

Phylogenetic and Morphological Analyses Support the Resurrection of *Dendroconche* and the Recognition of Two New Genera in Polypodiaceae Subfamily Microsoroideae

Weston L. Testo,¹ Ashley R. Field,² Emily B. Sessa,¹ and Michael Sundue³

¹Department of Biology, University of Florida, 521 Bartram Hall, Gainesville, Florida 32611, USA; wtesto@ufl.edu; emilysessa@ufl.edu

²Queensland Herbarium, Department of Environment and Sciences; Australian Tropical Herbarium, James Cook University, Box 6811, Cairns, Queensland, Australia 4878; ashley.field@jcu.edu.au

³The Pringle Herbarium, University of Vermont, Burlington, 27 Colchester Drive, Vermont 05405, USA; sundue@gmail.com
Author for correspondence (wtesto@ufl.edu)

Communicating Editor: Alejandra Vasco

Abstract—The taxonomy of the Polypodiaceae subfamily Microsoroideae is highly problematic, especially with respect to the circumscription of the highly variable and non-monophyletic genus *Microsorium*. Using phylogenetic analyses and morphological evidence, we demonstrate that sixteen taxa typically treated in the genera *Microsorium* and *Colysis* are not closely related to those groups and instead belong to three clades that are successive sister groups to the Old-World ant-fern genus, *Lecanopteris*. We use the available genus name *Dendroconche* for one of these clades and propose the new genera *Bosmania* and *Zealandia* to accommodate the remaining two groups. We provide a description and identify morphological synapomorphies for each of the genera, make new combinations and designate lectotypes where necessary, and present keys and descriptions for all relevant species. We also discuss the evolution of ant-fern associations in the lecanopteroid ferns and highlight the need for additional taxonomic work in the subfamily. The following new combinations are provided: *Bosmania lastii*, *B. leandriana*, *B. membranacea*, *Dendroconche ampla*, *D. latilobata*, *D. linguiforme*, *D. sayeri*, *D. scandens*, *D. varians*, *Zealandia novae-zealandiae*, *Z. powellii*, *Z. pustulata*, *Z. pustulata* subsp. *hovensis*, and *Z. vieillardii*.

Keywords—Classification, fern, *Lecanopteris*, taxonomy.

Despite being the focus of considerable taxonomic (Bosman 1991; Nootboom 1997; Zhang et al. 2018) and phylogenetic study (Schneider et al. 2006; Kreier et al. 2008; Testo and Sundue 2014, 2016; Sundue et al. 2015; Nitta et al. 2018; Zhang et al. 2019), generic circumscription in the microsorooid ferns (Polypodiaceae subfamily Microsoroideae sensu PPG I, 2016) has remained uncertain. Taxonomic resolution of the subfamily has been hindered in large part by the morphological heterogeneity and non-monophyly of *Microsorium*, as demonstrated by Bosman (1991) in her monograph of the genus and later by a series of phylogenetic studies (Schneider et al. 2004, 2006; Kreier et al. 2008; Testo and Sundue 2014, 2016; Nitta et al. 2018). In each of these studies, several species of *Microsorium* and the allied genus *Colysis* were found not to be closely related to *Microsorium* s. s. but instead were resolved in a grade allied to the Old-World ant-fern genus *Lecanopteris*. Although this finding was discussed by the authors of each of these studies, they did not attempt to resolve the outstanding taxonomic issues, as this would require either naming several new genera or placing these taxa in a broadly construed and morphologically incoherent *Lecanopteris*. Here, we generate a molecular phylogeny and examine the morphology of this group to circumscribe monophyletic and morphologically cohesive clades and provide the appropriate taxonomic innovations to resolve the long-standing taxonomic problems associated with these species.

MATERIALS AND METHODS

Taxon Sampling and Sequence Data—We included sequence data from 167 taxa in this study, including representatives of all recognized genera of Polypodiaceae subfamily Microsoroideae. Included in our analyses were the type species of all 12 currently recognized genera in the subfamily (PPG I 2016) as well as those of *Colysis*, in which two of our focal species have been treated, and *Dendroconche*, which previous studies had indicated was closely related to our group of interest (Kreier et al. 2008). Sequence data for four chloroplast markers (*rbcl* gene, *rps4* gene, *rps4-trnS* intergenic spacer, and *trnL-trnF* intergenic spacer) were obtained from Genbank, using data generated from previous phylogenies of subfamily Microsoroideae

(Haufler et al. 2003; Schneider et al. 2004; Li and Lu 2005; Schneider et al. 2006; Kreier et al. 2008; Wang et al. 2009; Testo and Sundue 2014; Nitta et al. 2018) with the exception of *Dendroconche annabellae* and *Dendroconche sayeri*, for which new data were generated. For those two taxa, DNA extraction, amplification, and sequencing protocols follow those of Testo and Sundue (2014). Missing data percentages were 12% for *rbcl*, 28% for *rps4*, 27% for *rps4-trnS*, and 23% for *trnL-trnF*. Genbank accession numbers for all sequences are provided in Appendix 1.

Phylogenetic Analyses—Sequence alignment was performed for each marker using the MAFFT (Katoh and Standley 2013) plugin in Geneious 10.0.3 (Biomatters Ltd.) with a gap-open penalty of 1.3 and an offset cost of 0.123. The best-fit models of nucleotide substitution were selected using the AICc criterion in jModelTest2 (Darriba et al. 2012) on the Cipres Science Gateway portal (Miller et al. 2010); these were the GTR + Γ model for *rps4* and *trnL-trnF*, the HKY model for *rbcl*, and the TVM model for *rps4-trnS*. The four alignments obtained were concatenated for all tree-building analyses.

Maximum likelihood (ML) phylogenetic analysis was performed in RAxML 8.2.10 (Stamatakis 2014) on the Cipres Science Gateway portal. We partitioned the dataset by marker, retained the best-scoring tree, and performed 1000 bootstrap (BS) replicates. Bayesian inference (BI) analysis was performed using MrBayes 3.2.6 (Ronquist and Huelsenbeck 2003) on the Cipres Science Gateway portal. We partitioned the dataset by marker using the best-fit substitution models for each and ran two replicates of a MCMC for 5 million generations each, sampling every 2000 generations. We evaluated the output for convergence using Tracer 1.6 (Rambaut and Drummond 2004) and removed the first 25% of the run as burn-in; effective sample size for all parameters following trimming exceeded 800. The remaining 1875 trees were combined to create a 50% majority-rule consensus tree which was visualized using FigTree 1.4.3 (Rambaut 2009); support values reported are posterior probabilities (PP).

Morphological Analyses—To examine patterns of morphological evolution and identify synapomorphies for our focal clades, we used the “drop.tip” command in the R package ape (Paradis et al. 2004) to trim the 50% majority-rule consensus tree referenced above to include all members of *Lecanopteris* and the allied clades of interest (together, “lecanopteroids”) as well as a reduced set of representative outgroup taxa. The trimmed tree included all 25 lecanopteroids present in the original tree and three representatives each from *Leptochilus*, *Microsorium*, *Lepisorus*, and *Goniophlebium*.

We scored six morphological characters (growth habit, presence of sclerenchymatous strands in rhizome, presence of glaucous rhizomes, presence of rhizome cavities, association with ants, and presence of impressed sori that are visible on the adaxial laminar surface) from all species in our reduced data set based on study of herbarium specimens and live plants as well as descriptions from monographic treatments (Bosman

1991; Nootboom 1997). These characters were selected because they have been considered taxonomically informative in the microsoroid and lecanopteroid ferns (Hennipman and Verduyn 1987; Bosman 1991; Nootboom 1997). In cases where expression of a character in a species was variable, we coded the taxon with the more frequent state. A trait matrix is provided in Appendix 2. The herbarium specimens studied for these analyses were also used to generate distribution maps using the “mapBatch” function in the R package *monographaR* (Reginato 2016).

Character reconstruction was performed using the R package *phytools* (Revell 2012) under a continuous-time Markov chain model with equal rate character state transition matrix (Lewis 2001) using the “ace” function from the *ape* package (Paradis et al. 2004) and the *phytools* function “lik.anc.” For visualization purposes, the tree was ultrametricized using the “compute.brlen” function in *ape*.

RESULTS

Phylogeny—We recover a well-supported phylogeny (Fig. 1) with a topology that is generally concordant with previously published phylogenies of the Polypodiaceae subfamily Microsoroideae (Schneider et al. 2006; Kreier et al. 2008; Testo and Sundue 2014; Sundue et al. 2015; Nitta et al. 2018) with three principal clades in the core microsoroids. One of these clades (*Lepisorus* s. l.), is strongly supported (BS = 96%, PP = 1.0) as monophyletic and is comprised of *Lepisorus* s. s., *Lenmaphyllum*, *Lepidomicrosorium*, *Neocheiopteris*, *Neolepisorus*, *Paragramma*, and *Tricholepidium*. The second clade is comprised of *Microsorium* s. s. and *Leptochilus*, which are well-supported (BS = 92%, PP = 1.0) as sister to each other; the type species of *Colysis* (*Colysis hemionitidea* (C. Presl) C. Presl) is recovered within *Leptochilus*. The third clade is comprised of *Lecanopteris* and three small clades that are recovered in a grade of successive sister groups (BS = 89%, PP = 1.0). We find strong support (BS = 89%, PP = 1.0) that a small group of two species (*Bosmania*, gen. nov.) is sister to the remaining members of this clade. Within this group, a clade of six species (*Dendroconche*) is sister to *Lecanopteris* + *Zealandia* gen. nov., with strong support (BS = 99%, PP = 1.0); support for the relationship of *Zealandia* as sister to *Lecanopteris* is strong (BS = 89%, PP = 1.0).

Morphological Analyses—**GROWTH HABIT**—Our character state reconstructions indicate that epiphytism is likely ancestral in subfamily Microsoroideae, with a transition to terrestrial growth in the *Microsorium/Leptochilus* clade and another in *Bosmania* (Fig. 2A). A single transition to hemiepiphytic growth is inferred to have occurred in *Dendroconche*. Among the lecanopteroid ferns, terrestrial growth is a synapomorphy for *Bosmania*, hemiepiphytic growth is a synapomorphy for *Dendroconche*, and the symplesiomorphic state of epiphytic growth is retained in *Zealandia* and in *Lecanopteris*.

PRUINOSE RHIZOMES—Our character state reconstructions indicate that having a non-pruinose (green) rhizome is ancestral in subfamily Microsoroideae, with a transition to pruinose rhizomes occurring in *Zealandia*, followed by a reversal in *Z. powellii* (Fig. 2B). Among the lecanopteroid ferns, pruinose rhizomes are a synapomorphy for *Zealandia* (except in *Z. powellii*) and the plesiomorphic state of having non-pruinose rhizomes is retained in *Bosmania*, *Dendroconche*, and *Lecanopteris*.

SCLERENCHYMA STRANDS IN RHIZOME—Our reconstructions for this character for the subfamily are ambiguous, with approximately equal probabilities for sclerenchymatous strands being present or absent in the rhizome ground tissue (Fig. 2C). The absence of such strands is a

synapomorphy for the lecanopteroid ferns, with a single exception (*Z. powellii*) that frequently possesses them.

RHIZOME CAVITIES—Cavity-free rhizomes are inferred to be the ancestral character state for subfamily Microsoroideae, with high probability (Fig. 2D). We infer that transitions to cavity-bearing rhizomes occurred in the lecanopteroid ferns once in *Dendroconche* and separately in *Lecanopteris*, after the divergence of the cavity-less *Lecanopteris mirabilis* from the remainder of the genus. Based on our examination of specimens and the literature, we found that rhizome cavities were common but not always present in *Dendroconche* and the cavities in that genus are much smaller than those found in *Lecanopteris*, in which the cavities are always present.

ANT ASSOCIATION—Our reconstruction of the occurrence of an ant-fern association demonstrates that the ancestor of subfamily Microsoroideae lacked any such association (Fig. 2E). We infer a single transition of ants colonizing rhizomes in *Lecanopteris*; this is a synapomorphy for that genus.

IMPRESSED SORI—Reconstruction of this character across our phylogeny was ambiguous with respect to whether or not impressed sori are the ancestral character state for subfamily Microsoroideae (Fig. 2F). Non-impressed sori are favored as the ancestral character state of the lecanopteroid ferns; there is some ambiguity with respect to this reconstruction. Alternatively, if the ancestor of the clade had impressed sori, non-impressed sori would have most likely evolved twice, in *Bosmania* and *Dendroconche*.

