, *Pseudolarix* and *Tsuga* lack normal axial and radial resin canals, but all of them can form traumatic axial canals, and *Cedrus* also forms traumatic radial canals.

Mineral inclusions—the presence of mineral inclusions in Pinaceae, particularly in Abietoideae, has diagnostic value.

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