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review and synthesis**

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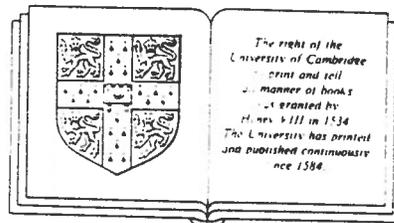
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Anatomy of vine and liana stems: a review and synthesis

SHERWIN CARLQUIST

Introduction

In the 19th century, the work of Westermeier & Ambronn (1881) and Schenck (1893) initiated appreciation of the many ways in which stem and wood anatomy of climbing plants differs from that of self-supporting plants. During the first half of the 20th century, data on stem and wood anatomy accumulated in the form of systematic comparisons, as particular taxonomic groups were investigated. The present chapter, as well as others in this volume, attempts to review this literature and present a new synthesis of the characteristics of vines and how they are related to habit, function, and ecology. After Haberlandt (1914), interest in a synthesis between form and function lagged, perhaps mostly because experimental work in plant physiology of scandent dicotyledons was relatively dormant; the recent renewed interest represented by the work in this volume permits new syntheses. A review of anatomical data is presented here by way of showing what comparative anatomical patterns suggest in terms of function, and thereby what correlations can be demonstrated or may in the future be demonstrated.

Cambial variants and cambial activity

Since the pioneering work of Schenck (1893), Pfeiffer (1926), and Obaton (1960), there has been general appreciation that lianas and vines, much more frequently than self-supporting woody plants, are characterized by the presence of cambial variants (the term from Carlquist, 1988; 'anomalous secondary thickening' of other authors). At the outset, one must note that cambial variants are by no means unique to scandent woody plants. For example, successive cambia (the 'concentric interxylary phloem' of some earlier authors) occur in various families of Chenopodiales (Centrospermae):

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Aizoaceae, Amaranthaceae, Basellaceae, Caryophyllaceae, Chenopodiaceae, Nyctaginaceae, Phytolaccaceae, and Rhabdodendraceae. Only a few of these (e.g. *Bougainvillea* of the Nyctaginaceae) are woody vines. Some of the complex forms of cambial variants (e.g. expansion of the woody stem by proliferation of parenchyma as in *Bauhinia*, *Flabellaria*, and *Mendoncia*) are found virtually only in lianoid plants (Pfeiffer, 1926). With attention to these facts, we may survey scandent dicotyledons with respect to cambial variants. The listing below is based on Carlquist (1988); genera of non-climbing plants have been omitted. For illustrations and detailed discussions of terminology and appropriate literature, see Carlquist (1988). Data are from compilations such as Solereder (1908) and Metcalfe & Chalk (1950) with additional sources as noted. These listings must be regarded as provisional, because more examples are likely to be discovered.

Successive cambia (centrifugal):

Amaranthaceae: *Chamissoa*.

Connaraceae: *Rourea* (Boureau, 1957), *Spiropetalum* (Obaton, 1960).

Convolvulaceae: *Argyrea*, *Calonyction*, *Convolvulus*, *Dicranostyles*, *Ericybe*, *Exogonium*, *Hewittia*, *Ipomoea*, *Maripa*, *Merremia*, and *Porana* (Carlquist & Hanson, 1991).

Cucurbitaceae: *Adenopus*, *Luffa*, *Melothria*, *Mormodica*, *Physedra*, *Sphaerosicyos* (Zimmermann, 1922).

Dilleniaceae: *Doliocarpus* (Chalk & Chattaway, 1937).

Dioncophyllaceae: *Dioncophyllum* (Boureau, 1957).

Fabaceae: *Machaerium*, *Milletia*, *Mucuna*, *Rhynchosia*, *Strongylodon*, *Wisteria* (Boureau, 1957).

Hippocrateaceae: *Cheiloclinium*, *Salacia*, *Salacighia* (Obaton, 1960).

Icacinaceae: *Icacina*, *Rhaphiostylis* (Obaton, 1960).

Menispermaceae: all lianoid genera.

Nyctaginaceae: *Bougainvillea* (Esau & Cheadle, 1969; Pulawska, 1973).

Passifloraceae: *Adesmia* (Ayensu & Stern, 1964), *Adenia* (Obaton, 1960).

Sapindaceae: *Serjania pinnata* (Pfeiffer, 1926).

Vitaceae: *Tetrastigma* sp. (Carlquist 1988).

In gymnosperms, lianoid species of *Gnetum* have successive cambia (Haberlandt, 1914; Martens, 1971).

Successive cambia (centripetal): This term is applied to cambia formed in the pith; Piperaceae and certain other families are excluded because they have bundles formed in the pith in the primary stem, and these may have cambial activity, but no cambia outside of these bundles are present in the pith.

Acanthaceae: *Afromendoncia* (Obaton, 1960).

Apocynaceae: *Willughbeia* (Scott & Brebner, 1891).

