WOOD ANATOMY AND STEM OF CHLORANTHUS; SUMMARY OF WOOD ANATOMY OF CHLORANTHACEAE, WITH COMMENTS ON RELATIONSHIPS, VESSELLESSNESS, AND THE ORIGIN OF MONOCOTYLEDONS

by

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Summary

In contrast to the monopodial Ascarina and Hedyosmum, Chloranthus and Sarcandra are sympodial. Sarcandra and C. erectus have woody canes of finite duration, whereas other species of Chloranthus have shoots of one year's duration; these latter species have second year wood only on rhizomes, not on upright shoots. Rhizome portions transitional to upright stems were selected for study. Chloranthus erectus has abundant septate fibres-tracheids, C. japonicus none, and two other species a few. Chloranthus (and Sarcandra) have rays of two distinct sizes in wood: rays that are extensions of primary rays, and uniseriate and biseriate rays in fascicular areas. Wood anatomy of each of the four genera can be characterised, and is summarised in the form of a key. Except for primitiveness of vessels, wood of Chloranthaceae is very similar to that of Lactoridaceae and Piperaceae, and this probably indicates a close phyletic relationship. The large rays of chloranthaceous wood, little modified from primary rays and with upright cells predominantly, are indicative of some degree of herbaceousness and some degree of secondary woodiness. Scattered bundles and multilacunar nodes, characteristics of monocotyledons, are absent in Chloranthaceae but present in Piperaceae. The sympodial habit of Chloranthus and Sarcandra, and the presence of vessels in roots but not in stems of Sarcandra are conditions like those basic to origin of monocotyledons. The possibility that Chloranthaceae are close to Piperales and that these groups are close to origin of monocotyledons should be considered. Some cladists have hypothesised that secondary vessellessness is polyphyletic in dicotyledons. While these cases are theoretically possible, the histological and ecological scenarios that must be hypothesised for these events are ignored by cladists; most of these scenarios are unlikely for reasons explored here, although a few are still worthy of consideration. Stem endodermis is reported for three species of Chloranthus.

Key words: Ascarina, Chloranthaceae, Chloranthus, endodermis in stems, Hedyosmum, monocotyledon origins, Piperales, Sarcandra, vessel evolution, wood anatomy.

Introduction

The present study offers new data on wood anatomy of the genus Chloranthus. This paper is the fourth in a series that deals with wood of the family; the other papers have dealt with Sarcandra (Carlquist 1987), Ascarina (Carlquist 1990), and Hedyosmum (Carlquist 1992a). A summary of wood anatomy of the family is offered; other papers that have contributed to this summary are those of Thierry (1912), Swamy & Bailey (1950), and Swamy (1953).

The inherent phylogenetic interest of Chloranthaceae is very great. The family has ethereal oil cells as well as other features that place it unmistakably in Magnoliidae sensu lato (now superorder Magnoliidae of some authors). However, the location of the family within the order is not at all certain: several recent treatments consider it in a separate order (Chloranthales) of the superorder Magnoliidae (e.g., Lammers et al. 1986), which merely states the uncertainty of its relation-
ships. Endress (1987), in a review of features of the family, cites more numerous resemblances of Chloranthaceae to Hamamelidales, which lack ethereal oil cells and are not placed in Magnoliidae, than to Laurales of Magnoliidae. Chloranthaceae have some highly primitive features (e.g., wood) plus some highly specialised features (floral structure). Few will agree with Leroy's (1983) idea that the inflorescences of Hedyosmum are actually multistaminate primitive flowers (see the response to that idea by Endress 1987). The phylogenetic problems posed by Chloranthaceae are not close to solution at present.

The habit, wood, and vascular bundles of Chloranthus in particular, and Chloranthaceae in general, contain features relevant to consideration with respect to origin of monocotyledons. Although Chloranthaceae have not been considered close to origin of monocotyledons because of such features as their rather specialised flowers, opposite leaves, and cylindrical arrangement of bundles, the family is definitely worthy of consideration in this respect. Features ancestral to origin of monocotyledons include sympodial growth habit, short-lived upright stems, minimal cambial activity, wide primary rays, and vessels in roots only (tracheids only in other organs): these are features of Sarcandra (and, except for distribution of vessels, Chloranthus). Trimer, basic to flowers of monocotyledons, is evident in flowers of Chloranthaceae (female flowers of Hedyosmum have three tepals).

