*Phytotaxa* 394 (3): 176–208
https://www.mapress.com/j/pt/


**Article**

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

https://doi.org/10.11646/phytotaxa.394.3.1

# Taxonomic novelties in grammitid ferns (Polypodiaceae) from the Neotropics and Madagascar supported by molecular data

VIACHESLAV SHALISKO[1], MICHAEL A. SUNDUE[2], ALMA ROSA VILLALOBOS-ARÁMBULA[3], MIGUEL ÁNGEL MUÑIZ-CASTRO[1] & J. ANTONIO VÁZQUEZ-GARCÍA[1*]

[1] *Laboratorio de Ecosistemática, Instituto de Botánica, Departamento de Botánica y Zoología, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Camino Ing. Ramón Padilla Sánchez No. 2100, La Venta del Astillero, Zapopan, 45200, Jalisco, Mexico*

[2] *Pringle Herbarium, Dept. of Plant Biology, University of Vermont, Burlington, VT, 50405 USA*

[3] *Laboratorio de Genética, Ecosistemática Molecular y Funcional, Departamento de Biología Celular y Molecular, Centro Universitario de Ciencias Biológicas y Agropecuarias, Universidad de Guadalajara, Camino Ing. Ramón Padilla Sánchez No. 2100, La Venta del Astillero, Zapopan, 45200, Jalisco, Mexico*

**Corresponding author. Email: talaumaofeliae@gmail.com*

## Abstract

Based on cpDNA data, we provide the phylogenetic position for 18 species of Neotropical grammitid ferns (Polypodiaceae) that were not previously included in a molecular phylogeny. These species were resolved in *Alansmia*, *Ceradenia*, *Enterosora*, *Grammitis*, *Lellingeria*, *Lomaphlebia*, *Melpomene*, *Moranopteris*, *Stenogrammitis,* and *Terpsichore*. Our results indicate that *Enterosora* is polyphyletic and in need of generic recircumscription. We maintain the identity of *Enterosora*, based on the position of *E. campbellii* subsp. *spongiosa,* a variety of the type species. This finding allowed us to conclude that the *E. parietina* clade should be excluded from *Enterosora*. To accommodate this clade we describe a new genus, *Parrisia*. It is related to *Adenophorus* and a clade that includes *Cochlidium*, *Grammitis* s.s., and *Lomaphlebia*. We further found that *Zygophlebia* is paraphyletic with respect to *Enterosora*, represented by two separate clades, *Zygophlebia* s. s. that includes *Z. cornuta*, the type species, *Z. sectifrons* and *Z. matthewsii*, and a second clade that includes another seven species of *Zygophlebia* as well as *E. barbatula*. As a separate clade, this *Zygophlebia* species could be maintained. However, we prefer to sink both *Zygophlebia* clades into *Enterosora*. We propose ten novel combinations for *Enterosora*, by moving *Zygophlebia* with a confirmed phylogenetic position to *Enterosora*. It is possible that the remaining *Zygophlebia* species should also be treated as *Enterosora*, but further research is necessary.

**Key words**. *Adenophorus*, *Enterosora*, *Parrisia*, spongiose mesophyll, *Zygophlebia*

## Introduction

The generic circumscription of ferns remains dynamic, owing to advances in molecular systematics, new insights into morphological evolution, and reevaluation of the utility of generic concepts (Schuettpeltz *et al*. 2018). In particular, genera of Grammitidoideae Parris & Sundue in PPG I (2016: 594) have been substantially revised (Lehnert *et al.* 2010, Hirai & Prado 2012, León-Parra 2012, Moguel-Velázquez & Kessler 2013, Labiak 2013, Lehnert 2013, Sundue *et al*. 2014) with eight new genera described in the last ten years using molecular phylogenetics and morphological trait data, in order to resolve the polyphyly of genera based solely upon morphology (e.g. *Grammitis* Swartz (1800: 3), *Lellingeria* A.R.Sm. & R.C.Moran in Smith *et al.* (1991: 76), *Micropolypodium* Hayata (1928: 31), and *Terpsichore* Smith (1993: 479)). These segregated genera include *Alansmia* Kessler *et al.* (2011: 238), *Ascogrammitis* Sundue (2010: 361), *Galactodenia* Sundue & Labiak in Sundue *et al.* (2012: 340), *Leucotrichum* Labiak in Labiak *et al.* (2010a: 915), *Moranopteris* R.Y.Hirai & J.Prado in Hirai *et al.* (2011: 1127), *Mycopteris* Sundue (2013: 175), *Notogrammitis* Parris in Perrie & Parris (2012: 465), and *Stenogrammitis* Labiak (2011: 141). Except for *Notogrammitis,* which is an austral genus primarily occurring in Australia and New Zealand, these segregate genera comprise primarily Neotropical species; with few occurring in Africa (*Alansmia*, *Stenogrammitis*), Madagascar (*Leucotrichum*, *Moranopteris*, *Stenogrammitis*), and Polynesia (*Stenogrammitis*). Partial molecular sampling available to date has further confirmed as monophyletic the genera *Adenophorus* Gaudichaud-Beaupré (1824: 508), *Ceradenia* Bishop (1988: 2), *Cochlidium* Kaulfuss (1820: 36),

 *Accepted by Marcus Lehnert: 10 Feb. 2019; published: 1 Mar. 2019*

and *Melpomene* Smith and Moran (1992: 426). Owing to the combined morphological and molecular approaches, most grammitid genera are now well characterized and easy to identify using unique combinations of characters (Sundue 2010). However, some exceptions remain. The Asian clade is still sparsely sampled in phylogenetic studies, several endemic genera from Malesia were described recently using morphological criteria (Parris 1997, 1998, 2007, 2013), and others appear to be paraphyletic (Sundue *et al.* 2014). Thus, taxonomic revision remains ongoing, particularly in *Ctenopterella* Parris (2007: 234), *Enterosora* Baker in Im Thurn (1886: 218), and *Grammitis,* and *Oreogrammitis*, that are are known to be artificial (Bauret *et al*. 2017).

Here, we address one of these questions in particular, the relations between *Enterosora* and *Zygophlebia* Bishop (1989: 107). Both genera occur in the Neotropics, Africa, Madagascar, and Mascarenes (Parris 2002). Both genera also lack hydathodes, a distinctive field character, and along with *Ceradenia* form the primarily neotropical anhydathodous clade. *Enterosora* is particularly distinctive, perhaps even "showy" for a fern because it features conspicuously thick and spongy laminae with large intercellular air spaces within the parenchyma (Bishop & Smith, 1992). Although no other group of ferns exhibits laminae as profoundly spongy as *Enterosora*, spongy leaves were shown by Sundue (2010) and Sundue *et al*. (2010) to be homoplastic, occurring to a lesser degree in a number of species scattered throughout the Grammitidioideae. Furthermore, Ranker *et al*. (2004) and Sundue (2010a) found no morphological synapomorphies that support segregation of *Enterosora* from *Zygoplebia*, and Sundue & Poinar (2016) found little morphological disparity between them. Thus, it was not a complete surprise when Bauret *et al*. (2017) showed that *Enterosora* is polyphyletic as currently circumscribed, with two clades nested within *Zygophlebia*. However, the lack of phylogenetic data for the type species of *Enterosora*, *E. campbellii* Baker in Im Thurn (1886: 218), has prevented them from resolving this problem because it was unclear which of the four "*Enterosora"* clades recovered by Bauret *et al*. (2017) it belonged to. The proposal of PPG I (2016) is to treat *Zygophlebia* as a synonym of *Enterosora* if the phylogenetic position of the type species of the latter supports it.

## Materials and methods

### Taxonomic sampling

The ingroup sampling within Grammitidoideae included 266 accessions representing 221 recognized species from 23 genera, from which a minor fraction (13 species) belongs to genera endemic to Asia, Australia, and the Pacific. The dataset represented 15 of 16 known Neotropical genera, excluding the monotypic *Luisma* Murillo & Smith (2003: 313) from Colombia, and including *Lomaphlebia* Smith (1875: 182) endemic to the Antilles. New sequence data were produced for 62 samples from 36 Neotropical species (Table 1). The vouchers for newly collected material were deposited in IBUG and VT (acronyms according to Thiers 2016). Leaf samples form preserved herbarium specimens were taken from US. From taxa with newly obtained sequences unequivocally identified up to species, 19 were not previously included in molecular phylogenetic studies. Most of the ingroup accessions (204 samples representing 201 species) were taken from the NCBI GenBank data cited in Sundue *et al*. (2014) and Bauret *et al.* (2017). In the case of Neotropical genera, the selection of accessions generally consisted of one sample per described species when required sequence data were available. The information on sampled species, their authors, herbarium vouchers, and GenBank accession numbers is listed in Appendix 1. The outgroup was defined by two species from Polypodiaceae Presl & Presl (1822: 159), that according to Schuettpelz & Pryer (2007) are closely related to the clade of Grammitidoideae: *Polypodium vulgare* Linnaeus (1753: 1085) and *Serpocaulon fraxinifolium* (Jacquin 1789: 187) A.R. Sm. in Smith *et al*. (2006: 928).

### DNA extraction, amplification, and sequencing

Total genomic DNA was extracted from silica-gel dried leaf tissue or leaf fragments from herbarium specimens using a modified 2×CTAB method (Doyle & Doyle 1987, Palomera *et al.* 2008). The three cpDNA markers (*rbcL*, *trnG-trnR*, *trnL-trnF*) were amplified by PCR, following a procedure described in Labiak *et al.* (2010). For *rbcL*, we used primers of Schuettpelz and Pryer (2007): ESRBCL1F and ESRBCL1361R for amplification, and additional internal primers ESRBCL628F and ESRBCL654R for sequencing. For *trnG-trnR*, we used a set of primers TRNG1F, TRNR22R, TRNG43F1, and TRNG63R (Nagalingum *et al.* 2007), with the last two only being used for sequencing. For *trnL-trnF,* the primers were TRNLF and TRNLE (Taberlet *et al.* 1991). Amplified fragments were purified with GFX columns (GE Healthcare, Chicago, IL, USA) using the manufacturer's protocols. The purified PCR products were sent for sequencing to the htSEQ High Throughput Genomics Unit of the University of Washington (Seattle, WA, USA) and

University of Arizona Genetics Core (Tucson, AZ, USA). The chromatogram processing, assembling of contigs, and production of consensus sequences were accomplished with Geneious® 8.1.9 (Biometters Ltd., San Francisco, CA, USA). All newly obtained consensus sequences were submitted to GenBank (accession numbers included in Table 1).

**TABLE 1.** Samples used to generate new sequences in this study. Species with an asterisk (*) were for the first time included in molecular phylogeny. Order of GenBank accession numbers is following: *rbcL*, *trnG-trnR, trnL-trnF*. Missing sequences are indicated by a dash (—).

| Species | Voucher | Herbarium | Collecting locality | GenBank |
|---|---|---|---|---|
| *Alansmia elastica* (Bory ex Willdenow 1810: 183) Moguel & M. Kessler in Kessler *et al*. (2011: 240) | *Shalisko 254* | IBUG | Costa Rica | MK319093, MK319045, MK318991 |
| *A. elastica* | *Shalisko 255* | IBUG | Costa Rica | MK319094, MK319046, MK318992 |
| *A. elastica* | *Sundue 3386* | VT, IBUG | Costa Rica | MK319095, MK319047, MK318993 |
| *Alansmia smithii* (A. Rojas in Rojas-Alvarado 2008: 15–16) Moguel & M. Kessler in Kessler *et al*. (2011: 242) | *Evans et al. 34* | US | Costa Rica | MK319096, MK319048, MK318994 |
| *Alansmia turrialbae* (Christ in Duraud & Pittier 1896: 226) Moguel & M. Kessler in Kessler *et al*. (2011: 240) | *Lellinger & White 996* | US | Costa Rica | MK319097, MK319049, MK318995 |
| *Ascogrammitis anfractuosa* (Kunze ex Klotzsch 1847: 375) Sundue (2010: 365) | *Sundue 3133* | VT | Oaxaca, Mexico | MK319098, MK319050, MK318996 |
| *A. anfractuosa* | *Sundue 3381* | VT, IBUG | Costa Rica | MK319099, MK319051, MK318997 |
| *Ceradenia knightii** (Copeland 1955: 419) Bishop (1988: 5) | *Lellinger & White 1583* | US | Costa Rica | MK319106,—,— |
| *Ceradenia kookenamae** (Jenman in im Thurn 1886: 215) Bishop (1988: 5) | *Lellinger & White 1048* | US | Costa Rica | MK319100, MK319052, MK318998 |
| *Ceradenia meridensis** (Klotzsch 1847: 380) Bishop (1988: 5) | *Evans & Lellinger 271* | US | Costa Rica | MK319130,—, MK318999 |
| *Cochlidium jungens** Bishop (1978: 84) | *Proctor 40989* | US | Puerto Rico | MK319131,—, MK319000 |
| *Cochlidium linearifolium** (Desvaux 1811: 302) Maxon ex Christensen (1929: 23) | *Sundue 3016* | VT | Oaxaca, Mexico | MK319103, MK319055, MK319001 |
| *C. linearifolium* | *Sundue 3530* | VT, IBUG | Oaxaca, Mexico | MK319104, MK319056, MK319002 |
| *Cochlidium serrulatum* (Swartz 1788: 128) Bishop (1978: 80) | *Shalisko 250* | IBUG | Costa Rica | MK319105, MK319057, MK319003 |
| *C. serrulatum* | *Shalisko 314* | IBUG | Chiapas, Mexico | MK319132,—, MK319004 |
| *C. serrulatum* | *Shalisko 333* | IBUG | Chiapas, Mexico | KT156610, KT156613, KT156611 |
| *Cochlidium rostratum* (Hooker 1864: 122) Maxon ex Christensen (1929: 23) | *Sundue 3379* | VT, IBUG | Costa Rica | MK319101, MK319053,— |
| *Enterosora campbellii** subsp. *spongiosa* (Maxon 1939: 113) L.E. Bishop in Bishop & Smith (1992: 531) | *Lellinger & White 1540* | US | Costa Rica | MK319107, MK319059, MK319005 |

...*continued on next page*

**TABLE 1.** (Continued)

| Species | Voucher | Herbarium | Collecting locality | GenBank |
|---|---|---|---|---|
| *Galactodenia delicatula* (Martens & Galeotti 1842: 35) Sundue & Labiak in Sundue *et al*. (2012: 340) | *Mickel 1152* | US | Oaxaca, Mexico | MK319101, MK319054,— |
| *Galactodenia* sp. | *Evans et al. 78* | US | Costa Rica | MK319149,—, MK319150 |
| *Galactodenia subscabra* (Klotzsch 1847: 377) Sundue & Labiak in Sundue *et al.* (2012: 341) | *Sundue 3423* | VT, IBUG | Costa Rica | MK319108, MK319060, MK319006 |
| *Grammitis bufonis** L.D. Gómez (1982: 154) | *Valdespino & Arande 179* | US | Panama | MK319109, MK319061, MK319007 |
| *Grammitis limbata** Fée (1852: 233) | *Valdespino & Arande 165* | US | Panama | MK319141,—, MK319008 |
| *Lellingeria apiculata* (Kunze ex Klotzsch 1847: 378) A.R. Sm. & R.C. Moran in Smith *et al.* (1991: 83) | *Shalisko 319* | IBUG | Chiapas, Mexico | MK319111, MK319063, MK319009 |
| *Lellingeria tmesipteris** (Copeland 1955: 410) A.R. Sm. & R.C. Moran in Smith *et al.* (1991: 88) | *Evans et al. 171* | US | Costa Rica | MK319112, MK319064, MK319010 |
| *Lomaphlebia linearis** (Swartz 1800: 17) Smith (1875: 183) | *Wilson & Murrey 635* | US | Jamaica | MK319113, MK319065, MK319011 |
| *Melpomene* cf. *flabelliformis* (Poiret 1804: 519) A.R. Sm. & R.C. Moran (1992: 430) | *Sundue 3036* | VT | Oaxaca, Mexico | MK319114, MK319066, MK319012 |
| *M.* cf. *flabelliformis* | *Sundue 3421* | VT, IBUG | Costa Rica | MK319115, MK319067, MK319013 |
| *Melpomene moniliformis* (Lagasca & Segura ex Swartz 1806: 33) A.R. Sm. & R.C. Moran (1992: 430) | *Sundue 3042* | VT | Oaxaca, Mexico | MK319118, MK319070, MK319016 |
| *M. moniliformis* | *Sundue 3047* | VT | Oaxaca, Mexico | MK319142,—, MK319017 |
| *M. moniliformis* var. *adnata** (Kunze 1851: 80) Lehnert (2010: 55) | *Sundue 3531* | VT, IBUG | Oaxaca, Mexico | MK319123, MK319075, MK319021 |
| *Melpomene pilosissima* (M. Martens & Galeotti 1842: 39) A.R. Sm. & R.C. Moran (1992: 431) | *Sundue 3082* | VT | Oaxaca, Mexico | MK319121, MK319073, MK319019 |
| *Melpomene personata* Lehnert (2008: 237) | *Sundue 3420* | VT, IBUG | Costa Rica | MK319120, MK319072, MK319018 |
| *Melpomene xiphopteroides* (Liebmann 1849: 196) A.R. Sm. & R.C. Moran (1992: 431) | *Shalisko 305B* | IBUG | Chiapas, Mexico | MK319124, MK319076, MK319022 |
| *M. xiphopteroides* | *Shalisko 315* | IBUG | Chiapas, Mexico | MK319125, MK319077, MK319023 |
| *M.* aff. *xiphopteroides* | *Shalisko 316* | IBUG | Chiapas, Mexico | MK319116, MK319068, MK319014 |
| *M.* aff. *xiphopteroides* | *Shalisko 317* | IBUG | Chiapas, Mexico | MK319117, MK319069, MK319015 |
| *M.* aff. *xiphopteroides* | *Sundue 3514* | VT | Oaxaca, Mexico | MK319122, MK319074, MK319020 |

