LIANA ANATOMY: A BROAD PERSPECTIVE ON STRUCTURAL EVOLUTION OF THE VASCULAR SYSTEM

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OVERVIEW

The vascular system of lianas exhibits a number of shared features that result from convergent evolution and are independent of their taxonomic affinities. In this chapter we explore the vascular system of lianas in major lineages addressing different aspects of their anatomy, development, seasonal growth, and evolution. Since lianas are twining plants that climb in the search of light, various special features favor this habit and guarantee an efficient fluid conduction throughout their long stems. Both xylem and phloem of lianas are conspicuous for their wide conducting cells. In xylem it is also common to find a reduced volume of fibers associated with an increased amount of axial parenchyma. The flexibility required to twine seems to have been facilitated by the widespread presence of variant secondary growth, which derives from the activity of one or multiple cambia. The evolution of cambial variants in different lineages seems to have led to an increase in anatomical complexity in lineages in which variants occur. Cambial variants also affect xylem differentiation and seasonal response to environmental cues. Lianas may have active cambia for a very short period of time, from two months to up to a year, most likely a taxon-dependent feature. The vascular system of lianas provides a wealth of features to explore the link between habit, development, and the evolution of complex anatomies.

INTRODUCTION: THE UNIQUE VASCULAR SYSTEM OF LIANAS

The study of the vascular system of lianas has a long history. It flourished in the works of Heinrich Schenck (1892, 1893), who traveled from Germany to Brazil and compiled a treatise on both morphological (Schenck 1892) and anatomical aspects (Schenck 1893) of lianas. Most textbooks dealing with liana anatomy subsequently used Schenck's work and his detailed hand-line drawings as a basis for their treatments (Solereder 1908; Boureau 1957; Metcalfe & Chalk 1950). Most recently, Obaton (1960) on lianas of Africa, and Carlquist (1991, and references therein) on lianas of different continents, have introduced a large volume of new data, enriching the knowledge in this field. In this chapter we summarize general aspects of the vascular system of lianas, and provide new data that show how the vascular anatomy of lianas has evolved and diversified, and how lianas respond to environmental cues. A neotropical bias will be evident inasmuch as this is our research expertise, though aspects of paleotropical lianas are also covered based on the literature (Obaton 1960; Rajput & Rao 1999, 2003; Rajput et al. 2009; Patil et al. 2011). An Appendix of glossary terms is also given.

The lianescent habit evolved many times during the evolutionary history of plants (Gentry 1991; Burnham 2009; Spicer & Groover 2010; Isnard & Feild, Chapter 17 in this volume), being present in lycophytes, monilophytes (ferns), fossil pteridosperms, gymnosperms and angiosperms (Fig. 19.1). Several convergences evolved along with these multiple origins, including the development of modified organs specialized for climbing, such as tendrils, spines, or adventitious roots that enable vines to reach the canopy (Darwin 1865; Schenck 1892; Isnard & Silk 2009). Additionally, the development of a highly specialized vascular system has been key to the success of lianas, and this is the focus of this chapter. The vascular system of lianas is special since scandent plants must cope with very specific physical constraints inherent to their habit, including water transport along extremely long stems (Isnard & Feild, Chapter 17 in this volume), and the demand for flexibility to accommodate twining (or circumnutation). Lianas do not support their own body, but instead use external supports, usually other plants, as the means to reach the canopy and keep their bodies erect, a characteristic that gave them the epithet of "structural parasites" (Stevens 1987).

The fact that lianas are not self-supporting has enabled them, along their evolutionary trajectory, to favor conduction and flexibility at the expense of mechanical stiffness. This reliance on host support may explain why lianas have narrower stems than trees, even though they frequently sustain a leaf area comparable to that of trees (Ewers & Fisher 1991). The broad canopies of lianas, in turn, are only made possible by the development of a highly specialized vascular system with very wide vessels (or wider than those from closely related self-supporting species), low density, and intermixed soft and stiff tissues, features that ensure both optimal water conduction, flexibility, and toughness. Together these traits may be termed the "lianescent vascular syndrome," and they are common to most scandent plants.
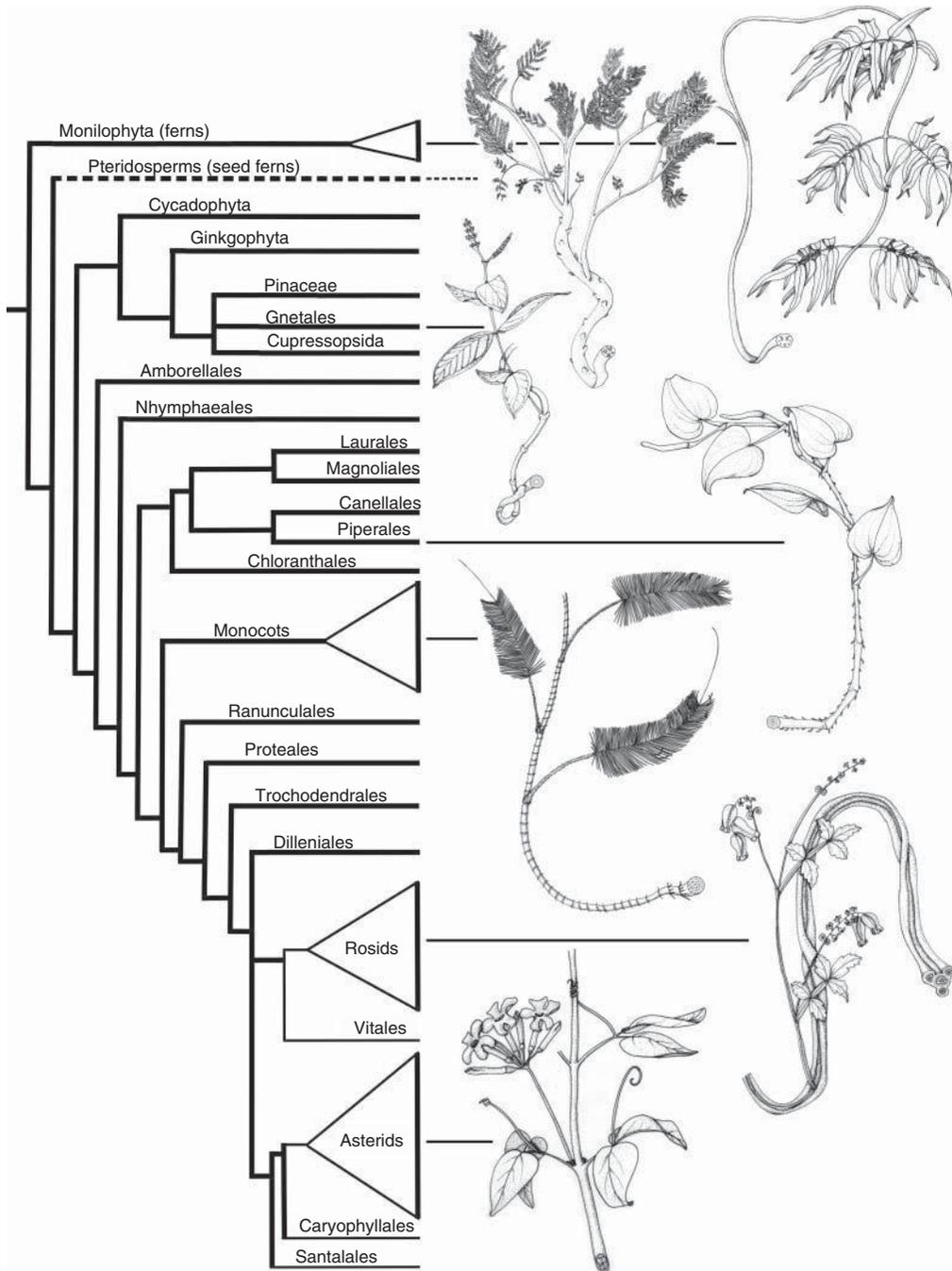
Fig. 19.1 Tracheophytes phylogeny, according to APweb (Stevens 2001 onwards, excluding lycophytes), showing examples of liana species that evolved independently in major lineages of vascular plants. Monilophyta: Blechnaceae, *Salpichlaena volubilis*. Pteridosperms: Medullosaceae, *Medullosa steinii* (fossil; dotted line). Gymnosperms: Gnetales, *Gnetum* sp. Angiosperms: Magnoliids, Piperales, Piperaceae, *Manekia obtusa*. Monocots: Arecales, Arecaceae, *Calamus* sp. Eudicots, Rosids, Sapindales, Sapindaceae, *Serjania* sp. Eudicots: Asterids, Lamiales, Bignoniaceae, *Lundia longa*. (Source: Illustrator L.W. Gussella. Reproduced with permission.)

THE LIANESCENT VASCULAR SYNDROME

Regardless of whether the vine is a fern (e.g., *Salpichlaena volubilis*, Fig. 19.2A), gymnosperm (e.g., *Gnetum* spp., Fig. 19.2B), magnoliid (e.g., *Piper nigrum* or *Aristolochia gigantea*, Fig. 19.2C), monocot (e.g. *Desmoncus orthacanthos*, Fig. 19.2D), or eudicot (various families, including Acanthaceae, Bignoniaceae, Leguminosae, Menispermaceae, and Sapindaceae, Figs. 19.2E, 19.2F), vines generally show a very similar vascular system. Xylem may be characterized by very wide conducting cells, fewer fibers, and the presence of soft tissues, usually parenchyma and/or phloem, interspersed in the stiff xylem and/or sclerenchyma

(Schenck 1893; Obaton 1960; Carlquist 1985a). In lianas with secondary growth, the combination of wide and narrow vessels or vasicentric tracheids (termed vessel dimorphism by Carlquist 1981), the presence of non-lignified axial and ray parenchyma, high and wide rays, and cambial variants are also common. Together, these characters make up what can be termed the lianescent vascular syndrome.

In contrast, self-supporting plants typically show xylem with narrower vessels, no vessel dimorphism, less parenchyma, and more fibers compared with the secondary xylem of their lianescent counterparts. This can be seen, for example, in some species with a facultative scandent habit in the Euphorbiaceae (*Manihot*, Ménard et al. 2009) and the Leguminosae
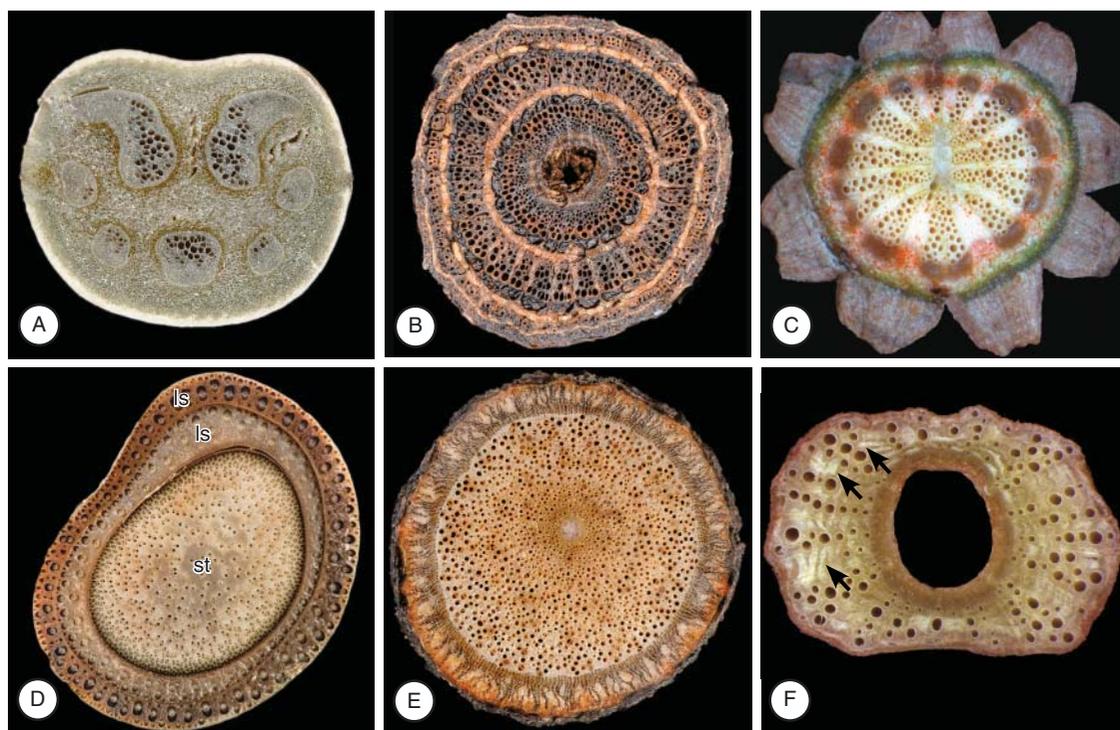
Fig. 19.2 Macroscopic transverse sections of tracheophyte liana stems, figures not to scale. (A) *Salpichlaena volubilis* (Blechnaceae, Monilophytes) stem showing wide tracheary elements, twining rachis. (B) *Gnetum paniculatum* (Gnetaceae, Gymnosperm) stem showing wide vessels and successive cambia. (C) *Aristolochia gigantea* (Aristolochiaceae, Magnoliid) stem showing thick periderm, wide vessels and secondary vascular cylinder marked by very wide rays alternating with the axial elements of the xylem and phloem. Wide rays are derived from the interfascicular cambium. (D) *Desmoncus orthacanthos* (Arecaceae, Monocots) main stem (st) and two surrounding leaf sheaths (ls). (E) *Dioclea rufescens* (Leguminosae, Eudicot Rosid) stem with very wide vessels (up to 500 μm). (F) *Thunbergia grandiflora* (Acanthaceae, Eudicot Lamiid) stem showing wide vessels and islands of included phloem (arrows) produced by interfascicular cambium. *See plate section for color representation of this figure*.
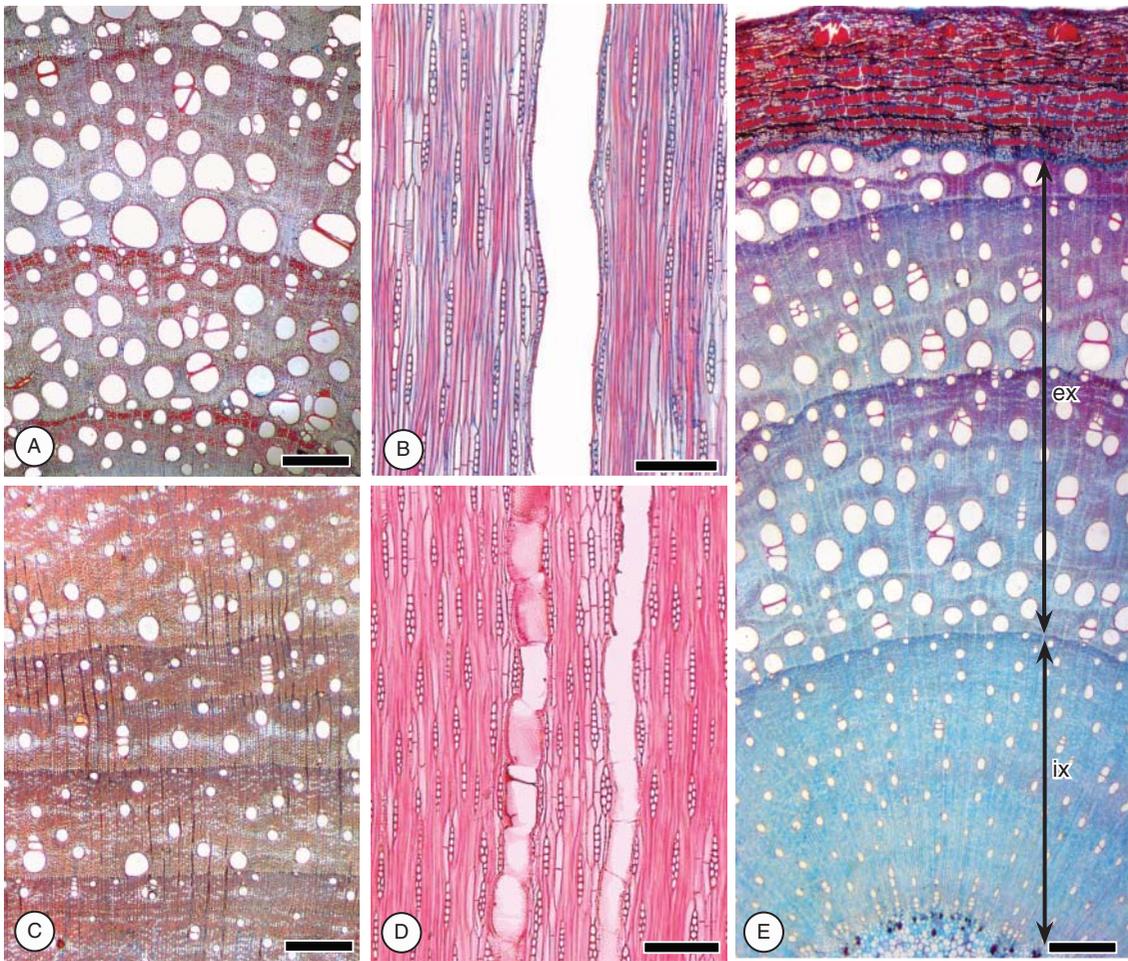
Fig. 19.3 Anatomical comparison between wood of a liana and a tree of *Dalbergia frutescens* (Leguminosae). (A, B, E), liana; (C, D), tree. (A) Wood transverse section, wide and narrow vessels combined, abundant banded paratracheal parenchyma. (B) Wood tangential section, showing lack of clear storied structure (rays irregularly storied), rays taller than those of the trees. (C) Wood transverse section, narrow vessels, aliform paratracheal parenchyma, forming short confluences. (D) Wood tangential section, showing storied structure (rays, axial parenchyma, vessel elements), narrow and short rays. (E) Stem transverse section from pith to cambium. Note the difference between the inner, dense, secondary xylem of self-supporting phase (ix) and the subsequent xylem with lianescent xylem syndrome (ex). Note: Scale bars: A, C, E = 500 µm, B, D = 200 µm. *See plate section for color representation of this figure.*