Chloranthaceae have a range of habits: Ascarina and Hedyosmum are monopodial shrubs to trees, whereas Chloranthus and Sarcandra have a sympodial growth form; Sarcandra, C. erectus, and C. spicatus have upright shoots that last for several years and can branch somewhat, whereas the remaining species of Chloranthus form upright stems that last only a single year. This range of habits is obviously of interest with respect to wood anatomy. An attempt is made here to characterise the wood of the species and genera studied. In this regard, the reader should be aware that species names commonly encountered in Chloranthus and Sarcandra have been supplanted in accord with the studies of Verdcourt (1985). A synonymy is offered in the Materials and Methods section.

Whether vessellessness is primary or secondary in particular dicotyledon phylads is an issue that has received comments in recent years. For several reasons, Chloranthaceae are pertinent in this regard, and a section of this paper is devoted to a discussion of this matter.

Stem endodermis is reported here for three species of Chloranthus. This feature is scarce in angiosperms, so occurrences are worthy of being recorded.

**Materials and Methods**

Stems and roots of Chloranthus serratus (Carlquist 15684 RSA) were collected in the forest of Mt. Unzen, Kyushu, Japan, in 1982 and preserved in formalin-acetic-alcohol. The kindness of Prof. Mikio Ono in aiding my field work is gratefully acknowledged. Material of other species of Chloranthus was derived from herbarium specimens: C. erectus (Stone 12116 KLU), Templer Park, Selangor, Malaysia; C. japonicus (Gorovoy 8 June 1968 RSA), N of the River Komarovka, Primorye Terr., Siberia, USSR; C. multistachys (Sino-American Botanical Expedition 1185 RSA).

Stems of Chloranthus erectus were boiled in water, stored in 50% aqueous ethyl alcohol, and sectioned on a sliding microtome. Sections for study by SEM were dried between clean glass slides. Material of C. serratus was infiltrated, embedded in paraffin and sectioned. Material of C. japonicus and C. multistachys was from herbarium specimens and was treated with 2% NaOH to expand tissues, then stored in 50% aqueous ethyl alcohol, infiltrated, embedded in paraffin, and sectioned. Sections of all species were stained with a safranin-fast green combination. Paraffin sections for SEM study were mounted on aluminum stubs followed by removal of paraffin by means of xylene. Macerations of all species were prepared by means of Jeffrey's fluid and stained with safranin.

Terms used are according to the IAWA Committee on Nomenclature (1964). Primary wall presence in perforations is referred to as membrane remnants (Carlquist 1992b). Vessel diameter is taken as lumen diameter at widest point. In scanning a section with the light microscope to determine vessels per mm², ray
areas were not excluded (but only secondary xylem was included).

The species names in *Chloranthus* and *Sarcandra* are according to Verdcourt (1984, 1985): *Chloranthus erectus* (Buch.-Ham.) Verdcourt (= *C. officinalis* Blume); *C. japonicus* Siebold; *C. multistachys* Pei; *C. serratus* Roem & Schult.; *Sarcandra chloranthoides* Gardner (= *S. irvingbaileyi* Swamy); *S. glabra* (Thunb.) Nakai [= *C. brachystachys* Blume, *S. hainanensis* (Pei) Swamy & Bailey]. *Sarcandra* thus consists of two species; *Chloranthus*, which has not been monographed as a genus, contains about 10.

**Anatomical descriptions of wood**

*Chloranthus erectus* (Figs. 1–11). Diffuse-porous (Fig. 1). Vessels mostly solitary (Fig. 1); mean number of vessels per group, 1.15. Mean diameter of vessels, 32 μm. Mean number of vessels per mm², 107. Mean vessel wall thickness, 2.0 μm. Mean vessel element length, 1207 μm. Perforation plates scalariform (Fig. 6), mean number of bars, 78. Membrane remnants in perforations varying from extensive (Fig. 7) to nearly absent (Fig. 8). Remnants present as a series of flakes (Figs. 9, 10) or as bands in the lateral ends of the perforations (Fig. 11). Lateral wall pitting of vessels consisting of circular pits about 5 μm in diameter, these pits usually in unisierate vertical rows, corresponding to vessel walls facing fibre-tracheids. All imperforate tracheary elements are septate fibre-tracheids (Figs. 4, 5), pits sparse with apertures obliquely oriented (Figs. 4, 5). Pits bordered, pit cavity diameter varying from 2 μm to 5 μm. Mean fibre-tracheid diameter, 21 μm. Mean fibre-tracheid length, 1333 μm. Axial parenchyma not observed. Rays formed from interfascicular areas wide (Fig. 2), mean width at widest point, 11.4 cells. Mean ray height more than 5 mm, accurate estimation on the basis of sections impossible. Occasional uniseriate and biseriate rays present in axial xylem formed from fascicular areas; mean height biseriate rays, 1004 μm; mean height uniseriate rays, 700 μm. All ray cells upright, prominently elongate (Fig. 3). Ray cell walls lignified, wall thickness about 3 μm. Pits interconnecting ray cells conspicuously bordered. Wood nonstoried. Starch present in ray cells and occasionally in septate fibres.