*...continued on next page*

**TABLE 1.** (Continued)

| Species | Voucher | Herbarium | Collecting locality | GenBank |
|---|---|---|---|---|
| *Melpomene zempoaltepetlensis** (Mickel & Beitel 1988: 205) Smith (1995: 21) | *Sundue 3050* | VT | Oaxaca, Mexico | MK319126, MK319078, MK319024 |
| *Moranopteris setulosa** (Rosenstock 1912: 277) A. Rojas in Rojas-Alvarado (2017: 153) | *Evans et al. 15* | US | Costa Rica | MK319143,—, MK319025 |
| *Moranopteris taenifolia** (Jenman 1897: 114) R.Y. Hirai & J. Prado in Hirai *et al.* (2011: 1132) | *Shalisko 253* | IBUG | Costa Rica | MK319127, MK319079, MK319026 |
| *M. taenifolia* | *Shalisko 257* | IBUG | Costa Rica | MK319128, MK319080, MK319027 |
| *M. taenifolia* | *Shalisko 332* | IBUG | Chiapas, Mexico | MK319129, MK319081, MK319028 |
| *M. taenifolia* | *Shalisko 336* | IBUG | Chiapas, Mexico | —, MK319082, MK319029 |
| *M. taenifolia* | *Shalisko 337* | IBUG | Chiapas, Mexico | —, MK319083, MK319030 |
| *M. taenifolia* | *Sundue 3385* | VT, IBUG | Costa Rica | MK319144,—, MK319031 |
| *M. taenifolia* | *Sundue 3411* | VT | Costa Rica | MK319145,—, MK319032 |
| *Mycopteris* aff. *semihirsuta* (Klotzsch 1847: 379) Sundue (2014: 182–183) | *Sundue 3108* | VT | Oaxaca, Mexico | —, MK319084, MK319033 |
| *M.* aff. *semihirsuta* | *Sundue 3112* | VT | Oaxaca, Mexico | MK319133, MK319085, MK319034 |
| *Mycopteris zeledoniana* (Lellinger 1985: 383) Sundue (2014: 183) | *Shalisko 259* | IBUG | Costa Rica | —, MK319058,— |
| *Stenogrammitis delitescens** (Maxon 1904: 74) Labiak (2011: 145) | *Proctor 4350* | US | Jamaica | MK319134, MK319086, MK319035 |
| *Stenogrammitis jamesonii** (Hooker 1861: t. 14) Labiak (2011: 146) | *Sundue 3422* | VT, IBUG | Costa Rica | MK319138, MK319090, MK319042 |
| *Stenogrammitis hartii* (Jenman 1886: 272) Labiak (2011: 145) | *Lellinger 572* | US | Dominica | MK319146,—, MK319036 |
| *Stenogrammitis hellwigii* (Mickel & Beitel 1988: 199) Labiak (2011: 145–146) | *Sundue 3037* | VT | Oaxaca, Mexico | MK319135, MK319087, MK319037 |
| *S. hellwigii* | *Sundue 3044* | VT | Oaxaca, Mexico | MK319147,—, MK319038 |
| *Stenogrammitis limula* (Christ 1909: 218) Labiak (2011: 146) | *Shalisko 251* | IBUG | Costa Rica | MK319136, MK319088, MK319039 |
| *S. limula* | *Shalisko 256* | IBUG | Costa Rica | MK319137, MK319089, MK319040 |
| *Stenogrammitis nutata** (Jenman 1886: 272) Labiak (2011: 147) | *Proctor 5714* | US | Jamaica | MK319148,—, MK319041 |
| *Terpsichore alfaroi** (Donnell Smith 1902: 262) Smith (1993: 485) | *Lellinger & White 998* | US | Costa Rica | MK319110, MK319062,— |
| *Terpsichore staheliana** (Posthumus 1927: 401) Smith (1993: 488) | *Cremers G. 13084* | US | French Guiana | MK319119, MK319071,— |
| *Zygophlebia cornuta** (Lellinger 1985: 381) Bishop (1989: 112) | *Lellinger & While 1062* | US | Costa Rica | MK319139, MK319091, MK319043 |

*...continued on next page*

**TABLE 1.** (Continued)

| Species | Voucher | Herbarium | Collecting locality | GenBank |
|---|---|---|---|---|
| *Zygophlebia sectifrons* (Kunze ex Mettenius 1856: 99) Bishop (1989: 110) | *Lellinger & White 1535* | US | Costa Rica | MK319140, MK319092, MK319044 |

### Sequence alignment and phylogenetic analysis

Phylogenetic analysis was based entirely on cpDNA sequences from six markers: two protein coding (*atpB*, *rbcL*) and four intergenic spacers (*trnG-trnR*, *trnL-trnF*, *rps4-trnS*, *atpB-rbcL*). The alignments were produced separately for each region with the MAFFT plugin 7.017 for Geneious (Katoh & Toh 2008). Alignments were visually inspected for ambiguities and concatenated in a single dataset, maintaining six partitions for markers. The search for a best-fitting nucleotide substitution model was performed in jModelTest 2.1.10 (Darriba *et al.* 2012) independently in each partition. Following recommendations of Luo *et al.* (2010), we used the Bayesian Information Criteria for model selection.

Phylogenetic relations were reconstructed using Maximum Likelihood (ML) and Bayesian Inference (BI). Both analyses used the same concatenated partitioned sequence dataset and the same nucleotide substitution models, with gaps treated as missing data. An ML search for the best scoring tree was performed in 1,000 bootstrap replicates with RAxML-HPC2 8.2.10 (Stamatakis 2014) on the CIPRES web server (Miller *et al.* 2010), with support values (BS) annotated to each tree node. MrBayes 3.2.6 (Ronquist *et al.* 2012) was used to conduct BI analysis via two simultaneous runs of a Markov chain Monte Carlo simulation in ten million generations with four chains each, taking samples every 1,000 generations. The first 2,500 tree samples were discarded as burn-in samples. Convergence and stationarity and the equivalent sample size for parameter estimates of the BI analysis after the burn-in were confirmed in Tracer 1.7.1 (Rambaut *et al.* 2018). The set of BI trees after burning were used to produce the 50% majority-rule consensus topology with average branch length and to estimate node posterior probability (PP) values. Consensus trees produced in ML and BI were visualized and annotated with ggtree (Yu 2017).

## Results

The dataset of six aligned and concatenated cpDNA markers was 6,897 characters long, from which 2,298 were phylogenetically informative. Availability of sequence data was unequal between partitions, with overall 51.2% of data missing; the *rbcL* was of the highest availability with 259 accessions, and intergenic spacer *atpB-rbcL* was available in 61. The best-fitting nucleotide substitution models were all with unequal base frequencies and gamma distributed rate variation between sites but varied in the scheme of substitution rates and the presence of invariable sites (Table 2).

**TABLE 2.** Best fitted nucleotide substitution models and parameters of alignments for six cpDNA partitions. Missing data include missing sequences, gaps and ambiguities.

| Locus | Best nucleotide model | Number of accessions | Missing data (%) | Aligned length | Phylogenetically informative characters |
|---|---|---|---|---|---|
| *atpB* | TPM3uf+I+Γ | 179 | 43.1 | 1408 | 335 |
| *rbcL* | TPM2uf+I+Γ | 259 | 17.2 | 1442 | 411 |
| *atpB-rbcL* | GTR+I+Γ | 61 | 80.7 | 1018 | 200 |
| *rps4-trnS* | TVM+Γ | 137 | 70.2 | 711 | 342 |
| *trnG-trnR* | TVM+I+Γ | 194 | 59.4 | 1637 | 714 |
| *trnL-trnF* | TPM1uf+Γ | 247 | 63.1 | 681 | 296 |
| Concatenated dataset | GTR+I+Γ | 269 | 51.2 | 6897 | 2298 |


**FIGURE 1.** The phylogenetic position of newly sequenced samples of Neotropical grammatid ferns (indicated as bold text) shown at the best maximum likelihood (ML) tree of the combined six cpDNA loci dataset. Bootstrap support (BS) values from ML and posterior probability (PP) from Bayesian inference analysis are indicated as numbers above nodes. Dots represent nodes with BS>70 or PP>0.9. "-" indicates absence of node in the consensus topology in Bayesian inference. Clades included in taxonomic treatment are indicated on the right.

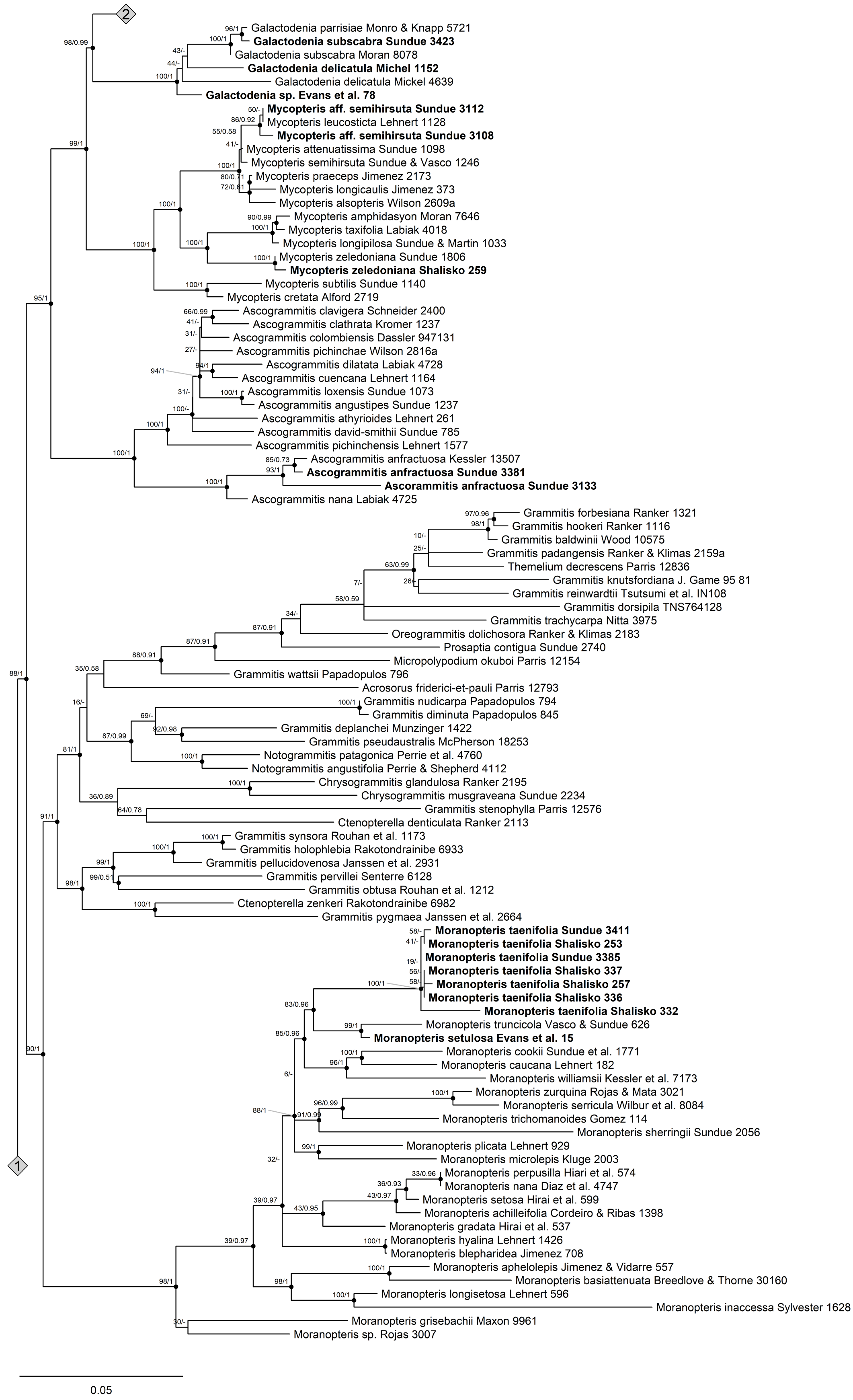


**FIGURE 1.** (Continued).

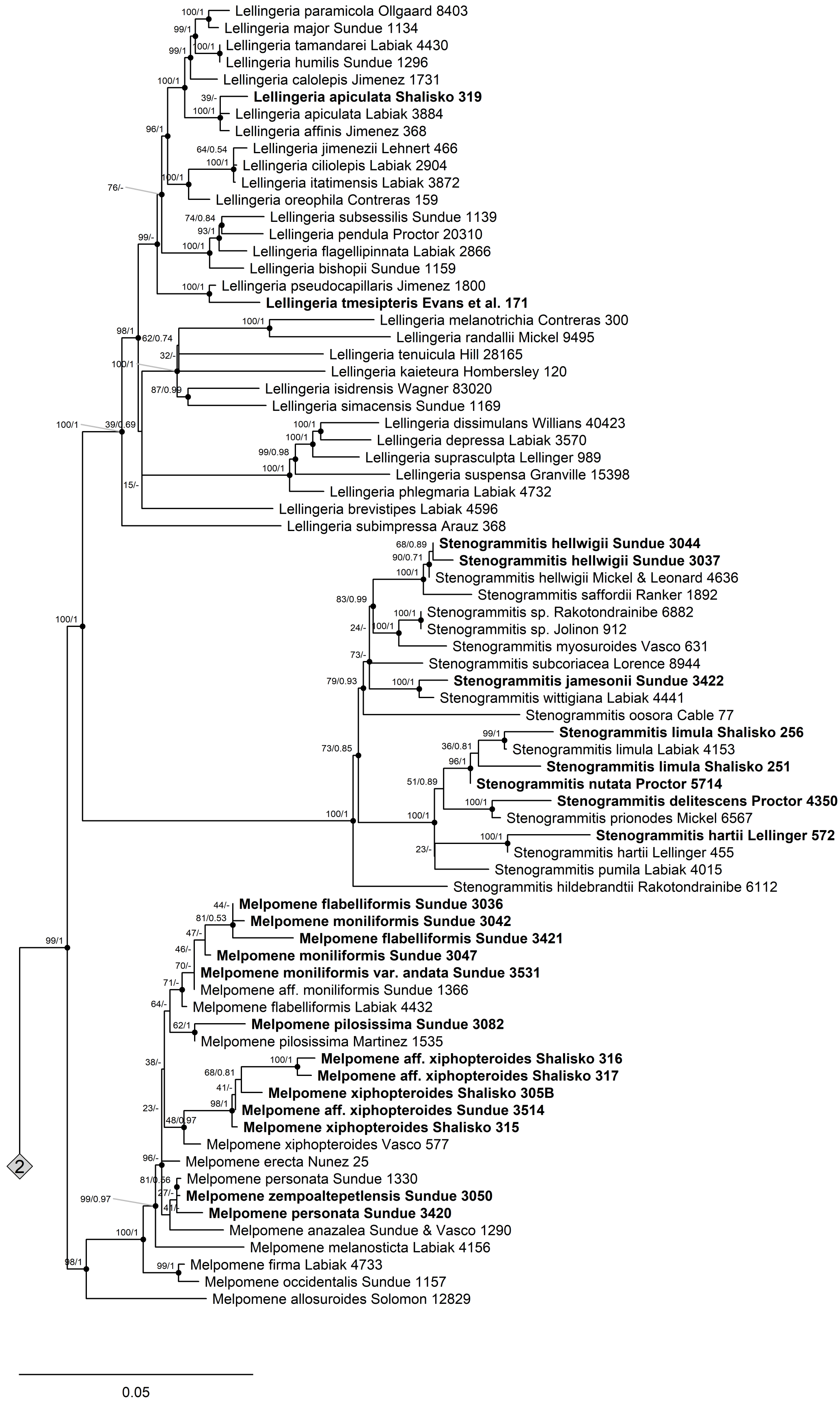


**FIGURE 1.** (Continued).

The ML and BI analysis produced rather similar ingroup topologies that differed in minor details for weakly supported nodes. The tree selected in ML is shown in Figure 1 with annotations of BS values, and corresponding PP values from BI analysis where this was applicable. Genera supported by both analyses as monophyletic with highest support (BS = 100%, PP = 1) were *Adenophorus*, *Alansmia*, *Ascogrammitis*, *Cochlidium*, *Galactodenia*, *Lellingeria*, *Leucotrichum*, *Lomaphlebia*, *Mycopteris*, and *Stenogrammitis*. Slightly lower support was observed for *Ceradenia* (BS = 95%, PP = 0.83), *Melpomene* (BS = 98%, PP = 1), *Moranopteris* (BS = 98%, PP = 1), and *Terpsichore* (BS = 99%, PP = 1). The monophyly was not found in the case of *Ctenopterella*, *Grammitis*, *Enterosora* and *Zygophlebia*. However, *Grammitis* s.s. did resolve as monophyletic (BS = 84%, PP = 0.91).

