WOOD ANATOMY OF MODERN AND FOSSIL FAGALES IN RELATION TO PHYLOGENETIC HYPOTHESES, FAMILIAL CLASSIFICATION, AND PATTERNS OF CHARACTER EVOLUTION

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The wood anatomy of fagalean families is summarized. Each family and most genera are wood anatomically distinct and can be distinguished by features such as vessel grouping and arrangement, vessel-ray parenchyma pit type, imperforate element type, ray structure, and axial parenchyma distribution. For each family, we review the published fossil wood record (with particular attention to Cretaceous and Paleogene occurrences) that we consider to be reliably identified on the basis of diagnostic character syndromes, giving insights into their stratigraphic range and former geographic ranges. Fossil woods with characteristics of the Fagaceae (Castaneoideae) occurred as early as the Late Cretaceous (Campanian) of the Northern Hemisphere and were widespread in the Cenozoic. Nothofagaceae wood occurred in the Late Cretaceous and Early Tertiary of Antarctica. Ring-porous Castaneoideae were not common until after the Eocene, reflecting the increase in seasonality that occurred in the Northern Hemisphere at that time. Woods diagnostic of Betulaceae, Juglandaceae, and Myricaceae occurred in the Eocene. With the recognition of Morella Lour. as a genus distinct from Myrica L., we propose two new combinations for fossil woods of Myricaceae. Reliably identified Casuarinaceae wood did not occur until the Miocene. There are no reports of Ticodendraceae fossil wood, although there are reports of fossil woods with its combination of features from the Cretaceous onward, but these are assigned to different families or are of unknown affinities. Most fagalean fossil woods have anatomy similar to that of modern genera, but some Paleogene taxa have combinations of characters not found in present-day genera. We discuss the utility of wood anatomy in assessing phylogenetic relationships within and among families of Fagales, with reference to clades supported by molecular sequence data. Generally, wood anatomical groupings are consistent with recent phylogenetic analyses of the order and of its constituent families. We propose hypotheses about adaptive character evolution in the order based on previously presented phylogenetic relationships inferred from DNA sequence data and the current ecological preferences of individual families.

Keywords: Betulaceae, Casuarinaceae, Fagaceae, Juglandaceae, Myricaceae, Nothofagaceae, Ticodendraceae, fossil wood, secondary xylem, Cretaceous, Paleocene, Eocene.

Introduction

Among the currently recognized orders of angiosperms, the Fagales stand out for their economic importance and predominance in many ecosystems. The Fagales are exclusively woody, consisting mostly of substantial trees whose distribution ranges from tropical to cool-temperate areas. Seven families are included in the order (Stevens 2001–). Five include important elements of distinct community types in the Southern (Nothofagaceae, Casuarinaceae) and Northern (Betulaceae, Fagaceae, Juglandaceae) Hemispheres. One of them, that is, Ticodendraceae, is monospecific, with a narrow present-day distribution (Ticodendron incognitum Gómez-Laur & L.D. Gómez) in Central America. Myricaceae is the most widespread, with species in North and South America, Africa, Europe, and Asia (Mabberley 2017).

Our concept of Fagales through the 1980s was mainly that it consisted of the families Fagaceae, Betulaceae, and Nothofagaceae (Takhtajan 1980; Cronquist 1988). Subsequently, cladistic analyses of existing morphological data and newly acquired molecular characters resulted in the concept of a more inclusive monophyletic Fagales, requiring the addition of some families that once had been placed in their own orders, for example, Juglandaceae.
Myricaceae, and Casuarinaceae (Stevens 2001; APG IV 2016). Li et al. (2004) supported this broader concept of the order and also included the recently recognized family Ticodendraceae. They used nucleotide sequences of six regions from three plant genomes—trnL-F, matK, rbcL, atpB (plastid), matR (mtDNA), and 18S rDNA (nuclear)—with a sampling of 31 extant genera. Subsequent investigations have upheld the monophyly of this order and depicted similar patterns of relationships among the families (Sauquet et al. 2012; Xing et al. 2014; Larson-Johnson 2016). The recurrent phylogenetic topology from all these investigations is that Nothofagaceae are sister to all other Fagales (fig. 1), in which Fagaceae (clade 1 in fig. 1) are sister to all other families of the order. Casuarinaceae are consistently placed as sister to a clade of Ticodendraceae and Betulaceae (clade 2 in fig. 1), and this clade is consistently sister to Juglandaceae (clade 3 in fig. 1). *Rhoiptelea* Diels & Hand.-Mazz., formerly treated in its own family, is consistently found paired with Juglandaceae and currently is subsumed within that family (APG IV 2016). The position of Myricaceae is inconsistent in molecular phylogenetic analyses. According to Li et al. (2004) and Larson-Johnson (2016), Myricaceae are sister to Juglandaceae, but, in the work of Sauquet et al. (2012) and Xing et al. (2014), the Myricaceae are the direct sister to the clade that includes Betulaceae, Casuarinaceae, and Ticodendraceae, which collectively form a clade that is sister to Juglandaceae.

The Fagales is one of the most thoroughly studied orders of the rosids. The order includes many important timber trees, and, consequently, their wood anatomy has been investigated in detail over the past century. These data invite broader comparisons to assess patterns of variation and character evolution across the entire clade. Also, this order has an excellent micro- and macrofossil record, with occurrences of each family extending back to the early Cenozoic and with relatives extending back to the Cretaceous. Here, we review the wood anatomical patterns characterizing each of the families and summarize records of Cretaceous and Paleogene woods assigned to the Fagales to help our understanding of the geological history of the order and its component families.

We have chosen to use the phylogenetic analysis of Li et al. (2004) as a reference point for discussing the relationships among families (fig. 1). More recent analyses of the order have included fossil taxa (mainly reproductive structures) in addressing questions of the rates and timing of diversification (e.g., Xing et al. 2014; Larson-Johnson 2016). The wood anatomical characteristics that will be discussed herein are those that historically have been used to distinguish among these families, as follows: vessel grouping and arrangement, perforation plate type, vessel-ray parenchyma pits, imperforate tracheary element type, and ray structure. There is a large body of literature on the wood anatomy of

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Fig. 1  Phylogenetic diagram depicting inferred relationships among fagalean families and genera based on Li et al. (2004) and mostly corroborated in subsequent analyses (Sauquet et al. 2012; Xing et al. 2014; Larson-Johnson 2016). Major subclades discussed in the text are labeled 1, 2, and 3. Bootstrap percentages and Bayesian posteriority values indicated at the nodes are those from figure 2 of Li et al. (2004), a single most parsimonious tree based on a combined matrix of 27 species with a length of 2558 steps (consistency index = 0.770, retention index = 0.812).
the families and genera of the Fagales (see Gregory 1994). The compendium by Metcalfe and Chalk (1950) included summaries for all families except Ticrodendraceae, which was not yet known. Subsequent treatments have dealt with individual families, for example, Fagaceae (Shimaji 1962), Myricaceae (Carlquist 2002), Ticrodendraceae (Carlquist 1991), and woods of a single family from a single region (e.g., Juglandaceae of the United States; Stark 1953) or of a single genus from one region (e.g., Betula L. of the United States; Miller and Cahow 1989; Quercus of Japan: Shimaji 1954a, 1954b).

The objectives of this article are to address the following questions. First, what are the secondary xylem characteristics of the families and genera that make up the Fagales? Second, what are the wood anatomical distinctions between families and genera? Third, how does the distribution of these characteristics compare to recent phylogenetic analyses, and do wood anatomical patterns support or contradict the relationships hypothesized for the order? Fourth, what are the Cretaceous-Paleogene records for woods distinctive to families and genera, and are there extinct wood types? And fifth, to what extent can diversity patterns in fossil and extant Fagales be understood in terms of functional adaptations?

Material and Methods

We used data on extant and fossil woods of Fagales compiled from multiple sources and recorded on the InsideWood website (http://insidewood.lib.ncsu.edu; Wheeler 2011; Wheeler et al. 2020). The coded descriptions therein are based on the IAWA List of Microscopic Features for Hardwood Identification of the IAWA Committee (1989). The abbreviations of Index Xylariorum 4.1 or individual collector’s numbers are used for the wood specimens featured in figures 2–12; additional images are available on the InsideWood website.

Review of Wood Anatomical Features and the Fossil Record

Families are discussed in alphabetical order. Tables 1 and 2 compare selected features of the families and genera, showing that the families have distinctive wood anatomy.

Betulaceae s.l.

The Betuloideae (fig. 2) and Coryloideae (fig. 3) have been treated variously as subfamilies within the Betulaceae or as separate families, Betulaceae and Corylaceae. The Li et al. (2004) analysis did not recover a clear grouping of Alnus Miller and Betula versus the Coryloideae (Carpinus L., Corylus L., Ostrya Scop., Ostryopsis Decne.), but Forest et al.’s (2005), which used a different set of genes and examined a different number of species, did. Vessels in the Coryloideae typically have radial/diagonal/dendritic arrangements, while those in Alnus and Betula are randomly arranged (table 1).

Isolated pieces of Betula wood are easy to identify because of their unique combination of vessels that are solitary and in short radial multiples that are randomly arranged (fig. 2A), minute alternate intervessel pitting (fig. 2B), vessel-ray parenchyma pits similar to intervessel pits (fig. 2C), exclusively scalariform perforation plates (fig. 2C), and homocellular rays (fig. 2B, 2C). Alnus woods are also distinctive, with vessels that are solitary and in radial multiples that are randomly arranged (fig. 2E), scalariform perforation plates (fig. 2F, 2G), opposite to alternate intervessel pits (fig. 2G), and, in many species, aggregate homocellular rays (fig. 2E, 2F; e.g., Tippo 1938; Hall 1952; Brazier and Franklin 1961; Panshin and deZeeuw 1980; Schweinigruber 1990). Coryloideae woods often have a radial/diagonal vessel arrangement (fig. 3A–3C); aggregate rays occur in Carpinus and Corylus (fig. 3A), and simple perforation plates occur in Ostrya and some Carpinus and Corylus. Crystals are unknown in the Betuloideae, but crystalliferous ray cells occur in some Coryloideae (table 2; fig. 3G).

