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Source: Systematic Botany, 43(2):397-413.
Published By: The American Society of Plant Taxonomists
URL: http://www.bioone.org/doi/full/10.1600/036364418X697166

Systematic Botany (2018), 43(2): pp. 397–413

DOI 10.1600/036364418X697166
Date of publication June 21, 2018

Microsorum × *tohieaense* (Polypodiaceae), a New Hybrid Fern from French Polynesia, with Implications for the Taxonomy of *Microsorum*

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Communicating Editor: Alejandra Vasco

Abstract—A new hybrid microsoroid fern, ***Microsorum* × *tohieaense*** (*Microsorum commutatum* × *Microsorum membranifolium*) from Moorea, French Polynesia is described based on morphology and molecular phylogenetic analysis. *Microsorum* × *tohieaense* can be distinguished from other French Polynesian *Microsorum* by the combination of sori that are distributed more or less in a single line between the costae and margins, apical pinna wider than lateral pinnae, and round rhizome scales with entire margins. Genetic evidence is also presented for the first time supporting the hybrid origin of *Microsorum* × *maximum* (*Microsorum grossum* × *Microsorum punctatum*), and possibly indicating a hybrid origin for the Hawaiian endemic *Microsorum spectrum*. The implications of hybridization for the taxonomy of microsoroid ferns are discussed, and a key to the microsoroid ferns of the Society Islands is provided.

Keywords—*gapCp*, Moorea, *rbcL*, Society Islands, Tahiti, *trnL–F*.

Hybridization, or interbreeding between species, plays an important role in evolutionary diversification (Anderson 1949; Stebbins 1959). Hybridization can increase species diversity through reinforcement if hybrids have reduced fitness relative to parents (Barton and Hewitt 1985) or by the generation of completely new taxa if hybrids are fertile (Chapman and Burke 2007). Alternatively, hybridization may also decrease diversity by allowing gene flow between previously separated lineages (Mayr 1966). Hybridization is particularly significant in the diversification of ferns, which have high numbers of hybrid taxa. For example, in Japan, hybrids account for ca. one third of the pteridophyte flora (380 hybrid vs. 720 non-hybrid taxa, including species, subspecies, and varieties; Ebihara 2016). Furthermore, ferns have high rates of both polyploidy and apogamy (i.e. asexual reproduction via unreduced spores), which allow them to overcome hybrid sterility with relative ease (Barrington et al. 1989). Hybridization has been documented in a wide range of fern lineages (e.g. Wagner 1954; Barrington 1990; Beck et al. 2010; Rothfels et al. 2014). However, many reported cases of fern hybrids are based solely on morphological evidence (e.g. Manickam et al. 1997; Moran and Watkins 2004; Testo et al. 2015). While morphology intermediate between putative parent taxa provides a useful basis for establishing hypotheses of hybrid origin, morphological variation may arise through various processes including phenotypic plasticity and intraspecific variation. Furthermore, morphology alone is insufficient to detect complicated evolutionary processes associated with hybridization, such as repeated origins (e.g. Beck et al. 2012; Sigel et al. 2014). Thus, investigations of putative hybrid taxa should include biparentally inherited genetic markers, in addition to other sources of data (Zhang et al. 2013).

Here, we investigate a putative case of hybridization between species of microsoroid ferns (Polypodiaceae, subfamily Microsoroideae), a diverse (12 genera; ca. 183 spp.) clade of terrestrial, hemiepiphytic, epiphytic, or epilithic ferns distributed mainly in the paleotropics (Schneider et al. 2004b; Testo and Sundue 2014; Pteridophyte Phylogeny Group I 2016). Generic taxonomy of the microsoroid ferns is in flux. Some of the segregate genera are monophyletic with clearly defined apomorphies, such as *Lecanopteris*, which forms symbiotic associations with ants (Haufler et al. 2003; Kreier et al. 2008). However, many species formerly placed in the genus *Microsorum* on the basis of morphology (Bosman 1991; Nooteboom 1997) have been shown to be nested within other genera in molecular investigations (Schneider et al. 2004a, b; Kreier et al. 2008; Wang et al. 2010a, b; Wei et al. 2017), and *Microsorum* is badly in need of taxonomic revision (Schneider et al. 2004b; Kreier et al. 2008). Studies of hybridization may provide evidence for the genetic distinctness of taxa to help inform delimitation of species and genera (Tejero-Díez et al. 2009). Although various hybrid taxa have been described previously in the microsoroid ferns (Nooteboom 1997), we are unaware of any cases that have been verified genetically.

As part of another study, we recently conducted a field survey of the ferns of Moorea and Tahiti, Society Islands, French Polynesia (Nitta et al. 2017). There are seven taxa of microsoroid ferns known from the Society Islands: *Lepisorus spicatus* (L.f.) Li Wang, *Microsorum commutatum* (Blume) Copel., *Microsorum grossum* (Langsd. & Fisch.) S.B.Andrews, *Microsorum membranifolium* (R.Br.) Ching, *Microsorum powellii* (Baker) Copel. [=*Microsorum parksii* (Copel.) Copel.], *Microsorum punctatum* (L.) Copel., and *Microsorum* × *maximum* (Brack.) Copel. (a putative hybrid between *M. punctatum* and *M. grossum*) (Copeland 1932; Sykes and Game 1996; Murdock and Smith 2003; Nitta et al. 2011; Florence in press). During our field survey, we encountered a population of *Microsorum* on Moorea that did not match any of these species in gross morphology, and that we therefore suspected could be a previously undescribed taxon. Here, we present results of our morphological and molecular analyses that support recognition of this plant as a new hybrid, *Microsorum* × *tohieaense*, between *M. commutatum* and *M. membranifolium*. Furthermore, we include samples of endemic *Microsorum spectrum* (Kaulf.) Copel. from Hawaii, and discuss the taxonomic implications of our results for *Microsorum*.

Materials and Methods

Morphological Analysis—We observed morphological characters in multiple specimens of each microsoroid species from our study area (Society Islands, French Polynesia; Fig. 1) using herbarium specimens at GH, images of herbarium specimens downloaded from the P Vascular Plants database (https://science.mnhn.fr/institution/mnhn/collection/p/item/search/form), or fresh material. Herbarium abbreviations follow

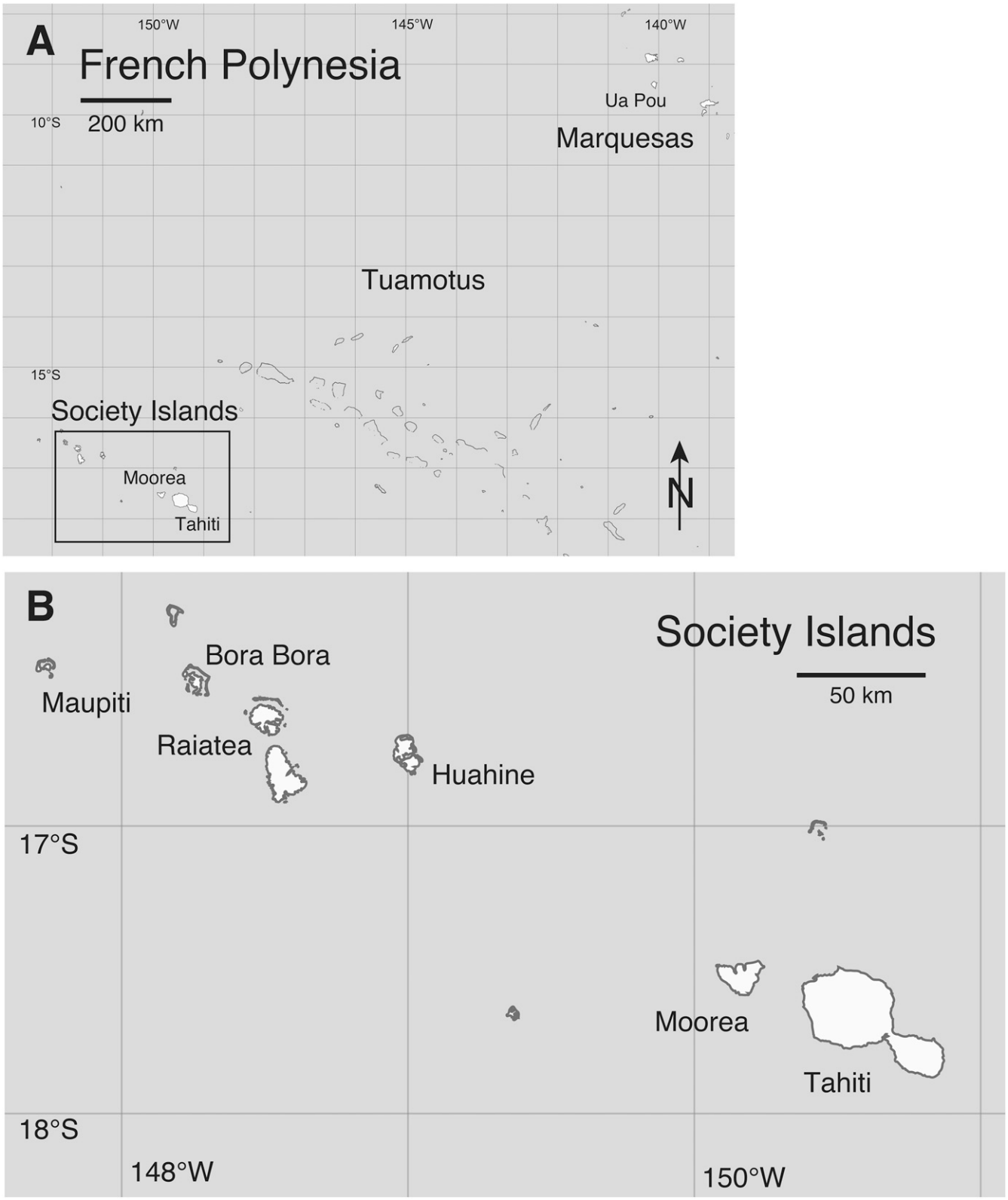

FIG. 1. Map of the study area. A. French Polynesia, showing the locations of Moorea (Society Islands) and Ua Pou (Marquesas Islands). Location of inset (B) indicated by rectangle. B. Society Islands. Maps adapted from Wikimedia Commons under Creative Commons License.

Thiers (2018). Morphological characters include: arrangement of sori, degree of immersion of sori in lamina, spore color, rhizome scales, rhizome diameter, frond length, frond width, stipe length, degree of lamina dissection, and number of pinna pairs. Quantitative frond traits were measured on the single largest frond per specimen, and rhizome diameter measured at the widest point of the rhizome. We examined spores of the unknown plant using a compound microscope (photographs taken with Olympus DP70 digital microscope camera). Spore length was measured across the widest part of the spore excluding the perine, and spore width was measured in a similar way approximately perpendicular to spore length. Measurements made on digital images used ImageJ (Abramoff et al. 2004). Voucher specimens collected for this study are deposited in UC and GH.

DNA Extraction, Marker Selection, and Sequencing—DNA extraction was performed on frond tissue preserved in silica gel either using a modified CTAB protocol (Doyle and Doyle 1987) or the DNeasy kit (Qiagen, Valencia, California) following the manufacturer's instructions.

Plastid *rbcL* and *trnL–F* (including the *trnL–trnF* intergenic spacer alone or the *trnL* intron and the *trnL–trnF* intergenic spacer together) have been used in previous studies of microsoroid ferns including a broad taxonomic sampling (Schneider et al. 2004b; Kreier et al. 2008; Wang et al. 2010a, b; Wei et al. 2017), and are useful to place the Society Islands microsoroid ferns in a global context. We therefore selected these two markers for sequencing, and complemented our data with all available accessions of microsoroid ferns for the same markers on GenBank. Special care was taken to ensure that *rbcL* and *trnL–F* accessions originated from the same voucher specimen for all GenBank data used here (Appendix 1).

It is impossible to detect hybridization events using only plastid loci, as these are maternally inherited in almost all known cases in ferns (Gastony and Yatskievych 1992; Vogel et al. 1998a). We therefore sequenced two nuclear markers, the "long" and "short" copies of *gapCp* (Schuettpelz et al. 2008; hereafter *gapCp long* and *gapCp short*) in multiple specimens from all microsoroid ferns from the Society Islands, as well as two specimens of *M. membranifolium* from the Marquesas Islands, one specimen of *M. spectrum* (Kaulf.) Copel. var. *pentadactylum* (Hillebr.) D.D.Palmer from Hawaii, and one specimen of *Leptochilus ellipticus* (Thunb. ex Murray) Noot. var. *pothifolius* (Buch.-Ham. ex D.Don) X.C.Zhang from Okinawa. *Microsorum spectrum* was included to investigate the phylogenetic affinities of this Hawaiian endemic species to other Pacific *Microsorum*, and *L. ellipticus* var. *pothifolius* was included to test the monophyly of *Microsorum* with nuclear data. Outgroup species were selected from other taxa in Polypodiaceae (*rbcL*, *trnL–F*, *gapCp long*, and *gapCp short*) or Davalliaceae (*gapCp short* only).

The PCR amplification was performed using TRNLF-f (Taberlet et al. 1991) and FernL 1Ir1 (Li et al. 2009) for *trnL–F* (including both the *trnL* intron and the *trnL–trnF* intergenic spacer), ESRBCL1F and ESRBCL1361R (Schuettpelz and Pryer 2007) for *rbcL*, and ESGAPCP8F1 and ESGAPCP11R1 (Schuettpelz et al. 2008) for *gapCp*. The PCR protocols and thermocycler settings followed those of Schuettpelz and Pryer (2007) for *rbcL* and *trnL–F* (except for annealing temperature set to 56°C) and Schuettpelz et al. (2008) for *gapCp*. Amplification success was visually inspected by gel electrophoresis including 3 μL PCR product per lane on a 1% agarose gel, with a current of 80 V applied for 1 hr.