New accessions that were resolved with high support (BS > 90% and PP > 0.95) as a part of the immediate sister group for previously sequenced samples of the same species include three nodes for *Alansmia elastica*, two for *Ascogrammitis anfractuosa*, three for *Cochlidium serrulatum*, one for *Mycopteris zeledoniana*, two for *Stenogrammitis hellwigii*, a node for *S. limula* (another sample belong to this species clade with low support (BS = 36%, PP = 0.81)), and a node of *Zygophlebia sectifrons*. *Alansmia smithii* (*Evans et al. 34*, US !) had an original identification equivalent to *A. lanigera* (Desvaux 1811: 316) Moguel & M. Kessler in Kessler *et al*. (2011: 240–241), but it had not resolved jointly to *A. lanigera* (*B. Leon 3647*, UC, USM), instead belonging to a clade with *A. cultrata* (Willdnew 1810: 187) Moguel & M.Kessler (2011: 239) and *A. smithii* (BS = 98%, PP = 1). Our *A. turrialbae* (*Lellinger & White 996*, US!) appeared as a sister to previously sequenced *A. turrialbae* (*Sundue 1765*, NY!, in GenBank as *A. glandulifera*) (BS = 100%, PP = 1). First time sequenced *Ceradenia kookenamae*, *C. knightii*, and *C. meridensis* appeared in one clade with *C. aulaeifolia* L.E. Bishop ex A.R. Sm. in Smith (1993a: 182), *C. ayopayana* Kessler & Smith (2008: 167), *C. intonsa* L.E. Bishop ex Leon-Parra & J. Mostacero in León-Parra (2012: 38), *C. intricata* (Morton 1967: 101) L.E. Bishop ex Smith (1993a: 185), *C. kalbreyeri* (Baker in Im Thurn 1886: 215) Bishop (1988: 5), *C. madidiensis* Kessler & Smith (2008: 168), and *C. spixiana* (Martius ex Mettenius 1856: 57) Bishop (1988: 5) (BS = 92%, PP = 0.68) but relations between these ten species remained uncertain due to low support levels within this clade, and differences in topology recovered by ML and BI. Two accessions of *Cochlidium linearifolium* were resolved as a crown group (BS = 100%, PP = 1) related to paraphyletic *C. rostratum*, with good node support (BS = 97%, PP = 0.99). The latter clade and *C. serrulatum* participate in a poorly resolved group (BS = 55%, PP = 0.77) with newly sequenced *C. jungens*, and *C. punctatum* (Raddi 1825: 11) Bishop (1978: 86) was resolved as an immediate external branch. *Enterosora campbellii* subsp. *spongiosa* was resolved as a sister to *E. percrassa* (Baker 1887: 26) L.E. Bishop in Bishop & Smith (1992: 352) (BS = 100%, PP = 1) and nested within the clade that also includes *E. enterosoroides* (Christ 1907: 260) A. Rojas in Rojas-Alvarado (2006: 11), *E. trichosora* (Hooker 1891: pl. 12) L.E. Bishop in Bishop & Smith (1992: 357), and *E. trifurcata* (Linnaeus 1753: 1084) L.E. Bishop in Bishop and Smith (1992: 353) (BS = 87%, PP = 0.99). In contrast, the species *E. sprucei* (Hooker 1861: pl. 10) Parris (2002: 426) and *E. parietina* (Klotzsch 1847: 373) L.E. Bishop in Bishop and Smith (1992: 357–358) were resolved as a clade (BS = 100%, PP = 1) separate from other *Enterosora*. It was a sister clade to *Adenophorus* in ML (BS = 61%), which in turn appeared as a sister clade to a well-supported group of *Cochlidium*, *Grammitis*, and *Lomaphlebia* (BS = 99%, PP = 1). In *Galactodenia*, new accessions were provided for *G. delicatula* and *G. subscabra*, proving their close relation to *G. parrisiae* Sundue & Labiak in Sundue *et al.* (2012: 345). The clade of *G. subscabra* and *G. parrisiae* is monophyletic (BS = 100%, PP = 1), but within this clade, the former species resulted paraphyletic with respect to the latter. In the case of *G. delicatula,* the node support was insufficient in ML to consider paraphyly, but in BI it was not resolved, remaining as a part of a polytomic node that includes *Galactodenia* sp. (*Evans et al. 78*, US !) and the clade of *G. subscabra* and *G. parrisiae*. Two new accessions for neotropical *Grammitis* were resolved as expected within the clade of *Grammitis* s.s.; *G. bufonis* and *G. limbata* appear as single clade (BS = 89%, PP = 1), with *G. ebenina* (Maxon 1915: 224) Tardieu (1953: 211) as an immediate relative (BS = 73%, PP = 0.93). *Lellingeria apiculata* (*Shalisko 319*, IBUG!) appeared as a part of an unresolved clade with another accession for the same species and *L. affinis* Labiak (2013: 14) (BS = 100%, PP = 1). The newly sequenced *L. tmesipteris* was resolved as sister taxon to *L. pseudocapillaris* (Rosenstock 1913: 17) A.R. Sm. & R.C. Moran in Smith *et al.* (1991: 86) (BS = 100%, PP = 1). *Lomaphlebia linearis* was resolved as sister group to *L. turquina* Sundue & Ranker in Sundue *et al.* (2014: appendix 2) (BS = 100%, PP = 1). Five accessions of *Melpomene* identified as *M. moniliformis* and *M. flabelliformis* were resolved within the same cluster (BS = 71%) sister to *M. pilosissima*. Data do not support separation between *M. moniliformis* and *M. flabelliformis*. The new accession of *M. pilosissima* was resolved as a sister to a previously known sample of this species (BS = 62%, PP = 1). The clade formed by several accessions of *M. xiphopteroides* had low support in ML (BS = 48%, PP = 0.97). *Melpomene zempoaltepetlensis* was resolved within the poorly supported clade (BS = 41%) that includes *M. anazalea* Sundue & Lehnert (2008: 209) and *M. personata* Lehnert (2008: 237). *Moranopteris setulosa* was the new species sampled in *Moranopteris*, that was found to be closely related to *M. truncicola* (Klotzsch 1847: 374) R.Y. Hirai & J. Prado in *Hirai et al.* (2011: 1132)

(BS = 99%, PP = 1). Seven new accessions of *M. taenifolia* were resolved as a strongly supported monophyletic clade (BS = 100%, PP = 1) sister to *M. setulosa* and *M. truncicola*. Two new accessions of *Mycopteris* aff. *semihirsuta* were resolved as a clade that includes *M. leucosticta* (Smith 1875: 185) Sundue (2014: 182) (BS = 86%, PP = 0.92), separate from the known position of *M. semihirsuta* (*Sundue & Vasco 1246*, NY!). The position of *Stenogrammitis delitescens* was found to be close to *S. prionodes* (Mickel & Beitel 1988: 203) Labiak (2011: 147) (BS = 100%, PP = 1); *S. nutata* (Jenman 1886: 272) Labiak (2011: 147) was resolved as a sister branch to *S. limula* (BS = 96%, PP = 1). *S. jamesonii* (*Sundue 3422*) was close to *S. wittigiana* (Fée & Glaziou ex Fée 1873: 50) Labiak (2011: 148) (BS = 100%, PP = 1). The position of *Terpsichore alfaroi* (*Lellinger & White 998*, US!) was resolved sister to *T. chrysleri* (BS = 100%, PP = 1) Another newly sampled species, *T. staheliana,* is sister to *T. asplenifolia* (Linnaeus 1753: 1084) Smith (1993: 485) with low support in ML (BS = 44%) and their closest relative is *T. lehmanniana* (Hieronymus 1904: 513) Smith (1993: 487) (BS = 61%, PP = 0.78). Newly sampled *Zygophlebia cornuta* was resolved as sister branch to *Z. sectifrons*, represented by two accessions; the clade of two species had maximal support (BS = 100%, PP = 1).

## Discussion

The general topology in the results of phylogenetic analysis resembles that of Sundue *et al.* (2014) and Bauret *et al.* (2017). Our results confirmed recognition of monophyletic clades as in Bauret *et al.* (2017), as well as the artificial nature of *Ctenopterella*, *Enterosora*, and *Grammitis* s.l. Similarly, we found *Zygophlebia* to be paraphyletic with respect to *Enterosora*. *Lomaphlebia linearis,* as type species of *Lomaphlebia,* is sequenced here for the first time and was confirmed as a sister to *Lomaphlebia turquina*.

Our data, based on the specimen of *Evans et al. 15* (US!) confirmed the proposal of Rojas-Alvarado (2017) to recognize *Moranopteris setulosa* as being independent from *M. nana* (Fée 1852: 238) Hirai & Prado (2011: 1131), contrary to the point of view of Moran (1995). Our specimen of *Terspichore alfaroi* (*Lellinger & White 998*; US!) resolved within *Terpsichore* rather than *Alansmia*; it was tentatively treated in the latter by Moguel & M. Kessler (2013) [as *Alansmia alfaroi* (Donnell Smith 1902: 262) Moguel & M. Kessler in Kessler *et al*. (2011: 239)] who noted that it lacked the *Alansmia* synapmorphy of stellate setae (Kessler *et al.* 2011). Thus, placement in *Tersichore* is in fact more congruent with morphology.

In our results, *Enterosora campbellii* subsp. *spongiosa* was resolved within the main clade of *Enterosora*. Although this is a subspecies of the type species, we expect that it indicates the position of the type because the two described subspecies differ only in degree of leaf dissection, and intermediate forms between them were observed (Bishop & Smith, 1992). The only other distinction is geographic, with E. *campbellii* subsp. *campbellii* occurring in Jamaica and Venezuela and *E. campbellii* subsp. *spongiosa* being found in Costa Rica and Panama. Our specimen (*Lellinger & White 1540*, F!, US!) from Costa Rica morphologically belongs to *E. campbellii* as understood by Bishop & Smith (1992).

The species of *Enterosora* resolved along with *E. campbellii* included *E. percrassa*, *E. enterosoroides*, *E. trichosora*, and *E. trifurcata*. These five species of *Enterosora* formed a topology compatible with informal groups discussed in Bishop & Smith (1992), excluding *E. enterosoroides* that is morphologically intermediate between two groups. The independent clades of polyphyletic *Enterosora* include *E. barbatula* (Baker in Hooker & Baker 1867: 323) Parris (2002: 426) from Africa and Madagascar, represented in our data by sample *Rakotondrainibe 6951* (P!), which is resolved within *Zygophlebia*. The results of Bauret *et al.* (2017) indicate that *E. barbatula* may include cryptic species because other samples of this species not included in our sampling are related to *Ceradenia*.

Finally, the remaining *Enterosora* clade was formed by samples of *E. parietina* and *E. sprucei*. These samples were resolved distantly from the others, and formed a clade with *Adenophorus*, *Cochlidium*, *Grammitis* s.s., and *Lomaphlebia*. The presence of this independent clade of *Enterosora* was first shown by Bauret *et al.* (2017), who sampled seven accessions of *E. sprucei* from Madagascar and two of *E. parietina* from the Neotropics. Furthermore, the morphological characters shared by *E. parietina* and *E. sprucei* that are not observed in other *Enterosora* sensu Bishop and Smith (1992) include placement of sori in the middle of the vein, and a somewhat higher number of annulus cells in sporangia (13–16) compared with 11–15 in other neotropical *Enterosora* species. The number of species in this clade, however, remains unclear. Bauret *et al.* (2017) revealed the possible polyphyletic nature of *E. parietina* in their sampling, if *E. sprucei* is recognized. The position of samples of *E. parietina, Sundue 3097* (VT!) and *Schuettpelz 230* (DUKE) in the above-mentioned study is resolved independently from each other, both relative to *E. sprucei*, however, based on different cpDNA markers. There are no genetic markers shared by two samples of *E. parietina,* and therefore the actual topology of relations between samples of *E. parietina* and *E. sprucei* remains uncertain. The recommendation of Bauret *et al.* (2017) is to treat *E. sprucei* as a synonym to *E. parietina*, following Bishop & Smith (2002). Another species with the same combination of characters is the African *E. gilpinae* (Baker 1877: 204) Bishop & Smith (1992: 359) that closely resembles *E. parietina*, differing from the latter in size and rhizome scales. Parris (2002, 2005) treats *E. gilpinae* as a synonym of *E. sprucei*. Thus, until a more robust data set can be analyzed, geography compels us to maintain two species for the time being, one neotropical and one Malagasy.

Our results indicate that *Zygophlebia* is paraphyletic with respect to *Enterosora* sensu Bishop and Smith (1992) in our study, and in the data of Bauret *et al.* (2014). Our data did not confirm the existence of two morphologically defined groups of *Zygophlebia* from Rakotondrainibe & Deroin (2006). Instead, the phylogenetic data were consistent with the definition of clades based on biogeography and leaf venation pattern: the Neotropical clade that includes *Z. cornuta*, *Z. matthewsii*, and *Z. sectifrons* mostly present distal or intramarginal areoles, while another seven species of *Zygophlebia* from Madagascar and Africa located in a separate clade have irregular and occasional vein anastomoses. We resolve the paraphyly of *Enterosora* and *Zygophlebia* by recognizing a single genus as suggested by PPG I (2016). Morphologically, *Enterosora* and *Zygophlebia* are quite similar, the main difference being the conspicuous spongiose mesophyll of *Enterosora* and that sori are mostly elongated, somewhat sunken in *Enterosora*, and round superficial in *Zygophlebia* (Bishop & Smith, 1992). However, most other characters are shared by both genera including leaves with anastomosing veins and without hydathodes with straight setae but without whitish or brownish glands (Sundue 2010, Sundue *et al.* 2010). *Enterosora* is one of the first grammitid fern genera described from the Neotropics; thus, it has priority over *Zygophlebia*. The new combinations provided here for ten species were based on their positions in molecular phylogeny, confirmed by morphology. We suggest that most other *Zygophlebia* should also be combined as *Enterosora* but refrain from proposing combinations until phylogenetic analyses can be performed. These remaining species are namely: *Zygophlebia anjanajaribensis* Rakotondr. in Rakotondrainibe & Deroin (2006: 147), *Z. dudleyi* Bishop (1989: 113), *Z. eminens* (Morton 1967: 99) Bishop (1989: 113), *Z. humbertii* (C. Christensen 1928: 215) Parris in Roux (2009: 166), *Z. longipilosa* (Christensen 1903: 78) Bishop (1989: 109), *Z. major* (Reimers 1933: 937) Parris (2002: 433), *Z. rouxii* Rakotondrainibe & Parris (2018: 158), and *Z. werffii* Bishop (1989: 115).

*Evolution of spongiose mesophyll*.—Thick spongiosa and air-filled parenchyma have always been considered diagnostic for *Enterosora* as traditionally defined (Bishop & Smith, 1992). Although few species outside of the traditional *Enterosora* exhibit laminae quite as thick and spongy, previous phylogenetic analyses integrating morphological and molecular evidence indicate that this trait is in fact homoplastic and widespread among grammitid ferns (Sundue 2010, Sundue *et al.* 2010). Our results further extend this pattern and show that *Parrisia* is an additional example of the independent convergent evolution of this trait. The functional significance of spongiose mesophyll and whether it is an adaptive trait remains to be seen, and its repeated occurrence across grammitids provides an excellent opportunity for further investigation.

## Taxonomic treatment

***Parrisia*** Shalisko & Sundue, *gen. nov.* (Fig. 2)

**Type species:**—*Parrisia parietina* (Klotzsch) Shalisko & Sundue (=*Polypodium parietinum* Klotzsch).

**Basyonym:**—*Polypodium parietinum* Klotzsch. VENEZUELA. Aragua: ad saxor. parietes humidas Colonia Tovar, *Moritz 253* (holotype B!, fragment NY!, isotypes BM!, K!, P!).

