RESEARCH ARTICLE

A global phylogeny of grammitid ferns (Polypodiaceae) and its systematic implications

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Abstract Grammitidoideae are the largest subfamily in Polypodiaceae and contain about 911 species. Progress has been made in understanding the overall phylogeny and generic boundaries in the light of recent molecular works. However, the majority of species, especially Asian species, and some critical type species of genera remain unsampled. In this study, a dataset of six plastid markers of 1003 (112 new) accessions representing ca. 412 species of Grammitidoideae including the type species of *Ctenopterella*, *Grammitis*, *Moranopteris*, *Radiogrammitis*, and *Themelium*, was assembled to infer a phylogeny. Our major results include: (1) the type species of *Grammitis* is successfully sequenced using a next-generation sequencing technique and is resolved in *Grammitis* s.str. as expected; (2) *Ctenopterella* is found to be polyphyletic and a new clade consisting of *C. khaoluangensis* is resolved as sister to *Tomophyllum*; (3) the type species of *Ctenopterella* is resolved in a clade sister to the *C. lasiostipes* clade; (4) *Oreogrammitis* is found to be polyphyletic and three clades outside of the core *Oreogrammitis* are identified containing *O. subevenosa* and allies, *O. orientalis*, and *O. beddomeana* (+ *O.* cf. *beddomeana*); (5) *Prosaptia* is found to be paraphyletic with *P. nutans* being sister to a clade containing the rest of *Prosaptia* and *Archigrammitis*; (6) the intergeneric and major relationships within the Asia-Pacific clade are well resolved and strongly supported except for a few branches; (7) extensive cryptic speciation is detected in the Asia-Pacific clade; and (8) based on the polyphyly of *Ctenopterella* we describe three new genera, *Boonkerdia*, *Oxygrammitis*, and *Rouhania*, for species formerly in *Ctenopterella*; because the type species of *Grammitis* belongs to *Grammitis* s.str., we describe five new genera, *Aenigmatogrammitis*, *Grammitastrum* (stat. nov.), *Howeogrammitis*, *Nanogrammitis*, and *Thalassogrammitis* for species formerly in *Grammitis* s.l. A key to the 35 Old-World genera is given, a taxonomic treatment is presented, and the morphology of all new genera is shown with either a color plate and/or a line drawing.

Keywords *Archigrammitis*; Asia-Pacific clade; *Ctenopterella*; *Grammitis*; *Oreogrammitis*; *Prosaptia*

Supporting Information may be found online in the Supporting Information section at the end of the article.

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■ INTRODUCTION

As one of the nine subfamilies in the fern family Polypodiaceae (Wei & Zhang, 2022), Grammitidoideae contain about 911 species (PPG I, 2016) or about two-thirds of the species diversity in the family (Sundue & al., 2014). Grammitidoideae were recognized by many botanists (Evans, 1963; Ranker & al., 2004; Sundue & al., 2014; Bauret & al., 2017) but sometimes were placed in their own family, Grammitidaceae (Ching, 1940; Parris, 1990; Ranker & al., 2004; Schneider & al., 2004). Notably, they are not recognized as a separate family now because they are nested within Polypodiaceae (Schneider & al., 2004; Schuettpelz & Pryer, 2007; Du & al., 2021). Primarily epiphytic ferns (Parris, 1990), Grammitidoideae are a natural group characterized in general by small size, scales usually present on rhizomes but absent from laminae, rhizome usually short-creeping, a single vascular strand in the petiole, exindusiate sori, sporangial stalk of one row of cells, and trilete spores with chlorophyll (Ching, 1940; Wagner, 1985; Parris, 1990; Sundue, 2010a; Sundue & al., 2010; Mellado-Mansilla & al., 2021). Grammitidoideae are a characteristic and important component of rainforests in tropical montane regions of the Old World and the New World, extending to the North Temperate Zone, not beyond 40°N and to the South Temperate Zone to 56°S. Seasonal dryness is the major limiting factor in their distribution (Parris, 2003). In the tropics, the average daily lower limit of cloud formation is an important determiner of the lower limits of distribution (Parris, 2003). A few species are found in tropical lowland forest associated with rivers, either as epiphytes on trees overhanging the water or as facultative or obligate rheophytes on rocks in and by water (Parris, 2003). They are estimated to have diverged from their closest relatives, subfamily Polypodioideae, 40.8 million years ago (Testo & Sundue, 2016), and evidence from a Dominican amber fossil showed that Grammitidoideae inhabited the Neotropics in the Tertiary (Sundue & Poinar, 2016).

Generic circumscription has changed considerably in Grammitidoideae as new studies have revealed that some taxonomic characters traditionally relied upon were homoplastic (Ranker & al., 2004; Sundue, 2010a). For most of the 20th century, most species of Grammitidoideae were placed in three genera based on the degree of frond dissection: *Grammitis* Sw., with fronds ± entire, *Xiphopteris* Kaulf., with fronds lobed, and *Ctenopteris* Blume ex Kunze with fronds deeply pinnately divided to tripinnatifid. Indeed, the generic classification in Grammitidoideae has changed dramatically in the last ca. 40 years, beginning with morphology-based additions and more recently mostly in the light of molecular phylogenies. So far 38 genera have been generally recognized in the subfamily (PPG I, 2016; Shalisko & al., 2019; Yang & al., 2023; but see Parris & Sundue, 2020, below), 26 of which were newly established between 1988 and 2023: *Alansmia* M.Kessler & al., (Kessler & al., 2011), *Archigrammitis* Parris (Parris, 2013a), *Ascogrammitis* Sundue (Sundue, 2010b), *Calligrammitis* Parris & al. (Yang & al., 2023), *Ceradenia* L.E.Bishop (Bishop, 1988), *Chrysogrammitis* Parris (Parris, 1998), *Ctenopterella* Parris (Parris, 2007), *Dasygrammitis* Parris (Parris, 2007), *Devolia* Li Bing Zhang & al. (Yang & al., 2023), *Galactodenia* Sundue & Labiak (Sundue & al., 2012), *Glabrigrammitis* Li Bing Zhang & al. (Yang & al., 2023), *Lellingeria* A.R.Sm. & R.C.Moran (Smith & al., 1991), *Leucotrichum* Labiak (Labiak & al., 2010), *Luisma* M.T.Murillo & A.R.Sm. (Murillo & Smith, 2003), *Melpomene* A.R.Sm. & R.C.Moran (Smith & Moran, 1992), *Moranopteris* R.Y.Hirai & J.Prado (Hirai & al., 2011), *Mycopteris* Sundue (Sundue, 2014), *Notogrammitis* Parris (Perrie & Parris, 2012), *Parrisia* Shalisko & Sundue (Shalisko & al., 2019), *Radiogrammitis* Parris (Parris, 2007), *Stenogrammitis* Labiak (Labiak, 2011), *Terpsichore* A.R.Sm. (Smith, 1993), *Themelium* (T.Moore) Parris (Parris, 1997), *Tomophyllum* (E.Fourn.) Parris (Parris, 2007), *Xiphopterella* Parris (Parris, 2007), and *Zygophlebia* L.E.Bishop (Bishop, 1989). Recently, a monophyletic clade (ORT clade; Sirimalwatta, 2019) including *Oreogrammitis* Copel., *Radiogrammitis*, and *Themelium* has been united in *Oreogrammitis* (Parris & Sundue, 2020), which reduced the number of recognized genera in Grammitidoideae to 36. In contrast to the earlier 20th century genera, these more recently described genera are much better defined morphologically, albeit often with obscure characters.

Molecular data so far have resolved many backbone relationships within Grammitidoideae (Ranker & al., 2004; Perrie & Parris, 2012; Sundue & al., 2014; Bauret & al., 2017; Shalisko & al., 2019; Sirimalwatta, 2019). Parris (2003) first pointed out that there are two major phytogeographical zones in grammitids: the Americas plus Africa, and Asia-Malesia-Pacific. Subsequent phylogenetic analyses have shown that the American and some African taxa (ca. 17 genera/clades) together form a grade (amphi-Atlantic grade; Bauret & al., 2017), whereas the Asia-Pacific taxa (ca. 19 genera/clades) together are monophyletic (Asia-Pacific clade ["paleotropical clade"]; Sundue & al., 2014; Bauret & al., 2017). Biogeographical studies suggested that Grammitidoideae originated in Neotropical regions, and the current distribution pattern is driven by numerous transatlantic long-distance dispersal events (Sundue & al., 2014; Bauret & al., 2017).

Whereas the phylogeny of the amphi-Atlantic grade in Grammitidoideae has recently been updated, providing strong support for a number of relationships found earlier (Shalisko & al., 2019), relationships within the Asia-Pacific clade remain largely unresolved or only weakly/moderately supported except those between a portion of *Ctenopterella* and a portion of *Grammitis* + *Notogrammitis* even in the latest global phylogeny (Bauret & al., 2017).

At the generic level, molecular studies have sampled 31 out of the 36 genera recognized and the only 5 genera that have not yet been sampled are *Archigrammitis* and *Luisma* (Bauret & al., 2017; Shalisko & al., 2019) plus the three newly described genera, *Calligrammitis*, *Devolia*, and *Glabrigrammitis* (Yang & al., 2023). Molecular data have also supported the monophyly of 27 genera in Grammitidoideae, whereas

3 genera, *Ctenopterella*, *Grammitis*, and *Oreogrammitis* sensu Parris & Sundue (2020), have not been supported as monophyletic, with *Ctenopterella* and *Grammitis* being highly polyphyletic (Ranker & al., 2004; Sundue & al., 2014; Bauret & al., 2017; Shalisko & al., 2019). Only one species of *Acrosorus* Copel. had been included in previous studies, and thus the monophyly of that genus was unknown (Sundue & al., 2014; Bauret & al., 2017) until a recent study by Liu & al. (2022), who included two species and supported the monophyly of the genus. Previous studies included 27 type species of accepted genera (Ranker & al., 2004; Perrie & Parris, 2012; Sundue & al., 2014; Bauret & al., 2017; Shalisko & al., 2019), whereas the remaining 9 type species had not yet been included in earlier molecular works (Appendix 1). Those nine type species included those of the highly polyphyletic *Ctenopterella* and *Grammitis*, preventing the accurate delimitation of these species-rich genera.

At the species level, earlier studies were based on relatively large taxon sampling by including 202, 266, and 396 accessions representing 190, 221, and 224 species by Sundue & al. (2014), Shalisko & al. (2019), and Bauret & al. (2017), respectively. The species included were from both the New World and the Old World (especially Africa and Madagascar; Bauret & al., 2017). However, the majority (ca. 75%) of ca. 911 species of Grammitidoideae (PPG I, 2016) have not yet been sampled. This is particularly true for the ca. 515 (Parris, unpub. data) Asia-Pacific species. The largest taxon sampling so far sampled 55 accessions representing only 42 (less than 10%) of Asian-Pacific species (Bauret & al., 2017).

In this study we aimed: (1) to infer a comprehensive phylogeny of Grammitidoideae based on the largest taxon sampling so far with particular focus on Asian-Pacific species; (2) to further resolve the relationships and the delimitations of the genera in Grammitidoideae, especially those in the Asian-Pacific clade including *Archigrammitis*; (3) to further test the monophyly of the genera in Grammitidoideae by including the types of *Moranopteris*, *Radiogrammitis*, and *Themelium*; (4) to assess and redefine the circumscription of *Ctenopterella* and *Grammitis* by including the type species of each of the two genera for the first time; (5) to detect new clades, if any, and to make new taxonomic treatments, if needed; and (6) to discover new species complexes and cryptic speciation by including multiple accessions of widely distributed taxa for future morphological and taxonomical studies.

■ MATERIALS AND METHODS

Taxon sampling. — A total of 112 accessions representing 48 species were newly sequenced. Of the 112 new accessions, 100 representing ca. 40 species were from Asia and 21 of the 40 Asian species were newly sampled. Combined with published molecular data, a total of 1003 (891 + 112) accessions representing ca. 412 (ca. 45%) species in 35 out of 36 (except *Luisma*) accepted genera of Grammitidoideae were used as the ingroup. One accession of *Archigrammitis* was sampled for the first time for a grammitid phylogeny in maximum parsimony and maximum likelihood analyses, but five accessions with nearly identical sequences were used in Bayesian inference analysis (unpub. data of the four accessions were from GenBank). Type species of two genera, *Ctenopterella* and *Grammitis*, also were included for the first time in addition to that of *Moranopteris*, which was included for the third time. The yet to be sampled type species included those of *Archigrammitis*, *Calymmodon* C.Presl, *Cochlidium* Kaulf., and *Oreogrammitis*.

Two species, *Davallia trichomanoides* Blume and *D. yunnanensis* Christ, of Davalliaceae, and 15 species from seven out of the remaining eight subfamilies in Polypodiaceae were chosen as the outgroups (Wei & Zhang, 2022). Voucher information and GenBank accession numbers for each sampled taxon in this study are listed in Appendix 2.

Morphology. — Morphological data were derived from field observations, herbarium specimen examination (CDBI, KUN, MO, P, PYU), and published studies (e.g., Parris, 2003, 2005, 2007, 2013a,b, 2018; Sundue & al., 2010, 2014; Knapp, 2011; Perrie & Parris, 2012; Zhang & al., 2013; Parris & al., 2015; Bauret & al., 2017; Knapp & Hsu, 2017; Shalisko & al., 2019; Parris & Sundue, 2020). Field observations were mainly conducted by X-MZ, RP, RK, BP, MS, TAR, Z-LL, NTL, TTL, LZ, and L-BZ. Relevant specimens in JSTOR Global Plants (https://plants.jstor.org/), GBIF (https://www.gbif.org), and some other online images (e.g., BM, E, P, K, U) were examined.

DNA extraction, amplification, and Sanger sequencing. — Sanger sequencing was conducted for 107 out of the 112 new accessions. Genomic DNA was extracted using a TIANGEN plant genomic DNA extraction kit (TIANGEN Biotech., Beijing, China) under the manufacturer's protocols from silica-dried materials. For the plastid regions, three coding genes (*rbcL*, *atpB*, *rps4*), and three non-coding intergenic spacers (*rps4-trnS*, *trnG-R*, *trnL-F*) were sequenced similar to previous phylogenetic studies of Grammitidoideae (Sundue & al., 2014; Bauret & al., 2017). The *rbcL* sequences were amplified with primers F1 (Fay & al., 1997) and 1379R designed by Zurawski & al. (1984). The *atpB* sequences were amplified with ESATPB172F (Schuettpelz & Pryer, 2007) and ESATPE45R (Schuettpelz & Pryer, 2007). The *trnG-R* sequences were amplified with TRNG1F (Nagalingum & al., 2007) and TRNR22R (Nagalingum & al., 2007). The *rps4* gene and *rps4-trnS* intergenic spacer sequences were amplified with primer TRNS (Souza-Chies & al., 1997) and an unnamed primer derived from Li & Lu (2006). The *trnL* intron and *trnL-F* intergenic spacer sequences were amplified together using the primers FERN1 (Trewick & al., 2002) and F (Taberlet & al., 1991). All polymerase chain reaction conditions followed previous studies. PCR products were sequenced by Tsingke Biotechnology (Kunming, China).

Plastome assembly and annotation. — We attempted to sequence the plastomes of 11 samples from six genera using the next-generation sequencing (NGS) technology described in Zhou & al. (2022). These 11 relatively old samples were all from herbarium specimens and Sanger sequencing did not work.

DNA extraction, library preparation, and Illumina sequencing were carried out by the Molecular Biology Experiment Center, Germplasm Bank of Wild Species in Southwest China. Plastomes were assembled using the GetOrganelle toolkit v.1.7.5 (Jin & al., 2020). Complete circular chloroplast genomes from our study and GenBank were initially annotated using CPGAVAS2 (Shi & al., 2019), GeSeq (Tillich & al., 2017), and PGA (Qu & al., 2019). Due to DNA degradation, scaffolds of some materials were annotated using the three tools mentioned above. The positions of starts, stops, and introns of the annotated sequences were all manually adjusted in Geneious Prime 2021.2.2 by referring to published plastomes of Polypodiaceae (*Lepisorus clathratus* Ching, NC035739; *Selliguea yakushimensis* Fraser-Jenk., MN623352). The chloroplast genome composition of *Grammitis marginella* (Sw.) Sw. was elucidated using Chloroplot (Zheng & al., 2020). Six DNA regions (*atpB*, *rbcL*, *rps4*, *rps4-trnS*, *trnG-R*, *trnL-F*) were extracted from the plastid genomes and used for phylogenetic analyses.

Sequence alignment and phylogenetic analysis. — Sequencher v.4.1.4 was used to assemble contigs and edit amphibolous loci based on chromatograms. Sequences of each plastid region from GenBank and the newly generated data were aligned using MAFFT v.7 (Katoh & Standley, 2013) and adjusted manually in BioEdit (Hall, 1999). Based on the Akaike information criterion, the selection of the appropriate nucleotide substitution model of maximum likelihood (ML) was carried out using ModelFinder (Kalyaanamoorthy & al., 2017) for each DNA region and concatenated data. The best-fitting models and parameter values are provided in Table 1.

For each plastid gene region and the combined data with a governing model, ML tree searches and ML bootstrapping were conducted using RAxML-HPC2 v.8.2.12 with 1000 rapid bootstrap (BS) analyses followed by a search for the best-scoring tree in a single run (Stamatakis, 2014).

Equally weighted maximum parsimony (MP) analyses for each locus and the combined dataset were conducted in PAUP* v.4.0b10 (Swofford, 2002) using 1000 tree-bisection-reconnection (TBR) searches with MAXTREES set to increase without limit. Gaps were coded as missing data. Parsimony jackknife (JK) analyses (Farris & al., 1996) were conducted using PAUP* with the removal probability set to approximately 37%, and "jac" resampling emulated. One thousand replicates were performed with 10 TBR searches per replicate and a maximum of 100 trees held per TBR search.

Bayesian inference (BI) was conducted using MrBayes v.3.27 (Ronquist & Huelsenbeck, 2003) on CIPRES (Miller & al., 2010). Four Markov Chain Monte Carlo (one cold, three heated) were run and started with a random tree. A total of 10 million generations were run with sampling every 1000

Table 1. Best-fitting models and parameter values for separate and concatenated plastid datasets in this study.

		Base frequencies				Substitution model (rate matrix)								
Region	AIC selected model	A	C	G	T	A-C	A-G	A-T	C-G	C-T	G-T	Ti/Tv	I	G
Plastid *atpB* gene	GTR+F+I+G4	0.282	0.201	0.246	0.271	1.66639	7.56842	0.61832	0.76165	9.83296	1.00000	–	0.468	0.678
Plastid *rbcL* gene	GTR+F+I+G4	0.271	0.204	0.248	0.277	2.08804	8.69939	1.32367	1.05295	13.31010	1.00000	–	0.425	0.622
Plastid *rps4* gene & *rps4-trnS* spacer	GTR+F+I+G4	0.337	0.152	0.178	0.333	0.97100	2.89464	0.25627	0.77283	3.28433	1.00000	–	0.179	2.012
Plastid *trnL* intron & *trnL-F* spacer	GTR+F+I+G4	0.320	0.187	0.179	0.315	0.99437	2.67583	0.36317	0.52147	2.43630	1.00000	–	0.129	1.949
Plastid *trnG-R* spacer	GTR+F+I+G4	0.344	0.168	0.162	0.325	1.22273	3.30207	0.32487	0.72825	2.80242	1.00000	–	0.148	1.085
Concatenated	GTR+F+I+G4	0.294	0.192	0.223	0.290	1.32658	3.98016	0.55559	0.61145	4.63677	1.00000	–	0.336	1.000

"G" = gamma distribution shape parameter (Yang, 1994). "GTR" = general-time-reversible model (Tavaré, 1986). "I" = proportion of invariable sites. "Ti/Tv" = transition/transversion ratio.

generations. Convergence among generations was checked using Tracer v.1.4 (Rambaut & al., 2018) and the first 25% of samples from the cold chain were discarded as burn-in. The remaining 7.5 million trees were used to calculate a 50% majority-rule consensus topology and posterior probability (PP) values.

Criteria for defining genera. — When proposing a new genus, we used two main criteria: (1) well-supported monophyly reflecting evolutionary distinction; and (2) morphological discontinuity allowing diagnosability. We also found that, in some cases, geographical distribution was informative when the second criterion was ambiguous.

■ RESULTS

A total of 444 Sanger sequences were generated for this study (Appendix 2). Five out of the 11 accessions from six genera were successful in plastome sequencing. Three out of these five accessions represented types of *Grammitis marginella* (*A. Rojas 8597*), *Moranopteris basiattenuata* (Jenman) R.Y. Hirai & J.Prado (*G. Davidse 34809*), and *Themelium tenuisectum* (Blume) Parris (*B.C. Stone 13773*). The plastome of *Grammitis marginella* is shown in suppl. Fig. S1. Six DNA regions were extracted from the plastid genomes and aligned with other Sanger data. The final aligned dataset consisted of 5854 sites, of which 2849 (48.7%) were parsimony informative (Table 2). Comparisons of tree topologies from the MLBS analyses of the individual markers (*rps4* and *rps4-trnS* combined) and the combined plastid dataset did not identify any well-supported conflicts (MLBS ≥ 70%; Mason-Gamer & Kellogg, 1996; Zhang & Simmons, 2006). The simplified ML tree is shown in Fig. 1 and the detailed tree is shown in suppl. Fig. S2. The alignment and ML tree are deposited in TreeBase (http://purl.org/phylo/treebase/phylows/study/TB2:S29551).

Grammitidoideae were monophyletic (MLBS: 100%, BIPP: 0.51, MPJK: 100%; Fig. 1, suppl. Fig. S2) and were resolved into a paraphyletic amphi-Atlantic grade and a monophyletic Asia-Pacific clade (MLBS: 94%, BIPP: –, MPJK: –; "–" means a value <50% or <0.5). Within the amphi-Atlantic grade, clade A (*Adenophorus* Gaudich., *Cochlidium*, *Grammitis*, *Lomaphlebia* J.Sm., *Parrisia*, *Terpsichore*) (MLBS: 72%, BIPP: 0.6, MPJK: 81%) was sister (MLBS: 100%, BIPP: 0.51, MPJK: 99%) to the rest, followed by the *Alansmia* + *Leucotrichum* clade (MLBS: 62%, BIPP: 0.58, MPJK: 52%), and further by the *Ceradenia* + *Enterosora* clade (MLBS: 56%, BIPP: 0.97, MPJK: –), and by clade B (*Ascogrammitis*, *Galactodenia*, *Lellingeria*, *Melpomene*, *Mycopteris*, *Stenogrammitis*) (MLBS: 99%, BIPP: 1.0, MPJK: 92%), which was sister to *Moranopteris* + the Asia-Pacific clade. Within the clade A, *Terpsichore* was sister (MLBS: 72%, BIPP: 0.60, MPJK: 81%) to the rest, followed by the *Adenophorus* + *Parrisia* clade (MLBS: 82%, BIPP: 0.65, MPJK: 58%), which was sister to *Lomaphlebia* + (*Cochlidium* + *Grammitis*) (MLBS: 100%, BIPP: 0.94, MPJK: 99%). The relationships within clade A were all well supported. Within clade B, *Ascogrammitis* was sister to the rest, sequentially followed by *Mycopteris*, *Galactodenia*, *Melpomene*, *Lellingeria*, and *Stenogrammitis*. The relationships within clade B were all well supported except the one between *Mycopteris* and its sister, which was supported by moderate values (MLBS: 69%, BIPP: 1.0, MPJK: 71%).

Within the Asia-Pacific clade, the *Nanogrammitis* Parris & al. (*Grammitis holophlebia* (Baker) Copel. & allies) + *Rouhania* Li Bing Zhang & al. (*Ctenopterella zenkeri* (Hieron.) Parris & allies) clade (MLBS: 98%, BIPP: 1.0, MPJK: 98%) was sister (MLBS: 94%, BIPP: –, MPJK: –) to the rest, followed by *Chrysogrammitis*, and further by clade C (*Boonkerdia* [*Ctenopterella khaoluangensis* and allies], *Calymmodon*, *Dasygrammitis*, *Devolia* Li Bing Zhang & al. [*Oreogrammitis orientalis*], *Micropolypodium* Hayata, *Scleroglossum* Alderw., *Tomophyllum*, *Xiphopterella*) (MLBS: 98%, BIPP: 0.78, MPJK: 97%), which was sister (MLBS: 78%, BIPP: 0.51, MPJK: –) to a clade containing clade D (*Ctenopterella*, *Grammitastrum* [*Grammitis pseudaustralis* E.Fourn.], *Howeogrammitis* [*Grammitis diminuta* Copel.], *Notogrammitis*, *Thalassogrammitis* [*Grammitis deplanchei* (Baker) Copel.]) (MLBS: 95%, BIPP: 0.50, MPJK: 81%) and clade E (*Acrosorus*, *Aenigmatogrammitis*, *Oxygrammitis*) (MLBS: 80%, BIPP: 0.99, MPJK: 81%) + clade F (*Archigrammitis*, *Calligrammitis* [*Oreogrammitis beddomeana* & allies], *Glabrigrammitis* [*Oreogrammitis subevenosa* & allies], *Oreogrammitis*, *Prosaptia* C.Presl) (MLBS: 96%, BIPP: –, MPJK: 81%). Clade F was sister (MLBS:

Table 2. Data statistics.

Matrix	# accessions	# characters	PI characters (%)	Missing data (%)
Plastid *atpB* gene	676	1382	440 (31.8)	13.8
Plastid *rbcL* gene	928	1316	442 (33.6)	5.9
Plastid *rps4* gene & *rps4-trnS* spacer	492	1017	644 (63.3)	49.2
Plastid *trnL* intron & *trnL-F* spacer	682	1011	585 (57.9)	65.0
Plastid *trnG-R* spacer	429	1128	738 (65.4)	13.7
Concatenated	1003	5854	2849 (48.7)	51.4

Missing data include missing sequences, uncertain bases (R, A or G; Y, C or T; S, G or C; W, A or T; K, G or T; M, A or C) and gaps (–). PI, parsimony-informative.

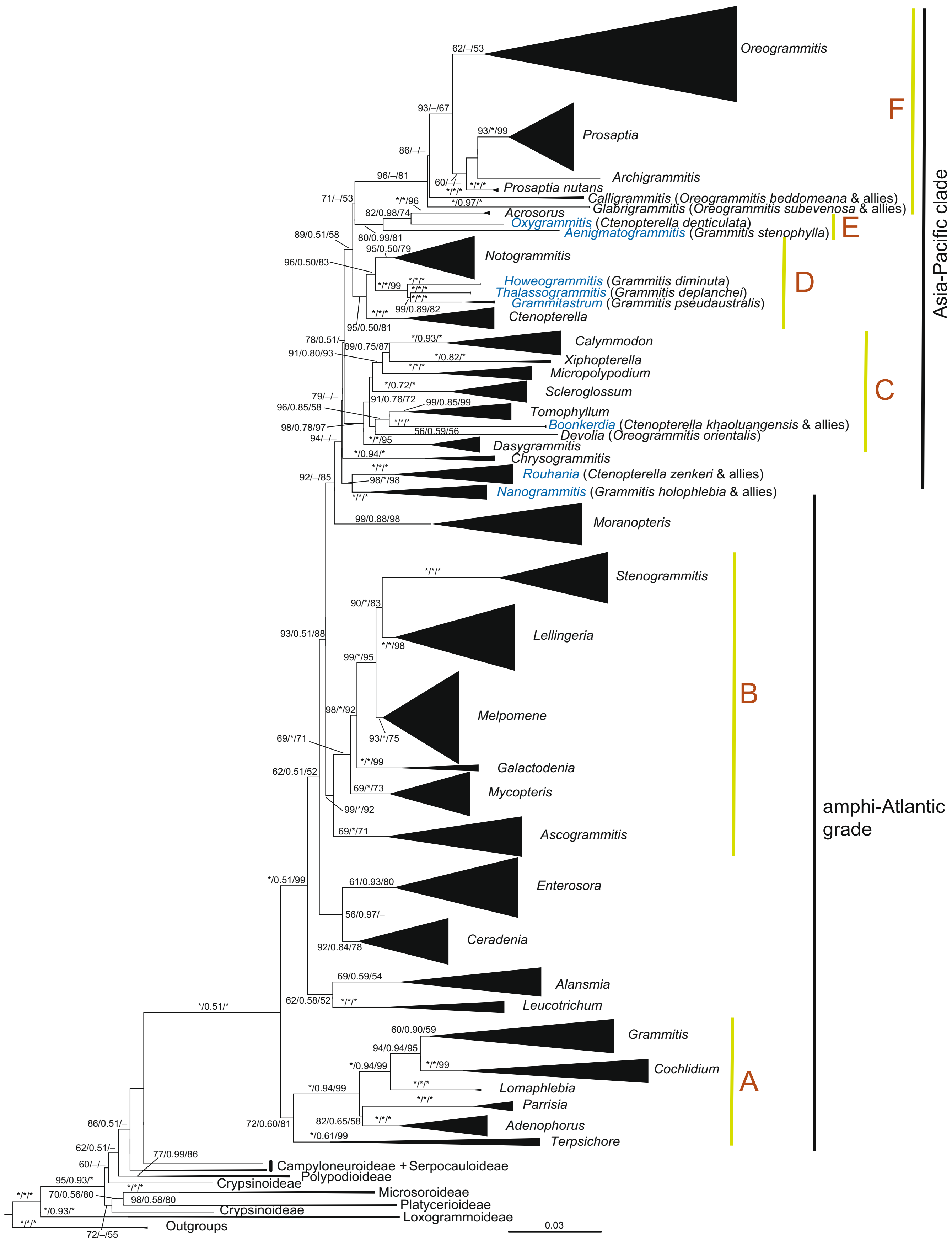

Fig. 1. Legend on next page.

71%, BIPP: –, MPJK: 53%) to clade E. Within clade C, *Dasygrammitis* was sister (MLBS: 98%, BIPP: 0.78, MPJK: 97%) to the rest, followed by *Devolia* + (*Boonkerdia* + *Tomophyllum*), which were sister to *Scleroglossum* + (*Micropolypodium* + (*Calymmodon* + *Xiphopterella*)). Within clade D, *Ctenopterella* was sister (MLBS: 95%, BIPP: 0.50, MPJK: 81%) to the rest, followed by *Notogrammitis*, which was sister to *Howeogrammitis* + (*Grammitastrum* + *Thalassogrammitis*). Within clade E, *Aenigmatogrammitis* was sister to *Acrosorus* + *Oxygrammitis*. Within clade F, *Glabrigrammitis* (*Oreogrammitis subevenosa* & allies) was sister (MLBS: 96%, BIPP: –, MPJK: 81%) to the rest, followed by *Calligrammitis* (*Oreogrammitis beddomeana* & allies), and further by *Oreogrammitis*, which was sister to *Archigrammitis* + *Prosaptia*. Most relationships described above except a few were strongly supported.

The relationships in the amphi-Atlantic grade matched those in Shalisko & al. (2019). The type species of *Grammitis*, *G. marginella*, was resolved in the *Grammitis* s.str. clade (Africa-Mascarenes + New World + eastern Pacific), which was sister to *Cochlidium*. The relationships in the Asia-Pacific clade were similar to those in Bauret & al. (2017) but with a number of new findings: (1) the newly sampled *Archigrammitis* was resolved within a paraphyletic *Prosaptia*; (2) *Prosaptia nutans* (Blume) Mett. was resolved as sister to *Archigrammitis* + the core *Prosaptia* with weak support; (3) the newly sampled *Ctenopterella khaoluangensis* (Tagawa & K.Iwats.) Parris (*Boonkerdia*) was resolved as sister to *Tomophyllum* with strong support; (4) the newly sampled *Oreogrammitis orientalis* (*Devolia*) was weakly supported as sister to a clade containing *Ctenopterella khaoluangensis* and *Tomophyllum*; (5) *Oreogrammitis subevenosa* (Baker) Parris and allies (*Glabrigrammitis*) were resolved outside of *Oreogrammitis* and as sister to the rest in clade F; (6) the newly sampled *Oreogrammitis beddomeana* (*Calligrammitis*) formed a clade with *O.* cf. *beddomeana* resolved outside of *Oreogrammitis* and as the second branching lineage in clade F; (7) the type species of *Ctenopterella*, *C. blechnoides* (Grev.) Parris, and allies, were resolved in a clade (*Ctenopterella*) sister to another containing the *Grammitis deplanchei* clade and *Notogrammitis*; (8) the type species of *Moranopteris* and *Themelium* each were resolved with other congeneric species; (9) the type species of *Radiogrammitis* was resolved as part of *Oreogrammitis* sensu Parris & Sundue (2020); and (10) most intergeneric and major relationships in the Asia-Pacific clade were well resolved and strongly supported.

■ DISCUSSION

Usefulness of next-generation sequencing for old herbarium materials. — The polyphyly of *Ctenopterella* s.l. and *Grammitis* s.l. has been well documented in earlier molecular works (Ranker & al., 2004; Perrie & Parris, 2012; Sundue & al., 2014; Bauret & al., 2017; Shalisko & al., 2019), but it had not been clear to which clades the two generic names should be applied because neither of the type species had been sampled in previous studies. There are specimens of the two type species in some herbaria, but they are too old or not well preserved for Sanger sequencing. Earlier studies so far have included 27 type species out of 33 genera and the main reason for the missing six type species was that there were no appropriate DNA materials. In this study, we included types of eight genera, five of which were sequenced using the Sanger method, and one of which was sequenced using both Sanger and NGS technology, while the entire plastomes of the remaining two were sequenced using relatively old herbarium materials (13–33 years old) via NGS technology. Our study demonstrates that NGS technology can make good use of herbarium material for fern phylogenetic studies, consistent with earlier studies on ferns sequencing entire plastomes (Du & al., 2021; Zhou & al., 2022; Zhang & Zhang, 2022).

Phylogeny within the Asia-Pacific clade of Grammitidoideae. — With the largest taxon (1003 accessions of ca. 412 species) and character (6 plastid markers) sampling so far, our study provided several new findings and better support values for intergeneric and major clade relationships in the Asia-Pacific clade. In a few cases, however, our support values decreased in comparison with those in earlier studies probably because of our larger taxon sampling. Below we summarize our new findings relative to the results in Bauret & al. (2017), who presented the previously largest phylogeny of the Asia-Pacific clade.

In clade F, the core *Oreogrammitis* is resolved as monophyletic and the type of *Themelium* is part of it. Bauret & al. (2017) resolved *O. jagoriana* (Mett. ex Kuhn) Parris & Sundue as sister to the rest of *Oreogrammitis* + *Prosaptia*, whereas our data resolved *O. jagoriana* as part of *Oreogrammitis*.

In clade D, *Notogrammitis* is strongly supported (but weakly in BI analysis) as sister to a clade containing *Grammitastrum*, *Howeogrammitis*, and *Thalassogrammitis*. Bauret & al. (2017) also found this relationship but with support values <50%. *Grammitastrum*, *Howeogrammitis*, and *Thalassogrammitis*, together with *Ctenopterella* s.str., are moderately supported as sister to a clade containing clade E and clade F.

In clade C, all but two major relationships are strongly supported. The weakly supported relationships include: the sister relationship between *Oreogrammitis orientalis* (*Devolia*) and *Boonkerdia* + *Tomophyllum*, and that between *Scleroglossum* and *Micropolypodium* + (*Calymmodon* + *Xiphopterella*). *Micropolypodium* is strongly supported as sister to a well-supported clade containing *Calymmodon* and *Xiphopterella*. Bauret & al. (2017) found *Micropolypodium* to be sister to *Xiphopterella* with weak support.

Fig. 1. Simplified maximum likelihood phylogeny of grammitid ferns (Polypodiaceae) based on six plastid markers (*atpB*, *rbcL*, *rps4*, *rps4-trnS*, *trnG-R*, *trnL* & *trnL-F*). Values of maximum likelihood bootstrap support, Bayesian inference posterior probability, and maximum parsimony jackknife support are along/above the branches. "*" means a support value of 100% or 1.0. "-" means a support value of below 50% or 0.5.

Resolution of *Archigrammitis*. — *Archigrammitis* contains seven species (Parris, 2013a; Chen & al., 2022). This genus shares dorsiventral rhizomes with stipes articulated to phyllopodia and ciliate rhizome scales with *Prosaptia*, but has setose sporangia like *Oreogrammitis* (Parris, 2013a). *Archigrammitis* was included in a phylogenetic analysis by Nitta & al. (2017) with seven Grammitidoideae only. We included their *Archigrammitis* in our study and it is resolved within a paraphyletic *Prosaptia*, consistent with the morphological similarities of the two genera (Parris, 2013a). It remains to be tested whether the type species of *Archigrammitis* will be resolved in the same clade. The sister relationship between *Archigrammitis* and the core *Prosaptia* is not strongly supported possibly because of insufficient data from more species of *Archigrammitis*. Liu & al. (2022) also found this relationship.

Resolutions of type species of *Moranopteris*, *Radiogrammitis*, and *Themelium*. — The type of *Moranopteris*, *M. basiattenuata*, is for the third time included in a study of Grammitidoideae after Hirai & al. (2011) and Sundue & al. (2015). Our accession is resolved as sister to the one in Hirai & al. (2011) and Sundue & al. (2015), but with quite a bit of molecular divergence.

The type of *Radiogrammitis*, *R. setigera* (Blume) Parris, is included for the third time in a grammitid phylogeny and is resolved as part of *Oreogrammitis* sensu Parris & Sundue (2020). The type of *Themelium*, *T. tenuisectum*, was included in a grammitid phylogeny for the first time by Ranker & al. (2004). We included it here again and sampled two accessions from Malaysia and Samoa, respectively, which are resolved in the same subclade as *Oreogrammitis conjunctisora* (Baker) Parris & Sundue, *O. curtisii* (Baker) Parris & Sundue, and *O. halconensis* (Copel.) Parris & Sundue. The placement of *T. tenuisectum* is consistent with that in Ranker & al. (2004) and the synonymization of *Themelium* with *Oreogrammitis* as proposed by Kuo & al. (2019) and Parris & Sundue (2020). Interestingly, all of these closely related species were placed in *Themelium* based on morphological similarities (Parris, 1997, 2004).

Polyphyly of *Ctenopterella* s.l. and *Boonkerdia* gen. nov. and *Oxygrammitis* gen. nov. — *Ctenopterella* was described by Parris (2007) and contains about 20 species (Sundue & al., 2014) mainly in Africa, Southeast Asia, and Pacific islands (Parris, 2007) including *Grammitis denticulata* Blume and *Xiphopteris khaoluangensis*, which were transferred to *Ctenopterella* by Parris (2007). Bauret & al. (2017) sampled about seven species and resolved the genus as highly polyphyletic and divided into three clades: (1) the *C. lasiostipes* (Mett.) Parris clade (about 3 species); (2) the *C. denticulata* (Blume) Parris clade (only one species); and (3) the *C. zenkeri* clade (*C. parvula* (Bory ex Willd.) Parris and the polyphyletic “species” *C. zenkeri*). In the *C. zenkeri* clade, some samples formed a well-supported clade with *Grammitis pygmaea* (Mett. ex Kuhn) Copel. However, they did not include the type of *Ctenopterella*, *C. blechnoides* (Grev.) Parris, in their study. With four accessions of *C. blechnoides* included, our study confirmed the polyphyly of *Ctenopterella* and the three clades detected by the earlier study (Bauret & al., 2017). The type of the genus and *C. nhatrangensis* (C.Chr. & Tardieu) Parris are resolved in a clade sister to the *C. lasiostipes* clade. The samples we identified as *C. blechnoides* are paraphyletic in relation to *C. nhatrangensis*. We detected substantial molecular divergence among the four accessions of *C. blechnoides* suggesting that this complex may contain multiple species. In addition, we identified a new clade with three accessions of *C. khaoluangensis* as sister to *Tomophyllum* with strong support.

Ctenopterella denticulata, endemic to Indonesia (Sumatra, Java, Lesser Sunda Islands, Sulawesi, Maluku), Malaysia (Sabah), and the Philippines, has been consistently resolved as sister to *Acrosorus* (Sundue & al., 2014; Bauret & al., 2017; our study). Together they are sister to *Grammitis stenophylla* Parris (*Aenigmatogrammitis*). These three taxa are morphologically divergent from one another (Sundue & al., 2014; our Appendix 3).