(*Dalbergia*, Figs. 19.3A–D). These differences are also true for lineages of shrubs that evolved from lianescent ancestors, e.g., Apocynaceae (Lahaye et al. 2005), Bignoniaceae (Pace et al. 2009), and Aristolochiaceae (Wagner et al. 2012). In addition, a number of lianas start their development as self-supporting shrubs or with stiff searching branches. At these stages, they have not developed the lianescent vascular syndrome and are characterized, instead, by a few narrow vessels and thick fibers, which may be modified as they are established on a support, switching to a lianescent vascular anatomy (Fisher & Ewers 1991; Rowe &

Speck 1996, 2004; Gallenmüller et al. 2001; Rowe et al. 2004; Angyalossy et al. 2012; Fig. 19.3E). Here, we discuss the anatomy and functional biology of this unique set of characters that develop both in herbaceous vines and lianas.

Vessel dimensions and morphology

Herbaceous vines and lianas are well known for possessing some of the widest (Figs. 19.2, 19.3A, 19.3E, 19.4A–C) and longest vessels in the plant kingdom (Klotz 1978; Ewers 1985; Ewers et al. 1990; Jacobsen et al. 2012). The widest vessel was found in the eudicot *Dioclea*, Leguminosae, with vessels up to 500 μm wide (measured in this study) and the longest vessel, i.e., a series of vessel elements, was found in *Amphilophium* (= *Pithecoctenium*) *crucigerum*, Bignoniaceae, at 7.73 m long (Ewers et al. 1990). In addition, lianas have xylem that remains conductive for a longer time than trees (Ewers & Fisher 1989; Gartner et al. 1990; Ewers et al. 1991, Holbrook & Putz 1996). Increases in vessel lumen raise water flow exponentially to the 4th power, as described by the Hagen-Poiseuille equation (Sperry et al. 2006). Thus, the wide vessels of lianas are extremely efficient in water conduction. In addition, the abundance of vessels in liana stems is often closer to their theoretical packing limit, i.e., the maximum number of conduits of a given width per square millimeter (McCulloh et al. 2010), compared with that of self-supporting plants growing under similar conditions (Crivellaro et al. 2012). Furthermore, in clades in which multiple perforation plates are common, the vessels of lianas usually bear a higher frequency of simple perforation plates than self-supporting species (e.g., Dilleniaceae, Carlquist 1991; Gnetaceae, Fisher & Ewers 1995; European species, Baas & Schweingruber 1987). Simple perforation plates are known to be less resistant to water flow than scalariform perforation plates (Christman & Sperry 2010). The large diameters and long lengths of vessels, together with the prevalence of simple perforation plates, allow lianas to construct a very efficient hydraulic system (Ewers & Fisher 1991; Schnitzer 2005; Isnard & Feild, Chapter 17 in this volume).

Wide vessels, however, have the shortcoming of being more susceptible to failure by embolism (Zimmermann & Jeje 1981; Ewers et al. 1990), a phenomenon that may explain why the diversity and abundance of lianas are reduced at higher latitudes (Gentry 1991) and

altitudes (Jiménez-Castillo et al. 2007). However, even in tropical forests, embolisms can occur, especially during the dry season. This constraint might have been overcome, in part, by the ubiquitous presence of narrow vessels or vasicentric tracheids associated with the very wide vessels (vessel dimorphism; Figs. 19.4C, 19.4E–F). Vessel dimorphism guarantees water conduction when wide vessels embolize, by creating anastomoses within the water path (Carlquist 1985a). Narrow vessels act also as "vessel relays," creating "hydraulic bridges" between wide vessels and guaranteeing efficient radial water flow throughout the stem (Brodersen et al. 2013). This safety mechanism ensures conduction while root pressure (Ewers et al. 1997) or other mechanisms cope with vessel refilling. However, root pressure alone was shown not to be sufficient for vessel refilling in most lianas studied (Ewers et al. 1997). Other mechanisms may also participate in vessel refilling, such as the development of new tracheary elements to compensate for those lost by embolism (Sperry et al. 1987; Stiller & Sperry 2002), horizontal water redistribution from the secondary phloem to the secondary xylem (Salleo et al. 2004; Nardini et al. 2011; Sokołowska & Zagórska-Marek 2012), as well as growth of leaves and small branches in shade as to limit evaporative stress (Secchi & Zwieniecki 2012). Despite the mechanisms of action for embolism repair in lianas, it is a fact that most of their vascular system remains conductive for their entire lifespan (Ewers et al. 1991; Fisher & Ewers 1992).

Axial parenchyma

A higher abundance of axial parenchyma has been recorded in many lianas species in comparison to closely related trees and shrubs. Indeed, sometimes even the same species growing within different habits show these differences (e.g., *Machaerium floribundum*, Angyalossy et al. 2012; *Dalbergia frutescens*, Figs. 19.3A, 19.3C). This holds true also for the presence of non-lignified parenchyma (both axial and radial, Figs. 19.4D–G). Both features have been related to increased flexibility, storage capacity, and injury repair for liana stems (Carlquist 1985a, 1991; Fisher & Ewers 1991; Ewers et al. 1991). The lianas in the Bignoniaceae are an exception to this trend (Pace & Angyalossy 2013). They have less axial parenchyma than the self-supporting lineages in the family, with the
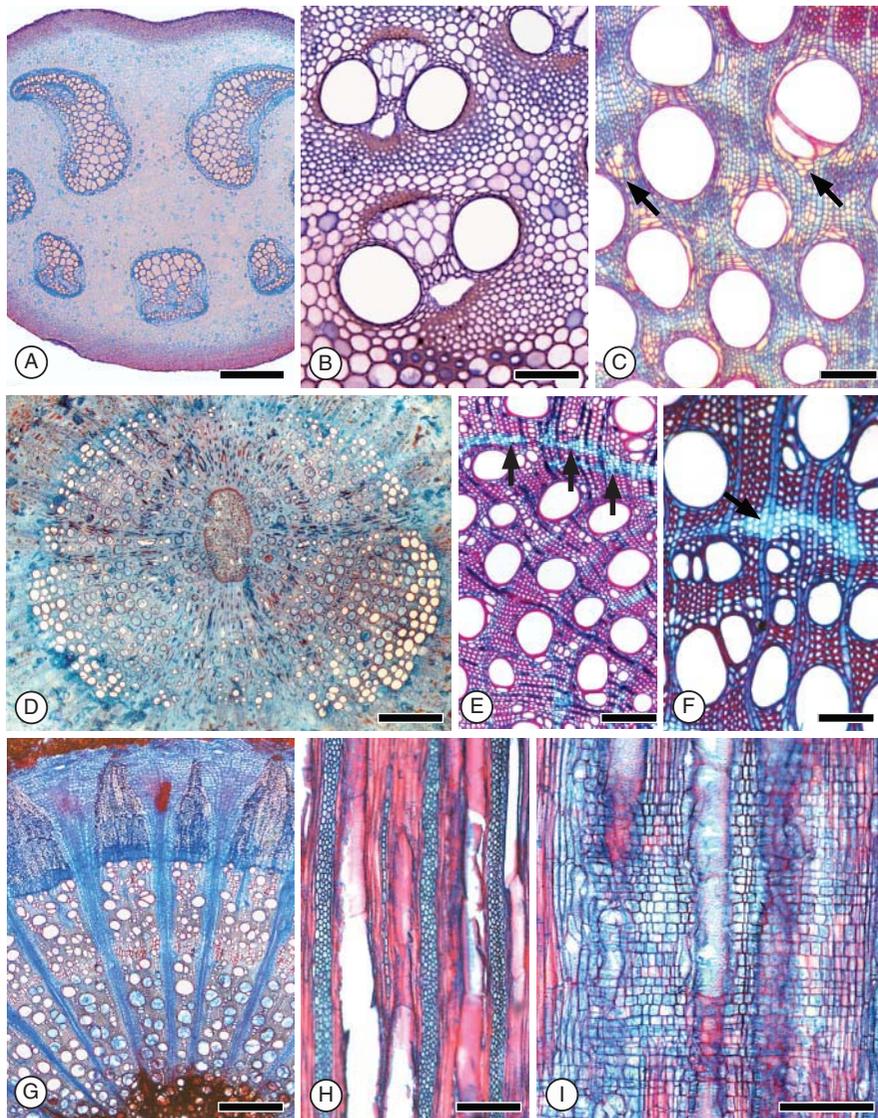
Fig. 19.4 Lianescent vascular syndrome. (A–G) Transverse section (TS). (A–C) Wide tracheary elements. (A) *Salpichlaena volubilis* (Blechnaceae, Monilophyte). (B) *Merostachys neesii* (Poaceae, Monocot). (C) *Gouania mollis* (Rhamnaceae Eudicot, narrow vessels (arrows) combined with wide vessels). (D) *Cissus sulcicaulis* (Vitaceae, Eudicot), the secondary xylem is composed of a matrix of non-lignified parenchyma where the vessels and their surrounding fibers are embedded. (E) *Heteropterys nordestina* (Malpighiaceae, Eudicot), non-lignified axial parenchyma in the secondary xylem (arrows). (F) *Dolichandra unguis-cati* (Bignoniaceae, Eudicot), rays are normally lignified, except when crossing islands of non-lignified axial parenchyma (arrow) in the secondary xylem. (G) *Cissampelos andromorpha* (Menispermaceae, Eudicot), wide and non-lignified rays. (H) *Bignonia campanulata* (Bignoniaceae, Eudicot), tall and wide rays, as seen in longitudinal tangential section (LT). (I) *Lundia corymbifera* (Bignoniaceae, Eudicot), heterogeneous rays, with procumbent, square and upright cells mixed, as seen in longitudinal radial section (LR). Note: Scale bars: A = 500 μm, B = 100 μm, C, E, H, I = 200 μm, D = 3mm, F = 50 μm G = 800 μm. *See plate section for color representation of this figure.*

flexibility and storage function probably being taken over by the ubiquitous presence of cambial variants, which typically mixes soft and stiff tissues with its phloem wedges, enhancing flexibility, and also by septate fibers, which resemble axial parenchyma in function, since they store starch (Harrar 1946; Pace et al. 2009, 2011; see Pace & Angyalossy 2013, for a discussion of this topic; see section on "furrowed xylem" in this chapter).

Non-lignified parenchyma is more common in lianas than in self-supporting species, and in some genera and/or species, such as *Cissus* (Vitaceae, Fig. 19.4D), *Heteropterys nordestina* (Malpighiaceae, Fig. 19.4E), *Stigmaphyllon* (Malpighiaceae), and *Dolichandra* (Bignoniaceae, Fig. 19.4F, Pace et al. 2009), non-lignified axial and radial parenchyma occupies spaces in which fibers, vessels, or lignified parenchyma normally are present. This replacement of one structure by another likely represents homeosis in plant anatomy (Sattler 1988), and is believed to be an important developmental mechanism in evolution (West-Eberhard 2003; Arthur 2011). Non-lignified parenchyma plays an important role in the development of the vascular system since non-lignified cells maintain the ability to divide, altering and transforming the secondary xylem after its formation. In *Dolichandra* (Bignoniaceae), the proliferation of non-lignified parenchyma is so intense that a multiple-dissected xylem is formed (Pace et al. 2009). Lianas of this genus were described as the most mechanically flexible in the entire group of 21 genera and more than 300 species (Bignonieae; Gentry 1980). Given this high division capacity, non-lignified parenchyma also plays an important role in injury repair (Carlquist 1985a; Dobbins & Fisher 1986; Fisher & Ewers 1991).

