The distribution of Grammitidaceae (Filicales) inside and outside Malesia

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Abstract

B. S. Parris (Fern Research Foundation, 21 James Kemp Place, Kerikeri, Bay of Islands, New Zealand) 2003. Distribution of Grammitidaceae (Filicales) inside and outside Malesia. Telopea 10(1): 451-466. Over 750 species of Grammitidaceae are known. At least 250 occur in the New World and at least 450 are found in the Old World. Of the Old World species, 262 are in Malesia, 127 in the Pacific including Australia and New Zealand, 63 in Asia excluding Malesia and 54 in Africa including Macaronesia, Madagascar and the Mascarene Islands. Lomaphlebia (2 spp.) and Luisma (1 sp.) are endemic to the New World; Ceradenia (54 spp.), Cochlidium (16 spp.), Enterosora (10 spp.), Melpomene (25 spp.) and Terpsichore (57 spp.) are centred in the New World, each with less than half their species in Africa; Micropolypodium (25 spp.) is New World-centred with 3 Asian/Malesian species; Lellingeria (63 spp.) is New World-centred with 11 African species and 2 Pacific species; Grammitis s. str. has 11 New World species, 7 African species and 4 Pacific species; Zygophlebia has 7 African species and 7 New World species. Acrosorus (5 spp.), Calymmodon (30 spp.), Chrysogrammitis (2 spp.), Prosaptia (53 spp.), Scleroglossum (10 spp.) and Themelium (7 spp.) are centred in Malesia and extend to Asia and/or the Pacific, as are several species groups of Ctenopteris, Grammitis s. lat. and Xiphopteris. Adenophorus (9 spp.) is endemic to the Pacific. Two species groups of Grammitis s. lat. are endemic to Africa. The Ctenopteris blechnoides species group has 11 species in the Asia-Malesia-Pacific region and 5 in Africa. The Grammitis billardierei species group is largely in Old and New World south temperate regions (16 spp.), with 1 species in Malesia and 2 in Africa. Numbers of groups, species and endemic species are given for the 93 countries in which the family occurs. Old World countries with the most species are Indonesia (162), Papua New Guinea (131), Malaysia (97) and Philippines (68). New World countries with the most species are Venezuela (86), Colombia (83), Ecuador (82) and Costa Rica (78). 364 species are endemic to a single country. Old World countries with the most endemics are Indonesia (48), Papua New Guinea (46) and Australia, Malaysia and Hawaiian Islands (all with 13). New World countries with the most endemics are Brazil (19), Venezuela (17), Peru (12) and Colombia (11).

Introduction

The fern family Grammitidaceae is a characteristic and important component of rainforest in tropical montane regions of the Old World and the New World, extending to the north and south temperate zones. In the northern hemisphere it does not occur beyond c. 40°N, but in the southern hemisphere it extends to 56°S. Seasonal dryness is the major limiting factor in its 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 facultative rheophytes on rocks in and by water.

For many years Grammitidaceae was one of the least studied of large groups of ferns, but in the last three decades it has been the subject of numerous taxonomic studies, some still ongoing, and including both morphological and molecular investigations. More than 750 species are now known (Parris 1998c). Floristic treatments, many recent and written by taxonomists who have prepared monographic accounts of the family, are also available. Enough is now known about the taxa of Grammitidaceae to enable

a preliminary compilation of their distribution and centres of diversity to be made, although our knowledge is as yet incomplete. In the light of current concerns on the loss of biodiversity it is also useful to highlight the areas with high species numbers and endemicity.

In the New World 11 genera of Grammitidaceae are currently recognised, nearly all of which have been recently revised or described. They are *Ceradenia* L.E.Bishop (Bishop 1988), *Cochlidium* Kaulf. (Bishop 1978), *Enterosora* Baker (Bishop & Smith 1992), *Grammitis* Sw. sect. *Grammitis* (Bishop 1977), *Lellingeria* A.R.Sm. & R.C.Moran (Smith et al. 1991), *Lomaphlebia* J.Sm. (Smith 1875), *Luisma* M.T.Murillo & A.R.Sm., *Melpomene* A.R.Sm. & R.C.Moran (Smith & Moran 1992), *Micropolypodium* Hayata (Smith 1992), *Terpsichore* A.R.Sm. (Smith 1993) and *Zygophlebia* L.E.Bishop (Bishop 1989).

