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Structure and development of the secondary xylem in ten species of *Passiflora* from Taiwan

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ABSTRACT: Studies on secondary growth of the genus *Passiflora* (Passifloraceae) in Taiwan are scarce. This study aimed to investigate the patterns of cambial variants in 10 *Passiflora* species. Stem diameters were measured to determine structural and developmental differences in the secondary xylem of *Passiflora* species. Cambial variants observed included irregular conformations, furrowed xylem, external secondary vascular cylinders, and successive cambia. An external secondary vascular cylinder was evaluated to distinguish *Passiflora coccinea* from *Passiflora vitifolia. Passiflora edulis* stems were thick and cylindrical, with two rings of successive cambia. *Passiflora suberosa* subsp. *litoralis* had fissured xylems with shallow phloem wedges in small stems and exhibited circular and cylindrical structures with more secondary rays in large stems. *Passiflora laurifolia* and *Passiflora quadrangularis* had secretory tissues around the cortex, where the stem of the former was regular in conformation, and that of the latter was four-ridged. Among the species studied, *P. quadrangularis* exhibited aggregated rays in stem xylem cylinders. All investigated species had a diffuse-porous secondary xylem and vasicentric paratracheal parenchyma, except for *P. suberosa litoralis,* which had semi-ring-porous and indistinct growing rings. The cambial variants of the genus *Passiflora* described in the present study could increase the significances of this study in relation to ecological and functional contexts and it will provide the primary information for future morphological studies.

KEY WORDS: Aggregate rays, external secondary vascular cylinder, interfascicular rays, Passifloraceae, phloem wedge.

INTRODUCTION

The family Passifloraceae comprises approximately 16 genera and about 600 species, which are primarily distributed in the tropics and subtropics, particularly in the New World tropics (Wang *et al.,* 2007). In Taiwan, eight species of *Passiflora* have been reported by earlier researchers (Kao, 1993; Chen et al., 2022). All these members are either lianas or herbaceous vines. Ayensu and Stern (1964) studied the systematic anatomy and ontogeny of the stems of 28 *Passiflora* species. Rajput and Baijnath (2016) reported the stem anatomy of six *Passiflora viz*: *P. edulis* Sims *f. edulis, P. edulis* Sims *f. flavicarpa* O.Deg., *P. foetida* L. var. *ellisonii* Vanderplank, *P. suberosa* L. subsp. *litoralis* (Kunth) Port.-Utl. ex M.A. M. Azevedo, Baumgratz and Gonç.-Estev., *P. subpeltata* Ortega, and *P. vesicaria* L. var. *vesicaria.* Secondary cambial growth may form irregular structures or cambial variants. Ayensu and Stern (1964) defined four keys for characterizing the stem transverse section of the mature vascular cylinder of the genus *Passiflora*: normal type in *P. laurifolia* L., included phloem type in *P. auriculata* H.B.K., and interrupted type in *P. coccinea* Aubl., *P. edulis* f. *edulis, P. foetida* var. *ellisonii*, and *Passiflora vitifolia* Kunth, and a dispersed type in *P. multiflora* L. The genus *Passiflora* has a cylindrical to deeply lobed stem with a lobed xylem (Acevedo-Rodriguez, 2005). *P. edulis* and *P. vesicaria* var. *vesicaria* had a furrowed xylem with phloem wedges, similar to those of Bignoniaceae. However, phloem wedges in Bignoniaceae are formed through alterations in cell division activity of the vascular cambium and the pattern of secondary xylem and phloem differentiation (Pace et al., 2009).

The climbing habits of lianas differ from their self-supporting habits in various ways. The most noticeable features are the mechanical properties (Rowe and Speck, 1996; Isnard *et al*., 2003, Isnard and Silk, 2009) and anatomical alterations in lignified and non-lignified tissues. A previous study investigated the *P. edulis* secondary growth and observed the presence of wide vessels. As the plants shifted to climbing habits, structure of the secondary xylem changed significantly and it was characterized by the presence of wide vessels. *P. edulis* had five pairs of interfascicular rays (Rajput and Baijnath, 2016) that made the xylem cylinder separate into segments equidistantly; however, the pairs of wider rays of *P. vesicaria* var. *vesicaria* were unevenly distributed. *P. foetida* var. *ellisonii*, *P. suberosa* subsp. *litoralis,* and *P. vesicaria* had phloem wedges owing to the unequal deposition of the secondary xylem by small segments of cambium in the cambial cylinder. Similarly, Angyalossy *et al*. (2015) also demonstrated that Malpighiaceae had phloem wedges and successive cambia, while Yang *et al*. (2022) reported a continuity of the cambium in phloem wedges external to the furrowed xylem.

Table 1. Voucher specimens of the investigated ***Passiflora*** species.

Species	Collectors	Herbarium /voucher no.	Collection information
Passiflora biflora Lam.	P.H. Chen & A.C. Chung	TAIF/1309	Daxiangshan, Xindian District, New Taipei City
Passiflora coccinea Aubl.	S.Z. Yang	PPI/81374	Shiwai Garden, Niaosong District, Kaohsiung city
-	S.M. Ku	PPI/54853	Wunluan, Wugoushuei, Pingtung County
-	C.H. Tseng	PPI/53128	Futian, Neipu Township, Pingtung County
Passiflora edulis Sims	S.Z. Yang	PPI/28871	Tengchih, Kaohsiung City
Passiflora foetida L.*foetida*	S.Z. Yang	PPI/617	Baoli, Pingtung County
Passiflora laurifolia L.	P.H. Chen	PPI/1083	Shuanghsi, Kaohsiung City
Passiflora ligularis Juss.	P.H. Chen & A.C. Chung	PPI/1905	Fenqihu, Zhuqi, Chiayi County
Passiflora quadrangularis L.	P.H. Chen	PPI/880	Taipo, Chiayi County
Passiflora suberosa L. subsp. *litoralis* (Kunth) Port.-Utl. ex M.A.M.Azevedo, Baumgratz & Gonç.-Estev.	S.Z. Yang	PPI/1069	Xinhua, Tainan County
Passiflora vesicaria L. var. *vesicaria*	P.H. Chen	PPI/1569	Hengchun, Pingtung County
Passiflora vitifolia Kunth	S.Z. Yang	PPI/81373	Pomelo garden, Linluo Township, Pingtung County
-	S.Z. Yang	PPI/59033	Chinchu elementary school, Neimen Township, Kaohsiung City