**Diagnosis:**—*Parrisia* is similar to *Enterosora*, but differs from the latter by radial rhizomes (vs. dorsiventral), the location of sori in the medium of the vein and the presence of setae around the sori. It is distinguished from *Grammitis* s.s. by the absence of a dark-colored sclerotized leaf margin, and by the presence of setae on the blade. It differs from *Adenophorus* in lacking the uniseriate reddish glandular paraphyses and hairs, present in the latter.

**Description:**—*Plants* epiphytic, *rhizomes* radial, rarely dorsiventral, with golden brown or brown non-clathrate scales. *Fronds* monomorphic, stipes setose, brown or blackish, laminae simple, linear, linear-spathulate or linear-elliptic, rounded at the apex, attenuate at the base, sinuate, sometimes lobed up to 1/3 of the distance to midrib, somewhat thick and spongy; fronds covered with septate setae, from castaneous to brown, clustered close to sori, at midrib and on the margin, as well as with simple or branched glandular hairs on both leaf surfaces; hydathodes absent; veins free, from simple to forked, rarely two times forked. *Sori* round or nearly so, superficial or subimpressed, exindusiate, without waxy or glandular paraphyses, located abaxially on blades in a single row on both sides from the midrib, that start at some distance from blade base, and extend up to leaf apex, sori born medially on the one-time forked vein. *Sporangia* with 13 to 16 thickened annulus cells.

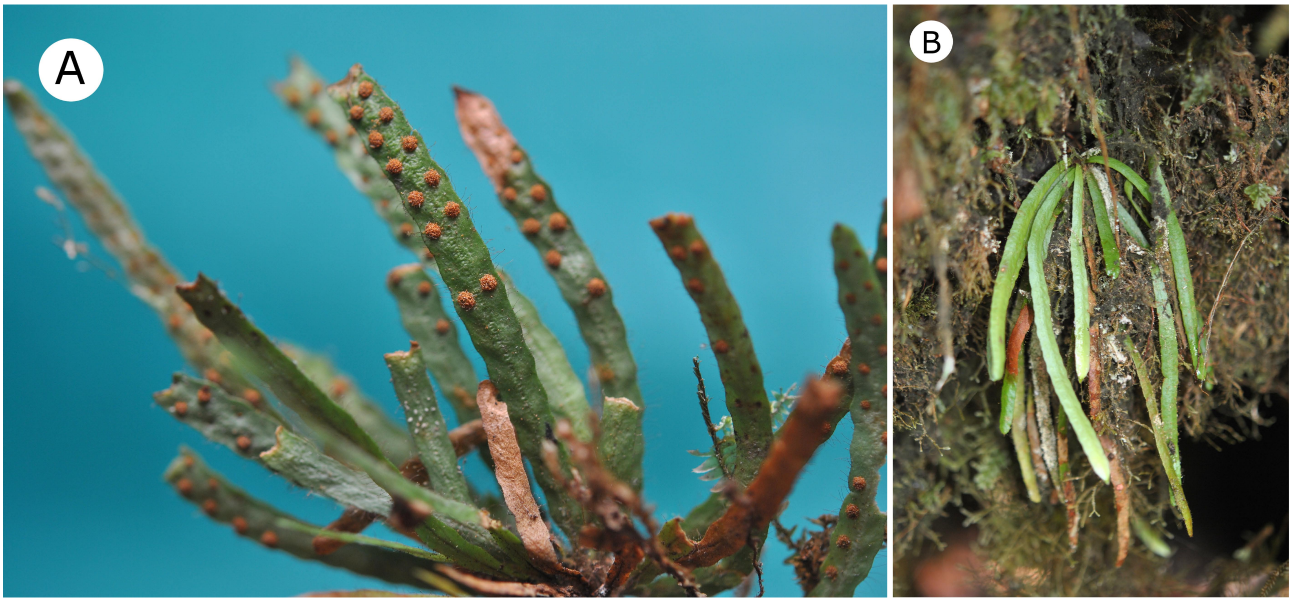


**FIGURE 2.** *Parrisia parietina* (Klotzsch) Shalisko & Sundue. A–B. Habit (*Sundue et al. 3233*). Photos by M. Sundue.

**Etymology:**—Named after Barbara S. Parris (*1945), honoring her enormous contributions to grammitid ferns, particularly in the paleotropics.

**Distribution:**—Mexico, Guatemala, Costa Rica, Panama, Jamaica, Hispaniola, Colombia, Venezuela, Ecuador, Peru, Bolivia, Africa, Madagascar, Mascarene islands.

**Generic comparison:**—*Parrisia* belongs to grammitid genera without clearly defined hydathodes (anhydathodous), among them are *Adenophorus*, *Chrysogrammitis* Parris (1998: 909), *Ceradenia, Enterosora* (including *Zygophlebia*), *Grammitis* s.s., *Lomaphlebia*, *Prosaptia* C.Presl (1836: 165–166) and *Scleroglossum* Alderwerelt van Rosenburgh (1912: 37–39). Compared to the phylogenetically related genera, it is distinguished from *Grammitis* s.s. by the absence of a dark-colored sclerotized leaf margin, and by the presence of setae on the blade. *Adenophorus* differs from *Parrisia* by their unique uniseriate reddish glandular paraphyses and hairs (Ranker 2008) that are lacking *Parrisia*. *Lomaphlebia* is distinguished from *Parrisia* by the presence of a commissure vein at the margin of the leaf blade, thus presenting a row of areoles along the margin. *Cochlidium* is distinguished from *Parrisia* by the presence of hydathodes, the absence of dark colored setae, and presence of a coenosorus deeply immersed into the lamina in several species. *Ceradenia* is distinguished from *Parrisia* by the presence of waxy deposits of a white, yellowish, or tan color, produced by paraphyses, as well as a lack of circumsoral setae. *Parrisia* is distinguished from *Enterosora* by radial rhizomes (vs. dorsiventral), the location of sori in the medium of the vein and the presence of setae around the sori.

The following species are transferred to the new genus:

***Parrisia parietina*** (Klotzsch) Shalisko & Sundue *comb. nov.* (Fig. 2)

Basionym:—*Polypodium parietinum* Klotzsch (1847: 373).

Homotypic synonyms:—*Grammitis parietina* (Klotzsch) Fée (1852: 233). *Enterosora parietina* (Klotzsch) L.E. Bishop in Bishop & Smith (1992: 357). Type:—VENEZUELA. Aragua: ad saxor. parietes humidas Colonia Tovar, *Moritz 253* (holotype B!, fragment NY!, isotypes BM!, K!, P!).

Heterotypic synonyms:—*Polypodium sprucei* Hooker (1861: pl. 10). *Grammitis sprucei* (Hook.) J. Smith (1875: 181). *Enterosora sprucei* (Hook.) Parris (2002: 426). Type:—PERU. San Martín: Tarapoto, Cerro Pelado, *Spruce 4746* (holotype K!, isotypes P!, US!).

*Polypodium rosulatum* Christ in Bommer & Christ (1896: 662). *Grammitis rosulata* (Christ) Lellinger (1977: 715). Type:—COSTA RICA. Forêts du Rio Naranjo, March 1893, *Pittier 7953* (holotype BR!, photos BM, US!).

*Polypodium yarumalense* Hieronymus (1904: 499). *Grammitis yarumalensis* (Hieron.) Proctor (1953: 36). Type:—COLOMBIA. Antioquía: Yarumal, *Lehmann 7390* (holotype B, isotypes BM!, K!, US!).

**Distribution:**—Southern Mexico, Guatemala, Costa Rica, Panama, Jamaica, Hispaniola, Colombia, Venezuela, Ecuador, Peru.

**Additional specimens examined:**—COLOMBIA. Antioquia: Municipio Frontino, Corregimiento Carauta, Parque Nacional Natural Las Orquídeas, sector Tres Bocas, cañón del Río Tercero, cerca a la finca la Pradera, 1740–1800 m, 06 September 2012, *Sundue et al. 3233* (NY!, MO).—COSTA RICA. Cartago: SE of Orosi, ca. 2.2 km SSE of Purisil, above Finca La Concordia, at the head of the valley, 1800–2300 m, 9–11 August 1970, *Lellinger & White 1531* (US!, F!); Ca. 22 km E of Turrialba, high ride above Platanillo, 1200–1450 m, 22 August 1967, *Mickel 3386* (NY!), *3640* (NY!); Heredia: between Abra and Aromal de Barba, 1900 m, 1 May 1969, *Gómez-P. 2198* (NY!, F!); Río Vueltas, 2100 m, 23 May 1969, *Gómez-P. 2214* (NY!, F!). Puntarenas: Monteverde, Reserva Bosque Nuboso Santa Elena, Sendero Caño Negro Cloud Forest, 1700 m,10°20′24″N, 84°47′10″W, 29 January 2013, *Matos & Matos 2139* (NY!).—DOMINICAN REPUBLIC. Monte Cristi: Cordillera Central, Monción, high ridge between Río Cenobi and Río San Juan, 1900 m, 11 June 1929, *Ekman 12819a* (NY!).—ECUADOR. Azuay: Forest along the road from Gualacea to Limon, 2838 m, 3.007185°N, 78.626204°S, *Olivares et al. 219* (VT!, Z!); Loja: Estación Científica San Francisco, forest at 5 m from trail along Transect 1, 2200 m, 3.9790445°, -79.073995°, *Olivares et al. 10* (VT!, Z!); Tungurahua: Cantón Baños, Parroquia Río Verde, sendero para la Cascada Manto del Ángel, justo después de la Puente Machay y antes del Túnel Churosinguna en la carretera Baños-Puyo, 1530 m, 01°23′56″S, 78°16′53″W, 9 August 2014, *Matos 2503* (NY!).—JAMAICA. Morge's gap, 1524 m, 2 February 1903, *Underwood 540a* (NY!); Blue Mountains, May 1903, *Watt s.n.* (NY!, US!).—MEXICO. Oaxaca: Ixtlán, 79 km N of Ixtlán de Juárez on Route 175, 1 km S of Campamento Vista Hermosa, 1173–1402 m, 27 July 1971, *Mickel 5739* (NY!, UC); Santiago Comaltepec, Relampago, área communal protegida de Comaltepec, along carettera principal MEX 175, 1752 m, 17°34.341′N, 96°23.039′W, *Sundue & Torres-C. 3097* (MEXU!, VT!); Villa Alta, moist woods along trial from Yetzelalag toward Lovani, 1067 m, 2 December 1971, *Hallberg 1515* (NY!, UC); valley of the Yelagago River, ca. 20 mi, NE of Villa Alta, 1067–1219 m, 17°25′N, 96°05′W, 29 July 1962, *Mickel 1064* (NY!). PERU. Bagua: ca. 12–20 km (by trail) E of La Peca, 1900–2400 m, 14 July 1978, *Barbour 2723* (F!).—VENEZUELA. Mérida: distrito Andres Bello, municipio Zerpa, La Carbonera, Bosque San Eusebio, 2400–2800 m, 18 January 1982, *Martín et al. 131* (F!).

**Notes:—**Position based on molecular and morphological data.

***Parrisia gilpinae*** (Baker) Shalisko & Sundue *comb. nov.*

Basionym:—*Polypodium gilpinae* Baker (1877: 204).

Homotypic synonyms:—*Enterosora gilpinae* (Baker) Bishop & Smith (1992: 359), *Grammitis gilpinae* (Baker) Tardieu (1960: 59). Type:—MADAGASCAR. Antananarivo, March 1877, *Gilpin s.n.* (holotype K, fragment BM!).

Heterotypic synonyms:—*Polypodium microphyllum* Baker (1897: 299). Type:—MADAGASCAR. Tanala: forest of Ambohimitombo, 1450–1560 ft alt., 31 December 1894, *C.I. Forsyth Major 477* (holotype K!, isotypes B, BM!, P!, UC!).

*Polypodium pseudopoolii* Reimers in Mildbraed (1933: 934) as "*pseudo-Poolii*". Type:—TANZANIA. Tanganyika, Uluguru-Gebirge, NW, Parata Pass, ca. 1910 m, 18 October 1932, *Schlieben 2827a* (holotype B!).

**Distribution:—**Tanzania, Madagascar.

**Additional specimens examined:**—MADAGASCAR. Massif al Manangarcio, 1909, *Perrier de la Bâthie 7478* (US!). Alaotra-Mangoro: Massif de l'Andrangovalo au sud-est du lac Alaotra, Réserve Naturelle No. 3 dite de Zakamena, bassin de l'Onibe, 1200–1500 m, October 1937, *Humbert & Cours 17839* (P!); Moramanga, Andasibe, Parc National de Mantadia, piste commencant au PK14 et s'élevant vers la crête, 1050 m, 18°50′44″S, 48°26′17″E, 12 November 2004, *Rouhan & Janssen 414* (P!); Parc National Mantadia, aux alentours de la piste au départ de PK14, circuit Tsakoka, sur la crête, 950 m, 18°47′50″S, 48°25′54″E, 8 November 2011, *Rouhan et al. 1343* (P!); Parc National Mantadia, aux alentours de la piste au départ de PK9, circuit Rianasoa-Chutes sacrées, 910 m, 18°49′50″S; 48°26′7″E, 10 November 2011, *Rouhan et al. 1381* (P!). Haute Matsiatra: Ambalavao-Aantanifotsy, p. N de l'Andringitra Forêt d'Imaitso, 1600–1650 m, 22°8′S, 46°56′E, 18 November 2004, *Rakotondrainibe et al. 6936* (P!). Mahajanga: Mangindrano, Massif du Tsaratanana, Montagnes au N de Mangindrano, crête menant de Matsaborimaiky vers Bepia, entre le point culminant de la crête menant vers Bepia, 2480–2490 m, 14°8′39″S, 48°58′23″E, 12 May 2005, *Janssen et al. 2925* (P!). Fianarantosa [Vatovavy-Fitovinany]: PN Ranomafana forêt de Vohiparara, 1100–1150 m, 21°14′03″S, 47°23′52″E, 27 April 2005, *Janssen 2837* (P!). Sava: Andapa, Parc National de Marojejy, sur le site dit du Takhtajania, au dessus du Camp 2, 1000 m, 14°26′23″S; 49°45′34″E, 21 October 2011, *Rouhan et al. 1145* (P!); Parc National de Marojejy, dans la pente du versant exposé Nord entre Camp 3 et Camp 2, plus proche du Camp 3, 14°26′10″S; 1210 m, 49°44′44″E, 26 October 2011, *Rouhan et al. 1227* (P!).

**Notes:—**Based upon molecular and morphological data. We suggest treating all samples of *Enterosora sprucei* from Madagascar presented in Bauret *et al.* (2017) as *Parrisia gilpinae*.

We propose the following combinations to transfer species from *Zygophlebia* to *Enterosora*:

***Enterosora cornuta*** (Lellinger) Shalisko & Sundue, *comb. nov*. Basionym:—*Grammitis cornuta* Lellinger (1985: 381). Homotypic synonym:—*Zygophlebia cornuta* (Lellinger) Bishop (1989: 112). Type:—COSTA RICA: San Jose, Las Nubes, ca. 1500–1900 m, *Standley 38843* (holotype US!, photo CR, isotype GH!).

***Enterosora devoluta*** (Baker) Shalisko & Sundue, *comb. nov*. Basionym:—*Polypodium devolutum* Baker (1876: 419–420). Homotypic synonyms:—*Ctenopteris devoluta* (Baker) Tardieu (1959: 445), *Zygophlebia devoluta* (Baker) Parris (2002: 432), *Grammitis devoluta* (Baker) Christenhusz (2018: 43). Type:—MADAGASCAR. *Pool s.n.* (holotype K!).

***Enterosora forsythiana*** (Baker) Shalisko & Sundue, *comb. nov.* Basionym:—*Polypodium forsythianum* Baker (1897: 300). Homotypic synonyms:—*Ctenopteris forsythiana* (Baker) Tardieu (1959: 445), *Zygophlebia forsythiana* (Baker) Parris (2002: 432), *Grammitis forsythiana* (Baker) Christenhusz (2018: 44). Type:—MADAGASCAR. Tanala: forest of Ambohimitombo, 442–476 m, *C.I. Forsyth Major 200* (holotype K!).

***Enterosora goodmanii*** (Rakotondr.) Shalisko & Sundue, *comb. nov*. Basionym:—*Zygophlebia goodmanii* Rakotondr. in Rakotondrainibe & Deroin (2006: 145–147). Homotypic synonym:—*Grammitis goodmanii* (Rakotondr.) Christenhusz (2018: 44).Type:—MADAGASCAR. Province de Fianarantsoa, foret de Vinanitelo, alt. 1225 m, 30 Oct 2000, *Rakotondrainibe, Andriambololona & Rasolohery 6168* (holotype P!, isotype TEF).

***Enterosora humbertii*** (C. Chr.) Shalisko & Sundue, *comb. nov*. Basionym:—*Polypodium humbertii* Christensen (1928: 215–216). Homotypic synonyms:—*Ctenopteris humbertii* (C.Chr.) Tardieu (1959: 445), *Grammitis humbertii* (C.Chr.) Christenhusz (2018: 44), *Zygophlebia humbertii* (C.Chr.) Parris in Roux (2009: 166). Type:—MADAGASCAR. Massif de l'Andringitra, vallée de la Riambava, 27 November 1924, *H. Humbert 3752* (BM!).

