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Tracheid Dimorphism: A New Pathway in Evolution of Imperforate Tracheary Elements

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ABSTRACT

Certain dicotyledon families characteristically have tracheids as their imperforate tracheary element type. Of these, six families are anomalous by having septate (or nonseptate but living) fiber-tracheids or libriform fibers coexisting with the tracheids in some species or genera (Austrobaileyaceae, Celastraceae, Convolvulaceae, Ericaceae, and Grossulariaceae, and Rosaceae). Data from the literature and original data on wood anatomy of these families are presented. A theory of tracheid dimorphism is developed to account for these instances of tracheids combined with fiber-tracheids or libriform fibers. According to this theory, septate or living fiber-tracheids or libriform fibers are produced in addition to tracheids, starting with ancestors that contain tracheids as the only imperforate tracheary element type, in response to selection for a rapidly increased photosynthate storage capacity, while maintaining the advantage of tracheids in providing conductive safety. Borders are phyletically lost rapidly on the septate (or nonseptate but living) imperforate tracheary elements because they are not water-conducting cells. Genera cited in this study can be ranged into a phyletic series with respect to differentiation from the hypothetical monomorphic-tracheid ancestors with respect to (1) loss of borders on pits of the septate or living elements; (2) distribution of tracheids with respect to vessels; and (3) retention of axial parenchyma. *Austrobaileya* is the most primitive genus in these respects, while genera such as *Holodiscus* and *Spiraea* are specialized. Tracheid dimorphism is compared to vessel dimorphism, fiber-tracheid dimorphism, fiber dimorphism, and the dimorphism related to origin of vessels. All these pathways except the last named one are confined to small numbers of families, and are considered minor trends superimposed on the major trends described by I. W. Bailey and coworkers. Basic to all of the dimorphic behaviors described is selection for two divergent cell types as a way of performing two distinctive wood functions.

Key words: Austrobaileyaceae, Celastraceae, Convolvulaceae, Ericaceae, fiber dimorphism, fiber-tracheid dimorphism, Grossulariaceae, Rosaceae, tracheid dimorphism, vessel dimorphism, vessel origin, wood anatomy.

INTRODUCTION

Working under the leadership of I. W. Bailey, Frost (1930*a, b,* 1931) advanced our understanding of wood evolution by showing that more tracheidlike vessel elements are statistically correlated with other primitive wood features. As a corollary, one could say that if *imperforate* tracheary elements in a wood are more tracheidlike (pit cavities larger in diameter, pits more densely placed, with wider borders on pits), they are more primitive (as opposed to imperforate tracheary elements in which pits are fewer, smaller, and unbordered, as in libriform fibers). This was confirmed (with the kind of correlations Frost used) by Metcalfe and Chalk (1950:xlv), who find more fully bordered pits on imperforate tracheary elements are much more common in woods with primitive vessel elements than in those with specialized vessel elements. Imperforate tracheary elements with pit cavities large in diameter, pits more fully bordered, and with pits densely

placed were termed tracheids by Bailey (1936) and the IAWA Committee on Nomenclature (1964); that usage is followed in the present paper.

The pattern of imperforate tracheary elements evolution accepted has been one in which there is a linear and gradual evolution within a dicotyledon phylad from tracheids to fiber-tracheids to libriform fibers. However, there are reasons to believe that additional evolutionary pathways occur in certain dicotyledon families. One such phenomenon that has been identified has been termed fiber dimorphism (Carlquist 1958). Fiber dimorphism represents in essence a way in which parenchyma bands are formed in a ground mass of libriform fibers by production of two kinds of libriform fibers—those in the bands parenchymalike. In the Asteraceae in which this process occurs, progressively greater degrees of fiber dimorphism are found in species with more seasonal climates (e.g., alpine species of *Argyroxiphium* and *Dubautia*), in which large parenchyma volume serves for storage related to seasonality. In these two genera as well as in virtually all other Asteraceae, vasicentric scanty parenchyma is present. One can hypothesize that alteration of the vasicentric scanty parenchyma pattern in terms of both position and quantity is genetically more difficult to achieve than fiber dimorphism (e.g., large sheaths would have to be formed around vessels during years when more storage parenchyma is of value, and such fluctuation is unknown in dicotyledon woods). Although discovered in Asteraceae, fiber dimorphism has been reported in other families, such as Lythraceae (Baas and Zweypfenning 1979), and Urticaceae (Bonsen and Welle 1984). Reports of fusiform parenchyma cells in wood of some Moraceae, such as *Cudrania* and *Maclura* (Tippo 1938), are referable to this concept.

The reader should note that fiber dimorphism is not at all the same as origin of nucleated (often septate) fibers from nonnucleated fibers (dead at maturity) by acquisition of greater protoplast longevity in the libriform fibers (Arnold 1951). Only in function is there a resemblance, namely, utilization of imperforate tracheary elements as parenchymalike cells. In the case of ordinary acquisition of nucleated fibers, the entire ground tissue of the wood—all its libriform fibers—is converted to nucleated fibers, whereas in fiber dimorphism, only localized zones of fibers retain protoplasts. Fiber dimorphism also differs from ordinary instances of nucleated fiber occurrence in that in a phylad with fiber dimorphism, the nucleated fibers become progressively more like axial parenchyma, and eventually are indistinguishable from axial parenchyma. In ordinary instances of nucleated fibers, the morphology of the fibers is the same as that of libriform fibers dead at maturity, differing at most only in formation of septa that reflect a division of the protoplast.

Another kind of fiber dimorphism may be claimed in *Cercidium* and related caesalpinoid Fabaceae in which some libriform fibers contain strands of crystals (the crystals separated from each other by thin primary walls), whereas other fibers are identical except for absence of these crystals (Carlquist 1988a). The function of crystal-containing fibers is presumably deterrence of boring insects.

There is also a phenomenon that has been termed vessel dimorphism (Carlquist 1981). Vessel dimorphism is easily demonstrated in vining species in which notably wide vessels and narrow vessels are formed, but relatively smaller numbers of vessels intermediate in diameter occur. In some instances, the narrow "vessel elements" are so narrow that they lack perforation plates, and thus by definition

become vasicentric tracheids. Vessel dimorphism would account for occurrence of vasicentric tracheids in such a species as *Antigonon leptopus* H. & A. (Carlquist 1985*b*), a vine in which only a few vasicentric tracheids occur but very narrow vessel elements are also produced. One may also think of vascular tracheids as a product of vessel dimorphism (or perhaps polymorphism) in which extremely narrow vessel elements grade into perforation-free "vessel elements" (the vascular tracheids) at the terminus of a growth ring.

