Stem cambial variants of Taiwan lianas

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Original Article

Keywords: centrifugal xylem, lianas, parenchymatization, secondary growth, Taiwan

Posted Date: May 16th, 2022

DOI: https://doi.org/10.21203/rs.3.rs-1568515/v1

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 the cambium in Taiwan lianas, with 21 variants, were diverse. 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 external primary vascular bundle cylinder combined with axial vascular elements in segments; Vitaceae had axial vascular elements in segments combined with irregular conformation. Axial vascular elements in segments and intraxylary phloem appeared in six or seven combination types, showing that these two types combined with many variants are helpful for the identification of lianas. Only one species, *Momordica charantia* var. *abbreviata,* had a cambium element in the cortical bicollateral vascular bundles and formed directional layers of successive cambia.

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

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). 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 or anomalous structures (Isnard and Silk, 2009). The differences in these structures can be used to distinguish liana families (Caballé 1993; Angyalossy et al. 2012).

The stem development in several lianas species begins with stiff searching branches or a self-supporting shrub structure, followed by the formation of the lianescent vascular syndrome (Angyalossy et al. 2015). 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. These climbing phase traits can be summarized as the lianescent xylem syndrome.

The characteristics of lianescent vascular syndrome in lianas are related to the secondary growth, which results in special attributes of vascular bundles, 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). 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-Rodriguez 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). 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 ℃, 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 species of climbing plants 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 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 (v 1.50h) software (Ferreira and Rasband 2011). 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 at the National Pingtung University of Science and Technology, Pingtung, Taiwan, for subsequent identification.

Table 1
Cambial variants of each species in Taiwan lianas

Families	Scientic name	Cambial variants
Acanthaceae	*Thunbergia alata* Bojer ex Sims	FD
	Thunbergia grandiflora Roxb.	TE
	Thunbergia laurifolia Lindl.	TE
Actinidiaceae	*Actinidia arguta* (Sieb. & Zucc.) Planch. ex Miquel	RC
	Actinidia callosa var. *discolor* C. F. Liang Feng	RC
	Actinidia latifolia (Gardner & Champ.) Merr.	RC
	Actinidia rufa (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 oldhamii (Hemsl.) Merr.	RC
Apocynaceae	*Alyxia sibuyanensis* Elmer	TR
	**Alyxia taiwanensis* S. Y. Lu & Yuen P. Yang	TR
	Anodendron affine (Hook. & Arn.) Druce	TR
	* *Anodendron benthamiana* Hemsl.	TR
	Cryptolepis sinensis (Lour.) Merr.	TR
	Dregea volubilis (L. f.) Benth.	TR
	Gymnema sylvestre (Retz.) Schultes	TR, FC
	* *Heterostemma brownii* Hayata	TR, FC
	Marsdenia formosana Masam.	TR
	Marsdenia tinctoria R. Br.	TR
	* *Melodinus angustifolius* Hayata	TR
	Parsonsia alboflavescens (Dennst.) Mabb.	TR
	* *Trachelospermum formosanum* Y. C. Liu & C. H. Ou	TR
	Trachelospermum gracilipes Hook. f.	TR, ES
	Trachelospermum jasminoides (Lindl.) Lemaire	TR, FC
	**Trachelospermum lanyuense* C. E. Chang	TR
	Urceola micrantha (Wallich *ex* G. Don) D. J. Middleton	TR
	Urceola 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 cucurbitifolia* Hayata	VS
	Aristolochia elegans Mast.	VS

Note: *: endemic species. cambia normal in production and round in conformation (RC); cambia normal in production but stem with irregular conformation (IC); axial vascular elements in segments (VS); furrowed xylem of cambium continuity (FC); furrowed xylem of cambium discontinuity (FD); dissected xylem (DX); external primary vascular cylinders (EP); external secondary vascular cylinders (ES); successive cambia (SC); intraxylary phloem (TR); interxylary phloem (TE).

Families	Scientic name	Cambial variants
	Aristolochia shimadae Hayata	VS
	Aristolochia zollingeriana Miq.	VS
Asteraceae	*Blumea riparia* (Blume) DC. var. *megacephala* Randeria	VS
	Microglossa pyrifolia (Lam.) Kuntze	AB
	Mikania micrantha Kunth	FD
	Senecio scandens Buch.-Ham. ex D. Don var. *scandens*	RC
	Vernonia gratiosa Hance	VS
Basellaceae	*Anredera cordifolia* (Tenore) van Steenis	VS, TR, SC
Bignoniaceae	*Anemopaegma chamberlaynii* (Sims) Bureau & K.Schum.	FD
	Pyrostegia venusta (Ker-Gawl.) Miers	FD
Cannabaceae	*Humulus scandens* (Lour.) Merr.	IC
Capparaceae	**Capparis formosana* Hemsl.	RC
	Capparis lanceolaris DC.	RC
Caprifoliaceae	*Lonicera acuminata* Wall.	RC
	Lonicera hypoglauca Miq.	RC
	Lonicera japonica Thunb.	RC
Cecropiaceae	*Poikilospermum acuminata* (Trécul) Merr.	RC
Celastraceae	*Celastrus hindsii* Benth.	FC
	Celastrus kusanoi Hayata	VS
	Celastrus paniculatus Willd.	RC
	Celastrus punctatus Thunb.	FC
	* *Euonymus spraguei* Hayata	IC
	Tripterygium wilfordii Hook. f.	RC
Combretaceae	*Quisqualis indica* L.	TR, FC
Connaraceae	*Rourea minor* (Gaertn.) Leenhouts	SC
Convolvulaceae	**Argyreia akoensis* S. Z. Yang, P. H. Chen & G. W. Staples	TR, SC
	**Argyreia formosana* Ishigami ex T. Yamaz.	TR, SC
	Argyreia nervosa Boj.	TR, SC
	Camonea vitifolia (Burm.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 cairica (L.) Sweet	TR, SC
	Ipomoea carnea Jacq. subsp. *fistulosa* (Mart. ex Choisy) D. F. Austin	TR
	Ipomoea hederifolia L.	TR, SC
	Ipomoea indica (Burm. f.) Merr.	TR, SC
	Ipomoea littoralis Blume	TR, SC
	Ipomoea nil (L.) Roth.	TR, SC