Based on our present results, we propose that the currently defined *Ctenopterella* sensu Parris (2007) be divided into four genera: *Ctenopterella* s.str. (the *C. lasiostipes* clade), *Boonkerdia* gen. nov. (*C. khaoluangensis*), *Oxygrammitis* gen. nov. (*C. denticulata*), and *Rouhania* gen. nov. (the *C. zenkeri* clade + *Grammitis pygmaea* and *G. nanodes* (Peter) Ching; see below). *Boonkerdia* is different from *Ctenopterella* s.str. in lacking setae and branched hairs with setae as branches. *Boonkerdia* can be distinguished from *Tomophyllum* by having a dorsiventral rather than a radial rhizome and in lacking setae. *Oxygrammitis* differs from *Ctenopterella* s.str. in having the lamina bipinnately to tripinnately divided, with the ultimate divisions of the lamina apically acute to acuminate. *Rouhania* is different from *Ctenopterella* only in geographical range and the two are not phylogenetically close to each other.

We suggest that *Boonkerdia*, *Oreogrammitis orientalis* (now *Devolia*, Yang & al., 2023), and *Tomophyllum* should not be placed in one genus, although they formed a clade that received low support values in all analyses (<50%/<0.5). Morphologically, they are quite different from one another (Appendix 3). These three taxa share stipes that are not articulated to rhizomes, concolorous rhizome scales, presence of hydathodes, superficial sori, and glabrous sporangia. However, *Boonkerdia* has dorsiventral rhizomes, glabrous rhizome scales, pinnatisect or pinnate to tripinnate lamina, 1-forked, dimidiately branched or pinnately branched veins, catenate simple hairs present, and sometimes branched hairs with catenate branches present. In contrast, *Devolia* has dorsiventral rhizomes, rhizome scales glabrous or with an apical seta, simple lamina, simple veins, setae present, and branched hairs with setae as branches present; *Tomophyllum* has radially symmetric rhizomes, rhizome scales glabrous or ciliate, sometimes absent, lobed to tripinnatifid lamina, pinnate veins, and setae, catenate simple hairs, branched hairs with setae as branches.

Species of *Boonkerdia* were placed in *Ctenopterella* s.l., and *Devolia* in *Oreogrammitis* (see below).

Polyphyly of *Grammitis* s.l. and six new genera: *Aenigmatogrammitis*, *Grammitastrum*, *Howeogrammitis*, *Nanogrammitis*, *Rouhania*, *Thalassogrammitis*. — The type genus of Grammitidoideae, *Grammitis* s.l., has long been known to be polyphyletic (Ranker & al., 2004; Schuettpelz & Pryer, 2007; Sundue & al., 2010, 2014; Bauret & al., 2017; Shalisko & al., 2019). Bauret & al. (2017) resolved *Grammitis* s.l. into five clades: the *Grammitis* s.str. clade, the *G. deplanchei* clade (*G. deplanchei*, *G. pseudaustralis*, *G. diminuta*), the *G. holophlebia* clade (*G. holophlebia*, *G. obtuse* Willd. ex Kaulf., *G. pellucidovenosa* (Bonap.) Copel., *G. pervillei* (Mett. ex Kuhn) Tardieu, *G. synsora* (Baker) Copel.), the *G. pygmaea* clade (*G. pygmaea*), and the *G. stenophylla* clade. Notably, the type of the genus, *G. marginella*, had never been included in any previous studies. Based on the lamina with blackish sclerotic margins, Bauret & al. (2017) hypothesized that the type should be a member of *Grammitis* s.str. Thanks to the NGS technology, our current study included *G. marginella* for the first time based on herbarium material and confirmed the type species as belonging to *Grammitis* s.str. With the inclusion of *G. marginella*, *Grammitis* s.str. is resolved into three deeply diverged subclades: two of them were detected by Bauret & al. (2017), and the third one consists of *G. marginella* only. This, along with the weakly supported monophyly of *Grammitis* s.str., highlights the molecular heterogeneity within the genus, although most members have blackish lamina margins (Bauret & al., 2017). Species of *Grammitis* s.str. are widespread in Africa, West Indian Ocean islands (La Réunion, Madagascar), Pacific islands, and Central and South America.

For the other clades of *Grammitis* s.l. resolved by Ranker & al. (2004), Perrie & Parris (2012), Sundue & al. (2014), Bauret & al. (2017), and our current study, we propose to recognize six new genera: *Aenigmatogrammitis* (*G. stenophylla*), *Grammitastrum* (*Grammitis pseudaustralis*), *Howeogrammitis* (*G. diminuta*), *Nanogrammitis* (the *G. holophlebia* clade), *Rouhania* (the *G. pygmaea* clade + *Ctenopterella parvula* + *C. zenkeri* and allies; see also above), and *Thalassogrammitis* (*G. deplanchei*).

Grammitastrum, *Howeogrammitis*, and *Thalassogrammitis* formed a strongly supported clade in clade D and could be united into one genus, but we suggest that because they are so morphologically distinct, treating the species in three genera would be most appropriate. Phylogenetically, each of them has a long branch indicating their molecular distinctness, too (Fig. 1). In addition, there are no obvious morphological characters to define the clade formed by the three. *Howeogrammitis* is endemic to Lord Howe Island, whereas the other two genera are endemic to New Caledonia. These three genera together are weakly to strongly supported as sister to *Notogrammitis* and the four together are sister to *Ctenopterella* s.str. (Sundue & al., 2014; Bauret & al., 2017; our Fig. 1).

Notogrammitis, *Howeogrammitis*, *Grammitastrum*, and *Thalassogrammitis* share some characters, e.g., dorsiventral rhizomes, lamina simple (except one species of *Notogrammitis*), veins 1–2-forked (except one species of *Notogrammitis*), and superficial to slightly sunken sori. *Notogrammitis* has glabrous rhizome scales and glabrous sporangia, as does *Howeogrammitis*. *Grammitastrum* is distinct from the other three genera in having clathrate, not concolorous rhizome scales and in having basally stellate hairs that are absent from the other three genera. *Grammitastrum* and *Thalassogrammitis* have rhizome scales with setae on the margin and setose sporangia with hairs on the cell walls of the annulus, and differ from the other two genera in having ciliate, rather than glabrous, rhizome scales and in having setae on the cell walls of the annulus, rather than glabrous sporangia as in the other two genera (Perrie & Parris, 2012). *Thalassogrammitis* has concolorous rhizome scales and lacks both setae and basally stellate hairs on the lamina. *Notogrammitis* and *Howeogrammitis* are morphologically very similar, but the latter cannot be included in the former because of its position in our tree (Fig. 1). These four genera are different from *Ctenopterella* s.str. in having simple (but pinnatisect to tripinnatifid in *N. heterophylla* (Labill.) Parris) laminae, whereas *Ctenopterella* s.str. has pinnatisect laminae.

Species of *Nanogrammitis* and *Rouhania* are distributed in Africa and West Indian Ocean islands and the genera are sister to each other in phylogenetic analyses (Sundue & al., 2014; Bauret & al., 2017; our Fig. 1). These two genera could be united into one genus or separated into three. Considering the deep divergence and lamina morphology, we separate them here into two. All species of *Nanogrammitis* have simple laminae like those of *Grammitis* s.str., while all except two of *Rouhania* have pinnatisect laminae like those of *Ctenopterella* s.str. It seems better to treat the two simple-fronded *Grammitis pygmaea* and *G. nanodes* in a *Ctenopterella*-dominant (pinnatisect-fronded) genus than to treat 6+ pinnatisect-fronded species of *Ctenopterella* in a simple-fronded genus.

Polyphyly of *Oreogrammitis*. — Among the three genera, *Oreogrammitis*, *Radiogrammitis*, and *Themelium* (the ORT clade; Sirimalwatta, 2019), *Oreogrammitis* is the oldest name (Copeland, 1917). Its type, *O. clemensiae* Copel., has not yet been sampled in any molecular study. Sundue & al. (2014) and Bauret & al. (2017) suggested that these three genera, though distinguishable from one another morphologically (Parris, 2007), should be united. Hsu in Knapp & Hsu (2017) described an interesting species from mainland China, Taiwan, and Japan, *O. orientalis* T.C.Hsu, with simple soriferous lateral veins. Based on an earlier molecular study (Sundue & al., 2014), Kuo & al. (2019) transferred the names of seven fern species of Taiwan to *Oreogrammitis* including *Radiogrammitis beddomeana* and *R. subnervosa* T.C.Hsu. Parris & Sundue (2020) formally reduced *Radiogrammitis* and *Themelium* to synonymy with *Oreogrammitis* and transferred the remaining 36 names to *Oreogrammitis*. Two additional related species, *Grammitis adspersa* Blume and *G. nuda* Tagawa, were transferred to *Oreogrammitis* earlier by Parris (2007, 2013b).

Our study provides evidence that *Oreogrammitis* sensu Parris (2007, 2013b), Kuo & al. (2019), and Parris & Sundue (2020) is polyphyletic but can be resolved into four clades:

the core *Oreogrammitis*, the *O. beddomeana* clade (*O. beddomeana* + *O.* cf. *beddomeana*), the *O. subevenosa* clade (*O. nuda* + *G. subevenosa*), and the monospecific *O. orientalis* clade. The *O. beddomeana* clade and the *O. subevenosa* clade are paraphyletic in relation to the core *Oreogrammitis* + (*Archigrammitis* + *Prosaptia* s.l.). The *O. orientalis* clade is distantly related to the core *Oreogrammitis* and weakly supported as sister to a clade containing *Ctenopterella khaoluangensis* (*Boonkerdia*) and *Tomophyllum*.

The three clades outside of the core *Oreogrammitis* have been recently described as *Calligrammitis* (*Oreogrammitis beddomeana* and allies), *Devolia* (*Oreogrammitis orientalis*), and *Glabrigrammitis* (*Oreogrammitis subevenosa* and allies), respectively (Yang & al., 2023).

In addition to the three new clades, we made a few new findings in core *Oreogrammitis*: (1) identification of a Sino-Vietnamese subclade with *O. hainanensis* Parris, *O. sinohirtella* Parris, etc.; (2) the *O. jagoriana* (Christ) Parris subclade with O. *dorsipila*, *O. jagoriana*, *O. scleroglossoides* (Copel.) Parris, etc. resolved as part of the monophyletic core *Oreogrammitis*, in contrast to the paraphyly of the genus in relation to *Prosaptia* by Bauret & al. (2017); and (3) the *Themelium* subclade with the type included (see above).

Paraphyly of *Prosaptia*. — *Prosaptia* has consistently been confirmed as monophyletic in recent molecular studies (Ranker & al., 2004; Sundue & al., 2014; Bauret & al., 2017). As shown by Liu & al. (2022), the addition of *Archigrammitis* and *P. nutans* makes *Prosaptia* paraphyletic in relation to *Archigrammitis* because *P. nutans* is resolved as sister to core *Prosaptia* + *Archigrammitis*. The type of *Prosaptia*, *P. contigua* (G.Forst.) C.Presl, has previously been sampled and was resolved within *Prosaptia* in earlier studies (Ranker & al., 2004; Sundue & al., 2014; Bauret & al., 2017; Liu & al., 2022; our current study), and thus *P. nutans* appears to be better accommodated in a different genus.

Bauret & al. (2017) also sampled an unidentified accession of *Prosaptia* belonging to the *Prosaptia nutans* clade, but *Archigrammitis* was not included and their *Prosaptia* was still monophyletic. *Ranker & Trapp 1765* from Papua New Guinea, from which the first DNA data of *P. nutans* were obtained (Ranker & al., 2004), was not included in Bauret & al. (2017). The combination of superficial or slightly sunken sori and rachis darker on the adaxial surface of *P. nutans* distinguish *P. nutans* from the other sampled species of *Prosaptia*.

We suggest that *Archigrammitis*, *Prosaptia* s.str., and *P. nutans* should not be united into one genus. The clade formed by them is only weakly supported by ML analysis (Fig. 1). Morphologically, *Archigrammitis* has concolorous rhizome scales (vs. clathrate in the other two) and setose sporangia (vs. sporangia not setose in the other two; Parris, 2013a; our Appendix 3). *Prosaptia nutans* might be best treated in a new genus but further sampling and research are needed.

Extensive cryptic speciation in the Asia-Pacific clade. — By including multiple accessions of numerous species we discovered that many of the species currently defined/identified in Asian-Pacific Grammitidoideae are polyphyletic or paraphyletic (suppl. Fig. 2S), illustrating the complexity of the taxonomy within the subfamily. In fact, all 12 genera in the Asia-Pacific clade with four or more accessions sampled are found to contain at least one polyphyletic or paraphyletic or highly divergent species, and one genus (*Grammitastrum*) with three accessions sampled is found to contain a cryptic species. These 13 Asia-Pacific genera contain at least 32 species with cryptic species currently undetected. More taxonomic studies are needed.

These 32 polyphyletic/paraphyletic/highly divergent "species" in the Asia-Pacific clade include (from clade F to C: suppl. Fig. S2) 8 spp. of *Oreogrammitis* (clade F): *O. adspersa* (Blume) Parris, *O. congener* (Blume) Parris, *O. hirtelloides* Parris & Sundue, *O. holttumii* (Copel.) Parris & Sundue, *O. jagoriana*, *O. locellata* (Baker) Parris, *O. multifolia* (Copel.) Parris & Sundue, and *O. reinwardtii* (Blume) Parris; 7 spp. of *Prosaptia* (clade F): *P. alata* (Blume) Christ, *P. barathrophylla* (Baker) M.G.Price, *P. contigua*, *P. obliquata* (Blume) C.Chr. & Tardieu, *P. palauensis* Hosok., *P. pectinata* T.Moore, and *P. urceolaris* (Hayata) H.Ito; 3 spp. of *Notogrammitis* (clade D): *N. billardierei* (Willd.) Parris, *N. ciliata* (Colenso) Parris, and *N. crassior* (Kirk) Parris; 1 sp. of *Grammitastrum* (clade D): *G. pseudaustrale* (E.Fourn.) Parris & al.; 1 sp. of *Ctenopterella* (clade D): *C. blechnoides*; 1 sp. of *Calymmodon* (clade C): *C. gracilis* Copel.; 1 sp. of *Micropolypodium* (clade C): *M. sikkimensis* (Hieron.) X.C.Zhang; 3 spp. of *Scleroglossum* (clade C): *S. pusillum* (Blume) Alderw., *S. sulcatum* (Kuhn) Alderw., and *S. wooroonooran* (F.M.Bailey) C.Chr.; 1 sp. of *Tomophyllum* (clade C): *T. macrum* (Copel.) Parris; 2 spp. of *Dasygrammitis* (clade C): *D. mollicoma* (Nees & Blume) Parris, *D. purpurascens* (Nadeaud) Parris; 1 sp. of *Chrysogrammitis* (clade C): *C. glandulosa* (J.Sm.) Parris; 2 spp. of *Rouhania* (clade C): *R. parvula* (Bory ex Willd.) Li Bing Zhang & al., and *R. zenkeri* (Hieron.) Li Bing Zhang & al.; and 1 sp. of *Nanogrammitis* (clade C): *N. obtusa* (Willd. ex Kaulf.) Parris & al.

■ TAXONOMIC TREATMENT

The only unsampled genus in Grammitidoideae in our phylogeny is *Luisma* from Colombia (Murillo & Smith, 2003). All the proposed new genera here are from the Old World and morphologically different from *Luisma*, and morphology would suggest that *Luisma* is similar to or even congeneric with *Lellingeria* (M. Sundue, pers. comm.). There has long been need of new genera for portions of the polyphyletic *Ctenopterella* s.l., *Grammitis* s.l., and *Oreogrammitis* s.l. (Ranker & al., 2004; Sundue & al., 2014; Bauret & al., 2017; Shalisko & al., 2019). We here treat the parts of the polyphyletic *Ctenopterella* s.l. and *Grammitis* s.l., but not those of the polyphyletic *Oreogrammitis* s.l., which have been treated elsewhere (Yang & al., 2023). The new genera we are proposing each have an isolated placement in our phylogeny and are supported by morphology and/or geographical distribution. The proposed new genera include all of the Asia-Pacific species formerly referred to *Ctenopterella* s.l. and

Grammitis s.l. except *G. nudicarpa* Copel. and *G. pulchella* Ching from Lord Howe Island. There are 42 genera in total now in the subfamily including the little-known *Luisma*. A morphological comparison of the 35 Old-World genera in Grammitidoideae is presented in Appendix 3. A key to these genera is presented below and the taxonomic treatment of the new genera follows.

A key to the Old-World genera of Grammitidoideae

1. Laminae simple to slightly crenate 2
1. Laminae lobed to tripinnatifid......................................26
2. Margin with dark sclerotic band (Africa, Pacific) .... ***Grammitis***
2. Margin without dark sclerotic band 3
3. Sori deeply sunken in lamina, in two separate grooves, one each side of midrib (Asia, Pacific) ....***Scleroglossum***
3. Sori superficial or slightly sunken, or if sunken, not in two grooves 4
4. Rhizomes radially symmetric 5
4. Rhizomes dorsiventral 7
5. Sporangia with setae (Asia, Pacific)................................ .... ***Oreogrammitis*** p.p. (***Radiogrammitis***)
5. Sporangia without setae 6
6. Rhizome scales absent (Asia)................. ***Calligrammitis***
6. Rhizome scales present (Africa)........................ ***Parrisia***
7. Sporangia with setae...8
7. Sporangia without setae 10
8. Rhizome scales glabrous (Asia, Pacific)......................... .... ***Oreogrammitis*** p.p. (s.str.)
8. Rhizome scales ciliate 9
9. Rhizome scales concolorous (Asia, Pacific) ....***Archigrammitis***
9. Rhizome scales clathrate (Pacific) .... ***Grammitastrum***
10. Sori on both acroscopic and basiscopic vein branches, nearer to margin than to midrib, rhizome scales ciliate (Pacific).. ***Thalassogrammitis***
10. Sori on acroscopic vein branch, usually midway between margin and midrib or nearer to midrib, and rhizome scales not ciliate 11
11. Rhizome scales with catenate hairs or glandular hairs (Africa) .... ***Enterosora*** p.p.
11. Rhizome scales glabrous or with apical hairs only 12
12. Hydathodes absent from vein endings on adaxial surface of lamina 13
12. Hydathodes present on vein endings on adaxial surface of lamina..16
13. Setae present on fronds (South Temperate regions)......... .... ***Notogrammitis*** p.p.
13. Setae absent from fronds 14
14. Rhizome scales acuminate and terete at apex and/or catenate glandular hairs frequent in sori as receptacular paraphyses (Pacific).............................. ***Adenophorus*** p.p.
14. Rhizome scales not acuminate at apex or, if acuminate, apex flat, not terete, receptacular soral paraphyses absent 15
15. Rhizome scales (5.8–)6.0–11.5(–12.0+) mm long (Lord Howe Island) ....***Howeogrammitis***
15. Rhizome scales (0.4–)1.4–4.3(–6.5) mm long (South Temperate regions).......................... ***Notogrammitis*** p.p.
16. Rhizome scales clathrate 17
16. Rhizome scales concolorous 18
17. Setae present on fronds (Africa)...... ***Nanogrammitis*** p.p.
17. Setae absent from fronds, however branched hairs with setae as branches present (Africa) ...***Stenogrammitis*** p.p.
18. Setae present on fronds 19
18. Setae absent from fronds 24
19. Rhizomes long-creeping (Africa) .... ***Nanogrammitis*** p.p.
19. Rhizomes short-creeping..20
20. White deposit present on hydathodes on adaxial surface of lamina (Asia).................................. ***Glabrigrammitis***
20. White deposit absent from hydathodes on adaxial surface of lamina 21
21. Longest setae ca. 0.1 mm long....................................22
21. Longest setae (0.2–)0.5–1.0(–1.7) mm long 23
22. An apical seta sometimes present at apex of rhizome scale; fertile veins always simple (Asia)............. ***Devolia***
22. Setae absent from rhizome scales; fertile veins simple or 1-branched (Africa). .... ***Rouhania*** p.p.
23. Fertile veins simple (Africa)........... ***Nanogrammitis*** p.p.
23. Fertile veins 1-forked (South Temperate regions)........... .... ***Notogrammitis*** p.p.
24. Fronds glabrous or with catenate simple hairs and/or catenate branched hairs with flattened cells; indurated cells of annulus 7–10(–14) (Asia, Pacific) ....***Aenigmatogrammitis***
24. Fronds glabrous or with catenate simple hairs and/or catenate branched hairs with cells not flattened; indurated cells of annulus (7–)10–14(–20) 25
25. Fronds glabrous or with catenate simple hairs and catenate hairs with catenate branches (South Temperate region) .... ***Notogrammitis*** p.p.
25. Fronds glabrous or with catenate simple hairs and sometimes catenate hairs with setae as branches (Africa) .... ***Nanogrammitis*** p.p.
26. Apical part of lamina more or less entire when fertile, sori in two rows, confluent across midrib at maturity, basal part of lamina sterile, pinnatifid (Africa) ..... ***Cochlidium***
26. Fertile upper part of lamina and sterile basal part of lamina similar..27
27. Rhizomes radially symmetric 28
27. Rhizomes dorsiventral 41
28. Rhizome scales subclathrate to clathrate 29
28. Rhizome scales concolorous 30
29. Rhizome scales ciliate (Africa) ....***Leucotrichum***
29. Rhizome scales glabrous or with an apical hair (Africa).. .... ***Stenogrammitis*** p.p.
30. Rhizome scales ciliate 31
30. Rhizome scales absent, glabrous or with an apical hair ... .34
31. Hydathodes absent from vein endings on adaxial surface of lamina (Asia, Pacific).............***Dasygrammitis***

31. Hydathodes present on vein endings on adaxial surface of lamina 32
32. Veins pinnately branched (Asia, Pacific) .... ***Tomophyllum*** p.p.
32. Veins simple to few-forked 33
33. Pale yellow to pale red-brown setae present, no other hair types (Africa) .... ***Alansmia*** p.p.
33. Red-brown setae and translucent branched hairs present (Africa) .... ***Moranopteris***
34. Rhizome scales absent.. 35
34. Rhizome scales glabrous or with an apical hair 36
35. Sporangia with setae on annulus and sporangial face (Africa). .... ***Alansmia*** p.p.
35. Sporangia glabrous (Asia, Pacific)..... ***Tomophyllum*** p.p.
36. Sporangia with setae at apex adjacent to annulus (Asia, Pacific) .... ***Oreogrammitis*** (s.str.)
36. Sporangia glabrous.. 37
37. Veins simple.. 38
37. Veins few-forked or pinnate.. 39
38. Pinnae dimorphic, sterile pinnae flat, fertile pinna variously folded over sori (Asia, Pacific) .... ***Calymmodon***
38. Pinnae monomorphic (Asia) .... ***Micropolypodium***
39. Veins pinnate (Asia, Pacific)............. ***Tomophyllum*** p.p.
39. Veins few-forked... 40
40. Setae, including setae as branches of branched hairs, medium to dark red-brown, hydathodes absent (Asia, Pacific) .... ***Acrosorus***
40. Setae, including setae as branches of branched hairs, pale yellow-brown or pale to medium red-brown, hydathodes sometimes present (Asia) .... ***Xiphopterella***
41. Sporangia with setae at apex adjacent to annulus (Asia, Pacific) .... ***Oreogrammitis*** p.p (s.str.)
41. Sporangia without setae 42
42. Rhizome scales subclathrate to clathrate...................... 43
42. Rhizome scales concolorous 47
43. Rhizome scales ciliate (Asia, Pacific) .... ***Prosaptia***
43. Rhizome scales glabrous or with one or more apical hairs 44
44. Setae absent from frond (Africa)..... ***Stenogrammitis*** p.p.
44. Setae present on frond... 45
45. Rhizome scales with glandular hairs at apex and sometimes also on margin (Africa)....................... ***Melpomene***
45. Rhizome scales glabrous 46
46. Setae dense in sorus as receptacular paraphyses (Pacific) .... ***Ctenopterella*** p.p.
46. Setae absent from sorus, or sometimes occasional to frequent around it, but not in sorus as receptacular paraphyses (Asia, Pacific)....... ***Oreogrammitis*** p.p. (***Themelium***)
47. Hydathodes present at vein endings on adaxial surface of lamina 48
47. Hydathodes absent from vein endings on adaxial surface of lamina 53
48. Setae absent from fronds 49
48. Setae present on fronds 52
49. Veins 1-forked.. 50
49. Veins dimidiately branched or pinnately branched 51
50. Simple glandular hairs present (Africa).... ***Rouhania*** p.p.
50. Catenate simple and catenate branched hairs present (Asia) .... ***Boonkerdia*** p.p.
51. Veins dimidiately branched (Asia)........ ***Boonkerdia*** p.p.
51. Veins pinnately branched; hair types identical, simple glandular hairs, catenate simple hairs and branched catenate hairs present...................... ***Boonkerdia*** p.p. (Asia), ***Notogrammitis*** p.p. (Pacific), ***Rouhania*** p.p. (Africa)
52. Catenate branched hairs with catenate branches present (Pacific) .... ***Notogrammitis*** p.p
52. Catenate branched hairs absent or, if present, with setae as branches (Asia, Pacific) .... ***Ctenopterella*** p.p.
53. Setae present on frond 54
53. Setae absent from frond 55
54. Glands white (Africa) .... ***Ceradenia*** p.p.
54. Glands translucent or pale to dark yellow to red-brown (Africa) .... ***Enterosora*** p.p.
55. Rhizome scales glabrous, ultimate segments of lamina acute to acuminate at apex, glandular or eglandular receptacular paraphyses sometimes present (Asia).................. .... ***Oxygrammitis***
55. Rhizome scales with glandular hairs at apex or more widely distributed, rarely glabrous, glandular receptacular paraphyses present 56
56. Glands white (Africa) .... ***Ceradenia*** p.p.
56. Glands translucent or pale to dark yellow to red-brown 57
57. Rhizome scales with apical glands (Pacific) .... ***Adenophorus***
57. Rhizome scales with marginal glandular hairs, rarely glabrous 58
58. Veins 1-forked or pinnately branched with 1–4 pairs of branches in longest pinnae (Asia, Pacific) .... ***Chrysogrammitis***
58. Veins pinnately branched with 4–8 pairs in longest pinnae (Africa) .... ***Enterosora*** p.p.

Aenigmatogrammitis Parris, **gen. nov.** – Type: *Aenigmatogrammitis stenophylla* (Parris) Parris.

Etymology. – Latin, *aenigma* = enigma, and Greek, *Grammitis*, the genus of ferns in which the type species was originally described, referring to the mystery of its relationships.

Diagnosis. – *Aenigmatogrammitis* differs from other genera of Grammitidoideae by the following combination of characters: rhizomes dorsiventral, rhizome scales glabrous, concolorous, fronds not articulated to rhizome, laminae simple, without sclerotic margin, sometimes glabrous, setae absent, sometimes with catenate simple hairs and branched hairs with flattened catenate branches present, veins 1-forked, vein endings with conspicuous pale to dark hydathodes 0.1–0.8 × 0.1–0.2 mm on adaxial surface of lamina, sporangia glabrous, with 7–10(–14) thickened cells in annulus.

Description. – Rhizomes erect to short-creeping, rhizome scales pale to medium red-brown, stipes absent, laminae oblanceolate to linear-oblanceolate or linear-elliptic, obtuse to acute at apex, long-attenuate at base, thinly coriaceous, frond base glabrous, veins usually not visible in transmitted light, acroscopic branch usually ± as long as basiscopic branch, sori ± circular to broadly elliptic, superficial or slightly sunken in broad shallow depressions in lamina, receptacle sometimes slightly prominent on adaxial surface, in one row each side of midrib. (Figs. 2, 3)

Notes. – *Aenigmatogrammitis* was included in *Grammitis* in previous studies (Perrie & Parris, 2012; Sundue & al., 2014; Bauret & al., 2017). Species of this genus are currently known in Australia and Indonesia.

Aenigmatogrammitis kairatuensis (M.Kato & Parris) Parris, **comb. nov.** ≡ *Grammitis kairatuensis* M.Kato & Parris in J. Fac. Sci. Univ. Tokyo, Sect. 3, Bot. 15(2): 129–130, fig. 3. 1992 – Holotype: Indonesia, Maluku, West Seram, Kairatu District, Tihulale to Gunung Totaniwel, 980–1190 m, 19 Aug 1986, *Kato, Ueda & Fanani C-13399* (TI!).

The species is known only from the type collection and differs from *Aenigmatogrammitis stenophylla* in the absence of catenate simple hairs.

Aenigmatogrammitis stenophylla (Parris) Parris, **comb. nov.** ≡ *Grammitis stenophylla* Parris in Bot. J. Linn. Soc. 70(1): 35. 1975 – Holotype: Australia, Northeast Queensland, Mt Bellenden Ker, summit of south peak, 1524 m, 6 Apr 1948, *Brass 18307* (BRI barcode BRI-AQ0004529!; isotype A barcode 00021268!).

The species is endemic to the east coast of Australia, from Far North Queensland to New South Wales. Its range overlaps that of the tropical genus *Oreogrammitis* in Queensland and the South Temperate genus *Notogrammitis* in New South Wales.

Boonkerdia Li Bing Zhang, Pollawatn, X.M.Zhou & Liang Zhang, **gen. nov.** – Type: *Boonkerdia khaoluangensis* (Tagawa & K.Iwats.) Li Bing Zhang, Pollawatn, X.M. Zhou & Liang Zhang.

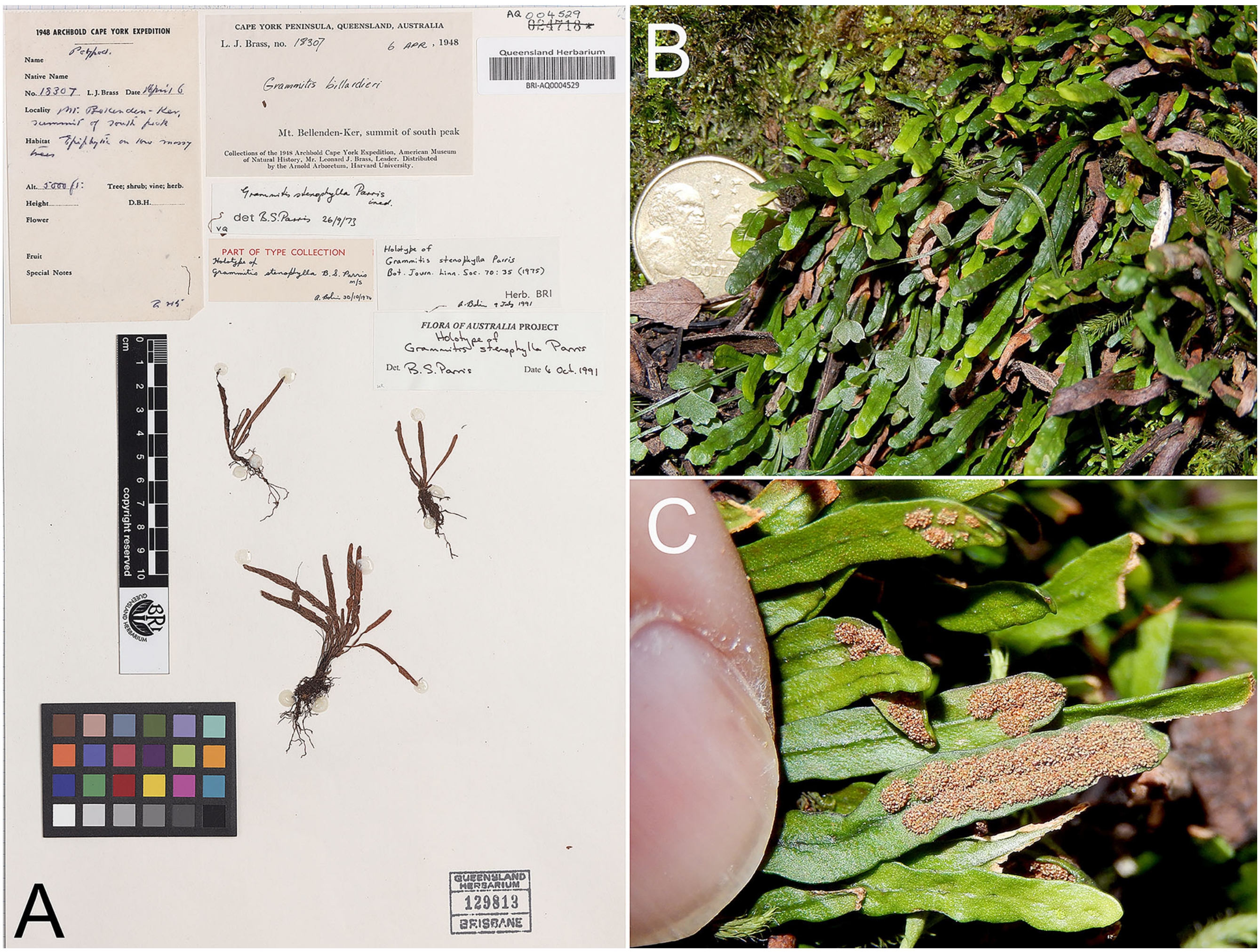

Fig. 2. *Aenigmatogrammitis stenophylla* (Parris) Parris. **A**, Holotype (*L.J. Brass 18307*; BRI-AQ0004529); **B**, Habit and habitat; **C**, Upper portions of laminae. — Photos: A, JSTOR; B & C, Poyt @ flickr.

Etymology. – In honor of Thawesakdi Boonkerd based at BCU for his contributions to the fern flora of Thailand (e.g., Boonkerd & Pollawatn, 2000; Boonkerd, 2006; Pongkai & al., 2018). In fact, nearly all currently active pteridologists in Thailand were trained by him.

Diagnosis. – *Boonkerdia* differs from the other genera of Grammitidoideae by the following combination of characters: rhizomes dorsiventral, rhizome scales glabrous, concolorous, fronds not articulated to rhizome, stipes absent or very short, glabrous or with catenate simple glandular hairs, branched catenate hairs with catenate branches sometimes present, setae absent, laminae pinnatisect, pinnate or deeply bipinnatisect, without sclerotic border, pinnae with one or more lobes on acroscopic margin, sometimes one or two on basiscopic margin also, catenate simple glandular hairs present, sometimes branched hairs with catenate branches present, setae absent, vein endings with hydathodes on adaxial surface of lamina, sori one on each pinna or primary lobe, sporangia glabrous.

Boonkerdia differs from its sister genus *Tomophyllum* in having a dorsiventral rather than a radial rhizome and in lacking setae.

Description. – Rhizome short-creeping to erect; rhizome scales pale to medium red-brown or pale to medium yellow-brown, ovate-lanceolate or narrowly lanceolate, acute to apiculate. Stipes short, green or castaneous, sometimes narrowly winged to the base. Laminae linear, narrowly lanceolate,

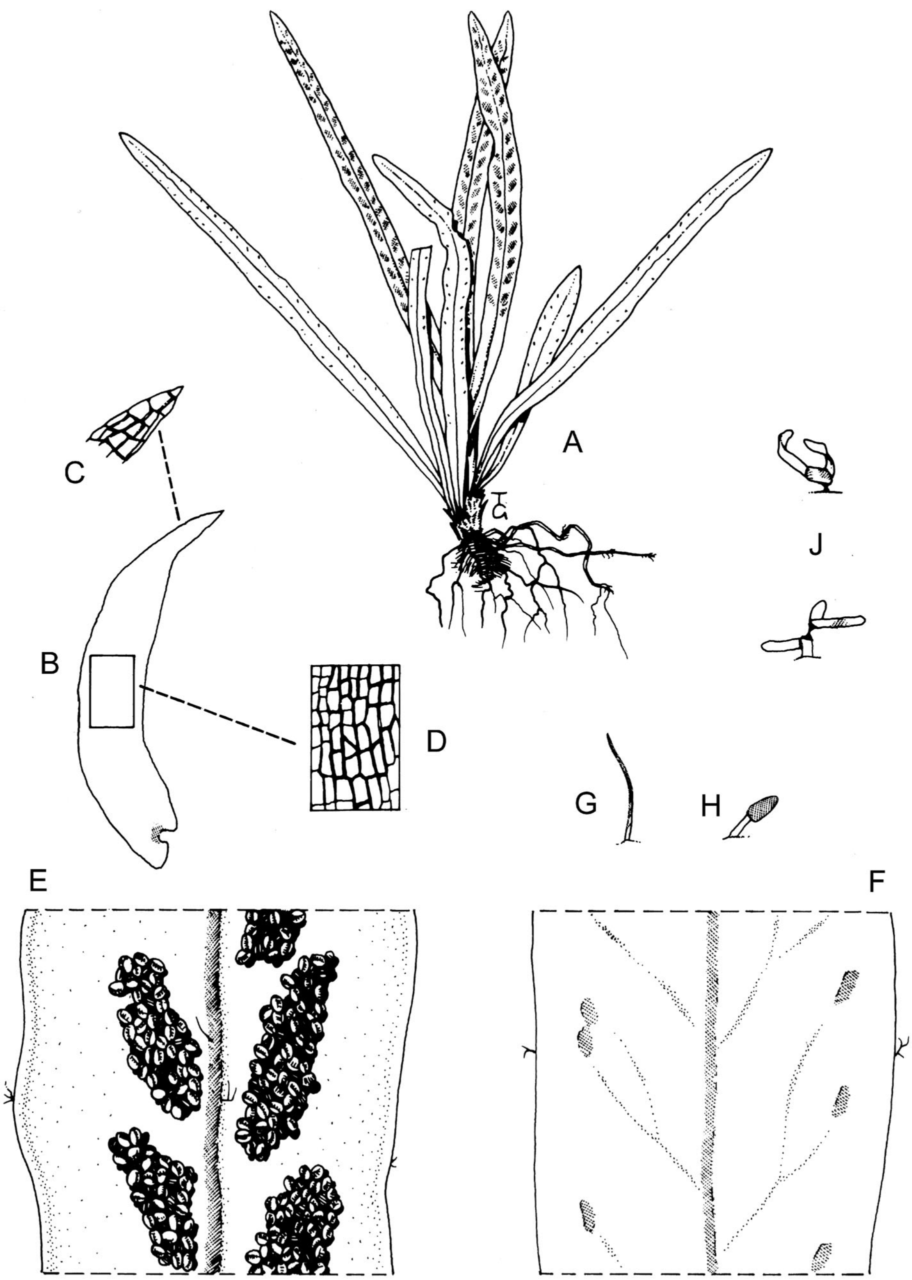

Fig. 3. *Aenigmatogrammitis stenophylla* (Parris) Parris. **A**, Habit ×1.4; **B**, Rhizome scale ×27; **C**, Apex of rhizome scale ×55; **D**, Cells from center of rhizome scale ×55; **E**, Detail of abaxial surface of lamina ×17; **F**, Detail of adaxial surface of lamina ×17; **G**, Catenate simple eglandular hair from margin ×55; **H**, Simple glandular hair from abaxial surface of lamina ×55; **J**, Branched hairs from margin ×55. — Based on *Dockrill 1513* (QRS); drawn by Tim Galloway.

elliptic, narrowly elliptic or narrowly oblanceolate in outline, gradually narrowing towards both ends, obtuse to acuminate at apex; veins visible or not in transmitted light. Sori ± circular to broadly elliptic, superficial. (Fig. 4)

Notes. – Parris (2007) treated the type of *Boonkerdia* as a member of *Ctenopterella*, and this was accepted by subsequent botanists (Lindsay & Middleton, 2012–; Chen & al., 2020). Our phylogeny shows that it is not part of *Ctenopterella* but sister to *Tomophyllum*.

Boonkerdia cornigera (Baker) Parris, **comb. nov.** ≡ *Polypodium cornigerum* Baker in Hooker & Baker, Syn. Fil., ed. 2: 508. 1874 ≡ *Grammitis cornigera* (Baker) Ching in Bull. Fan Mem. Inst. Biol. 10(5): 240. 1941 ≡ *Xiphopteris cornigera* (Baker) Copel., Gen. Fil. [Ann. Cryptog. Phytopathol. 5]: 215. 1947 ≡ *Micropolypodium cornigerum* (Baker) X.C.Zhang in Y.X. Lin, Fl. Reipubl. Popularis Sin. 6(2): 301–302. 2000 – Holotype: Ceylon, Horton Plains, 7500 feet, *Thwaites C.P. 4005* (PDA!).