Redefinition of generic limits in the Old World is as yet incomplete, with 18 genera currently accepted (Parris 2001, 2002, Moran & Smith 2001, Smith 1992). They are *Acrosorus* Copel., *Adenophorus* Gaudich., *Calymmodon* C.Presl, *Ceradenia*, *Chrysogrammitis* Parris, *Cochlidium*, *Enterosora*, *Grammitis* s. str. (sect. or subgenus *Grammitis*), *Lellingeria*, *Melpomene*, *Micropolypodium*, *Prosaptia* C.Presl, *Scleroglossum* Alderw., *Terpsichore*, *Themelium* (T.Moore) Parris and *Zygophlebia*; *Ctenopteris* s. lat., *Grammitis* s. lat. and *Xiphopteris* p.p. (Old World) have also been accepted, with the proviso that within *Ctenopteris* and *Grammitis* a number of distinct species groups can also be recognised (Parris 2001). As the type species of *Ctenopteris*, *C. venulosa* Blume ex Kunze, is now treated as *Prosaptia venulosa* (Blume ex Kunze) M.G.Price (e.g. Parris 2001), the type species of *Xiphopteris*, *X. serrulata* (Sw.) Kaulf., has been transferred to *Cochlidium* (Bishop 1978) and *Grammitis* is now only accepted as a genus in the strict sense (e.g. Moran & Smith 1995), the remaining species of these three genera in the Old World need to be assigned to other genera.

Thirty-two groups of Grammitidaceae have been recognised for this paper. Some groups are genera that have already been described, while most (or all) of the others may be described as genera in the future. The groups are listed in Table 1, together with the number of species in each.

Acrosorus	5 (Parris unpublished data)
Adenophorus	9 (Palmer 2002)
Calymmodon	20 (Parris unpublished data)
Ceradenia	54 (Bishop 1988, Parris 2002)
Chrysogrammitis	2 (Parris 1998a)
Cochlidium	16 (Bishop 1978)
Enterosora	10 (Bishop & Smith 1992, Parris 2002)
Grammitis s. str.	22 (Bishop 1977, Parris 1997a, Parris unpublished data)
Lellingeria	63 (Smith et al. 1991, Parris 2002, Parris unpublished data)
Lomaphlebia	2 (Parris unpublished data)
Luisma	1 (Murillo & Smith 2003)
Melpomene	25 (Smith & Moran 1992)
Micropolypodium	25 (Smith 1992)
Prosaptia	53 (Parris unpublished data)
Scleroglossum	10 (Parris unpublished data)

Table 1.	Groups o	f Grammitidaceae	and the number	r of species in	n each group.
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Terpsichore	57 (Smith & Moran 1995, Parris 2002)
Themelium	7 (Parris 1997b, Parris unpublished data)
Zygophlebia	14 (Bishop 1989, Parris 2002)
Ctenopteris blechnoides (Grev.) W.H.Wagner & Grether group	16 (Parris unpublished data)
Ctenopteris curtisii (Baker) Copel. group	10 (Parris unpublished data)
Ctenopteris lasiostipes (Mett.) Brownlie group	2 (Parris unpublished data)
Ctenopteris mollicoma (Nees & Blume) Kunze group	9 (Parris unpublished data)
Ctenopteris nutans (Blume) J.Sm. group	10 (Parris unpublished data)
Ctenopteris repandula (Mett.) C.Chr. & Tardieu group	27 (Parris unpublished data)
Ctenopteris whartoniana (C.Chr.) Copel. group	4 (Parris unpublished data)
Grammitis billardierei Willd. group	16 (Parris unpublished data)
G. cryptophlebia (Baker) Copel. group	2 (Parris unpublished data)
G. pervillei (Mett. ex Kuhn) Tardieu group	4 (Parris unpublished data)
G. reinwardtii Blume group	c. 146 (Parris unpublished data)
G. samoensis (Baker) Ching group	7 (Parris unpublished data)
G. universa (Baker) Copel. group	4 (Parris unpublished data)
Xiphopteris hieronymusii (C.Chr.) Holttum group	6 (Parris unpublished data)

Distribution

It is convenient to divide the world into five regions for the purpose of examining the distribution of Grammitidaceae: 1, New World (North, Central and South America, the West Indies and the islands of the Galapagos, Falklands and South Georgia); 2, Africa (continental Africa, Madagascar and the islands of the Azores, Canaries, Ascension, St Helena, Tristan da Cunha group, Seychelles, Comoros, Mauritius, Réunion, Marion, Crozets and Kerguelen); 3, Asia excluding Malesia (India, Sri Lanka, Nepal, Thailand, Cambodia, Laos, Vietnam, China, Taiwan and Japan); 4, Malesia (Malaysia, Singapore, Brunei Darussalam, Indonesia, Philippines and Papua New Guinea), and 5, Pacific (Australia, New Zealand and the islands of Micronesia, Melanesia and Polynesia).