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Families	Scientic name	Cambial variants
	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
	Lepistemon binectariferum (Wall.) Kuntze var. *trichocarpum* (Gagnep.) Ooststr.	TR, SC
	Merremia gemella (Burm.f.) Hallier f.	TR, SC
	Operculina turpethum (L.) S. Manso	TR, SC
	Stictocardia tilifolia (Desr.) Hallier f.	TR, SC
Cucurbitaceae	*Coccinia grandis* (L.) Voigt	IC, VS
	Gynostemma pentaphllum (Thunb.) Makino	IC, VS
	Melothria pendula L.	IC, VS
	Momordica charantia L.	IC, VS, SC
	Momordica charantia L. var. *abbreviata* Ser.	IC, VS, SC
	Momordica cochinchinensis (Lour.) Spreng.	FD, VS
	Neoalsomitra integrifolia (Cogn.) Hutch.	FD, VS
Elaeagnaceae	*Elaeagnus formosana* Nakai	RC
	Elaeagnus glabra Thunb.	RC
	**Elaeagnus grandifolia* Hayata	RC
	**Elaeagnus thunbergii* Serv.	RC
	Elaeagnus triflora Roxb.	RC
Euphorbiaceae.	*Mallotus repandus* (Willd.) Müll. Arg.	IC
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
	**Derris laxiflora* Benth.	RC
	Derris trifoliata Lour.	RC
	**Dolichos rilobus* L. var. *kosyunensis* (Hosok.) H. Ohashi & Tateishi	FC
	Dunbaria merrillii Elmer	RC

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Families	Scientic name	Cambial variants
	**Dumasia truncata* Siebold & Zucc.	RC
	Entada phaseoloides (L.) Merr. subsp. *phaseoloides*	SC
	Entada phaseoloides (L.) Merr. subsp. *tonkinensis* (Gagnep.) H. Ohashi	SC
	Entada rheedei Spreng.	SC
	Lablab purpureus (L.)Sweet	ES,AB
	Macroptilium atropurpureum (DC.) Urb.	RC
	Macroptilium lathyroides (L.) Urb.	RC
	Millettia pachycarpa Benth.	RC
	Mimosa diplotricha C. Wright ex Sauvalle	FC
	Mucuna gigantea (Willd.) 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
	Paraderris canarensis (Dalzell) Adema	RC
	Paraderris elliptica (Wallich) Adema	RC
	Psophocarpus tetragonolobus (L.) DC.	RC
	Pueraria lobata (Willd.) Ohwi subsp. *thomsonii* (Benth.) Ohashi & Tateishi	SC
	Pueraria montana (Lour.) Merr.	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 sarmentosum* (Lam.) Craven	RC
Hernandiaceae	*Illigera luzonensis* (C. Presl) Merr.	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
Lardizabalaceae	*Akebia longeracemosa* Matsum.	VS
	Akebia chingshuiensis T. Shimizu	VS
	Stauntonia hexaphylla (Thunb.) Dcene.	VS
	Stauntonia obovata Hemsl.	VS
	* *Stauntonia purpurea* Y. C. Liu & F. Y. Lu	VS
Loganiaceae	*Gardneria multiflora* Makino	FD, TR
	Gardneria nutans Siebold & Zucc.	FD, TR
	Strychnos cathayensis Merr.	TE, TR
Malpighiaceae	*Hiptage benghalensis* (L.) Kurz.	RC
	Tristellateia australasiae A. Rich.	FC
Melastomataceae	**Medinilla formosana* Hayata	RC
	**Medinilla hayataina* H. Keng	TR

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Families	Scientic name	Cambial variants
Menispermaceae	*Cissampelos pareira* L. var. *hirsuta* (DC.) Forman	VS
	Cocculus orbiculatus (L.) DC.	VS
	* *Cyclea gracillima* Diels	VS
	Cyclea insularis (Makino) Hatus.	VS
	* *Cyclea ochiaiana* (Yamam.) S. F. Huang & T. C. Huang	VS
	* *Paratinospora dentata* (Diels) Wei Wang	VS
	Pericampylus glaucus (Lam.) Merr.	VS
	Sinomenium acutum (Thunb.) Rehder & E. H. Wils.	VS
	Stephania japonica (Thunb.) Miers	VS
	Stephania longa Lour.	VS
	Stephania merrillii Diels	VS
	Stephania tetraandra S. Moore	VS
	Tinospora crispa (L.) J. D. Hook. & Thom.	VS
	Tinospora sinensis (Lour.) Merr.	VS
Moraceae	*Ficus aurantiaca* Griff. var. *parvifolia* (Corner) Corner	IC
	Ficus pumila L. var. *awkeotsang* (Makino) Corner	IC
	Ficus pumila L. var. *pumila*	IC
	Ficus sarmentosa 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 cochinchinensis (Lour.) Corner	RC
	Malaisia scandens (Lour.) Planch.	RC
Nyctaginaceae	*Bougainvillea spectabilis* Willdenow	SC
	Pisonia aculeata L.	TE
Oleaceae	*Jasminum lanceolarium* 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.	FD
	Passiflora edulis Sims	FD
	Passiflora laurifolia L.	RC
	Passiflora quadrangularis L.	AB
	Passiflora suberosa L. subsp. *litoralis* (Kunth) K.Port.-Utl. ex M.A.M.Azevedo, Baumbratz & Gonç.-Estev.	FC
	Passiflora vesicaria L.	FC
Phyllanthaceae	*Phyllanthus reticulatus* Poiret	FC
Piperaceae	*Piper arborescens* Roxb.	EP, VS
	Piper betle L.	EP, VS
	Piper interruptum Opiz	EP, VS