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Asclepiadaceae: *Periploca* (Scott & Brebner, 1891).

Convolvulaceae: *Bonamia*, *Prevostea* (Obaton, 1960); *Exogonium* (Carlquist & Hanson, 1991).

Icacinaceae: a ring of inverted bundles with secondary growth between the first-formed secondary xylem and outer rings formed by successive cambial is illustrated for *Icacina mannii* by Obaton (1960).

Interxylary phloem derived from a single cambium:

Acanthaceae: *Mendoncia*, *Thunbergia* (Carlquist & Zona, 1987).

Asclepiadaceae: *Ceropegia*, *Leptadenia* (Singh, 1943).

Combretaceae: *Calycopteris*, *Combretum*, *Guiera*, *Thiloa* (van Vliet, 1979).

Convolvulaceae: *Ipomoea versicolor* (Solereider 1908).

Cucurbitaceae: *Cucurbita*, *Lagenaria*.

Fabaceae: *Entada* (Haberlandt, 1914), *Mucuna pruriens* (Obaton, 1960).

Icacinaceae: lianoid genera of the tribe Sarcostigmateae (Bailey & Howard, 1941a).

Loganiaceae: *Strychnos*, *Usteria* (Scott & Brebner, 1891; Obaton, 1960; Menega, 1980).

Cambial normal in products but abnormal in conformation or dispersion:

Stems oval in transection because of differential amounts of xylem deposition (but other variants not present):

Celastraceae: *Celastrus*.

Combretaceae: *Quisqualis* (van Vliet, 1979).

Icacinaceae: *Iodes ovalis* (Bailey & Howard, 1941a).

Malpighiaceae: *Heteropteris*.

Marcgraviaceae: *Marcgravia*.

Moraceae: *Ficus*.

Piperaceae: *Piper*.

Polygonaceae: *Atraphaxis*.

Verbenaceae: *Lantana*, *Petrea*.

Stems markedly flattened in transection:

Apocynaceae: *Landolphia owariensis* (Obaton, 1960).

Aristolochiaceae: *Aristolochia*, *Pararistolochia*.

Fabaceae: *Abrus*, *Bauhinia*, *Rhynchosia*.

Vitaceae: *Cissus*.

Stems lobed in transection:

Celastraceae: *Celastrus*.

Combretaceae: *Combretum dolichandrone* (Obaton, 1960).

Fabaceae: *Acacia pennata* (Obaton, 1960).

Rubiaceae: *Mussaenda* (Obaton, 1960).

Verbenaceae: *Lantana* (Bhambie, 1972).

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Stems with xylem furrowed (cambium becoming unilateral to various degrees at places on the stem, so that less secondary xylem than secondary phloem is produced at those places):

Bignoniaceae: *Adenocalymma*, *Anemopaegma*, *Arrabidaea*, *Bignonia*, *Callichlamys*, *Cuspidaria*, *Distictis*, *Doxantha*, *Fridericia*, *Glaziova*, *Haplolophium*, *Lundia*, *Melloa*, *Paragonia*, *Petastoma*, *Phaedranthus*, *Phryganocydia*, *Pithecoctenium*, *Pleonotoma*, *Pyrostegia*, *Stizophyllum*, *Tanaecium* (Schenck, 1893; Pfeiffer 1926).

Convolvulaceae: *Bonamia*, *Neuropeltis*, *Prevostea*.

Fabaceae: *Centrosema plumieri*.

Hippocrateaceae: *Hippocratea*, *Salacia*.

Icacinaceae: *Neostachyanthus*, *Pyrenacantha*.

Malpighiaceae: *Triapsis odorata*.

Passifloraceae: *Crossostemma*, *Passiflora* (Ayensu & Stern, 1964).

Xylem in plates (wide rays lacking in cell wall lignification and not altering during secondary growth, so that 'fibrous' xylem is separated by thin-walled ray cells):

Aristolochiaceae: *Aristolochia*.

Asclepiadaceae: *Ceropegia* (some species).

Asteraceae: *Mikania* (Pfeiffer, 1926; van der Walt *et al.*, 1973).

Cucurbitaceae: *Coccinia* (Fisher & Ewers, 1990).

Menispermaceae: *Menispermum* (Pfeiffer, 1926).

Vitaceae: *Cissus* (Obaton, 1960).

Wood parts ('fibrous' woody parts) dispersed by parenchyma proliferation:

Acanthaceae: *Afromendoncia*, *Mendoncia* (Schenck, 1895, Obaton, 1960).

Bignoniaceae: *Macfadyena mollis* (Schenck, 1895).

Convolvulaceae: *Ipomoea umbellata* (Schenck, 1895), *Merremia*, *Neuropeltis*, *Prevostea*.

Fabaceae: *Bauhinia* (*B. championi*, *B. japonica*, *B. langsdorffiana*: Scheck, 1895), *Kunstleria ridleyi*.

Icacinaceae: *Icacina*, *Iodes*, *Phytocrene*, *Pyrenacantha*.