A provisional world list of Grammitidaceae species and their distribution has been compiled (Parris, unpublished) from the sources listed in Table 1, together with the following: Baksh-Comeau (2000), Bishop (1995), Bishop & Smith (1995), Braithwaite (1986), Brown and Brown (1931), Brownlie (1969, 1977), Christensen (1943), Copeland (1932), Dorr et al. (2000), Iwatsuki (1995), Kato and Parris (1992), Kramer (1978), Labiak (2000, 2002), Manickam and Irudayaraj (1992), Mickel and Beitel (1988), Moran and Smith (1995a, 1995b, 1995c, 1995d), Parris (1983, 1990, 1993, 1997a, 1998b, 1998c, in press), Parris and Given (1976), Parris and Glenny (in prep.), Parris and Latiff (1997), Ponce (1996), Proctor (1977, 1985, 1989), Rodriguez (1995), Sledge (1967), Smith (1985, 1995a, 1995b), Smith and Bishop (1995), Smith et al. (1999), Stolze (1981), Tagawa and Iwatsuki (1989), Tardieu-Blot and Christensen (1941), Tryon and Stolze (1993), Werff and Smith (1980), Zhang (2000). Parris' unpublished data cited in Table 1 is based on fieldwork in Malesia and the study of herbarium material from the institutes acknowledged below, particularly for Africa, Malesia and the Pacific.

The provisional world list was used as the basis for the data in Figure 1, which shows the number of groups, species and endemics in each of the phytogeographical regions. It should be noted that Table 1 does not include monotypic groups and distinct species

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whose affinities are not yet clear; however, they are included in the following species counts for the phytogeographical regions. Taxa in unresolved species complexes in African *Ceradenia* and *Zygophlebia*, Malesian and Pacific *Calymmodon*, Malesian *Ctenopteris* and undescribed species from South America (particularly Bolivia, Paulo Labiak and Alan Smith pers. comm.) are not included in the counts. Preliminary investigations suggest that more than 60 species are involved and they bring the number of species in the family to over 750.

The groups, their disposition in the five regions, the number of species in each region and the number of species endemic to each region, are shown in Table 2..

Group N	lew World	Africa	Asia	Malesia	Pacific
Lomaphlebia	2/2	-	-	-	-
Luisma	1/1	-	-	-	-
Ceradenia	48/46	8/6	-	-	-
Cochlidium	16/15	1/0	-	-	-
Enterosora	9/8	2/1	-	-	-
Melpomene	25/24	1/0	-	-	-
Terpsichore	55/55	2/2	-	-	-
Zygophlebia	7/7	7/7	-	-	-
Grammitis billardierei	3/0	3/1	-	1/0	15/11
Grammitis s. str.	11/11	7/7	-	-	4/4
Lellingeria	50/50	11/11	-	-	2/2
Micropolypodium	22/22	-	2/2	1/1	-
G. cryptophlebia	-	2/2	-	-	-
G. pervillei	-	4/4	-	-	-
Ctenopteris blechnoide	s -	5/5	4/1	6/2	6/4
Acrosorus	-	-	2/0	5/2	1/0
Calymmodon	-	-	4/1	20/14	7/5
Chrysogrammitis	-	-	2/0	2/0	1/0
Prosaptia	-	-	11/4	40/32	12/10
Scleroglossum	-	-	2/0	8/5	5/2
Themelium	-	-	1/0	7/5	2/0
Ctenopteris mollicoma	-	-	3/0	7/4	3/2
Ctenopteris repandula	-	-	6/4	23/18	4/2
G. reinwardtii	-	-	16/8	105/94	40/31
Ctenopteris curtisii	-	-	1/0	10/9	-
G. universa	-	-	1/1	3/3	-
Xiphopteris hieronymus	<i>sii -</i>	-	1/0	6/5	-
Ctenopteris nutans	-	-	-	8/8	2/2
G. samoensis	-	-	-	2/2	5/5
Ctenopteris whartoniar	na -	-	-	4/4	-
Adenophorus	-	-	-	-	9/9
Ctenopteris lasiostipes	-	-	-	-	2/2
Unassigned	1/1	1/1	7/7	6/6	7/7
Total	250/243	54/47	63/28	262/217	179/98

Table 2. Distribution of groups of Grammitidaceae showing the number of species and the number of endemic species in each region.

Table 2 shows that there are two major phytogeographic zones for Grammitidaceae: the New World and Africa, and Asia-Malesia-Pacific. The boundaries between them lie 1) in the Pacific Ocean, between the New World/African groups that extend no further west than continental Central and South America and the Galapagos Islands, and the Asia-Malesia-Pacific groups that extend no further east than the Hawaiian Islands and the Marquesas, and 2) in the Indian Ocean, between the New World/African groups that extend no further east than the Hawaiian Islands and the Seychelles, and the Asia-Malesia-Pacific groups that extend no further west than Sri Lanka and India. They delimit the New World-centred and the Malesian-centred areas of diversity within the family and are marked on Figure 1.