Boonkerdia khaoluangensis (Tagawa & K.Iwats.) Li Bing Zhang, Pollawatn, X.M.Zhou & Liang Zhang, **comb. nov.** ≡ *Xiphopteris khaoluangensis* Tagawa & K.Iwats. in Acta Phytotax. Geobot. 23(5–6): 177, fig. 14. 1969 ≡

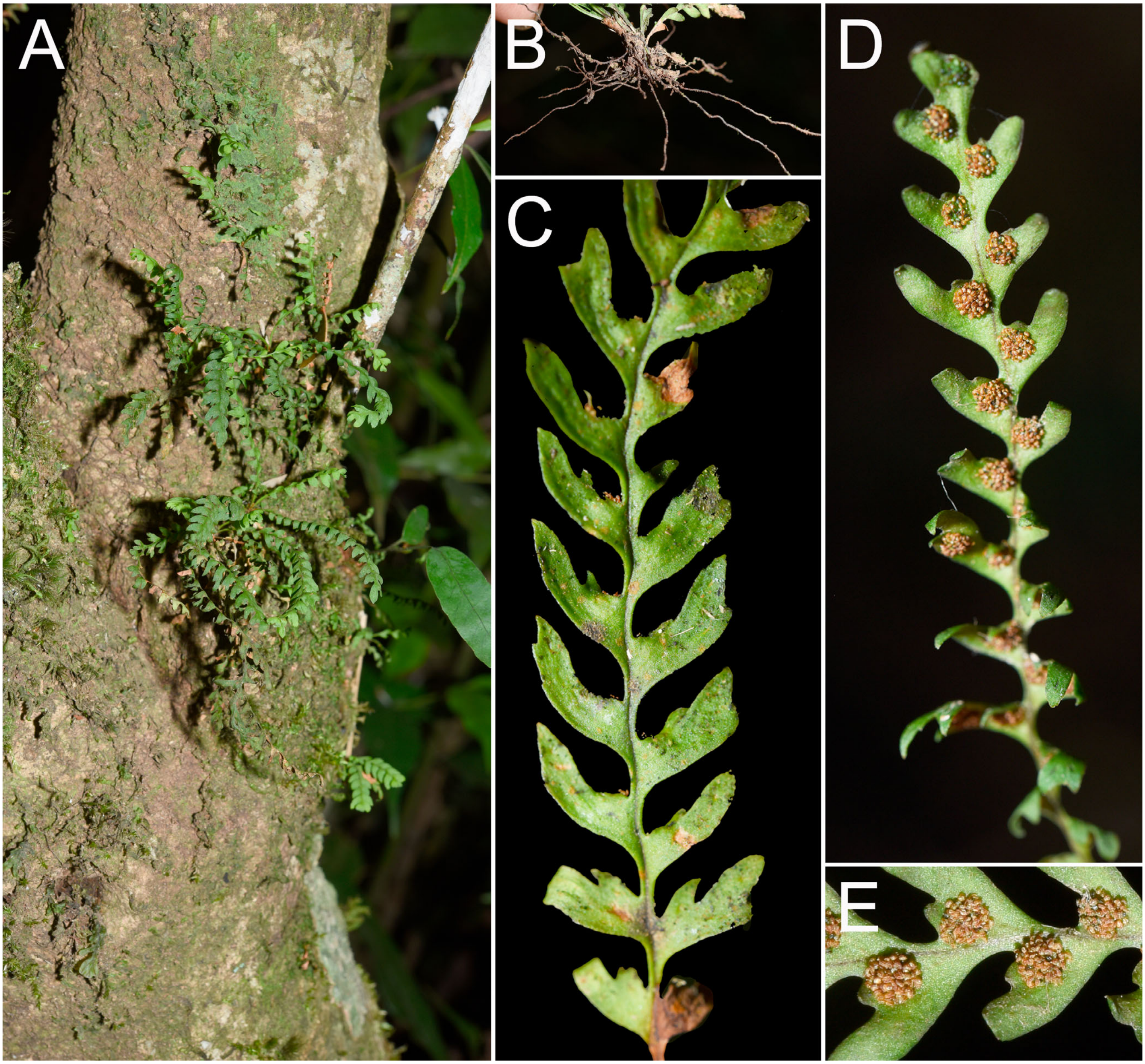

Fig. 4. *Boonkerdia khaoluangensis* (Tagawa & K.Iwats.) Li Bing Zhang, Pollawatn, X.M.Zhou & Liang Zhang. **A**, Habit and habitat; **B**, Lower portion of plant; **C**; Adaxial view of lamina; **D**, Abaxial view of lamina showing sori; **E**, Abaxial view of upper portion of lamina. — Photos: Liang Zhang.

Ctenopterella khaoluangensis (Tagawa & K.Iwats.) Parris in Gard. Bull. Singapore 58(2): 236. 2007 – Holotype: Peninsular Thailand, Nakhon Si Thammarat, Khao Luang, *Iwatsuki, Koyana, Hutoh & Chintayungkun T-14594* (KYO [image!]; isotypes: BFC n.v., K barcode K001044421!, KYO [image!], L barcode L 0052403!).

= *Ctenopteris malayana* Parris in Kew Bull. 41: 494. 1986 – Holotype: Peninsular Malaysia, Pahang/Selangor, Gunung Ulu Kali, *Piggott 1285* (K barcode K000474002!).

This species occurs in southern Thailand, Peninsular Malaysia, and southern Vietnam (Lindsay & Middleton, 2012–; Chen & al., 2020).

Boonkerdia thwaitesii (Bedd.) Parris, **comb. nov.** ≡ *Polypodium thwaitesii* Bedd., Ferns Brit. India: t. 188. 1866 ≡ *Ctenopteris thwaitesii* (Bedd.) Sledge in Bull. Brit. Mus. (Nat. Hist.), Bot. 2(5): 155. 1960 ≡ *Ctenopterella thwaitesii* (Bedd.) Parris in Fern Gaz. 20(2): 98. 2015 – Lectotype (designated by Parris in Fern Gaz. 16(5): 243. 2002): Ceylon, *Thwaites C.P. 3900* (K barcode K001040225!; isolectotypes: BM barcodes BM000053168!, BM001039870 [image!], CAL No. CAL20454 [image!], CGE!, E barcode E00195204!, GH barcode 00065921!, K barcodes K001040226!, K001040227!, K001040228!, K001040229!, P barcode P02141982!, PDA!).

Grammitastrum (E.Fourn.) Parris, Sundue, Li Bing Zhang & X.M.Zhou, **stat. nov.** ≡ *Polypodium* sect. *Grammitastrum* E.Fourn. in Ann. Sci. Nat., Bot., ser. 5, 18: 282. 1873 – Type (designated by Morton in Contr. U. S. Natl. Herb. 38(3): 89. 1973): *Grammitis pseudaustralis* E.Fourn.

Etymology. – Greek, *Grammitis*, the fern genus it resembles, and *astrum*, star, referring to the basally stellate hairs.

Diagnosis. – *Grammitastrum* differs from the other genera of Grammitidoideae by the following combination of characters: rhizomes dorsiventral, rhizome scales clathrate, ciliate, fronds not articulated to rhizome, laminae simple, without sclerotic margin, setae, branched hairs with setae as branches and basally stellate hairs present, fertile veins 1-forked, hydathodes absent from vein endings on adaxial surface of lamina, sporangia setose, setae on annulus and sporangial faces.

Description. – Sori ± circular to broadly elliptic, superficial or slightly sunken in broad shallow depressions, in one row each side of midrib. (Figs. 5, 6)

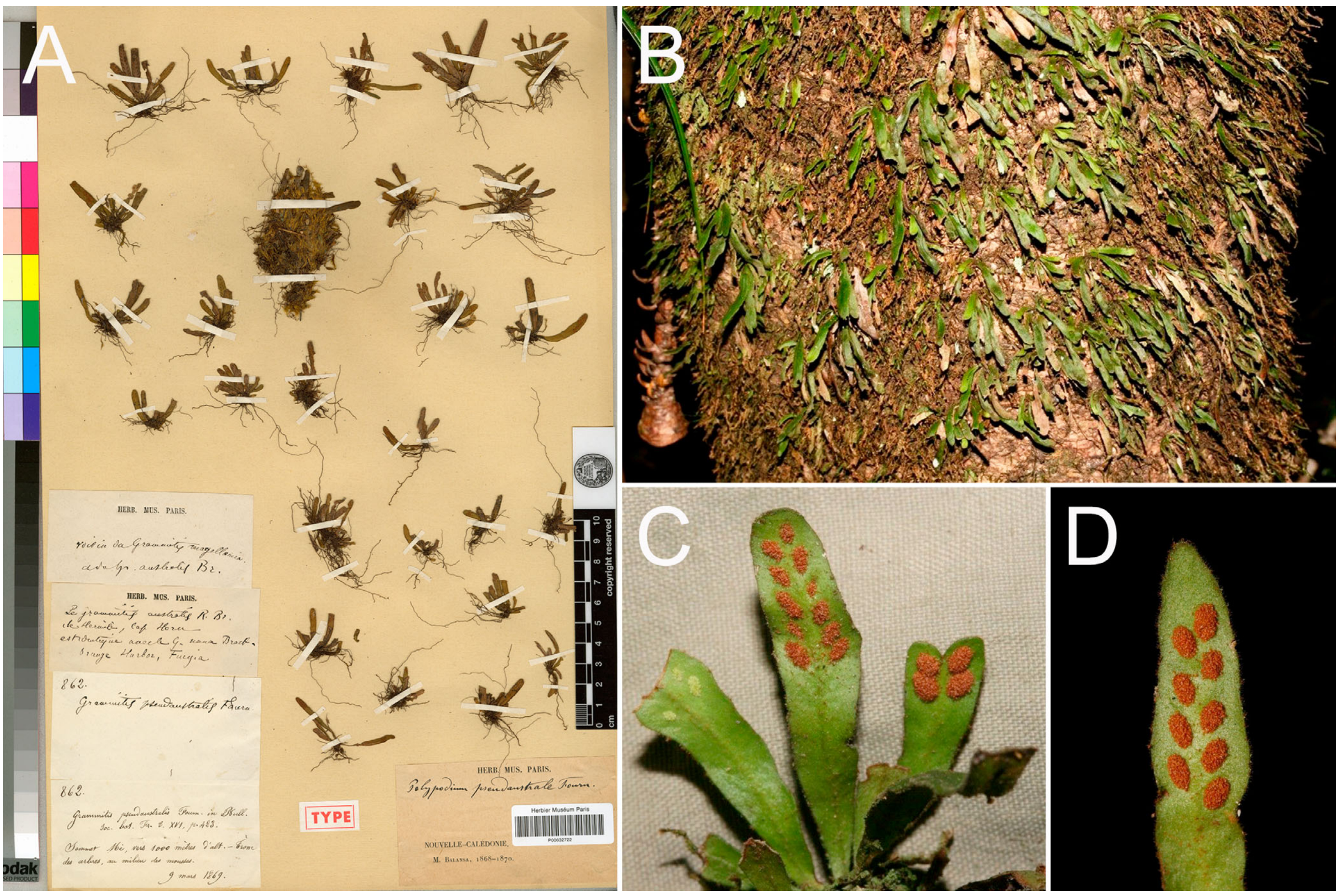

Fig. 5. *Grammitastrum pseudaustrale* (E.Fourn.) Parris, Sundue, Li Bing Zhang & X.M.Zhou. **A**, A syntype (*B. Balansa 863*; P00632722); **B**, Habit and habitat; **C** & **D**, Adaxial views of laminae showing sori. — Photos: B–D, Rémy Amice.

Notes. – *Grammitastrum* is separated from *Grammitis* s.l. and is resolved as sister to *Thalassogrammitis*. These two genera are sister to *Howeogrammitis* and together they form a clade that is sister to *Notogrammitis*. The three genera resemble most species of *Notogrammitis* in having dorsiventral rhizomes and simple laminae. *Grammitastrum* can be distinguished from *Howeogrammitis*, *Notogrammitis* and *Thalassogrammitis* by its clathrate ciliate rhizome scales and setose sporangia with hairs on the annulus cells and the faces of the sporangia.

Grammitastrum is monospecific and is endemic to New Caledonia. There is substantial divergence among three accessions of *G. pseudaustralis* as detected by Bauret & al. (2017) suggesting that there might be another species in the genus in New Caledonia.

Grammitastrum pseudaustrale (E.Fourn.) Parris, Sundue, Li Bing Zhang & X.M.Zhou, **comb. nov.** ≡ *Grammitis pseudaustralis* E.Fourn. in Bull. Soc. Bot. France 16: 423. 1869 ≡ *Polypodium pseudaustrale* (E.Fourn.) E.Fourn. in Ann. Sci. Nat., Bot., ser. 5, 18: 282. 1873 – **Lectotype (designated here):** New Caledonia, Mt. Mi, 1000 m, 9 Mar 1869, *M. Balansa 863* (P barcode P00632722 [image!]; isolectotypes: K!, MICH barcode 1191404!, UC barcode UC361298! [UC specimen does not have a collector's number]).

= *Polypodium pumilio* Hieron. in Hedwigia 44: 102. 1905, non Fée (1852) – Synypes: New Caledonia, *Vieillard 2260* (B!, K barcode K001044382!, NSW!, P? n.v.).

A lectotype for *Polypodium pumilio* has not been chosen because not all type material has been examined. This species occurs in New Caledonia.

Howeogrammitis Parris, Sundue, Li Bing Zhang & X.M. Zhou, **gen. nov.** – Type: *Howeogrammitis diminuta* (Baker) Parris, Sundue, Li Bing Zhang & X.M.Zhou.

Etymology. – Howe, from Lord Howe Island where the species occurs, and Greek, *Grammitis*, the fern genus in which it has been placed.

Diagnosis. – *Howeogrammitis* differs from the other genera of Grammitidoideae by the following combination of characters: rhizomes dorsiventral, rhizome scales concolorous, glabrous, fronds not articulated to rhizome, laminae simple, without sclerotic margin, with catenate simple hairs and sometimes with branched hairs with catenate hairs as branches, veins 1-forked, hydathodes absent from vein endings on adaxial surface of lamina, sporangia glabrous.

Description. – Stipes usually evident, rarely ± winged to base, articulated to phyllopodia, glabrous or with catenate simple hairs, or laminae linear-lanceolate to linear-oblanceolate, bluntly acute to acute at apex and long-attenuate at base, sori ± circular to narrowly oblong, superficial, one row each side of midrib. One species is recognized, from Lord Howe Island. (Fig. 7)

Notes. – *Howeogrammitis* is separated from *Grammitis* s.l. and is recovered as sister to the clade of *Grammitastrum* and *Thalassogrammitis*. These three genera form a clade that is sister to *Notogrammitis*.

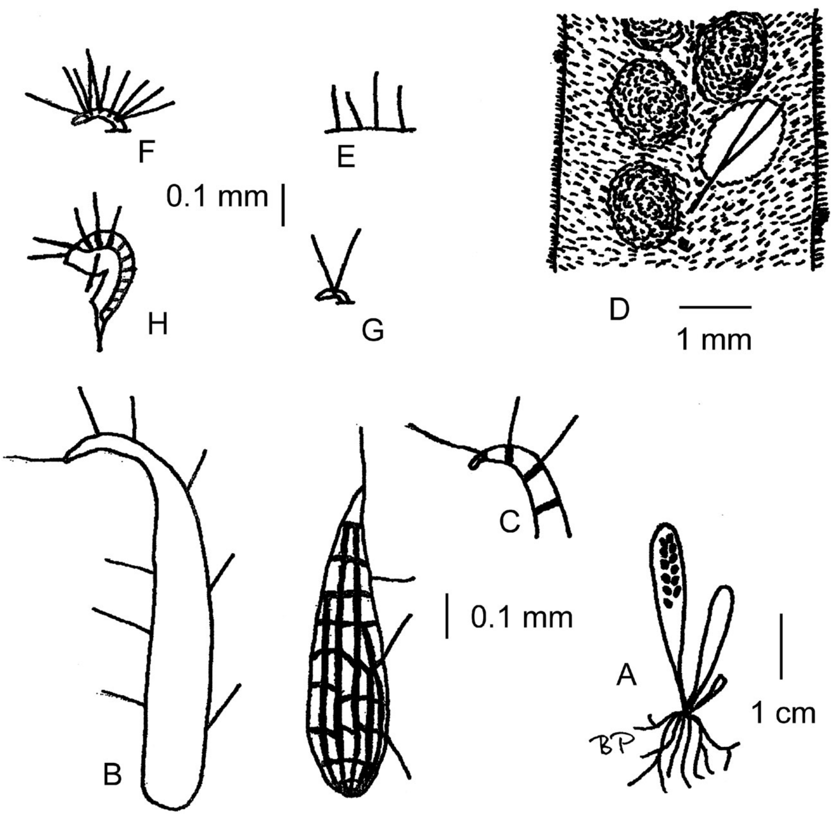

Fig. 6. *Grammitastrum pseudaustrale* (E.Fourn.) Parris, Sundue, Li Bing Zhang & X.M.Zhou. **A**, Habit; **B**, Rhizome scales showing cell arrangement; **C**, Apex of rhizome scale; **D**, Detail of abaxial surface of lamina; **E**, Simple eglandular hairs from lamina margin; **F**, Catenate hair with setae as branches from margin; **G**, Catenate hair with setae as branches from adaxial surface of lamina; **H**, Sporangium. — Based on *Schlechter 14992* (K); drawn by Barbara Parris.

Howeogrammitis diminuta (Baker) Parris, Sundue, Li Bing Zhang & X.M.Zhou, **comb. nov.** ≡ *Polypodium diminutum* Baker in Hooker & Baker, Syn. Fil., ed. 2: 507. 1874 ≡ *Grammitis diminuta* (Baker) Copel. in Philipp. J. Sci. 80(2): 141, fig. 13. 1952 – Lectotype (designated by Green in Fl. Austral. 49: 577. 1994): Lord Howe Island, *C. Moore* [31] (K barcode K001044367!).

= *Polypodium howeanum* Watts in J. Proc. Roy. Soc. New South Wales 49: 388. 1915 – Lectotype (designated by Green in Fl. Austral. 49: 577. 1994): Lord Howe Island, Mt Gower, Aug 1911, *Watts s.n.* (NSW!; isolectotypes: BRI!, MO!).

Grammitis nudicarpa Copel. and *G. pulchella* Ching [based on *Polypodium pulchellum* Watts (1916) non Willem. (1796) nec Salisb. (1796)] might be members of *Howeogrammitis* pending more evidence.

Nanogrammitis Parris, Li Bing Zhang, X.M.Zhou & Liang Zhang, **gen. nov.** – Type: *Nanogrammitis holophlebia* (Baker) Parris, Li Bing Zhang, X.M.Zhou & Liang Zhang.

Etymology. – Greek, *nanos* = dwarf, and *Grammitis*, a genus of ferns in which the species were previously placed referring to the small size of the species.

Diagnosis. – *Nanogrammitis* differs from the other genera of Grammitidoideae by the following combination of characters: rhizomes dorsiventral, rhizome scales glabrous, clathrate or concolorous, stipes absent or very short, fronds usually not

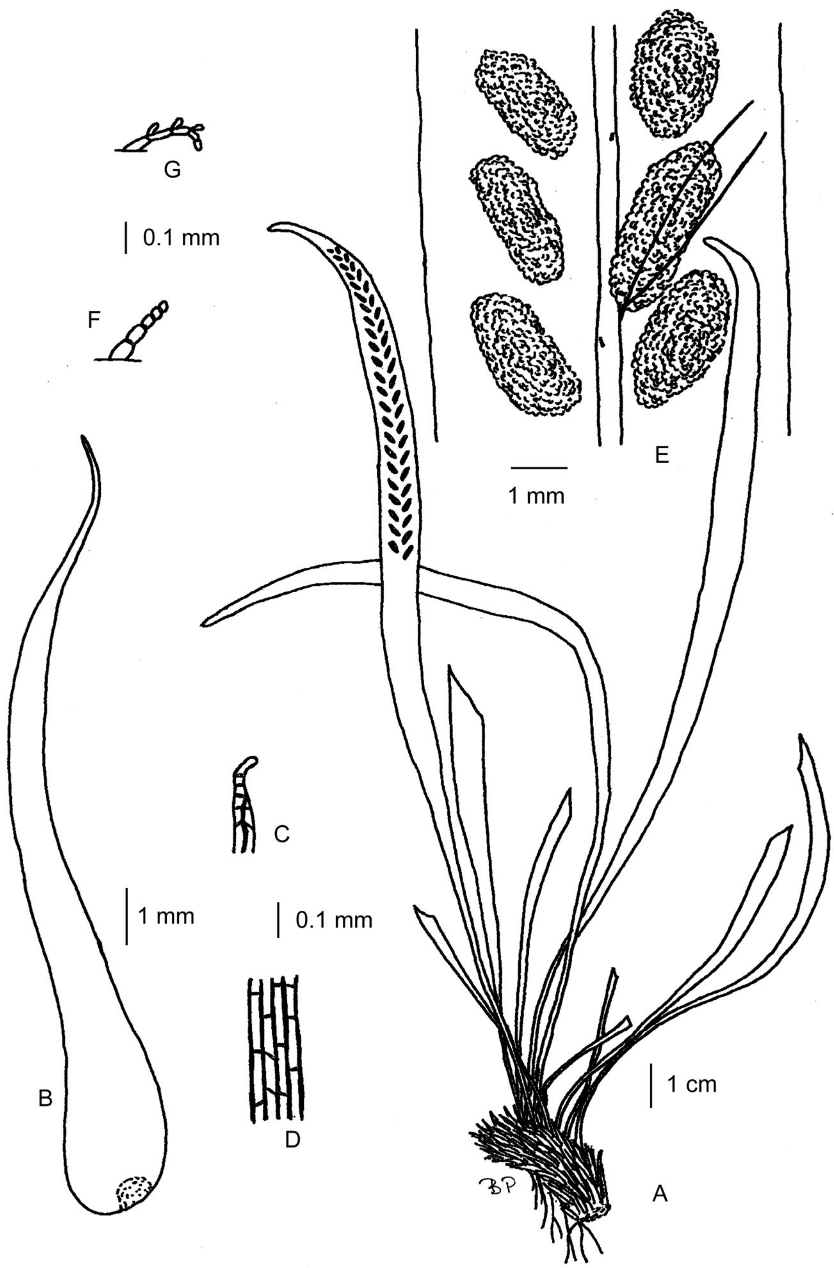

Fig. 7. *Howeogrammitis diminuta* (Baker) Parris, Sundue, Li Bing Zhang & X.M.Zhou. **A**, Habit; **B**, Rhizome scale; **C**, Apex of rhizome scale; **D**, Cells from center of rhizome scale; **E**, Detail of abaxial surface of lamina; **F**, Catenate simple glandular hair from abaxial surface of midrib; **G**, Catenate branched glandular hair from abaxial surface of midrib. — A & E, *Watts BRI 151749* (BRI); B & F, *Fullager 31* (MEL); C & D, *Percival BRI 192199* (BRI); G, *Beauglehole 5380* (MEL); drawn by Barbara Parris.

articulated to rhizome, laminae simple, without sclerotic margin, glabrous or setae often present, branched hairs and catenate simple hairs sometimes present, veins usually simple, sometimes 1(–2)-forked, vein endings usually with hydathodes present on adaxial surface of lamina, sporangia glabrous.

Description. – Rhizomes short-creeping to long-creeping. Laminae ovate, elliptic, narrowly elliptic, narrowly lanceolate, linear-lanceolate to linear-oblanceolate, texture membranous to coriaceous, hairs whitish to dark red-brown, veins usually free, rarely anastomosing at margin, sometimes prominent on adaxial surface of lamina, sori in one row each side of midrib. (Fig. 8)

Notes. – *Nanogrammitis* is resolved as sister to *Rouhania*. It differs from *Grammitis* s.str. in not having sclerotic blackish lamina margins.

Currently eight species are known in the genus and five have been sequenced. The species are distributed in the West Indian Ocean islands and tropical eastern Africa.

Nanogrammitis anisophylla (Rakotondr. & Parris) Parris, **comb. nov.** ≡ *Grammitis anisophylla* Rakotondr. & Parris in Adansonia, sér. 3, 40(11): 150. 2018 – Holotype: Madagascar, Toamasina, Maroantsetra, sur les berges de la rivière Andranobe, à 6 km au sud d'Ambanizana, 15° 41′S, 49°58′E, 40 m, 18 Dec 1993, *Rakotondrainibe & Raharamalala 1832* (P barcode P006028!; isotypes: AK!, MO!, TAN!).

Nanogrammitis dauphinensis (Rakotondr. & Parris) Parris, **comb. nov.** ≡ *Grammitis dauphinensis* Rakotondr. & Parris in Adansonia, sér. 3, 40(11): 152. 2018 – Holotype: Madagascar, Toliara, Tolanaro, Iabakho, Antstso-Avaratra, Ivohibe, 24°34′13″S, 47°12′02″E, 334 m, 21 May 2006, *Birkenshaw & al. 1630* (P barcode P01625745!).

Nanogrammitis holophlebia (Baker) Parris, Li Bing Zhang, X.M.Zhou & Liang Zhang, **comb. nov.** ≡ *Polypodium holophlebia* Baker in J. Bot. 18: 370. 1880 ≡ *Grammitis holophlebia* (Baker) Copel. in Philipp. J. Sci. 80: 136. 1951 – **Lectotype (designated here):** Madagascar, Tanala, *Kitching s.n.* (K barcode K000227549!)
= *Polypodium tanalense* Baker in Kew Bull. 1897: 300. 1897 – Holotype: Madagascar, Province of Tanala, forest of Ambohimatombo, *Forsyth Major 185* (K!).

This species occurs in Madagascar.

Nanogrammitis obtusa (Willd. ex Kaulf.) Parris, Li Bing Zhang, X.M.Zhou & Liang Zhang, **comb. nov.** ≡ *Grammitis obtusa* Willd. ex Kaulf., Enum. Filic.: 94. 1824 – Holotype: Mauritius, *herb. Willd. 19595* (B [photo!]).

This species occurs in La Réunion, Mauritius, and Madagascar.

Nanogrammitis pellucidovenosa (Bonap.) Parris, Li Bing Zhang, X.M.Zhou & Liang Zhang, **comb. nov.** ≡ *Polypodium pellucidovenosum* Bonap., Notes Ptérid. 10: 189. 1920 ≡ *Grammitis pellucidovenosa* (Bonap.) Ching in Bull. Fan Mem. Inst. Biol. 10: 241. 1940 – Syntypes: Madagascar, Centre, massif de Manongarivo, ca. 1200 m, May 1909, *Perrier de la Bâthie 7471* (BM barcode BM000585309!, P barcodes P00114042, P00462082, P00462083 [images!]), *Perrier de la Bâthie 7471** (P?), *Perrier de la Bâthie 7704* (P?).

This species occurs in Madagascar.

Nanogrammitis pervillei (Mett. ex Kuhn) Parris, Li Bing Zhang, X.M.Zhou & Liang Zhang, **comb. nov.** ≡ *Polypodium pervillei* Mett. ex Kuhn, Filic. Afr.: 150. 1868 ≡ *Grammitis pervillei* (Mett. ex Kuhn) Tardieu in Notul. Syst. (Paris) 15(4): 424. 1959 – **Lectotype (designated here):** Seychelles, *Pervillé s.n.*, Buchinger herb. (B!; isolectotypes: UC barcode UC2048269 [as *Perville s.n.*, image!]; P barcode P00462088 [as *Pervillé 217*; image!], UC barcode UC2048270 [as *Pervillé 217*]).

This species occurs in the Seychelles.

Nanogrammitis synsora (Baker) Parris, Li Bing Zhang, X.M. Zhou & Liang Zhang, **comb. nov.** ≡ *Polypodium synsorum* Baker in J. Linn. Soc. 16: 203. 1877 ≡ *Grammitis synsora* (Baker) Copel. in Philipp. J. Sci. 80(2): 137. 1952 – **Lectotype (designated here):** Madagascar, Antananarivo, *Gilpin s.n.* (K barcode K000435891!; isolectotype: P barcode P00114081 [image!]).

This species occurs in Madagascar and Tanzania.

Oxygrammitis Parris & Sundue, **gen. nov.** – Type: *Oxygrammitis denticulata* (Blume) Parris & Sundue.

Etymology. – Greek, *oxys* = sharp, and *Grammitis*, a fern genus in which the type species was formerly placed, referring to the sharp teeth on the margin of the lamina

Diagnosis. – *Oxygrammitis* differs from the other genera of Grammitidoideae in the following combination of characters: rhizomes dorsiventral, rhizome scales glabrous, concolorous, stipes present, sometimes very short, fronds sometimes articulated to phyllopodia on rhizome, lamina without sclerotic margin, bipinnately to tripinnately divided, ultimate divisions acute to acuminate at apex, texture thickly coriaceous, fronds glabrous or with setae and/or catenate simple hairs, simple glandular hairs, and 1–3-forked hairs with catenate base and catenate branches, veins invisible in transmitted light, pinnately branched, prominent and concolorous with lamina on adaxial surface, hydathodes absent from vein endings on adaxial surface of lamina, sporangia glabrous.

Description. – Rhizomes short-creeping to long-creeping, rhizome scales pale to medium red-brown or pale to medium yellow-brown, sori in one row each side of costa, one per primary lobe, ± circular to broadly elliptic, superficial or slightly sunken in broad shallow depressions, receptacles sometimes prominent on adaxial surface of lamina. (Fig. 9)

Notes. – There are two species in the genus, distributed from Indonesia (Sumatra) to Papua New Guinea.

Oxygrammitis denticulata (Blume) Parris & Sundue, **comb. nov.** ≡ *Grammitis denticulata* Blume in Blume & Fischer, Fl. Javae, Filices: 121, t. 50, fig. 4. 1830 ≡ *Polypodium denticulatum* (Blume) C.Presl, Tent. Pterid.: 178. 1836 ≡ *Calymmodon denticulatus* (Blume) T.Moore, Index Fil.: lxii. 1857 ≡ *Ctenopteris denticulata* (Blume) C.Chr. & Tardieu in Notul. Syst. (Paris) 8: 181. 1939 ≡ *Ctenopterella denticulata* (Blume) Parris in Gard. Bull.

Fig. 8. *Nanogrammitis holophlebia* (Baker) Parris, Li Bing Zhang & X.M.Zhou. **A**, Holotype (K000227549); **B** & **C**, Habit and habitats. — Photos: B & C, Germinal Rouhan.

Singapore 58(2): 235. 2007 – **Lectotype (designated here):** Java, *Blume s.n*. (L barcode L 0051199!).

= *Polypodium solidum* Mett. in Abh. Senckenberg. Naturf. Ges. 2: 53. 1857 ≡ *Ctenopteris solida* (Mett.) J.Sm., Hist. Fil.: 184. 1875 ≡ *Grammitis solida* (Blume) Ching in Bull. Fan. Mem. Inst. Biol. 10: 241. 1941 – Type: Java, *Zollinger 165* (G?).

= *Polypodium sibarongae* Christ in Ann. Jard. Bot. Buitenzorg 19 [= ser. 2, 4]: 36. 1904 – Type: Celebes (= Sulawesi), Mt Sibaronga, 20 Jul 1902, *F. & P. Sarasin 2011* (BAS?).

= *Polypodium serratodentatum* Alderw. in Bull. Dép. Agric. Indes Néerl. 18: 20. 1908 – **Lectotype (designated here):** Java, Pasir Orai, Kosala, Bantam, 2900 feet a.s.l., Oct 1879, *H.O. Forbes 244* (CAL No. CAL22444 [image!]; isolectotype: BO n.v.).

= *Polypodium serratodentatum* var. *major* Alderw. in Bull. Jard. Bot. Buitenzorg, sér. 2, 16: 59. 1914 – **Lectotype (designated here):** Sumatra, Kapahiang-barisan, *Matthew 230* (L!; isolectotype: K barcode K000474256!). The L collection is labelled by Alderwerelt so is a better choice for lectotype than the K material, which is labelled by Matthew and lacks a number.

= *Polypodium scalpturatum* C.Chr. in Svensk Bot. Tidskr. 16(1): 100. 1922 – **Lectotype (designated here):** Celebes (Sulawesi), Bolaang to Mongondou, above Modajag, *Kaudern 37* (S No. S-P-6809 [image!]).

The species occurs in Indonesia (Sumatra, Java, Lesser Sunda Islands, Sulawesi, Maluku), Malaysia and the Philippines.

Oxygrammitis undosa (Baker) Parris & Sundue, **comb. nov.** ≡ *Polypodium undosum* Baker in J. Bot. 28: 108. 1890 ≡ *Ctenopteris undosa* (Baker) Copel. in Philipp. J. Sci. 81(2): 103. 1953 ≡ *Ctenopterella undosa* (Baker) Parris in Fern. Gaz. 20(2): 98. 2015 – **Lectotype (designated here):** [Papua] New Guinea, Mt Musgrave, 1889, *MacGregor 61* (K barcode K000507064!; isolectotype: MEL!).

= *Polypodium solidum* var. *bolanicum* Rosenst. in Repert. Spec. Nov. Regni Veg. 12: 177. 1913 ≡ *Polypodium bolanicum* (Rosenst.) Copel. in Univ. Calif. Publ. Bot. 12(15): 403. 1931 ≡ *Ctenopteris bolanica* (Rosenst.) Copel. in Philipp. J. Sci. 81(2): 103. 1953 – **Lectotype (designated here):** Nova Guinea germanica, Bolan Mts, 3400–3800 m, 1912, *C. Keysser B. 21.39* (UC barcode UC391432!).

= *Polypodium vernicosum* Alderw. in Nova Guinea 14: 46. 1924 – **Lectotype (designated here):** [Indonesian] New

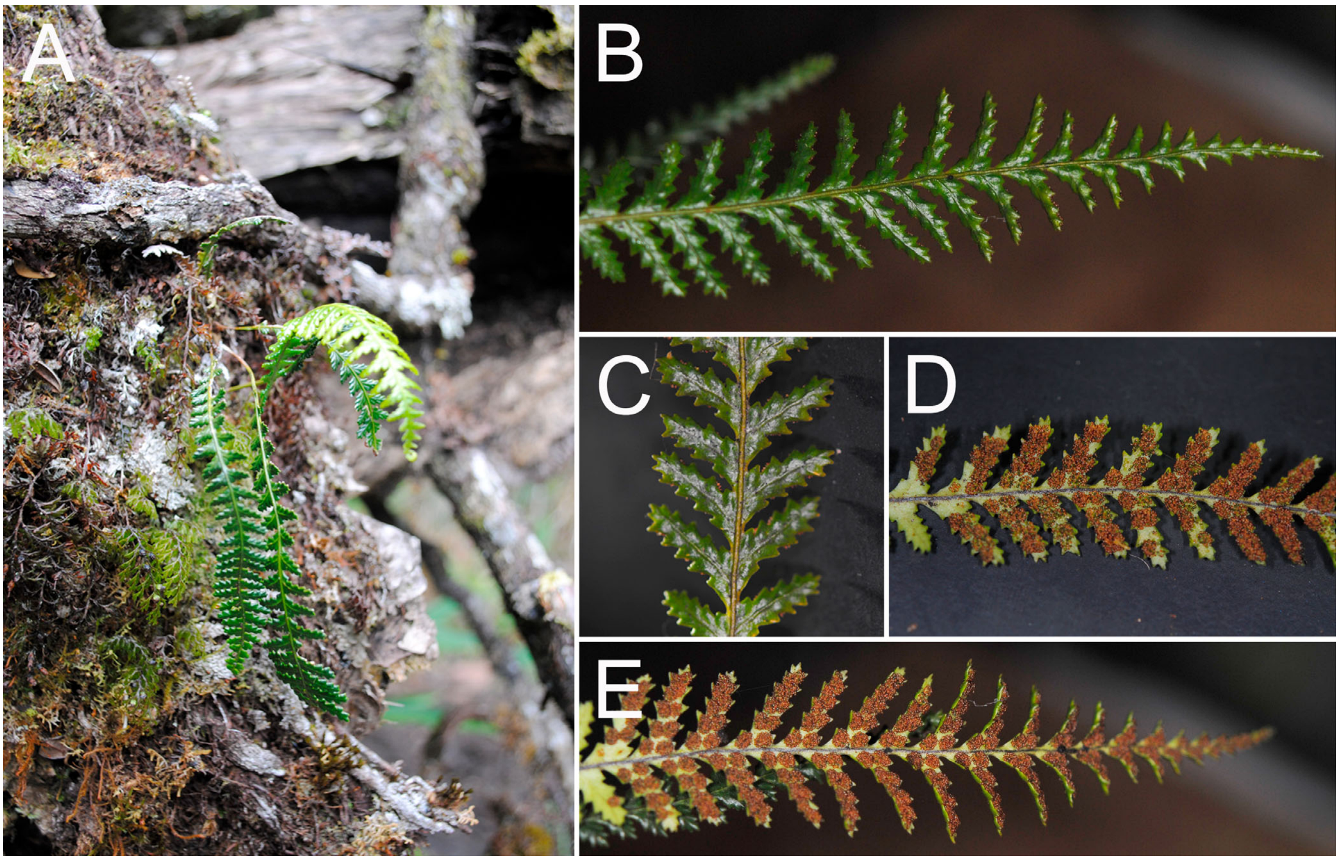

Fig. 9. *Oxygrammitis undosa* (Baker) Parris & Sundue. **A**, Habit and habitat; **B** & **C**, Portions of adaxial lamina; **D** & **E**, Portions of abaxial lamina showing sori. — Photos: Michael Sundue.

Guinea, Doormantop, 2500 m, 30 Oct 1920, *Lam 1850* (BO No. 1347986!).

= *Polypodium pycnophyllum* C.Chr. in Brittonia 2(4): 308. 1937 ≡ *Ctenopteris pycnophylla* (C.Chr.) Copel. in Philipp. J. Sci. 81(2): 102. 1953 – **Lectotype (designated here):** Papua [New Guinea], Central Division, Mt Albert Edward, 3680 m, 5 Jul 1933, *Brass 4421* (NY barcode 00127770 [image!]; isolectotypes: BRI barcode BRI-AQ0024868!, MICH barcode 1115954!).

The species is endemic to New Guinea.

Rouhania Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Liang Zhang, **gen. nov.** – Type: *Rouhania zenkeri* (Hieron.) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Liang Zhang.

Etymology. – In honor of Germinal Rouhan based at P for his contributions to pteridology, especially that of Madagascar (e.g., Rouhan & al., 2007, 2012; Bauret & al., 2017, 2018; Duan & al., 2017). Half of the vouchers of DNA data of this clade were collected by him and colleagues.

Diagnosis. – *Rouhania* differs from the other genera of Grammitidoideae by the following combination of characters: rhizomes dorsiventral, rhizome scales glabrous, concolorous, fronds sometimes articulated to phyllopodia, laminae simple (*R. nanodes*, *R. pygmaea*) or pinnate or pinnatisect (*R. parvula*, *R. zenkeri*), without sclerotic margin, sometimes glabrous, simple glandular hairs usually present, catenate simple hairs, setae and branched hairs with setae or catenate hairs as branches sometimes present, veins simple, 1-forked or pinnately branched, vein endings with hydathodes present on adaxial surface of lamina, sporangia glabrous.

Description. – Rhizomes long or short-creeping. Stipes sometimes articulated to phyllopodia, sometimes ± winged to base, short or long. Laminae oblanceolate to linear-oblanceolate; with pinnae oblique or at right angle to the rachis. Sori ± circular to broadly elliptic, superficial or slightly sunken in broad shallow depressions in lamina, in one row each side of midrib or costa. (Fig. 10)

Notes. – Currently eight species are known for this genus and four have been sequenced. They occur in Africa and the Indian Ocean islands.

Rouhania boivinii (Mett. ex Kuhn) Parris, **comb. nov.** ≡ *Polypodium boivinii* Mett. ex Kuhn, Filic. Afr.: 146. 1868 ≡

Fig. 10. *Rouhania zenkeri* (Hieron.) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Liang Zhang. **A**, Holotype (K000435906); **B**, Habit and habitat; **C**, Abaxial view of fronds. — Photos: B & C, Germinal Rouhan.