The dendrogram of Passifloraceae obtained from the qualitative data revealed distinct groupings among the distant accessions, including *P. coccinea* (subgenus *Passiflora*/supersection *Passiflora*) and *P. vitifolia* (subgenus *Passiflora*/supersection *Distephana*), were distinct from the other subgenera. *P. vitifolia* has three-lobed leaves, a tubular corona, and conspicuous nectary glands on the leaf sinuses and bracts (Ocampo and Coppens d'Eeckenbrugge, 2017). *P. foetida* and *P. vesicaria* (subgenus *Passiflora*/section *Dysosmia*) have pinnatisect bracts (Ocampo and Coppens d'Eeckenbrugge, 2017).

In this study, we aimed to investigate the cambial variants, and elucidate the anatomical variations in the secondary growth of ten species of *Passiflora* growing in Taiwan.

MATERIALS AND METHODS

In this study, 10 *Passiflora* species were observed: *P. biflora* Lam., *P. coccinea* Aubl., *P. edulis*, *P. foetida* var. *foetida*, *P. laurifolia, P. ligularis* Jus., *P. quadrangularis* L., *P. suberosa* subsp. *litoralis*, *Passiflora vesicaria* var. *vesicaria,* and *P. vitifolia* (Table 1). *P. ligularis* is a recently naturalized species in Taiwan (Chen *et al.*, 2022), whereas *P. foetida* var. *taininiana* was observed to be identical to *P. foetida* var. *foetida* (Govaerts *et al.*, 2021). *P. biflora* climbs a larger tree along the roadside; *P. coccinea* is planted in a private garden covers the canopy layer; the fruits of *P. edulis* are edible and easy to collect; *P. foetida* var. *foetida*, *P. quadrangularis*, *P. suberosa* subsp. *litoralis,* and *P. vesicaria* always grow along roadsides or climbing hedges, widely distributed in Taiwan lowlands; *P. laurifolia* just grows in Shuangxi Botanical Garden; only a few individuals of *P. ligularis* are found growing in the field; while *P. vitifolia* is collected in a private pomelo orchard.

Thick stems with barks were collected from the field and stored in a collection bag to keep the materials fresh and retain humidity. Plants with various stem diameters were collected to assess the positions of various vascular bundle tissues and to observe the characteristics of secondary growth. One or three samples with defined and easy-to-observe cambial variants were selected per species for imaging and scoring of morphological characteristics. The morphological features of the cross sections of the stems of the different species under investigation were used to construct a comparative table.

In the laboratory, fresh materials were cut into approximately 5-cm pieces, and a freehand cross-section of each stem was made using a razor blade. Stem cross sections were imaged using a Nikon D7100 SLR digital camera with a 1:1 lens (Lens AF Micro Nikon 60 mm 1:2.8D; Nikon Corporation, Tokyo, Japan). Cambial characteristics were depicted and described. Quantitative anatomical traits, such as stem diameter, cork thickness, and mean ray width, were determined using ImageJ software (National Institute of Health, Bethesda, MD, USA [Ferreira and Rasband, 2011]). All specimens were oven dried at 60 °C for 4–5 days and stored at -20 °C for 3–4 days to keep insects prevention. Subsequently, the specimen data included collectors, voucher number, and collection location were deposited in the herbarium of Provincial Pingtung Institute at the National Pingtung University of Science and Technology, Pingtung, Taiwan, and the herbarium of Taiwan Forest Research Institute at the Ministry of Agriculture for subsequent identification. The nomenclature used in this study followed that of the Flora of Taiwan, Volume III (Kao, 1993).

The following stem features were investigated for each species: habit (including liana and vine; lianas are woody climbers, and vines are herbaceous climbing plants), stem diameter and shape, cork, cortex, ducts, cambial variant types, shallow or deep phloem wedge, vessels arrangement, vessel minimum and maximum diameters, mean vessel diameter, interfascicular rays, ray numbers, axial parenchyma, ray minimum and maximum width, mean ray width, secondary and wider rays, ray dilatations, pith cavities, or crushed. The bark characteristics (Angyalossy *et al.* 2016) and stem cross-sections in this study were described considering the definitions by Angyalossy *et al.* (2015) and Yang *et al.* (2021, 2022, and 2023). Terms used for ray and type of axial parenchyma are adopted from Carlquist (2001) and the International Association of Wood Anatomists Committee on Nomenclature (1964).

RESULTS

***Passiflora* species stem characterization**

1. ***P. biflora***: vining shrubs; stem cross-section octagonal when stem diameter was approximately 2.5 mm, the xylem cylinder was divided by rays into six segments, and phloem fibers were observed (Fig. 1A). The thickness of the cortexes ranged from 331–800 µm, with an average of 609 µm. The cambial variant was a furrowed xylem with shallow phloem wedges when stem diameter was approximately 9.4 mm. The vessels were diffuse-porous, tiny, with solitary and few multiple pores, with diameters ranging from 8–77 µm and an average of 34 µm. The axial parenchyma was vasicentric paratracheal. The rays were numerous with widths ranging from 70 to 221 µm and an average of 114 µm when the stem diameter was approximately 9.4 mm and cylindrical (Fig. 1B). Numerous secondary rays, wider ray tissue within the xylem, and ray dilatation were observed, and the pith was crushed or flecked.