Wide and tall rays

Although some lianas, such as the Combretaceae, have generally narrow, uniseriate to biseriate rays, very wide and tall rays are more common in lianas (Figs. 19.4G, 19.4H), and they represent another feature correlated with the lianescent vascular syndrome. Anatomically, these rays are often five or more cells in width and can reach more than one millimeter in height in tangential section (Fig. 19.4H). In the families in which their composition has been described, they were also heterocellular (Klaassen 1999 for Sapindaceae; Tamaio 2006 for Menispermaceae; Rajput et al. 2012b for Leguminosae; Pace & Angyalossy 2013 for Bignoniaceae), marked by the presence of procumbent, square, and upright cells mixed throughout the rays (Fig. 19.4I). The presence of wide and tall rays increases the flexibility of the stem of lianas, allowing the twining around supports, and also avoiding damage to the vascular system when lianas' hosts fall or are dislodged (Schenck 1893; Carlquist 1985a, 1991).

In lianas of several lineages, the rays are remarkably wide and tall, such as in Dilleniaceae, Menispermaceae, and the entire order Piperales (Figs. 19.2C, 19.4G), and they originate from the interfascicular cambium that exclusively possesses ray initials (Esau 1967, 1977; Mennega 1982; Isnard et al. 2012; and personal observations). In the Piperales, the presence of wide and tall rays has even been suggested as acting as a preaptation (a process in which a feature becomes adaptive even though not primarily selected for that function, *sensu* Gould & Vrba, 1982) in the multiple evolution of the lianescent habit in this order (Isnard et al. 2012).

Conducting ray cells

Perforated ray cells (Figs. 19.5A–C) and sieve ray cells are conducting elements originated by ray initials. These are usually found connecting vessels or sieve tubes that are present at opposite sides of the rays (Fig. 19.5B). More information is available about perforated ray cells than sieve ray cells, due to the difficulties in working with phloem. Perforated ray cells occur frequently in lianas and are common even in families in which closely related self-supporting species lack them completely, such as in the Leguminosae and Bignoniaceae (Angyalossy et al. 2009, 2012; Pace & Angyalossy 2013). Specifically, in Bignoniaceae the lianescent habit evolved many times, accompanied each time by the evolution of perforated ray cells (Pace & Angyalossy 2013; Figs. 19.5D, 19.5E). Perforated ray cells are usually found connecting narrow and wide vessels, constituting by-passes when the wide vessels are embolized (Angyalossy et al. 2009). Future studies should address the possible role of perforated ray cells in vessel refilling, a mechanism thus far largely neglected.
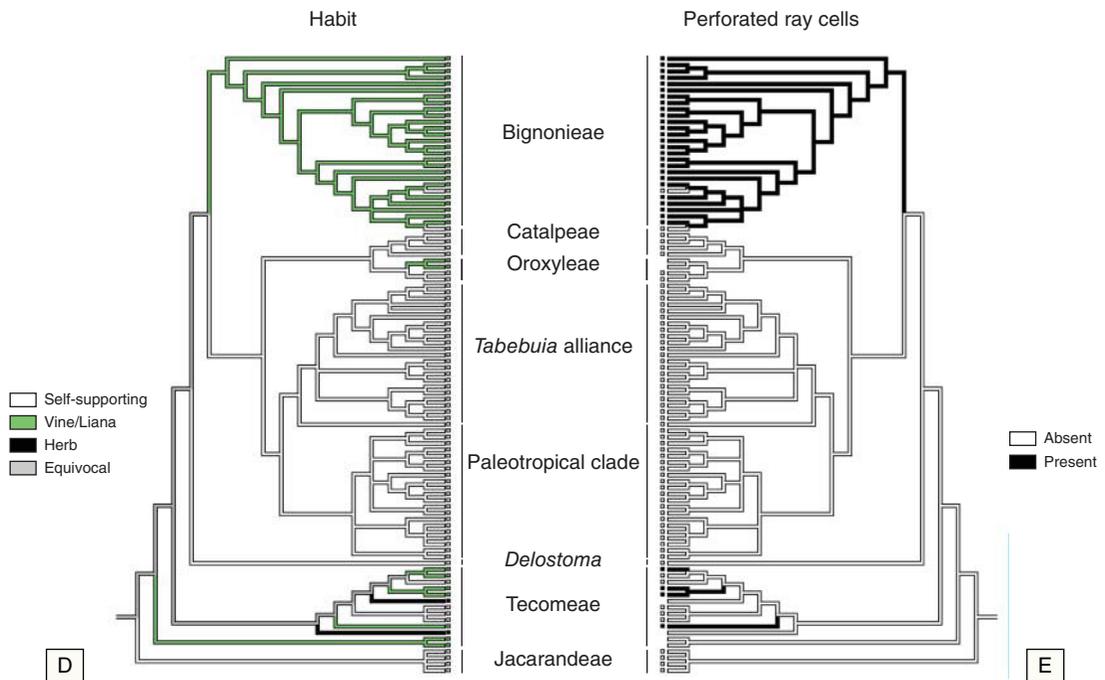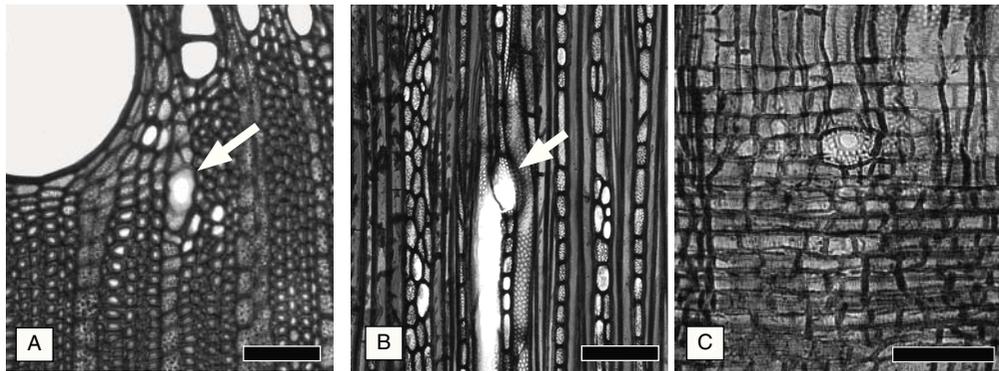
Fig. 19.5 Perforated ray cells in Bignoniaceae. (A) *Callichlamys latifolia*, perforated ray cell (arrow), in transverse section (TS). (B) *Stizophyllum riparium*, perforated ray cell (arrow) connecting two adjacent vessels, in longitudinal tangential section (LT). (C) *Campsis radicans*, perforated ray cell, in longitudinal radial section (LR). (D) Ancestral character state reconstruction of habits of Bignoniaceae. (E) Ancestral character state reconstruction of perforated ray cells in the wood of the Bignoniaceae. Note correlation between lianescent habit and presence of perforated ray cells. Note: Scale bars: A, C = 100 μm, B = 80 μm. (Source: Pace & Angyalossy 2013. Reproduced with permission of the University of Chicago Press.)
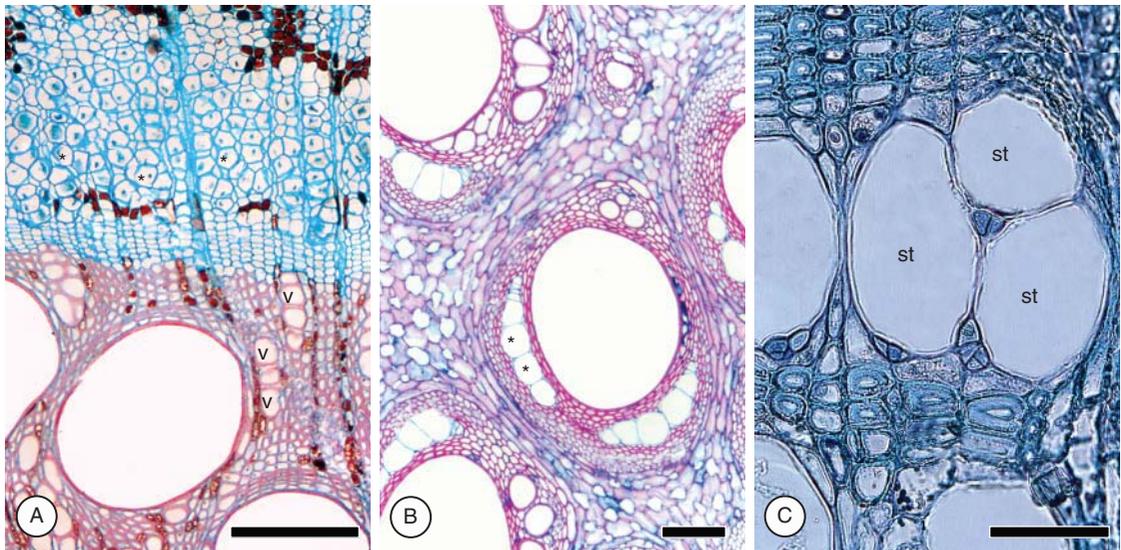
Phloem

In contrast to xylem, not much information is available on the possible correlations between the scandent habit and phloem anatomical modifications. Scientific literature suggests that lianas usually have very wide sieve tubes (Carlquist 1975, 1991; Pace et al. 2011), sometimes as wide as the small vessels found in the xylem of the same plant (Figs. 19.6A, 19.6B). Wide sieve tubes ensure higher photosynthate transport across the plant. Examples of wide sieve tubes are seen in both monocot and eudicot scandents. In *Calamus* palms (Fig. 19.6B) and in Bignoniaceae lianas, sieve tubes as wide as 70 μm can be found (Pace et al. 2011). In addition, these wide sieve tubes may bear more than one companion cell per sieve tube element, as seen in transverse section, possibly a response to the demands made by such a wide cell (Fig. 19.6C). Furthermore, in Bignoniaceae, where the lianas have both a regular and a variant phloem occurring side-by-side, it is notable that the sieve tubes of the phloem wedges are remarkably wider than those of the regular phloem, occupying a higher total area in that tissue, and possibly indicating that the variant phloem in these plants may have specialized in conduction, while the regular phloem has taken over the storage function (Pace et al. 2011), something that has been recently suggested also for plants with interxylary phloem (Carlquist 2013).

Cambial variants

Cambial variants (Carlquist 2001) are an alternative form of secondary growth that deviates from the most common secondary growth pattern found in vascular plants. Most vascular plants have a single vascular cambium, with fusiform and ray initials, which produce more secondary xylem to the inside than secondary phloem to the outside, in equal proportions around the organ circumference. Cambial variants are present in both self-supporting plants and lianas, though they are much more common in the latter (Putz & Mooney 1991; Angyalossy et al. 2012). Although not all lianas have cambial variants, in a quantitative report on the frequency of lianas

Fig. 19.6 The phloem of lianas (wide sieve tubes), as seen in transverse section (TS). (A) *Serjania lethalis* (Sapindaceae, Eudicot), sieve tubes (asterisks) as wide as the narrow vessels (v). (B) *Calamus trachycoleus* (Arecaceae, Monocot), wide sieve tubes (asterisks) in vascular bundles of a climbing palm. (C) *Tynanthus cognatus* (Bignoniaceae, Eudicot), the wide sieve tubes of Bignoniaceae lianas may have more than one companion cell. Note: Scale bars: A = 200 μm, B = 100 μm, C = 50 μm.

with variant secondary growth in the rain forests of Gabon (Africa), 56% of all lianas did have some sort of cambial variant (Caballé 1986). Cambial variants may represent another key feature in the evolution of lianas. Since most cambial variants differ in development and diversity, they are treated separately and in detail below.

## DIVERSITY AND EVOLUTION OF THE CAMBIAL VARIANTS

Similar to the lianescent habit, cambial variants also evolved many times in the evolutionary trajectory of vascular plants (Fig. 19.7), being present in fossil pteridosperms (*Medullosa*, Dunn et al. 2003), gymnosperms (*Gnetum*, Fisher & Ewers 1995, Carlquist 1996; Fig. 19.2B), magnoliids (Aristolochiaceae, Carlquist 1991; Wagner et al. 2012; Fig. 19.2C), and eudicots (Apocynaceae, Bignoniaceae, Leguminosae, Malpighiaceae, Menispermaceae, Sapindaceae, among others; Schenck 1893; Carlquist 1991; Spicer & Groover 2010; Angyalossy et al. 2012; Fig. 19.2F). Cambial variants have been studied since the nineteenth century (Schenck 1893, Radlkofer 1875) and are especially notable for generating new architectures in organs in which they occur, forming ladder-like stems (*Phanera splendens*, Leguminosae), cables (tribe Paullinieae, Sapindaceae), and cross-vines (Bignonieae, Bignoniaceae), among other architectural forms. Cambial variants are commonly taxon-specific, such as the four, to multiples of four, equidistant phloem wedges of Bignonieae (Bignoniaceae; Lohmann 2006) or the successive cambia with wide rays of Menispermaceae (Mennega 1982; Carlquist 1996; Ortiz et al. 2007). This allows the identification of many individual plants to family or genus, even in the absence of leaves and flowers (Caballé 1993). Cambial variants have been suggested as playing a key role in providing higher flexibility to the stem of climbers (Putz & Holbrook 1991; Rowe et al. 2004), to actively participate in injury repair (Dobbins & Fisher 1986; Fisher & Ewers 1991), to store water and carbohydrates (Mooney & Gartner 1991; Carlquist 2001), to influence xylem development (Lima et al. 2010), and to provide a more efficient system for the conduction of photosynthates (Pace et al. 2011). Table 19.1 summarizes all cambial variants and the orders/families in which they occur.

Cambial variants are extraordinarily diverse, but, overall, they can be divided into two major groups: (1) those derived from a single cambium; and (2) those derived from multiple cambia (Carlquist 1991, 2001; Angyalossy et al. 2012). Within each category, new subgroups can be delimited. These categories are detailed below.

