



Cambial variants of liana species (Fabaceae) in Taiwan

Sheng-Zehn YANG*, Po-Hao CHEN and Kung-Cheng LIN

National Pingtung University of Science and Technology, No. 1, Shuefu Rd., Neipu, Pingtung, Taiwan.

* Corresponding author Tel: 886-8-7703202 ext. 7408; Email: yangsz@mail.npust.edu.tw

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ABSTRACT: In order to better understand variation in cambium in lianas in Taiwan and to aid identification of liana species, we examined the stem structure of ten species of lianas belonging to the family Fabaceae. Samples were collected mainly from southern and eastern Taiwan and were selected from plants with different stem diameters in order to compare the structural similarities of plants. The results showed that cambium had a normal appearance and stems were round in *Caesalpinia bonduc* (L.) Roxb., *Caesalpinia crista* L., and *Caesalpinia minax* Hance. We noted a combination of furrowed xylem and dissected xylem in *Bauhinia championii* (Benth.) Benth., shallowly furrowed xylem in *Acacia caesia* (L.) Willd., *Centrosema pubescens* Benth., and *Mimosa diplotricha* C. Wright ex Sauvalle, a combination of flattened stem and interxylary phloem in *Entada koshunensis* Hayata & Kaneh. and *Entada phaseoloides* (L.) Merr., and a combination of external vascular cylinder and flattened stem in *Pueraria montana* (Lour.) Merr. Of these lianas, three species, *A. caesia*, *B. championii*, and *C. crista*, -experienced two distinct developmental growth phases. We concluded that variations in cambium and xylem deposition are associated with the size of the stems. Medullary bundles occurred in the pith of *P. montana*, an observation that has not previously been recorded. We present the first description and photographs of these bundles and the external vascular cylinder in the pith, and it is recommended that further study of this species be conducted.

KEY WORDS: Cambial variants, Fabaceae, Interxylary phloem, Lianas, Taiwan, Xylem.

INTRODUCTION

Lianas are climbing vines that are among the most important components of tropical forests (Schnitzer and Bongers, 2002). Their roots are generally buried in the soil, while their stems that rise by various climbing mechanisms and are dependent on external supports. They have two stages of development, the autologous support stage and the climbing stage. The autologous support stage of lianas is characterized by the presence of a few narrow vessels and thick fibers. During the climbing stage, a special internal structure of the liana stem develops that is either a standard structure or anomalous (Isnard and Silk, 2009). Morphological variation in liana stems is mainly associated with the geometry of the phloem and xylem structure, and the irregular shapes within the stems are classified into several types (Angyalossy *et al.*, 2015).

Most vascular plants contain a single vascular cambium, which originates from an initial fusiform cell and an initial ray cell. More secondary xylem is produced near the inside of the stem than near the outside of the stem, and all the secondary xylem and secondary phloem grow along the peripheral organs. Cambial variants are the most common features of the secondary growth mode of vascular plants, and they are more common in lianas than in trees or shrubs (Putz and Mooney, 1991; Carlquist, 2001; Angyalossy *et al.*, 2012; Yang *et al.*, 2015, 2016). When leaves and flowers are missing, cambial variants provide unique means of identification and they can be used in the classification of many families and genera (Caballé, 1993).

Lianas show diverse stem structure and cambial variants (Angyalossy *et al.*, 2012). Mauseth (1988) described the unusual appearance and organization of the cambium, xylem, and phloem, known as an anomalous structure, in some lianas. The shapes of liana stem cross-sections and the structures and cambial variants of the corresponding orders and families have been studied previously (Angyalossy *et al.*, 2012, 2015), including those of the family Fabaceae.

Within this family, there are multiple types of cambial variants. Previous reports indicated that some species in this family had diverse anomalous structures (Metcalf and Chalk, 1985; Carlquist, 1991, 2001; Caballé, 1993; Sun *et al.*, 2014). Taiwan is located in the subtropical climate zone, so it is warm and humid year-round and is suitable for the growth of lianas, including those of the family Fabaceae. This family includes 79 climbers recorded in the Flora of Taiwan (Huang and Ohashi, 1993), including 70 species in Papilionoideae, five species in Mimosoideae, and four species in Caesalpinioideae. The family includes six cambial variants: irregular stem conformation, interxylary phloem, phloem arcs/wedges, xylem dispersed by parenchyma divisions, successive cambia, and intraxylary phloem (Angyalossy *et al.*, 2012, 2015). However, data regarding the patterns and complex characteristics of stem transverse sections in this family are lacking.