Twenty-seven of the 32 groups dealt with here do not cross either of the boundaries, only five of the groups do, and they show several distribution patterns. Lellingeria and Grammitis s. str. both occur in Africa, the New World and the Pacific, but do not extend into Asia-Malesia; Lellingeria is mainly New World, with 11 species endemic to Africa, one (L. saffordii (Maxon) A.R.Sm. & R.C.Moran) endemic to the Hawaiian Islands and one (L. subcoriacea (Copel.) A.R.Sm. & R.C.Moran) found on the Society Islands and the Marquesas; Grammitis s. str. has 11 species in the New World, seven species endemic to Africa and four species endemic in the Pacific, ranging from Vanuatu (New Hebrides) to the Marquesas. Micropolypodium is another mainly New World genus that does not extend into the Pacific, but has c. three species in Asia-Malesia. The group of Ctenopteris blechnoides has 11 Asian-Malesian-Pacific species, and five endemic to Africa. In contrast to all other groups of Grammitidaceae, which are largely restricted to the tropics, the group of Grammitis billardierei is essentially south temperate and circum-antarctic in distribution, with one species (G. stenophylla Parris, syn G. kairatuensis M.Kato & Parris) extending to the tropics of Australia and Seram in the Moluccas.

All 17 groups occurring only in the Asia-Malesia-Pacific areas are most diverse in Malesia, as is the group of *Ctenopteris blechnoides*. Of the groups found in Asia, Malesia and the Pacific, only six occur in all of the regions of Malesia: Peninsular Malaysia, Sumatra, Java, Lesser Sunda Islands, Borneo, Sulawesi, the Moluccas, the Philippines and New Guinea. They are the *Grammitis reinwardtii* group, *Prosaptia*, the *Ctenopteris blechnoides* group and the *Ctenopteris blechnoides* group. *Acrosorus, Calymmodon, Chrysogrammitis* and *Themelium* are found in Asia, the Pacific and part of Malesia. The groups of *Ctenopteris curtisii* and *Grammitis universa, Micropolypodium*, and the group of *Xiphopteris hieronymusii* are present in Asia and part of Malesia, but are absent from the Pacific; in contrast, the groups of *Ctenopteris nutans, Grammitis billardierei* and *Grammitis samoensis* are absent from Asia, but are in part of Malesia and in the Pacific. The group of *Ctenopteris whartoniana* is endemic to part of Malesia.

It is constructive to examine the distribution of diversity and endemicity within the family in detail for each of the regions to establish which countries are richest in terms of species numbers and numbers of endemics and are thus important for conservation. The provisional world checklist for the family has been used to build tables for each of the regions. Information on the distribution of species within countries is sometimes unavailable in floras, although endemic status is usually cited. In the discussion of endemics following each table, distribution is cited at the level of primary political unit within a country, when known, with the number of endemics followed by the total number of species, except for Sri Lanka, where distribution of Grammitidaceae is confined to a small area delimited by co-ordinates, and Tanzania, Madagascar and Malesia, where distribution is cited by major geographical units, sometimes within major political units. Countries without endemic species are omitted from the regional tables, but are listed above them, with the number of groups preceding number of

species for each. They are countries at the edge of the distribution of the family or apparently with little suitable habitat. A few have limited information available (Hispaniola, Guyana and French Guiana).

Table 3 shows the distribution of Grammitidaceae endemic to New World countries. The regions can be subdivided into areas that are often treated as floristic units based upon species distribution and numbers of endemics. They are listed here, but space prohibits a detailed discussion of regional endemicity. Data on endemics in the following New World list is sometimes limited to country level and for countries where floristic accounts are unavailable it has been acquired from monographs. Countries without endemics are United States (1/1), Belize (4/7), Honduras (8/30), Nicaragua (7/21), El Salvador (6/26), Hispaniola (9/34), Tobago (2/3), Guyana (7/25), Surinam (7/18), French Guiana (3/8), Argentina (2/4), Chile (1/3), Falkland Islands (1/1) and South Georgia (1/1).

Area	No. of groups in area	No. of species in area	No. of species endemic to area
Southern Mexico & Central America	9	101	25
Mexico	7	37	3
Guatemala	7	38	1
Costa Rica	9	78	3
Panama	9	68	2
Antilles	10	67	26
Greater Antilles	10	62	17
Cuba	8	23	3
Jamaica	10	50	6
Puerto Rico	7	20	2
Lesser Antilles	9	28	5
South America	11	192	111
Trinidad	5	12	1
Brazil	8	55	19
Colombia	10	83	11
Venezuela	9	86	17
Ecuador	9	82	7
Peru	9	72	12
Bolivia	9	55	7

Table 3. Distribution of New World Grammitidaceae.

Mexican endemics are found in Chiapas (1/37) and Oaxaca (3/33). The sole Guatemala endemic comes from Alta Verapaz (1/23) and Huehuetenango (1/9). For Costa Rica and Panama the distribution of endemic taxa within the country is unknown.

In Cuba the majority of species (or all?) including endemics occur in Oriente; no modern account is available. In Jamaica the majority of species and all endemics occur in St Andrew (2/29), Portland (6/36) and St Thomas (2/30) in the Blue Mountains, John Crow Mountains and the Port Royal Mountains. The Puerto Rico endemics and the

majority of species are found in Jayuya (1/10), Naguabo (1/10) and Río Grande (1/12); the endemics are also known from Adjuntas (1/3), Caguas (1/2) and San Lorenzo (1/3). In the Lesser Antilles the majority of species and the endemics occur on St Kitts (2/10), Montserrat (1/5), Nevis (1/6), Guadeloupe (5/22), Dominica (4/17), Martinique (3/16), St Vincent (2/14) and Grenada (2/12). The New World endemic genus *Lomaphlebia* is restricted to the Greater Antilles, with one species in Cuba and one in Jamaica.