Successful plastid PCR products were sent without further modification for enzymatic cleaning and Sanger sequencing to GENEWIZ (South Plainfield, New Jersey). In addition to the forward and reverse PCR primers, internal primers ESRBCL628F and ESRBCL654R were used to sequence *rbcL* (Schuettpelz and Pryer 2007). The resulting AB1 files were imported into Geneious v. 9.1.3 (Kearse et al. 2012), assembled into contigs, manually edited, and a single consensus sequence obtained for each plastid marker per specimen. Flanking regions containing PCR primer sequences were trimmed, and the consensus sequences were exported in FASTA format.

The *gapCp* primers used here typically amplify both *gapCp long* (ca. 900 bp) and *short* (ca. 600 bp), in addition to shorter bacterial fragments lacking introns, in a single PCR reaction (Schuettpelz et al. 2008). We separated the two *gapCp* copies by gel electrophoresis as follows: each 25 μL *gapCp* PCR product was mixed with 5 μL 6 × loading dye, loaded on a 1.25% agarose gel in modified 1 × TAE buffer (Millipore, Billerica, Massachusetts), and subjected to a 60 V current for 2 hr. This allowed the bands to be visually distinguished under UV light and excised using a clean razor blade. Excised bands were purified using the Montage gel extraction kit (Millipore, Billerica, Massachusetts) following the manufacturer's instructions. We first attempted to direct-sequence the excised, purified *gapCp* PCR products using ESGAPCP8F1 and ESGAPCP11R1 in the same way as the plastid products. In the case that direct sequencing did not result in a clean sequence (i.e. multiple peaks were present), we separated alleles within each *gapCp* copy by cloning using the TOPO TA kit (Thermo Fisher Scientific, Waltham, Massachusetts) following the manufacturer's instructions. 12–16 colonies were selected per region (*gapCp short* or *long*) per specimen, and amplified using vector-based primers M13F and M13R. Verification of amplification success and sequencing were performed in the same way as for plastid regions, except that we only used the reverse primer (M13R) for sequencing to reduce costs. Typically, at least one colony per allele was obtained in the forward orientation and obviated the need for sequencing with the forward primer (M13F); if this was not the case, we selected a single PCR sample of known genotype from the first sequencing reaction to sequence using M13F. AB1 files were imported into Geneious, and ends automatically trimmed with an error cutoff of 4.0% per base.

GapCp alleles were identified while accounting for chimeras and other sequencing errors using a similar approach to that of Grusz et al. (2009): for each *gapCp* copy per specimen, all trimmed AB1 files were aligned using MAFFT (Katoh et al. 2002) as implemented within Geneious, primer regions were trimmed from the alignment, and a phylogenetic analysis was performed using RAxML (Stamatakis 2006) as implemented within Geneious. This generally resulted in a phylogenetic tree with 2–4 clades containing most of the sequences, with chimeric sequences (i.e. artifacts consisting of fragments of distinct sequences that became fused together during PCR) either sister to all other sequences within a clade or occupying intermediate positions between clades. Obviously chimeric sequences were excluded, and monophyletic groups containing sequences each with less than 5 bp difference from the consensus were considered to belong to the same allele. Lists of sequences representing putative alleles were then selected, exported from the alignment, and assembled into contigs. Consensus sequences (i.e. the final alleles) were obtained from the resulting contigs and exported in FASTA format. All newly generated sequences have been deposited in GenBank (Appendix 1).

Phylogenetic Analysis—DNA sequences in FASTA format were analyzed using MAFFT (Katoh et al. 2002) under default settings to generate alignments of each marker separately. Ends of the resulting alignments with more than 90% missing data (50% for *trnL–F*, which had sequences of varying length due to different primers used in previous studies) were trimmed using the "trimEnds" function of the "ips" package (Heibl 2014) in R (R Core Team 2016). Preliminary maximum likelihood (ML) analysis of *rbcL* and *trnL–F* separately did not reveal any strongly supported conflicts, so we concatenated these two markers into a single plastid alignment for all subsequent analyses.

Maximum likelihood (ML) phylogenetic analyses of the concatenated plastid alignment and each nuclear gene separately were carried out using RAxML (Stamatakis 2006) with a GTR + G model of sequence evolution (GTRGAMMA) on the CIPRES Science Gateway computing platform (Miller et al. 2010). We searched for the best likelihood tree, conducted 1000 bootstrap (BS) replicates, and wrote the results of the bootstrap analysis to the best likelihood tree using the rapid analysis option (-f a).

Maximum parsimony (MP) phylogenetic analyses of the same datasets as those analyzed by ML were carried out in PAUP* 4.0b (Swofford 2002) on CIPRES. A heuristic search for the most parsimonious tree(s) was conducted for 1000 random addition replicates with tree-bisection-reconnection (TBR) branch swapping, saving no more than two trees with a score ≥ 5 per replicate, and swapping on the best trees only. Statistical support was evaluated using 1000 BS replicates with 10 random addition sequences per replicate under the same settings as the heuristic search.

For phylogenetic analysis using Bayesian inference (BI), we first identified the most appropriate model of DNA sequence evolution for *rbcL*, *trnL–F*, *gapCp long*, and *gapCp short* separately using Akaike's information criterion as implemented in SMS (Lefort et al. 2017) on the PhyML webserver (http://www.atgc-montpellier.fr/sms/). This resulted in the selection of the GTR + I + G, GTR + I + G, GTR + G, and GTR + I models, respectively. We partitioned the concatenated plastid alignment into two partitions, one for *rbcL* and one for *trnL–F*, and unlinked all parameters except for topology and branchlengths between partitions. No partitioning was used for *gapCp* alignments, which were analyzed separately. We carried out searches of treespace in MrBayes 3 (Ronquist and Huelsenbeck 2003) on CIPRES with two independent runs of four chains each (three hot, one cold) using flat priors. Chains were allowed to run for 10,000,000 generations, sampling the cold chain once every 1000 generations. We confirmed that chains had converged when the average standard deviation of split frequencies reached 0.01 or less. The initial 25% of trees were discarded as burn-in, and the remaining trees summed to produce a 50% (majority rule) tree.

During our initial phylogenetic analysis (ML only), we observed an unexpectedly high number of *gapCp* alleles in three putatively non-hybrid specimens (*M. membranifolium Nitta 573*, *M. punctatum Nitta 1399*, and *M. punctatum Nitta 3818*) that matched other, non-hybrid species (i.e. "rogue alleles"). We believe these are artifacts due to the protocol we used (cloning), which is highly sensitive to even small amounts of contaminating DNA (Ruecker et al. 2011). There are several lines of evidence that support this conclusion: each rogue allele was recovered only for *gapCp long* or *short* (never for both); plastid sequences of these specimens matched others of the same species exactly; nothing about the morphology of these specimens indicate hybrid origin; and other accessions of the same species do not show such a pattern. We therefore excluded these specimens from our final analysis, as we could not be confident of their homology.

Data associated with this study including morphological measurements, alignments, phylogenetic trees, and preliminary analyses are available on the Dryad Digital Repository (Nitta et al. 2018).

Results

Morphology—The morphology of the unknown plant does not match that of any previously described microsoroid fern from the Society Islands (Tables 1, 2; Figs. 2, 3). It is close in overall size and degree of lamina dissection to *M. grossum, M. commutatum*, and *M. powelli*, but differs in lamina texture from *M. grossum* (membranaceous in the unknown plant, vs. coriaceous in *M. grossum*), differs in soral arrangement from *M. commutatum* (one or sometimes two lines of sori on either side of the costae in the unknown plant, but with irregularities, vs. many scattered sori in *M. commutatum*), and can be distinguished from *M. powellii* by growth habit (terrestrial or epipetric in the unknown plant, vs. epiphytic in *M. powellii*) and rhizome scales (entire margins in the unknown plant, vs. denticulate margins in *M. powellii*). The unknown plant matches well with *M. membranifolium* in lamina texture, but is much smaller and usually with fewer pinna pairs than the latter (Table 2). The unknown plant has clear, occasionally misshapen spores. The occurrence of irregularly arranged sori in the unknown plant appears to be intermediate between species with regularly arranged sori (*M. grossum*, *M. powellii*, *M. membranifolium*) and those with scattered sori (*M. commutatum*, *M. punctatum*).

Plastid Phylogeny—We generated a total of 50 new plastid sequences from 28 individuals representing 10 taxa. The final concatenated plastid alignment was 2175 bp including 242 individuals representing 149 taxa (Table 3). 106 *trnL–F* sequences from GenBank out of 211 total (50.2%) were missing the first ca. 600 bp of the alignment due to use of the *trnL–F* "e" and "f" primer set (Taberlet et al. 1991) by previous studies (e.g. Kreier et al. 2008) that only amplified the intergenic spacer between the *trnL* (UAA) 3′ exon and *trnF*, without the *trnL* intron. Topologies obtained by ML, MP, and BI were mostly consistent with no strongly supported conflicts. We therefore present a summary tree based on the ML phylogeny in Fig. 4, and refer the reader to our dataset on Dryad for individual phylogenies produced by each analysis (Nitta et al. 2018). Microsoroid ferns were recovered as monophyletic (designated "M" in Fig. 4; MLBS = 100%; MPBS = 100%; BIPP = 1.00). As in previous studies, *Microsorum* is not monophlyetic (Schneider et al. 2004a, b; Kreier et al. 2008; Wang et al. 2010a, b; Wei et al. 2017). Relationships of other previously sampled taxa were broadly consistent with previous studies and not the focus of this study, so we do not discuss those in detail.

Society Islands microsoroid ferns occupy a range of positions in the plastid tree (Fig. 4). *Microsorum grossum*, *M. punctatum,* and *M.* × *maximum* are closely related and belong to a strongly supported clade also including *Microsorum scolopendria* (Burm.f.) Copel., *Microsorum papuanum* (Baker) Parris, *Microsorum musifolium* Copel., *Microsorum whiteheadii* A.R. Sm. & Hoshiz., and *Microsorum thailandicum* Booknerd & Noot. (MLBS = 98%; MPBS = 93%; BIPP = 1.00), which is in turn weakly supported as sister to *M. commutatum* (MLBS = 53%; MPBS < 50%; BIPP = 0.64). Most *M.* × *maximum* plastid sequences match those of *M. grossum*, but one specimen from Maupiti matches with *M. punctatum*. Sequences of the unidentified *Microsorum* plant from Moorea are nested within a clade of *M. membranifolium* including accessions from the Marquesas (Ua Pou), the Society Islands (Huahine, Moorea, and Tahiti), a cultivated specimen of unknown origin, an unidentified *Microsorum* species from Laos, and *Microsorum rubidum* (Kunze) Copel. from Japan (MLBS = 100%; MPBS = 100%; BIPP = 1.00). *Microsorum spectrum* is nested within a clade containing *Microsorum cuspidatum* (D.Don) Tagawa, *Microsorum lucidum* (Roxb.) Copel., and *Microsorum hainanense* Noot. (MLBS = 80%; MPBS = 86%; BIPP = 1.00). The *M. membranifolium* clade and *M. spectrum* clade are sister to each other (MLBS = 98%; MPBS = 87%; BIPP = 1.00). The *grossum–punctatum–commutatum* clade, *membranifolium* clade, *spectrum* clade, and *Leptochilus* together form the "microsoroid s. s." clade sensu Kreier et al. (2008) (MLBS = 64%; MPBS < 50%; BIPP = 0.98), but relationships between these four groups are not well resolved. The other two Society Islands microsoroid ferns, *L. spicatus* and *M. powellii*, are more distantly related, and nested within the lepisoroid clade in the case of the former, and the lecanopteroid clade (including *Lecanopteris* and other taxa named *Microsorum* mostly from New Zealand, New Caledonia, and Australia) in the latter.

Nuclear Phylogeny—We produced 69 new nuclear sequences in total from 20 specimens representing 13 taxa. Alignment statistics are summarized in Table 3. Results of the ML, MP, and BI analyses were similar and lacked any strongly conflicting topologies, so we present summary trees based on the ML phylogenies in Figs. 5 and 6. As in the plastid

Table 1. Qualitative morphological traits of microsoroid ferns from the Society Islands, French Polynesia. Degree of soral immersion as follows: None = Sori superficial, not noticeable adaxially; Slight = Sori immersed, adaxially visible but not forming raised bumps, or bumps very slight; Moderate = Sori immersed, clearly visible adaxially and forming raised bumps to 1 mm; Deep = Sori immersed, forming conspicuously raised bumps to 2–5 mm.

	Dissection	Soral arrangment	Soral immersion	Spore color	Rhizome scale shape	Rhizome scale color	Rhizome scale margin
Lepisorus spicatus	Simple	Coenosorus	None	Yellow	Ovate-lanceolate-linear	Clathrate	Denticulate
Microsorum commutatum	Pinnatifid	Scattered	Slight	Yellow	Round	Weakly clathrate, dark in center	Entire
Microsorum grossum	Pinnatifid	Regular	Moderate	Yellow	Ovate-lanceolate	Strongly clathrate	Denticulate
Microsorum membranifolium	Pinnatifid	Regular	Deep	Yellow	Irregularly round	Non-clathrate, light-brown	Entire
Microsorum powellii	Pinnatifid	Regular	Slight	Yellow	Ovate-lanceolate	Strongly clathrate	Denticulate
Microsorum punctatum	Simple	Scattered	None	Yellow	Ovate-lanceolate	Non-clathrate, lustrous	Denticulate
Microsorum × *maximum*	Irregularly pinnatifid	Scattered	None to moderate	Clear	Ovate-lanceolate	Clathrate	Denticulate
Microsorum × *tohieaense*	Pinnatifid	Mostly regular	Slight	Clear	Round	Clathrate, light in the center	Entire

TABLE 2. Quantitative morphological traits of microsoroid ferns from the Society Islands, French Polynesia. Data shown as mean ± SD (range, sample size).

