American Journal of Plant Sciences, 2019, 10, 545-554
http://www.scirp.org/journal/ajps
ISSN Online: 2158-2750
ISSN Print: 2158-2742

Cambial Variations of Three Lianoid Genera, *Akebia*, *Stauntonia*, and Sabia (Lardizabalaceae and Sabiaceae), in Taiwan

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How to cite this paper: Yang, S.-Z., Chen, P.-H. and Chen, J.-J. (2019) Cambial Variations of Three Lianoid Genera, *Akebia*, *Stauntonia*, and Sabia (Lardizabalaceae and Sabiaceae), in Taiwan. *American Journal of Plant Sciences*, **10**, 545-554.
https://doi.org/10.4236/ajps.2019.104039

Received: March 18, 2019
Accepted: April 15, 2019
Published: April 18, 2019

Abstract

Descriptions of the cambial variants of the lianoids in two families, Lardizabalaceae and Sabiaceae, were lacking in Taiwan. This study aimed to diagnose the stem characteristics of seven lianoid species from these two families to update existing knowledge. Specifically, the transverse sections of fresh stems were diagnosed to generate a key. The results showed that all seven species develop one of ten cambial variant types, viz. axial vascular elements in segments. Of these species, *Sabia swinhoei* Hemsley, *Stauntonia obovata* Hemsley, and *S. obovatifoliola* Hayata formed secondary rays. The thick and successive periderm was apparent in *Stauntonia obovata* and *S. obovatifoliola* at older stem. The sclerenchyma ring was continuous or discontinuous in two genera (*Akebia* and *Stauntonia*), but was absent in Sabia. Four diagnostic features could be used to distinguish Lardizabalaceae and Sabiaceae; namely, the periderm, cortical sclerenchyma, vessel arrangement, and cortex ducts. The cambial variations documented for these seven lianoid species in Taiwan update existing information, facilitating comparisons between Lardizabalaceae and Sabiaceae.

Keywords

Cambium, Lardizabalaceae, Parenchyma, Sabiaceae, Secondary Ray

1. Introduction

The family Lardizabalaceae contains approximately seven genera and 40 species that are mainly distributed in E Asia [1] [2] [3], of which five species from two genera are found in Taiwan [4]. The family Sabiaceae contains approximately 66 species from three genera that are distributed in tropical and East Asia, as well as Central and South America [4] [5]. Six species from two of these genera are found in Taiwan [6]. Lardizabalaceae and Sabiaceae contain scandent (climbing) genera. In comparison, the species of Lardizabalaceae found in Taiwan are lianoid (woody vines), including the species from the genera *Akebia* Decaisne and *Stauntonia* de Candolle. Furthermore, all species of Sabiaceae are woody, but only the genus *Sabia* Colebr. is lianoid. Variation in the activity of vascular bundles leads to unusual variation in the distribution patterns of xylem and phloem, which influences stem shape [7]. One cambial variant has been documented in *Akebia* and *Stauntonia*, namely axial vascular elements in segments [8]; however, the types of cambial variants in Sabiaceaere are mainly poorly documented.

The woody morphological characteristics of lianoids in the Lardizabalaceae and Sabiaceae families include the primary form of vascular bundles maintained by wider rays. Specific characteristics include distinct growth rings, dimorphic vessels and porous rings. Vessel diameter is >100 μm for large vessels and 25 - 40 μm for small vessels, while vessel density is 100 - 200 mm^2. Large vessels tend to be solitary, while small vessels tend to be grouped. The axial parenchyma is vasicentric paratracheal, and occasionally apotracheal. The axial parenchyma can be diffuse or form aggregates, with distinct ray dilatations [9] [10].

For example, the interfascicular area of *Akebia quinata* Decne. (Lardizabalaceae) is sunken compared to fascicular areas. This phenomenon results in the stem cambium exhibiting slower activity in xylem ray areas. Sclerenchyma that forms in phloem ray areas can extend into xylem rays, and is interconnected outwardly with cortical sclerenchyma [9]. The species *A. trifoliata* (Thunb.) Koidz. has a growth ring, large unlignified rays at the transverse section of the periphery, and a belt of sclerenchyma below the phellogen [10]. The diagnostic features of *Stauntonia hexapetala* Decasn. include ray dilatations in the secondary phloem, and a group of sclerenchyma in the cortex area [10]. *S. hexaphylla* Decne has a growth ring, numerous vessels in earlywood and narrower and poor vessels in latewood [9]. The growth ring of *Sabia japonica* Maxim. (Sabiaceae) is type 3, whereby vessels are at least twice as wide in earlywood compared to latewood [11].

