INTRODUCTION

The fern family Grammitidaceae is a characteristic and important epiphytic component of montane forests in the wet tropics of both the Old World and the New World, extending to the north and south temperate zones. It is a medium-sized family with at least 750 species, c. 250 in the New World and c. 500 in the Old World. There are two centres of diversity, one in the New World tropics, extending west as far as Hawaii, the Marquesas and the Society Islands and east as far as Africa, Madagascar, the Mascarene Islands and the Seychelles, and one in the Old World tropics, centred in Malesia and extending west to Africa and east to Hawaii, the Marquesas and the Society Islands.

The family was described by Newman (1840), but other 19th century authors regarded it as not distinct from Polypodiaceae. One hundred years later Ching (1940) re-established the family and subsequently authors of fern floras, particularly in the Old World, including Copeland (1960) in the Philippines and Holtum (1955) in Malesia maintained the family as distinct from Polypodiaceae. The treatment of the phylogenetic position of the family has varied widely. Some authors, e.g. Holtum (1955), regarded it as rather primitive, while others, e.g. Copeland (1960), regarded it as very advanced. Recent morphological and molecular data support Copeland’s view. Grammitidaceae originated from New World Polypodiaceae and is nested within it (Ranker et al. 2004, Schneider et al. 2004) in the crown of the fern evolutionary tree. The Old World taxa are considered more evolutionarily derived (Ranker et al. 2004) and the major centre of diversification is in Malesia.

Grammitidaceae differs from Polypodiaceae as follows:

Grammitidaceae have leaf traces with a single vascular strand, fronds without scales, sporangial stalks of 1 row of cells, at least basally, thin-walled short-lived chlorophyllous spores with more or less immediate germination and gametophytes with gemmae.

Polypodiaceae, in contrast, have leaf traces with more than one vascular strand, fronds with scales, sporangial stalk consisting of more than one row of cells, thick-walled long-lived non-chlorophyllous spores whose germination may be delayed and gametophytes without gemmae.

CLASSIFICATION OF GRAMMITIDACEAE

Traditionally the three major genera in the family were delimited by frond division. Grammitis Sw. had simple fronds with one row of sori on each side of the midrib. Xiphopteris Kaulf. had fronds pinnately lobed to pinnate, with one sorus per lobe or pinna. Ctenopteris Blume ex Kunze had fronds like Xiphopteris or more highly divided, with two or more soris per lobe or pinna. There are problems involved with the use of all three generic names. Ctenopteris cannot be used because its type species, X. venulosa Blume ex Kunze, has been transferred to Prosaptia C.Presl, a Southeast Asian–Malesian–Pacific genus. Grammitis is now restricted to the species with a blackish sclerotic frond margin, found in the New World, Africa and the Pacific. Xiphopteris cannot be used because its type species, X. serrulata (Sw.) Kaulf., has been transferred to Cochlidium Kaulf., a New World–African genus.

The modern generic classification of the family is based on characters of the rhizomes, rhizome scales and frond hairs, rather than on laminar dissection, and 24 genera are currently recognised. They are Acrosorus Copel. (9 species), Adenophorus Gaudich. (10 spp.), Calymmodon C.Presl (44 spp.), Ceradenia L.E.Bishop (68 spp.), Chrysogrammitis Parris (2 spp.), Cohilidium (16 spp.), Ctenopterella Parris (20 spp.), Dasygrammitis Parris (9 spp.), Enterosora Baker (11 spp.), Grammitis (25 spp.), Lellingeria A.R.Sm. & R.C.Moran (70 spp.), Lomaphlebia J.Sm. (2 spp.), Luisma M.T.Murillo & A.R.Sm. (1 sp.), Meipomene A.R.Sm. & R.C.Moran (30 spp.), Micropolyplodium Hayata (25 spp.), Oreoagrammitis Copel. (141 spp.), Prosaptia (76 spp.), Radiogrammitis Parris (30 spp.), Scleroglossum Alderw. (9 spp.), Terpsichore A.R.Sm. (66 spp.), Themelium T.Moore Parris (26 spp.), Tomophyllum E.Fourn. Parris (34 spp.), Xiphopterella Parris (8 spp.) and Zygophlebia L.E.Bishop (17 sp.). Another three genera will be described from the Southeast Asia–Malesia–Pacific region.