Müller-Stoll and Mädel (1959) reviewed occurrences of fossil betulaceous woods. The earliest occurrence of wood with features of Betula is from the middle Eocene Clarno Nut Beds, Oregon (Scott and Wheeler 1982, Wheeler and Manchester 2001). Alnus-like woods with the abovementioned combination of features are more common and are reported from the Paleocene of England (Crawley 2001) and the Denver Basin of the United States (Wheeler and Michalski 2003), the Paleocene-Eocene of the Russian Far East (Blokhina and Snezhkova 1999), and the early Eocene of Yellowstone National Park (Wheeler et al. 1977). This is congruent with the fruit and seed record (Forest et al. 2005; Liu et al. 2014). Unequivocal Coryloideae woods have been recovered from the Upper Cretaceous (Campanian) of California (Carpinoxylon ostryopsoides Page 1970), the early Eocene of Yellowstone National Park (Carpinus absarokensis Wheeler, Scott & Barghoorn and Carpinus saximontana Wheeler, Scott & Barghoorn; Wheeler et al. 1977), and the Oligocene of Europe (Coryloxyylon nemejci Prakash, Bězinová & Bůžek and Coryloxyylon tertiarum Prakash, Bězinová & Bůžek; Prakash et al. 1971).

Casuarinaceae

Moseley (1948) surveyed Casuarinaceae wood anatomy. Since that time, Casuarina has been split into four genera: Allocasuarina L.A.S. Johnson, Casuarina L. s.s., Ceuthostoma L.A.S. Johnson, and Gymnostoma L.A.S. Johnson (Johnson and Wilson 1989; Wilson and Johnson 1989). Steane et al.’s (2003) phylogenetic analysis supports the recognition of these four genera. Some Casuarina species appear similar to some Quercus L. species (the evergreen oaks) because they share solitary vessels (fig. 4A–4D), vasicentric tracheids (fig. 4E), two size classes of rays (fig. 4H–4J), and a pocked axial parenchyma (fig. 4A–4D). However, vessel-ray pits in Casuarinaceae do not have markedly reduced borders and are not irregularly shaped (fig. 4G), whereas they are in the Castaneoideae (fig. 7A–7D).

In the 1990s, M. Molenaar (Rijksherbarium, Leiden University; M. Molenaar, unpublished data) began a wood anatomical study of the family, sectioning woods of Allocasuarina, Casuarina, and Gymnostoma from a variety of habitats; samples of Ceuthostoma were not available. He observed variation in vessel diameter and density correlating with variation in habitat and habitat, with shrubby species that grow in arid regions having narrower, more numerous vessels than tree species that grow in moist habitats. Descriptions based on Molenaar’s work and photographs of his sections are available on the InsideWood website. These data show that there is potential for using wood anatomy to distinguish the genera (tables 1, 2), to investigate how wood anatomical features correlate with xeric conditions, and to use fossil woods to track the history of the family.
Table 1
Distribution of Vessel-Related Features

| Family          | Genus      | Por | VArr | VGrp | PP | IVP | VRP | HT | MVTD |
|-----------------|------------|-----|------|------|----|-----|-----|-----|------|
| Betulaceae:     |            |     |      |      |    |     |     |     |      |
| Betuloideae:    |            |     |      |      |    |     |     |     |      |
| Alnus           |            | D   | N    | RM   | Sc | O, A | B   | N   | VS, S |
| Betula          |            | D   | N    | RM   | Sc | A   | B   | N   | (VS, M), S |
| Coryloideae:    |            |     |      |      |    |     |     |     |      |
| Carpinus        |            | D   | R/Dg, Dd, (N) | RM, (4+) | Si, Sc | A, (O) | B, (R) | Y, (N) | VS, S |
| Corylus         |            | D   | R/Dg, Dd, (N) | RM, (4+) | Si, Sc | A, (O) | B, (R) | Y, (N) | VS, S |
| Ostrya          |            | D   | Dg   | RM, (4+) | Si, Sc | A, (O) | B   |     | Y    | VS, S |
| Ostryopsis      |            | D   | Dg, Dd, N | RM, 4+  | Sc   | A   | B   |     | Y    | VS, S |
| Casuarinaceae:  |            |     |      |      |    |     |     |     |      |
| Allocasuarina   | D, (S)     | R/Dg, N | ExSol | Si, (Sc) | (A) | B   | N   | Y   | VS, S, M |
| Casuarina       | D, (S)     | R/Dg, N | ExSol | Si, (Sc) | (A) | B   | N   | S   | M    |
| Gymnostoma      | D          | R/Dg, N | ExSol | Si, (Sc) | (A) | B   | N   | S, M, (L) |
| Juglandaceae:   |            |     |      |      |    |     |     |     |      |
| Rhoipteleoideae|            |     |      |      |    |     |     |     |      |
| Rhoiptelea      | S          | R/Dg, Dd | RM   | Sc   | A   |     | B/R | N   | S, M* |
| Engelhardioideae|            |     |      |      |    |     |     |     |      |
| Alfaroa         | D          | R/Dg | RM   | Si, Sc | A   | R   | N   | M   |      |
| Engelhardia     | D          | N, (R/Dg) | RM   | Si, (Sc) | A   | R, (B) | N   | M    |
| Oreomunnea      | D          | N, (R/Dg) | RM   | Si, (Sc) | A   | R, (B) | N   | M    |
| Juglandioideae: |            |     |      |      |    |     |     |     |      |
| Anamamocarya    | D          | N    | RM   | Si   | A   |     | B   | N   | M    |
| Carya           | R, (S, D)  | N    | RM   | Si   | A   |     | B   | N   | M, L |
| Cyclocarya      | S          | N, R/Dg | RM   | Si   | A   | B, (R) | N   | M, (L) |
| Juglans         | S, D       | N, (R/Dg) | RM   | Si   | A   | B, (R) | N   | M, (L) |
| Petterocarya    | S, D       | N, R/Dg | RM   | Si   | A   | B, (R) | N   | M, (L) |
| Platycaryoideae|            |     |      |      |    |     |     |     |      |
| Platycarya      | R          | R/Dg, Dd | RM   | Si   | A   |     | B, (R) | Y   | M, (L) |
| Myricaceae:     |            |     |      |      |    |     |     |     |      |
| Canacomyrica    | D, (S)     | N    | ExSol | Sc   | A/O | B   | N   | S   |
| Comptonia       | D          | N    | ExSol | Sc   | A/O | B   | N   | S   |
| Morella         | D          | N    | ExSol | Sc   | A/O | B   | N   | VS, S |
| Myrica          | S, (R)     | N    | RM   | Sc   | A/O | B   | N   | VS, S |
| Nothofagaceae:  |            |     |      |      |    |     |     |     |      |
| Brassospora     | D          | N    | RM   | Si   | A/O | R   | N   | S   |
| Temperate species| D, (S) | N    | RM   | Si, (Sc) | O/Sc | R   | Y/N | VS, S |
| Ticodendraceae: |            |     |      |      |    |     |     |     |      |
| Ticodendron     | D          | N    | ExSol | Sc   | Sc  |     |     |     |      |

Note. Parentheses indicate a feature that occurs variably or rarely. N = not present; Y = present. Por = porosity; D = diffuse-porous; S = semi-ring-porous; R = ring-porous. VArr = vessels arranged in a distinct pattern: R = radial; Dg = diagonal; Dd = dendritic. VGrp = vessel grouping: RM = radial multiples present; 4+ = radial multiples of four or more common; ExSol = more than 90% of vessels solitary. PP = perforation plate type: Sc = scalariform; Si = simple. IVP = intervessel pitting: O = opposite; A = alternate; Sc = scalariform. Italics indicate pits between vessel elements and vasicentric tracheids. VRP = vessel-ray parenchyma pits: B = bordered and similar to intervessel pits; R = pits with reduced to simple borders. HT = helical thickenings present in vessel elements. MVTD = mean vessel tangential diameter: VS = <50 μm; S = <100 μm; M = 100–200 μm; L = >200 μm. For ring-porous woods, earlywood diameter is recorded.