Several authors have claimed that the lianoids of Lardizabalaceae and Sabiaceae are similar. The family Lardizabalaceae is placed in Ranunculales (Berberidales) [9]. There is much controversy over us whether this family is related to-Rutales (Sapindales) [9] or Proteales [3]. The family Sabiaceae is placed in Proteales; however, Sabiaceae is placed in Sabialesrather than Proteales [10]. Although the wood anatomy of *A. quinata*, *A. trifoliata*, *S. hexapetala*, *S. hexaphylla* and *S. japonica* has been described previously, cambial variations of more lianoids from Lardizabalaceae and Sabiaceae in Taiwan are needed. Such information would allow the identification of distinctive features, providing more evidence to advance phylogenetic studies.

2. Materials and Methods

2.1. Research Materials

From 2015 to 2017, multiple samples of seven species, *Akebia chingshuiensis* T. Shimizu, *Akebia longeracemosa* Matsum, *Stauntonia obovata* Hemsley, *Stauntonia obovatifoliola* Hayata, *Stauntonia purpurea* Y. C. Liu & F. Y. Lu, *Sabia swinhoei* Hemsley, and *Sabia transarisanensis* Hayata were collected. Stems with a lignified epidermis were selected to compare and identify structural variations using known secondary growth characteristics for their transections. Out of these species, *A. chingshuiensis*, *S. purpurea*, and *S. transarisanensis* are endemic species of Taiwan [4] [6] [12].

2.2. Research Methods

For each species, only one sample, exhibiting clear cambial variations that were easy to observe, was selected to photograph and describe. The fresh materials were cut into pieces of about 5 cm long. A flat, freehand cross-section of each stem was made with a razor blade. Cambial variation of the stems was measured and described based on certain parameters; namely, stem diameter (mm), periderm thickness (mm), periderm successive (+/−), cortical sclerenchyma (+/−), cortex with ducts (+/−), semi-ring porous arrangement (+/−), diffuse porous arrangement (+/−), sclerenchyma rings (+/−), sclerenchyma continuous (+/−), xylem ray widening centrifugally (+/−), secondary rays, collateral vascular bundle, xylem min-max width (mm), xylem average width (mm), xylem ray min-max width (μm), xylem ray average width (μm), vessel min-max diameter (μm), vessel average diameter (μm), and axial parenchyma. Cambial variants were identified based on Carlquist (1993) [11] [13] [14] [15] [16].

In the present study, vessel arrangement was defined as follows: If the vessels in early wood are 6 to >10× larger in diameter than those in latewood, they are called ring-porous; if vessel diameter is constant throughout the growth ring, it is called diffuse-porous; and if vessels in early wood are 3 to 5× larger in diameter than those in the latewood, they are called semi-ring-porous [10]. Ray width size is defined by Chatta way (1933) [17]. This cambial variant type was derived from a single cambium, according to the report by Angyalossy *et al.* (2012) [14].

The stem surface was immediately photographed using a Nikon D7100 SLR digital camera (Lens AF Micro Nikon 60 mm 1:2.8D, Nikon Corporation, Tokyo, Japan). Quantitative anatomical traits were determined using Image-J software [18]. The specimens were dried in an oven (60˚C) for 4 - 5 days, and were then stored at −20˚C for one week. All of the plant collections will be deposited in the herbarium, Provincial Pingtung Institute (PPI), National Pingtung University of Science and Technology, for subsequent identification. The nomenclature follows Flora of Taiwan Volume 2 [4] [6]. Information on specimens was assimilated, including the scientific name of species, herbarium, collector, voucher number, date, phenology, and locality. Morphological descriptions, photographs, and a key to the congeners were created to aid identification.

3. Results

3.1. Photographs and Explanations of Cambial Variants

Information on the voucher specimens of the seven species from the two families, Lardizabalaceae and Sabiaceae, are presented (Table 1). In general, these seven species develop axial vascular elements in segments. The xylems are separated by broad rays (0.1 - 0.2 mm width) and moderately broad rays (0.05 - 0.1 mm width). Some of the morphological characteristics of these two families were similar, including the presence of solitary vessels solitary, vessel dimorphism, and round stem transverse type.