The present paper develops evidence for tracheid dimorphism and also considers another phenomenon, fiber-tracheid dimorphism. Tracheid dimorphism is proposed as an explanation for certain instances of vasicentric tracheid occurrence, as well as instances in which a condition antecedent to presence of vasicentric tracheids may be claimed (*Austrobaileya*).

We may briefly consider the various pathways that could lead to occurrence of vasicentric tracheids. One possibility is cited above for *Antigonon leptopus:* vessel dimorphism leading to formation of a vew vasicentric tracheids adjacent to wide vessels. A second potential pathway to vasicentric tracheid presence begins with another product of vessel dimorphism, vascular tracheids. Vascular tracheids are considered as confined to the terminal layers of a growth ring, whereas vasicentric tracheids accompany vessels in a portion of or all of a growth ring, or throughout diffuse-porous woods (Carlquist 1985*a*). In some woods with libriform fibers, vascular tracheids are relatively abundant (certain Asteraceae and Lamiaceae); by virtue of their abundance, vessels in the later portions of growth rings in certain species of these families are surrounded by tracheids. In such instances, vasicentric tracheids are present (although one should recognize the transitional nature of such an instance), as in *Salvia* (Carlquist 1985*a*). In *Salvia,* wider growth rings may have vascular tracheids only in a small terminal portion of the ring, but a narrow ring (in which vessels are scattered) may consist almost wholly of tracheids and vessels, in which case the concept of vasicentric tracheids obviously applies. Phylesis in a group with vascular tracheids toward production of wood like that found in narrow *Salvia* growth rings would constitute a second mode of origin of vasicentric tracheids. A third possible pathway may be called fiber-tracheid dimorphism (Carlquist 1988*b*), and is reviewed in the concluding section of this paper.

A fourth possible pathway, tracheid dimorphism, is considered here. This phenomenon is hypothesized to occur in six families (Austrobaileyaceae, Celastraceae, Convolvulaceae, Ericaceae, Grossulariaceae, and Rosaceae), although other instances very likely remain to be discovered. This pathway is hypothesized to account for peculiar anatomical circumstances that are applicable neither to the traditional concepts of evolution of imperforate tracheary element cited in the opening paragraph of this Introduction nor to the three pathways to vasicentric tracheids cited above. The following facts are cited in connection with the woods of the six families cited.

All of the six families have notably primitive wood (e.g., scalariform perforation plates present except in more xeromorphic phylads). True tracheids are present to the exclusion of fiber-tracheids or libriform fibers in at least some of the portions of these families. For example, if one looks at the wood of *Mortonia* (Celastraceae), *Dicranostyles* (Convolvulaceae), *Rhododendron* (Ericaceae), or *Cercocarpus* (Rosaceae), one sees as tracheary elements only vessel elements plus tracheids. In

none of these families does one see a series of genera representing gradual trans-
formation of the tracheids into fiber-tracheids and thence into libriform fibers.
Yet in some genera such as *Austrobaileya* (Austrobaileyaceae), *Celastrus* (Celas-
traceae), *Ipomoea* (Convolvulaceae), *Arctostaphylos* (Ericaceae), *Ribes* (Grossu-
lariaceae), and *Spiraea* (Rosaceae), one sees wood in which tracheids are present,
but also, coexisting with the tracheids, living fibers or fiber-tracheids (in most of
these, septate fibers or fiber-tracheids). This gives the appearance of a sudden
intercalation of living fibers into woods that otherwise are clearly primitive.

The lack of range of imperforate tracheary elements in these families is evident.
If a range were present, one could hypothesize that the septate libriform fibers
represented an end product or gradual evolution from tracheid to libriform fiber.
Another peculiar circumstance in the families cited is that fiber-tracheids or li-
briform fibers, where present, are always nucleated (in many instances septate, a
condition that is evidence of prolonged cell longevity).

Examples of woods featuring the above peculiar characters can be found in the
literature, although these occurrences have not been collected into a theoretical
framework. *Austrobaileya* was found to have tracheids plus septate fiber-tracheids
(with variations in pit diameter) by Bailey and Swamy (1949).

In Celastraceae, Metcalfe and Chalk (1950:394) mention that there are "mul-
tiseriate bands of septate fibers among the fiber-tracheids [=tracheids in the present
usage] in *Cassine, Celastrus* p.p., *Elaeodendron* p.p., *Frauenhofera* p.p., *Gym-
nosporia* p.p., *Hartogia, Maurocenia, Maytenus* p.p., and *Plenckia*." They add
that "these bands of septate fibers are exactly comparable in distribution with the
multiseriate bands of parenchyma occurring in other species, and in a single genus
the bands may be composed of septate fibers in one species and of parenchyma
in another."

In Convolvulaceae, wood is basically composed of true tracheids in addition
to vessels and axial parenchyma (Metcalfe and Chalk 1950). This is shown by
such genera as *Dicranostyles* (Mennega 1969) and the Canarian species of *Con-
volvulus* (Carlquist, unpublished data). However, in *Argyreia,* tracheids, fiber-
tracheids, and libriform fibers are reported to coexist in the same wood (Pant and
Bhatnagar 1975). In *Ipomoea hederifolia* L., wood contains vessels, fibriform
vessel elements, tracheids, and fiber-tracheids (Lowell and Lucansky 1986).

In Ericaceae, the drawings of Greguss (1959) indicate co-occurrence of tracheids
and of libriform fibers (usually septate) in *Erica, Vaccinium* p.p. and in the genera
of Arbutoideae (*Arbutus, Arctostaphylos*). Metcalfe and Chalk (1950) report co-
occurrence of libriform fibers (supposedly with simple pits, although vestigially
bordered pits and thereby fiber-tracheids are reported in the present paper) in
Agauria, Arbutus, Arctostaphylos, Oxydendrum, and *Vaccinium*. This co-occur-
rence of tracheids and fiber-tracheids in the arbutoid genera has been reported in
terms of vasicentric tracheid occurrence (Carlquist 1985*a*).

In Grossulariaceae, the most reliable work on wood anatomy is that of Stern,
Sweitzer, and Phipps (1970). These authors report co-occurrence of tracheids and
septate fiber-tracheids in the woods of the *Ribes* species they examined.

