Comparative anatomy of Grammitidaceae genera in Peninsular Malaysia

A.T. Nor-Ezzawanis

Forest Research Institute Malaysia, 52109 Kepong, Selangor, Malaysia
ezzawanis@frim.gov.my

ABSTRACT. Grammitidaceae is represented by 12 genera and 52 species in Peninsular Malaysia. The rhizome morphology and anatomy of Peninsular Malaysian Grammitidaceae were studied to determine whether it can be used as a supplementary character in generic delimitation. Two types of rhizome (creeping dorsiventral or erect), three types of stipe arrangement on the rhizome (in horizontal rows, in whorls or spiral) and two types of stele (solenostele or dictyostele) were identified.

Keywords. Anatomy, Grammitidaceae, morphology, Peninsular Malaysia, rhizomes

Introduction

Grammitidaceae is an important family for rainforest biodiversity in tropical montane regions with over 750 species worldwide (Parris 2003, 2010). For Peninsular Malaysia, 12 genera, namely, *Acrosorus* Copel., *Calymmodon* C.Presl, *Chrysogrammitis* Parris, *Ctenopterella* Parris, *Dasygrammitis* Parris, *Oreogrammitis* (Copel.) Parris, *Prosaptia* C.Presl, *Radiogrammitis* Parris, *Themelium* (T.Moore) Parris, *Tomophyllum* (E.Fourn.) Parris, *Scleroglossum* Alderw. and *Xiphopterella* Parris and 52 species are currently recognised (Parris 2007, 2010). Lately, the morphological and molecular aspects of this family have been intensively studied (Ranker et al. 2003, 2004; Schneider et al. 2004).

The Grammitidaceae have been treated in various ways taxonomically. Tryon and Tryon (1982) treated the entire Grammitidaceae as a single genus based on spore and sporangial characters while others established natural groupings based on the type of the rhizome, rhizome scales, stipe and rachis, types of frond hairs, venation patterns, soral arrangement and sporangial ornamentation (Parris 1983, 1986, 1995, 1997, 1998; Ranker et al. 2004). Parris (1995) also pointed out that neither cladistic nor cytological studies were helpful in the generic inter-relationships in the family; reticulate evolution possibly is one of the causes of failure.

For Peninsular Malaysia, all previous studies on this family were mainly based on morphological characters, ecology and phytogeography (Holttum 1955; Parris 1986, 1995, 1997, 1998, 2001, 2003, 2007, 2010). Rakotondrainabe & Deroin (2006) have shown that rhizome anatomy is a useful character in generic delimitation and can improve understanding of phylogeny of the family. Hence a study on rhizome anatomy of selected species of Grammitidaceae in Peninsular Malaysia was conducted

in order to determine whether it can be used as a supplementary character in generic delimitation.

Material and methods

Fresh specimens of the rhizome were used for anatomical study. A list of specimens used is attached in Appendix A. Transverse sections 25–50 μm thick were made using the sliding microtome following the methods used by Sass (1958). These sections were stained with safranin and alcian green, then mounted with euparal. Anatomical data analysis was made with a Leica Diaplan microscope equipped with a CCTV camera. The photomicrographs were obtained from the camera through a computer using the Analysis software.

Results and discussion

Out of the 12 genera of the Grammitidaceae in Peninsular Malaysia, 11 were studied. The genus *Chrysogrammitis* Parris was excluded due to the limitation in obtaining fresh specimens. Two types of rhizome, three types of stipe arrangement and two types of vasculature were identified in this study (Table 1).

Two types of rhizome were observed, i.e., creeping dorsiventral and erect. Creeping dorsiventral rhizomes were found in *Ctenopterella* (Fig. 1: A1), *Dasygrammitis* (Fig. 1: A2), *Oreogrammitis* (Fig. 1: A3), *Prosaptia* (Fig. 1: A4) and *Themelium* (Fig. 1: A5) while erect rhizomes occur in *Acrosorus* (Fig. 2: A1), *Calymmodon* (Fig. 3: A1), *Radiogrammitis* (Fig. 2: A2), *Scleroglossum* (Fig. 3: A3 & A4), *Tomophyllum* (Fig. 2: A3) and *Xiphopterella* (Fig. 3: A4). In comparison with Hovenkamp (1990), the results in the current study agreed with the creeping dorsiventral type of rhizome in *Prosaptia.* However for *Dasygrammitis*, instead of the radial type of rhizome found by Hovenkamp (1990), the current study found only the creeping dorsiventral type of rhizome for both *D. brevivenosa* and *D. fuscata*.

