"Primitive" Wood Characters are Adaptive: Examples from Paracryphiaceae

Sherwin Carlquist
Santa Barbara Botanic Garden, Santa Barbara, California

"PRIMITIVE" WOOD CHARACTERS ARE ADAPTIVE: EXAMPLES FROM PARACRYPHIACEAE

Sherwin Carlquist

Santa Barbara Botanic Garden, 1212 Mission Canyon Road, Santa Barbara, California 93105

ABSTRACT

Why plants rich in plesiomorphic ("primitive") features are alive today is a question that receives little comment. Apomorphies in angiosperms are often interpreted as valuable adaptations. However, both apomorphies and plesiomorphies can be keyed to ecological and physiological features. If a particular habitat remains little modified for long periods of geological time, plesiomorphic features should theoretically persist. The Bailey-Frost-Kribs correlations (usually between tracheary element length and character states in other wood features), deemed useful in their day, did not include adaptation to ecology, nor did they have the advantages that molecular-based phylogenies bring to us today. Montane cloud forests or cool wet forests in geologically older areas (New Zealand, New Caledonia, New Guinea, northern Queensland), especially closer to the equator, contain many species rich in wood plesiomorphies. Wood plesiomorphies can also occur in areas frozen in winter but with moderate transpiration rates during the growing season. Wood plesiomorphies that correlate with these conditions include long and narrow vessel elements with scalariform perforation plates that have wider bars and narrower perforations sometimes occluded by pit membrane remnants. These remnants often take the form of axially-oriented strands, the retention of which correlates with the nature of flow in vessels. The direction of these strands contrasts with that in circular bordered pits of conifers, and is basic to the differences in wood of the two groups. Other plesiomorphic features form a coherent grouping of characters related to low conductivity and moderate peak tensions in water columns: scalariform lateral wall pitting in vessels, tracheids as the imperforate tracheary element, thin porose membranes in bordered pits of tracheids and vessels, rays numerous per mm, abundant upright cells in rays, and diffuse axial parenchyma. Details about the woods and other features of Paracryphiaceae are offered as examples of these tendencies. Flower and fruit characters in Paracryphiaceae show clear apomorphies. Scalariform perforation plates are not acquired secondarily; once extinguished in a clade, the genetic basis for their formation cannot be completely restored, and other features (tracheids, vessel grouping, etc.) provide better methods for achieving conductive safety. Woody plants in drier areas, as well as annuals, caudex perennials, and drought-deciduous trees and shrubs have fewer plesiomorphic features.

Key words: conductive safety, mesic ecology, vessel morphology and ultrastructure, wood physiology.

INTRODUCTION

Apomorphic ("specialized") character states in groups or clades seem to command more attention than the plesiomorphic ("primitive") ones because they are regarded by some as representing optimal adaptations. Yet putatively plesiomorphic states in wood are still present today and in some highly successful groups, and hypotheses for why this should be true are few. Are plants with such woods occupants in ecological regimens that are much the same as those of their ancestors? If so, we still have to explain why they co-exist with plants that show remarkable modifications in wood cell types and tissues.

Paracryphiaceae (3 genera, ca. 35 spp.) exemplify a plesiomorphy-rich vessel-bearing clade of Campanulidae (asterids II). Wood anatomy plesiomorphies are held here to be not relics of doubtful selective value, but adaptive in conditions that are stable, highly mesic, and free from climatic extremes. Such a combination of features is much less common (and such areas tend to shrink over time) than conditions that favor wood with any of various apomorphies. The numerical correlations among wood characters in the Bailey-Frost-Kribs papers,

valuable as they were in providing an initial framework for hypothesizing evolutionary change, are now superseded because of the precision of molecular phylogenetics, which forms a matrix for evolutionary interpretation. Olson (2012) has offered further critiques of the Baileyan methodology. In addition to wood histology, data from ecology, habit, wood physiology, and wood ultrastructure can form a synthesis; all relevant features must be included, and species should be analyzed individually. No synthesis methodology with reliability as high as that of the molecular tree itself is at hand. Plesiomorphic features in Paracryphiaceae and other families, especially in geologically old cloud-forest areas, are hypothesized to include the following (probable functions, as cited in Carlquist [2012b], in parentheses after each feature): longer vessel elements providing less conductive resistance (fewer end walls per unit length); long scalariform perforation plates occur on long end walls (greater length compensating for the resistance of the bars; the resistance a byproduct of safety). Perforations are axially narrow, with correspondingly wide bars. Pit membrane remnants are present in perforations (increased safety). Lateral wall pitting is scalariform (better conduction, but wall less strong than with alternate pitting). Vessels are narrow (lower peak flows), with thin walls (lower negative pressures) and diffuse (grouping less effective for safety than with uniform distribution of more numerous conductive imperforate tracheary elements). Pit membranes of tracheary elements are thin and porose (better conduction, possible because water column tensions low). Rays

are numerous per mm (measured horizontally on a tangential section). Rays are multiseriate and uniseriate, but with upright cells predominant (radial transport of sugars in procumbent cells is aided by procumbent shape of cells). Axial parenchyma (commonly thought to control the conductive process in woods) is diffuse rather than paratracheal.

We do not often attempt hypotheses to account for these shifts in anatomical terms. And yet, morphogenetically, the answers may be simpler than we think. For example, the wood of the mint family (Lamiaceae) contains vessels plus libriform fibers—the latter a mechanical cell type that does not function for conduction. However, the wood of one genus, *Rosmarinus* (rosemary), contains in addition vasicentric tracheids—conducting cells that are adjacent to vessels. We need not imagine some gradual form of origin or dramatic reversal to the tracheid, which is a conductive cell (to be distinguished from fiber-tracheids, in which bordered pits are too few, small, or sparse to permit an active conductive function (Carlquist 1988; Sano et al. 2011; Lens et al. 2016). *Rosmarinus*, in common with other angiosperm woods, has bordered pits on vessels; thus, the genetic information to form bordered pits is present; it need only be activated in the formation of imperforate tracheary elements. Vasicentric tracheids are useful for woody species that inhabit seasonally very dry areas, because they offer conductive cells that do not embolize as readily as vessels under most conditions (Carlquist 1985). *Rosmarinus* occupies dry lowland coastal sites along Mediterranean coasts where xeromorphic wood features permit survival of a woody plant through the summer season. But presence of tracheids in woods has been statistically linked to other plesiomorphic features (Metcalfe and Chalk 1950: xlv, "fibers with bordered pits"). Why should this be true? The tracheids in *Rosmarinus* and *Krameria* are almost certainly "secondary tracheids" or "neotracheids" rather than a continuation of an unbroken history of tracheid presence.

A family often cited as having "primitive wood," Illiciaceae, now contains the genera *Schisandra* and *Kadsura*, formerly excluded in Schisandraceae. *Illicium* has tracheids plus vessels with scalariform perforation plates with pit membrane remnants in the perforations (Carlquist 1982, 1992; Carlquist and Schneider 2002). These vessel characteristics are widely thought to represent plesiomorphic wood features. *Schisandra* and *Kadsura* have tracheids plus vessels with either scalariform or simple perforation plates. The vessels with simple perforation plates in these two genera are more common than has been appreciated (Carlquist 1999). The occurrence of wide-diameter vessels with simple perforation plates in *Schisandra* and *Kadsura* can be attributed to the lianoid habit of these two genera (as compared to the shrubby to arboreal nature of species of *Illicium*). *Kadsura* and *Schisandra* show that elimination of bars on a perforation plate can occur readily in evolutionary terms (narrower vessels in these two genera have scalariform perforation plates). Thus, the schisandroids demonstrate that wood thought to be rich in plesiomorphic features can shift dramatically to apomorphic ones in relation to changes in habit and ecology.

Thus, *Rosmarinus* has evolved tracheids, an apomorphic feature not otherwise reported in Lamiales, whereas in Illiciaceae, there has been a departure from a syndrome of plesiomorphic features in the acquisition of vessels with simple perforation plates. That wood characters can change independently of each other is not a surprise. What is unexpected is the fact that while some woods do retain plesiomorphic features in abundance, they are evidently capable of shifting to apomorphies in some cases. The implication here is that there must be some selective value in the scalariform perforation plate, so widespread in woody angiosperms (Carlquist 1988), and that vessel elements with this end-wall configuration should not be viewed as merely relictual. They must have functional value in those contemporary angiosperms that contain them. Otherwise, we have to think that numerous angiosperm families, such as Bruniaceae, Cornaceae and Hamamelidaceae, are competing well despite a physiological handicap. Paracryphiaceae have woods that are informative with respect to the significance of scalariform perforation plates—and tracheids—in the functioning of woods. Unfortunately, the behavior of water columns at high levels of magnification (i.e., the behavior of water traversing a perforation plate *in vivo*) has not at present been adequately studied. Comparative wood anatomy, while not an alternative to studies in wood physiology, has much to offer in providing extensive circumstantial evidence. Foliar anatomy and physiology of plants with woods rich in plesiomorphies are definitely also relevant to studies on water conduction in woods. And while fiber-tracheids (sensu Bailey 1936; Carlquist 1988; Sano et al. 2011; Lens et al. 2016) and libriform fibers serve mechanical purposes, the remainder of wood cells are involved, directly or indirectly, with the translocation process. Thus, we must analyze more than the nature of vessel structure.

Because vessels of Paracryphiaceae and certain other families (Carlquist 1992) contain pit membrane remnants in perforations, further examination of this phenomenon is in order. These remnants often take the form of porose planar membranes, or of webs at lateral ends of perforations, or of strands that run axially across the perforations. What possible significance do these conformations have? Are any of the strands that persist after maturation of a vessel element and the lysis and sweeping action of the conductive stream formed before a vessel matures, or are they structures that are randomly left behind after the conductive stream becomes active? What function might they serve? Like the bars on perforation plates, the occurrence of webs, strands, and shreds of the primary wall in perforations probably have some functional significance. To think otherwise, we would have to imagine that this wood character has been rather extensively retained in unrelated clades despite being non-functional or even detrimental to the flow of sap in wood. The present paper takes the viewpoint that we should look to possible function before concluding that a structure has little or no function, and that we should consider wood evolution an efficient process.

Character evolution in the Hennigian sense of cladistics considers morphological characters to be either present or absent. Is this an accurate view of character evolution in wood? Some wood characters seem to have some plasticity or indeterminate variation, and thus one cannot designate a 0 or 1 character state. The presence of various degrees of pit membrane remnants in perforation plates is one such example. In Paracryphiaceae, as in Illiciaceae (Carlquist and Schneider 2002; Schneider and Carlquist 2003) and other families, there is a range from perforations that are completely occluded at maturity with pit membranes to those that are devoid of remnants. The three genera of Paracryphiaceae have imperforate tracheary elements that are not easily categorized within the gamut between libriform fibers and tracheids (tracheids in the sense of Bailey [1936]; Carlquist 1988; Sano et al. 2011; Lens et al. 2016). From such intermediate expressions in various families of angiosperms, imperforate

tracheary elements that correspond more closely to the extremes can be evolved. Likewise, we have dimorphism in other cell types in wood: fiber [= libriform fiber] dimorphism is one example of this tendency (Carlquist 2014): mechanical fibers and storage fibers can result side by side in such woods as *Acacia* and *Acer*. Character intermediacy was proposed for evolution of bordered vs. non-bordered perforation plates in Caryophyllales (Carlquist 2010). The principle of intermediacy in character state expression may run throughout wood histology and may deserve further exploration.

The wood anatomy of Paracryphiaceae in the most recent (trigeneric) sense as derived from molecular data (Lundberg 2001; Tank and Donoghue 2010) has not been studied as a unit, although separate accounts of the wood of *Paracryphia* (Dickison and Baas 1977), *Sphenostemon* (Baas 1975) and *Quintinia* (Meylan and Butterfield 1978) have been offered. By comparing the wood of the three genera, one can see the evolution of Paracryphiaceae as a whole and judge the role of plesiomorphy and apomorphy in the evolution of wood features and in other features (reproductive, foliar). One can also compare the three genera with the ecology of their component species and thus find evidence regarding how wood anatomy and ecology (and thereby wood physiology) are linked. Data from scanning electron microscopy (SEM) are provided here as a way of showing the evolution and plasticity of wood characters on an ultrastructural level as well as by means of light microscopy.

MATERIAL AND METHODS

The collections studied are as follows: *Paracryphia alticola* (Schltr.) Steenis, depressed wet area near summit of Mont Panié, New Caledonia, *Carlquist 15575* (RSA, RSAw); this collection used for all features; summit of Mont Panié, New Caledonia, *McKee 4993* (P, MADw); this collection used for perforation plate pit membrane features. *Quintinia serrata* A. Cunn., New Zealand, *Braggins s.n.* (wood sample provided by Botany Division, DSIR, Christchurch). *Sphenostemon lobosporus* (F. Muell.) L.S. Sm., West Line of Atherton Forest, Atherton Plateau, Queensland, Australia, *Carlquist 15213* (RSA, RSAw). *Sphenostemon pachycladus* Baill., between end of road and summit, Montagne des Sources, New Caledonia, *Carlquist 15604* (RSA, RSAw).

Liquid preservation of wood samples was not possible for logistical reasons; dried wood samples were available and are judged to be adequate for the present study. Most artifacts in pit membranes of perforation plates take the form of cracks or tears that are readily evident and are caused by handling of wood samples and wood sections. Some artifacts probably would have occurred even in liquid-preserved material because of handling.

