Stem cambial variants of Taiwan lianas

Sheng-Zehn Yang¹*, Po-Hao Chen² and Jian-Jhong Chen³

Abstract

Background: Cambium in lianas, responsible for secondary growth, develop diverse and diagnostic traits during the climbing phase. Studies on the cross-section of Taiwanese liana cambial variants are scarce. We collected multiple stem cross-sections from 287 liana species belonging to 52 families. Each sample was examined on five occasions, and the observations were documented.

Results: The results showed that approximately 22 cambial variants types were displayed in Taiwan lianas. Among these, axial vascular elements in radial segments were the most common, followed by the variants with the irregular conformation and intraxylary phloem. Based on our assessment, we provide the following identification features of a few families: Apocynaceae had intraxylary phloem; Convolvulaceae had intraxylary phloem combined with successive cambia; Lardizabalaceae, Menispermaceae, and Ranunculaceae possessed axial vascular elements in segments; Piperaceae had axial vascular elements in segments combined with irregular conformation. Axial vascular elements in segments and intraxylary phloem appeared in six or five combination types, showing that these two types combined with many variants are helpful for the identification of lianas. Two species, Momordica charantia var. abbreviata, and Momordica cochinchinensis had a cambium element in the outer cylinder of cortical bicollateral vascular bundles and formed directional layers of successive cambia.

Conclusions: Our study documented regular secondary growth with a single cambium in 36 species and cambial variants present in 16 species of Taiwanese lianas. Furthermore, we provide crucial baseline data on liana cambial variations, thereby improving our understanding of their morphology and identification.

Keywords: Centrifugal xylem, Lianas, Parenchymatization, Secondary growth, Taiwan

Background

The climbing plants can be divided into lianas and herbaceous vines based on the degree of stem lignification. Lianas, a group of perennial climbing shrubs, have fibrous, thick, and truly lignified stems. On the contrary, herbaceous vines have slender and herbaceous stems (Gentry 1991; Putz and Mooney 1991). Most lianas grow without any external stem support, gradually forming unique stem variations. These variations originate in the cambium, changing the shape and structure of the stems into irregular forms, called cambial variants (Carlquist 2001). The differences in these structures can be used to distinguish liana families (Caballé 1993; Angyalossy et al. 2012).

The stem of several lianas species begins with stiff searching branches or a self-supporting shrub structure. Transverse sections of the stem from the pith to the cambium revealed that the inner secondary xylem of the self-supporting phase is characterized by the presence of shrub-type xylem, a few narrow vessels, and thick fibers. However, the xylem of the ensuing, non-self-supporting (climbing) phase is characterized by very wide vessels, low density, and intermixed soft and stiff tissues referred to as liana-type xylem.

The characteristics of lianescent vascular syndrome in lianas are related to the secondary growth, which results in special attributes, such as wide conducting cells in...
xylem and phloem, high abundance of parenchyma, fewer fibers, wide rays, and variations in the cambium (Angyalossy et al. 2015; Dias-Leme et al. 2021). Numerous studies have been conducted on the secondary growth of liana stems of different families (Metcalfe and Chalk 1985; Carlquist 1991, 2001, 2007, 2013; Caballé 1993; Jansen et al. 2002; Acevedo-Rodríguez 2005; Isnard and Silk 2009; Angyalossy et al. 2012, 2015; Pace et al. 2018). In Taiwan, liana cambial variants of stem cross-sections were studied in Fabaceae (Yang et al. 2016), Menispermaceae (Yang and Chen 2016), Piperaceae (Yang and Chen 2017), Lardizabalaceae and Sabiaceae (Yang et al. 2019), Convolvulaceae (Yang et al. 2020), Ranunculaceae (Yang et al. 2021), and in families with xylem in plate type (Yang and Chen 2015). Carlquist (2001) and Angyalossy et al. (2015) listed the angiosperm orders and families of climbing plants that possess the cambial variants, promoting the identification of certain families and genera.

Taiwan is located in the subtropical monsoon region; the climate is warm and humid throughout the year, approximately 22–24 °C, and annual average rainfall is about 2000–2500 mm precipitation. Due to the favorable climate, diverse species, including climbing plants, naturally occur in this region. Approximately 553 species of climbing plants belonging to 65 families are documented in Taiwan, accounting for approximately 11% of the native flora (Stevens 2001). Of these, 101 plants (23% of the climbing plants in Taiwan) are endemic to this region, indicating a high degree of endemism. Sixty one percent of the climbers (337 species) are lianas, of which 62 (18.3% of lianas) are endemic. The remaining 39% (216 species) is composed of vines, of which 39 (18.1% of vines) are endemic. In this study, we investigated the cambial variants of Taiwan lianas families. Our results contribute to the classification and ecology of climbing plants and ultimately integrate with the conservation research of global vine diversity.

Materials and methods

We collected plant stems of various sizes from 287 lianas from 52 families in the different habitats of Taiwan (Table 1), to observe the vascular bundle development in stem cross-sections. The samples were collected at 1.3 m height to obtain comparable measurements of the diameter at breast height. The fresh materials were divided into approximately 5 cm long pieces, and a flat cross-section of each stem was cut using a cutter blade. We immediately took pictures of the stem cross sections using a Nikon D80 SLR digital camera (Lens AF Micro Nikon 60 mm f: 2.8D, Nikon Corporation, Tokyo, Japan), and qualitative and quantitative anatomical traits were determined using Image-J (v 1.50 h) software (Ferreira and Rasband 2011). All our photographs are made from macroscopic observations. The specimens were dried in an oven (60 °C) for 4–5 days and then stored at −20 °C for 3–4 days. Liana species were identified using a field guide (Boufford et al. 2003). All the collected specimens were deposited in the Provincial Pingtung Institute herbarium (PPI) at the National Pingtung University of Science and Technology, Pingtung, Taiwan, for subsequent identification.

The cambial variants were divided into two categories, a single cambium and multiple cambia, as defined by Angyalossy et al. (2015). Single cambial variants were subdivided into five types, including irregular conformation, interxylary phloem, furrowed xylem, axial vascular elements in segments, and fissured stem/dispersed xylem, and are described below:

1. Irregular conformation (IC): Vascular cambium has a regular activity, the proportions of xylem and phloem produced varied around the girth, and the stem with irregular conformation can be divided into lobes and flattened.

2. Interxylary phloem (TE): Interxylary phloem is defined as strands or bands of phloem embedded within the secondary xylem of a stem of a plant that has a single vascular cambium (Carlquist 2001, 2013). Interxylary phloem have four different ontogenetic origins (Angyalossy et al. 2015), (a) the cambium produces phloem in both directions (inside and outside), followed by the formation of xylem only towards the inside, as a result, the phloem enclosd in the wood; (b) the cambium produces less xylem than phloem at the certain portions of stem, creating small phloem arcs, including strands (Caballé 1993), bands (Metcalfe and Chalk 1985) or umbrellas; (c) the result of the inclusion of phloem wedges within the xylem; and (d) the cambium varies from the differentiation of xylem parenchyma into sieve tubes. The evenly distributions or round islands of interxylary phloem generate patterns that are available in the identification of species.

3. Furrowed xylem (FX): 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; it is characterized by a regular gap between the xylem and phloem or irregular arrangements of the two. One of the furrowed xylem has a regular cambium, forms four equidistant phloem arcs/wedges, and then develops into a multiple of four phloem arcs/wedges (Angyalossy et al. 2012). This process result in multiple phloem arcs/wedges evenly spread across the stem. The other of the furrowed xylem is irregular spacing of phloem arcs/wedges. Caballé (1993) identified the furrowed
Table 1  Cambial variants of each species in Taiwan lianas