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Families	Scientic name	Cambial variants
	Piper kadsura (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
	Reynoutria multiflorum (Thunb.) Moldenke var. *hypoleuca* (Ohwi) S.S. Ying	VS
Primulaceae	* *Embelia laeta* (L.) Mez var. *papilligera* (Nakai) Walker	VS
	* *Embelia lenticellata* Hayata	VS
	Embelia rudis Hand.-Mazz.	VS
Ranunculaceae	*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 lasiandra Maxim.	VS
	Clematis leschenaultiana DC.	VS
	Clematis meyeniana Walp.	VS
	Clematis montana Buch.-Ham. *ex* DC.	VS
	**Clematis parviloba* 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 fenchifuensis* 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 pyrifolius Sm.	RC
	Rubus rolfei S. Vidal	RC

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Families	Scientic name	Cambial variants
	Rubus swinhoei Hance var. *swinhoei*	RC
	Rubus wallichianus Wight & Arn.	IC
Rubiaceae	*Coptosapelta diffusa* (Champ. ex Benth.) Steenis	FC, IC
	Dimetia hedyotidea (DC.) T. C. Hsu	DX, TR, IC
	Morinda parvifolia Bartl.	FC
	Morinda umbellata L.	FC
	Mussaenda formosanum (Matsum.) T. Y. Aleck Yang & K. C. Huang	RC
	Mussaenda parviflora Miq.	RC
	Mussaenda pubescens W. T. Aiton	RC
	* *Mussaenda taihokuensis* Masam.	RC
	Paederia cavaleriei H. Lév.	IC, VS
	Paederia foetida L.	IC, VS
	Psychotria serpens L.	RC
	Randia sinensis (Lour.) 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 swinhoei* Hemsl.	VS
	**Sabia transarisanensis* Hayata	VS
Schisandraceae	*Kadsura japonica* (L.) Dunal	RC
	Kadsura matsudae Hayata	RC
	**Schisandra arisanensis* Hayata	RC
Solanaceae	*Solanum lyratum* Thunb.	TR
	Solanum pittosporifolium Hemsl.	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 maritime B. R. Jackes	VS
	Cissus assamica (Laws.) Craib	IC,VS
	**Cissus pteroclada* Hayata	IC,VS
	Cissus repens Lam.	IC,VS
	Cissus sp.	IC,VS
	Cissus verticillata (L.) Nicolson & C.E.Jarvis	IC,VS
	Nekemias cantoniensis (Hook. & Arn.) J.Wen & Z.L.Nie	VS
	Nekemias cantoniensis (Hook. & Arn.) J.Wen & Z.L.Nie var. *leecoides* (Maxim.) F.Y.Lu	VS
	Parthenocissus tricuspidata (Siebold & Zucc.) Planch	IC,VS

Note: *: endemic species. cambia normal in production and round in conformation (RC); cambia normal in production but stem with irregular conformation (IC); axial vascular elements in segments (VS); furrowed xylem of cambium continuity (FC); furrowed xylem of cambium discontinuity (FD); dissected xylem (DX); external primary vascular cylinders (EP); external secondary vascular cylinders (ES); successive cambia (SC); intraxylary phloem (TR); interxylary phloem (TE).

Families	Scientic name	Cambial variants
	**Tetrastigma formosanum* (Hemsley) Gagnepain	IC,VS, SC
	**Tetrastigma hemsleyanum* 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 heyneana* Roemer & Schultes	IC
	Vitis heyneana Roemer & Schultes subsp. *ficifolia* (Bunge) C. L. Li	IC
	Vitis sinocinerea W. T. Wang	IC
52 families	287 species	

Note: *: endemic species. cambia normal in production and round in conformation (RC); cambia normal in production but stem with irregular conformation (IC); axial vascular elements in segments (VS); furrowed xylem of cambium continuity (FC); furrowed xylem of cambium discontinuity (FD); dissected xylem (DX); external primary vascular cylinders (EP); external secondary vascular cylinders (ES); successive cambia (SC); intraxylary phloem (TR); interxylary phloem (TE).

Table 2
Cambial variant types of lianas of different families in Taiwan

Family	RC	VS	IC	TR	FC	SC	FD	TE	TR +SC	IC +VS	EP + VS	FC + TR	FD +VS	FD +TR	FC +IC	ES +TR	TE + TR	ES + IC	IC +DX	IC +\ +.
Acanthaceae	-	-	-	-	1	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-
Actinidiaceae	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Amaranthaceae	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anacardiaceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Annonaceae	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Apocynaceae	-	-	-	14	-	-	-	-	-	-	-	3	-	-	-	1	-	-	-	-
Araliaceae	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Areacaceae	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aristolochiaceae	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Asteraceae	1	2	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-
Basellaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Bignoniaceae	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Cannabaceae	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Capparaceae	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Caprifoliaceae	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cecropiaceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Celastraceae	2	1	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Combretaceae	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Connaraceae	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Convolvulaceae	-	-	-	4	-	-	-	-	20	-	-	-	-	-	-	-	-	-	-	-
Cucurbitaceae	-	-	-	-	-	-	-	-	-	3	-	-	2	-	-	-	-	-	-	2
Elaeagnaceae	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Euphorbiaceae	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Fabaceae	24	-	4	-	3	6	-	-	-	-	-	-	-	-	-	-	-	1	1	-
Gesneriaceae	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Heliotropiaceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hernandiaceae	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Hydrangeaceae	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Lardizabalaceae	-	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Loganiaceae	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	1	-	-	-
Malpighiaceae	1	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Melastomataceae	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Menispermaceae	-	14	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Moraceae	4	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Nyctaginaceae	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-
Oleaceae	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Opiliaceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Pandanaceae	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Note: stem cambia normal in production and round in conformation (RC); stem cambia normal in production but stem with irregular conformation (IC); axial v (VS); furrowed xylem of cambium continuity (FC); furrowed xylem of cambium discontinuity (FD); dissected xylem (DX); external primary vascular cylinders (I cylinders (ES); successive cambia (SC); intraxylary phloem (TR); interxylary phloem (TE); cambium variant types in each family (Types No.), not include RC, S