In the present study, we examined the stem transverse sections of ten species belonging to Fabaceae in Taiwan. As the cambial variations constitute an extremely diverse morphology, the present study attempts to (1) carefully revise the descriptors used, (2)



provide detailed photographs of features discussed, and (3) provide a key based on morphological characters of transverse sections to facilitate the identification of irregular cambial activity in this family.

MATERIALS and METHODS

From 2012 to 2015, we collected samples of ten species in seven genera belonging to Fabaceae in Taiwan (Table 1). Members of these species are extensively distributed in the low mountainous forest of Taiwan. The dataset included three native species [*Bauhinia championii* (Benth.) Benth., *Caesalpinia bonduc* (L.) Roxb., and *Caesalpinia crista* L.] and one cultivated species (*Caesalpinia minax* Hance) in the subfamily Caesalpinioideae, four native species [*Acacia caesia* (L.) Willd., *Entada koshunensis* Hayata & Kaneh., *Entada phaseoloides* (L.) Merr., and *Mimosa diplotricha* C. Wright ex Sauvalle] in the subfamily Mimosoideae, and two species [*Centrosema pubescens* Benth. and *Pueraria montana* (Lour.) Merr.] in the subfamily Papilionoideae. The species *E. koshunensis* is endemic to Taiwan and distributed at low altitudes in southern Taiwan.

We collected plant stems of various sizes from each species in order to observe the similarities or differences in their stem cross-sections. All the specimens were collected at chest height in order to obtain comparable measurements of the diameter at breast height (DBH). The fresh materials were cut into pieces about 5 cm long and a flat cross-section of each stem was cut using a cutter blade. After the cross-section was cut, we immediately took pictures of the stem surface using a Nikon D80 SLR digital camera (Lens AF Micro Nikon 60 mm 1: 2.8D, Nikon Corporation, Tokyo, Japan), and qualitative and quantitative anatomical traits were determined using Image-J software (Ferreira and Rasband, 2011). The specimens were dried in an oven (temp. 60°C) for 4–5 days and were then stored at –40°C for 3–4 days. All the collected specimens were deposited in the Provincial Pingtung Institute herbarium at the National Pingtung University of Science and Technology, Pingtung, Taiwan, for subsequent identification. The scientific names of plants were found in Flora of Taiwan Volume 3 (Huang and Ohashi, 1993).

Angyalossy *et al.* (2015) divided cambial variants into two types: those that originate from a single cambium and those that originate from multiple cambia. Single cambial variants are subdivided into six types: 1. Irregular conformation. Varying proportions of xylem and phloem are produced around the girth of the stem. 2. Interxylary phloem, also called included phloem. The cambium produces phloem that grows both on the inside and outside of the stem. This type of variant does not contain cambium (included cambium). 3. Phloem arcs.

The cambium produces more phloem than xylem. This type of variant contains included cambium. 4. Furrowed xylem. The xylem is furrowed by arcs and/or wedges of phloem, a trait termed wedge phloem. This type of variant is derived from the part of the cambium that contains a relatively small amount of xylem and a relatively large amount of phloem. 5. Axial vascular elements in segments (xylem in plates). Axial elements of the xylem and phloem are present in segments alternating with very wide xylem and phloem rays. 6. Dissected xylem (dispersed xylem segments). This type of variant is derived from the proliferation of non-lignified parenchyma.

Multiple cambial variants are subdivided into four types: 1. Successive cambia. New cambia arise successively due to cell divisions in the external secondary vascular system. Each new cambium in the stem successively generates an inward-pointing secondary xylem and an outward-pointing secondary phloem. 2. Compound stem. Multiple vascular cylinders in a single stem, which creates a cable-like structure, form the stem. 3. Intraxylary phloem. Cambium is formed between the primary xylem and the pith. 4. External vascular cylinders. This type of multiple cambial variant is formed either by neof ormation of secondary vascular cylinders or secondary growth of external primary vascular bundles.