Cambial variants derived from a single cambium

Five different types represent this category. In the first type there is a cambium with regular activity, producing more xylem to the inside than phloem to the outside, but in different proportions around the stem's girth. This generates a stem with an irregular conformation, found, for example, in some Apocynaceae, Leguminosae, Malpighiaceae and Rubiaceae (Fig. 19.8A). In the second type there is a cambium which alternates its activity, sometimes producing xylem to the inside and phloem to the outside, and sometimes producing phloem in both directions (outside and inside), generating interxylary phloem, found, for instance, in some Acanthaceae, Combretaceae, and Malpighiaceae (Fig. 19.8B). In the third type there is a cambium that produces less xylem than phloem at certain portions of the stem, creating small phloem arcs that later become included with the coalescence of the cambium around the arcs. This generates interxylary phloem in which the included phloem strands possess a portion of cambium within them, as in some Loganiaceae (Fig. 19.8C). In the fourth type, the xylem is furrowed by the presence of phloem arcs/wedges, derived from portions of the cambium that decrease the production of xylem, but increase the production of phloem, found, for instance, in most lianas of Bignoniaceae (Fig. 19.8D) and in some Celastraceae, Icacinaceae, and Malpighiaceae. Finally, in the fifth type, axial elements of the xylem and phloem are present in segments alternating with very wide xylem and phloem rays (in wood anatomy also called xylem in plates by Pfeiffer, 1926, and others subsequently). In some groups these axial elements are derived exclusively from the fascicular cambium that produces only fusiform derivatives in the younger stems, while the interfascicular cambium produces only rays (Figs. 19.2C, 19.4G, 19.8E). Sometimes this variant can be combined with other ones, such as in the successive cambia of Menispermaceae (Fig. 19.8F).
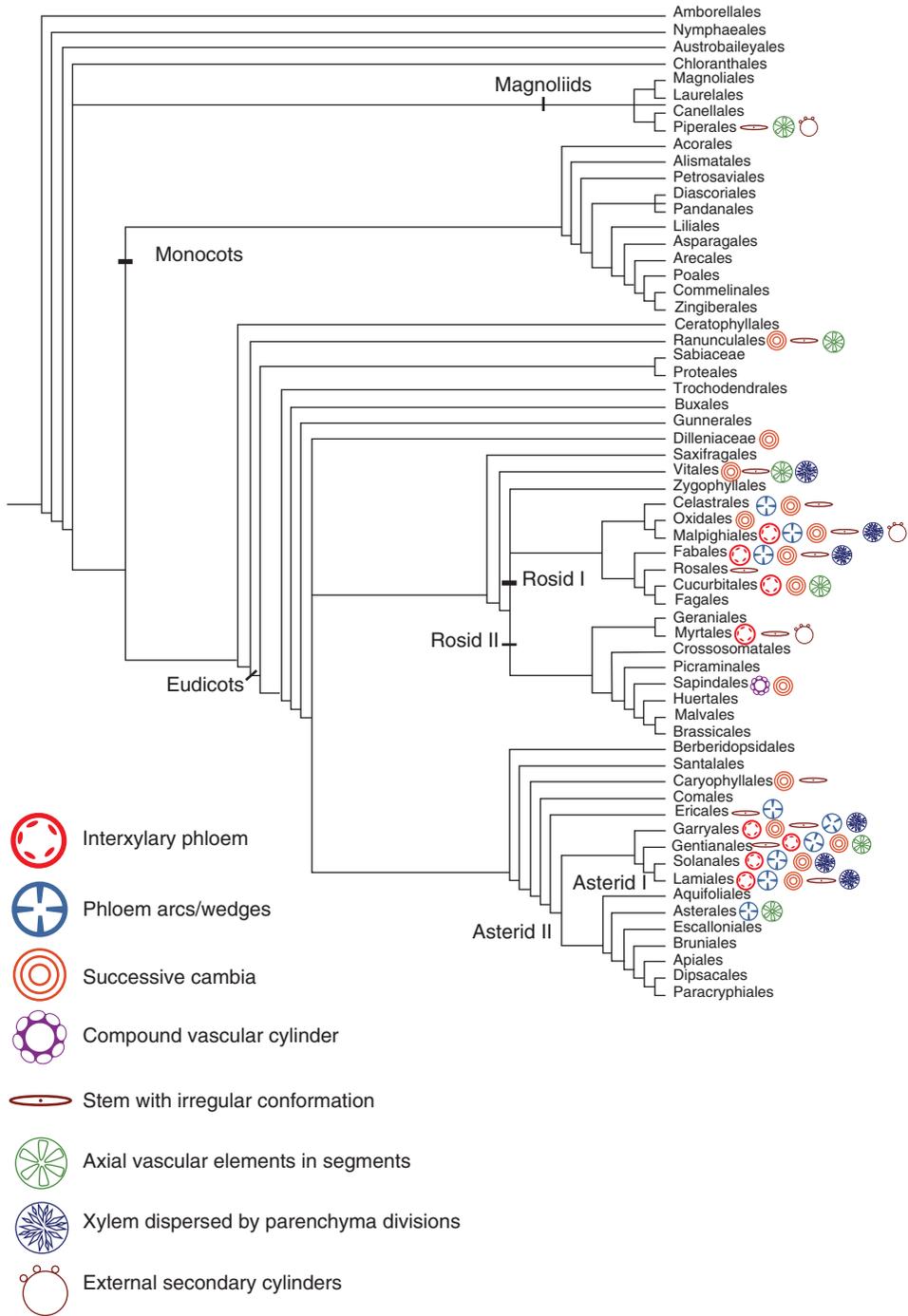
Fig. 19.7 Phylogeny of angiosperms (after Stevens 2001 onwards, APweb) illustrating distribution of cambial variants in the phylogeny. Note the higher concentration of cambial variants in the Eudicots, especially in the Rosids and the Asterids (inspired by Spicer & Groover 2010). For more detailed references on the distribution of cambial variants by family, see Table 19.1. (Source: Adapted from Angyalossy et al. 2012. Reproduced with permission of Taylor & Francis Ltd.)

Table 19.1 List of angiosperm orders and families of lianas that possess cambial variants, with their type specified and source information.

| Order	Family	Cambial variant type	References	Additional references
Asterales	Asteraceae	Axial vascular elements in segments*. Phloem arc/wedges.	Schenck 1893, Pfeiffer 1926, Carlquist 1991	Carlquist 1992a, 1966
Caryophyllales	Amaranthaceae	Successive cambia.	Schenck 1893, Pfeiffer 1926, Carlquist 1991	Rajput & Rao 1999, 2000, Carlquist 2003a
Caryophyllales	Dionchophyllaceae	Successive cambia.	Carlquist 1991	–
Caryophyllales	Nyctaginaceae	Successive cambia.	Schenck 1893, Pfeiffer 1926, Carlquist 1991	Esau & Cheadle 1969, Carlquist 2004, Hernández-Ledesma et al. 2011
Caryophyllales	Polygonaceae	Stem with irregular conformation. Successive cambia. Intraxylary phloem.	Schenck 1893, Pfeiffer 1926, Carlquist 1991	Joshi 1936, Carlquist 2003b
Celastrales	Celastraceae s.l.	Phloem arc/wedges. Stem with irregular conformation. Successive cambia. Interxylary phloem.	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	Mennega 1997
Cucurbitales	Begoniaceae	Axial vascular elements in segments. Stem with irregular conformation	Schenck 1893	Carlquist 1985b
Cucurbitales	Cucurbitaceae	Successive cambia. Interxylary phloem. Axial vascular elements in segments	Schenck 1893, Pfeiffer 1926, Carlquist 1991	Carlquist 1992a, 1992b, Patil et al. 2011
Dilleniales	Dilleniaceae	Successive cambia. Axial vascular elements in segments.	Schenck 1893, Pfeiffer 1926, Carlquist 1991	Dickison 1967
Ericales	Marcgraviaceae	Stem with irregular conformation.	Carlquist 1991	
Fabales	Leguminosae	Successive cambia. Interxylary phloem. Stem with irregular conformation. Phloem arc/wedges. Xylem parts dispersed by parenchyma. Intraxylary phloem.	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	Kuo & Pate 1981, Nair et al. 1990, Nair 1993, Brandes and Barros 2008, Rajput et al. 2012b
Fabales	Polygalaceae	Successive cambia.	Schenck 1893, Pfeiffer 1926, Carlquist 1991	Caballé 1993, Rajput et al. 2012a

Table 19.1 (*continued*).

Order	Family	Cambial variant type	References	Additional references
Gentianales	Apocynaceae *s.l.*	Stem with irregular conformation. Successive cambia. Interxylary phloem. Axial vascular elements in segments. Phloem arc/wedges.	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	Patil & Rajput 2008
Gentianales	Gentianaceae	Interxylary phloem.	Pfeiffer 1926	Carlquist 1992a
Gentianales	Loganiaceae	Interxylary phloem.	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	Scott & Brebner 1889, Veenendal & Den Outer 1993, Rajput et al. 2010
Gentianales	Rubiaceae	Phloem arc/wedges. Stem with irregular conformation.	Schenck 1893, Pfeiffer 1926, Carlquist 1991	
Lamiales	Acanthaceae	Successive cambia. Interxylary phloem. Xylem parts dispersed by parenchyma.	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	Carlquist 1992a
Lamiales	Bignoniaceae	Phloem arc/wedges. Xylem parts dispersed by parenchyma.	Schenck 1893, Pfeiffer 1926, Dobbins 1969, 1970, 1971, 1981, Pace et al. 2009	Carlquist 1991, Gasson & Dobbins 1991, Dos Santos 1995, Ozório-Filho 2002, Pace et al. 2011.
Lamiales	Verbenaceae	Stem with irregular conformation.	Schenck 1893, Pfeiffer 1926, Carlquist 1991	–
Malpighiales	Malpighiaceae	Phloem arc/wedges. Xylem parts dispersed by parenchyma. Successive cambia. Interxylary phloem. Stem with irregular conformation.	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	–
Malpighiales	Passifloraceae	Successive cambia. Phloem arc/wedges.	Obaton 1960, Carlquist 1991	Hearn 2009
Malpighiales	Euphorbiaceae	External vascular cylinders.	Schenck 1893, Pfeiffer 1926	Ménard et al. 2009
Myrtales	Combretaceae	Interxylary phloem. Stem with irregular conformation. External vascular cylinders.** Intraxylary phloem.	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	Den Outer & Fundter 1976, Den Outer & Van Veenendaal 1995, Rajput et al. 2009, Zózimo et al. 2011
near Garryales	Icacinaceae	Successive cambia. Interxylary phloem. Stem with irregular conformation. Phloem arc/wedges. Xylem parts dispersed by parenchyma.	Pfeiffer 1926, Obaton 1960, Carlquist 1991	Bailey & Howard 1941, Lens et al. 2008, Utteridge et al. 2005

Order	Family	Description	References	References
Oxalidales	Connaraceae	Successive cambia.	Obaton 1960, Carlquist 1991	
Piperales	Piperaceae	Axial vascular elements in segments*. Stem with irregular conformation. External vascular cylinders.**	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	Isnard et al. 2012
PIperales	Aristolochiaceae	Axial vascular elements in segments. Stem with irregular conformation.	Schenck 1893, Obaton 1960, Carlquist 1991	Isnard et al. 2012
Ranunculales	Ranunculaceae	Axial vascular elements in segments.	Schenck 1893, Pfeiffer 1926	Carlquist 1995, Isnard et al. 2003
Ranunculales	Menispermaceae	Successive cambia. Axial vascular elements in segments. Stem with irregular conformation. Intraxylary phloem.	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	Mennega 1982, Rajput & Rao 2003, Tamaio et al. 2009,
Rosales	Ulmaceae	Stem with irregular conformation.	Schenck 1893, Pfeiffer 1926	
Rosales	Moraceae	Stem with irregular conformation.	Schenck 1893, Pfeiffer 1926, Carlquist 1991	Koek-Noorman et al. 1984
Sapindales	Sapindaceae	Compound vascular cylinders. Divided and corded cylinder. Successive cambia.	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	Raldkofer 1932, Acevedo-Rodriguez 1993, Klaassen 1999, Araújo & Costa 2006, Tamaio & Somner 2010, Tamaio et al. 2011
Solanales	Convolvulaceae s.l.	Successive cambia. Interxylary phloem. Phloem arc/wedges. Xylem parts dispersed by parenchyma. Intraxylary phloem.	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	Scott 1891, Mikesell & Schroeder 1984, Rajput et al. 2008, Patil et al. 2009, Patil et al. 2009, Ceja-Romero & Perez-Olvera 2010, Terrazas et al. 2011
Vitales	Vitaceae	Axial vascular elements in segments. Stem with irregular conformation. Successive cambia. Xylem parts dispersed by parenchyma.	Schenck 1893, Pfeiffer 1926, Obaton 1960, Carlquist 1991	June Adkinson 1913, Carlquist 1985a

Notes:
*Terminology according to Tamaio et al. (2009).
**Terminology according to this chapter, grouping: (1) new formation of secondary vascular cylinders as in Euphorbiaceae, Combretaceae, Sapindaceae; and (2) secondary growth of the external primary vascular bundle as in Piperaceae.
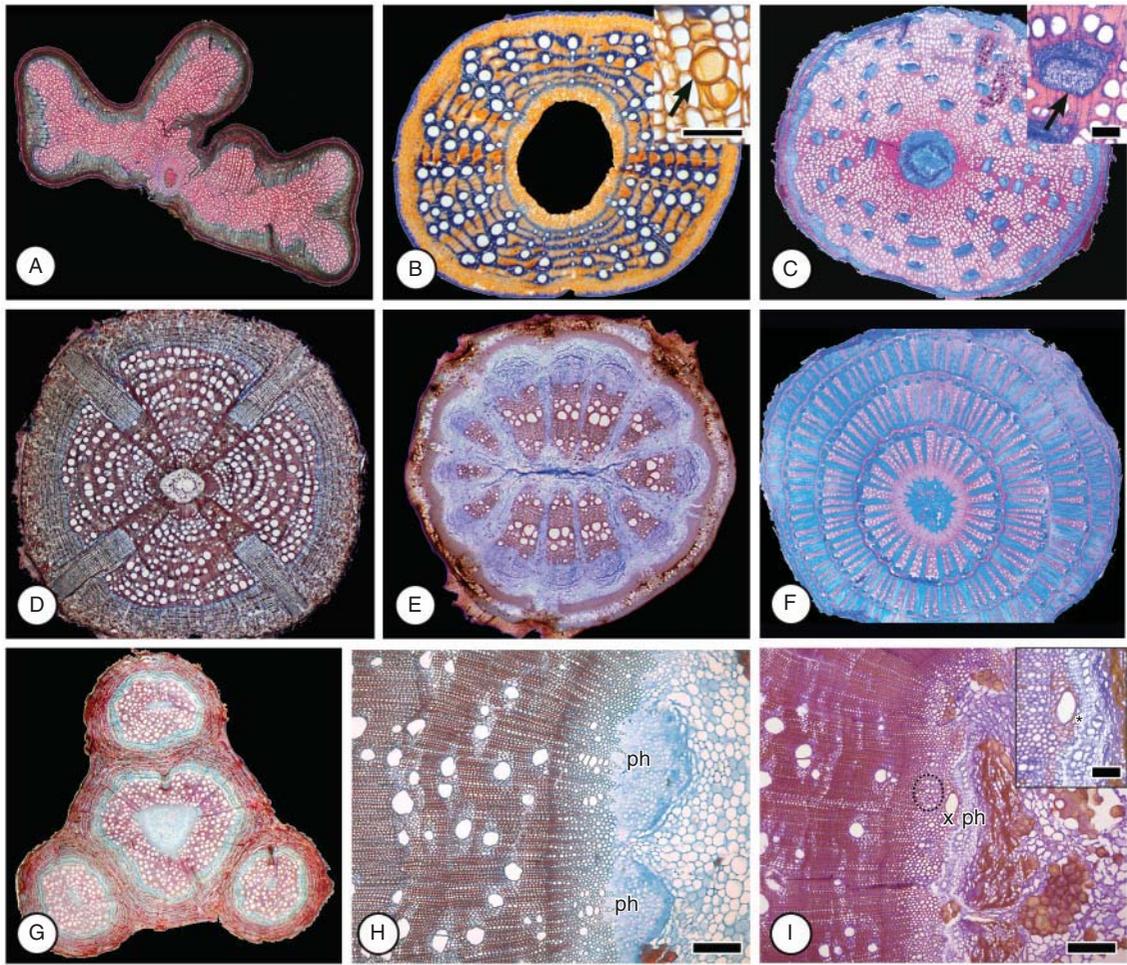
Fig. 19.8 Cambial variant types, as seen in transverse section (TS). (A) *Heteropterys nordestina* (Malpighiaceae), asymmetrical stem. (B) *Thunbergia grandiflora* (Acanthaceae), interxylary phloem without cambial inclusion (detail: sieve tube with simple sieve plate, arrow). (C) *Strychnos millepunctata* (Loganiaceae), interxylary phloem with cambial inclusion (detail: included cambium, arrow). (D) *Tanaecium pyramidatum* (Bignoniaceae), xylem furrowed by phloem wedges. (E) *Aristolochia gigantea* (Aristolochiaceae), axial vascular elements in segments alternating with wide vascular rays. (F) *Chondrodendron platyphyllum* (Menispermaceae), successive cambia. (G) *Serjania lethalis* (Sapindaceae), compound stem. (H) *Maripa glabra* (Convolvulaceae), intraxylary phloem (ph) produced by a perimedullar cambium. (I) *Telitoxicum duckei* (Menispermaceae), intraxylary phloem (ph) and xylem (x) produced by a perimedullar cambium shown in the detail (asterisk). Note primary xylem before the neoformed intraxylary xylem (dotted circle). Note: Scale bars: B = detail 50 μm, C = detail = 100 μm, H-I = 300 μm, I = detail = 100 μm. *See plate section for color representation of this figure.*