| Families    | Scientific name                  | Cambial variants |
|-------------|----------------------------------|------------------|
| Acanthaceae | *Thunbergia alata* Bojer ex Sims | FD               |
|             | *Thunbergia grandiflora* Roxb    | TE               |
|             | *Thunbergia laurifolia* Lindl    | TE               |
| Actinidiaceae | *Actinidia anguta* (Sieb. & Zucc.) Planch. ex Miquel | RC             |
|             | *Actinidia callosa* var. discolor *C. F. Liang Feng | RC             |
|             | *Actinidia latifolia* (Gardner & Champ.) Merr | RC             |
|             | *Actinidia rufula* (Sieb. & Zucc.) Planch. ex Miquel | RC             |
|             | *Actinidia setosa* (H. L. Li) C. F. Liang & A. R. Ferguson | RC             |
| Amaranthaceae | *Deeringia amaranthoides* (Lam.) Merr | SC             |
| Anacardiaceae | *Rhus ambigua* Lav. ex Dippel | RC               |
| Annonaceae  | *Artabotrys hexapetalus* (Linnaeus f.) Bhandari | RC             |
|             | *Fissistigma glaucescens* (Hance) Merr | RC             |
|             | *Fissistigma olfhamii* (Hemsli) Merr | RC             |
| Apocynaceae | *Alyxia sibuyanensis* Elmer | TR               |
|             | *Alyxia tawianensis* S. Y. Lu & Yuen P. Yang | TR             |
|             | *Anodendron affine* (Hook. & Arn.) Druce | TR             |
|             | *Anodendron benthamiana* Hemsli | TR             |
|             | *Cryptolepis sinensis* (Lout.) Merr | TR             |
|             | *Dregea voluibilis* (L. f.) Benth | TR             |
|             | *Gymnema sylvestre* (Retz.) Schultes | TR, FC          |
|             | *Heterostemma brownii* Hayata | TR, FC          |
|             | *Mansonia formosana* Masam | TR             |
|             | *Mansonia tintoria* R. Br | TR             |
|             | *Melodinus angustifolius* Hayata | TR             |
|             | *Panurria alboflavescens* (Dennst.) Mabb | TR             |
|             | *Trachelospermum formosanum* Y. C. Liu & C. H. Ou | TR             |
|             | *Trachelospermum gracilipes* Hook. f | TR, ES          |
|             | *Trachelospermum jasminoides* (Lindl) Lemaire | TR             |
|             | *Trachelospermum tanyuense* C. E. Chang | TR             |
|             | *Urecola micrantha* (Wallich ex G. Don) D. J. Middleton | TR             |
|             | *Urecola rosea* (Hook. & Arn.) D. J. Middleton | TR             |
| Araliaceae  | *Eleutherococcus trifoliatus* (L.) S. Y. Hu var. setusus (H. L. Li) H. Ohashi | IC             |
|             | *Eleutherococcus trifoliatus* (L.) S. Y. Hu var. trifoliatus | RC             |
|             | *Hedera rhombea* (Miq.) Bean var. formosana (Nakai) H. L. Li | RC             |
| Areacaceae  | *Calamus formosanus* Becc | RC             |
|             | *Calamus siphonospathus* Martius | RC             |
| Aristolochiaceae | *Aristolochia cucubitifolia* Hayata | VS             |
|             | *Aristolochia elegans* Mast | VS             |
|             | *Aristolochia shimadai* Hayata | VS             |
|             | *Aristolochia zollingeniana* Miq | VS             |
| Asteraceae  | *Blumea riparia* (Blume) DC. var. megacephala Randeria | VS             |
|             | *Microglossa pyrifolia* (Lam.) Kuntze | IC             |
|             | *Mikania micrantha* Kunth | FD             |
|             | *Senecio scandens* Buch.-Ham. ex D. Don var. scandens | RC             |
|             | *Vernonia gnataosa* Hance | VS             |
| Basellaceae | *Annedrea cordifolia* (Tenore) van Steenis | VS, SC         |
| Bignoniacese | *Anemopaegma chamberliyonii* (Sims) Bureau & K.Schum | FD             |
|             | *Pyrostegia venusta* (Ker-Gawl.) Miers | FD             |
| Cannabaceae | *Humulus scandens* (Lour.) Merr | IC             |
| Capparaceae | *Capparis formosana* Hemsli | RC             |
|             | *Capparis lanceolans* DC | RC             |
| Families          | Scientific name | Cambial variants |
|-------------------|-----------------|------------------|
| **Caprifoliaceae**| Lonicera acuminata Wall | RC               |
|                   | Lonicera hypoglauca Miq | RC               |
|                   | Lonicera japonica Thunb | RC               |
| **Cecropiaceae**  | Pokiospernum acuminata (Trécul) Merr | RC               |
| **Celastraceae**  | Celastrus hindsii Benth | FC               |
|                   | Celastrus kusanoi Hayata | VS               |
|                   | Celastrus paniculatus Willd | RC               |
|                   | Celastrus punctatus Thunb | FC               |
|                   | *Euonymus sprzuei Hayata | IC               |
|                   | Tripterygium willoordii Hook. f | RC               |
| **Combretaceae**  | Quisqualis indica L | TR, FC           |
| **Connaraceae**   | Rourea minor (Gaertn.) Leenhouts | SC               |
| **Convolvulaceae**| *Argyrea akiensis S. Z. Yang, P. H. Chen & G. W. Staples | TR, SC           |
|                   | *Argyrea fassosanui Ishigami ex T. Yamaz | TR, SC           |
|                   | Argyrea nervosa Boj | TR, SC           |
|                   | Camanea vitifolia (Burn.f.) A. R. Simões & Staples | TR, SC           |
|                   | Distimake quinquefolius (L.) A.R.Simões & Staples | TR               |
|                   | Distimake tuberosus (L.) A.R.Simões & Staples | TR, SC           |
|                   | Erycibe henryi Prain | TR, SC           |
|                   | Ipomoea alba L | TR, SC           |
|                   | Ipomoea batatas (L.) Lam | TR, SC           |
|                   | Ipomoea canica (L.) Sweet | TR, SC           |
|                   | Ipomoea carnea Jacq. subsp. fistulosa (Mart. ex Choisy) D. F. Austin | TR   |
|                   | Ipomoea hederifolia L | TR, SC           |
|                   | Ipomoea indica (Bur. f) Merr | TR, SC           |
|                   | Ipomoea littoralis Blume | TR, SC           |
|                   | Ipomoea nil (L.) Roth | TR, SC           |
|                   | Ipomoea obscura (L.) Ker Gawl | TR, SC           |
|                   | Ipomoea pes-caprae (L.) R. Br. subsp. brasiliensis (L.) Oostst | TR, SC           |
|                   | Ipomoea quamoclit L | TR               |
|                   | Ipomoea triloba L | TR, SC           |
|                   | Ipomoea violacea L | TR               |
|                   | Lepistemum binecetatiflorum (Wall.) Kuntze var. trichocarpum (Gagnep.) Ooststr | TR, SC           |
|                   | Merremia gemela (Bur. f) Hallier f | TR, SC           |
|                   | Operculina turpethum (L.) S. Manso | TR, SC           |
|                   | Stictocardia tillifolia (Desz) Hallier f | TR, SC           |
| **Cucurbitaceae** | Cocinia grandis (L.) Voigt | IC, VS           |
|                   | Gymnostemma pentaphillum (Thunb.) Makino | IC, VS           |
|                   | Melothria pendula L | IC, VS           |
|                   | Momordica charantia L | IC, VS           |
|                   | Momordica charantia L. var. abbreviata Ser | IC, VS, SC       |
|                   | Momordica cochinchinensis (Lour.) Spreng | FD, VS, SC       |
|                   | Neosolomitra integrifolia (Cogn.) Hutch | FD, VS           |
| **Elaeagnaceae**  | Elaeagnus formosana Nakai | RC               |
|                   | Elaeagnus glutol Thunb | RC               |
|                   | *Elaeagnus grandifolia Hayata | RC               |
|                   | *Elaeagnus thunbergii Serv | RC               |
|                   | Elaeagnus nitiflor Roxb | RC               |
| **Euphorbiaceae** | Mallotus repandus (Wild.) Müll. Arg | IC               |
| Families       | Scientific name                        | Cambial variants |
|---------------|----------------------------------------|------------------|
| Fabaceae      | Abrus precatorius L                    | IC               |
|               | Bauhinia championii (Benth.) Benth     | DX, IC           |
|               | Caesalpinia bonduc (L.) Roxb           | RC               |
|               | Caesalpinia crista L                   | RC               |
|               | Caesalpinia decapetala (Roth) Alston   | RC               |
|               | Caesalpinia minax Hance                | RC               |
|               | Callerya nitida (Benth.) R. Geesink    | RC               |
|               | Calopogonium mucunoides Desv           | IC               |
|               | Canavalia cathartica Thouars           | RC               |
|               | Canavalia lineata (Thunb.) DC          | RC               |
|               | Canavalia rosea (Sw.) DC               | RC               |
|               | Centrosema pubescens Benth             | FC               |
|               | Clitoria ternatea L                    | RC               |
|               | Dalbergia benthamii Prain              | RC               |
|               | *Dermis laxiflora Benth                | RC               |
|               | *Dermis trifoliata Lour                | RC               |
|               | *Dolichos ribolus L. var. kosyunensis (Hosok.) H. Ohashi & Tateishi | FC |
|               | Dunbaria merrillii Elmer               | RC               |
|               | *Dumasia truncata Siebold & Zucc       | RC               |
|               | Entada phaseoloides (L.) Merr. subsp. phaseoloides | SC |
|               | Entada phaseoloides (L.) Merr. subsp. tonknensis (Gagnep.) H. Ohashi | SC |
|               | Entada rheedei Spreng                 | SC               |
|               | Lablab purpureus (L.) Sweet            | ES, IC           |
|               | Macroptilium atropurpureum (DC.) Urb   | RC               |
|               | Macroptilium lathyroides (L.) Urb      | RC               |
|               | Millettia pachycarpa Benth             | RC               |
|               | Mimosa diplotricha C. Wright ex Sauvalle | RC         |
|               | Mucuna gigantea (Wild.) DC.subsp. tashiroi (Hayata) H. Ohashi & Tateishi | RC |
|               | Mucuna macrocarpa Wall                 | SC               |
|               | Mucuna membranacea Hayata              | RC               |
|               | Mucuna pruriens (L.) DC. var. utilis (Wall. ex Wight) Burck | IC |
|               | Neonotonia wightii (Wight & Arn.) Lackey | RC         |
|               | Paradenis canarensis (Dalzell) Adema   | RC               |
|               | Paradenis elliptica (Wallich) Adema    | RC               |
|               | Psophocarpus tetragonolobus (L.) DC    | RC               |
|               | Pueraria lobata (Wild.) Ohwi subsp. thomsonii (Benth.) Ohashi & Tateishi | SC |
|               | Pueraria montana (Lour.) Meer          | SC               |
|               | Senegalia caesia (L.) Maslin, Seigler & Ebinger | IC |
|               | Wisteriopsis reticulata (Benth.) J. Compton & Schrire | RC |
| Gesneriaceae  | Aeschynanthus acuminatus Wall. ex A. DC | FC |
| Heliotropiaceae| Heliotropium sammentosum (Lam.) Craven | RC |
| Hernandiaeae  | Illigera luzonensis (C. Presl) Meer    | FC               |
| Hydrangeaceae | Hydrangea anomala D. Don               | RC               |
|               | *Hydrangea fauriei (Hayata) Y. De Smet & Granados | RC |
|               | Hydrangea integrifolia Hayata          | RC               |
|               | Hydrangea viburnoides (Hook. f. & Thomson) Y. De Smet & Granados var. parviflora Oliv. ex Maxim | RC |
| Landizabalaceae| Akebia longissimosa Matsum             | VS               |
|               | Akebia chingshuensis T. Shimizu        | VS               |
|               | Stauntonia hexaphylla (Thunb.) Dcne    | VS               |
|               | Stauntonia obovata Hemsl               | VS               |
|               | * Stauntonia purpurea Y. C. Liu & F. Y. Lu | VS |
Table 1 (continued)