DISCUSSION

As has been shown in earlier studies, several species typically treated in the genera *Microsorium* and *Colysis* are resolved in our phylogeny as allied to *Lecanopteris* (Bosman 1991; Schneider et al. 2006; Kreier et al. 2008; Testo and Sundue 2014). As a whole, this group (including *Lecanopteris*) is morphologically heterogeneous, but all species are united by their lack of sclerenchymatous strands in the rhizome ground tissue, which are present in all other members of Polypodiaceae subfamily Microsoroideae. These taxa are resolved as three clades that are successive sister groups to *Lecanopteris*, all are well-supported as monophyletic (Fig. 1), and have clear morphological synapomorphies (Fig. 2). The taxonomic issues posed by the position of these taxa can be resolved either by expanding *Lecanopteris* to include all members of this clade or recognizing three genera of lecanopteroid ferns in addition to *Lecanopteris* itself. We prefer the latter course of action, as it preserves the long-standing and uncontroversial generic concept of *Lecanopteris*, which is one of the most distinctive fern genera.

A previously published name (*Dendroconche* Copel.) is available for one of the three clades of interest. *Dendroconche* was described by Copeland (1911) based on *Dendroconche annabellae* (H.O. Forbes) Copel. from New Guinea, a peculiar species with orbicular sterile leaves and fertile leaves with an orbicular proximal portion and a caudate apex that bears the sporangia. This species was sampled in our phylogenetic analyses and thus allows us to confidently apply the name *Dendroconche* to six species included in our phylogeny and an additional two taxa that we place here on morphological grounds. These species are united by a combination of a hemiepiphytic growth habit (Figs. 2A, 3A, B), non-pruinose rhizomes (Figs. 2B, 3B), non-impressed sori (not prominently

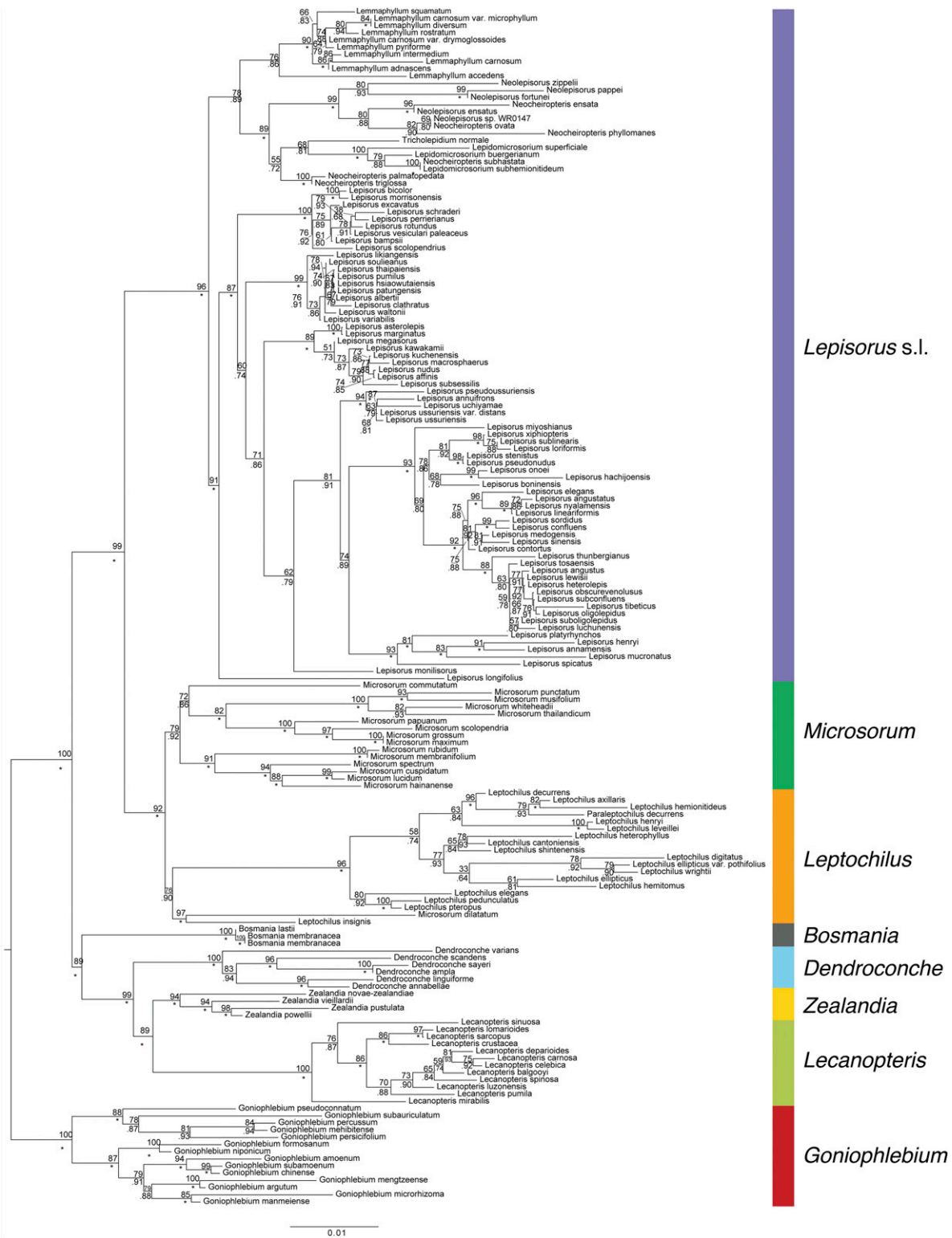


FIGURE 1. Maximum likelihood phylogeny of Polypodiaceae subfamily Microsoroideae. Support values above branches are ML bootstrap values; those below branches are BI posterior probabilities.

visible on the adaxial lamina surface; Figs. 2F, 3A), bright yellow verrucate spores, and presence of specialized clasping roots that are laterally inserted (Fig 3B). Several species also have orbicular leaves or clasping leaf bases (Fig. 4C).

We are unable to find any available names for the remaining two clades and thus propose the recognition of two new

genera, *Bosmania* Testo and *Zealandia* Testo & A. R. Field. *Bosmania* is comprised of three very similar species and can be distinguished by their membranaceous laminae (Fig. 3), generally terrestrial growth habit (Fig. 3A), and simple leaves that are deciduous in the dry season (Bosman 1991). *Zealandia* includes four species that are resolved in our phylogeny as

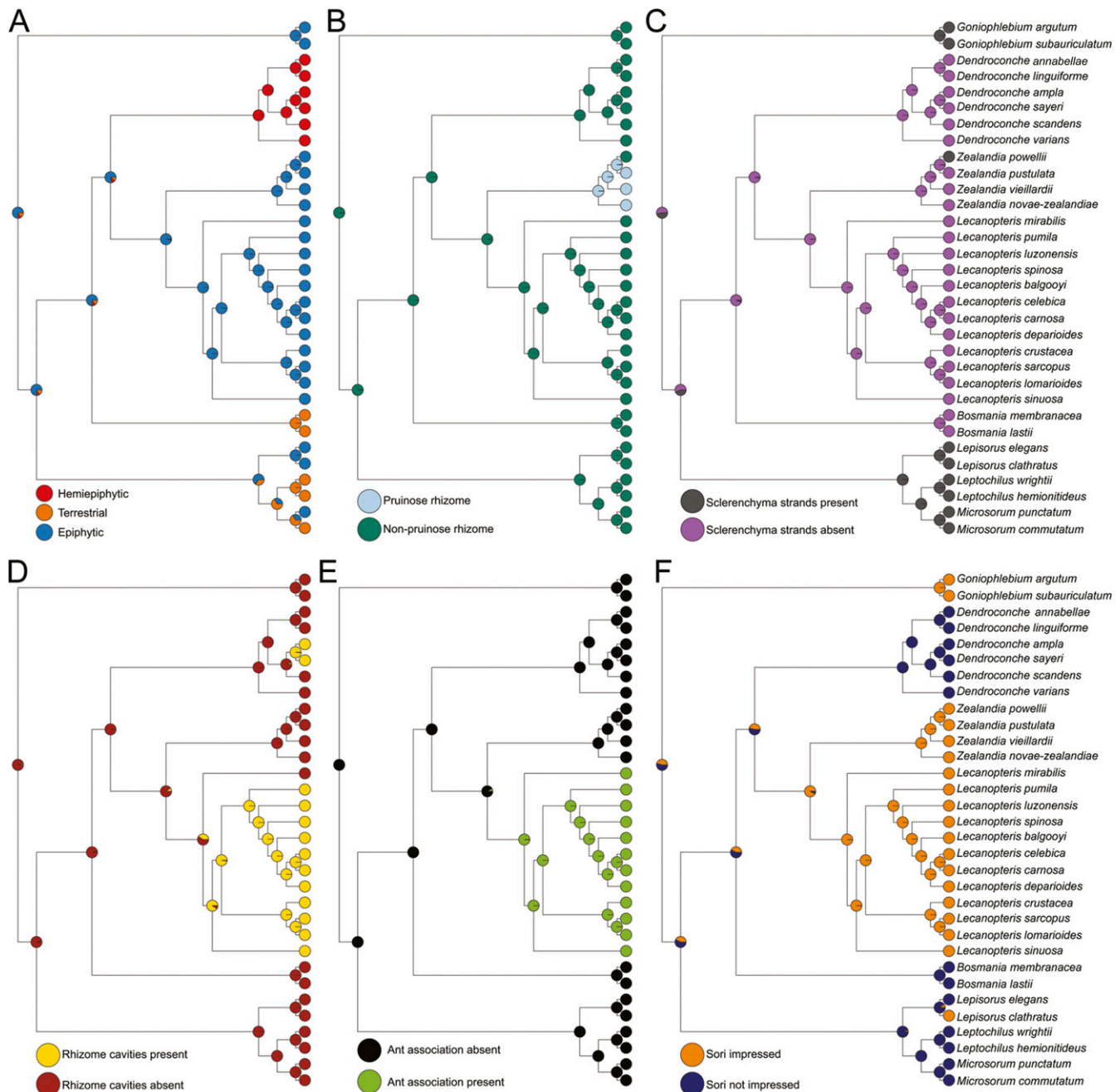


FIGURE 2. Maximum likelihood ancestral character state reconstructions for six traits across Polypodiaceae subfamily Microsoroideae. A. Growth habit. B. Occurrence of pruinose rhizomes. C. Presence of sclerenchymatous strands in rhizome ground tissue. D. Presence of cavities in rhizome. E. Association with ants. F. Presence of impressed sori.

sister to *Lecanopteris*; members of this genus are characterized by their (mostly) epiphytic growth habit, deeply impressed sori that are readily visible on the adaxial lamina surface (Fig. 5A, C), generally prominent venation (Fig. 5B), and pruinose rhizomes (Fig. 5D).

In addition to contributing to the clarification of phylogenetic relationships and generic circumscription in Polypodiaceae subfamily Microsoroideae, this study provides insight into the evolution of growth habit and adaptations to stressful habitats. Though the common ancestor of the lecanopteroid ferns was probably epiphytic, members of this lineage have radiated into terrestrial and hemiepiphytic niches in addition to holoepiphytic growth, which occurs in

Zealandia and *Lecanopteris* (Fig. 2A). These shifts in growth habit and associated attributes suggest that the lecanopteroid ferns have developed a range of ecological strategies that allow them to occupy ecological niches with significant nutrient and/or water stress. The leaves of *Bosmania* are seasonally deciduous, presumably as an adaptation to the extended dry period they experience. The hemiepiphytic growth habit of *Dendroconche* is thought to provide a suite of ecological advantages, including improved light acquisition in dense forest understories (Putz and Holbrook 1986), consistent access to water and nutrients (Watkins et al. 2010), and release from competitive forest floor habitats (Testo and Sundue 2014). In addition, *D. annabellae*, *D. kingii*,