The Trinidad endemic and most other species are restricted to the Northern Range in St George. Brazil's endemic species are found either in the north or in the southeast, and most of the other species are restricted to either or both of these areas. No modern account is available for Colombia and the distribution of endemic taxa within the country is unknown. The monotypic endemic *Luisma* is known only from the Colombian type. Venezuela endemics and the majority of species, occur in Amazonas (5/46) and Bolívar (8/51) in the Venezuelan Guayana and in Aragua (2/21), Mérida (1/24), Tachira (1/13) and Trujillo (3/27) in the Venezuelan Andes. In Ecuador the endemics and the majority of species are found in Azuay (3/16), Carchi (1/28), Loja (1/20), Pichincha (2/42), Tunguragua (1/26) and Zamora (1/23). Peruvian endemics and most species are in Amazonas (1/22), Cuzco (7/40), Huánuco (2/28), Pasco (2/27) and San Martín (1/21). No modern account is available for Bolivia and the distribution of endemic taxa within the country is unknown. The New World Grammitidaceae are most numerous in the Andes from Venezuela to Bolivia, with 141 species known from the mountain chain.

The distribution of Grammitidaceae in African countries having endemic species is shown in Table 4. Countries with no endemic species are Azores (2/2), Canary Islands (1/1), Guinea (3/3), Sierra Leone (3/3), Liberia (4/4), Ivory Coast (3/3), Ghana (1/1), Cameroon (6/6), Bioko (5/5), Equatorial Guinea (1/1), Annobon (1/1), Popular Republic of the Congo (2/2), Democratic Republic of the Congo (4/4), Rwanda (3/3), Uganda (1/1), Kenya (3/3), Zimbabwe (3/3), Mozambique (3/3), Mauritius (9/10), South Africa (2/2), South Atlantic Ocean Islands (2/2) and South Indian Ocean Islands (1/1).

Area	No. of groups	No. of species	No. of species endemic
San Tomé & Principe	5	6	1
Gabon	3	3	1
Ethiopia	2	2	1
Tanzania	9	14	3
Malawi	6	6	1
Madagascar	12	28	12
Comoro Islands	2	2	2
Seychelles	4	4	1
Réunion	11	12	2
Ascension Island	1	1	1
St Helena	1	1	1

Table 4. Distribution of Grammitidaceae in African countries having endemic species.

Cochlidium serrulatum (Sw.) L.E.Bishop, Lellingeria oosora (Baker) A.R.Sm. & R.C.Moran, Melpomene flabelliformis (Poir.) A.R.Sm. & R.C.Moran) and Terpsichore elastica (Bory ex Willd.) A.R.Sm. are widespread in tropical Africa. Some or all four occur in the countries without endemics listed above. The endemic species of San Tome, Gabon, Ethiopia and Malawi are each known from a single gathering. In Tanzania an endemic species and the majority of other species are found on the Uluguru Mounts (1/10). The other endemics occur on Kilimanjaro (1/2) and the Nguru Mounts (1/6). Madagascar endemics and other species are known from Ambazinana (1/3), Ambohimitombo (2/3), Andrangovalo (2/5), Anjenaharibe (2/4), Andohahela (1/4), Andringitra (2/4), Ankafina (2/6), Befingotra (3/7), Manongarivo (4/13), Mantadia (2/7), Marojejy (2/7), Ranomafana (3/8) and Tsaratanana (2/6). The Comoro endemics are found on Anjouan (2 species) and Grande Comore (1 species). All Seychelles species including the endemic are known from Mahé while one species is also found on Silhouette. The endemic and other species of Réunion are found in forest, often above 800-1000 m (Badré and Cadet 1978). The endemic species of Ascension Island and St Helena occur on the summit peaks of the islands. Two groups are endemic to Africa, those of Grammitis cryptophlebia and G. pervillei. The former extends from San Tomé to Mauritius and Réunion while the latter occurs in Tanzania, Madagascar and the Seychelles.

The distribution of Grammitidaceae in Asian countries, excluding Malesia, having endemic species is shown in Table 5. Bhutan (1/1), Nepal (2/2), Thailand (11/27), Cambodia (3/4) and Laos (1/1) have no endemic species.

	No. of groups	No. of species	No. of species endemic
Japan	4	6	5
China	7	13	1
Taiwan	10	19	1
North & Northeast India	3	3	1
South India	5	8	2
Sri Lanka	9	22	9
Vietnam	10	19	1

Table 5. Distribution of Grammitidaceae in Asia (excluding Malesia), having endemic species.