Three types of stipe arrangement were found in this study:

1) In horizontal rows, which occur in *Ctenopterella* (Fig. 1: A1 & B1), *Dasygrammitis* (Fig. 1: A2 & B2), *Oreogrammitis* (Fig. 1: A3 & B3), *Prosaptia* (Fig. 1: A4 & B4) and *Themelium* (Fig. 1: A5 & B5);
2) In whorls, in *Calymmodon* (Fig. 3: A1 & B1), *Scleroglossum* (Fig. 3: A2 & B2; A3 & B3) and *Xiphopterella* (Fig. 3: A4 & B4); and
3) Spirally in *Acrosorus* (Fig. 2: A1 & B1), *Radiogrammitis* (Fig. 2: A2 & B2) and *Tomophyllum* (Fig. 2: A3 & B3).

   In the spiral arrangement, transverse sections of the rhizome show that the stipes were in fact arranged in a more-or-less "2+1" arrangement i.e. two stipes were at the same stage of development but there is another stipe in an another stage of development. This proved that the three stipes are not exactly a true whorl.

Table 1. Rhizome characteristics of Grammitidaceae taxa studied.

Species	Rhizome habit	Stipe arrangement	Vasculature
Acrosorus friderici-et-pauli	erect	spiral	solenostele
Acrosorus streptophyllus	erect	spiral	solenostele
Calymmodon curtus	erect	whorls	dictyostele
Ctenopterella blechnoides	creeping dorsiventral	horizontal rows	solenostele
Dasygrammitis brevivenosa	creeping dorsiventral	horizontal rows	solenostele
Dasygrammitis fuscata	creeping dorsiventral	horizontal rows	solenostele
Oreogrammitis adspersa	creeping dorsiventral	horizontal rows	solenostele
Oreogrammitis congener	creeping dorsiventral	horizontal rows	solenostele
Oreogrammitis malayensis	creeping dorsiventral	horizontal rows	solenostele
Oreogrammitis reinwardtii	creeping dorsiventral	horizontal rows	solenostele
Prosaptia alata	creeping dorsiventral	horizontal rows	solenostele
Prosaptia contigua	creeping dorsiventral	horizontal rows	solenostele
Prosaptia obliquata	creeping dorsiventral	horizontal rows	solenostele
Radiogrammitis holttumii	erect	spiral	solenostele
Radiogrammitis multifolia	erect	spiral	solenostele
Scleroglossum pusillum	erect	whorls	dictyostele
Scleroglossum sulcatum	erect	whorls	dictyostele
Themelium tenuisectum	creeping dorsiventral	horizontal rows	solenostele
Tomophyllum subminutum	erect	spiral	solenostele
Xiphopterella hieronymusii	erect	whorls	dictyostele
Xiphopterella sparsipilosa	erect	whorls	dictyostele

Two types of vasculature were identified, i.e., solenostele and dictyostele, similar to those results of Ogura (1972), Bishop (1988, 1989), Rakotondrainibe & Deroin (2006). Ogura (1972) also described the type of vasculature in the grammitids *Polypodium subpinnatifidum* (currently known as *Radiogrammitis subpinnatifida* (Blume) Parris) as solenosteles. The other type, the perforated dictyostele, occurs in *Ctenopteris sodiroi* (currently known as *Melpomene sodiroi* (Christ & Rosenst.) A.R.Sm. & R.C.Moran), *Grammitis* sp. and *Scleroglossum* sp. The results of the current study are similar to his study. The solenostele was found in *Acrosorus* (Fig. 2: B1), *Radiogrammitis* (Fig. 2: B2), *Tomophyllum* (Fig. 2: B3) (all with erect rhizomes and the stipes arranged spirally); and *Ctenopterella* (Fig. 1: B1), *Dasygrammitis* (Fig. 1: B2), *Oreogrammitis* (Fig. 1: B3), *Prosaptia* (Fig. 1: B4) and *Themelium* (Fig. 1: B5) (all with creeping dorsiventral rhizomes and the stipes arranged horizontally). The dictyostele occurs in *Calymmodon* (Fig. 3: B1), *Scleroglossum* (Fig. 3: B2 & B3) and *Xiphopterella* (Fig. 3: B4) (all with erect rhizomes and the stipes arranged in whorls).