*Chloranthus japonicus* (Figs. 12–15). Wood diffuse-porous (Fig. 12), although the second year’s wood (on rhizomes and bases of upright stems) has smaller vessels, often irregular in shape and size (Fig. 15, left third of photograph), whereas the first year’s vessels are arranged in orderly rows (Fig. 12). Vessels at the end of first year wood are narrower and more tracheid-like (Fig. 14, middle); some may actually be tracheids. During the second year’s growth (Fig. 14, top), wider vessels are intermixed with narrower vessels; narrower vessels bear scalariform end wall pitting typical of wider vessels (Fig. 15). Vessels as seen in transection in large groups by virtue of absence of imperforate tracheary elements. Mean vessel diameter, 33 μm. Mean vessel wall thickness, 2.2 μm. Mean vessel element length, 1188 μm. Perforation plates all scalariform (Fig. 20). Mean number of bars per plate, 76. Lateral wall pitting of vessels transitional, opposite, or alternate. Axial parenchyma not present in the ordinary sense; parenchyma cells between vessels in metaxylem grade into rays within the fascicular areas. Rays of two sorts, the large rays essentially extensions of primary rays (Fig. 13, left and right), whereas uniseriate or biseriate rays are present in fascicular areas (Fig. 13, centre). Mean height of the large rays more that 5 mm; mean height of uniseriate rays, 1265 μm. Ray cells all upright (Fig. 15, bottom). Ray cell walls lignified but thin (1.2 μm thick). Wood nonstoried. Starch present in ray cells.

*Chloranthus multistachys* (Fig. 19). Wood diffuse-porous, although the second year’s wood has vessels irregular in shape and size. Second year wood present only in rhizomatous stems and at bases of upright stems. Vessels often not solitary, often in radial rows, mean number of vessels per group, 1.93. Mean vessel diameter, 39 μm. Mean number of vessels per mm², 64. Mean vessel wall thickness, 1.8 μm. Mean vessel element length, 1248 μm. Perforation plates scalariform, membrane remnants common in perforations. Mean number of bars per perforation plates, 72. Lateral wall pitting of vessels opposite or alternate. Imperforate tracheary ele-
Figs. 1–5. Wood sections of *Chloranthus serratus*. – 1: Transection, showing abundance of fibre-tracheids compared to vessels. – 2: Tangential section; two large multiserate rays are evident. – 3: Radial section, showing upright ray cells and, at right, septate fibre-tracheids. – 4: Two septate fibre-tracheids from radial section; pit sizes are different. – 5: SEM photograph of septate fibre-tracheids from radial section; pit apertures are oblique. — Figs. 1 & 2, scale above Fig. 1 (divisions = 10 μm); Fig. 3, scale above Fig. 3 (divisions = 10 μm); Fig. 4, scale above Fig. 4 (divisions = 10 μm); Fig. 5, bar at upper right = 5 μm.
Figs. 6–11. SEM photographs of perforations plates from radial sections of *Chloranthus erectus* wood. – 6: Entire perforation plate; remnants can be seen in perforations. – 7: Perforation plate with maximal retention of membrane remnants. – 8: Perforation plate with only a few thread-like remnants of membrane. – 9: Flake-like membrane remnants in perforations. – 10: Small vestiges of membranes along margins of perforations. – 11: Membrane remnants in lateral ends of perforations. — Fig. 6, bar = 5 μm; Figs. 7–11, bar in upper right of Fig. 7 = 1 μm.
Figs. 12–15. Sections of wood of *Chloranthus japonicus*. — 12: Transection, pith at right; two years accumulation of secondary xylem are present. — 13: Tangential section; large multiseriate rays at left and right, uniseriate rays in fascicular portion, centre. — 14: Transection; cells with thicker walls, center, represent end of first year’s growth, second year’s wood above. — 15: Radial section; the irregular cells in left third of photographs represent the second year’s wood. — Fig. 12 & 13, scale above Fig. 1; Fig. 14 & 15, Scale above Fig. 3.
Figs. 16–20. Wood sections of *Chloranthus*. – 16–18: *C. serratus*. – 16: Transection; a single year’s wood is shown. – 17: Radial section; vessels with scalariform perforation plates, above; ray cells, below center; septate fibre-tracheids, bottom. – 18: Perforation plate from tangential section; membranes in perforations are intact. – 19: *C. multistachys*, SEM photograph of perforations showing membrane remnants. – 20: *C. japonicus*; SEM photograph of perforations nearly free of membrane remnants. — Fig. 16, scale above Fig. 1; Fig. 17, scale above Fig. 3; Fig. 18, bar = 5 μm. Figs. 19, scale in Fig. 8. Fig. 20, scale in Fig. 7.
ments are all septate fibre-tracheids, less abundant in number than vessel elements, with pits sparser than on lateral walls of vessels, pits about 4 μm in diameter. Mean fibre-tracheid length, 1352 μm. Axial parenchyma not observed. Larger multiseriate rays are essentially extensions of primary rays; mean height of multiseriate rays more than 5 mm. Mean width of multiseriate rays, 6.2 cells. A few uniseriate or biseriate rays are present within the axial xylem formed in the fascicular areas. All ray cells are upright. Ray cell walls are lignified, about 1.4 μm thick. Pits among ray cells simple or very slightly bordered. Wood nonstoried. Starch present in ray cells.

