

THE *FLORA MALESIANA* ACCOUNT OF GRAMMITID FERNS
(POLYPODIACEAE): A PROGRESS REPORT WITH AN
ILLUSTRATED SYNOPTIC KEY TO MALESIAN GENERA

*Barbara S. Parris*¹

ABSTRACT

Fourteen genera and approximately 373 species of grammitid ferns (formerly Grammitidaceae, now Polypodiaceae) occur in Malesia. The *Flora Malesiana* account of the group is 75% complete (280 species). The genera are illustrated and briefly described. Current studies involve working through species that have long been herbarium dumping grounds containing numerous undescribed species, such as *Calymmodon cucullatus* (Nees & Blume) C.Presl, *Prosaptia contigua* (G.Forst.) C.Presl, *Radiogrammitis hirtella* (Blume) Parris (as *Grammitis hirtella*) and *Tomophyllum subfalcatum* (Blume) Parris (as *Ctenopteris subfalcata*).

INTRODUCTION

Grammitids are a characteristic and important component of rain forest in tropical montane regions of the world, extending to the north and south temperate zones. Seasonal dryness is the major limiting factor for distribution within both tropical and temperate regions. In the tropics the average daily lower limit of cloud formation is an important demarcator of the lower altitudinal limits of distribution. A few species are found in tropical lowland forest associated with rivers, either as epiphytes on trees overhanging the water or as rheophytes on rocks in and by water (Parris, 2003).

Grammitid ferns were formerly treated in their own family, Grammitidaceae, e.g. Holttum (1968), Kato & Parris (1992) and Parris *et al.* (1992), until molecular studies showed that the family was nested in Polypodiaceae (Schneider *et al.*, 2004). Grammitidaceae are currently recognised as subfamily Grammitidoideae of Polypodiaceae (PPG 1, 2016). Grammitidoideae are distinguished from the other subfamilies of Polypodiaceae by having the sporangial stalk of one row of cells at least in part (Wilson, 1959) rather than three rows, one vascular strand or two vascular strands that fuse above the base of the petiole (Parris, 1990; Sundue, 2010) rather than several vascular strands, and spores chlorophyllous, globose and trilete (Parris, 1990) rather than non-chlorophyllous, elliptic and monolete.

Taxonomic concepts in grammitid ferns have changed considerably with the advent of molecular phylogenetics (Ranker *et al.*, 2004; Sundue *et al.*, 2014). *Ctenopteris* (Blume ex Kunze), *Grammitis* Sw. and *Xiphopteris* Kaulf. were widely used in the past, for example by Holttum (1968), but are now considered to be unsatisfactory

1. Barbara S. Parris is Research Director at the Fern Research Foundation, Kerikeri, Northland, New Zealand.
Address: 21 James Kemp Place, Kerikeri, Bay of Islands, New Zealand.
Email: barbara2parris@gmail.com

artificial genera based on frond dissection (Ranker *et al.*, 2004). Recent developments in grammitid taxonomy have involved the recognition of new genera based on additional morphological characters, and both *Ctenopteris* and *Xiphopteris* are no longer recognised. The type species of *Ctenopteris*, *C. venulosa* Blume ex Kunze, has been transferred to *Prosaptia* C.Presl (Price, 1982; Price, 1987) and the type species of *Xiphopteris*, *X. serrulata* (Sw.) Kaulf., has been transferred to *Cochlidium* Kaulf. (Bishop, 1978), while *Grammitis sensu stricto* now includes only the species with a dark sclerified frond margin (Parris, 2007). *Oreogrammitis* Copel. (Copeland, 1917) was reinstated (Parris, 2007) and *Themelium* (T.Moore) Parris (Parris, 1997), *Chrysogrammitis* Parris (Parris, 1998), *Ctenopterella* Parris (Parris, 2007), *Dasygrammitis* Parris (Parris, 2007), *Radiogrammitis* Parris (Parris, 2007), *Tomophyllum* (E.Fourn.) Parris (Parris, 2007), *Xiphopterella* Parris (Parris, 2007), *Notogrammitis* Parris (Perrie & Parris, 2012) and *Archigrammitis* Parris (Parris, 2013) were described to accommodate Asia-Pacific species formerly included in *Ctenopteris*, *Grammitis sensu lato* and *Xiphopteris*.