* Measurement of a juvenile wood sample for Rhoiptelea.
Table 2

Imperforate Cell Types, Axial Parenchyma Distribution, and Ray Features

|                | VT | FP | AP | Ex1s | Agg   | Ray2 | RayCmp | Cry |
|----------------|----|----|----|------|-------|------|--------|-----|
| **Betulaceae:**|     |    |    |      |       |      |        |     |
| Betuloideae:   |     |    |    |      |       |      |        |     |
| *Alnus*        | (Y) | I  | D  | DA, | M     | N    | Y, (N) | N   | Ho | N   |
| *Betula*       | (Y) | I  | D  | DA, | M     | N    | Y, (N) | N   | Ho | N   |
| **Coryloideae:**|    |    |    |      |       |      |        |     |
| *Carpinus*     |     | N  | I  | D  | DA, | M     | N    | Y     | N   | Ho | (He) | (RP, I) |
| *Corylus*      | (Y) | I  | D  | DA, | M     | N, (Y)| Y     | N   | Ho | He | (RP) |
| *Osryfas*      | (Y) | I  | D  | DA, | M     | N, (Y)| Y     | N   | Ho | (He) | (RP) |
| *Osrytopsis*   | N   | I  | D  |     |       | N    | Y     | N   | Ho | (He) | (RP) |
| **Casuarinaceae:**|    |    |    |      |       |      |        |     |
| *Allocasuarina*| Y   | D, | I  | B   |      | (Y), | N     | Y   | N   | Ho | (He) | (RP, AP) |
| *Casuarina*    | Y   | D, | I  | (D, | DA), | B    | (Y),  | N   | N   | Ho | (RP, AP) |
| *Gymnostoma*   | Y   | D, | I  | D, | DA, | B    | (Y),  | N   | N   | Ho | (RP, AP) |
| **Fagaceae:**  |     |    |    |      |       |      |        |     |
| Fagoideae:     |     |    |    |      |       |      |        |     |
| *Fagus*        | N   | D  | I  | D, | DA   | N    | N     | (Y) | He | (RP, AP) |
| **Castaneoideae:**|     |    |    |      |       |      |        |     |
| *Castanea*     | Y   | I  | D  | DA, | ScP  | Y    | N     | N   | Ho | (AP) |
| *Catanopsis*   | Y   | D, | I  | (D, | DA), | B    | Y     | Y   | N   | N   | Ho | (RP, AP) |
| *Chrysolepis*  | Y   | D  | I  | D, | DA, | ScP, | B    | Y,  | N   | N   | Y   | Ho | (RP, AP) |
| *Lithocarpus*  | Y   | D, | I  | D, | DA, | ScP, | B    | Y,  | (N) | Y   | N   | Ho | (RP, AP) |
| *Notholithocarpus*| Y | D, | I  | D, | DA, | ScP, | B    | Y,  | (Y) | Y   | (Y) | Ho | AP |
| *Quercus*      | Y   | D, | I  | D, | DA, | ScP, | B    | N   | (Y) | Y   | Ho | (RP, AP) |
| *Trigonobalanus*| Y  | D, | I  | D, | DA, | B    | Y    | Y   | N   | Ho | He | (RP, AP) |
| **Juglandaceae:**|    |    |    |      |       |      |        |     |
| **Juglandoideae:**|    |    |    |      |       |      |        |     |
| *Alfaroa*      | N   | I  | ScP, | Vc, | M, | B    | N    | N     | N   | He | N   |
| *Engelhardia*  | N   | D, | I  | ScP, | (Vc, | M), | B    | N    | N     | N   | He | N   |
| *Oreomunnea*   | N   | I  | ScP, | (D, | DA, | M), | B    | N    | N     | N   | He | (AP, RP, I) |
| **Juglandeae:**|    |    |    |      |       |      |        |     |
| *Annamocarya*  | N   | I  | ScP, | Vc, | B   | N    | N     | N   | N   | He | AP, (RP, I) |
| *Carya*        | N   | I  | ScP, | Vc, | B, | M    | N    | N     | N   | Ho, | (He) | (AP, I) |
| *Cyclocarya*   | N   | I  | ScP, | B, | M   | N    | N     | N   | N   | He | N   |
| *Juglans*      | N   | I  | ScP, | (Vc), | B, | M   | N    | N     | N   | Ho, | He | (AP, I) |
| *Pterocarya*   | N   | I  | ScP, | B, | M   | N    | N     | N   | Ho, | He | N   |
| **Platycaryoideae:**|    |    |    |      |       |      |        |     |
| *Platycarya*   | Y   | I  | ScP, | Vc, | B, | M   | N    | N     | N   | He | RP |
| **Myricaceae:**|    |    |    |      |       |      |        |     |
| *Canacomyrica* | N   | D  | D  | DA, | ScP  | N    | N     | N   | N   | He | AP, RP |
| *Comptonia*    | N   | D  | D  | DA, | ScP  | N    | N     | N   | N   | He | N   |
| *Morella*      | N   | D  | D  | DA, | ScP  | N    | N     | N   | N   | He | AP, (RP) |
| *Myrica*       | N   | D  | D  | DA, | ScP  | N    | N     | N   | N   | He | N   |
| **Nothofagaceae:**|    |    |    |      |       |      |        |     |
| *Brassospora*  | N   | I  | (D), | B   | N    | N     | N   | N   | He | AP |
| *Temperate species*| Y, | N | I, | (D)| R, | D, | (M) | Y, | N   | N   | Ho, | (He) | (AP) |
| **Ticodendraceae:**|    |    |    |      |       |      |        |     |
| *Ticodendron*  | N   | D  | D  | DA, | N    | N     | N   | N   | He | (RP) |

Note. Parentheses indicate a feature that occurs variably or rarely. N = not present; Y = present. VT = vasicentric tracheids present. Italics indicate that vascular tracheids intergrade with narrow latewood vessel elements. FP = fiber pits; I = indistinct (minutely bordered to simple); D = distinctly bordered. AP = axial parenchyma occurrence; D = diffuse; DA = diffuse-in-aggregates; M = marginal; B = banded; ScP = scanty paratracheal; Vc = vasicentric; R = rare. Ex1s = exclusively uniseriate rays. This is also coded present for woods with other rays that are aggregate rays. Agg = aggregate rays. Ray2 = rays of two distinct sizes. RayCmp = cellular composition: Ho = homocellular, composed of procumbent cells; He = heterocellular, composed of procumbent and square/upright cells. Cry = crystal presence and location: RP = in ray parenchyma; I = in idioblasts; AP = in axial parenchyma.
However, reliable reports of fossil woods of Casuarinaceae are rare, and the descriptions of putative Cretaceous and Paleogene woods of the family do not include the details necessary to confirm their affinities with the family. In 1937, Shimakura thought that large compound rays as seen in a poorly preserved small axis with pith from the Cretaceous of Japan occurred only in Casuarinaceae, Fagaceae, and Proteaceae. He considered its vessel arrangement most similar to that of Casuarinaceae and so named it *Casuaroxylon japonicum* Shimakura. However, large rays and predominantly solitary vessels also occur in other families (e.g., Betulaceae, Cardiopteridaceae, Cunoniaceae, Dilleniaceae, Ericaceae, Icacinaceae, Menispermaceae). Shimakura’s (1937) description mentions simple perforation plates with a question about the occurrence of scalariform perforation plates; a line drawing shows a scalariform perforation plate, and photographs show only steeply inclined vessel element end walls, so it is not clear what type of perforation plate predominates. Vessel-ray parenchyma pits are not described or illustrated. The pith of this Cretaceous wood sample has sclereids; however, the pith of *Allocasuarina stricta* (Macklin) L.A.S. Johnson does not have sclereids (Moseley...
Fig. 3 Betulaceae. Coryloideae. A, Diffuse-porous wood, vessels that are solitary and in short radial multiples, and aggregate rays. *Carpinus caroliniana* Walter, BWCw 8056a, TS. B, Diffuse-porous wood, vessels that are solitary and in short radial multiples, and, at top, loose aggregate rays. *Corylus cornuta* subsp. *californica* (A.DC.) A.E.Murray, BWCw 8610, TS. C, Diffuse-porous wood, vessels that are solitary and in short radial multiples, and a tendency to a diagonal vessel arrangement. *Ostrya virginiana* (Mill.) K.Koch, BWCw 8417, TS. D, Simple perforation plate (PP), alternate intervessel pitting (IVP), vessel-ray parenchyma pits (VRP) similar to intervessel pits, and fine helical thickenings (HT) in vessel elements. *Carpinus caroliniana*, BWCw 8056a, RLS. E, Scalariform perforation plates and alternate intervessel pitting. *Corylus cornuta* subsp. *californica*, BWCw 8610, RLS. F, Rays composed of procumbent cells and simple perforation plates in narrow latewood vessel elements. *Ostrya knowltonii* Coville, BWCw 8697, RLS. G, Aggregate ray with crystals in enlarged cells. *Carpinus caroliniana*, BWCw 8056a, TLS. H, Scalariform perforation plates in side view, alternate intervessel pitting, and narrow rays. *Corylus cornuta* subsp. *californica*, PACw USGSw.524, TLS. I, Narrow rays and vasicentric tracheids (VT). *Ostrya knowltonii*, BWCw 8697, TLS. Scale bars = 500 µm (A), 200 µm (B, C, G), 50 µm (D, E, H, I), 100 µm (F).
Fig. 4 Casuarinaceae. A–D, Exclusively solitary vessels, wide rays, and banded axial parenchyma. TS. A, Allocasuarina huegeliana (Miq.) L.A.S. Johnson, DBRw 12479. B, Allocasuarina torulosa (Aiton) L.A.S. Johnson, Lw D10.151.102. C, Casuarina cristata Miq., USw 11018. D, Gymnostoma papuanum (S. Moore) L.A.S. Johnson, Hoogland 9011. E, Vasicentric tracheids. Casuarina cristata, USw 11018, RLS. F, Series of vessel elements with simple perforation plates (left) and rays with procumbent cells. Allocasuarina torulosa, Lw D10.151.102, RLS. G, Small vessel-ray parenchyma pits. Allocasuarina torulosa (Miq.) L.A.S. Johnson, Lw R939, RLS. H, Rays of two distinct sizes; widest rays ≥10-seriate. Allocasuarina huegeliana, Lw DBR(DPF) 12470, TLS. I, Aggregate and uniseriate rays. Allocasuarina decussata (Benth.) L.A.S. Johnson, SFCw R336-2, TLS. J, Aggregate and uniseriate rays. Gymnostoma glaucescens (Schltr.) L.A.S. Johnson, Lw 6299, TLS. Scale bars = 200 μm (A–D, H–J), 50 μm (E, G), 100 μm (F).
1948, fig. 27). The wood collection of the Naturalis Biodiversity Center has slides of two other Allocasuarina species and two Casuarina species with pith included in the sections; there were no sclereids.

Hofmann (1944) assigned an Oligocene wood from Europe (Austria) to Casuarinaceae. However, the description of this wood was brief, and some important diagnostic characters (e.g., vessel-ray parenchyma pits) were not mentioned, so the familial assignment is questionable. Vessel-ray parenchyma pit type is particularly useful for distinguishing Casuarinaceae from Fagaceae (table 1).

Moore and Wallace (2000) reported that multiple samples of Casuarinaceae wood occurred in the Miocene of New Zealand. They did not provide anatomical details, but the one cross section figured shows anatomy consistent with Casuarinaceae, particularly with those species from moist habitats. More recently, Vanner (2019) described Casuarinoxylon ildephonsi Vanner from the Miocene of New Zealand, also hypothesized to be from a mesic site.

**Fagaceae**

The Fagaceae are often treated as having three subfamilies, Fagoideae, Quercoideae, and Castaneoideae (Kubitzki 1993), but phylogenetic analyses reveal that the Castaneoideae are paraphyletic, with *Quercus* intervening (Oh and Manos 2008; Larson-Johnson 2016), supporting Nixon’s (1989) recognition of just two subfamilies, Fagoideae and Castaneoideae. Consistent with the phylogenetic topology of Li et al. (2004) and as known for decades (Metcalfe and Chalk 1950), the Fagoideae (fig. 5; vessels solitary and in multiples, random vessel arrangement, and heterocellular

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**Fig. 5**  Fagaceae. Fagoideae. A, Vessels that are solitary and in pairs; latewood vessels are narrower than earlywood vessels. *Fagus crenata* Blume, TWTw 14917, TS. B–G, *Fagus japonica* Maxim., USw 537, TS. B, Growth ring boundary and diffuse and diffuse-in-aggregates axial parenchyma. TS. C, Simple perforation plate and intervessel pitting. RLS. D, Scalariform perforation plates and intervessel pitting. RLS. E, Vessel-ray parenchyma pits. RLS. F, G, Rays of varying sizes; the widest ray is >10-seriate. TLS. Scale bars = 200 μm (A, F), 50 μm (B–E), 100 μm (G).
rations in size—ranging from narrow to wide—have anatomy distinct from that of the Castaneoideae (figs. 6, 7); vessels exclusively solitary, usually in a radial/diagonal to dendritic arrangement, rays exclusively uniseriate or of two distinct sizes—uniseriate plus very wide and tall or uniseriate plus aggregate rays—and predominantly homocellular; tables 1, 2). Vascincent tracheids, the occurrence of which is often correlated with wide and exclusively solitary vessels (Carlquist 1984, 2001), are common in the Castaneoideae and rare in the Fagioideae. Grimmson et al. (2016) suggested that *Fagus* L. split from other Fagaceae by the Late Cretaceous.