2. ***P. coccinea***: vine, the stem cross-section was cylindrical when the stem diameter was approximately 12 mm, and the thickness of the cortexes ranged from 1,270–2,070 µm, with an average of 1,530 µm. The cambial variant was a furrowed xylem with shallow phloem wedges (Fig. 1C) and an external secondary vascular cylinder. Vascular bundles were observed near the cortex (Fig. 1D) when the stem diameter was approximately 16 mm. Secondary rays were numerous. The vessels were diffuse-porous, tiny, with solitary and few multiple pores, with diameters ranging from 24–144 µm and an average of 78 µm. The axial parenchyma was vasicentric paratracheal. The rays were numerous, ranging from 87–164 µm and an average of 127 µmin width with distinct cylindrical pith.

3. ***P. edulis***: liana, the stem cross-section was pentagonal with a green epidermis when the stem diameter was approximately 14 mm, and the stem was cylindrical with a diameter of approximately 32 mm. The thickness of the cortexes ranged from,520–3,150 µm, with an average of 2,360 µm. The phloem fibers were flame-like. The cambial variant had a furrowed xylem with deep phloem wedges when the stem diameter was approximately 14 mm. When the stem diameter was approximately 32 mm (Fig. 1F), the stem was cylindrical, and the cambial variant consisted of two layers of successive cambia. The vessels were diffuse-porous, with solitary and few multiple pores, rounded, and diameters ranging from 43–330 µm with an average of 153 µm. The axial parenchyma was vasicentric paratracheal. The xylem cylinder was divided into segments by five pairs of interfascicular rays distributed equidistantly, each pair was separated by a narrow plate of axial elements (Fig. 1E). The width of the rays ranged from 660 to 1,810 µm, with an average of 980 µm, and secondary rays were numerous. The pith had a suborbicular cavity.

4. ***P. foetida* var. *foetida***: vine, the stem cross-section was pentagonal. Phloem fiber bundles were ring-like, presented near the epidermis when the stem diameter was approximately 3 mm (Fig. 2A), and black. The xylem cylinder was separated by four to five rays. The thickness of the cortexes ranged from 201–599 µm, with an average of 418 µm when the stem diameter was approximately 4.7 mm (Fig. 2B). The cambial variant had the furrowed xylem of the shallow phloem wedges. The vessels were diffuse-porous, with solitary pores, rounded, and with diameters ranging from 21–129 µm and an average of 64 µm. The axial parenchyma was vasicentric paratracheal. The ray width ranged from 403–493 µm, with an average of 458 µm, and was evenly or regularly distributed, and possessed rounded pith.

5. ***P. laurifolia***: liana, the stem cross-section was cylindrical when the stem diameters ranged from 14–16 mm. Ducts were distributed along the cortex, and phloem fibers were flame-like (Fig. 2C). The thickness of the cortexes ranged from 1,080–1,940 µm, averaging 1,470 µm. The cambial variant was a furrowed xylem with shallow phloem wedges. The vessels were diffuse-porous, with solitary and multiple pores, and diameters ranging from 86–234 µm with an average of 148 µm. The axial parenchyma was vasicentric paratracheal. The wide rays within the xylem were abundant; among them, five were wide, with widths ranging from 200–1,104 µm and an average of 550 µm. Furthermore, the rays had an irregular distribution, secondary rays were numerous, and possessed rounded pith.

6. ***P. ligularis***: vine; the stem cross-section was cylindrical when the stem was approximately 13 mm in diameter and wavy in outline with inner xylem near the pith (shrub type) and external xylem near the periderm (liana type). The cortical thickness ranged from 2–2.5 mm with conspicuous ducts. The cambial variant was a furrowed xylem with deep phloem wedges. The vessel was diffuse-porous, with solitary and few multiple pores, and the diameters ranged from 56–219 µm. The axial parenchyma was vasicentric paratracheal. The xylem cylinder was divided into equidistantly distributed segments by five pairs of interfascicular rays with an equidistance ranging from 56–300 µm (Fig. 2D). The pith was cylindrical, and the cavity was 2.4 mm in diameter.