Malpighiaceae: *Banisteria*, *Flabellaria*, *Mascagnia*, *Tetrapteris* (Schenck, 1895).

Vitaceae: *Cissus*.

Divided xylem cylinder (a furrowed xylem cylinder ontogenetically subdivides into segments, each of which becomes surrounded by a cambium):
Sapindaceae: *Serjania corrugata* and allied species.

Compound secondary xylem (in addition to a normal cylinder of secondary xylem, cambium forms around cortical bundles and adds secondary xylem to them):

Sapindaceae: *Paullinia* (16 of 122 species), *Serjania* (91 of 172 species).

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Combinations of cambial variants:

Acanthaceae: *Afromendoncia*, *Mendoncia* (dispersed xylem segments plus interxylary phloem formed from a single cambium: Obaton, 1960; Carlquist & Zona, 1987).

Fabaceae: *Bauhinia* (flattened stems with dispersed xylem segments); *Machaerium*, *Milletia* (flattened stems with successive cambia).

Icacinaceae: *Icacina mannii* (successive cambia, with tendency of cambium to become unilateral in action in places, so that there are grooves in the xylem rings: Metcalfe & Chalk, 1983).

Menispermaceae: *Anomospermum* (flattened stems with successive cambia: Schenck, 1893).

Polygalaceae: *Securidaca* (successive cambia, grooved stems: Schenck, 1893).

Sapindaceae: *Thinouia* (lobed stem outline, successive cambia).

Why is the 'normal' cambium so pervasive in self-supporting trees and shrubs, but characteristic of a smaller proportion of vining and lianoid dicotyledons? The answer very likely involves several factors. For self-supporting trees and shrubs, a dense wood is achieved with the greatest certainty by means of a 'normal' cambium. Successive cambia, xylem dispersed (by parenchyma proliferation), and xylem in plates result inevitably in a greater proportion of parenchyma interspersed among 'fibrous' wood than is the case in most 'normal' cambia. A higher proportion of parenchyma in a dicotyledonous stem is not disadvantageous if there is a selective advantage for interspersed parenchyma. One possible selective advantage is 'cable construction' (flexibility of the stem without damage to vessels: Schenck, 1893; Putz & Holbrook, Chapter 3). Other potential advantages include sites for wound healing (Fisher & Ewers, 1990) or storage of water or photosynthates.

Vessel restriction patterns, and unusual ontogenetic change in vessel presence and diameter

In many dicotyledons, vessels tend to increase in diameter as a stem grows, and although this can be observed readily (Carlquist, 1984a), it is not often reported explicitly. Neither this tendency, nor the annual change in vessel diameter involved in ring porosity, is under discussion here. Rather, in certain lianas there are drastic and sudden increases in diameter of vessel elements shortly after the onset of secondary growth. This takes place in some lianas – for example, *Acacia pennata*, *Cissus afzelii*, *C. barteri*, *Salacia bipindensis*, and *Strychnos densiflora* (Obaton, 1960).

In a more extreme phenomenon, secondary xylem begins with a 'fibrous' wood in which vessels are either lacking or are of the same diameter as imperforate tracheary elements or apparently so (i.e. narrow vessels are very

similar to imperforate tracheary elements as seen in transection). Later-formed secondary xylem – often abruptly initiated – contains wider vessels. Attention was called to this phenomenon by Haberlandt (1914), who considered this a way of achieving mechanical strength at first, followed by development of a wood efficient at water conduction. This can be considered a form of vessel restriction (non-random distribution of vessels within the secondary xylem), a term originally devised for a different pattern of vessel distributions: absence of vessels adjacent to rays, as in Papaveraceae (Carlquist & Zona, 1988). Examples of a vessel restriction pattern in which wood appears vessel-free at first but in which subsequent wood contains wide vessels can be found in Convolvulaceae (*Prevestea*: Obaton, 1960; *Exogonium*: Carlquist & Hanson, 1991) and Icacinaceae (*Iodes liberica*, *I. ovalis*: Bailey & Howard, 1941a; *Pyrenacantha klaineana*: Obaton, 1960). In Convolvulaceae and Icacinaceae, tracheids are the imperforate tracheary element type present (Carlquist, 1988), so that in the first-formed secondary xylem these cells offer a conductive potential absent in a wood in which the background to the vessels is composed of libriform fibers or fiber-tracheids.

A second type of vessel restriction pattern in scandent dicotyledons is constituted by presence of vessels in localized patches (with vessels apparently absent elsewhere) with no reference to ontogeny. Examples of this are illustrated photographically for *Pyrenacantha repanda*, *Hosiea sinense*, *Iodes liberica*, and *I. philippinensis* by Bailey & Howard (1941a). The explanation of this phenomenon is not readily apparent.