Of these three genera, *Akebia* and *Stauntonia*, developed discontinuous (Figure 1) and continuous (Figure 2, Figure 3) sclerenchyma, respectively. The *Sabia* genus lacked this characteristic. The stems of the *Stauntonia* genus tended to develop a thick periderm, that was successive or non-successive around the stem (Figure 2, Figure 3). The thickness of the periderm was relative to the old stem. The periderm of *S. obovatifoliola* was approximately 0.2 - 1.9 mm thick, with a stem diameter of approximately 13.2 mm (Table 2, Figure 3(a)). The stem diameter of *S. obovata* and *S. purpurea* was approximately 25.7 mm and 12.8 mm, with periderms of 2.40 - 4.60 mm and 0.07 - 0.54 mm thickness, respectively. Rays that widened centrifugally were clearly visible in *S. swinhoei*, *S. transarisanensis* (Figure 4), and *S. obovatifoliola* (Figure 3(a)). Out of the seven species, *S. swinhoei*, *S. obovata* and *S. obovatifoliola* formed 2 - 3 secondary rays through the proliferation of parenchyma.

Out of all the characteristics measured and described (Table 2), *S. obovatifoliola* was the largest for four features, including the average width of the xylem (0.63 ± 0.20 mm), average width of xylem ray (195 ± 0.68 μm), and average diameter of vessels (108 ± 35 μm). The diameter of the largest vessels was approximately 5× larger than that of the smallest vessels (Table 2), showing that the diameter of vessels is subject to dimorphism (Figure 3(a)). The vessel arrangement of Lardizabalaceae was semi-ring-porous, whereas that of Sabiaceae was diffuse-porous.

Table 1. Collections of the seven species from the three genera *Akebia*, *Stauntonia*, and *Sabia* deposited in the Herbarium of Provincial Pingtung Institute (PPI) referred to in this study.

Scientific name	Herbarium	Collector	Voucher number	Date	Phenology	Locality
Akebia chingshuiensis	PPI	P. H. Chen	1109	May	fruits	Hsinchu County, Cinsbu
Akebia longeracemosa	PPI	S. T. Chiu, S. C. Mou & K. C. Yang	6238	May	flowers	Hualien County, Hoping Forest road
Stauntonia obovata	PPI	Y. P. Liu	026	October	fruits	Taitung County, Dazan forest station
Stauntonia obovatifoliola	PPI	P.H. Chen	293	March	flowers	Taitung County, Dazan forest station
Stauntonia purpurea	PPI	S. T. Chiu, S. C. Mou & K. C. Yang	6190	May	flowers	Hualien County, Hoping Forest road
Sabia swinhoei	PPI	P.H. Chen	478	August	fruits	Pingtung County, Chenlishan
Sabia transarisanensis	PPI	S. Z. Yang	26551	May	Flowers and fruits	Kaohsiung County, Tienchi

Table 2. Morphological characteristics of stem transverse section of five Lardizabalaceae species and two Sabiaceae species in Taiwan.