Regarding the similarity in type of vasculature between genera, there are two probabilities. The first is that the similarities are possibly caused by the close

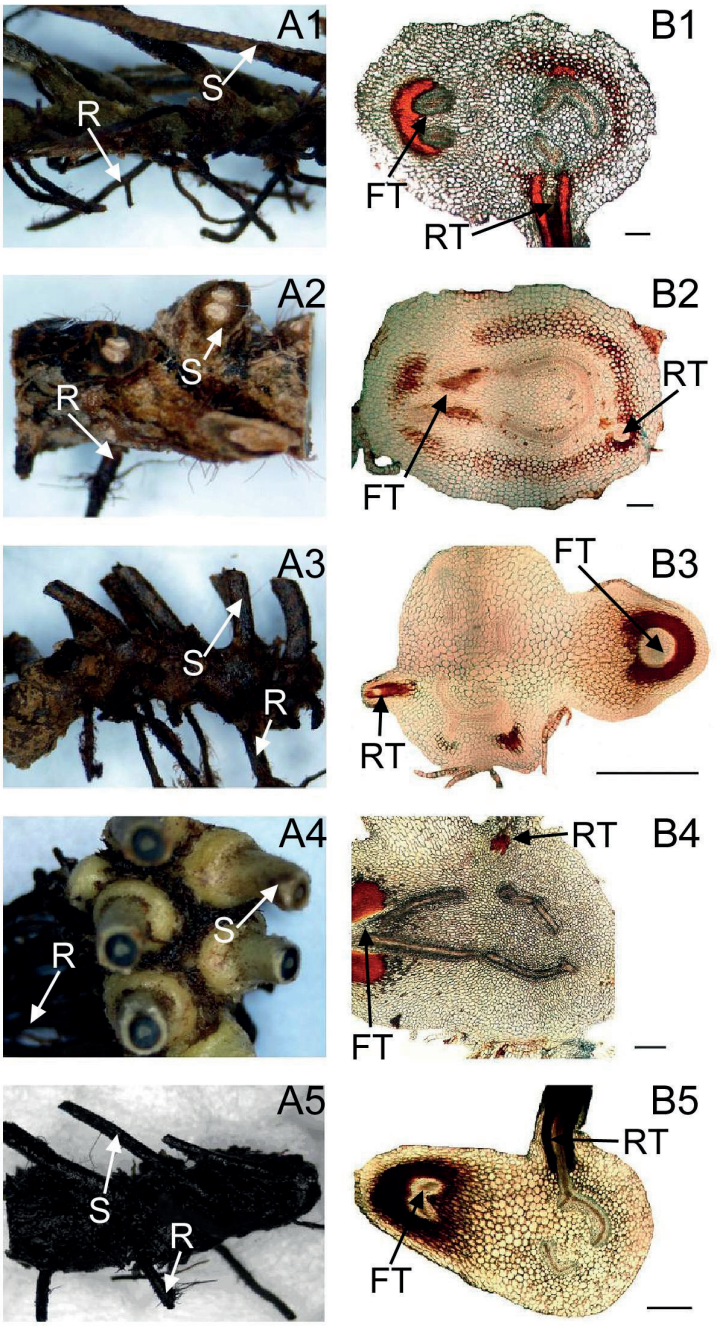

Fig. 1. Rhizome habit (A1–5) and anatomy (B1–5) in Grammitid species of the Solenostele group with creeping dorsiventral rhizomes and stipes arranged in horizontal rows. **A1 & B1.** *Ctenopterella blechnoides*; **A2 & B2.** *Dasygrammitis fuscata*; **A3 & B3.** *Oreogrammitis congener*; **A4 & B4.** *Prosaptia alata*; **A5 & B5.** *Themelium tenuisectum*. Bar equals 200 µm in B1, B2; 500 µm in B4 & B5 and 1000 µm in B3. Abbreviations used: S = stipe, R = root, FT = frond trace, RT = root trace.