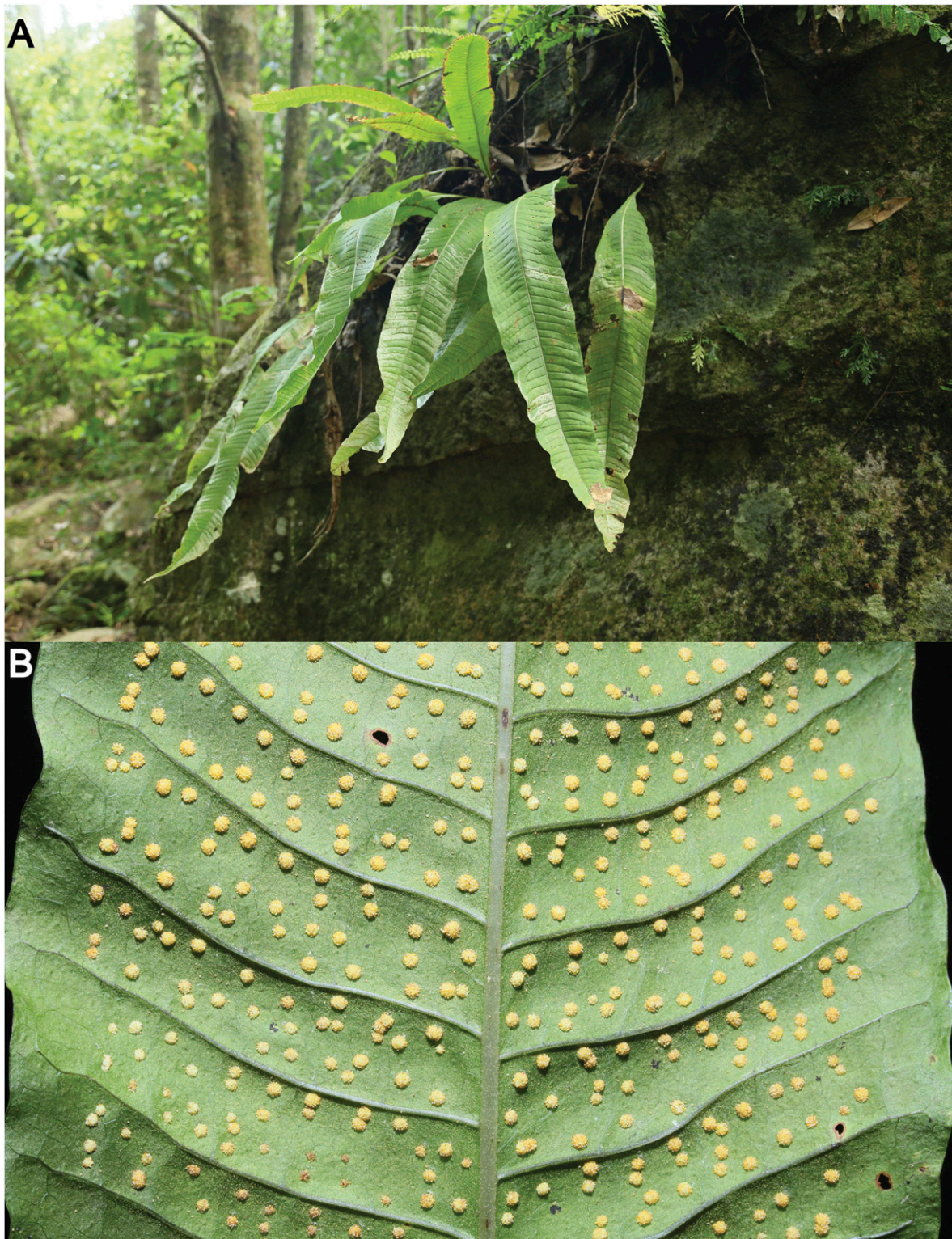


FIGURE 3. *Bosmania*. A. Growth habit and thin lamina of *Bosmania membranacea*. B. Thin lamina, simple leaves, and bright yellow spores of *Bosmania membranacea*. Photos by Cheng-Wei Chen.

and *D. linguiforme* have clasping leaf bases that catch leaf litter fall-through, which presumably aid in nutrient acquisition and water retention (Fig. 4). As indicated by Bosman (1991) and Testo and Sundue (2014), some *Dendroconche* have large cavities in their rhizomes that occasionally open to the rhizome exterior, and we recently observed ants living under

the rhizomes of some plants of *D. ampla*. Our morphological analyses indicate these likely evolved independently from those found in *Lecanopteris*, in which ants live in domatia underneath or inside the highly specialized rhizomes of that genus, but further investigation of myrmecophily in the lecanopteroid ferns is needed. Specializations are not as



FIGURE 4. *Dendroconche*. A. Gross morphology of *Dendroconche kingii*. B. Hemiepiphytic growth habit and dimorphic roots of *Dendroconche ampla*. C. Clasp-like leaf bases of *Dendroconche kingii*. Photos by Michael Sundue.

obvious in *Zealandia*, but the waxy rhizomes and coriaceous laminae present in that genus may represent adaptations to frequently dry epiphytic niches. The morphological disparity among lecanopteroid genera suggests that the clade has undergone an adaptive radiation (sensu Givnish 2015) driven by exploration of varied ecological strategies, but

further work is needed to better understand patterns of niche evolution in the group.

The resurrection of *Dendroconche* and recognition of *Bosmania* and *Zealandia* resolve long-standing issues with circumscription of genera in Polypodiaceae subfamily Microsoroideae and contribute to the taxonomic resolution

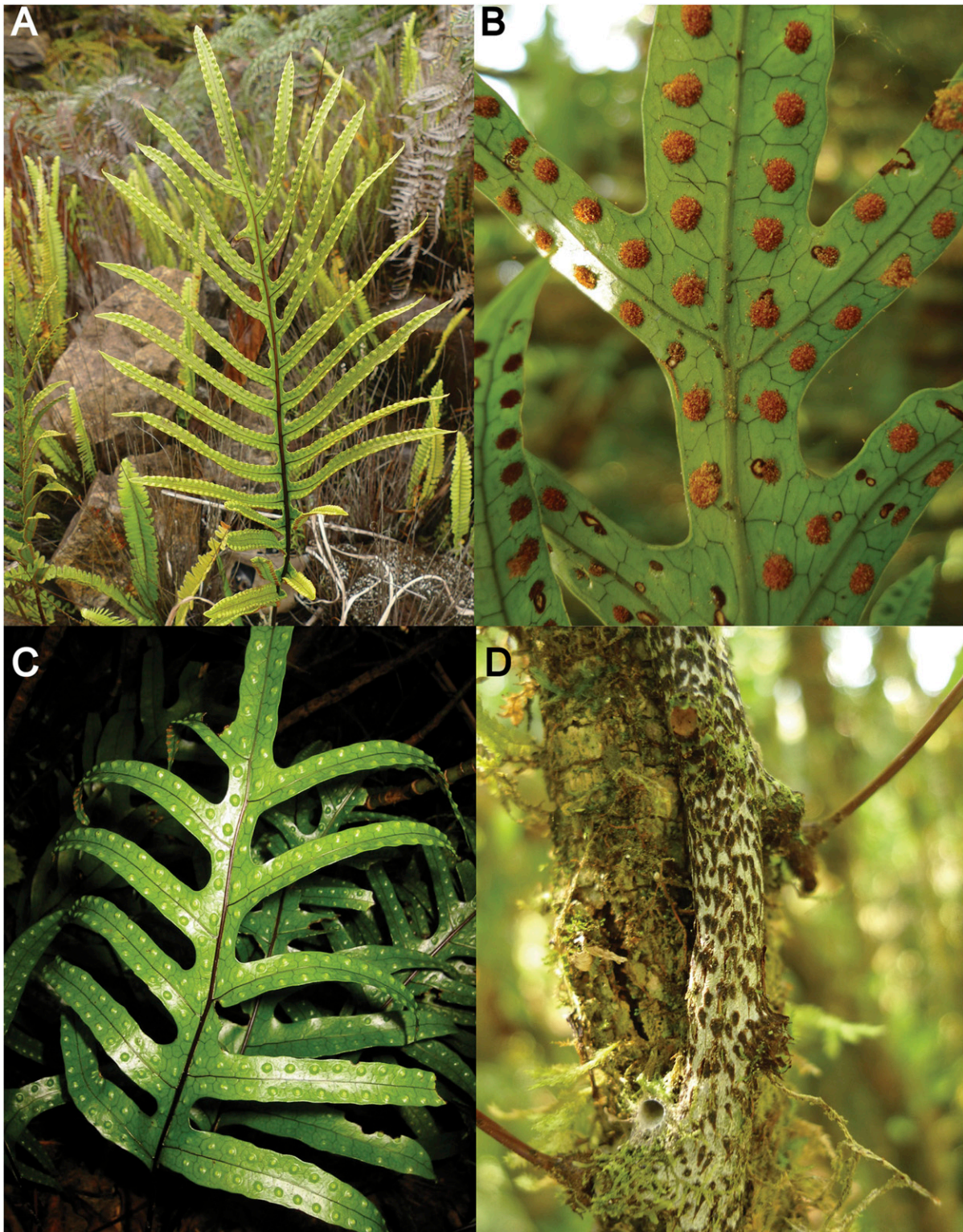


FIGURE 5. *Zealandia*. A. Growth habit and impressed sori of *Zealandia vieillardii*. B. Sori and prominent venation of *Zealandia pustulata* subsp. *pustulata*. C. Leaf morphology and impressed sori of *Zealandia pustulata* subsp. *pustulata*. D. Glauccous rhizome of *Zealandia pustulata* subsp. *pustulata*. Photos A, B, D by Leon Perrie, C by Jon Sullivan.

of this challenging group of ferns. To aid in the identification of members of this clade, we present a key to the genera of lecanopteroid ferns, which are distinct among members of Polypodiaceae subfamily Microsoroideae by lacking free strands of sclerenchyma scattered in the rhizome

ground tissue. We also provide a taxonomic treatment for *Bosmania*, *Dendroconche*, and *Zealandia*, including a description of each genus and its species, a key to the species in each genus, and a discussion of their ecology, distribution, and morphology.

KEY TO THE GENERA OF LECANOPTEROID FERNS

1. Plants with ants living in conspicuously hollow rhizome (under arched rhizome in *L. mirabilis*), sori marginal (medial in *L. mirabilis* and *L. sinuosa*) *Lecanopteris*
1. Plants without ants living in rhizome, sori submarginal to inframedial 2.
 2. Leaves deciduous in dry season; lamina membranaceous; plants usually terrestrial or epilithic on limestone *Bosmania*
 2. Leaves not deciduous in dry season; lamina membranaceous to coriaceous; plants hemiepiphytic or epiphytic, rarely terrestrial 3.
 3. Rhizomes typically pruinose; plants mostly holoepiphytes; lacking laterally inserted climbing roots; sori deeply impressed in lamina *Zealandia*
 3. Rhizomes not pruinose; plants hemiepiphytes; possessing laterally inserted climbing roots; sori not deeply impressed in lamina *Dendroconche*

TAXONOMIC TREATMENT

Bosmania Testo gen. nov. TYPE: NEPAL. *Polypodium membranaceum* D. Don, Prodr. Fl. Nepal. 2. 1825.

Plants terrestrial, epilithic, or epiphytic. **Rhizome** moderately to long-creeping, terete or slightly dorsiventrally flattened. **Rhizome scales** brown, slightly spreading, lanceolate, 1.5–9 mm long, 1–3 mm wide. **Roots** of one type, ventrally inserted and attaching to soil. **Petiole** 1–15 cm long, not winged. **Leaves** seasonally deciduous, simple, elliptic, 20–110 cm long, 4.5–15 cm wide. **Lamina** membranaceous. **Venation** prominent, anastomosing, forming regular areoles. **Sori** round to slightly elongate. **Spores** yellow, ellipsoid, monolete, verrucate. Figure 3.

Distribution and Habitat—*Bosmania* species occur in Bhutan, China, Laos, Madagascar, Myanmar, Nepal, Philippines, Sri Lanka, Taiwan, Thailand, and Vietnam (Fig. 6A). They are generally terrestrial and epilithic on limestone and limestone-derived soils, or occasionally epiphytic.

Etymology—This genus is named in honor of Dutch botanist Monique T. M. Bosman (1958–), who first characterized this group of species in her 1991 monograph of *Microsorium*.

Notes—Members of this genus are readily distinguished by their simple, membranaceous leaves that are shed during dry periods (Fig. 3). Although *B. membranacea* is a widespread and common species in Southeast Asia, the remaining two species in the genus are narrowly distributed in Madagascar and appear to be very rare.

KEY TO THE SPECIES OF *BOSMANIA*

1. Sori present in costal areoles, plants of southern and southeastern Asia *B. membranacea*
1. Sori absent in costal areoles, plants restricted to Madagascar 2.
 2. Rhizome generally < 3 mm wide, lamina generally 2.5–4× as long as wide, base of lamina typically broadly cuneate *B. lastii*
 2. Rhizome generally 3–5 mm wide, lamina generally 5–7× as long as wide, base of lamina typically narrowly tapered *B. leandriana*

Bosmania lastii (Baker) Testo comb. nov., *Polypodium lastii* Baker, J. Bot. 29: 5. 1891. *Microsorium lastii* (Baker) Tardieu, Fam. 5: 116. 1960. TYPE: MADAGASCAR. Dec 1890, *Last s.n.* (holotype: K, barcode: K000435917, image!).

designated here: P, barcode: P00482647, image!; isolectotype: P, barcode: P00482648, image!).

Plants terrestrial. **Rhizome** long-creeping, dorsiventrally slightly flattened 1–3 mm in diam. **Rhizome scales** brown, slightly spreading, lanceolate, 2–3 mm long, 1–1.5 mm wide. **Roots** of one type, ventrally inserted and attaching to soil. **Petiole** 5–20 cm long, not winged. **Leaves** seasonally deciduous, simple, 15–55 cm long, 5–10 cm wide. **Lamina** membranaceous, cuneate at base, attenuate at apex. **Venation** prominent, forming areoles. **Sori** round to slightly elongate, absent from costal areoles. **Spores** yellow, ellipsoid, monolete, verrucate.