Lellingeria boivinii (Mett. ex Kuhn) A.R.Sm. & R.C. Moran in Amer. Fern J. 81(3): 83. 1991 ≡ *Stenogrammitis boivinii* (Mett. ex Kuhn) Labiak in Brittonia 63(1): 145. 2011 ≡ *Grammitis boivinii* (Mett. ex Kuhn) Christenh. in Global Flora 4: 47. 2018 ≡ *Ctenopterella boivinii* (Mett. ex Kuhn) Rakotondr. & Parris in Adansonia, ser. 3, 40(11): 160. 2018 – **Lectotype (designated here):** Madagascar, *Boivin s.n.* (B barcode B20 087466!).

This species is endemic to Madagascar.

Rouhania gabonensis (Parris) Parris, **comb. nov.** ≡ *Ctenopterella gabonensis* Parris in Fern Gaz. 19(3): 89. 2012 – Holotype: Gabon, Chantier CEB, Monts Doudou, ca. 20 km WSW of Doussala, 02°25′S 10°30′E, ca. 650–700 m, 20 May 1985, *J.M. & B. Reitsma 1081, Breteler & A.M. Louis* (WAG barcode WAG0014897!).

This species occurs in Equatorial Africa and Gabon.

Rouhania lastii (Parris & Rakotondr.) Parris, **comb. nov.** ≡ *Ctenopterella lastii* Parris & Rakotondr. in Adansonia, sér. 3, 40(11): 148. 2018 – Holotype: Madagascar, Be Kilus Mts, Apr–May 1890, *Last s.n.* (BM barcode BM000585367!).

This species is endemic to Madagascar.

Rouhania macrorhyncha (Baker) Parris, **comb. nov.** ≡ *Polypodium macrorhynchum* Baker in J. Bot. 18: 370. 1880 ≡ *Ctenopterella macrorhyncha* (Baker) Parris in Gard. Bull. Singapore 58(2): 237. 2007 ≡ *Grammitis macrorhyncha* (Baker) Christenh. in Global Flora 4: 52. 2018 – **Lectotype (designated here):** Madagascar, Tanala, *Kitching s.n.* (K barcode K000435901!).

This species is endemic to Madagascar.

Rouhania nanodes (Peter) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Liang Zhang, **comb. nov.** ≡ *Polypodium nanodes* Peter in Repert. Spec. Nov. Regni Veg. Beih. 40(1): 27. 1929 ≡ *Grammitis nanodes* (Peter) Ching in Bull. Fan Mem. Inst. Biol. 10: 241. 1941 – **Lectotype (designated here):** Deutsch-Ostafrika, W Usumbara, Kisimba, üb. Mazumbai, 1900 m, Apr 1915, *Peter 16492* (K barcode K000435892!; isolectotypes: B?, UC barcode UC611143!).

This species is reinstated here from the synonymy of *Grammitis pygmaea* (Parris, 2005) considering the geographical and molecular divergence (Bauret & al., 2017; our suppl. Fig. S1). This species occurs in eastern Africa.

Rouhania parvula (Bory ex Willd.) Li Bing Zhang, X.M. Zhou, Jian Jun Yang & Liang Zhang, **comb. nov.** ≡ *Polypodium parvulum* Bory ex Willd., Sp. Pl. 5(1): 182. 1810 ≡ *Ctenopteris parvula* (Bory ex Willd.) J.Sm., Hist. Fil.: 185. 1875 ≡ *Grammitis parvula* (Bory ex Willd.) C.V. Morton in Contr. U. S. Natl. Herb. 38: 261. 1973 ≡ *Ctenopterella parvula* (Bory ex Willd.) Parris in Gard. Bull. Singapore 58(2): 237. 2007 – **Lectotype (designated here):** Réunion, Bourbon, *Bory 96* (B barcode B -W 19667 -01 0!; isolectotypes: FI [image!], P barcode P00462092!).

This species occurs in the West Indian Ocean islands.

Rouhania pygmaea (Bory ex Willd.) Li Bing Zhang, X.M. Zhou, Jian Jun Yang & Liang Zhang, **comb. nov.** ≡ *Polypodium pygmaeum* Mett. ex Kuhn, Filic. Afr.: 152. 1868 ≡ *Grammitis pygmaea* (Mett. ex Kuhn) Copel. in Philipp. J. Sci. 80(2): 138. 1952 – Holotype: Ins. Borboniae, *Buchinger herb.* (B barcode 20 0136781!).

This species occurs in the West Indian Ocean islands. The eastern African material is referred to *R. nanodes*.

Rouhania zenkeri (Hieron.) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Liang Zhang, **comb. nov.** ≡ *Polypodium zenkeri* Hieron. in Bot. Jahrb. Syst. 46(3): 385. 1911 ≡ *Ctenopteris zenkeri* (Hieron.) Tardieu in Aubreville, Fl. Cameroun 3: 327. 1964 ≡ *Xiphopteris zenkeri* (Hieron.) Schelpe in Contr. Bolus Herb. 1: 12. 1969 ≡ *Ctenopterella zenkeri* (Hieron.) Parris in Gard. Bull. Singapore 58(2): 237. 2007 – Lectotype (designated by Parris in Gard. Bull. Singapore 58: 237. 2007): Kamerun, Yaunde, 4 Aug 1897, *Zenker 1507* (B barcode B20 122283!; isolectotypes: BM barcodes BM000585411!, BM000585412!, E barcode E00194040!, K barcode K000435906!, P barcode P00462090!).

= *Polypodium decorum* var. *excaudatum* Bonap., Notes Ptérid. 4: 79. 1917 ≡ *Polypodium excaudatum* (Bonap.) C.Chr. in Arch. Bot. Mém. 2(12): 215. 1928 – Syntypes: [Madagascar], Région floristique de l'Est et du Centre, Forêt d'Analamazaotra, 800 m d'altitude, [*Perrier de la Bâthie*] *7533* (BM barcode BM000585410!, P?); Région floristique du Centre, Imerina occidentale, Manankazo au Nord-Est d'Ankazohe, vers 1500 m d'altitude, Nov 1913, [*Perrier de la Bâthie*] *7593* (P?); Région floristique cu Centre, Montagnes du Sambirano, vers 1000 m d'altitude, Oct 1908, *Perrier de la Bâthie 7643* (P?).

This species occurs in Africa and the West Indian Ocean islands.

Thalassogrammitis Parris, Sundue, Li Bing Zhang & X.M. Zhou, **gen. nov.** – Type: *Thalassogrammitis deplanchei* (Baker) Parris, Sundue, Li Bing Zhang & X.M.Zhou.

Etymology. – Greek, *Thalassa* = sea, and *Grammitis*, the genus in which the species has been included, referring to the distribution of the genus on New Caledonia, an island in the southwest Pacific Ocean.

Diagnosis. – *Thalassogrammitis* differs from the other genera of Grammitidoideae by the following combination of characters: rhizomes dorsiventral, rhizome scales concolorous, ciliate, stipes ± winged to base, lamina simple, without sclerotic margin, glabrous at maturity, sometimes with simple glandular hairs and 1-forked hairs with a seta as branch when young, veins 1(–2)-forked, usually each branch with a sorus, hydathodes absent from vein endings on adaxial surface of lamina, sori nearer margin than midrib, sporangia setose, setae at apex of sporangium on walls of annulus cells.

Description. – Lamina coriaceous, veins free or rarely anastomosing, sori ± circular to broadly elliptic, superficial or slightly sunken in broad shallow depressions, in one each side of midrib, nearer margin than midrib. (Fig. 11)

Notes. – *Thalassogrammitis* is segregated from *Grammitis* s.l. and is resolved as sister to *Grammitastrum*. These two genera are sister to *Howeogrammitis* and together they form a clade that is sister to *Notogrammitis*. The three genera resemble most species of *Notogrammitis* in having dorsiventral rhizomes and simple laminae. *Thalassogrammitis* can be distinguished from *Grammitastrum*, *Howeogrammitis* and *Notogrammitis* by having concolorous ciliate rhizome scales, sori on most vein branches that are nearer the margin than the midrib and setose sporangia with hairs on the cell walls of the annulus.

Thalassogrammitis is monospecific and is endemic to New Caledonia.

Thalassogrammitis deplanchei (Baker) Parris, Sundue, Li Bing Zhang & X.M.Zhou, **comb. nov.** ≡ *Polypodium deplanchei* Baker in Hooker & Baker, Syn. Fil.: 322. 1867 ≡ *Austrogramme deplanchei* (Baker) E.Fourn. in Ann. Sci. Nat., Bot., ser. 5, 18: 279. 1873 ≡ *Grammitis deplanchei* (Baker) Copel., Gen. Fil. [Ann. Cryptog. Phytopathol. 5]: 211. 1947 – **Lectotype (designated here):** New Caledonia, *Deplanche 5* (K barcode K001044391!).

= *Grammitis athroosperma* E.Fourn. in Bull. Soc. Bot. France 16: 423. 1869 – Syntypes: New Caledonia, *Deplanche s.n.* (K barcodes K001044390!, K001044392!, P?), *Baudouin s.n.* (P?).

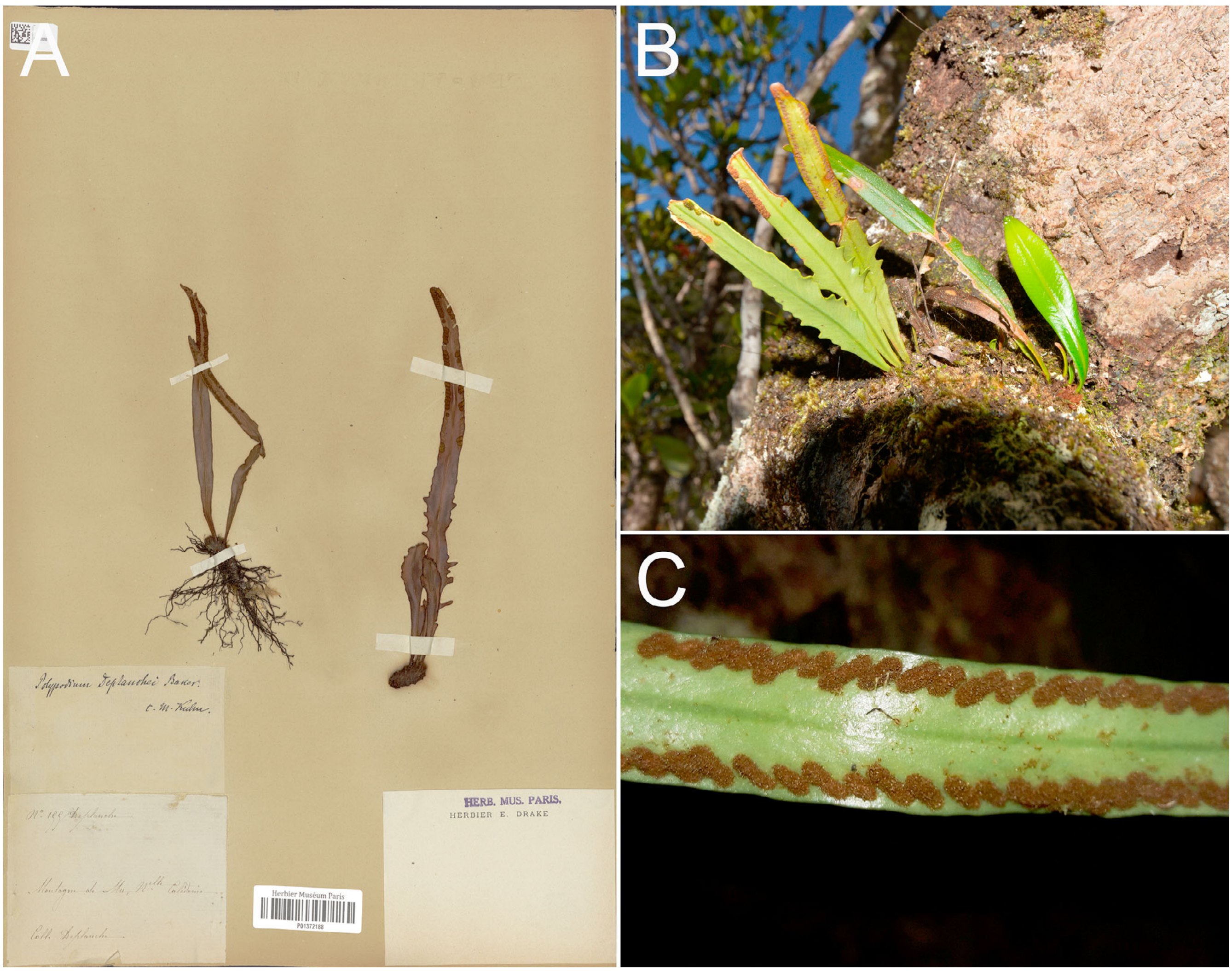

Fig. 11. *Thalassogrammitis deplanchei* (Baker) Parris, Sundue, Li Bing Zhang & X.M.Zhou. **A**, A specimen (P01372188); **B**, Habit; **C**, Abaxial view of portion of lamina. — Photos: B, Pierre-Louis Stenger; C, Lara Shepherd.

AUTHOR CONTRIBUTIONS

Conceptualization: LBZ, Liang Zhang & XMZ; Investigation: XMZ, JJY, RP, RK, BP, MS, TAR, ZLL, Lin Zhou, NTL, TTL, XW, ZRH, JZ, Liang Zhang, LBZ; Writing: LBZ & BP; Reviewing and Editing: XMZ, JJY, RP, RK, BP, MS, TAR, Liang Zhang & LBZ; Visualization: XMZ, JJY, BP & LBZ; Supervision: XMZ, Liang Zhang & LBZ.
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Appendix 1. List of types of genera included in previous and current studies.

No.	Genus	Type species	Sampled by
1	*Acrosorus*	**A. exaltatus* (Copel.) Copel. = *A. friderici-et-pauli* (Christ) Copel.	Sundue & al. (2014), Bauret & al. (2017)
2	*Adenophorus*	*A. tripinnatifidus* Gaudich.	Ranker & al. (2003), Nitta & Schuettpelz (unpub.)
3	*Aenigmatogrammitis*	*A. stenophylla* (Parris) Parris	Perrie & Parris (2012)
4	*Alansmia*	*A. lanigera* (Desv.) Moguel & M.Kessler	Ranker & al. (2004), Sundue & al. (2010)
5	*Archigrammitis*	*A. friderici-et-pauli* (Christ) Parris	-
6	*Ascogrammitis*	*A. athyrioides* (Hook.) Sundue	Sundue & al. (2010)
7	*Boonkerdia*	**B. khaoluangensis* (Tagawa & K.Iwats.) Li Bing Zhang, Pollawatn, X.M.Zhou & Liang Zhang	This study
8	*Calligrammitis*	*C. beddomeana* (Alderw.) Parris, Sundue, Li Bing Zhang, X.M.Zhou & Ralf Knapp	This study
9	*Calymmodon*	*C. cucullatus* (Nees & Blume) C.Presl	-
10	*Ceradenia*	*C. curvata* (Sw.) L.E.Bishop	Sundue & al. (2014)
11	*Chrysogrammitis*	*C. glandulosa* (J.Sm.) Parris	Hirai & al. (2011), this study
12	*Cochlidium*	*C. graminoides* (Sw.) Kaulf.	-
13	*Ctenopterella*	*C. blechnoides* (Grev.) Parris	Nitta & al. (2017), Nitta & Schuettpelz (unpub.)
14	*Dasygrammitis*	*D. mollicoma* (Nees & Blume) Parris	Sundue & al. (2014), this study
15	*Devolia*	**D. orientalis* (T.C.Hsu) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Ralf Knapp	This study
16	*Enterosora*	*E. campbellii* subsp. *spongiosa* (Maxon) L.E.Bishop	Shalisko & al. (2019)
17	*Galactodenia*	*G. delicatula* (M.Martens & Galeotti) Sundue & Labiak	Labiak & al. (2010), Shalisko & al. (2019)
18	*Glabrigrammitis*	*G. subevenosa* (Baker) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Parris	This study
19	*Grammitastrum*	*G. pseudaustrale* (E.Fourn.) Parris, Sundue, Li Bing Zhang & X.M.Zhou	Sundue & al. (2014), Bauret & al. (2017)
20	*Grammitis*	*G. marginella* (Sw.) Sw.	This study
21	*Howeogrammitis*	*H. diminuta* (Baker) Parris, Sundue, Li Bing Zhang & X.M.Zhou	Papadopulos & al. (2011)
22	*Lellingeria*	*L. apiculata* (Kunze ex Klotzsch) A.R.Sm. & R.C.Moran	Ranker & al. (2004), Labiak & al. (2010), Shalisko & al. (2019)
23	*Leucotrichum*	*L. organense* (Gardner) Labiak	Labiak & al. (2010)
24	*Lomaphlebia*	*L. linearis* (Sw.) J.Sm. = *L. graminea* (Sw.) Parris	Shalisko & al. (2019)
25	*Luisma*	***L. bivascularis* M.T.Murillo & A.R.Sm.	-
26	*Melpomene*	*M. moniliformis* (Lagasca ex Sw.) A.R.Sm. & R.C.Moran	Ranker & al. (2004), Lehnert & al. (2009), Labiak & al. (2010), Shalisko & al. (2019)
27	*Micropolypodium*	*M. pseudotrichomanoides* (Hayata) Hayata = *M. okuboi* (Yatabe) Hayata	Ebihara & al. (2010), Hirai & al. (2011), Wei & al. (2021), this study
28	*Moranopteris*	*M. basiattenuata* (Jenman) R.Y.Hirai & J.Prado	Hirai & al. (2011), this study
29	*Mycopteris*	*M. taxifolia* (L.) Sundue	Sundue & al. (2010)
30	*Nanogrammitis*	*N. holophlebia* (Baker) Parris, Li Bing Zhang, X.M.Zhou & Liang Zhang	Bauret & al. (2017)
31	*Notogrammitis*	*N. billardierei* (Willd.) Parris	Perrie & Parris (2012), Sundue & al. (2014), Richardson & Morse (unpub.)
	ORT clade		
32 (1)	*Oreogrammitis*	*O. clemensiae* Copel.	-
32 (2)	*Radiogrammitis*	*R. setigera* (Blume) Parris = *O. setigera* (Blume) T.C.Hsu	Sundue & al. (2014), this study

(Continues)

Appendix 1. Continued.

No.	Genus	Type species	Sampled by
32 (3)	*Themelium*	*T. tenuisectum* (Blume) Parris = *O. tenuisecta* (Blume) T.C.Hsu	Ranker & al. (2004), Nitta & Schuettpelz (unpub.), this study
33	*Oxygrammitis*	*O. denticulata* (Blume) Parris	Hirai & al. (2011)
34	*Parrisia*	*P. parietina* (Klotzsch) Shalisko & Sundue	Schuettpelz & Pryer (2007), Hennequin & al. (2014), Bauret & al. (2017)
35	*Prosaptia*	*P. contigua* (G.Forst.) C.Presl	Sundue & al. (2014), Bauret & al. (2017), Nitta & al. (2017), Nitta & Schuettpelz (unpub.), Steier & Schuettpelz (unpub.), this study
36	*Rouhania*	*R. zenkeri* (Hieron.) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Liang Zhang	Bauret & al. (2017)
37	*Scleroglossum*	*S. pusillum* (Blume) Alderw.	Sundue & al. (2014), Bauret & al. (2017), Liu & al. (2019), Nitta & Schuettpelz (unpub.), Steier & Schuettpelz (unpub.)
38	*Stenogrammitis*	*S. myosuroides* (Sw.) Labiak	Labiak & al. (2010), Ranker & al. (2010)
39	*Terpsichore*	*T. asplenifolia* (L.) A.R.Sm.	Hirai & al. (2011)
40	*Thalassogrammitis*	*T. deplanchei* (Baker) Parris, Sundue, Li Bing Zhang & X.M.Zhou	Schuettpelz & Pryer (2007), Bauret & al. (2017), Nitta & Schuettpelz (unpub.)
41	*Tomophyllum*	*T. subsecundodissectum* (Zoll.) Parris	Bauret & al. (2017)
42	*Xiphopterella*	*X. hieronymusii* (C.Chr.) Parris	Sundue & al. (2014)

* only type species sampled, ** no species sampled.

Appendix 2. List of taxa sampled with voucher information, GenBank accession numbers (*atpB*, *rbcL*, *rps4 & ps4-trnS*, *trnG-R*, *trnL & trnL-F*), and references: [1] Sundue & al., 2014; [2] Bauret & al., 2017; [3] Ranker & al., 2003; [4] Nitta, J. & Schuettpelz, E. 2020. Biogeography of Pacific pteridophytes in a global context (unpublished); [5] Perrie & Parris, 2012; [6] Labiak & al., 2010; [7] Rouhan & al., 2012; [8] Sundue & al., 2010; [9] Hennequin & al., 2014; [10] Shalisko & al., 2019; [11] Ranker & al., 2004; [12] Schneider & al., 2002; [13] Nitta & al., 2020; [14] Nitta & al., 2017; [15] Sundue & al., 2018; [16] Geiger & al., 2007; [17] Steier, J. & Schuettpelz, E. 2020. The evolution of overrepresentation: Exploring the biogeography of Marquesan pteridophytes (unpublished); [18] Lehnert & al., 2009; [19] Wei & al., 2017; [20] Papadopulos & al., 2011; [21] Hirai & al., 2011; [22] Shalisko,V., Vazquez Garcia, J.A., Villalobos Arambula, A.R. & Muniz Castro, M.A. 2015. Phylogenetic and biogeographic inference from six cpDNA loci reveals Neotropical origin of grammitid ferns (unpublished); [23] Zuniga, J.D., Mulcahy, D.G., Funk, V.A. & Coddington, J.A. 2017. DNA barcodes from plants collected as part of the biological diversity of the Guiana Shield Program (unpublished); [24] Schneider & al., 2004; [25] Ebihara & al., 2010; [26] Wei & al., 2021; [27] Du & al., 2021; [28] Sundue, M.A. 2014. Direct submission: https://www.ncbi.nlm.nih.gov/nuccore/KP027642, KP050355, KP050357, KP027643; [29] Chau & al., 2020; [30] Richardson, S. & Morse, C. 2013. Symbiotic convergence over ecosystem retrogression (unpublished); [31] Tsutsumi & Kato, 2006; [32] Schuettpelz & Pryer, 2007; [33] Liu & al., 2019; [34] Ranker & al., 2010; [35] Kim & al., 2013; [36] Li & al., 2012; [37] Smith & al., 2006; [38] Schneider & al., 2006; [39] Haufler & al., 2003; [40] Testo & Sundue, 2014; [41] Wang & al., 2010; [42] Salino & al., 2008; [43] Assis & al., 2016; [44] Otto & al., 2009; "this study" indicates accessions newly sequenced in this study.

Acrosorus friderici-et-pauli (Christ) Copel., Vietnam, *C.-W. Chen 1630* (TAIF), KM218817, KM218751, KM106104, –, –, [1]; ***Acrosorus friderici-et-pauli***, Peninsular Malaysia, *M. Allen 2282* (US), –, KM218752, KM106105, KM105963, KM106046, [1]; ***Acrosorus friderici-et-pauli***, Sabah, Malaysia, *J.H. Beaman 8041* (US), –, KM218753, KM106106, KM105964, KM106047, [1]; ***Acrosorus friderici-et-pauli***, Vietnam, *Averyanov 3673* (P), –, –, KY712388, –, KY711717, [2]; ***Adenophorus abietinus*** K.A.Wilson, Hawaii, *Ranker 1100* (COLO), AF469778, AF468202, –, –, AF469791, [3]; ***Adenophorus abietinus***, Hawaii, *K.R. Wood 17837* (PTBG), –, MT657566, –, –, –, [4]; ***Adenophorus epigaeus*** (L.E.Bishop) W.H.Wagner, Hawaii, *Ranker 1103* (COLO), AF469779, AF468203, –, –, AF469792, [3]; ***Adenophorus epigaeus***, Hawaii, *K.R. Wood 12514* (PTBG), –, MT657569, –, –, –, [4]; ***Adenophorus haalilioanus*** (Brack.) K.A.Wilson, Hawaii, *Ranker 1561* (COLO), AF469775, AF468200, –, –, AF469788, [3]; ***Adenophorus haalilioanus***, Hawaii, *K.R. Wood 17973* (PTBG), –, MT657571, –, –, –, [4]; ***Adenophorus hymenophylloides*** (Kaulf.) Hook. & Grev., Hawaii, *Ranker 1203* (COLO), AF469780, AF468204, –, –, AF469793, [3]; ***Adenophorus hymenophylloides***, Hawaii, *K.R. Wood 12274* (PTBG), –, MT657568, –, –, –, [4]; ***Adenophorus montanus*** (Hillebr.) W.H.Wagner, Hawaii, *Ranker 1351* (COLO), AF469781, AF468205, –, –, AF4697942, [3]; ***Adenophorus oahuensis*** (Copel.) L.E.Bishop, Hawaii, *Ranker 969* (COLO), AF469776, AY057382, –, –, AF469789, [3]; ***Adenophorus periens*** L.E.Bishop, Hawaii, *Ranker 1114* (COLO), AF469774, AF468199, –, –, AF469787, [3]; ***Adenophorus pinnatifidus*** Gaudich., Hawaii, *K.R. Wood 17508* (PTBG), –, MT657572, –, –, –, [4]; ***Adenophorus pinnatifidus***, Hawaii, *Ranker 1559* (COLO), AF469777, AF468201, –, –, AF469790, [3]; ***Adenophorus pinnatifidus*** var. ***rockii*** (Copel.) D.D.Palmer, Hawaii, *K.R. Wood 15740* (PTBG), –, MT657573, –, –, –, [4]; ***Adenophorus pinnatifidus*** var. ***rockii***, Hawaii, *K.R. Wood 15627* (PTBG), –, MT657574, –, –, –, [4]; ***Adenophorus tamariscinus*** Hook. & Grev., Hawaii, *Ranker 1031* (COLO), AF469782, AF468206, –, –, AF469795, [3]; ***Adenophorus tamariscinus***, Hawaii, *K.R. Wood 17505* (PTBG), –, MT657567, –, –, –, [4]; ***Adenophorus tenellus*** (Kaulf.) Ranker, Hawaii, *Ranker 1352* (COLO), AF469773, AF468198, –, –, AF469786, [3]; ***Adenophorus tenellus***, Hawaii, *K.R. Wood 12401* (PTBG), –, MT657575, –, –, –, [4]; ***Adenophorus tripinnatifidus*** Gaudich., Hawaii, *Ranker 1102* (COLO), AF469783, AF468207, –, –, AF469796, [3]; ***Adenophorus tripinnatifidus***, Hawaii, *K.R. Wood 14155* (PTBG), –, MT657570, –, –, –, [4]; ***Aenigmatogrammitis stenophylla*** (Parris) Parris, Australia, *Parris 12576* (AK), JX499239, JQ904084, –, –, JQ911714, [5]; ***Alansmia cultrata*** (Willd.) Moguel & M.Kessler, Ecuador, *Sundue 1136* (NY), GU376475[6], GU376494[6], JN654940[7], JN654953[7], JN654966[7], [6][7]; ***Alansmia cultrata***, Colombia, *Dassler 94-7-19-1* (ILLS), GU476806, GU476828, –, –, –, [8]; ***Alansmia cultrata***, Colombia, *Sundue 1214* (NY), GU376476[6], GU376496, KM106107 [JN654943][1,7], JN654956[7], JN654969[7], [1][6][7]; ***Alansmia cultrata***, Ecuador, *Sundue 1162* (NY), GU376477[6], GU376495[6], JN654942[7], JN654955[7], JN654968[7], [6][7]; ***Alansmia cultrata***, Mauritius, *S. Hennequin 336* (P, MAU), –, KF992522, –, –, –, [9]; ***Alansmia elastica*** (Bory ex Willd.) Moguel & M.Kessler, Madagascar, *Ravelonarivo & al. 2841* (MO), –, OQ708599, OQ717188, OQ717049, –, **this study**; ***Alansmia elastica***, Bolivia, *Kessler 13443* (UC), –, –, –, –, GU476727, [8]; ***Alansmia elastica***, Costa Rica, *Shalisko 254* (IBUG), –, MK319093, –, MK319045, MK318991, [10]; ***Alansmia elastica***, Costa Rica, *Shalisko 255* (IBUG), –, MK319094, –, MK319046, MK318992, [10];

Appendix 2. Continued.

Alansmia elastica, Costa Rica, *Sundue 3386* (VT), –, MK319095, –, MK319047, MK318993, [10]; ***Alansmia elastica***, Madagascar, *J. Kluge 7863* (Z), KM218858, KM218795, –, KM105965, KM106048, [1]; ***Alansmia elastica***, Madagascar, *Rakotondrainibe 5833* (P), KY711747, KY711921, KY712248, KY712089, KY711574, [2]; ***Alansmia elastica***, Madagascar, *Rouhan & al. 1138* (P), KY711745, KY711919, KY712245, KY712087, KY711572, [2]; ***Alansmia elastica***, Madagascar, *Rouhan & al. 1150* (P), KY711746, KY711920, KY712247, KY712088, KY711573, [2]; ***Alansmia elastica***, Madagascar, *Rouhan & al. 1171* (P), KY711831, KY712007, KY712323, KY712171, KY711656, [2]; ***Alansmia elastica***, Madagascar, *Rouhan & al. 1376* (P), KY711832, KY712008, KY712324, KY712172, KY711657, [2]; ***Alansmia elastica***, Mauritius, *Hennequin & al. 339* (P), KY711748, KY711922, KY712249, KY712090, KY711575, [2]; ***Alansmia elastica***, Seychelles, *Senterre 6125* (P), KY711889, KY712063, KY712381, KY712229, KY711709, [2]; ***Alansmia glandulifera*** (A.Rojas) Moguel & M.Kessler, Costa Rica, *Sundue 1765* (NY), GU376472[6], GU376497[6], JN654944[7], JN654957[7], JN654970[7], [6][7]; ***Alansmia heteromorpha*** (Hook. & Grev.) Moguel & M.Kessler, Ecuador, *Sundue 2609* (NY), –, KM218803, –, KM105966, –, [1]; ***Alansmia lanigera*** (Desv.) Moguel & M.Kessler, Costa Rica, *A. Rojas & al. 3207* (UC, CR, INB, MO), AY459504, AY460671, –, –, –, [11]; ***Alansmia lanigera***, Peru, *B. Leon 3647* (USM), GU476809, GU476844, –, –, GU476718, [8]; ***Alansmia senilis*** (Fée) Moguel & M.Kessler, Costa Rica, *A. Rojas & al. 3196* (INB), AY459510[11], AY096208[11], AY096237[12], –, GU476736[8], [8][11][12]; ***Alansmia senilis***, Ecuador, *Sundue 1156* (NY), GU376474[6], GU376498[6], JN654941[7], JN654954[7], JN654967[7], [6][7]; ***Alansmia smithii*** (A.Rojas) Moguel & M.Kessler, Mexico, *Kessler 13511* (UC), –, –, –, –, GU476712, [8]; ***Alansmia smithii***, Costa Rica, *J.H. Nitta 865* (UC, CR), –, MW138159, –, –, –, [13]; ***Alansmia smithii***, Costa Rica, *Lellinger & Bowes 34* (US), –, MK319096, –, MK319048, MK318994, [10]; ***Alansmia stella*** (Copel.) Moguel & M.Kessler, Ecuador, *Sundue 1083* (NY), GU376473[6], GU376499[6], JN654939[7], JN654952[7], JN654965[7], [6][7]; ***Alansmia turrialbae*** (Christ) Moguel & M.Kessler, Costa Rica, *Lellinger & White 996* (US), –, MK319097, –, MK319049, MK318995, [10]; ***Archigrammitis tahitensis*** (C.Chr.) Parris, Moorea, *Nitta 656* (UC), –, KY099756, –, –, –, [14]; ***Ascogrammitis anfractuosa*** (Kunze ex Klotzsch) Sundue, Ecuador, *Lehnert 1035* (GOET), GU476783[8], GU476853[8], KM106108[1], KM105967[1], GU476675[8], [1][8]; ***Ascogrammitis anfractuosa***, Bolivia, *Jimenez 1399* (LPB), GU476779, GU476833, –, –, GU476672, [8]; ***Ascogrammitis anfractuosa***, Bolivia, *Lehnert 499* (GOET), GU476780, GU476859, –, –, GU476673, [8]; ***Ascogrammitis anfractuosa***, Costa Rica, *A. Rojas & al. 3321* (INB), AY459501, AY460668, –, –, –, [11]; ***Ascogrammitis anfractuosa***, Costa Rica, *Moran s.n.* (NY), GU476781, GU476916, –, –, GU476674, [8]; ***Ascogrammitis anfractuosa***, Costa Rica, *Sundue 3381* (VT), –, MK319099, –, MK319051, MK318997, [10]; ***Ascogrammitis anfractuosa***, Ecuador, *Kessler 14867* (VT), MG948936, MG948938, MG966515, MG966519, MG966517, [15]; ***Ascogrammitis anfractuosa***, Ecuador, *Moran 7567* (NY), GU476782, GU476919, –, –, –, [8]; ***Ascogrammitis anfractuosa***, Mexico, *Kessler 13507* (UC), GU476784, GU476845, –, –, GU476676, [8]; ***Ascogrammitis anfractuosa***, Mexico, *Kessler 13517* (NY), –, GU476847, –, –, GU476677, [8]; ***Ascogrammitis anfractuosa***, Oaxaca, Mexico, *Sundue 3133* (VT), –, MK319098, –, MK319050, MK318996, [10]; ***Ascogrammitis anfractuosa***, Peru, *Lehnert 212* (GOET), GU476793, GU476855, –, –, –, [8]; ***Ascogrammitis anfractuosa***, Peru, *Lehnert 315* p.p. (GOET), GU476785, GU476858, –, –, –, [8]; ***Ascogrammitis angustipes*** (Copel.) Sundue, Colombia, *Sundue 1237* (NY), KM218837[1], GU476891[8], KM106109[1], KM105968[1], GU476703[8], [1][8]; ***Ascogrammitis angustipes***, Colombia, *Rodriguez 5124* (NY), –, –, –, –, GU476702, [8]; ***Ascogrammitis athyrioides*** (Hook.) Sundue, Peru, *Lehnert 261* (UC), KM218840[1], GU476856[8], KM106110[1], KM105969[1], GU476704[8], [1][8]; ***Ascogrammitis clathrata*** (Sundue & M.Kessler) Sundue, Bolivia, *Kromer 1237* (UC), KM218838[1], GU476843[8], KM106111[1], KM105970[1], GU476708[8], [1][8]; ***Ascogrammitis clavigera*** A.R.Sm. & Sundue, Venezuela, *Schneider 2400* (UC), KM218839, GU476925, KM106112, –, GU476709, [1][8]; ***Ascogrammitis colombiensis*** Sundue, Colombia, *Dassler 94-7-13-1* (OS), GU476805[8], GU476827[8], KM106113[1], –, –, [1][8]; ***Ascogrammitis colombiensis***, Colombia, *Sundue & Vasco 1316* (NY), GU476804, GU476900, –, –, GU476710, [8]; ***Ascogrammitis cuencana*** (Hieron.) Sundue, Ecuador, *Lehnert 1164* (GOET), –, GU476851, KM106114, KM105971, GU476714, [1][8]; ***Ascogrammitis david-smithii*** (Stolze) Sundue, Bolivia, *Sundue 785* (NY), GU376639, GU387012, GU387122, GU387205, GU387284, [6]; ***Ascogrammitis david-smithii***, Bolivia, *Jimenez 1215* (UC), –, GU476830, –, –, GU476689, [8]; ***Ascogrammitis david-smithii***, Bolivia, *Jimenez 1246* (UC), GU476795, GU476832, –, –, GU476690, [8]; ***Ascogrammitis david-smithii***, Bolivia, *Jimenez 1452* (UC), –, GU476834, –, –, GU476691, [8]; ***Ascogrammitis david-smithii***, Bolivia, *Jimenez 894* (UC), –, GU476841, –, –, GU476692, [8]; ***Ascogrammitis dilatata*** (Sundue & M.Kessler) Sundue, Bolivia, *Labiak 4728* (UPCB), GU376640, GU387033, GU387124, GU387206, GU387285, [6]; ***Ascogrammitis dilatata***, Bolivia, *Jimenez 1156* (UC), GU476808, GU476829, –, –, GU476717, [8]; ***Ascogrammitis dilatata***, Bolivia, *Jimenez 954*(UC), GU476807, GU476842, –, –, GU476716, [8]; ***Ascogrammitis lehnertii*** Sundue, Ecuador, *Olivares 142* (VT), MG948937, MG948939, MG966516, MG966520, MG966518, [15]; ***Ascogrammitis loxensis*** Sundue, Ecuador, *Sundue 1073* (NY), GU376641, GU386995, GU387125, GU387207, GU387286, [6]; ***Ascogrammitis loxensis***, Ecuador, *Lehnert 1233* p.p. (UC), –, GU476852, –, –, GU476722, [8]; ***Ascogrammitis loxensis***, Ecuador, *Sundue 1125* (NY), –, GU476870, –, –, GU476723, [8]; ***Ascogrammitis loxensis***, Ecuador, *Sundue 1164* (NY), GU476812, GU476881, –, –, GU476721, [8]; ***Ascogrammitis nana*** (Sundue & M.Kessler) Sundue, Bolivia, *Labiak 4725* (UPCB), GU376642, GU387031, –, GU387208, GU387287, [6]; ***Ascogrammitis nana***, Bolivia, *Sundue 866* (NY), GU476815, GU476912, –, –, GU476728, [8]; ***Ascogrammitis pichinchae*** (Sodiro) Sundue, Ecuador, *K.A. Wilson 2816a* (UC), –, GU476928[8], KM106115[1], –, GU476730[8], [1][8]; ***Ascogrammitis pichinchae***, Colombia, *C. Dassler 94-7-13-1* (ILLS), –, AY460675, –, –, –, [11]; ***Ascogrammitis pichinchensis*** (Hieron.) Sundue, Ecuador, *Lehnert 1577* (UC), GU476816[8], GU476854[8], KM106116[1], –, GU476732[8], [1][8]; ***Ascogrammitis pichinchensis***, Ecuador, *Rodriguez 646* (QCA), –, GU476924, –, –, GU476731, [8]; ***Boonkerdia khaoluangensis*** (Tagawa & K.Iwats.) Li Bing Zhang, Pollawatn, X.M.Zhou & Liang Zhang, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11081* (KUN, CDBI, BCU), OQ702675, OQ708586, OQ717278, –, OQ717097, **this study**; ***Boonkerdia khaoluangensis***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11080* (KUN, CDBI, BCU, MO, PYU), OQ702709, OQ708580, OQ717282, –, OQ717098, **this study**; ***Boonkerdia khaoluangensis***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11091* (KUN), OQ702676, OQ708572, OQ717279, –, OQ717099, **this study**; ***Calymmodon asiaticus*** Copel., Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11119* (KUN, CDBI, BCU, MO, PYU, XTBG), OQ702728, OQ708562, OQ717187, –, OQ717106, **this study**; ***Calymmodon asiaticus***, China, *X.-C. Zhang 3531* (PE), –, MF450450, –, –, –, [9]; ***Calymmodon asiaticus***, Khanh Hoa, Vietnam, *L.-B. Zhang & al. 8818* (CDBI, MO, PHH), OQ702680, OQ708582, OQ717189, OQ717054, OQ717107, **this study**; ***Calymmodon clavifer*** (Hook.) T.Moore, Sabah, Malaysia, *Sundue 2235* (VT), KM218818, KM218804, KM106117, –, KM106049, [1]; ***Calymmodon* cf. *cucullatus***, New Caledonia, *H. van der Werff & Bruce Gray 17042* (MO), OQ702726 [OQ968267], OQ708614 [OQ968267], OQ717288 [OQ968267], OQ717050 [OQ968267], OQ717100 [OQ968267], **this study**; ***Calymmodon* cf. *curtus***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 10990* (KUN, CDBI, BCU, MO), OQ702693, OQ708581, OQ717276, –, OQ717102, **this study**; ***Calymmodon* cf. *curtus***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11118* (KUN, CDBI, BCU, MO, PYU), OQ702694, OQ708512, OQ717272, –, OQ717103, **this study**; ***Calymmodon gracilis*** (Fee.) Copel., Lam Dong, Vietnam, *L.-B. Zhang & al. 8566* (CDBI, MO, PHH), OQ702678, OQ708573, OQ717230, OQ717052, OQ717104, **this study**; ***Calymmodon gracilis***, Khanh Hoa, Vietnam, *L.-B. Zhang & al. 8670* (CDBI, MO, PHH), OQ702679, OQ708578, OQ717233, OQ717053, OQ717105, **this study**; ***Calymmodon gracilis***, Philippines, *Fei Wei Li 980* (TAIF), –, –, –, KM105972, –, [1]; ***Calymmodon gracilis***, Philippines, *Kuo 2023* (TAIF), –, –, –, KY712080, –, [2]; ***Calymmodon gracilis***, Taiwan Island, *Chiou 97-09-12-01* (COLO, TAIF, UC), AY459451[11], AY362341[11], –, –, GU476618[8], [8][11]; ***Calymmodon grantii*** Copel., Marquesas Islands, *Schuettpelz 1935* (US), –, MT215995, –, –, –, [17]; ***Calymmodon* cf. *grantii***, French Polynesia, *D.H. Lorence 8945* (PTBG), –, MT657576, –, –, –, [4]; ***Calymmodon latealatus*** Copel., Savaii, Samoa, *K.R. Wood 17012* (PTBG), –, MT657578, –, –, –, [4]; ***Calymmodon latealatus***., Tanna, Vanuatu, *T.A. Ranker 2249* (NYBG), –, MT657579, –, –, –, [4]; ***Calymmodon luerssenianus*** (Domin) Copel., Australia, *Kessler 14264* (VT), KM218819, KM218806, KM106118, KM105973, KM106050, [1]; ***Calymmodon luerssenianus***, Queensland, Australia, *H. van der Werff & G. McPherson 16031* (MO), OQ702727, OQ708615, OQ717287, OQ717051, OQ717101, **this study**; ***Calymmodon orientalis*** Copel., Moorea, *Nitta 682* (UC), –, KY099779, –, –, –, [14]; ***Calymmodon pectinatus*** Parris, West Papua, Indonesia, *Karger 1675* (Z), KM218820, KM218807, KM106120, –, KM106052, [1]; ***Calymmodon ponapensis*** Copel., Pohnpei, Micronesia, *K.R. Wood 13558* (PTBG), –, MT657577, –, –, –, [4]; ***Calymmodon* sp. 1**, Vanuatu, *Rouhan & al. 601* (P), KY711749, KY711923, KY712250, KY712091, KY711576, [2]; ***Calymmodon* sp. 1**, Vanuatu, *Rouhan & al. 662* (P), KY711750, KY711924, KY712251, KY712092, KY711577, [2]; ***Calymmodon* sp. 2**, Sabah, Malaysia, *Sundue 2218* (VT), –, KM218805, KM106119, –, KM106051, [1]; ***Calymmodon* sp. 3**, Papua New Guinea, *Ranker & Trapp 1771* (COLO, UC), AY459452, AY460618, –, –,

Appendix 2. Continued.