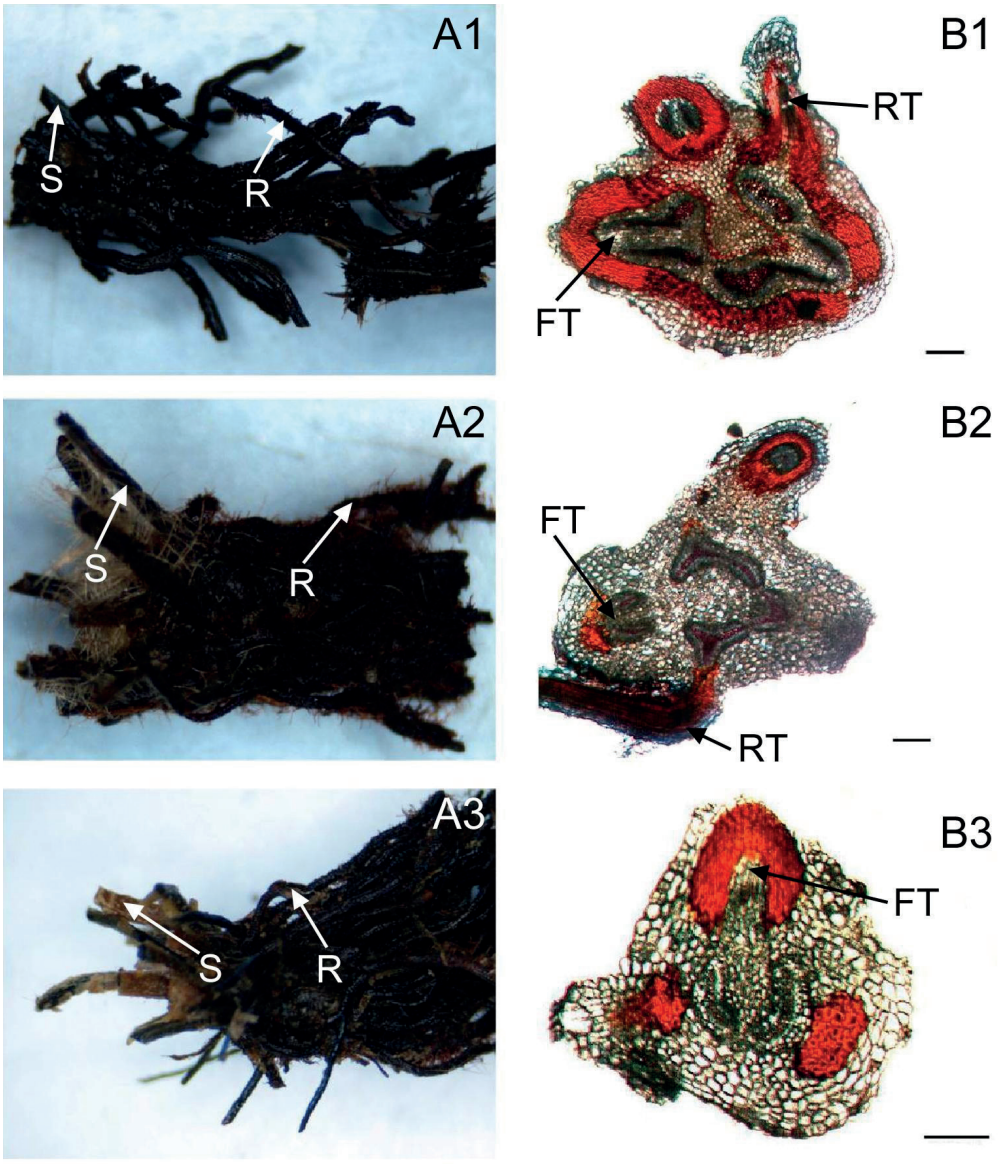

Fig. 2. Rhizome habit (A1–3) and anatomy (B1–3) in Grammitid species of the Solenostele group with erect rhizomes and stipes arranged spirally. **A1 & B1.** *Acrosorus friderici-et-pauli*; **A2 & B2.** *Radiogrammitis multifolia*; **A3 & B3.** *Tomophyllum subminutum*. Bar equals 200 µm in B1–B3. Abbreviations used: S = stipe, R = root, FT = frond trace, RT = root trace.

relationship between genera. For the solenostele group in the current study (*Acrosorus*, *Ctenopterella*, *Dasygrammitis*, *Oreogrammitis*, *Prosaptia*, *Radiogrammitis*, *Themelium* and *Tomophyllum*); the close resemblance between certain genera, e.g., (*Oreogrammitis* and *Radiogrammitis*; *Ctenopterella* and *Themelium*; *Dasygrammitis* and *Tomophyllum*) has been discussed by Parris (2007). The genera *Radiogrammitis*,