Cambial variants derived from multiple cambia

This category can be divided into four main types. The first type is characterized by successive cambia, in which new cambia arise successively by cell divisions of external portions of the secondary vascular system. Each new cambium produces secondary xylem to the inside and secondary phloem to the outside of the stem successively, found, for instance, in some Dilleniaceae, Gnetaceae, Menispermaceae and Leguminosae (Fig. 19.8F). The second type includes those species with a compound stem, which is formed by multiple vascular cylinders forming a single stem, creating a cable-like structure. The compound stem may originate in the primary growth, with the formation of 4–12 procambial cylinders that develop into discrete vascular bundles. Later on, a cambium is formed within each vascular bundle, each of which start secondary growth, forming 4–12 complete secondary vascular cylinders, such as in *Serjania caracasana* (Tamaio & Angyalossy 2009). In other species, the compound stem is formed later during secondary growth of the stem, with the dedifferentiation of pericycle parenchyma cells into new cambia that produce external vascular cylinders without pith (Tamaio & Somner 2010). The compound stem is found exclusively in the Sapindaceae (Fig. 19.8G). The third type consists of species exhibiting intraxylary phloem (Fig. 19.8H), and sometimes also intraxylary xylem (Fig. 19.8I), derived from a cambium formed between primary xylem and the pith. The last type is comprised of species showing external vascular cylinders that can be formed by (1) neoformation of secondary vascular cylinders, as in Euphorbiaceae (Fig. 19.9A) and Combretaceae, or (2) secondary growth of the external primary vascular bundles, as in Piperaceae (Figs. 19.9B, 19.9C).

Furthermore, a single plant can exhibit more than one type of cambial variant, a case found, for example, in the stems of Sapindaceae and Bignoniaceae, which in addition to the compound stems and furrowed xylem, respectively, can also exhibit neoformation of the vascular system in some genera. In the compound stems of lianescent Sapindaceae, new vascular cylinders are formed in older stems between the original vascular cylinders. New cambia arise by cell divisions of parenchyma cells of the nonconducting phloem of one or more of the original cylinders (Tamaio & Angyalossy 2009; Figs. 19.9D, 19.9E). In the Bignoniaceae, new vascular portions arise from new cambia, perpendicularly to the original cambium, derived from anticlinal cell divisions of the dilated phloem rays of the nonconducting phloem, resulting in new vascular portions (parallel to the rays of the original vascular system; Figs. 19.9F, 19.9H).

Another common trait of lianas is the parenchymatization of the stem associated with one type of cambial variant, as seen in the multiple-dissected wood of *Dolichandra* (see Fig. 9 in Pace et al. 2009). Parenchymatization occurs through the presence of non-lignified parenchyma in the stems, which may subdivide later on in the ontogeny of a species and create novel anatomical architectures.

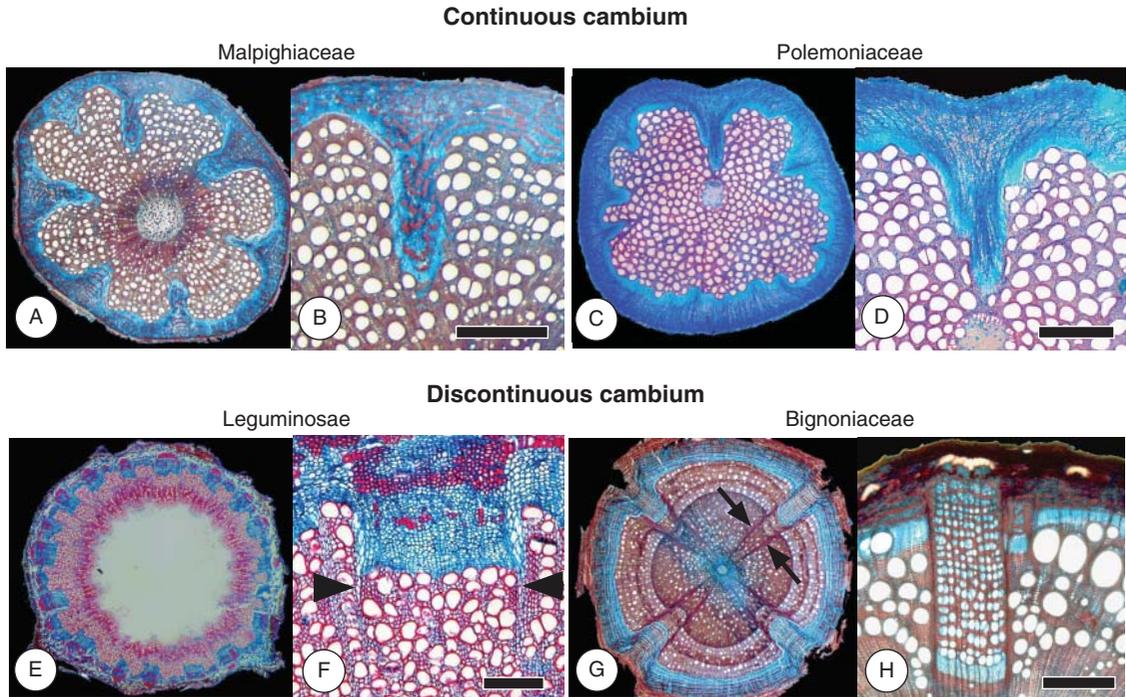## DEVELOPMENT AND MULTIPLE ORIGINS OF CAMBIAL VARIANTS

Although different types of cambial variant can be considered typical of certain families (Caballé 1993), most variants are not exclusive to a single lineage, having evolved multiple times (Fig. 19.7). However, as expected in homoplasious evolution, even though some variations are included under the same category, they commonly differ in development and fine anatomy, a phenomenon explored in detail here for the lianas with furrowed xylem and successive cambia.

Furrowed xylem (phloem arcs/wedges)

Finding furrowed xylem in lianas is not unusual and although commonly related to lianas of Bignoniaceae – one of the top three most abundant liana families in the Neotropics (Gentry 1991) – it can be found in at least nine other orders/families of the eudicots (Fig. 19.7; labeled as phloem arcs/wedges), clearly the result of independent origins. Phloem wedges furrowing the xylem have evolved at least five times in the rosids (Celastraceae, Euphorbiaceae, Leguminosae, Malpighiaceae and Passifloraceae) and six times in the asterids (Apocynaceae, Asteraceae, Bignoniaceae, Convolvulaceae, Icacinaceae and Polemoniaceae). Although they appear similar, they include marked differences. First, in some, phloem wedges appear at regular intervals, e.g., Apocynaceae, Bignoniaceae, Leguminosae, and Malpighiaceae, while rather irregularly in other families. The Bignoniaceae are easily distinguished from the others by the constant number of four to multiples of four phloem wedges that
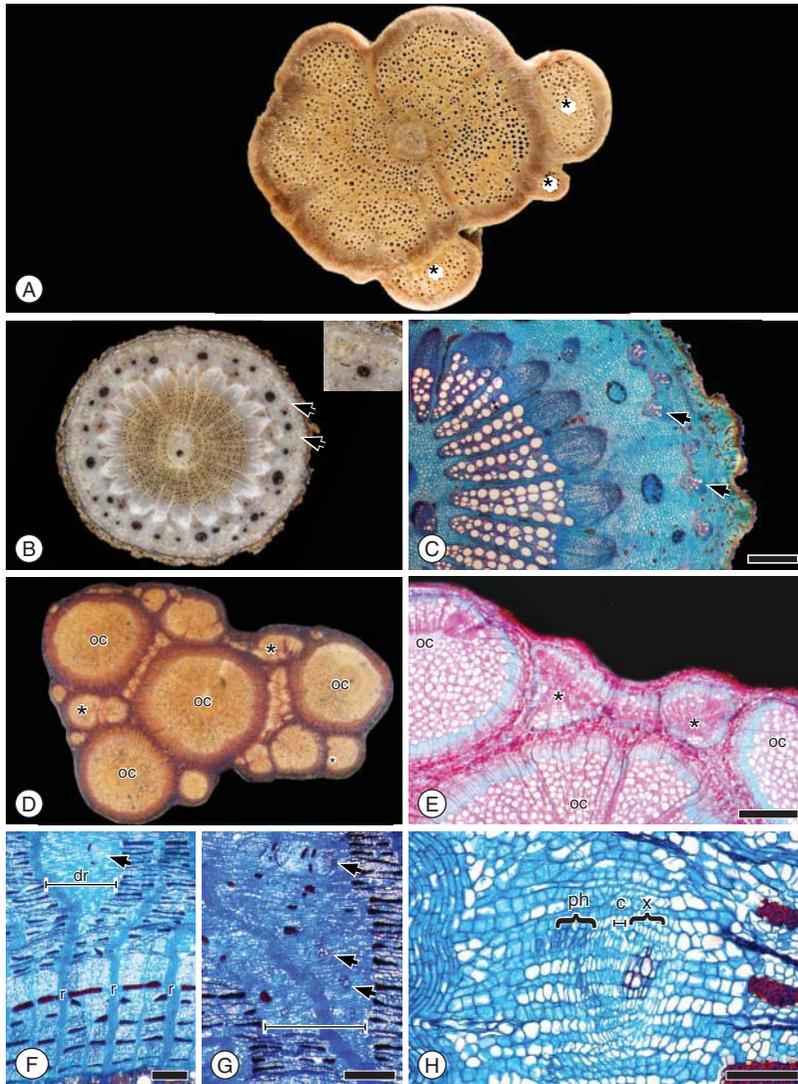
Fig. 19.9 Cambial variant types, as seen in transverse section (TS). (A–C) External vascular cylinders. (A) *Dalechampia ficifolia* (Euphorbiaceae), lateral vascular cylinders (asterisks) derived from neoformations. (B, C) *Manekia obtusa* (Piperaceae), secondary growth of external primary vascular bundle (detail: two external vascular cylinders). (D–H) Neoformations of vascular cylinders associated with another type of cambial variant. (D, E) Compound stem of *Serjania laruotteana* (Sapindaceae) with neoformed vascular cylinders (asterisks) between four original cylinders (oc). (F–H) *Amphilophium crucigerum* (Bignoniaceae), new vascular portions (arrows) derived from new cambia, perpendicular to original cambium, at dilated portion (dr) of phloem rays (r) in the nonconducting phloem. Note in H the detail of one new vascular portion with its phloem (ph) and xylem (x) derived from a neoformed cambium (c). Note: Scale bars: C = 1mm, E = 250 μm, F–G = 500 μm, H = 150 μm. *See plate section for color representation of this figure.*

Continuous cambium

Malpighiaceae

Polemoniaceae

Discontinuous cambium

Leguminosae

Bignoniaceae

Fig. 19.10 Four examples of families with furrowed xylem (phloem arcs/wedges), as seen in transverse section (TS). (A–D) Continuous cambium. (A, B) *Mascagnia sepium* (Malpighiaceae). (C, D) *Cobaea scandens* (Polemoniaceae). (E–H) Discontinuous cambium (cambia included). (E–F) *Mimosa velloziana* (Leguminosae), arrows indicate limiting rays. (G) *Fridericia chica* (Bignoniaceae), arrows indicate limiting rays. (H) *Tynanthus cognatus* (Bignoniaceae), detail of a phloem wedge. Note: Scale bars: B, D = 500 μm; F = 350 μm; H = 450 μm. *See plate section for color representation of this figure.*

are regularly spaced (Schenck 1893; Dobbins 1971; Pace et al. 2009; Figs. 19.8D, 19.10G, 19.10H). This characteristic has been related to the decussate leaves typical of the Bignoniaceae (Dobbins 1970). In fact, the wedges are always found in alternation with the leaves (Schenck 1893; Pace et al. 2011) and traveling in a spiral throughout the stem.

From a broad perspective, the furrowed xylem (phloem wedges) cambial variant can be divided into two major groups, depending on the continuity of the cambium, as in Apocynaceae, Celastraceae, Convolvulaceae, Euphorbiaceae, Malpighiaceae, Passifloraceae, and Polemoniaceae (Figs. 19.10A–D), or its discontinuity, as in Bignoniaceae, Icacinaceae, and Leguminosae (Figs. 19.10E–H).