–, [11]; ***Ceradenia argyrata*** (Bory ex Willd.) Parris, Reunion, *Rakotondrainibe 6904* (P), KY711751, KY711925, KY712252, KY712093, KY711578, [2]; ***Ceradenia argyrata***, Reunion, *Janssen & al. 2716* (P), KY711752, KY711926, KY712253, KY712094, KY711579, [2]; ***Ceradenia argyrata***, Reunion, *T. Janssen 2688* (P, REU), –, KF992463, –, –, –, [9]; ***Ceradenia aulaeifolia*** L.E.Bishop ex A.R.Sm., Costa Rica, *A. Rojas & al. 3232* (UC, CR, INB, MO), AY459453[11], AY460619[11], KM106122[1], KM105974[1], GU476623[8], [1][8][11]; ***Ceradenia aulaeifolia***, Costa Rica, *Sundue 1705* (NY), GU476748, GU476902, –, –, –, [8]; ***Ceradenia ayapoyana*** M.Kessler & A.R.Sm., Bolivia, *I. Jimenez 1114* (GOET, LPB, UC), –, KM218811, KM106123, KM105975, KM106053, [1]; ***Ceradenia comorensis*** (Bak.) Parris, Madagascar, *Janssen & al. 2452* (P), KY711760, KY711935, KY712262, KY712103, KY711588, [2]; ***Ceradenia curvata*** (Sw.) L.E.Bishop, Bolivia, *I. Jiménez 1559* (UC, LPB), KM218821, KM218788, –, KM105976, KM106054, [1]; ***Ceradenia deltodon*** (Bak.) Parris, Madagascar, *Rouhan & al. 1217* (P), KY711753, KY711927, KY712254, KY712095, KY711580, [2]; ***Ceradenia deltodon***, Madagascar, *Janssen & al. 2924* (P), –, KY711932, KY712259, KY712100, KY711585, [2]; ***Ceradenia deltodon***, Madagascar, *Kessler 12741* (UC), –, –, –, –, KY711565, [2]; ***Ceradenia deltodon***, Madagascar, *Rakotondrainibe 6402* (P), KY711757, KY711931, KY712258, KY712099, KY711584, [2]; ***Ceradenia deltodon***, Madagascar, *Rouhan & al. 1250* (P), KY711754, KY711928, KY712255, KY712096, KY711581, [2]; ***Ceradenia deltodon***, Madagascar, *Rouhan & al. 1250bis* (P), KY711755, KY711929, KY712256, KY712097, KY711582, [2]; ***Ceradenia deltodon***, Madagascar, *Rouhan & al. 1350* (P), KY711756, KY711930, KY712257, KY712098, KY711583, [2]; ***Ceradenia farinosa*** (Hook.) L.E.Bishop, Ecuador, *David Neill 11985* (MO), KM218823, KM218790, KM106124, KM105977, KM106055, [1]; ***Ceradenia fucoides*** (Christ) L.E.Bishop, Costa Rica, *Sundue 1766* (NY), GU476749[8], GU476907[8], KM106125[1], –, GU476625[8], [1][8]; ***Ceradenia intonsa*** L.E.Bishop ex Leon-Parra & Mostacero, Colombia, *Sundue & Vasco 1321* (NY), GU476750[8], GU476901[8], KM106126[1], –, GU476626[8], [1][8]; ***Ceradenia intricata*** (C.V.Morton) L.E.Bishop ex A.R.Sm., Bolivia, *Lehnert 1108* (UC, LPB), KM218833, KM218791, KM106127, KM105978, KM106056, [1]; ***Ceradenia jungermannioides*** (Klotzsch) L.E.Bishop, Costa Rica, *A.R. Smith 2576* (UC), AY459454, AY460620, –, –, –, [11]; ***Ceradenia kalbreyeri*** (Baker) L.E.Bishop, Colombia, *Vasco & Sundue 701* (NY), GU476747[8], GU476825[8], KM106121[1], –, GU476622[8], [1][8]; ***Ceradenia kalbreyeri***, Colombia, *Sundue & Vasco 1213* (NY), GU476745, GU476887, –, –, GU476619, [8]; ***Ceradenia kalbreyeri***, Costa Rica, *J.H. Nitta 828* (UC), –, MW138183, –, –, –, [13]; ***Ceradenia kalbreyeri***, Costa Rica, *Rojas & al. 3323* (Unknown), AY459455, AY460621, –, –, –, [11]; ***Ceradenia kalbreyeri***, Costa Rica, *Sundue 1759* (NY), GU476744[8], GU476905[8], KM106128[1], KM105979[1], GU476617[8], [1][8]; ***Ceradenia knightii*** (Copel.) L.E.Bishop, Costa Rica, *Lellinger & White 1583* (US), –, MK319106, –, –, –, [10]; ***Ceradenia kookenamae*** (Jenman) L.E.Bishop, Colombia, *Sundue & Vasco 1242* (NY), GU476751, GU476893, –, –, GU476627, [8]; ***Ceradenia kookenamae***, Costa Rica, *Lellinger & White 1048* (US), –, MK319100, –, MK319052, MK318998, [10]; ***Ceradenia leucosora*** (Boj. ex Hook.) Parris, Reunion, *Rakotondrainibe 6908* (P), KY711758, KY711933, KY712260, KY712101, KY711586, [2]; ***Ceradenia leucosora***, Reunion, *Janssen & al. 2689* (P), KY711759, KY711934, KY712261, KY712102, KY711587, [2]; ***Ceradenia leucosora***, Reunion, *T. Janssen 2689* (P, REU), –, KF992464, –, –, –, [9]; ***Ceradenia madidiensis*** M.Kessler & A.R.Sm., Bolivia, *I. Jimenez 1089* (UC), KM218834, –, KM106129, –, KM106057, [1]; ***Ceradenia madidiensis***, Costa Rica, *Evans & Lellinger 271* (US), –, MK319130, –, –, MK318999, [10]; ***Ceradenia pearcei*** (Baker) L.E.Bishop, Bolivia, *A.F. Fuentes & Villalobos 13997* (MO), KM218822, KM218789, KM106130, KM105980, KM106058, [1]; ***Ceradenia pilipes*** (Baker) L.E.Bishop, Costa Rica, *A. Rojas & al. 3233* (INB), AY459456, AY460622, –, –, GU476620, [11]; ***Ceradenia pilipes***, Ecuador, *Sundue 1120* (NY), GU476746, GU476869, –, –, GU476621, [8]; ***Ceradenia sechellarum*** (Bak.) Parris, Seychelles, *Senterre 6122* (P), KY711886, KY712060, KY712378, KY712226, KY711706, [2]; ***Ceradenia* sp. 1**, Colombia, *Sundue & Vasco 1238* (NY), GU476752, GU476892, –, –, GU476628, [8]; ***Ceradenia* sp. 1**, Pasco, Peru, *C.J. Rothfels & al. 4918* (UC), OQ702666, OQ708600, OQ717221, OQ717055, OQ717108, **this study**; ***Ceradenia* sp. 2**, Ecuador, *Moran 7520* (QCA), GU476753, GU476918, –, –, GU476629, [8]; ***Ceradenia* sp. 3**, Pasco, Peru, *C.J. Rothfels & al. 4948* (UC), OQ702672, OQ708601, OQ717220, OQ717056, OQ717109, **this study**; ***Ceradenia spixiana*** (Mart. ex Mett.) L.E.Bishop, Brazil, *Salino 3008* (UC), AY459457, AY460623, –, –, –, [11]; ***Chrysogrammitis glandulosa*** (J.Sm.) Parris, Taiwan Island, *R. Knapp 3422* (P), –, OQ708513, OQ717211, OQ717057, OQ717110, **this study**; ***Chrysogrammitis glandulosa***, Malaysia, *Ranker 2195* (BORH, SAN, SNP, COLO), JF514082, JF514014, –, –, JF514048, [21]; ***Chrysogrammitis musgraviana*** (Baker) Parris, Sabah, Malaysia, *Kessler 12570* (US), AY459458[11], AY460624[11], KM106131[1], –, GU476630[8], [1][8][11]; ***Chrysogrammitis musgraviana***, Sabah, Malaysia, *Sundue 2234* (VT), KM218825, KM218797, KM106132, KM105981, KM106059, [1]; ***Chrysogrammitis* sp.**, Dak Lak, Vietnam, *L.-B. Zhang & al. 8860* (CDBI, MO, PHH), OQ702663, OQ708535, OQ717192, –, OQ717112, **this study**; ***Chrysogrammitis* sp.**, Dak Lak, Vietnam, *L.-B. Zhang & al. 8910* (CDBI, MO, PHH), OQ702662, OQ708593, OQ717193, OQ717058, OQ717111, **this study**; ***Cochlidium jungens*** L.E.Bishop, Puerto Rico, *Proctor 40989* (US), –, MK319131, –, –, MK319000, [10]; ***Cochlidium linearifolium*** (Desv.) Maxon ex C.Chr., Oaxaca, Mexico, *Sundue 3016* (VT), –, MK319103, –, MK319055, MK319001, [10]; ***Cochlidium linearifolium***, Oaxaca, Mexico, *Sundue 3530* (VT), –, MK319104, –, MK319056, MK319002, [10]; ***Cochlidium punctatum*** (Raddi) L.E.Bishop, Brazil, *Salino 3127* (UC, BHCB), AY459520, AY460625, –, –, –, [11]; ***Cochlidium punctatum***, Brazil, *Silva 3914* (UC), JF514057[21], JF513987[21], –, –, GU476631[8], [8][21]; ***Cochlidium rostratum*** (Hook.) Maxon ex C.Chr., Panama, *I. Valdespino & J. Aranda 180* (UC), AY459459[11], AY460626[11], –, KM105982[1], –, [1][11]; ***Cochlidium rostratum***, Costa Rica, *J.H. Nitta 827* (UC), –, MW138255, –, –, – [13]; ***Cochlidium rostratum***, Costa Rica, *Sundue 3379* (VT), –, MK319101, –, MK319053, –, [10]; ***Cochlidium seminudum*** (Willd.) Maxon, Dominican Republic, *S.R. Hill 29102A* (no voucher), AY459460[11], AY460627[11], –, –, KM106060[1], [1][11]; ***Cochlidium serrulatum*** (Sw.) L.E.Bishop, Brazil, *Hirai & Schwartsburd 541* (SP), JF514078[21], JF514010[21], KM106133[1], KM105983[1], JF514044[21], [1][21]; ***Cochlidium serrulatum***, Chiapas, Mexico, *Shalisko 314* (IBUG), –, MK319132, –, –, MK319004, [10]; ***Cochlidium serrulatum***, Chiapas, Mexico, *Shalisko 333* (IBUG), –, KT156610, –, KT156613, KT156611, [22]; ***Cochlidium serrulatum***, Costa Rica, *J.H. Nitta 2292* (UC, GH, Nectandra), –, MW138121, –, –, –, [13]; ***Cochlidium serrulatum***, Costa Rica, *Rojas 3004* (UC), –, EF178614, –, –, –, [16]; ***Cochlidium serrulatum***, Costa Rica, *Shalisko 250* (IBUG), –, MK319105, –, MK319057, MK319003, [10]; ***Cochlidium serrulatum***, Dominican Republic, *S.R. Hill 29102* (UC), EF178632, EF178615, –, –, –, [16]; ***Cochlidium serrulatum***, Kako River, Guyana, *Redden 6492*(US), –, MF786357, –, –, –, [23]; ***Cochlidium serrulatum***, Madagascar, *Rouhan & al. 1142* (P), KY711761, KY711936, KY712263, KY712104, KY711589, [2]; ***Cochlidium serrulatum***, Madagascar, *Rouhan & al. 1314* (P), KY711762, KY711937, KY712264, KY712105, –, [2]; ***Cochlidium serrulatum***, Madagascar, *Rouhan & al. 383* (P), KY711766, KY711941, KY712268, KY712108, KY711593, [2]; ***Cochlidium serrulatum***, Mauritius, *Rouhan & al. 172* (P), KY711765, KY711940, KY712267, KY712107, KY711592, [2]; ***Cochlidium serrulatum***, Reunion, *Rakotondrainibe 6903* (P), KY711763, KY711938, KY712265, –, KY711590, [2]; ***Cochlidium serrulatum***, Reunion, *T. Janssen 2699* (P, REU), –, KF992454, –, –, –, [9]; ***Cochlidium serrulatum***, Seychelles, *Rouhan & al. 141* (P), KY711764, KY711939, KY712266, KY712106, KY711591, [2]; ***Ctenopterella blechnoides*** (Grev.) Parris, Moorea, *Nitta 658* (UC), –, KY099786, –, –, –, [14]; ***Ctenopterella blechnoides***, Huahine, French Polynesia, *K.R. Wood 11009* (PTBG), –, MT657584, –, –, –, [4]; ***Ctenopterella blechnoides***, Savaii, Samoa, *K.R. Wood 16986* (PTBG), –, MT657582, –, –, –, [4]; ***Ctenopterella blechnoides***, Upolu, Samoa, *K.R. Wood 16877* (PTBG), –, MT657581, –, –, –, [4]; ***Ctenopterella lasiostipes*** (Mett.) Parris, New Caledonia, *Munzinger & McPherson 773* (MO), OQ702681, OQ708602, OQ717222, OQ717059, OQ717113, **this study**; ***Ctenopterella lasiostipes***, New Caledonia, *Hodel 1448* (US), AY459463, AY460630, –, –, –, [11]; ***Ctenopterella lasiostipes***, New Caledonia, *Mackee 17342* (P), KY711896, KY712068, KY712389, KY712231, KY711719, [2]; ***Ctenopterella lasiostipes***, New Caledonia, *Mackee 42028* (P), KY711898, KY712070, KY712391, –, KY711721, [2]; ***Ctenopterella lasiostipes***, New Caledonia, *Mackee 43573* (P), –, –, KY712392, –, KY711722, [2]; ***Ctenopterella lasiostipes***, New Caledonia, *Mackee 45654* (P), KY711899, KY712071, KY712393, –, KY711723, [2]; ***Ctenopterella lasiostipes***, New Caledonia, *Munzinger 1166* (P), KY711777, KY711952, KY712278, KY712119, KY711604, [2]; ***Ctenopterella lasiostipes***, New Caledonia, *Munzinger 1673* (P), KY711778, KY711953, KY712279, KY712120, KY711605, [2]; ***Ctenopterella lasiostipes***, New Caledonia, *Munzinger 687* (P), KY711897, KY712069, KY712390, KY712232, KY711720, [2]; ***Ctenopterella nhatrangensis*** (C.Chr. & Tardieu) Parris, Dak Lak, Vietnam, *L.-B. Zhang & al. 8848* (CDBI, MO, PHH), OQ702682, OQ708594, OQ717232, OQ717060, OQ717114, **this study**; ***Ctenopterella nhatrangensis***, Khanh Hoa, Vietnam, *L.-B. Zhang & al. 8815* (CDBI, MO, PHH), OQ702683, OQ708603, OQ717216, OQ717061, OQ717115, **this study**; ***Ctenopterella pacifica*** Parris, Aneityum, Vanuatu, *G.M. Plunkett 4088* (NYBG), –, MT657580, –, –, –, [4]; ***Ctenopterella pacifica***, Vanuatu, *Rouhan & al. 618* (P), KY711767, KY711942, KY712269, KY712109, KY711594, [2]; ***Ctenopterella* sp. 1**, New Caledonia, *Le Rat 912* (P), KY711891, KY712065, KY712384, –, –, [2]; ***Ctenopterella* sp. 1**, New Caledonia, *Mackee 18525* (P),

Appendix 2. Continued.

KY711908, KY712076, KY712401, –, KY711737, [2]; ***Ctenopterella* sp. 1**, New Caledonia, *Mackee 6387* (P), –, –, KY712383, –, KY711711, [2]; ***Ctenopterella* sp. 1**, New Caledonia, *Perrie P026561* (WELT), –, KY711917, –, –, KY711558, [2]; ***Ctenopterella* sp. 2**, New Caledonia, *Munzinger & Mcpherson 580* (MO), OQ702665, OQ708604, OQ717210, OQ717062, OQ717116, **this study**; ***Dasygrammitis brevivenosa*** (Alderw.) Parris, Sabah, Malaysia, *Sundue 2222* (VT), KM218828, KM218774, KM106135, KM105985, –, [1]; ***Dasygrammitis brevivenosa***, Sabah, Malaysia, *Sundue 2206* (VT), KM218829, KM218775, KM106136, KM105986, KM106061, [1]; ***Dasygrammitis crassifrons*** (Baker) Parris, Fiji, *J. Game 95-80* (UC), JF514062[21], JF513992[21], KM106137[1], –, JF514026[21], [1][21]; ***Dasygrammitis fuscata*** (Blume) Parris, Peninsular Malaysia, *Parris 12784* (AK), –, KM218778, KM106138, KM105987, –, [1]; ***Dasygrammitis malaccana*** (Baker) Parris, Peninsular Malaysia, *Parris 12796* (AK), –, KM218779, KM106139, KM105988, –, [1]; ***Dasygrammitis malaccana***, Indonesia, *Winkler s.n.* (P), –, –, –, –, KY711726, [2]; ***Dasygrammitis mollicoma*** (Nees & Bl.) Parris, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11038* (KUN, CDBI, BCU), OQ702710, OQ708595, OQ717218, –, OQ717117, **this study**; ***Dasygrammitis mollicoma***, Taiwan Island, *R. Knapp 3423* (P), –, OQ708526, OQ717283, –, –, **this study**; ***Dasygrammitis mollicoma***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11089* (KUN), OQ702729, OQ708574, OQ717259, –, OQ717118, **this study**; ***Dasygrammitis mollicoma***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. s.n.* (KUN), OQ702684, OQ708543, OQ717275, –, OQ717119, **this study**; ***Dasygrammitis mollicoma***, Peninsular Malaysia, *Parris 12797* (AK), –, KM218776, –, KM105989, KM106063, [1]; ***Dasygrammitis purpurascens*** (Nadeaud) Parris, Moorea, *Nitta 694* (UC), –, KY099788, –, –, –, [14]; ***Dasygrammitis purpurascens***, French Polynesia, *1936945* (US), –, MT216009, –, –, –, [17]; ***Dasygrammitis purpurascens***, French Polynesia, *Wood17719* (PTBG), –, MT216008, –, –, –, [17]; ***Dasygrammitis purpurascens***, Marquesas Islands, *1014855* (US), –, MT216010, –, –, –, [17]; ***Dasygrammitis purpurascens***, Marquesas Islands, *Schuettpelz 1933* (US), –, MT216011, –, –, –, [17]; ***Enterosora barbatula*** (Baker) Parris, Madagascar, *Rouhan & al. 1186* (P), KY711782, KY711957, KY712282, KY712123, KY711608, [2]; ***Enterosora barbatula***, Reunion, *Tamon 53* (P), KY711781, KY711956, KY712281, KY712122, KY711607, [2]; ***Enterosora barbatula***, Madagascar, *Rakotondrainibe 6951* (P), KY711783, KY711958, KY712283, KY712124, KY711609, [2]; ***Enterosora barbatula***, Reunion, *D. Strasberg 28-5-93* (REU), –, MT657607, –, –, –, [4]; ***Enterosora barbatula***, Reunion, *Rouhan & al. 223* (P), KY711784, KY711959, KY712284, –, –, [2]; ***Enterosora barbatula***, Reunion, *S. Hennequin R174* (BM, REU), –, KF992490, –, –, –, [9]; ***Enterosora barbatula***, Tanzania, *Rouhan & al. 524* (P), KY711785, KY711960, KY712285, KY712125, KY711610, [2]; ***Enterosora campbellii*** subsp. ***spongiosa*** (Maxon) L.E.Bishop, Costa Rica, *Lellinger & White 1540* (US), –, MK319107, –, MK319059, MK319005, [10]; ***Enterosora cornuta*** (Lellinger) Shalisko & Sundue, Costa Rica, *Lellinger & While 1062* (US), –, MK319139, –, MK319091, MK319043, [10]; ***Enterosora devoluta*** (Baker) Shalisko & Sundue, Madagascar, *Kluge 7937* (Z), KM218827, KM218793, KM106199, KM106042, KM106100, [1]; ***Enterosora devoluta***, Madagascar, *Kessler 12687* (UC), –, –, –, –, KY711563, [2]; ***Enterosora devoluta***, Madagascar, *Kessler 12688* (UC), –, –, KY712240, –, KY711564, [2]; ***Enterosora devoluta***, Madagascar, *Kluge 7940* (Z), KM218826, KM218792, –, KM106041, KM106099, [1]; ***Enterosora devoluta***, Madagascar, *Rakotondrainibe 6023* (P), KY711883, KY712058, KY712375, KY712223, KY711704, [2]; ***Enterosora devoluta***, Madagascar, *Rakotondrainibe 6953* (P), KY711856, KY712031, KY712348, KY712196, KY711680, [2]; ***Enterosora devoluta***, Madagascar, *Rouhan & al. 1157* (P), KY711868, KY712043, KY712360, KY712208, KY711690, [2]; ***Enterosora devoluta***, Madagascar, *Rouhan & al. 1226* (P), KY711852, KY712027, KY712344, KY712192, KY711676, [2]; ***Enterosora devoluta***, Madagascar, *Rouhan & al. 1290* (P), KY711853, KY712028, KY712345, KY712193, KY711677, [2]; ***Enterosora devoluta***, Madagascar, *Rouhan & al. 1336* (P), KY711869, KY712044, KY712361, KY712209, KY711691, [2]; ***Enterosora devoluta***, Madagascar, *Rouhan & al. 1351* (P), KY711854, KY712029, KY712346, KY712194, KY711678, [2]; ***Enterosora devoluta***, Madagascar, *Rouhan & al. 1379* (P), KY711855, KY712030, KY712347, KY712195, KY711679, [2]; ***Enterosora devoluta***, Madagascar, *Rouhan & al. 286* (P), KY711857, KY712032, KY712349, KY712197, KY711681, [2]; ***Enterosora enterosoroides*** (Christ) A.Rojas, Ecuador, *Sundue 1172* (NY), GU476756[8], –, KM106140[1], –, GU476634[8], [1][8]; ***Enterosora forsythiana*** (Baker) Shalisko & Sundue, Madagascar, *Rouhan & al. 1380* (P), KY711858, KY712033, KY712350, KY712198, KY711682, [2]; ***Enterosora forsythiana***, Madagascar, *Rouhan & al. 1344* (P), KY711859, KY712034, KY712351, KY712199, KY711683, [2]; ***Enterosora goodmanii*** (Rakotondr.) Shalisko & Sundue, Madagascar, *Kessler 12778* (UC), –, –, KY712242, –, KY711567, [2]; ***Enterosora goodmanii***, Madagascar, *Rakotondrainibe 6345* (P), KY711862, KY712037, KY712354, KY712202, –, [2]; ***Enterosora goodmanii***, Madagascar, *Rouhan & al. 1164* (P), KY711850, KY712025, KY712342, KY712190, KY711674, [2]; ***Enterosora goodmanii***, Madagascar, *Rouhan & al. 1189* (P), KY711851, KY712026, KY712343, KY712191, KY711675, [2]; ***Enterosora goodmanii***, Madagascar, *Rouhan & al. 1338* (P), KY711870, KY712045, KY712362, KY712210, KY711692, [2]; ***Enterosora goodmanii***, Madagascar, *Rouhan & al. 1382* (P), KY711871, KY712046, KY712363, KY712211, KY711693, [2]; ***Enterosora goodmanii***, Madagascar, *Rouhan & al. 424* (P), KY711863, KY712038, KY712355, KY712203, KY711686, [2]; ***Enterosora humbertii*** (C.Chr.) Shalisko & Sundue, Madagascar, *Rouhan & al. 1182* (P), KY711864, KY712039, KY712356, KY712204, KY711687, [2]; ***Enterosora humbertii***, Madagascar, *Rakotondrainibe 6954* (P), KY711866, KY712041, KY712358, KY712206, KY711689, [2]; ***Enterosora humbertii***, Madagascar, *Rouhan & al. 1248* (P), KY711865, KY712040, KY712357, KY712205, KY711688, [2]; ***Enterosora mathewsii*** (Kunze ex Mett.) Shalisko & Sundue, Colombia, *Sundue & Vasco 1254* (NY), KY775306[2], GU476895[8], KY775305[2], –, GU476743[8], [2][8]; ***Enterosora mathewsii***, Ecuador, *Sundue 1119* (NY), –, GU476868, –, –, –, [8]; ***Enterosora percrassa*** (Baker) L.E.Bishop, Costa Rica, *Sundue 1665* (NY), GU476757[8], GU476882[8], KM106141[1], –, GU476635[8], [1][8]; ***Enterosora percrassa***, Costa Rica, *Moraga & Rojas 508* (UC), GU476758[8], AY460635[11], –, –, GU476635[8], [8][11]; ***Enterosora sectifrons*** (Kunze ex Mett.) Shalisko & Sundue, Costa Rica, *Sundue 1757* (NY), –, GU476904[8], KY775304[2], KM106044[1], KM106101[1], [1][2][8]; ***Enterosora sectifrons***, Costa Rica, *Lellinger & White 1535* (US), –, MK319140, –, MK319092, MK319044, [10]; ***Enterosora* sp. 1**, Comoros, *Pignal & al. 3380* (P), KY711872, KY712047, KY712364, KY712212, KY711694, [2]; ***Enterosora* sp. 1**, Comoros, *Pignal & al. 3382* (P), KY711873, KY712048, KY712365, KY712213, KY711695, [2]; ***Enterosora* sp. 1**, Comoros, *Pignal & al. 3390* (P), KY711874, KY712049, KY712366, KY712214, KY711696, [2]; ***Enterosora* sp. 2**, Madagascar, *Massawe & Phillipson 467* (MO), –, KM218796, KM106200, –, KM106102, [1]; ***Enterosora subpinnata*** (Baker) Shalisko & Sundue, Madagascar, *Rakotomalaza & al. 129* (MO), –, –, KY712243, –, KY711568, [2]; ***Enterosora subpinnata***, Madagascar, *Rakotondrainibe 5935* (P), KY711876, KY712051, KY712368, KY712216, –, [2]; ***Enterosora subpinnata***, Madagascar, *Rouhan & al. 1378* (P), KY711875, KY712050, KY712367, KY712215, KY711697, [2]; ***Enterosora subpinnata***, Madagascar, *Rouhan & al. 1387* (P), KY711877, KY712052, KY712369, KY712217, KY711698, [2]; ***Enterosora torulosa*** (Baker) Shalisko & Sundue, Reunion, *Tamon 2* (P), KY711878, KY712053, KY712370, KY712218, KY711699, [2]; ***Enterosora torulosa***, Madagascar, *Rakotondrainibe 6177* (P), KY711884, –, KY712376, KY712224, –, [2]; ***Enterosora torulosa***, Madagascar, *Rakotondrainibe 6937* (P), KY711881, KY712056, KY712373, KY712221, KY711702, [2]; ***Enterosora torulosa***, Madagascar, *Rouhan & al. 1249* (P), KY711879, KY712054, KY712371, KY712219, KY711700, [2]; ***Enterosora torulosa***, Madagascar, *Rouhan & al. 1352* (P), KY711880, KY712055, KY712372, KY712220, KY711701, [2]; ***Enterosora torulosa***, Reunion, *S. Hennequin R107* (BM, REU), –, KF992465, –, –, –, [9]; ***Enterosora trichosora*** (Hook.) L.E.Bishop, Ecuador, *Moran 7659* (NY), –, GU476920, –, –, GU476637, [8]; ***Enterosora trifurcata*** (L.) L.E.Bishop, Costa Rica, *J.H. Nitta 811* (UC, CR), –, MW138196, –, –, –, [13]; ***Enterosora trifurcata***, Costa Rica, *J.H. Nitta 738* (UC, CR), –, MW138254, –, –, –, [13]; ***Enterosora trifurcata***, Costa Rica, *Sundue 1774* (NY), GU476754, GU476909, –, –, GU476632, [8]; ***Enterosora trifurcata***, Ecuador, *Moran 7515* (NY), GU476755, GU476917, –, –, GU476633, [8]; ***Enterosora trifurcata***, Puerto Rico, *Ranker 1608* (COLO), AY459521, AY460636, –, –, –, [11]; ***Enterosora villosissima*** (Hook.) Shalisko & Sundue, Equatorial Guinea, *Carvalho 3688* (P), KY711892, KY712066, KY712385, –, KY711713, [2]; ***Enterosora villosissima***, Equatorial Guinea, *Carvalho 3639* (P), KY711903, –, KY712395, KY712233, KY711728, [2]; ***Enterosora villosissima***, Sierra Leone, *Jaeger 9654* (P), KY711902, –, KY712394, –, KY711727, [2]; ***Galactodenia delicatula*** (M.Martens & Galeotti) Sundue & Labiak, Mexico, *Mickel 4639* (NY), –, –, GU387123[6], –, KM106064[1], [1][6]; ***Galactodenia delicatula***, Oaxaca, Mexico, *Mickel 1152* (US), –, MK319102, –, –, –, [10]; ***Galactodenia parrisiae*** Sundue & Labiak, Panama, *Monro & Knapp 5721* (NY), –, KM218794, –, KM105990, –, [1]; ***Galactodenia* sp.**, Costa Rica, *Evans Lellinger & Bowes 78* (US), –, MK319149, –, –, MK319150, [10]; ***Galactodenia subscabra*** (Klotzsch) Sundue & Labiak, Costa Rica, *Moran 8078* (NY), GU476821[8], GU476860[8], GU387127[6], GU387209[6], GU476739[8], [6][8]; ***Galactodenia subscabra***, Costa Rica, *A. Rojas & al. 3211* (UC, CR, INB, MO), AY459511, AY460677, –, –, GU476740, [11]; ***Galactodenia subscabra***, Costa Rica, *Sundue 3423* (VT), –, MK319108, –, MK319060, MK319006, [10]; ***Grammitastrum pseudaustrale*** (E.Fourn.) Parris, Sundue, Li Bing Zhang

Appendix 2. Continued.