Our observations were supplemented by published images and descriptions (Metcalf e and Chalk, 1985; Carlquist, 1991, 2001; Caballé, 1993; Acevedo-Rodriguez, 2005; Isnard and Silk, 2009; Angyalossy *et al.*, 2012, 2015; Yang and Chen, 2015) on the external morphology and transverse xylem of lianas to describe the morphological characteristics of lianas and integrate the characters to make a key. The photographs and observations of all 10 investigated lianas are new. We described these 10 species according to location (county), number of collection, stem diameter (mm), water content of stem, thorns on epidermis, shape of pith, pith diameter (mm), pith color, medullary bundles, parenchyma proliferation, cambial variants, vessel dimorphism, and phloem fibers (Table 1). Terminology for the description partly follows Chiang (1973), Metcalf e and Chalk (1979, 1985), Carlquist (1991), and Beck (2010).

RESULTS

The identifying details for the ten species appear in Table 1, as well as in figures as follows: *A. caesia* (Fig. 1a), *B. championii* (Fig. 1b, 1c), *C. bonduc* (Fig. 1d), *C. crista* (Fig. 1e), *C. minax* (Fig. 1f), *C. pubescens* (Fig. 2a), *E. koshunensis* (Fig. 2b), *E. phaseoloides* (Fig. 2c), *M. diplotricha* (Fig. 2d), and *P. montana* (Fig. 2e, 2f). Some figures were indicated by the abbreviate labels and symbols to show the diagnostic parts of stem transverse



Table 1. Morphological characteristics of stem transverse sections in ten Fabaceae species in Taiwan

Species	Locations (county)	Number of collection	Stem diameter (mm)	Water juice of stem	Thorns on epidermis	Shape of pith	Pith diameter (mm)	Pith color	Medullary bundles	Parenchyma proliferation	Cambial variants	Vessel dimorphism	Phloem fibers
<i>Acacia caesia</i> (L.) Willd.	Taitung	3	10-11	0	1	pentagon	1.8-2.0	yellow	0	0	shallowly furrowed xylem	1	conspicuous
<i>Bauhinia championii</i> (Benth.) Benth.	Taitung, Kaohsiung, Pingtung, Taichung	5	15-18; 40-50	0	0	4-5 angulars	0.7-0.8, absent in older stage	brown	0	1	furrowed xylem; dissected xylem in larger stem	1	obscure
<i>Caesalpinia bonduc</i> (L.) Roxb.	Hsienchu	1	12-14	0	1	orbicular	6.1-6.2	white	0	0	regular	0	conspicuous
<i>Caesalpinia cristata</i> L.	Pingtung	2	8-10	0	1	orbicular	1.5-2.0	yellow	0	0	regular	1	obscure
<i>Caesalpinia minax</i> Hance	Taichung	1	10-13	0	1	5-7 angulars	8.0-8.2	white	0	0	regular	0	none
<i>Centrosema pubescens</i> Benth.	Pingtung	1	13-15	0	1	flat	1-1.2	yellow	0	0	shallowly furrowed xylem; 2-4 lobed stem	0	conspicuous
<i>Entada koshunensis</i> Hayata & Kaneh.	Pingtung	1	30-45	1	0	orbicular	2.5-3.0	gray	0	1	interxylary phloem; flattened stem	0	conspicuous
<i>Entada phaseoloides</i> (L.) Merr.	Taichung	1	80-100	1	0	nearly absent	-	-	0	1	interxylary phloem; flattened stem	0	conspicuous
<i>Mimosa diplotricha</i> C. Wright ex Sauvalle	Pingtung	1	15-18	0	1	suborbicular	3.5-4.0	yellow	0	0	shallowly furrowed xylem	0	conspicuous
<i>Pueraria montana</i> (Lour.) Merr.	Nantou, Chiayi, Pingtung, Taitung	11	5-8; 15-23	1	0	orbicular	1.1-1.3	white	1/0	0	external vascular cylinder; flattened stem	0	conspicuous

Note: Water juice of stem: 0 = absent, 1 = present; Thorns on epidermis: 0 = absent, 1 = present; Medullary bundle: 0 = absent, 1 = present; Parenchyma proliferation: 0 = absent, 1 = present; Vessel dimorphism: 0 = absent, 1 = present.