Worldwide there are c. 911 species of grammitids in 33 genera (PPG 1, 2016). Fourteen genera and c. 373 species are currently known from Malesia; 122 of the species are new, i.e. around 33% of the group. Of the published family or group accounts of pteridophytes so far treated in *Flora Malesiana*, only Thelypteridaceae (Holttum, 1982), with more than 400 species, is larger. Flora accounts of 280 grammitid species are complete, i.e. around 75% of the group. Map 1 shows the distribution of grammitids in Malesia.



Map 1 Distribution of grammitids in Malesia. Map drawn by Barbara S. Parris.

THE GENERA

Grammitid genera are defined by unique assemblages of the following characters:

1. Rhizomes: a) dorsiventral, with stipes produced in two dorsal rows; b) rhizomes radial, with stipes produced in whorls or spirals.
2. Stipes: a) articulated to rhizome; b) not articulated to rhizome.
3. Rhizome scales: a) glabrous; b) setose; c) glandular; d) absent.
4. Rhizome scales: a) concolorous; b) clathrate; c) absent.
5. Lamina: a) simple; b) lobed to tripinnate.
6. Veins: a) simple or few-forked; b) pinnately to quadripinnately branched.
7. Hydathodes: a) present; b) absent.
8. Sori: a) superficial; b) protected by folded pinnae i) acroscopic and basiscopic margin folded; ii) basiscopic margin folded; c) deeply sunken in grooves in lamina; d) deeply sunken in pits in lamina; e) deeply sunken in marginal or submarginal pouches.
9. Sporangia: a) glabrous; b) setose.
10. Hairs: a) setose (Fig. 1); b) simple glandular; c) simple catenate (Fig. 2); d) branched glandular; e) branched catenate, setae as branches (Fig. 3); f) branched catenate, branches catenate; g) absent.

1. ACROSORUS Copel. (Fig. 4)

Rhizome radial; stipes not articulated to rhizome; rhizome scales glabrous and concolorous; lamina lobed to pinnate; veins few-forked; hydathodes absent; sori protected by pinnae folded on acroscopic and basiscopic margin; sporangia glabrous; hairs setose, simple catenate, branched catenate with setae as branches.



Fig. 1 Setae, c. 0.3–0.5 mm long. Photo: Peter Edwards, reproduced with permission.

Fig. 2 Simple catenate hair, c. 0.2 mm long. Photo: Peter Edwards, reproduced with permission.

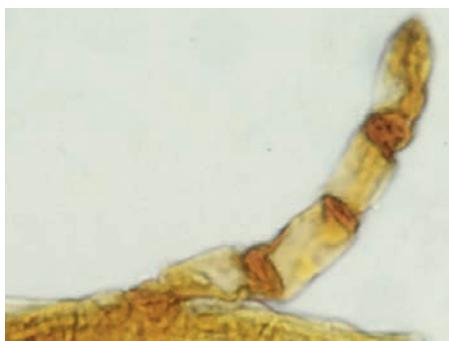


Fig. 3 Branched catenate hair with setae as branches, longer branches c. 0.5 mm long. Photo: Peter Edwards, reproduced with permission.



Monophyly not confirmed (Sundue *et al.*, 2014).

Nine species, SE Asia, Malesia and Pacific Islands. Nine species in Malesia; genus account complete.

2. *ARCHIGRAMMITIS* Parris (Fig. 5)

Rhizome dorsiventral; stipes articulated to prominent phyllopodia; rhizome scales setose and concolorous; lamina simple; veins pinnately branched; hydathodes present (in Malesian species); sori superficial; sporangia setose; hairs setose, simple catenate, branched catenate with setae as branches.

Monophyly not confirmed (no published data on genus).

Seven species, Borneo to Pacific Islands. Two species in Malesia; genus account complete.



Fig. 4 *Acrosorus streptophyllus* (Baker) Copel., abaxial surface of lamina, pinnae c. 1 mm wide at base. *Wade* 4331. Photo: Cheng-Wei Chen, reproduced with permission.