Family	RC	VS	IC	TR	FC	SC	FD	TE	TR +SC	IC +VS	EP + VS	FC + TR	FD +VS	FD +TR	FC +IC	ES +TR	TE + TR	ES + IC	IC +DX	IC +V +
Passifloraceae	1	-	1	-	2	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
Phyllanthaceae	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Piperaceae	-	-	-	-	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-
Polygonaceae	-	2	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Primulaceae	-	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Ranunculaceae	-	15	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-
Rhamnaceae	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rosaceae	4	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Rubiaceae	8	-	1	-	2	-	-	-	-	2	-	-	-	-	1	-	-	-	-	-
Rutaceae	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Sabiaceae	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Schisandraceae	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Solanaceae	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vitaceae	-	3	7	-	-	-	-	-	-	8	-	-	-	-	-	-	-	-	-	4
Sum of family	25	11	11	4	10	5	3	2	1	3	1	2	2	1	1	1	1	1	1	2
Sum of species	96	51	23	21	15	10	5	3	20	13	8	4	3	2	1	1	1	1	1	6
Percentage %	33.4	17.7	8.0	7.3	5.2	3.5	1.7	1.0	7.0	4.5	2.8	1.4	1.0	0.7	0.3	0.3	0.3	0.3	0.3	2.

Note: stem cambia normal in production and round in conformation (RC); stem cambia normal in production but stem with irregular conformation (IC); axial (VS); furrowed xylem of cambium continuity (FC); furrowed xylem of cambium discontinuity (FD); dissected xylem (DX); external primary vascular cylinders (cylinders (ES); successive cambia (SC); intraxylary phloem (TR); interxylary phloem (TE); cambium variant types in each family (Types No.), not include RC, S

The cambial variants were divided into two categories, single cambial 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 dissected xylem, and are described below

1. Irregular conformation (IC): Cambia were normal in production, 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): The cambium typically exhibits regular activity in the stem until the parenchyma cells outside the phloem produce a new cambium, which in turn produces phloem that grows towards the inside and outside of the stem. It results in an irregular distribution and arrangement of the phloem. These additional secondary phloems are embedded in the secondary xylem (Isnard and Silk 2009; Angyalossy et al. 2012) and produce different shapes, including strands (Caballé, 1993), bands (Metcalfe and Chalk 1985) or umbrellas.
3. Furrowed xylem(FX): It is characterized by a regular gap between the xylem and phloem or irregular arrangements of the two. The xylem is furrowed by phloem arcs or wedges, and this trait is termed phloem arcs/wedges. The furrowed xylem has a regular cambium, forms four equidistant phloem arcs/wedges, and then develops into a multiple of four phloem wedges in Bignoniaceae (Angyalossy et al. 2012). This type can be divided into furrowed xylem of cambium continuity (FC) and the cambium discontinuity of furrowed xylem (FD). Based on the depth of the phloem arcs/wedges, this furrowed xylem of cambium continuity can be divided into shallow or deep split types (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. Dissected xylem (DX): This cambial variant type is derived from non-lignified parenchyma proliferation and is also called dispersed xylem segments. Dissected xylem, also known as fissured/blocks xylem, is more cracked than the normal xylem. The primary xylem is severed by the proliferation of phloem or parenchyma cells (Metcalfe and Chalk 1985; Carlquist 2001).

Multiple cambia, derived from the parenchyma of the cortex to generate lateral meristems, produce conjunctive tissue and vascular bundle cambium inward and the epidermis outward. Multiple cambial variants were subdivided into four types:

1. Successive cambia (SC): Successive cambia from new cambia arising through cell division in the external secondary vascular system were formed by alternating concentric rings of xylem and phloem. The xylem and phloem produced by the cambium are present in their normal positions (Metcalfe and Chalk 1985), whereas the ribbon-shaped vascular tissue is separated by a band of parenchyma or sclerenchyma (conjunctive tissue). 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 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. Intraxylary phloem (TR): Intraxylary phloem is derived from the formation of a secondary cambium between the primary xylem and the pith. The secondary cambium either produces a phloem ring that appears inside the xylem or forms two phloem arcs toward the pith (Metcalfe and Chalk 1985). This newly formed phloem is also called internal or medullary phloem.
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 into cylindrical vascular bundles 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 and Chen (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. Among the 191 species, seven cambial variants were exhibited in 128 species, and fourteen combinations of cambial variants were present in 63 species. Furthermore, of these 191 species, 51 had axial vascular elements in segments, e.g., *Pericampylus formosanus* (Fig. 1A), 23 species had irregular conformation, e.g., *Jasminum lanceolarium* (Fig. 1B), 21 species had intraxylary phloem, e.g., *Melodinus suaveolens* (Fig. 1C), 15 species had furrowed xylem of cambium continuity, e.g., *Morinda parvifolia* (Fig. 1D), 10 species had successive cambia, e.g., *Mucuna macrocarpa* (Fig. 1E), five species had furrowed xylem of cambium discontinuity, e.g., *Pyrostegia venusta* (Fig. 1F), and three species had interxylary phloem, e.g., *Thunbergia grandiflora* (Fig. 2A).

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 intraxylary phloem combined with successive cambia, e.g., *Merremia gemella* (Fig. 2B), 13 species with irregular conformation combined with axial vascular elements in segments, e.g., *Tetrastigma obtectum* 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 intraxylary phloem combined with furrowed xylem of cambium continuity, e.g., *Gymnema sylvestre* (Fig. 2E), three 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 intraxylary phloem combined with furrowed xylem of cambium discontinuity, e.g., *Gardneria multiflora* (Fig. 3A), one species with furrowed xylem of cambium continuity combined with irregular conformation, e.g., *Coptosapelta diffusa* (Fig. 3B), one species having external secondary vascular cylinders combined with intraxylary phloem, e.g., *Trachelospermum gracilipes* (Fig. 3C), one species possessing an interxylary phloem combined with intraxylary 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 dissected xylem combined with irregular conformation, e.g., *Bauhinia championii* (Fig. 3F).