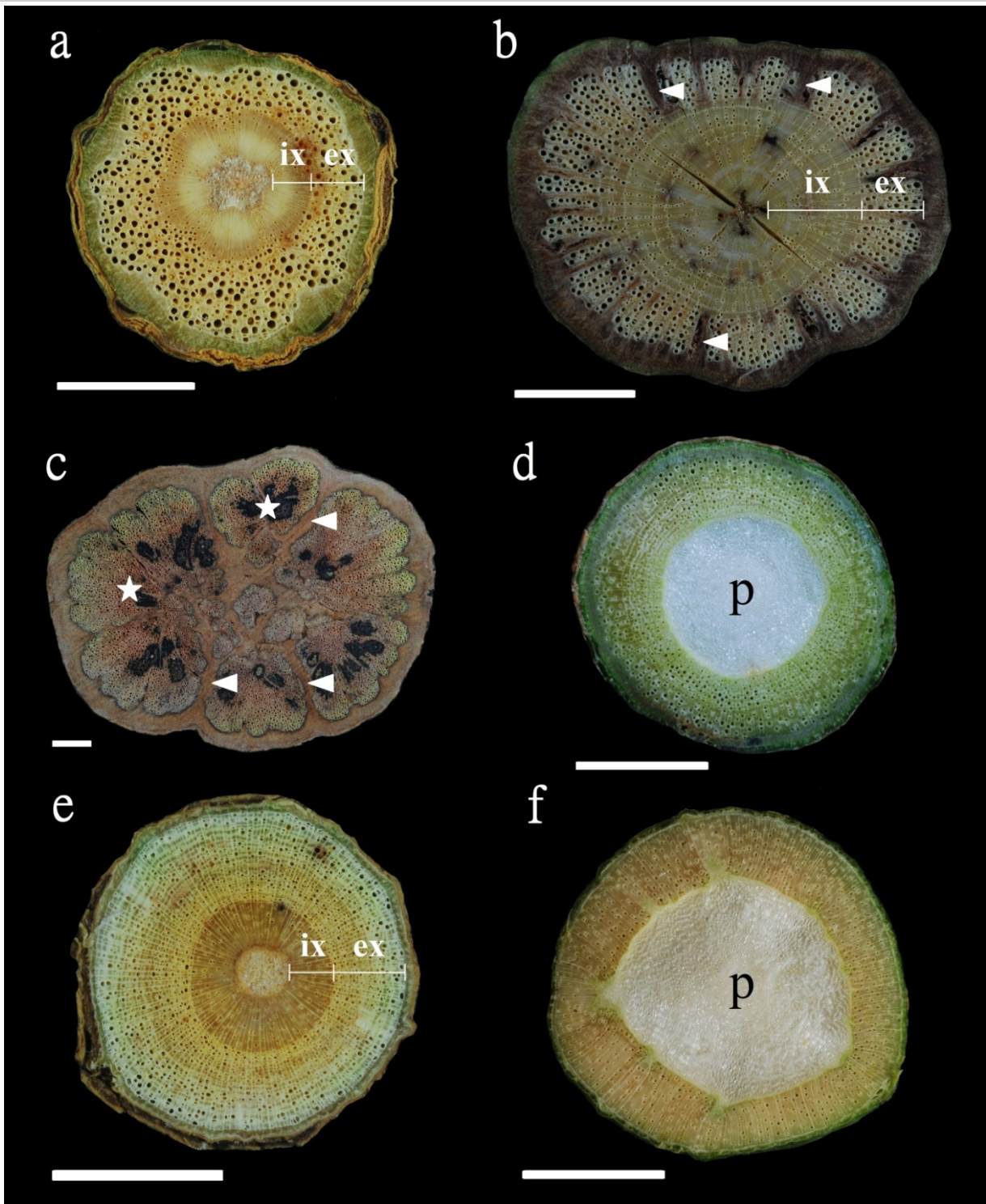


Fig. 1. Stem transverse sections of members of the family Fabaceae. **(a)** *Acacia caesia* (L.) Willd. showing self-supporting phase with a few narrow vessels in inner xylem and climbing phase with very wide vessels in external xylem. **(b)** *Bauhinia championii* (Benth.) Benth., in younger stage, showing self-supporting phase with a few narrow vessels in inner xylem and climbing phase with very wide vessels in external xylem; furrowed xylem by parenchyma proliferation (arrowhead). **(c)** *Bauhinia championii*, in older stage, showing dissected xylem (star) by parenchyma proliferation (arrowhead). **(d)** *Caesalpinia bonduc* (L.) Roxb., pith round, white in color. **(e)** *Caesalpinia crista* L., showing self-supporting phase with a few narrow vessels in inner xylem and climbing phase with very wide vessels in external xylem. **(f)** *Caesalpinia minax* Hance., pith 5–7-sided, white in color. Labels: ix = inner xylem, ex = external xylem, p = pith. Scale bars: (a)–(f) = 5 mm.