***Enterosora mathewsii*** (Kunze ex Mett.) Shalisko & Sundue, *comb. nov*. Basionym:—*Polypodium mathewsii* Kunze ex Mettenius (1856: 74). Homotypic synonyms:—*Grammitis mathewsii* (Kunze ex Mett.) Morton (1970: 66), *Zygophlebia mathewsii* (Kunze ex Mett.) Bishop (1989: 108). Type:—PERU. Amazonas: Chachapoyas, *Mathews 1811* (lectotype B!, designated by Bishop 1989: 108,, photo F, isolectotype B!, BM, K!, P!).

***Enterosora sectifrons*** (Kunze ex Mett.) Shalisko & Sundue, *comb. nov*. Basionym:—*Polypodium sectifrons* Kunze ex Mettenius (1856: 99). Homotypic synonyms:—*Grammitis sectifrons* (Kunze ex Mett.) Seymour (1975: 180), *Zygophlebia sectifrons* (Kunze ex Mett.) Bishop (1989: 110). Type:—PUERTO RICO. *Schwanecke s.n.* (lectotype GH, designated by Proctor 1985: 585).

***Enterosora subpinnata*** (Baker) Shalisko & Sundue, *comb. nov*. Basionym:—*Polypodium subpinnatum* Baker (1876: 419). Homotypic synonyms:—*Grammitis subpinnata* (Baker) Christenhusz (2018: 49), *Xiphopteris villosissima* subsp. *subpinnata* (Baker) Schelpe (1969: 8). *Zygophlebia subpinnata* (Baker) L.E. Bishop ex Parris (2002: 433). Type:—MADAGASCAR. Antananarivo, *Pool s.n.* (holotype K!, isotype K!).

***Enterosora torulosa*** (Baker) Shalisko & Sundue, *comb. nov*. Basionym:—*Polypodium torulosum* Baker (1877: 204). Homotypic synonyms:—*Ctenopteris torulosa* (Baker) Tardieu (1959: 445), *Zygophlebia torulosa* (Baker) Parris in Roux (2009: 166), *Grammitis torulosa* (Baker) Christenhusz (2018: 50). Type:—MADAGASCAR. Antananarivo: "On a tree at Andrangaloaka", March 1877, *H. Gilpin s.n.* (holotype K!).

***Enterosora villosissima*** (Hook.) Shalisko & Sundue, *comb. nov*. Basionym:—*Polypodium villosissimum* Hooker (1862: 197). Homotypic synonyms:—*Grammitis villosissima* (Hook.) Ching (1941: 241), *Ctenopteris villosissima* (Hook.) Harley (1955: 92–93), *Xiphopteris villosissima* (Hook.) Alston (1956: 27), *Zygophlebia villosissima* (Hook.) Bishop (1989: 117). Type:—SIERRA LEONE. Sugar-loaf Mountains, *C. Barter s.n.* (lectotype K!, designated by Schelpe 1960: 8).

## Acknowledgments

The research was partially funded by CONACYT scholarship No. 256271/275105 for Viacheslav Shalisko. We thank Eric Schuettpelz as a curator of the fern collection in the US for the facilities to study specimens and obtain samples for DNA extraction, Robbin Moran for the opportunity to study specimens in NY and providing useful bibliographic references, and Miguel Ángel Pérez Farrera and Neptalí Ramírez Marcial for support during the field work in Chiapas in January of 2014. We thank reviewers Marcus Lehnert and Weston Testo for helpful comments, and further thank Marcus Lehnert for identification of *Melpomene* specimens.


## References


Alston, A.H.G. (1956) New African ferns. *Boletim da Sociedade Broteriana* Sér. 2, 30: 5–27.

Alderwerelt van Rosenburgh, C.R.W.K. (1912) New or interesting Malayan ferns 4. *Bulletin du Jardin Botanique de Buitenzorg* Sér. 2, 2 (7): 1–41.

Baker, J.G. (1876) On a collection of ferns made by Mr. William Pool in the interior of Madagascar. *The Journal of the Linnean Society, Botany* 15: 411–422.
https://doi.org/10.1111/j.1095-8339.1876.tb00251.x

Baker, J.G. (1877) On a collection of ferns made by Miss Helem Gilpin in the interior of Madagascar. *The Journal of the Linnean Society, Botany* 16: 197–205.
https://doi.org/10.1111/j.1095-8339.1877.tb00173.x

Baker, J.G. (1887) Mr. J. J. Cooper's Costa Rica ferns. *Journal of Botany, British and Foreign* 25: 24–26.

Baker, J.G. (1897) Diagnoses Africanae, X. *Bulletin of Miscellaneous Information, Kew* 1897 (128–129): 243–300.

Bauret, L., Gaudeul, M., Sundue, M.A., Parris, B.S., Ranker, T.A., Rakotondrainibe, F., Hennequin, S., Ranaivo, J., Selosse, M.-A. & Rouhan, G. (2017) Madagascar sheds new light on the molecular systematics and biogeography of grammitid ferns: new unexpected lineages and numerous long-distance dispersal events. *Molecular Phylogenetics and Evolution* 111: 1–17.
https://doi.org/10.1016/j.ympev.2017.03.005

Bishop, L.E. (1978) Revision of the genus *Cochlidium* (Grammitidaceae). *American Fern Journal* 68 (3): 76–94.
https://doi.org/10.2307/1546453

Bishop, L.E. (1988) *Ceradenia*, a new genus of Grammitidaceae. *American Fern Journal* 78 (1): 1–5.
https://doi.org/10.2307/1547596

Bishop, L.E. (1989) *Zygophlebia*, a new genus of Grammitidaceae. *American Fern Journal* 79 (3): 103–118.
https://doi.org/10.2307/1547292

Bishop, L.E. & Smith, A.R. (1992) Revision of the fern genus *Enterosora* (Grammitidaceae) in the New World. *Systematic Botany* 17 (3): 345–362.
https://doi.org/10.2307/2419476

Bommer, J.-E. & Christ, K.H.H. (1897) Filices novae. *Bulletin de l'Herbier Boissier* 4 (10): 657–663.

Ching, R.C. (1941) New family and combinations of ferns. *Bulletin of the Fan Memorial Institute of Biology, Botany* 10 (5): 235–256.

Christenhusz, M.M.J., Fay, M.F. & Byng, J.W. (2018) *The global flora, a practical guide to vascular plant species of the world. Special Edition, GLOVAP Nomenclature Part 1, Vol. 4.* Plant Gateway, Bradford, U.K., 155 pp.

Christensen, C. (1903) New ferns from Brazil. *Botanisk Tidsskrift* 25: 77–81.

Christensen, C. (1928) Fougères nouvelles ou peu connues de Madagascar récoltées par H. Humbert en 1924. *Archives de Botanique (Caen), Bulletin mensual* 2 (12): 209–216.

Christensen, C. (1929) Taxonomic fern-studies I–II. *Dansk Botanisk Arkiv* 6: 1–102.

Christ, K.H.H. (1907) Primitiae florae costaricensis, Filices V. *Bulletin de l'Herbier Boissier* Série 2, 7 (4): 257–276.

Christ, K.H.H. (1909) Primitiae florae costaricensis, Filices, VI. *Bulletin de la Société Botanique de Genève* Série 2, 1 (5): 216–236.

Copeland, E.B. (1955 [1956]) *Ctenopteris* in America. *Philippine Journal of Science* 84 (4): 381–471.

Darriba, D., Taboada, G.L., Doallo, R. & Posada, D. (2012) jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9 (8): 772.
https://doi.org/10.1038/nmeth.2109

Desvaux, N.A. (1811) Observations sur quelques nouveaux genres de fougères et sur plusieures espèces nouvelles de la même famille. *Der Gesellschaft Naturforschender Freunde zu Berlin Magazin für die neuesten Entdeckungen in der gesammten Naturkunde* 5:

297–330.
Donnell Smith, J. (1902) Undescribed plants from Guatemala and other central American republics, XXIII. *Botanical Gazette* 33 (4): 249–262.
https://doi.org/10.1086/328223
Doyle, J.J. & Doyle, J.L. (1987) A rapid DNA isolation procedure from small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11–15.
Duraud, T. & Pittier, H. (1896) Primitiae florae costaricensis. *Bulletin de la Société Royale de Botanique de Belgique* 35 (1): 151–198.
Feé, A.L.A. (1852) Genera filicum. Exposition des genres de la famille des polypodiacées (classe des fougères). *Mémoires sur les familles des fougères* 5: 1–387.
Fée, A.L.A. (1873) *Cryptogames vasculaires (Fougères, Lycopodiacées, Hydropteridées, Equisetacées) du Brésil, II Partie, Supplément et révision*. J.B. Baillière, Paris, 115 pp.
Gómez-P., L.D. (1982) Plantae mesoamericanae novae, VI. *Phytologia* 52 (3): 153–156.
Gaudichaud-Beaupré, M. (1824) Descriptions du *Pinonia*, du *Schizoloma*, de l'*Adenophorus* et du *Freycinetia*, nouveaux genres de plantes recuillies. *Charles Annales des Sciences Naturelles (Paris)* 3: 507–510.
Harley, W.J. (1955) The ferns of Liberia. *Contributions from the Gray Herbarium of Harvard University* 177: 58–101.
Hayata, B. (1928) On the Systematic Importance of the stelar system in the Filicales, III. *Botanical Magazine, Tokyo* 42 (499): 334–348.
https://doi.org/10.15281/jplantres1887.42.334
Hieronymus, G. (1904 [1905]) Plantae Lehannianae in Guatemala, Columbia et Ecuador regionibusque finitimis collectae, additis quibusdam ab aliis collectoribus ex iisdem regionibus allatus determinatat et descriptae, Pteridophyta. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 34: 417–582.
Hirai, R.Y., Rouhan, G., Labiak, P.H., Ranker, T.A. & Prado, J. (2011) *Moranopteris*: A new Neotropical genus of grammitid ferns (Polypodiaceae) segregated from Asian *Micropolypodium*. *Taxon* 60 (4): 1123–1137.
Hirai, R.Y. & Prado, J. (2012) Monograph of *Moranopteris* (Polypodiaceae). *Pteridologia* 4: 1–113.
https://doi.org/10.5962/bhl.title.124914
Hooker, W.J. (1861) *A second century of ferns: being figures with brief descriptions of one hundred new, or rare, or imperfectly known species of ferns from various parts of the world.* William Pamplin, London.
Hooker, W.J. (1862) *Polypodium*. *Species Filicum* 4: 163–273.
Hooker, W.J. & Baker, J.G. (1867) *Synopsis Filicum, or a synopsis of all known ferns*. Robert Hardwicke, London, 482 pp.
Im Thurn, E.F. (1886) Notes on the plants observed during the Roraima expedition of 1884. *Timehri* 5: 145–223.
Jacquin, N.J. (1789 [1791]) *Collectanea ad botanicam, chemiam, et historiam naturalem, spectantia, cum figuris*. *Vol. 3.* Vindobonae, Ex Officina Wappleriana, 306 pp.
Jenman, G.S. (1886) Some additional Jamaica ferns. *Journal of Botany, British and Foreign* 24 (288): 265–273.
Jenman, G.S. (1897) Ferns – synoptical list, XLVI. *Bulletin of the Botanical Department, Jamaica* New series, 4: 112–141.
Katoh, K. & Toh, H. (2008) Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* 9 (4): 286–298.
https://doi.org/10.1093/bib/bbn013
Kaulfuss, G.F. (1820) Kurze Anleitung zum Selbststudium der kryptogamischen Gewächse. *Berlinisches Jahrbuch fur die Pharmacie und fur die Damit Verbundenen Wissenschaften* 21: 20–54.
Kessler, M. & Smith, A.R. (2008) New species of grammitid ferns (Polypodiaceae, Polypodiopsida) from Bolivia. *Organisms Diversity & Evolution* 8 (3): 167.e1–e18.
https://doi.org/10.1016/j.ode.2007.04.003
Kessler, M., Moguel-Velásquez, A.L., Sundue, M. & Labiak, P.H. (2011) *Alansmia*, a new genus of grammitid ferns (Polypodiaceae) segregated from *Terpsichore*. *Brittonia* 63 (2): 233–244.
https://doi.org/10.1007/s12228-010-9156-y
Klotzsch, J.F. (1847) Beiträge zu einer Flora der Äquinoctial-Gegenden der neuen Welt, Filices. *Linnaea* 20: 337–432.
Kunze, G. (1851) *Jamesonia adnata* Kunze. *Die Farrnkräuter* 2: 80.
Labiak, P.H. (2011) *Stenogrammitis*, a new genus of grammitid ferns segregated from *Lellingeria*. *Brittonia* 63 (1): 139–149.
https://doi.org/10.1007/s12228-010-9148-y
Labiak, P.H. (2013) Grammitid ferns (Polypodiaceae): I. *Lellingeria*. *Flora Neotropica Monograph* 111: 1–129.
Labiak, P., Sundue, M. & Rouhan, G. (2010) Molecular phylogeny, character evolution, and biogeography of the grammitid fern genus *Lellingeria* (Polypodiaceae). *American Journal of Botany* 97 (8): 1354–1364.
https://doi.org/10.3732/ajb.0900393
Labiak, P., Rouhan, G. & Sundue, M. (2010a) Phylogeny and taxonomy of *Leucotrichum* (Polypodiaceae): a new genus of grammitid ferns from the Neotropics. *Taxon* 59 (3): 911–921.

https://doi.org/10.1002/tax.593019
Lehnert, M. (2008) Eleven new species in the grammitid fern genus *Melpomene* (Polypodiaceae). *American Fern Journal* 98 (4): 214–250.
https://doi.org/10.1640/0002-8444-98.4.214
Lehnert, M. (2010) On the recognition of varieties in the grammitid fern genus *Melpomene* (Polypodiaceae–Polypodiopsida). *Phytotaxa* 5: 47–63.
https://doi.org/10.11646/phytotaxa.5.1.3
Lehnert, M. (2013) Grammitid ferns (Polypodiaceae): II. *Melpomene*. *Flora Neotropica Monograph* 112: 1–122.
Lehnert, M., Kessler, M., Schmidt-Lebuhn, A.N., Klimas, S.A., Fehlberg, S.D. & Ranker, T.A. (2009) Phylogeny of the fern genus *Melpomene* (Polypodiaceae) inferred from morphology and chloroplast DNA analysis. *Systematic Botany* 34: 17–27.
https://doi.org/10.1600/036364409787602276
Lellinger, D.B. (1977) Nomenclatural and taxonomic notes on the pteridophytes of Costa Rica, Panama, and Colombia, I. *Proceedings of the Biological Society of Washington* 89 (61): 703–732.
Lellinger, D.B. (1985) Nomenclatural and taxonomic notes on the pteridophytes of Costa Rica, Panama, and Colombia, II. *Proceedings of the Biological Society of Washington* 98 (2): 366–390.
León-Parra, A. (2012) *Ceradenia* (Polypodiaceae). *Flora de Colombia* 29: 7–82.
Liebmann, F.M. (1849) Mexicos Bregner, en systematisk, critisk, plantegeographisk Undersögelse. *Kongelige Danske videnskabernes Selskabs Skrifter, Naturvidenskabeli Mathematisk Afdeling* 1: 151–322.
Linnaeus, C. (1753) *Species plantarum*, Vol. 2. Salvius, Stockholm, 640 pp.
Luo, A., Qiao, H., Zhang, Y., Shi, W., Ho, S.Y., Xu, W., Zhang, A. & Zhu, C. (2010) Performance of criteria for selecting evolutionary models in phylogenetics: a comprehensive study based on simulated datasets. *BMC Evolutionary Biology* 10: 242.
https://doi.org/10.1186/1471-2148-10-242
Martens, M. & Galeotti, H. (1842) Mémoire sur les Fougères du Mexique, et considérations sur la geographie botanique de cetle contrée. *Nouveaux Mémoires de l'Academie Royale des Sciences et belles Lettres de Bruxelles* 15 (5): 1–95.
Maxon, W.R. (1904) On the names of the Jamaican species of *Polypodium*. *Bulletin of the Torrey Botanical Club* 32: 73–76.
https://doi.org/10.2307/2478508
Maxon, W.R. (1915) *Polypodium marginellum* and its immediate allies. *Bulletin of the Torrey Botanical Club* 42: 219–225.
https://doi.org/10.2307/2479651
Maxon, W.R. (1916) Studies of tropical American fern No. 6. *Contributions from the United States National Herbarium* 17 (7): 541–608.
Maxon, W.R. (1939) Fern miscellany, V. *Proceedings of the Biological Society of Washington* 52: 113–120.
Mettenius, G.H. (1856) Ueber einige Farngattungen, I, *Polypodium*. *Abhandlungen herausgegeben von der Senckenbergischen Naturforschenden Gesellschaft* 2: 1–138.
Mickel, J.T. & Beitel, J.M. (1988) Pteridophyte flora of Oaxaca, Mexico. *Memories of The New York Botanical Garden* 46: 1–568.
Mildbraed, J. (1933) Neue und seltene Arten aus Ostafrika (Tanganyika-Territ. Mandat) leg. H. J. Schlieben, IV. *Notizblatt des Königl. botanischen Gartens und Museums zu Berlin* 11: 912–945.
https://doi.org/10.2307/3994649
Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Proceedings of the Gateway Computing Environments Workshop (GCE)* 14: 1–8.
https://doi.org/10.1109/GCE.2010.5676129
Moguel-Velázquez, A.L. & Kessler, M. (2013) Grammitid ferns (Polypodiaceae): III. *Alansmia*. *Flora Neotropica Monograph* 113: 1–68.
Moran, R.C. (1995) *Micropolypodium*. *In:* Moran, R.C. & Riba, R. (Eds.) *Flora Mesoamericana*, *Volumen 1, Psilotaceae a Salviniaceae*. Universidad Nacional Autónoma de México, México D. F., pp. 383–385.
Morton, C.V. (1967) The genus *Grammitis* in Ecuador. *Contributions from the United States National Herbarium* 38: 85–123.Morton, C.V. (1970) A peculiar species of *Grammitis*. *American Fern Journal* 60 (2): 65–67.
https://doi.org/10.2307/1546932
Murillo, M.T. & Smith, A.R. (2003) *Luisma*, a new genus of Grammitidaceae (Pteridophyta) from Colombia. *Novon* 13 (3): 313–317.
https://doi.org/10.2307/3393265
Nagalingum, N.S., Schneider, H. & Pryer, K.M. (2007) Molecular phylogenetic relationships and morphological evolution in the heterosporous fern genus *Marsilea*. *Systematic Botany* 32 (1): 16–25.
https://doi.org/10.1600/036364407780360256
Palomera, V., Castro-Félix, P. & Villalobos-Arámbula, A.R. (2008) High yield of high quality DNA from vegetative and sexual tissues of Mexican white pine (*Pinus ayacahuite*). *African Journal of Biotechnology* 7: 51–54.