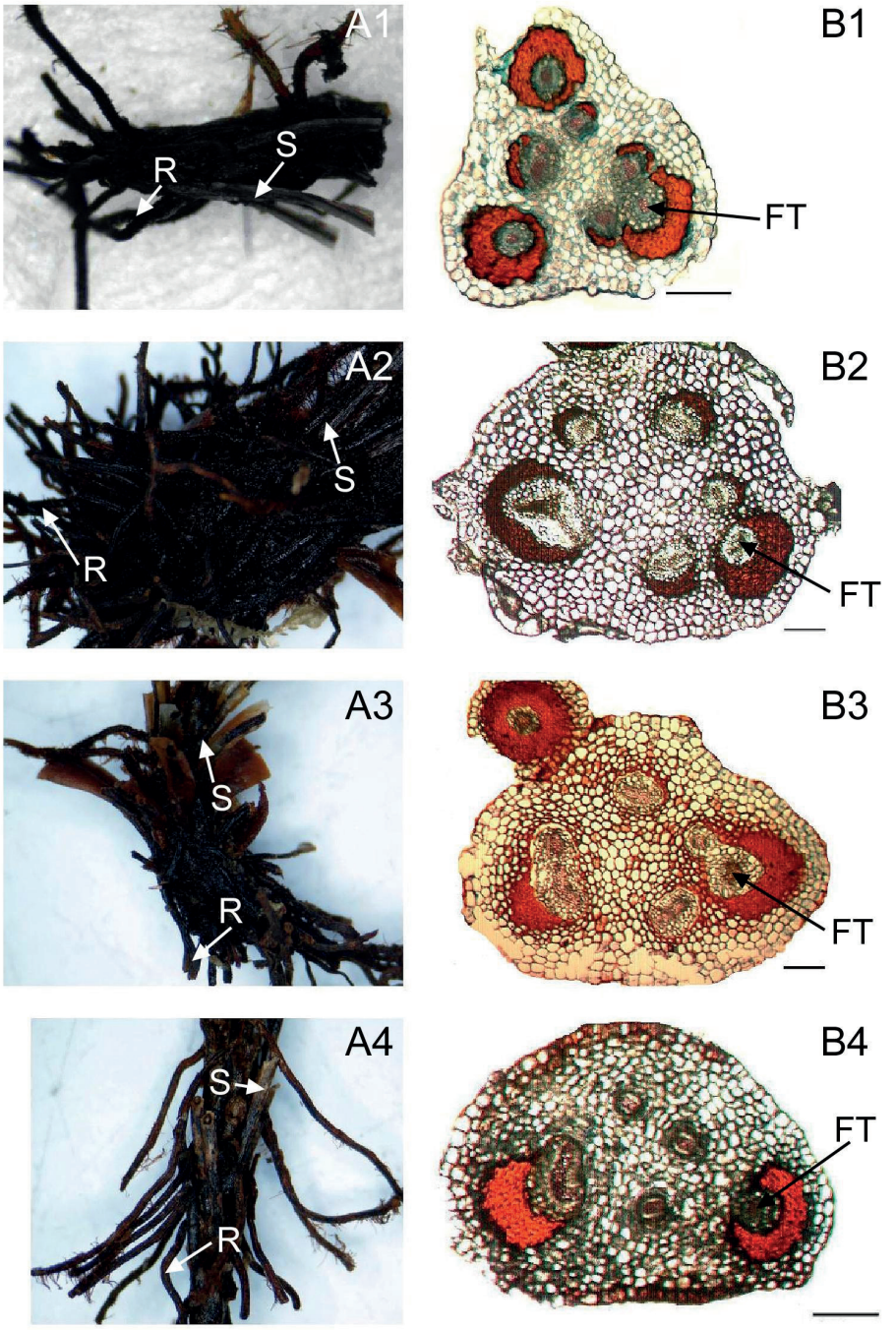

Fig. 3. Rhizome habit (A1–4) and anatomy (B1–4) in Grammitid species of the Dictyostele group with erect rhizomes and stipes arranged in whorls. **A1 & B1.** *Calymmodon curtus*; **A2 & B2.** *Scleroglossum pusillum*; **A3 & B3.** *Scleroglossum sulcatum*; **A4 & B4.** *Xiphopterella hieronymusii*. Bar equals 200 µm in B2–B4; 500 µm in B1. Abbreviations used: S = stipe, R = root, FT = frond trace.