	Stipe length (cm)	Frond length (cm)	Frond width (cm)	Rhizome diam (mm)	No. pinna pairs
L. spicatus	2.8 ± 1.5 (0–6.4, n = 23)	33.2 ± 8.7 (19.6–51.4, n = 23)	1.6 ± 0.5 (0.8–2.6, n = 23)	4.1 ± 1.3 (2.5–8, n = 23)	0 ± 0 (0–0, n = 23)
M. commutatum	36.7 ± 14.8 (10.4–74, n = 17)	97.7 ± 31.3 (39.7–150, n = 17)	24 ± 5.9 (15.1–36, n = 17)	7.1 ± 3 (5.1–17, n = 17)	14 ± 4.5 (6–20, n = 16)
M. grossum	27.8 ± 13.5 (9.6–61.4, n = 30)	63.4 ± 21.5 (31.4–109.1, n = 30)	20 ± 6.2 (2.1–29.2, n = 30)	5.3 ± 1.4 (3.4–9.2, n = 30)	6.3 ± 3.5 (0–14, n = 30)
M. membranifolium	69.4 ± 20.1 (50–105, n = 7)	170.1 ± 61.8 (111–278.8, n = 7)	42.5 ± 15.2 (25–64.8, n = 7)	9 ± 3.5 (6–15, n = 7)	6.6 ± 8.6 (0–20, n = 7)
M. powellii	19.8 ± 10.6 (4.8–42, n = 16)	47.6 ± 19.7 (18.5–84.2, n = 16)	18.6 ± 5.5 (9.3–27.3, n = 16)	5.9 ± 1.6 (4–9.7, n = 15)	7.2 ± 3.4 (3–13, n = 16)
M. punctatum	0 ± 0 (0–0, n = 25)	72.1 ± 16.7 (40.5–100.2, n = 25)	7.4 ± 1.2 (5–10.7, n = 25)	6 ± 1.2 (3.4–9, n = 25)	0 ± 0 (0–0, n = 25)
M. × *maximum*	10.9 ± 9.8 (0.6–38, n = 16)	92.8 ± 33.6 (27.4–155, n = 16)	17.1 ± 8.7 (3.7–29, n = 16)	6.8 ± 1.1 (5.2–8.8, n = 16)	2.6 ± 2.9 (0–10, n = 16)
M. × *tohieaense*	25.6 ± 6.8 (20.8–30.4, n = 2)	55.5 ± 2.4 (53.9–57.2, n = 2)	16 ± 0.5 (15.6–16.3, n = 2)	4.8 ± 0.4 (4.5–5, n = 2)	6 ± 0 (6–6, n = 2)

phylogeny, nuclear data show that the microsoroid ferns as a whole are monophyletic (*gapCp long* MLBS = 81%, MPBS = 100%, BIPP = 0.81; *gapCp short* MLBS = 99%, MPBS = 100%, BIPP = 1.00), but *Microsorum* is not. We detected some of the same deeper divergences observed in the plastid tree in the nuclear trees. These split the non-hybrid species into two main clades: one including *M. grossum*, *M. punctatum*, and *M. commutatum,* and the other including *M. membranifolium* and *L. spicatus* (Figs. 5, 6). However, the structure of some internal nodes varies between the two copies of *gapCp*. Excluding putative hybrids, in *gapCp short*, *M. grossum* is sister to *M. punctatum* (MLBS = 85%; MPBS = 70%; BIPP = 0.98), which together are sister to *M. commutatum* (MLBS = 99%; MPBS = 99%; BIPP = 1.00). In *gapCp long*, *M. grossum* is sister to *M. commutatum* (MLBS = 99%; MPBS = 97%; BIPP = 1.00), which together are sister to *M. punctatum* (MLBS = 98%; MPBS = 96%; BIPP = 1.00). The placement of *M. powellii* also varies between the two phylogenies: in *gapCp short*, it is sister to the clade containing *M. membranifolium* (MLBS = 87%; MPBS = 85%; BIPP = 1.00), whereas in *gapCp long*, it is sister to the *punctatum–commutatum–grossum* clade (MLBS = 100%; MPBS = 92%; BIPP = 0.94).

Microsorum × *maximum* has multiple distinct alleles that match exactly with those of *M. grossum* and *M. punctatum*. The unknown plant from Moorea has multiple distinct alleles that match closely to *M. membranifolium* and exactly (*gapCp short* and *long*) or very closely (*gapCp short*) to *M. commutatum*. These data support the hypotheses for hybrid origins in both instances (i.e. *M.* × *maximum* and the unknown plant from Moorea). Furthermore, multiple divergent alleles were also recovered for *M. spectrum*, one sister to *M. commutatum* (*gapCp short* and *long*) and one sister to the clade including *M. membranifolium* and *L. ellipticus* var. *pothifolius* (observed in *gapCp short* only). *Microsorum grossum* and *M. punctatum* each contain two distinct alleles for *gapCp short* and *gapCp long*, and these both appear in the accession of *M.* × *maximum* from Maupiti for *gapCp short*. Multiple alleles were recovered within some other non-hybrid species as well (e.g. *M. powellii*, *L. spicatus*) but it is unclear if these represent allelic diversity in diploid populations, PCR-introduced error, or additional duplications of *gapCp*. One *gapCp short* allele from *L. spicatus* appears to be a pseudogene based on a 53 bp deletion in exon 9.

Discussion

Patterns of Hybridization in Microsorum—The results of our morphological and phylogenetic analyses strongly support the status of the unknown plant from Moorea as a hybrid between *M. membranifolium* and *M. commutatum*, which we describe as *Microsorum* × *tohieaense* (see Taxonomic Treatment). Furthermore, we provide the first genetic evidence that *M.* × *maximum* is indeed a hybrid between *M. punctatum* and *M. grossum*, and that the Hawaiian endemic *M. spectrum* may also be of hybrid origin, although elucidating its progenitor taxa requires further investigation. We describe each of these cases in turn below and discuss the implications of hybridization for the taxonomy of *Microsorum*.

MICROSORUM × TOHIEAENSE—The phylogenetic placement of sequences obtained from *M.* × *tohieaense* provides more insight into the details of its origins. We detected an exact match between one set of *gapCp short* and *long* alleles recovered from *M.* × *tohieaense* with those of *M. commutatum* from the Society Islands, suggesting that *M. commutatum* from nearby

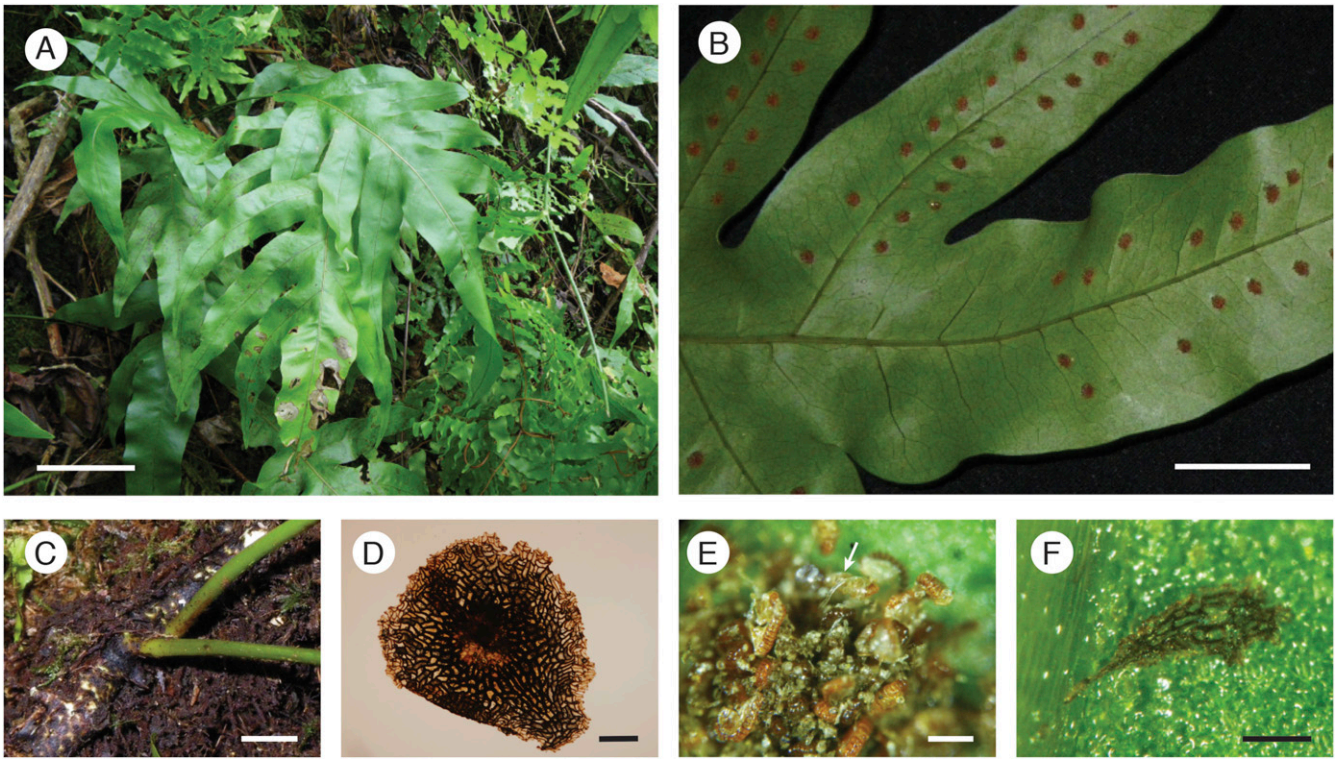

FIG. 2. Photographs of *Microsorum* × *tohieaense*. A. Whole plant in situ. B. Abaxial surface of lamina. C. Rhizome in situ. D. Rhizome scale. E. Sorus. Arrow indicates acicular paraphysis. Note clear spores. F. Costal scale. Scalebars: A = 5 cm; B–C = 2 cm; D–E = 250 μm; F = 100 μm. A–C, E–F: *Nitta 3929* (GH); D: *Nitta 1040* (GH). Photographs by J. H. Nitta.

the type population of *M.* × *tohieaense* directly contributed to formation of the hybrid. Furthermore, we observed a close match between plastid genes and the other set of *gapCp* alleles of *M.* × *tohieaense* with *M. membranifolium*, suggesting that *M. membranifolium* is the mother, and *M. commutatum* is the father, of *M.* × *tohieaense*. However, none of the plastid or nuclear sequences from *M.* × *tohieaense* match exactly with sequences of *M. membranifolium* from the Society Islands. Rather, *M.* × *tohieaense* plastid sequences are clearly more closely related to accessions of *M. membranifolium* from Ua Pou (Marquesas Islands), ca. 1380 km distant (Figs. 1A, 4). This disjunct pattern has several conceivable explanations. First, it is possible that there are additional plastid haplotypes of *M. membranifolium* currently present in the Society Islands near the type location of *M.* × *tohieaense* that contributed to hybrid formation that we failed to sample. However, our plastid sequences of *M. membranifolium* from Moorea, Tahiti, and Huahine are all identical, indicating a single plastid haplotype of *M. membranifolium* in the Society Islands. Alternatively, there could have been a more widely distributed plastid haplotype of *M. membranifolium* in the past that contributed to hybrid formation and subsequently became extirpated from the Society Islands, but survived in the Marquesas. Another possibility is that *M.* × *tohieaense* could be the result of recent long-distance spore dispersal by *M. membranifolium* from the Marquesas Islands. The phylogenetic position of two Asian taxa (an unidentified *Microsorum* accession from Laos and *M. rubidum* from Japan) sister to the *M. membranifolium* Ua Pou–*M.* × *tohieaense* clade (Fig. 4), indicates the possibility of multiple independent colonizations of Pacific islands by *M. membranifolium* from Asia. Additional sequencing of specimens from throughout the South Pacific region and Asia is needed to distinguish between these scenarios.

Another factor that should be considered is that *M. membranifolium* itself may be a complex including multiple species and hybrids. *GapCp* accessions of *M. membranifolium* from Moorea required cloning to separate multiple alleles, indicating either allopolyploidy or intraspecific variation, whereas those of *M. membranifolium* from Ua Pou as well as *M. commutatum* could be direct-sequenced, consistent with sexual diploids. The nuclear data do not show the disjunct pattern as clearly as the plastid data, but neither do they contradict it: only considering the alleles not derived from *M. commutatum*, in the *gapCp long* tree, *M.* × *tohieaense* is sister to *M. membranifolium* from Ua Pou, which together nest within a clade including *M. membranifolium* from Moorea (Fig. 6). In the *gapCp short* tree, *M.* × *tohieaense* is nested within a clade including *M. membranifolium* from Moorea and Ua Pou (Fig. 5). More intensive sampling of *M. membranifolium* across its range including ploidy level analysis is needed to determine if this taxon is a species complex.

The clear, occasionally misshapen spores and limited range (currently known only from the type locality) of *M.* × *tohieaense* suggest that it is incapable of sexual reproduction or apogamy. It is unknown when the type population became established, or how it is maintained. One possibility is continuous growth of long-creeping rhizomes; such vegetative reproduction is estimated to have supported a sterile hybrid population of *Osmunda* in West Virginia, USA for ca. 1100 yr (Barrington 2011). Microsoroid ferns have gametophytes capable of clonal growth by branching (Nayar and Kaur 1971), so it is also possible that long-lived gametophytes of the two parent species may exist together at this site and repeatedly produce hybrid sporophytes by crossing (Ebihara et al. 2009).