*Chloranthus serratus* (Figs. 16–18). Wood diffuse-porous, although diminution in vessel diameter is evident at the end of the growth ring (representing a single year) (Fig. 16). Vessels often in radial rows (Figs. 16, 17). Mean number of vessels per group, 2.2. Mean vessel diameter, 44 μm. Mean vessel wall thickness, 2.7 μm. Mean vessel element length, 1264 μm. Perforation plates scalariform (Fig. 17, above). Many perforations observed to contain membrane remnants that are intact (Fig. 18). Mean number of bars per plate, 82. Lateral wall pitting mostly alternate, rarely opposite. Imperforate tracheary elements all septate fibre-tracheids (Fig. 17, bottom); pit diameter 2 μm, borders vestigial. Mean fibre-tracheid diameter, 25 μm; mean length, 1372 μm. Axial parenchyma not observed. Multiserate rays wide, little altered extensions of primary rays; mean height of multiseriate rays more than 5 mm. Uniseriate and biseriate rays present in axial secondary xylem formed in fascicular areas. Most ray cells upright, a few procumbent cells in which horizontal dimension only slightly exceeds vertical dimension present (Fig. 17). Ray cell walls lignified (Figs. 16, 17). Ray cell walls about 2.0 μm thick. Pits among ray cells simple or with narrow borders. Wood nonstoried. Starch present in ray cells.

**Stem endodermis**

The layer of cells external to phloem fibres is differentiated as an endodermis in stems of *C. erectus, C. multistachys, and C. serratus*. The endodermis in these species has a typical Caspian strip which stains rose with safranin in contrast to the remainder of the cell wall, which stains green with fast green. An endodermis of this sort has not previously been reported in stems of Chloranthaceae, although Thierry (1912) figures an endodermis for *C. oldhamii* Solms. The endodermis he figures is like a layer of thin-walled sclereids rather than cells with thin primary walls bearing Caspian strips.

**Stem endodermis** is not a common phenomenon in dicotyledons, but the instances reported thus far do not appear to have phylogenetic significance within dicotyledons at large (presence and absence within a single family may be significant). For example, stem endodermis with clear Caspian strips occurs in helianthoid Asteraceae such as *Fitchia* (Carlquist 1957). Metcalfe and Chalk (1950) report a number of genera of Lamiaceae with various types of endodermis, including some with typical Caspian strips. Asteraceae and Lamiaceae are not considered families extremely close to each other, and stem endodermis has been reported, in any case, in only a small number of dicotyledon families. The occurrence of stem endodermis in monocotyledons may be more significant with relation to the stem endodermis in Chloranthus. Stem endodermis may be found in rhizomes of Araceae such as *Acorus*. The reports of stem endodermis in *Chloranthus* are from bases of upright stems; these regions are very close to the prostrate stem portions that form the rhizomes, and are histologically essentially the same as the rhizomes.

**Differences in wood of Chloranthus**

The wood of the few species of *Chloranthus* differs with respect to quantitative features, but these are of relatively little significance. The qualitative differences are distinctive and relate to habit. The selection of the species was designed to cover the range within the genus in woodiness. *Chloranthus erectus* is the woodiest, with canes that add wood along their length, although that wood accumulation is finite: only 2–3 mm thickness of secondary xylem. *Chloranthus japonicus, C. multistachys,* and *C. serratus* have upright stems that cannot be called woody: they do not develop secondary xylem along
most of their length after the first year, and only the rhizomes and the transitions between rhizomes and upright stems add secondary xylem after the first year, and this added xylem tends to be irregular in configuration (e.g., Fig. 12). Of the three species mentioned, _C. japonicus_ qualifies as the most nearly herbaceous (its range is also the most northerly).