There is considerable overlap in the wood anatomical characteristics of *Lithocarpus* Blume and *Quercus*. There is also overlap in the wood anatomy of *Castanea* Miller, *Castanopsis* (D. Don) Spach, and *Chrysolepis* Hjelmq. (tables 1, 2). The molecular analyses of Li et al. (2004) did not find clear distinctions among these genera. The overlap in the appearance of diffuse-porous *Quercus* and diffuse-porous *Lithocarpus* is such that, at present, it is not clear whether their woods are distinguishable, supporting the merger of Quercoideae and Castaneoideae. Manos et al. (2008) recognized the western North American endemic *Notobothriotrichia densiflora* (Hook. & Arn.) Manos, Cannon & S.H. Oh (synonym: *Lithocarpus densiflorus* (Hook. & Arn.) Rehder) and considered it more closely related to *Castanopsis* than to *Lithocarpus*. InsideWood’s images of tangential and transverse sections of these two genera give some support for that proposed relationship: aggregate rays in *Lithocarpus* are composed of wider rays than those that occur in *Notobothriotrichia* Manos, Cannon & S.H. Oh and some species of *Castanopsis*.

**Trigonobalanus** Forman was recognized as sister to the castaneoid genera in the analyses of Li et al. (2004) and Larson-Johnson (2016). Nixon and Crepet (1989) proposed that the three species of *Trigonobalanus* be split into three monospecific genera. Available wood anatomical information for *Trigonobalanus* does not provide support for such a split. *Trigonobalanus* wood is diffuse-porous and has uniseriate and aggregate rays and so is similar to that of *Lithocarpus* and diffuse-porous *Quercus* spp. (Forman and Cutler 1967), supporting Forman’s (1964) placement of the genus in the Quercoideae sensu Kubitzki. The three trigonobalanoid taxa form a clade that is sister to a clade of both quercoid and castaneoid genera in the analysis of Larson-Johnson (2016).

Being able to recognize different species of *Quercus* has been a preoccupation of North American and European wood scientists since the 1800s (Abromeit 1884, cited in Tillson and Muller 1942). It was also an issue in producing the endangered species *Quercus mongolica* (CITES app. III; https://trade.cites.org.org, a white oak from the Russian Far East that has been mixed with American and European oaks in flooring and furniture (https://eia-global.org/subinitiatives/russia). The accepted wisdom is that all ring-porous red oaks (subgenus *Quercus*, section *Lobatae*) have latewood pores that are thick walled and rounded in outline, while ring-porous white oaks (subgenus *Quercus*, section *Quercus*) have latewood pores that are thin walled and angular in outline (e.g., Panshin and DeZeeuw 1980); evergreen oaks often have semi-ring-porous to diffuse-porous wood with vessels in a diagonal to radial arrangement (table 1). Identification of individual species is considered impractical, however. Although it would be of value to museum conservators and antique dealers who are interested in the provenance of materials made of oak wood, there does not appear to be a reliable way to use wood anatomy to distinguish European white oaks from American white oaks (e.g., Brazier and Franklin 1961).

**Fossil Fagioideae wood.** In his monograph on *Fagus*-like fossil woods, Süss (1986) accepted *Fagoxylon bokkaidense* Stopes and Fuji (1910) from the Late Cretaceous of Japan as *Fagus*-like. However, Takahashi and Suzuki (2003) were not able to locate and reexamine material of *F. bokkaidense* and consider that the original diagnosis lacks details necessary for showing that the wood can be only *Fagus*. We concur with Takahashi and Suzuki.

Paleogene fossil woods that were thought to have features of *Fagus* include *Fagus grandiflorus* Beyer (1954) from the early middle Eocene of Yellowstone National Park, Wyoming, and *Fagoxylon kraeuselii* Hofmann (1952) from the Oligocene of Austria. The description of *F. grandiflorus* by Beyer (1954, p. 563) mentions “intervessel . . . pits not as abundant as in living species,” and the paper illustrates only widely spaced alternate intervessel pits; vessel-ray parenchyma pits were not described or figured. It is questionable that the affinities of this fossil wood are with *Fagus*. Unfortunately, the description of the Austrian wood is not detailed, so it is not possible to reevaluate the affinities of this wood. Denk (2003) and Denk and Grimm (2009) suggested that *Fagus* originated in the northern Pacific Basin during the early Tertiary and spread to Europe and Central Asia during the Oligocene. At least 10 *Fagus*-like woods are known from the Mio-Pliocene of Europe and the United States (http://inside.wood.lib.ncsu.edu; Süss 1986; Gregory et al. 2009). There are late Eocene woods from Oregon with features of *Fagus* (E. A. Wheeler and S. R. Manchester, unpublished data).

**Fossil Castaneoideae wood.** *Quercinium centenaeo* Estrada-Ruiz, Martinez-Cabrera & Cevallos-Ferriz (Estrada-Ruiz et al. 2007) from the late Campanian/early Maastrichtian Olmos Formation of Mexico and *Paraquercinium cretaceum* Wheeler, Lee & Matten from the Maastrichtian McNairy Formation of southeastern Illinois (Wheeler et al. 1987) are the oldest known occurrences of woods with features of the Castaneoideae. Both have diffuse-porous to slightly semi-ring-porous wood, few and relatively wide exclusively solitary vessels in a somewhat radial/diagonal arrangement, aggregate rays and exclusively uniseriate rays that are predominantly homocellular, and vascincent tracheids.

*Quercus cretaceoxylon* Suzuki & Ohba (1991) from Hokkaido, Japan, has characteristics of a ring-porous oak, but the sample was a pebble in a modern river deposit, so its exact stratigraphic placement is not known, and in spite of its name it is likely Cenozoic (Takahashi and Suzuki 2003). A distinctly ring-porous wood would be unusual in the Cretaceous. Ring-porous wood, considered an adaptation to seasonal climates, did not become common until after the Eocene (Wheeler and Baas 1991, 1999). Ring-porous Castaneoideae woods were common in the Miocene-Pliocene of Asia, Europe, and North America (e.g., Watari 1952; Müller-Stoll and Mädel 1957; Prakash and Barghoo 1961). Ring-porous *Castanea* type had occurred. A wood from the Paleocene Williamsburg Formation, South Carolina, was assigned to *Fagaceoxylon* Scott & Wheeler (Mclchior 1998), but it has exclusively solitary vessels, which is not a characteristic of *Fagaceoxylon* (a fossil combining features of the Betulaceae and Fagaceae; Scott and Wheeler 1982). Exclusively solitary vessels, along with uniseriate and aggregate rays and
Fig. 6  Fagaceae. Castaneoideae. A–C, Diffuse-porous to semi-ring-porous; exclusively solitary vessels arranged in a radial/diagonal pattern; diffuse, diffuse-in-aggregates, and irregularly banded axial parenchyma; and aggregate rays. TS. A, Lithocarpus edulis Makino (Nakai), Tiw 4823. B, Notholithocarpus densiflorus (Hook. & Arn.) Manos, Cannon, & S.H. Oh, BWCw 8593. C, Quercus virginiana Mill., BWCw 8432. D–F, Ring-porous woods; vessels are exclusively solitary. TS. D, Rays of two distinct sizes and latewood vessels that are rounded in outline, typical of the red oak group. Quercus falcata Michx., BWCw 8432. E, Rays of two distinct sizes and latewood vessels that are angular in outline, typical of the white oak group. Quercus alba L., BWCw 8007. F, All rays narrow and numerous narrow latewood vessels. Castanea dentata (Marshall) Borkh., TWTw 4619. G, Numerous ring-porous narrow latewood vessels. Chrysolepis chrysophylla (Douglas ex Hook.) Hjelmq., BWCw 8591. H, Semi-ring-porous; diagonal arrangement of solitary vessels. Castanopsis cuspidata (Thunb.) Schottky, Tiw 4822. I, All rays narrow, predominantly uniseriate, and numerous narrow latewood vessels. Castanopsis eyrei (Champ. ex Benth.) Hutch., TWTw 7432. TS. Scale bars = 200 µm.
Fig. 7  Fagaceae. Castaneoideae.  

A–D, Vessel-ray parenchyma pits with reduced borders, vertically elongate (palisade), and vasicentric tracheids with circular bordered pits. RLS. A, *Castanopsis fordii* Hance, PACw 21168. B, *Quercus falcata*, BWCw 8165. C, *Lithocarpus edulis*, TI 4823. D, *Notholithocarpus densiflorus*, BWCw 8593. 

E, F, Uniseriate rays and aggregate rays. TLS. E, *Lithocarpus edulis*, TI 4823. F, *Notholithocarpus densiflorus*, BWCw 8593. 

G–J, Rays of two distinct sizes, uniseriate and wider than 10 cells. TLS. G, *Quercus alba*, BWCw 8034. H, *Quercus falcata*, BWCw 8037. I, J, Exclusively uniseriate rays. I, *Chrysolepis chrysophylla*, BWCw 8591. J, *Castanea pumila* (L.) Mill., BWCw 8675. Scale bars = 50 μm (A, B, D), 20 μm (C), 200 μm (E–H), 100 μm (I, J).
irregularly shaped vessel-ray parenchyma pits, suggest that Melchior’s Palaeocene wood belongs in the semi-ring-porous to diffuse-porous Quercus and Lithocarpus group and would be better placed in Quercinimum Unges or Lithocarpoxylon Petrescu. Castanoxylon philipii Crawley (2001) from the Palaeocene Thanet Sands, England, is a semi-ring-porous to diffuse-porous Castanopsis-like wood. There are mammified woods from the upper Oligocene of South China assigned to Lithocarpoxylon and Castanopsis (Huang et al. 2018); the Castanopsis woods had a combination of distinctly ring-porous woods, but their growth ring boundaries were not delineated by thick-walled imperforate elements, a combination suggested to be confined to the tropics.