In Rosaceae, Solereder (1908) mentions presence of occasional "fibers with
simple pits" in woods that otherwise have tracheids: *Kerria, Potentilla, Rhodo-
typos,* and *Spiraea*. The drawings of Greguss (1959) indicate co-occurrence of
tracheids and libriform fibers in *Cotoneaster* p.p., *Crateagus* p.p., *Cydonia, Kerria,
Rubus,* and *Spiraea.*

In order to see if all the above disparate examples represent manifestations of the same evolutionary phenomenon, I have examined representatives of most of the abovementioned genera. Particular attention was paid to four anatomical issues: (1) whether the imperforate tracheary elements other than tracheids have bordered or simple pits; (2) whether the imperforate tracheary elements are living, as evidenced by presence of septa, nuclei, or starch; (3) whether species with imperforate tracheary elements in addition to tracheids have axial parenchyma or not, and to what degree; (4) whether in the species examined tracheids are distributed with relation to vessels or not.

In a genus of Rosaceae other than those mentioned above, another pattern occurs. Some species of *Prunus,* such as *P. amygdalus* Batsch, *P. fremontii* Wats. and probably the majority of species in the genus, have only tracheids as their sole type of imperforate tracheary element. *Prunus lyonii* (Eastw.) Sarg., *P. ilicifolius* (Nutt.) Walp. and a few other species have vasicentric tracheids plus fiber-tracheids (Carlquist 1985*a*). The latter group of species is believed to represent an instance of what is called fiber-tracheid dimorphism here. Anatomical details of selected species of *Prunus* are presented here in order to document this instance.

MATERIALS AND METHODS

The following wood samples were used in this study. Those available preserved in liquid (which therefore give more reliable data about starch or nuclear presence) are indicated by an asterisk (*).

Austrobaileyaceae
  *Austrobaileya scandens C. T. White, *Carlquist 1930* (RSA)
Celastraceae
  Catha edulis Forsk., *Carlquist 1555* (RSA)
  Celastrus scandens L., *USw-5851* (RSAw)
  Elaeodendron dioicum Griseb., *USw-5929* (RSAw)
  *E. capense Eckl. & Zeyh. (cult. Vavra Estate UCLA)
  Maytenus boaria Molina, *USw-9457* (RSAw)
Convolvulaceae
  Ipomoea arborescens Sweet, *Henrickson and Christman 2087* (RSA)
  I. macrorhiza Michaux, *USw-1843* (RSAw)
Ericaceae
  *Arbutus menziesii Pursh, *Bissing 124* (RSA)
  A. texana Buckl., *USw-19051 (RSAw)*
  *Arctostaphylos auriculata Eastw., *cult. RSA*
  A. mariposa Dudl. in Eastw., *Wolf 5071* (RSA)
  A. patula Greene, *Carlquist s.n.* (Mt. San Jacinto)
  *A. viscida Parry, *Wallace 1519* (RSA)
  *Comarostaphylis diversifolia (Parry) Greene, *Wallace 1388* (RSA)
  Vaccinium arboreum Marsh., *USw-19399* (RSAw)
  V. ovatum Pursh, *cult. RSA*
  Xylococcus bicolor Nutt., *Wallace 1380* (RSA)
Grossulariaceae
  *Ribes aureum Pursh, *RSA prop. no. 6539*
  R. cereum Douglas, *Everett 21900* (RSA)
  R. montigenum McClatchie, *Warnock 9* (RSA)
  *R. sanguineum Pursh, *RSA prop. no. 11390*
  *R. viburnifolium Gray, *RSA prop. no. 7602*
Rosaceae
  *Cotoneaster microphylla Lindl., *Carlquist 15938* (RSA)
  *Holodiscus discolor (Pursh) Maxim., *RSA prop. no. 8548*

H. microphyllus Rydb., *Carlquist 15847* (RSA)
Prunus fremontii Wats., *RSA prop. no. 6524*
P. ilicifolius (Nutt.) Walp., *Carlquist s.n.* (San Antonio Canyon)
P. lyonii (Eastw.) Sarg., *cult. RSA*
Rubus spectabilis Pursh, *Carlquist 1 July 1972*
Spiraea douglasii Hook., *RSA prop. no. 7546*

Dried wood samples were boiled in water and stored in aqueous 50% ethyl alcohol. All woods were sectioned on a sliding microtome. Sections were stained with safranin; in most instances, they also were counterstained with fast green, which permitted detection of vestigial borders on pits of the living imperforate tracheary elements. A simple polarizing apparatus aided in revealing presence of starch. Macerations were prepared with Jeffrey's Fluid and stained with safranin.

RESULTS

Because the object of this study is not purely comparative, the data collected are restricted to the four anatomical features specified in the last paragraph of the Introduction. Although an attempt has been made to locate families in which wood characteristically has tracheids plus living (often septate) libriform fibers or fiber-tracheids, that objective can be realized only in limited terms. If the hypothesis of tracheid dimorphism is valid, early stages will feature in a given wood the presence of conductive tracheids plus living fiber-tracheids (e.g., *Austrobaileya*). Tracheids may at first not be distributed primarily with relation to vessels (e.g., *Austrobaileya*). If woods with tracheids plus septate fibers evolve over time, however, the tracheids would be expected to develop a vasicentric pattern (because of the advantage of this pattern with relation to conductive safety: Carlquist 1985*a*), and the fibers may not remain septate (or otherwise with living contents). For example, the woods of *Ceanothus* (Rhamnaceae) or *Quercus* would be of this description. Are the woods of *Ceanothus* and *Quercus* ultimately derived from tracheid dimorphism, or do they represent a result of another pathway? In genera such as these, the criteria whereby tracheid dimorphism can be established in earlier stages of evolution of this pathway are now not present. Therefore, phylads in which the vasicentric tracheid habit has become well established cannot be cited here, and only those families in which some genera have true tracheids as the sole imperforate tracheary element type, whereas other genera in those same families have tracheids plus living fibers, are cited here. Even within these, some appear to represent earlier stages (*Austrobaileya*) than others (*Maytenus*).