7. ***P. quadrangularis***: vine, the stem cross-section

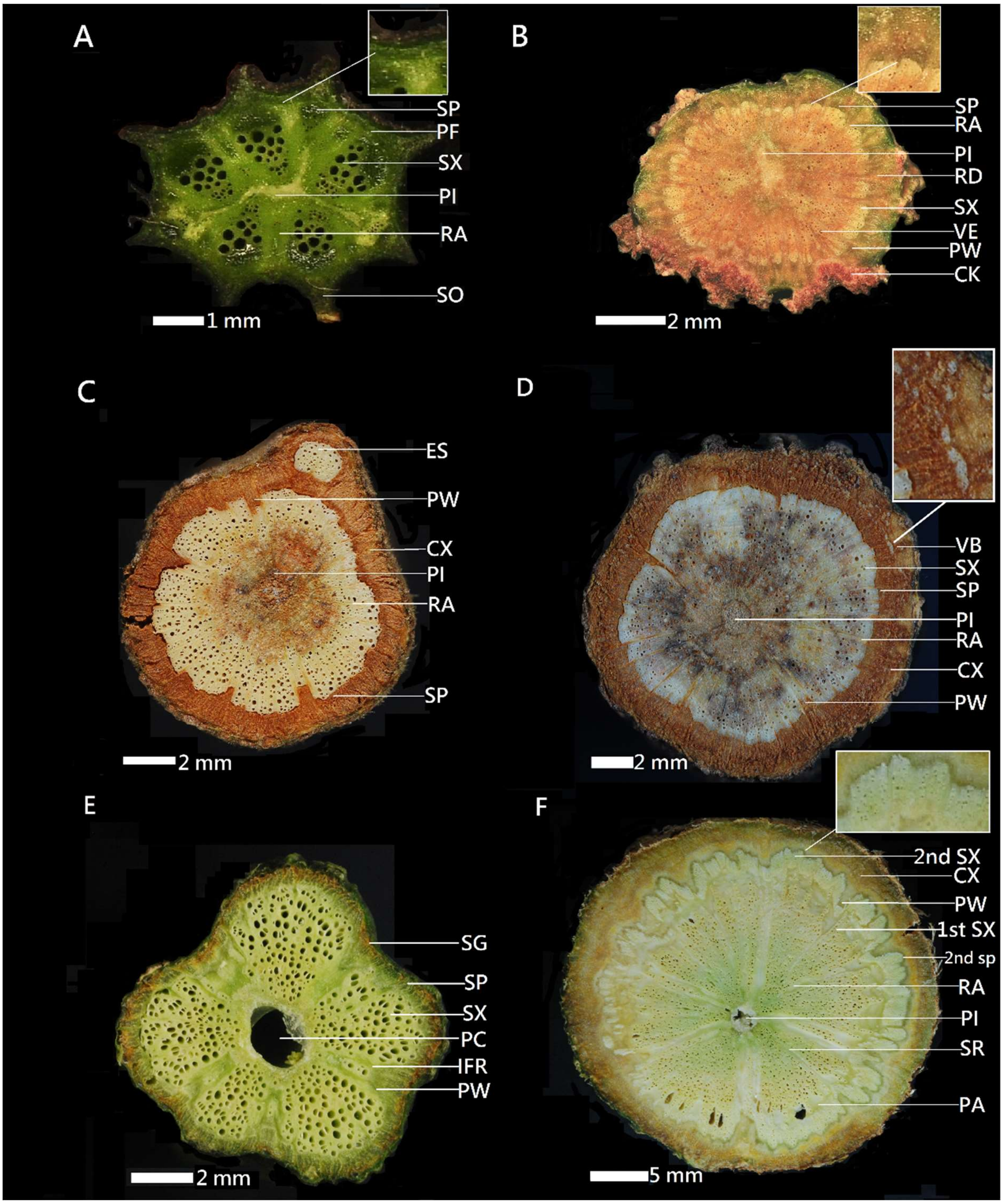

Fig. 1. A. Relatively young stem of ***Passiflora biflora***: stem cross-section octagonal, xylem cylinder divided into six segments while central portion showing crushed pith; phloem fibers (enlarged part). **B.** ***P. biflora***: mature stem with thin cork and phloem wedges (enlarged part), ray dilatation, and numerous secondary rays. A and B sampled from the same individual. **C.** ***Passiflora coccinea***: stem cross-section with an external secondary vascular cylinder, and phloem wedges. Samples collected in Neipu Township, Pingtung County. **D.** ***P. coccinea***: stem cross-section with vascular bundles (enlarged part) and phloem wedges. Samples collected in Shiwai Garden, Niaosong District, Kaohsiung City. **E.** ***Passiflora edulis***: stem grooved, phloem fiber flamelike, five pairs of interfascicular rays equidistantly, deep phloem wedges, wider rays, and pith cavity. **F.** ***P. edulis***: stem diameter with two layers of successive cambia (enlarged part). E and F samples collected from the same individual in Tengchih, Kaohsiung City. Abbreviations: PW, phloem wedges; RA, rays; RD, ray dilatation; SR, secondary rays; PI, pith; PF, phloem fibers; IFR, interfascicular rays; 1st SX, first secondary xylem; 2nd SX, second secondary xylem; 2nd SP, second secondary phloem. PC, pith cavity; SO, stem octagon; CK, cork; ES, external secondary vascular cylinder. CX, cortex; SG. stem grooved; VE. vessel; VB, vascular bundle; PA, parenchyma proliferation.