The main molecular study involving Grammitidaceae is that of Ranker et al. (2004), with additional data in Geiger et al. (2007) and Ranker et al. (2003). In total little more than 10 % of the family has been sampled. These studies demonstrate that as sampled, Adenophorus (10 of 10 spp.), Calymmodon (2 of 44 spp.), Ceradenia (5 of 64 spp.), Cohilidium (4 of 16 spp.), Enterosora (2 of 11 spp.), Grammitis s.s. (3 of 25 spp.),
**MALESIAN GRAMMITIDACEAE**

The following 13 genera are currently recognised in Malesia (figures after the genus are the number of species in Malesia, with the total number of species in the genus in brackets): Acrosorus 9 (9), Calymmodo 35 (44), Chrysogrammitis 2 (2), Ctenopterella 6 (20), Dasygrammitis 7 (9), Micropolypodium 1 (25), Oreoagrammitis 101 (141), Prosapta 64 (76), Radiogrammitis 22 (30), Scleroglossum 7 (9), Themelium 26 (26), Tomophilium 27 (34) and Xiphopterella 6 (8). Figures for the undescribed genera are: new genus one 2 (7), new genus two 1 (17) and new genus three 1 (1).

Some of the Malesian genera have been recognised for more than 50 years: they are Acrosorus, described in 1906, Calymmodo and Prosapta, described in 1836 and Scleroglossum, described in 1912. Two other old genera have been recently re-instated: Micropolypodium was described in 1928, with species formerly treated as Xiphopteris, and Oreoagrammitis was described in 1917, with most species formerly in Grammitis, with a few in Ctenopteris and Xiphopteris.

The remaining seven genera have been described in the last 11 years for species formerly in Ctenopteris, Grammitis or Xiphopteris. They are Chrysogrammitis (Parris 1998, species formerly in Ctenopteris and Xiphopteris), Ctenopterella (Parris 2007, most species formerly in Ctenopteris, a few in Xiphopteris), Dasygrammitis (Parris 2007, species formerly in Ctenopteris), Radiogrammitis (Parris 2007, most species formerly in Grammitis, a few in Xiphopteris), Themelium (Parris 1997, 2004, most species formerly in Ctenopteris, a few in Grammitis and Xiphopteris), Tomophilium (Parris 2007, species formerly in Ctenopteris) and Xiphopterella (Parris 2007, species formerly in Xiphopteris).

The Malesian genera are characterised as follows:

1. **Acrosorus** has radial rhizomes with stipes in whorls, medium to dark brown non-clathrate glabrous rhizome scales, laminae deeply pinnately divided to pinnate, one sorus per lobe or pinna, protected by acrosopic and/or basiscopic margin of pinna folded towards the plane of the abaxial surface of lamina, sometimes sunken in lamina, medium to dark red-brown simple and branched hairs present, hydathodes sometimes present and glabrous sporangia.

2. **Calymmodo** has radial rhizomes with stipes in whorls, pale to medium brown non-clathrate rhizome scales that are glabrous or with hairs at apex only, laminae deeply pinnately divided to pinnate, one sorus per lobe or pinna, protected by basiscopic margin of pinna folded towards the apex of the lamina, hairs pale to medium brown, simple and branched hairs present, hydathodes usually present and sporangia glabrous.

3. **Chrysogrammitis** has dorsiventral rhizomes with stipes in two rows, whitish, yellowish or pale to dark brown non-clathrate rhizome scales with glandular hairs on margin, laminae deeply pinnately divided to pinnate, one or more sori per lobe or pinna, whitish, yellowish or pale to dark brown simple and branched glandular hairs on all parts of the frond, hydathodes absent and glabrous sporangia.

4. **Ctenopterella** has dorsiventral rhizomes with stipes in two rows, pale to medium brown non-clathrate glabrous rhizome scales, laminae deeply pinnately divided to pinnate, more than one sorus per lobe or pinna, pale to dark brown simple and branched hairs present, hydathodes sometimes present and glabrous sporangia.