Given that oak woods are relatively easy to recognize, even without prepared thin sections, it would be possible to examine hand specimens from localities with good age control to see whether the timing of the appearance of ring porosity in the Castanoeidae could be better defined. The diffuse to semi-ring-porous condition seen in Late Cretaceous and Paleogene Castaneoidea wood is apparently a precursor to the more strongly ring-porous woods seen in the Neogene (e.g., Selmeier 1971; Suzuki and Terada 1996; Wheeler and Dillhoff 2009; Imandei et al. 2011). Present-day ring-porous woods are deciduous (Boura and DeFranceschi 2007), so comparing changes in porosity to changes in leaf characters would provide information on the history of the relationship between leaf physiology and xylem physiology.

**Juglandaceae**

Among the useful studies of the wood anatomy of the Juglandaceae are those by Heimsch and Wetmore (1939), Müller-Stoll and Mädel (1960), Miller (1976), Manchester (1983), and Dupéron (1988), as well as that by Withner (1941) on *Rhoiptelea*. *Rhoiptelea*, native to China and northern Vietnam, was formerly treated in its own family, Rhoipteleaceae, distinguished by its bisexual flowers, but recent phylogenetic analyses treat it as a genus of the Juglandaceae and the sole member of the subfamily Rhoipteleoideae. Juglandaceae are the only extant Fagales with compound leaves. *Rhoiptelea* wood differs from other Juglandaceae woods because it has exclusively scalariform perforation plates, usually with 3–12 bars (fig. 8F; 8C; Tipp 1938; Withner 1941; table 1). We had access to only a tangential section of juvenile wood, but its rays are markedly taller than those of other Juglandaceae (cf. fig. 8C with figs. 8E, 9E, 9F). One of the four samples that Withner described also had exceptionally tall rays. The pore distribution pattern is consistent with that of other Juglandaceae (table 1). There are no reports of fossil wood of *Rhoiptelea*.

Manos and Stone (2001) investigated relationships within extant members of Juglandaceae using ITS, chloroplast DNA, morphological, and chemical data. Their results supported the continued recognition of two major clades within the family, Engelhardioideae and Juglandoideae. In the Engelhardioideae (*Alfaroa* Standl., *Engelhardia* Lesch. ex Blume, *Oreomunnea* Oerst.), there are predominantly simple perforation plates accompanied by occasional scalariform perforation plates and vessel-ray parenchyma pits of various shapes (fig. 8G). Recognition of *Alfarpodis* Iljin., with the single species *Alfarpodis roxburghiana* (Wall.) Iljin., has received support for its segregation from *Engelhardia* (Stone 2010). However, we did not find any anatomical features that distinguish the wood of *Engelhardia roxburghiana* Lindl. from other *Engelhardia* species (table 1).

In the Juglandoideae (*Carya* Nutt., *Cyclocarya* Iljin., *Juglans* L., *Platycarya* Siebold and Zucc., *Pterocarya* Kunth), there are exclusively simple perforation plates and vessel-ray parenchyma pits that are similar in shape to the intervessel pits (although at times with the pit borders reduced; table 1; fig. 9). The Juglandoideae are further divided into two tribes, Juglandae and Platycaryoideae (*Platycarya*). *Platycarya* wood has vascular/vascincent tracheids, vessels with helical thickenings, and crystals in idioblastic ray parenchyma cells, features not found in Juglandae wood (table 2; fig. 9H, 9I). Manos and Stone (2001) proposed the recognition of two subtribes within the Juglandae, Juglandinae (*Juglans*, *Pterocarya*, *Cyclocarya*) and Caryinae (*Carya*). Septate pith, a feature not found elsewhere in the Juglandaceae or other Fagales, characterizes *Juglans*, *Pterocarya*, and *Cyclocarya*. Miller (1976) found that woods of the different sections of *Juglans* could be distinguished by aspects of their wood anatomy. The butternuts (sections Cardiocaryon and Trachycaryon) were observed to have procumbent ray cells that were “flattened”/oval when viewed in tangential section, whereas black walnuts (section Rhysoxyyn) had ray cells that were circular when viewed in tangential section. Crystals in the axial parenchyma were observed in long chains (tropical black walnuts) or short chains (temperate black walnuts) or were absent (butternuts and English walnuts).

There is overlap in the wood anatomical features of the subtribes Juglandinae and Caryinae, for example, in the anatomy of the semi-ring-porous species of *Carya* (e.g., *Carya illinoinensis* (Wangen.) K. Koch) and some *Juglans* species (e.g., *Juglans regia* L. (e.g., *Juglans nigra* L.) Dupéron 1988). *Annamocarya* A. Chev. is considered a monotypic genus in the Flora of China (http://www.efloras.org/flora_detail.aspx?flora_id=28&taxon_id=10460) but is treated as *Carya sinensis* Dode in Kew’s Plants of the World (http://www.plantslecture.org). Its wood anatomy is consistent with placement in the Juglandae (tables 1, 2), and it has rhomboidal crystals in idioblasts of axial parenchyma—a distinctive feature of *Carya*—and rarely in ray parenchyma. Its differences from the temperate species of *Carya* are as would be expected from its geographic origin in tropical and subtropical southwest China and Vietnam (Leroy 1953); growth ring boundaries are not as distinct, and marginal parenchyma is lacking. Within the Juglandae, *Annamocarya* also stands out because its multisericrate rays are exclusively heterocellular, a feature shared with the Engelhardiodeae.

Fossil woods of Engelhardiodeae assigned to Engelhardiobia- l. *Manchester* occurred in the middle Eocene of Oregon and Texas (Manchester 1983), the late Eocene of western Europe (Gottwald 1992), and the Oligocene of the Russian Far East (Blokhina et al. 2002). The earliest known Juglandaceae woods occurred in the early middle Eocene (Yellowstone National Park: Wheeler et al. 1977; Denver Basin: Wheeler and Michalski 2003) and are referable to *Pterocarya* Muller-Stoll & Mädel, a genus used for woods that have characteristics seen in both *Pterocarya* and the “soft walnuts” (*Juglans*, section Trachycaryon and section Cardiocaryon).

Dupéron (1988) reviewed fossil wood of the Juglandaceae, updated the work of Müller-Stoll and Mädel (1960), emended the diagnosis of *Eucaryoxylon* Müller-Stoll & Mädel, and agreed that it should be used for fossil woods with clear affinities to *Carya*. He also proposed a new genus, *Rhysocarya* Dupéron, for
Fig. 8  Juglandaceae. A–C, Rhoipteleoideae. *Rhoiptelea chiliantha* Diels & Hand.-Mazz. A, Semi-ring-porous wood and vessels that are solitary and in short radial multiples, with a tendency to a diagonal/dendritic arrangement. Hw 23044, TS. B, Scalariform perforation plates with fewer than 10 bars and alternate intervessel pitting (ivp). Hw 23762, RLS. C, One- to three-seriate rays. Hw 23762, TLS. D–G, Engelhardioideae. D, Narrow tangential bands of axial parenchyma and vessels tending to a diagonal arrangement. *Alfarsa costaricensis* Standl., Hw 19093, TS. E, One- to two-seriate narrow rays and alternate intervessel pitting. *Alfarsa costaricensis*, MADw 37726, TLS. F, Strands of axial parenchyma associated with vessel elements and crystals in chambered axial parenchyma (C). *Oreomunnea pterocarpa* Oerst., SJRw 10769, TLS. G, Perforation plate with one bar, alternate intervessel pitting, and vessel-ray pitting with reduced borders. *Engelhardia roxburghiana* Lind., PACw ChinaA_184, RLS. H–J, Juglandoideae. *Annamocarya sinensis* (Dode) J-F Leroy, CAFw 17510. H, Diffuse-porous wood, vessels that are solitary and in short radial multiples, and banded axial parenchyma. TS. I, Crystals in idioblasts, multiseriate rays that are more than four-seriate, and common uniseriate rays. TLS. J, Heterocellular ray with procumbent body cells and marginal rows of square and upright cells; short rays (uniseriate) composed of upright and square cells. RLS. Scale bars = 1 mm (A, D), 50 μm (B, F), 100 μm (C, E, I), 20 μm (G), 500 μm (H), 200 μm (J).
Fig. 9  Juglandaceae. Juglandoideae. A, Ring-porous wood, vessels that are solitary and in radial multiples, and narrow axial parenchyma bands absent from the earliest earlywood. Carya alba (L.) Nutt. ex Elliott, BWCw 8238, TS. B, Semi-ring-porous wood, vessels that are solitary and in short radial multiples, and narrow bands of axial parenchyma throughout the growth ring. Carya illinoensis (Wangenh.) K.Koch, BWCw 8399, TS. C, Semi-ring-porous wood with a diagonal vessel arrangement and thin-walled fibers. Pterocarya rhoifolia Siebold & Zucc., FHOw 2096, TS. D, Alternate intervessel pitting and vessel-ray parenchyma pitting of a similar size and shape as the intervessel pitting. Pterocarya rhoifolia, FHOw 2096, RLS. E, One- to four-seriate rays and prismatic crystals in solitary inflated axial parenchyma cells. Carya pallida (Ashe) Engelm. & Graebn., BWCw 8479, TLS. F, One- to four-seriate rays and prismatic crystals in chambered axial parenchyma. Juglans nigra, BWCw 8614, TLS. G, H, Platycarya strobilacea Siebold & Zucc. G, Ring-porous wood and latewood vessels in clusters in wavy tangential bands. TWTw 18441, TS. H, Six-seriate ray and narrow vessel elements intergrading with vascular tracheids, with both helical thickenings and alternate intervessel pitting. Hw 18623, TLS. I, Prismatic crystals in enlarged ray parenchyma cells; the body of the ray is composed of procumbent cells with a single marginal row of square cells. Hw 18623, RLS. Scale bars = 200 μm (A–C), 50 μm (D, H), 100 μm (E, F, I), 500 μm (G).
woods resembling the “black walnut” group, *Juglans*, section *Rhysocaryon*. *Rhysocaryoxylon* was subsequently recognized from the early Eocene of Denmark (Sakala and Gryc 2011), which is significant in that extant black walnuts are confined to the Americas.

Strongly ring-porous woods of Juglandaceae, like those seen today in species of *Carya* and *Platycarya*, did not appear until after the Eocene. This post-Eocene timing coincides with the appearance of the same condition in Fagaceae.