The three cambial variants combination included: five 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 with axial vascular elements in segments combined with intraxylary phloem and successive cambia, e.g., *Anredera cordifolia* (Fig. 4B); one species having dissected xylem combined with intraxylary phloem with irregular conformation, e.g., *Dimetia hedyotidea* (Fig. 4D).

Axial vascular elements in segments types and intraxylary phloem appeared in six and seven combination types, respectively. Therefore, these two variant types are always combined with many variants, so they are more helpful to the lianas identification. Fourteen combinations types of cambial variants were found, indicating the presence of multiple cambial variants in Taiwan lianas. 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. Among them, Fabaceae and Rubiaceae had five cambial variants, the highest amongst the other families. While Vitaceae had four variants, other families like Apocynaceae, Asteraceae, Celastraceae, Cucurbitaceae, Passifloraceae, and Polygonaceae, had only three types (Table 3).

Table 3

List of orders and families of Taiwan lianas that possess the cambial variants

Orders	Families	Cambial variants (this study)	Angyalossy et al. (2015)
Asterales	Asteraceae	VS, FC, FD	VS, FX
Apiales	Araliaceae	RC	-
Arecales	Areacaceae	RC	-
Austrobaileyales	Schisandraceae	RC	-
Boraginales	Heliotropiaceae	RC	-
Brassicales	Capparaceae	RC	-
Caryophyllales	Amaranthaceae	SC	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 + ES + SC, FD + VS	SC, TE, VS
Dipsacales	Caprifoliaceae	RC	-
Ericales	Actinidiaceae	RC	-
	Primulaceae	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	-
Magnoliales	Annonaceae	RC	-
Malpighiales	Euphorbiaceae	IC	ES
	Malpighiaceae	FC	FX, DX, SC, TE, IC
	Passifloraceae	FD, 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	Menispermaceae	VS	SC, VS, IC, TR
	Ranunculaceae	VS, VS + FD	VS

Note: cambial normal in production and stem is round in conformation (RC); stem with irregular conformation (IC); axial vascular elements in segments (VS); furrowed xylem of cambium continuity (FC); furrowed xylem of cambium discontinuity (FD); dissected xylem (DX); external primary vascular cylinders (EP); external secondary vascular cylinders (ES); successive cambia (SC); intraxylary phloem (TR); interxylary phloem (TE).

Orders	Families	Cambial variants (this study)	Angyalossy et al. (2015)
	Lardizabalaceae	VS	-
Rosales	Cannabaceae	IC	-
	Cecropiaceae	RC	-
	Elaeagnaceae	RC	-
	Rhamnaceae	RC	-
	Rosaceae	RC	-
	Moraceae	IC	IC
Santalales	Opiliaceae	RC	-
Solanales	Convolvulaceae	TR, TR + SC	SC, TE, FX, DX, TR
	Solanaceae	TR	-
Vitales	Vitaceae	IC, VS, IC + VS + SC, VS + IC	VS, IC, SC, DX
18 orders	49 families		

Note: cambial normal in production and stem is round in conformation (RC); stem with irregular conformation (IC); axial vascular elements in segments (VS); furrowed xylem of cambium continuity (FC); furrowed xylem of cambium discontinuity (FD); dissected xylem (DX); external primary vascular cylinders (EP); external secondary vascular cylinders (ES); successive cambia (SC); intraxylary phloem (TR); interxylary phloem (TE).

Ten species belonging to Amaranthaceae, Connaraceae, Fabaceae, Nyctaginaceae, and Polygonaceae displayed successive cambia. In Fabaceae family, *Mucuna macrocarpa, Pueraria lobata* subsp. *thomsonii*, and *Pueraria montana* (Fig. 21), have 3–4 layers of regular concentric rings. *Entada koshunensis, 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 et al. 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 baselloides* had axial vascular elements in segments in smaller stem and 2–3 layers of successive cambia in a wider stem (Fig. 4B).

In this study, two species of Bignoniaceae had furrowed xylem of cambium discontinuity. Furrowed xylem of cambium discontinuity had two patterns. One was wedge-shaped phloem with 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) 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.

The diagnostic feature of the bicollateral vascular bundle (Cucurbitaceae) had outer and inner phloem at both ends. 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 intervascular 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 discontinuity formed by shallowly phloem wedges (Rajput and Baijnath 2016). The other diagnostic feature of *P. edulis* was the presence of five pairs of rays distributed equidistantly with secondary rays. The cambial variant of four *Passiflora* species in this study also exhibited furrowed xylem of cambium continuity or discontinuity, but the cambia of *Passiflora laurifolia* had regular secondary growth and the stem was round in conformation, *Passiflora quadrangularis* was irregular conformation.

The cambial variants of Rubiaceae exhibiting furrowed or lobed xylem were reported in *Atractogyne* and *Chiococca* (Jansen et al. 2002.). In this study, *Coptosapelta diffusa, Morinda parvifolia*, and *Morinda umbellata* also possessed this cambial variant. Four genera, *Coptosapelta, Mussaenda, Randia*, and *Uncaria* (Table 1), show lignified parenchyma, and three genera, *Dimetia, Morinda, Paederia*, showed unlignified parenchyma (lianescent habit), and aggregate rays were found only in *Paederia* as reported by 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. Since the stem is larger (about 3.5 cm in size), the second layer of vascular bundles developed near the cortex and formed the successive cambia (Fig. 4F). Pace et al. (2018) indicated *Tetrastigma retinervum* and *Tetrastigma voinierianum* (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 observed 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 species of the genus *Tetrastigma* might have a combination of axial vascular elements in segments with successive cambia, and the species without successive cambia might be related to the stem size.