The development of phloem wedges involves at least two steps. First, in the onset of secondary growth a continuous cambium is installed with regular activity throughout its girth. Second, sooner or later depending on the species, grooves appear in some regions of the cambium. These correspond to zones that reduce the production of xylem and increase the production of phloem. Given this differential production of secondary tissues, phloem arcs/wedges are formed (Figs. 19.10B, 19.10D). In plants with a continuous cambium, this is the final stage of development.

In plants with a discontinuous cambium, on the other hand, there is a third step. In the places where the phloem wedges had first appeared, a cambium disruption with inclusion occurs. In Bignoniaceae and, most likely, other families where phloem wedges are accompanied by cambial disruption (Icacinaceae, Leguminosae), this phenomenon is correlated with the loss of anticlinal division capacity by the variant cambia (Pace et al. 2009). In the Bignoniaceae, the four equidistant portions of the cambium that

change their activity lack anticlinal divisions, while the regular portions of the cambium go on increasing in girth by anticlinal divisions, leading to cambial disruption while growth proceeds. At the margins of the phloem wedges, wide and tall rays start to form.

The presence of wide and tall rays bordering the phloem wedges is typical of the furrowed xylem (phloem wedges) cambial variant, and it is especially evident in those families displaying cambial inclusion, although not exclusively. These wide rays were recognized by Schenck in 1893, who named them "limiting rays," given their marginal position (Schenck 1893; Figs. 19.10F, 19.10G). These wide rays were suggested as acting as a physiological barrier in Bignoniaceae, canalizing hormones originating from the leaves and promoting the development of the phloem wedges in this family (Dobbins 1990, 2005). However, this proposition does not seem to hold since the phloem wedges start their formation in Bignoniaceae before the appearance of limiting rays (Pace et al. 2009). It is therefore more likely that the limiting rays in the furrowed xylem cambial variant simply represent an architectural by-product (a spandrel, *sensu* Gould & Lewontin 1979). The limiting rays are present exactly at sharp notches in the limits of the phloem wedges, a zone of mechanically fragile tissue that could easily facilitate fracture propagation. Rays likely enlarge as a way to adjust for the differential growth rates between the regular and variant cambia and to avoid tissue fracture, similar to the dilating rays of the secondary phloem of various vascular plants that dilate to adjust to the increase in the circumference of the axis (Evert 2006). Ray divisions also allows the new cells produced by the included cambium to move outward while they differentiate, since they are within the phloem wedges and surrounded by stiff secondary xylem (Obaton 1960). Therefore, limiting rays in this cambial variant have probably not appeared as a result of adaptive selection, but as a by-product of architectural constraint in the dynamic of the tissues in the secondary body of these plants.

Although the variant cambium reduces the production of xylem, it is important to note that it never really ceases or becomes unidirectional, and both xylem and phloem continue to be produced throughout the plant's lifespan (Pace et al. 2011). In some Malpighiaceae, the presence of tilted axial xylem cells is noticeable, most likely because of the position of the cambium in the margins of the phloem wedges. The same pattern is noticeable in *Perianthomega*, the only genus of the Bignonieae tribe (Bignoniaceae) that possesses phloem arcs with a continuous cambium (Pace et al. 2009).

Successive cambia

Successive cambia are one of the most frequent types of cambial variant, having evolved independently at least eighteen times, in both gymnosperms (e.g., *Gnetum*, Fig. 19.11A) and angiosperms (Fig. 19.7, Table 19.1). Successive cambia refers to the appearance of multiple concentric cambia in the stem. It is especially frequent in the Caryophyllales (Amaranthaceae, Dionchophyllaceae, Nyctaginaceae, Fig. 19.11D), but it is also present in some Acanthaceae, Apocynaceae, Dilleniaceae (*Doliocarpus*, Fig. 19.11B), Celastraceae, Connaraceae, Convolvulaceae, Cucurbitaceae, Icacinaceae, Leguminosae (Fig. 19.11C), Malpighiaceae (some *Banisteriopsis*), Menispermaceae (Fig. 19.11E), Passifloraceae, Polygalaceae, Sapindaceae, and Vitaceae.

Similar to most cambial variants, at the onset of secondary growth the stems have regular growth with a single cambium of equal activity throughout the girth. Subsequently, successive cambia appear. These may be derived from: (1) divisions of the pericyclic cells, as reported for Convolvulaceae, Dilleniaceae and Menispermaceae (Eames & MacDaniels 1925; Tamaio et al. 2009; Terrazas et al. 2011; Fig. 19.11E); (2) cortex cells, such as reported for some Menispermaceae (Carlquist 2007) and Leguminosae (Rajput et al. 2012b; Fig. 19.11C); or even (3) parenchyma cells of the nonconducting phloem, as in some Leguminosae (Schenck 1893; Nair & Mohan-Ram 1990; Dias-Leme 1999; personal observations).

In the most common case, as in Caryophyllales, Dilleniaceae, and Menispermaceae, pericyclic or cortical cells divide and develop into a large meristematic zone. New successive cambia will periodically develop in the middle of this meristematic zone, with secondary phloem originating to the outside and secondary xylem to the inside. Part of the meristematic zone differentiates into parenchymatic tissue and/or sclerenchymatic tissue, termed conjunctive tissue (Fig. 19.11D). The outermost part of this meristematic tissue/cells, near the cortex or periderm, will form new successive cambia sequentially.
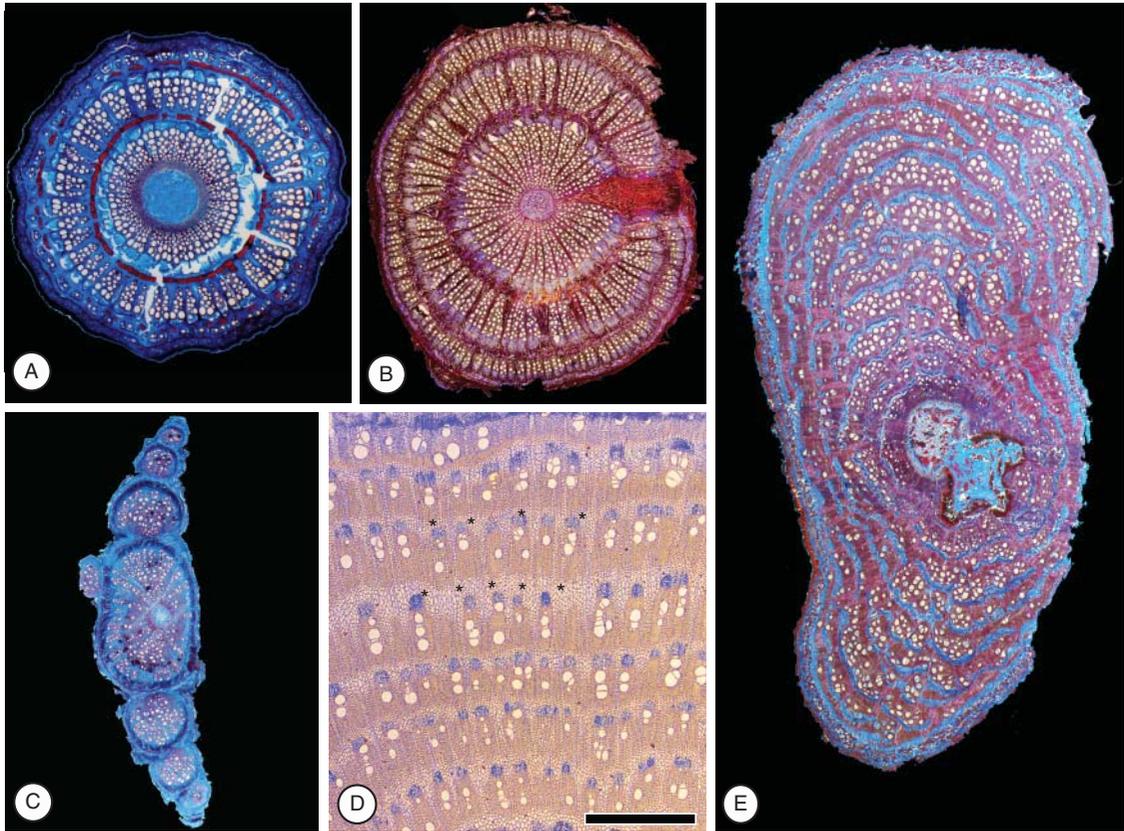
Fig. 19.11 Successive cambia of different types, seen in transverse section (TS). (A, B) Successive cambia resulting in a round stem. (C, E) Successive cambia resulting in flattened stem. (D) Conjunctive tissue (asterisks) one of the products of the successive cambia. (A) *Gnetum paniculatum* (Gnetaceae). (B) *Doliocarpus dentatus* (Dilleniaceae). (C) *Rhynchosia phaseoloides* (Leguminosae). (D) *Bouganvillea spectabilis* (Nyctaginaceae). (E) *Telitoxicum duckei* (Menispermaceae). *See plate section for color representation of this figure.*

In the legume species *Rhynchosia phaseoloides*, successive cambia arise from cells of the cortex (Schenck 1893; Rajput et al. 2012b; Fig. 19.11C). These cortical cells originate meristematic cells in radial files, which in the mid region differentiate into a vascular cambium and in the inner region a parenchymatic conjunctive tissue (Rajput et al. 2012b). The outermost part of this meristematic zone will give rise to new successive cambia. For some lianas species of the genus *Machaerium* (*M. tounateifolium*, Schenck 1893; *M. oblongifolium*, Dias-Leme 1999; personal observations), new cambia arise from the differentiation of axial parenchyma cells of the nonconductive secondary phloem. This axial phloem parenchyma does not produce a meristematic

zone, but differentiates directly into a cambium. As a consequence, no conjunctive tissue is formed.

The successive cambia found in the nineteen families (Table 19.1) are not anatomically identical. For instance, in some, the successive cambia have more pronounced activity at certain portions than others, generating asymmetrical stems, typical of some Connaraceae, Leguminosae (Fig. 19.11C), and Menispermaceae (Fig. 19.11E). Other families exhibit successive cambia with more or less equal amounts of tissue through the stem girth, resulting in stems with a round external appearance, as in some Asteraceae, Dilleniaceae (Fig. 19.11B), Gnetaceae (Fig. 19.11A), Menispermaceae, and Nyctaginaceae (Fig. 19.11D).

CAMBIAL VARIANTS ENHANCE ANATOMICAL COMPLEXITY

Cambial variants result from a myriad of completely different developmental pathways. However, most of them seem to be initially derived from a stem with regular secondary growth. A remarkable exception is the compound stem of some Sapindaceae, which exhibit a different vascular structure initiated at primary growth (Araújo & Costa 2006; Tamaio & Angyalossy 2009).

More commonly, though, lianas seem to have evolved into gradually more complex forms, as is the case for species of the Bignonieae (Bignoniaceae). In these lianas, different anatomical architectures have evolved, but they are all linked by a sequence of gradual changes. The first anatomical variation to evolve in the tribe was the formation of four phloem arcs, and subsequently four phloem wedges, the most common pattern in the family (for details, see Pace et al. 2009; Fig. 19.12). These four phloem arcs/wedges are equally spaced (Figs. 19.12B–F), and between them, in the interwedges, the cambium maintains regular secondary growth. However, in three lineages within the Bignonieae (the "multiples of four clade," some *Adenocalymma* and *Lundia*), additional phloem wedges form between the first four, creating stems with 8, 16, 32, and 64 phloem wedges or more, also equally spaced (Figs. 19.12G–I). In another lineage, *Dolichandra*, sister to the "multiples of four clade," non-lignified rays and axial parenchyma are present in addition to the multiple phloem wedges (Figs. 19.12K, 19.12L, 19.13). This ray and axial parenchyma, in turn, subdivide during development, tearing the lignified cells of the secondary xylem into pieces due to parenchymatization. Both variations seem to increase the flexibility of the stem (Gentry 1980), but biomechanical tests are needed to confirm this perspective. Another lineage, *Amphilophium*, reunites six genera of earlier classifications (*Amphilophium*, *Distictella*, *Distictis*, *Glaziova*, *Haplolophium*, *Pithecoctenium*; Fischer et al. 2004; Lohmann & Taylor 2014) and develops normally four, or multiples of four, phloem wedges; however, these phloem wedges seem to disappear in adult stems. Careful anatomical analysis shows that the phloem wedges have not disappeared, but have been included in the secondary xylem (Fig. 19.12J), something detected by the interruption of the wood cells in four to multiple of four sites of the stem. At a certain stage in the development of *Amphilophium*, the regular cambium flanking the phloem wedges coalesces and includes the wedges. Apparently, the variant secondary phloem of *Amphilophium* remains conductive for a shorter period than that of other Bignonieae and this could be one reason why the regular cambium coalesces and includes the wedge in *Amphilophium*, but not in other lianas of Bignonieae. Interestingly, as seen in Fig. 19.13, the evolution of the cambial variant of Bignonieae is accompanied by an increase in anatomical complexity (more stages in their ontogenies) towards the terminal nodes of the phylogeny.

Other families in which multiple types of cambial variants occur, such as the Leguminosae, Malpighiaceae, and Sapindaceae, might also reproduce a similar evolutionary pattern by virtue of similar small-scale changes in the development of the stems. The Malpighiaceae, for instance, shows a remarkable diversity of cambial variants (Fig. 19.14), as well as lianas with regular secondary growth (Fig. 19.14A). The cambial variants include species with unequal production of xylem, generating lobed stems, that may be asymmetrical (Fig. 19.14B) or symmetrical (Fig. 19.14C), intraxylary phloem, furrowed xylem (Figs. 19.14D, 19.14E), and dissected xylem, caused by the proliferation of non-lignified parenchyma (Figs. 19.14F–H), as well as successive cambia (Fig. 19.14I). These variations may also be found in combination. How these variants have evolved within the family and whether or not they are developmentally interconnected is under evaluation (Pace & Angyalossy, in preparation).