Fig. 5 *Archigrammitis friderici-et-pauli* (Christ) Parris, abaxial surface of lamina, lamina c. 2 cm wide. *Ranker* 2156. Photo: Barbara S. Parris.

3. *CALYMMODON* C.Presl. (Fig. 6)

Rhizome radial; stipes not articulated to rhizome; rhizome scales glabrous or with apical setae and concolorous; lamina lobed to pinnate; veins simple; hydathodes usually present; sori protected by pinna folded on basisopic margin; sporangia glabrous; hairs setose, simple catenate, branched catenate with setae as branches.

Monophyletic (Sundue *et al.*, 2014).

Sixty-three species, South, East and SE Asia, Malesia, Australia and Pacific Islands. Forty-eight species in Malesia; 41 species accounts complete.

4. *CHRYSOGRAMMITIS* Parris (Fig. 7)

Rhizome dorsiventral; stipes not articulated to rhizome; rhizome scales glandular and concolorous; lamina lobed to pinnate; veins few-forked or pinnately divided; hydathodes absent; sori superficial; sporangia glabrous; hairs simple glandular and branched glandular.

Fig. 6 *Calymmodon concinnus* Parris; abaxial surface of lamina, folded fertile pinnae c. 1 mm wide. *Hsu 7406*. Photo: Tian-Chuan Hsu, reproduced with permission.



Fig. 7 *Chrysogrammitis musgraviana* (Baker) Parris; adaxial surface of lamina, pinnae c. 1.5 mm wide. *Wade 4352*. Photo: Cheng-Wei Chen, reproduced with permission.



Monophyletic (Sundue *et al.*, 2014).

Two species, South Asia, Malesia and Pacific Islands. Two species in Malesia; genus account complete.

5. *CTENOPTERELLA* Parris (Fig. 8)

Rhizome dorsiventral; stipes not articulated to rhizome; rhizome scales glabrous and concolorous (in Malesian species); lamina lobed to pinnate; veins pinnately branched; hydathodes present or absent; sori superficial; sporangia glabrous; hairs setose, simple catenate, branched catenate with setae as branches, branched catenate with branches catenate.

Monophyly not confirmed (Sundue *et al.*, 2014).

Twenty-four species, Africa, South, East and SE Asia, Malesia, Australia and Pacific Islands. Eight species in Malesia; genus account complete.

6. *DASYGRAMMITIS* Parris (Fig. 9)

Rhizome radial; stipes not articulated to rhizome; rhizome scales setose and concolorous; lamina lobed to bipinnate; veins pinnately branched; hydathodes absent; sori superficial; sporangia usually glabrous, rarely setose; hairs setose, simple catenate, branched catenate with setae as branches.



Fig. 8 *Ctenopterella blechnoides* (Grev.) Parris; abaxial surface of lamina, pinnae c. 2 mm wide. *James* 1646. Photo: Michael Sundue, reproduced with permission.



Fig. 9 *Dasygrammitis malaccana* (Baker) Parris; abaxial surface of lamina, pinnae c. 2 mm wide. *Chew FRI* 53601. Photo: Barbara S. Parris.

Monophyletic (Sundue *et al.*, 2014).

Twelve species, South, East and SE Asia, Malesia and Pacific Islands. Ten species in Malesia; nine species accounts complete.

7. *MICROPOLYPODIUM* Hayata (Fig. 10)

Rhizome radial; stipes not articulated to rhizome; rhizome scales glabrous and concolorous; lamina lobed to pinnate; veins simple; hydathodes present; sori superficial; sporangia glabrous; hairs setose, simple catenate.

Monophyletic (Sundue *et al.*, 2014).

Three species, East and SE Asia to the Philippines. One species in Malesia; genus account complete.

8. *OREOGRAMMITIS* Copel. (Fig. 11)

Rhizome dorsiventral; stipes usually not articulated to rhizome, rarely articulated to prominent phyllopodia; rhizome scales glabrous and usually concolorous, rarely clathrate; lamina usually simple, rarely lobed to pinnate; veins usually few-forked, rarely



Fig. 10 *Micropolypodium okuboi* (Yatabe) Hayata; abaxial surface of lamina, pinnae c. 1.5 mm wide at base. *Bellingham* 659. Photo: Barbara S. Parris.