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. Cambium 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, eight orders (Table 3) were added in this study. The cambial variants of Sapindales had a compound stem (Angyalossy et al. 2015), and this type was not found in Taiwan Sapindaceae.

Three combination types of cambial variants in Cucurbitales were added. The cambial variants of interxylary and intraxylary phloem in Fabales were not found, and an external secondary vascular cylinder was added. Gentianales consisted of three families with diverse cambial variants and exhibited combinations of cambial variants; only successive cambia type was not found. Malpighiales and Myrtales had multiple types of cambial variants; however, only furrowed xylem and intraxylary phloem were found. Piperales had a combination of external primary vascular cylinders with axial vascular elements in segments, and few species of the stem had irregular conformation. Ranunculales only had one type of axial vascular element in the segment, but successive cambia, irregular conformation, and intraxylary phloem were not found; furrowed xylem of cambium discontinuity was added. Diverse cambial variants were reported in Solanales; however, only intraxylary phloem and successive cambia were found in the Taiwanese specimens. In Vitales, only dissected xylem was not found in Taiwan. All the additional information presented in our study would be helpful for future researchers.

The xylem of rosids and asterids had a furrowed xylem. Therefore, the phylogenetic relationship between rosids and asterids is relatively stronger than that of other families (Angyalossy et al. 2015). Furrowed xylem was one of the important characteristics for identifying woody vines. The differences in cambial variants types between the orders should be related to the dominant families in the survey regions. The cambial variants we added will be available for academic study. Accurate relationships among the order and families of lianas may be established with additional information on liana cambial variants.

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. Therefore, wider and freshly cut stems in each liana should be investigated further.

Conclusion

This study explored the species diversity and the cambial variants of the stem cross-section of Taiwan lianas. The results showed that there were about 553 species of climbing plants in Taiwan, including 337 lianas and 216 herbaceous vines. Approximately seven cambial variants and fourteen 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. For a single family, five cambial variants types of Fabaceae and Rubiaceae are the highest, followed by Vitaceae with four types. Most species in Apocynaceae, Convolvulaceae, Menispermaceae, and Ranunculaceae had the same cambial variant in each family, such as intraxylary phloem, combination of intraxylary phloem with successive cambia, and axial vascular element in segments, respectively, and could be used as diagnostic characteristics of that family. Comparing the orders/families from the previous data, we added data on the cambium secondary growth of 52 lianas, including 36 lianas with regular secondary growth with rounded stem and 16 lianas with different cambial variants. Approximately 50 species are still needed to investigate all the Taiwan lianas. Studying the cambium 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 allow the identification of many individual plants to families of genera without leaves or flowers.

Declarations

Authors' contributions

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

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.

Competing interests

The authors declare that they have no competing interests.

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Figures

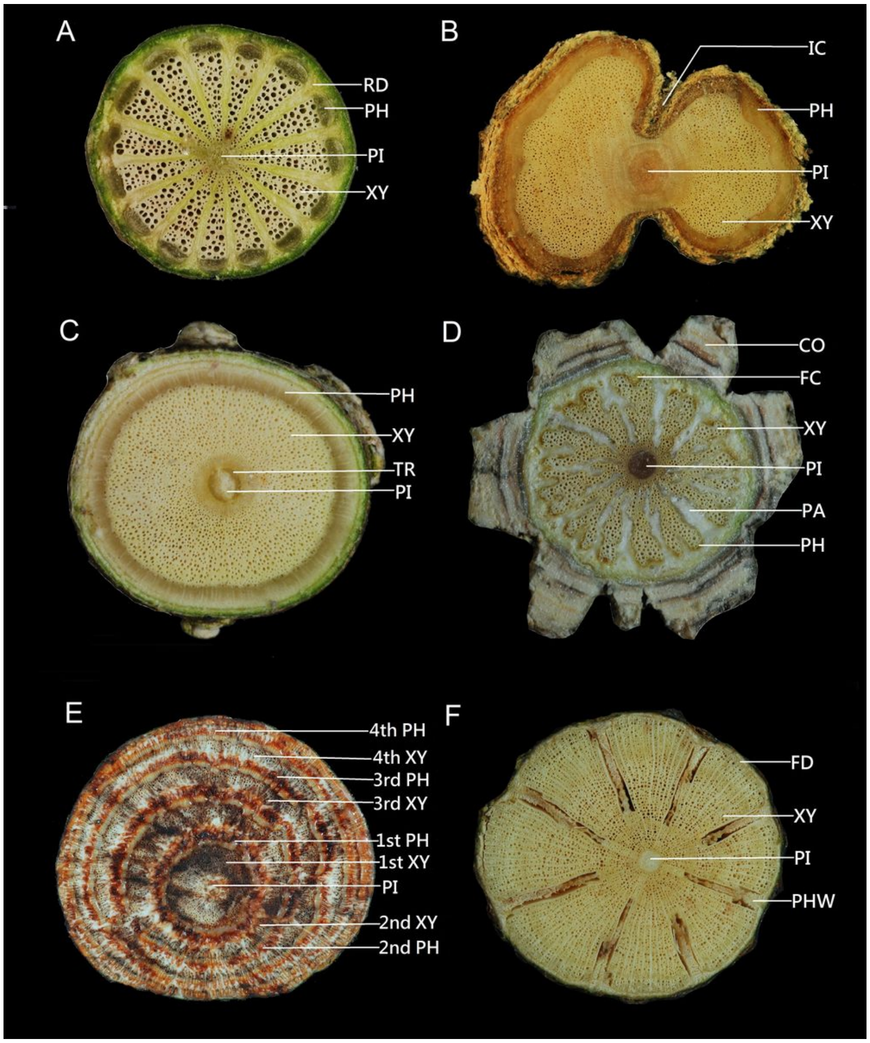

Figure 1

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 suaveolens*. D. Furrowed xylem of cambium continuity: *Morinda parvifolia*. E. successive cambia: *Mucuna macrocarpa*. F. furrowed xylem of cambium discontinuity: *Pyrostegia venusta*. Abbreviations: 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 XP: second xylem, 3rd XP: 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.