Portions of wood samples were boiled in hot water to remove air, and sectioned by means of usual sliding microtome techniques. Sections were stained with a safranin-fast green combination. Sections were mounted in Canada balsam. Macerations were prepared by means of Jeffrey's Solution, stained with safranin, and mounted in Canada balsam. All data provided are original. Although quantitative data on some of these species were provided by Baas (1975) and Dickison and Baas (1977), presentation of new data was thought advisable in order to provide uniformity in comparisons. Wood samples were judged to

be relatively large and thus to show mature patterns, and no twig samples were studied.

The term "plesiomorphic" should, strictly speaking, be used only with reference to a particular clade, and that clade should be defined. "Plesiomorphic" is used in this paper in a more general sense, corresponding more to the "primitive" of earlier authors. The term "F/V ratio" is the ratio between length of imperforate tracheary elements (F) and the length of vessel elements (V).

RESULTS

Paracryphia alticola

The presentation of leaves (Fig. 1A) and flowers (Fig. 1B) here is intended to provide photographic representations otherwise not present in the literature. Drawings of habit and of floral and fruit details are offered by Baker (1921) and photographs of light microscope preparations have been published by Dickison and Baas (1977).

The leaves of the sole species of *Paracryphia* are coriaceous (section illustrated by Dickison and Baas 1977). We should note that leaf texture of highly mesophytic angiosperms is often coriaceous rather than membranous, a fact discussed later. Dickison and Baas (1977) illustrate leaf sections showing two layers of palisade, but epidermal cutinization is not mentioned by them.

The short spike of flowers (Fig. 1A, B) contains both bisexual and male flowers (Baker 1921; Dickison and Baas 1977). The bisexual flower illustrated (Fig. 1B) has about eight stamens with filiform filaments and a syncarpous gynoecium composed of about 12 carpels. Male flowers have stamens with wide filaments (Baker 1921; Dickison and Baas 1977) like those illustrated here for *Sphenostemon pachycladus* (Fig. 5A, B).

The wood of *Paracryphia* (Fig. 1C–F, Fig. 2) is plesiomorphic and mesomorphic in most features. Growth rings are minimally expressed (Fig. 1C). The number of vessels per group is 1.37, but varies within a section. The number of vessels per mm^2 is 107. Vessel lumen diameter averages 53 μm. Mean vessel element length is 1612 μm. Perforation plates are not well defined (Fig. 2A, B); upper and lower ends transition gradually into lateral wall pitting. Lateral wall pitting is scalariform (Fig. 2C). Mean length of perforation plates is 693 μm. The mean number of bars per plate is 159 (Fig. 2A). The presence of pit membranes in perforations varies in extent and type. Briefly illustrated earlier (Carlquist 1992), the full range is shown here (Fig. 2D–H). Pit membranes may be laminar and homogeneous in surface texture (Fig. 2D; fractures due to handling). In a few perforation plates, axially-oriented strands overlie a laminar or porose pit membrane (Fig. 2E). Some perforation plate pit membranes have numerous small pores, the pores tending to be elongate in an axial direction (Fig. 2F). More extensive spaces in the perforate pit membranes, probably due to lysis and sweeping action of the conductive stream, can be seen in Fig. 2G. Pit membrane remnants are most abundant in the lateral ends of perforations. Axially-oriented strands without laminar membranes occur in perforations of some plates. The most minimal pit membrane remnants are present as lumps along the bars of the plate (Fig. 2H). Both collections of *Paracryphia* studied had wide ranges of pit membrane presence in perforations; there is a tendency for axially wider perforations to retain fewer remnants of pit membranes than narrower perforations.
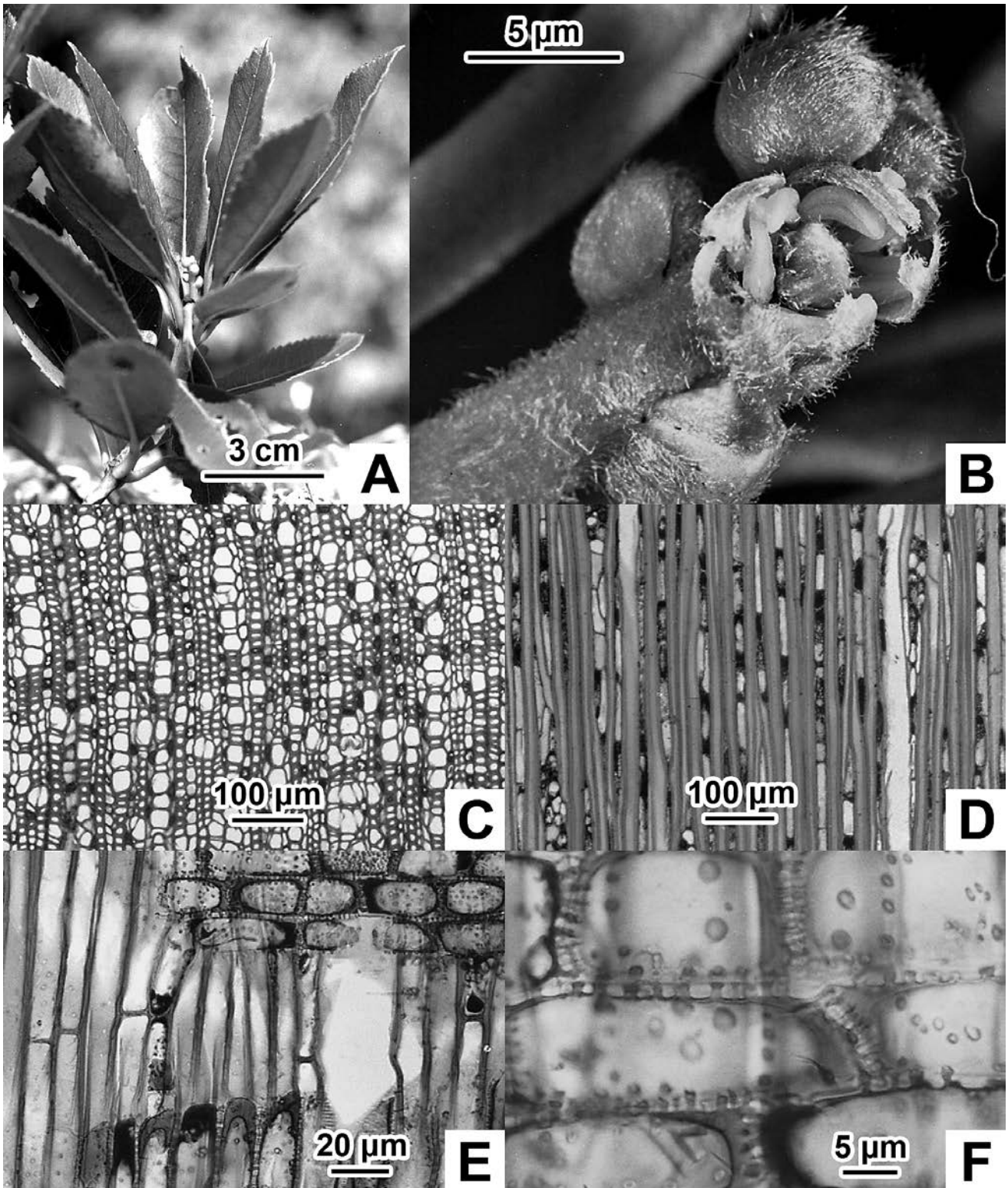
Fig. 1. A–F. *Paracryphia alticola, Carlquist 15575.*—A. Branch with inflorescence at tip.—B. Inflorescence; a bisexual flower is open.—C. Transverse section of wood; vessels are solitary or in small groups, radially aligned.—D. Tangential section; multiseriate rays up to three cells wide; uniseriate rays and uniseriate wings of multiseriate rays abundant.—E. Radial section; multiseriate portion of ray, procumbent cells, above right. Axial parenchyma, left.—F. Radial section, procumbent ray cells; tangential walls densely pitted; horizontal walls prominently pitted; most pits are bordered.
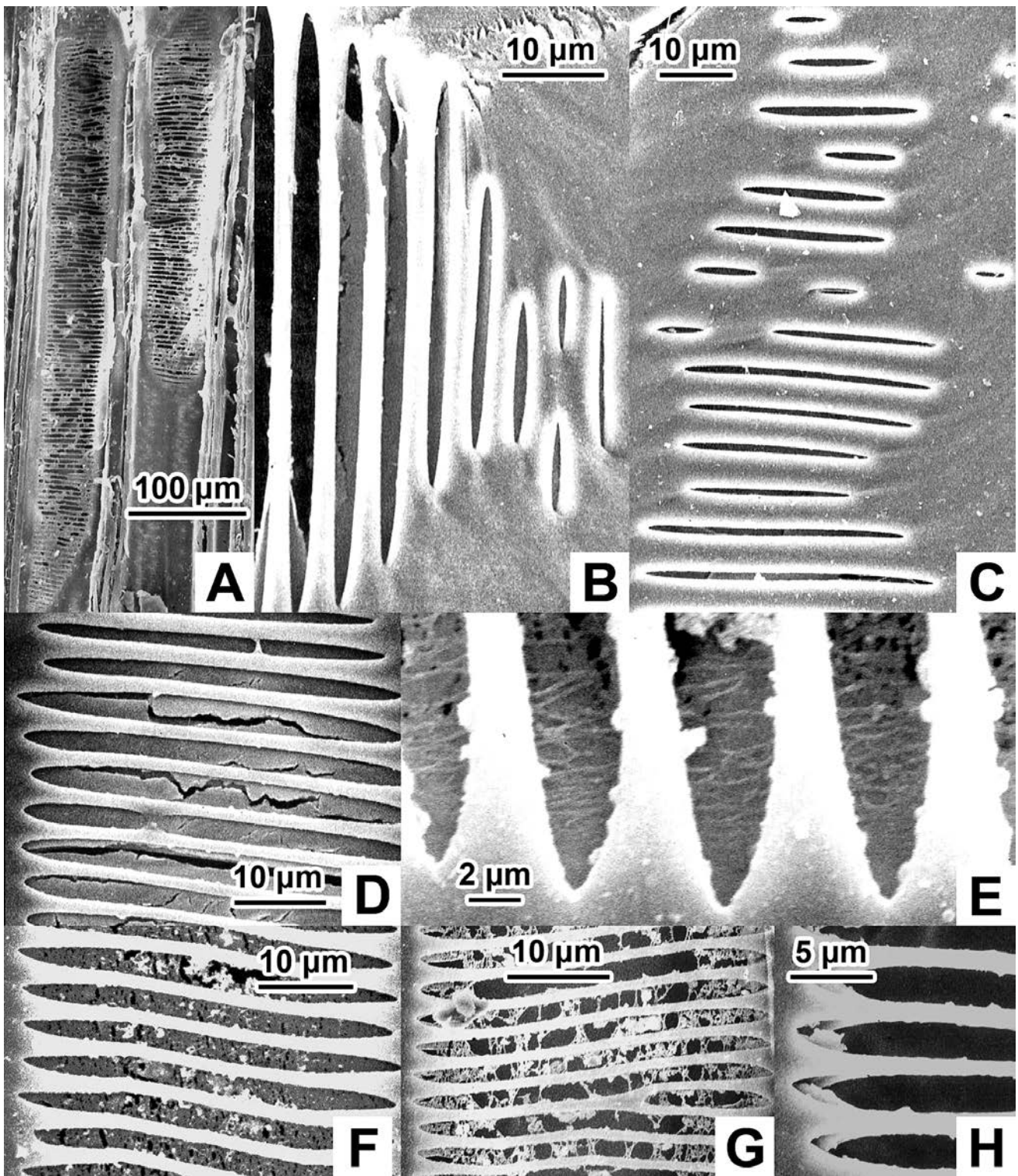
Fig. 2.   A–H. *Paracryphia alticola, Carlquist 15575* (B–D, F, H) and *McKee 4993* (E, G). SEM (scanning electron microscope) images of radial sections.—A. Two perforation plates.—B. Transition between end of perforation plate (left) and scalariform lateral wall pitting (right).—C. Scalariform lateral wall pitting.—D–H. Perforation plate portions.—D. Pit membranes intact (cracking an artifact due to handling).—E. Pit membranes intact, with axially-oriented thickenings and a few pores.—F. Pit membranes present, but some pores and axially-running gaps present.—G. Axially-arranged threads in central portions of perforations, pit membranes denser at lateral ends of perforations.—H. Pit membrane remnants present only as small lumps along bars.

Imperforate tracheary elements average 2764 μm in length and 27 μm in diameter (Fig. 7C). Pits are bordered, with elliptical apertures (Fig. 7B); some splitting due to shrinkage of the dehydrated wall is present (Fig. 7A). Pit borders are 3–4 μm in diameter. A few wider imperforate tracheary elements with more than one series of pits per facet were observed. The F/V ratio is 1.71.

Rays are uniseriate, biseriate and triseriate (Fig. 1D). Most multiseriate rays have uniseriate wings. Mean height of multiseriate rays is 1553 μm. Mean height of uniseriate rays is 1516 μm. Central portions of multiseriate rays are composed of radially elongate cells (Fig. 1E, F), mostly 1.5 to 2 times as long as broad. Pits are denser on tangential walls (Fig. 1F), and often bordered; pits are sparser on horizontal walls, many of these inconspicuously bordered. Uniseriate rays and wings of multiseriate rays are composed of upright cells (Fig. 1E).