Plants terrestrial. **Rhizome** long-creeping, dorsiventrally slightly flattened, 3–5 mm in diam. **Rhizome scales** brown, slightly spreading, lanceolate, 2–4 mm long, 1–3 mm wide. **Roots** of one type, ventrally inserted and attaching to soil. **Petiole** 5–10 cm long, not winged. **Leaves** seasonally deciduous, simple, 35–65 cm long, 4.5–8 cm wide. **Lamina** membranaceous, narrowly cuneate at base, attenuate at apex. **Venation** prominent, forming areoles. **Sori** round to slightly elongate, absent from costal areoles. **Spores** yellow, ellipsoid, monolete, verrucate.

Distribution and Habitat—This species is endemic to western Madagascar, from 400–600 m elevation. It occurs in forests with limestone outcrops and limestone-derived soils.

Notes—When Tardieu-Blot described this species, she distinguished it from *Bosmania lastii* (as *Polypodium lastii*) on the basis of its relatively narrower leaves and more narrowly tapered lamina base. It is only known from a few collections, and its distinctness from *B. lastii* is uncertain.

Representative Specimens—Madagascar.—ANTANANARIVO PROVINCE: Cremers 3688 (MO); Rasolohery 160 (MO).—TOLIARA PROVINCE: DuPuy MB758 (MO).

Distribution and Habitat—This species is endemic to northwestern Madagascar, from 250–1000 m elevation. It is reported to be a terrestrial species, growing in forest over limestone.

Notes—This species is very similar to *B. leandriana*, which is also restricted to northwestern Madagascar and also occurs solely on limestone and limestone-derived soils. It is known from few collections; additional work is needed to determine if *B. lastii* and *B. leandriana* warrant recognition as distinct species.

Representative Specimens—Madagascar.—ANTSIRANANA PROVINCE: Humbert 18581 (P, image!); Nusbaumer 932 (P, image!); Rakotondrainibe 902 (P, image!); Rakotondrainibe 1402 (P, image!).—MAHAJANGA PROVINCE: Leandri 810 (P, image!); Leandri 2859 (P, image!).

Bosmania leandriana (Tardieu) Testo comb. nov., *Microsorium leandrianum* Tardieu, Notul. Syst. 15: 444. 1959. TYPE: MADAGASCAR. Environs de Tsiandro (oust) Sud du village 500–600 m, 26 Nov 1952, Léandri et al. 1900 (lectotype

Bosmania membranacea (D. Don) Testo comb. nov., *Polypodium membranaceum* D. Don, Prodr. Fl. Nepal. 2. 1825. *Microsorium membranaceum* (D. Don) Ching, Bull. Fan Mem. Inst. Biol. 4: 9. 1933.—TYPE: NEPAL. *Wallich s.n.* (lectotype, designated by Bosman, 1991: BM, barcode: BM001038408, image!; isolectotype: B, n.v.).

Polypodium transparens Presl ex Ettingsh., Denkschrift Akad. Wiss. Wien 22: 95. 1864.—TYPE: NEPAL. Hügel 269

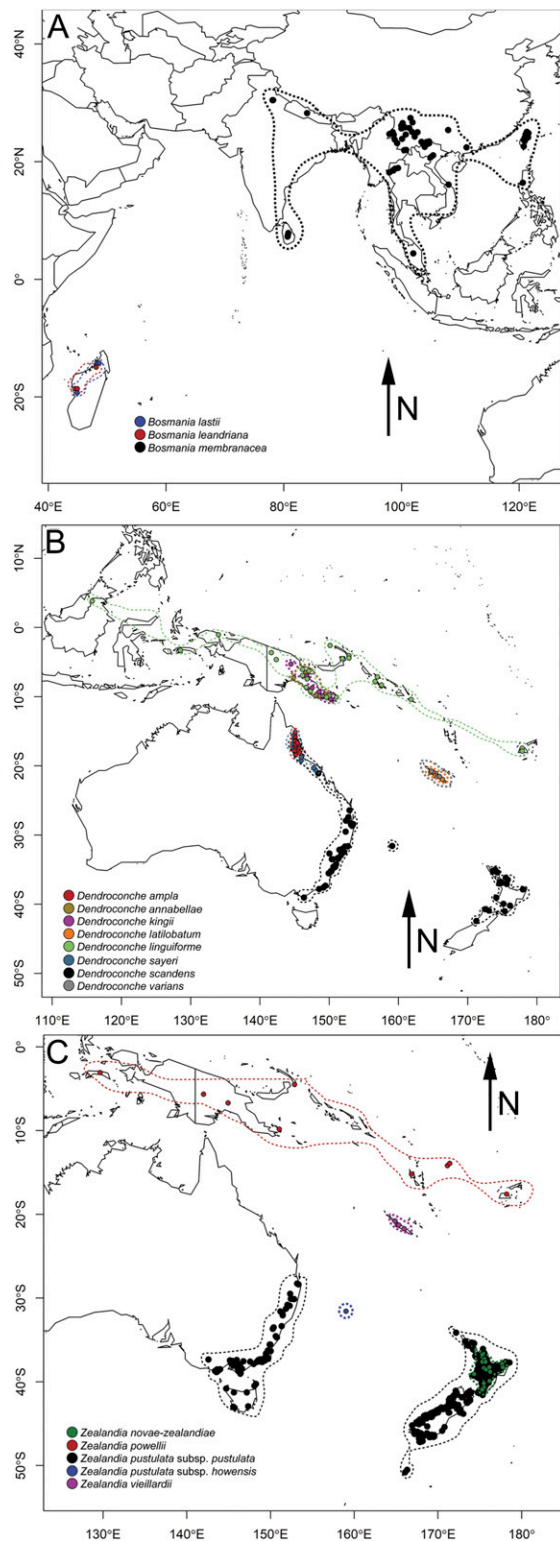


FIGURE 6. Distributions of lecanopteroid fern genera. A. *Bosmania*. B. *Dendroconche*. C. *Zealandia*. Dots indicate species occurrences based on georeferenced herbarium collections; dotted lines indicated approximate species distributions.

(lectotype, designated by Bosman, 1991: W, barcode W0061326, image!).

Plants epiphytic, rupicolous, or terrestrial. **Rhizome** long-creeping, terete dorsiventrally slightly flattened, 3–10 mm in diam. **Rhizome scales** brown, slightly spreading, lanceolate,

2–9 mm long, 1–3 mm wide. **Roots** of one type, ventrally inserted and attaching to soil. **Petiole** 2–15 cm long, not winged. **Leaves** seasonally deciduous, simple, 25–110 cm long, 5–15 cm wide. **Lamina** membranaceous, narrowly cuneate at base, acuminate at apex; margins often undulate. **Venation** prominent, forming areoles. **Sori** round to slightly elongate, present in costal areoles. **Spores** yellow, ellipsoid, monolete, verrucate.

Distribution and Habitat—*Bosmania membranacea* has been reported from Bhutan, China, India, Laos, Myanmar, Philippines, Thailand, and Vietnam, from 600–3600 m elevation.

Notes—This is by far the most widespread species of *Bosmania*; it appears to be most abundant in the Himalayan region. The leaves of this species are yellow-green when dried and frequently have conspicuously undulate margins.

Representative Specimens—**China**.—YUNNAN PROVINCE: *Sino-American Botanical Expedition 1273* (US). **India**.—ASSAM STATE: *Mamm s.n.* (US);—KARNATAKA STATE: *Ramamoorthy 286* (US); *Saldanha 421* (US);—UTTARAKHAND STATE: *Koelz 21894* (US). **Nepal**.—LALITPUR DISTRICT: *Nicolson 2207* (US). **Philippines**.—BEGUET: *Topping 263* (US). **Sri Lanka**.—CENTRAL PROVINCE: *Anon. s.n.* (P, image!). **Taiwan**.—TAO YUAN COUNTY: *Knapp 3880* (P, image!). **Thailand**.—CHIANG MAI PROVINCE: *Hennipman 3360* (P, image!);—NORTHERN PROVINCE: *Murata 15642* (US). **Vietnam**.—LAM DONG PROVINCE: *Schmid 117* (P, image!).

DENDROCONCHE Copel. TYPE: PAPUA NEW GUINEA. *Polypodium annabellae* H.O. Forbes J. Bot. 26: 33. 1888.

Plants hemiepiphytic. **Rhizome** long-creeping, dorsiventrally flattened, with occasional cavities in some species. **Rhizome scales** brown, spreading to appressed. **Roots** of two types, one type laterally inserted and clasping, the other type ventrally inserted and attaching to soil. **Leaves** simple to deeply pinnatifid, 15–70 cm long, 10–40 cm wide, monomorphic or hemidimorphic. **Petiole** absent to 30 cm long, when present, usually winged to base. **Venation** prominent, anastomosing to form regular areoles. **Sori** round to elongate. Figure 4.

Distribution and Habitat—Members of the genus occur in Australia, Fiji, India, Indonesia, New Caledonia, New Guinea, New Zealand, and the Solomon Islands (Fig. 6B) in low- to mid-elevation rain forests. They are hemiepiphytes or in some species, occasionally terrestrial.

Etymology—From the Greek “dendron,” meaning “tree,” and “konche,” meaning “shell.” The genus name apparently refers to the orbicular leaves and growth habit of the type species, *D. annabellae*.

Notes—When Copeland (1911: 91) described *Dendroconche*, he based the genus on a single species from New Guinea (*D. annabellae*) that possessed highly specialized orbicular leaves that tightly clasp the tree on which the plant grows. Because of this peculiar leaf morphology, Copeland suggested that the genus was closely allied to *Drynaria*, but that the two “represent distinct lines of development.” Later, Copeland expanded the genus to include another New Guinean endemic, *D. kingii*, which possesses similar but less-specialized clasping leaves. These taxa were later treated as synonyms of *Microsorium linguiforme*, and *Dendroconche* was relegated to synonymy under *Microsorium*. Later studies (Schneider et al. 2006; Kreier et al. 2008; Testo and Sundue 2014) indicated that *Microsorium* was not monophyletic and that *M. linguiforme* was more closely allied to *Lecanopteris*; however, the taxonomy of the group remained unresolved.

As construed here, *Dendroconche* includes eight species that are united by their dorsiventrally flattened rhizomes, rhizome

cavities, laterally inserted clasping roots, and non-glaucous rhizomes (Fig. 4). The flattened rhizomes and clasping roots found in the genus correspond closely to the “hemiepiphyte syndrome” proposed by Testo and Sundue (2014) in a study on *Dendroconche ampla* (as *Colysis ampla*); indeed, it appears that all *Dendroconche* species are at least facultative hemiepiphytes. The genus is represented in Malesia, Australia, New Zealand, New Caledonia, the Solomon Islands, and Fiji. A single species, *D. linguiforme*, is very widespread and ranges from India to Fiji (the Indian populations likely represent escapes from

cultivation; Bosman 1991); most others are narrowly distributed, single-island endemics. Species richness is highest in New Guinea and Australia with three species (two endemics) each; another two species are restricted to New Caledonia. Several poorly understood taxa that we did not sample but appear allied to *D. linguiforme* may belong to *Dendroconche*; these include *Microsorium cinctum* Bosman, *Microsorium egregium* (Brause) Bosman, *Microsorium longissimum*, *Microsorium rampans* (Baker) Parris, and *Microsorium samarense* (J. Sm.) Bosman.

KEY TO THE SPECIES OF *DENDROCONCHE*

1. Leaves of mature plants simple 2.
 2. Fertile leaves lanceolate to pandurate, without conspicuous rounded base *D. linguiforme*
 2. Fertile leaves unguiculate, with conspicuous rounded base 3.
 3. Apical portion of fertile leaves lanceolate, 2–5 cm wide *D. kingii*
 3. Apical portion of fertile leaves caudate, < 1.5 cm wide *D. annabellae*
1. Leaves of mature plants deeply lobed 4.
 4. Fertile and sterile fronds strongly dimorphic, fertile fronds with segments < 1 cm wide, plants from New Caledonia 5.
 5. Rhizome scales appressed, round; pinna apex acute *D. varians*
 5. Rhizome scales spreading, lanceolate; pinna apices rounded *D. latilobatum*
 4. Fertile and sterile fronds monomorphic or weakly dimorphic, fertile fronds with segments > 1.5 cm wide, plants from Australia and New Zealand 6.
 6. Mature leaves typically with one row of areoles between the costa and leaf margin; sori round *D. scandens*
 6. Mature leaves typically with two rows of areoles between the costa and leaf margin; sori elongate 7.
 7. Petioles typically winged their entire length; sori mostly extending from near costa almost to the leaf margin; spores generally 45–60 µm long *D. ampla*
 7. Petioles typically not winged near base, sori extending approximately halfway from costa to leaf margin; spores 65–80 µm long *D. sayeri*

Dendroconche ampla (F. Muell. ex Benth.) Testo, Sundue, & A.R. Field comb. nov., *Grammitis ampla* F. Muell. ex Benth., Fl. Austr. 7: 777. 1878. *Polypodium amplum* (F. Muell. ex Benth.) Domin, Bibl. Bot. 85: 182. 1913. *Colysis ampla* (F. Muell. ex Benth.) Copel., Gen. Fil. 199. 1947. *Leptochilus amplus* (F. Muell. ex Benth.) Noot., Blumea 42: 277. 1997. TYPE: AUSTRALIA. Queensland. Rockingham Bay, 18 Aug. 1866, J. Dallachy s.n. (lectotype, designated here: MEL, barcode MEL2166912 image!; isolectotypes: MEL, barcode MEL1061215 image!; MEL, barcode MEL2166916 image!; P, barcode P00626877!; BM, barcode BM001038460 image!; BM, barcode BM001038461 image!).