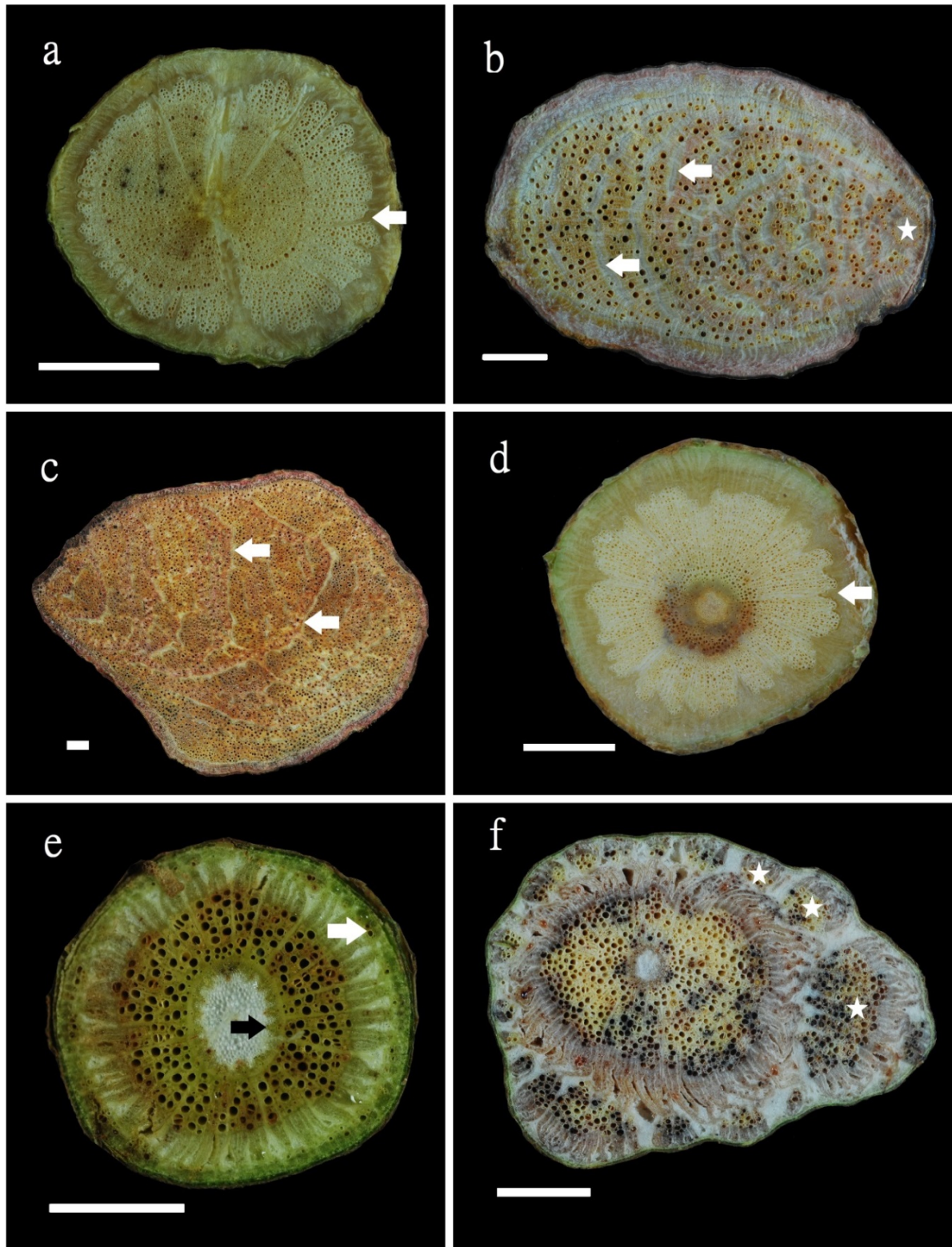


Fig. 2. Stem transverse sections in members of the family Fabaceae. **(a)** *Centresema pubescens* Benth., showing 2–4-lobed stem and shallowly furrowed xylem (arrow). **(b)** *Entada koshunensis* Hayata & Kaneh., showing the pith (star) located on the edge of stem and flattened stem with interxylary phloem (arrow). **(c)** *Entada phaseoloides* (L.) Merr., showing flattened stem with interxylary phloem (arrow). **(d)** *Mimosa diplotricha* C. Wright ex Sauvalle., showing shallowly furrowed xylem (arrow). **(e)** *Pueraria montana* (Lour.) Merr., in younger stage, showing muellary bundles (black arrow) within the pith and cortex vascular bundle (white arrow). **(f)** *Pueraria montana*, in older stage, showing external vascular cylinder (star) with irregular flattened stem. Scale bars: (a)–(f) = 5 mm.



section. In the present study, three species had transverse sections of stems in which the cambium was normal and the stem was round—*C. bonduc*, *C. crista*, and *C. minax*. The cambial variants of the other seven species were furrowed xylem in *B. championii* at a young stage, dissected xylem in *B. championii* at an older stage, furrowed xylem with shallow lobes in *A. caesia*, *C. pubescens* and *M. diplotricha*; flattened stem and interxylary phloem in *E. koshunensis*, irregular stem and interxylary phloem in *E. phaseoloides*; and external vascular cylinder and flattened stem in *P. montana*.

Using the characteristics of the stem transverse cross-sections described above, we constructed the following key to the ten climber species.

- | | |
|--|------------------------|
| 1a. Cambium normal in products | 2 |
| 1b. Cambium with variations | 4 |
| 2a. Pith with 5–7 sides, 8.0–8.2 mm in size | <i>C. minax</i> |
| 2b. Pith round in shape | 3 |
| 3a. Pith white in color, 6.1–6.2 mm in size | <i>C. bonduc</i> |
| 3b. Pith yellow in color, 1.5–2 mm in size | <i>C. crista</i> |
| 4a. Multiple cambia; stem irregular with cortical vascular bundles | <i>P. montana</i> |
| 4b. Single cambium | 5 |
| 5a. Combination of cambial variants | 6 |
| 5b. Shallowly furrowed xylem | 8 |