**Myricaceae**

The position of the Myricaceae with respect to the other families of the Fagales is considered somewhat uncertain (Stein 2001–), as is the number of species within this geographically widespread family (Huguet et al. 2005). Li et al.’s (2004) analysis recovered Myricaceae as sister to Juglandaceae (including the Rhoipteleaceae), but there was not strong support for this relationship. Myricaceae (fig. 10) and Juglandaceae (figs. 8, 9) share few wood anatomical features (tables 1, 2). Carlquist (2001) studied the wood anatomy of the Myricaceae’s four genera (*Canocomyrica* Guillaumin, *Comptonia* Banks ex Gaertn., *Myrica* L., and *Morella* Lour.) and found them to be distinct from one another.

Huguet et al. (2005) used ITS and rbcL sequence data to analyze *Myrica* species. They found that *Myrica gale* L. (the lectotype of *Myrica*) and *Myrica hartwegii* S. Watson formed a clade distinct from other *Myrica*. The “other” *Myrica* species are now treated as the separate genus *Morella*, leaving *Myrica sensu stricto* as a relatively depauperate genus. Wood anatomy supports this distinction: both *M. gale* and *M. hartwegii* are semi-ring-porous, with an earlywood that includes vessel multiples and a latewood with very few vessels (fig. 8C), whereas *Morella* species are diffuse-porous and have predominantly solitary vessels (table 1; fig. 10A, 10B).

Fossil woods assigned to *Myrica* are reported from the early Eocene of Eden Valley (*Myrica scalariforme* Kruse (1954)) and the early middle Eocene of Yellowstone National Park, Wyoming (*Myrica absarokensis* Wheeler, Scott & Barghoorn; Wheeler et al. 1978). However, these Eocene fossil woods have features of *Morella* rather than *Myrica*, as they have exclusively solitary vessels, multiserate rays are as common as uniseriate rays, and crystals occur in chambered axial parenchyma. *Myrica sensu stricto*, as exemplified by *M. gale* and *M. hartwegii*, is distinguished by radial multiples, mostly uniseriate rays with rare partially multiserate rays, and a lack of crystals. Consequently, we propose the following new combinations.

**Morella Lour.**

*Morella scalariforme* (Kruse) Wheeler & Manchester comb. nov.

**Basionym.** *Myrica scalariformis* Kruse 1954, *Ohio Journal of Science* 54(4):243–244.

*Morella absarokensis* (Wheeler, Scott, Barghoorn) Wheeler & Manchester comb. nov.

**Basionym.** *Myrica absarokensis* Wheeler, Scott, & Barghoorn 1978, *Journal of the Arnold Arboretum* 59(1):10–11.

There is one putative *Myrica* wood from the Paleocene of South Carolina (Melchior 1998) based on a small axis with a stellate pith and fewer than three growth rings. The wood shares the following features with Myricaceae: scalariform perforation plates, alternate to opposite intervessel pitting, vessel-ray parenchyma pits similar to intervessel pits, diffuse-in-aggregates axial parenchyma, and narrow heterocellular rays. However, it is not a “match” for any of the modern genera: *Canocomyrica* *Comptonia*, and *Morella* have exclusively solitary vessels, and this wood has some radial multiples. *Myrica* has some radial multiples, but it has exclusively uniseriate rays, semi-ring porosity, and very thin-walled fibers (table 1). It is possible that there is some relationship to Myricaceae, but the same combination of features occurs in other families, including the Cornaceae, Cunoniaceae, Curtisiaceae, Pentaphylacaceae, Styracaceae, Symlocaceae, and Viburnaceae, although these families usually have more bars per perforation plate than does Melchior’s fossil, which has fewer than 20 bars. Wood of *Comptonia* has not been identified in the fossil record despite the widespread occurrence of this genus from the Eocene onward in North America, Europe, and Asia on the basis of distinctive leaves (Liang et al. 2010).

**Nothofagaceae**

*Nothofagus* Blume was formerly placed in the Fagaceae, but it has long been recognized that it has distinct wood anatomy (Metcalfe and Chalk 1950), and it is positioned as sister to the other Fagales in phylogenetic analyses (e.g., Li et al. 2004; Larson-Johansen 2016). This genus is characterized by radial multiples of vessels (fig. 9A–9C) and narrow heterocellular rays (fig. 11D–11F, 11H, 11J). These features do not characterize the Castaneoideae or Fagoideae, although there are rare reports of narrow heterocellular rays in *Lithocarpus*. Within *Nothofagus* there are differences between the tropical subgenus *Brassospora* Philipson & M.N. Philipson from New Guinea and New Caledonia and the temperate clades from South America, New Zealand, and Australia. *Brassospora* has irregularly spaced conspicuous parenchyma bands and relatively wide vessels in low densities (table 1; fig. 9B). Temperate species have narrow and numerous vessels, rare axial parenchyma that is largely restricted to growth ring boundaries, and, in some species, very narrow latewood vessels intergrading with vascular tracheids (Dadswell and Ingle 1954). Septate fibers occur in varying frequencies together with nonseptate fibers in the temperate group, but they are virtually absent from tropical *Brassospora*. *Nothofagus* wood differs from that of other Fagales, and it might be difficult to recognize that it belongs in the same clade only on the basis of wood.

Fossil woods similar to *Nothofagus* are usually assigned to *Nothofagoxylon* Gothen. Poole (2002) reviewed the fossil record of woods of the Nothofagaceae as well as the characteristics of the modern species. In extant species of this family, there is variation in intervessel pitting (scalariform to opposite to alternate; fig. 11D–11F), ray width (exclusively uniseriate or one- to three-seriate; fig. 11E, 11F, 11J), and fiber types (septate [fig. 11J] and/or nonseptate [fig. 11E, 11F]; tables 1, 2). Nothofagaceae is the only fagaceous family in which some septate fibers occur (13 of the 20 InsideWood *Nothofagus* descriptions). It is uncertain whether this is a retained primitive feature or a novelty (adaptation).

According to Poole (2002), anatomically distinct groups, that is, groups that resemble the extant subgenera *Lophozonia* and
Fig. 10  Myricaceae. A, Diffuse-porous wood, solitary vessels tending to be angular in outline, and diffuse axial parenchyma. *Morella rubra* Lour., TI 4820, TS. B, Near-continuous row of narrow vessels in earlywood, solitary vessels that are angular in outline, vessels of similar widths throughout the growth ring, and diffuse axial parenchyma. *Morella cerifera* (L.) Small. BWCw 8306, TS. C, Earlywood with a continuous band of narrow vessels followed by a zone with vessel groups, the rest of the growth ring without vessels, very thin-walled fibers, and diffuse to diffuse-in-aggregates axial parenchyma. *Myrica gale* L., FHOw 2040, TS. D, Scalariform perforation plate (PP) with a few thick bars, vessel-ray parenchyma pits (VRP) similar to the intervessel pits, and imperforate elements with distinctly bordered pits. *Morella rubra*, TI 4820, RLS. E, Simple perforation plate. *Morella californica*, BWCw 8594, RLS. F, Scalariform perforation plate and vessel-ray parenchyma pits. *Morella californica* (Cham.) Willbur, BWCw 8594, RLS. G, Heterocellular rays, mostly one- to three-seriate. *Morella rubra*, TI 4820, TLS. H, Heterocellular rays, one- to four-seriate. *Morella cerifera*, TLS. I, Rays that are exclusively uniseriate, alternate intervessel pits, and scalariform perforation plates. *Myrica gale*, UNw 769, TLS. J, K, Rays with procumbent body cells and square to upright marginal cells and prismatic crystals in chambered axial parenchyma. RLS. J, *Morella californica*, BWCw 8594. K, *Morella cerifera*, BWCw 8306. Scale bars = 200 µm (A, B, G, H), 100 µm (C, D), 20 µm (E, F), 50 µm (I–K).
Fig. 11  Nothofagaceae.  A–C, Diffuse-porous woods with vessels that are solitary and commonly in radial multiples.  TS.  A, Nothofagus truncata (Colenso) Cockayne (subgenus Fuscospora), FPAw 16763.  B, Nothofagus pullei Steenis (subgenus Brassospora), Hoogland 7332.  Tangential bands of axial parenchyma.  C, Nothofagus pumilio (Poepp. & Endl.) Krasser (subgenus Nothofagus), MADw 13718.  D, Simple perforation plate (PP), alternate (+subopposite) intervessel pits, and thin-walled tyloses.  Nothofagus pumilio (subgenus Nothofagus), MADw 13718, TLS.  E, Opposite intervessel pits, one- to two-seriate rays, and nonseptate fibers.  Nothofagus menziesii (Hook.f.) Oerst. (subgenus Lophozonia), Kw 4157, TLS.  F, Scalariform intervessel pits, uniseriate rays, thin-walled, widely spaced tyloses, and nonseptate fibers.  Nothofagus antarctica (G.Forst.) Oerst. (subgenus Nothofagus), Kw Nothant.Argentina, TLS.  G, Vessel-ray parenchyma pits with reduced borders, horizontally elongate.  Nothofagus grandis Steenis (subgenus Nothofagus), FPAw ngf.5366, RLS.  H, Vessel-ray parenchyma pits with reduced borders, circular in outline.  Nothofagus pumilio (subgenus Nothofagus), MADw 13718, RLS.  I, Septate fibers; rays mostly two-seriate.  Nothofagus moorei (F.Muell.) Krasser (subgenus Lophozonia), Kw Nothmoo.1953, TLS.  Scale bars = ca. 100 μm (A, C, I), 500 μm (B), 50 μm (D–F, H), 20 μm (G).
Nothofagus, occurred by the Late Cretaceous (Campanian to Maastrichtian). No Cretaceous or early Tertiary wood with characteristics of the tropical subgenus Brassospora is known.