Axial parenchyma is diffuse, randomly distributed, so that some axial parenchyma strands touch rays, some touch vessels, but a clear paratracheal pattern is not evident. Axial parenchyma strands are 4–9 cells in length. Axial parenchyma cells average 212 μm in length.

Dark deposits are present in ray cells (Fig. 1D–F) and occasionally in some axial parenchyma cells (Fig. 1E). Styloid crystals are common in bark and present but scarce in wood.

Quintinia serrata

Quintinia is a wet forest genus of about 25 species (species limits of the New Zealand species uncertain) that ranges from the Philippines to New Guinea, Vanuatu, Australia, New Caledonia and mainland New Zealand (Allan 1982). Wood of only one species was available for study. Quintinia serrata occurs on North Island, New Zealand (Allan 1982).

Growth rings are perceptible, but not strongly marked (Fig. 3A, latewood at bottom). Mean number of vessels per group is 1.07. Mean number of vessels per mm^2 is 298 (Fig. 3A). Vessel lumen diameter averages 32 μm. The mean vessel element length is 1082 μm. Average length of perforation plates is 237 μm (Fig. 3E–F). Mean number of bars per perforation plate is 48. Lateral wall pitting of vessels is scalariform-transitional (Fig. 3D) or sparse. Perforation plates have relatively clearly defined limits, but upper and lower ends of perforation plates grade into lateral wall pitting to a limited extent (Fig. 3F, upper left). Cross-bar patterns occasional (Fig. 4G). Pit membrane remnants occur to various extents in almost all of the perforations (Fig. 3E, 4A–F), but are nearly absent in the perforations shown in Fig. 3F–G). Where most abundant, pit membrane remnants take the form of a porose thin and fragile primary wall (Fig. 4A, C), Secretion of secondary substances may inhibit lysis of some pit membranes (Fig. 4B). The pit membranes of Fig. 4B show a tendency for strands of wall material to be aligned in an axial direction. This tendency is also evident in the centers of perforations, in which filiform strands can be seen (Fig. 4F). At the lateral ends of the perforations, pit membranes form networks that tend to be resistant to removal by the conductive stream (Fig. 4D–F). These observations are in accord with the illustrations for Q. acutifolia Kirk by Meylan and Butterfield (1978), who use the term "microfibrillar webs" for this appearance.

Imperforate tracheary elements average 1403 μm in length. As seen from the lumen side, pit apertures are lenticular. The pits are rather densely placed (Fig. 7C), and are fully bordered (Fig. 7D).

Rays are uniseriate, biseriate, and multiseriate (Fig. 3C). Meylan and Butterfield (1978), who studied wood from large-diameter wood samples, reported multiseriate portions of multiseriate rays to vary from 2 to 7 cells in width. Multiseriate rays mostly terminate vertically in uniseriate wings (Fig. 3C). Ray cells are radially square to three times as long as broad, and have dense pitting on tangential walls. Multiseriate rays average 953 μm in axial height. Uniseriate rays and uniseriate wings of multiseriate rays are composed of upright cells. Uniseriate rays average 855 μm in height.

Axial parenchyma is composed of strands up to 7 cells in length. The average axial length of strand cells is 178 μm. Axial parenchyma is predominantly diffuse (Fig. 3B). Contacts between axial parenchyma cells and vessels or rays are essentially random, and no genuine paratracheal pattern is evident.

Dark-staining deposits in rays and axial parenchyma are minimal (Fig. 3C). Styloids were not observed, nor are they reported for the two Quintinia species studied by Meylan and Butterfield (1978).

Sphenostemon

Sphenostemon consists of nine species, native to New Guinea, Queensland, and New Caledonia. Wood of tree species was studied by Baas (1975), who offered a composite description of wood anatomy of the genus. As Baas (1975) noted, differences among the species are not major ones. A separate description of wood of two species is offered here, if only as a way of presenting quantitative data. Quantitative data in woods are related to ecology, but, within a species, whether the sample comes from a small-diameter or a large-diameter sample is important; vessels tend to become wider in diameter, and multiseriate rays greater in thickness and height with increase in stem diameter. This also applies to length of vessel elements and imperforate tracheary elements (Bailey and Tupper 1918).

Sphenostemon pachycladus

The perianth segments of S. pachycladus flowers are brownish and fimbriate at the tips (Fig. 5A, B). On the flower illustrated there is a cycle of stamens, convex on outer surfaces (Fig. 5A), but flat facing the two carpels (Fig. 5B). Fruits are very shortly pedicellate; the leaves are coriaceous (Fig. 5C). Longitudinal sections of fruits reveal one (rarely two) pyrene-like seeds occupying most of the volume of the fruit (Fig. 5D), which is at this stage green and parenchymatous.

Growth rings are very weakly developed (Fig. 5E). Mean number of vessels per group is 1.30. Mean number of vessels per mm^2 is 87.5. Vessel lumen diameter is 48 μm. Vessel element length averages 1347 μm. Mean perforation plate length is 416 μm. Perforation plates are scalariform (Fig. 6E). The mean number of bars per plate is 108. Perforation plates grade into the lateral wall pitting. Some perforation plates have axially-oriented thread-like pit membrane remnants (Fig. 6E, F), whereas others are devoid of pit membrane remnants. More extensive remnants based on fresh material were illustrated by Carlquist (2012b: Fig. 4E).

Imperforate tracheary elements are moderately thick-walled (Fig. 6E, Fig. 7E) and average 1700 μm in length. Pit borders are
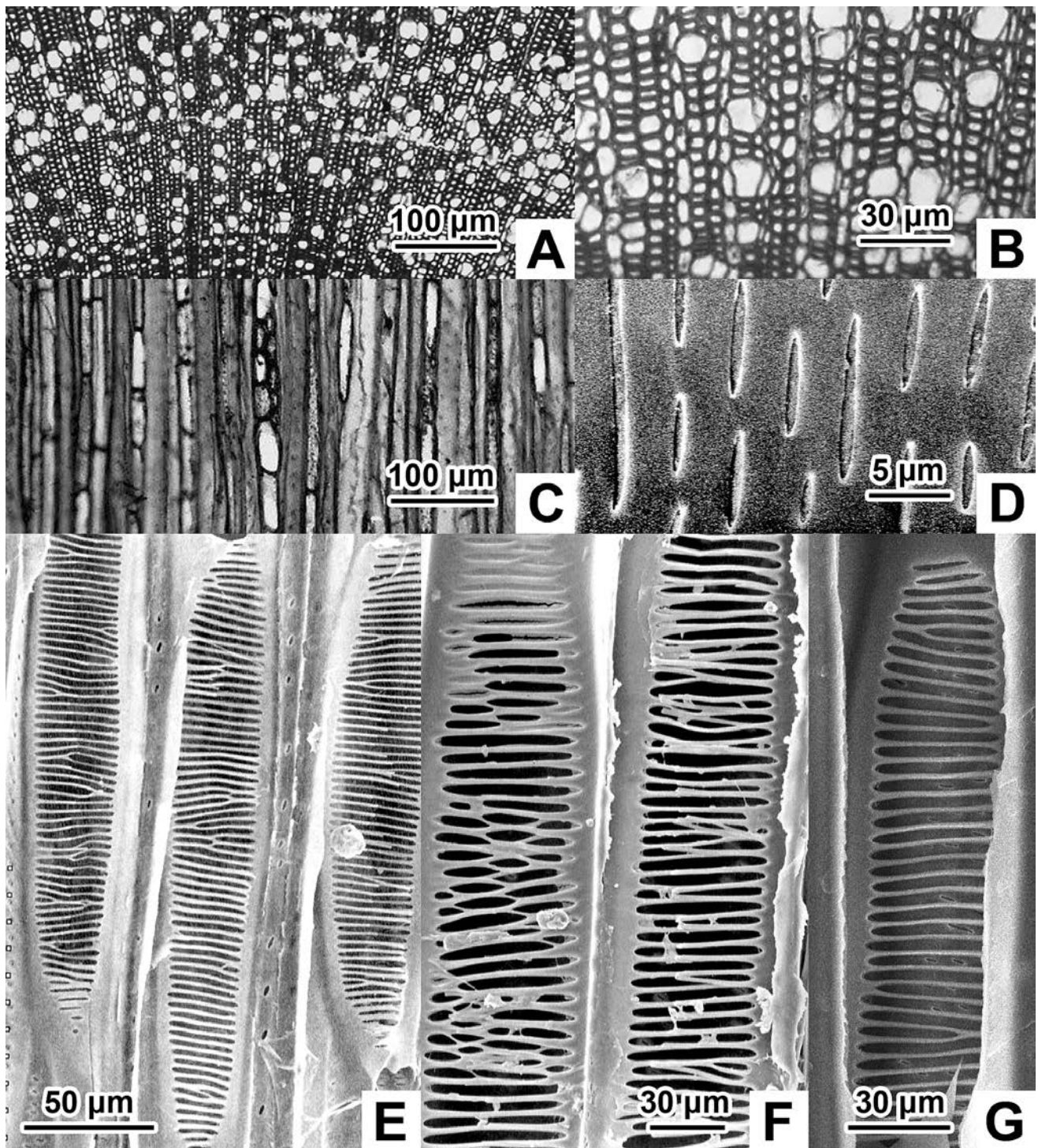
Fig. 3.   A–G. *Quintinia serrata*, *Braggins s.n.*, light microscope photographs (A–C) and SEM images (D–G) of wood.—A. Transverse section, latewood below, earlywood above; vessels are mostly solitary.—B. Transverse section. Axial parenchyma is sparse, diffuse.—C. Tangential section; rays are mostly uniseriate; multiseriates up to three cells wide.—D. Transitional pattern of lateral vessel wall pitting. E–G. Perforation plates on radial sections.—E. Three perforation plates; axially-orientated pit membrane remnants are faintly visible in the perforations.—F. Portions of two perforation plates; pit membranes absent in perforations, some bar anomalies in perforation plate at left.—G. Most of a perforation plate; pit membranes are absent; upper end of perforation plate at top.
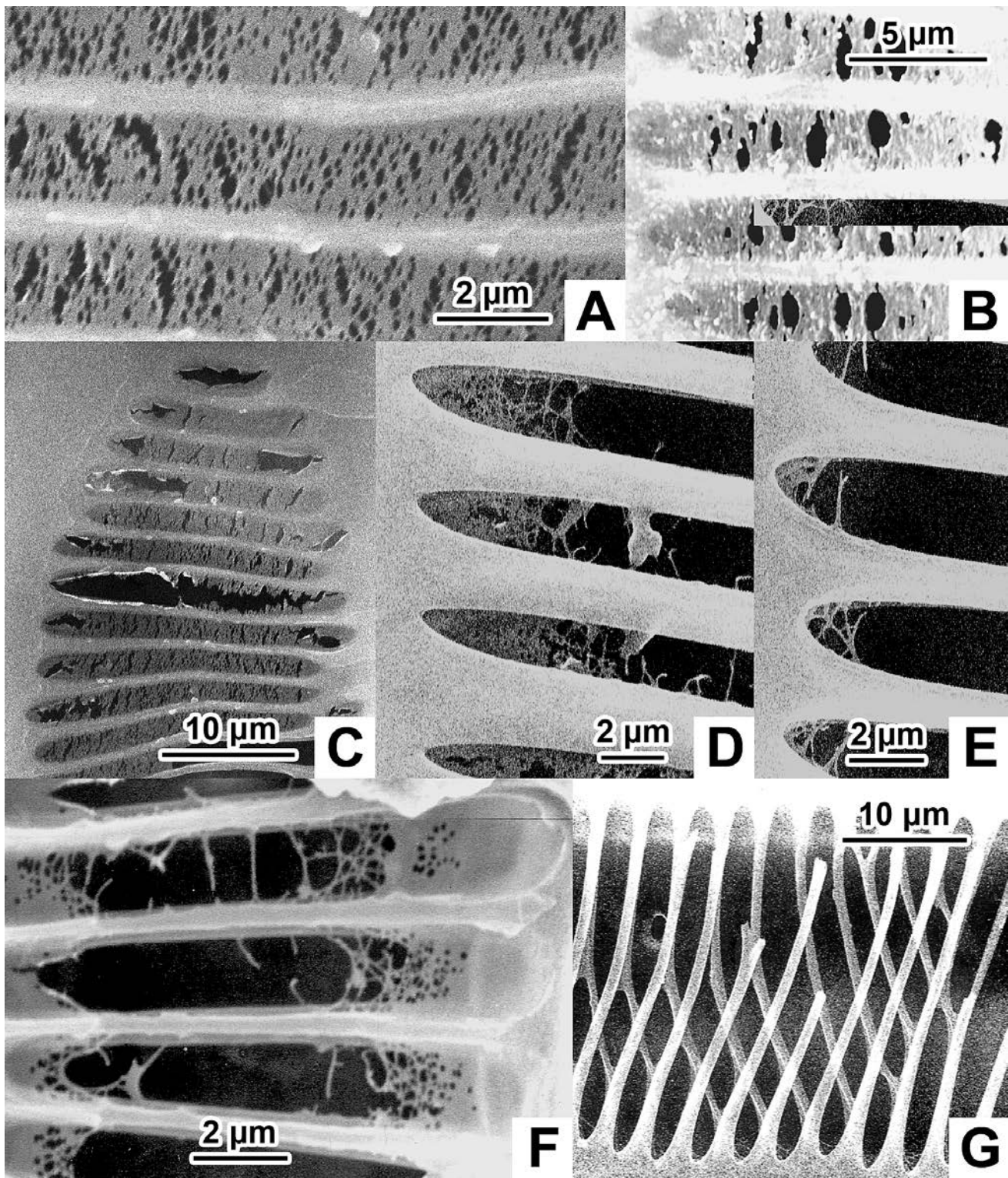
Fig. 4. A–G. *Quintinia serrata, Braggins s.n.*, SEM images of perforation plate portions from radial sections.—A. Pit membrane remnants present, porosities apparently natural and tending to be elongate in an axial direction.—B. Pit membranes present, some gaps present; pit membrane dissolution may have been inhibited by presence of a secondary compound.—C. Tip of perforation plate; pit membranes present, porosities are axially elongate.—D. Pit membranes present as dense webs at lateral ends of perforations, left, but sparse in central portions of perforations, right.—E. A few threads of pit membranes at ends of perforations, left.—F. Pit membranes laminar and porose at perforation lateral ends, right and left, but present only as a few threads in central portions of perforations.—G. Adjacent perforation plates with bars oriented in opposing directions; pit membranes absent.
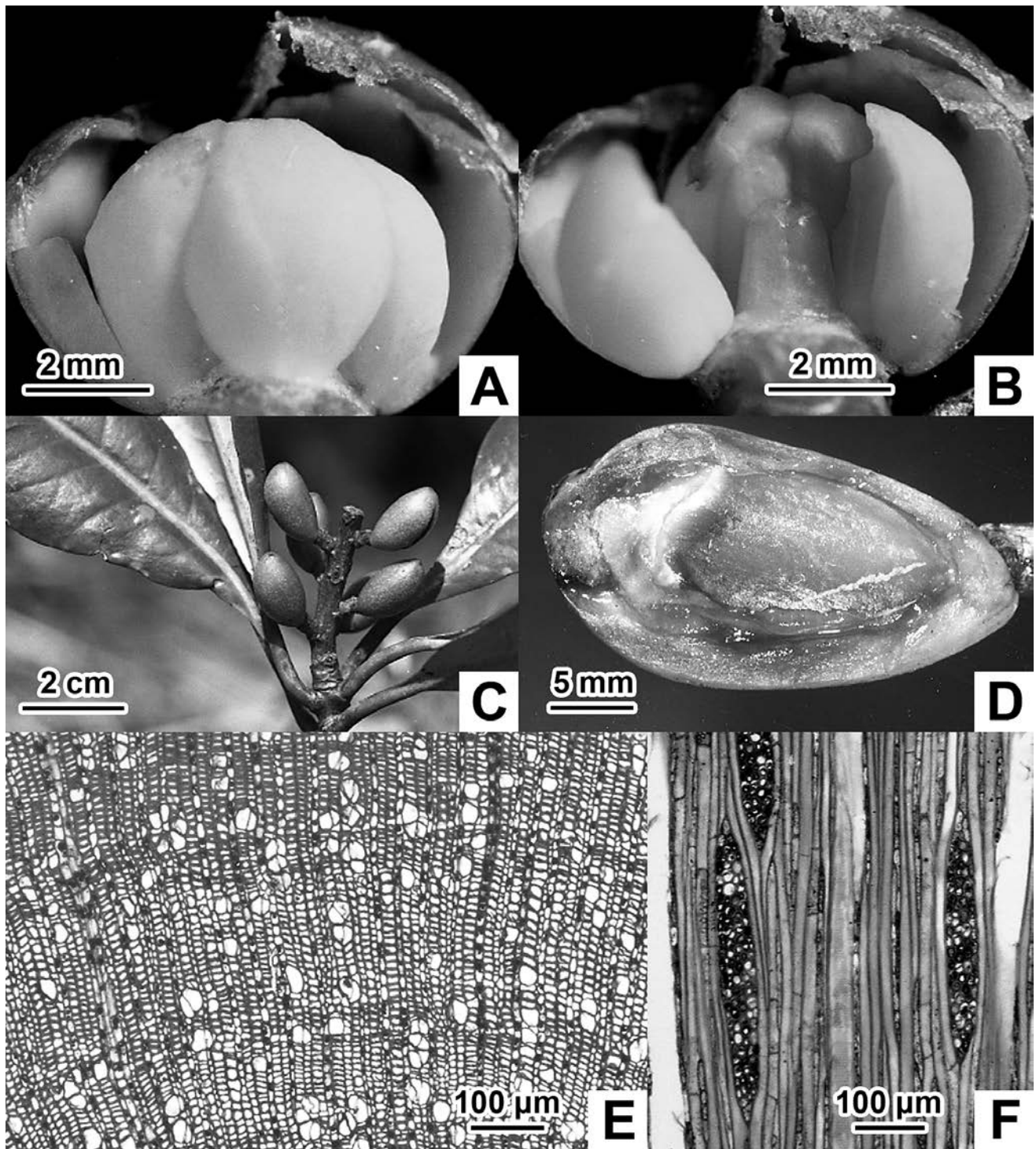
Fig. 5. A–F. *Sphenostemon pachycladus*, *Carlquist 15604*.—A. Flower dissection, tepal removed to show stamens.—B. Flower dissection, stamen removed to show bicarpellate gynoecium.—C. Terminal inflorescence with fruits.—D. Fruit dissection; exocarp removed to show one seed.—E, F. Light photomicrographs of wood sections.—E. Transverse section; growth rings very faintly demarcated, some vessels grouped.—F. Tangential section; three multiseriate rays almost without wings present; the remainder of the rays are uniseriate.