| 6a. Furrowed xylem and dissected xylem | <i>B. championii</i> |
| 6b. Flattened stem and interxylary phloem | 7 |
| 7a. Stem oval in shape | <i>E. koshunensis</i> |
| 7b. Stem irregular in shape | <i>E. phaseoloides</i> |
| 8a. Pith with 5 sides, each side divided into two lobes | <i>A. caesia</i> |
| 8b. Pith round or irregular, without well-defined sides | 9 |
| 9a. Stem 2–4 lobes in shape | <i>C. pubescens</i> |
| 9b. Stem round in shape | <i>M. diplotricha</i> |

DISCUSSION

We summarized descriptions in previous reports (Metcalf and Chalk, 1985; Carlquist, 1991, 2001; Caballé, 1993; Sun *et al.*, 2014) that used different terms, such as block or fissured xylem, to describe the transverse sections of the same genus, such as *Bauhinia* (Table 2). In the present study, three species had transverse sections of stems in which the cambium was normal and the stem was round—*C. bonduc*, *C. crista*, and *C. minax*. The cambial variants of the other seven species matched descriptions in previous studies (Angyalossy *et al.*, 2012, 2015) with the exception of *P. montana*, which demonstrated an external vascular cylinder (Table 2), originating from multiple cambia. An external vascular cylinder type is created by the neoformation of secondary vascular cylinders or secondary growth of external primary vascular bundles. Angyalossy *et al.* (2015) mentions only formation by the secondary growth of external primary vascular bundles. In addition, our observations constitute the first report of medullary bundles in the pith of *P. montana* (Table 1).

The cambial variant of *E. rheedii* of concentrically alternating xylem and phloem (succession cambium) was described by Sun *et al.* (2014) and differs from the

interxylary phloem reported for this type by Metcalfe and Chalk (1985) and Carlquist (1991). A closer examination of the cortex of this species revealed that the phloem fibers were significantly present in the cortex when the stem DBH was > 15 cm. Therefore, we suggest that *E. rheedii* should be considered an interxylary phloem type and that the wood portions of the genus *Entada* are dispersed or separated by the proliferation of the parenchyma.