Parris, B.S. (1997) *Themelium*, a new genus of Grammitidaceae (Filicales). *Kew Bulletin* 52: 737–741.
https://doi.org/10.2307/4110307

Parris, B.S. (1998) *Chrysogrammitis*, a new genus of Grammitidaceae (Filicales). *Kew Bulletin* 53: 909–918.
https://doi.org/10.2307/4118878

Parris, B.S. (2002) New species and new combinations in African Grammitidaceae (Filicales). *Kew Bulletin* 57: 423–434.
https://doi.org/10.2307/4111120

Parris, B.S. (2005) Grammitidaceae. *In:* Beentje, H.J. & Ghazanfar, S.A. (Eds.) *Flora of Tropical East Africa*. Royal Botanic Gardens, Kew, 22 pp.

Parris, B.S. (2007) Five new genera and three new species of Grammitidaceae (Filicales) and the re-establishment of *Oreogrammitis*. *Gardens' Bulletin of Singapore* 58: 233–274.

Parris, B.S. (2013) *Archigrammitis*, a new genus of grammitid fern (Polypodiaceae) from Malesia and Polynesia. *Fern Gazette* 19: 135–138.

Perrie, L.R. & Parris, B.S. (2012) Chloroplast DNA sequences indicate the grammatid ferns (Polypodiaceae) in New Zealand belong to a single clade, *Notogrammitis* gen. nov. *New Zeeland Journal of Botany* 50: 457–472.
https://doi.org/10.1080/0028825X.2012.735247

Poiret, J.L.M. (1804) *Polypode flabelliforme*. *Encyclopédie Méthodique, Botanique* 5: 519.

Posthumus, O. (1927 [1926]) Notes on Guiana Ferns. *Recueil des Travaux Botaniques Néerlandais* 23: 396–402.

Presl, C.B. (1836) *Tentamen Pteridographiae: seu genera filicacearum praesertim juxta venarum decursum et distributionem exposita. Vol. 3.* Typis Filiorum Theophili Haase, Prague, 290 pp.
https://doi.org/10.5962/bhl.title.630

Presl, J.S. & Presl, C.B. (1822) Plantarum novarum Brasiliae praesertim Filicum Linnei diagnoses et descriptiones. *Deliciae Pragenses* 1: 155–198.

Proctor, J.R. (1953) A preliminary checklist of Jamaican pteridophytes. *Bulletin of the Institute of Jamaica* Science Series, 5: 1–89.

Proctor, J.R. (1985) *Ferns of Jamaica: a guide to the Pteridophytes*. British Museum (Natural History), London, 631 pp.

PPG I [Pteridophyte Phylogeny Group I] (2016) A community-derived classification for extant lycophytes and ferns. *Journal of Systematics and Evolution* 54 (6): 563–603.
https://doi.org/10.1111/jse.12229

Raddi, G. (1825) *Plantarum brasiliensium nova genera et species novae, vel minus cognitae* (Pars 1, Filices). Aloisii Pezzati, Florentiae, 101 pp.

Rakotondrainibe, F. & Deroin, T. (2006) Comparative morphology and rhizome anatomy of two new species of *Zygophlebia* (Grammitidaceae) from Madagascar and notes on the generic circumscription of *Zygophlebia* and *Ceradenia*. *Taxon* 55 (1): 145–152.
https://doi.org/10.2307/25065536

Rakotondrainibe, F., Jouy, A., Rouhan, G., Bauret, L. & Parris, B.S. (2018) Nouveautés taxonomiques et nomenclaturales chez les fougères grammitides (Pteridophyta, Polypodiaceae, Grammitidoideae) de Madagascar. *Adansonia* 40 (2): 141–162.
https://doi.org/10.5252/adansonia2018v40a11

Rambaut, A., Drummond, A.J., Xie, D., Baele, G.M. & Suchard, M.A. (2018) Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology* 67 (5): 901–904.
https://doi.org/10.1093/sysbio/syy032

Ranker, T.A., Smith, A.R., Parris, B.S., Geiger, J.M.O., Haufler, C.H., Straub, S.C.K. & Schneider, H. (2004) Phylogeny and evolution of grammitid ferns (Grammitidaceae): a case of rampant morphological homoplasy. *Taxon* 53 (2): 415–428.
https://doi.org/10.2307/4135619

Ranker, T.A. (2008) A New Combination in *Adenophorus* (Polypodiaceae). *American Fern Journal* 98 (3): 170–171.
https://doi.org/10.1640/0002-8444(2008)98[170:ANCIAP]2.0.CO;2

Reimers, H. (1933) Pteridophyta in Neue und seltene Arten leg. H.J. Schlieben, III. *Notizblatt des Königl. botanischen Gartens und Museums zu Berlin* 11: 912–943.

Rojas-Alvarado, A.F. (2006) Notas sobre *Enterosora* Baker (Filicales: Grammitidaceae) en Costa Rica. *Lankesteriana International Journal on Orchidology* 6: 9–13.
https://doi.org/10.15517/lank.v6i1.19752

Rojas-Alvarado, A.F. (2008) Novelties of grammitid ferns (Polypodiaceae) from Costa Rica, Panama and Colombia. *Métodos en Ecología y Sistemática (MES)* 3 (2): 12–22.

Rojas-Alvarado, A.F. (2017) Novedades en *Moranopteris* R.Y. Hirai & J. Prado (Polypodiaceae) para el Neotrópico. *Acta Botanica Malacitana* 42: 149–154.
https://doi.org/10.24310/Actabotanicaabmabm.v42i2.3023

Ronquist, F., Teslenko, M., Van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P.

(2012) MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61 (3): 539–542.
https://doi.org/10.1093/sysbio/sys029

Rosenstock, E.R. (1912) Filices costaricenses, II. *Repertorium Specierum Novarum Regni Vegetabilis* 10: 274–280.
https://doi.org/10.1002/fedr.19120101803

Rosenstock, E.R. (1913) Die von Dr. Th. Herzog auf seiner zweiten Reise durch Bolivien in den Jahren 1910 und 1911 gesammelten Pflanzen (Filicales). *Mededeelingen van's Rijks-Herbarium* 19: 3–26.

Roux, J.P. (2009) Synopsis of the Lycopodiophyta and Pteridophyta of Africa, Madagascar, and neighbouring islands. *Strelitzia* 23: 1–296.

Schelpe, E.A.C.L.E. (1969) Reviews of tropical African Pteridophyta. *Contributions from the Bolus Herbarium* 1: 1–132.

Schuettpelz, E. & Pryer, K.M. (2007) Fern phylogeny inferred from 400 leptosporangiate species & three plastid genes. *Taxon* 56 (4): 1037–1050.
https://doi.org/10.2307/25065903

Schuettpelz, E., Rouhan, G., Pryer, K.M., Rothfels, C.J., Prado, J., Sundue, M.A., Windham, M.D., Moran, R.C. & Smith, A.R. (2018) Are there too many fern genera? *Taxon* 67 (3): 473–480.
https://doi.org/10.12705/673.1

Seymour, F.C. (1975) *Polypodium* in Nicaragua. *Phytologia* 31 (2): 129–192.
https://doi.org/10.5962/bhl.part.12119

Smith, A.R. (1993) *Terpsichore*, a new genus of Grammitidaceae (Pteridophyta). *Novon* 3 (4): 478–489.
https://doi.org/10.2307/3391398

Smith, A.R. (1993a) New species and combinations in *Ceradenia* (Grammitidaceae). *Novon* 3 (2): 182–185.
https://doi.org/10.2307/3391532

Smith, A.R. (1995) New combinations in neotropical Grammitidaceae (Pteridophyta). *Novon* 5 (1): 20–21.
https://doi.org/10.2307/3391823

Smith, A.R. & Moran, R.C. (1992) *Melpomene*, a new genus of Grammitidaceae (Pteridophyta). *Novon* 2 (4): 426–432.
https://doi.org/10.2307/3391505

Smith, A.R., Moran, R.C. & Bishop, L.E. (1991) *Lellingeria*, a new genus of Grammitidaceae. *American Fern Journal* 81 (3): 76–88.
https://doi.org/10.2307/1547576

Smith, A.R., Kreier, H.P., Haufler, C.H., Ranker, T.A. & Schneider, H. (2006) *Serpocaulon*, a new genus segregated from *Polypodium*. *Taxon* 55 (4): 919–930.
https://doi.org/10.2307/25065686

Smith, J. (1875) *Historia filicum*. Macmillan, London, 429 pp.

Stamatakis, A. (2014) RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. *Bioinformatics* 30 (9): 1312–1313.
https://doi.org/10.1093/bioinformatics/btu033

Sundue, M.A. (2010) A monograph of *Ascogrammitis*, a new genus of grammitid ferns (Polypodiaceae). *Brittonia* 62 (4): 357–399.
https://doi.org/10.1007/s12228-009-9108-6

Sundue, M.A. (2010a) A morphological cladistic analysis of *Terpsichore* (Polypodiaceae). *Systematic Botany* 35 (4): 716–729.
https://doi.org/10.1600/036364410X539808

Sundue, M.A. (2014) *Mycopteris*, a new neotropical genus of grammitid ferns (Polypodiaceae). *Brittonia* 66 (2): 174–185.
https://doi.org/10.1007/s12228-013-9322-0

Sundue, M.A., Labiak, P.H., Mostacero, J. & Smith, A.R. (2012) *Galactodenia*, a new genus of grammitid fern segregated from *Terpsichore* (Polypodiaceae). *Systematic Botany* 37 (2): 339–346.
https://doi.org/10.1600/036364412X635395

Sundue, M.A. & Lehnert, M. (2008) *Melpomene anazalea*, a new species of grammatid fern (Polypoiaceae). *American Fern Journal* 98 (4): 208–213.
https://doi.org/10.1640/0002-8444-98.4.208

Sundue, M.A., Parris, B.S., Ranker, T.A., Smith, A.R., Fujimoto, E.L., Zamora-Crosby, D., Morden, C.W., Chiou, W.-L., Chen, C.-W., Rouhan, G., Hirai, R.Y. & Prado, J. (2014) Global phylogeny and biogeography of grammitid ferns (Polypodiaceae). *Molecular Phylogenetics and Evolution* 81: 195–206.
https://doi.org/10.1016/j.ympev.2014.08.017

Sundue, M. & Poinar, G. (2016) An extinct grammitid fern genus from Dominican amber, with revision of Grammitis succinea. *Review of Palaeobotany and Palynology* 233: 193–198.
https://doi.org/10.1016/j.revpalbo.2016.04.004

Swartz, O.P. (1788) *Nova genera et species plantarum seu prodromus descriptionum vegetalium, maximam partem incognitorum quæ sub itinere in Indiam occidentalem annis 1783-1787*. M. Swederi, Stockholm [Holmiae], Upsala & Abo, 166 pp.

Swartz, O.P. (1800 [1801]) Genera et species filicum. *Journal für die Botanik* 2: 1–120.

Swartz, O.P. (1806) *Synopsis filicum carum genera etspecies systematice complectens*. Impensis Bibliopolii novi academici, Kiliae, 445 pp.

Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17 (5): 1105–1109. https://doi.org/10.1007/BF00037152

Tardieu, M.L. (1953) Les Ptéridophytes de l'Afrique intertropicale Française. *Mémoires de l'Institut Français d'Afrique Noire* 28: 1–241.

Tardieu, M.L. (1959) Combinaisons et espèces Nouvelles de "*Ctenopteris*", "*Xiphoopteris*" et "*Microsorium*" de Madagascar et des Mascareignes. *Notulae Systematicae. Herbier du Museum de Paris* 15 (4): 443–447.

Tardieu, M.L. (1960) Grammitidacées. *Flore de Madagascar et des Comores* 5 (2): 71–133.

Thiers, B. (2016 [constantly updated]) Index Herbariorum: A global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/ih (accessed 28 February 2019)

Willdenow, C.L. (1810) *Species Plantarum, ed. 4, Vol. 5*. GC Nauck, Berlin, 542 pp.

Yu, G., Smith, D.K., Zhu, H., Guan, Y. & Lam, T.T.Y. (2017) ggtree: an R package for visualization and annotation of phylogenetic trees with their covariates and other associated data. *Methods in Ecology and Evolution* 8 (1): 28–36. https://doi.org/10.1111/2041-210X.12628

**APPENDIX 1.** Accession numbers for previously known sequences downloaded from GenBank for phylogenetic analysis. Missing sequences are indicated by a dash (—).