A third type of vessel restriction pattern is represented by lianas in which vessels are large and are sheathed by imperforate tracheary elements – libriform fibers in the examples cited here. Parenchyma rarely if ever occurs near a vessel. Instances of this have been figured for *Thunbergia grandiflora* of the Acanthaceae by Obaton (1960), for *T. alata* (Carlquist & Zona, 1987), and for *Mucuna pruriens* of the Fabaceae (Obaton, 1960). A similar condition is illustrated for *Afromendocia* (Obaton, 1960), *Mendocia gigas*, and *Thunbergia laurifolia* (Carlquist & Zona, 1987). In these, a few smaller vessels are present in addition to larger vessels, but vessel groupings are sheathed by libriform fibers. These conditions can be called vessel restriction patterns because vessels tend never to be adjacent to thin-walled parenchyma; only the sheathing libriform fibers abut on the thin-walled parenchyma. Because this pattern has not been recognized as a form of a vessel restriction pattern, further examples are likely to be found; a number of these may occur in lianas with xylem dispersed by parenchyma proliferation (e.g. *Bauhinia*). The significance of this type of vessel restriction, as in the first type mentioned above (*Thunbergia*) is very likely the protection of large vessels from injury by sheathing them with fibers.

Vessel element dimensions and morphology

Vessel elements in vines and lianas are notably wide. This condition was observed early by such authors as Westermeier & Ambronn (1881), who note that vessels in some species of *Passiflora* average more than 500 μm in diameter. The occurrence of notably wide vessels in lianas is mentioned prominently by Haberlandt (1914), who says, 'in such plants, the construction of the conductive system is governed by two factors, namely, the great length of the conductive region and the relatively small cross-sectional area available for the disposition of the conductive elements'. Haberlandt's (1914) idea that longer stems (such as those vines and lianas may have) produce friction, and that this friction must be compensated by wider vessels, is probably an incorrect concept. However, Haberlandt's idea that few, wide vessels produce less friction than more numerous, narrower vessels is certainly valid and operative in scandent plants.

Various authors since Westermeier & Ambronn (1881) have given data that dramatize the wideness of vessels in vines and lianas. Notable among these are Bailey & Howard (1941b), who contrast vessel diameters in three categories of Icacinaceae: trees and shrubs; scrambling shrubs; and vines and lianas. The scrambling shrubs are intermediate in vessel diameter, as one might expect if they precede vines and lianas in an evolutionary series. The fact that Icacinaceae contain all three categories is important, in that one is dealing with a monophyletic group that has evolved into different habitats, much like an experimental material subdivided into three experimental conditions, and thus one has a reliable measure of by how much vessels have widened as a result of evolution into scandent habits of various kinds and degrees. The comparison by Fisher & Ewers (Chapter 4) of shrubby and lianoid *Bauhinia* species is pertinent in this regard.

Quantitative vessel element figures on a sampling of vines and lianas (Carlquist, 1975, p. 206) showed mean vessel diameter to be greater than in any other category based on habit or habitat. The vessel density in climbing plants is accordingly low, but one must remember that vessel diameter figures may inadvertently omit small vessels that are similar in diameter to imperforate tracheary elements. Even despite a low figure for number of vessels per mm^2 of wood transection, the conductive area cited for the sampling of vines and lianas (mean vessel area multiplied by mean number of vessels per mm^2) is higher than for any other habit or habitat category. In that survey, the mean conductive area (0.36 mm^2 per mm^2 of transection) exceeds a third of the secondary xylem area. This figure is confirmed in Lardizabala-ceae (Carlquist, 1984c), although a relatively high number of vessels per mm^2 characterizes the lianas in that family.

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The implication in all of the above studies is clear that because vines are not self-supporting, 'fibrous' cells (imperforate tracheary elements) comprise a smaller proportion of wood of scandent dicotyledons than they do in other growth form categories. Related to this consideration is the tendency for the area of foliage of a liana to be comparable in quantity to that of a tree, whereas the transectional area of the liana stem is relatively smaller than that of a tree, as hinted by the Haberlandt quote cited above. Data have been provided by Putz (1983).

Emphasis on the notably wide vessels of vines and lianas is justifiable, but one must remember that throughout the mature wood of vines and lianas, one may find narrower vessels – often much narrower – as well. To call attention to this phenomenon, the term 'vessel dimorphism' was used (Carlquist, 1981). In using this term, I did not intend to imply that vessel diameters in a scandent species would form a bimodal curve when graphed, although that occasionally does happen (Ewers & Fisher, 1989). Rather, I wished to include under this term any deviation from a normal distribution curve of vessel diameters. In fact, such attenuation of normal distribution curves is common in the data reported by Fisher & Ewers (1989). Vessel diameters in roots of lianas and vines are rarely recorded, but may be wider than in stems (Ewers, Fisher & Fichtner, Chapter 5). This follows the pattern for non-vining dicotyledons (Patel, 1965).