about 3 µm in diameter; pits are moderately sparse. Pit apertures are lenticular (Fig. 7E, F), some splitting with dehydration (Fig. 7E). The F/V ratio is 1.26.

Rays are multiseriate and uniseriate, the former more common (Fig. 5F). The multiseriate portion of multiseriate rays is 4–6 cells wide at widest point. Uniseriate wings are often lacking on the multiseriate rays. Mean multiseriate ray height is 578 µm, mean uniseriate ray height is 418 µm. Multiseriate portions of multiseriate rays are composed of square to procumbent cells (Fig. 6A). Uniseriate rays and uniseriate portions of multiseriate
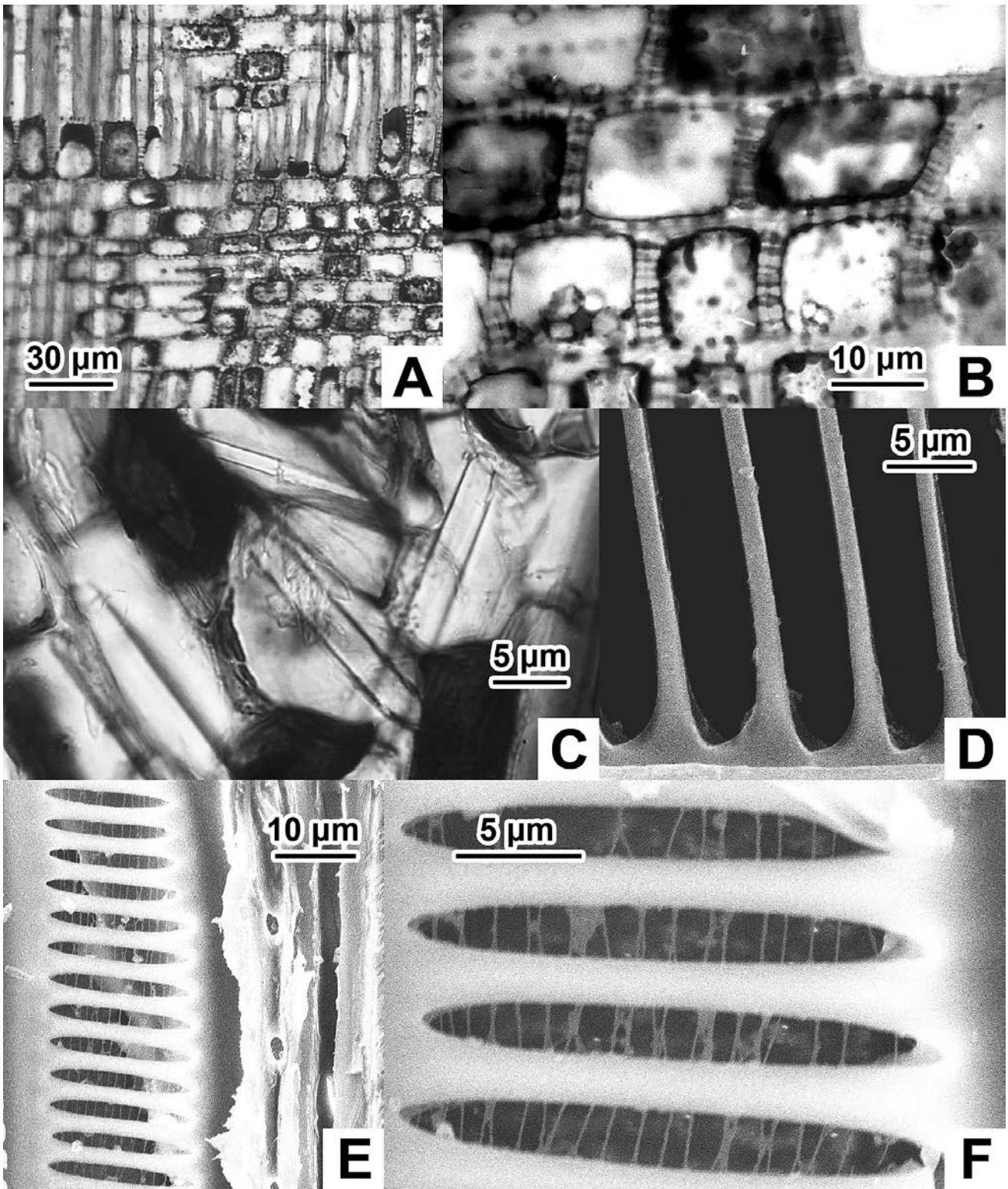
Fig. 6. A–F. *Sphenostemon pachycladus, Carlquist 15604* (A–C, E–F) and *S. lobosporus, Carlquist 15213* (D).—A–C. Light photomicrographs.—A. Radial section of wood; some upright cells at tips of multiseriate ray (upper left; bottom); most ray cells are square to procumbent.—B. Radial section; dense pitting, pits bordered, on tangential walls; pits somewhat less dense, many bordered on horizontal walls.—C. Portion of radial section of bark; some styloid portions visible.—D–F. Portions of perforation plates from radial sections.—D. Perforation plate with no pit membrane remnants.—E. Perforation plate with relatively thick bars, perforation plate remnants.—F. Pit membrane remnants are present as axially-oriented threads.
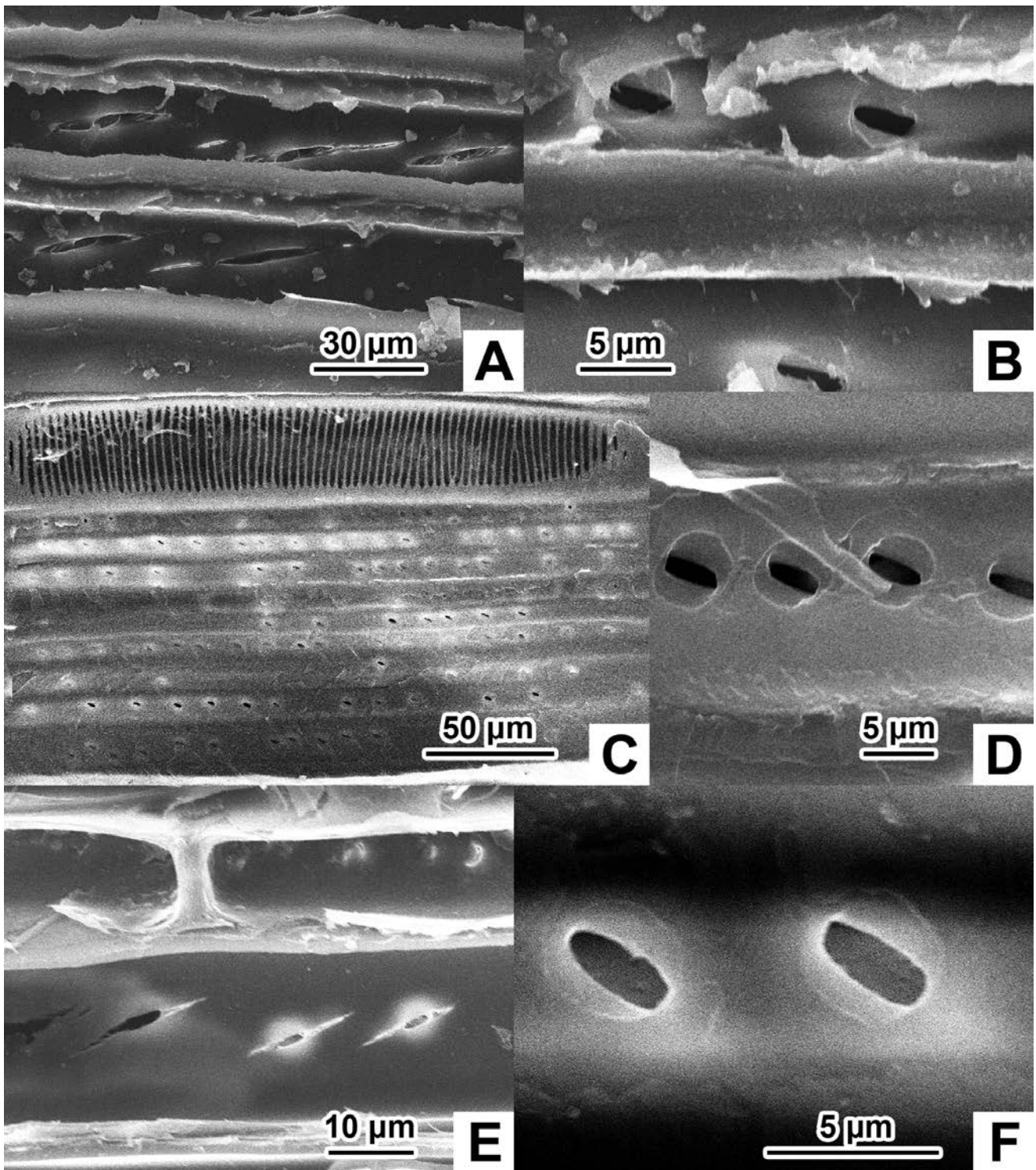
Fig. 7.   A–F. SEM images of imperforate tracheary elements from radial sections of wood. A–B, *Paracryphia alticola*, *Carlquist 15575*.—A. View of inner surfaces of imperforate tracheary elements; splits extend from pit apertures.—B. Outer surfaces of imperforate tracheary elements; bordered pits relatively sparse.—C–D. *Quintinia serrata*, *Braggins s.n.*—C. Entirety of a perforation plate, above, and outer surfaces of numerous imperforate tracheary elements.—D. Outer surface, bordered pits densely placed.—E–F. *Sphenostemon pachycladus*, *Carlquist 15604*.—E. Inner surface, splits extend from pit apertures; two axial parenchyma cells, above.—F. Outer surface of imperforate tracheary elements to show bordered pits.