| Families                  | Scientific name                        | Cambial variants |
|---------------------------|----------------------------------------|------------------|
| Loganiaceae               | *Gardneria multiflora* Makino          | FD, TR           |
|                           | *Gardneria nutans* Siebold & Zucc      | FD, TR           |
|                           | *Strychnos cathayensis* Merr           | TE, TR           |
| Malpighiaceae             | *Hiptage benghalensis* (L.) Kurz       | RC               |
|                           | *Tristellatea australiae* A. Rich      | FC               |
| Melastomataceae           | *Medinilla formosana* Hayata           | RC               |
|                           | *Medinilla hayataiara* H. Keng         | TR               |
| Menispermaceae            | *Cissampelos pareio* L. var. *hirsuta* (DC.) *Forman* | VS               |
|                           | *Cocculus arboiculatus* (L.) DC        | VS, SC           |
|                           | *Cyclea gracillima* Diels              | VS               |
|                           | *Cyclea insulans* (Makino) Hatus       | VS               |
|                           | *Cyclea ochisiana* (Yamam.) S. F. Huang & T. C. Huang | VS               |
|                           | *Paratinospora dentata* (Diels) Wei Wang | VS               |
|                           | *Percyamylius giancusc* (Lam.) Merr   | VS               |
|                           | *Smorumenium acuturn* (Thunb.) Rehder & E. H. Wils | VS               |
|                           | *Stephania japonica* (Thunb.) Miers    | VS               |
|                           | *Stephania longa* Lour                 | VS               |
|                           | *Stephania menllii* Diels              | VS               |
|                           | *Stephania tetraanda* S. Moore         | VS               |
|                           | *Tinospora crispa* (L.) J. D. Hook. & Thom | VS               |
|                           | *Tinospora sinensis* (Lour.) Merr      | VS               |
| Moraceae                  | *Ficus aurantiaca* Griff. var. *parvifolia* (Comer) Corner | IC               |
|                           | *Ficus pumila* L. var. *aw PERF* (Makino) Corner | IC               |
|                           | *Ficus pumila* L. var. *pumila*        | IC               |
|                           | *Ficus sarmentosia* Buch.-Ham. ex Sm. var. *nipponica* (Franch. & Sav.) Corner | IC               |
|                           | *Ficus trichocarpa* Blume var. *obtusa* (Hassk.) Corner | IC               |
|                           | *Ficus vaccinioides* Hemsl. ex King    | RC               |
|                           | *Maclura cochinchinesis* (Lour.) Corner | RC               |
|                           | *Malaisia scandens* (Lour.) Planch     | RC               |
| Nyctaginaceae             | *Bougainvillea spectabilis* Willdenov  | SC               |
|                           | *Pisonia aculeata* L                   | TE               |
| Oleaceae                  | *Jasminum lanceolatum* Roxb            | IC               |
|                           | *Jasminum nervosum* Lour               | RC               |
|                           | *Jasminum sinense* Hemsl               | RC               |
|                           | *Jasminum urophyllum* Hemsl            | RC               |
| Opiliaceae                | *Cansjera rheedei* J. F. Gmelin        | RC               |
| Pandanaceae               | *Freycinetia formosana* Hemsl          | RC               |
| Passifloraceae            | *Passiflora biflora* Lam               | FC               |
|                           | *Passiflora edulis* Sims               | FC               |
|                           | *Passiflora launfola* L                | RC               |
|                           | *Passiflora quadrangularis* L          | IC               |
|                           | *Passiflora suberosa* L. subs. *litoralis* (Kunth) K.Port.-Utl. ex M.A.M.Azevedo, Baumbratz & Gonç.-Estev | FC               |
|                           | *Passiflora vesicaria* L               | FC               |
| Phyllanthaceae            | *Phyllanthus reticulatus* Poiret       | FC               |
| Families    | Scientific name                          | Cambial variants |
|------------|-----------------------------------------|------------------|
| Piperaceae | *Piper arborescens* Roxb                | EP, VS           |
|            | *Piper betle* L                         | EP, VS           |
|            | *Piper interruptum* Opiz                | EP, VS           |
|            | *Piper kadiura* (Choisy) Ohwi           | EP, VS           |
|            | *Piper kawakamii* Hayata                | EP, VS           |
|            | *Piper lanyuense* K.N. Kung & Kun C. Chang | EP, VS       |
|            | *Piper sintenense* Hatusima             | EP, VS           |
|            | *Piper taiwanense* T.T. Lin & S.Y. Lu   | EP, VS           |
| Polygonaceae | *Antigonon leptopus* Hook. & Arn    | SC               |
|            | *Persicaria chinense* (L.) H. Gross     | VS               |
|            | *Persicaria perfoliata* (L.) H. Gross   | FC               |
| Primulaceae | *Reynoutria multiflora* (Thunb.) Moldenke var. hypoleuca (Ohwi) S.S. Ying | VS |
| Ranunculaceae | *Embelia laeta* (L.) Mez var. papilligera (Naikai) Walker | VS |
|            | *Embelia lenticellata* Hayata           | VS               |
|            | *Embelia rudis* Hand.-Mazz              | VS               |
|            | *Clematis chinensis* Osbeck var. chiensis | VS            |
|            | *Clematis crassifolia* Benth           | VS               |
|            | *Clematis formosana* Kuntz             | VS               |
|            | *Clematis gouriana* Roxb. ex DC. subsp. lishanensis Yang & Huang | VS, FD          |
|            | *Clematis grata* Wall                   | VS               |
|            | *Clematis henryi* Oliv. var. henryi    | VS               |
|            | *Clematis lassandra* Maxim              | VS               |
|            | *Clematis leschenaultiana* DC           | VS               |
|            | *Clematis meyeniana* Walp               | VS               |
|            | *Clematis montana* Buch.-Ham. ex DC.    | VS               |
|            | *Clematis parviflora* Gard. ex Champ. subsp. bartlettii (Yamamoto) Yang & Huang | VS |
|            | *Clematis tamurae* T.Y.A. Yang & T.C. Huang | VS |
|            | *Clematis tashiroi* Maxim. var. tashiroi | VS           |
|            | *Clematis terniflora* DC. var. garanbiensis (Hayata) M.C. Chang | VS |
|            | *Clematis uncinata* Champ. ex Benth. var. okinawensis (Ohwi) Ohwi | VS |
|            | *Clematis uncinata* Champ. ex Benth. var. uncinata | VS |
| Rhamnaceae | *Berchemia arisanensis* Y.C. Liu & F.Y. Lu | RC             |
|            | *Berchemia fenchiiensis* C.M. Wang & F.Y. Lu | RC          |
|            | *Berchemia formosana* C.K. Schneid      | RC               |
|            | *Berchemia racemosa* Siebold & Zucc. var. magna Makino | RC |
|            | *Rhamnus formosana* Matsum              | RC               |
|            | *Sageretia randaiensis* Hayata          | RC               |
|            | *Sageretia thea* (Osbeck) M.C. Johnston var. thea (Osbeck) M.C. Johnston | RC |
|            | *Ventilago elegans* Hemsl               | RC               |
|            | *Ventilago leiocarpa* Benth             | RC               |
| Rosaceae   | *Rubus formosensis* Kuntze             | RC               |
|            | *Rubus penifolius* Sm                   | RC               |
|            | *Rubus rolfei* S.Vidal                 | RC               |
|            | *Rubus swinhoei* Hance var. swinhoei   | RC               |
|            | *Rubus wallichianus* Wight & Ann       | IC               |
Table 1 (continued)

| Families         | Scientific name                              | Cambial variants |
|------------------|---------------------------------------------|------------------|
| Rubiaceae        | Coptosapelta diffusa (Champ. ex Benth.) Steenis | FC, IC           |
|                  | Dimetia hedycdea (DC.) T. C. Hsu              | DX               |
|                  | Morinda parvifolia Bartl                     | FC               |
|                  | Morinda umbellata L                         | FC               |
|                  | Musaenda formosanum (Matsum.) T.Y. Aleck Yang & K. C. Huang | RC   |
|                  | Musaenda parviflora Miq                      | RC               |
|                  | Musaenda pubescens W. T. Atton                | RC               |
|                  | *Musaenda taihokuensis Masam                 | RC               |
|                  | Paedea calavalei H. Lev                     | IC, VS           |
|                  | Paedea foetida L                            | IC, VS           |
|                  | Psychotria serpens L                        | RC               |
|                  | Randia sinensis (Lou.) Roem. &Schult         | RC               |
|                  | Uncaria hirsuta Havil                        | RC               |
|                  | Uncaria lanosa Wall. var. appendiculata Ridsdale | IC   |
|                  | Uncaria rhynchophylla (Miq.) Miq. ex Havil   | RC               |
| Rutaceae         | Toddalia asiatica (L.) Lam                   | RC               |
|                  | Zanthoxylum nitidum (Roxb.) DC               | RC               |
|                  | Zanthoxylum scandens Blume                   | RC               |
| Sabiaceae        | Sabia spinhovei Hemsli                       | VS               |
|                  | *Sabia transanensis Hayata                  | VS               |
| Schisandraceae   | Kaduna japonica (L.) Dunal                   | RC               |
|                  | Kaduna matsudae Hayata                      | RC               |
|                  | *Schisandra arisanensis Hayata               | RC               |
| Solanaceae       | Solanum lyratum Thunb                       | TR               |
|                  | Solanum pettisporfolium Hemsli               | TR               |
| Vitaceae         | Ampelopsis brevipedunculata (Maxim.) Trautv. var. ciliata (Nakai) F.Y. Lu | IC   |
|                  | Ampelopsis brevipedunculata (Maxim.) Trautv. var. hancei (Planch.) Rehder | IC   |
|                  | Cayratia corniculata (Benth.) Gagnep         | IC, VS, SC       |
|                  | Cayratia japonica (Thunb.) Gagnep            | IC, VS           |
|                  | Cayratia maritima B. R. Jackes               | VS               |
|                  | Cissus assamica (Laws.) Craib                | IC, VS           |
|                  | *Cissus pterocladus Hayata                   | IC, VS           |
|                  | Cissus repens Lam                            | IC, VS           |
|                  | Cissus sp.                                   | IC, VS           |
|                  | Cissus verticillata (L.) Nicolson & C.E.Jarvis | IC, VS         |
|                  | Nekemias cantoniensis (Hook. & Am.) J.Wen & Z.L.Nie | VS  |
|                  | Nekemias cantoniensis (Hook. & Am.) J.Wen & Z.L.Nie var. leecoides (Maxim.) F.Y.Lu | VS  |
|                  | Parthenocissus tricuspida (Siebold & Zucc.) Planch | IC, VS |
|                  | *Tetrastigma formosanum (Hemsley) Gagnepain  | IC, VS, SC       |
|                  | *Tetrastigma hymenlayanum Diels &Gilg        | IC, VS, SC       |
|                  | *Tetrastigma lanyuense C. E. Chang           | IC, VS, SC       |
|                  | Tetrastigma obtectum (Wallich ex M. A. Lawson) Planchon ex Franchet var. glabrum (H. Léveillé) Gagnepain | IC, VS |
|                  | Vitis amurenensis Rupr                       | IC               |
|                  | Vitis flexuosa Thunberg                      | IC               |
|                  | *Vitis heynaeus Roemer & Schultes            | IC               |
|                  | Vitis heynaeus Roemer & Schultes subsp. ficifolia (Bunge) C. L. Li | IC   |
|                  | Vitis sinocinerata W. T. Wang                | IC               |