MICROSORUM × MAXIMUM—This species was previously considered to be a hybrid on the basis of its intermediate

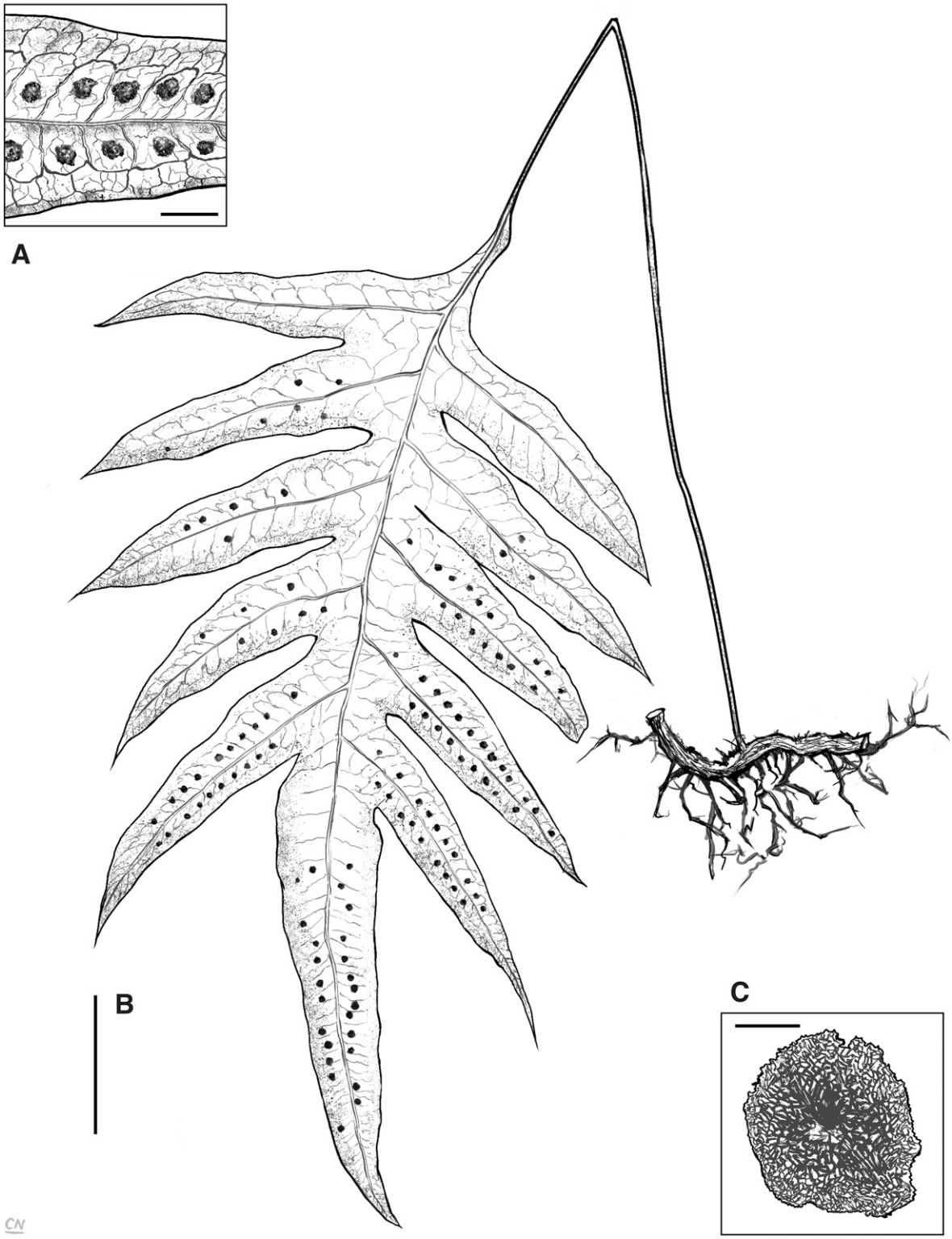

FIG. 3. Illustration of *Microsorum* × *tohieaense*. A. Detail of abaxial surface showing arrangement of sori and veins. B. Habit. C. Rhizome scale. Scalebars: A = 1 cm; B = 5 cm; C = 500 μm. A, B: *Nitta 3929* (GH). C: *Nitta 1040* (GH). Illustrations by C. C. Nitta.

morphology between *M. punctatum* (simple laminae) and *M. grossum* (deeply pinnatifid laminae) (Copeland 1932). The laminae of *M.* × *maximum* are more or less simple, but often have irregularly shaped lobes and irregularly scattered sori (Table 1). Recently, Nitta et al. (2017) detected matching plastid sequences (*rbcL* and *trnHpsbA*) between accessions of *M.* × *maximum* and *M. grossum* from Moorea, consistent with the hypothesis that *M. grossum* is the mother of *M.* × *maximum*. Our phylogenetic analysis of nuclear *gapCp* shows that *M.* × *maximum* contains alleles from both putative parents, further confirming its status as a hybrid between these two species. Interestingly, of the four samples included in our analysis,

TABLE 3. Alignment statistics by gene region. Percent missing data calculated as number of cells in the alignment that are not A, C, T, or G out of total.

	No. accessions	No. individuals	No. taxa	No. characters	% missing data	No. (%) parsimony-informative characters
rbcL	240	240	149	1180	1.1%	269 (22.8%)
trnL–F	237	237	148	995	46.3%	416 (41.8%)
rbcL + trnL–F	242	242	149	2175	22.7%	685 (31.5%)
gapCp long	32	21	12	1138	25.3%	337 (29.6%)
gapCp short	38	23	13	767	21.8%	300 (39.1%)

three (from Huahine, Moorea, and Tahiti) have plastid sequences matching *M. grossum*, while one (from Maupiti) has plastid sequences matching *M. punctatum* (Fig. 4). We recovered one additional *M.* × *maximum* specimen from Moorea (*Vinette 34*, UC) not included in the current phylogenetic analysis with plastid sequences matching *M. grossum* (data not shown). Thus, there appears to be a bias in parentage of *M.* × *maximum*, a phenomenon that has been observed in several other hybrid fern taxa (Vogel et al. 1998b; Xiang et al. 2000; Zhang et al. 2013; Testo et al. 2014; Yamada et al. 2016). Maupiti, the site of the sole *M.* × *maximum* with an *M. grossum* plastid genotype, is the westernmost and smallest of the main Society Islands, with a lower maximum altitude (380 m), drier climate, and less diverse flora than the others (Fosberg and Sachet 1987; Fig. 1B). Geographical and/or ecological processes could be involved in structuring the hybridization bias we observed (Sigel et al. 2014), but our sample size is insufficient to test such hypotheses. Phylogeographic splits between the Leeward (Huahine, Raiatea, Bora Bora, and Maupiti) and Windward (Moorea, Tahiti) Society Islands have been observed in diverse organisms including insects, birds, and plants (Hembry and Balukjian 2016). *Microsorum punctatum* and *M. grossum* themselves each have two distinct copies of *gapCp long* and *short* that appear to be the result of duplication, and *M.* × *maximum* has inherited both of these (Figs. 5, 6). Similar apparent duplications of *gapCp* within particular lineages in ferns have been observed in *Adiantum* (Rothfels and Schuettpelz 2014), *Astrolepis* (Beck et al. 2010), the common ancestor of *Culcita* and *Plagiogyria* (Rothfels et al. 2013), and within Lindsaeaceae (Rothfels et al. 2013).

MICROSORUM SPECTRUM—Unlike *M.* × *maximum*, we are unaware of any previous suggestions that Hawaiian endemic *M. spectrum* may be of hybrid origin. We detected two distinct *gapCp* alleles in *M. spectrum*, one closely related to *M. commutatum* (observed in both *gapCp short* and *long*; Figs. 5, 6), and one that forms a clade with *M. membranifolium* and *L. ellipticus* var. *pothifolius* (observed in *gapCp short* only; Fig. 5). Plastid sequences of *M. spectrum* were nested within a clade containing *M. cuspidatum* and *M. hainanense*, which is sister to the *M. membranifolium* clade (Fig. 4). It is therefore possible that *M. spectrum* is of hybrid origin with a mother from the *membranifolium–cuspidatum–Leptochilus* clade and a father closely related to *M. commutatum,* but we lack exact matches for either of these putative parents. *Microsorum spectrum* has a tetraploid chromosome count of either $2n = 148$ (Wagner 1963) or $2n = 144$ (Löve et al. 1977), which, in combination with our data, suggests that it may be an allopolyploid. *Microsorum spectrum* is a morphologically variable taxon, and has been treated as two varieties (var. *spectrum* and var. *pentadactylum*; Palmer 2003; Vernon and Ranker 2013). It is possible that some of this variation is due to its hybrid origins. Our nuclear sampling only includes one specimen of *M. spectrum* (var. *pentadactylum*), but additional sampling including multiple morphotypes may help clarify if any of the morphological variation is correlated with genetic diversity in this taxon. Furthermore, *M. spectrum* is the only native *Microsorum* occurring in Hawaii (Palmer 2003; Vernon and Ranker 2013), and the results of our phylogenetic analyses indicate that it is not derived from any of the other Pacific *Microsorum* sampled thus far. Additional sampling in Hawaii and elsewhere is needed to confirm whether this species is indeed of hybrid origin, and if so, where its parents occur.

Taxonomic Implications for Microsorum—The results of our phylogenetic analysis agree with previous studies showing that *Microsorum* is polyphyletic (Schneider et al. 2004a, b; Kreier et al. 2008), and furthermore demonstrate this for the first time with nuclear data. Although our sampling is not sufficient to allow for a taxonomic revision of the genus, the patterns of hybridization we observe here may be informative for future taxonomic studies. If *Microsorum* were expanded to include all species with this name, it would involve sinking multiple distinct monophyletic genera (e.g. *Lecanopteris*, *Lepisorus*) into synonymy, which does not seem warranted. An alternative is to restrict *Microsorum* to only *M. punctatum* (the type species of *Microsorum*) and closely related species including *M. musifolium*, *M. thailandicum*, and *M. whiteheadii*. *Phymatosorus* (type *M. scolopendria*) could be applied for the species *M. grossum*, *M. scolopendria*, and *M. papuanum* (Kreier et al. 2008). However, our results showing that hybrids (*M.* × *maximum*) between *M. punctatum* and *M. grossum* occur frequently and reciprocally (i.e. either species is capable of acting as the mother or father) indicate that these two clades are genetically similar, and lack absolute prezygotic mating barriers. Furthermore, all of these species are nested within a clade comprising other species of *Microsorum* and *Leptochilus*, corresponding to the "Microsoroid s. s. clade" of Kreier et al. (2008). The other hybridization events we detect (*M.* × *tohieaense*, possibly *M. spectrum*) also occur within this clade, again indicating the genetic affinity of the species involved. Hybridization events between fern genera are not unheard of, but they are extremely rare (Ranker and Sundue 2015; Rothfels et al. 2015; Schwartsburd et al. 2018). Were *Microsorum* split to recognize *Phymatosorus* and *Leptochilus*, it would result in at least two additional intergeneric hybrids.

Our study is the first to our knowledge to show genetic evidence of hybridization in microsoroid ferns. Nooteboom (1997) lists nine other putative hybrids or species of hybrid origin on the basis of morphology in this group. Inclusion of these taxa in future studies may help clarify the distinctness of proposed genera. Detailed studies into the dynamics of hybridization, including effect of antheridiogens, sperm and archegonia neck sizes, and the degree of niche overlap between progenitor taxa should also provide further insight into the maintenance of barriers to gene flow between microsoroid ferns (Sigel et al. 2014; Testo et al. 2014) and guide appropriate generic delimitation.

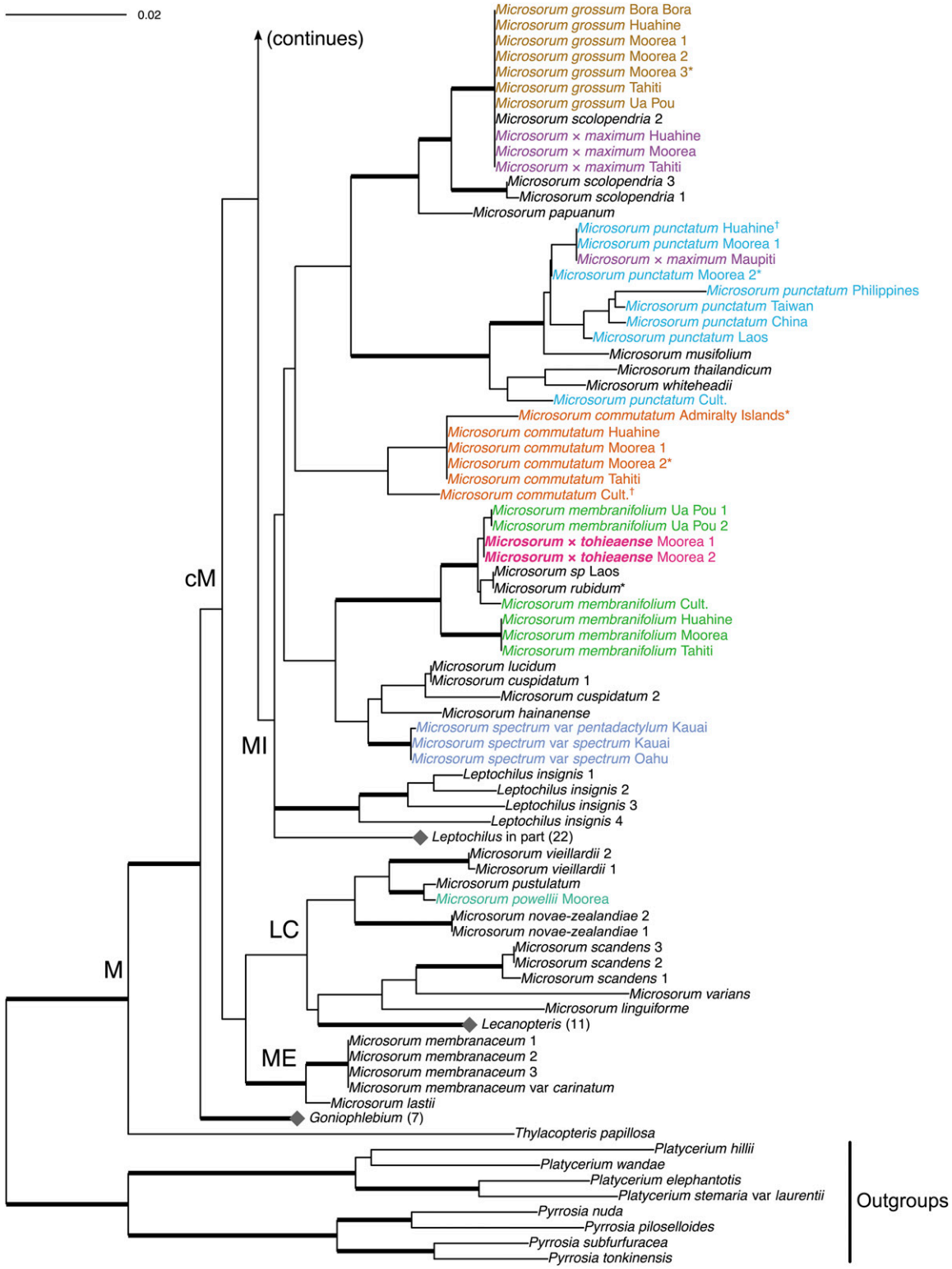

FIG. 4. Maximum-likelihood phylogenetic tree inferred using plastid markers (*rbcL* and *trnL–F*) including Society Islands microsoroid ferns and related taxa. Taxa occurring in Society Islands and Hawaii colored by taxon; taxa not occurring in these areas and outgroups in black. *Microsorum* × *tohieaense* in bold. Locality information and / or specimen individual code shown for taxa with multiple specimens. Diamonds indicate monophyletic genera or large clades within genera that do not contain any Society Islands species and have been collapsed for plotting; number of collapsed species indicated in parenthesis. Diamonds placed at first divergence within the collapsed clade. Extremely short branchlengths ($< 1 \times 10^{-5}$ substitutions per site) have been collapsed to zero. Strongly supported nodes (maximum likelihood bootstrap > 95%; maximum parsimony bootstrap > 95%; Bayesian inference posterior probability > 0.95) indicated by thickened lines. Abbreviations at nodes indicate major clades following Kreier et al. (2008): M = microsoroid ferns; ME = membranaceoid clade; LC = lecanopteroid clade; LP = lepisoroid clade; cM = core microsoroids; MI = microsoroid (s. s.) clade. Scalebar indicates substitutions per site. * missing *rbcL*. † missing *trnL–F*.