Narrow vessels (in wood of lianas in which wide vessels also occur) may take the form of fusiform cells, little wider than imperforate tracheary elements. In fact, Woodworth (1935) invented the term 'fibriform vessel elements' for narrow vessel elements of this kind in *Passiflora* wood. Fibriform vessel elements are not only fusiform in shape, they tend to have perforation plates placed laterally (but often near the tips) on the vessel elements instead of terminally. Fibriform vessel elements of this sort occur in Nepenthaceae (Carlquist, 1981) and other woods of vines (notably Convolvulaceae: Carlquist & Hanson, 1991). Fibriform vessel elements, although they will likely prove to be characteristic of vines and lianas when these groups are studied more thoroughly, may also occur in certain shrubby plants, such as *Eriodictyon* (Carlquist, Eckhart & Michener, 1983).

Narrower vessels in vines may function in a variety of ways in scandent dicotyledons: mechanical support, water storage, and conductive safety (redundancy that permits conduction to continue if larger vessels are embolized), and as juncture cells in the conductive system are among the ideas entertained by Ewers *et al.* (Chapter 5). The idea that the relatively high number of vessels per mm² in climbing Lardizabalaceae may represent adaptation to conductive safety was advanced earlier (Carlquist, 1984c).

The length of vessel elements in vines may not differ greatly from that in woody self-supporting plants. In some families, such as Trimeniaceae

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(Carlquist, 1984a) and Loasaceae (Carlquist, 1984b), the vining representatives have vessel elements somewhat longer than those of most non-vining relatives. However, the mean vessel element length in a sampling of vines and lianas, 334 μm (Carlquist, 1975, p. 206) is appreciably lower than that of woody dicotyledons at large, 649 μm (Metcalf & Chalk, 1950, p. 1360). To be sure, the Metcalfe & Chalk figure may be biased in favor of trees of wet tropical (and to a lesser extent, temperate) trees, but even if the figure represented trees exclusively, one would have to conclude that lianas as known at present have relatively short vessel elements. This trend is confirmed by the data of Bailey & Howard (1941c); in Icacinaceae, the scandent genera (tribes Iodeae, Phytocreneae, and Sarcostigmataeae) have by far the shortest vessel elements in the family.

The length of vessels – the vertical series of interconnected vessel elements – is relatively great in lianas (Ewers, *et al.*, Chapter 5). On account of the exceptionally good conductive characteristics of scandent dicotyledons, these figures are not surprising.

Vessel element morphology

Perforation plates of vines and lianas are predominantly simple; this accords with the idea that simple plates offer the minimal impedance to water flow, and thereby promote conductive efficiency. One must note in this connection that considerations from flow physics suggest that bars in a conductive stream would have a slight negative impact at slow flow rates, but are of greater significance as flow rates accelerate. Vines and lianas do occur in some taxonomic groups in which scalariform perforation plates occur, and the nature of perforation plates in these groups is particularly instructive. In Trimeniaceae, the arboreal genus *Trimenia* has more numerous bars per perforation plate than does the scandent shrub *Piptocalyx*, and borders on perforations are reduced in *Piptocalyx* (Carlquist, 1984a). In Dilleniaceae, woods of shrubs and trees have scalariform perforation plates, but the three genera that are scandent (*Davilla*, *Doliocarpus*, and *Tetracera*) have simple perforation plates. In Lardizabalaceae, the single shrubby genus, *Decaisnea*, has scalariform perforation plates, but all the other genera, which are woody vines, have simple perforation plates (Carlquist, 1984c). In Actinidiaceae, the woody vine *Actinidia* has simple perforation plates on wider vessels and scalariform plates on narrower vessels, whereas the tree genus *Saurauia* has exclusively scalariform perforation plates (Metcalf & Chalk, 1950). In the three tribes of Icacinaceae that are comprised of scandent plants (Iodeae, Phytocreneae, Sarcostigmataeae), perforation plates are simple, whereas non-scandent genera of the family have scalariform perforation plates (Bailey & Howard, 1941b). Schisandraceae, a family of vines, has perforation plates

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with relatively few, non-bordered bars, whereas in the closely related family of trees and shrubs, Illiciaceae, perforation plates have more numerous, thicker bars with borders (Bailey & Nast, 1948).

With respect to lateral wall pitting of vessels, scalariform pitting occurs in a number of families with climbing representatives: Actinidiaceae, Aristolochiaceae, Dilleniaceae, Hydrangeaceae, Lardizabalaceae, Piperaceae, Trimeniaceae, and Vitaceae. This list may have little significance, because the vessels in these groups may have retained the scalariform condition (considered a primitive feature in dicotyledonous woods) independently. Scalariform lateral wall pitting may not be of negative selective value in scandent dicotyledons. A lateral wall pitting in which pits are circular and alternate is thought to form a mechanically stronger pattern than does scalariform pitting (Carlquist, 1975). Alternate pits may have greater selective value in self-supporting growth forms than in vines or lianas. Although deformation of vessels due to tensions in water columns may not be a problem, vines and lianas have lower tensions than do trees and shrubs, in general – in fact, positive pressures may be present (Ewers *et al.*, Chapter 5). If tensions in water columns of climbing plants were lower than those of non-climbing plants, scandent plants might not experience selection for maximally strong vessel walls. However, stronger vessel walls may result from selection for resistance to breakage and for support more than for resistance to deformation due to water column tensions.