## SEASONALITY OF CAMBIAL ACTIVITY AND GROWTH RINGS IN LIANAS

There is still surprisingly little information on the seasonality of secondary growth of lianas, resulting from switches in cambial activity. In temperate lianas, such as *Celastrus scandens* (Celastraceae), *Parthenocissus inserta*, *Vitis riparia* and *Vitis vinifera* (Vitaceae), the cambium is active from one and a half to four months annually (Esau 1948; Davis & Evert 1970). Although the resumption of cambial activity every year was not well synchronized among the individuals – varying by one and a half months, from early to late spring – all species exhibited a dormant cambium before the onset of winter. Temperature has been highlighted as the most likely factor influencing dormancy and resumption of the cambium in temperate species (Kozlowski et al. 1991; Begum et al. 2007, 2008).
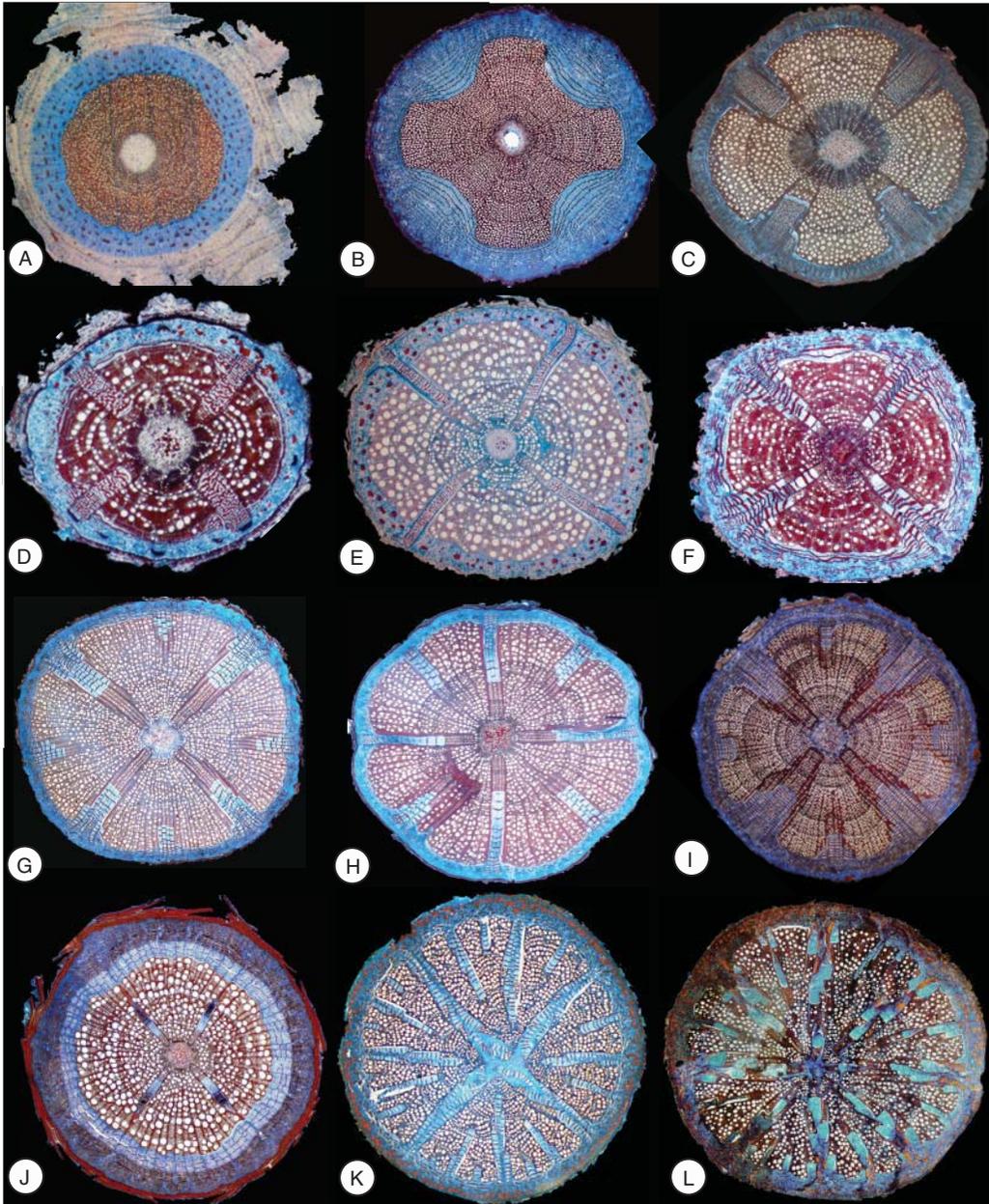
Fig. 19.12 Diversity of stem architectures in Bignoniaceae lianas, as seen in transverse section (TS). (A) Liana of tribe Tecomeae. (B–L) Lianas of tribe Bignonieae. (A) *Podranea ricasoliana*, stem with regular secondary growth. (B) *Perianthomega vellozoi*, stem with 4 arcs. (C–F) Stems with 4 phloem wedges. (C) *Fridericia samydoides*. (D) *Lundia longa*. (E) *Pleonotoma tetraquetra*. (F) *Manaosella cordifolia*. (G–I) Stems with multiple of 4 phloem wedges. (G) *Mansoa difficilis*. (H) *Pyrostegia venusta*. (I) *Adenocalymma divaricatum*. (J) *Amphilophium crucigerum*, stem with included phloem wedges. (K, L) Stems with multiple dissected phloem wedges. (K) *Dolichandra unguis-cati*. (L) *Dolichandra unguiculata*. *See plate section for color representation of this figure.*
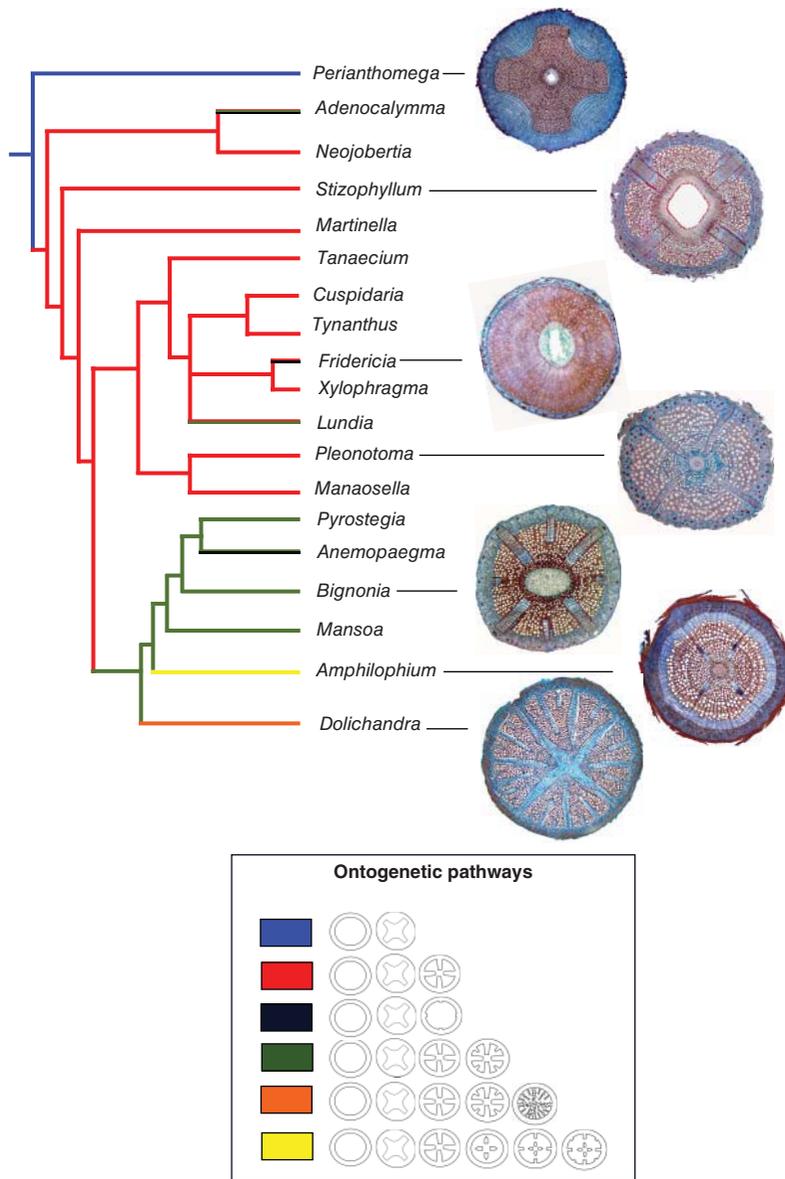
Fig. 19.13 Ancestral character state reconstruction of the ontogenetic pathways of tribe Bignonieae (Bignoniaceae). In Bignonieae the presence of four phloem arcs (blue) is ancestral in the family (synapomorphic), and different stem anatomical architectures have evolved from it, four phloem wedges (red) correspond to the majority of the tribe, multiple of four phloem wedges (green), multiple dissected (black) and included phloem wedges (yellow) have evolved in the terminal nodes of the phylogeny. *See plate section for color representation of this figure.*
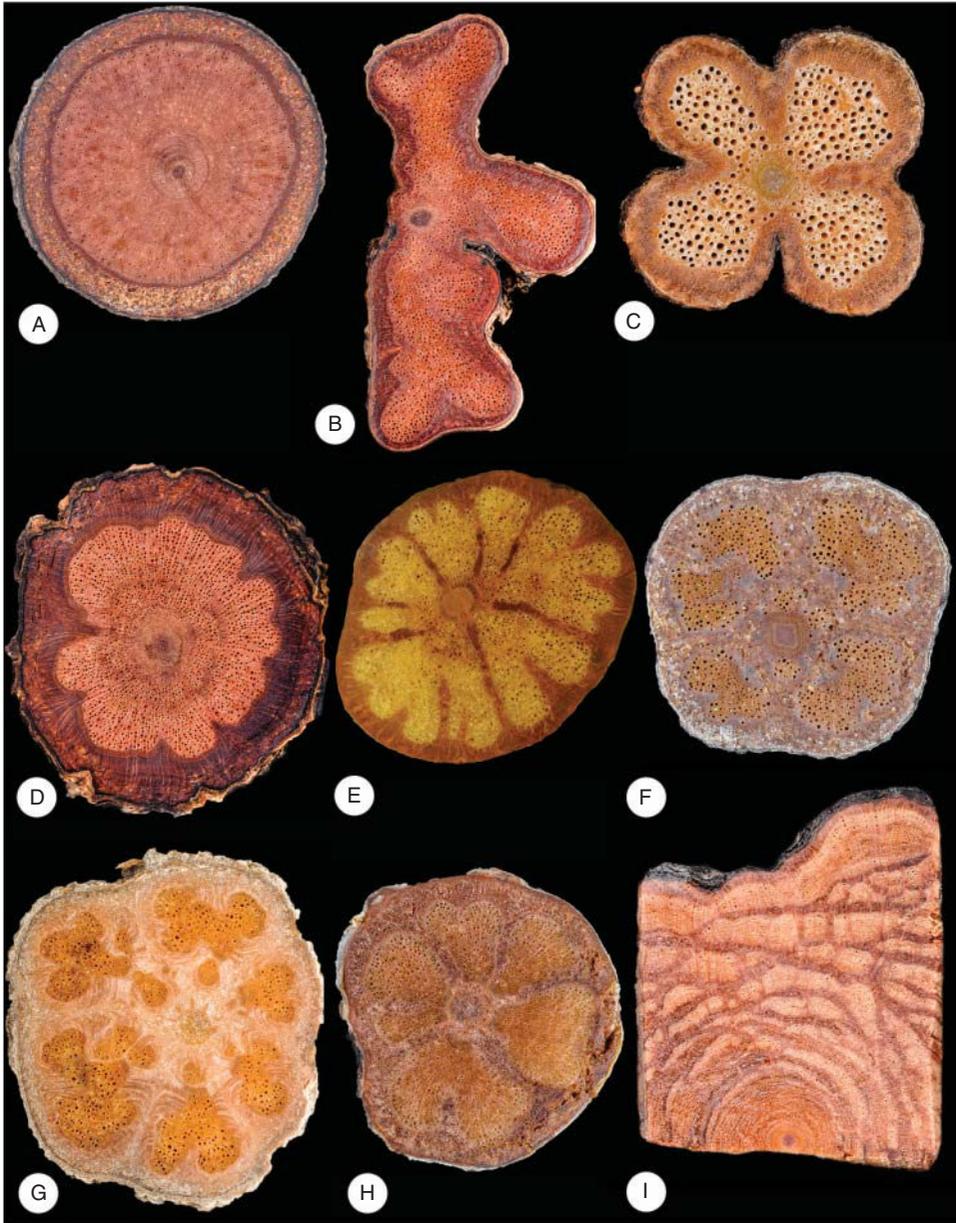
Fig. 19.14 Diversity of stem architectures in Malpighiaceae lianas, as seen in transverse section (TS). (A) *Heteropterys nitida* stem with regular secondary growth. (B) *Heteropterys nordestina* stem lobed with asymmetrical conformation. (C) *Stigmaphyllon blanchetii*, stem lobed with symmetrical conformation (D) *Heteropterys megaptera*, stem with shallow phloem wedges. (E) *Mascagnia sepium*, stem with deep phloem wedges. (F–H) Stems with dissected xylem. (F) *Mezia mariposa*. (G) *Alicia anisopetala*. (H) *Heteropterys cordifolia*. (I) *Banisteropsis nummifera*, stem with successive cambia. *See plate section for color representation of this figure.*

In contrast to temperate regions, the main factor affecting cambial activity in tropical tree species is the seasonal dry periods (Worbes 1995) or floods in floodplains (Worbes 1985; Schöngart et al. 2002). It was previously believed that growth rings of lianas were too irregular to have been produced annually (Schenck 1893); however, new analyses, including periodic sampling of stems (Léon-Gómez & Monroy-Ata 2005; Lima et al. 2010; Lima 2012), dendrochronology (Heuzé et al. 2009; Brandes et al. 2011), and cambial wounding (Brandes et al. 2011) have demonstrated that growth rings are indeed annual and positively correlated with precipitation in the tropics.