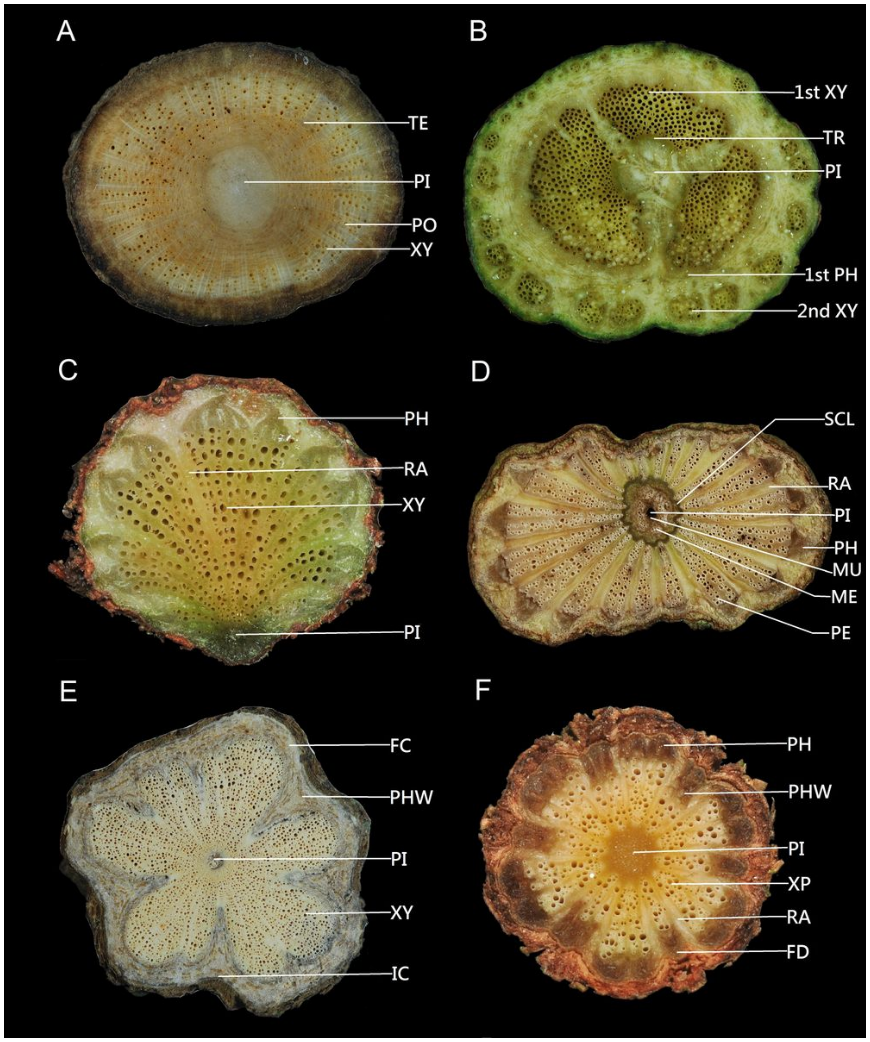

Figure 2

Single cambial variant or combination of two cambial variants of stem cross section. A. interxylary phloem: *Thunbergia grandiflora*. B. intraxylary phloem combined with successive cambia: *Merremia tuberosa*. C. irregular conformation combined with axial vascular elements in segments: *Tetrastigma obtectum* var. *glabrum.* D. external primary vascular cylinders combined with axial vascular elements in segments: *Piper kadsura*. E. furrowed xylem of cambium continuity combined with intraxylary phloem: *Gymnema sylvestre*. F. furrowed xylem of cambium discontinuity combined with axial vascular elements in segments: *Clematis gouriana* subsp. *lishanensis*. Abbreviations: PI: pith, PO: pore,TE: interxylary phloem, TR: intraxylary phloem, 1st XY: first xylem, 2nd XP: 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, PHW: phloem wedges-like, IC: irregular conformation.