Austrobaileyaceae

AUSTROBAILEYA (Fig. 1–4).—In the wood of *Austrobaileya scandens* imperforate tracheary elements include tracheids (thicker-walled cells, Fig. 1–2; Fig. 4) and septate fiber-tracheids (Fig. 3, center). Pits in fiber-tracheids are conspicuously to vestigially bordered, but no simple pits were observed on imperforate tracheary elements. The range of pit diameter in tracheids and fiber-tracheids is shown in Fig. 3–4. Fiber-tracheids have nuclei, but starch was not observed in this material. Axial parenchyma is present in a vasicentric scanty pattern (Fig. 1, 2). Distribution of tracheids and fiber-tracheids is approximately random with respect to vessels and vasicentric parenchyma.
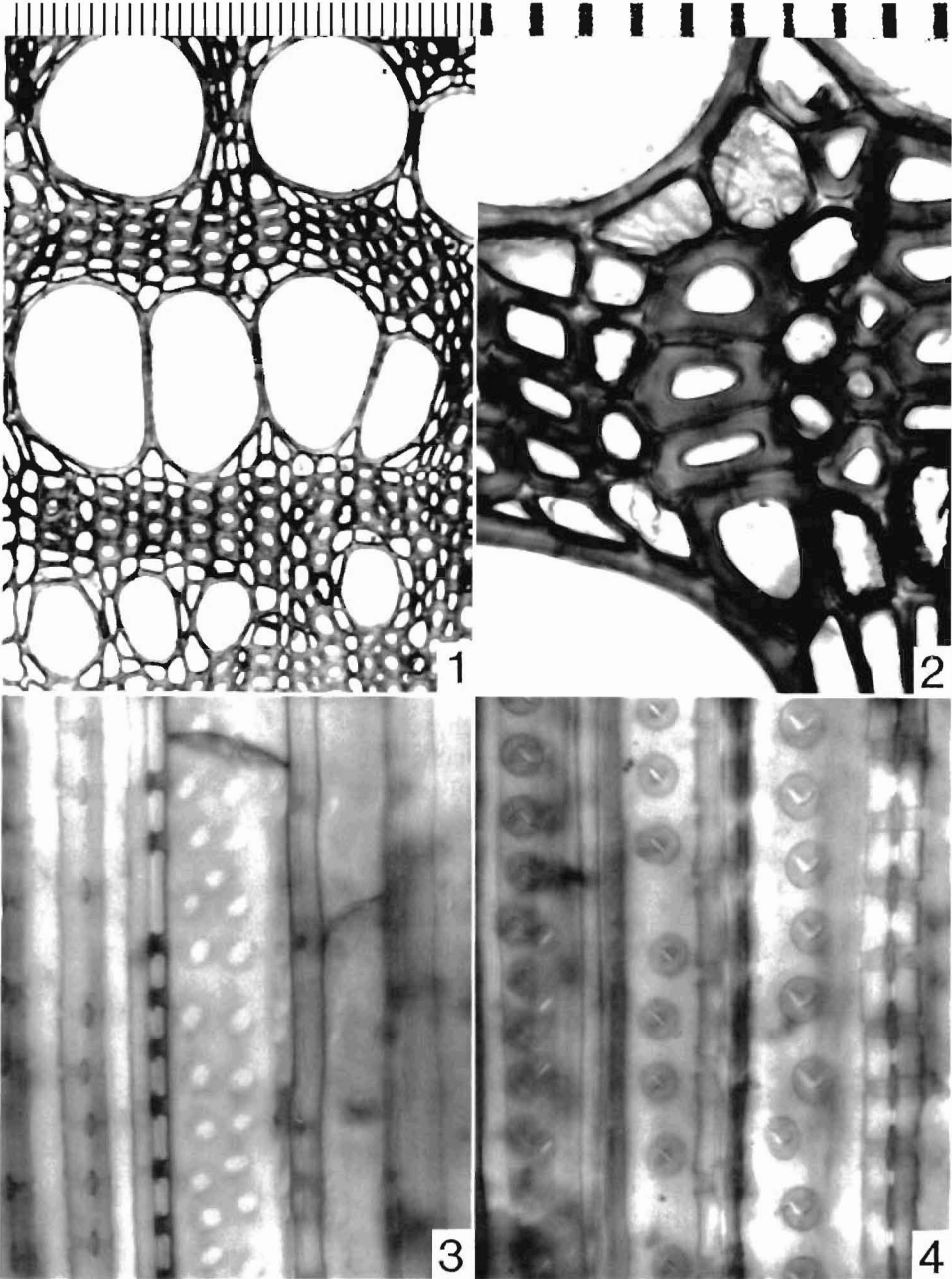
Fig. 1–4.   Wood sections of *Austrobaileya scandens* (*Carlquist 1390*, RSA).—1. Transection, show-ing vessels of various sizes surrounded by axial parenchyma.—2. Transection portion, showing thick-walled tracheids (center), somewhat thinner-walled septate fiber-tracheids (left), and vasicentric paren-chyma (cross walls visible in two cells, above).—3. Septate fiber-tracheids in radial section, showing septa (right above) and pits in transection (center).—4. Tracheids from radial section, showing pits in face and sectional view. (Fig. 1, magnification scale above Fig. 1 [divisions = 10 μm]); Fig. 2–4, scale above Fig. 2 [divisions = 10 μm].)

Celastraceae

CATHA (Fig. 5–8).—In *Catha edulis,* imperforate tracheary elements are septate libriform fibers (thinner-walled cells in Fig. 5 and 6; Fig. 8, cells to left and right of middle ray) and tracheids (Fig. 7). Borders are absent or apparently so on pits of septate fibers (Fig. 8). Starch was not observed in this material. Axial parenchyma is not present. Septate fibers are in tangential bands (Fig. 5, 6).

CELASTRUS.—In *Celastrus scandens,* imperforate tracheary elements are tracheids and septate fibers. Pits on septate fibers are apparently simple. Axial parenchyma is present in earlywood, together with septate fibers and wider vessels. Latewood consists of narrower vessels plus tracheids.

ELAEODENDRON.—The two collections of *Elaeodendron* examined have wood features corresponding to those specified for *Catha edulis.*

MAYTENUS.—In *Maytenus boaria,* imperforate tracheary elements are tracheids plus septate fiber-tracheids. Borders are vestigial on the pits of fiber-tracheids. Tracheids are nearly all vasicentric, although several terminal layers composed of tracheids occur in growth rings also; except for those layers, septate fiber-tracheids are distributed throughout growth rings. Starch was not observed in fiber-tracheids.