Japanese endemic and other species are found in Honshu (2/3), Shikoku (1/2) and Kyushu (3/4), while the species of Ryukyu (2/2) and Iwo-jima (1/1) are all endemic. In China the endemic and other species occur in Fujian (1/3), Guangxi (1/3) and Zhejiang (1/2). Hainan (6/8) is the most species-rich area of China. The endemic species of Taiwan is known from Takaio (probably in southern Taiwan), where the majority of species are found. The Indian endemic occurs in Meghalaya and Assam, while the other two Indian species are in Sikkim (2), Manipur (1), Meghalaya (1) and Nagaland (1). In South India the endemic species and all other species are in Tamil Nadu. The Sri Lanka endemics and the majority of other species are confined to the upland areas between c. $6^{\circ}30'-7^{\circ}30'N 80^{\circ}20'-81^{\circ}20'E$. In Vietnam the endemic species occurs in Nhatrang (1/13), as do the majority of other species, but no groups are endemic to this area.

The distribution of Grammitidaceae in Malesian phytogeographic regions having endemic species is shown in Table 6. Singapore (1/1) and the Lesser Sunda Islands (6/17) have no endemics.

Table 6.	Distribution	of Malesian	Grammitidaceae.
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Area	No. of groups	No. of species	No. of species endemic
Peninsular Malaysia	13	48	6
Sumatra	12	57	4
Java	10	50	5
Borneo	16	91	14
Sulawesi	14	45	5
Moluccas	13	66	9
Philippines	13	68	12
New Guinea	14	161	91

In Peninsular Malaysia the endemic and other species are found in Pahang/Selangor (Cameron Highlands (1/23), Gunung Tahan (1/21), Fraser's Hill (1/19), Gunung Ulu Kali (1/11)), Perak (Larut Hills (1/17), Melaka (Gunung Ledang (1/6)), Johor (Gunung Belumut (2/4), Gunung Mering (1/3)) and Kedah (Gunung Jerai (1/3)). Sumatran endemics and most other species occur on Gunung Kerinci/Gunung Tujuh (1/22), Gunung Singalang (1/17) and Gunung Kemiri (1/16); other endemics are known from Gunung Dempo (2/2), Laë Pondom (1/8), Goh Lembuh (1/4) and Bukit Sipitai (1/3); Gunung Losir has 12 species, none endemic. In Java nearly all of the species, and all endemics are on Mount Gede/Pangrango (5/41); the only other site with more than 5 species is Gunung Patuha (1/7). In Borneo most endemics and the majority of species occur on Mount Kinabalu in Sabah (10/77); other endemics are known from Gunung Mulu (3/40+), Pueh Range (1/11), Mount Penrissen (1/8), Mount Dulit (2/7), Ba Kelalan (1/3) and Kelabit Highlands (1/3) in Sarawak, the Crocker Range (1/13) in Sabah, Gunung Besar (1/5), Bukit Raja (1/4), Gunung Murud (1/3) and Gunung Kemul (1/2) in Kalimantan, and Mt Galegas (1/1) in Brunei. Sulawesi endemics and the majority of species occur on Mt Roroka Timbu (3/25), while other endemics are known from Gunung Matinang (1/2) and Mt Busu (1/1). In the Moluccas all of the endemics and nearly all of the species are found on Seram (9/60). The Philippine endemics and the majority of other species are found on Luzon (5/44), Mindanao (7/48) and Mindoro (1/12), with the greatest number of species occurring on Mount Apo (27) and Mount Dulang-Dulang (17) in Mindanao, and Mount Banahaw (18) and Mount Pulog (16) in Luzon. In New Guinea the endemics are found in 79 localities, the most important of which are Mount Java (9/50), Mount Trikora (3/15), Lake Habbema (4/24) and Mount Doorman (6/21) in the Central Ranges of West Papua, and Mount Hagen (7/36) in Western Highlands, Tari Gap (4/15) in Enga District, Mount Giluwe (6/36) in Southern Highlands District, Mount Wilhelm (3/24) in Simbu District, Mount Otto (4/12) and Mount Piora (3/17) in Eastern Highlands District, Aseki (4/21), Matap (3/17), Rawlinson Range (8/32), Saruwaged Range (9/38) and Ekuti Range (3/20) in Morobe District, Boridi (3/7) and Mount Albert Edward (3/15) in Central District, Mount Suckling (5/20), Fergusson Island (3/12) and Normanby Island (3/8) in Milne Bay District, Papua New Guinea. The group of Ctenopteris whartoniana is endemic to East Malesia and ranges from Seram in the Moluccas to Papua New Guinea.

For Malesia the diversity and endemicity figures presented above are arranged in the floristic units that are recognised in the literature for Flora Malesiana, but it is expedient to list them also by political rather than geographic boundaries for conservation purposes (Table 7).

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Table 7. Distribution of Malesian Grammitidaceae by country.