Acrosorus and *Tomophyllum* share similarities in having solenosteles and stipes arranged spirally around the rhizome. However, on the basis of examining the close relationships between genera, the similarity of these characters does not agree with their placement in the phylogenetic tree in Ranker et al. (2004), where *Radiogrammitis* is placed near to *Oreogrammitis* and *Themelium* (due to its close resemblance to *Oreogrammitis* in many characters except its erect rhizome and the absence of rhizome scales in many species); while *Tomophyllum* falls within the same group with *Calymmodon* and *Scleroglossum*. However, not all the genera with solenosteles have been sampled for the cladistic analysis in Ranker et al. (2004). Four genera not yet included in the cladistic analysis are *Acrosorus*, *Ctenopterella*, *Dasygrammitis* and *Xiphopterella*. Hence, an explanation of the relationship between the genera in the solenostele group can only be proved once these four genera are included in the analysis. For the dictyostele group in the current study, the close relationship between *Calymmodon* and *Scleroglossum* was shown in the cladistic tree by Ranker et al. (2004), while the position of *Xiphopterella* in the same clade based on rhizome form and hair types, which was hypothesised in Parris (2007), agreed with the rhizome anatomy results.

The second probability is that the similarities might be due to a mechanical factor such as stipe arrangement on the rhizome. Ogura (1972) mentioned in general that the dictyostele occurs in species with overlapping leaf gaps. This is clearly seen with the occurrence of dictyosteles in genera with erect rhizomes and stipes arranged in whorls (*Calymmodon*, *Scleroglossum* and *Xiphopterella*); as well as the genera with creeping rhizomes and stipes arranged horizontally (*Ctenopterella*, *Dasygrammitis*, *Oreogrammitis*, *Prosaptia* and *Themelium*) that all have solenosteles. However, the occurrence of solenosteles in some species with erect rhizomes where the stipes are arranged spirally around the rhizome is not clearly understood. This is probably due to the non-overlapping of leaf gaps due to the spiral arrangement.

Ogura (1972) gave a brief description of the rhizome anatomy of the Polypodiaceae. The cortex and pith consist mostly of parenchyma. Sclerenchyma may occur in various forms and arrangements. In the current study, sclerenchyma around the vascular bundles was found in *Acrosorus friderici-et-pauli* (Christ.) Copel. (Fig. 4A), *Calymmodon curtus* Parris (Fig. 4B), *Scleroglossum pusillum* (Blume) Alderw. (Fig. 4C), *Xiphopterella hieronymusii* (C.Chr.) Parris (Fig. 4D) (all with erect rhizomes) and *Oreogrammitis malayensis* Parris (Fig. 4E) (with a creeping dorsiventral rhizome). One similarity between these plants is that almost all (except *Acrosorus friderici-et-pauli* and *Xiphopterella sparsipilosa*) are small-sized plants with the lamina length less than 10 cm. Hence, the sclerenchyma may function as supporting tissue in the plants.

Conclusions

Similarities in the type of vasculature among genera in the current study are seen as the result of the arrangement of stipes on the rhizome. It is consistent throughout the