Plants hemiepiphytic or rarely terrestrial. **Rhizome** long-creeping, dorsiventrally flattened, with occasional cavities, not pruinose. **Rhizome scales** dark brown, spreading, ovate, 2–6 mm long, 1–2.5 mm wide. **Roots** of two types, one type laterally inserted and clasping, the other type ventrally inserted and attaching to soil. **Petiole** 6–30 cm long, usually winged to base. **Leaves** deeply pinnatifid on mature plants, simple on young plants; mature leaves 15–70 cm long, 10–40 cm wide. **Venation** prominent, usually forming 2 areoles between the costa and leaf margin. **Sori** elongate, running from near the costa to the leaf margin.

Distribution and Habitat—This species is endemic to northeastern Queensland, Australia, from 0–800 m elevation. It typically occurs in lowland or lower montane complex mesophyll vine forests in wetlands, adjacent to creeks or in rocky areas, and usually occurs as a low to subcanopy hemiepiphyte on a range of host trees.

Notes—Testo and Sundue (2014) discussed the growth habit of this species and proposed a “hemiepiphyte syndrome” that is present in other members of *Dendroconche*. This species is closely allied to *D. scandens* and *D. sayeri* and they may constitute a reticulate polyploid complex; see comments

under *D. sayeri*. Recent field observations by one of us revealed that this species can harbor colonies of ants under its rhizomes. This is the first record of myrmecophily in *Dendroconche*; further study is needed to determine if this is common in *D. ampla* and if it occurs in other species.

Type Note—Mueller (in Bentham 1878) named this species from two syntypes and the most complete of the specimens examined by Mueller is chosen as the lectotype.

Representative Specimens—AUSTRALIA.—QUEENSLAND: Bean 4010 (BRI); Bostock 1592 (BRI); Brass 18267 (BRI); Chinnock 8343 (BRI); Forster 17221 (BRI, CNS); Jago 3632 (BRI); Gray 8234 (CNS); Kessler 14300 (CNS); Stocker 1767 (CNS); van der Werff 11488 (BRI, CNS).

DENDROCONCHE ANNABELLAE (H.O. Forbes) Copel., *Polypodium annabellae* H.O. Forbes, J. Bot. 26: 33. 1888. *Pleopeltis annabellae* (H.O. Forbes) Alderw., Bull. Dep. Agric. Indes Neerl. 27: 5. 1909. TYPE: PAPUA NEW GUINEA. New Guinea, 1887, C.H. Hartmann 86 (lectotype, designated here: BM, barcode: BM000036777, image!).

Polypodium cyclobasis Baker, Kew Bull. 110: 42. 1896. TYPE: PAPUA NEW GUINEA. Stirling Range, 1500 ft, 1894, Micholitz s.n. (lectotype, designated here: K, barcode K000959768, image!).

Plants hemiepiphytic. **Rhizome** long-creeping, dorsiventrally flattened, with occasional cavities, not pruinose. **Rhizome scales** dark brown, spreading, lanceolate, 4–7 mm long, 1.5–2.5 mm wide. **Roots** of two types, one type laterally inserted and clasping, the other type ventrally inserted and attaching to soil. **Petiole** absent or nearly so. **Sterile leaves** orbicular, 8–12 cm across. **Fertile leaves** hemidimorphic, with an orbicular base and caudate apex; proximal portion 8–12 cm across, distal portion 18–28 cm long, 0.5–1 cm across. **Venation** prominent, forming at least 6 rows of areoles between the rachis and leaf margin in sterile leaves and the proximal portion of fertile leaves, forming a single areole between the rachis and leaf margin in the distal portion of fertile leaves.

Sori round, restricted to distal portion of fertile leaves, in a single row between the rachis and leaf margin.

Distribution and Habitat—*Dendroconche annabellae* is endemic to Papua New Guinea, from 500–1300 m.

Notes—This species and *D. kingii* were treated as a synonym of *D. linguiforme* by Bosman (1991) and Nooteboom (1997) but we find them to be morphologically distinct and warrant recognition at the species rank. The leaves of this species are tightly appressed to the trunk of the tree on which the plant is growing. The sterile leaves are orbicular, whereas the fertile leaves are hemidimorphic, with an orbicular base and a caudate apex. The elongate sori-bearing portion of the fertile leaf curves away from the tree trunk, presumably to aid in spore dispersal. This species is known from very few collections.

Representative Specimens—**Papua New Guinea**.—UNKNOWN PROVINCE: *King s.n.* (P, image!); *Chambers s.n.* (P, image!); *Micholitz s.n.* (P, image!). —MILNE BAY PROVINCE: *Pell 911* (NY).

Type Note—The collector is not cited in the protologue and we have not been able to locate any material collected by H. E. Forbes. A specimen collected by C. H. Hartmann and matching Forbes' printed description as well as including his handwritten notes is present in BM and is selected as the lectotype. The printed type locality "Murray River" differs from Forbes' handwritten description of "Musgrave River." The Murray is in Western Province and is incorrect, whereas the Musgrave is in Central Province and drains from the Owen Stanley Range as presented in the description.

DENDROCONCHE KINGII Copel., Univ. Calif. Publ. Bot. 12: 407. 1931. TYPE: PAPUA NEW GUINEA. Papua, Mt Tuan, 1911, *King 387* (lectotype designated here: MICH, barcodes: MICH 1003428A &, image!; isolectotype: MICH, barcode: MICH 1003428B, image!).

Plants hemiepiphytes. **Rhizome** long-creeping, dorsiventrally flattened, with occasional cavities, not pruinose. **Rhizome scales** brown, spreading, lanceolate, 4–8 mm long, 2–2.5 mm wide. **Roots** of two types, one type laterally inserted and clasping, the other type ventrally inserted and attaching to soil. **Petiole** absent or nearly so. **Sterile leaves** orbicular to sub-orbicular, 6–9 cm across. **Fertile leaves** hemidimorphic, with an orbicular base and lanceolate apex; proximal portion 6–9 cm across, distal portion 10–18 cm long, 3.5–5 cm across. **Venation** prominent, forming at least 5 rows of areoles between the rachis and leaf margin on sterile leaves and the base of fertile leaves, forming 3–5 rows on the distal portions of fertile leaves. **Sori** round, restricted to distal portion of fertile leaves, in 3–6 rows between the rachis and leaf margin.

Distribution and Habitat—This species is apparently endemic to Papua New Guinea, and occurs from 500–1300 m.

Notes—Like *D. annabellae*, this species produces leaves that are tightly appressed to the trunk of the tree on which it grows; however, it lacks the caudate fertile leaf apices of that species. The few collections we have seen of this species are from eastern Papua New Guinea.

Representative Specimens—**Papua New Guinea**.—MILNE BAY PROVINCE: *Brass 27434* (US).—MOROBE PROVINCE: *Brass 29407* (US); *Weinland s.n.* (P, image!).—NORTHERN PROVINCE: *James & Sundue 1616* (BISH, LAE, VT).

Dendroconche latilobata (Hennipman & Hett.) Testo, Sundue, & A.R. Field comb. nov., *Acrostichum varians* f. *major* Mett., Ann. Sci. Nat. Bot. Ser. 4: 57. 1861. *Microsorium latilobatum* Hennipman & Hett., Jahrb. Syst. 105: 6. 1984. TYPE: NEW CALEDONIA. 16 Apr 1868, *Viellard 1528* (holotype: B,

barcode: 20-0054328, image!; isotype: P, barcode: P01545165, image!).

Plants hemiepiphytic or rarely terrestrial. **Rhizome** long-creeping, dorsiventrally flattened, not pruinose. **Rhizome scales** dark brown, appressed, lanceolate, 2–8 mm long, 1–2.5 mm wide. **Roots** of two types, one type laterally inserted and clasping, the other type ventrally inserted and attaching to soil. **Petiole** 4–25 cm long, not winged. **Sterile leaves** deeply pinnatifid on mature plants, simple to lobed on young plants; mature leaves 20–75 cm long, 20–40 cm wide; pinnae 8–20 cm long, 2–6 cm wide. **Fertile leaves** pinnatisect, with lamina strongly contracted; 15–50 cm long, 12–45 cm wide; pinnae 3–8 cm long, 0.3–0.8 cm wide. **Venation** prominent, usually forming 2–3 areoles between the costa and leaf margin. **Sori** acrostichoid, covering abaxial lamina surface.

Distribution and Habitat—This species is endemic to New Caledonia, from 300–800 m elevation.

Notes—This species is closely related to *D. varians* and these species are unique within the lecanopteroids for their highly reduced fertile leaves with acrostichoid sori. In addition to the characters provided in the key, it differs from *D. varians* by having more complex venation, as illustrated by Hennipman and Hetterscheid (1984) in their description of the species.

Representative Specimens—**New Caledonia**.—NORTH PROVINCE: *Montrouzier 250* (P, image!).—SOUTH PROVINCE: *Guillamin et al. 10415* (US); *Mackee 196* (P, image!).—UNKNOWN PROVINCE: *Cribs 453* (P, image!); *Franc 656* (US); *Germain s.n.* (P, image!); *Henecart 4* (P, image!); *Le Ral 74* (P, image!).

Dendroconche linguiforme (Mett.) Testo, Sundue, & A.R. Field comb. nov., *Polypodium linguiforme* (as 'linguaeforme') Mett. In Miq., Ann. Mus. Bot. Lugd.-Bat. 2: 228. 1866. *Pleopeltis linguiformis* (Mett.) Alderw., Bull. Dep. Agric. Indes Neerl. 27: 6 (1909: 6). *Microsorium linguiforme* (Mett.) Copel., Univ. Calif. Publ. Bot. 16: 116. 1929. TYPE: INDONESIA. *Zippelius s.n.* (lectotype designated by Bosman, 1991: L, barcode: L0051905, image!).

Polypodium schumannianum Diels in K. Schum & Lauterb., Fl. Schutzgeb. Suudsee 139. 1900.; *Microsorium schumannianum* (Diels) Copel., Gen. Fil. 196. 1947. TYPE: PAPUA NEW GUINEA. Sattellberg, Jan 1889, *Hellwig 238* (B, image!).

Pleopeltis dendroconchoides Alderw., Bull. Jard. Bot. Buitenzorg III 2: 165. 1920. TYPE: INDONESIA. Sumatra, Boekit Batoe Banting, 1200 m, 16 June 1918, *Jacobson s.n.* (holotype BO, n.v., isotype: L, barcode: L0051902, image!).

Plants hemiepiphytic, less commonly terrestrial or holoepiphytic. **Rhizome** long-creeping, dorsiventrally flattened, with occasional cavities, not pruinose. **Rhizome scales** dark brown, appressed to slightly spreading, lanceolate, 4–10 mm long, 1–2.5 mm wide. **Roots** of two types, one type laterally inserted and clasping, the other type ventrally inserted and attaching to soil. **Petiole** 1–12 cm long, not winged. **Leaves** simple, often narrowed in the middle, 7.5–50 cm long, 5–15 cm wide. **Venation** prominent, usually forming one principal row of areoles between the rachis and leaf margin. **Sori** round, in 2–7 rows between the rachis and the leaf margin.

Distribution and Habitat—*Dendroconche linguiforme* occurs in Indonesia, Malaysia, New Guinea, Solomon Islands, and Fiji, from 0–1600 m elevation.

Notes—This is the most widespread and variable species in the genus. It is generally a larger plant than its close relatives

D. annabellae and *D. kingii* and differs from those species by its monomorphic lanceolate leaves without an orbicular base. Bosman (1991) noted that "uncooked, salted fronds are eaten locally in New Guinea."