Fig. 11 *Oreogrammitis knutsfordiana* (Baker) Parris; abaxial surface of lamina, sori c. 1 mm wide. *Wade* 4422. Photo: Cheng-Wei Chen, reproduced with permission.

simple or pinnately branched; hydathodes present or absent; sori superficial; sporangia setose; hairs setose, simple catenate, rarely branched catenate with setae as branches.

Polyphyletic (Sundue *et al.*, 2014).

One hundred and fifty-eight species, South, East and SE Asia, Malesia, Australia and Pacific Islands. One hundred and thirteen species in Malesia; 80 species accounts complete.

9. *PROSAPTIA* C.Presl (Fig. 12)

Rhizome dorsiventral; stipes articulated to prominent phyllopodia; rhizome scales setose and clathrate; lamina usually lobed to pinnate, rarely simple; veins usually pinnately branched, rarely few-forked; hydathodes absent; sori rarely superficial, usually deeply sunken in pits in lamina or in marginal or submarginal pouches; sporangia glabrous; hairs setose, simple catenate, branched catenate with setae as branches.

Monophyletic (Sundue *et al.*, 2014).

Eighty-eight species, South, East and SE Asia, Malesia, Australia and Pacific Islands. Seventy-six species in Malesia; 43 species accounts complete.



Fig. 12 *Prosaptia contigua* (G.Forst.) C.Presl; abaxial surface of lamina, pinnae c. 3 mm wide at base. *Perrie* NC 72. Photo: Leon Perrie, reproduced with permission.

10. *RADIOGRAMMITIS* Parris (Fig. 13)

Rhizome radial; stipes not articulated to rhizome; rhizome scales glabrous and concolorous, rarely clathrate, sometimes absent; lamina usually simple, rarely lobed; veins simple or few-forked; hydathodes present or absent; sori superficial; sporangia setose; hairs setose, simple catenate, rarely branched catenate with setae as branches.

Polyphyletic (Sundue *et al.*, 2014).

Thirty-four species, South, East and SE Asia, Malesia and Pacific Islands. Twenty-seven species in Malesia; 25 species accounts complete.



Fig. 13 *Radiogrammitis cheesemani* (Parris) Parris; whole plant, lamina c. 5 mm wide. *De Lange* s. n. Photo: Peter de Lange, reproduced with permission.

11. *SCLEROGLOSSUM* Alderw. (Fig. 14)

Rhizome radial; stipes not articulated to rhizome; rhizome scales glabrous and concolorous; lamina simple; veins few-forked; hydathodes absent; sori deeply sunken in grooves in lamina; sporangia glabrous; hairs simple catenate, branched catenate with setae as branches, branched catenate with catenate branches.

Monophyletic (Sundue *et al.*, 2014).

Seven species, South, East and SE Asia, Malesia, Australia and Pacific Islands. Five species in Malesia; genus account complete.



Fig. 14 *Scleroglossum pusillum* (Blume) Alderw.; abaxial surface of lamina, lamina c. 2.5 mm wide below sori. *Wade* 4337. Photo: Cheng-Wei Chen, reproduced with permission.

12. *THEMELIUM* (T.Moore) Parris (Fig. 15)

Rhizome dorsiventral; stipes sometimes articulated to rhizome, phyllopodia absent; rhizome scales glabrous and usually clathrate, rarely concolorous; lamina simple or lobed to bipinnate; veins few-forked or pinnate; hydathodes usually present; sori superficial; sporangia usually glabrous, very rarely setose; hairs setose, simple catenate.



Fig. 15 *Themelium yoderi* (Copel.) Parris; abaxial surface of lamina, pinnae c. 6 mm wide. *Sundue* 3619. Photo: Michael Sundue, reproduced with permission.

Monophyletic, but nested within a large clade containing *Oreogrammitis* and *Radiogrammitis* (Sundue *et al.*, 2014). *Oreogrammitis* is the earliest name for this clade.

Twenty-eight species, East and SE Asia, Malaysia and Pacific Islands. Twenty-seven species in Malaysia; 20 species accounts complete.