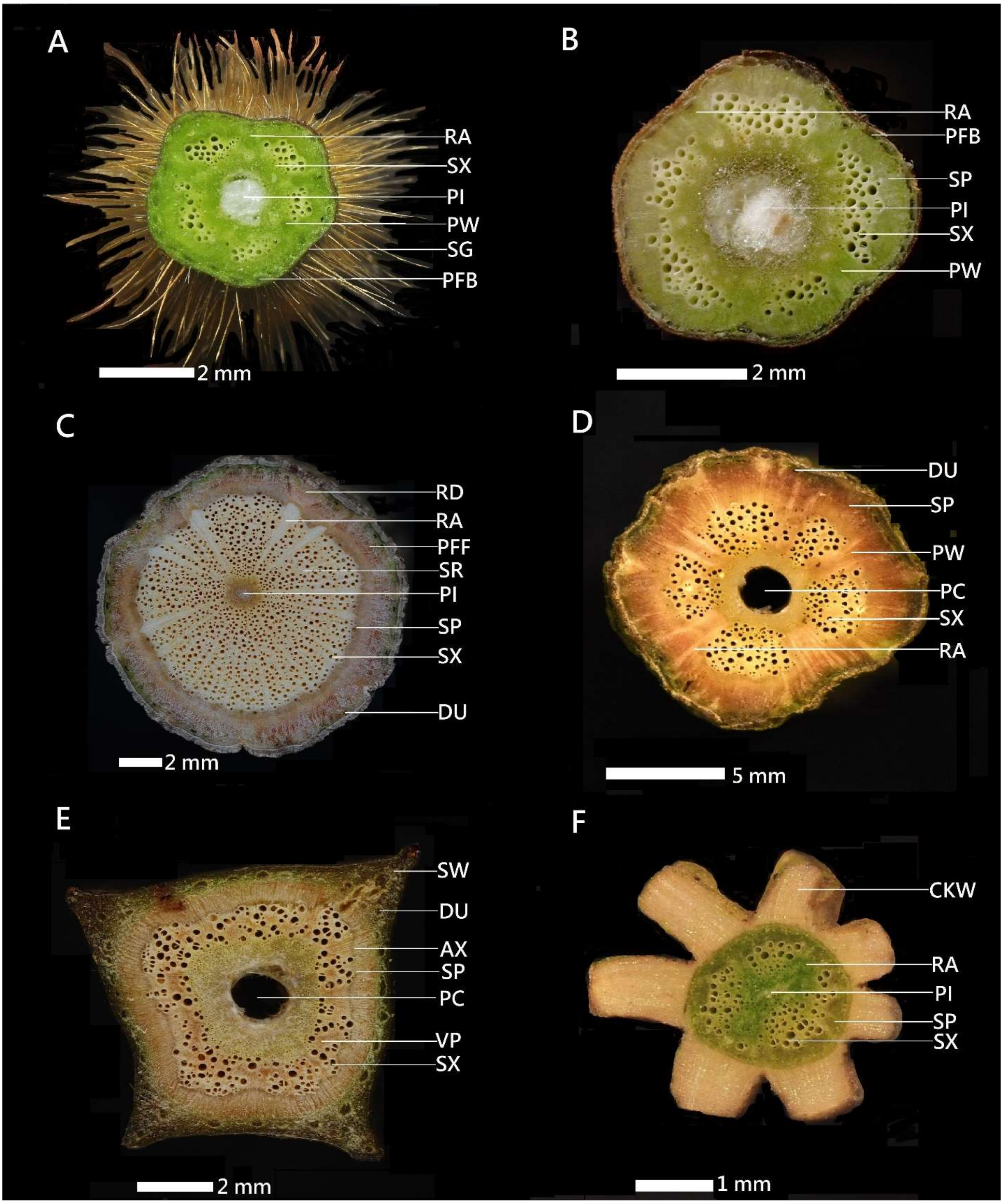

Fig. 2. A. *Passiflora foetida* var. *foetida*: stem cross-section pentagonal, phloem fibers bundles near the epidermis, and xylem cylinder separated into 4–5 segments. Samples collected in Longjing District, Taichung. **B. *P. foetida* var. *foetida*,** the epidermis glabrous, phloem wedges formed. Samples collected in Wanan, Pingtung County. **C. *Passiflora laurifolia***: cortex thick with ducts, phloem fibers flame-like, rays widened centrifugally and dilated. **D. *Passiflora ligularis***: phloem wedges formed, and with pith cavity. **E. *Passiflora quadrangularis***: stem four-winged, cortex thick with ducts, pith cavity, and rays aggregated. **F. *Passiflora suberosa* subsp. *litoralis***: cork-winged-like, thick, and with three xylem segments divided by three rays. Abbreviations: CKW, cork fissured and winged-like; RA, rays; RD, ray dilatation; SR, secondary rays; PI, pith; PFB, phloem fiber bundles; PFF, phloem fibers flame-like; SP, secondary phloem; SX, secondary xylem; DU, duct; PC, pith cavity; SW, stem-winged; PW, phloem wedge; VP, vasicentric paratracheal; AX, aggregated xylem.

was square and four-winged, the thickness of the cortexes ranged between 740–1,350 µm thick, with an average of 1,000 µm, and larger secretory tissues were observed around the cortex. The cambial variants had a furrowed xylem of shallow phloem wedges. The vessels were diffuse-porous, mainly solitary with few multiple pores, rounded, with diameters ranging from 34–286 µm and an average of 145 µm. The axial parenchyma was vasicentric paratracheal. The rays were numerous, thin, and aggregated (Fig. 2E). The pith had a cavity.

8. ***P. suberosa* subsp. *litoralis***: vine, the stem cross-section was cylindrical when the stem diameter was approximately 2–3 mm, corks were thick, fissured and winged-like, and the thickness of the cortexes ranged from 195–942 µm, with an average of 661 µm (Figs 2F and 3A). The cambial variant was a furrowed xylem with shallow phloem wedges. The vessels were semi-ring-porous, with solitary and multiple pores, and diameters ranging from 20–80 µm and an average of 51 µm. The axial parenchyma was scanty, vasicentric paratracheal. The phloem fibers were triangular, flame-like, and black. Three segments of the xylem were separated by rays, and three to four wider rays developed in each xylem segment, giving totals ranging from 11–13 per xylem (Fig. 3B). Furthermore ray dilatation was observed. The ray width ranged from 53–213 µm, with an average of 130 µm. Secondary rays ranged from 10–12 mm long when the stem diameter was approximately 10 mm. The pith was flecked with a rounded, eccentric, and green color.

9. ***P. vesicaria* var. *vesicaria***: vine, the cross-section of the stem was pentagonal (Fig. 3C), the thickness of the cortexes ranged from 130–620 µm, with an average of 450 µm, and a cylinder of phloem fiber bundles was arranged in the cortex. The cambial variant was a furrowed xylem with shallow phloem wedges when the stem diameter was approximately 5 mm (Fig. 3D). The vessels were diffuse-porous, with solitary and few multiple pores, rounded, and diameters ranging from 52–152 µm with an average of 90 µm. The axial parenchyma was vasicentric paratracheal. The xylem cylinder was divided into segments by five to six pairs of interfascicular rays that were not equidistantly distributed, and each pair was separated by a narrow plate of axial elements. The widths of the rays ranged from 201–273 µm, with an average of 234 µm, when the stem diameter was approximately 20 mm (Fig. 3E), and there were numerous secondary rays. The pith was either rounded or contained cavities.