Representative Specimens—**Fiji.** *Smith* 5253 (US); *Smith* 8450 (US). **Indonesia.**—MALUKU: *Robinson* 1961 (US). **Malaysia.**—SABAH: *Parris* 11029 K, image!).—SARAWAK: *Anon. s.n.* (US). **Papua New Guinea.**—CENTRAL PROVINCE: *Brass* 5157 (US).—MANUS PROVINCE: *Grether* 3535 (US).—MOROBE PROVINCE: *Brass* 29407 (US); *Brass* 32678 (US). **Philippines.**—LUZON: *McGregor* 19801 (US); *Merrill* 699 (US). **Solomon Islands.**—BOUGAINVILLE ISLAND: *Kajewski* 1972 (P, image!).

Dendroconche sayeri (F. Muell. & Baker) Testo, Sundue, & A.R. Field, comb. nov., *Gymnogramma sayeri* F. Muell. & Baker, J. Bot 25: 163. 1887. *Polypodium selligaea* var. *sayeri* (F. Muell. & Baker) Domin, Bibl. Bot. 85: 186. 1913. *Colysis sayeri* (F. Muell. & Baker) Copel., Gen. Fil. 199. 1947. TYPE: AUSTRALIA. Queensland, Bellenden Ker Range, 5200 ft, 1887, *Sayer & Davidson* 72 (K, barcode: K000959615, image!).

Gymnogramma baileyi Baker, Kew Bull. 64: 86. 1892. *Colysis baileyi* (Baker) Ching, Sunyatsenia 5: 261. 1940. TYPE: AUSTRALIA. Queensland, Bellenden Ker, *F.M. Bailey s.n.* (K000959614 image!).

Plants hemiepiphytic or rarely terrestrial. **Rhizome** long-creeping, dorsiventrally flattened, with occasional cavities, not pruinose. **Rhizome scales** dark brown, spreading, ovate, 2–8 mm long, 1–3 mm wide. **Roots** of two types, one type laterally inserted and clasping, the other type ventrally inserted and attaching to soil. **Petiole** 1–20 cm long, usually not winged except in distal portion. **Leaves** deeply pinnatifid on mature plants, simple on young plants; mature leaves 12–65 cm long, 8–35 cm wide. **Venation** prominent, usually forming 2 areoles between the costa and leaf margin. **Sori** elongate, situated midway between the costa and leaf margin.

Distribution and Habitat—This species is endemic to northeastern Queensland, Australia and occurs from 500–1300 m elevation. This species usually is a low-growing hemiepiphyte and occurs in montane simple to complex notophyll vine forest near creeks, on adjacent ridges in rocky areas.

Notes—This species is narrowly distributed in northeastern Queensland, where it is restricted to mid- to high-elevation rain forests. *Dendroconche sayeri* is morphologically intermediate to *D. ampla* and *D. scandens* in leaf dissection, sorus shape, and petiole wing length; it also occurs where the ranges of those species overlap. Since *D. sayeri* is tetraploid and the other two species are diploid (Tindale and Roy, 2002) the possibility that *D. sayeri* is an allopolyploid derived from *D. ampla* and *D. scandens* warrants further investigation. Nooteboom (1997) and Bostock and Spokes (1998) place *Gymnogramma baileyi* Baker as a synonym of *D. ampla* but based on the soral arrangement and the locality of the type collection, we believe it is better considered a synonym of *D. sayeri*.

Type Note—Bostock and Spokes (1998 p. 471) list that the 'holotype' is housed in BRI citing Nooteboom (1997 p. 277) but Nooteboom does not cite this institution and no such specimen is present in BRI. The matching specimen, including the accession date at K, is here considered to be the holotype, being the only known original material available.

Representative Specimens—**Australia.**—QUEENSLAND: *Brass* 20049 (BRI); *Conors* 8387 (CANB); *Crayn* 1413 (CNS); *Ford* 3868 (CNS); *Ford* 5166

(CNS); *Jago* 6945 (CNS); *Jones & Gray* 18741 (CNS); *Jones* 101 (CANB, CNS); *Webb* 11278 (CNS); *van der Werff* 11826(CNS).

Dendroconche scandens (G. Forst.) Testo, Sundue, & A.R. Field, comb. nov., *Polypodium scandens* G. Forst., Fl. Insl. Austr. 81. 1786. *Phymatodes scandens* (G. Forst.) C. Presl, Tent. Pterid. 196. 1836. *Microsorium scandens* (G. Forst.) Tindale, Am. Fern J. 50: 241. 1960. *Phymatosorus scandens* (G. Forst.) Pic. Serm., *Webbia* 28: 459. 1973. TYPE: NEW ZEALAND. *Forster s.n.* (lectotype, designated by Pichi-Sermolli, 1951: BM, barcode: BM000066255, image!; isolectotypes: K, barcode: K000959807, image!; GOET, barcode: GOET012802, image!).

Plants hemiepiphytic or rarely terrestrial. **Rhizome** long-creeping, dorsiventrally flattened, with occasional cavities, rarely pruinose. **Rhizome scales** dark brown, spreading, ovate, 2–8 mm long, 1–2.2 mm wide. **Roots** of two types, one type laterally inserted and clasping, the other type ventrally inserted and attaching to soil. **Petiole** 1–16 cm long, usually not winged except in distal portion. **Leaves** deeply pinnatifid on mature plants, simple or irregularly lobed on young plants; mature leaves 8–58 cm long, 5–25 cm wide. **Venation** prominent, usually forming a single areole between the costa and leaf margin. **Sori** round, in a single row between the costa and leaf margin.

Distribution and Habitat—This species is found in Australia and New Zealand, where it occurs from 0–1500 m elevation. It is typically restricted to montane rain forest, especially in the northern part of its Australian range.

Notes—The type collection is probably from New Zealand, not the Society Islands, as Forster indicated (Tindale 1961). Live and freshly dried plants often have a strong musky smell. This species occasionally has pruinose rhizomes, a character that is otherwise present in *Zealandia*.

Representative Specimens—**Australia.**—NEW SOUTH WALES: *Boorman s.n.* (US); *Canning* 5754 (US); *Constable* P8103 (US); *Fraser & Vickery s.n.* (US).—QUEENSLAND: *Forster* 7347 (CANB); *Gray* 2271 (CANB, image!); *Jones* 11621 (CANB); *New Zealand.*—NORTH ISLAND: *Fosberg* 30459 (US); *Walker* 4394 (US); *Walker* 5175 (US).—SOUTH ISLAND: *Brame s.n.* (US); *Wiggins* 21037 (US); *Wright* 13410 (AK, image!).

Dendroconche varians (Mett.) Testo, Sundue, & A.R. Field comb. nov., *Acrostichum varians* Mett., Ann. Sci. Nat. Bot. 15:56. 1861. *Leptochilus varians* (Mett.) E. Fourn., Bull. Soc. Bot. France 15: 394. 1869. *Gymnopteris varians* (Mett.) Diels, Bot. Jahrb. Syst. 39: 7. 1906. *Christiopteris varians* (Mett.) Copel., Philipp. J. Sci. 12: 333. 1917. *Microsorium varians* (Mett.) Hennisman & Hett., Bot. Jahrb. Syst. 105: 5. 1984. TYPE: NEW CALEDONIA. 16 Apr 1868, *Vieillard* 1526 (holotype: B, n.v.; isotype: P, barcode: P01545167, image!).

Acrostichum varians Mett. var. *contracta* Mett., Ann. Sci. Nat. Bot. 15: 57. 1861. TYPE: NEW CALEDONIA. 16 Apr 1868, *Vieillard* 1525 (holotype: B, n.v.; isotype: P, barcode: P02141952, image!).

Plants hemiepiphytic or rarely terrestrial. **Rhizome** long-creeping, slightly dorsiventrally flattened, not pruinose. **Rhizome scales** dark brown, appressed, round or oblong, 1–3 mm long, 0.7–2.2 mm wide. **Roots** of two types, one type laterally inserted and clasping, the other type ventrally inserted and attaching to soil. **Petiole** 2–15 cm long, not winged. **Sterile leaves** deeply pinnatifid on mature plants, simple to lobed on young plants; mature leaves 20–55 cm long, 20–40 cm wide; pinnae 5–20 cm long, 0.5–3.5 cm wide. **Fertile leaves** pinnatisect, with lamina strongly contracted; 20–40 cm

long, 12–50 cm wide; pinnae 4–12 cm long, 0.2–0.7 cm wide. **Venation** prominent, usually forming 2–3 areoles between the costa and leaf margin. **Sori** acrostichoid, covering abaxial lamina surface.

Distribution and Habitat—*Dendroconche varians* is endemic to New Caledonia, where it occurs in montane cloud forest from 300–1100 m elevation.

Notes—This species is closely related to *D. latilobata* and differs principally by the characters provided in the key. Hennipman and Hettterscheid (1984: 5) reported that the spores of this species are very large (70–85 µm), suggesting that it may be polyploid. If this is the case, *D. latilobata* is a likely putative progenitor.

Representative Specimens—**New Caledonia**.—NORTH PROVINCE: Guillamin & Baumann-Bodenheim 8787 (US); Guillamin & Baumann-Bodenheim 8788 (US); Schmid 3413 (P, image!).—SOUTH PROVINCE: Baumann 5441 (US); Franc 616 (P, image!); Le Ral 63 (P, image!); Mackee 12141 (P, image!); Veillon 7642 (P, image!). Unknown: Franc 1081 (P, image!); Veillon 1529 (P, image!); Vieillard 1528 (B, image!).

Zealandia Testo & A. R. Field gen. nov., TYPE: NEW ZEALAND.
Polypodium pustulatum G. Forst., Fl. Ins. Austr. 81. 1786.

Plants terrestrial, epipetric, or epiphytic. **Rhizome** long-creeping, terete or slightly dorsiventrally flattened, usually

pruinose. **Rhizome scales** brown, appressed to spreading, lanceolate to ovate. **Petiole** 1–40 cm long, not winged. **Leaves** simple to pinnatisect, 10–140 cm long, 10–45 cm wide. **Lamina** membranaceous to coriaceous. **Venation** prominent, anastomosing, forming regular areoles; hydathodes usually evident. **Sori** round to slightly elongate, usually impressed into the lamina and visible adaxially. **Spores** yellow, ellipsoid, monolete, tuberculate. Figure 5.

Distribution and Habitat—This genus occurs in Australia, the Cook Islands, Indonesia, New Caledonia, New Zealand, Papua New Guinea, Samoa, the Solomon Islands, and Vanuatu (Fig. 6C). Species of *Zealandia* may be terrestrial or epiphytic, and frequently occur in wet montane forests from 200–2000 m elevation.

Etymology—The genus name refers to the fact that most species in the genus are restricted to the sunken continent of Zealandia, which comprises New Caledonia, New Zealand, Norfolk Island, and Lord Howe Island (Australia).

Notes—As construed here, *Zealandia* is comprised of four species (one represented by two varieties) that possess (in almost all plants) pruinose rhizomes and deeply lobed leaves with sori that are deeply impressed into the lamina (Fig. 5).

KEY TO THE SPECIES OF ZEALANDIA

1. Rhizome scales basifixed 2.
2. Plants from New Zealand, venation generally not prominent, 5–20 pairs of lobes on leaves of mature plants *Z. novae-zealandiae*
2. Plants widely distributed in Pacific Islands, venation generally prominent, 15–30 pairs of lobes on leaves of mature plants *Z. powellii*
1. Rhizome scales peltate 3.
3. Plants from New Caledonia, sori submarginal, lamina of fertile leaves strongly contracted relative to sterile leaves *Z. vieillardii*
3. Plants from Australia, sori inframedial, lamina of fertile leaves not or only weakly contracted relative to sterile leaves *Z. pustulata*

Zealandia novae-zealandiae (Baker) Testo & A. R. Field comb. nov., *Polypodium novae-zealandiae* Baker in Hook. & Baker, Icon. Pl. 1674. 1868. *Microsorium novae-zealandiae* (Baker) Copel., Gen. Fil. 196. 1947. *Phymatosorus novae-zealandiae* (Baker) Pic. Serm., Webbia 28: 459. 1973. TYPE: NEW ZEALAND. Pirongia Mt., Upper Waikato District, May 1879, T. F. Cheeseman 361 (lectotype designated by Brownsey & Perrie, 2012: K, K000959805 and K000959806, images!).

Plants epiphytic, rarely terrestrial. **Rhizome** long-creeping, terete, 4.5–9 mm in diam. **Rhizome scales** basifixed orange-brown, spreading and squarrose, narrowly ovate, 5–15 mm long, 2–3 mm wide. **Roots** of one type, ventrally inserted and attaching to substrate. **Petiole** 6–30 cm long, not winged. **Leaves** pinnatifid, 20–85 cm long, 18–38 cm wide. **Lamina** coriaceous, cuneate at base, acute to acuminate at apex, generally with 5–20 pinna pairs. **Venation** usually not prominent, forming areoles; hydathodes present. **Sori** round, usually impressed into the lamina and visible adaxially. **Spores** yellow, ellipsoid, monolete, smooth.