Convolvulaceae

IPOMOEA.—In *Ipomoea arborescens,* tracheary elements include ordinary vessel elements, fibriform vessel elements, tracheids, and septate fiber-tracheids. Borders are much reduced on the fiber-tracheids. The septate fiber-tracheids are scattered at random throughout the wood. Axial parenchyma is diffuse, with some vasicentric scanty and some apotracheal banded distributions. Starch was not observed in the fiber-tracheids. In *Ipomoea macrorhiza,* the tracheary elements are vessels and septate fiber-tracheids, and no tracheids are present. Axial parenchyma is scarce. Starch was not observed, but resinlike deposits occur in the septate fiber-tracheids.

Ericaceae

ARBUTUS.—In *Arbutus menziesii,* tracheids and septate fiber-tracheids are present. Borders on pits of fiber-tracheids are very small. Nuclei were observed, but not starch. Axial parenchyma is not present. Tracheids are vasicentric, commoner in earlywood than in latewood; a few layers of tracheids terminate growth rings. The wood of *A. texana* is similar, differing in that septa are lacking in some of the fiber-tracheids.

ARCTOSTAPHYLOS *and allied genera.*—In *Arctostaphylos auriculata* (Fig. 9–12), imperforate tracheary elements are septate fiber-tracheids (Fig. 9, upper right; Fig. 11, at left adjacent to ray; Fig. 12, lower right) and tracheids (Fig. 9, below; Fig. 10, left; Fig. 12, left). Fiber-tracheids have vestigial borders (best shown in Fig. 11, fiber-tracheid adjacent to ray). Axial parenchyma not present. Starch was observed in septate fiber-tracheids. Earlywood (Fig. 9, above) consists of wide vessels plus septate fiber-tracheids, but tracheids can be observed adjacent to most vessels. Latewood (Fig. 9, below) consists of numerous narrow vessels associated
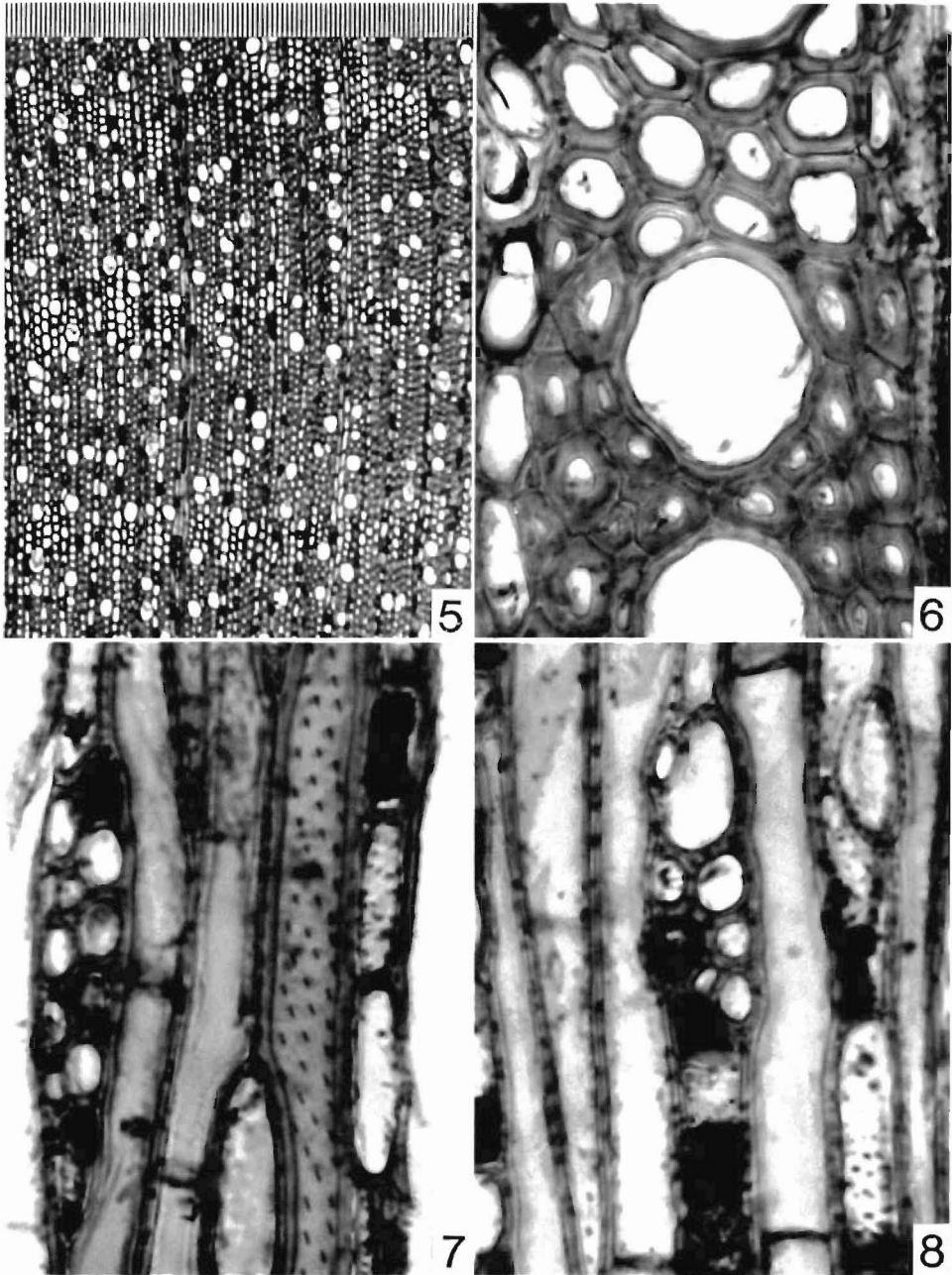
Fig. 5–8. Wood sections of *Catha edulis* (*Carlquist 1555*, RSA).—5. Transection; three tangential bands of septate libriform fibers, difficult to distinguish from remainder of wood, are present in this portion.—6. Transection portion, showing libriform fibers above vessel, tracheids to left and right of and below vessel.—7. Tangential section; tracheid to right of center illustrates dense pitting.—8. Tangential section showing ray portions and septate libriform fibers pits (sectional view) simple or nearly so. (Fig. 5, magnification scale above Fig. 5 [divisions = 10 μm]; Fig., 6–8, scale above Fig. 2.)
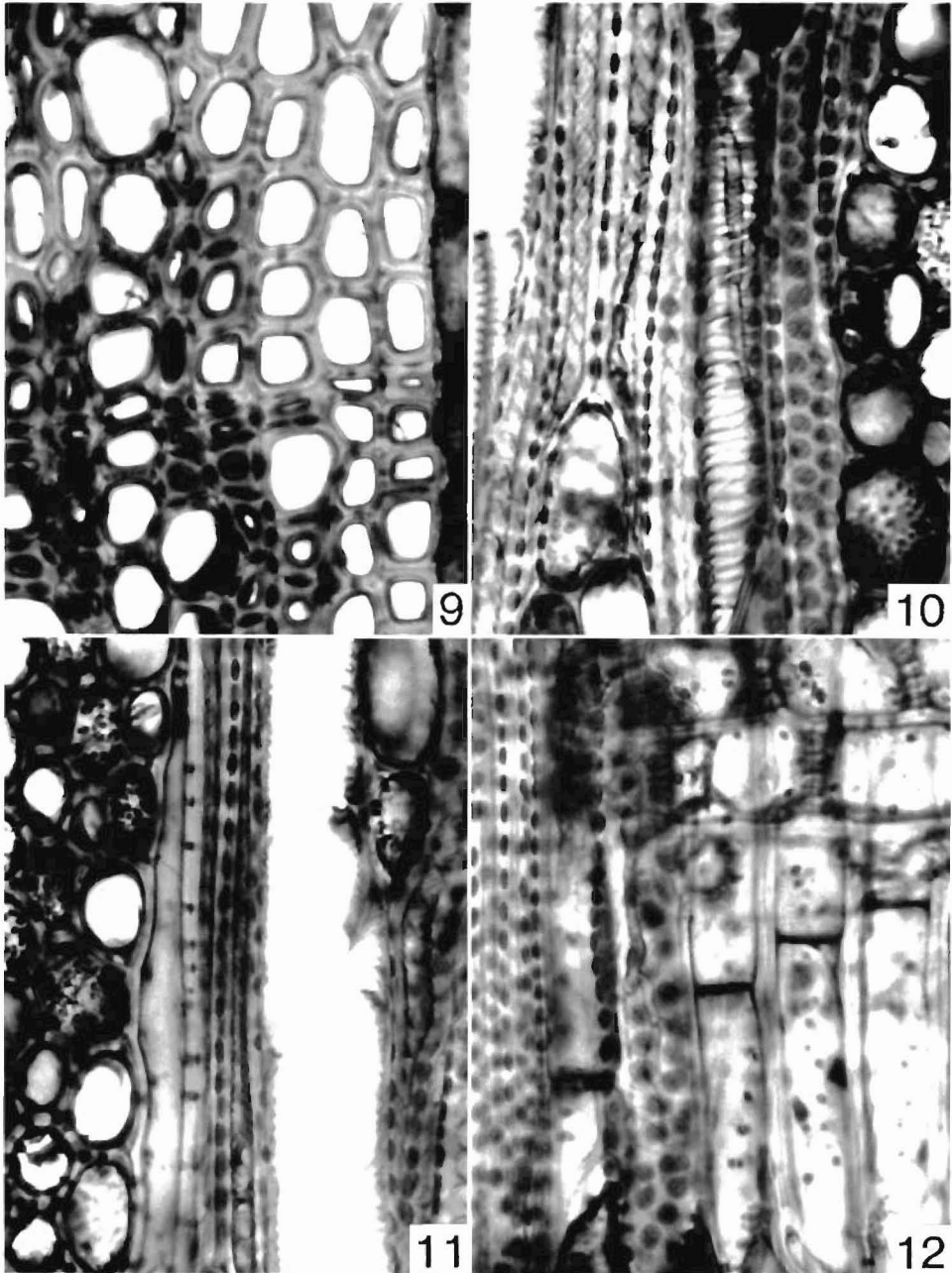
Fig. 9–12. Wood sections of *Arctostaphylos auriculata* (*cult. RSA*).—9. Transection; end of growth ring just below center; septate fiber tracheids in upper half of photograph.—10. Tangential section; vessel (center) with helical thickenings and vasicentric tracheids (left half of photograph).–11. Tangential section, showing vessel and vasicentric tracheids; a septate fiber tracheid (pits in sectional view) to right of ray at left.—12. Radial section, showing ray (above) and septate fiber-tracheids (lower right); dark spots in fiber-tracheids are air spaces in starch grain hila resulting from dehydration. (Fig. 9–12, magnification scale above Fig. 2.)