& X.M.Zhou, New Caledonia, *L. Tibell 19878* (AK), –, KM218785, KM106150, –, KM106068, [1]; ***Grammitastrum pseudaustrale***, New Caledonia, *McPherson 18253* (MO), KY711867, KY712042, KY712359, KY712207, –, [2]; ***Grammitastrum pseudaustrale***, New Caledonia, *Munzinger 1676* (P), KY711822, KY711997, KY712316, KY712161, KY711646, [2]; ***Grammitis bryophila*** (Maxon) F.Seym., Costa Rica, *Rojas & al. 3240* (UC), AF469784, AF468208, –, –, AF469797, [3]; ***Grammitis bufonis*** L.D.Gómez, Panama, *Valdespino & Arande 179* (US), –, MK319109, –, MK319061, MK319007, [10]; ***Grammitis cincta*** Copel. ex Parris, Marquesas Islands, *Schuettpelz 1930* (US), –, MT216033, –, –, –, [17]; ***Grammitis copelandii*** Tard., Madagascar, *Rouhan & al. 1190* (P), KY711793, KY711968, KY712292, KY712133, KY711618, [2]; ***Grammitis copelandii***, Madagascar, *Janssen & al. 2515* (P), KY711795, KY711970, –, –, –, [2]; ***Grammitis copelandii***, Madagascar, *Miller 3556* (MO), –, –, –, –, KY711562, [2]; ***Grammitis copelandii***, Madagascar, *Rouhan & al. 1241* (P), KY711882, KY712057, KY712374, KY712222, KY711703, [2]; ***Grammitis coriaceifolia*** Rakotondr. & Parris, Madagascar, *Rouhan & al. 1181* (P), KY711796, KY711971, KY712294, KY712135, KY711620, [2]; ***Grammitis cryptophlebia*** (Baker) Copel., Madagascar, *Kluge 7936* (Z), KM218815, KM218799, KM106144, KM105992, KM106065, [1]; ***Grammitis cryptophlebia***, Madagascar, *Rakotondrainibe 6930* (P), KY711800, KY711975, KY712298, KY712139, KY711624, [2]; ***Grammitis cryptophlebia***, Madagascar, *Rouhan & al. 1247* (P), KY711797, KY711972, KY712295, KY712136, KY711621, [2]; ***Grammitis cryptophlebia***, Madagascar, *Rouhan & al. 1337* (P), KY711827, KY712003, KY712321, KY712167, KY711652, [2]; ***Grammitis cryptophlebia***, Reunion, *Rakotondrainibe 6912* (P), KY711885, KY712059, KY712377, KY712225, KY711705, [2]; ***Grammitis cryptophlebia***, Reunion, *S. Hennequin R103* (BM, REU), –, KF992491, –, –, –, [9]; ***Grammitis cryptophlebia***, Reunion, *Tamon 16* (P), KY711798, KY711973, KY712296, KY712137, KY711622, [2]; ***Grammitis ebenina*** (Maxon) Tard., Madagascar, *Rouhan & al. 1180* (P), KY711804, KY711979, KY712302, KY712143, KY711628, [2]; ***Grammitis ebenina***, Madagascar, *Rouhan & al. 1165* (P), KY711825, KY712001, KY712320, KY712165, KY711650, [2]; ***Grammitis ebenina***, Madagascar, *Rouhan & al. 1242* (P), KY711805, KY711980, KY712303, KY712144, KY711629, [2]; ***Grammitis ebenina***, Saint Helena, *Eastwood 199* (E), KY711890, KY712064, KY712382, –, KY711710, [2]; ***Grammitis kyimbilensis*** (Brause ex Brause & Hieron.) Copel., Madagascar, *Kessler 12773* (UC), EF178641, EF178624, KM106147, KM105993, EF178659, [1][16]; ***Grammitis kyimbilensis***, Madagascar, *Janssen & al. 2391* (P), KY711813, KY711988, KY712310, KY712152, KY711637, [2]; ***Grammitis kyimbilensis***, Madagascar, *Kluge 7857* (UC), KY711742, KY711915, KY712238, KY712082, KY711560, [2]; ***Grammitis kyimbilensis***, Madagascar, *Rakotondrainibe 6347* (P), KY711812, KY711987, KY712309, KY712151, KY711636, [2]; ***Grammitis kyimbilensis***, Madagascar, *Rouhan & al. 1242bis* (P), KY711806, KY711981, KY712304, KY712145, KY711630, [2]; ***Grammitis kyimbilensis***, Madagascar, *Rouhan & al. 1341* (P), KY711794, KY711969, KY712293, KY712134, KY711619, [2]; ***Grammitis kyimbilensis***, Tanzania, *Janssen & al. 2663* (P), KY711814, KY711989, KY712311, KY712153, KY711638, [2]; ***Grammitis kyimbilensis***, Tanzania, *Rouhan & al. 518* (P), KY711815, KY711990, KY712312, KY712154, KY711639, [2]; ***Grammitis limbata*** Fée, Reunion, *Valdespino & Arande 165* (US), –, MK319141, –, –, MK319008, [10]; ***Grammitis marginella*** (Sw.) Sw., Costa Rica, *A. Rojas 8597*(CR, MO), OQ702731 [OQ968266], OQ708616 [OQ968266], OQ717213 [OQ968266], OQ717063 [OQ968266], OQ717120 [OQ968266], **this study**; ***Grammitis marginelloides*** (J.W.Moore) Copel., Moorea, *Nitta 666* (UC), –, KY099803, –, –, –, [14]; ***Grammitis melanoloma*** (Cordemoy) Tardieu, Reunion, *Ranker & Adsersen 1504* (COLO), GU476760[8], AY460643[11], KM106148[1], –, GU476641[8], [1][8][11]; ***Grammitis melanoloma***, Reunion, *Rakotondrainibe 6907* (P), KY711816, KY711991, KY712313, KY712155, KY711640, [2]; ***Grammitis melanoloma***, Reunion, *S. Hennequin R115* (BM, REU), –, KF992492, –, –, –, [9]; ***Grammitis paramicola*** L.E.Bishop, Bolivia, *Jiménez & Gallegos* (UC), KM218816, KM218801, KM106149, KM105994, KM106067, [1]; ***Howeogrammitis diminuta*** (Baker) Parris, Sundue, Li Bing Zhang & X.M.Zhou, Lord Howe Island, *Papadopulos AP845* (NSW), –, JF950809, –, –, JF950910, [20]; ***Howeogrammitis diminuta***, Lord Howe Island, *Papadopulos AP794* (NSW), –, JF950810, –, –, JF950911, [20]; ***Lellingeria affinis*** Labiak, Bolivia, *Jimenez 368* (LPB), GU376570, GU386982, GU387044, GU387130, GU387212, [6]; ***Lellingeria affinis***, Peru, *van der Werff 21196* (MO), GU376571, GU387041, GU387045, GU387131, GU387213, [6]; ***Lellingeria apiculata*** (Kunze ex Klotzsch) A.R.Sm. & R.C.Moran, Brazil, *Salino 3009* (UC), –, AY362343, AY362690, –, –, [11][24]; ***Lellingeria apiculata***, Brazil, *Labiak 3884* (UPCB), GU376572, GU387021, GU387046, GU387132, GU387214, [6]; ***Lellingeria apiculata***, Brazil, *Labiak 4223* (UPCB), GU376573, –, GU387047, GU387133, GU387215, [6]; ***Lellingeria apiculata***, Chiapas, Mexico, *Shalisko 319* (IBUG), –, MK319111, –, MK319063, MK319009, [10]; ***Lellingeria bishopii*** Labiak, Ecuador, *Sundue 1159* (NY), GU376574, –, GU387048, GU387134, GU387216, [6]; ***Lellingeria bishopii***, Ecuador, *Van der Werff & Palacios 9343a* (MO), HQ599531, HQ599522, –, –, HQ599516, [34]; ***Lellingeria brevistipes*** (Mett. ex Kuhn) A.R.Sm. & R.C.Moran, Brazil, *Labiak 3633* (UPCB), GU376575, GU387018, GU387049, GU387135, GU387217, [6]; ***Lellingeria brevistipes***, Brazil, *Labiak 4596* (UPCB), GU376576, GU387030, GU387050, GU387136, GU387218, [6]; ***Lellingeria calolepis*** Labiak, Bolivia, *Jimenez 1731* (LPB), GU376577, GU386979, GU387051, GU387137, GU387219, [6]; ***Lellingeria calolepis***, Bolivia, *Labiak 2904* (UPCB), GU376578, GU387016, GU387052, GU387138, GU387220, [6]; ***Lellingeria depressa*** (C.Chr.) A.R.Sm. & R.C.Moran, Brazil, *Labiak 3570* (UPCB), GU376579, GU387017, GU387053, GU387139, GU387221, [6]; ***Lellingeria dissimulans*** (Maxon) A.R.Sm., Guatemala, *Willians 40423* (NY), GU376580, GU387043, GU387054, GU387140, GU387222, [6]; ***Lellingeria flagellipinnata*** M.Kessler & A.R.Sm., Bolivia, *Labiak 2866* (UPCB), GU376581, GU387015, GU387055, GU387141, GU387223, [6]; ***Lellingeria flagellipinnata***, Bolivia, *Labiak 4726* (UPCB), GU376582, –, GU387056, GU387142, GU387224, [6]; ***Lellingeria hirsuta*** A.R.Sm. & R.C.Moran, Costa Rica, *A. Rojas & E. Fletes 3145* (UC), AY459482, AY460649, –, –, –, [11]; ***Lellingeria hombersleyi*** (Maxon) A.R.Sm., Costa Rica, *J.H. Nitta 1867* (UC, GH, Nectandra), –, MW138141, –, –, –, [13]; ***Lellingeria humilis*** (Mett.) A.R.Sm. & R.C.Moran, Colombia, *Sundue 1296* (NY), –, –, GU387060, GU387146, –, [6]; ***Lellingeria humilis***, Colombia, *Sundue & Vasco 1289* (NY), GU476763, GU476897, –, –, GU476649, [8]; ***Lellingeria isidrensis*** (Maxon ex Copel.) A.R.Sm. & R.C.Moran, Costa Rica, *Wagner 83020* (NY), GU376586, GU387042, GU387061, GU387147, GU387228, [6]; ***Lellingeria itatimensis*** (C.Chr.) A.R.Sm. & R.C.Moran, Brazil, *Labiak 3872* (UPCB), GU376587, GU387020, GU387062, GU387148, GU387229, [6]; ***Lellingeria jimenezii*** Labiak, Bolivia, *Jimenez 2139* (LPB), GU376588, GU386981, GU387063, GU387149, –, [6]; ***Lellingeria jimenezii***, Bolivia, *Lehnert 466* (UC), GU376589, GU386986, GU387064, GU387150, GU387230, [6]; ***Lellingeria kaieteura*** (Jenman) Labiak, Trinidad and Tobago, *Hombersley 120* (NY), GU376590, GU386978, GU387065, GU387151, GU387231, [6]; ***Lellingeria major*** (Copel.) A.R.Sm. & R.C.Moran, Ecuador, *Sundue 1134* (NY), GU476766, GU476873, GU387068, GU387154, GU476652, [8]; ***Lellingeria major***, Ecuador, *M. Lehnert 895* (GOET), EF178644, EF178627, –, –, –, [16]; ***Lellingeria major***, Ecuador, *Sundue 1147* (NY), GU376592, –, GU387069, GU387155, GU387233, [6]; ***Lellingeria major***, Ecuador, *Sundue 1171* (NY), GU476768, GU476886, –, –, GU476654, [8]; ***Lellingeria melanotrichia*** (Baker) A.R.Sm. & R.C.Moran, Colombia, *Contreras 300* (NY), GU376593, GU386973, GU387070, GU387156, GU387234, [6]; ***Lellingeria melanotrichia***, Costa Rica, *J.H. Nitta 818* (UC, CR), –, MW138190, –, –, –, [13]; ***Lellingeria oreophila*** (Maxon) A.R.Sm. & R.C.Moran, Colombia, *Contreras 159* (NY), –, GU386974, GU387080, GU387165, GU387243, [6]; ***Lellingeria paramicola*** Labiak, Ecuador, *Ollgaard 8403* (NY), GU376601, GU387014, GU387081, GU387166, GU387244, [6]; ***Lellingeria pendula*** (Sw.) A.R.Sm. & R.C.Moran, Venezuela, *Meier 706* (VEN), –, –, GU387082, –, GU387245, [6]; ***Lellingeria pendula***, Guadeloupe, *Proctor 20310* (US), GU376602, GU387036, GU387083, GU387167, GU387246, [6]; ***Lellingeria phlegmaria*** (J.Sm.) A.R.Sm. & R.C.Moran, Colombia, *Sundue 1345* (NY), GU376603, GU387008, GU387084, GU387168, GU387247, [6]; ***Lellingeria phlegmaria***, Bolivia, *Labiak 4732* (UPCB), GU376604, GU387034, GU387085, GU387169, GU387248, [6]; ***Lellingeria pseudocapillaris*** (Rosenst.) A.R.Sm. & R.C.Moran, Bolivia, *Jimenez 1800* (LPB), GU376606, GU386980, GU387087, GU387171, GU387250, [6]; ***Lellingeria pseudocapillaris***, Ecuador, *Laegaard 20186* (US), GU376607, GU386983, GU387088, GU387172, GU387251, [6]; ***Lellingeria randallii*** (Maxon) A.R.Sm. & R.C.Moran, Trinidad and Tobago, *Mickel 9495* (NY), KM218860[1], –, GU387090[6], KM105996[1], GU387253[6], [1][6]; ***Lellingeria randallii***, Panama, *Valdespino 345* (NY), GU376609, GU387039, GU387091, GU387174, GU387254, [6]; ***Lellingeria simacensis*** (Rosenst.) A.R.Sm. & R.C.Moran, Ecuador, *Sundue 1169* (NY), GU376610, –, GU387092, GU387175, GU387255, [6]; ***Lellingeria simacensis***, Ecuador, *Sundue 1126* (NY), GU476769, GU476871, –, –, GU476658, [8]; ***Lellingeria* sp. 1**, Ecuador, *M. Lehnert 718* (GOET), EF178648, EF178631, –, –, –, [16]; ***Lellingeria* sp. 2**, Bolivia, *M. Lehnert 1232* (GOET), EF178647, EF178630, –, –, –, [16]; ***Lellingeria subimpressa*** (Copel.) Labiak, Panama, *Araúz 368* (US), GU376611, GU386967, GU387093, GU387176, GU387256, [6]; ***Lellingeria subimpressa***, Costa Rica, *Rojas & Fletes 3124* (UC), HQ599536, HQ599528, –, –, HQ599518, [34]; ***Lellingeria subsessilis*** (Baker) A.R.Sm. & R.C.Moran, Ecuador, *Sundue 1124* (NY), GU376612, GU386996, GU387094, GU387177, GU387257, [6]; ***Lellingeria subsessilis***, Costa Rica, *A. Rojas 3022 & M. Mata* (UC), AY459485[11],

Appendix 2. Continued.

AY460653[11], –, –, GU476643[8], [8][11]; ***Lellingeria subsessilis***, Ecuador, *Sundue 1139* (NY), GU376613, –, GU387095, GU387178, GU387258, [6]; ***Lellingeria subsessilis***, Ecuador, *Sundue 1170* (NY), GU476761, GU476885, –, –, GU476644, [8]; ***Lellingeria suprasculpta*** (Christ) A.R.Sm. & R.C.Moran, Costa Rica, *Lellinger 989* (US), GU376614, –, GU387096, GU387179, GU387259, [6]; ***Lellingeria suprasculpta***, Costa Rica, *Sundue 1767* (NY), GU476770, GU476908, –, –, GU476659, [8]; ***Lellingeria suspensa*** (L.) A.R.Sm. & R.C.Moran, Colombia, *Vasco 632* (NY), GU376615, GU386969, GU387097, GU387180, GU387260, [6]; ***Lellingeria suspensa***, Brazil, *Labiak 3644* (UPCB), GU376619, GU387019, GU387101, GU387184, GU387264, [6]; ***Lellingeria suspensa***, Colombia, *Vasco 717* (NY), GU376616, GU386970, GU387098, GU387181, GU387261, [6]; ***Lellingeria suspensa***, Colombia, *Vasco & Sundue 625* (NY), GU476771, GU476824, –, –, GU476660, [8]; ***Lellingeria suspensa***, Colombia, *Vasco & Sundue 704* (NY), GU476772, GU476826, –, –, GU476661, [8]; ***Lellingeria suspensa***, Costa Rica, *J.H. Nitta 706* (UC), –, MW138274, –, –, –, [13]; ***Lellingeria suspensa***, Costa Rica, *J.H. Nitta 718* (UC), –, MW138265, –, –, –, [13]; ***Lellingeria suspensa***, Ecuador, *Sundue 1047* (NY), GU376618, –, GU387100, GU387183, GU387263, [6]; ***Lellingeria suspensa***, French Guiana, *Granville 15398* (US), GU376617, GU386976, GU387099, GU387182, GU387262, [6]; ***Lellingeria suspensa***, Guadeloupe, *Proctor 20312* (US), GU376620, GU387037, GU387102, GU387185, GU387265, [6]; ***Lellingeria tamandarei*** A.R.Sm. & R.C.Moran, Brazil, *Labiak 4430* (UPCB), GU376621, GU387027, GU387103, GU387186, GU387266, [6]; ***Lellingeria tenuicula*** (Fée) A.R.Sm. & R.C.Moran, Dominican Republic, *Hill 28165* (US), GU376622, GU386977, GU387104, GU387187, GU387267, [6]; ***Lellingeria tmesipteris*** (Copel.) A.R.Sm. & R.C.Moran, Costa Rica, *Evans Lellinger & Bowes 171* (US), –, MK319112, –, MK319064, MK319010, [10]; ***Leucotrichum madagascariense*** Rakotondr. & Rouhan, Madagascar, *Rakotondrainibe & al. 6957* (P), JN654923, JN654924, JN654949, JN654962, JN654975, [7]; ***Leucotrichum mitchelliae*** (Baker ex Hemsl.) Labiak, Mexico, *Breedlon & Almeda 48307* (NY), GU376479[6], GU376488[6], JN654937[7], JN654950[7], JN654963[7], [6][7]; ***Leucotrichum mitchelliae***, Cuba, *Morton & Acuna 3141* (NY), GU376480[6], GU376487[6], JN654938[7], JN654951[7], JN654964[7], [6][7]; ***Leucotrichum mitchelliae***, Panama, *Valdespino 195* (NY), GU376481[6], GU376486[6], JN654948[7], JN654961[7], JN654974[7], [6][7]; ***Leucotrichum mortonii*** (Copel.) Labiak, Dominican Republic, *Liogier 16026* (NY), GU376478, GU376489, –, –, –, [6]; ***Leucotrichum organense*** (Gardner) Labiak, Brazil, *Labiak 3630* (UPCB), GU376483[6], GU376490[6], JN654945[7], JN654958[7], JN654971[7], [6][7]; ***Leucotrichum organense***, Brazil, *Labiak 4232* (UPCB), GU376485[6], GU376492[6], JN654946[7], JN654959[7], JN654972[7], [6][7]; ***Leucotrichum organense***, Brazil, *Labiak 4302* (UPCB), GU376484[6], GU376491[6], JN654947[7], JN654960[7], JN654973[7], [6][7]; ***Leucotrichum pseudomitchelliae*** (Lellinger) Labiak, Costa Rica, *A. Rojas 3005* (MO), AY459484, AY460652, –, –, –, [11]; ***Leucotrichum schenckii*** (Hieron.) Labiak, Brazil, *Salino 4538* (UC, BHCB), AY459483[11], AY460651[11], –, –, KM106072[1], [1][11]; ***Leucotrichum schenckii***, Brazil, *Prado 1664* (SP), GU376482, GU376493, –, –, –, [6]; ***Leucotrichum schenckii***, Brazil, *Salino 4547* (UC), –, –, –, –, GU476657, [8]; ***Lomaphlebia linearis*** (Sw.) J.Sm., Jamaica, *Wilson & Murrey 635* (US), –, MK319113, –, MK319065, MK319011, [10]; ***Lomaphlebia turquina*** (Maxon) Sundue & Ranker, Cuba, *C. Sanchez 82061* (HAJB), KM218814, KM218800, –, –, KM106069, [1]; ***Melpomene albicans*** Lehnert, Bolivia, *M. Lehnert 514* (GOET), FJ011007, FJ011044, –, –, –, [18]; ***Melpomene albicans***, Bolivia, *M. Lehnert 601* (GOET), FJ011008, FJ011045, –, –, –, [18]; ***Melpomene albicans***, Bolivia, *M. Lehnert 717* (GOET), FJ011009, FJ011046, –, –, –, [18]; ***Melpomene allosuroides*** (Rosenst.) A.R.Sm. & R.C.Moran, Bolivia, *Solomon 12829* (NY), GU376628, GU387038, GU387109, GU387192, GU387273, [6]; ***Melpomene anazalea*** Sundue & Lehnert, Colombia, *Sundue & Vasco 1290* (NY), GU476773[8], GU476898[8], KM106152[1], KM105997[1], GU476662[8], [1][8]; ***Melpomene caput-gorgonis*** Lehnert, Bolivia, *M. Lehnert 372* (GOET), FJ011010, FJ011047, –, –, –, [18]; ***Melpomene erecta*** (C.V.Morton) A.R.Sm. & R.C.Moran, Bolivia, *Nuñez 25* (NY), GU376629, GU387013, GU387110, GU387193, GU387274, [6]; ***Melpomene erecta***, Ecuador, *M. Lehnert 1570* (GOET), FJ011011, FJ011048, –, –, –, [18]; ***Melpomene firma*** (J.Sm.) A.R.Sm. & R.C.Moran, Colombia, *Sundue 1253* (NY), –, GU387003, GU387111, GU387194, GU387275, [6]; ***Melpomene firma***, Bolivia, *Labiak 4733* (UPCB), GU376630, GU387035, GU387112, GU387195, GU387276, [6]; ***Melpomene firma***, Bolivia, *M. Lehnert 516* (GOET, LPB, UC), FJ011013, FJ011050, –, –, –, [18]; ***Melpomene firma***, Ecuador, *M. Lehnert 1003* (GOET), FJ011012, FJ011049, –, –, –, [18]; ***Melpomene firma***, Ecuador, *Sundue 1072* (NY, QCA, QCNE, UC), GU476774, GU476864, –, –, GU476663, [8]; ***Melpomene flabelliformis*** (Poir.) A.R.Sm. & R.C.Moran, Colombia, *Sundue 1303* (NY), GU376631, GU387005, GU387113, GU387196, GU387277, [6]; ***Melpomene flabelliformis***, Bolivia, *I. Jimenez 1874* (GOET), –, FJ011082, –, –, –, [18]; ***Melpomene flabelliformis***, Brazil, *Labiak 4432* (UPCB), GU376632, GU387028, GU387114, GU387197, GU387278, [6]; ***Melpomene flabelliformis***, Colombia, *C. Dassler 94-7-14-2* (UC), FJ011018, FJ011055, –, –, –, [18]; ***Melpomene flabelliformis***, Colombia, *P. Sanchez-B. 183* (UC), AY459488, AY460656, –, –, –, [11]; ***Melpomene flabelliformis***, Costa Rica, *J. Kluge 1189* (GOET), –, FJ011081, –, –, –, [18]; ***Melpomene flabelliformis***, Costa Rica, *Sundue 3421* (VT), –, MK319115, –, MK319067, MK319013, [10]; ***Melpomene flabelliformis***, Ecuador, *M. Lehnert 955* (GOET), FJ011019, FJ011056, –, –, –, [18]; ***Melpomene flabelliformis***, Madagascar, *Rakotondrainibe 6940* (P), KY711835, KY712011, KY712327, KY712175, KY711660, [2]; ***Melpomene flabelliformis***, Madagascar, *Rouhan & al. 1179* (P), KY711833, KY712009, KY712325, KY712173, KY711658, [2]; ***Melpomene flabelliformis***, Madagascar, *T. Janssen 2927* (P), –, FJ011083, –, –, –, [18]; ***Melpomene flabelliformis***, Oaxaca, Mexico, *Sundue 3036* (VT), –, MK319114, –, MK319066, MK319012, [10]; ***Melpomene flabelliformis***, Reunion, *M. Kessler 13834* (GOET, REU), –, KF992503, –, –, –, [9]; ***Melpomene flabelliformis***, Reunion, *Rakotondrainibe 6906* (P), KY711834, KY712010, KY712326, KY712174, KY711659, [2]; ***Melpomene flabelliformis***, Tanzania, *A. Hemp s.n.* (UBT), FJ011016, FJ011053, –, –, –, [18]; ***Melpomene flabelliformis***, Tanzania, *A. Hemp s.n.* (UBT), FJ011017, FJ011054, –, –, –, [18]; ***Melpomene flabelliformis***, Tanzania, *Janssen & al. 2669* (P), KY711836, KY712012, KY712328, KY712176, KY711661, [2]; ***Melpomene flagellata*** Lehnert, Bolivia, *M. Lehnert 555* (GOET), –, FJ011084, –, –, –, [18]; ***Melpomene gracilis*** (Hook.) A.R.Sm., Ecuador, *M. Lehnert 1554* (GOET), FJ011006, FJ011043, –, –, –, [6]; ***Melpomene jimenezii*** Lehnert, Bolivia, *I. Jimenez 1859* (GOET), –, FJ011085, –, –, –, [18]; ***Melpomene leptostoma*** (Fée) A.R.Sm. & R.C.Moran, Mexico, *M. Kessler 13515* (GOET), –, FJ011087, –, –, –, [18]; ***Melpomene leptostoma***, Mexico, *M. Kessler 13528* (GOET), –, FJ011088, –, –, –, [18]; ***Melpomene melanosticta*** (Kunze) A.R.Sm. & R.C.Moran, Brazil, *Labiak 4156* (UPCB), GU376633, GU387024, GU387115, GU387198, GU387279, [6]; ***Melpomene melanosticta***, Ecuador, *M. Lehnert 1533* (GOET, QCA, UC), FJ011020, FJ011057, –, –, –, [18]; ***Melpomene michaelis*** Lehnert, Bolivia, *M. Lehnert 519* (GOET), –, FJ011086, –, –, –, [18]; ***Melpomene moniliformis*** (Lag. ex Sw.) A.R.Sm. & R.C.Moran, Colombia, *Sundue 1366* (NY), GU376626, GU387010, GU387107, GU387190, GU387271, [6]; ***Melpomene moniliformis***, Costa Rica, *M. Moraga & A. Rojas 446* (INB), AY459486, AY460654, –, –, GU476664, [11]; ***Melpomene moniliformis***, Ecuador, *M. Lehnert 1110* (GOET), FJ011021, FJ011058, –, –, –, [18]; ***Melpomene moniliformis***, Ecuador, *M. Lehnert 122* (GOET), FJ011022, FJ011059, –, –, –, [18]; ***Melpomene moniliformis***, Mexico, *Farrar 94-9-21-1* (no voucher), AY459487, AY460655, –, –, –, [11]; ***Melpomene moniliformis***, Oaxaca, Mexico, *Sundue 3042* (VT), –, MK319118, –, MK319070, MK319016, [10]; ***Melpomene moniliformis***, Oaxaca, Mexico, *Sundue 3047* (VT), –, MK319142, –, –, MK319017, [10]; ***Melpomene moniliformis***, Oaxaca, Mexico, *Sundue 3531* (VT), –, MK319123, –, MK319075, MK319021, [10]; ***Melpomene moniliformis***, Peru, *M. Lehnert 273* (GOET), FJ011023, FJ011060, –, –, –, [18]; ***Melpomene moniliformis***, Peru, *M. Lehnert 435* (GOET), FJ011024, FJ011061, –, –, –, [18]; ***Melpomene occidentalis*** Lehnert, Ecuador, *M. Lehnert 1343* (GOET), FJ011014, FJ011051, –, –, –, [18]; ***Melpomene occidentalis***, Ecuador, *Lehnert 1558a* (GEOT), FJ011015, FJ011052, –, –, –, [18]; ***Melpomene occidentalis***, Ecuador, *Sundue 1157* (NY), GU476776, GU476877, –, –, GU476666, [8]; ***Melpomene occidentalis***, Ecuador, *Sundue 1168* (NY), GU476775, GU476884, –, –, GU476665, [8]; ***Melpomene paradoxa*** Lehnert, Bolivia, *M. Lehnert 388* (GOET), FJ011025, FJ011062, –, –, –, [18]; ***Melpomene paradoxa***, Bolivia, *M. Lehnert 539* (GOET), FJ011026, FJ011063, –, –, –, [18]; ***Melpomene personata*** Lehnert, Colombia, *Sundue 1330* (NY), GU376634, GU387007, GU387116, GU387199, GU387280, [6]; ***Melpomene personata***, Colombia, *Sundue 1281 & Vasco* (NY), GU476777, GU476896, –, –, GU476667, [8]; ***Melpomene personata***, Colombia, *Sundue 1365* (NY), GU376635, GU387009, GU387117, GU387200, –, [6]; ***Melpomene personata***, Costa Rica, *J. Kluge 6949* (GOET), FJ011027, FJ011064, –, –, –, [18]; ***Melpomene personata***, Costa Rica, *R. Kirkpatrick 1126* (UC), FJ011028, FJ011065, –, –, –, [18]; ***Melpomene personata***, Costa Rica, *Sundue 3420* (VT), –, MK319120, –, MK319072, MK319018, [10]; ***Melpomene personata***, Ecuador, *M. Lehnert 145* (GOET), FJ011029, FJ011066, –, –, –, [18]; ***Melpomene peruviana*** (Desv.) A.R.Sm. & R.C.Moran, Argentina, *M. Lehnert 571* (GOET), FJ011030, FJ011067, –, –, –, [18]; ***Melpomene peruviana***, Bolivia, *M. Lehnert 775* (GOET), FJ011031, FJ011068, –, –, –, [18]; ***Melpomene pilosissima*** (M.Martens & Galeotti) A.R.Sm. & R.C.Moran, Mexico, *Martinez 1535* (NY), GU376636, GU386993, GU387118, GU387201, GU387281, [6]; ***Melpomene pilosissima***, Mexico, *Kroemer 2738* (GOET), –, FJ011089, –, –, –, [18]; ***Melpomene pilosissima***, Mexico, *M. Kessler 13514* (GOET), –,

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FJ011090, –, –, –, [18]; ***Melpomene pilosissima***, Oaxaca, Mexico, *Sundue 3082* (VT), –, MK319121, –, MK319073, MK319019, [10]; ***Melpomene pseudonutans*** (Christ & Rosenst.) A.R.Sm. & R.C.Moran, Ecuador, *K.A. Wilson 2806* (UC), AY459489, AY460657, –, –, –, [11]; ***Melpomene pseudonutans***, Ecuador, *M. Lehnert 119* (GOET), FJ011032, FJ011069, –, –, –, [18]; ***Melpomene pseudonutans***, Ecuador, *M. Lehnert 1558* (GOET), FJ011033, FJ011070, –, –, –, [18]; ***Melpomene sklenarii*** Lehnert, Ecuador, *M. Lehnert 1465* (GOET), FJ011034, FJ011071, –, –, –, [18]; ***Melpomene sodiroi*** (Christ & Rosenst.) A.R.Sm. & R.C.Moran, Ecuador, *M. Lehnert 1106* (GOET), FJ011035, FJ011072, –, –, –, [18]; ***Melpomene sodiroi***, Ecuador, *M. Lehnert 173* (GOET), –, FJ011091, –, –, –, [18]; ***Melpomene vernicosa*** (Maxon ex Copel.) A.R.Sm. & R.C.Moran, Ecuador, *M. Lehnert 1333* (GOET), FJ011036, FJ011073, –, –, –, [18]; ***Melpomene vernicosa***, Ecuador, *Sundue 1112* (NY), GU476778, GU476867, –, –, GU476668, [8]; ***Melpomene vernicosa***, Mexico, *M. Kessler 13502* (GOET), –, FJ011092, –, –, –, [18]; ***Melpomene vulcanica*** Lehnert, Ecuador, *M. Lehnert 176* (GOET), FJ011037, FJ011074, –, –, –, [18]; ***Melpomene wolfii*** (Hieron.) A.R.Sm. & R.C.Moran, Ecuador, *M. Lehnert 1229* (GOET), FJ011038, FJ011075, –, –, –, [18]; ***Melpomene wolfii***, Ecuador, *M. Lehnert 985* (GOET), FJ011039, FJ011076, –, –, –, [18]; ***Melpomene xiphopteridoides*** (Liebmann) A.R.Sm. & R.C.Moran, Brazil, *Labiak 4301* (UPCB), GU376627, GU387026, GU387108, GU387191, GU387272, [6]; ***Melpomene xiphopteridoides***, Bolivia, *M. Lehnert 477* (GOET), FJ011041, FJ011078, –, –, –, [18]; ***Melpomene xiphopteridoides***, Bolivia, *Vasco 577* (NY), GU376638, GU387040, GU387120, GU387203, GU387283, [6]; ***Melpomene xiphopteridoides***, Chiapas, Mexico, *Shalisko 305B* (IBUG), –, MK319124, –, MK319076, MK319022, [10]; ***Melpomene xiphopteridoides***, Chiapas, Mexico, *Shalisko 315* (IBUG), –, MK319125, –, MK319077, MK319023, [10]; ***Melpomene xiphopteridoides***, Chiapas, Mexico, *Shalisko 316* (IBUG), –, MK319116, –, MK319068, MK319014, [10]; ***Melpomene xiphopteridoides***, Chiapas, Mexico, *Shalisko 317* (IBUG), –, MK319117, –, MK319069, MK319015, [10]; ***Melpomene xiphopteridoides***, Chiapas, Mexico, *Sundue 3514* (VT), –, MK319122, –, MK319074, MK319020, [10]; ***Melpomene xiphopteridoides***, Colombia, *Sundue 1300* (NY), GU376637, GU387004, GU387119, GU387202, GU387282, [6]; ***Melpomene xiphopteridoides***, Ecuador, *M. Lehnert 187* (GOET), FJ011040, FJ011077, –, –, –, [18]; ***Melpomene xiphopteridoides***, Ecuador, *M. Lehnert 792* (GOET), FJ011042, FJ011079, –, –, –, [18]; ***Melpomene xiphopteridoides***, Mexico, *M. Kessler 13484* (GOET), –, FJ011093, –, –, –, [18]; ***Melpomene zempoaltepetlensis*** (Mickel & Beitel) A.R.Sm., Chiapas, Mexico, *Sundue 3050* (VT), –, MK319126, –, MK319078, MK319024, [10]; ***Micropolypodium okuboi*** (Yatabe) Hayata, Cao Bang, Vietnam, *L.-B. Zhang & al. 6812* (CDBI, MO, VNMN), –, OQ708536, OQ717248, –, –, **this study**; ***Micropolypodium okuboi***, Guangxi, China, *X.-C. Zhang 6000* (PE), MW876340, MW876338, –, –, –, [26]; ***Micropolypodium okuboi***, Japan, *Parris 12154* (AK), JF514064, JF513994, –, –, –, [21]; ***Micropolypodium okuboi***, Japan, *Wilson 2387* (UC), JF514086, JF514018, –, –, JF514053, [21]; ***Micropolypodium okuboi***, Miyazaki, Japan, *762780* (TNS), –, AB575300, –, –, –, [25]; ***Micropolypodium okuboi***, Taiwan Island, *Kanebira & Sasaki 21672* (UC), –, JF513998, –, –, –, [21]; ***Micropolypodium sikkimensis*** (Hieron.) X.C.Zhang, Xizang, China, *YLZB1783* (CDBI), OQ702711, OQ708606, OQ717191, OQ717064, OQ717123, **this study**; ***Micropolypodium sikkimensis***, Bhutan, *Miehe 00-093-32* (UC), JF514068, JF513999, –, –, JF514032, [21]; ***Micropolypodium sikkimensis***, China, *Xian & al. s.n.* (UC), JF514087, JF514019, –, –, JF514054, [21]; ***Micropolypodium sikkimensis***, Xizang, China, *Z.-Y. Li 2763*, MW876339, MW876339, –, –, –, [26]; ***Micropolypodium sikkimensis***, Yunnan, China, *Q. Wei WQ408* (KUN), MT130599, MT130599, –, –, –, [27]; ***Micropolypodium sikkimensis***, Yunnan, China, *Z.-L. Liang 1111* (CDBI, KUN), OQ702713, OQ708545, OQ717201, OQ717067, OQ717126, **this study**; ***Micropolypodium sikkimensis***, Yunnan, China, *Z.-L. Liang 1122* (CDBI, KUN), OQ702712, OQ708544, OQ717204, OQ717066, OQ717125, **this study**; ***Micropolypodium sikkimensis***, Yunnan, China, *Z.-L. Liang 939* (PYU), OQ702699, –, OQ717190, OQ717065, OQ717124, **this study**; ***Moranopteris achilleifolia*** (Kaulf.) R.Y.Hirai & J.Prado, Brazil, *J. Cordeiro & O. Ribas 1398* (UC), AY459499[11], AY460666[11], KM106153[1], KM105999[1], –, [1][11]; ***Moranopteris aphelolepis*** (C.V.Morton) R.Y.Hirai & J.Prado, Bolivia, *Jiménez & Vidarre 557* (UC), JF514066, JF513996, –, –, JF514030, [21]; ***Moranopteris basiattenuata*** (Jenman) R.Y.Hirai & J.Prado, Lempira, Honduras, *G. Davidse 34809* (MO), OQ702660, OQ708515, OQ717289, –, OQ717127, **this study**; ***Moranopteris basiattenuata***, Mexico, *Breedlove & Thorne 30160* (NY), JF514058, JF513988, –, –, JF514022, [21]; ***Moranopteris blepharidea*** (Copel.) R.Y.Hirai & J.Prado, Bolivia, *Jimenez 708* (GOET), JF514065[21], JF513995[21], KM106154[1], KM106000[1], JF514029[21], [1][21]; ***Moranopteris caucana*** (Hieron.) R.Y.Hirai & J.Prado, Ecuador, *Lehnert 182* (GOET), JF514071[21], JF514002[21], KM106155[1], KM106001[1], JF514035[21], [1][21]; ***Moranopteris caucana***, Ecuador, *Van der Werff & al. 13445* (UC), JF514061, JF513991, –, –, –, [21]; ***Moranopteris cookii*** (Underw. & Maxon ex Maxon) R.Y.Hirai & J.Prado, Costa Rica, *Sundue & al. 1771* (NY), JF514076[21], JF514007[21], KM106156[1], KM106002[1], JF514040[21], [1][21]; ***Moranopteris gradata*** (Baker) R.Y.Hirai & J.Prado, Brazil, *Hirai & al. 537* (SP), JF514077, JF514009, –, –, JF514043, [21]; ***Moranopteris grisebachii*** (Underw. ex C.Chr.) R.Y.Hirai & J.Prado, Jamaica, *Maxon 9961* (NY), –, JF514008, –, –, –, [21]; ***Moranopteris hyalina*** (Maxon) R.Y.Hirai & J.Prado, Costa Rica, *A. Rojas & al. 3210* (UC, CR, INB, MO), AY459490[24], AY362344[24], AY362691[24], –, GU476670[11], [11][24]; ***Moranopteris hyalina***, Ecuador, *Lehnert 1426* (GOET), JF514070[21], JF514001[21], KM106157[1], KM106003[1], JF514034[21], [1][21]; ***Moranopteris hyalina***, Ecuador, *Sundue 1148* (NY), JF514075, JF514006, –, –, JF514039, [21]; ***Moranopteris inaccessa*** Sundue & Sylvester, Peru, *Sylvester 1628* (CUZ, VT, Z), KP050355, KP027642, –, –, KP050357, [28]; ***Moranopteris longisetosa*** (Hook.) R.Y.Hirai & J.Prado, Bolivia, *Lehnert 596* (GOET), JF514072[21], JF514003[21], KM106158[1], KM106004[1], JF514036[21], [1][21]; ***Moranopteris longisetosa***, Costa Rica, *A. Rojas & al. 3209* (UC, CR, INB, MO), AY459507, AY460674, –, –, –, [11]; ***Moranopteris microlepis*** (Rosenst.) R.Y.Hirai & J.Prado, Costa Rica, *Smith 2584* (UC), JF514056, JF513986, –, –, JF514020, [21]; ***Moranopteris microlepis***, Costa Rica, *Kluge 2003* (UC), JF514067, JF513997, –, –, JF514031, [21]; ***Moranopteris nana*** (Fée) R.Y.Hirai & J.Prado, Venezuela, *Diaz & al. 4747* (NY), –, JF513990, –, –, –, [21]; ***Moranopteris perpusilla*** (Maxon) R.Y.Hirai & J.Prado, Brazil, *Hiari & al. 574* (SP), JF514079, JF514011, –, –, JF514045, [21]; ***Moranopteris plicata*** (A.R.Sm.) R.Y.Hirai & J.Prado, Ecuador, *Lehnert 929* (GOET, UC), JF514074[21], JF514005[21], KM106159[1], KM106005[1], JF514038[21], [1][21]; ***Moranopteris serricula*** (Fée) R.Y.Hirai & J.Prado, Dominican Republic, *Wilbur & al. 8084* (NY), JF514085, JF514017, –, –, JF514052, [21]; ***Moranopteris setosa*** (Kaulf.) R.Y.Hirai & J.Prado, Brazil, *Hirai & al. 599* (SP), JF514080, JF514012, –, –, –, [21]; ***Moranopteris setulosa*** (Rosenst.) A.Rojas, Costa Rica, *Evans Lellinger & Bowes 15* (US), –, MK319143, –, –, –, [10]; ***Moranopteris sherringii*** (Baker) R.Y.Hirai & J.Prado, Puerto Rico, *Sundue 2056* (NY, VT, UPRP), –, KP027643, –, –, –, [28]; ***Moranopteris* sp.**, Madagascar, *Bauret & al. 107* (P), –, KY711912, –, –, –, [2]; ***Moranopteris taenifolia*** (Jenman) R.Y.Hirai & J.Prado, Costa Rica, *A. Rojas 3007* (UC), AY459491, AY460658, –, –, HQ599515, [11]; ***Moranopteris taenifolia***, Chiapas, Mexico, *Shalisko 332* (IBUG), –, MK319129, –, MK319081, MK319028, [10]; ***Moranopteris taenifolia***, Chiapas, Mexico, *Shalisko 336* (IBUG), –, –, –, MK319082, MK319029, [10]; ***Moranopteris taenifolia***, Chiapas, Mexico, *Shalisko 337* (IBUG), –, –, –, MK319083, MK319030, [10]; ***Moranopteris taenifolia***, Costa Rica, *J.H. Nitta 715* (UC, CR), –, MW138266, –, –, –, [13]; ***Moranopteris taenifolia***, Costa Rica, *Rothfels 08-116* (DUKE), JF514060, –, –, –, JF514023, [21]; ***Moranopteris taenifolia***, Costa Rica, *Shalisko 253* (IBUG), –, MK319127, –, MK319079, MK319026, [10]; ***Moranopteris taenifolia***, Costa Rica, *Shalisko 257* (IBUG), –, MK319128, –, MK319080, MK319027, [10]; ***Moranopteris taenifolia***, Costa Rica, *Sundue 3385* (VT), –, MK319144, –, –, MK319031, [10]; ***Moranopteris taenifolia***, Costa Rica, *Sundue 3411* (VT), –, MK319145, –, –, MK319032, [10]; ***Moranopteris taenifolia***, Costa Rica, *Triano-Moreno s.n.* (SP), JF514083, JF514015, –, –, JF514050, [21]; ***Moranopteris trichomanoides*** (Sw.) R.Y.Hirai & J.Prado, Honduras, *Gomez 114* (NY), JF514063, JF513993, –, –, JF514027, [21]; ***Moranopteris trichomanoides***, Dominican Republic, *Zanoni & al. 45973* (NY), –, –, –, –, JF514055, [21]; ***Moranopteris truncicola*** (Klotzsch) R.Y.Hirai & J.Prado, Colombia, *Vasco & Sundue 626* (NY), JF514084[21], JF514016[21], KM106160[1], KM106006[1], JF514051[21], [1][21]; ***Moranopteris truncicola***, Ecuador, *Lehnert 862* (GOET), JF514073, JF514004, –, –, JF514037, [21]; ***Moranopteris williamsii*** (Maxon) R.Y.Hirai & J.Prado, Bolivia, *Kessler & al. 7173* (UC), JF514069, JF514000, –, –, JF514033, [21]; ***Moranopteris zurquina*** (Copel.) R.Y.Hirai & J.Prado, Costa Rica, *A. Rojas 3021 & M. Mata* (UC), AY459492, AY460659, –, –, –, [11]; ***Mycopteris alsopteris*** (C.V.Morton) Sundue, Bolivia, *Jimenez 1451* (LPB), GU476798, GU476835, –, –, GU476696, [8]; ***Mycopteris alsopteris***, Bolivia, *Jimenez 1487* (LPB), GU476796, GU476836, –, –, GU476693, [8]; ***Mycopteris alsopteris***, Bolivia, *Jimenez 1491* (LPB), GU476797, GU476837, –, –, GU476694, [8]; ***Mycopteris alsopteris***, Bolivia, *Jimenez 1504* (LPB), –, GU476838, –, –, GU476695, [8]; ***Mycopteris alsopteris***, Costa Rica, *J.H. Nitta 752* (UC, CR), –, MW138245, –, –, –, [13]; ***Mycopteris alsopteris***, Costa Rica, *Moran s.n.* (NY), GU476799, GU476915, –, –, GU476697, [8]; ***Mycopteris alsopteris***, Ecuador, *K.A. Wilson 2609a* (UC), –, AY460667, –, –, –, [11]; ***Mycopteris amphidasyon*** (Kunze ex Mett.) Sundue, Ecuador, *Moran 7646* (NY), GU476759[8], GU476922[8], KM106161[1], KM106007[1], GU476638[8], [1][8]; ***Mycopteris amphidasyon***, Ecuador, *Sundue 1129* (NY), –, GU476872, –, –,

Appendix 2. Continued.