The four species fall into three groups with respect to fibre-tracheid presence: _Chloranthus erectus_: in the transition from metaxylem to secondary xylem, parenchyma among vessels is supplanted by fibre-tracheids; as in most dicotyledon woods, imperforate tracheary elements (septate fibre-tracheids in this genus) are much more abundant than vessel elements. _Chloranthus spicatus_ (Thunb.) Maxim. agrees with _C. erectus_ with respect to fibre-tracheid morphology and presence (Takahashi 1985). — _Chloranthus multi-stachys_ and _C. serratus_: in the transition from metaxylem to secondary xylem, parenchyma among the vessels is supplanted by fibre-tracheids, but the number of vessels increases at this point, so that fibre-tracheids are relatively few in number compared to the vessel elements, and the secondary xylem is composed mostly of vessel elements. — _Chloranthus japonicus_: in the transition from metaxylem to secondary xylem, parenchyma among the vessels is supplanted by rays composed of upright cells. Fibre-tracheids are absent, and the axial portion of the secondary xylem consists wholly of vessels.

The shift from abundance to paucity to absence of fibre-tracheids is a significant trend. The most obvious correlation is with woody versus herbaceous. _Chloranthus erectus_ is clearly the woodiest, and tallness of its canes and the fact that they can branch during a second or third year relate to the greater mechanical support provided by the abundant fibre-tracheids (_C. spicatus_ is similar to _C. erectus_ in habit and fibre-tracheid presence: Takahashi 1985). In the other species, which are relatively herbaceous, fibre-tracheids are few or (_C. japonicus_) none. Addition of secondary xylem in these species occurs only on rhizomes and the bases of upright shoots transitional to the rhizomes; for these species, phloem fibres likely offer sufficient mechanical support for the relatively short duration and stature of the upright stems. _Chloranthus japonicus_ represents the ultimate end point in such a series.

The series formed by these _Chloranthus_ species can be read from woody to herbaceous, although there is no evidence for unidirectional evolution of that sort. The important correlation is with the cane-like habit, which, in turn, is related to a sympodial habit. Fibre-tracheids would not likely be lost if a monopodial habit were retained. A series such as that cited above is instructive with relation to origin of monocotyledons, because they have xylem lacking in dimorphism of tracheary elements (strength provided instead by extraxylary fibres) and sympodial growth habit: both of these conditions have been completely achieved by _C. japonicus_.

**Chloranthaceae and the origin of monocotyledons: relationships of Chloranthaceae**

The preceding paragraph shows how two interrelated conditions that must be hypothesised as basic to origin of monocotyledons: sympodial growth habit and monomorphism of tracheary elements. However, the monomorphism in _C. japonicus_ is achieved by presence of vessels without any fibre-tracheids, yet a primitive monocotyledon ought to have not vessels throughout, but tracheids throughout the plant body or in roots only. Cheadle's (1942) data shows that the most primitive monocotyledons already have vessels in roots only, although Cheadle (1953) hypothesises independent origin of vessels in monocotyledons and dicotyledons. Tracheids throughout a plant but with vessels in roots is a condition found in _Sarcandra_ (Carlquist 1987). If a species of _Sarcandra_ had the herbaceous habit of _Chloranthus japonicus_, it would, in terms of bundle structure and tracheary element type and distribution throughout the plant satisfy the criteria required for a dicotyledon ancestral to a monocotyledon (the _Sarcandra_ type of dicotyledon was not considered by Cheadle, 1953, in his hypothesis of origin of vessels in monocotyledons). Criteria other than these would have to be met for plants like Chloranthaceae to be ancestral to monocotyledons, however, and extant
Chloranthaceae do not satisfy all of these criteria.

Among the criteria not satisfied by Chloranthaceae as potential ancestors of monocotyledons are the opposite leaves, cylinder of bundles, and unilacunar-two trace nodes (Swamy 1953). These nodes, however, are believed to be the most primitive type in dicotyledons (Bailey 1956). The family Piperaceae, however, has alternate leaves and scattered bundles. These are significant as an example of how the leaf position, nodal anatomy, and bundle configuration likely basic to monocotyledons are present in a phylad closely related to Chloranthaceae provided that Piperaceae are, in fact, closely related to Chloranthaceae. Are Chloranthaceae and Piperaceae closely related?