rays are composed of upright cells (Fig. 6A, left center). Pits are dense on tangential walls of the multiseriate portion of multiseriate rays; the pits are often bordered (Fig. 6B).

Axial parenchyma is diffuse (Fig. 5E); a few short diffuse-in-aggregates were observed. Number of cells per strand is 4–7. Axial parenchyma cells average 206 μm in length.

Dark-staining compounds occur in ray cells and, less commonly, axial parenchyma cells (Fig. 6A, B). Styloids are present in phloem parenchyma (Fig. 6C) and, rather sparsely, in axial parenchyma of the secondary xylem.

Sphenostemon lobosporus

Faint growth rings are present. The mean number of vessels per group is 1.45 (grouping varies according to location in wood) and the mean number of vessels per mm^2 is 66. Vessel lumen diameter averages 36 μm and vessel element length 1702 μm. Perforation plates average 815 μm in length and are scalariform, some well-defined at axial ends, some grading into the scalariform lateral wall pitting. The mean number of bars per plate is 163. Pit membranes are present in perforations in the form of delicate strands (Carlquist 1992) or porose thin membranes (Carlquist 2012*b*: Fig. 4A, B) or are absent (present paper, Fig. 6D).

Imperforate tracheary elements average 1863 μm in length. The diameter of pit borders is 5 μm. The pits are not densely placed. The F/V ratio is 1.10.

Rays are multiseriate and uniseriate, the former less common. Multiseriate rays are 2–7 cells wide at the widest point; more than half of the multiseriate rays lack uniseriate wings. Radial length of ray cells in the multiseriate portion of multiseriate rays is about three times as long as broad. Uniseriate rays and uniseriate wings of multiseriate rays are composed of upright cells. Borders are present on many of the pits on tangential walls of the ray cells. Mean multiseriate ray height is 1392 μm. Uniseriate ray height averages 602 μm.

Axial parenchyma is diffuse or aggregated into small (fewer than four cells) groupings. Some axial parenchyma cells touch vessels or rays, but most do not, so no true paratracheal pattern is present. The average number of cells per strand is 4–9. Average length of cells in a strand is 228 μm.

Dark-staining deposits are present in axial parenchyma and ray cells. Styloids are common in phloem parenchyma of bark, but very rarely present in axial parenchyma of the secondary xylem.

CONCLUSIONS 1: CHARACTER STATES WITHIN PARACRYPHIACEAE

1. **Autapomorphies**.

Nearly all of the apomorphies within Paracryphiaceae appear to be flower and fruit characteristics. These can be more clearly interpreted now that we have molecular trees of Paracryphiaceae, which are sister to Adoxaceae and Caprifoliaceae (s.s.) of the Dipsacales (*sensu* Tank and Donoghue 2010).

Flowers

Paracryphia: Flowers have four decussate caducous perianth segments (one larger and covering the others (Fig. 1B). The floral condition is andromonoecious, with male flowers lower on the spicate inflorescence; male flowers lacking gynoecium remnants and with four stamens with a thick filament (much like those of *Sphenostemon*, Fig. 5A, B). Bisexual flowers with eight stamens with filiform one-trace filaments; gynoecium composed of 8–15 laterally fused carpels, each with four unitegmic ovules borne axially; the syncarp is topped by a single stigma (Fig. 1B; description details from Dickison and Baas 1977).

Quintinia: Racemes bear pedicillate flowers; ovaries are semi-inferior with 5 persistent calyx lobes. Petals are imbricate, ovate, 5, and separate. The ovary is 3–5 celled with a 3–5 lobed capitate stigma (from Allan 1982).

Sphenostemon: The inflorescence is a raceme with short pedicels. The perianth consists of 4 imbricate, free perianth segments. The stamens are 4 (Fig. 5A, B), each with a thick fleshy filament; the carpels are 2, adherent but with separate stigmas (description based on *S. pachycladus, Carlquist 15604*).

Fruits

Paracryphia: The fruit is a dry syncarp, the component follicles separating from the axis and opening ventrally, dispersing dry flat seeds (Dickison and Baas 1977).

Quintinia: The fruit is a capsule; the component carpels open apically and disperse the dry flat seeds (Allan 1982).

Sphenostemon: The fruit is a drupoid berry usually with one, but sometimes two seeds with sclerenchymatous testa (Fig. 5C, D).

The precise sequence of morphological divergences is not evident from this summary; Tank and Donoghue (2010) show *Quintinia* as sister to the other two genera, suggesting a dry fruit may have been plesiomorphic and that the drupoid berries of *Sphenostemon* are an autapomorphy. The tetramerous condition of *Sphenostemon* flowers is vaguely evident in *Paracryphia* flowers (perianth, but not androecium or gynoecium) but not in *Quintinia*, which seems pentamerous except for the gynoecium.

The stamens of male flowers of *Paracryphia* are quite distinct from the filiform stamens of bisexual flowers in the genus. The fleshy connective of male *Paracryphia* flowers (which have stamens like those of *Sphenostemon*) would have been considered "primitive" in past decades, but in fact, the co-occurrence of fleshy stamens and filiform stamens in male and bisexual flowers of *Paracryphia* should have been noted long ago as indicating functional significance rather than phylogenetic significance. Likewise, ontogenetic studies have shown that "conduplicate" carpels mostly originate as a cup-like meristem outgrowth ("ascidiate" carpels), different from foliar ontogeny (Endress and Igersheim 1997; Endress 2005). The thick stamens of male *Paracryphia* flowers, like those of *Sphenostemon* flowers, may function in opening of the flowers by swelling rapidly, as in *Belliolum* (Carlquist 1983) or *Zygogynum* of Winteraceae, or they may be fodder for foraging beetles, along with pollen. Paracryphiaceae have exclusively cyclic flowers, and that should probably be considered a plesiomorphy in most clades of angiosperms, including the magnoliids (+ monocots) or Nymphaeales (*Cabomba*). The early angiosperms entered the beetle-pollination niche early (Gottsberger 1977; Hu et al. 2007), and crowded helices (stamens of Magnoliaceae; the

family has trimerous perianths) are now best interpreted in terms of function, usually as bribes for foraging beetles (Carlquist 1969), rather than relicts of some ancient sporophyll pattern. *Amborella* suggests trimery rather than helical organization, and this is true of Piperales, Chloranthales, and most monocots as well.

2. **Synapomorphies**

Synapomorphies in Paracryphiaceae include the styloids (common in secondary phloem, rare in secondary xylem) of *Sphenostemon* (present paper) and *Paracryphia* (Dickison and Baas 1977). The fiber-tracheids in these two genera may also represent a synapomorphy as compared to the tracheids of *Quintinia.*

3. **Plesiomorphies**

Bailey became interested in what were called "woody Ranales" (of Engler), and studied wood anatomy of many of them. Because Bailey was not a field botanist, his foraging for materials took place mostly in the Harvard herbaria. Certainly he was intrigued by the vesselless nature of *Amborella*, a fact discovered by van Tieghem (1900). Bailey focused on the "ancient" lands of southern Indomalaysia, where many of these genera occur. These regions include New Caledonia, New Zealand, Queensland, and New Guinea especially, but also include such lands as Fiji and high-montane Madagascar. Bailey did not have a clear idea of angiosperm phylogeny, and he never presented any phylogenetic treatment of these plants, but he must have suspected that early angiosperms, regardless of where they may have originated, persisted in these lands, cut off as they were from the radiations of many later-arising angiosperm groups (Bailey 1948). Today we would assign the groups that interested Bailey mostly to magnoliids, chloranthoids, and piperoids. These three groups have in common ethereal oil cells (lacking in monocots except for *Acorus*). However, none of the campanulids, to which *Paracryphia* belongs, have ethereal oil cells, nor do Nymphaeales, so those clades must stem from ancestors that lacked ethereal oil cells (which are, interestingly, absent in *Amborella* as well, a fact that should have suggested to earlier workers that *Amborella* cannot be grouped with Monimiaceae or other magnoliid families).

Wood features of Paracryphiaceae can almost without exception be considered plesiomorphic for a vessel-bearing woody angiosperm. This is true of wood of some other families, also, such as Chloranthaceae, Hydrangeaceae (some), and Illiciaceae—all of which represent independent groups, phylogenetically. Today we would say that wood plesiomorphy of this sort may show the homoplasious origin of many apomorphic wood features (e.g., the simple perforation plate must have originated numerously times, as mentioned for *Kadsura* and *Schisandra* (Illiciaceae s. l.) above. *Amborella* may exceed any other genus of angiosperms in its assemblage of plesiomorphic features, because its wood is primitively vesselless, and its tracheid pits have very thin, porose, fragile pit membranes (Carlquist and Schneider 2001); wider tracheids have scalariform end-wall pitting. What these plesiomorphies are, what their adaptive value may be, and hypotheses concerning how they function as a syndrome and separately are considered in the next section.

CONCLUSIONS 2: PLESIOMORPHY IN ANGIOSPERM WOODS

The methods of Bailey and his students Frost and Kribs in establishing character states in angiosperm woods still influence us, although they have been superseded in some important respects. The Baileyan "trends" were based on comparative anatomy alone; the phylogenetic ideas of that era were vague and intuitive. The findings of molecular phylogeny for angiosperms as a whole and within particular natural groups (clades) cannot be overemphasized: they provide reference points for understanding how wood evolves. Concepts of wood physiology and how they affect our ideas of wood phylogeny had not been discovered in Baileyan times, and likewise, because wood anatomists rarely did field work in that era, the importance of ecological data in understanding "primitive" and "specialized" character states was not appreciated (Olson 2012). Ultrastructural data were not available. A "new synthesis" based on combining all of this new information is needed (Carlquist 2012*b*). From such a synthesis, the earlier character states can now be analyzed: in group after group, early branches from clades provide the basis for understanding plesiomorphic character states. Interpretation of character states must be cautious, because molecular systematics is not based on (for example) wood characters. All relevant information should be used, and congruence in evolution of character states is one criterion that can be followed, despite its fallibility. Paracryphiaceae, although a small group, shows us how such synthesis of methodologies can reveal ancestral character states. These methodologies can be applied to other systematic groups as defined by molecular phylogeny.

1. Bailey and Tupper (1918) compiled lengths of vessel elements and imperforate tracheary elements for a wide range of woods. The implication was that longer fusiform cambial initials were plesiomorphic, and thereby one could use those lengths as quantitative indicators of degrees of primitiveness. This idea was expanded by finding strong correlations between long fusiform cambial initials and other features which were thereby thought to be "primitive" (plesiomorphic): long vessel elements with many-barred scalariform perforation plates, scalariform lateral wall pitting (Frost 1930), Heterogeneous Type I rays (Kribs 1935), and diffuse axial parenchyma (Kribs 1937). Several problems emerge from these schemes. (a) Fusiform cambial initials are not stable within a species; they tend to elongate in woody species (Bailey and Tupper 1918), whereas they shorten in less woody species (Carlquist 1962). (b) The length of fusiform cambial initials as an indicator of primitiveness did not involve comparison to a secure phylogenetic system; such a system was not in place until the last decade of the 20th century, when global phylogenetic systems based on molecular data came into play. (c) Data from plant physiology were not extensive during the Bailey-Frost-Kribs era, and none of the wood anatomists of that era was able to take a physiological view of the character states in wood cells and tissues. Ecological and physiological wood anatomy had not come into existence. With the introduction of this synthesis (Carlquist 1966), tentative explanations of why "specialized" conditions (apomorphies) evolved could be offered. There was, however, much less attention paid to why plesiomorphic xylary conditions were in existence or why they might even be advantageous in some situations.