GU476701, [8]; ***Mycopteris amphidasyon***, Ecuador, *Sundue 1135* (NY), –, GU476874, –, –, GU476700, [8]; ***Mycopteris attenuatissima*** (Copel.) Sundue, Ecuador, *Sundue 1098* (NY), GU476801[8], GU476866[8], GU387121[6], GU387204[6], GU476705[8], [6][8]; ***Mycopteris attenuatissima***, Ecuador, *K.A. Wilson 2609a* (UC), AY459500[11], GU476927[8], –, –, –, [8][11]; ***Mycopteris attenuatissima***, Ecuador, *Lehnert & Kessler 1162* (NY), GU476802, GU476850, –, –, GU476706, [8]; ***Mycopteris attenuatissima***, Ecuador, *Sundue 1038* (NY), GU476803, GU476863, –, –, GU476707, [8]; ***Mycopteris costaricensis*** (Rosenst.) Sundue, Costa Rica, *J.H. Nitta 707* (UC, CR), –, MW138273, –, –, –, [13]; ***Mycopteris cretata*** (Maxon) Sundue, Dominican Republic, *Alford 2719* (NY), –, GU476823, –, –, GU476713, [8]; ***Mycopteris leucosticta*** (J.Sm.) Sundue, Ecuador, *Lehnert 1128* (UC), GU476811[8], GU476848[8], KM106162[1], –, GU476720[8], [1][8]; ***Mycopteris leucosticta***, Ecuador, *Moran 7590* (QCA), GU476810, GU476921, –, –, GU476719, [8]; ***Mycopteris longicaulis*** (Sundue & M.Kessler) Sundue, Bolivia, *Jimenez 373* (UC), GU476813, GU476840[8], KM106163[1], –, GU476724[8], [1][8]; ***Mycopteris longipilosa*** Sundue, Ecuador, *Sundue & Martin 1033* (NY), GU476814[8], GU476861[8], KM106164[1], KM106008[1], GU476726[8], [1][8]; ***Mycopteris longipilosa***, Ecuador, *Sundue & Martin 1037* (NY), –, GU476862, –, –, GU476725, [8]; ***Mycopteris praeceps*** (Sundue & M.Kessler) Sundue, Bolivia, *Jimenez 2173* (UC), GU476817[8], GU476839[8], KM106165[1], –, GU476734[8], [1][8]; ***Mycopteris semihirsuta*** (Klotzsch) Sundue, Bolivia, *Jimenez 1238* (LPB), GU476786, GU476831, –, –, GU476678, [8]; ***Mycopteris semihirsuta***, Bolivia, *Nuñez 524* (MO), GU476787, GU476913, –, –, –, [8]; ***Mycopteris semihirsuta***, Colombia, *Sundue & Vasco 1234* (NY), –, GU476889, –, –, GU476680, [8]; ***Mycopteris semihirsuta***, Colombia, *Sundue & Vasco 1246* (NY), GU476818, GU476894, –, –, GU476735, [8]; ***Mycopteris semihirsuta***, Colombia, *Sundue & Vasco 1313* (NY), GU476788, GU476899, –, –, GU476681, [8]; ***Mycopteris semihirsuta***, Costa Rica, *Moran 8077* (NY), GU476790, GU476923, –, –, GU476684, [8]; ***Mycopteris semihirsuta***, Ecuador, *Lehnert 1144* (NY), GU476789, GU476849, –, –, GU476682, [8]; ***Mycopteris semihirsuta***, Mexico, *Kessler 13508* (NY), GU476791, GU476846, –, –, GU476685, [8]; ***Mycopteris semihirsuta***, Oaxaca, Mexico, *Sundue 3108* (VT), –, –, –, MK319084, MK319033, [10]; ***Mycopteris semihirsuta***, Oaxaca, Mexico, *Sundue 3112* (VT), –, MK319133, –, MK319085, MK319034, [10]; ***Mycopteris semihirsuta***, Peru, *B. Leon 3655* (USM, UC), AY459509, AY460676, –, –, –, [11]; ***Mycopteris semihirsuta***, Peru, *Lehnert 313* (NY), –, GU476857, –, –, GU476683, [8]; ***Mycopteris subtilis*** (Kunze ex Klotzsch) Sundue, Ecuador, *Lehnert 1396* (UC), GU376643, GU386984, GU387128, GU387210, GU387288, [6]; ***Mycopteris subtilis***, Costa Rica, *M. Moraga & A. Rojas 505* (INB), AY459512, AY460678, –, –, –, [11]; ***Mycopteris subtilis***, Ecuador, *Sundue 1140* (NY), KY711743, KY711916, KY712244, KY712085, KY711569, [2]; ***Mycopteris subtilis***, Ecuador, *Sundue 1142* (NY), –, GU476875, –, –, GU476741, [8]; ***Mycopteris subtilis***, Ecuador, *Sundue & Schuettpelz 1077* (NY), –, GU476865[8], KM106166[1], –, GU476687[8], [1][8]; ***Mycopteris taxifolia*** (L.) Sundue, Brazil, *Labiak 4018* (NY), GU476800[8], GU476914[8], KM106167[1], KM106009[1], GU476699[8], [1][8]; ***Mycopteris taxifolia***, Colombia, *Sundue & Vasco 1215* (NY), –, GU476888, –, –, GU476698, [8]; ***Mycopteris taxifolia***, Ecuador, *Sundue & Werner 1161* (NY, QCA, UC), GU476792, GU476880, –, –, GU476686, [8]; ***Mycopteris zeledoniana*** (Lellinger) Sundue, Costa Rica, *Sundue 1806* (NY), –, GU387011, GU387129, GU387211, –, [6]; ***Mycopteris zeledoniana***, Costa Rica, *Shalisko 259* (IBUG), –, –, –, MK319058, –, [10]; ***Nanogrammitis holophlebia*** (Baker) Parris, Li Bing Zhang, X.M.Zhou & Liang Zhang, Madagascar, *Rouhan & al. 1160* (P), KY711807, KY711982, KY712305, KY712146, KY711631, [2]; ***Nanogrammitis holophlebia***, Madagascar, *Janssen & al. 2514* (P), KY711809, KY711984, –, KY712148, KY711633, [2]; ***Nanogrammitis holophlebia***, Madagascar, *Rakotondrainibe 6933* (P), KY711808, KY711983, KY712306, KY712147, KY711632, [2]; ***Nanogrammitis holophlebia***, Madagascar, *Rouhan & al. 1311* (P), KY711786, KY711961, –, KY712126, KY711611, [2]; ***Nanogrammitis obtusa*** (Willd. ex Kaulf.) Parris, Li Bing Zhang, X.M.Zhou & Liang Zhang, Madagascar, *Rouhan & al. 1212* (P), KY711817, KY711992, KY712314, KY712156, KY711641, [2]; ***Nanogrammitis obtusa***, Madagascar, *Rouhan & al. 230* (P), KY711819, KY711994, –, KY712158, KY711643, [2]; ***Nanogrammitis obtusa***, Reunion, *Janssen & al. 2696* (P), KY711818, KY711993, KY712315, KY712157, KY711642, [2]; ***Nanogrammitis obtusa***, Reunion, *Ranker 1505* (COLO), –, –, –, –, KY711561, [2]; ***Nanogrammitis obtusa***, Reunion, *T. Janssen 2674* (P, REU), –, KF992493, –, –, –, [9]; ***Nanogrammitis pellucidovenosa*** (Bonap.) Parris, Li Bing Zhang, X.M.Zhou & Liang Zhang, Madagascar, *Janssen & al. 2415* (P), KY711820, KY711995, –, KY712159, KY711644, [2]; ***Nanogrammitis pellucidovenosa***, Madagascar, *Janssen & al. 2931* (P), KY711821, KY711996, –, KY712160, KY711645, [2]; ***Nanogrammitis pervillei*** (Mett. ex Kuhn) Parris, i Bing Zhang, X.M.Zhou & Liang Zhang, Seychelles, *Senterre 6128* (P), KY711887, KY712061, KY712379, KY712227, KY711707, [2]; ***Nanogrammitis synsora*** (Baker) Parris, i Bing Zhang, X.M. Zhou & Liang Zhang, Madagascar, *Rouhan & al. 1173* (P), KY711826, KY712002, –, KY712166, KY711651, [2]; ***Nanogrammitis synsora***, Madagascar, *Rakotondrainibe 6932* (P), KY711830, KY712006, –, KY712170, KY711655, [2]; ***Nanogrammitis synsora***, Madagascar, *Rouhan & al. 1316* (P), KY711829, KY712005, –, KY712169, KY711654, [2]; ***Notogrammitis angustifolia*** (Jacq.) Parris, Australia, *Lendemer 30006* (NY), KM218824, KM218770, KM106168, KM106010, KM106074, [1]; ***Notogrammitis angustifolia***, Amsterdam Island, *Jolinon 1089* (P), KY711907, KY712075, KY712400, KY712234, KY711735, [2]; ***Notogrammitis angustifolia***, Harihari, New Zealand, *Perrie & Shepherd 4112* (WELT), JX499251, JQ904093, –, –, JQ904114, [5]; ***Notogrammitis angustifolia***, Lake Rotopounamu, New Zealand, *Parris 12423* (AK), JX499252, JQ904083, –, –, JQ904113, [5]; ***Notogrammitis billardierei*** (Willd.) Parris, New Zealand, *Perrie & Shepherd 4038* (WELT), JX499244, JQ904089, –, –, JQ904101, [5]; ***Notogrammitis billardierei***, Australia, *Sundue s.n.* (VT), –, KM218755, –, KM106012, KM106075, [1]; ***Notogrammitis billardierei***, Lake Rotopounamu, New Zealand, *Parris 12421* (AK), AY459469[11], JQ904094[5], –, KM106011[1], JQ904102[11], [1][5][11]; ***Notogrammitis billardierei***, New Zealand, *Allan Herbarium CHR 630315* (CHR), –, –, –, –, KF591325, [30]; ***Notogrammitis billardierei***, Tasmania, Australia, *Brownsey TAS1* (WELT), JX499250, JQ904096, –, –, JQ904103, [5]; ***Notogrammitis ciliata*** (Colenso) Parris, New Zealand, *A.R. Smith 2615* (UC), AY459470, AY460638, –, –, –, [11]; ***Notogrammitis ciliata***, Anaura Bay, New Zealand, *Perrie & Shepherd 4421* (WELT), –, –, –, –, JQ904108, [5]; ***Notogrammitis ciliata***, Charleston, New Zealand, *Parris 12657* (AK), JX499248, JQ904095, –, –, JQ904106, [5]; ***Notogrammitis ciliata***, Dannevirke, New Zealand, *Perrie & Shepherd 4477* (WELT), –, –, –, –, JQ904109, [5]; ***Notogrammitis ciliata***, Hunua Ranges, New Zealand, *Jane s.n.* (AK), JX499249, JQ904097, –, –, JQ904105, [5]; ***Notogrammitis ciliata***, Kerikeri, New Zealand, *Parris 12630* (AK), JX499247, JQ904078, –, –, JQ904104, [5]; ***Notogrammitis ciliata***, Palmerston, New Zealand, *Perrie & Shepherd 3976* (WELT), JX499243, JQ904081, –, –, JQ904107, [5]; ***Notogrammitis crassior*** (Kirk) Parris, Kerguelen Archipelago, *Quetel & Chambrin 2* (P), KY711744, KY711918, KY712246, KY712086, KY711571, [2]; ***Notogrammitis crassior***, Australia, *Weber 13772* (COLO), AY459478, AY460646, –, –, –, [11]; ***Notogrammitis crassior***, Cass, New Zealand, *Perrie 3742* (WELT), JX499241, JQ904077, –, –, JQ904115, [5]; ***Notogrammitis crassior***, Chile, *C. Taylor 6072* (UC), AY459479, AY460647, –, –, –, [11]; ***Notogrammitis crassior***, Falkland Islands, *Corner 333* (P), –, –, –, –, KY711734, [2]; ***Notogrammitis crassior***, Fiordland, New Zealand, *Perrie & Shepherd 4065* (WELT), –, JQ904090, –, –, JQ904116, [5]; ***Notogrammitis crassior***, Kerguelen Archipelago, *Boulangeat 11* (P), KY711810, KY711985, KY712307, KY712149, KY711634, [2]; ***Notogrammitis crassior***, Kerguelen Archipelago, *Boulangeat 19* (P), KY711811, KY711986, KY712308, KY712150, KY711635, [2]; ***Notogrammitis crassior***, Marion Island, South Africa, Unknown, –, MN854685, –, –, –, [29]; ***Notogrammitis crassior***, South Africa, *Huntley 721* (P), –, –, –, –, KY711733, [2]; ***Notogrammitis givenii*** (Parris) Parris, Maruia, New Zealand, *Perrie & Shepherd 3842* (WELT), JX499242, JQ904079, –, –, –, [5]; ***Notogrammitis givenii***, Fiordland, New Zealand, *Sneddon s.n.* (WELT), –, JQ904092, –, –, JQ904112, [5]; ***Notogrammitis givenii***, Unknown, *LRP 6325* (WELT), –, –, –, –, JQ904111, [5]; ***Notogrammitis heterophylla*** (Labill.) Parris, New Zealand, *A.R. Smith 2614* (UC), AY459461, AY460628, –, –, –, [11]; ***Notogrammitis heterophylla***, Fox, New Zealand, *Perrie & Shepherd 4089* (WELT), JX499237, JQ904091, –, –, JQ904099, [5]; ***Notogrammitis heterophylla***, New Zealand, *Allan Herbarium CHR 630373* (CHR), –, –, –, –, KF591319, [30]; ***Notogrammitis heterophylla***, New Zealand, *Allan Herbarium CHR 630374* (CHR), –, –, –, –, KF591335, [30]; ***Notogrammitis heterophylla***, New Zealand, *B. Parris 12419* (AK), –, MT657587, –, –, –, [4]; ***Notogrammitis heterophylla***, New Zealand, *Parris 12419* (AK), AY459462, AY460629, –, –, JQ904100, [11]; ***Notogrammitis patagonica*** (C.Chr.) Parris, Unknown, *LRP 3947* (WELT), –, JQ904087, –, –, –, [5]; ***Notogrammitis patagonica***, Ruahine, New Zealand, *Perrie & al. 4760* (WELT), JX499246, JQ904088, –, –, JQ904075, [5]; ***Notogrammitis pseudociliata*** (Parris) Parris, Waipoua, New Zealand, *Parris 12420* (AK), JX499245, JQ904080, –, –, –, [5]; ***Notogrammitis pseudociliata***, Mount Somers, New Zealand, *Perrie & Shepherd 3947* (WELT), AY459477, JQ904098, –, –, JQ904074, [5]; ***Notogrammitis pseudociliata***, New Zealand, *B. Parris 12420* (AK), –, MT657605, –, –, –, [4]; ***Notogrammitis rawlingsii*** (Parris) Parris, Warkworth, New Zealand, *Young s.n.* (AK), JX499240, JQ904085, –, –, JQ904119, [5]; ***Notogrammitis rawlingsii***, Warkworth, New Zealand, *Young s.n.* (AK), –, JQ904086, –, –, JQ904120, [5]; ***Notogrammitis rigida*** (Hombron) Parris, Fiordland, New Zealand, *Rance s.n.* (WELT P022031), JX499238, JQ904082, –, –, JQ904121, [5]; ***Oreogrammitis adspersa*** (Blume) Parris, Sabah, Malaysia,

Appendix 2. Continued.

Sundue 2233 (VT), –, KM218808, KM106171, KM106013, KM106076, [1]; ***Oreogrammitis adspersa***, Taiwan Island, *R. Knapp 4532* (P), –, OQ708519, OQ717212, –, –, **this study**; ***Oreogrammitis baldwinii*** (Baker) Parris, Hawaii, *K.R. Wood 10575* (PTBG), EF178633, EF178616, –, –, EF178649, [16]; ***Oreogrammitis baldwinii***, Hawaii, *K.R. Wood 17977* (PTBG), –, MT657588, –, –, –, [4]; ***Oreogrammitis beddomeana*** (Alderw.) Parris, Sundue, Li Bing Zhang & X.M.Zhou, Taiwan Island, *R. Knapp 4527* (P), OQ702725, OQ708541, OQ717273, –, –, **this study**; ***Oreogrammitis beddomeana***, Sabah, Malaysia, *T.A. Ranker & S.K. Klimas 2179* (BORH, SAN, SNP, COLO), EF178636, EF178619, –, –, EF178652, [16]; ***Oreogrammitis beddomeana***, Taiwan Island, *R. Knapp 4531* (P), –, OQ708542, OQ717271, –, –, **this study**; ***Oreogrammitis caespitosa*** (Blume) Parris, Taiwan Island, *R. Knapp 3599* (P), OQ702714, OQ708517, OQ717258, –, –, **this study**; ***Oreogrammitis cheesemanii*** (Parris) Parris & Sundue, Cook Islands, *John Game 8553* (UC), KM218861, –, KM106183, –, KM106087, [1]; ***Oreogrammitis conformis*** (Brack.) Parris, Fiji, *B. Parris 12025* (AK), –, MT657610, –, –, –, [4]; ***Oreogrammitis congener*** (Blume) Parris, Lam Dong, Vietnam, *L.-B. Zhang & al. 8612* (CDBI, MO, PHH), OQ702717, OQ708609, OQ717225, OQ717072, OQ717137, **this study**; ***Oreogrammitis congener***, Peninsular Malaysia, *Parris 12782* (AK), KM218845, KM218762, KM106172, KM106014, KY711570, [1]; ***Oreogrammitis congener***, Malaysia, *J.H. Beaman & al. 8662* (US), –, –, –, KM105991, –, [1]; ***Oreogrammitis congener***, Malaysia, *Ranker 2126* (BORH), –, –, –, –, KM106077, [1]; ***Oreogrammitis congener***, Sabah, Malaysia, *Ranker & Klimas 2126* (COLO), –, –, –, KY712081, –, [2]; ***Oreogrammitis congener***, Sabah, Malaysia, *T.A. Ranker 2126 & S.K. Klimas* (BORH, SAN, SNP, COLO), EF178634, EF178617, –, –, EF178650, [16]; ***Oreogrammitis congener***, Taiwan Island, *R. Knapp 3633* (P), OQ702667, OQ708596, –, –, OQ717129, **this study**; ***Oreogrammitis conjunctisora*** (Baker) Parris & Sundue, Papua New Guinea, *Ranker 1758 & Trapp* (COLO, UC), AY459514, AY460680, –, –, –, [11]; ***Oreogrammitis curtisii*** (Baker) Parris & Sundue, Taiwan Island, *R. Knapp 4243* (P), OQ702735, OQ708537, OQ717234, –, –, **this study**; ***Oreogrammitis curtisii***, Philippines, *Parris 12836* (K), –, KM218758, KM106193, KM106034, KM106093, [1]; ***Oreogrammitis dolichosora*** (Copel.) Parris, Sabah, Malaysia, *T.A. Ranker 2183 & S.K. Klimas* (BORH, SNP), EF178635, EF178618, –, –, –, [16]; ***Oreogrammitis dorsipila*** (Christ) Parris, Kagoshima, Japan, *764128* (TNS), –, AB575257, –, –, –, [25]; ***Oreogrammitis fenicis*** (Copel.) Parris, Taiwan Island, *R. Knapp 4073* (P), OQ702686, OQ708607, OQ717223, OQ717068, OQ717130, **this study**; ***Oreogrammitis forbesiana*** (W.H.Wagner) Parris, Hawaii, *K.R. Wood 17162* (PTBG), –, MT657589, –, –, –, [4]; ***Oreogrammitis forbesiana***, Hawaii, *Ranker 1321* (COLO), AY459472, AY460640, –, –, EF178651, [11]; ***Oreogrammitis graniticola*** Parris, Sabah, Malaysia, *Sundue 2212* (VT), KM218846, KM218757, –, KM106015, KM106078, [1]; ***Oreogrammitis halconensis*** (Copel.) Parris & Sundue, Sabah, Malaysia, *Sundue 2226* (VT), KM218844, –, KM106194, KM106035, KM106094, [1]; ***Oreogrammitis hirtelloides*** (Copel.) Parris & Sundue, Vanuatu, *Rouhan & al. 615* (P), KY711841, KY712017, KY712333, KY712181, KY711666, [2]; ***Oreogrammitis hirtelloides***, Fiji, *J. Game 95-81* (UC), –, AY460641, –, –, –, [11]; ***Oreogrammitis hirtelloides***, Vanuatu, *Rouhan & al. 663* (P), KY711842, KY712018, KY712334, KY712182, KY711667, [2]; ***Oreogrammitis holttumii*** (Copel.) Parris & Sundue, Sabah, Malaysia, *Sundue 2208* (VT), KM218856, KM218771, KM106184, KM106028, –, [1]; ***Oreogrammitis holttumii***, Sabah, Malaysia, *Ranker 2175* (BORH, SAN, SNP, COLO), EF178638, EF178621, –, –, EF178654, [16]; ***Oreogrammitis hookeri*** (Brack.) Parris, Hawaii, *Ranker 1116* (COLO), AY459473, AY460642, –, –, EF178655, [11]; ***Oreogrammitis hookeri***, Hawaii, *K.R. Wood 17901* (PTBG), –, MT657590, –, –, –, [4]; ***Oreogrammitis jagoriana*** (Mett. ex Kuhn) Parris & Sundue, Sabah, Malaysia, *T.A. Ranker 2152 & S.K. Klimas* (SNP), EF178639, EF178622, –, –, EF178656, [16]; ***Oreogrammitis*** cf. ***jagoriana***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11000* (KUN, CDBI), OQ702734, OQ708575, OQ717207, –, OQ717128, **this study**; ***Oreogrammitis kinabaluensis*** (Copel.) Parris & Sundue, Sabah, Malaysia, *Sundue 2211* (VT), KM218855, KM218773, KM106185, –, KM106088, [1]; ***Oreogrammitis knutsfordiana*** (Baker) Parris, Fiji, *J. Game 95-81* (UC), AY459474, AY362342, –, –, EF178657, [11]; ***Oreogrammitis knutsfordiana***, Sabah, Malaysia, *T.A. Ranker 2176 & S.K. Klimas* (BORH, SAN, SNP, COLO), EF178640, EF178623, –, –, EF178658, [16]; ***Oreogrammitis ligulata*** (Baker) Parris & Sundue, Huahine, French Polynesia, *Nitta 3975* (UC), –, KY099804, –, –, –, [14]; ***Oreogrammitis ligulata***, Huahine, French Polynesia, *K.R. Wood 11047* (PTBG), –, MT657606, –, –, –, [4]; ***Oreogrammitis locellata*** (Baker) Parris, Papua New Guinea, *M.S. Clemens 12380* (UC), –, MT657592, –, –, –, [4]; ***Oreogrammitis locellata***, Papua New Guinea, *M.S. Clemens 12380* (UC), –, KM218763, KM106173, –, KM106079, [1]; ***Oreogrammitis locellata***, Sabah, Malaysia, *Ranker 2228* (COLO), –, –, KM106174, –, –, [1]; ***Oreogrammitis medialis*** (Baker) Parris, Sri Lanka, *Ballard 1082* (P), –, –, KY712397, –, KY711730, [2]; ***Oreogrammitis monticola*** (Sledge) Parris, Savaii, Samoa, *K.R. Wood 17022* (PTBG), –, MT657591, –, –, –, [4]; ***Oreogrammitis multifolia*** (Copel.) Parris & Sundue, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11034* (KUN, CDBI, BCU, MO, PYU, XTBG), OQ702736, OQ708584, OQ717285, –, OQ717131, **this study**; ***Oreogrammitis multifolia***, Malaysia, *Jaman 6000* (UC), –, –, AY362689, –, –, [24]; ***Oreogrammitis multifolia***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11076* (KUN, CDBI, BCU, MO, PYU, XTBG), OQ702715, OQ708564, OQ717284, –, OQ717132, **this study**; ***Oreogrammitis multifolia***, Thailand, *M. Tagawa, K. Iwatsuki, & N. Fukuoka T4797* (US), –, KM218772, KM106146, –, KM106066, [1]; ***Oreogrammitis neocaledonica*** (Copel.) Parris, New Caledonia, *Munzinger 1721* (P), KY711843, KY712019, KY712335, KY712183, KY711668, [2]; ***Oreogrammitis neocaledonica***, New Caledonia, *Lowry 6815* (P), KY711904, –, KY712396, –, KY711729, [2]; ***Oreogrammitis nuda*** (Tagawa) X.M.Zhou, Liang Zhang, Jian Jun Yang & Ralf Knapp, Taiwan Island, *R. Knapp 4528* (P), OQ702733, OQ708563, OQ717203, –, –, **this study**; ***Oreogrammitis orientalis*** (T.C.Hsu) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Ralf Knapp, Taiwan Island, *R. Knapp 3964* (P), OQ702730, OQ708527, OQ717274, –, –, **this study**; ***Oreogrammitis padangensis*** (Baker) Parris, Sabah, Malaysia, *T.A. Ranker 2159a & S.K. Klimas* (BORH, SAN, SNP, COLO), EF178642, EF178625, –, –, EF178660, [16]; ***Oreogrammitis parva*** (Brause) Parris & Sundue, Papua New Guinea, *Ranker 1763a & Trapp* (COLO, UC), AY459476, AY460644, –, –, –, [11]; ***Oreogrammitis raiateensis*** (J.W.Moore) Parris, Moorea, *Nitta 681* (UC), –, KY099840, –, –, –, [14]; ***Oreogrammitis reinwardtii*** (Blume) Parris, Taiwan Island, *R. Knapp 4536* (P), –, OQ708538, OQ717241, –, –, **this study**; ***Oreogrammitis reinwardtii***, Gunung Gede, Indonesia, *IN108* (TI), –, AB232398, –, –, –, [31]; ***Oreogrammitis reinwardtii***, Java, Indonesia, *R. Wei & al. 523*, MW876347, MW876347, –, –, –, [26]; ***Oreogrammitis reinwardtii***, Khanh Hoa, Vietnam, *L.-B. Zhang & al. 8668* (CDBI, MO, PHH), OQ702738, OQ708579, OQ717226, OQ717070, OQ717134, **this study**; ***Oreogrammitis reinwardtii***, Lam Dong, Vietnam, *L.-B. Zhang & al. 8547* (CDBI, MO, PHH), OQ702737, OQ708591, OQ717231, OQ717069, OQ717133, **this study**; ***Oreogrammitis reinwardtii***, Taiwan Island, *R. Knapp 4539* (P), –, OQ708520, OQ717242, –, –, **this study**; ***Oreogrammitis reinwardtioides*** (Copel.) Parris, Sabah, Malaysia, *T.A. Ranker 2160 & S.K. Klimas* (BORH, SAN, SNP, COLO), EF178643, EF178626, –, –, EF178661, [16]; ***Oreogrammitis reinwardtioides***, Sabah, Malaysia, *Sundue 2202* (VT), KM218847, KM218756, –, KM106016, KM106080, [1]; ***Oreogrammitis scleroglossoides*** (Copel.) Parris, Pohnpei, Micronesia, *D.H. Lorence 9597b* (PTBG), –, MT657612, –, –, –, [4]; ***Oreogrammitis setigera*** (Blume) T.C.Hsu, Taiwan Island, *R. Knapp 3325* (P), –, –, OQ717280, –, –, **this study**; ***Oreogrammitis setigera***, Malaysia, *Karger 813* (Z), –, KM218759, KM106186, –, KM106089, [1]; ***Oreogrammitis setigera***, Taiwan Island, *R. Knapp 3473* (P), OQ702701, OQ708521, OQ717281, –, –, **this study**; ***Oreogrammitis*** cf. ***sinohirtella***, Cao Bang, Vietnam, *L.-B. Zhang & al. 6811* (CDBI, MO, VNMN), –, OQ708518, OQ717277, –, –, **this study**; ***Oreogrammitis* sp.**, Hainan Island, *Wei Q. & al. FB819* (KUN), MT130563, MT130563, –, –, –, [27]; ***Oreogrammitis* sp. 2**, Guangxi, China, *J.S. Kang 1201-11*, MW876345, MW876345, –, –, –, [26]; ***Oreogrammitis* sp. 2**, Jiangxi, China, *H.-M. Liu B294*, MW876346, MW876346, –, –, –, [26]; ***Oreogrammitis* sp. 3**, Hainan Island, *Z.-L. Liang 743* (PYU), OQ702718, OQ708547, OQ717239, OQ717074, OQ717139, **this study**; ***Oreogrammitis* sp. 3**, Hainan Island, *Z.-L. Liang 744* (PYU), OQ702668, –, OQ717205, OQ717075, OQ717140, **this study**; ***Oreogrammitis* sp. 3**, Hainan Island, *Z.-L. Liang 746* (PYU), OQ702702, OQ708546, OQ717195, OQ717073, OQ717138, **this study**; ***Oreogrammitis* sp. 3**, Hainan Island, *Z.-L. Liang 797* (PYU), OQ702719, OQ708548, OQ717199, OQ717076, OQ717141, **this study**; ***Oreogrammitis* sp. 3**, Hainan Island, *Z.-L. Liang 798* (PYU), OQ702720, OQ708549, OQ717200, OQ717077, OQ717142, **this study**; ***Oreogrammitis* sp. 3**, Hainan Island, *Z.-L. Liang 799* (PYU), OQ702722, OQ708556, OQ717209, OQ717079, OQ717144, **this study**; ***Oreogrammitis* sp. 3**, Hainan Island, *Z.-L. Liang 800* (PYU), OQ702721, OQ708550, OQ717196, OQ717078, OQ717143, **this study**; ***Oreogrammitis* sp. 3**, Hainan Island, *Z.-L. Liang HF0718* (PYU), OQ702695, OQ708551, OQ717215, OQ717080, OQ717145, **this study**; ***Oreogrammitis* sp. 4**, Hainan Island, *Z.-L. Liang 994* (PYU), OQ702723, OQ708552, OQ717194, OQ717081, OQ717146, **this study**; ***Oreogrammitis* sp. 5**, Sabah, Malaysia, *Sundue 2223* (VT), –, –, –, KM106045, –, [1]; ***Oreogrammitis* sp. 6**, Vanuatu, *Rouhan & al. 614* (P), KY711837, KY712013, KY712329, KY712177, KY711662, [2]; ***Oreogrammitis* sp. 7**, Taiwan Island, *R. Knapp 4530* (P), –, OQ708528, OQ717208, –, –, **this study**; ***Oreogrammitis* sp. 8**, Sabah, Malaysia, *T.A. Ranker & S.K. Klimas 2181* (BORH, SAN, SNP, COLO), EF178637, EF178620, –, –, EF178653, [16]; ***Oreogrammitis subevenosa*** (Baker) X.M.Zhou, Liang Zhang, Jian Jun Yang & Ralf Knapp, Lam Dong,

Appendix 2. Continued.

Vietnam, *L.-B. Zhang & al. 8543* (CDBI, MO, PHH), OQ702685, OQ708587, OQ717186, –, –, **this study**; ***Oreogrammitis subspathulata*** (Brack.) Parris, Tahiti, French Polynesia, *Nitta 3187* (UC, GH), –, KY099841, –, –, –, [14]; ***Oreogrammitis taiwanensis*** (Parris & Ralf Knapp) T.C.Hsu, Taiwan Island, *R. Knapp 3971* (P), OQ702687, OQ708608, OQ717198, –, –, **this study**; ***Oreogrammitis tenuisecta*** (Blume) T.C.Hsu, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11037* (KUN, CDBI, BCU, MO, PYU), OQ702716, OQ708565, OQ717237, –, OQ717135, **this study**; ***Oreogrammitis tenuisecta***, Pahang, Malaysia, *B.C. Stone 13773* (MO), OQ702739 [OQ968265], OQ708617 [OQ968265], OQ717286 [OQ968265], OQ717071 [OQ968265], OQ717136 [OQ968265], **this study**; ***Oreogrammitis tenuisecta***, Savaii, Samoa, *K.R. Wood 16991* (PTBG), –, MT657593, –, –, –, [4]; ***Oreogrammitis tenuisecta***, Taiwan Island, *Chiou 97-09-12-02* (COLO, TAIF, UC), –, AY362346[11], AY362693[24], –, –, [11][24]; ***Oreogrammitis tuyamae*** (H.Ohba) Parris, Tokyo, Japan, *Takayama 07062194* (TNS), –, AB575258, –, –, –, [25]; ***Oreogrammitis uapensis*** (E.D.Br.) Parris, Marquesas Islands, *K.R. Wood 10825* (US), –, KM218787, –, KM105995, KM106070, [1]; ***Oreogrammitis uapensis***, French Polynesia, *1936824* (US), –, MT216073, –, –, –, [17]; ***Oreogrammitis uapensis***, French Polynesia, *Wood17618* (PTBG), –, MT216074, –, –, –, [17]; ***Oreogrammitis uapensis***, Marquesas Islands, *Schuettpelz 1877* (US), –, MT216075, –, –, –, [17]; ***Oreogrammitis uapensis***, Marquesas Islands, *Schuettpelz 1892* (US), –, MT216076, –, –, –, [17]; ***Oreogrammitis ultramaficola*** Parris, Sabah, Malaysia, *Ranker 2153* (COLO), KM218841, KM218754, KM106151, –, KM106071, [1]; ***Oreogrammitis wurunuran*** (Parris) Parris, Australia, *Kessler 14307* (VT), KM218842, KM218760, KM106175, KM106017, –, [1]; ***Oreogrammitis wurunuran***, Australia, *Kessler 14251* (VT), KM218843, KM218761, KM106176, KM106018, –, [1]; ***Oxygrammitis denticulata*** (Blume) Parris, Malaysia, *Ranker 2113* (BORH, SAN, SNP, COLO), JF514081, JF514013, –, –, JF514047, [21]; ***Parrisia gilpinae*** (Baker) Shalisko & Sundue, Madagascar, *Kessler 12770* (UC), –, KY711914, KY712241, KY712084, KY711566, [2]; ***Parrisia gilpinae***, Madagascar, *Janssen & al. 2925* (P), KY711790, KY711965, KY712289, KY712130, KY711615, [2]; ***Parrisia gilpinae***, Madagascar, *Rakotondrainibe 6936* (P), KY711789, KY711964, KY712288, KY712129, KY711614, [2]; ***Parrisia gilpinae***, Madagascar, *Rouhan & al. 1145* (P), KY711828, KY712004, KY712322, KY712168, KY711653, [2]; ***Parrisia gilpinae***, Madagascar, *Rouhan & al. 1227* (P), KY711787, KY711962, KY712286, KY712127, KY711612, [2]; ***Parrisia gilpinae***, Madagascar, *Rouhan & al. 1343* (P), KY711788, KY711963, KY712287, KY712128, KY711613, [2]; ***Parrisia gilpinae***, Madagascar, *Rouhan & al. 1381* (P), KY711791, KY711966, KY712290, KY712131, KY711616, [2]; ***Parrisia parietina*** (Klotzsch) Shalisko & Sundue, Mexico, *Sundue 3097* (VT), –, –, KY712237, –, KY711559, [2]; ***Parrisia parietina***, Ecuador, *Schuettpelz 230* (DUKE), EF463494, EF463248, –, –, –, [32]; ***Parrisia parietina***, Reunion, *S. Hennequin R104* (BM, REU), –, KF992494, –, –, –, [9]; ***Prosaptia alata*** Ching, Kosrae Island, Micronesia, *T. Flynn 6004* (UC, AD, BISH, PTBG, US), AY459493[11], AY460660[11], –, KM106019[1], KM106081[1], [1][11]; ***Prosaptia alata***, Huahine, French Polynesia, *K.R. Wood 11027* (PTBG), –, MT657596, –, –, –, [4]; ***Prosaptia alata***, Kosrae Island, Micronesia, *D.H. Lorence 10154* (PTBG), –, MT657595, –, –, –, [4]; ***Prosaptia alata***, Savaii, Samoa, *K.R. Wood 17006* (PTBG), –, MT657600, –, –, –, [4]; ***Prosaptia alata***, Upolu, Samoa, *K.R. Wood 16897* (PTBG), –, MT657599, –, –, –, [4]; ***Prosaptia barathrophylla*** (Baker) M.G.Price, Dak Lak, Vietnam, *L.-B. Zhang & al. 8945* (CDBI, MO, PHH), OQ702696, OQ708597, OQ717238, OQ717085, OQ717155, **this study**; ***Prosaptia barathrophylla***, Ha Giang, Vietnam, *L.-B. Zhang & al. 6881* (CDBI, MO, VNMN), –, OQ708539, OQ717254, –, –, **this study**; ***Prosaptia barathrophylla***, Guangxi, China, *X.-C. Zhang 6038* (PE), MW876356, MW876356, –, –, –, [26]; ***Prosaptia barathrophylla***, Vinh Phuc, Vietnam, *L.-B. Zhang & al. 6446* (CDBI, MO, VNMN), –, OQ708523, OQ717240, –, –, **this study**; ***Prosaptia celebica*** (Blume) Tagawa & K.Iwats., Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11039* (KUN, CDBI, BCU, MO, PYU) OQ702669, OQ708567, OQ717251, –, OQ717156, **this study**; ***Prosaptia celebica***, Taiwan Island, *R. Knapp 3331* (P), OQ702740, OQ708557, OQ717266, –, –, **this study**; ***Prosaptia celebica***, Philippines, *Parris 12835* (K), KM218849, KM218786, KM106178, KM106021, –, [1]; ***Prosaptia contigua*** (G.Forst.) C.Presl, New Caledonia, *Munzinger & McPherson 652* (MO), OQ702670, OQ708610, OQ717219, OQ717082, OQ717147, **this study**; ***Prosaptia contigua***, Aneityum, Vanuatu, *G.M. Plunkett 4087* (NYBG), –, MT657601, –, –, –, [4]; ***Prosaptia contigua***, Australia, *Sundue 2740* (VT), KM218851, KM218767, KM106180, KM106025, –, [1]; ***Prosaptia contigua***, French Polynesia, *Wood17704* (PTBG), –, MT216093, –, –, –, [17]; ***Prosaptia contigua***, Marquesas Islands, *Schuettpelz 1923* (US), –, MT216094, –, –, –, [17]; ***Prosaptia contigua***, Marquesas Islands, *Schuettpelz 1925* (US), –, MT216095, –, –, –, [17]; ***Prosaptia contigua***, Marquesas Islands, *Wood17729* (PTBG), –, MT216096, –, –, –, [17]; ***Prosaptia contigua***, Moorea, *Nitta 310* (UC), –, KY099849, –, –, –, [14]; ***Prosaptia contigua***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 10974* (KUN, CDBI, BCU, MO, PYU, XTBG), OQ702705, –, OQ717252, –, OQ717157, **this study**; ***Prosaptia contigua***, Nakhon Si Thammarat, Thailand, *L.-B Zhang & al. 11078* (KUN, CDBI, BCU, MO, PYU), OQ702661, OQ708576, –, –, OQ717158, **this study**; ***Prosaptia contigua***, New Caledonia, *Munzinger 1271* (P), KY711838, KY712014, KY712330, KY712178, KY711663, [2]; ***Prosaptia contigua***, Sabah, Malaysia, *Sundue 2219* (VT), KM218850, KM218765, –, KM106022, KM106083, [1]; ***Prosaptia contigua***, Taiwan Island, *Chiou 97-09-12-05* (TAIF, COLO, UC), AY459494[24], AY362345[24], AY362692[24], –, EF178663[11], [11][24]; ***Prosaptia contigua***, Taiwan Island, *R. Knapp 3464* (P), OQ702704, –, OQ717263, –, OQ717149, **this study**; ***Prosaptia contigua***, Taiwan Island, *R. Knapp 3464A* (P), OQ702742, OQ708530, OQ717262, –, OQ717151, **this study**; ***Prosaptia contigua***, Taiwan Island, *R. Knapp 3464B* (P), OQ702741, OQ708529, OQ717260, –, OQ717150, **this study**; ***Prosaptia contigua***, Taiwan Island, *R. Knapp 3476* (P), OQ702703, OQ708566, OQ717243, –, OQ717148, **this study**; ***Prosaptia contigua***, Taiwan Island, *R. Knapp 3601* (P), OQ702743, OQ708531, OQ717247, –, OQ717152, **this study**; ***Prosaptia contigua***, Tanna, Vanuatu, *G.M. Plunkett 2860* (NYBG), –, MT657602, –, –, –, [4]; ***Prosaptia contigua***, Tanna, Vanuatu, *G.M. Plunkett 3061* (NYBG), –, MT657603, –, –, –, [4]; ***Prosaptia contigua***, Upolu, Samoa, *K.R. Wood 16856* (PTBG), –, MT657597, –, –, –, [4]; ***Prosaptia contigua***, Vanuatu, *Rouhan & al. 669* (P), KY711839, KY712015, KY712331, KY712179, KY711664, [2]; ***Prosaptia davalliacea*** (F.Muell. & Baker) Copel., Sabah, Malaysia, *Sundue 2210* (VT), KM218852, KM218798, KM106179, KM106023, KM106084, [1]; ***Prosaptia formosana*** (Hayata) T.C.Hsu, Taiwan Island, *R. Knapp 3475* (P), OQ702745, OQ708568, OQ717181, –, OQ717159, **this study**; ***Prosaptia formosana***, Taiwan Island, *R. Knapp 3328* (P), OQ702746, OQ708522, OQ717244, –, OQ717161, **this study**; ***Prosaptia formosana***, Taiwan Island, *R. Knapp 3465* (P), OQ702706, OQ708532, OQ717217, –, OQ717160, **this study**; ***Prosaptia kanashiroi*** (Hayata) Nakai, Okinawa, Japan, *759271* (TNS), –, AB575253, –, –, –, [25]; ***Prosaptia maidenii*** (Watts) Parris, Australia, *Kessler 14243* (VT), –, KM218766, –, KM106024, –, [1]; ***Prosaptia nutans*** (Blume) Mett., Taiwan Island, *R. Knapp 3424* (P), OQ702750, OQ708524, OQ717268, –, –, **this study**; ***Prosaptia nutans***, Papua New Guinea, *Ranker 1765 & Trapp* (COLO, UC), AY459464, AY460631, –, –, –, [11]; ***Prosaptia nutans***, Taiwan Island, *R. Knapp 3606* (P), OQ702751, OQ708525, OQ717269, –, –, **this study**; ***Prosaptia obliquata*** (Blume) Mett., Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 10955* (KUN, CDBI, BCU, MO, PYU, XTBG), OQ702747, OQ708569, OQ717249, –, OQ717162, **this study**; ***Prosaptia obliquata***, Taiwan Island, *R. Knapp 3474* (P), OQ702744, OQ708558, OQ717267, –, –, **this study**; ***Prosaptia obliquata***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11057* (KUN, CDBI, BCU, MO, PYU, XTBG), OQ702700, OQ708553, OQ717245, –, OQ717163, **this study**; ***Prosaptia obliquata***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11070* (KUN, CDBI, BCU, MO, PYU, XTBG), OQ702671, OQ708540, OQ717255, –, OQ717165, **this study**; ***Prosaptia obliquata***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11074* (KUN, CDBI, BCU, MO, PYU, XTBG), OQ702689, OQ708577, OQ717253, –, OQ717164, **this study**; ***Prosaptia obliquata***, Philippines, *Karger 166* (Z), KM218854, KM218768, KM106181, KM106026, KM106085, [1]; ***Prosaptia obliquata***, Sulawesi, Indonesia, *R.Wei 246*, MW876357, MW876357, –, –, –, [26]; ***Prosaptia obliquata***, Taiwan Island, *Chiou 97-09-12-04* (TAIF, COLO, UC), AY459495, AY460661, –, –, –, [11]; ***Prosaptia obliquata***, Thailand, *Larsen 33479* (P), KY711894, KY712067, KY712387, KY712230, KY711716, [2]; ***Prosaptia palauensis*** Hosok., Palau, *Rondeau & Rodda 93-011 &* (UC), –, AY460662[11], –, KM106027[1], –, [1][11]; ***Prosaptia palauensis***, Babeldaob, Palau, *S. Perlman 20781* (PTBG), –, MT657604, –, –, –, [4]; ***Prosaptia pectinata*** T.Moore, Taiwan Island, *R. Knapp 3326* (P), OQ702748, –, OQ717270, –, –, **this study**; ***Prosaptia pectinata***, Dak Lak, Vietnam, *L.-B. Zhang & al. 8905* (CDBI, MO, PHH), OQ702692, OQ708514, OQ717264, –, OQ717169, **this study**; ***Prosaptia pectinata***, Lam Dong, Vietnam, *L.-B. Zhang & al. 8454* (CDBI, MO, PHH), OQ702690, OQ708585, OQ717228, OQ717086, OQ717166, **this study**; ***Prosaptia pectinata***, Lam Dong, Vietnam, *L.-B. Zhang & al. 8509* (CDBI, MO, PHH), OQ702691, OQ708611, OQ717229, OQ717087, OQ717167, **this study**; ***Prosaptia pectinata***, Lam Dong, Vietnam, *L.-B. Zhang & al. 8592* (CDBI, MO, PHH), OQ702707, OQ708589, OQ717235, OQ717088, OQ717168, **this study**; ***Prosaptia pectinata***, Vietnam, *Averyanov 3376* (P), KY711893, –, –, –, KY711715, [2]; ***Prosaptia pinnatifida*** C.Presl, Philippines, *Karger 608* (Z), KM218848, KM218764, KM106177, KM106020, KM106082, [1]; ***Prosaptia pubipes*** Copel., Fiji, *J. Game 95-65* (UC), AY459496[11], AY460663[11], –, –, EF178664[16], [11][16]; ***Prosaptia rhodocarpa*** (Copel.) Parris, Papua New Guinea,

Appendix 2. Continued.