Distribution and Habitat—*Zealandia novae-zealandiae* is endemic to the North Island of New Zealand, where it is found in montane forests from 350–1250 m.

Representative Specimens—**New Zealand**.—NORTH ISLAND: Barltrop s.n. (US); Brame s.n. (US); Cheeseman s.n. (US); Gardner 878 (CBG); Grace 1022 (US); Hutchison s.n. (US); Sledge 176 (US).

Zealandia powellii (Baker) Testo & A. R. Field comb. nov., *Polypodium powellii* Baker in Hook. & Baker, Syn. Fil. 364. 1868. *Phymatosorus powellii* (Baker) Pic. Serm., Webbia 28: 459. 1973. TYPE: SAMOA. Upolu, 2000 ft, Aug 1864, T. Powell 135 (holotype: K, barcode: K000804531 and K K000804532

[associated sheets]; possible isotypes [without collection number]: GH, barcode GH00021885 image!; MEL, barcode MEL2424290 and MEL2424291, images!).

Plants terrestrial or epiphytic. **Rhizome** long-creeping, terete, 2.5–5 mm in diam; sclerenchymatous strands sometimes present. **Rhizome scales** basifixed, brown, slightly spreading, narrowly ovate, 3–12 mm long, 2–5 mm wide. **Roots** of one type, ventrally inserted and attaching to substrate. **Petiole** 20–40 cm long, not winged. **Leaves** pinnatifid, 40–140 cm long, 25–45 cm wide. **Lamina** membranaceous, cuneate at base, acute to acuminate at apex, generally with 15–30 pinna pairs. **Venation** prominent, forming areoles. **Sori** round. **Spores** yellow, ellipsoid, monolete, smooth.

Distribution and Habitat—This species occurs in the Cook Islands, Fiji, French Polynesia, Indonesia (Moluccas), New Guinea, Pitcairn Islands, Samoa, the Solomon Islands, and Vanuatu. It generally grows in montane forests from 100–1700 m elevation.

Notes—This is the only member of *Zealandia* that occurs exclusively outside of Australia, New Caledonia, and New Zealand. It differs from other members of the lecanopteroid clade by the presence of sclerenchymatous strands in the rhizome ground tissue and is the only species of *Zealandia* that lacks a pruinose rhizome. Nitta et al. (2018) hypothesized that this species may be of hybrid origin, based on incongruent phylogenetic placement across the loci they analyzed in their study. We think this possibility is likely, given the morphological disparity between this taxon and the remaining *Zealandia* species. Additional study is needed to better understand the origin of this taxon; we place it in *Zealandia* for a lack of other appropriate options.

Microsorium rubidium (J. Sm.) Copel. and *Microsorium sibomense* Copel. are morphologically similar and may belong to *Zealandia*; their taxonomic affinities should be reassessed once molecular data are available.

Representative Specimens—Cook Islands.—RAROTONGA: Wright 14623 (AK, image!); Wright 14624 (AK, image!); Cheeseman s.n. (AK, image!). FIJI: Thurn 125 (K, image!). **French Polynesia**.—SOCIETY ISLANDS: Florence et al. 11066 (US); Florence & Jourdan 11465 (US); Nitta 654 (UC, image!). **Indonesia**.—MOLUCCAS: Kato et al. 14044 (L, image!); Kato et al. 3214 (L, image!); Kato et al. 7402 (L, image!). **Papua New Guinea**.—MADANG PROVINCE: Walker 8882 (L, image!).—MILNE BAY PROVINCE: Brass 27124 (US); Brass 24720 (US); Croft 523 (L, image!).—NEW IRELAND PROVINCE: Croft et al. 1871 (CBG, L, image!).—ORO PROVINCE: Hoogland 4395 (K, image!). **Pitcairn Islands**. Florence & Waldren 11046 (US). **Samoa**. Hochreutiner 3291 (L, image!); Vaupel 350 (AK, image!). **Solomon Islands**.—GUADALCANAL: Braithwaite 4720 (CBG). **Vanuatu**. Braithwaite 2397 (K, image!).

Zealandia pustulata (G. Forst.) Testo & A. R. Field comb. nov., *Polypodium pustulatum* G. Forst., Fl. Ins. Austr. 81. 1786. *Microsorium pustulatum* (G. Forst.) Copel., Gen. Fil. 196. 1947. *Phymatosorus pustulatus* (G. Forst.) M. F. Large, J. E. Braggins, & P. S. Green, New Zeal. J. Bot. 30: 207. 1992. —TYPE: NEW ZEALAND. Forster s.n. (lectotype designated by Pichi Sermolli 1951: BM, barcode: BM000066256, image!; isolectotypes: GOET, barcode: GOET012801, image!; LE, barcode: LE00008784, image!).

Polypodium diversifolium Willd., Sp. Pl. 5(1): 166. 1810. —TYPE: AUSTRALIA (Tasmania). *de Labillardiere s.n.* (lectotype, designated by Brownsey and Perrie, 2012: FI, image!; isolectotype: L, image!).

Polypodium billardierei R. Br., Prodr. 147. 1810.—TYPE: AUSTRALIA Tasmania, Port Dalrymple. *R. Brown Iter. Austral. 11* (lectotype, chosen by Tindale, 1961: BM, barcode: BM001038373; isolectotypes: E, barcode: E00146814, image!; K, n.v.; MEL, barcode: MEL672378).

Plants terrestrial, epipetric, or epiphytic. **Rhizome** long-creeping, terete, 3–8.5 mm in diameter, typically glaucous. **Rhizome scales** peltate, dark brown, appressed, ovate, 3–7 mm long, 1–3 mm wide. **Roots** of one type, ventrally inserted and attaching to substrate. **Petiole** 5–20 cm long, not winged. **Leaves** simple on young plants and pinnatifid on mature plants, 5–60 cm long, 5–38 cm wide. **Lamina** herbaceous, cuneate at base, acute at apex. **Venation** prominent, forming areoles. **Sori** round, inframedial. **Spores** yellow, ellipsoid, monolete, tuberculate.

Distribution and Habitat—Australia, New Zealand, Norfolk Island, and Lord Howe Island. From 0–1400 m elevation.

Zealandia pustulata (G. Forst.) Testo & A. R. Field subsp. *pustulata*

Plants terrestrial, epipetric, or epiphytic. **Rhizome** long-creeping, terete, 3–5 mm in diameter, typically glaucous. **Rhizome scales** peltate, dark brown, appressed, ovate, 3–7 mm long, 1–3 mm wide. **Roots** of one type, ventrally inserted and attaching to substrate. **Petiole** 5–20 cm long, not winged. **Leaves** simple on young plants and pinnatifid on mature plants, 5–50 cm long, 5–33 cm wide. **Lamina** herbaceous, cuneate at base, acute at apex. **Venation** prominent, forming areoles. **Sori** round, inframedial. **Spores** yellow, ellipsoid, monolete, tuberculate.

Distribution and Habitat—Australia, New Zealand, Norfolk Island. From 0–1400 m elevation.

Representative Specimens—AUSTRALIA: NEW SOUTH WALES: *Constable 6751* (NSW, image!); *Craven 591* (US); Taylor et al. 414 (NSW, image!). QUEENSLAND: *Blake 20421* (BRI); *Forster 15741* (BRI); *Forster 34134* (BRI); *Guymier 27* (BRI). TASMANIA: *Brown s.n.* (E, image!). VICTORIA: *Jobson 3509* (NSW, image!). NEW ZEALAND: NORTH ISLAND: *Brown s.n.* (AK, image!). SOUTH ISLAND: *Calvo 5814* (MA, image!). NORFOLK ISLAND: *North 169* (CANB, image!); *Taylor s.n.* (AK, image!).

Zealandia pustulata (G. Forst.) Testo & A. R. Field subsp. *howensis* (Tindale & P. S. Green) Testo & A. R. Field comb. nov., *Phymatosorus pustulatus* subsp. *howensis* Tindale & P. S. Green, Fl. Austr. 49: 617. 1994. *Microsorium pustulatum* subsp. *howense* (Tindale & P. S. Green) Bostock, Fl. Austr. 48: 715. 1998. —TYPE: AUSTRALIA: Lord Howe Island, Transit Hill. *R.D. Hoogland 8673* (holotype: NSW, barcode: NSW536359, image!; isotype: CANB, barcode: CANB130948).

Plants terrestrial, epipetric, or epiphytic. **Rhizome** long-creeping, terete, 4–8.5 mm in diameter, sometimes glaucous. **Rhizome scales** peltate, dark brown, appressed, lanceolate, 3–5 mm long, 1–3 mm wide. **Roots** of one type, ventrally inserted and attaching to substrate. **Petiole** 10–20 cm long, not winged. **Leaves** simple on young plants and pinnatifid on mature plants, 20–60 cm long, 8–38 cm wide. **Lamina** herbaceous, cuneate at base, acute at apex. **Venation** prominent, forming areoles. **Sori** round, inframedial. **Spores** yellow, ellipsoid, monolete, tuberculate.

Distribution and Habitat—Endemic to Lord Howe Island, 100–600 m elevation.

Notes—This subspecies differs from subsp. *pustulata* by having sori closer to the leaf margin, broader rhizome scales, and generally more regularly pinnatisect lamina.

Representative Specimens—AUSTRALIA: LORD HOWE ISLAND: *van Balgooy 1011* (CANB); *Croft 1021* (CBG); *Hoogland 8683* (CANB); *Telford 7002* (CBG).

Zealandia vieillardii (Mett.) Testo & A. R. Field comb. nov., *Polypodium vieillardii* Mett., Ann. Sci. Nat. Bot. 15: 77. 1861. *Microsorium vieillardii* (Mett.) Copel., Gen. Fil. 196. 1947. *Phymatosorus vieillardii* (Mett.) Pic. Serm., Webbia 31: 249. 1977. TYPE: NEW CALEDONIA. Poila. 1855–1860, *Vieillard 1598* (lectotype designated by Brownlie, 1969: P, barcode: P00626841, image!).

Polypodium lenormandii Baker in Hook. & Baker, Syn. Fil. 514. 1874. TYPE: NEW CALEDONIA. 1861–1867, *DePlanche 1599* (K, barcode: K000826160, image!).

Plants epiphytic, rarely epipetric. **Rhizome** long-creeping, terete, 5–10 mm in diam, not glaucous. **Rhizome scales** peltate, dark brown, appressed, ovate, 3–7 mm long, 1.5–4 mm wide. **Roots** of one type, ventrally inserted and attaching to substrate. **Petiole** 15–30 cm long, not winged. **Leaves** simple or lobed on young plants and pinnatifid on mature plants, 30–75 cm long, 18–33 cm wide. **Lamina** herbaceous, cuneate at base, acute at apex; fertile leaves with strongly contracted lamina. **Venation** not prominent, forming areoles. **Sori** round, submarginal. **Spores** yellow, ellipsoid, monolete, smooth.

Distribution and Habitat—This species is endemic to New Caledonia, where it occurs in montane forests from 200–950 m.

Notes—This is the only species of *Zealandia* present on New Caledonia. In addition, it can readily be distinguished from

other members of the genus by its slightly dimorphic fertile leaves and submarginal sori.

Representative Specimens—**New Caledonia**.—ISLE OF PINES: *Bernardi* 9713 (US).—PROVINCE NORD: *Pignal* 5178 (P, image!); *Pignal* 5305 (P, image!).—PROVINCE SUD: *Baumann* 8274 (US); *Franç* 330 (US); *Guillaumin* 7621 (US); *Guillaumin* 10335 (US); *Guillaumin & Baumann* 7735 (US).—UNKNOWN PROVINCE: *Pancher* 119 (US).

ACKNOWLEDGMENTS

The authors thank Robbin Moran (NY) and Susan Pell (US National Conservatory) for providing material of *Dendroconche annabellae* and Peter Hovenkamp for insight into the taxonomy of microsorioid ferns. Leon Perrie, Cheng-Wei Chen, and Jon Sullivan provided images of several taxa. The Alice and Rolla Tryon Pteridophyte Library at the Pringle Herbarium at the University of Vermont provided access to literature that was central to this work. We thank Associate Editor Alejandra Vasco and two anonymous reviewers for their helpful comments on an earlier version of this manuscript.

AUTHOR CONTRIBUTIONS

WT performed lab work and carried out the phylogenetic analyses. WT, MS, and AF scored morphological characters and compiled the morphological matrix. MS and AF conducted field work and made collections of *Dendroconche* and *Zealandia*. WT and AF wrote the taxonomic treatment. WT was the primary author of the manuscript, with contributions by AF, ES, and MS.