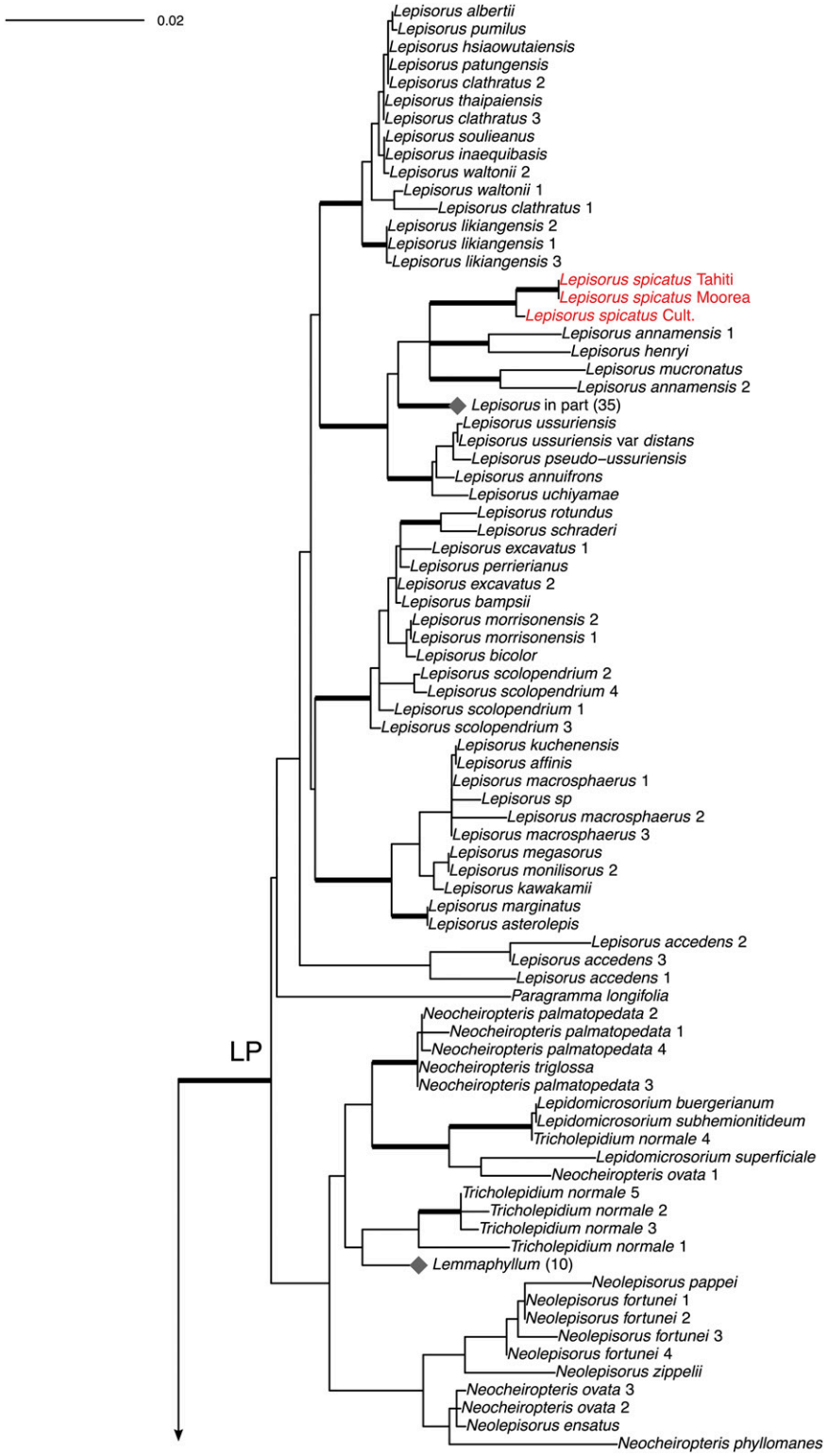

FIG. 4. (Continued)

Evolution of Nuclear Genomes in Microsorum—In addition to the clear evidence we recover for hybrid origins of *M.* × *maximum* and *M.* × *tohieaense*, our dataset also reveals the complicated nature of nuclear genome evolution in this group. We observed statistically supported, conflicting topologies for non-hybrid species between the two *gapCp* phylogenies: *M. grossum* and *M. punctatum* form a clade (MLBS = 85%; MPBS = 70%; BIPP = 0.98), which is then sister to *M. commutatum* (MLBS = 99%; MPBS = 99%; BIPP = 1.00) in the *gapCp short* phylogeny (Fig. 5), whereas *M. grossum* and *M. commutatum* form a clade (MLBS = 99%; MPBS = 97%; BIPP = 1.00), which is in turn sister to *M. punctatum* (MLBS = 98%; MPBS = 96%; BIPP = 1.00) in the *gapCp long* phylogeny (Fig. 6). Furthermore, the position of *M. powellii* also varies

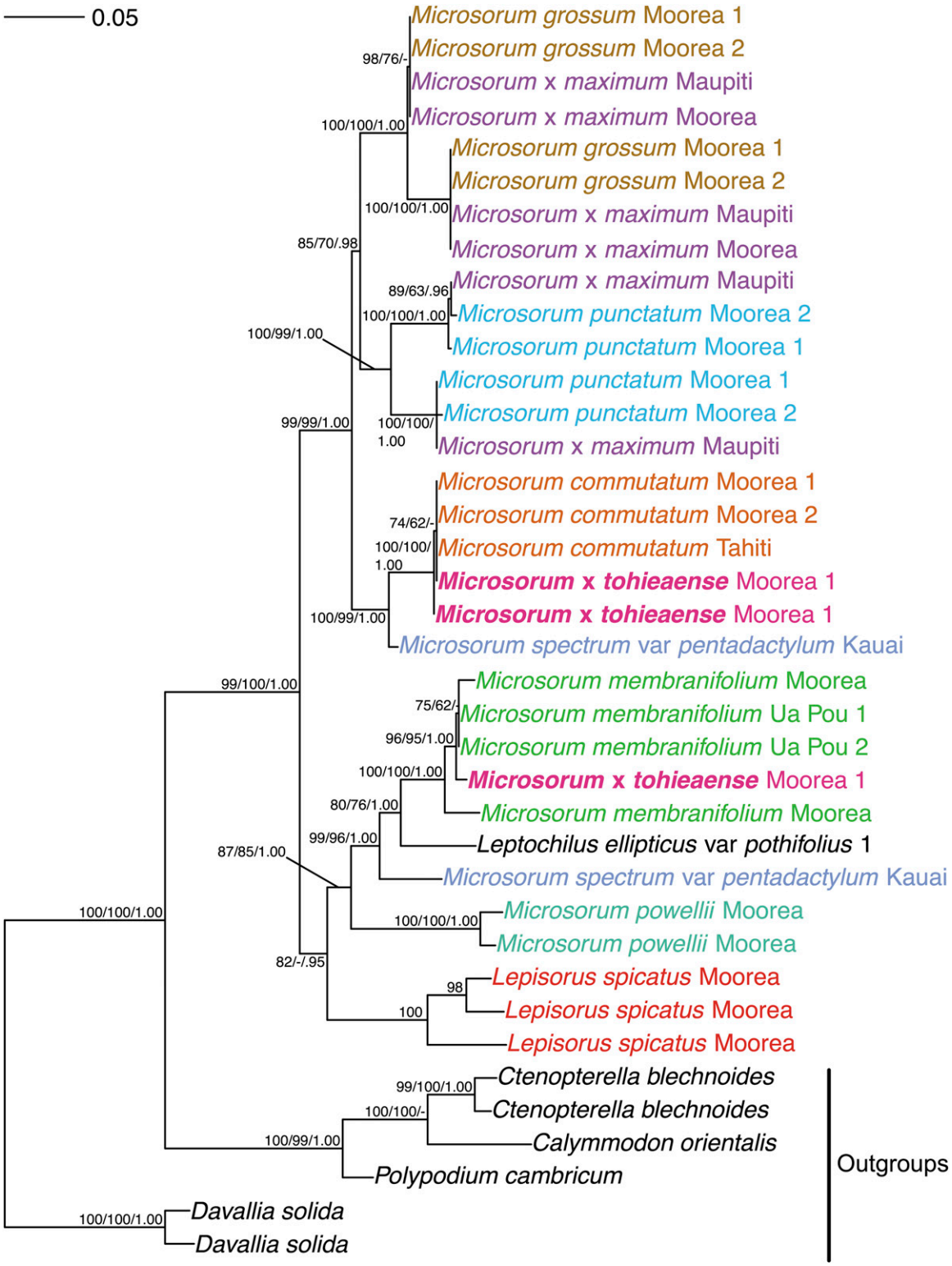

FIG. 5. Maximum-likelihood phylogenetic tree inferred using nuclear *gapCp short* including Society Islands microsoroid ferns and related taxa. Taxa occurring in Society Islands and Hawaii colored by taxon; taxa not occurring in these areas and outgroups in black. *Microsorum* × *tohieaense* in bold. Maximum likelihood bootstrap (MLBS), maximum parsimony bootstrap (MPBS), and Bayesian inference posterior probability (BIPP) values shown at nodes separated by slashes; values less than 50% (MLBS, MPBS) or 0.5 (BIPP) indicated with dash. Extremely short branchlengths ($< 1 \times 10^{-5}$ substitutions per site) have been collapsed to zero. Scalebar indicates substitutions per site.

between nuclear phylogenies, appearing amongst other more distantly related groups in the plastid and *gapCp short* phylogenies (Figs. 4, 5), but sister to "core *Microsorum*" (i.e. *M. punctatum*, *M. grossum*, and *M. commutatum*; MLBS = 100%; MPBS = 92%; BIPP = 0.94) in the *gapCp long* tree (Fig. 6). Such conflict between nuclear genes at internal nodes may indicate processes of incomplete lineage sorting or introgression. It is therefore possible that hybridization has played an important

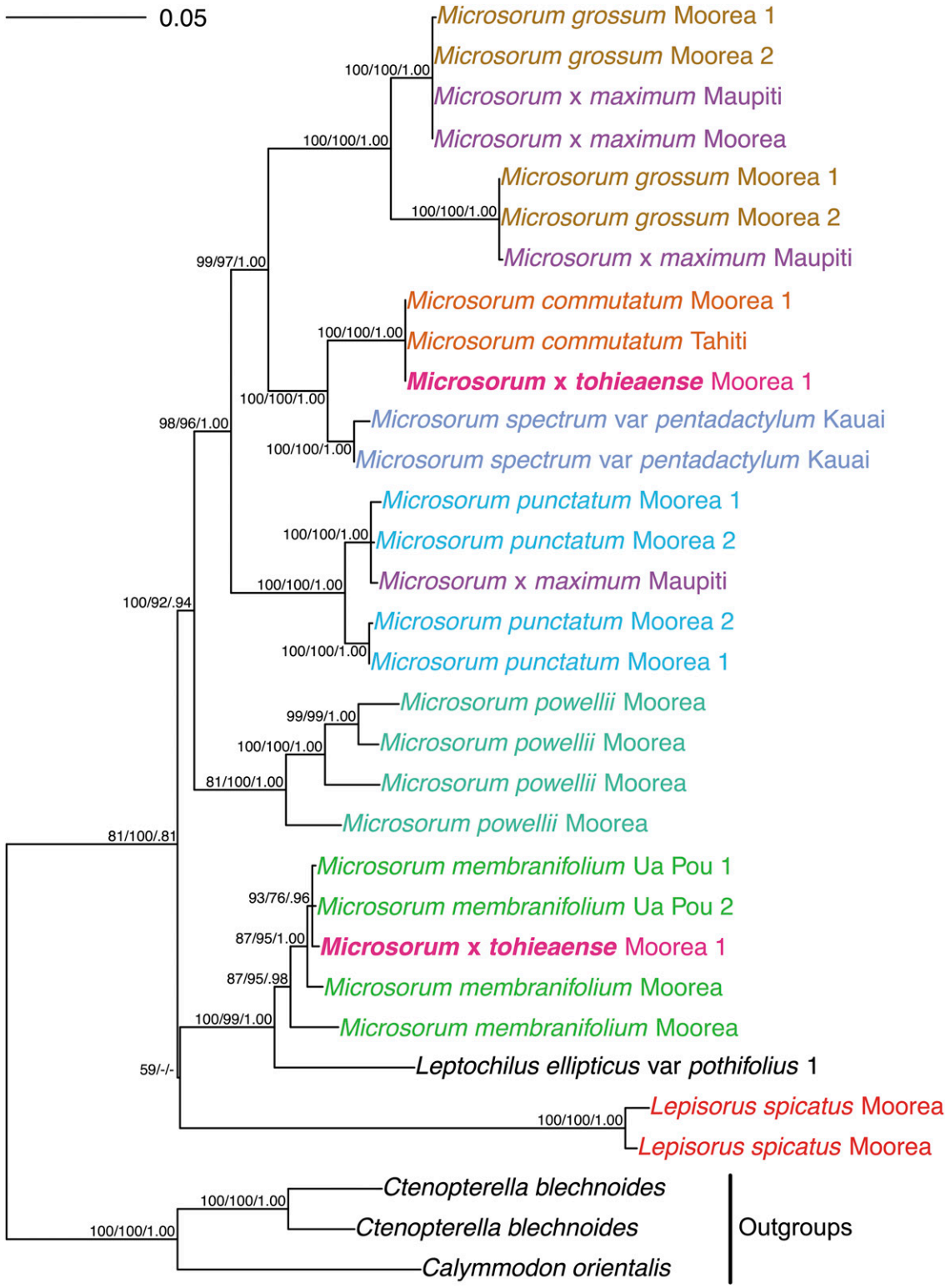

FIG. 6. Maximum-likelihood phylogenetic tree inferred using nuclear *gapCp long* including Society Islands microsoroid ferns and related taxa. Taxa occurring in Society Islands and Hawaii colored by taxon; taxa not occurring in these areas and outgroups in black. *Microsorum* × *tohieaense* in bold. Maximum likelihood bootstrap (MLBS), maximum parsimony bootstrap (MPBS), and Bayesian inference posterior probability (BIPP) values shown at nodes separated by slashes; values less than 50% (MLBS, MPBS) or 0.5 (BIPP) indicated with dash. Extremely short branchlengths ($< 1 \times 10^{-5}$ substitutions per site) have been collapsed to zero. Scalebar indicates substitutions per site.

role in the evolution of microsoroid ferns over long time scales. The method used here, cloning, is labor-intensive and cannot accommodate a large number of samples / loci. Application of recently developed next-generation DNA sequencing methods for polyploid species complexes (Rothfels et al. 2017) that can produce datasets for a much larger number of unlinked loci, combined with species-tree methods (Edwards 2009), should provide better insight into the complex evolutionary history of this group.