2. Character width/plasticity. We had been accustomed, even before cladistics, to consider a character state present (1) or

absent (0). The convenience of this method of evolutionary accounting did not take into account characters that are variably expressed within a plant and can take place largely because of shifts in production of growth hormones (Aloni and Zimmermann 1983). The ability to vary degrees of bordering on perforation plates was cited as a labile character in Caryophyllales (Carlquist 2010), but that is a minor character of uncertain physiological significance. In Paracryphiaceae, characters with built-in flexibility include degrees of pit membrane retention in perforations, and degrees of growth ring formation. Control of vessel diameter and density as a result of hormone gradients has been demonstrated experimentally by Aloni and Zimmermann (1983). Other characters in which wood features change ontogenetically may be included here, such as length of fusiform cambial initials. We do not know the genetic basis for an important ontogenetic feature, timing of change from juvenile to adult to wood features. The shutdown of cambial activities in vascular bundles of monocots may be under more genetic control, for instance. Other shifts found within a given wood include vessel diameter and vessel density (often in relation to growth rings), grouping of parenchyma, localization of axial parenchyma, etc. (Carlquist 1988). The nature of characters that can shift because of environmental or other factors versus those that are genetically fixed within narrow ranges may be more than merely just phenotypic modification (as opposed to genetic programming), because phenotypic diversity has some basis (e.g., hormone control).

3. Dimorphisms of various sorts are basic to the origin of particular wood characters—especially apomorphic ones. The origin of vessels in early angiosperms involved a dimorphism from an ancestral cell we would call a tracheid into vessel elements and accompanying tracheids. We tend to recognize the various features of the plesiomorphic vessel element (see below), but we tend to forget that the accompanying tracheids in this dimorphism show changes in some features. For example, the circular borders of tracheid pits in *Amborella* are about 11–12 μm in diameter, and tracheid end walls have scalariform pits in earlywood, whereas in woody vessel-bearing angiosperms, the end walls of tracheids are not differentiated into areas of scalariform pitting, and borders of pits are smaller, usually in the 4–7 μm range.

One important question that has not been addressed is why the scalariform pattern (rather than variously distributed alternate pits) is present on end walls of tracheids in vesselless angiosperms such as *Amborella, Trochodendron, Tetracentron*, and various Winteraceae, and, more importantly, why does the end-wall of the plesiomorphic vessel in angiosperms bear scalariform perforations rather than circular perforations as in *Ephedra* and *Gnetum*? One can say that lateral expansion of tracheary elements, as in earlywood tracheids of vesselless angiosperms and plesiomorphic vessel elements of angiosperms, tends to favor scalariform perforation outlines rather than a series of circular perforations because vessels are laterally-widened versions of tracheids (and wider tracheids in vesselless angiosperms have scalariform end wall pitting), but more may be involved, as gnetalean vessels show us. The vessels of *Welwitschia* are so narrow that their simple perforation plates are not like perforation plates of *Ephedra* and *Gnetum* (Carlquist and Gowans 1995). Zimmermann (1983) thought that scalariform perforation plates "sieved out" air bubbles that formed after frozen water in vessels thaws; this may be true, but it does

not explain the scalariform perforation plates of many tropical genera that grow in frost-free places (nor does it explain the simple perforation plates of Arctic shrubs such as *Salix*). Scalariform perforation plates increase resistance to flow (Jeje and Zimmermann 1979), so phylogenetic removal of bars in numerous clades independently suggests selection for less resistance. If the numerous bars on a perforation plate have some physiological basis that accounts for their retention in numerous clades, confining embolisms seems the most probable function.

Numerous bars in a scalariform perforation plate could sieve out air bubbles even in mesic situations: the photograph of wilting foliage on new growth of *Illicium* under field conditions (Carlquist 1975) illustrates that embolisms can form in vessels with scalariform perforation plates on a hot day, even though the soil remains moist. The numerous bars on perforation plates of *Illicium* may prevent embolisms from spreading the length of a vessel. Bars on a perforation plate may resist tension in a vessel: this would apply in perforation plates with few, wide bars, such as *Liquidambar, Magnolia*, and *Rhizophora* (but the reduced number of bars in those genera removes them from the most plesiomorphic conditions). The retention of borders on bars may confer greater strength than absence of borders. The multiperforate perforation plates of *Ephedra* vessels very likely have better resistance to tension than do angiosperm perforation plates with numerous thin bars.

4. The plesiomorphic vessel element has been characterized as having greater length, a long perforation plate with numerous bordered bars, and scalariform lateral wall pitting (Frost 1930). To this list, I would add greater length of vessels (Frost considered only vessel element length), gradual transition between perforations and lateral wall pits at top and bottom ends of perforation plates, and retention of pit membrane remnants in perforations. Paracryphiaceae have all of these features. Longer vessel elements have longer end walls, which would lead one to conclude that longer perforation plates with more numerous bars is the plesiomorphic condition. In Paracryphiaceae, *Quintinia serrata* has shorter vessel elements with fewer bars. *Paracryphia* may be near the upper limit reported for length of perforation plates and number of bars per plates (I know of no data comparing pertinent genera in this regard). More numerous bars should not be used ipso facto as a measure of "primitiveness," however. Selection for flow volume per unit time may be involved: if flow volume is lower, more numerous bars may have positive selective value by being associated with a larger conductive area of a perforation plate.

5. Pit membrane remnants in perforations certainly do not confer strength to a perforation, and they undoubtedly slow the conductive stream, and thus are not of positive value where flow considerations are involved. The prominent pit membrane remnants in perforations of *Hydrangea macrophylla* (Thunb.) Ser. probably result in water uptake falling short of transpiration, inducing daytime wilt in shrubs planted out in locations where humidity is low, as in southern California (original observations). In Japan, where the species is native, this probably happens more rarely because of more moderate ranges of temperature and humidity. Pit membrane remnants are thus of negative selective value in achieving flow. The value of pit membrane remnants may well be one of confining embolisms. One should take into account that tracheids of some ferns (Carlquist and Schneider 2007) and vessel elements of some monocots (Carlquist 2012*a*) have pit membrane remnants in end walls, or sometimes porose

pit membranes on end wall pits. The selective value for retention of pit membranes in end wall pits/perforations appears to be that of confining hydraulic failure (embolisms) to fewer tracheary elements. In this respect, vessel elements with pit membrane remnants are retaining as much of the safety of tracheids as possible in a given species without lowering the value of end wall conductivity of vessel elements excessively.

6. Pit membrane remnants in perforations of plesiomorphic vessels are now well enough known so that further conclusions and hypotheses about their conformation can be offered. All three genera of Paracryphiaceae, as well as genera from unrelated orders and families, are known to have strands that are predominantly axially oriented—except in many cases at lateral ends of the perforations, where webs of randomly-oriented microfibrils are common (see Fig. 4). The axially-orientated threads of microfibrils may in part exist prior to lysis and dissolution of the pit membrane (e.g., Fig. 2E, F). However, the survival of axially-oriented (parallel to the long axis of the vessel element, or to the axis of the plant) threads seems to have a physical explanation. If the threads were randomly oriented, more pressure of the conductive stream would be exerted on them, and they would tend to be lost. Axial orientation of the threads subjects them to minimal force. In the lateral ends of the perforations, the area of pit membrane remnants is small, and thus exposed to minimal force (progressing to zero at the lateral ends of the perforation). Thus, these perforation ends (Fig. 4D–F) tend to retain a web of short threads and porose planar pit membrane areas. These results are in accord with those recorded by Meylan and Butterfield (1978) for several New Zealand genera (*Atherosperma, Quintinia, Weinmannia*) as well as genera of Aextoxicaceae (Carlquist 2003), Hydrangeaceae (Carlquist and Schneider 2004) and other families (Carlquist 1992). The wide systematic occurrence of these pit membrane remnants, most of which are in families that have scalariform perforation plates and are rich in plesiomorphic wood character states, suggests more than a functionless relictual phenomenon. An increase in conductive safety (confining potential embolisms within one or a few vessel elements rather than allowing embolism spread the length of a vessel) is one possible hypothetical function. Slower conductive rates may be less likely to sweep away pit membrane remnants. Long vessels occur in more "primitive" families, shorter vessels in apomorphy-rich families, so confining embolisms to portions of a vessel may, in fact, be more important in woods of those families with long vessels. We do not have good comparative data on the degree to which pit membrane remnants are retained under different conditions of specimen preservation and handling. However, the axially-oriented pit membrane strands in Paracryphiaceae are significant in contrast with the radially-oriented strands in the margos of coniferous and gnetalean pits, an important distinction explained elsewhere (Carlquist 2017).

7. Although vessel diameter and density vary within a plant in physiologically significant ways, angiosperms as a whole frequently have relatively narrow vessels with scalariform perforation plates, both features providing greater resistance to conductive flow, but probably also conductive safety. Wider vessels are more vulnerable to cavitation, and are incompatible with scalariform perforation plates. The breakthrough to simple perforation plates can be measured by means of speciation, which is a rough indicator of ecological diversity to which a clade is adapted (Carlquist 2012*b*: Fig. 14).

8. Pit membrane thickness and porosity are undoubtedly significant characters with respect to the hydraulic nature of a plant and the plesiomorphic or apomorphic state of its assemblage of wood characters (Choat et al. 2008). We do not as yet have comparative data over a wide spectrum of angiosperms.

9. Imperforate tracheary elements have been considered relative to the shift from plesiomorphy to apomorphy in woods. Metcalfe and Chalk (1950: xlv) on the basis of Baileyan character-association methods (which in turn depend on widespread homoplasy of character shifts) found bordered pits on imperforate tracheary elements to precede simple pits phylogenetically. This is plausible across large portions of angiosperms, but not without exception. Species with vasicentric tracheids combine both tracheids (with larger bordered pits) and libriform fibers (which have simple pits), or in some cases, fiber-tracheids and libriform fibers. The latter results from dimorphism in cell type evolution. A distinction between tracheids (conductive) versus fiber-tracheids and libriform fibers (non-conductive) has been made by many workers because of the conductive nature of tracheids (Sano et al. 2011). Although the demonstration of *Amborella* as sister to the remainder of angiosperms shows that an all-tracheid condition probably preceded vessel presence, we do not know for sure whether the earliest vessel-bearing angiosperms had tracheids or fiber-tracheids in addition to vessels.

The example of Paracryphiaceae is particularly relevant, because in this small clade of three genera, *Paracryphia* and *Sphenostemon* have fiber-tracheids, whereas *Quintinia* has what I believe might be called tracheids. There is obviously relatively little difference: slightly larger bordered pits, more densely placed, on imperforate tracheary elements of *Quintinia*. However, an ancillary character can be used to establish whether a species has tracheids or fiber-tracheids. Species with tracheids as the imperforate tracheary element type group vessels to a lower degree (1.20 vessels per group or fewer, usually) than do species with fiber-tracheids or libriform fibers, which usually have about 1.30 vessels per group or more (Carlquist 1984). Tracheids apparently are a method of achieving conductive safety that outdoes vessel grouping in effectiveness. *Quintinia* has less vessel grouping (and more tracheid characters) as compared to *Paracryphia* and *Sphenostemon*, although the difference is not great. Intermediate conditions also appear in *Ilex* (Aquifoliaceae), an early-departing clade of Campanulidae. This capability to evolve more numerous and larger pits versus fewer and smaller (and borderless) pits is the important aspect. Although tracheids are more common in plesiomorphic woods than fiber-tracheids or libriform fibers, tracheids can be developed at various sites within a phylogenetic tree. Woody angiosperms have the genetic information to form bordered pits (present on all lateral vessel walls) and simple pits (present on phloem fibers, sclereids, and other wood cells), and thus evolution of particular imperforate tracheary element types is merely a matter of activating that capability more widely or less widely within a given wood. Reversibility (0 to 1, followed by 1 to 0) in the Hennigian sense is not involved here. For example, Illiciaceae have what one could call "archeotracheids" like those found in early angiosperms, whereas Krameriaceae have "neotracheids" probably evolved from fiber-tracheids in the zygophyllalean ancestors of Krameriaceae (Carlquist 2005).

10. The F/V ratio (imperforate tracheary element length divided by vessel element length) is theoretically a measure of degree of differentiation between the cell types. One can say

that an F/V ratio of less than about 2.0 is plesiomorphic and that an F/V ratio of more than 3.0 is apomorphic. We do not, however, have data on a large number of angiosperms in this regard. The advantage of greater tensile strength conferred by longer fibriform cells, or, concurrently, the advantage of shorter vessel elements (possibly isolating air bubbles in smaller portions of the conductive network) may be the underlying physiological factors leading to these expressions, and numerical values of the F/V ratio should not be used as markers without reference to function.

11. The ray types of Kribs (1935), once mentioned by numerous workers in wood anatomy, are probably less popular now because applying the definitions given by Kribs is sometimes difficult or inexact. Also, the proportion of procumbent cells to upright cells increases during growth of a particular stem (Barghoorn 1941). These definitions had to be modified to include instances of protracted juvenilism in woods (Carlquist 1988). The terminology in more common use today emphasizes whether procumbent cells are present in addition to upright cells (heterocellular) or only procumbent cells are present (homocellular). The occurrence of uniseriate rays exclusively, composed only of upright cells, is a different matter because such rays are juvenilistic (paedomorphic: Carlquist 1962, 1988).