10. ***P. vitifolia***: vine, the stem cross-section was pentagonal when the stem diameters ranged from 14–16 mm. The thickness of the cortexes ranged from 720–1760 µm, with an average of 1,200 µm. The cambial variant was a furrowed xylem with shallow phloem wedges (Fig. 3F). The vessels were diffuse-porous, tiny, with solitary and few multiple pores, and diameters ranging from 34–198 µm, averaging 108 µm. The axial parenchyma was vasicentric paratracheal. The xylem cylinder was divided into segments by five to six pairs of interfascicular rays that were not equidistantly distributed, with widths ranging from 39–232 um, averaging 147 µm, and with an irregular distribution. The pith was cylindrical.

Key to the identification of *Passiflora* species

A bracket key for ten *Passiflora* species is provided below for their identification.

1. Cork thick, winged-like .... ***Passiflora suberosa*** subsp. ***litoralis***
1. Cork not winged-like 2
2. Stems with four broad angular .... ***Passiflora quadrangularis***
2. Stems without angular 3
3. Stem cylindrical and regular conformation 4
3. Stem pentagonal or octagon or irregular 5
4. Without interfascicular rays .... ***Passiflora laurifolia***
4. With interfascicular rays equidistantly .... ***Passiflora ligularis***
5. With external secondary vascular cylinder or successive cambia ... 6
5. With furrowed xylem of shallow phloem wedges 7
6. Stem with external secondary vascular cylinder .. ***Passiflora coccinea***
6. With successive cambia .... ***Passiflora edulis***
7. Without secondary rays .... ***Passiflora foetida*** var. ***foetida***
7. Secondary rays numerous 8
8. Pith cavity .... ***Passiflora vesicaria*** var. ***vesicaria***
8. Pith without cavity 9
9. With interfascicular rays unequidistantly .... ***Passiflora vitifolia***
9. Without interfascicular rays .... ***Passiflora biflora***

DISCUSSION

According to Ayensu and Stern (1964) and the identification keys using cambial variants from Angyalossy *et al.* (2015), *P. biflora, P. laurifolia,* and *P. suberosa* subsp. *litoralis* have cylindrical stems with conspicuous rays. *Passiflora* species exhibited furrowed xylem at shallow and deep phloem wedges. *P. coccinea* and *P. edulis* had external secondary vascular cylinders and successive cambia in their mature stems, respectively, inconsistent with the findings observed by Rajput and Baijnath (2016) or Yang *et al.* (2022) in their order/family data. These variations may associated with the stem thickness studied in the present study. Ayensu and Stern (1964) suggested that the cambial variant of *P. edulis* exhibited an irregular or interrupted conformation. However, Rajput and Baijnath (2016) revealed that *P. edulis* has a regular conformation, consistent with the findings of this study. Furthermore, no phloem or dispersed type were observed among *P. edulis* species. In a previous study, the *P. coccinea* cambial variant exhibited an interrupted type with a marginal series of steps (Ayensu and Stern, 1964), inconsistent with the findings from this study. The interrupted type developed a step-like configuration of phloem wedges owing to the unequal production of secondary xylem and phloem, and the marginal series of steps may be related to habitat conditions or different developmental stages.

Based on the definitions of developmental stages in the earlier studies (Ayensu and Stern, 1964; Isnard et al., 2003), we referred the ontogeny to classify these species. The primary phloem fibers and vascular cylinders were in