5. **Dasygrammitis** has radial rhizomes with stipes in whorls, medium to dark brown non-clathrate ciliate rhizome scales, laminae deeply pinnately divided to pinnate, more than one sorus per lobe or pinna, medium to dark brown simple and branched hairs present, hydathodes absent and glabrous sporangia.

6. **Micropolypodium** has radial rhizomes with stipes in whorls, pale to medium brown non-clathrate glabrous rhizome scales, laminae deeply pinnately divided to pinnate, one sorus per lobe or pinna, medium to dark brown simple hairs present and branched hairs absent, hydathodes present and glabrous sporangia.

7. **Oreoagrammitis** has dorsiventral rhizomes with stipes in two rows, pale to dark brown or blackish usually non-clathrate, rarely clathrate, glabrous rhizome scales, laminae usually simple with one or more rows of sori on each side of the midvein rarely deeply pinnately divided to pinnate with one or more sori per lobe or pinna, pale to dark brown simple hairs present, branched hairs usually absent, hydathodes sometimes present and setose sporangia.

8. **Prosapta** has dorsiventral rhizomes with stipes in two rows, medium to dark brown or blackish subclathrate to clathrate ciliate rhizome scales, lamina simple with one row of sori on each side of the midvein in pinnate with usually more than one sorus per pinna, pale to dark brown simple and branched hairs present, hydathodes absent, and glabrous sporangia.

9. **Radiogrammitis** has radial rhizomes with stipes in whorls, pale to dark brown non-clathrate glabrous rhizome scales or scales absent, lamina simple or lobed, one or more rows of sori on each side of the midvein pale to dark brown simple and branched hairs present, hydathodes sometimes present and setose sporangia.

10. **Scleroglossum** has radial rhizomes with stipes in whorls, pale to medium brown non-clathrate glabrous rhizome scales, lamina simple, sori in one row on each side of the midvein deeply sunken in more or less parallel grooves, pale to dark brown simple and branched hairs present, hydathodes absent and glabrous sporangia.

11. **Themelium** has dorsiventral rhizomes with stipes in two rows, medium to dark brown, sometimes greyish, usually subclathrate to clathrate glabrous rhizome scales, lamina lobed, with one row of sori on each side of the midvein to bipinnate with more than one sorus per pinna, medium to
dark brown simple hairs present, branched hairs absent, hydathodes present, sometimes only in the basal part of pinnae and usually glabrous, very rarely setose, sporangia.

12. *Tomophyllum* has radial rhizomes with stipes in whorls, pale to medium brown non-clathrate rhizome scales with hairs on margin and/or at apex, or scales absent, lamina deeply lobed to bipinnate, more than one sorus per lobe or pinna, pale to medium red-brown simple and branched hairs present, hydathodes present and sporangia glabrous or very rarely setose.

13. *Xiphopterella* has radial rhizomes with stipes in whorls, pale to medium brown non-clathrate rhizome scales glabrous or with hairs at apex, lamina deeply lobed to pinnate, one sorus per lobe or pinna, pale to medium red-brown simple and branched hairs present, hydathodes sometimes present and sporangia glabrous.

Revisionary work still needs to be done on some of the accepted Malesian genera of *Grammitidaceae* and numerous new species remain to be described. *Acrosorus*, *Chrysogrammitis*, *Ctenopterella*, *Micropolypodium*, *Oreogrammitis* and *Radio-grammitis* pose few or no taxonomic problems, on the basis of specimens so far examined, but there are complex problems to be resolved in *Calymmodon*, *Dasygrammitis*, *Prosapta*, *Themelium* and *Tomophyllum*.

CONCLUSIONS

Just over 10% of the c. 750 species of *Grammitidaceae* have published molecular phylogenetic data (Geiger et al. 2007, Ranker et al. 2003, 2004), and some genera remain unsampled, so we only have a very basic outline of relationships based on DNA data.

We cannot afford the time to wait for molecular phylogenies when writing accounts for floras such as Flora Malesiana, and we must still rely on morphology for our generic and specific delimitations.

REFERENCES