Imperforate tracheary elements

A listing of vining or lianoid genera with true tracheids (Carlquist, 1985) is quite impressive: 28 families of dicotyledons were listed as containing scandent genera with true tracheids. To this list, *Durandea* of the Linaceae should be added. One should also mention in this connection the two genera of Gnetales with vessels in addition to tracheids: *Ephedra* (a few species scandent, such as *E. pedunculata*) and *Gnetum* (most species lianoid).

Vasicentric tracheids were once thought to be limited to a small number of families (about 30, according to Metcalfe & Chalk, 1950), but have now been found in more than 70 (Carlquist, 1988). Vasicentric tracheids occur in a high proportion of dicotyledon families that contain climbing genera, 24 (Carlquist, 1988). *Mendoncia* and *Thunbergia* of the Acanthaceae were not included in the latter listing, but do have vasicentric tracheids (Carlquist & Zona, 1987).

If one examines both the true tracheid and vasicentric tracheid lists (see Carlquist, 1988, for detailed discussion of these concepts), one finds numerous instances in which the scandent representatives have these cells, but in which non-scandent relatives have fiber-tracheids or libriform fibers instead.

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For example, in Icacinaceae the scandent genera (tribes Iodeae, Phytocreneae, and Sarcostigmataeae) have true tracheids whereas the non-scandent genera of the family have fiber-tracheids (Bailey & Howard, 1941c). *Hedera* is the only genus of Araliaceae in which vasicentric tracheids have been reported, just as *Beaumontia*, *Mandevilla*, and *Trachelospermum* have vasicentric tracheids but non-scandent Apocynaceae lack them. In the genus *Solanum*, only a few species have vasicentric tracheids; most of these (notably section *Basarthrum*) are scandent (Carlquist, 1991).

Thus, scandent dicotyledons have true tracheids and vasicentric tracheids to an extraordinarily high degree. The possible explanation cited (Carlquist, 1985) is that tracheids can serve as a subsidiary conductive system when vessels embolize, and on the basis of the abundance of tracheids in climbing dicotyledons, these species may have vessels that occasionally suffer air embolisms under extreme conditions. To be sure, the tracheids in these species could only account for a small proportion of the conduction that occurs, but they could, in case of embolism formation in the vessels, serve for a slow rate of conduction and maintain water columns to leaves until large vessels could become embolism-free and resume their role in conduction. The small collective lumen diameter of tracheids in a given scandent dicotyledon species makes it unlikely that tracheids serve for water storage to any marked extent.

Axial parenchyma

A survey that compares axial parenchyma in scandent species to that in non-scandent species is not at hand, and would be difficult to assemble. Nevertheless, patterns are evident in a number of cases, and these may point the way toward discovering other parenchyma distributions that may represent functional correlations in scandent dicotyledons.

Attention was called to the presence of starch-rich parenchyma adjacent to vessels in a number of scandent dicotyledons (Carlquist, 1985). To be sure, liquid-preserved specimens of these species permitted observation of starch, and comparable material of non-scandent dicotyledon wood would reveal more starch presence than is commonly reported. Starch may be less frequently present in wood prepared from dried specimens, and is often not reported in the anatomical literature in any case. However, the central theme with respect to vines and lianas is that there tends to be an abundance of paratracheal parenchyma, and that this may contain starch. Bailey & Howard (1941d) report that in 'Icacinaceae with a scrambling or climbing habit of growth . . . there is a more or less conspicuous reduction in the amount of banded apotracheal parenchyma. The associated paratracheal parenchyma tends to persist as the apotracheal is reduced'. Moreover, abundant paratracheal parenchyma (cited as having somewhat 'unstable' distribution: Bailey

& Howard, 1941d) occurs in the lianoid tribes Iodeae and Phytocreneae of Icacinaceae.

Parenchymatization is certainly an abundant byproduct in those species in which parenchyma proliferation breaks apart a woody cylinder. The listing above of genera in which this happens (e.g. *Mendoncia* of the Acanthaceae, or lianoid species of *Bauhinia*) is indicative of this phenomenon. Separation of the wood into strands of this sort was the basis for the concept of the cable principle of construction in lianas and vines by Schenck (1893, 1895) and Haberlandt (1914). Certainly Fisher & Ewers (1989) have demonstrated that axial parenchyma can serve a role in regeneration of vascular tissue following wounding, and Putz & Holbrook (Chapter 3) show how it contributes to liana stem flexibility.