Country	No. of groups	No. of species	No. of species endemic
Malaysia	15	97	13
Singapore	1	1	0
Brunei Darussalam	8	12	1
Indonesia	16	162	48
Philippines	13	68	12
Papua New Guinea	14	131	46

Table 8 shows the distribution of Grammitidaceae in the Pacific countries with endemic species. Tonga (1/1) has no endemic.

No. of groups	No. of species	No. of species endemic
7	24	13
1	12	5
10	28	5
8	14	3
7	11	5
7	16	7
9	18	8
2	2	1
2	2	2
9	15	10
	No. of groups 7 1 10 8 7 7 9 2 2 2 2 9	No. of groupsNo. of species72411210288147117169182222915

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Table 8. Distribution of Pacific Grammitidaceae.

Marguesas Islands

Hawaiian Islands

Federated States of Micronesia

In Australia the highest number of species and endemics are in northeast Queensland, mostly between 16–19°S 145–146°E (9/14), other endemics are on Lord Howe Island (3/3) and Tasmania (1/7). The endemic and the majority of other species in New Zealand are in North Auckland (2/6), South Auckland (3/8), Taranaki (2/7), Gisborne (2/7), Wellington (2/8), Nelson (2/8), Marlborough (2/7), Westland (2/7), Canterbury (2/7), Otago (1/7) and Southland (3/10), endemics are also known from Stewart Island (2/6), Auckland Islands (2/6), Antipodes Island (1/3) and Chatham Islands (1/3). In the Solomon Islands the endemic and most of the other species occur on Guadalcanal (2/16), Kolombangara (2/14) and Bougainville (2/13); another endemic is on San Cristobal (1/3). In Vanuatu the endemic and most other species are on Espiritu Santo (2/8) and Tanna (1/4); Aneitum also has 8 species, none endemic. The Grammitidaceae of New Caledonia, including the endemic species, are distributed in

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13

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the forest areas along the centre and east of the island in numerous localities. The Fijian endemic and most other species are on Viti Levu (4/12), Vanua Levu (4/11), Taveuni (2/6) and Ovalau (1/3). In Samoa the endemics and the majority of species occur on Upolu (5/14) and Savai'i (5/13); other islands with endemic species are Tutuila (2/5), T'au (1/4) and Olosina (1/3). The species of the Cook Islands are restricted to Rarotonga (1/2) and the two endemic species of Rapa are known only from Mount Perahu. In the Society Islands the endemics and most of the species are found on Raiatea (6/8) and Tahiti (5/11), with endemics also occurring on Huahine (2/3) and Tahaa (2/3). The Marquesas Islands endemics and most of the species are known from Nuku Hiva (3/5) and Hiva Oa (2/6), with another endemic on Ua Pou (1/2). In the Hawaiian Islands the endemics and all species are found on Hawaii (6/7), Kauai (12/13), Lanai (7/8), Maui (8/9), Molokai (8/9) and Oahu (9/10). The endemic and all other species in the Federated States of Micronesia are found on Ponape, Caroline Islands (3/6) and Babeldoab, Palau Islands (3/4). In the Pacific the group of Ctenopteris lasiostipes is endemic to New Caledonia and Adenophorus is endemic to the Hawaiian Islands.

Discussion

This treatment of the distribution of Grammitidaceae must be regarded as preliminary, providing an outline of the areas of group and species richness and indicating areas of species endemism. Essentially it summarises our current knowledge concerning what is where and is of course incomplete. The hows and whys of distribution within the family may be addressed with some hope of success later, when we have a family phylogeny.

Grammitidaceae are known from a total of 93 countries. The countries with the highest number of groups in the Old World are Indonesia (16), Malaysia (15) and Papua New Guinea (14); in the New World they are Colombia (10) and Jamaica (10). Old World countries with the most species are Indonesia (162), Papua New Guinea (131), Malaysia (97) and Philippines (68). New World countries with the most species are Venezuela (86), Colombia (83), Ecuador (82) and Costa Rica (78). It is useful to compare the areas of high diversity in Grammitidaceae with the areas identified by Groombridge and Jenkins (2002) as important centres of plant diversity at regional and global levels. In Indonesia areas of significant diversity are Murkele Ridge in Seram, Moluccas (55 species), Mount Jaya in West Papua (50 species), and Mount Gede/Pangrango (3000 m) in Java, Indonesia (41 species). Mount Java is identified as important by Groombridge and Jenkins (2002), but the other two Indonesian areas are not. In Papua New Guinea the Saruwaged Range (38 species) and Mount Hagen and Mount Giluwe in Papua New Guinea (both with 36 species) are important for Grammitidaceae and also important for plant diversity as a whole. In Malaysia, Mount Kinabalu in Sabah (77 species), Gunung Mulu in Sarawak (40 species) and Cameron Highlands in Peninsular Malaysia (23 species) are important for Grammitidaceae and also for plant diversity in general. In the Philippines, Mount Apo (27 species) and Mount Dulang-Dulang (17 species) in Mindanao, and Mount Banahaw (18 species) and Mount Pulog (16 species) in Luzon have the greatest diversity of Grammitidaceae. None of these areas is identified as important by Groombridge and Jenkins (2002). In the New World, areas of diversity in Colombia and Costa Rica have not been identified because of the paucity of information about distribution within these countries. In Venezuela the states of Amazonas (46 species) and Bolívar (51 species) in the Venezuelan Guayana (total 54 species), and Trujillo (27 species) and Mérida (24 species) in the Venezuelan Andes are important centres for Grammitidaceae. The Venezuelan Guayana is identified as important by Groombridge and Jenkins (2002),