The woody parts of *Bauhinia japonica* Maxim., *Bauhinia langsdorffiana* Bong., and *B. championii* were dispersed by parenchyma proliferation (Carlquist, 1991, 2001), a phenomenon termed dissected xylem type (Angyalossy *et al.*, 2015). In the present study, the dissected xylem type occurred in the woody parts of older-stage *B. championii* and in the furrowed xylem type of younger-stage specimens. Therefore, the axial parenchyma plays a role in regeneration of vascular tissue at different developmental stages (Angyalossy *et al.*, 2012). The species *B. championii* has a shrubby growth form and the lianoid phase is pertinent in this regard.

The characteristics of the pith differed among the ten investigated species. The pith was located in the stem center of all of them except *E. koshunensis* and *E. phaseoloides*, in which the pith was located on the edge of the stem or not present (Fig. 2b, 2c). The pith of the genus *Caesalpinia* was larger in diameter and generally whiter in color, especially *C. bonduc* and *C. crista* (Fig. 1d, 1e), than the pith of other genera. Members of the genus *Caesalpinia* showed regular cambium activity.

A previous study reported that the cambial variant of *Millettia reticulata* Benth is a combination of xylem in plates and strands of included phloem (Sun *et al.*, 2014). We suggest that the species has xylem in plates but no strands of included phloem after checking the original materials from Sun *et al.* (2014). The absence of strands of included phloem is a better diagnostic feature than the distribution of the axial parenchyma in the secondary xylem. The vessels of this species are surrounded by or in contact with vasicentric parenchyma, one of the types of paratracheal parenchyma described by Beck (2010). It is worth noting that the characteristic wide rays from the pith to the cortex in *M. reticulata* differ from those of *Millettia pulchra* Kurz. var. *microphylla* Dunn. and *Millettia pachycarpa* Benth. We suggest that the diagnostic character of wide rays in *M. reticulata* is justification for transferring members of the genus *Millettia* into the genus *Callerya* (Table 2). The shape of the rays in cross-section has diagnostic value.

The cambial variants in *Derris laxiflora* Benth., *Dalbergia benthamii* Benth., *M. pachycarpa*, and *M. pulchra* var. *microphylla* are strands or rings of included phloem, as described in previous literature (Table 2). The vessels of these species are surrounded or contacted by confluent parenchyma, which is paratracheal parenchyma (Beck, 2010). The absence of strands and rings of



Table 2. Cambium variants of eleven genera in the family Fabaceae

Genus (Subfamily)	Metcalfe and Chalk (1985)	Carlquist (1991)	Caballé (1993)	Carlquist (2001)	Sun <i>et al.</i> (2014)	Present study
<i>Bauhinia</i> (Caesalpinioideae)	1. concentrically alternating xylem and phloem. 2. flattened stem. 3. furrowed or lobed stem. 4. fissured xylem (<i>B. langsdorffiana</i>).	1. flattened stem. 2. wood parts dispersed by parenchyma. 3. flattened stem with dispersed xylem segments.	block	flattened stem.		a combination of furrowed xylem and dissected xylem (<i>B. championii</i>)
<i>Caesalpinia</i> (Caesalpinioideae)						cambium normal (<i>C. bonduc</i> , <i>C. crista</i> , <i>C. minax</i>)
<i>Callerya</i> (Caesalpinioideae)						xylem in plates with vascentric parenchyma (<i>C. reticulata</i>)
<i>Centrosema</i> (Papilionoideae)		shallowly furrowed xylem (<i>C. plumieri</i>)				shallowly furrowed xylem (<i>C. pubescens</i>)
<i>Dalbergia</i> (Papilionoideae)			duplicate xylem cylinder	successive cambia	rings and strands interxylary phloem (<i>D. benthamii</i>)	cambium normal with confluent parenchyma (<i>D. benthamii</i>)
<i>Derris</i> (Papilionoideae)	1. cortical vascular bundle. 2. concentrically alternating xylem and phloem.				strands interxylary phloem (<i>D. laxiflora</i>)	cambium normal with confluent parenchyma (<i>D. laxiflora</i>)
<i>Milletia</i> (Papilionoideae)	1. concentrically alternating xylem and phloem. 2. flattened stem.	flattened stem with successive cambia	successive cambia rings (<i>M. duchesnei</i>)	flattened stem	1. strands interxylary phloem (<i>M. pachycarpa</i>). 2. rings interxylary phloem (<i>M. pulchra</i> var. <i>microphylla</i>). 3. wider rays with strand interxylary phloem (<i>M. reticulata</i>).	cambium normal with confluent parenchyma (<i>M. pachycarpa</i> , <i>M. pulchra</i> var. <i>microphylla</i>)
<i>Mucuna</i> (Papilionoideae)	1. cortical vascular bundle. 2. interxylary phloem. 3. concentrically alternating xylem and phloem.	interxylary phloem (<i>M. pruriens</i>)		successive cambia	concentrically alternating xylem and phloem (<i>M. macrocarpa</i>)	successive cambia (<i>M. macrocarpa</i>)
<i>Pueraria</i> (Papilionoideae)	concentrically alternating xylem and phloem.					a combination of external vascular cylinder (<i>P. montana</i>) and flattened stem
<i>Acacia</i> (Mimosoideae)	furrowed xylem.		deeply lobed stem		5-deeply lobed stem	shallowly furrowed xylem (<i>A. caesia</i>)
<i>Entada</i> (Mimosoideae)	interxylary phloem	interxylary phloem (single cambium)			concentrically alternating xylem and phloem (<i>E. rheedii</i>)	a combination of flattened stem and interxylary phloem (<i>E. koshunensis</i> , <i>E. phaseoloides</i>)