Key to the Microsoroid Ferns of the Society Islands, French Polynesia

1. Sporangia covering entire fertile surface of frond (i.e. forming a coenosorus), concentrated at apical segment; apical segment abruptly narrowed; rhizome short-creeping. . . . . *Lepisorus spicatus*
1. Sporangia arranged in distinct sori, not restricted to the apical segment; apical segment not abruptly narrowed; rhizome long-creeping. 2
   2. Laminae simple, base truncate to obtuse; stipe absent or broadly alate along nearly entire length. . . . . *Microsorum punctatum*
   2. Laminae rarely simple, usually at least irregularly lobed to deeply pinnatifid, base cuneate; stipe present, not or only narrowly alate. 3
      3. Sori scattered. 4
      3. Sori more or less in regular lines between costae and margins. 5
         4. Laminae irregularly lobed; sori 1–2 mm diam, sometimes fusing together. . . . . *Microsorum* × *maximum*
         4. Laminae deeply pinnatifid; sori < 1 mm diam, not fusing. . . . . *Microsorum commutatum*
            5. Laminae coriaceous; secondary veins obscured. . . . . *Microsorum grossum*
            5. Laminae membranaceous to subcoriaceous; secondary veins at least partly visible to very distinct. 6
               6. Plants epiphytic; laminae subcoriaceous. . . . . *Microsorum powellii*
               6. Plants terrestrial; laminae membranaceous. 7
                  7. Fronds to 2(–3) m; apical pinna more or less same size as lateral pinnae; sori deeply immersed, forming raised bumps ca. 2(–5) mm high adaxially. . . . . *Microsorum membranifolium*
                  7. Fronds < 1 m; apical pinna wider than lateral pinnae; sori slightly immersed, only forming slightly raised bumps < 1 mm high adaxially. . . . . *Microsorum* × *tohieaense*

Taxonomic Treatment

Microsorum* × *tohieaense J.H.Nitta, hyb. nov. Type: French Polynesia. Society Islands: Moorea, Mt. Tohiea, 393 m, 12 Jul 2012, *J.H. Nitta 1040* (holotype: GH!; isotypes: P!, PAP!, UC!).

Similar to *Microsorum grossum* and *Microsorum commutatum* in size and habit, but with membranaceous laminae (vs. coriaceous in *M. grossum*) and sori more or less in regular rows (vs. scattered in *M. commutatum*); similar to *Microsorum membranifolium* in texture, but differs in smaller size (fronds less than 1 m vs. fronds to 2 m in *M. membranifolium*) and apical pinna wider than lateral ones (vs. more or less conform apical pinnae in *M. membranifolium*).

Plants terrestrial or lithophytic. **Rhizomes** 4.5–5(7) mm wide, long creeping, moderately to densely scaly, pale green; rhizome scales 1–1.5 mm wide, round, peltate, clathrate, light in center, dark brown between center and margins, lighter towards the margins, margins entire; phyllopodia distinct. **Fronds** 50–60 cm long, set 2–5 cm apart, monomorphic. **Stipes** 20–30 cm long, glabrous except for a few scattered scales near the base, stramineous; scales similar to those on rhizome. **Laminae** 32–37 × 15–17 cm, ovate-lanceolate, deeply pinnatifid, apically subconform, membranaceous, surfaces glabrous, with a slightly sweet (coumarin) fragrance; pinnae 9–11 × 2.5 cm, 5–6(7) pairs, linear-lanceolate, slightly ascending, entire; apical pinnae 13–19 × 3–4 cm, larger than lateral pinnae, with primary veins more evident, slightly narrowing at the base; rachises and costae with few scattered scales, stramineous; costal scales 0.5 × 0.1–0.2 mm, clathrate, ovate, apex acuminate. **Veins** reticulate; main lateral veins 5–6 mm apart, distinct; connecting veins forming one row of large areolae parallel to the costa; smaller veins variously anastomosing. **Sori** 1.5–2 mm, round, located in a single row (or sometimes two rows) between costae and pinna margins, occasionally irregularly placed, slightly immersed, appearing slightly raised adaxially, with uniseriate paraphyses. **Spores** 29–44 × 10–31 μm, occasionally misshapen, clear, presumably not fertile. Figures 2, 3.

Ecology and Distribution*—Microsorum* × *tohieaense*** is known from a single population less than ca. 10 m^2 in extent located at ca. 400 m on the slope of Mt. Tohiea, Moorea, French Polynesia. Plants were observed growing terrestrially, but on a steep and rocky surface, so they are considered both terrestrial and epipetric.

***Etymology*—**The new hybrid is named after the type locality.

***Notes*—**This is a hybrid between *Microsorum commutatum* (Blume) Copel. and *Microsorum membranifolium* (R.Br.) Ching.

Conservation Status*—Microsorum* × *tohieaense*** is only known from the type locality and is extremely rare; however, as a hybrid it is excluded from the IUCN red list (IUCN 2017).

***Additional Specimen Examined*—French Polynesia.**—Society Islands: Moorea. Mt. Tohiea, 410 m, 9 Jul 2014, *J.H. Nitta 3929* (GH, P, PAP, UC).

Acknowledgments. We are grateful to Alan R. Smith and Jean-François Butaud for helpful discussions on the possible origins of *M.* × *tohieaense*. Weston Testo and an anonymous reviewer provided comments that greatly improved the manuscript. Atsushi Ebihara kindly provided use of the microscope for observations of rhizome scales and spores. Colin C. Nitta drew the illustrations. Suzanne Vinette, Tohei Theophilus, and Tristan Wang assisted with fieldwork. Staff at the University of California, Berkeley Richard B. Gump South Pacific Research Station provided logistical support for fieldwork. We thank the staff of PTBG for lending us their specimens of *M. membranifolium* and *M. spectrum*. Funding for this project was provided in part by the National Science Foundation (Doctoral Dissertation Improvement Grant DEB-1311169 to JHN and CCD), Setup Funds from Harvard University to CCD, the American Society of Plant Taxonomists (Research Grant for Graduate Students to JHN), the Garden Club of America (Award in Tropical Botany to JHN), the Harvard University Herbaria (Fernald Fieldwork Fellowship to JHN), the Society of Systematic Biologists (Graduate Student Research Award to JHN), and the Systematics Association (Systematics Research Fund to JHN).

Author Contributions. JHN conceived the study, gathered the data, conducted analyses, and was the primary author of the manuscript. SA collected specimens and measured traits. CCD provided lab space and materials and revised the manuscript.

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APPENDIX 1. GenBank accession numbers for plant material used in this study. Data presented as follows: taxon, individual code used during phylogenetic analysis followed by colon if more than one individual sampled for that taxon, voucher specimen (herbarium), locality if known, *rbcL* accession number, *trnL–F* accession number, *gapCp long* accession number(s) if available, *gapCp short* accession number(s) if available. Missing *rbcL* or *trnL–F* indicated by —. Accessions of *gapCp* given in order of arbitrarily assigned allele number (e.g., the first accession number corresponds to allele 1, the second to allele 2, etc.). Newly generated sequences are accession numbers MG452009–MG452032 (*rbcL*), MG427052–MG427077 (*trnL–F*), MG451945–MG451976 (*gapCp long*), and MG550279–MG550315 (*gapCp short*). Herbarium abbreviations follow Thiers (2018). Botanical garden abbreviations as follows: BGB, Botanical Garden Berlin-Dahlem; BGG, Old Botanical Garden of the University of Göttingen; BGH, Botanical Garden of the University of Heidelberg; BGZ, Botanical Garden Zurich; CAG, Garden of Charles Alford (Florida, USA); DBG, Duke Botanical Garden; LBG, Leiden Botanical Garden; KBG, Kunming Botanical Garden; NYBG, New York Botanical Garden; RBGE, Royal Botanic Garden Edinburgh; TBG, Tüebingen Botanic Garden; UBG, Utrecht Botanical Garden; UCBG, University of California, Berkeley Botanical Garden; XTBG, Xishuangbanna Tropical Botanical Garden.

Calymmodon orientalis Copel. *Nitta 682* (GH) Moorea, French Polynesia, —, —, *gapCp long* MG451945, *gapCp short* MG550279. ***Ctenopterella blechnoides*** (Grev.) Parris *Nitta 658* (GH) Moorea, French Polynesia, —, —, *gapCp long* MG451946, MG451947, *gapCp short* MG550280, MG550281. ***Davallia solida*** (G.Forst.) Sw. *Ranker 1935* (UC) Moorea, French Polynesia, —, —, *gapCp short* MG550282, MG550283. ***Goniophlebium argutum*** (Wall. ex Hook.) J.Sm. ex Hook. 1: *Cranfill TW075* (UC) Taiwan, DQ164442, DQ164505; 2: *Kim 2012-9 (cult. KBG)* (KUN) China, JX103721, JX103805; 3: *Wu 2440* (KUN) Laos, JX103709, JX103793. ***Goniophlebium mehibitense*** (C.Chr.) Parris *Hovenkamp 05-278* (L) East Kalimantan, Indonesia, EU482932, EU483026. ***Goniophlebium persicifolium*** (Desv.) Bedd. *cult. BGB 239-12-90-33* (B), EU482933, EU483028. ***Goniophlebium pseudoconnatum*** Copel. *cult. BGB 239-36-90-30* (B), EU482934, EU483029. ***Goniophlebium subauriculatum*** (Blume) C.Presl *Kreier s.n. (cult. BGG)* (GOET), AF470342, AY083645. ***Lecanopteris balgooyi*** Hennipman *David Klein s.n.* (L) Sulawesi, AF470328, AY083631. ***Lecanopteris carnosa*** (Reinw.) Blume *David Klein s.n.* (L) Sulawesi, AF470322, AY083625. ***Lecanopteris celebica*** Hennipman *Hennipman s.n. (UBG 85GR00170)* (L) Sulawesi, AF470323, AY083626. ***Lecanopteris crustacea*** Copel. *Franken and Roos 341* (L) Philippines, AF470329, AY083632. ***Lecanopteris deparioides*** (Ces.) Baker *Hennipman 7865 (UBG 87GR00136)* (U) Malaysia, AF470324, AY083627. ***Lecanopteris lomarioides*** (Kunze ex Mett.) Copel. *Hennipman s.n. (LBG 912010)* (L) Malaysia, AF470326, AY083629. ***Lecanopteris luzonensis*** Hennipman *Hennipman 7820 (UBG 87GR00084)* (U, L) Philippines, AF470325, AY083628. ***Lecanopteris pumila*** Blume *Woodhams 551* (L) Malaysia, AF470331, AY083634. ***Lecanopteris sarcopus*** (Teijsm. & Binn.) Copel. *cult. RBGE 171* (E), EU482935, EU483030. ***Lecanopteris sinuosa*** (Hook.) Copel. *Hennipman 7821 (UBG 87GR00087)* (U) Philippines, AF470321, AY083624. ***Lecanopteris spinosa*** Jermy & T.G.Walker *Jaarsma s.n. (UBG 92GR01365)* (U) Sulawesi, AF470327, AY083630. ***Lemmaphyllum adnascens*** Ching *Zhang 4237* (PE) Sichuan, China, GU126694, GU126724. ***Lemmaphyllum carnosum*** (Wall. ex J.Sm.) C.Presl 1: *collector unknown (UCBG 50.0326)* (UC) Japan, AF470332, AY083635; 2: *Schneider s.n. (cult. BGZ)* (GOET), EU482938, EU483033; 3: *Zhang 4364* (PE) Japan, GU126698, GU126728. ***Lemmaphyllum diversum*** (Rosenst.) Tagawa 1: *Ranker 2079* (COLO) Taiwan, EU482937, GU126729; 2: *Zhang 1854* (PE) China, EU482939, EU483034. ***Lemmaphyllum intermedium*** (Ching) Li Wang *Zhang 5162* (PE) Sichuan, China, GU126696, GU126726. ***Lemmaphyllum pyriforme*** (Ching) Ching *Zhang 4363 (cult. TBG)* (PE), GU126695, GU126725. ***Lemmaphyllum rostratum*** (Bedd.) Tagawa *Shui 80676* (PE) Yunnan, China, GU126697, GU126727. ***Lemmaphyllum squamatum*** (A.R. Sm. & X.C.Zhang) Li Wang *WB Xu 07087* (PE) Guangxi, China, GU126692, GU126721. ***Lepidomicrosorium buergerianum*** (Miq.) Ching & K.H.Shing *Shui 80894* (PE) China, GQ256315, GQ256242. ***Lepidomicrosorium subhemionitideum*** (Christ) P.S.Wang *Zhang 4111* (PE) Guangxi, China, GU126693, GU126723. ***Lepidomicrosorium superficiale*** (Blume) Li Wang *SG Lu J17* (PYU) Yunnan, China, AY725055, AY725049. ***Lepisorus accedens*** (Blume) Hosok. 1: *Hovenkamp 05-298* (L) East Kalimantan, Indonesia, EU482936, EU483031; 2: *Kuo LY kuo2072* (TAI) Philippines, KX891369, KX891354; 3: *Schneider H FJ11-129* (BM) Philippines, KX891368, KX891353. ***Lepisorus affinis*** Ching *Zhang 4219 (cult. SZBG)* (PE) China, GQ256256, GQ256173. ***Lepisorus albertii*** (Regel) Ching *Zhang 4325* (PE) Xinjiang, China, GQ256257, GQ256174. ***Lepisorus angustus*** Ching *Z.H. Shen S25* (PE) Tibet, China, GQ256290, GQ256214. ***Lepisorus annamensis*** (C.Chr.) Li Wang 1: *D Li 873* (PE) Hainan, China, GQ256252, GQ256166; 2: *Hovenkamp 05-277* (L) East Kalimantan, Indonesia, EU482931, EU483025. ***Lepisorus annuifrons*** (Makino) Ching *Kokubo s.n.* (TI) Japan, GQ256258, GQ256176. ***Lepisorus asterolepis*** (Baker) Ching ex S.X.Xu *Zhang 5171* (PE) Sichuan, China, GQ256259, GQ256177. ***Lepisorus bampsii*** Zink *R. Viane 11233* (PE) Kenya, GQ256260, GQ256178. ***Lepisorus bicolor*** (Takeda) Ching *Zhang 5157* (PE) Tibet, China, GQ256261, GQ256179. ***Lepisorus boninensis*** (Christ) Ching *cult. TBG 54022* (herbarium unknown) Japan, GQ256262, GQ256180. ***Lepisorus clathratus*** (C.B.Clarke) Ching 1: *Dickore 12430* (GOET) Tibet, China, DQ642154, DQ642236; 2: *Zhang 4515* (PE) Yunnan,