Ranker 1764 & Trapp (COLO, UC), AY459467, AY460634, –, –, –, [11]; ***Prosaptia samoensis*** (C.Chr.) Parris, Savaii, Samoa, *D.H. Lorence 10630* (PTBG), –, MT657598, –, –, –, [4]; ***Prosaptia serriformis*** Christ, Thailand, *Middleton 5509* (E), KY711910, KY712078, KY712403, KY712235, KY711740, [2]; ***Prosaptia* sp.**, Lam Dong, Vietnam, *L.-B. Zhang & al. 8455* (CDBI, MO, PHH), OQ702708, OQ708598, OQ717224, OQ717089, OQ717170, **this study**; ***Prosaptia* sp.**, Vanuatu, *Rouhan & al. 605* (P), KY711840, KY712016, KY712332, KY712180, KY711665, [2]; ***Prosaptia* sp. 2**, Khanh Hoa, Vietnam, *L.-B. Zhang & al. 8716* (CDBI, MO, PHH), OQ702677, OQ708592, OQ717227, OQ717083, OQ717153, **this study**; ***Prosaptia* sp. 2**, Lam Dong, Vietnam, *L.-B. Zhang & al. 8615* (CDBI, MO, PHH), OQ702688, OQ708588, OQ717236, OQ717084, OQ717154, **this study**; ***Prosaptia subnuda*** (Mett. ex Kuhn) Copel., Moorea, *Nitta 662* (UC), –, KY099850, –, –, –, [14]; ***Prosaptia urceolaris*** (Hayata) Copel., Taiwan Island, *R. Knapp 3498* (P), OQ702749, OQ708533, OQ717265, –, –, **this study**; ***Prosaptia venulosa*** (Blume) M.G.Price, Philippines, *Karger 859* (Z), KM218853, KM218769, KM106182, –, KM106086, [1]; ***Pyrrosia stigmosa*** (Sw.) Ching, Laos, *Wu 2586* (KUN), JX103674, JX103716, JX103758, –, JX103800, [35]; ***Rouhania nanodes*** (Peter) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Liang Zhang, Tanzania, *Janssen & al. 2664* (P), –, KY712000, KY712319, KY712164, KY711649, [2]; ***Rouhania parvula*** (Bory ex Willd.) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Liang Zhang, Reunion, *Rakotondrainibe 6898* (P), KY711769, KY711944, KY712271, KY712111, KY711596, [2]; ***Rouhania parvula***, Comoros, *Pignal & al. 3378* (P), KY711771, KY711946, KY712273, KY712113, KY711598, [2]; ***Rouhania parvula***, Madagascar, *Janssen & al. 2455* (P), KY711770, KY711945, KY712272, KY712112, KY711597, [2]; ***Rouhania parvula***, Reunion, *S. Hennequin R167* (BM, REU), –, KF992462, –, –, –, [9]; ***Rouhania pygmaea*** (Bory ex Willd.) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Liang Zhang, Madagascar, *Rouhan & al. 1313* (P), KY711799, KY711974, KY712297, KY712138, KY711623, [2]; ***Rouhania pygmaea***, Madagascar, *Rakotondrainibe 6983* (P), KY711824, KY711999, KY712318, KY712163, KY711648, [2]; ***Rouhania pygmaea***, Madagascar, *Rouhan & al. 1184* (P), KY711823, KY711998, KY712317, KY712162, KY711647, [2]; ***Rouhania pygmaea***, Seychelles, *Senterre 5986* (P), KY711888, KY712062, KY712380, KY712228, KY711708, [2]; ***Rouhania* sp.**, New Caledonia, *Tronchet 551* (P), KY711780, KY711955, –, –, –, [2]; ***Rouhania zenkeri*** (Hieron.) Li Bing Zhang, X.M.Zhou, Jian Jun Yang & Liang Zhang, Madagascar, *Kessler 12659* (UC), –, KY711913, KY712239, KY712083, –, [2]; ***Rouhania zenkeri***, Madagascar, *Rakotondrainibe 6081* (P), KY711775, KY711950, –, KY712117, KY711602, [2]; ***Rouhania zenkeri***, Madagascar, *Rakotondrainibe 6082* (P), KY711776, KY711951, KY712277, KY712118, KY711603, [2]; ***Rouhania zenkeri***, Madagascar, *Rouhan & al. 1254* (P), KY711792, KY711967, KY712291, KY712132, KY711617, [2]; ***Rouhania zenkeri***, Madagascar, *Rouhan & al. 1287* (P), KY711860, KY712035, KY712352, KY712200, KY711684, [2]; ***Rouhania zenkeri***, Madagascar, *Rouhan & al. 1308* (P), KY711768, KY711943, KY712270, KY712110, KY711595, [2]; ***Rouhania zenkeri***, Madagascar, *Rouhan & al. 1312* (P), KY711861, KY712036, KY712353, KY712201, KY711685, [2]; ***Rouhania zenkeri***, Madagascar, *Rouhan & al. 1347* (P), KY711772, KY711947, KY712274, KY712114, KY711599, [2]; ***Rouhania zenkeri***, Madagascar, *Rouhan & al. 1354* (P), KY711773, KY711948, KY712275, KY712115, KY711600, [2]; ***Rouhania zenkeri***, Madagascar, *Rouhan & al. 1354bis* (P), KY711774, KY711949, KY712276, KY712116, KY711601, [2]; ***Scleroglossum pusillum*** (Blume) Alderw., Peninsular Malaysia, *Parris 12779* (AK), –, KM218812, KM106187, KM106030, KM106090, [1]; ***Scleroglossum pusillum***, Thailand, *Middleton 5137* (E), KY711911, KY712079, KY712404, KY712236, KY711741, [2]; ***Scleroglossum pusillum***, Yunnan, China, *J.-Y. Shen 1162*, –, MK936467, –, –, –, [33]; ***Scleroglossum pyxidatum*** Alderw., Khanh Hoa, Vietnam, *L.-B. Zhang & al. 8757* (CDBI, MO, PHH), OQ702673, OQ708590, OQ717184, OQ717090, OQ717171, **this study**; ***Scleroglossum pyxidatum***, Dak Lak, Vietnam, *L.-B. Zhang & al. 8901* (CDBI, MO, PHH), OQ702674, OQ708612, OQ717185, OQ717091, OQ717172, **this study**; ***Scleroglossum sulcatum*** (Kuhn) Alderw., Pohnpei, Micronesia, *K.R. Wood 13557* (PTBG), –, MT657608, –, –, –, [4]; ***Scleroglossum sulcatum***, Hainan Island, YGL-032a, –, MK936470, –, –, –, [33]; ***Scleroglossum sulcatum***, Hainan Island, YGL-032b, –, MK936471, –, –, –, [33]; ***Scleroglossum sulcatum***, Kon Tum, Vietnam, WP0228, –, MK936468, –, –, –, [33]; ***Scleroglossum sulcatum***, Kosrae Island, Micronesia, *K.R. Wood 13953* (PTBG), –, MT657609, –, –, –, [4]; ***Scleroglossum sulcatum***, Lam Dong, Vietnam, *L.-B. Zhang & al. 8542* (CDBI, MO, PHH), OQ702664, OQ708613, OQ717182, OQ717092, OQ717175, **this study**; ***Scleroglossum sulcatum***, Lam Dong, Vietnam, WP1204, –, MK936469, –, –, –, [33]; ***Scleroglossum sulcatum***, Marquesas Islands, *Schuettpelz 1931* (US), –, MT216107, –, –, –, [17]; ***Scleroglossum sulcatum***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 10973* (KUN, CDBI, BCU, MO, PYU, XTBG), OQ702753, OQ708559, OQ717257, –, OQ717174, **this study**; ***Scleroglossum sulcatum***, Nakhon Si Thammarat, Thailand, *L.-B. Zhang & al. 11114* (KUN), OQ702752, OQ708570, OQ717246, –, OQ717173, **this study**; ***Scleroglossum sulcatum***, Philippines, *Whitford 1503* (P), –, –, –, –, KY711738, [2]; ***Scleroglossum sulcatum***, Pohnpei, Micronesia, *Bowden-Kerby in Raulerson 24182b* (UC, GUAM), AY459498[11], AY460665[11], KM106188[1], –, JF514049[21], [1][11][21]; ***Scleroglossum sulcatum***, Pohnpei, Micronesia, *T. Flynn 6287* (UC, PTBG, US), AY459497, AY460664, –, –, –, [11]; ***Scleroglossum sulcatum***, Raiatea, French Polynesia, *Nitta 3695* (UC, GH), –, KY099861, –, –, –, [14]; ***Scleroglossum wooroonooran*** (F.M.Bailey) C.Chr., Australia, *Kessler 14289* (VT), KM218835, KM218809, KM106189, KM106031, KM106091, [1]; ***Scleroglossum wooroonooran***, Australia, *Kessler 14304* (VT), KM218836, KM218810, KM106190, KM106032, KM106092, [1]; ***Scleroglossum wooroonooran***, New Caledonia, *Mackee 18207* (P), –, –, KY712386, –, KY711714, [2]; ***Stenogrammitis delitescens*** (Maxon) Labiak, Jamaica, *Proctor 4350* (US), –, MK319134, –, MK319086, MK319035, [10]; ***Stenogrammitis hartii*** (Jenman) Labiak, Dominican Republic, *Lellinger 455* (US), GU376583, GU386985, GU387057, GU387143, GU387225, [6]; ***Stenogrammitis hartii***, Dominican Republic, *Lellinger 572* (US), –, MK319146, –, –, MK319036, [10]; ***Stenogrammitis hellwigii*** (Mickel & Beitel) Labiak, Mexico, *Mickel & Leonard 4636* (NY), GU376584, GU386990, GU387058, GU387144, GU387226, [6]; ***Stenogrammitis hellwigii***, Mexico, *Mickel & Hellwig 4324* (NY), HQ599533, HQ599524, –, –, HQ599517, [34]; ***Stenogrammitis hellwigii***, Oaxaca, Mexico, *Sundue 3037* (VT), –, MK319135, –, MK319087, MK319037, [10]; ***Stenogrammitis hellwigii***, Oaxaca, Mexico, *Sundue 3044* (VT), –, MK319147, –, –, MK319038, [10]; ***Stenogrammitis hildebrandtii*** (Hieron.) Labiak, Madagascar, *Rakotondrainibe 6112* (P), GU376585, GU386975, GU387059, GU387145, GU387227, [6]; ***Stenogrammitis hildebrandtii***, Madagascar, *Rouhan & al. 1213* (P), KY711844, KY712020, KY712336, KY712184, KY711669, [2]; ***Stenogrammitis hildebrandtii***, Madagascar, *Rouhan & al. 1375* (P), KY711845, KY712021, KY712337, KY712185, KY711670, [2]; ***Stenogrammitis limula*** (Christ) Labiak, Costa Rica, *Sundue 1736* (NY), GU476765, GU476903, GU387066, GU387152, GU476651, [8]; ***Stenogrammitis limula***, Brazil, *Labiak 4153* (UPCB), GU376591, GU387023, GU387067, GU387153, GU387232, [6]; ***Stenogrammitis limula***, Costa Rica, *J.H. Nitta 812* (UC, CR), –, MW138195, –, –, –, [13]; ***Stenogrammitis limula***, Costa Rica, *Moraga & Rojas 501* (UC), AY459523, AY460650, –, –, –, [11]; ***Stenogrammitis limula***, Costa Rica, *Shalisko 251* (IBUG), –, MK319136, –, MK319088, MK319039, [10]; ***Stenogrammitis limula***, Costa Rica, *Shalisko 256* (IBUG), –, MK319137, –, MK319089, MK319040, [10]; ***Stenogrammitis limula***, Costa Rica, *Sundue 1761* (NY), GU476764, GU476906, –, –, GU476650, [8]; ***Stenogrammitis myosuroides*** (Sw.) Labiak, Colombia, *Vasco 631* (NY), GU376594, GU386968, GU387071, GU387157, GU387235, [6]; ***Stenogrammitis myosuroides***, Bolivia, *Bach 1840* (LPB), GU376595, GU386971, GU387072, GU387158, GU387236, [6]; ***Stenogrammitis myosuroides***, Colombia, *Sundue 1248* (NY), GU376597, GU387002, GU387075, GU387161, GU387238, [6]; ***Stenogrammitis myosuroides***, Colombia, *Sundue 1318* (NY), GU376598, GU387006, GU387076, GU387162, GU387239, [6]; ***Stenogrammitis myosuroides***, Dominican Republic, *Liogier 17085* (NY), HQ599534[34], HQ599525[34], –, –, GU476647[8], [8][34]; ***Stenogrammitis myosuroides***, Ecuador, *Sundue 1149* (NY), GU376596, GU386999, GU387074, GU387160, GU387237, [6]; ***Stenogrammitis myosuroides***, Guatemala, *Liogier 4* (NY), GU376599, GU386988, GU387077, GU387163, GU387240, [6]; ***Stenogrammitis nutata*** (Jenman) Labiak, Jamaica, *Proctor 5714* (US), –, MK319148, –, –, MK319041, [10]; ***Stenogrammitis oosora*** (Baker) Labiak, Cameroon, *Cable 77* (K), GU376600, GU386972, GU387078, GU387164, GU387241, [6]; ***Stenogrammitis oosora***, Madagascar, *Rakotondrainibe 6929* (P), HQ599535, HQ599527, –, –, –, [34]; ***Stenogrammitis oosora***, Madagascar, *Rakotondrainibe 6929* (P), KY711848, KY712024, KY712340, KY712188, KY711673, [2]; ***Stenogrammitis oosora***, Madagascar, *Rouhan & al. 1188* (P), KY711846, KY712022, KY712338, KY712186, KY711671, [2]; ***Stenogrammitis oosora***, Madagascar, *Rouhan & al. 1246* (P), KY711847, KY712023, KY712339, KY712187, KY711672, [2]; ***Stenogrammitis oosora***, Rwanda, *Christiansen 1379* (US), –, –, GU387079, –, GU387242, [6]; ***Stenogrammitis prionodes*** (Mickel & Beitel) Labiak, Mexico, *Mickel 6567* (NY), GU376605, GU386991, GU387086, GU387170, GU387249, [6]; ***Stenogrammitis pumila*** (Labiak) Labiak, Brazil, *Labiak 4015* (UPCB), GU376608, GU387022, GU387089, GU387173, GU387252, [6]; ***Stenogrammitis saffordii*** (Maxon) Labiak, Hawaii, *T.A. Ranker 1892* (BISH, COLO), EF178645[16], EF178628[16], KM106191[1], –, EF178662[16], [1][16]; ***Stenogrammitis saffordii***, Hawaii, *Ranker 1892* (PTPG), –, GU476926, –, –, GU476656, [8]; ***Stenogrammitis saffordii***, Hawaii, *Ranker 1989* (COLO), HQ599532, HQ599523, –, –, –, [34]; ***Stenogrammitis saffordii***, U.S.A.: Kauai, *K.R. Wood 18133*

Appendix 2. Continued.

(PTBG), –, MT657646, –, –, –, [4]; ***Stenogrammitis* sp. 1**, Amsterdam Island, *Jolinon 912* (P), KY711905, KY712073, KY712398, –, KY711731, [2]; ***Stenogrammitis* sp. 1**, Amsterdam Island, *Noel 35* (P), KY711906, KY712074, KY712399, –, KY711732, [2]; ***Stenogrammitis* sp. 1**, Amsterdam Island, *Noel 85* (P), KY711909, KY712077, KY712402, –, KY711739, [2]; ***Stenogrammitis* sp. 2**, Reunion, *Rakotondrainibe 6882* (P), KY711849, –, KY712341, KY712189, –, [2]; ***Stenogrammitis subcoriacea*** (Copel.) Labiak, Marquesas Islands, *D. Lorence 8944* (PTBG), EF178646, EF178629, –, –, –, [16]; ***Stenogrammitis subcoriacea***, French Polynesia, *Wood17692* (PTBG), –, MT216128, –, –, –, [17]; ***Stenogrammitis subcoriacea***, Marquesas Islands, *Schuettpelz 1891* (US), –, MT216129, –, –, –, [17]; ***Stenogrammitis subcoriacea***, Marquesas Islands, *Schuettpelz 1927* (US), –, MT216127, –, –, –, [17]; ***Stenogrammitis subcoriacea***, Marquesas Islands, *Wood 10823* (PTBG), HQ599537, HQ599529, –, –, HQ599519, [34]; ***Stenogrammitis subcoriacea***, Tahiti, French Polynesia, *Nitta 3316* (UC, GH), –, KY099867, –, –, –, [14]; ***Stenogrammitis wittigiana*** (Fee & Glaziou ex Fee) Labiak, Brazil, *Sylvestre 1885* (UPCB), GU376624, GU386989, GU387073, GU387159, GU387269, [6]; ***Stenogrammitis wittigiana***, Costa Rica, *Sundue 3422* (VT), –, MK319138, –, MK319090, MK319042, [10]; ***Stenogrammitis wittigiana***, Brazil, *Condack 552* (RB), GU376623, –, GU387105, GU387188, GU387268, [6]; ***Stenogrammitis wittigiana***, Brazil, *Labiak 4441* (UPCB), GU376625, GU387029, GU387106, GU387189, GU387270, [6]; ***Terpsichore asplenifolia*** (L.) A.R.Sm., Costa Rica, *Moraga & Rojas 506* (INB), JF514059[21], JF513989[21], KM106192[1], –, –, [1][21]; ***Terpsichore atroviridis*** (Copel.) A.R.Sm., Costa Rica, *J.H. Nitta 704* (UC, CR), –, MW138276, –, –, –, [13]; ***Terpsichore chrysleri*** (Proctor ex Copel.) A.R.Sm., Bolivia, *I. Jimenez 1369* (UC, LPB), KM218859, KM218813, –, KM106033, –, [1]; ***Terpsichore chrysleri***, Costa Rica, *Lellinger & White 998* (US), –, MK319110, –, MK319062, –, [10]; ***Terpsichore eggersii*** (Baker) A.R.Sm., Dominican Republic, *S.R. Hill 29109* (UC), AF469785[24], AF468209[24], AY362694[11], –, –, [11][24]; ***Terpsichore hanekeana*** (Proctor) A.R.Sm., Puerto Rico, *Ranker 1610* (COLO), AY459503, AY460670, –, –, –, [11]; ***Terpsichore lehmanniana*** (Hieron.) A.R.Sm., Ecuador, *K.A. Wilson 2589* (UC), AY459506, AY460673, –, –, –, [11]; ***Terpsichore staheliana*** (Posth.) A.R.Sm., Guiana, *G. Cremers 13084* (US), –, MK319119, –, MK319071, –, [10]; ***Thalassogrammitis deplanchei*** (Baker) Parris, Sundue, Li Bing Zhang & X.M.Zhou, New Caledonia, *Hodel 1450* (UC), AY459471[11], AY460639[11], KM106145[1], –, GU476639[8], [1][8][11]; ***Thalassogrammitis deplanchei***, New Caledonia, *Gaudeul 99* (P), KY711801, KY711976, KY712299, KY712140, KY711625, [2]; ***Thalassogrammitis deplanchei***, New Caledonia, *Munzinger 1242* (P), KY711802, KY711977, KY712300, KY712141, KY711626, [2]; ***Thalassogrammitis deplanchei***, New Caledonia, *Munzinger 1422* (P), KY711803, KY711978, KY712301, KY712142, KY711627, [2]; ***Thalassogrammitis deplanchei***, New Caledonia, *Tronchet 529* (P), KY711779, KY711954, KY712280, KY712121, KY711606, [2]; ***Tomophyllum donianum*** (Spreng.) Fraser-Jenk. & Parris, Yunnan, China, *PYU-S-2315* (PYU), OQ702698, OQ708555, OQ717206, OQ717096, OQ717180, **this study**; ***Tomophyllum donianum***, Yunnan, China, *Z.-L. Liang 1118* (CDBI, KUN), OQ702754, OQ708560, OQ717197, OQ717093, OQ717176, **this study**; ***Tomophyllum donianum***, Yunnan, China, *X. Cheng & al. FB486* (KUN), MT130584, MT130584, –, –, –, [27]; ***Tomophyllum donianum***, Yunnan, China, *Z.-L. Liang 1133* (CDBI, KUN), OQ702697, OQ708554, OQ717202, OQ717094, OQ717177, **this study**; ***Tomophyllum macrum*** (Copel.) Parris, Philippines, *Karger 532* (Z), –, KM218780, –, –, –, [1]; ***Tomophyllum macrum***, Philippines, *Karger 165* (Z), KM218830, –, –, –, –, [1]; ***Tomophyllum perplexum*** (Parris) Parris, Sri Lanka, *Faden 77/12* (P), KY711901, –, –, –, KY711725, [2]; ***Tomophyllum repandulum*** (Mett.) Parris, Papua New Guinea, *Ranker 1766 & Trapp* (COLO, UC), AY459465, AY460632, –, –, –, [11]; ***Tomophyllum repandulum***, Papua New Guinea, *Ranker 1767 & Trapp* (COLO, UC), AY459466, AY460633, –, KM106036, –, [11]; ***Tomophyllum repandulum***, Sri Lanka, *Onraedt 3747* (P), KY711900, KY712072, –, –, KY711724, [2]; ***Tomophyllum sakaguchianum*** (Koidz.) Parris, Nara, Japan, *776372* (TNS), –, AB575254, –, –, –, [25]; ***Tomophyllum secundum*** (Ridl.) Parris, Sabah, Malaysia, *Ranker 2193* (COLO), KM218832, KM218781, KM106195, KM106037, KM106095, [1]; ***Tomophyllum* sp. 1**, Taiwan Island, *R. Knapp 2982* (P), –, OQ708516, OQ717261, –, OQ717178, **this study**; ***Tomophyllum* sp. 1**, Taiwan Island, *R. Knapp 3421* (P), –, OQ708571, OQ717256, OQ717095, –, **this study**; ***Tomophyllum* sp. 2**, Taiwan Island, *R. Knapp 3173* (P), OQ702724, OQ708561, OQ717183, –, OQ717179, **this study**; ***Tomophyllum subsecundodissectum*** (Zoll.) Parris, New Caledonia, *Mackee 11829* (P), KY711895, –, –, –, KY711718, [2]; ***Tomophyllum walleri*** (Maiden & Betche) Parris, Australia, *Kessler 14250* (VT), KM218831, KM218782, KM106196, KM106038, KM106096, [1]; ***Xiphopterella devolii*** S.J.Moore, Parris & W.L.Chiou, Taiwan Island, *R. Knapp 4634* (P), –, OQ708534, OQ717250, –, –, **this study**; ***Xiphopterella hieronymusii*** (C.Chr.) Parris, Peninsular Malaysia, *Parris 12781* (AK), –, KM218783, KM106197, KM106039, KM106097, [1]; ***Xiphopterella sparsipilosa*** (Holttum) Parris, Peninsular Malaysia, *Parris 12790* (AK), –, KM218784, KM106198, KM106040, KM106098, [1]; **— OUTGROUP.** ***Campyloneurum angustifolium*** (Sw.) Fée, Costa Rica, *Chisaki & Carter 1004* (UC), AY459515[11], AF470344[39], AY362645[24], –, AY083647[39], [11][24][39]; ***Davallia trichomanoides*** Blume, Laos, *Wu 2463* (KUN), JX103675, JX103717, JX103759, –, JX103801, [35]; ***Davallia yunnanensis*** Christ, Laos, *Wu 2458* (KUN), JX103676, JX103718, JX103760, –, JX103802, [35]; ***Dendroconche ampla*** (F.Muell. ex Benth.) Testo, Sundue & A.R.Field, Queensland, Australia, *Kessler 14358* (VT), –, KF570108, KF570109, –, KF570110, [40]; ***Dictymia mckeei*** Tindale, Cult., *Schneider s.n.* (E), EF463492, EF463246, –, –, –, [32]; ***Lepisorus miyoshianus*** (Makino) Fraser-Jenk. & Subh. Chandra, Sichuan, China, *C.-C. Liu DB06104* (PE), –, GQ256255, GQ256327, –, GQ256172, [41]; ***Leptochilus digitatus*** (Baker) Noot., Hanoi, Vietnam, *L.-B. Zhang & al. 6487* (CDBI, MO, VNMN), OQ702732, OQ708583, OQ717214, –, OQ717121, **this study**; ***Loxogramme grammitoides*** (Baker) C.Chr., Taiwan Island, *R. Knapp 3652* (P), –, OQ708605, OQ717290, –, OQ717122, **this study**; ***Microgramma microsoroides*** Salino, T.E.Almeida & A.R.Sm., Brazil, *Almeida 681 & al.* (BHCB, CVRD, UC), –, EU292730, EU292731, –, EU292732, [42]; ***Pecluma macedoi*** (Brade) M.Kessler & A.R.Sm., Brazil, *Lehn 1054* (CGMS), –, KT780738, KT794116, –, KT780798, [43]; ***Platycerium coronarium*** (O.F.Müll.) Desv., Laos, *Wu 2597* (KUN), JX103669, JX103711, JX103753, –, JX103795, [35]; ***Pleopeltis myriolepis*** (Christ) A.R.Sm. & Tejero, Costa Rica, *Krieger 2327* (COLO), –, EU650131, EU650170, –, EU650092, [44]; ***Pleopeltis pyrrholepis*** (Fée) A.R.Sm. & Tejero, Mexico, *Lautner 02-44* (GOET), –, EU650133, EU650172, –, EU650094, [44]; ***Selliguea oxyloba*** (Wall. ex Kunze) Fraser-Jenk., Yunnan, China, *Lu S-G/SG79*, –, JQ685432, JQ685496, –, JQ700500, [36]; ***Serpocaulon appressum*** (Copel.) A.R.Sm., Bolivia, *Jimenez 862* (LPB), –, DQ151905, DQ151930, –, DQ151957, [37]; ***Synammia intermedia*** (Muhl. ex Willd.) G.Kunkel, Juan Fernández Islands, *Danton & Perrier s.n.* (UC), –, DQ168811, DQ168816, –, DQ168822, [38].

Appendix 3. Morphological comparison of the 35 genera in the Asia-Pacific clade of grammitid ferns (Polypodiaceae).

	Rhizomes	Stipes	Rhizome scales	Rhizome scales	Lamina	Veins	Hydathodes	Sori	Sporangia	Hairs
Acrosorus	radially symmetric	not articulated to rhizome	glabrous	concolorous	lobed to pinnate	few-forked	absent	protected by pinnae folded on acroscopic and basiscopic margin	glabrous	setae, simple catenate hairs, branched hairs with setae as branches
Adenophorus	dorsiventral	sometimes articulated to rhizome	glabrous or with glandular hairs, usually only at apex, rarely at margin	concolorous	simple to tripinnatifid	few-forked or pinnate	absent	superficial	glabrous	simple glandular hairs, catenate simple glandular, branched with catenate branches, branched with glands as branches
Aenigmatogrammitis	dorsiventral	not articulated to rhizome	glabrous	concolorous	simple	1-forked	present	superficial or slightly sunken in lamina	glabrous	sometimes absent, sometimes with catenate simple hairs and branched hairs with flattened catenate branches
Alansmia	radially symmetric	not articulated to rhizome	ciliate or absent	concolorous or absent	deeply pinnately divided or pinnate	1-forked	present	superficial or very slightly sunken	glabrous or setose	setae, sometimes with branched hairs with setae as branches and basally stellate hairs
Archigrammitis	dorsiventral	articulated to rhizome	ciliate	concolorous	simple	pinnately branched	present	superficial	setose	setae, catenate simple hairs, branched hairs with setae as branches
Boonkerdia	dorsiventral	not articulated to rhizome	glabrous	concolorous	pinnatisect or pinnate to tripinnate	1-forked, dimidiately branched or pinnately branched	present	superficial	glabrous	catenate simple hairs present, sometimes branched hairs with catenate branches present
Calligrammitis	radially symmetric	not articulated to rhizome	absent	absent	simple	simple, 1-forked or pinnately branched	present	superficial	glabrous	setae present, branched hairs with setae as branches present, basally stellate hairs present
Calymmodon	radially symmetric	not articulated to rhizome	glabrous or with apical setae	concolorous	lobed to pinnate	simple	usually present	protected by pinna folded on basiscopic margin	glabrous	setae, catenate simple hairs, branched hairs with setae as branches
Ceradenia	dorsiventral	articulated to rhizome	rarely glabrous, usually with glandular hairs	concolorous	deeply pinnately divided or pinnate	pinnately branched	absent	superficial or very slightly sunken	glabrous	setae sometimes present, simple glandular hairs, catenate simple glandular hairs, branched hairs with catenate glandular and/or glandular branches, glands white

(Continues)

Appendix 3. Continued.

	Rhizomes	Stipes	Rhizome scales	Rhizome scales	Lamina	Veins	Hydathodes	Sori	Sporangia	Hairs
Chrysogrammitis	dorsiventral	not articulated to rhizome	with glandular hairs	concolorous	lobed to bipinnatifid	few-forked or pinnately divided	absent	superficial	glabrous	simple glandular hairs, catenate simple glandular hairs, and branched hairs with simple glandular hairs as branches
Cochlidium	radially symmetric	not articulated to rhizome	glabrous	concolorous	lobed	simple, rarely 1-forked	absent	superficial or very slightly sunken	glabrous	simple glandular, rarely catenate simple
Ctenopterella	dorsiventral	not articulated to rhizome	glabrous	usually concolorous	lobed to pinnate	pinnately branched	present or absent	superficial	glabrous	setae, catenate simple hairs, branched hairs with setae as branches, branched hairs with catenate hairs as branches
Dasygrammitis	radially symmetric	not articulated to rhizome	ciliate	concolorous	lobed to bipinnate	pinnately branched	absent	superficial	usually glabrous, rarely with setae adjacent to annulus at base of sporangium or part way between stalk and annulus	setae, catenate simple hairs, branched hairs with setae as branches
Devolia	dorsiventral	not articulated to rhizome	glabrous or with an apical seta	concolorous	simple	simple	present	superficial	glabrous	setae present, branched hairs with setae as branches present
Enterosora	dorsiventral	sometimes articulated to rhizome	glabrous or with glandular or catenate glandular hairs	concolorous	simple to bipinnatifid	few-forked to pinnately branched	absent	superficial or sunken in lamina	glabrous	setae usually present, simple glandular hairs, catenate simple hairs, catenate hairs with catenate branches or glands as branches, glands translucent to pale yellow-brown or pale red-brown
Glabrigrammitis	dorsiventral	not articulated to rhizome	glabrous	concolorous	simple	simple or 1-forked	present	superficial or sunken in lamina	glabrous or with setae at apex adjacent to annulus	setae present, branched hairs with setae as branches present
Grammitastrum	dorsiventral	not articulated to rhizome	ciliate	clathrate	simple	1-forked	absent	superficial or slightly sunken in lamina	setose with hairs on the cell walls of the annulus	setae, branched hairs with setae as branches and basally stellate hairs present
Grammitis	dorsiventral & radially symmetric	not articulated to rhizome	glabrous	concolorous	simple margin sclerotic	simple or few-forked	usually absent, sometimes present	superficial	glabrous	setae, catenate simple, catenate branched with setae or catenate hairs as branches may be present
Howeogrammitis	dorsiventral	sometimes articulated to rhizome	glabrous or with a few apical setae or ciliate	concolorous	simple	1(–2–3)-forked	absent	superficial or slightly sunken in lamina	glabrous	catenate simple hairs or setae or branched hairs with setae as branches or branched hairs with catenate branches

(Continues)

Appendix 3. Continued.

	Rhizomes	Stipes	Rhizome scales	Rhizome scales	Lamina	Veins	Hydathodes	Sori	Sporangia	Hairs
Leucotrichum	radially symmetric	not articulated to rhizome	ciliate	clathrate	lobed	1-forked	present, more obvious when young	superficial	glabrous	setae, branched hairs with setae as branches
Melpomene	dorsiventral	not articulated to rhizome	glabrous or with a few hairs at apex	clathrate	deeply pinnately divided to pinnate	pinnately branched	present	superficial or very slightly sunken in lamina	glabrous	setae, catenate simple hairs, branched hairs with setae or catenate hairs as branches
Micropolypodium	radially symmetric	not articulated to rhizome	glabrous	concolorous	lobed to pinnate	simple	present	superficial	glabrous	setae, catenate simple hairs
Moranopteris	radially symmetric	not articulated to rhizome	ciliate	concolorous	deeply pinnately divided	simple to few-forked	present	superficial	glabrous	setae, branched hairs with catenate branches or glandular hairs for branches
Nanogrammitis	dorsiventral	not articulated to rhizome	glabrous	usually concolorous, sometimes clathrate	simple	usually simple, sometimes 1–(2–)-forked	present	superficial or slightly sunken in lamina	glabrous	setae often present, simple glandular hairs, branched hairs with setae as branches and catenate simple hairs sometimes present
Notogrammitis	dorsiventral	rarely articulated to rhizome	glabrous	usually concolorous	usually simple, sometimes pinnate to tripinnatifid	usually 1-forked, sometimes pinnately branched	sometimes present	superficial or slightly sunken in lamina	glabrous	setae, catenate simple hairs, branched hairs with setae or catenate hairs as branches
Oreogrammitis	dorsiventral or radial	sometimes articulated to rhizome	glabrous	usually concolorous	simple to tripinnatifid	1–2(–4)-forked or pinnately branched	present or absent	superficial or sunken in lamina	setae at apex of sporangium	sometimes glabrous, setae often present, catenate simple hairs and basally stellate hairs sometimes present
Oxygrammitis	dorsiventral	sometimes articulated to rhizome	glabrous	concolorous	bipinnately to tripinnately divided	pinnately branched	absent	superficial or slightly sunken in lamina	glabrous	glabrous or with setae and/or catenate simple hairs, and 1–3-forked hairs with catenate base and catenate branches
Parrisia	radially symmetric	not articulated to rhizome	glabrous, with a few hairs at apex or ciliate	concolorous	simple	simple or 1-forked	absent	superficial or very slightly sunken in lamina		setae present, sometimes catenate simple, catenate branched with glandular or catenate hairs as branches present
Prosaptia	dorsiventral	articulated to rhizome	ciliate	clathrate	lobed to pinnate, rarely simple	usually pinnately branched, rarely few-forked	absent	deeply sunken in pits in lamina or in marginal or submarginal pouches	glabrous	setae, catenate simple hairs, branched catenate with setae as branches present, basally stellate hairs sometimes persent

(Continues)

Appendix 3. Continued.

	Rhizomes	Stipes	Rhizome scales	Rhizome scales	Lamina	Veins	Hydathodes	Sori	Sporangia	Hairs
Rouhania	dorsiventral	sometimes articulated to rhizome	glabrous	concolorous	simple or pinnate or pinnatisect	simple, 1-forked or pinnately branched	present	superficial or slightly sunken in lamina	glabrous	simple glandular hairs usually present, catenate simple hairs, setae and branched hairs with setae or catenate hairs as branches sometimes present
Scleroglossum	radially symmetric	not articulated to rhizome	glabrous	concolorous	simple	few-forked	absent	deeply sunken in grooves in lamina	glabrous	catenate simple hairs, branched hairs with setae as branches, branched hairs with catenate hairs as branches
Stenogrammitis	dorsiventral & radially symmetric	not articulated to rhizome	glabrous or with a solitary seta or branched hair with seta as branch at apex	subclathrate to clathrate	simple to lobed	simple	present	superficial	glabrous	branched hairs with setae as branches
Thalassogrammitis	dorsiventral	sometimes articulated to rhizome	ciliate	concolorous	simple	1–(2–)-forked	absent	superficial or slightly sunken in lamina	setose, setae at apex of sporangium on walls of annulus cells	glabrous at maturity, sometimes with simple glandular hairs and 1-forked hairs with a seta as branch when young
Tomophyllum	radially symmetric	not articulated to rhizome	glabrous or ciliate, sometimes absent	concolorous	lobed to tripinnatifid	pinnate	present	superficial	glabrous	setae, catenate simple hairs, branched hairs with setae as branches
Xiphopterella	radially symmetric	not articulated to rhizome	glabrous or with apical setae	concolorous	lobed to pinnate	few-forked	present or absent	superficial	glabrous	setae, catenate simple hairs, branched hairs with setae as branches sometimes branched hairs with catenate hairs as branches