Note: interxylary phloem means as included phloem



included phloem of these four species is a better diagnostic feature than the distribution of the axial parenchyma in the secondary xylem. The confluent parenchyma consists of bands that enclose or are in contact with vessels. We concluded the cambium is normal in these four species. We also note that the species *D. benthamii* contains mucilage cavities distributed in the cortex after checking the original materials from Sun *et al.*, (2014). This finding was similar to the results of a previous study (Metcalf and Chalk, 1985).

The genus *Acacia* includes two cambial variants: furrowed xylem and deeply lobed stems (Caballé, 1993). In the present study, we determined that *A. caesia* contains shallowly furrowed xylem and the pith is five-sided, each side being divided into two lobes. A transverse section of the stem in *C. pubescens* revealed shallowly furrowed xylem, consistent with results obtained by Carlquist (1991). Transverse sections of *M. diplotricha* (in the present study) and *Mimosa velloziana* Mart. (Angyalossy *et al.*, 2015) revealed a furrowed xylem type, with continuous cambium and relatively deep phloem wedges in the former and discontinuous cambium in the latter. The interspecific variations within the genus *Mimosa* appear to be associated with the relative sizes of the stems or derived from the proliferation of non-lignified parenchyma.

A number of lianas start their development as self-supporting shrubs or with stiff searching branches, after which they develop lianescent vascular syndrome (Angyalossy *et al.*, 2015). Transverse sections of the stem from the pith to the cambium revealed that the secondary xylem of the self-supporting phase (ix) (Fig. 1a, 1b, 1e) is characterized by a few narrow vessels and thick fibers, whereas the xylem of the later, non-self-supporting (climbing) phase is characterized by very wide vessels, low density, and intermixed soft and stiff tissues. Those traits, in the climbing phase, may be termed the lianescent xylem syndrome. In the present study, three species showed significant differences in transverse sections from the pith to the cambium associated with these two growth stages: *A. caesia*, *B. championii*, and *C. crista*. Angyalossy *et al.* (2015) reported that the species *Dalbergia frutescens* (Vell.) Britton included a self-supporting phase and a subsequent lianescent xylem syndrome phase. The secondary xylem development of *D. benthamii* (Sun *et al.*, 2014) was the same that of *D. frutescens* in terms of the two growth phases. Future studies should measure the length of these two stages to reveal whether the self-supporting phase is longer than the climbing phase.

CONCLUSIONS

A comparison of the cambial variants of ten liana species belonging to seven genera in the Fabaceae

family in Taiwan showed that the cambium of three species in the genus *Caesalpinia* is regular in form. The remaining seven species included the cambial variants of furrowed xylem and dissected xylem (in the same species during different growth phases), interxylary phloem, successive cambia, and flattened stem and interxylary phloem. Three species (*A. caesia*, *B. championii*, and *C. crista*), experience two developmental phases in their growth stage. Different-sized stems may display different cambial variants in the genus *Bauhinia*. We suggest that the cambial variant and the function of parenchyma are influenced by the relative size of the stem and other plant components. The abundance and function of parenchyma in the stems of lianas and vines, and the types and distribution of interxylary phloem, merit further study.

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