with large numbers of tracheids, although a few septate fiber-tracheids are present also.

Although the proportions of septate fiber-tracheids to tracheids vary from species to species within *Arctostaphylos,* the same conditions given for *A. auriculata* were observed in *A. mariposa, A. patula,* and *A. viscida.* In the last two species, septate fiber-tracheids are more common, tracheids accordingly less common, in roots than in stems. Wood of *Xylococcus bicolor* and *Comarostaphylis diversifolia* differs from that of *Arctostaphylos* in that diffuse axial parenchyma is moderately common.

VACCINIUM.—In *V. arboreum* and *V. ovatum,* the imperforate tracheary elements are tracheids plus fibers. Pits are apparently simple on the septate fibers. Axial parenchyma is rare or absent. Starch was observed in septate fibers. Tracheids form the ground mass of the wood, and both vessels and septate fibers are scattered diffusely among the tracheids.

Grossulariaceae

RIBES.— *Ribes aureum* has tracheids plus septate fiber-tracheids. Borders on fiber-tracheid pits are vestigial but readily observed. Axial parenchyma was not observed. Starch is abundant in septate fiber-tracheids. The tracheids are not abundant, but they are arranged in vasicentric fashion; many vessels are accompanied by one or two files of tracheids.

The same features were observed in *R. sanguineum* and *R. viburnifolium.* Vasicentric tracheids are more abundant (septate fiber-tracheids accordingly less abundant) in *R. cereum* and *R. montigenum.*

Rosaceae

COTONEASTER.— *Cotoneaster microphylla* has tracheids plus septate fiber-tracheids. Septate fiber-tracheids have easily-discernible vestigial pit borders. Septate fiber-tracheids are densely filled with starch. Axial parenchyma is absent. Tracheids are relatively few in number and vasicentric in distribution; the ground mass of the wood thus consists of septate fiber-tracheids.

HOLODISCUS.—The wood of *H. discolor* contains tracheids plus nonseptate nucleated living fibers. The living fibers have apparently simple pits. Diffuse axial parenchyma is present, but not common. Tracheids are distributed in a vasicentric fashion, and are also present as a few terminal layers in latewood.