13. *TOMOPHYLLUM* (E.Fourn.) Parris (Fig. 16)

Rhizome radial; stipes not articulated to rhizome; rhizome scales glabrous or setose and concolorous, sometimes absent; lamina lobed to tripinnatifid; veins pinnate; hydathodes present; sporangia glabrous; hairs setose, simple catenate, branched catenate with setae as branches.

Monophyletic (Sundue *et al.*, 2014).



Fig. 16 *Tomophyllum subrepandum* (Christ) Parris; abaxial surface of lamina, pinnae c. 2 mm wide. *James* 1566. Photo: Michael Sundue, reproduced with permission.

Forty-two species, South, East and SE Asia, Malesia, Australia and Pacific Islands. Thirty-six species in Malesia; 26 species accounts complete.

14. *XIPHOPTERELLA* Parris (Fig. 17)

Rhizome radial; stipes not articulated to rhizome; rhizome scales glabrous or with apical setae and concolorous; lamina lobed to pinnate; veins few-forked; hydathodes present or absent; sori superficial; sporangia glabrous; hairs setose, simple catenate, branched catenate with setae as branches.

Monophyletic (Sundue *et al.*, 2014).

Ten species, East and SE Asia and Malesia; ten species in Malesia, genus account complete.



Fig. 17 *Xiphopterella sparsipilosa* (Holttum) Parris; abaxial surface of lamina, pinnae c. 1.5 mm wide. Parris 10937. Photo: Barbara S. Parris.

[*GRAMMITIS* Sw. *sensu lato*, not yet placed in genus.]

One species, Indonesia (Moluccas); description complete.

Current work involves the taxonomy of the larger genera, *Calymmodon*, *Oreogrammitis*, *Prosaptia*, *Themelium* and *Tomophyllum*, which contain most of the 122 undescribed species of the group. Table 1 summarises the characters and character states of the grammitid genera.

CURRENT WORK

New grammitid species are still being collected; expeditions to Sabah, the Philippines and Papua New Guinea over the last 11 years have produced several novelties. The folders of unidentified ferns and the folders of taxa identified only to genus in herbaria are expected to be an important source of new species of grammitids. The folders of some well-known species have also proved to be an interesting source of misidentified and new taxa. These 'dumping ground' species were mostly described by Blume in the early part of the 19th century and they are found in all major herbaria with Malesian collections. In some cases, any specimen with only a generic resemblance to a Blume species was filed with it. The following species are the largest sources of misidentified and undescribed species: *Calymmodon cucullatus* (Nees & Blume) C.Presl, *Prosaptia contigua* (G.Forst.) C.Presl, *Radiogrammitis hirtella* (Blume) Parris (as *Grammitis*

Genera	1	2	3	4	5	6	7	8	9	10
<i>Acrosorus</i>	b	b	a	a	b	a	b	bi	a	e
<i>Archigrammitis</i>	a	a	b	a	a	b	a	a	b	ace
<i>Calymmodon</i>	b	b	ab	a	b	a	a(b)	bii	a	ace
<i>Chrysogrammitis</i>	a	b	c	a	b	ab	a	a	a	bd
<i>Ctenopterella</i>	a	b	a	a	b	b	ab	a	a	acef
<i>Dasygrammitis</i>	b	b	b	a	b	b	b	a	a(b)	ace
<i>Micropolypodium</i>	b	b	a	a	b	a	a	a	a	ac
<i>Oreogrammitis</i>	a	(a)b	a	a(b)	a(b)	a(b)	ab	a	b	ac(e)
<i>Prosaptia</i>	a	a	b	b	(a)b	(a)b	b	(a)de	a	ace
<i>Radiogrammitis</i>	b	b	ad	a(b)c	a(b)	a	ab	a	b	ac(e)
<i>Scleroglossum</i>	b	b	a	a	a	a	b	c	a	cef
<i>Themelium</i>	a	ab	(a)b	b	(a)b	(a)b	ab	a	a(b)	ac
<i>Tomophyllum</i>	b	b	abd	ac	b	b	a	a	a	ace
<i>Xiphopterella</i>	b	b	ab	a	b	a	ab	a	a	ace
<i>Grammitis s.l.</i>	a	b	a	a	a	a	a	a	a	f

Table 1 Genera of Malesian grammitids and characters with character states.

hirtella (Blume) Tuyama) and *Tomophyllum subfalcatum* (Blume) Parris (as *Ctenopteris subfalcata* (Blume) Kunze).