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Polypodium vulgare* Linnaeus | *Larsson 13* | JF832178 | JF832081 | — | — | JF832234 | — |
| *P. vulgare* | *Schneider s.n.* | EF463510 | EF551065 | — | EF551081 | — | EF551119 |
| *Serpocaulon fraxinifolium* (Jacquin) A.R. Smith | *Jiménez 1354* | — | EF551070 | — | EF551095 | — | EF551133 |
| *Acrosorus friderici-et-pauli* (H. Christ) Copeland | *Parris 12793* | — | KM218752 | — | KM106105 | KM105963 | KM106046 |
| *Adenophorus oahuensis* L.E. Bishop | *Ranker 969* | AF469776 | AY057382 | — | — | — | AF469789 |
| *Adenophorus periens* L.E. Bishop | *Ranker 1114* | AF469774 | AF468199 | — | — | — | AF469787 |
| *Adenophorus tenellus* (Kaulfuss) Ranker | *Ranker 1352* | AF469773 | AF468198 | — | — | — | AF469786 |
| *Alansmia* aff. *cultrata* (Willdenow) Moguel & M. Kessler | *Sundue 1162* | GU376475 | GU376494 | JN654929 | JN654940 | JN654953 | JN654968 |
| *A. cultrata* | *Dassler 947191* | AY459502 | AY460669 | — | — | — | — |
| *Alansmia elastica* (Bory ex Willdenow) Moguel & M. Kessler | *Hennequin et al. 339* | KY711748 | KY711922 | — | KY712249 | KY712090 | KY711575 |
| *Alansmia heteromorpha* (Hooker & Grevile) Moguel & M. Kessler | *Sundue 2609* | — | KM218803 | — | — | KM105966 | — |
| *Alansmia lanígera* (Desvaux) Moguel & M. Kessler | *Leon 3647* | GU476809 | GU476844 | — | — | — | GU476718 |
| *Alansmia senilis* (Fée) Moguel & M. Kessler | *Sundue 1156* | — | — | JN654928 | JN654941 | JN654954 | JN654967 |
| *Alansmia smithii* (A. Rojas) Moguel & M. Kessler | *Kessler 13511* | — | — | — | — | — | GU476712 |
| *Alansmia stella* (Copeland) Moguel & M. Kessler | *Sundue 1083* | — | — | JN654926 | JN654939 | JN654952 | JN654965 |
| *Alansmia turrialbae* (Christ) Moguel & M. Kessler | *Sundue 1765* | GU376472 | GU376497 | JN654931 | JN654944 | JN654957 | JN654970 |
| *Ascogrammitis anfractuosa* (Kunze ex Klotzsch) Sundue | *Kessler 13507* | GU476784 | GU476845 | — | — | — | GU476676 |
| *Ascogrammitis angustipes* (Copeland) Sundue | *Sundue 1237* | KM218837 | GU476891 | — | KM106109 | KM105968 | GU476703 |

*...continued on next page*

**APPENDIX 1.** (Continued)

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Ascogrammitis athyrioides* (Hooker) Sundue | *Lehnert 261* | KM218840 | GU476856 | — | KM106110 | KM105969 | GU476714 |
| *Ascogrammitis clathrata* (Sundue & M. Kessler) Sundue | *Kromer 1237* | KM218838 | GU476843 | — | KM106111 | KM105970 | GU476708 |
| *Ascogrammitis clavigera* A.R. Smith & Sundue | *Schneider 2400* | KM218839 | GU476925 | — | KM106112 | — | GU476709 |
| *Ascogrammitis colombiensis* Sundue | *Dassler 947131* | GU476805 | GU476827 | — | KM106113 | — | GU476711 |
| *Ascogrammitis cuencana* (Hieronymus) Sundue | *Lehnert 1164* | — | GU476851 | — | KM106114 | KM105971 | GU476714 |
| *Ascogrammitis david-smithii* (Stolze) Sundue | *Sundue 785* | GU376639 | GU476911 | GU386960 | GU387122 | GU387205 | GU387284 |
| *Ascogrammitis dilatata* (Sundue & M. Kessler) Sundue | *Labiak 4728* | GU376640 | GU387033 | GU386962 | GU387124 | GU387206 | GU387285 |
| *Ascogrammitis loxensis* Sundue | *Sundue 1073* | GU376641 | GU386995 | GU386963 | GU387125 | GU387207 | GU387286 |
| *Ascogrammitis nana* (Sundue & M. Kessler) Sundue | *Labiak 4725* | GU376642 | GU387031 | GU386964 | GU387126 | GU387208 | GU387287 |
| *Ascogrammitis pichinchae* (Sodiro) Sundue | *Wilson 2816a* | — | GU476928 | — | KM106115 | — | GU476730 |
| *Ascogrammitis pichinchensis* (Hieronymus) Sundue | *Lehnert 1577* | GU476816 | GU476854 | — | KM106116 | — | GU476732 |
| *Ceradenia argyrata* (Bory ex Willdenow) Parris | *Janssen et al. 2716* | KY711752 | KY711926 | — | KY712253 | KY712094 | KY711579 |
| *Ceradenia aulaeifolia* L.E. Bishop ex A.R. Smith | *Rojas 3232* | AY459453 | AY460619 | — | KM106122 | KM105974 | GU476623 |
| *Ceradenia ayopayana* M. Kessler & A.R. Smith | *Jiménez 1114* | — | KM218811 | — | KM106123 | KM105975 | KM106053 |
| *Ceradenia comorensis* (Baker) Parris | *Janssen et al. 2452* | KY711760 | KY711935 | — | KY712262 | KY712103 | KY711588 |
| *Ceradenia curvata* (Swartz) L.E. Bishop | *Jiménez 1559* | KM218821 | KM218788 | — | — | KM105976 | KM106054 |
| *Ceradenia deltodon* (Baker) Parris | *Rouhan et al. 1217* | KY711753 | KY711927 | — | KY712254 | KY712095 | KY711580 |
| *Ceradenia farinosa* (Hooker) L.E. Bishop | *Neill 11985* | KM218823 | KM218790 | — | KM106124 | KM105977 | KM106055 |
| *Ceradenia fucoides* (Christ) L.E. Bishop | *Sundue 1766* | GU476749 | GU476907 | — | KM106125 | — | GU476625 |

*...continued on next page*

**APPENDIX 1.** (Continued)

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Ceradenia intonsa* L.E. Bishop ex Leon-Parra & Mostacero | *Sundue & Vasco 1321* | GU476750 | GU476901 | | | | GU476626 |
| *Ceradenia intricata* (C.V. Morton) L.E. Bishop ex A.R. Smith | *Lehnert 1108* | KM218833 | KM218791 | — | KM106127 | KM105978 | KM106056 |
| *Ceradenia jungermannioides* (Klotzsch) L.E. Bishop | *Smith 2576* | AY459454 | AY460620 | — | — | — | — |
| *Ceradenia kalbreyeri* (Baker) L.E. Bishop | *Sundue 1759* | GU476744 | GU476905 | — | KM106128 | KM105979 | GU476617 |
| *Ceradenia leucosora* (Bojer ex Hooker) Parris | *Janssen et al. 2689* | KY711759 | KY711934 | — | KY712261 | KY712102 | KY711587 |
| *Ceradenia madidiensis* M. Kessler & A.R. Smith | *I. Jiménez 1089* | KM218834 | — | — | KM106129 | — | KM106057 |
| *Ceradenia pearcei* (Baker) L.E. Bishop | *Fuentes & Villalobos 13997* | KM218822 | KM218789 | — | KM106130 | KM105980 | KM106058 |
| *Ceradenia pilipes* (Hooker) L.E. Bishop | *Sundue 1120* | GU476746 | GU476869 | — | — | — | GU476621 |
| *Ceradenia sechellarum* (Baker) Parris | *Senterre 6122* | KY711886 | KY712060 | — | KY712378 | KY712226 | KY711706 |
| *Ceradenia spixiana* (Martius ex Mettenius) L.E. Bishop | *Salino 3008* | AY459457 | AY460623 | — | — | — | |
| *Chrysogrammitis glandulosa* (J. Smith) Parris | *Ranker 2195* | JF514082 | JF514014 | — | — | — | JF514048 |
| *Chrysogrammitis musgraveana* (Baker) Parris | *Sundue 2234* | KM218825 | KM218797 | — | KM106132 | KM105981 | KM106059 |
| *Cochlidium punctatum* (Raddi) L.E. Bishop | *Silva 3914* | JF514057 | JF513987 | — | — | — | GU476631 |
| *Cochlidium rostratum* (Hooker) Maxon ex C. Christensen | *Valdespino & Aranda 180* | AY459459 | AY460626 | — | — | KM105982 | — |
| *Cochlidium serrulatum* (Swartz) L.E. Bishop | *Rouhan et al. 172* | KY711765 | KY711940 | — | KY712267 | KY712107 | KY711592 |
| *Ctenopterella denticulata* (Blume) Parris | *Ranker 2113* | JF514081 | JF514013 | | | | JF514047 |
| *Ctenopterella zenkeri* (Hieronymus) Parris | *Rakotondrainibe 6982* | KY711776 | KY711951 | — | KY712277 | KY712118 | KY711603 |
| *Enterosora barbatula* (Baker) Parris | *Rakotondrainibe 6951* | KY711783 | KY711958 | — | KY712283 | KY712124 | KY711609 |
| *Enterosora enterosoroides* (Christ) A. Rojas | *Sundue 1172* | GU476756 | — | — | KM106140 | — | GU476634 |

*...continued on next page*

**APPENDIX 1.** (Continued)

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Enterosora parietina* (Klotzsch) L.E. Bishop | *Schuettpelz 230* | EF463494 | EF463248 | | | | |
| *Enterosora percrassa* (Baker) L.E. Bishop | *Sundue 1665* | GU476757 | GU476882 | — | KM106141 | — | GU476635 |
| *Enterosora sprucei* (Hooker) Parris | *Janssen et al. 2925* | KY711790 | KY711965 | — | KY712289 | KY712130 | KY711615 |
| *Enterosora trichosora* (Hooker) L.E. Bishop | *Moran 7659* | — | GU476920 | — | — | — | GU476637 |
| *Enterosora trifurcata* (Linnaeus) L.E. Bishop | *Sundue 1774* | GU476754 | GU476909 | — | — | — | GU476632 |
| *Galactodenia delicatula* (M. Martens & Galeotti) Sundue & Labiak | *Mickel 4639* | — | — | GU386961 | GU387123 | — | KM106064 |
| *Galactodenia parrisiae* Sundue & Labiak | *Monro & Knapp 5721* | — | KM218794 | — | — | KM105990 | — |
| *Galactodenia subscabra* (Klotzsch) Sundue & Labiak | *Moran 8078* | GU476821 | GU476860 | GU386965 | GU387127 | GU387209 | GU476739 |
| *Grammitis baldwinii* Copeland | *Wood 10575* | EF178633 | EF178616 | — | — | — | EF178649 |
| *Grammitis bryophila* (Maxon) F. Seymour | *Rojas et al. 3240* | AF469784 | AF468208 | — | KM106143 | — | AF469797 |
| *Grammitis copelandii* Tardieu | *Rouhan et al. 1190* | KY711793 | KY711968 | — | KY712292 | KY712133 | KY711618 |
| *Grammitis cryptophlebia* (Baker) Copeland | *Kluge 7936* | KM218815 | KM218799 | — | KM106144 | KM105992 | KM106065 |
| *Grammitis deplanchei* Copeland | *Munzinger 1422* | KY711803 | KY711978 | — | KY712301 | KY712142 | KY711627 |
| *Grammitis diminuta* (Baker) Copeland | *Papadopulos 845* | — | JF950809 | — | — | — | — |
| *Grammitis dorsipila* (Christ) C. Christensen & Tardieu | *TNS764128* | — | AB575257 | — | — | — | — |
| *Grammitis ebenina* (Maxon) Tardieu | *Rouhan et al.1180* | KY711804 | KY711979 | — | KY712302 | KY712143 | KY711628 |
| *Grammitis forbesiana* W.H. Wagner | *Ranker 1321* | AY459472 | AY460640 | — | — | — | EF178651 |
| *Grammitis holophlebia* (Baker) Copeland | *Rakotondrainibe 6933* | KY711808 | KY711983 | — | KY712306 | KY712147 | KY711632 |
| *Grammitis hookeri* Copeland | *Ranker 1116* | AY459473 | AY460642 | — | — | — | EF178655 |
| *Grammitis knutsfordiana* (Baker) Copeland | *Game 95-81* | AY459474 | AY362342 | — | — | — | EF178657 |
| *Grammitis kyimbilensis* (Brause) Copeland | *Kessler 12773* | EF178641 | EF178624 | — | KM106147 | KM105993 | EF178659 |

*...continued on next page*

**APPENDIX 1.** (Continued)

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Grammitis marginelloides* (J.W. Moore) Copeland | *Nitta 666* | — | KY099803 | — | — | — | — |
| *Grammitis melanoloma* (Cordemoy) Tardieu | *Ranker 1504 & Adsersen* | AY459475 | AY460643 | — | KM106148 | — | GU476641 |
| *Grammitis nudicarpa* Copeland | *Papadopulos AP794* | — | JF950810 | — | — | — | — |
| *Grammitis obtusa* Willdenow ex Kaulfuss | *Rouhan et al. 1212* | KY711817 | KY711992 | — | KY712314 | KY712156 | KY711641 |
| *Grammitis padangensis* (Baker) Copeland | *Ranker 2159a & Klimas* | EF178642 | EF178625 | — | — | — | EF178660 |
| *Grammitis paramicola* L.E. Bishop | *Jiménez &. Gallegos s.n.* | KM218816 | KM218801 | — | KM106149 | KM105994 | KM106067 |
| *Grammitis pellucidovenosa* (Bonaparte) Copeland | *Janssen et al. 2931* | KY711821 | KY711996 | — | — | KY712160 | KY711645 |
| *Grammitis pervillei* Tardieu | *Senterre 6128* | KY711887 | KY712061 | — | KY712379 | KY712227 | KY711707 |
| *Grammitis pseudaustralis* E. Fournier | *McPherson 18253* | KY711867 | KY712042 | — | KY712359 | KY712207 | |
| *Grammitis pygmaea* (Mettenius ex Kuhn) Copeland | *Janssen et al. 2664* | — | KY712000 | — | KY712319 | KY712164 | KY711649 |
| *Grammitis reinwardtii* Blume | *Tsutsumi et al. IN108* | — | AB232398 | — | — | — | — |
| *Grammitis stenophylla* Parris | *Parris 12576* | JX499239 | JQ904084 | — | — | — | JQ911714 |
| *Grammitis synsora* (Baker) Copeland | *Rouhan et al. 1173* | KY711826 | KY712002 | — | — | KY712166 | KY711651 |
| *Grammitis trachycarpa* (Mettenius) Copeland | *Nitta 3975* | — | KY099804 | — | — | — | — |
| *Grammitis wattsii* Copeland | *Papadopulos AP796* | — | — | — | — | — | JF950912 |
| *Lellingeria affinis* Labiak | *Jiménez 368* | GU376570 | GU386982 | GU386884 | GU387044 | GU387130 | GU387212 |
| *Lellingeria apiculata* (Kunze ex Klotzsch) A.R. Smith & R.C. Moran | *Labiak 3884* | GU376572 | GU387021 | GU386886 | GU387046 | GU387132 | GU387214 |
| *Lellingeria bishopii* Labiak | *Sundue 1159* | GU376574 | GU476878 | GU386888 | GU387048 | GU387134 | GU387216 |
| *Lellingeria brevistipes* (Mettenius ex Kuhn) A.R. Smith & R.C. Moran | *Labiak 4596* | GU376576 | GU387030 | GU386890 | GU387050 | GU387136 | GU387218 |
| *Lellingeria calolepis* Labiak | *Jiménez 1731* | GU376577 | GU386979 | GU386891 | GU387051 | GU387137 | GU387219 |
| *Lellingeria ciliolepis* (C. Christensen) A.R. Smith | *Labiak 2904* | GU376578 | GU387016 | GU386892 | GU387052 | GU387138 | GU387220 |

...continued on next page

**APPENDIX 1.** (Continued)

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Lellingeria depressa* (C. Christensen) A.R. Smith & R.C. Moran | *Labiak 3570* | GU376579 | GU387017 | GU386893 | GU387053 | GU387139 | GU387221 |
| *Lellingeria dissimulans* (Maxon) A.R. Smith | *Willians 40423* | GU376580 | GU387043 | GU386894 | GU387054 | GU387140 | GU387222 |
| *Lellingeria flagellipinnata* M. Kessler & A.R. Smith | *Labiak 2866* | GU376581 | GU387015 | GU386895 | GU387055 | GU387141 | GU387223 |
| *Lellingeria humilis* (Mettenius) A.R. Smith & R.C. Moran | *Sundue 1296* | — | — | GU386900 | GU387060 | GU387146 | — |
| *Lellingeria isidrensis* (Maxon ex Copeland) A.R. Smith & R.C. Moran | *Wagner 83020* | GU376586 | GU387042 | GU386901 | GU387061 | GU387147 | GU387228 |
| *Lellingeria itatimensis* (C. Christensen) A.R. Smith & R.C. Moran | *Labiak 3872* | GU376587 | GU387020 | GU386902 | GU387062 | GU387148 | GU387229 |
| *Lellingeria jimenezii* Labiak | *Lehnert 466* | GU376589 | GU386986 | GU386904 | GU387064 | GU387150 | GU387230 |
| *Lellingeria kaieteura* (Jenman) Labiak | *Hombersley 120* | GU376590 | GU386978 | GU386905 | GU387065 | GU387151 | GU387231 |
| *Lellingeria major* (Copeland) A.R. Smith & R.C. Moran | *Sundue 1134* | GU476766 | GU476873 | GU386908 | GU387068 | GU387154 | GU476652 |
| *Lellingeria melanotrichia* (Baker) A.R. Smith & R.C. Moran | *Contreras 300* | GU376593 | GU386973 | GU386910 | GU387070 | GU387156 | GU387234 |
| *Lellingeria oreophila* (Maxon) A.R. Smith & R.C. Moran | *Contreras 159* | — | GU386974 | GU386919 | GU387080 | GU387165 | GU387243 |
| *Lellingeria paramicola* Labiak | *Ollgaard 8403* | GU376601 | GU387014 | GU386920 | GU387081 | GU387166 | GU387244 |
| *Lellingeria pendula* (Swartz) A.R. Smith & R.C. Moran | *Proctor 20310* | GU376602 | GU387036 | GU386921 | GU387083 | GU387167 | GU387246 |
| *Lellingeria phlegmaria* (J. Smith) A.R. Smith & R.C. Moran | *Labiak 4732* | GU376604 | GU387034 | GU386923 | GU387085 | GU387169 | GU387248 |
| *Lellingeria pseudocapillaris* (Rosenstock) A.R. Smith & R.C. Moran | *Jiménez 1800* | GU376606 | GU386980 | GU386925 | GU387087 | GU387171 | GU387250 |
| *Lellingeria randallii* (Maxon) A.R. Smith & R.C. Moran | *Mickel 9495* | KM218860 | GU386992 | GU386928 | GU387090 | KM105996 | GU387253 |