52 families 287 species

RC: stem cambium normal in production and round in conformation; VS: axial vascular elements in segments; IC: stem cambium normal in production but stem with irregular conformation; TR: intraxylary phloem; FC: furrowed xylem of cambium continuity; SC: successive cambia; FD: furrowed xylem of cambium discontinuity; TE: interxylary phloem; EP: external primary vascular cylinders; ES: external secondary vascular cylinders; DX: fissured stem/dispersed xylem

* endemic species
Table 2  Cambial variant types of lianas of different families in Taiwan

| Family           | RC | VS | IC | TR | FC | SC | FD | TE | DX | TR+SC | IC+VS | EP+VS | FC+TR | FD+VS |
|------------------|----|----|----|----|----|----|----|----|----|-------|-------|-------|-------|-------|
| Acanthaceae      |    |    |    |    |    | 1  |    |    |    |       |       |       |       |       |
| Actinidiaceae    | 5  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Amaranthaceae    |    |    |    |    |    |    |    |    | 1  |       |       |       |       |       |
| Anacardiaceae    | 1  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Annonaceae       | 3  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Apocynaceae      |    |    |    |    | 14 |    |    |    |    |       |       | 3     |       |       |
| Araliaceae       | 3  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Areaceae         | 2  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Aristolochiaceae |    | 4  |    |    |    |    |    |    |    |       |       |       |       |       |
| Asteraceae       | 1  | 2  | 1  |    |    |    |    |    |    |       |       |       |       |       |
| Basellaceae      |    |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Bignoniaceae     |    |    |    |    |    |    |    |    | 2  |       |       |       |       |       |
| Cannabaceae      |    |    |    | 1  |    |    |    |    |    |       |       |       |       |       |
| Capparaceae      | 2  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Caprifoliaceae   | 3  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Celastraceae     | 2  | 1  | 1  |    |    |    |    |    |    |       |       |       |       |       |
| Combretaceae     |    |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Conneraceae      |    |    |    |    |    |    |    |    | 1  |       |       |       |       |       |
| Convolvulaceae   |    |    | 4  |    |    |    |    |    |    |       |       | 20    |       |       |
| Cucurbitaceae    |    |    |    |    |    |    |    |    |    |       |       | 3     |       | 1     |
| Elaeagnaceae     | 5  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Euphobriaceae    |    | 1  |    |    |    |    |    |    |    |       |       |       |       |       |
| Fabaceae         | 24 | 4  | 3  | 6  |    |    |    |    |    |       |       |       |       |       |
| Gesneriaceae     |    |    |    |    |    |    |    |    | 1  |       |       |       |       |       |
| Heliotropiaceae  | 1  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Hernandiaceae    |    |    |    |    | 1  |    |    |    |    |       |       |       |       |       |
| Hydrangeaceae    | 4  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Lardizabalaceae  |    | 5  |    |    |    |    |    |    |    |       |       |       |       |       |
| Loganiaceae      |    |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Malpighiaceae    | 1  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Melastomataceae  | 1  |    | 1  |    |    |    |    |    |    |       |       |       |       |       |
| Menispermaceae   | 13 |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Moraceae         | 4  | 4  |    |    |    |    |    |    |    |       |       |       |       |       |
| Nyctaginaceae    |    |    |    |    | 1  | 1  |    |    |    |       |       |       |       |       |
| Oleaceae         | 3  | 1  |    |    |    |    |    |    |    |       |       |       |       |       |
| Opiliaceae       | 1  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Pandanaceae      | 1  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Passifloraceae   | 1  | 1  | 4  |    |    |    |    |    |    |       |       |       |       |       |
| Phyllanthaceae   |    |    |    |    | 1  |    |    |    |    |       |       |       |       |       |
| Piperaceae       |    |    |    |    |    | 8  |    |    |    |       |       |       |       |       |
| Polygonaceae     | 2  | 1  | 1  |    |    |    |    |    |    |       |       |       |       |       |
| Primulaceae      | 3  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Ranunculaceae    | 15 |    |    |    |    |    |    |    |    |       |       |       |       | 1     |
| Rhamnaceae       | 9  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Rosaceae         | 4  | 1  |    |    |    |    |    |    |    |       |       |       |       |       |
| Rubiaceae        | 8  | 1  | 2  |    |    |    |    |    | 1  |       |       | 2     |       |       |
| Rutaceae         | 3  |    |    |    |    |    |    |    |    |       |       |       |       |       |
| Sabiaceae        |    | 2  |    |    |    |    |    |    |    |       |       |       |       |       |
Table 2 (continued)

| Family              | RC | VS   | IC  | TR  | FC  | SC  | FD  | TE  | TR + SC | IC + VS | EP + VS | FC + TR | FD + VS |
|---------------------|----|------|-----|-----|-----|-----|-----|-----|---------|---------|---------|---------|---------|
| Schisandraceae      | 3  | –    | –   | –   | –   | –   | –   | –   | –       | –       | –       | –       | –       |
| Solanaceae          | –  | 7    | 2   | –   | –   | –   | –   | –   | –       | –       | –       | –       | –       |
| Vitaceae            | –  | 3    | 8   | –   | –   | –   | –   | –   | 1       | 1       | 2       | 2       | 2       |
| Sum of family       | 25 | 11   | 11  | 4   | 10  | 5   | 2   | 2   | 1       | 1       | 3       | 1       | 2       |
| Sum of species      | 96 | 50   | 23  | 21  | 17  | 10  | 3   | 3   | 1       | 20      | 13      | 8       | 4       |
| Percentage %        | 33.4 | 17.4 | 8.0 | 7.3 | 5.5 | 3.5 | 1.0 | 1.0 | 0.3     | 7.0      | 4.5      | 2.8      | 1.4      |