Calymmodon cucullatus is the type of the genus and is restricted to high altitudes in Peninsular Malaysia, Java, Sabah and New Guinea. Material of *C. asiaticus* Copel. (China, Peninsular Thailand, Vietnam and Peninsular Malaysia), *C. atrichus* Copel. (New Guinea), *C. glabrescens* Copel. (Sri Lanka), *C. gracilis* (Fée) Copel. (Taiwan, Vietnam, Malesia, Solomon Islands), *C. gracillimus* (Copel.) Nakai ex H.Ito (Malesia except Peninsular Malaysia and Lesser Sunda Islands), *C. luerssenianus* (Domin) Copel. (Australia) and *C. pergracillimus* (Alderw.) Copel. (New Guinea) has been identified as *C. cucullatus*. New species recognised from material previously identified as *C. cucullatus* are *C. curtus* Parris (Thailand, Peninsular Malaysia) and five undescribed species from New Guinea, two from Borneo, one from Malesia except Peninsular Malaysia, Lesser Sunda Islands and Sulawesi, one from Borneo to New Guinea and one from Borneo and Sulawesi.

Prosaptia contigua is the type of the genus and is widespread, in South India, Sri Lanka, China, Thailand, Malesia, Australia and Pacific Ocean Islands as far east as the Marquesas Islands. *Prosaptia pectinata* T.Moore and *P. rosenstockii* Copel. are commonly misidentified as *P. contigua*. As yet undescribed species recognised from material previously identified as *P. contigua* include four from New Guinea, one from Sulawesi and one from Borneo.

Radiogrammitis hirtella (syn. *Grammitis hirtella*) is probably endemic to Java. Material of *Oreogrammitis bongoensis* (Copel.) Parris (Borneo), *R. holttumii* (Copel.) Parris (probably endemic to Peninsular Malaysia), *R. multifolia* (Copel.) Parris (Thailand, Peninsular Malaysia, Sumatra and Java), *O. mollipila* (Baker) Parris (New Guinea), *O. nana* (Fée) Parris (Java), *O. reinwardtii* (Blume) Parris (Sri Lanka, Taiwan, Vietnam, Malesia, Australia and Solomon Islands) and *O. trichopoda* (F.Muell.) Parris (New Guinea) has been misidentified as *R. hirtella*. One new species is recognised from material previously identified as *G. hirtella*: *O. sinohirtella* Parris (China, Thailand and Vietnam).

Tomophyllum subfalcatum (syn. *Ctenopteris subfalcata*) is probably endemic to Java. Material of *T. brachyphlebium* (Baker) Parris (Sumatra and Borneo), *T. donianum* (Spreng.) Fraser-Jenk. & Parris (China, northern India, Nepal, Bhutan, Myanmar, northern Thailand and Vietnam), *T. lividum* (Mett.) Parris (Java), *T. macrum* (Copel.) Parris (Philippines), *T. subminutum* (Alderw.) Parris (Java) and *T. subrepandulum* (Christ) Parris (Malesia except Lesser Sunda Islands and Solomon Islands) has been misidentified as *C. subfalcata*. New species recognised from material previously identified as *C. subfalcata* are *T. epaleatum* (Parris) Parris (Sri Lanka and Java) and three as yet undescribed species, one from the Philippines, one from Sumatra and one from Java.

CONCLUSION

The *Flora Malesiana* treatment of grammitid ferns is 75% complete. The current estimate for completion of the account is the end of 2020, if everything goes to plan.