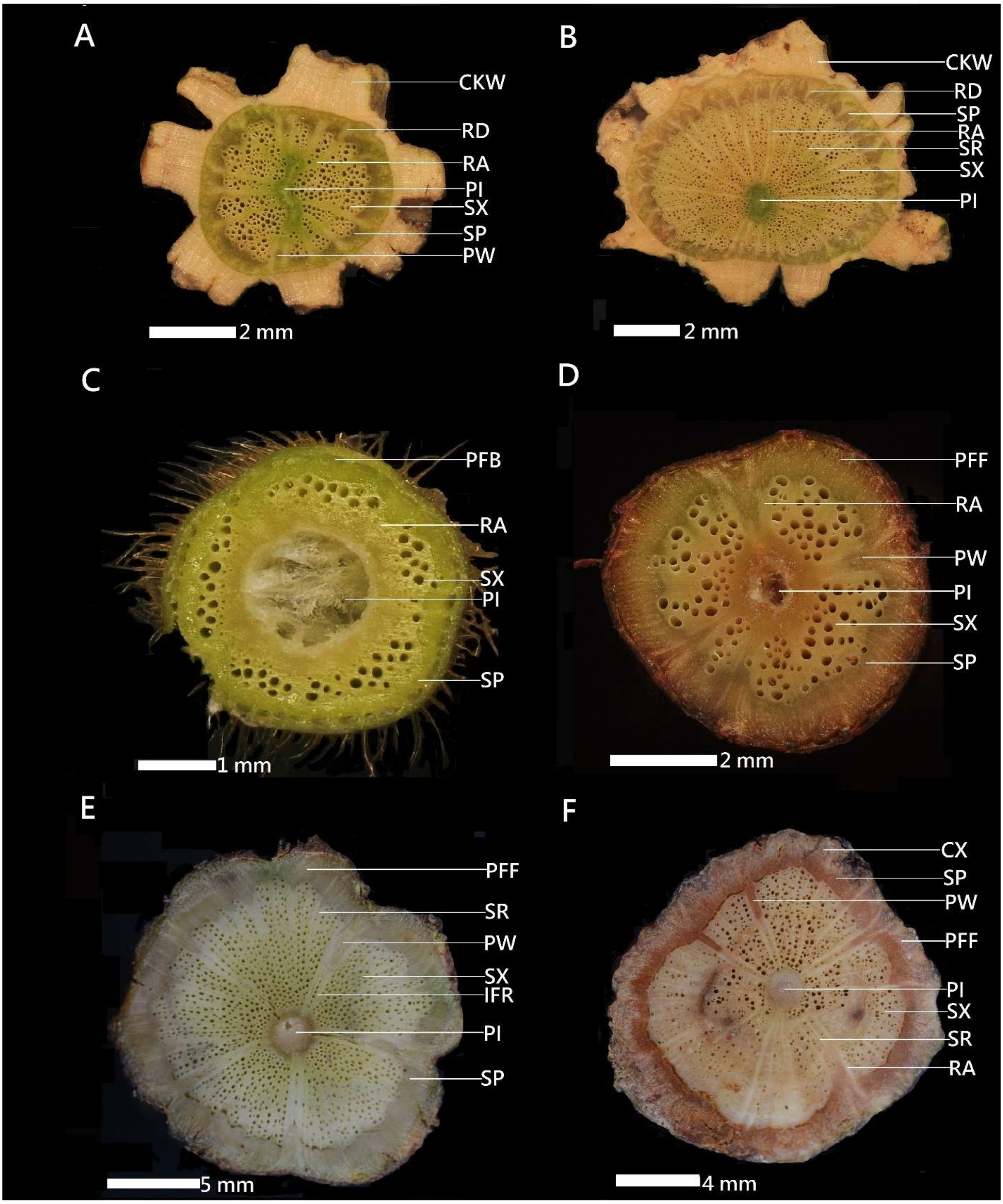

Fig. 3. A. *Passiflora suberosa* subsp. *litoralis*: phloem wedges, 3–4 rays developed in each xylem segment, 11–13 rays, ray dilatation, and pith flecks. **B. *P. suberosa* subsp. *litoralis***: phloem fibers triangular or flame-like, pith eccentric. A and B samples collected from the same individual in Xinhua District, Tainan. **C. *Passiflora vesicaria* var. *vesicaria***: phloem fiber bundles arranged in the cortex, xylem cylinder separated into 4–5 segments, and pith cavity. **D. *P. vesicaria* var. *vesicaria***: phloem wedges formed. **E. *P. vesicaria* var. *vesicaria***: stem with 4–5 pairs of interfascicular rays, phloem fibers flame-like, shallow phloem wedges, and secondary rays numerous. C samples collected in Hengchun, Pingtung County, and those of D and E in Dashe District, Kaohsiung City. **F. *Passiflora. vitifolia***: shallow phloem wedges formed, 4-6 pairs of interfascicular rays unequidistantly. Abbreviations: CX, cortex; CKW, cork fissured and winged-like; PW, phloem wedges; RA, rays; RD, ray dilatation; SR, secondary rays; PI, pith; PFB, phloem fiber bundles; IFR, interfascicular rays; PFF, phloem fibers flame-like; SP, secondary phloem; SX, secondary xylem.

Table 2. Morphological characteristics determined from stem cross-sections of Taiwanese ***Passiflora*** species

Characters	*P. biflora*	*P. coccinea*	*P. edulis*	*P. foetida* var. *foetida*	*P. laurifolia*	*P. ligularis*	*P. quadrangularis*	*P. suberosa* ssp. *litoralis*	*P. vesicaria* var. *vesicaria*	*P. vitifolia*
Habit	vine	vine	liana	vine	liana	vine	vine	vine	vine	vine
SD (mm)	2.5, 9.4	12,16	14, 32	3, 4.7	14–16	13	7.0–8.5	3, 10	5, 21	14–16
SS	OCT, CYL	CYL	PEN, CYL	PEN	CYL	CYL	SQU	CYL	PEN	CYL
Cork (+/–)	+	–	–	–	+	–	–	+	–	–
CKW(+/–)	–	–	–	–	–	–	–	+	–	–
Cortex (μm)	331–800	1270–2070	1520–3150	201–599	1080–1940	200–250	740–1350	195–942	130-620	720–1760
MCO (μm)	609	1530	2360	418	1470	225	1000	661	450	1200
ST (+/–)	–	–	–	–	+	+	+	–	–	–
CV	PW	ES,PW	SC,PW	PW	PW	PW	PW	PW	PW	PW
PWS	+	+	–	+	+	–	+	+	–	–
PWD	–	–	+	–	–	+	–	–	+	+
SRP (+/–)	–	–	–	–	–	–	–	+	–	–
DP (+/–)	+	+	+	+	+	+	+	–	+	+
VD (μm)	8–77	24–144	43–330	21–129	86–234	56–219	34–286	20–80	52–152	34–198
MVD (μm)	34	78	153	64	148	138	145	51	90	108
AR (+/–)	–	–	–	–	–	–	+	–	–	–
IRE (+/–)	–	–	+	–	–	+	–	–	–	–
IRU (+/–)	–	–	–	–	–	–	–	–	+	+
RN	>20	>20	10	4–5	10–13	–	+	11-13	>20	+
RAW (μm)	70–221	87–164	660–1810	403–493	200–1104	56–300	<50	53–213	201–273	39–232
MRA (μm)	114	127	980	458	550	280	-	130	234	147
SR	>20	>20	17–18	–	10–12	–	–	10-12	+	+
WR (+/–)	+	–	+	–	+	–	–	+	+	+
RD (+/–)	+	–	+	–	+	–	–	+	–	–
PC (+/–)	–	–	+/–	+	–	+	+	–	+	–
PIF(+/–)	+	–	+/–	–	–	–	–	+	–	–