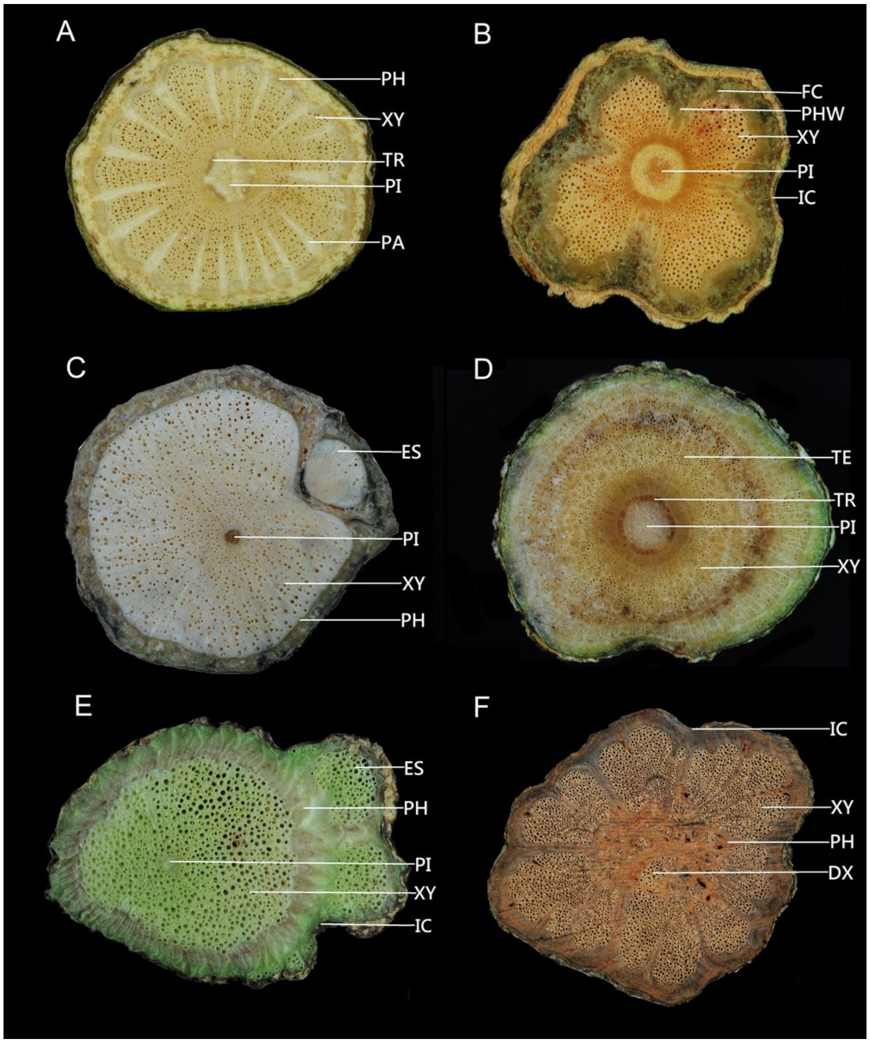

Figure 3

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. interxylary phloem combined with intraxylary phloem: *Strychnos cathayensis*. E. external secondary vascular cylinders combined with irregular conformation: *Lablab purpureus*. F. dissected xylem combined with irregular conformation: *Bauhinia championii*. Abbreviations: PI: pith, FC: furrowed xylem of cambium continuity, PHW: phloem wedges-like, IC: irregular conformation, PA: parenchyma, DX: dissected xylem, TR: intraxylary phloem, ES: external secondary vascular cylinders, XY: xylem, PH: phloem, DX: dissected xylem, TE: interxylary phloem.

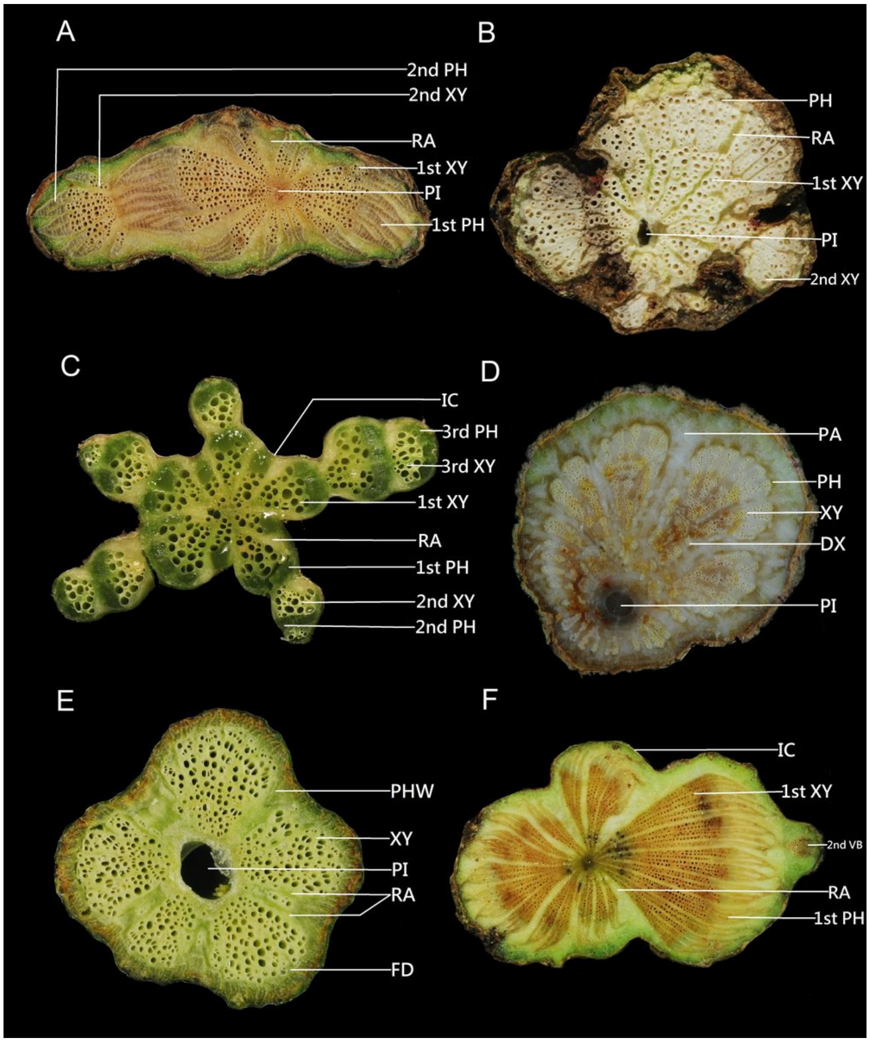

Figure 4

Combination of three cambial variants or single cambial variant of stem cross section. A. successive cambia combined with axial vascular elements in segments and irregular conformation: *Tetrastigma formosanum.* B. axial vascular elements in segments combined with intraxylary phloem and successive cambia: *Anredera cordifolia.* C. external secondary vascular cylinders combined with axial vascular elements in segments and successive cambia: *Momordica charantia* var. *abbreviata.* D. dissected xylem combined with intraxylary phloem and irregular conformation: *Dinetia hedyotidea.* E. furrowed xylem of cambium discontinuity: *Passiflora edulis.* F. irregular in conformation combined with axial vascular elements in segments and successive cambia: *Cayratia corniculata.* Abbreviations: PI: pith, FD: furrowed xylem of cambium discontinuity, RA: ray, PHW: phloem wedges-like, 1st XY: first xylem, 2nd XY: second xylem, 3rd XY: third xylem, 1st PH: first phloem: 2nd PH: second phloem: 3rd PH: third phloem, 2nd VB: second vascular bundle, IC: irregular conformation, PA: parenchyma, DX: dissected xylem.