The wood anatomy of Lactoridaceae proves to be essentially identical to that of Piperaceae (Carlquist 1990b). This by itself proves nothing about the relationships of Chloranthaceae, but it does widen our concepts of Piperales, in which order Lactoridaceae must be placed if evidence from wood is as significant as I believe it to be. The wood features of Chloranthaceae are very much like those of Lactoridaceae and Piperaceae: the only two differences of significance are the presence of scalariform perforation plates and nonstoried wood in Chloranthaceae; perforation plates are simple (occasionally scalariform in Lactoridaceae) and wood is storied in Lactoridaceae and Piperaceae. These are both differences of evolutionary level rather than systematic divergence per se. Both storied wood and simple perforation plates have evolved in many phylads independently, so that they are much more likely to be homoplasies than synapomorphies. Such interesting features as presence of living septate fibre-tracheids with vestigially bordered pits, wide tall multiseriate rays little altered from primary rays, and upright ray cells exclusively or nearly so are common to the three families. Certainly the wood anatomy of the three families is compatible with the idea that they are more closely related to each other than each is to the nearest outgroup.

Loss of cambial activity is thought to be characteristic of origin of monocotyledons. Certainly Chloranthus shows minimal cambial activity, combined with wide primary rays. Arber (1917) claimed there was vestigial cambial activity within vascular bundles of monocotyledons, although this statement has been disputed by some (e.g., Katherine Esau, personal communication). Philipson et al. (1971) have carefully examined this question, and concluded that some monocotyledon genera (Gliriosa, Veratrum) have cambial activity that adds vascular tissue within a bundle during a second growing season. Philipson et al. (1971) note that monocotyledons lack both intrafascicular cambia and initiation of rays within bundles. However, the presence of residual cambia in Liliaceae (because of its primitive xylem and other reasons a family often considered as primitive within monocotyledons) is significant in that it indicates derivation of monocotyledons from a group of dicotyledons with at least some cambial activity. Vascular bundles like those cited by Philipson et al. (1971) could be derived from vascular bundles like those in Sarcandra or Chloranthus merely by reduction of cambial activity—a matter of degree rather than a presence or absence difference.

The large multiseriate rays of Chloranthaceae, Lactoridaceae, and Piperaceae are mostly little-altered continuations of primary rays. Rays in all of these families are composed of upright cells exclusively or predominantly. Both features suggest paedomorphosis, using the criteria of Carlquist (1962). In fact, a species of Piperaceae (Macropiper excelsum Miq.) was cited as having the paedomorphic descending curve of vessel element length with age, a curve contrary to the curve for typical woody dicotyledons (Carlquist 1962). Paedomorphosis characterises wood of dicotyledons that are either secondarily woody or are herbaceous or very nearly herbaceous (Carlquist 1988a). Because the herbaceous habit is basic to monocotyledons, the occurrence of paedomorphic rays and vessel elements in Chloranthaceae and possibly allied families offers yet another reason why Chloranthaceae should be considered in connection to origin of monocotyledons. Although there is no decisive evidence on whether the monopodial (Ascarina, Hedyosmum) or symподial (Chloranthus, Sarcandra) habit is primitive in Chloranthaceae, there are reasons to
believe the arboreal habit in *Hedyosmum* is derived (e.g., the axial parenchyma type in *Hedyosmum*, the most arboreal genus, is more specialised than axial parenchyma conditions elsewhere in the family; male flowers of *Hedyosmum* are quite reduced).

Other features of Chloranthaceae bear consideration with respect to origin of monocotyledons. Trimery, characteristic of flowers of monocotyledons, is prominent in flowers of Saururaceae of the Piperales (Tucker 1985) and in flowers of Lactoridaceae (Carlquist 1964). The flowers of Chloranthaceae are highly reduced, but *Chloranthus* retains trimery in its androecium, and *Hedyosmum* retains trimery in tepals of female flowers (Endress 1987). Monosulcate pollen grains, the type basic to monocotyledons, occur in *Ascarina* (Swamy 1953); the other genera of Chloranthaceae have types that are closely related to monosulcate pollen grains. Burger (1977) hypothesised that Piperales are closely related to monocotyledons. The evidence adduced by Burger, including such features as floral anatomy, is different from that cited by the above authors, but it deserves reconsideration.