but not the other two. In Ecuador, Pichincha (42 species), Carchi (28 species) and Tunguragua (23 species) are richest in Grammitidaceae. Parts of these areas have been identified as important by Groombridge and Jenkins (2002). It is evident that on a world scale areas of diversity in Grammitidaceae do not overlap completely with those of plants as a whole. Apart from the areas cited above with high species numbers there are other locations, e. g. in Cuba, Tanzania and Madagascar that are important for Grammitidaceae rather than plants in general. It is hoped that their diversity and endemicity is adequately protected.

Old World countries with the most endemics are Indonesia (48), Papua New Guinea (46) and Australia, Malaysia and Hawaiian Islands (all with 13). New World countries with the most endemics are Brazil (19), Venezuela (17), Peru (12) and Colombia (11). It is interesting to compare the percentage of endemics in countries with high numbers of endemic species in Grammitidaceae with the figures for plant endemicity cited by Groombridge and Jenkins (2002) in their survey of biodiversity at country level. Indonesia has the highest number of endemic species in the family, comprising 30% of the total, which is similar to the figure of 27% for plants as a whole there. Papua New Guinea has 35% of Grammitidaceae endemic, but no figures are available for plants. Australia has high plant endemism (90%) but the figure for Grammitidaceae is much lower, 54%. Malaysian endemic Grammitidaceae are 13% of the total, compared with 23% for plants in general. The Hawaiian Islands have the highest percentage of endemism in Grammitidaceae (93%). Separate figures for Hawaiian Islands plants are not provided by Groombridge and Jenkins (2002), but Palmer (2002) gives a figure of 77% for endemicity in Hawaiian Islands pteridophytes and Wagner et al. (1990) cite a figure of 89% for angiosperms. Brazil endemic Grammitidaceae form 35% of the total, but no plant figures are available. The proportion of Grammitidaceae in Venezuela (20%), is much lower than that of plants in general (37%), in Peru 17% of Grammitidaceae are endemic, compared with 31% of plants and in Colombia 13% of Grammitidaceae are endemic, compared with 29% of plants.

The percentage figures for endemicity in Australia, Colombia, Malaysia, Peru and Venezuela for Grammitidaceae are probably lower than those for plants in general because of the greater vagility of wind-blown spores. The figure for the Hawaiian Islands Grammitidaceae is high largely because of the species radiation of *Adenophorus*.

The total number of species endemic to a single country is 364, i. e. 49% of species in the family. It is likely to rise when the unresolved complexes in *Calymmodon, Ceradenia, Ctenopteris* and *Zygophlebia* are dealt with. The taxonomic status of some endemic species in groups yet to be revised needs to be confirmed, and the continued existence of some endemics needs to be verified. For example, *Grammitis tomensis* Schelpe has not been recorded during the 20th century (Figueiredo 2000), and *Terpsichore kirkii* Parris is known only from the type, collected in the 19th century. Many endemic species are known only from the type collection or from one locality and their conservation status remains unknown. Some may well be extinct. It is matter of some urgency to document them more fully.

The pteridophyte flora of Seram has been estimated by Kato (1990) as over 700 species, a surprisingly high figure. The number of species of Grammitidaceae, 60, is also unexpectedly high. The Murkele Ridge, including Gunung Binaiya (3000 m), supports 55 species, but even much lower areas, such as Gunung Kobipoto (16 species) and Gunung Roihelu (13 species) that are c. 1500 m alt., have significantly greater numbers of species than areas of similar altitude elsewhere. The Moluccas lie between the two great centres of botanical diversity in eastern and western Malesia and part of the species richness of Seram is due to an overlap of elements from both centres. Elsewhere in the Moluccas there appear to be far fewer species of Grammitidaceae.

Ambon has 4, Bacan 6, Buru 4, Halmahera 4 and Tidore 3, but based on the figures for Seram, far more would be expected. Another of the reasons for Seram's diversity appears to be that the four botanical expeditions responsible for nearly all of the material gathered there have included experienced pteridologists who have been assiduous in collecting the smaller and less obvious species. If the collecting of Grammitidaceae were carried out to the same standard elsewhere it would probably lead to a significant increase in the numbers of species in most areas, an increase in new species and possibly significant range extensions of already described species.

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