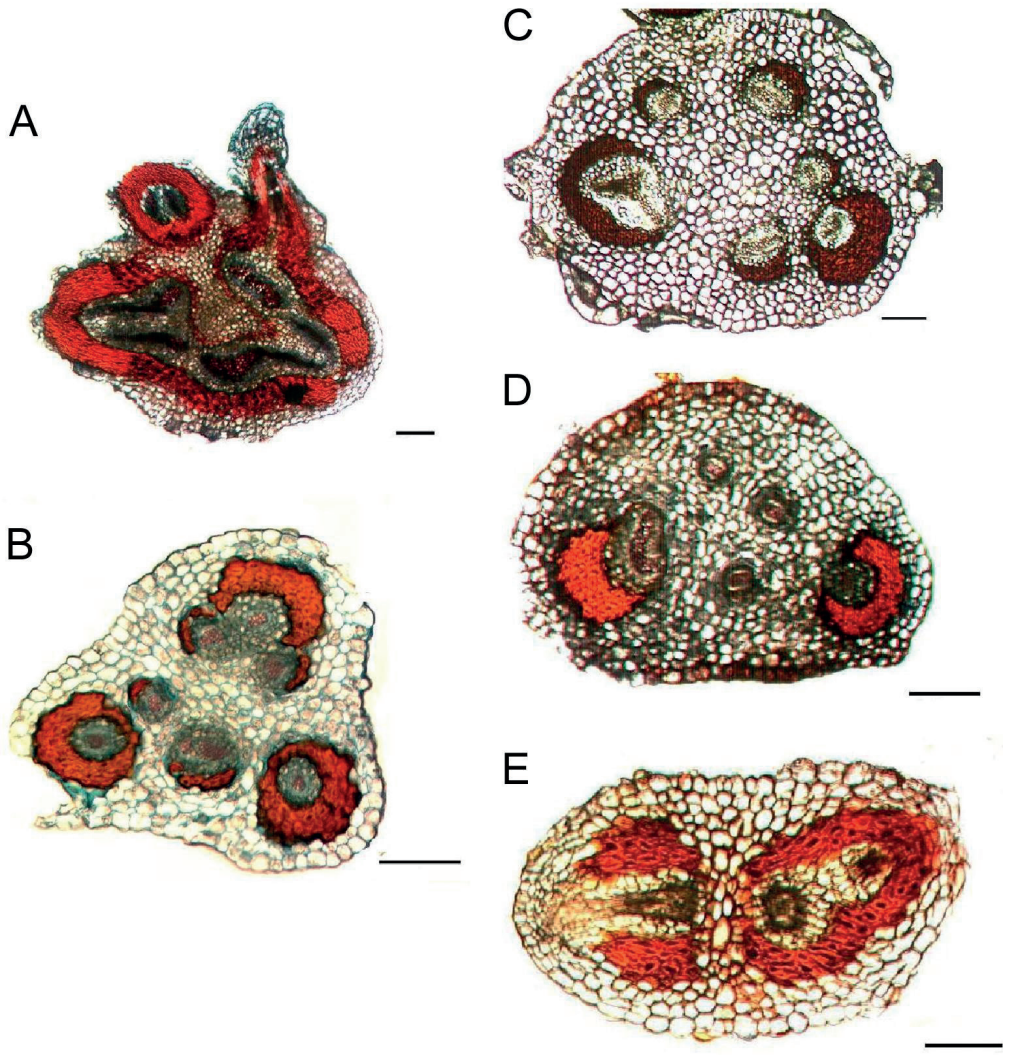

Fig. 4. Rhizome sections with red staining highlighting sclerenchyma tissue surrounding the vascular bundles. **A.** *Acrosorus friderici-et-pauli*; **B.** *Calymmodon curtus*; **C.** *Scleroglossum pusillum*; **D.** *Xiphopterella hieronymusii*; **E.** *Oreogrammitis malayensis*. Bar equals 200 µm in A, C–E; 500 µm in B.

study that overlapping of leaf gaps influences the formation of stele type. Whether the similarities are the result of close relationship among genera, it is only proven in certain cases, especially in the dictyostele group. For the solenostele group, a larger sampling is needed in the DNA analysis before such relationships can be assessed.

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Appendix A. List of specimens used for rhizome anatomy study. Bkt = Bukit (Malay for Hill), FR = Forest Reserve; G = Gunung (Malay for Mount)

Taxa	Specimens examined
Acrosorus friderici-et-pauli (Christ.) Copel.	*Nor Ezzawanis* FRI 52526, Cameron Highlands, G Brinchang, c. 1729 m asl, 17 Jan 2007 (KEP).
Acrosorus streptophyllus (Baker) Copel.	*Nor Ezzawanis* FRI 52395, Cameron Highlands, G Berembun, c. 1500 m asl, 19 Aug 2006 (KEP).
Calymmodon curtus Parris	*Nor Ezzawanis* FRI 52530, FRI 52531, Cameron Highlands, G Brinchang, c. 1729 m asl, 13 Jan 2007 (KEP).
Ctenopterella blechnoides (Grev.) Parris	*Nor Ezzawanis* FRI 54527, G Ledang, c. 1225 m asl, 15 Jan 2008 (KEP).
Dasygrammitis brevivenosa (Alderw.) Parris	*Nor Ezzawanis* FRI 52525, Cameron Highlands, G Brinchang, c. 1729 m asl, 13 Jan 2007 (KEP).
Dasygrammitis fuscata (Blume) Parris	*Nor Ezzawanis* FRI 52420, Cameron Highlands, G Berembun, c. 1500 m asl, 19 Aug 2006 (KEP), *Nor Ezzawanis* FRI 52521, FRI 52527, Cameron Highlands, G Brinchang, c. 1729 m asl, 13 Jan 2007 (KEP).