REFERENCES

- BISHOP, L.E. (1978). Revision of the genus *Cochlidium* (Grammitidaceae). *American Fern Journal*, 68: 76–94.
- COPELAND, E.B. (1917). New species and a new genus of Borneo ferns, chiefly from the Kinabalu collections of Mrs. Clemens and Mr. Topping. *Philippine Journal of Science. C: Botany*, 12: 45–65.
- HOLTTUM, R.E. (1968). *A Revised Flora of Malaya* vol. 2 (2nd edn). Government Printing Office, Singapore, pp. 212–236.
- HOLTTUM, R.E. (1982). Thelypteridaceae. *Flora Malesiana*, ser. II, vol. 1(5): 331–599.
- KATO, M. & PARRIS, B.S. (1992). Taxonomic studies of pteridophytes of Ambon and Seram (Moluccas) collected by Indonesian-Japanese botanical expeditions. VII: Grammitidaceae. *Journal of the Faculty of Science, University of Tokyo*, 3(15): 111–133.
- PARRIS, B.S. (1990). Grammitidaceae. In: KRAMER, K.U. & GREEN, P.S. (eds), *The Families and Genera of Vascular Plants* vol. 1. Springer-Verlag, Berlin & Heidelberg, pp. 153–157.
- PARRIS, B.S. (1997). *Themelium*, a new genus of Grammitidaceae (Filicales). *Kew Bulletin*, 52: 737–741.

- PARRIS, B.S. (1998). *Chrysogrammitis*, a new genus of Grammitidaceae (Filicales). *Kew Bulletin*, 53: 909–918.
- PARRIS, B.S. (2003). The distribution of Grammitidaceae (Filicales) inside and outside Malasia. *Telopea*, 10: 451–466.
- PARRIS, B.S. (2007). Five new genera and three new species of Grammitidaceae (Filicales) and the re-establishment of *Oreogrammitis*. *Gardens' Bulletin Singapore*, 58: 233–274.
- PARRIS, B.S. (2013). *Archigrammitis*, a new genus of grammitid ferns (Polypodiaceae). *The Fern Gazette*, 19: 135–138.
- PARRIS, B.S., BEAMAN, R.S. & BEAMAN, J.H. (1992). *The Plants of Mount Kinabalu 1. Ferns and Fern Allies*. Royal Botanic Gardens, Kew, pp. 61–77.
- PERRIE, L.R. & PARRIS, B.S. (2012). Chloroplast DNA sequences indicate the grammitid ferns (Polypodiaceae) in New Zealand belong to a single clade, *Notogrammitis* gen. nov. *New Zealand Journal of Botany*, 50: 457–472.
- PPG 1 (2016). A community-derived classification for extant lycophytes and ferns. *Journal of Systematics and Evolution*, 54(6): 563–603.
- PRICE, M.G. (1982). The ferns of Steere and Harrington. *Contributions from the University of Michigan Herbarium*, 15: 197–204.
- PRICE, M.G. (1987). Sabah Ferns collected by John H. Beaman. *Contributions from the University of Michigan Herbarium*, 16: 189–200.
- RANKER, T.A., SMITH, A.R., PARRIS, B.S., GEIGER, J.M.O., HAUFLE, C.H., STRAUB, S.C.K. & SCHNEIDER, H. (2004). Phylogeny and evolution of grammitid ferns (Grammitidaceae): a case of rampant morphological homoplasy. *Taxon*, 53: 415–428.
- SCHNEIDER, H., SMITH, A.R., CRANFILL, R., HILDEBRAND, T.J., HAUFLE, C.H. & RANKER, T.A. (2004). Unravelling the phylogeny of polygrammoid ferns (Polypodiaceae and Grammitidaceae): exploring aspects of the diversification of epiphytic plants. *Molecular and Phylogenetic Evolution*, 31: 1041–1063.
- SUNDUE, M.A. (2010). A morphological cladistic analysis of *Terpsichore* (Polypodiaceae). *Systematic Botany*, 35: 716–729.
- SUNDUE, M.A., PARRIS, B.S., RANKER, T.A., SMITH, A.R., FUJIMOTO, E.L., ZAMORA-CROSBY, D., MORDEN, C.W., CHIOU, W.L., CHEN, C.W., ROUHAN, G., HIRAI, R.Y. & PRADO, J. (2014). Global phylogeny and biogeography of grammitid ferns (Polypodiaceae). *Molecular and Phylogenetic Evolution*, 81: 195–206.
- WILSON, K.A. (1959). Sporangia of the fern genera allied with *Polypodium* and *Vittaria*. *Contributions from the Gray Herbarium of Harvard University*, 185: 97–127.