*...continued on next page*

**APPENDIX 1.** (Continued)

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Lellingeria simacensis* (Rosenstock) A.R. Smith & R.C. Moran | *Sundue 1169* | GU376610 | GU387001 | GU386930 | GU387092 | GU387175 | GU387255 |
| *Lellingeria subimpressa* (Copeland) Labiak | *Arauz 368* | GU376611 | GU386967 | GU386931 | GU387093 | GU387176 | GU387256 |
| *Lellingeria subsessilis* (Baker) A.R. Smith & R.C. Moran | *Sundue 1139* | GU376613 | GU386997 | GU386933 | GU387095 | GU387178 | GU387258 |
| *Lellingeria suprasculpta* (Christ) A.R. Smith & R.C. Moran | *Lellinger 989* | GU376614 | GU386987 | GU386934 | GU387096 | GU387179 | GU387259 |
| *Lellingeria suspensa* (Linnaeus) A.R. Smith & R.C. Moran | *Granville 15398* | GU376617 | GU386976 | GU386937 | GU387099 | GU387182 | GU387262 |
| *Lellingeria tamandarei* A.R. Smith & R.C. Moran | *Labiak 4430* | GU376621 | GU387027 | GU386941 | GU387103 | GU387186 | GU387266 |
| *Lellingeria tenuicula* (Fée) A.R. Smith & R.C. Moran | *Hill 28165* | GU376622 | GU386977 | GU386942 | GU387104 | GU387187 | GU387267 |
| *Leucotrichum madagascariense* Rakotondrainibe & Rouhan | *Rakotondrainibe et al. 6957* | JN654923 | JN654924 | JN654936 | JN654949 | JN654962 | JN654975 |
| *Leucotrichum mitchelliae* (Baker) Labiak | *Morton & Acuna 3141* | GU376480 | GU376487 | JN654925 | JN654938 | JN654951 | JN654964 |
| *Leucotrichum mortonii* (Copeland) Labiak | *Liogier 16026* | GU376478 | GU376489 | — | — | — | — |
| *Leucotrichum organense* (Gardner) Labiak | *Labiak 3630* | GU376483 | GU376490 | JN654932 | JN654945 | JN654958 | JN654971 |
| *Leucotrichum pseudomitchellae* (Lellinger) Labiak | *Rojas 3005* | AY459484 | AY460652 | — | — | — | — |
| *Leucotrichum schenckii* (Hieronymus) Labiak | *Salino 4538* | AY459483 | AY460651 | — | — | — | KM106072 |
| *Lomaphlebia turquina* (Maxon) Sundue & Ranker | *Sanchez 82061* | KM218814 | KM218800 | — | — | — | KM106069 |
| *Melpomene* aff. *moniliformis* (Lagasca y Segura ex Swartz) A.R. Smith & R.C. Moran | *Sundue 1366* | GU376626 | GU387010 | GU386945 | GU387107 | GU387190 | GU387271 |
| *Melpomene allosuroides* (Rosenstock) A.R. Smith & R.C. Moran | *Solomon 12829* | GU376628 | GU387038 | GU386947 | GU387109 | GU387193 | GU387273 |
| *Melpomene anazalea* Sundue & Lehnert | *Sundue & Vasco 1290* | GU476773 | GU476898 | — | — | — | GU476662 |

*...continued on next page*

**APPENDIX 1.** (Continued)

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Melpomene erecta* (C.V. Morton) A.R. Smith & R.C. Moran | *Nunez 25* | GU376629 | GU387013 | GU386948 | GU387110 | GU387193 | GU387274 |
| *Melpomene firma* (J. Smith) A.R. Smith & R.C. Moran | *Labiak 4733* | GU376630 | GU387035 | GU386950 | GU387112 | GU387195 | GU387276 |
| *Melpomene flabelliformis* (Poiret) A.R. Smith & R.C. Moran | *Labiak 4432* | GU376632 | GU387028 | GU386952 | GU387114 | GU387197 | GU387278 |
| *Melpomene melanosticta* (Kunze) A.R. Smith & R.C. Moran | *Labiak 4156* | GU376633 | GU387024 | GU386953 | GU387115 | GU387198 | GU387279 |
| *Melpomene occidentalis* Lehnert | *Sundue 1157* | GU476776 | GU476877 | — | — | — | GU476666 |
| *Melpomene personata* Lehnert | *Sundue 1330* | GU376634 | GU387007 | GU386954 | GU387116 | GU387199 | GU387280 |
| *Melpomene pilosissima* (M. Martens & Galeotti) A.R. Smith & R.C. Moran | *Martinez 1535* | GU376636 | GU386993 | GU386956 | GU387118 | GU387201 | GU387281 |
| *Melpomene xiphopteroides* (Liebmann) A.R. Smith & R.C. Moran | *Vasco 577* | GU376638 | GU387040 | GU386958 | GU387118 | GU387203 | GU387283 |
| *Micropolypodium okuboi* (Yatabe) Hayata | *Parris 12154* | JF514064 | JF513994 | — | — | — | JF514028 |
| *Moranopteris achilleifolia* (Kaulfuss) R.Y. Hirai & J. Prado | *Cordeiro & Ribas 1398* | AY459499 | AY460666 | — | KM106153 | KM105999 | |
| *Moranopteris aphelolepis* (C.V. Morton) R.Y. Hirai & J. Prado | *Jiménez & Vidarre 557* | JF514066 | JF513996 | — | — | — | JF514030 |
| *Moranopteris basiattenuata* (Jenman) R.Y. Hirai & J. Prado | *Breedlove & Thorne 30160* | JF514058 | JF513988 | — | — | — | JF514030 |
| *Moranopteris blepharidea* (Copeland) R.Y. Hirai & J. Prado | *Jiménez 708* | JF514065 | JF513995 | — | KM106154 | KM106000 | JF514029 |
| *Moranopteris caucana* (Hieronymus) R.Y. Hirai & J. Prado | *Lehnert 182* | JF514071 | JF514002 | — | KM106155 | KM106001 | JF514035 |
| *Moranopteris cookii* (Underwood & Maxon) R.Y. Hirai & J. Prado | *Sundue et al. 1771* | JF514076 | JF514007 | — | KM106156 | KM106002 | JF514040 |
| *Moranopteris gradata* (Baker) R.Y. Hirai & J. Prado | *Hirai et al. 537* | JF514077 | JF514009 | — | — | — | JF514043 |

*...continued on next page*

**APPENDIX 1.** (Continued)

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Moranopteris grisebachii* (Underwood ex C. Christensen) R.Y. Hirai & J. Prado | *Maxon 9961* | — | JF514008 | — | — | — | JF514041 |
| *Moranopteris hyalina* (Maxon) R.Y. Hirai & J. Prado | *Lehnert 1426* | JF514070 | JF514001 | — | KM106157 | KM106003 | JF514034 |
| *Moranopteris inaccessa* Sundue & Sylvester | *Sylvester 1628* | KP050355 | KP027642 | — | — | — | KP050357 |
| *Moranopteris longisetosa* (Hooker) R.Y. Hirai & J. Prado | *Lehnert 596* | JF514072 | JF514003 | — | KM106158 | KM106005 | JF514036 |
| *Moranopteris microlepis* (Rosenstock) R.Y. Hirai & J. Prado | *Kluge 2003* | JF514067 | JF513997 | — | — | — | JF514031 |
| *Moranopteris nana* (Fée) R.Y. Hirai & J. Prado | *Diaz et al. 4747* | — | JF513990 | — | — | — | — |
| *Moranopteris perpusilla* (Maxon) R.Y. Hirai & J. Prado | *Hiari et al. 574* | JF514079 | JF514011 | — | — | — | JF514045 |
| *Moranopteris plicata* (A.R. Smith) R.Y. Hirai & J. Prado | *Lehnert 929* | JF514074 | JF514005 | — | KM106159 | KM106005 | JF514038 |
| *Moranopteris serricula* (Fée) R.Y. Hirai & J. Prado | *Wilbur et al. 8084* | JF514080 | JF514017 | — | — | — | JF514052 |
| *Moranopteris setosa* (Kaulfuss) R.Y. Hirai & J. Prado | *Hirai et al. 599* | JF514080 | JF514012 | — | — | — | JF514046 |
| *Moranopteris sherringii* (Baker) R.Y. Hirai & J. Prado | *Sundue 2056* | — | KP027643 | — | — | — | KP050356 |
| *Moranopteris* sp. | *Rojas 3007* | AY459491 | AY460658 | — | — | — | HQ599515 |
| *Moranopteris trichomanoides* (Swartz) R.Y. Hirai & J. Prado | *Gómez 114* | JF514063 | JF513993 | — | — | — | JF514027 |
| *Moranopteris truncicola* (Klotzsch) R.Y. Hirai & J. Prado | *Vasco & Sundue 626* | JF514084 | JF514016 | — | KM106160 | KM106006 | JF514051 |
| *Moranopteris williamsii* (Maxon) R.Y. Hirai & J. Prado | *Kessler et al. 7173* | JF514069 | JF514000 | — | — | — | JF514033 |
| *Moranopteris zurquina* (Copeland) R.Y. Hirai & J. Prado | *Rojas 3021 & Mata* | AY459492 | AY460659 | — | — | — | — |
| *Mycopteris alsopteris* (C.V. Morton) Sundue | *Wilson 2609a* | AY459500 | AY460667 | — | — | — | — |

*...continued on next page*

**APPENDIX 1.** (Continued)

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Mycopteris amphidasyon* (Kunze ex Mett.) Sundue | *Moran 7646* | GU476759 | GU476922 | | KM106161 | KM106007 | GU476638 |
| *Mycopteris attenuatissima* (Copeland) Sundue | *Sundue 1098* | GU476801 | GU476866 | GU386959 | GU387121 | GU387204 | GU476705 |
| *Mycopteris cretata* (Maxon) Sundue | *Alford 2719* | — | GU476823 | — | — | — | GU476713 |
| *Mycopteris leucosticta* (J. Smith) Sundue | *Lehnert 1128* | GU476811 | GU476848 | — | KM106162 | — | GU476720 |
| *Mycopteris longicaulis* (Sundue & M. Kessler) Sundue | *Jiménez 373* | GU476813 | GU476840 | — | KM106163 | — | GU476724 |
| *Mycopteris longipilosa* Sundue | *Sundue & Martin 1033* | GU476814 | GU476861 | — | KM106164 | KM106008 | GU476726 |
| *Mycopteris praeceps* (Sundue & M. Kessler) Sundue | *Jiménez 2173* | GU476817 | GU476839 | — | KM106165 | — | GU476734 |
| *Mycopteris semihirsuta* (Klotzsch) Sundue | *Sundue & Vasco 1246* | GU476818 | GU476894 | — | — | — | GU476735 |
| *Mycopteris subtilis* (Kunze ex Klotzsch) Sundue | *Sundue 1140* | KY711743 | KY711916 | — | KY712244 | KY712085 | KY711569 |
| *Mycopteris taxifolia* (Linnaeus) Sundue | *Labiak 4018* | GU476800 | GU476914 | — | KM106167 | KM106009 | GU476699 |
| *Mycopteris zeledoniana* (Lellinger) Sundue | *Sundue 1806* | — | GU387011 | — | GU387129 | GU387211 | — |
| *Notogrammitis angustifolia (Jacquin) Parris* | *Perrie 4112 & Shepherd* | JX499251 | JQ904093 | — | — | — | JQ904114 |
| *Notogrammitis patagonica* (C. Christensen) Parris | *Perrie et al. 4760* | JX499246 | JQ904088 | — | — | — | — |
| *Oreogrammitis dolichosora* (Copeland) Parris | *T. A. Ranker 2183 & S. K. Klimas* | EF178635 | EF178618 | — | — | — | — |
| *Prosaptia contigua* (G. Forster) C. Presl | *Sundue 2740* | KM218851 | KM218767 | — | KM106180 | KM106025 | — |
| *Stenogrammitis hartii* (Jenman) Labiak | *Lellinger 455* | GU376583 | GU386985 | GU386897 | GU387057 | GU387143 | GU387225 |
| *Stenogrammitis hellwigii* (Mickel & Beitel) Labiak | *Mickel & Leonard 4636* | GU376584 | GU386990 | GU386898 | GU387058 | GU387144 | GU387226 |
| *Stenogrammitis hildebrandtii* (Hieronymus) Labiak | *Rakotondrainibe 6112* | GU376585 | GU386975 | GU386899 | GU387059 | GU387145 | GU387227 |
| *Stenogrammitis limula* (Christ) Labiak | *Labiak 4153* | GU376591 | GU387023 | GU386907 | GU387067 | GU387153 | GU387232 |

*...continued on next page*

**APPENDIX 1.** (Continued)

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Stenogrammitis myosuroides* (Swartz) Labiak | *Vasco 631* | GU376594 | GU386968 | GU386911 | GU387071 | GU387157 | GU387235 |
| *Stenogrammitis oosora* (Baker) Labiak | *Cable 77* | GU376600 | GU386972 | GU386918 | GU387078 | GU387164 | GU387241 |
| *Stenogrammitis prionodes* (Mickel & Beitel) Labiak | *Mickel 6567* | GU376605 | GU386991 | GU386924 | GU387086 | GU387170 | GU387249 |
| *Stenogrammitis pumila* (Labiak) Labiak | *Labiak 4015* | GU376608 | GU387022 | GU386927 | GU387089 | GU387173 | GU387252 |
| *Stenogrammitis saffordii* (Maxon) Labiak | *Ranker 1892* | EF178645 | GU476926 | — | KM106191 | — | GU476656 |
| *Stenogrammitis* sp. | *Jolinon 912* | KY711905 | KY712073 | — | KY712398 | — | KY711731 |
| *Stenogrammitis* sp. | *Rakotondrainibe 6882* | KY711849 | — | — | KY712341 | KY712189 | — |
| *Stenogrammitis subcoriacea* (Copeland) Labiak | *Lorence 8944* | EF178646 | EF178629 | — | — | — | HQ599520 |
| *Stenogrammitis wittigiana* (Fée & Glaziou ex Fée) Labiak | *Labiak 4441* | GU376625 | GU387029 | GU386944 | GU387106 | GU387189 | GU387270 |
| *Terpsichore aspleniifolia* (Linnaeus) A.R. Smith | *Moraga & Rojas 506* | JF514059 | JF513989 | — | KM106192 | — | — |
| *Terpsichore chrysleri* (Proctor ex Copeland) A.R. Smith | *I. Jiménez 1369* | KM218859 | KM218813 | — | — | KM106033 | — |
| *Terpsichore eggersii* (Baker ex Hooker) A.R. Smith | *Hill 29109* | AF469785 | AF468209 | — | — | — | AF469798 |
| *Terpsichore hanekeana* (Proctor) A.R. Smith | *Ranker 1610* | AY459503 | AY460670 | — | — | — | — |
| *Terpsichore lehmanniana* (Hieronymus) A.R. Smith | *Wilson 2589* | AY459506 | AY460673 | — | — | — | — |
| *Themelium decrescens* Parris | *Parris 12836* | — | KM218758 | — | KM106193 | KM106034 | KM106093 |
| *Zygophlebia devoluta* (Baker) Parris | *Kluge 7937* | KM218827 | KM218793 | — | KM106199 | KM106042 | KM106100 |
| *Zygophlebia forsythiana* (Baker) Parris | *Rouhan et al. 1380* | KY711858 | KY712033 | — | KY712350 | KY712198 | KY711682 |
| *Zygophlebia goodmannii* Rakotondrainibe | *Rouhan et al. 424* | KY711863 | KY712038 | — | KY712355 | KY712203 | KY711686 |
| *Zygophlebia humbertii* (C. Christensen) Parris | *Rakotondrainibe 6954* | KY711866 | KY712041 | — | KY712358 | KY712206 | KY711689 |
| *Zygophlebia mathewsii* (Kunze ex Mettenius) L.E. Bishop | *Sundue & Vasco 1254* | KY775306 | GU476895 | — | KY775305 | — | GU476743 |

*...continued on next page*

**APPENDIX 1.** (Continued)

| Species | Voucher | *atpB* | *rbcL* | *rbcL-atpB* | *rps4-trnS* | *trnG-trnR* | *trnL-trnF* |
|---|---|---|---|---|---|---|---|
| *Zygophlebia sectifrons* (Kunze ex Mettenius) L.E. Bishop | *Sundue 1757* | — | GU476904 | — | KY775304 | KM106044 | KM106101 |
| *Zygophlebia subpinnata* (Baker) L.E. Bishop ex Parris | *Rouhan et al. 1378* | KY711875 | KY712050 | — | KY712367 | KY712215 | KY711697 |
| *Zygophlebia torulosa* (Baker) Parris | *Tamon 2* | KY711878 | KY712053 | — | KY712370 | KY712218 | KY711699 |
| *Zygophlebia villosissima* (Hooker) L. E. Bishop | *Carvalho 3688* | KY711892 | KY712066 | — | KY712385 | — | KY711713 |