Noted: SD: stem diameter, SS: stem shape, OCT: octagon, CYL: cylindrical, PEN: pentagonal, SQU: square, CKW: cork winged-like, MCO (μm): mean cortex thickness, ST: secretory tissues, CV: cambial variant, IC: irregular conformation, SC: successive cambia, ES: external secondary vascular cylinder, PWS: phloem wedges shallowly, PWD: phloem wedges deeply, SRP: semi-ring-porous vessel, DP: diffuse-porous vessel, VD (μm): vessel min-max diameter (n=50), MVD (μm): mean vessel diameter (mean± SD, n=50), AR: aggregate rays, IRE: interfascicular rays equidistantly, IRU: interfascicular rays unequidistantly, RN: rays numbers, RAW (μm): ray min-max width, MRA (μm): mean ray width, SR: secondary rays, WR: wide rays, RD: ray dilatations, PC: pith cavity, PIF: pith flecks, (+/–): present/absent.

an early developmental stage. The initial periderm, and secondary phloem fibers were in the middle developmental stages. The amount of ray-like parenchyma, larger vessels, and secondary phloem fibers were in an older developmental stage. According to the definitions described above, secondary cambium growth of *P. biflora* (Fig. 1A), *P. foetida* var. *foetida* (Figs 2A and B), *P. suberosa* subsp. *litoralis* (Fig. 2F), and *P. vesicaria* var. *vesicaria* (Fig. 3C) were at the younger developmental stages. *P. coccinea* (Figs 1C and D), *P. edulis* (Figs 1E and F), *P. laurifolia* (Fig. 2C), *P. ligularis* (Fig. 2D), *P. quadrangularis* (Fig. 2E), *P. suberosa* subsp. *litoralis* (Fig. 3B), *P. vesicaria* var. *vesicaria* (Fig. 3E), and *P. vitifolia* (Fig. 3F) were at the older developmental stages. However, there is a need to investigate young to mature stem to establish the complete ontogeny for each species. The growth of these plants is affected by extensive human activity in their natural habitat. We collected materials from one area; therefore, there were cases where the targeted plant species were missing or their stem diameters were too small to measure, affecting the assessment of cambial variants.

Rajput and Baijnath (2016) reported that *P. foetida* var. *foetida* stems lobed when their stems were approximately 2–2.3 cm in size. In the present study, this species had ring-like phloem fiber bundles when the stem diameter was 3 mm and 4–5 medullary rays when the stem was 4.7 mm. We hypothesized that the features of the fissured xylem of the phloem wedge exhibited in this study will become deeply lobed stems, and there is a need to observe the mature stem. The *P. suberosa* subsp. *litoralis* stem cross-section revealed three xylem segments separated by rays (Fig. 2F) when the stem diameter ranged from 2–2.3 mm. However, the stem diameter was approximately 3 mm, three to four wider rays developed in each xylem segment, giving totals ranging from 11–13 rays (Fig. 3A), and it had a phloem wedge. When the stem diameter was approximately 10 mm, the phloem fibers became triangular or flame-like, and 10–12 secondary rays were formed (Fig. 3B). The features of the fissured xylems exhibited in this study were consistent with those observed by Rajput and Baijnath (2016) and Acevedo-Rodríguez (2005) in the stems of plants at the younger and older developmental stages, respectively. Feuillet and Acevedo-Rodríguez (2020) observed cylindrical stems with lobed xylem or a normal type.

P. coccinea and *P. vitifolia* have similar leaf morphologies and red flowers (Gentry, 1981) and are cultivated as ornamental and shade plants, respectively, in Taiwan. In the present study, *P. coccinea* cambial variant exhibited an external secondary vascular cylinder, whereas that of *P. vitifolia* had a phloem wedge. The *P. coccinea* (Fig. 1D, enlarged part) cortex exhibited vascular bundles that developed into an external secondary vascular cylinder or successive cambium. These characteristics might increase the functions of adaption or evolutionary significantly. Therefore, different stem sizes need to be investigated in future studies. The external secondary vascular cylinder has different roles in *P. coccinea* and *P. vitifolia*.

The climbing phase of climbers differs from the self-supporting phase, considering various characteristics and anatomical changes in the lignified and non-lignified tissues in the stem. The early stages of secondary growth in *P. edulis* (liana) and *P. quadrangularis* (herbaceous vine and climber, respectively) xylems were characterized by relatively narrow vessels and many lignified cells around the pith. As the plants shifted to the climbing phase, the secondary xylem exhibited wider vessels, increasing stem flexibility and storage capacity (Rowe and Speck, 2005). The *P. edulis* and *P. quadrangularis* exhibited liana and climber growth habits. *P. quadrangularis* was the only species with thin and numerous rays, forming aggregates (Fig. 2E). The *P. edulis* xylem rings had five interfascicular ray divisions equidistantly, and those of *P. vesicaria* var. *vesicaria* and *P. vitifolia* were not equidistantly divided (Table 2).

The genus *Passiflora* has three cambial variant types, and most species have furrowed xylem of the phloem wedges and pith cavities resulting from non-lignified walls in the innermost pith parenchyma. Winged corks, pith flecks, wider rays, interfascicular rays, external secondary vascular cylinders, and successive cambia were observed as the key identification characteristics distinguishing species in the genus *Passiflora* in this study, providing additional identification keys for plants.

CONCLUSIONS

This study explored cambial variants of the stem cross-sections of *Passiflora* species in Taiwan. *P. coccinea* had xylems furrowed by phloem wedges and an external secondary vascular cylinder. Phloem wedges were observed in all the species. A novel cambial variant of an external secondary vascular cylinder and the presence of successive cambium are added to the currently available data on the family Passifloraceae. Future studies need to determine how the development of different stem diameters of climbers influences cambial variants of secondary growth, such as dispersed or interrupted xylem types. Information on secondary stem growth and cambial variants in different species of *Passiflora* occurring in Taiwan enables the establishment of cambial variants that are commonly taxon-specific, and combinations of cambial variant could be of more broader implications for taxonomy and phylogenetic value.

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