The significance of the sympodial habit for distribution of vessels in monocotyledons as compared to dicotyledons has not been sufficiently appreciated. Bailey (1944, 1953) believed that vessels originated in secondary xylem of roots and stems of dicotyledons, whereas Cheadle (1942) presented evidence that in monocotyledons, vessels originated in the root and then progressed upward in the plant phyletically. Because there is a continuity between the root and the stem secondary xylem formed in a given year in a typical monopodial dicotyledon, simultaneous vessel origin is likely: for efficient conduction, vessels in the root should be intercontinuous with vessels formed in the stem. This is not true in a monocotyledon because of the sympodial habit. With the sympodial habit of monocotyledons, new roots are constantly initiated on the newly-formed rhizome portions, so that all roots are adventitious and no roots have secondary xylem. Therefore, interconnections between vessels of roots, not formed ontogenetically at the same time as the tracheary elements of the stems from which the roots branch, are not to be expected. In *Sarcandra*, there is a transitional kind of sympodial habit, in which rhizomes, roots, and stems last more than one year (although only for a few years at most). One might expect that a vessel condition more like the dicotyledon condition than the monocotyledon condition would be present in *Sarcandra* because of the brevity of secondary xylem activity in stems and roots. In a sympodial dicotyledon with longer lasting stems and roots (e.g., a woody *Piper*), interconnection between vessels in roots and those of stems on which the roots have formed is to be expected.

If one looks at recent attempts to use cladistics to elucidate relationship of families mentioned above as well as other families with notably primitive features, one sees quite disparate results. The cladograms offered by Young (1981), Lammers *et al.* (1986) and Donoghue and Doyle (1989) dealing with these families differ markedly from each other with respect to key families. For example, Lammers *et al.* (1986) show Piperales and Chloranthales as distant outgroups, isolated from each other, of Magnoliidae (in which they include Lactoridaceae). Donoghue and Doyle (1989), on the other hand, show families traditionally placed in Magnoliidae and/or Laurales branching off their clade both above and below Hamamelidae. Donoghue and Doyle (1989) place Chloranthaceae close to Trimeniaceae, Austrobaileyaceae, Monimiaceae, and Amborellaceae; they place Lactoridaceae close to Piperaeae and Lactoridaceae but also, curiously, close to Aristolochiaceae. One especially pertinent feature of the Donoghue & Doyle scheme is that Piperaeae, Saururaceae, and Lactoridaceae (but not Chloranthaceae) are placed close together and close to origin of monocotyledons, as represented by the single monocotyledon family they include, Liliaceae. It would be easy to say that Donoghue and Doyle (1989) are ‘correct’ except that they have misplaced Chloranthaceae (a close relationship between Chloranthaceae and Trimeniaceae, also suggested by Endress, 1987, is hypothesised by Donoghue and Doyle). The matter cannot be resolved by such statements. The three cladograms of primitive dicotyledon families cited are strikingly differ
ent, and there is no reason to believe that any of the workers has been less than diligent. The problem appears to lie with the relictual nature of these families. In such families, characters of phyletic significance are relatively few – so many have been lost in the course of evolution. The paucity of significant characters means that an attempt at cladistic analysis will by this circumstance over-stress some characters. The solution to this problem lies not so much in attempts to reuse information (largely from gross morphology) the information already at hand, but to construct cladograms with the aid of new, more highly significant, kinds of data. Various types of DNA data are likely to yield data of decisive phyletic importance. Therefore, my recommendation is that hypotheses such as the idea that Chloranthaceae may be close to Piperales, that Lactoridaceae is in Piperales, and that Chloranthaceae and Piperales are close to origin of monocotyledons, should be compared to results provided by new DNA data.

**Phylesis within Chloranthaceae**

Because of divergences among species of *Chloranthus* with respect to wood anatomy, as discussed above, xylary features of *Chloranthus* are more difficult to summarise than are those of the other genera. However, the salient differences can be summarised in the form of a key:

<table>
<thead>
<tr>
<th>Rays of two sorts (wide, tall multiseriate rays are extensions of primary rays, uniseriate and biseriate rays are formed by cambium of the fascicular areas); cambial action restricted because of sympodial habit; ray cells contain starch.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Vessels in roots only, not in upright stems; axial parenchyma diffuse</td>
</tr>
<tr>
<td>Vessels in stems and roots; axial parenchyma absent or nearly so</td>
</tr>
<tr>
<td>Multiseriate rays of various widths, not just biseriate and wide multiseriate; cambial action indefinite because of monopodial habit; droplets or amorphous deposits of yellow-staining compounds in ray cells.</td>
</tr>
<tr>
<td>Axial parenchyma vasieentric; uniseriate rays present only in young stems; fibre-tracheoids all septate</td>
</tr>
</tbody>
</table>

The axial parenchyma and ray type of *Ascarina* are more primitive than the corresponding condition in *Hedyosmum*. *Ascarina* has nonseptate fibre-tracheids or even tracheids. *Ascarina* has more primitive inflorescences than *Hedyosmum* in the interpretation of Endress (1987).