	Lardizabalaceae					Sabiaceae	
Characters	*Akebia chingshuiensis*	*Akebia longeracemosa*	*Stauntonia obovata*	*Stauntoniaobo vatifoliola*	*Stauntonia purpurea*	*Sabia swinhoei*	*Sabia transarisanensis*
Stem diameter (mm)	6.2	4.4	6.9	13.2	6.7	16.6	13
Periderm thick (mm)	0.04 - 0.14	0.02 - 0.15	0.07 - 0.38	0.20 - 1.90	0.05 - 0.36	–	–
Periderm successive (+/–)	+	–	+	+	+	–	–
Cortical sclerenchyma (+/–)	+	+	+	+	+	–	–
Cortex with ducts (+/–)	–	–	–	–	–	+	+
Semi-ring-porous	+	+	+	+	+	–	–
Diffuse-porous	–	–	–	–	–	+	+
Sclerenchyma rings (+/–)	+	+	+	+	+	–	–
Sclerenchyma continuous (+/–)	+	–	+	+	+	–	–
Xylem rays widening centrifugally (+/–)	–	–	–	+	–	+	+
Secondary rays (+/–)	–	–	+	+	–	+	–
Collateral vascular bundle number	29	20	35	30	35	19	25
Xylem min-max width (mm)	0.13 - 0.60	0.14 - 0.57	0.14 - 0.47	0.19 - 1.00	0.20 - 0.43	0.49 - 1.31	0.29 - 1.62
Xylem average width (mean ± SD) (mm)	0.39 ± 0.12 (n = 29)	0.41 ± 0.11 (n = 20)	0.34 ± 0.10 (n = 35)	0.63 ± 0.20 (n = 30)	0.32 ± 0.06 (n = 35)	0.95 ± 0.31 (n = 10)	0.90 ± 0.38 (n = 22)
Xylem ray min-max width (μm)	37 - 119	22 - 81	19 - 114	69 - 337	12 - 143	114 - 253	69 - 221
Xylem ray average width (mean ± SD) (μm)	72 ± 19 (n = 29)	54 ± 19 (n = 20)	63 ± 23 (n = 35)	195 ± 68 (n = 30)	59 ± 23 (n = 35)	177 ± 34 (n = 19)	156 ± 31 (n = 25)
Vessel min-max diameter (μm) (n = 50)	27 - 143	26 - 139	26 - 143	53 - 195	17 - 103	13 - 78	53 - 147
Vessel average diameter (mean ± SD) (μm) (n = 50)	74 ± 25	78 ± 29	88 ± 28	108 ± 35	52 ± 19	33 ± 12	81 ± 16
Axial parenchyma	vasicentric	vasicentric	vasicentric	vasicentric scanty and few diffuse	vasicentric, confluent	vasicentric, confluent	vasicentric

Note: +/–: prescence/absent; minimum-maximum: min-max.

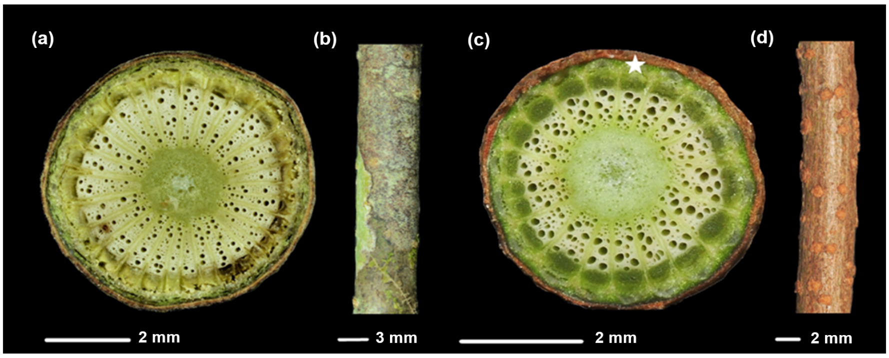

Figure 1. Transverse section of the stem and epidermis of *Akebia chingshuiensis* T. Shimizu (a)-(b), and *Akebia longeracemosa* Matsum. (c)-(d) (Lardizabalaceae). (a) Enlargement of cortical sclerenchyma extending into xylem rays; (b) Stem round, epidermis covered with few lenticels and glabrous; (c) Discontinuous gray sclerenchyma (star), phloem deep-green in color; (d) Stem round, epidermis covered numerous lenticels.

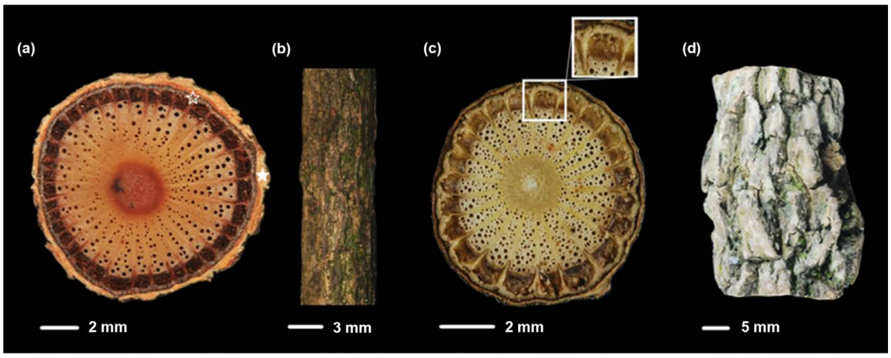

Figure 2. Transverse sections of stem and epidermis of *Stauntonia obovata* Hemsley from three specimens (Lardizabalaceae). (a) Section description from the pith to the outside of the stem: pith red in color, semi-ring porous, phloem rectangular in shape and deep-brown when dried, white cortical sclerenchyma and black sclerenchyma ring (white star), stem surrounded by periderm (solid white star); (b) Epidermis glabrous at younger stage; (c) Enlargement of cortical sclerenchyma connected with plate of sclerenchyma that formed in the phloem rays; (d) Stem diameter is approximately 2.6 cm, surrounded by a 2.4 - 4.6 mm thick periderm.