| Family              | FD + TR | SC + VS | FC + IC | ES + TR | TE + TR | ES + IC | IC + DX | IC + VS + SC | FD + VS + SC | SP No. | Types No. |
|---------------------|---------|---------|---------|---------|---------|---------|---------|-------------|-------------|-------|-----------|
| Acanthaceae         | –       | –       | –       | –       | –       | –       | –       | –           | –           | 3     | 2         |
| Actinidiaceae       | –       | –       | –       | –       | –       | –       | –       | –           | –           | 5     | 0         |
| Amaranthaceae       | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 1         |
| Anacardiaceae       | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 0         |
| Annonaceae          | –       | –       | –       | –       | –       | –       | –       | –           | –           | 3     | 0         |
| Apocynaceae         | –       | –       | 1     | –       | –       | –       | –       | –           | –           | 18    | 3         |
| Araliaceae          | –       | –       | –       | –       | –       | –       | –       | –           | –           | 3     | 0         |
| Areaceae            | –       | –       | –       | –       | –       | –       | –       | –           | –           | 2     | 0         |
| Aristolochiaceae    | –       | –       | –       | –       | –       | –       | –       | –           | –           | 4     | 1         |
| Asteraceae          | –       | –       | –       | –       | –       | –       | –       | –           | –           | 5     | 3         |
| Basellaceae         | –       | –       | 1     | –       | –       | –       | –       | –           | –           | 1     | 1         |
| Bignoniaceae        | –       | –       | –       | –       | –       | –       | –       | –           | –           | 2     | 1         |
| Cannabaceae         | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 1         |
| Capparaceae         | –       | –       | –       | –       | –       | –       | –       | –           | –           | 2     | 0         |
| Caprifoliaceae      | –       | –       | –       | –       | –       | –       | –       | –           | –           | 3     | 0         |
| Cercropiaceae       | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 0         |
| Celastraceae        | –       | –       | –       | –       | –       | –       | –       | –           | –           | 6     | 3         |
| Combretaceae        | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 1         |
| Conneraceae         | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 1         |
| Convolvulaceae      | –       | –       | –       | –       | –       | –       | –       | –           | –           | 24    | 2         |
| Cucurbitaceae       | –       | –       | –       | –       | –       | –       | –       | –           | 2           | 1     | 7         |
| Elaeagnaceae        | –       | –       | –       | –       | –       | –       | –       | –           | –           | 5     | 0         |
| Euphorbiaceae       | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 1         |
| Fabaceae            | –       | –       | –       | –       | –       | 1     | 1     | –           | –           | 39    | 5         |
| Gesneriaceae        | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 1         |
| Heliotropiaceae     | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 0         |
| Hernandiaceae       | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 1         |
| Hydrangeaceae       | –       | –       | –       | –       | –       | –       | –       | –           | –           | 4     | 0         |
| Lardizabalaceae     | –       | –       | –       | –       | –       | –       | –       | –           | –           | 5     | 1         |
| Loganiiaceae        | 2       | –      | –      | –      | –      | 1     | –     | –           | –           | 3     | 2         |
| Malpighiaceae       | –       | –       | –       | –       | –       | –       | –       | –           | –           | 2     | 1         |
| Melastomataceae     | –       | –       | –       | –       | –       | –       | –       | –           | –           | 2     | 1         |
| Menispermaceae      | –       | –       | 1     | –      | –      | –      | –      | –           | –           | 14    | 1         |
| Moraceae            | –       | –       | –       | –       | –       | –       | –       | –           | –           | 8     | 1         |
| Nyctaginaceae       | –       | –       | –       | –       | –       | –       | –       | –           | –           | 2     | 2         |
| Oleaceae            | –       | –       | –       | –       | –       | –       | –       | –           | –           | 4     | 1         |
| Opiliaceae          | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 0         |
| Pandanaceae         | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 0         |
| Passifloraceae      | –       | –       | –       | –       | –       | –       | –       | –           | –           | 6     | 3         |
| Phyllanthaceae      | –       | –       | –       | –       | –       | –       | –       | –           | –           | 1     | 1         |
| Piperaceae          | –       | –       | –       | –       | –       | –       | –       | –           | –           | 8     | 1         |
| Polygonaceae        | –       | –       | –       | –       | –       | –       | –       | –           | –           | 4     | 3         |
xylem of four regular gaps as quarter-lobes. The furrowed xylem is divided into two groups according to the discontinuity (FD) or continuity (FC) of the cambium. Discontinuity cambium results in the inclusion of fragments of the original concentric cambium within the phloem wedges, which are radially lined by wide rays (Pace et al. 2009). A continuous cambium produces secondary phloem that contains tanniferous cells and druse crystals, or the sclerenchyma is composed of large sclereid clusters or bands of fiber-sclereids to form a stratified phloem (Pace et al. 2009). The cambium continuity also can be divided into shallow or deep split types by the depth of the phloem wedges (Angyalossy et al. 2015).

4. Axial vascular elements in segments (VS): Axial elements of the xylem and phloem are present in segments alternating with very wide xylem and phloem rays, and also called as xylem in plates (Carquist 1991, 2001). Angyalossy et al. (2012) defined this feature as axial vascular elements in segments.

5. Fissured stem/dispersed xylem (DX): this cambial variant is defined as: irregularly shaped, disoriented strands of xylem and phloem associated with fragments of vascular cambium spread throughout a parenchymatous matrix; or the dispersed nature of xylem and phloem strands results from the rupturing of the vascular cambium by parenchyma cells (Ayensu and Stern 1964; Cabanillas et al. 2017). This cambial variant type is derived from non-lignified parenchyma proliferation and is called dispersed xylem segments, or is more cracked than the normal xylem, also known as fissured/blocks xylem. The primary xylem is severed by the proliferation of phloem or parenchyma cells (Metcalfe and Chalk 1985; Carquist 2001).

Multiple cambia are derived from the parenchyma of the cortex in order to generate lateral meristems, which begin to produce conjunctive tissue and vascular bundle cambium inward, and the epidermis outward. The cambial variants of this category can be divided into four types:

1. Successive cambia (SC): Successive cambia are formed from new cambia arising through cell division in the external secondary vascular system. Each new cambia in the stem successively generates a secondary inward xylem and a secondary outward phloem. The process involves pericyclic, cortex, and parenchyma cell division. Pericyclic or cortical cell division causes a meristematic zone, which differentiates into parenchyma or sclerenchyma, called conjunctive tissue. The successive cambia are formed by alternating concentric rings of xylem and phloem. The xylem and phloem produced by the cambium are in their normal positions (Metcalfe and Chalk 1985), and vascular tissue is separated by a band of parenchyma or sclerenchyma (conjunctive tissue). The continuous cambium is also referred to as the alternation of bands of vascular tissue with connective tissue (Acevedo-Rodríguez 2005). The successive cambia are further subdivided into two types, concentric and non-concentric bands. The pith of concentric and non-concentric bands is usually located in the

---

**Table 2 (continued)**

| Family      | FD + TR | SC + VS | FC + IC | ES + TR | TE + TR | ES + IC | IC + DX | IC + VS + SC | FD + VS + SC | SP No. | Types No. |
|-------------|---------|---------|---------|---------|---------|---------|---------|-------------|-------------|--------|-----------|
| Primulaceae | –       | –       | –       | –       | –       | –       | –       | –           | –           | 3      | 1         |
| Ranunculaceae | –     | –       | –       | –       | –       | –       | –       | –           | –           | 16     | 2         |
| Rhamnaceae  | –       | –       | –       | –       | –       | –       | –       | –           | –           | 9      | 0         |
| Rosaceae    | –       | –       | –       | –       | –       | –       | –       | –           | –           | 5      | 1         |
| Rubiaceae   | –       | –       | –       | –       | –       | –       | –       | –           | –           | 15     | 5         |
| Rutaceae    | –       | –       | –       | –       | –       | –       | –       | –           | –           | 3      | 0         |
| Sabiaceae   | –       | –       | –       | –       | –       | –       | –       | –           | –           | 2      | 1         |
| Schisandraceae | –  | –         | –       | –       | –       | –       | –       | –           | –           | 3      | 0         |
| Solanaceae  | –       | –       | –       | –       | –       | –       | –       | –           | –           | 2      | 1         |
| Vitaceae    | –       | –       | –       | –       | –       | –       | –       | –           | –           | 4      | 2         |

Sum of family: 1 2 1 1 1 1 1 2 1

Sum of species: 2 2 1 1 1 1 1 6 1 287

Percentage %: 0.7 0.7 0.3 0.3 0.3 0.3 0.3 2.1 0.3 100

RC, stem cambium normal in production and round in conformation; VS, axial vascular elements in segments; IC, stem cambium normal in production but stem with irregular conformation; TR, intraxylary phloem; FC, furrowed xylem of cambium discontinuity; SC, successive cambia; FD, furrowed xylem of cambium discontinuity; TE, interxylary phloem; EP, external primary vascular cylinders; ES, external secondary vascular cylinders; DX, fissured stem/dispersed xylem; SP No., species number; Types No., cambium variant types in each family, RC not included.
Fig. 1  Single cambial variant of stem cross section. A Axial vascular elements in segments: Pericampylus formosanus. B Irregular in conformation: Jasminum lanceolarium. C Intraxylary phloem: Melodinus angustifolius. D Furrowed xylem of cambium continuity: Morinda parvifolia. E Successive cambia: Mucuna macrocarpa. F Furrowed xylem of cambium discontinuity: Pyrostegia venusta. RD, ray dilatation, PI, pith, XY, xylem, PH, phloem, IC, irregular conformation, TR, intraxylary phloem, CO, cork, FC, furrowed xylem of cambium continuity, PA, parenchyma, 1st XY, first xylem, 2nd XY, second xylem, 3rd XY, third xylem, 4th XY, forth xylem, 1st PH, first phloem, 2nd PH, second phloem, 3rd PH, third phloem, 4th PH, forth phloem, FD, furrowed xylem of cambium discontinuity, PHW, phloem wedges-like
Among the 287 species (Table 1) of lianas in this study, 96 species had regular cambium development with a circular cross-section, and 191 species had other cambial variants (Table 2). Among the 191 species, eight cambial variants were exhibited in 128 species, and fourteen combinations of cambial variants were present in 63 species. Furthermore, of these 191 species, 50 had axial vascular elements in segments, e.g., Pericampylus formosanus (Fig. 1A), 23 species had irregular conformation, e.g., Jasminum lanceolatum (Fig. 1B), 21 species had intraxyllary phloem, e.g., Melodinus angustifolius (Fig. 1C), 17 species had furrowed xylem of cambium continuity, e.g., Morinda parvifolia (Fig. 1D), 10 species had successive cambia, e.g., Mucuna macrocarpa (Fig. 1E), three species had furrowed xylem of cambium discontinuity, e.g., Pyrostegia venusta (Fig. 1F), and three species had interxyllary phloem, e.g., Thunbergia grandiflora (Fig. 2A), one species had fissured stem/dispersed xylem, e.g., Dimetia hedyotidea (Fig. 4D).

Fourteen combination types of cambial variants were present, of which two or three combinations of cambial variants were present in 63 species. The two cambial variants combination included: 20 species having intraxyllary phloem combined with successive cambia, e.g., Distimake tuberosus (Fig. 2B), 13 species with irregular conformation combined with axial vascular elements in segments, e.g., Tetristigma obectum var. glabrum (Fig. 2C), eight species having external primary vascular cylinders combined with axial vascular elements in segments, e.g., Piper kadsura (Fig. 2D), four species having intraxyllary phloem combined with furrowed xylem of cambium continuity, e.g., Gymnema sylvestre (Fig. 2E), two species with axial vascular elements in segments combined with furrowed xylem of cambium discontinuity, e.g., Clematis gouriana subsp. lishanensis (Fig. 2F), two species possessing intraxyllary phloem combined with furrowed xylem of cambium discontinuity, e.g., Gardneria multiflora (Fig. 3A), two species with axial vascular elements in segments combined with successive cambia, e.g., Anredera cordifolia (Fig. 4B) and Cocculus orbiculatus, one species with furrowed xylem of cambium continuity combined with irregular conformation, e.g., Coptosapelta difusa (Fig. 3B), one species having external secondary vascular cylinders combined with intraxyllary phloem, e.g.,

Center or eccentric of these rings (Isnard and Silk 2009). However, the pith in this variety is not located in the center of the rings and is defined as successive and directional cambia (Isnard and Silk 2009).