China, GQ256275, GQ256197; 3: *Zhang 4533* (PE) Yunnan, China, GQ256263, GQ256181. ***Lepisorus confluens*** W.M.Chu *C.D. Xu s.n.* (PE) Yunnan, China, GQ256264, GQ256182. ***Lepisorus contortus*** (Christ) Ching 1: *Zhang 4699* (PE) Tibet, China, GQ256308, GQ256235; 2: *Zhang 5187* (PE) Sichuan, China, GQ256266, GQ256184; 3: *Zhang 5204* (PE) Chongqing, China, GQ256265, GQ256183. ***Lepisorus elegans*** Ching ex W.M.Chu *Zhang 4444* (PE) Yunnan, China, GQ256268, GQ256187. ***Lepisorus excavatus*** (Bory ex Willd.) Ching 1: *Rakotondrainibe 6785* (P) Grande Comore, Comoros, DQ642156, GQ256189; 2: *Hemp 3561* (DSM) Tanzania, DQ642155, GQ256188. ***Lepisorus hachijoensis*** Sa.Kurata *Zhang 4358* (PE) Japan, GQ256269, GQ256190. ***Lepisorus henryi*** (Hieron. ex C.Chr.) Li Wang *Shui 80679* (PE) Yunnan, China, GQ256253, GQ256167. ***Lepisorus heterolepis*** (Rosenst.) Ching *Zhang 5064* (PE) Tibet, China, GQ256270, GQ256191. ***Lepisorus hsiaowutaiensis*** Ching & S.K.Wu *Q.R. Liu s.n.* (PE) Hebei, China, GQ256271, GQ256192. ***Lepisorus inaequibasis*** ined. *Zhang 4615* (PE) Tibet, China, GQ256320, GQ256248. ***Lepisorus kawakamii*** (Hayata) Tagawa *Ranker 2051* (COLO) Taiwan, EU482940, GQ256193. ***Lepisorus kuchenensis*** (Y.C.Wu) Ching *J.M. Xi 08188* (PE) Guangxi, China, GQ256272, GQ256194. ***Lepisorus lewisii*** (Baker) Ching *Y Liu 05620* (PE) Anhui, China, GQ256273, GQ256195. ***Lepisorus likiangensis*** Ching & S.K. Wu 1: *Zhang 4468* (PE) Yunnan, China, GQ256267, GQ256186; 2: *Zhang 4488* (PE) Yunnan, China, GQ256274, GQ256196; 3: *Zhang 5117* (PE) Tibet, China, GQ256303, GQ256230. ***Lepisorus lineariformis*** Ching & S.K.Wu 1: *Zhang 4437* (PE) Yunnan, China, GQ256277, GQ256199; 2: *Zhang 4771* (PE) Tibet, China, GQ256276, GQ256198. ***Lepisorus loriformis*** (Wall. ex Mett.) Ching *Zhang 4440* (PE) Yunnan, China, GQ256278, GQ256201. ***Lepisorus luchunensis*** Y.X.Lin *Qi 097* (PE) Yunnan, China, HQ712000, HQ712019. ***Lepisorus macrosphaerus*** (Baker) Ching 1: *Kim 2012-3 (cult. KBG)* (KUN) China, JX103697, JX103781; 2: *Ranker TW018* (UC) Taiwan, EU482941, EU483036; 3: *Zhang 4794* (PE) Tibet, China, GQ256280, GQ256203. ***Lepisorus marginatus*** Ching *Zhang 3360* (PE) Hubei, China, GQ256281, GQ256204. ***Lepisorus medogensis*** Ching & Y.X.Lin *Z.D. Fang XZ-266* (PE) Tibet, China, GQ256282, GQ256205. ***Lepisorus megasorus*** (C.Chr.) Ching *Cranfill TW069* (UC) Taiwan, DQ642158, GQ256206. ***Lepisorus miyoshianus*** (Makino) Fraser-Jenk. & Subh.Chandra 1: *C.C. Liu DB06104* (PE) Sichuan, China, GQ256255, GQ256172; 2: *Cranfill TW087* (UC) Taiwan, AY362563, DQ179639. ***Lepisorus monilisorus*** (Hayata) Tagawa 1: *H.M. Zhang 20050117* (PE) Taiwan, GQ256283, GQ256207; 2: *Ranker TW012* (UC) Taiwan, EU482942, EU483037. ***Lepisorus morrisonensis*** (Hayata) H.Itô 1: *Zhang 4736* (PE) Tibet, China, GQ256285, GQ256209; 2: *Zhang 5113* (PE) Tibet, China, GQ256284, GQ256208. ***Lepisorus mucronatus*** (Fée) Li Wang *Jaman 5891* (UC) Malaysia, AY362562, GQ256168. ***Lepisorus obscurevenulosus*** (Hayata) Ching *Zhang 4151* (PE) Guangxi, China, GQ256286, GQ256210. ***Lepisorus oligolepidus*** (Baker) Ching *Zhang 5082* (PE) Tibet, China, GQ256287, GQ256211. ***Lepisorus onoei*** (Franch. & Sav.) Ching *Zhang 4352* (PE) Japan, GQ256288, GQ256212. ***Lepisorus patungensis*** Ching & S.K.Wu *Zhang 3413* (PE) Hubei, China, GQ256289, GQ256213. ***Lepisorus perrierianus*** (C.Chr.) Ching *EB 245* (herbarium unknown) Kenya, HQ711995, HQ712017. ***Lepisorus pseudonudus*** Ching *Zhang 4249* (PE) Sichuan, China, GQ256291, GQ256215. ***Lepisorus pseudo-ussuriensis*** Tagawa *Cranfill TW093* (UC) Taiwan, EU482943, GQ256216. ***Lepisorus pumilus*** Ching & S.K.Wu *M.Z. Wang 60667* (PE) Gansu, China, GQ256292, GQ256217. ***Lepisorus rotundus*** Ching *RV7675* (herbarium unknown) Tanzania, HQ711996, HQ712015. ***Lepisorus schraderi*** (Mett.) Ching *RV8253* (herbarium unknown) Reunion, HQ711998, HQ712016. ***Lepisorus scolopendrium*** (Ching) Mehra & Bir 1: *Wu 2441* (KUN) Laos, JX103698, JX103782; 2: *Y.D. Tang YD-076* (PE) Tibet, China, GQ256294, GQ256219; 3: *Zhang 2295* (PE) India, GQ256293, GQ256218; 4: *Zhang 4659* (PE) Tibet, China, GQ256295, GQ256220. ***Lepisorus sinensis*** (Christ) Ching *Shui 81069* (PE) Yunnan, China, GQ256296, GQ256221. ***Lepisorus sordidus*** (C.Chr.) Ching 1: *Zhang 0612* (PE) Sichuan, China, GQ256298, GQ256223; 2: *Zhang 3218* (PE) Yunnan, China, GQ256297, GQ256222. ***Lepisorus soulieanus*** (Christ) Ching & S.K.Wu *Zhang 5168* (PE) Sichuan, China, GQ256321, GQ256249. ***Lepisorus sp*** *Kim 2012-10* (KUN), JX103722, JX103806. ***Lepisorus spicatus*** (L.f.) Li Wang Cult: *Schneider s.n. (cult. BGG)* (GOET), DQ642153, DQ642234; Moorea: *Nitta 323* (GH) Moorea, French Polynesia, MG452009, MG427052, *gapCp long* MG451948, MG451949, *gapCp short* MG550284, MG550285, MG550286; Tahiti: *Ranker 1915* (COLO) Tahiti, French Polynesia, EF463244, GQ256170. ***Lepisorus stenistus*** (C.B.Clarke) Y.X.Lin *Z.D. Fang XZ-412* (PE) Tibet, China, GQ256279, GQ256202. ***Lepisorus subconfluens*** Ching *Zhang 4518* (PE) Yunnan, China, GQ256299, GQ256224. ***Lepisorus sublinearis*** (Baker ex Takeda) Ching 1: *Shui 80595* (PE) Yunnan, China, GQ256301, GQ256226; 2: *Shui 81060* (PE) Yunnan, China, GQ256300, GQ256225. ***Lepisorus thaipaiensis*** Ching & S.K.Wu *G.Y. Rao 2005-045A* (PE) Shanxi, China, GQ256302, GQ256229. ***Lepisorus thunbergianus*** (Kaulf.) Ching 1: *Ohora 2005042404* (TI) Japan, GQ256305, GQ256232; 2: *Zhang 4544* (PE) Yunnan, China, GQ256306, GQ256233; 3: *Zhang 5205* (PE) Chongqing, China, GQ256304, GQ256231. ***Lepisorus tibeticus*** Ching & S.K.Wu *Zhang 4694* (PE) Tibet, China, GQ256307, GQ256234. ***Lepisorus tosaensis*** (Makino) H.Itô *S. Fujimoto 2005042904* (TI) Japan, GQ256309, GQ256236. ***Lepisorus uchiyamae*** (Makino) H.Itô *S. Fujimoto 2005042902* (TI) Japan, GQ256310, GQ256237. ***Lepisorus ussuriensis*** (Regel & Maack) Ching *B.D. Liu s.n.* (PE) Heilongjiang, China, GQ256311, GQ256238. ***Lepisorus ussuriensis*** (Regel & Maack) Ching var. ***distans*** (Makino) Tagawa *S. Fujimoto SF05051602* (TI) Japan, GQ256312, GQ256239. ***Lepisorus waltonii*** (Ching) S.L.Yu 1: *Cranfill 94-266-29* (UC) China, EU482944, EU483039; 2: *Zhang 4639* (PE) Tibet, China, GQ256322, GQ256250. ***Lepisorus xiphiopteris*** (Baker) W.M.Chu ex Y.X.Lin *C.D. Xu A0303* (PE) Yunnan, China, GQ256313, GQ256240. ***Leptochilus axillaris*** (Cav.) Kaulf. 1: *Wu 2344* (KUN) Laos, JX103699, JX103783; 2: *Wu 2439* (KUN) Laos, JX103700, JX103784; 3: *Wu 2462* (KUN) Laos, JX103701, JX103785. ***Leptochilus cantoniensis*** (Baker) Ching 1: *Dong 172* (PE) China, EU482946, EU483042; 2: *Dong 743* (PE) China, EU482945, EU483041. ***Leptochilus decurrens*** Blume *Kim 2012-12 (cult. KBG)* (KUN) China, JX103724, JX103808. ***Leptochilus digitatus*** (Baker) Noot. 1: *Smith 00-036* (UC) Vietnam, EU482948, EU483044; 2: *Wu 2515* (KUN) Laos, JX103695, JX103779; 3: *Zhang 3509* (PE) China, EU482947, EU483043. ***Leptochilus ellipticus*** (Thunb. ex Murray) Noot. *Zhang 1923* (PE) China, EU482949, EU483045. ***Leptochilus ellipticus*** (Thunb. ex Murray) Noot. var. ***pothifolius*** (Buch.-Ham. ex D. Don) X.C. Zhang 1: *Nitta 377* (GH) Okinawa, Japan, MG452010, MG427053, *gapCp long* MG451950, *gapCp short* MG550287; 2: *Wu 2712* (KUN) Laos, JX103696, JX103780. ***Leptochilus hemionitideus*** (C.Presl) Noot. 1: *Moran s.n. (cult. NYBG)* (NY), EU482950, EU483046; 2: *Wu 2437* (KUN) Laos, JX103694, JX103778. ***Leptochilus hemitomus*** (Hance) Noot. *Zhang 3302* (PE) China, EU482951, EU483047. ***Leptochilus heterophyllus*** (S.K.Wu & K.L..Phan) Christenh. 1: *WP-136* (KUN) Vietnam, JX520933, JX520937; 2: *WP-201* (KUN) Vietnam, JX520934, JX520938; 3: *WP-135* (KUN) Vietnam, JX103688, JX103772. ***Leptochilus insignis*** (Blume) Fraser-Jenk. 1: *Liu 204* (PE) China, EU482957, EU483054; 2: *Liu 214* (PE) China, EU482958, EU483055; 3: *Wu 2435* (KUN) Laos, JX103703, JX103787; 4: *Zhang 3510* (PE) China, EU482959, EU483056. ***Leptochilus pteropus*** (Blume) Fraser-Jenk. *Kreier s.n. (cult. BGG)* (GOET), EU482965, EU483061. ***Leptochilus shintenensis*** (Hayata) X.C.Zhang & Noot. *Zhang 3800* (PE), EU482953, EU483049. ***Leptochilus wrightii*** (Hook. & Baker) X.C.Zhang 1: *Kim 2012-15 (cult. KBG)* (KUN) China, JX103727, JX103811; 2: *Tsutsumi 1067* (CT) Okinawa, Japan, EU482954, EU483050. ***Microsorum commutatum*** (Blume) Copel. Admiralty Islands: *Wagner & Grether 3481 (UCBG 55.0092)* (UC) Admiralty Islands, AY362571, —; Cult: *Smith 2901* (UC), —, EU483051; Huahine: *Nitta 4046* (GH) Huahine, French Polynesia, MG452011, MG427054; Moorea 1: *Sanchez-Baracaldo 175* (UC) Moorea, French Polynesia, MG452014, MG427056, *gapCp long* MG451952, *gapCp short* MG550289; Moorea 2: *Gulamhussein 2* (UC) Moorea, French Polynesia, MG452013, —, *gapCp short* MG550290; Tahiti: *Amer 13* (GH) Tahiti, French Polynesia, MG452012, MG427055, *gapCp long* MG451951, *gapCp short* MG550288. ***Microsorum cuspidatum*** (D.Don) Tagawa 1: *Kim 2012-6 (cult. KBG)* (KUN) China, JX103707, JX103791; 2: *collector unknown (LBG 3560)* (UC), AF470335, AY083638. ***Microsorum grossum*** (Langsd. & Fisch.) S.B.Andrews Bora Bora: *Nitta 3837* (GH) Bora Bora, French Polynesia, MG452015, MG427057; Huahine: *Dunn 504* (PTBG) Huahine, French Polynesia, MG452017, MG427059; Moorea 1: *Sanchez-Baracaldo 170* (UC) Moorea, French Polynesia, MG452019, MG427061, *gapCp long* MG451953, MG451954, *gapCp short* MG550291, MG550292; Moorea 2: *Vinette 33.3* (UC) Moorea, French Polynesia, KY099829, MG427062, *gapCp long* MG451955, MG451956, *gapCp short* MG550293, MG550294; Moorea 3: *Ranker 1941* (COLO) Moorea, French Polynesia, EF463253, —; Tahiti: *Amer 14* (GH) Tahiti, French Polynesia, MG452016, MG427058; Ua Pou: *Lorence 9155* (PTBG) Ua Pou, French Polynesia, MG452018, MG427060. ***Microsorum hainanense*** Noot. *Wang 1348 (cult. SCIB)* (PE), EU482960, EU483057. ***Microsorum lastii*** (Baker) Tardieu *Perier 7937* (P), EU482961, EU483058. ***Microsorum linguiforme*** Copel. *T. Ranker 1776* (UC) New Guinea, AF470334, AY083637. ***Microsorum lucidum*** (Roxb.) Copel. *Kim 2012-14 (cult. KBG)* (KUN) China, JX103726, JX103810. ***Microsorum*** × ***maximum*** (Brack.) Copel. Huahine: *Nitta 3972* (GH) Huahine, French Polynesia, MG452022, MG427065; Maupiti: *Nitta 3674* (GH) Maupiti, French Polynesia, MG452021, MG427064, *gapCp long* MG451957, MG451958, MG451959, *gapCp short* MG550295, MG550296, MG550297, MG550298; Moorea: *Hinkle 106* (UC) Moorea, French Polynesia, KY099833, MG427066, *gapCp long* MG451960, *gapCp short* MG550299, MG550300; Tahiti: *Nitta 1863* (GH) Tahiti, French Polynesia, MG452020, MG427063. ***Microsorum membranaceum*** (D.Don) Ching 1: *Kim 2012-2 (cult. KBG)* (KUN) China, JX103704, JX103788; 2: *Li 95 (cult. XTBG)* (PE), EU482962, EU483059; 3: *SG Lu J17* (PYU) Yunnan, China, AY725053, AY725051. ***Microsorum***