Oreogrammitis adspersa (Blume) Parris	*Nor Ezzawanis* FRI 54556, G Belumut, c. 1000 m asl, 22 to 24 Jan 2008 (KEP).
Oreogrammitis congener (Blume) Parris	*Nor Ezzawanis* FRI 52374, Cameron Highlands, G Brinchang, c. 1729 m asl, 18 Aug 2006 (KEP), *Nor Ezzawanis* FRI 52443, Cameron Highlands, G Berembun, c. 1500 m asl, 19 Aug 2006 (KEP).
Oreogrammitis malayensis Parris	*Nor Ezzawanis* FRI 54539, G Belumut, c. 1000 m asl, 22 Jan 2008 (KEP).
Oreogrammitis reinwardtii (Blume) Parris	*Nor Ezzawanis* FRI 52360, Cameron Highlands, G Brinchang, c. 1729 m asl, 18 Aug 2006 (KEP), *Nor Ezzawanis* FRI 52546, Cameron Highlands, G Brinchang, c. 1729 m asl, 14 Jan 2007 (KEP), *Nor Ezzawanis* FRI 52593, Genting Highlands, G Ulu Kali, c. 1767 m asl, 16 Feb 2007 (KEP).
Prosaptia alata (Blume) H. Christ.	*Nor Ezzawanis* FRI 54604, Berembun FR, Bkt Lantai, 9 Apr 2008 (KEP).
Prosaptia contigua (G. Forst.) C. Presl	*Nor Ezzawanis* FRI 52428, Bkt Larut FR, G Hijau, c. 1300 m asl, 20 Aug 2006 (KEP), *T.L. Yao* FRI 55924, Cameron Highlands, Parit Falls, 10 May 2007 (KEP).
Prosaptia obliquata (Blume) Mett.	*Nor Ezzawanis* FRI 52432, *FRI 52433*, Bkt Larut FR, G Hijau, c. 1300 m asl, 20 August 2006 (KEP), *Nor Ezzawanis* FRI 54460, Cameron Highlands, Ulu Telom, G Siku, c. 1486 m asl, 21 May 2007 (KEP).
Radiogrammitis holttumii (Copel.) Parris	*Nor Ezzawanis* FRI 54475, Cameron Highlands, Ulu Telom, G Siku, c. 1486 m asl, 21 May 2007 (KEP).
Radiogrammitis multifolia (Copel.) Parris	*Kueh H.L*. FRI 52544, Taman Negara, G Tahan, 3 to 4 Feb 2007 (KEP)
Scleroglossum pusillum (Blume) Alderw.	*Nor Ezzawanis* FRI 52592, Genting Highlands, G Ulu Kali, c. 1767 m asl, 16 Feb 2007 (KEP).
Scleroglossum sulcatum (Kuhn) Alderw.	*Nor Ezzawanis* FRI 52582*,* Genting Highlands, G Ulu Kali, c. 1767 m asl, 16 Feb 2007 (KEP).
Themelium tenuisectum (Blume) Parris	*Nor Ezzawanis* FRI 52591, Genting Highlands, G Ulu Kali, c. 1767 m asl, 16 Feb 2007 (KEP).
Tomophyllum subminutum (Alderw.) Parris	*Nor Ezzawanis* FRI 54482, Cameron Highlands, Ulu Telom, G Siku, c. 1486 m asl, 21 May 2007 (KEP).
Xiphopterella hieronymusii (C.Chr.) Parris	*Nor Ezzawanis* FRI 54464, Cameron Highlands, Ulu Telom, G Siku, c. 1486 m asl, 21 May 2007 (KEP).
Xiphopterella sparsipilosa (Holttum) Parris	*Kueh H.L*. FRI 52560, Taman Negara, G Tahan, 3 to 5 Feb 2007 (KEP)