2. Intraxyllary phloem (TR): Intraxyllary phloem is derived from the formation of a secondary cambium between the primary xylem and the pith (Angyalossy et al. 2015). The secondary cambium either produces a phloem ring that appears inside the xylem, or two arcs of phloem toward the pith (Metcalfe and Chalk 1985). Intraxyllary phloem refer to phloem strands that occur adjacent to protoxylem, at margins of the pith (Carlquist 2013). Internal phloem had been used to refer to intraxyllary phloem, but it is vague with respect to ontogeny as well as location of phloem. Due to conflicting usages, internal phloem had been rejected.

3. External primary vascular cylinders (EP): This type is formed by the secondary growth of external primary vascular bundles, such as in Piperaceae.

4. External secondary vascular cylinders (ES): This type is developed from the neoformation of secondary vascular cylinders. The cambium of the cortex is formed and developed into vascular bundles cylinders of different diameters, which surround the primary vascular bundle cylinders creating external secondary vascular cylinders (Angyalossy et al. 2012, 2015).

Other common traits of lianas, such as a single species exhibiting more than one type of cambial variant or the parenchyma proliferation of the stem association with one type of cambial variant (Angyalossy et al. 2015), should be investigated. Therefore, we recorded the combination type and parenchymatization in our samples. The features of bark and cross-section of the stem were described based on definitions provided by Yang et al. (2021).

**Results and discussion**

**Patterns of cambial variants of Taiwan lianas**

Among the 287 species (Table 1) of lianas in this study, 96 species had regular cambium development with a circular cross-section, and 191 species had other cambial variants (Table 2). Among the 191 species, eight cambial variants were exhibited in 128 species, and fourteen combinations of cambial variants were present in 63 species. Furthermore, of these 191 species, 50 had axial vascular elements in segments, e.g., Pericampylus formosanus (Fig. 1A), 23 species had irregular conformation, e.g., Jasminum lanceolatum (Fig. 1B), 21 species had intraxyllary phloem, e.g., Melodinus angustifolius (Fig. 1C), 17 species had furrowed xylem of cambium continuity, e.g., Morinda parvifolia (Fig. 1D), 10 species had successive cambia, e.g., Mucuna macrocarpa (Fig. 1E), three species had furrowed xylem of cambium discontinuity, e.g., Pyrostegia venusta (Fig. 1F), and three species had interxyllary phloem, e.g., Thunbergia grandiflora (Fig. 2A), one species had fissured stem/dispersed xylem, e.g., Dimetia hedyotidea (Fig. 4D).

Fourteen combination types of cambial variants were present, of which two or three combinations of cambial variants were present in 63 species. The two cambial variants combination included: 20 species having intraxyllary phloem combined with successive cambia, e.g., Distimake tuberosus (Fig. 2B), 13 species with irregular conformation combined with axial vascular elements in segments, e.g., Tetristigma obectum var. glabrum (Fig. 2C), eight species having external primary vascular cylinders combined with axial vascular elements in segments, e.g., Piper kadsura (Fig. 2D), four species having intraxyllary phloem combined with furrowed xylem of cambium continuity, e.g., Gymnema sylvestre (Fig. 2E), two species with axial vascular elements in segments combined with furrowed xylem of cambium discontinuity, e.g., Clematis gouriana subsp. lishanensis (Fig. 2F), two species possessing intraxyllary phloem combined with furrowed xylem of cambium discontinuity, e.g., Gardneria multiflora (Fig. 3A), two species with axial vascular elements in segments combined with successive cambia, e.g., Anredera cordifolia (Fig. 4B) and Cocculus orbiculatus, one species with furrowed xylem of cambium continuity combined with irregular conformation, e.g., Coptosapelta difusa (Fig. 3B), one species having external secondary vascular cylinders combined with intraxyllary phloem, e.g.,

(See figure on next page.)

**Fig. 2** Single cambial variant or combination of two cambial variants of stem cross section. A Intraxyllary phloem (enlargement): Thunbergia grandiflora. B Intraxyllary phloem (enlargement) combined with successive cambia: Distimake tuberosus. C Irregular conformation combined with axial vascular elements in segments: Tetristigma obectum var. glabrum. D External primary vascular cylinders combined with axial vascular elements in segments: Piper kadsura. E Furrowed xylem of cambium continuity combined with intraxyllary phloem: Gymnema sylvestre. F Furrowed xylem of cambium discontinuity combined with axial vascular elements in segments: Clematis gouriana subsp. lishanensis. PI, pith; TE, interxyllary phloem; TR, intraxyllary phloem; 1st XY, first xylem; 2nd XY, second xylem; 1st PH, first phloem; RA, ray; XY, xylem; PH, phloem; SCL, sclenchyma; MU, mucilage canal; ME, medullary vascular bundles; PE, peripheral vascular bundles; FD, furrowed xylem of cambium discontinuity; FC, furrowed xylem of cambium continuity; PW, phloem wedges.
Trachelospermum gracilipes (Fig. 3C), one species possessing an interxylary phloem combined with intraxyllary phloem, e.g., Strychnos cathayensis (Fig. 3D), one species having external secondary vascular cylinders with irregular conformation, e.g., Lablab purpureus (Fig. 3E), and one species having fissured stem/
Fig. 3 Combination of two cambial variants of stem cross section. A Furrowed xylem of cambium discontinuity combined with intraxylary phloem: *Gardneria multiflora*. B Furrowed xylem of cambium continuity combined with irregular conformation; *Coptosapelta diffusa*. C External secondary vascular cylinders combined with intraxylary phloem: *Trachelospermum gracilipes*. D Intersylyry phloem combined with intraxylary phloem: *Strychnos cathayensis*. E External secondary vascular cylinders combined with irregular conformation: *Lablab purpureus*. F Fissured stem/dispersed xylem combined with irregular conformation: *Bauhinia championii*. PI, pith; FC, furrowed xylem of cambium continuity; PW, phloem wedges; IC, irregular conformation; PA, parenchyma; DX, fissured stem/ dispersed xylem; TR, intraxylary phloem; ES, external secondary vascular cylinders; XY, xylem; PH, phloem; TE, interxylary phloem.
dispersed xylem combined with irregular conformation, e.g., Bauhinia championii (Fig. 3F).

The three cambial variants combination included: six species having successive cambia combined with axial vascular elements in segments and irregular conformation, e.g., Tetrastigma formosanum (Fig. 4A), Momordica charantia var. abbreviata (Fig. 4C), Cayratia corniculata (Fig. 4F), one species having furrowed xylem of cambium discontinuity combined with axial vascular elements in segments and successive cambia, such as Momordica cochinchinensis.

Axial vascular elements in segments type and intraxylary phloem type appeared in six and five combination types, respectively. These two variant types always appear in many combined variants, so they are more helpful to the lianas identification. Fourteen combinations types of cambial variants were found in Taiwan lianas, indicating multiple cambial variants type were found and could be a character of taxonomic values. The number and types of cambial variants in one family or genus might be related to the number of investigated species. Among the 52 families, most had only one type of variant. In this work Fabaceae and Rubiaceae showed to have the greatest diversity of cambial variants with five CV each one, followed by Cucurbitaceae and Vitaceae with four types. Other families like Apocynaceae, Asteraceae, Celastraceae, Passifloraceae, and Polygonaceae, had only three types (Table 3).

Ten species belonging to Amaranthaceae, Connnaraceae, Fabaceae, Nyctaginaceae, and Polygonaceae displayed successive cambia. In Fabaceae family, Mucuna macrocarpa, Pueraria lobata subsp. thomsonii, and Pueraria montana (Fig. 1E), have 3–4 layers of regular concentric rings. Entada phaseoloides subsp. phaseoloides, Entada phaseoloides subsp. tonkinensis, and Entada rheedei also have continuous cambium, but their stem cross-section consists of 5–12 layers of irregular concentric rings. The species Bougainvillea spectabilis (Nyctaginaceae) also had successive cambia with 5–6 layers of regular concentric rings.

Cambial variants of Taiwan lianas in each family or genus

The number of cambial variants in one family or genus might be related to the number of species investigated. Therefore, a family or genus with numerous species with only a single or few cambial variants may be easily identified using the unique cambial variants. For example, 14 out of 18 species of Apocynaceae possess intraxylary phloem; 19 out of 23 species of Convolvulaceae have a combination of intraxylary phloem and successive cambia; Lardizabalaceae (Yang et al. 2019), Menispermaceae (Yang et al. 2016), and Ranunculaceae (Yang et al. 2021), and 35 other species have axial vascular elements in segments; eight species of Piperaceae have a combination of external primary vascular bundle cylinder and axial vascular elements in segments (Yang and Chen 2017); 4 out of 6 species of Passiflora genus possess furrowed xylem; 12 out of 20 species of Vitaceae had a combination of axial vascular elements in segments and irregular in conformation.

Carquist (1999) indicated Anredera baselloides (Basellaceae) have combinations of three cambial variants, viz. successive cambia, interxylary phloem strands, and intraxylary phloem in a wider stem, with other features, such as restriction of vessels to central portions of fascicular areas, crystals and mucilage cells in cortex, and rays. We observed that the species Anredera cordifolia had axial vascular elements in segments in narrow stems and 2–3 layers of successive cambia in wider stems (Fig. 4B).