Holodiscus microphyllus is identical to *H. discolor* except that tracheids are somewhat more abundant and that axial parenchyma was not observed.

PRUNUS.—In wood of *P. fremontii,* imperforate tracheary elements are all tracheids, with pitting corresponding to the definition of this cell type by Bailey (1936). Starch is present in ray cells. Axial parenchyma is moderately scarce, and occurs in a diffuse distribution.

In *P. ilicifolius,* tracheids and fiber-tracheids are present. Fiber-tracheids are not septate or living and have bordered pits; pit diameter is about half that of the tracheid pits, borders are intermediate between fully bordered and vestigial, and pits are relatively sparse. Starch is abundant in rays and axial parenchyma, but is absent from imperforate tracheary elements. Axial parenchyma is mod-

erately sparse, and is present in diffuse and vasicentric distributions. The wood of *P. lyonii* is like that of *P. ilicifolius* in qualitative respects.

RUBUS.—In *R. spectabilis,* the imperforate tracheary elements are tracheids and septate fiber-tracheids. Pits on septate fiber-tracheids are vestigially bordered. Fiber-tracheids contain starch. Axial parenchyma is present in moderate quantities and distributed diffusely. Tracheids form the ground mass of the wood, and septate fiber-tracheids are scattered diffusely among the tracheids.

SPIRAEA.—Wood of *S. douglasii* contains tracheids plus septate fibers. The pits in septate fibers are apparently simple. Septate fibers are rich in starch. Axial parenchyma was not observed. Tracheids and septate fibers are arranged apparently at random.

CONCLUSIONS

A central hypothesis of this study is that in certain phylads with primitive wood, characteristically with tracheids, certain genera have undergone a process termed tracheid dimorphism, in which the result is presence of two types of imperforate tracheary elements: conductive tracheids and living (often septate) fiber-tracheids (or, in derived instances, libriform fibers). If this hypothesis is valid, one must propose an explanation for why dimorphism in imperforate tracheary elements should occur, and one should be able to demonstrate stages in the process.

The presence of starch in living imperforate tracheary elements is conspicuous in many of the woods studied here. In those in which abundant starch was not observed in imperforate tracheary elements, starch may possibly be present on a seasonal basis. The abundance of starch in the various taxa exemplifying tracheid dimorphism suggests that tracheid dimorphism is a way in which a large amount of photosynthate-storage tissue can be intercalated into wood. In all the genera cited here as exemplifying tracheid dimorphism, the living fibers are relatively wide and thin walled, characteristics that would make unlikely the origin of living fibers as a way of increasing mechanical strength.

Tracheid dimorphism might represent a phyletically more readily achieved way of enlarging the volume of starch storage in a wood than would increase in axial parenchyma (which would reduce mechanical strength of a wood) or increase in volume of ray tissue (which may be governed by similar constraints, as well as by a balance between ray tissue and axial wood tissues). Fiber dimorphism (Carlquist 1958) represents a mechanism for acquisition of parenchymalike fibers (presumably mostly with a storage function), beginning evolutionarily with libriform fibers. Other types of dimorphism in wood cells that do not involve increase in photosynthate storage will be discussed later.

If tracheid dimorphism is operative, one ought to be able to find opening stages in which the living imperforate tracheary elements are more tracheidlike. More tracheidlike living imperforate tracheary elements would be expected to have bordered pits (and thus be fiber-tracheids), although disappearance of borders on such cells would be expected to be phyletically rapid because these cells are no longer water-conducting cells. Among the species with septate fiber-tracheids, *Austrobaileya* is noteworthy because pits on fiber-tracheids vary in diameter from somewhat less than those of tracheids to much reduced (the type termed vestigial by some authors), as noted by Bailey and Swamy (1949).

Presence of borders on pits of the living imperforate tracheary elements in instances of tracheid dimorphism is considered important because these represent a remnant of a tracheidlike condition. Loss of borders is doubtless accelerated by the shift from conductive (tracheid) to nonconductive (living or septate fiber). Genera in the present study in which borders were observed on pits of living imperforate tracheary elements include *Arbutus, Arctostaphylos, Austrobaileya, Catha, Cotoneaster, Elaeodendron, Ipomoea, Maytenus, Ribes,* and *Rubus.* Except for *Austrobaileya,* borders are very vestigial and pits small in diameter (about 1–1.5 μm). All the genera studied here but not mentioned in this paragraph have living (mostly septate) libriform fibers, and can thus be considered to represent derivations of tracheid dimorphism in which imperforate tracheary elements are minimally tracheidlike and therefore more specialized.

One can also find a range in expressions from primitive to specialized among the genera studied with respect to presence of axial parenchyma. If tracheid dimorphism represents a mechanism for rapid introduction of a photosynthate storage tissue, one might expect that the phylads in this study would at first retain axial parenchyma but that axial parenchyma, much less in volume than the living imperforate tracheary elements, would disappear over time. This appears true. Among the genera studied, axial parenchyma is moderately common in *Arbutus, Austrobaileya, Celastrus, Comarostaphylis, Holodiscus, Ipomoea, Rubus,* and *Xylococcus.* Axial parenchyma is absent or nearly so in *Arctostaphylos, Catha, Elaeodendron, Maytenus, Ribes, Spiraea,* and *Vaccinium.* Thus, one can conclude that loss of axial parenchyma has been rapid in this assemblage of families. More significantly, the genera with more axial parenchyma are mostly the same genera cited here for other features alleged to represent primitive stages in tracheid dimorphism.

Early stages in the progress of tracheid dimorphism would be expected to feature random distribution of living imperforate tracheary elements with respect to tracheids. In *Austrobaileya,* there is no tendency for tracheids to be grouped around vessels, although some tracheids are in contact with vessels—approximately in proportion to random distribution. Thus, *Austrobaileya* cannot really be cited as an example of vasicentric tracheid distribution. A diffuse distribution of living imperforate tracheary elements with respect to tracheids may likewise be found in *Ipomoea, Rubus,* and *Vaccinium.* An intermediate degree of organization of tracheids with respect to living imperforate tracheary elements and to vessels is represented by *Celastrus* and *Maytenus* (tracheids a little more abundant in latewood); *Catha* and *Elaeodendron* (septate fibers in tangential bands); and *Celastrus* (tracheids plus narrow vessels in latewood, septate fibers plus vessels and axial parenchyma in earlywood). One can claim these as examples of vasicentric tracheids. A further advance is represented by *Arbutus, Arctostaphylos, Comarostaphylis, Holodiscus, Maytenus, Spiraea,* and *Xylococcus:* earlywood consists of vessels plus living septate fibers or living libriform fibers and vasicentric tracheids, whereas latewood contains narrow vessels plus more abundant vasicentric tracheids and a few living imperforate tracheary elements; tracheids form the terminal layers of latewood. Vasicentric tracheids clearly characterize these genera. An equally specialized degree of organization—all tracheids vasicentric in earlywood and latewood, septate fiber-tracheids or septate fibers abundant throughout—occurs in *Cotoneaster* and *Ribes.*