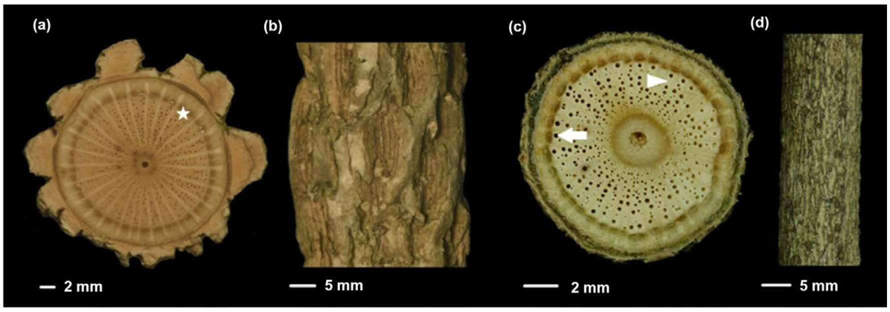

Figure 3. Transverse section of stem and epidermis of *Stauntonia obovatifoliola* Hayata (a), (b) and *Stauntonia purpurea* Y. C. Liu & F. Y. Lu (c), (d) (Lardizabalaceae). (a) Numberof collateral vascular bundle (white star) approximately 30, and stem covered by 0.2 - 1.9 mm thick periderm; (b) Stem surrounded by furrowed thick periderm; (c) Vessel dimorphism; showing the smallest (white arrow head) and largest (white arrow) vessels; (d) Epidermis broken ridges, pale-gray in color.

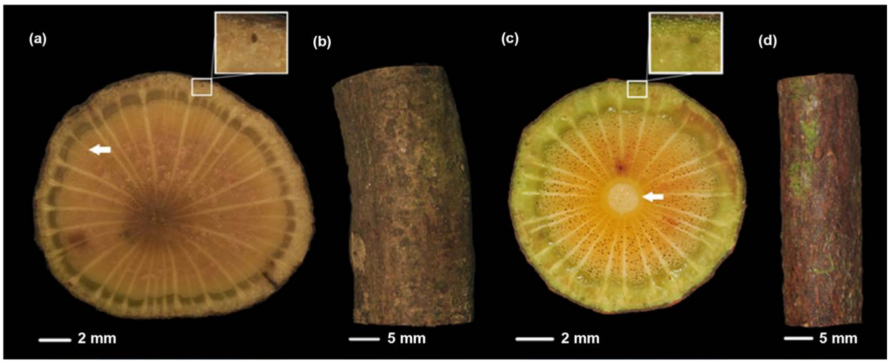

Figure 4. Transverse section of stem and epidermis of *Sabia swinhoei* Hemsl. (a), (b) and *Sabia transarisanensis* Hayata (c), (d) (Sabiaceae). (a) Secondary rays (split strips) (white arrow), enlargement of cortex with ducts; (b) Epidermis glabrous, gray in color; (c) Primary xylem ring (white arrow), clearly located around the pith, enlargement of cortex with ducts; (d) Epidermis glabrous, brown-green in color.

All five species of Lardizabalaceae were of the axial parenchyma type, whereby the vessels were surrounded by vasicentric paratracheal. However, the vessels of *S. obovatifoliola* and *S. purpurea* developed scandy, diffuse, and confluent parenchyma. The vessels of the two Sabiaceae species were surrounded by vasicentric and confluent parenchyma.

3.2. Characterization of Species

A key to the five Lardizabalaceae species and two Sabiaceae species in Taiwan is presented here, based on the characteristics of the bark and anomalous vascular bundles.