In this study, two species of Bignoniaceae had furrowed xylem of cambium discontinuity. Furrowed xylem of cambium discontinuity had two patterns. One where wedge-shaped phloem has a regular spacing, as found in Pyrostegia venusta (Bignoniaceae) (Fig. 1F) and Clematis gouriana subsp. lishanensis (Ranunculaceae) (Fig. 2F); the other had wedge-shaped phloem with irregular spacing, as in Passiflora edulis (Passifloraceae) (Fig. 4E). Furrowed xylem of cambium continuity had shallowly or deeply lobed patterns based on the depth of phloem arcs/wedges, as in Morinda parvifolia (Rubiaceae) (Fig. 1D) where the stem is deeply lobed, whereas Gymnema sylvestre (Apocynaceae) is shallowly lobed (Fig. 2E). However, four equidistant phloem arcs/wedges, a multiple of four phloem wedges (Angyalossy et al. 2015), cambium continuity/discontinuity, and the depth of phloem arcs/wedges in Bignoniaceae (Angyalossy et al. 2012) are the diagnostic characteristics available to the identification of furrowed xylem types. Although Angyalossy et al. (2012,
2015) distinguish some members of the subfamily Big-
noniae, but phloem wedges are present in more families
where they have a diversity of patterns and variability of
conformation (Cabanillas et al. 2017; Quintanar and Pace
2022). So, studying the variability of phloem arcs/wedges
in Taiwan lianas become more important.

The diagnostic feature of the bicollateral vascular bun-
dle (Cucurbitaceae) had outer and inner phloem at both

![Fig. 4](See legend on previous page.)
| Orders         | Families                | Cambial variants (this study) | Angyalossy et al. (2015) |
|---------------|-------------------------|-------------------------------|--------------------------|
| Asterales     | Asteraee                | VS, FC, FD                    | VS, FX                   |
| Apiales       | Araliaceae              | RC                            | –                        |
| Arecales      | Areaceae                | RC                            | –                        |
| Austrobaileyales | Schisandraceae         | RC                            | –                        |
| Boraginales   | Heliotropiaceae         | RC                            | –                        |
| Brassicales   | Capparaceae             | RC                            | –                        |
| Caryophyllales| Amaranthaceae           | SC                            | –                        |
|               | Nyctaginaceae           | TE, SC                        | SC                       |
|               | Polygonaceae            | SC, VS, FC                    | IC, SC, TR               |
|               | Basellaceae             | VS, TR, SC                    | –                        |
| Cornales      | Hydrangeaceae           | RC                            | –                        |
| Celastrales   | Celastraceae            | FC, VS, IC                    | FX, IC, SC, TE           |
| Cucurbitales  | Cucurbitaceae           | IC + VS, VS + IS + SC, FD + VS, FD + VS + SC | SC, TE, VS |
| Diosipes      | Caprifoliaceae          | RC                            | –                        |
| Ericales      | Actinidiaceae           | RC                            | –                        |
|               | Pimulaceae              | VS                            | –                        |
| Fabales       | Fabaceae                | IC, DX + IC, FC, SC, ES       | SC, TE, IC, FX, DX, TR   |
| Gentianales   | Apocynaceae             | TR, TR + FC, TR + ES          | IC, SC, TE, VS, FX       |
|               | Loganiaceae             | TR + FD, TR + TE              | TE                       |
|               | Rubiaceae               | FC + IC, IC, DX + TR + IC, IC + VS | FX, IC |
| Lamiales      | Acanthaceae             | FD, TE                        | SC, TE, DX               |
|               | Bignoniaceae            | FD                            | FX, DX                   |
|               | Gesneriaceae            | FC                            | –                        |
|               | Oleaceae                | IC                            | –                        |
| Laurales      | Hernandiaceae           | FC                            | –                        |
| Magnoliolae   | Annonaceae              | RC                            | –                        |
| Malpighiales  | Euphorbiaceae           | IC                            | ES                       |
|               | Malpighiaceae           | FC                            | FX, DX, SC, TE, IC       |
|               | Passifloraee            | FC                            | SC, FX                   |
|               | Phyllanthaceae          | FC                            | –                        |
| Myrtales      | Combretaceae            | TR + FC                       | TR, TE, ES, IC           |
| Oxalidales    | Connaraceae             | SC                            | SC                       |
| Pandanales    | Pandanaceae             | RC                            | –                        |
| Piperales     | Aristolochiaceae        | VS                            | VS, IC                   |
|               | Piperaceae              | EP + VS                       | VS, IC, EP               |
| Proteales     | Sabiaceae               | VS                            | –                        |
| Ranunculales  | Menispermacae           | VS, VS + SC                   | SC, VS, IC, TR           |
|               | Ranunculaceae           | VS, VS + FD                   | VS                       |
|               | Lardizabalaceae         | VS                            | –                        |
| Rosales       | Cannabaceae             | IC                            | –                        |
|               | Cecropiaceae            | RC                            | –                        |
|               | Elaeagnaceae            | RC                            | –                        |
|               | Rhamnaceae              | RC                            | –                        |
|               | Rosaceae                | RC                            | –                        |
|               | Moraceae                | IC                            | IC                       |
| Santalales    | Opilaceae               | RC                            | –                        |
| Solanales     | Convolvulaceae          | TR, TR + SC                   | SC, TE, FX, DX, TR       |
|               | Solanaceae              | TR                            | –                        |
| Vitals        | Vitaceae                | IC, VS, IC + VS + SC, VS + IC | VS, IC, SC, DX           |

18 orders 49 families

RC, stem cambium normal in production and round in conformation; VS, axial vascular elements in segments; IC, stem cambium normal in production but stem with irregular conformation; TR, interxylary phloem; FC, furrowed xylem of cambium continuity; SC, successive cambia; FD, furrowed xylem of cambium discontinuity; TE, interfylary phloem; EP, external primary vascular cylinders; ES, external secondary vascular cylinders; DX, fissured stem/dispersed xylem.
ends (Figs. 4C, 5). The distribution of the bicollateral vascular bundle on the stem cross-section had centripetal and centrifugal parts. The centripetal part of bicollateral vascular bundle was composed of centripetal phloem and centrifugal xylem, and no cambium was found between them. In contrast, the centrifugal part has centripetal xylem, a cambium, and centrifugal phloem. The wider primary rays split the bicollateral vascular bundle, secondary rays appeared in the xylem, and the larger the diameter, the secondary rays were produced. The interfascicular cambium was located between the vascular bundles and contributed to radial growth (Schweingruber et al. 2011). However, the cortical bicollateral vascular bundle of Momordica charantia var. abbreviata developed one to five layers of centrifugal vascular bundles, forming directional continuous successive cambia. This species exhibited a combination of three cambial variants (Fig. 4C) different from the other species of Cucurbitaceae. The cambial variants of Momordica cochinchinensis and Neoalsomitra integrifolia had furrowed xylem of cambium discontinuity combined with axial vascular elements in segments, which were special and different from other species of Cucurbitaceae.

The cambial variants of Passiflora edulis (Passifloraceae) had furrowed xylem of cambium continuity formed from very shallow depressions, via shallow to deep phloem wedges (Rajput and Bajnath 2016). The other diagnostic feature of P. edulis was the presence of five pairs of interfascicular rays distributed equidistantly. The cambial variant of four Passiflora species in this study exhibited furrowed xylem of cambium continuity, but the cambia of Passiflora laurifolia had regular secondary growth and the stem was round in conformation, and Passiflora quadrangularis was irregular conformation.

The cambial variants in Rubiaceae exhibited furrowed or lobed xylem in Atractogyne and Chiococca respectively (Jansen et al. 2002). In this study we found that Coptosapeltia diffusa, Morinda parvifolia, and Morinda umbellata also possessed this cambial variant type. Jansen et al. (2002) indicated that stem cross section generally develops lignified or unlignified parenchymas in some genera of Rubiaceae. In this study, four genera Coptosapeltia, Mussaenda, Randia, and Uncaria have lignified parenchyma and three genera Dimetia, Morinda, Paederia have significant unlignified parenchyma (lianescent habit), these results were consistent with Jansen et al. (2002). The lianescent habit or environmental influences presumably explains the variation in quantitative features or the distribution of axial parenchyma of M. parvifolia (Fig. 1D).

The cambial variant of Cayratia corniculata (Vitaceae) is a combination of irregular conformation and axial vascular elements in segments in the smaller stem. When the stem size is larger about 3.5 cm in diameter, the second vascular bundles developed near the cortex and will form the successive cambia (Fig. 4F). Pace et al. (2018) indicated Tetrastigma retinervum and Tetrastigma voineianum (Vitaceae) had a combination of axial vascular elements in segments with successive cambia, suggesting that the examination of mature stems of additional species of Tetrastigma should determine the distribution of this unique cambial variant type. We studied three endemic species, Tetrastigma formosanum, Tetrastigma hemsleyanum, Tetrastigma lanyuense, and one native species, Tetrastigma obtectum var. glabru, showing that only T. obtectum var. glabru had irregular conformation without successive cambia (Fig. 2C). We speculate that the stem diameter of this species we collected was too small to exhibit successive cambia development.

Cambial variants of Taiwan lianas in each order
All the differences between the comparisons of the cambial variants of orders/families reported by Angyalossy et al. (2015) are presented in Table 3. Just regular secondary growth of 36 species, belonging to 15 families, 12 orders (Table 3), e.g., Eleutherococcus trifoliatus var. trifoliatus and Hedera rhombea var. formosana (Araliaceae) (Table 1) and cambial variants of 16 species, belonging to nine families, and eight orders (Table 3) were added in this study.