Periodic sampling analyzing the most abundant liana families of the Neotropics, including Bignoniaceae, Leguminosae, and Sapindaceae, from the Brazilian semi-deciduous seasonal forest in the city of São Paulo, shed light on the periodicity of growth in tropical lianas (Lima et al. 2010; Lima 2012). Studies of the cambial activity in four species (*Tynanthus cognatus* and *Styzophyllum riparium* of the Bignoniaceae; *Dalbergia frutescens* of the Leguminosae; and *Serjania laruotteana* of the Sapindaceae) have shown that cambial activity is strongly correlated with the rainy season for these four species (Fig. 19.15A). It is shown that the entire period of growth for most of the species and the most intense growth period of the only continuously growing species analyzed, i.e., *Serjania laruotteana*, are concentrated during the last half of the rainy season. Periodic sampling also showed different responses of cambial activity extent in the four studied lianas growing under the same climatic conditions. The different responses
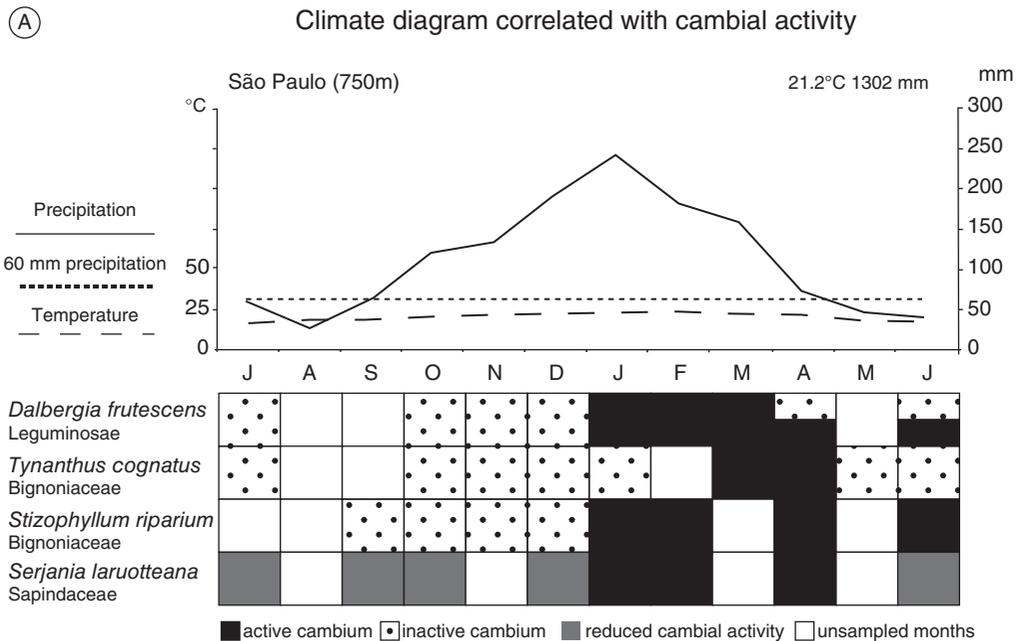
Fig. 19.15 (A) Climate diagram of São Paulo, Brazil, and the correlation with cambial activity of four species of lianas. Months in which the cambium was active are marked in black, inactive cambium is marked with dots. Gray indicates reduced activity. Black and dots together indicate periods in which the cambium was found both active and inactive in different specimens. White indicates unsampled months. (B) Diagram indicating cambial activity in the stem of the four studied liana species throughout the year. Active cambium is drawed by thick line and inactive by thin line. Note that the months depicted for each species are not the same, as the onset of cambial activity varied among them. The resumption of cambial activity in *Dalbergia frutescens* takes place in different regions of the stem in January and spread laterally until the end of the growth season in June. In *Tynanthus cognatus* and *Stizophyllum riparium* the cambial activity resumption takes place in the variant cambium inside the phloem wedges in March and January, respectively, and then spreads laterally to the regular cambium. *Serjania laruotteana* compound stem shows higher activity in the central cylinder and in portions of the peripheral cylinders of the cambium that face the central cylinder.
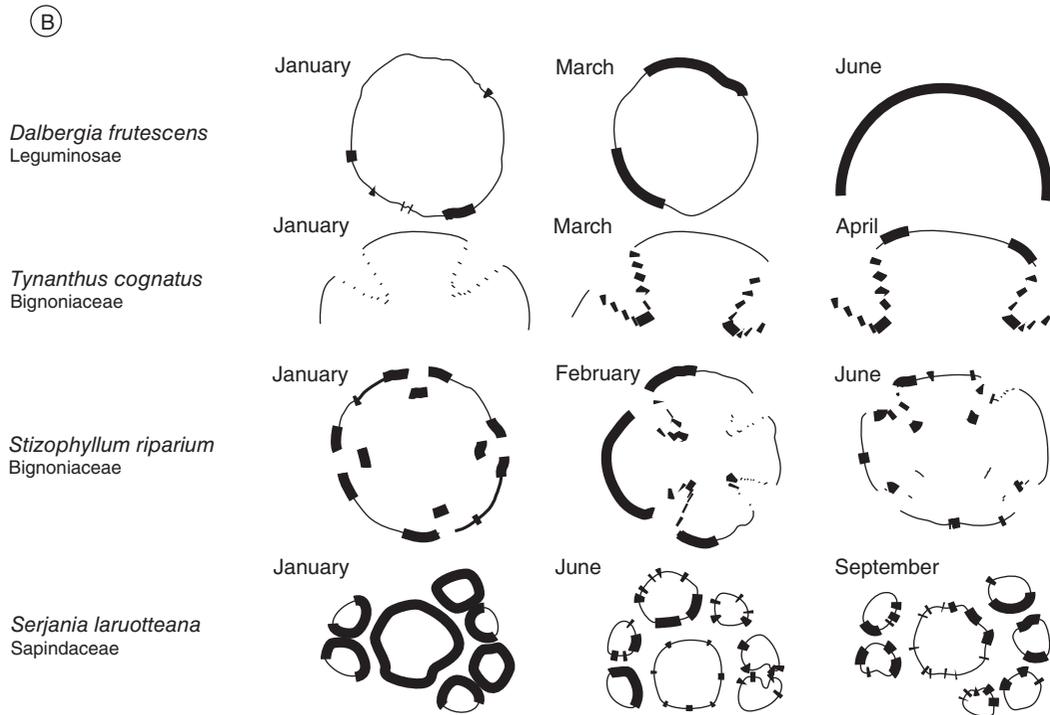
Fig. 19.15 (*continued*).

included a short cambial activity of only two months in *Tynanthus cognatus* (Lima et al. 2010), a longer period of six months in *Stizophyllum riparium* and *Dalbergia frutescens*, and continuous cambial activity in *Serjania laruotteana* (Lima 2012, Fig. 19.15A). Therefore, the different responses of cambial activities proved to be species-specific within a common environment. These idiosyncratic patterns of growth (Enquist & Leffler 2001) seen in different species may be controlled by the water relations of the plant, which is, in turn, influenced by both biotic and abiotic factors, such as the amount and seasonality of annual precipitation, the soil and wood water retention capacity, the size and depth of the root system, plant deciduousness, and seasonality of deciduousness (Borchert 1994a, 1994b).

Apart from temporal discontinuity, it is of significant interest that cambial activity is not spatially continuous throughout the stem circumference in all liana species studied. The cambial activity in *Dalbergia frutescens*, a species that lacks cambial variants, starts at different points scattered throughout the stem circumference and then spreads sideward, reaching all or most of the stem circumference by the end of the growing season (Fig. 19.15B).

The exact site where cambial activity resumes, or higher activity takes place, is not random, but is correlated with the cambial variant of the species. In *Tynanthus cognatus* and *Stizophyllum riparium* – species with furrowed xylem (phloem wedges, see Fig. 19.8D) – the resumption of cambial activity takes place first in the variant cambium located at the bottom of the phloem wedges, then spreads sideward to the regular portion of the cambium beside the phloem wedges, and then to the center of the regular portion of the cambium (Fig. 19.15B). Furthermore, in *Serjania laruotteana*, which has a compound stem and continuous cambial activity throughout the year, the higher activities are detected in the central cylinder and in portions of the cambium of the peripheral cylinders facing the central cylinder. Because of this activity, the piths are generally eccentric in the peripheral cylinders.

The seasonal cambium activity promotes a seasonal wood formation detectable by the presence of growth rings. In the studied species, annual growth rings occur in the three species that exhibit a dormant period of cambial activity (*Dalbergia frutescens* Fig. 19.16A; *Stizophyllum riparium* Fig. 19.16B; and *Tynanthus cognatus*); the only species with continuous growth during the year, *Serjania laruotteana*, lacks growth rings (Fig. 19.16C).

Several studies (Schenck 1893; Gasson & Dobbins 1991; Carlquist 1993; Brandes & Barros 2008; León 2009; Lima et al. 2010) shows that the most common earlywood growth markers found in the secondary xylem of lianas are marginal parenchyma, as found in Aristolochiaceae, Bignoniaceae (Fig. 19.16B), Combretaceae, Leguminosae (Fig. 19.16A), Rhamnaceae, Ulmaceae; and larger vessels, as found in Bignoniaceae (Fig. 19.16B), Leguminosae (Fig. 19.16A) and Verbenaceae. According to the same authors, the most common latewood markers are thick and radially flattened fibers, as found in Bignoniaceae, Combretaceae, Leguminosae, Rhamnaceae, Ulmaceae, Verbenaceae, and narrow vessels in Bignoniaceae (Lima et al. 2010). Less commonly, dilated rays and
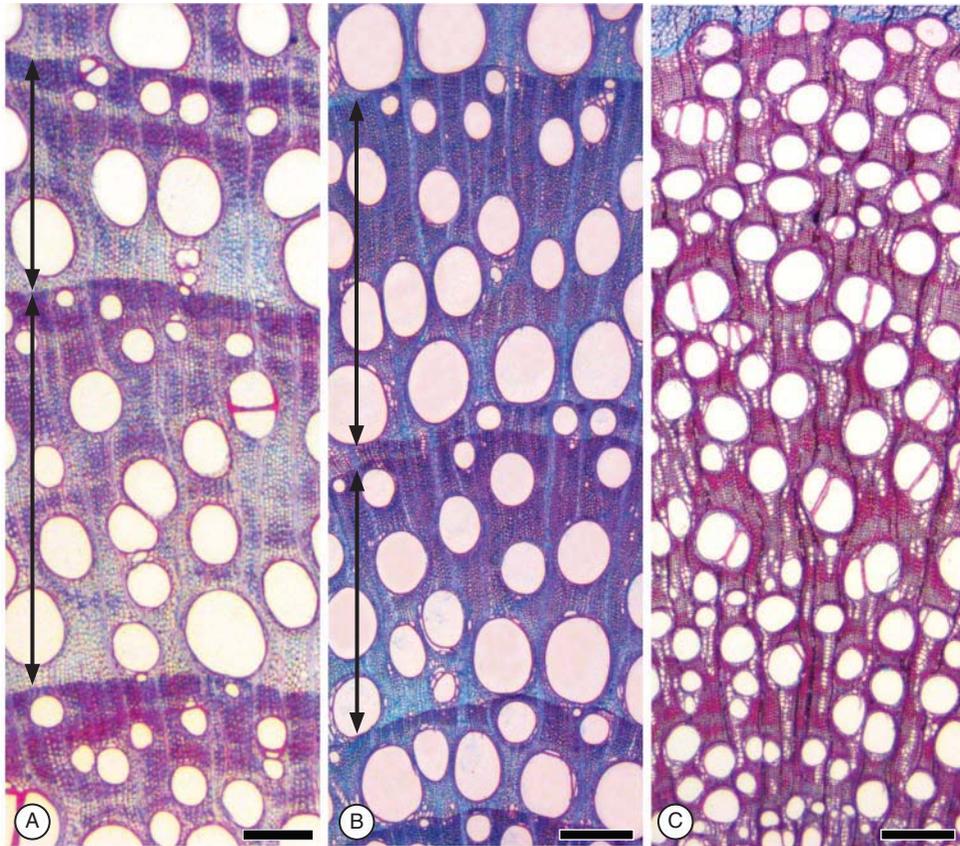
Fig. 19.16 Growth rings in secondary xylem of lianas, as seen in transverse section (TS). (A, B) Annual growth rings present (double-headed arrows). Annual growth rings marked by marginal parenchyma band and wide vessels in the earlywood and narrow vessels and radially flattened fibers in the latewood. (A) *Dalbergia frutescens* (Leguminosae). (B) *Stizophyllum riparium* (Bignoniaceae). (C) Growth rings absent in *Serjania laruotteana* (Sapindaceae). Scale bars: 400 μm.
See plate section for color representation of this figure.

radially shorter ray cells are also found as latewood markers in Bignoniaceae (Lima et al. 2010).

In addition, for the lianas of Bignoniaceae the latewood markers were shown to be the most reliable means of identifying growth rings, being found in all species that had growth rings, as opposed to earlywood markers that could be missing in several species (Lima et al. 2010).

CONCLUSION AND FUTURE DIRECTIONS

In this chapter, we have explored the anatomical characteristics of the vascular system of scandent plants, showing that they share common features that can be grouped under the term "lianescent vascular syndrome." These features include the presence of wide conducting cells of the xylem and phloem, a higher abundance of axial parenchyma, fewer fibers, broader rays, and cambial variants. New data on seasonal cambial activity and the formation of growth rings in Bignoniaceae, Leguminosae and Sapindaceae show that lianas respond differently to the presence of dry and wet seasons, depending on the taxon. Much more remains to be explored in liana anatomy, and the following are the most pressing topics:

1. The relationship between radial hydraulic water distribution from the secondary ray phloem towards the secondary ray xylem in taxonomically related liana and tree species to unravel the possible role of perforated ray cells in vessel refilling.

2. The seasonality of growth of lianas to confirm if (a) the observed timespan of cambial activity explored in the present study is shared by other lianas; and (b) whether different cambial variants induce different cambial activity.

3. The integration of ontogenetic and phylogenetic data of different families to learn whether optimization in photosynthate conduction of the cambial variant is a common feature in variant phloem of all lianas.

4. The integration of ontogenetic and phylogenetic studies to explore the mechanisms involved in the evolution of new architectures derived from cambial variants in the vascular system of lianas.

GLOSSARY

Anastomose: coalesce, get linked by anastomosis, like interconnected veins in a leaf join together.

Axial parenchyma: parenchyma cells in the axial system of the secondary vascular tissues, produced by the cambium.

Cambial variant: a term of convenience, use to indicate an alternative form of secondary growth different from the most common pattern, where a single cambium produces more secondary xylem to the inside than secondary phloem to the outside. Also known as anomalous secondary growth.

Fibers: in the secondary vascular tissue refers to axial elongated sclerenchyma cells with a lignified secondary wall.

Fusiform initials: elongated meristematic cells of the cambium that originate the elements of the axial system of the secondary xylem (vessel, tracheid, fiber, axial parenchyma) and secondary phloem (sieve tube elements, sieve cells, fibers, axial parenchyma).

Liana: any scandent plant that presents a conspicuous secondary growth.

Non-lignified axial parenchyma: axial parenchyma cells with non-lignified walls.

Perforated ray cell: cell within the rays that differentiates as vessel element and connect two adjacent vessels on each side of the ray.

Phloem wedges: a term of convenience that refers to the presence of wedges of phloem that penetrate into the secondary xylem. Also known as furrowed xylem.

Septate fiber: a fiber with a thin transverse wall (septum).

Rays: groups of cells of various shapes that are formed by the ray initials of the cambium, and that form a continuous radial system between phloem and xylem.

Ray initials: meristematic cells of the cambium that form the ray cells of both the secondary xylem and phloem.

Sieve ray cell: cell within the ray that differentiates as sieve tube element, usually connecting two adjacent sieve tubes at each side of the ray.

Vasicentric tracheids: tracheids adjacent to vessels in the secondary xylem.

Vessel dimorphism: a term of convenience coined by Carlquist (1981), which refers to the presence of very wide vessels co-occurring with very narrow vessels or tracheids in the secondary xylem, a feature very common in lianas.

Vine: any scandent plant.

*Most terms and definitions are based on Evert's (2006) *Esau's Plant Anatomy*.

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