The diffuse axial parenchyma of *Sarcandra* marks that genus as at least as primitive as *Ascarina*. The presence of vessels only in roots of *Sarcandra* and its diffuse parenchyma are best interpreted as primitive in comparison to *Chloranthus*, which has vessels in both roots and stems, clear differentiation between vessels and septate fibre-tracheids, and no appreciable amount of axial parenchyma. I am dubious about the report of diffuse axial parenchyma in *C. spicatus* by Takahashi (1985); such parenchyma does not appear in Takahashi’s figures, and must be quite scarce, if present.

If one attempts to say whether the sympodial genera *Chloranthus* and *Sarcandra* are more primitive than the monopodial genera *Ascarina* and *Hedyosmum* on the basis of wood anatomy, one cannot reach a conclusive distinction. Bisexual flowers, as in *Chloranthus* and *Sarcandra*, are traditionally considered more primitive than unisexual flowers (*Ascarina*, *Hedyosmum*), but that is a single character that should not be stressed. As with phylogeny of families potentially related to Chloranthaceae, DNA data that can be analysed so as to yield polarity in phyletic status are very much needed.

**Vessellessness in dicotyledons**

The presence of intact pit membrane remnants in perforations of vessel elements in *Chloranthus serratus* is interesting in that it indicates how readily the normal pattern of lysis of pit membranes can be reversed. However, this occurrence should not be read as a phyletic loss of vessels. As the preparations very clearly show, the tracheary elements are still dimorphic, septate fibre-tracheids are still present, and thus even if intact pit membranes occurred in all perforations of all individuals of *C. serratus*, the most important criteria of vessellessness would not have been satisfied. In order for secondary vessellessness to be
attained, not only would pit membranes have to be retained uniformly in all perforations, the imperforate tracheary elements accompanying the vessel elements would have to vanish—a change unlikely as long as there is selection for mechanical strength in stems (should both types of tracheary elements be retained, most criteria of vessellessness would not be satisfied). Even if such a change did occur, one would have to have retrograde evolution in order to erase any differences between end wall pitting and lateral wall pitting in the vessel elements—differences which characterise the vast majority of vessels in dicotyledons. Thus, secondary vessellessness in a woody dicotyledon is highly unlikely unless one invents a quite extreme scenario.

An extreme scenario that could lead to vessellessness has been described in the case of two nearly vesselless species of Ephedra (Carlquist 1988b). A phylad in which both vessel elements and tracheids were present would have to adapt to an extremely dry cold habitat, like the Ephedra species, in which tracheids are more advantageous than vessel elements at restricting the embolisms created by drought or freezing. Then such a phylad would have to shift back to more moderate conditions—in fact, all of the extant vesselless dicotyledons are restricted to the most mesic conditions possible.

Another scenario for secondary vessellessness—but one that will apply in only a few limited instances and that does not really involve loss of vessels is suggested by the stems of Sarcandra or stems of Nymphaeaceae. Comparative work on secondary xylem of dicotyledons led Bailey (1944, 1953) to conclude that in dicotyledons, vessels originated in secondary xylem (simultaneously in roots and stems), then progressed into primary xylem. There are dicotyledons in which vessels occur in secondary xylem but not in primary xylem. If such a dicotyledon lost secondary xylem entirely, it could become vesselless. But the outcome of this scenario would be an herbaceous plant. Nymphaeaceae, which are vesselless and have no secondary xylem, might be an example of this scenario or they might be primitively vesselless—until we know the ancestry of Nymphaeaceae, we cannot decide which hypothesis is correct. If stems of Sarcandra have less secondary xylem than do the roots, then possibly vessels may be absent because the development of wood is foreshortened in stems—although there are other possible scenarios, such as selective advantage of vessels in roots versus stems.

Some cladists, such as Young (1981) or Doyle and Donoghue (1989) have proposed events of secondary vessellessness in woody dicotyledons. They evade the responsibility of explaining the histological, ecological, and habital scenarios that must be proposed to account for such proposed events of vessel loss. The above discussion is intended to show what some of these unappreciated complexities may be. The extremeness of the scenarios that must be proposed should be considered by those who feel that more parsimonious cladograms can be achieved by such hypotheses.

References


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