**Ticodendraceae**

In the same volume in which Ticodendraceae was first described (Gómez-Laurito and Gómez 1991), Carlquist (1991) provided a detailed description of its wood. He considered it “exceptionally rich in primitive features” (Carlquist 1991, p. 101), that is, primitive in the Baileyan sense (e.g., Wheeler and Baas 2019). The monotypic genus *Ticodendron* Gómez-Laur. & L.D. Gómez, distributed in montane cloud forests from southern Mexico to Costa Rica and Panama, has numerous narrow vessels that are predominantly solitary and tend to be angular in outline (fig. 12A–12D), vessel element lengths of >1 mm, scalariform perforation plates with numerous bars (fig. 12F, 12H), imperfect perforation plates with distinctly bordered pits (fig. 12M), diffuse axial parenchyma and no obvious paratracheal parenchyma (fig. 12A–12D), and heterocellular rays (tables 1, 2). No fossil wood of *Ticodendron* has been reported. However, additional comparative work is needed to establish whether *Ticodendron* wood can be reliably distinguished from that of genera in families outside the Fagaceae that have these primitive characteristics. A search of InsideWood’s database indicates that *Ticodendron*’s suite of characters also occurs in these families (order): Clethraceae (Ericales), Cornaceae (Cornales), Cunoniaceae (Oxalidales), Daphniphyllaceae (Saxifragales), Ericaceae (Ericales), Hamamelidaceae (Saxifragales), Pentaphylacaceae (Ericales), Stachyuraceae (Crossosomatales), Symlocaceae (Ericales), Theaceae (Ericales), and Viburnaceae (Dipsacales). These families are spread throughout the eudicot phylogeny in an archetypal sense and are spread throughout the eudicot phylogeny in an archetypal sense.

**Extinct Fagalean Woods**

There are extinct Fagales recognized on the basis of other plant parts, including several genera of flowers and fruits from the Late Cretaceous (e.g., Herendeen et al. 1995; Friis et al. 2003, 2006; Takahashi et al. 2008). Although fossils referable to extinct genera were present by the Eocene, there are Eocene fagalean fruits that represent extinct taxa, for example, *Fagopsis* Hollick (Manchester and Crane 1983), *Palaeocarpinus* Crane (Pigg et al. 2003), *Cascadiacarpa* Mindell, Stockey & Beard (2007), *Alatomucula* Hermsen & Gandolfo (2016), and *Cruciptera* Manchester (1991). Thus, it is not surprising that there should be Eocene woods that have combinations of characters diagnostic of the Fagales but that do not conform to any one single genus.

*Fagacoxyylon ostroypsoide* Scott & Wheeler (middle Eocene Clarno Formation; Scott and Wheeler 1982; Wheeler and Manchester 2001) combines features seen in the Betulaceae and Fagaceae. It has vessels in radial multiples and clusters that are arranged in a radial to dendritic pattern, aggregate rays composed of narrow rays, and crystals that occur in slightly enlarged procumbent ray cells—features suggesting affinities with the Coryloideae. However, this wood has irregularly shaped vessel-ray parenchyma pits, which is a characteristic of the Fagaceae, not the Betulaceae.

*Clarnoxylon blanchardii* Manchester & Wheeler (1993; middle Eocene Clarno Formation) is diffuse-porous to semi-ring-porous and has a diagonal vessel arrangement, narrow, wavy bands of apotracheal parenchyma, simple perforation plates, alternate intervessel pits, vessel-ray parenchyma pits that are generally similar to the intervessel pits, and narrow rays. These features indicate affinities with the Juglandaceae and are features of *Pterocaryoxylon*. However, this Eocene stem is excluded from *Pterocarya* and *Juglans* in having solid rather than septate pith and prismatic crystals in enlarged procumbent ray cells, a feature that, among extant Juglandaceae, occurs only in *Platycarya*. It differs from *Platycarya*, however, in the absence of ring porosity, vasicentric tracheids, and helically thickened vessel walls.

*Manchesterxylon intermedium* Wheeler & Landon (1992; late Eocene, Nebraska) is also semi-ring-porous, with a tendency to a diagonal vessel arrangement, and it has narrow bands of apotracheal parenchyma, alternate intervessel pits, vessel-ray parenchyma pits that are generally similar to the intervessel pits, and narrow rays. However, it has some scalariform perforation plates, which is a characteristic of the Engelihardtioideae, and vasicentric tracheids, which is a characteristic of *Platycarya*.

**Discussion**

**Comments on the Fossil Record**

Although more than eight genera of small fagaceous flowers and fruits have been recognized on the basis of superbly preserved charcoalified remains from the Late Cretaceous of Europe and North America (e.g., Herendeen et al. 1995; Schönenberger et al. 2001; Friis et al. 2003), we do not have good records for the co-occurring vegetative organs. We do not know how the corresponding woods might have compared to extant woods of the families thought to be related to these remains, that is, Juglandaceae, Myricaceae, and Betulaceae. Fruits and flowers of a presumed fagaceous affinity are also known from the Late Cretaceous of the US state of Georgia (Herendeen et al. 1995), but, again, we lack information on any co-occurring fossil woods.

Nevertheless, there are a few indications of fagaceous diversity during the Cretaceous based on wood. These include *Carpinoxylon ostroypsoide* from the Campanian Panoche Formation of California (Page 1970), *Quercunium centenoae* (Estrada-Ruiz et al. 2007) from the late Campanian/early Maastrichtian Olmos Formation of Mexico, and *Pareguercinum cretaceum* from the Maastrichtian McNairy Formation of southern Illinois (Wheeler et al. 1987). Moreover, Page (1970) described a wood that had fagaceous features (sample CASG 60426 of her group VIB).
Nothofagaceae woods occurred in the Late Cretaceous of Patagonia and Antarctica, with subgenera beginning to diverge by the Campanian (Poole 2002).

Despite Paleocene occurrences of foliage and fruits of Juglandaceae, the woods diagnostic of this family are first known from the Eocene. These include species of *Pterocaryoxylon* with features of present-day *Pterocarya* and *Juglans* species that have similar wood anatomy; *Engelhardioxylon*, accommodating woods similar to extant *Alfaroa*, *Engelhardia*, and *Oreomunnea*; and the extinct *Clarnoxylon* and *Manchesteroxylon*, with

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Fig. 12  Ticodendraceae. *Ticodendron incognitum* Gómez-Laur. & L.D. Gómez. A–D, Diffuse-porous wood with exclusively solitary vessels. TS. A, C, Haber 7071. Axial parenchyma rare. B, D, McPherson 11659. Axial parenchyma primarily diffuse and diffuse-in-aggregates; some scantily paratracheal. E–G, Haber 7071, RLS. Heterocellular ray, ray body with procumbent cells, upright/square cells in the margins, and fibers with distinctly bordered pits. F, Scalariform perforation plate and scalariform intervessel pits. G, Vessel-ray parenchyma pits with reduced borders, horizontally elongate. H, I, McPherson 11659. Heterocellular ray and multiple perforation plate. J, Multiple perforation plate and opposite-scalariform intervessel pits. J, Vessel-ray parenchyma pits with reduced borders, horizontally elongate. K–N, Tangential sections. K, Rays of two distinct sizes; wider rays more than four-seriate and end walls of vessel elements steeply inclined. Haber 7071. L, Rays one- to three-seriate and end walls of vessel elements steeply inclined. McPherson 11659. M, Wider rays more than four-seriate, imperfect tracheary elements with distinctly bordered pits on tangential walls, and scalariform perforation plate in side view. Haber 7071. N, Rays one- to three-seriate and steeply inclined vessel element end wall. Scale bars = 200 μm (A, B, K, L), 100 μm (C–F, H, M, N), 50 μm (G, I, J).
combinations of features that indicate juglandaceous affinities but that do not occur in a single present-day genus.

Myricaceae wood is reported from the Eocene of Wyoming; reliable reports of Casuarinaceae wood are Miocene. There are no known fossil Ticodendraceae woods.

Wood Anatomy and Segregate Genera

The recognition of segregate genera during the past few decades is supported in some cases, but not in others, by wood anatomy. The distinction between Morella and Myrica is well supported by wood anatomy. There is some support for the recognition of Notholithocarpus as separate from Lithocarpus. On the other hand, wood anatomy does not support the segregation of the genera Columboobalanus and Formanodendron from Trigonobalanus or the recognition of Engelhardia roxburghiana as the monotypic Alfaropis. Annamocarya wood is very similar to that of Carafa, and the differences from other species of Carafa, such as diffuse versus ring porosity, are consistent with it being a tropical outlier of the genus. Its narrow, wavy tangential bands of axial parenchyma occur in several genera of Juglandaceae (table 1).

Wood Anatomical Character Evolution: Hypotheses of Ancestral States

To underpin hypotheses on character evolution and as a basis for discussing repeating patterns of wood anatomical syndromes, we plotted some characters from tables 1 and 2 on the Li et al. (2004) phylogeny (fig. 13).

Perforation plate type (fig. 13A). Most Fagales have simple perforations with a low percentage of scalariform perforations. Exclusively simple perforations characterize the Castaneoideae and Juglandoideae, whereas exclusively scalariform perforation plates characterize the Betuloideae, the Rhoipteleoideae, and the genera Canacomyrica, Morella, and Myrica (Myricaceae), as well as the Ticodendraceae (many bars). Plotting vessel perforation type on the molecular phylogeny would reconstruct mixed simple and scalariform perforations as the ancestral condition, with multiple derivations of exclusively scalariform or exclusively simple perforations and some reversals. An alternative interpretation would posit exclusively scalariform perforations as the ancestral condition. Lens et al. (2016), Carlquist (2018), Wheeler and Baas (2019), and Olson (2020) have presented arguments and evidence to support the hypothesis that scalariform to simple perforation plate transitions are largely irreversible (“Carlquist’s ratchet”) but that parallel transitions from scalariform to simple perforations were rampant. In this alternative interpretation, ancestral Fagales had exclusively scalariform perforation plates with multiple (approximately five) independent origins of simple perforations. Lens et al. (2016) reconstructed the vessel element evolution of the asterids, with almost all basal nodes along the spine of the molecular phylogeny of this superorder characterized by exclusively scalariform plates and multiple convergent origins of simple perforation plates.

However, in Fagales, the situation seems more complicated because Fagales are nested among clades with exclusively simple perforation plates (Cucurbitales, Rosales, Fabales) in the APG phylogeny. The few known Late Cretaceous fagalean woods have exclusively simple perforations (P. cretaceum, Q. centenoae) or both simple and scalariform perforations (C. ostryopsoides, Nothofagoxylon corrugatus, Nothofagoxylon menendezii, Nothofagoxylon scalariforme); we do not know of any Cretaceous fagalean woods with exclusively scalariform perforations, although such woods, that is, early Myricaceae or Ticodendraceae, which have a suite of primitive features found in other families, likely would be difficult to recognize as fagalean. Yet scalariform perforations appear to be in the early divergent branches within some families, including Juglandaceae and Fagaceae.