Axial parenchyma has been hypothesized to play other possible roles related to conduction or storage (Carlquist, 1985). Scholander, Love & Kanwisher (1955) showed that positive pressures can occur in the xylem in late winter, although they did not determine the mechanism for this. Plumb & Bridgman (1972) thought that carbohydrates can form a mechanism for sap ascent. If starch is hydrolyzed into sugar (a process observable through phosphatase staining reactions), and the sugar is released into vessels, osmotic pressure in the vessels rises, pulling water into them. This idea has been accepted by others (Sauter, 1972, 1980; Czaninski, 1977). This idea may be applicable not merely to temperate trees like the maple, but to tropical trees (Braun, 1983) or herbaceous perennials (Carlquist & Eckhart, 1984). Whether this process occurs in scandent plants is worthy of investigation. Another possibility is that starch stored in parenchyma is related to sudden flushes of growth or flowering.

The conjunctive tissue (parenchyma between the concentric vascular rings) in species with successive cambia is not axial parenchyma, because the conjunctive tissue is not part of the xylem (for a discussion, see Carlquist, 1988). Conjunctive tissue parenchyma may have the effect of protecting vascular tissue from torsion or permitting regeneration when stems are wounded (Putz & Holbrook, Chapter 3). However, other functions must also be attributed to conjunctive tissue in species with successive cambia. For example, in *Beta*, the conjunctive tissue between successive cambia in roots is a storage tissue. This may be true in lianoid species with successive cambia also. For example, large quantities of starch may be found in conjunctive tissue in species of *Ipomoea* of the Convolvulaceae (Carlquist & Hanson, 1991).

Rays

Westermeier & Ambronn (1881) signalled the prominence of rays in lianas, citing *Aristolochia*. *Aristolochia* is indeed a good example of this tendency for

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the rays are wide and during secondary growth do not subdivide very much. More significantly for this discussion, the rays are very wide and may be thin-walled (Fisher & Ewers, 1990). Notably wide rays composed of thin-walled cells are involved in the 'xylem in plates' cambial variant discussed above. Indeed, there may be little difference between that concept and the presence of wide, tall rays in dicotyledonous woods: if the ray cells are thin-walled and the rays alter little in ontogeny, the xylem is effectively subdivided into plates. Dicotyledonous families that contain scandent genera and that have wide, tall rays (thin-walled in some cases) include Actinidiaceae, Araliaceae, Cactaceae, Dilleniaceae, Hippocrateaceae, Icacinaceae, Lardizabalaceae, Marcgraviaceae, Passifloraceae, Piperaceae, Schisandraceae, and Vitaceae. The significance of such wide rays in vines may be as a means whereby vascular segments of the wood can yield to torsion without sustaining damage to vessels (Putz & Holbrook, Chapter 3).

An interesting question is formed by the wood of *Cobaea*, which proves to be rayless (Carlquist, Eckhart & Michener, 1984). Raylessness would seem to be a condition that runs contrary to the flexibility required by vine stems. However, axial parenchyma is rather abundant in stems of *Cobaea*. More significantly, one notes that stems of *Cobaea* never become very large; in fact, lack of rays may limit the duration or size of *Cobaea* stems.

Phloem

Phloem of vines is notable for presence of sieve-tube elements that are notably wide, and that have simple sieve plates with large pores (see Carlquist, 1975). Although this has been observed occasionally with respect to scandent dicotyledons, there is no quantitative documentation of dimensions of sieve-tube elements in climbing versus self-supporting woody plants, and one would like to see a study involving this feature.

Sieve-tube elements seem vulnerable to deformation caused by torsion because of their thin walls. The strands of interxylary phloem formed from a single cambium (e.g. *Strychnos*, Combretaceae) may be protected by being embedded within secondary xylem.

Stem sclerenchyma

Because the nature of xylem in dicotyledonous vines and lianas has been a topic of predominant interest, we do not have an image of presence of sclerenchyma in their stems. Certainly in some vines, sclerenchyma outside the phloem is scarce or virtually absent (e.g. *Cobaea* of the Polemoniaceae; various Convolvulaceae). In lianoid Lardizabalaceae, however, a prominent cylinder of sclerenchyma lies between the phloem and the periderm. In the shrub *Decaisnea* of the Lardizabalaceae, fibers are present as strands, not in a

continuous cylinder (Carlquist, 1984c). Stems in Lardizabalaceae increase in diameter slowly, according to my observations of *Akebia* in the field, so breakup of a sclerenchyma cylinder would be slow (allowing time for interpolation of new sclereids into the cylinder). Whether the sclerenchyma cylinder in Lardizabalaceae represents a deterrent to herbivores, or a mechanism for protection of xylem and phloem from crushing, would be interesting to know. Such scattered observations as these indicate that we do not have the beginnings of an understanding of how sclerenchyma fibers or brachysclereids function in stems of vines and lianas. Hopefully studies will address this question in the future.