membranaceum (D.Don) Ching var. ***carinatum*** W.M. Chu & Z.R. He *SG Lu J17* (PYU) Yunnan, China, AY725054, AY725050. ***Microsorum membranifolium*** (R.Br.) Ching Cult: *Schneider s.n. (cult. BGG)* (GOET), DQ642161, DQ642245; Huahine: *Nitta 4073* (GH) Huahine, French Polynesia, MG452023, MG427067; Moorea: *Nitta 1145* (GH) Moorea, French Polynesia, MG452024, MG427068, *gapCp long* MG451961, MG451962, *gapCp short* MG550301, MG550302; Tahiti: *Amer 15* (GH) Tahiti, French Polynesia, MG452025, MG427069; Ua Pou 1: *Dunn 250* (PTBG) Ua Pou, French Polynesia, MG452026, MG427070, *gapCp long* MG451963, *gapCp short* MG550303; Ua Pou 2: *Dunn 458* (PTBG) Ua Pou, French Polynesia, MG452027, MG427071, *gapCp long* MG451964, *gapCp short* MG550304. ***Microsorum musifolium*** Copel. *collector unknown (UCBG 58.0649)* (UC) Java, Indonesia, AF470333, AY083636. ***Microsorum novaezealandiae*** Copel. 1: *LRP 3558* (WELT) Thames, New Zealand, DQ401116, DQ401121; 2: *LRP 3584* (WELT) Wellington, New Zealand, DQ401120, DQ401124. ***Microsorum papuanum*** Parris *Schuettpelz 603 (cult. BGB)* (GOET), DQ642162, DQ642246. ***Microsorum powellii*** (Baker) Copel. *Nitta 654* (GH) Moorea, French Polynesia, MG452028, MG427072, *gapCp long* MG451965, MG451966, MG451967, MG451968, *gapCp short* MG550305, MG550306. ***Microsorum punctatum*** (L.) Copel. China: *Zhang 4194* (PE) China, GQ256316, GQ256244; Cult: *Schneider s.n. (cult. BGH)* (GOET), DQ164444, DQ164508; Huahine: *Nitta 4045* (GH) Huahine, French Polynesia, —, MG427073; Laos: *Wu 2506* (KUN) Laos, JX103705, JX103789; Moorea 1: *Vinette 32.2* (UC) Moorea, French Polynesia, KY099832, MG427074, *gapCp long* MG451971, MG451972, *gapCp short* MG550309, MG550310; Moorea 2: *Baltrushes s.n.* (UC) Moorea, French Polynesia, MG452029, —, *gapCp long* MG451969, MG451970, *gapCp short* MG550307, MG550308; Philippines: *C. Ridsdale (LBG 24091)* (UC) Philippines, AF470337, AY083640; Taiwan: *Ranker 2096* (COLO) Taiwan, EU482966, EU483063. ***Microsorum pustulatum*** Copel. *LRP 3575* (WELT) Wellington, New Zealand, DQ401117, DQ401122. ***Microsorum rubidum*** (Kunze) Copel. *TNS759256* (TNS) Okinawa, Japan, AB575280, —. ***Microsorum scandens*** Tindale 1: *Schneider s.n. (cult. BGG)* (GOET), DQ212057, DQ179641; 2: *LRP 3534* (WELT) Pohangina, New Zealand, DQ401118, DQ401123; 3: *LRP 3573* (WELT) Wellington, New Zealand, DQ401119, DQ401125. ***Microsorum scolopendria*** (Burm.f.) Copel. 1: *Schneider s.n. (cult. BGG)* (GOET), DQ642163, DQ642247; 2: *Ranker 1941* (COLO) Moorea, French Polynesia, DQ179633, DQ179642; 3: *Rakotondrainibe 660* (P) Mayotte, GQ256317, GQ256245. ***Microsorum sp*** *Wu 2367* (KUN) Laos, JX103708, JX103792. ***Microsorum spectrum*** (Kaulf.) Copel. var. ***pentadactylum*** (Hillebr.) D. D. Palmer *Wood 15756* (PTBG) Kauai, Hawaii, MG452030, MG427075, *gapCp long* MG451973, MG451974, *gapCp short* MG550311, MG550312. ***Microsorum spectrum*** (Kaulf.) Copel. var. ***spectrum*** Kauai: *Wood 10936* (PTBG) Kauai, Hawaii, EU482967, EU483064; Oahu: *HG 1350* (UC) Oahu, Hawaii, EU482968, EU483065. ***Microsorum thailandicum*** Boonkerd & Noot. *Schwertfeger s.n. (cult. BGG)* (GOET), EU482969, EU483066. ***Microsorum*** × ***tohieaense*** J.H.Nitta Moorea 1: *Nitta 3929* (GH) Moorea, French Polynesia, MG452032, MG427077, *gapCp long* MG451975, MG451976, *gapCp short* MG550313, MG550314, MG550315; Moorea 2: *Nitta 1040* (GH) Moorea, French Polynesia, MG452031, MG427076. ***Microsorum varians*** (Mett.) Hennipman & Hett. *Schneider s.n. (cult. BGG)* (GOET), AY362566, DQ179643. ***Microsorum vieillardii*** (Mett.) Copel. 1: *Smith s.n. (cult. CAG)* (UC), DQ179634, DQ179644; 2: *Schneider s.n. (cult. DBG)* (GOET), DQ179635, DQ179645. ***Microsorum whiteheadii*** A.R.Sm. & Hoshiz. *Whitehead s.n.* (UC) Sumatra, Indonesia, EU482970, EU483067. ***Neocheiropteris ovata*** (Fée) Fraser-Jenk. 1: *Kim 2012-8 (cult. KBG)* (KUN) China, JX103720, JX103804; 2: *X.Y. Du 0936* (KUN) Yunnan, China, HQ597011, HQ597020; 3: *Zhang 728/1* (PE) China, EU482972, EU483068. ***Neocheiropteris palmatopedata*** (Baker) Christ 1: *Schneider s.n. (cult. BGG)* (GOET), AY362567, DQ212059; 2: *Kim 2012-1 (cult. KBG)* (KUN) China, JX103706, JX103790; 3: *X.Y. Du 0961* (KUN) Yunnan, China, HQ597009, HQ597018; 4: *Zhang 4482* (PE) Yunnan, China, GQ256318, GQ256246. ***Neocheiropteris phyllomanes*** (Christ) Ching *Nicholson s.n. (cult. RGBE)* (E), EU482973, EU483069. ***Neocheiropteris triglossa*** (Baker) Ching *W.M. Zhu 57112* (KUN) Yunnan, China, HQ597010, HQ597019. ***Neolepisorus ensatus*** (Thunb.) Ching *Zhang 3611* (PE) South Korea, GQ256319, GQ256247. ***Neolepisorus fortunei*** (T.Moore) Li Wang 1: *Kim 2012-5 (cult. KBG)* (KUN) China, JX103702, JX103786; 2: *SG Lu J17* (PYU) Yunnan, China, AY725056, AY725052; 3: *Ranker 2087* (COLO) Taiwan, DQ642159, DQ642242; 4: *Zhang 3446* (PE) China, EU482955, EU483052. ***Neolepisorus pappei*** Li Wang *Schelpe 441/79 (LBG 901312)* (herbarium unknown) Madagascar, AF470336, AY083639. ***Neolepisorus zippelii*** (Blume) Li Wang *IN112* (TI) Gunung Gede, Indonesia, AB232411, GU126731. ***Paragramma longifolia*** (Blume) T.Moore *Cranfill BF012* (UC) Malay Peninsula, DQ642157, GQ256200. ***Platycerium elephantotis*** Schweinf. *Kreier GG0405 (cult. BGG)* (GOET), DQ164449, DQ164513. ***Platycerium hillii*** T.Moore *Kreier GG0407 (cult. BGG)* (GOET), DQ164452, DQ164516. ***Platycerium stemaria*** (Beauv.) Desv. var. ***laurentii*** De Wild. *Kreier GG0411 (cult. BGG)* (GOET), DQ164458, DQ164522. ***Platycerium wandae*** Racib. *Kreier GG0414 (cult. BGG)* (GOET), DQ164462, DQ164526. ***Polypodium cambricum*** L. *P.J.B. Woods 8-61* (E) Valencia, Spain, —, —, *gapCp short* KJ748235. ***Pyrrosia nuda*** (Giesenh.) Ching *Zhang et al. 6295* (CDBI, MO, VNMN) Hoa Binh, Vietnam, KY931116, KY931398. ***Pyrrosia piloselloides*** (L.) M.G.Price *Zhang et al. 7667* (CDBI, MO, VNMN) Thua Thien-Hue, Vietnam, KY931130, KY931409. ***Pyrrosia subfurfuracea*** (Hook.) Ching *Zhang et al. 6372* (CDBI, MO, VNMN) Hoa Binh, Vietnam, KY931051, KY931349. ***Pyrrosia tonkinensis*** (Giesenh.) Ching *Zhang et al. 9168* (CDBI) Guizhou, China, KY931175, KY931449. ***Thylacopteris papillosa*** (Blume) J.Sm. *Gravendeel 559* (L) Java, Indonesia, AY459175, AY459183. ***Tricholepidium normale*** (D.Don) Ching 1: *Kim 2012-4 (cult. KBG)* (KUN) China, JX103710, JX103794; 2: *Shen S4-1* (PE) China, EU482975, EU483071; 3: *Shui 80596* (PE) Yunnan, China, GQ256323, GQ256251; 4: *X.Y. Du 1004 (cult. KBG)* (KUN), HQ597012, HQ597022; 5: *Zhang 3100* (PE) China, EU482974, EU483070.