Vessel-ray pitting (fig. 13B). Vessel-ray pitting is typically simple or with strongly reduced borders and of various shapes in Nothofagaceae, Fagaceae, the Engelhardioideae of the Juglandaceae, and Ticodendraceae. The other taxa have bordered vessel-ray pits similar to the intervessel pits in shape and size, with some Juglandaceae tending toward slightly reduced borders in their vessel-ray parenchyma pits (table 1). Because vessel-ray pits that are simple or with reduced borders characterize the basal-most clades of the order, we hypothesize that they are the ancestral condition. This is relevant for recognizing Cretaceous and Paleogene fossils as potential members of the Fagales.

Vessel grouping and vessel patterns (fig. 13C, 13D). Exclusively solitary vessels occur in Ticodendraceae, Myricaceae (except Myrica), most Fagaceae (only Fagus has some small multiples in addition to solitary vessels), and Casuarinaceae. It is tempting to reconstruct solitary vessels as ancestral, but the basal-most genus Nothofagus has vessels in radial multiples. Vessel grouping shows considerable homoplasy within the order.

Diagonal to dendritic vessel patterns occur more frequently in Fagales than elsewhere in the angiosperms: in Fagaceae (except Fagus), some Casuarinaceae, coryloid Betulaceae, and some Juglandaceae (see table 1). These occurrences considered in light of the phylogenetic topology presented in figure 1 indicate that the condition has arisen convergently within the order at least three times. There are two Late Cretaceous fagalean woods with a diagonal/dendritic vessel arrangement (Page 1970; Wheeler et al. 1987).

Porosity. Most Fagales are diffuse-porous, and this can safely be assumed to be the ancestral character state for the order, as robustly supported by both the molecular phylogenies and the fossil record. Semi–ring porosity occurs in four families, and well-developed ring porosity is limited to the deciduous Castaneoideae of the Fagaceae and two extant genera of the Juglandaceae (Carya, Platycarya), apparently as part of convergent evolution in response to more seasonal climates. Almost all Cretaceous and Paleogene fagalean woods are diffuse-porous, with one report of a possible latest Eocene ring-porous Quercus (Brezina 1981).

Imperforate tracheary elements. Imperforate tracheary elements in Fagales show great diversity: there are vascular tracheids intergrading with narrow vessel elements in low frequencies in some Betulaceae (especially in the latewood) and temperate Nothofagus; vasicentric tracheids in Castaneoideae and trigonobalanoid Fagaceae and Casuarinaceae; ground tissue fibers with distinctly bordered pits (fiber tracheids or true tracheids sensu Carlquist) in Fagus, Ticodendron, and Myricaceae; fibers with simple to minutely bordered pits (libriform fibers) in Betulaceae and Juglandaceae (Juglandoideae and Rhoipteleoideae); and a mix of libriform fibers and fiber tracheids or an intermediate fiber type (Castaneoideae and Trigonobalanoidae, Casuarinaceae, and Engelhardia of the Juglandaceae) in some Fagales. Septate libriform fibers are unique to Nothofagus p.p.
Various wood anatomical characters considered in light of the Li et al. (2004) phylogeny indicate considerable homoplasy. Vasicentric tracheids are reconstructed as convergent specializations in Casuarinaceae, Castaneoideae, trigonobalanoid Fagaceae, and some Betulaceae. Vessel grouping is strongly associated with the type of background imperforate tracheary elements (Carlquist 1984, 2001), and this also holds true for Fagales. All clades with exclusively (>90%) solitary vessels have ground tissue fiber tracheids and/or vasicentric tracheids as backup hydraulic tissue. *Fagus*, with its high percentage of solitary vessels, also has fiber pits that are distinctly bordered as well as with reduced borders.

**Aggregate rays.** Aggregate rays—a “signature feature” of the Fagales—are in fact limited to Castaneoideae p.p. and trigonobalanoid Fagaceae, Casuarinaceae, and Betulaceae p.p., where they occur as aggregations either of uniseriate rays or of broader rays and can be interpreted as “dissected broad rays” or compound rays. Plotting this feature on the Li et al. (2004) phylogeny suggests that they arose twice in convergent evolution.

**Parenchyma distribution.** Axial parenchyma in Fagales is predominantly apotracheal, ranging from diffuse to diffuse-in-aggregates to narrow bands. Narrow marginal parenchyma bands occur in temperate *Nothofagus*, Betulaceae, and Juglandaceae. Relatively broad (more than three-seriate) and conspicuous bands are limited to tropical *Nothofagus*.

Paratracheal parenchyma is limited to scantily paratracheal in the Myricaceae to narrowly vasicentric in Juglandaceae; nonetheless, in these families and all other fagalean families, apotracheal parenchyma is the most common type. We hypothesize diffuse and diffuse-in-aggregates axial parenchyma as the ancestral state for the order, with paratracheal, banded, and marginal parenchyma as convergent and/or divergent specializations.

**Fig. 13** Selected wood anatomical traits plotted on the Li et al. (2004) tree. A, Perforation plate types. B, Vessel-ray parenchyma (VRP) pitting. IV = intervessel. C, Vessel grouping. D, Vessel arrangement.
Recurring Patterns

If the Li et al. (2004, fig. 1) phylogeny is accepted and *Nothofagus* is ignored as sister to the whole order, there are three major clades in the order: (1) Fagaceae (*Fagus* + Castaneoideae + *Trigonobalanus*), (2) Casuarinaceae + Tiscodendraceae + Betulaceae, and (3) Myricaceae + Juglandaceae. Wood anatomically, Casuariaceae is most similar to Castaneoideae, but its other features place it in a different clade. It is striking that in these three clades partially similar patterns have evolved. The clades in more or less basal positions have diffuse porosity and scalariform or mixed scalariform and simple perforation plates (*Fagus*, *Tiscodendron*, Myricaceae), while those in more derived positions have simple perforations, diagonal vessel patterns and/or ring porosity, and/or vasicentric tracheids and/or libriform fibers and/or aggregate rays (Fagaceae p.p., Casuarinaceae p.p., carpinioid Betulaceae, and Juglandaceae p.p.).

We hypothesize that wood anatomy in each of these three major clades shows convergent adaptive specializations toward (1) hydraulic efficiency, associated with simple perforation plates and wide vessels, as found in the earlywood of ring-porous woods (e.g., Spicer 2016; Robert et al. 2017), and (2) safety, associated with sectored xylem networks as caused by broad or aggregate rays and/or vessel patterning in radial, diagonal, or dendritic sectors that may facilitate bypassing areas with embolized vessels and also confine infections (Carlquist 1987, 2009; Zanne et al. 2006; Morris et al. 2016). However, not all of these adaptations have evolved in each of the three clades. It has been suggested that sectorality is associated with longevity (e.g., Lanner 2002; Bernard et al. 2020). *Quercus*, which has highly sectored wood, has some of the longest-lived eudicot trees, with multiple reliable reports of trees over 400 years in age (Di Filippo et al. 2015).

Ecological and Functional Adaptations

Herein, we discuss only the following aspects: alternative hydraulic strategies to optimize safety and efficiency and contrasts between tropical and temperate anatomies. Fagales include wood anatomical types that have been associated with contrasting strategies for hydraulic safety and efficiency, as follows: diffuse-porous woods with numerous relatively narrow vessels, ring-porous woods with efficient but vulnerable wide earlywood vessels, and hydraulic safety provided by vasicentric tracheids and narrow latewood vessels. It is noteworthy that these contrasting wood types often grow together in successful species assemblages. For instance, in northwestern Europe and the eastern United States, oak (*Quercus*), beech (*Fagus*), hornbeam (*Carpinus*), hazel (*Corylus*), alder (*Alnus*), and chestnut (*Castanea*) co-occur despite their very divergent wood anatomical structures (Braun 1950; Weeda et al. 1985; Dyer 2006). Apparently, the contrasting combinations of typically safe or efficient features function equally well in ecological settings that are almost identical with regard to water availability and temperature regime.

Fagales with exclusively scalariform plates (*Alnus*, *Betula*, Myricaceae, *Tiscodendron*) tend to grow in mesic sites partly subjected to winter frosts, confirming well-documented ecological trends (Baas 1976, 1986; Wheeler and Baas 2019). *Rhoiptelea* (Juglandaceae) is native to mountainous regions of southern China and Vietnam, regions where scalariform perforation plates with relatively few bars may not be a hydraulic disadvantage. *Tiscodendron*, from montane cloud forests, even fits the so-called xerophbic wood syndrome recognized by Feild et al. (2009).

Although most Fagales are restricted to the temperate zone and the subtropics, a few genera extend into the equatorial tropics. *Nothofagus*, with subgenus *Brassospora*, occurs in New Guinea and New Caledonia, and the other two subgenera are restricted to temperate South America, Australia, and New Zealand. The wood anatomical differences fit well-known ecological trends: the tropical clade has wider and fewer vessels and more axial parenchyma (cf. Wheeler et al. 2007; Morris et al. 2015). It would be interesting to analyze critically whether the differences in vessel diameter among *Nothofagus* species might be explained by differences in tree size and diameter, that is, by larger trees generally having wider vessels (e.g., Olson and Rosell 2013; Olson et al. 2020). The maximum heights reported for the tropical *Nothofagus* species that Dadswell and Ingle (1954) examined are 45 m; the maximum heights for some higher-latitude *Nothofagus* are very similar, 40–45 m (https://treesandshrubsonline.org).

In the Fagaceae, the tropical species of *Castanopsis*, *Lithocarpus*, and *Trigonobalanus* are diffuse-porous, while the deciduous *Quercus* species of the temperate zone are ring-porous. In *Quercus*, there is a correlation with phenology: deciduous oaks are ring-porous, while evergreen oaks are diffuse-porous to semi-ring-porous.

Conclusions

This review reafirms that fagalean families can be distinguished on the basis of their wood anatomy, with most subfamilies and genera having distinctive wood anatomy. Because of this, there is considerable potential for using fossil woods to better understand the history of the order. The wood anatomical variation in the Fagales is in part associated with adaptations to safety and efficiency in hydraulic conduction, and these adaptations are likely to have contributed to the success of the order, particularly of subfamily Castaneoideae in the Fagaceae. It would be useful to incorporate discrete wood anatomical characters in future phylogenetic analyses of the families and genera of Fagales.

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