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APPENDIX 1. GenBank accession numbers of samples used in this study. Order of data: Taxon name, *trnL-trnF* accession number, *rbcl* accession number, *rps4-trnS* accession number.

Bosmania lastii, EU483058, EU482961, –; *Bosmania membranacea*, AY725051, –, AY725046; *Bosmania membranacea*, AY725050, –, –; *Dendroconche ampla*, KF570110, KF570108, KF570109; *Dendroconche annabellae*, –, MN018180, –; *Dendroconche sayeri*, MN018178, MN18176, MN18177; *Dendroconche scandens*, DQ179641, DQ212057, DQ212058; *Dendroconche varians*, DQ179643, AY362566, AY362638; *Goniophlebium argutum*, DQ164505, DQ164442, DQ164473; *Goniophlebium formosanum*, DQ642235, AB043100, AY096224; *Goniophlebium mehibitense*, EU483026, EU482932, –; *Goniophlebium niponicum*, EU483027, AB043098, AY362626; *Goniophlebium persicifolium*, EU483028, AB043099, AY096225; *Goniophlebium pseudocannatum*, EU483029, EU482934, –; *Lecanopteris celebica*, AY083626, AF470323, –; *Lecanopteris crustacea*, AY083632, AF470329, –; *Lecanopteris pumila*, AY083634, AF470331, –; *Lecanopteris sarcopus*, EU483030, EU482935, –; *Lecanopteris sinuosa*, AY083624, AF470321, AY362634; *Lemmaphyllum accedens*, EU483031, EU482936, KX891400; *Lemmaphyllum adnascens*, GU126724, GU126694, GU126713; *Lemmaphyllum carnosum*, GU126728, AF470332, AY362631; *Lemmaphyllum carnosum*, KX891355, AF470332, AY362631; *Lemmaphyllum carnosum* var. *drymoglossoides*, GQ256241, –; *Lemmaphyllum carnosum* var. *microphyllum*, EU483033, –; *Lemmaphyllum diversum*, EU483032, EU482937, GU126718; *Lemmaphyllum intermedium*, GU126726, GU126696, GU126715; *Lemmaphyllum pyriforme*, GU126725, AB575261, GU126714; *Lemmaphyllum rostratum*, GU126727, GU126697, GU126716; *Lemmaphyllum squamatum*, GU126721, GU126692, GU126710; *Lepidomicrosorium buergerianum*, GQ256242, AB575277, EU363260; *Lepidomicrosorium subhemionitideum*, GU126722, GU126693, GU126711; *Lepidomicrosorium superficiale*, GU126730, AY362568, AY362641; *Lepisorus affinis*, GQ256173, –; GQ256328; *Lepisorus albertii*, GQ256174, –; GQ256329; *Lepisorus angustus*, GQ256175, –; GQ256330; *Lepisorus annamensis*, EU483025, EU482931, GQ256324; *Lepisorus annifrons*, GQ256176, AB575263; *Lepisorus asterolepis*, GQ256177, –; GQ256332; *Lepisorus bampsii*, GQ256178, –; GQ256333; *Lepisorus bicolor*, GQ256179, –; GQ256334; *Lepisorus boninensis*, GQ256180, AB575264, GQ256335; *Lepisorus clathratus*, DQ642236, AB575265, AY362633; *Lepisorus confluens*, GQ256182, –; GQ256337; *Lepisorus contortus*, GQ256183, –; GQ256338; *Lepisorus elegans*, GQ256187, –; GQ256342; *Lepisorus excavatus*, DQ642237, DQ642155, DQ642193; *Lepisorus hachijensis*, GQ256190, AB575266, GQ256343; *Lepisorus henryi*, GQ256167, –; GQ256325; *Lepisorus heterolepis*, GQ256191, –; GQ256344; *Lepisorus hsiaowutaiensis*, GQ256192, –; GQ256345; *Lepisorus kawakamii*, EU483035, EU482940, –; *Lepisorus kuchenensis*, GQ256194, –; GQ256346; *Lepisorus lewisii*, GQ256195, –; GQ256347; *Lepisorus likiangensis*, GQ256186, –; GQ256341; *Lepisorus lineariformis*, GQ256198, –; GQ256350; *Lepisorus longifolius*, DQ642239, DQ642157, DQ642195; *Lepisorus loriformis*, GQ256201, –; GQ256352; *Lepisorus luchunensis*, HQ712019, HQ712000, HQ712008; *Lepisorus macrosphaerus*, EU483036, EU482941, GQ256354; *Lepisorus marginatus*, GQ256204, –; GQ256355; *Lepisorus medogensis*, GQ256205, –; GQ256356; *Lepisorus megasorus*, DQ642240, DQ642158, DQ642196; *Lepisorus miyoshianus*, DQ179639, AB575255, AY362630; *Lepisorus monilisorus*, EU483037, EU482942, GQ256357; *Lepisorus morrisonensis*, GQ256208, –; GQ256358; *Lepisorus mucronatus*, DQ642232, AY362562, AY362629; *Lepisorus nudus*, HQ712018, AY362564, AY362639; *Lepisorus obscurevolulus*, GQ256210, –; GQ256360; *Lepisorus oligolepidus*, GQ256211, AB575267, GQ256361; *Lepisorus onoei*, GQ256212, AB575268, GQ256362; *Lepisorus patungensis*, GQ256213, –; GQ256363; *Lepisorus perrierianus*, HQ712017, HQ711995, –; *Lepisorus platyrhynchos*, DQ642233, DQ642152, DQ642190; *Lepisorus pseudonudus*, GQ256215, –; GQ256365; *Lepisorus pseudosussuriensis*, EU483038, EU482943, –; *Lepisorus pumilus*, GQ256217, –; GQ256366; *Lepisorus rotundus*, HQ712015, HQ711996, HQ712012; *Lepisorus schraderi*, HQ712016, HQ711998, HQ712010; *Lepisorus scolopendrius*, GQ256218, –; GQ256367; *Lepisorus sinensis*, GQ256221, –; GQ256370; *Lepisorus sordidus*, GQ256222, –; GQ256371; *Lepisorus soulieanus*, GQ256249, –; GQ256399; *Lepisorus spicatus*, DQ642234, DQ642153, DQ642191; *Lepisorus stenistus*, GQ256202, –; GQ256353; *Lepisorus subconfluens*, GQ256224, –; GQ256373; *Lepisorus sublinearis*, GQ256225, –; GQ256374; *Lepisorus suboligolepidus*, GQ256227, –; GQ256376;

Lepisorus subsessilis, GQ256228, –; GQ256377; *Lepisorus thaipaiensis*, GQ256229, –; GQ256378; *Lepisorus thunbergianus*, DQ642241, AB575269, AY096226; *Lepisorus tibeticus*, GQ256234, –; GQ256383; *Lepisorus tosaensis*, GQ256236, AB575270, GQ256385; *Lepisorus uchiyamae*, GQ256237, AB575271, GQ256386; *Lepisorus ussuriensis*, GQ256238, –; GQ256387; *Lepisorus ussuriensis* var. *distans*, GQ256239, –; *Lepisorus waltonii*, EU483039, EU482944, AY362632; *Lepisorus xiphopteris*, GQ256240, –; GQ256389; *Leptochilus axillaris*, EU483040, JX103699, JX103741; *Leptochilus cantoniensis*, EU483041, EU363245, –; *Leptochilus decurrens*, DQ179640, AB575273, EU363259; *Leptochilus digitatus*, EU483043, EU363232, EU363250; *Leptochilus ellipticus*, EU483045, AB575243, –; *Leptochilus ellipticus* var. *pothifolius*, JX103780, –; *Leptochilus hemionitideus*, EU483046, AB575244, –; *Leptochilus hemionus*, EU483047, EU363236, EU363252; *Leptochilus henryi*, EU483048, EU363237, EU363253; *Leptochilus heterophyllum*, JX103772, JX103688, JX103730; *Leptochilus insignis*, EU483054, EU482957, JX103745; *Leptochilus pteropus*, EU483061, AB575246, –; *Leptochilus shintenensis*, EU483049, U05612, –; *Leptochilus wrightii*, EU483050, AB232406, JX103769; *Microsorium commutatum*, EU483051, AY362571, AY362644; *Microsorium cuspidatum*, AY083638, AF470335, EU363252; *Microsorium grossum*, EU483053, EF463253, AY362695; *Microsorium hainanense*, EU483057, EU363249, EU363263; *Microsorium lucidum*, JX103810, JX103726, JX103768; *Microsorium membranifolium*, DQ642245, DQ642161, DQ642200; *Microsorium musifolium*, AY083636, AF470333, AY362636; *Microsorium papuanum*, DQ642246, DQ642162, –; *Microsorium punctatum*, DQ164508, AF470337, AY362637; *Microsorium scolopendria*, DQ179642, AB575281, DQ179636; *Microsorium spectrum*, EU483064, EU482967, –; *Microsorium thailandicum*, EU483066, EU482969, –; *Microsorium whiteheadii*, EU483067, EU482970, –; *Neochieopteris fortunei*, AY529477, AY529160, AY529184; *Neochieopteris oata*, EU483068, EU482972, JX103762; *Neochieopteris palmatopedata*, DQ212059, AY362567, AY362640; *Neochieopteris phyllomanes*, EU483069, EU482973, –; *Neochieopteris triglossa*, HQ597019, HQ597010, –; *Neolepisorus ensatus*, GQ256247, AY096204, GQ256397; *Neolepisorus fortunei*, AY725052, DQ164508, AY362642; *Neolepisorus pappi*, AY083639, AF470336, –; *Neolepisorus zippelii*, DQ642249, AB232411, DQ642203; *Tricholepidium normale*, EU483071, EU482975, HQ597013; *Zealandia novae-zealandiae*, DQ401121, DQ401116, DQ401126; *Zealandia pustulata* subsp. *pustulata*, DQ401122, AY362570, AY362643; *Zealandia vieillardii*, DQ179644, DQ179634, DQ179637.

APPENDIX 2. Matrix of morphological characters scored for this study. Order of data: Taxon name, growth habit (0 = terrestrial, 1 = hemiepiphytic, 2 = epiphytic), sclerenchymatous strands present in rhizome (0 = absent, 1 = present), glaucous rhizome (0 = absent, 1 = present), rhizome cavities (0 = absent, 1 = present), association with ants (0 = absent, 1 = present), sori impressed (0 = no, 1 = yes).

Dendroconche ampla 1, 0, 0, 1, 0, 0; *Dendroconche kingii* 1, 0, 0, 1, 0, 0; *Dendroconche latilobatum* 1, 0, 0, 0, 0, 0; *Dendroconche linguiforme* 1, 0, 0, 0, 0, 0; *Dendroconche sayeri* 1, 0, 0, 1, 0, 0; *Dendroconche scandens* 1, 0, 0, 0, 0, 0; *Dendroconche varians* 1, 0, 0, 0, 0, 0; *Dendroconche annabellae* 1, 0, 0, 0, 0, 0; *Bosmania lastii* 0, 0, 0, 0, 0, 0; *Bosmania membranacea* 0, 0, 0, 0, 0, 0; *Zealandia novae-zealandiae* 2, 0, 1, 0, 0, 1; *Zealandia vieillardii* 2, 0, 1, 0, 0, 1; *Zealandia pustulata* 2, 0, 1, 0, 0, 1; *Zealandia powellii* 2, 0, 0, 0, 0, 1; *Lecanopteris balgooyi* 2, 0, 0, 1, 1, 1; *Lecanopteris carnosata* 2, 0, 0, 1, 1, 1; *Lecanopteris celebica* 2, 0, 0, 1, 1, 1; *Lecanopteris crustacea* 2, 0, 0, 1, 1, 1; *Lecanopteris deparioides* 2, 0, 0, 1, 1, 1; *Lecanopteris lomarioides* 2, 0, 0, 1, 1, 1; *Lecanopteris luzonensis* 2, 0, 0, 1, 1, 1; *Lecanopteris mirabilis* 2, 0, 0, 0, 1, 1; *Lecanopteris pumila* 2, 0, 0, 1, 1, 1; *Lecanopteris sarcopus* 2, 0, 0, 1, 1, 1; *Lecanopteris sinuosa* 2, 0, 0, 1, 1, 1; *Lecanopteris spinosa* 2, 0, 0, 1, 1, 1; *Goniophlebium argutum* 2, 1, 0, 0, 0, 1; *Goniophlebium subauriculatum* 2, 1, 0, 0, 0, 1; *Leptochilus hemionitideus* 0, 1, 0, 0, 0, 0; *Leptochilus wrightii* 0, 1, 0, 0, 0, 0; *Microsorium punctatum* 2, 1, 0, 0, 0, 0; *Microsorium commutatum* 0, 1, 0, 0, 0, 0; *Lepisorus elegans* 2, 1, 0, 0, 0, 1; *Lepisorus clathratus* 2, 1, 0, 0, 0, 1.