The potential value of the Kribs ray types lies in an understanding of the physiology of a particular wood. Procumbent ray cells have a radial conductive function, as shown by the occurrence of greater pit density and borders on pits, on tangential walls of procumbent ray cells in many woods (Carlquist 2007). Upright cells are not so clearly identified with respect to role. They certainly have some vertical conductive capability, and bordered pits on transverse walls can be cited in this regard. Upright cells may also serve as intermediary pathways for photosynthate conduction between procumbent cells and axial parenchyma, or even as vicarious axial parenchyma (Carlquist 2012b). The finding by Barghoorn (1941) that procumbent cells become more common as a tree increases in diameter can be correlated with greater conduction of photosynthates radially in a larger tree trunk, whereas young stems have relatively little radial conduction of photosynthates in comparison with axial sugar movement. The axiom, rarely mentioned in plant anatomy, that elongate cells conduct in the direction in which they are elongate, needs mention more often. More numerous procumbent cells may be considered a criterion for accelerated adult patterns in wood, whereas abundance of upright cells indicates prolonged juvenilism (Carlquist 2012b). Thus, ray typology becomes a visual way of estimating degree of conductive activity.

If this is valid, why should greater abundance of uniseriate rays composed of upright cells, and abundance of uniseriate cells on wings of multiseriate rays be plesiomorphic? This is not clear, but one can cite less woodiness as more often characteristic of plants with other plesiomorphic features (one must remember that in recent years, wood samples are usually not obtained from cutting down large trees). Although greater degrees of arborescence were once regarded as a feature of "ancestral dicotyledons," trees are probably best regarded as a specialized growth form that has originated within various clades. Although Taylor and Hickey (1996), among others, emphasize early angiosperms as "paleoherbs," the sparse evidence we have from the fossil record suggests that early angiosperms are less woody than their derivatives, but not without secondary xylem (Philippe et al. 2008).

12. Kribs (1937) proposed types of axial parenchyma occurrence and ranked them in a putative tree of sorts. Although the defined types do exist, their phylogenetic relationships are not as clear as Kribs suggests, and more than one type can coexist in a wood. The hypothesized plesiomorphic configuraton is diffuse, or some slight modification of this. There is a discernible tendency, which can be confirmed by comparisons to molecular-based phylogenetic trees, to greater degrees of aggregation: sheathing of vessels, bands that include vessels, and at the beginning and end of a growth ring. This gives us some hint about the possible function of axial parenchyma. Release of sugar into vessels from axially elongate living cells, a means of enhancing sap volume osmotically and developing flow, was reported decades ago (Sauter et al. 1973). Why should diffusely scattered axial parenchyma strands be retained in plesiomorphic woods when aggregations of parenchyma would seemingly offer better conduits for this function?

There are statistically demonstrable associations between diffuse axial parenchyma and the diffuse (non-grouped) distribution of vessels. Also, a significant proportion of woods with numerous plesiomorphic features have tracheids, and for the water columns in these to function, they must be in contact with axial parenchyma. In this connection, one should note that vessel elements and tracheids in woods such as those of Paracryphiaceae are very long, so that an axial parenchyma strand is more likely to contact conductive cells than would be the case in a wood with short conductive cells. The precise mechanism for reversing embolisms in angiosperm wood may not be at hand yet, but ideas for which some data can be supplied are available (Zwieniecki and Holbrook 2000; Holbrook et al. 2002). In angiosperms with numerous plesiomorphic wood features, we would expect retention of intact water columns to prevail over repair of embolisms in water columns (Vogt 2001) so a hypothesis that involves axial parenchyma in preventing breakage of water columns is to be expected. Our understanding of axial parenchyma function would be aided if we could map the three-dimensional distribution of axial parenchyma with respect to rays and to tracheary elements, especially conductive tracheary elements. We need confirmation of the idea that axial parenchyma releases sugars into vessels (and tracheids) to maintain water columns. Our knowledge of wood anatomy is largely descriptive, and our descriptions of axial parenchyma occurrence are based on transverse sections rather than three-dimensional reconstructions. Ironically, parenchyma distribution types are best detected in transverse sections, whereas secure identification of axial parenchyma strands as distinct from other cell types often relies on radial sections, so one must shuttle between the two types of sections in order to understand fully the course of axial parenchyma in stems and roots.

13. Plesiomorphy-rich wood features moderate axial translocation rates because of narrower vessels and the resistance of scalariform perforation plates. Longer scalariform perforation plates compensate for their tendency to provide more resistance to the conductive flow. Thinner fragile pit membranes (lateral vessel walls, tracheids) that conduct better but would break if tension fluxes within vessels were higher, are adaptive in woods which do not experience strong fluctuations in negative pressures. Scalariform lateral wall pitting of vessels improves flow but has less strength than the alternate pitting in apomorphic vessels, in accord with the smaller negative pressures in vessels in plesiomorphy-rich woods. Rays are

axially longer and axial parenchyma strands are longer in accordance with the longer vessel elements; greater length assures more contact between living and non-living cells within the wood. Longer vessel elements and longer vessels compensate for greater resistance of the scalariform perforation plates (as opposed to simple perforation plates). Scalariform perforation plates and presence of tracheids as imperforate tracheary elements potentially confine embolisms to smaller portions of the conductive system, disabling less of the conductive system during extreme hydraulic stress. Embolisms probably occur relatively infrequently in plesiomorphy-rich woods compared with apomorphy-rich woods, which may refill embolisms rather than prevent them: wider (earlywood) vessels may embolize in woods with more apomorphic features (presence of tyloses in wider vessels, such as those of *Quercus*, demonstrates this visually). In plesiomorphy-rich woods, reliance on subsidiary conductive systems (vasicentric tracheids, larger groupings of very narrow vessels, vascular tracheids) to maintain flow is low compared to those features in apomorphy-rich woods.

Upright cells predominate over procumbent cells in plesiomorphy-rich woods. In trees with "primitive" woods, fluxes in photosynthate conduction in rays, promoted by procumbent cells, are less extreme than in woods with greater input and retrieval of stored carbohydrates. Plesiomorphic woods show less grouping of axial parenchyma into sheaths around vessels or in tangential bands, assuring contact between the living and non-living cells, but at the expense of lowering photosynthate storage capacity and rapidity of retrieval. Axial flow of photosynthates is more prominent in plesiomorphy-rich woods than in apomorphy-rich woods.

Disclaimers: the above generalizations are all subject to exceptions, because conductive strategies in angiosperm woods are varied and probably form a spectrum rather than a commonality in certain features. Evolutionary "trends" in one feature (e.g., perforation plate morphology) may not correlate with those in another feature: characters may change independently (which is one reason why angiosperms have adapted to more habitats). Experimental evidence on the characteristics of conduction in particular species are relatively few, and are much needed. Evidence from comparative anatomy is compelling, but the link between observed structure and how woods function in the native habitats of species is often weak because application of methodology depends on the skills of workers and the design breadth of a study. Physiological conclusions based on a few species should be subjected to confirmations based on species with different woods from different habitats than those in the original study.

14. Woods that are rich in plesiomorphic features are definitely adaptive, as is proved by their survival to the present day. The habitats to which such woods are adapted, however, may be small in area. During evolution over long periods of time, species with these woods remain adapted to particular conditions, and some presumably become even better adapted. The conditions to which most plesiomorphy-rich woods are adapted are more mesic, have less fluctuation in soil moisture availability, and feature less extreme fluctuations in temperature and humidity. Early angiosperms may have been confined to areas with these conditions, but they could be termed "well adapted" to these areas rather than evolutionarily "unstable." Early angiosperms had the great advantage of the shortened life cycle, less wasteful in photosynthate expenditure, compared to gym-

nosperms (note the fact that Gnetales have a diverse assemblage of conductive features but have not survived in broad areas). The conductive system of early angiosperms was not adapted to occupancy of a wide range of conditions because, among other reasons, conductive systems are more likely to be inadequate when there is extreme fluctuation of temperature, humidity, and soil moisture availability. When one visits the cloud forests of such places as New Caledonia, New Guinea, and Malaya (all "geologically old" areas), and when one knows the wood anatomy (which presumably reflects conductive characteristics well) of component species, one is struck by the relative commonness of species with plesiomorphic (or "primitive") wood features.

15. Wood features are supplemented by or can even be secondary to foliar features in determining hydraulic characteristics. Probably coriaceous leaves which buffer transpirational characteristics are relatively common in plesiomorphy-rich woods: *Paracryphia* and *Sphenostemon* have leaves typical of canopy leaves in mesic situations. Although such species may grow in perpetually moist soil in a cloud forest mountain, the sunny periods in such a habitat could trigger transpiration from the canopy that thinner leaves could not manage without wilting. Not surprisingly, few plesiomorphy-rich woods have such thin leaves, except for understory plants like *Cornus*. Bruniaceae is a family that grows mostly in scrub of cool but sunny mountains of Cape Province, South Africa (usually on south-facing slopes, which are less sunny in the Southern Hemisphere). Bruniaceae have woods with scalariform perforation plates the perforation plates of which contain porose pit membranes. The leaves of Bruniaceae are linear to scale-like, minimizing leaf heating in these localities and thereby coordinating with the likely moderate conductivity of the plesiomorphy-rich xylem. Each family will prove to have its own formulation, and those details, rather than generalizations, should be sought. There are many less obvious examples. Heteroblasty (long shoots plus short shoots) as well as linear leaves are characteristic of the Californian chaparral shrub *Adenostoma*, which has simple perforation plates in vessels in a background of tracheids, which probably can contain viable water columns when a proportion of vessels (which are, however, narrow and very likely less vulnerable than wide vessels) embolize. We frequently forget the many plants that utilize drought deciduousness as a way of minimizing transpirational loss. Annuals are the ultimate example of drought deciduousness. Drought deciduous plants are essentially incompatible with plesiomorphic wood characters, which feature flow stasis rather than wide conductive fluctuations. Conductive fluctuations are associated with occupation of ecologically unstable habitats with seasonal shift in water availability, especially near the soil surface. Deciduousness of woody plants can be seen in dry tropical forests, such as the winter-dry thorn forests of northern Mexico, and these mostly are plants with apomorphic wood characters. There are some woody species that exemplify leaf deciduousness with cold, such as *Cercidiphyllum, Euptelea*, and various Betulaceae, which have scalariform perforation plates. Winter-deciduous species of this sort are essentially mesomorphic, but with the capability for conductive shutdown during colder months; their woods are not unlike those of trees in forests wet throughout the year. Drought deciduousness in thorn-forest trees is associated with seasonal soil drying, so they are not mesomorphic in wood features: an appreciable number have wood that can store water. Simple equations like these may not seem as revelatory as experimental data, and they are not: but in

studying wood, we need a more comprehensive view that includes the habit and seasonal changes in water management by wood designs as well as by foliage and other features. If we are to understand apomorphies in wood adapted to high degrees of seasonality, we need to apply the same understanding to the wood of equatorial cloud forest trees also.

16. Bailey and his students offered correlations (never accompanied by statistical treatment, however) among wood features. The principal marker to which characters were compared was length of fusiform cambial initials, which can be approximated, for any given species, by vessel element length (vessel elements elongate little during the process of derivation from initials and maturation: Bailey and Tupper 1918). Bailey's "major trends" seemed viable precisely because there is so much homoplasy and parallel evolution in wood of angiosperms (but see Olson [2012] for a detailed critique). There was no reliable phylogeny of angiosperms available prior to the mid-1990s, when global molecular phylogenies emerged. Molecular phylogenies offer a high degree of probability, and therefore offer the best hope we have (short of tracing wood character genes in a large number of species, which is not feasible at present) as a basis for analyzing wood evolution. Molecular phylogenies remain the primary source of reliable data on evolution in angiosperms. Therefore, the proposal is made that we should use them as a basis for analysis of wood evolution within any given group. We all realize that evolution of wood characters and molecular phylogenies are not identical for any particular group, and objections may be raised that any method of associating wood characters with the cladograms from a molecular phylogeny is subjective and not capable of attaining a high degree of statistical probability. That may be true, but such associations are much more compelling than cladograms based on morphological characters alone, in which the evolutionary status of character status is scored by human perceptions or preconceptions. Even combinations of morphological and molecular data frequently suggest (when compared with subsequent molecular trees) that some characters are over-stressed. A superimposition on the Tank and Donoghue (2010) clade of Campanulidae (Carlquist 2012b: Fig. 14) of the systematic distribution of scalariform and simple perforation plates, which shows degrees of speciation following origin of simple plates in various clades, may represent a way of comparing wood evolution to phylogeny. Other methods are conceivable, but for the present, some degree of indirect evidence and interpretation seem inevitable. Integration of data from other fields, such as ecology and wood physiology, is highly desirable. The present essay, while advocating such a broader synthesis, does not claim to present the only possible methodology.