In this study, combination types of two or three cambial variants in Cucurbitales were added and the major differences were stems with irregular conformation and furrowed xylem and interxylary phloem. The cambial variants of external secondary vascular cylinder was added and interxylary and intraxylary phloems were
not found in Fabales. The cambial variants of Gentianales were diverse and exhibited combinations of two or three cambial variants; only successive cambia was not found. Malpighiales and Myrtales had furrowed xylem of cambium continuity, and furrowed xylem of cambium continuity combined with intraxylary phloem, but four types of cambial variants were not found. Piperales had a combination of external primary vascular cylinders with axial vascular elements in segments, and few species have stem with irregular conformation. In Ranunculales, two combination types were added but irregular conformation, and intraxylary phloem were not found. Six phloem wedges of furrowed xylem of cambium discontinuity are different from four equidistant phloem wedges in Bignoniaceae. Only intraxylary phloem and successive cambia were found in Solanales, but interxylary phloem, furrowed xylems and fissured stem/dispersed xylem were not reported. In Vitales, a combination of three cambial variants was added and only fissured stem/dispersed xylem was not found in Taiwanese species.

The cambial variants types had higher concentration in rosids and asterids (Stevens 2001), and furrowed xylem type was one of the important cambial variants for identification the climbers. The additional information of lianas cambial variants we added here will be available to assess the relationships among the order and families of climbers for academic study.

These reports provide basic data about cambial variants of lianas to establish cambial variants as commonly taxon-specific. The data allows the identification of many individual plants into families or/and genera, even without leaves or flowers.

The developmental processes of stem vascular elements were beneficial to understanding the changes of the vascular bundle of lianas. So in addition to sample larger and freshly stems, one should also sample earlier stages of development in each lianas should be investigated further.

**Conclusion**

This study explored the cambial variants of the stem cross-section of Taiwan lianas. The results showed that approximately seven cambial variants and sixteen combination types of cambial variants in 287 Taiwanese lianas were present, highlighting the occurrence of multiple cambial variants of lianas in this region. In most species, axial vascular elements in segments type were exhibited, followed by irregular conformation and intraxylary phloem. Five cambial variants types in Fabaceae and Rubiaceae are the highest, followed in Cucurbitaceae and Vitaceae with four types. Most species in Apocynaceae, Convolvulaceae, and Menispermaceae/ Ranunculaceae had intraxylary phloem, intraxylary phloem combined with successive cambia, and axial vascular element in segments, respectively, showing that these cambial variants could be as a diagnostic characteristics of that family. Comparing the orders/families from the previous data, we added data on the just secondary growth or just vascular bundles of 52 lianas, including 36 lianas with regular secondary growth with rounded stem and 16 lianas with different cambial variants. Approximately 50 remaining Taiwanese lianas are still needed to investigate. Studying the secondary growth, different diameters and corks developments, and the fundamental terms of cambial variants are extremely important for future lianas research. This information on cambial variants of Taiwan lianas will aid in the establishment of cambial variants as commonly taxon-specific and the combination of two or three cambial variants could be a character of taxonomic values, and allow the identification of many individual plants to families or genera without leaves or flowers.

**Acknowledgements**

We thank the Luodong Forest District Office, Forest Bureau, Council of Agriculture, Executive Yuan, for supporting the funding used to compile the book of lianas diversity in Taiwan. We also thank the staff members of the herbarium PPI for access to the collection and photography. The authors are extremely grateful to two reviewers who provided suggestions on improving this manuscript.

**Author contributions**

SZY conceived of and designed the experiments. PHC conducted the fieldwork and collected the plant specimens, and JJC performed the taxonomic study. SZY wrote the paper. All authors read and approved the final manuscript.

**Declarations**

**Competing interests**

The authors declare that they have no competing interests.

**Author details**

1 Department of Forestry, National Pingtung University of Science and Technology, No. 1, Shuefu Rd., Neipu, Pingtung 91201, Taiwan. 2 Graduate Institute of Bioresources, National Pingtung University of Science and Technology, No. 1, Shuefu Rd., Neipu, Pingtung 91201, Taiwan. 3 Luodong Forest District Office, Taiwan, No. 118, Zhongzheng North Rd., Luodong Town 263, Yilan, Taiwan.

**Received** 18 April 2022   **Accepted** 4 September 2022

**Published online:** 24 September 2022

**References**

Acvevedo-Rodríguez P (2005) Vines and climbing plants of Puerto Rico and the Virgin Islands. The US National Herbarium 51:483. Dept Bot, National Museum of Natural History, Washington, DC

Angyalossy V, Angeles GM, Pace R, Lima AC, Dias-Leme CL, Lohmann LG, Madero-Vega C (2012) An overview of the anatomy, development and evolution of the vascular system of lianas. Plant Ecol Divers 5(2):167–182

Angyalossy V, Pace MR, Lima AC (2015) Liana anatomy: a broad perspective on structural evolution of the vascular system. In: Schnitzer SA, Bongers F, Burnham RJ, Putz FE (eds) Ecology of lianas. Wiley Blackwell, West Sussex, pp 253–287
Ayensu ES, Stern WL (1964) Systematic anatomy and ontogeny of the stem in Passifloraceae. Contributions from the US Natl Herb 34(3):45–73
Boufford DE, Ohashi H, Huang TC, Hsien CF, Tsai JI, Yang KC, Peng CI, Kuoh CS, Hsiao H (2003) A checklist of the vascular plants of Taiwan. In: Huang TC et al (eds) Flora of Taiwan, vol 6, 2nd edn. Editorial committee of the Flora of Taiwan. Dept Bot NTU, Taipei, pp 15–139
Caballé G (1993) Liana structure, function and selection: a comparative study of xylem cylinders of tropical rainforest species in Africa and America. Bot J Linn Soc 113(1):41–60
Cabanillas PA, Pace MR, Angyalossy V (2017) Structure and ontogeny of the fissured stems of Callaeum (Malpighiaceae). IAWA J 38(1):49–66
Carlquist S (1991) Anatomy of vine and liana stems: a review and synthesis. In: Putz FE, Mooney HA (eds) The biology of vines. Cambridge University Press, Cambridge, pp 53–71
Carlquist S (1999) Wood, stem, and root anatomy of Basellaceae with relation to habit, systematics, and cambial variants. Flora 194:1–12
Carlquist S (2001) Comparative wood anatomy: systematic, ecological, and evolutionary aspects of dicotyledon wood. Springer-Verlag Press, Germany, p 448
Carlquist S (2007) Successive cambia revisited: ontogeny, histology, diversity, and functional significance. J Torrey Bot Soc 134:301–332
Carlquist S (2013) Interxylary phloem: diversity and functions. Brittonia 65(4):477–495
Dias-Leme CL, Pace MR, Angyalossy V (2021) The “Lianescent Vascular Syndrome” statistically supported in a comparative study of trees and lianas of Fabaceae subfamily Papilionoideae. Bot J Linn Soc 197(1):25–34. https://doi.org/10.1093/botlinn/en/boab015
Ferreira T, Rasband W (2011) The ImageJ user guide version 1.44. http://imagej.nih.gov/docs/user-guide.pdf
Gentry AH (1991) The distribution and evolution of climbing plants. In: Putz FE, Mooney HA (eds) The biology of vines. Cambridge University Press, Cambridge, pp 3–49
Isnard S, Silk WK (2009) Moving with climbing plants from Charles Darwin’s time into the 21st century. Am J Bot 96(7):1205–1221
Jansen S, Robbrecht E, Beeckman H, Smets E (2002) A survey of the systematic wood anatomy of the Rubiaceae. IAWA J 23(1):1–67
Metcalfe CR, Chalk L (1969) Wood structure and conclusion of the general introduction. Anatomy of the dicotyledons, vol II, 2nd edn. Oxford University Press, New York, p 330
Pace MR, Lohmann LG, Angyalossy V (2009) The rise and evolution of the cambial variant in Bignoniaceae (Bignoniinae). Evol Dev 11:465–479
Pace MR, Angyalossy V, Acevedo-Rodriguez P, Wen J (2018) Structure and ontogeny of successive cambia in Tetrastigma (Vitaceae), the host plants of Rafflesiae. J Syst Evol. https://doi.org/10.1111/jse.12303
Quintanar-Castillo A, Pace MR (2022) Phloem wedges in Malpighiaceae: origin, structure, diversification, and systematic relevance. EvoDevo 13:11
Rajput KS, Baijnath H (2016) Stem anatomy of some species of Passiflora (Passifloraceae). IAWA J 37(3):431–443
Schweingruber FH, Börner A, Schulze ED (2011) Atlas of stem anatomy in herbs, shrubs and trees, vol 1. Springer, Berlin
Stevens PF (2001 onwards) Angiosperm phylogeny website. Version 14, July 2017. [and more or less continuously updated since]. http://www.mobot.org/MOBOT/research/APweb/
Yang SZ, Chen PH (2015) Classify the radiating plates of xylem in Taiwan lianas. Taiwania 60(4):151–159
Yang SZ, Chen PH (2016) Cambial variants in the family Menispermaceae in Taiwan. Am J Plant Sci 7:841–854
Yang SZ, Chen PH (2017) Cambial variants of liana species (Piperaceae) in Taiwan. Bot Stud 58:17
Yang SZ, Chen PH, Lin KC (2016) Cambial variants of liana species (Fabaceae) in Taiwan. Taiwania 61(3):185–193
Yang SZ, Chen PH, Chen JJ (2019) Cambial variations of three lianoid genera, Akebia, Stauntonia, and Sobisa (Lardizabalaceae and Sabiaceae), in Taiwan. Am J Plant Sci 10:545–554
Yang SZ, Chen PH, Chen CF (2020) Cambial variants combine successive cambia and intraxylary phloem in Convolvulaceae in Taiwan. Am J Plant Sci 11:437–453
Yang SZ, Chen PH, Chen CF (2021) Stem cambial variants of the Clematis species (Ranunculaceae) in Taiwan. Taiwania 66(4):526–540

Publisher’s Note
Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Submit your manuscript to a SpringerOpen journal and benefit from:

- Convenient online submission
- Rigorous peer review
- Open access: articles freely available online
- High visibility within the field
- Retaining the copyright to your article