Scandent monocotyledons

When one considers that monocotyledons have stems of rather finite duration (except for palms) and that none of the scandent species have addition of bundles by means of a lateral meristem, climbing species are more abundant in monocotyledons than one might expect. Families that contain genera notable for their climbing habit include Araceae, Alstroemeriaceae, Arecaceae, Flagellariaceae, Pandanaceae (*Freycinetia*), Philesiaceae, and various families now being recognized as segregates from Liliaceae (e.g. Asparagaceae, Smilacaceae).

The monocotyledonous stem has many features that form intriguing structural parallels to the dicotyledonous picture described above. To date, little attention has been devoted to comparing vining with non-vining monocotyledons, although one has seen various citations, from the time of De Bary (1877) onwards, of the fact that vining monocotyledons tend to have wide vessels. The marked differentiation between protoxylem and metaxylem vessels in monocotyledons, with metaxylem vessels notably wider, offers a mechanism for achievement of vessel diameters comparable to that of scandent dicotyledons. The scattered bundles of the monocotyledon stem offer a mechanism for separation of vascular strands by means of thin-walled parenchyma, a mechanism achieved in dicotyledons by rays or else by successive cambia in which each cambium segment extends only for short tangential distances (e.g. the stem of *Pisonia* of the Nyctaginaceae looks as if it is composed of numerous scattered bundles in some species: Metcalfe & Chalk, 1950, 1983). The fibrous sheath around vascular bundles in monocotyledon stems offers an ideal protection to vascular tissue from damage due to torsion, if such a sheath serves that function, as we have reason to believe it may. Anchoring (climbing) roots of Araceae are richer in sclerenchyma than are 'feeding' roots (roots that penetrate a substrate and function primarily in water absorption). Monocotyledons offer an interesting potential comparison to dicotyledons in terms of functional anatomy. If parenchyma in

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dicotyledons serves to increase ability of liana or vine stems to resist torsion with minimal damage (Putz & Holbrook, Chapter 3), one would expect that this function is also achieved by the scattered bundles ('cable construction') of monocotyledons. Fisher & Ewers (1989) have stressed the potential role of parenchyma in dicotyledons in initiating regeneration following wounding or girdling. However, one must note that climbing monocotyledons are incapable of adding vascular tissue, so perhaps in dicotyledons also, the damage resistance inherent in cable construction is of overriding importance, and regeneration possibilities offered by parenchyma may be secondary. As our understanding of functional anatomy in stems of scandent dicotyledons increases, we may be in a better position to analyze stems and roots of climbing monocotyledons with respect to anatomical adaptation to the climbing habit.

Concluding remarks: an overview

The material covered above shows that we have developed some concepts of (i) how vines and lianas modally differ from non-climbing plants in terms of stem anatomy; and (ii) what the functional significance of these differences may be. These concerns are not new, and can be found in research of a century ago as well as in the most recent studies. The distinctive adaptations represented by vines and lianas may have compelled workers to compare anatomy with function to a greater extent than one finds in literature on anatomy of shrubs, trees, or herbs. Indeed, work on vines and lianas may be a model of the synthesis we ultimately hope to achieve, a synthesis between structural and functional ways of looking at plants.

With respect to acquiring knowledge on anatomical characteristics of vines and lianas, several comments are in order. There are two ways of developing information. One is to sample vines and/or lianas, and then to compare the data obtained with data from similar samplings of non-scandent plants. This method is valuable to the extent that one defines categories of growth forms carefully, and has extensive samplings. A second type of comparison, represented in studies of Lardizabalaceae (Carlquist, 1984c) and *Bauhinia* (Fisher & Ewers, Chapter 4), compares wood of scandent species with closely related non-scandent species. This type of comparison ought to be very informative about the nature of anatomical adaptation in climbing plants, and such studies are to be encouraged wherever there is a phyla in which both types of growth forms are represented. However, the potential drawback in such studies is that each group studied in this respect may represent distinctive modes. For example, *Piptocalyx* is a climbing shrub not strongly different in habit from shrubby to arboreal species of *Trimenia*, in the same family. However, lianoid species of *Bauhinia* may be markedly different in

construction from shrubby species of *Bauhinia*. This underlines the likelihood that each taxonomic group will represent adaptations in a slightly or appreciably distinctive way. Each study will suggest generalizations, but these generalizations cannot be applied to a particular group, only to a generalized image of scandent vs. non-scandent plants.

The generalizations obtained from comparative anatomy of vines suggest how those equipped to study physiological phenomena can design studies. With scandent plants, the cooperation between those who study structure and those who study function has been close and productive, as several of the co-authored chapters in this book illustrate. Collaborative efforts of this kind seem the optimal way of achieving a synthesis between anatomy and physiology. In such collaborative efforts, comparison between scandent and non-scandent plants, with appreciable contrast between the two categories, is of crucial importance. The synthesis between anatomy and function may not be as easy to achieve in other problems (e.g. functions of helical thickenings or vested pits in wood), but data on comparative anatomy, collected with reference to ecological and habitat categories, offer excellent points of departure for physiologists interested in building the structure-function synthesis.

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