17. Extinction of scalariform perforation plates in numerous clades of angiosperms independently speaks for the probability that better devices for preventing embolisms and insuring safety of water columns were developed, such as reliance on tracheids as a background cell type in wood. Grouping of vessels also has proved a common strategy in species that have fiber-tracheids or libriform fibers as imperforate tracheary element types. Narrowness of vessels is another strategy for lowering of embolisms and providing redundancy and thus greater safety in woods. Shortening of vessel elements tends of localize embolisms in smaller portions of the conductive system. Thus, there is no selective value for restoration of scalariform perforation plates in a clade once they have been lost. Various types of aberrant perforation plates can be found in clades in which scalariform perforation plates have been lost, such as Cichorieae of Asteraceae (Carlquist 1960). These aberrant plates are found in genera that have apparently experienced secondary woodiness, such as *Dendroseris* on the Juan Fernandez Islands. The fact that these plates are aberrant rather than clearly scalariform suggests that the scalariform perforation plate is genetically a somewhat complex feature, and thus has probably not been re-evolved.

18. Genera that have simple perforation plates in secondary xylem sometimes have scalariform perforation plates in primary xylem. *Eucommia* (Metcalfe and Chalk 1950), *Kadsura* (Carlquist 1999) and *Crossosoma* are notable in this regard. Bailey (1944) interpreted this as evidence that vessels originated in secondary xylem and phylogenetically extended into primary xylem. However, this does not provide a functional reason why scalariform perforation plates would be formed in primary xylem of these species. Likewise, it does not account for woods in which scalariform perforation plates with more numerous bars occur in metaxylem, followed by progressively fewer bars in secondary xylem, as in *Oreopanax* (Carlquist 2018) and other Araliaceae. Increasing volume of water transpired as shoots leaf out would provide an explanation for the shift to simple perforation plates in secondary xylem. Occurrence of scalariform perforation plates in primary xylem would correspond with confining air bubbles to individual vessel elements should wilting occur. The primary xylem in these instances, although providing more flow resistance with scalariform rather than simple perforation plates, offers more safety; narrower conduits in the primary xylem may also have this effect. In some woods that begin with scalariform plates and shift to simple plates, protracted juvenilism may explain occurrence of occasional scalariform plates in secondary xylem (campanuloid Campanulaceae, unpublished observations). "Mixed" simple and scalariform perforation plates, as in wood of Araliaceae, may provide degrees of safety combined with accommodation of lower flow resistance. In a number of angiosperm woods, such as *Styrax*, we can find scalariform perforation plates in latewood combined with simple perforation plates in earlywood, a pattern that seems to reinforce that interpretation.

REFERENCES

ALLAN, H. H. 1982. *Flora of New Zealand*, vol. **I**. P. D. Hasselberg, Government Printer, Wellington, New Zealand. 1085 p.

ALONI, R. AND M. H. ZIMMERMANN. 1983. The control of vessel size and density along the plant axis. A new hypothesis. *Differentiation* **24**: 203–208.

BAAS, P. 1975. Vegetative anatomy and the affinities of Aquifoliaceae, *Sphenostemon*, *Phelline*, and *Oncotheca*. *Blumea* **22**: 311–407.

BAILEY, I. W. 1936. The problem of differentiation and classification of tracheids, fiber-tracheids, and libriform fibers. *Trop. Woods* **45**: 18–23.

———. 1944. The development of vessels in angiosperms in morphological research. *Amer. J. Bot.* **31**: 421–428.

————. 1948. Origin of the angiosperms: need for a broadened outlook. *J. Arnold Arbor.* **30**: 64–70.

———— AND W. W. TUPPER. 1918. Size variation in tracheary cells. I. A comparison between the secondary xylems of vascular cryptogams, gymnosperms, and angiosperms. *Proc. Amer. Acad. Arts* **54**: 149–204.

BAKER, E. G. 1921. Systematic account of the plants collected in New Caledonia and the Isle of Pines by Prof. R. H. Compton, M.A., in 1914. Part I. Dicotyledons. Polypetalae. *J. Linn. Soc., Bot.* **45**: 264–325.

BARGHOORN, E. S. 1941. The ontogenetic development and phylogenetic specialization of rays in the xylem of dicotyledons. II. Modification of the multiseriate and uniseriate rays. *Amer. J. Bot.* **28**: 273–282.

CARLQUIST, S. 1960. Wood anatomy of Cichorieae (Compositae). *Trop. Woods* **112**: 65–91.

————. 1962. A theory of paedomorphosis in dicotyledonous woods. *Phytomorphology* **12**: 30–45.

————. 1966. Wood anatomy of Compositae: a summary, with comments on factors controlling wood evolution. *Aliso* **6**(2): 1–23.

————. 1969. Toward acceptable evolutionary interpretations of floral anatomy. *Phytomorphology* **19**: 332–362.

————. 1975. *Ecological strategies of xylem evolution*. University of California Press, Berkeley. 259 p.

————. 1982. Wood anatomy of *Illicium* (Illiciaceae): phylogenetic, ecological, and functional interpretations. *Amer. J. Bot.* **69**: 1587–1598.

————. 1983. Wood anatomy of *Belliolum* (Winteraceae); a note on floral opening. *J. Arnold Arbor.* **64**: 161–169.

————. 1984. Vessel grouping in dicotyledon woods: significance and relationship to imperforate tracheary elements. *Aliso* **10**: 505–525.

————. 1985. Vasicentric tracheids as a drought survival mechanism in the woody flora of southern California and similar regions; review of vasicentric tracheids. *Aliso* **11**: 37–68.

————. 1988. *Comparative wood anatomy*. Springer-Verlag, Heidelberg, Germany. 436 p.

————. 1992. Pit membrane remnants in perforation plates of primitive dicotyledons and their significance. *Amer. J. Bot.* **79**: 666–672.

————. 1999. Wood and bark anatomy of Schisandraceae: implications for phylogeny, habit, and vessel evolution. *Aliso* **19**: 45–55.

————. 2003. Wood anatomy of Aextoxicaceae and Berberidopsidaceae is compatible with their inclusion in Berberidopsidales. *Syst. Bot.* **28**: 317–325.

————. 2005. Wood anatomy of Krameriaceae, with comparisons with Zygophyllaceae: phylesis, ecology and systematics. *Bot. J. Linn. Soc.* **149**: 257–270.

————. 2007. Bordered pits in ray cells and axial parenchyma: the histology of conduction, storage, and strength in living wood cells. *Bot. J. Linn. Soc.* **153**: 157–168.

————. 2010. Caryophyllales: a key group for understanding wood character states and their evolution. *Bot. J. Linn. Soc.* **164**: 342–393.

————. 2012*a*. Monocot xylem revisited: new information, new paradigms. *Bot. Rev.* **78**: 87–153.

————. 2012*b*. How wood evolves: a new synthesis. *Botany* **90**: 901–940.

————. 2014. Fiber dimorphism: cell type diversification as an evolutionary strategy in angiosperm woods. *Bot. J. Linn. Soc.* **174**: 44–67.

————. 2017. Conifer tracheids resolve conflicting structural requirements: data, hypotheses, questions. *J. Bot. Res. Inst. Texas* **11**: 123–141.

————. 2018. Living cells in wood. 3. Overview; functional anatomy of the parenchyma network. *Bot. Rev.* **84**: 242–294.

———— AND D. A. GOWANS. 1995. *Secondary growth and wood histology of Welwitschia. Bot. J. Linn. Soc.* **118**: 107–121.

———— AND E. L. SCHNEIDER. 2001. Vegetative anatomy of the New Caledonian endemic *Amborella trichopoda*: relationships with the Illiciales and implications for vessel origin. *Pacific Sci.* **55**: 405–512.

———— AND ————. 2002. Vessels of *Illicium* (Illiciaceae): range of pit membrane presence in perforations and other details. *Int. J. Pl. Sci.* **163**: 755–763.

———— AND ————. 2004. Pit membrane remnants in perforation plates of Hydrangeales; comments on pit membrane remnant occurrence, physiological significance, and phylogenetic distribution in dicotyledons. *Bot. J. Linn. Soc.* **146**: 41–51.

———— AND ————. 2007. Tracheary elements in ferns: new techniques, observations, and concepts. *Amer. Fern J.* **97**: 199–211.

CHOAT, B., A. COBB AND S. JANSEN. 2008. Structure and function of bordered pits: new discoveries and impacts on whole plant hydraulic function. *New Phytol.* **177**: 608–626.

DICKISON, W. C. AND P. BAAS. 1977. The morphology and relationships of *Paracryphia. Blumea* **23**: 417–438.

ENDRESS, P. K. 2005. Carpels in *Brasenia* (Cabombaceae) are completely ascidiate despite a long stigmatic crest. *Ann. Bot. (Oxford)* **96**: 209–215.

———— AND A. IGERSHEIM. 1997. Gynoecium diversity and systematics of Laurales. *Bot. J. Linn. Soc.* **125**: 93–168.

FROST, F. H. 1930. Specialization in the secondary xylem of dicotyledons I. Origin of vessels. *Bot. Gaz.* **89**: 67–94.

GOTTSBERGER, G. 1977. Some aspects of beetle pollination in the evolution of flowering plants. *Pl. Syst. Evol., Suppl.* **1**: 211–226.

HOLBROOK, N. M., M. A. ZWIENIECKI, AND P. J. MELCHER. 2002. The mechanics of "dead wood": maintenance of water transport through plant stems. *Integrative and Comparative Biology* **42**: 492–496.

HU, S., D. DILCHER, D. M. JARZEN AND D. W. TAYLOR. 2007. Early steps of angiosperm-pollinator coevolution. *Proc. Natl. Acad. Sci. U.S.A.* **105**: 240–245.

JEJE, A. A. AND M. H. ZIMMERMANN. 1979. Resistance to flow in vessels. *J. Exp. Bot.* **30**: 817–827.

KRIBS, D. A. 1935. Salient lines of structural specialization in the wood rays of dicotyledons. *Bot. Gaz.* **96**: 547–557.

————. 1937. Salient lines of structural specialization in the wood parenchyma of dicotyledons. *Bull. Torrey Bot. Club* **64**: 177–186.

LENS, F., R. A. VOS, G. CHARRIER, T. VAN DER NIET, V. MERCKX, P. BAAS, J. AGUIRRE GUTIERREZ, B. JACOBS, L. C. DÓRIA, E. SMETS, S. DELZON AND S. B. JANSSENS. 2016. Scalariform-to-simple transition in vessel perforation plates triggered by differences in climate during the evolution of Adoxaceae. *Ann. Bot. (Oxford)* **118**: 1043–1056.

LUNDBERG, J. 2001. Phylogenetic studies in the euasterids II, with particular reference to Asterales and Escalloniaceae. *Comprehensive Summaries of Uppsala Dissertations from the Faculty of Science and Technology* **676**: 1–38.

METCALFE, C. R. AND L. CHALK. 1950. *Anatomy of the dicotyledons*. Clarendon Press, Oxford, UK. 1500 p.

MEYLAN, B. A. AND B. G. BUTTERFIELD. 1978. The structure of New Zealand woods. DSIR Publication 222. New Zealand Department of Scientific and Industrial Research, Wellington.

OLSON, M. E. 2012. Linear trends in botanical systematics and the major trends of xylem evolution. *Bot. Rev.* **78**: 154–183.

PHILIPPE, M., B. GOMEZ, V. GIRARD, C. COIFFARD, V. DAVIERO-GOMEZ, F. THEVENARD, J.-P. BILLON-BRUYAT, M. GUIOMAR, J.-L. LATIL, J. LE LOEUFF, D. NÉRAUDEAU, D. OLIVERO AND J. SCHLÖGL. 2008. Woody or not woody? Evidence for early angiosperm habit from the early Cretaceous fossil wood record of Europe. *Palaeoworld* **17**: 142–152.

SANO, Y., H. MORRIS, H. SHIMADA, L. P. RONSE DE CRAENE AND S. JANSEN. 2011. Anatomical features associated with water transport in imperforate tracheary elements of vessel-bearing angiosperms. *Ann. Bot. (Oxford)* **107**: 953–964.

SAUTER, J. J., W. I. ITEN AND M. H. ZIMMERMANN. 1973. Studies on the release of sugar into the vessels of sugar maple (*Acer saccharum*). *Canad. J. Bot.* **51**: 1–8.

SCHNEIDER, E. L. AND S. CARLQUIST. 2003. Perforation plate diversity in *Illicium floridanum* (Illiciaceae) with respect to organs, provenance, and microtechnical methods. *Sida* **20**: 1047–1057.

TANK, D. C. AND M. J. DONOGHUE. 2010. Phylogeny and phylogenetic nomenclature of the Campanulidae based on an extended sample of genes and taxa. *Syst. Bot.* **35**: 425–441.

TAYLOR, D. W. AND L. J. HICKEY. 1996. *Flowering plant origin, evolution, and phylogeny*. Chapman and Hall, New York. 403 p.

TIEGHEM, P. VAN. 1900. Sur les dicotylédones du groupe de homoxylées. *J. Bot. (Morot)* **14**: 259–297.

VOGT, U. K. 2001. Hydraulic vulnerability, vessel refilling, and seasonal courses of stem water potential of *Sorbus aucuparia* L. and *Sambucus nigra* L. *J. Exp. Bot.* **52**: 1527–1536.

ZIMMERMANN, M. H. 1983. *Xylem structure and the ascent of sap*. Springer-Verlag, Heidelberg, Germany. 143 p.

ZWIENIECKI, M. A. AND N. M. HOLBROOK. 2000. Bordered pit structure and vessel wall surface properties. Implications for embolism repair. *Pl. Physiol.* **123**: 1015–1020.