1) Stem without periderm; cortex with ducts 2
-1) Stem with periderm 3
2) Vessels about 33 μm in diameter; with secondary rays *Sabia swinhoei*
-2) Vessel about 81 μm in diameter; without secondary rays *Sabia transarisanensis*
3) With 2 - 3 secondary rays 4
-3) Without 2-3 secondary rays 5
4) Periderm 0.2 - 1.9 mm thick *Stauntonia obovatifoliola*
-4) Periderm 0.07 - 0.38 mm thick *Stauntonia obovata*
5) Periderm non-successive *Akebia longeracemosa*
-5) Periderm successive 6
6) Axial parenchyma surrounded by vasicentric *Akebia chingshuiensis*
-6) Axial parenchyma surrounded by vasicentric and confluent *Staun-tonia purpurea*

4. Discussion

The vessel diameter of the five Lardizabalaceae species found in Taiwan ranges from 103 to 195 μm for larger vessels and 17 to 53 μm for small vessels, supporting the description in [10]. Cariquist (1984) [9] stated that the periderm is thick and successive in old stems of Lardizabalaceae. In this study, the five species of Lardizabalaceae had successive (**Figure 2(d)**) or non-successive periderms, with this characteristic not being found in Sabiaceae. Thus, the characteristics of periderm could be used to differentiate these two genera. Phloem rays in the stems of *A. quinata* contained plates of sclerenchyma and were interconnected outwardly with cortical sclerenchyma [9]. These features were clearly detectable in *Akebia* and *Stauntonian* (**Figures 1-3**), but were not found in Sabia (**Figure 4**).

The transverse sections of *S. obovatifoliola* and *S. swinhoei* stems showed the presence of 2 - 3 secondary rays (**Figure 3(a)**, **Figure 4(a)**), which arose through the proliferation of parenchyma between some collateral vascular bundle. This feature was recorded in the species *Aristolochia macrophylla* of Aristolochiaceae [10] and the genus *Cyclea* of Menispermaceae [15]. These condary ray is also termed a split strip, which forms near the periphery with increasing stem diameter. However, the formation of secondary rays might depend on the diameter of the stem, requiring further investigation.

The average vessel diameter of *A. chingshuiensis* and *A. longeracemosa* was 74 μm and 78 μm (**Table 2**), respectively. These values were similar to those obtained for *A. trifoliata* (52 μm) reported in [9]. The scientific name *S. hexaphylla* was treated as the synonym of *S. obovatifoliola* [4]. The average vessel diameter of *S. obovatifoliola* was 108 μm larger than that of *S. hexaphylla* (52 μm), as recorded by Cariquist (1984) [9]. Because vessel density, size, and xylem length varied across individuals, classification was more difficult. In particular, differences in size might be relative to the growing regions. Only *S. swinhoi* and *S. transarisanensis* had a cortex with ducts (**Figure 4**). This diagnostic characteristic was not identified by previous reports. Thus, four diagnostic features (periderm, cortical sclerenchyma, vessel arrangement, and cortex ducts) may be used to distinguish Lardizabalaceae and Sabiaceae (**Table 2**).

The family Sabiaceae has wedge-shaped phloem rays [19]; however, this feature was not apparent in the two *Sabia* species from Taiwan. There remains controversy over whether Sabiaceaeis related to Rutales (Sapindales) [9], Proteales [3], or Sabiales [10]. The characteristics that were measured and described in this study could be used to compare functions and provide evidences to resolve systematic problems. Therefore, further study on the woody anatomy of Lardizabalaceae and Sabiaceaeis required.

5. Conclusion

Information about cambial variation in the three genera, *Akebia*, *Stauntonia*, and *Sabia* provided more evidence about congeners. In addition, a key was developed to aid the identification of these species. Seven species from two families, Lardizabalaceae and Sabiaceae, develop axial vascular elements in segments, which are separated by wider rays. Second rays were detected in older specimens of *S. swinhoei*, *S. obovata*, and *S. obovatifoliola*. Of these, the stems of *S. obovata* and *S. obovatifoliola* develop a thick periderm. The sclerenchyma ring is discontinuous or continuous in the genera, *Akebia* and *Stauntonia*, and was absent in the *Sabia* genus. The vessel arrangement, periderm, cortex with ducts, and cortical sclerenchyma in Lardizabalaceae differed to that in Sabiaceae. Thus, these four diagnostic features could be used to distinguish these two families. In conclusion, the information presented here could be used to help resolve the classification of Lardizabalaceae and Sabiaceae.

Acknowledgements

The authors thank the staff working in the Herbarium of PPI, National Pingtung University of Science and Technology, for providing assistance in the field and for providing the fresh stem material about the families Lardizabalaceae and Sabiaceae. The authors thank the anonymous reviewers for providing comments that improved an earlier draft of this manuscript.

Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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