Thus, all the genera studied here except *Prunus,* which is considered below, represent tracheid dimorphism, and show varying degrees in the progression of this phenomenon. Notably primitive in this series are *Austrobaileya, Ipomoea,* and *Rubus.* Although genera such as *Holodiscus* and *Spiraea* can be cited as specialized in this series, one must concede that genera with vasicentric tracheids not considered thus far in this paper might exceed them in degree of specialization, but cannot with certainty be identified as exemplifying tracheid dimorphism. For example, *Ceanothus* (Rhamnaceae) and *Quercus* (Fagaceae) have vasicentric tracheids, but these families lack genera with tracheids but no other kind of imperforate tracheary element, and the libriform fibers in these families are nonliving. Do *Ceanothus* and *Quercus* represent derivatives of tracheid dimorphism so specialized that neither they nor the families to which they belong show the identifying characteristics of the process cited in the genera studied here, or do these genera represent origin of vasicentric tracheids by some other mechanism? At present, the mode of origin of vasicentric tracheids can be hypothesized with any degree of assurance for only part of the known instances of occurrence of vasicentric tracheids.

If one looks at the families studied here, one sees that some shrubs from very dry habitats (e.g., *Cercocarpus, Mortonia*) have tracheids as the sole type of imperforate tracheary element, and do not exhibit tracheid dimorphism. Although more examples are needed to clarify the phyletic status of such genera, possibly the value of tracheids for their conductive safety is so great that maximal abundance of tracheids has been retained (air bubbles in one tracheid do not disable an entire series of tracheids because they cannot cross pit membranes). Consequently, tracheid presence in these taxa cannot be diminished, and photosynthate storage must be performed by parenchyma. Vasicentric tracheids are more common in alpine species of *Ribes* than in lowland or mid-elevation species, which suggests another series of instances in which maximization of tracheid presence has been achieved.

A scheme for the evolution of imperforate tracheary elements is being presented in a book appearing concurrently with this paper (Carlquist 1988*b*). In addition to tracheid dimorphism, another phenomenon is hypothesized, fiber-tracheid dimorphism. This pathway is postulated for families in which some species have true tracheids as the background cell type in wood, whereas other species have fiber-tracheids plus vasicentric tracheids. In this case, one may suggest that a phylad has an evolutionary range which includes tracheids in some groups, fiber-tracheids in others. This range may have been achievd in mesic conditions under which the conductive safety of tracheids, cited in the preceding paragraph, was of minimal selective value, and shift from tracheids to fiber-tracheids may have resulted from selection for greater mechanical strength as provided from the latter. In species with fiber-tracheids, the genetic information for formation of tracheids may be said still to be present, because tracheids and fiber-tracheids may be said to differ in degree, not in kind (presence or absence of a feature). A phylad with fiber-tracheids could develop vasicentric tracheids by relatively small changes in pitting of elements adjacent to a vessel—even slightly denser pits of the same size as on fiber-tracheids would result in presence of vasicentric tracheids if this change occurred in elements adjacent to vessels. Indeed, in the families in which fiber-tracheid dimorphism is postulated, the difference in any given species between

tracheids and fiber-tracheids may be little or appreciable. One can find such a range in *Eucalyptus* or *Melaleuca*. Families in which I claim fiber-tracheid dimorphism as the process that has led to presence of vasicentric tracheids include Dipterocarpaceae, Goupiaceae, Myrtaceae, and Zygophyllaceae. Interestingly, *Prunus* must also be added to this list, despite the fact that other Rosaceae exhibit tracheid dimorphism. The data developed above and previously (Carlquist 1985*a*) for *Prunus* show that evergreen species of the genus in dryland habitats have vasicentric tracheids plus fiber-tracheids, whereas deciduous species have true tracheids only.

Fiber dimorphism (Carlquist 1958) has led to development of parenchyma bands (presumably with photosynthate storage) in the mechanically strong libriform fiber tissue of various families (see Carlquist 1988*b*). Vessel dimorphism has led to wide plus narrow vessels in vines and, as a byproduct, some "vessel elements" are so narrow they lack perforation plates and are thereby vasicentric tracheids. Judging from the large number of vines with either true tracheids or vasicentric tracheids (Carlquist 1985*b*), presence of a high degree of conductive safety by virtue of tracheid presence appears a genuine phenomenon in scandent dicotyledons. Another form of vessel dimorphism is represented by vascular tracheids—the formation at the end of a growth ring of "vessel elements" so narrow they lack perforation plates and must be termed tracheids. In phylads in which vascular tracheids are formed abundantly (certain Asteraceae and Lamiaceae), the vasular tracheids phyletically come to surround at least a portion of the vessels and are thus functionally vasicentric tracheids (the latter term should then be used in such cases).

If the above hypotheses are valid, why have so many kinds of dimorphism evolved in dicotyledon wood? One can say, as a general principle, that if two functions are potentially to be served by imperforate tracheary elements but only one type of tracheary element is present, dimorphism in the imperforate tracheary elements will be evolved. The origin of wood containing vessel elements plus tracheids from wood that contains only tracheids is, in fact, the most dramatic example of all, and may be called dimorphism related to vessel origin. The two functions in this dimorphism are conductive efficiency and mechanical strength.

The inherent genetic capabilities of angiosperm woods are illustrated by all these kinds of dimorphisms—diversifications that have taken place many times independently in dicotyledons. We are indebted to I. W. Bailey and his students for explication of dimorphism related to vessel origin. These individuals could not at the same time have been expected to uncover the four tendencies—each characteristic of a limited number of dicotyledon families—called vessel dimorphism, tracheid dimorphism, fiber-tracheid dimorphism, and fiber dimorphism. These four kinds of dimorphisms are less common evolutionary pathways, superimposed on the major trends of evolution described by I. W. Bailey and his students Frederick H. Frost and David A. Kribs.

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