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

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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 *Microsorum*. Using phylogenetic analyses and morphological evidence, we demonstrate that sixteen taxa typically treated in the genera *Microsorum* 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 synonyms 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. linguforme*, *D. sayeri*, *D. scandens*, *D. varians*, *Zealandia novae-zealandiae*, *Z. pouelli*, *Z. pustulata*, *Z. pustulata subsp. howensis*, and *Z. vielardi*.

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

Despite being the focus of considerable taxonomic (Bosman 1991; Nooteboom 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 microsoroid 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 *Microsorum*, 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 *Microsorum* and the allied genus *Colysis* were found not to be closely related to *Microsorum 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, *rpo4* gene, *rpo4-trnS* intergenic spacer, and *trnL-trnF* intergenic space) were obtained from Genbank, using data generated from previous phylogenies of subfamily Microsoroideae (Hauffer 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 annabelae* and *Dendroconche sayeri*, for which new data were generated. For those two taxa, DNA extraction, amplification, and sequencing protocols followed those of Testo and Sundue (2014). Missing data percentages were 12% for *rbcL*, 28% for *rpo4*, 27% for *rpo4-trnS*, and 25% 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 Akc criterion in jModelTest2 (Darriba et al. 2012) on the Cipres Science Gateway portal (Miller et al. 2010); these were the GTR + Γ model for *rpo4* and *trnL-trnF*, the HKY model for *rbcL*, and the TVM model for *rpo4-trnS*. The four alignments obtained were concatenated for all tree-building analyses.

Maximum likelihood (ML) phylogenetic analysis was performed in RAxML v.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 Trace 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 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*, *Microsorum*, *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; Nooteboom 1997). These characters were selected because they have been considered taxonomically informative in the microsoroid and lecanopteroid ferns (Hennipman and Verdun 1987; Bosman 1991; Nooteboom 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 monographR (Reginato 2016).

Character reconstruction was performed using the R package phytools (Revell 2012) under a continuous-time Markov chain model with equal rate parameters for this character for the subfamily are ambiguous, with approximately equal probabilities for sclerenchyma strands in Rhizome (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*.

**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., Lemmaphyllum, Lepidomicroorum, Neocheiropteris, Neolepisorus, Paragymma, and Tricholepidium. The second clade is comprised of Microsorum s. s. and Leptochilus, which are well-supported (BS = 92%, PP = 1.0) as sister to each other; the type species of Colyis (Colyis hemionitidae (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 (Dendoconche) 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 Microsorum/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.

Discussion

As has been shown in earlier studies, several species typically treated in the genera Microsorum 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 annabellea* (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
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
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. annabeliae*, *D. kingii*, etc.
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
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 4. Dendroconche.** A. Gross morphology of *Dendroconche kingii*. B. Hemiepiphytic growth habit and dimorphic roots of *Dendroconche ampla*. C. Clasping leaf bases of *Dendroconche kingii*. Photos by Michael Sundue.
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.

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. Glaucous rhizome of Zealandia pustulata subsp. pustulata. Photos A, B, D by Leon Perrie, C by Jon Sullivan.
Key to the Species of Bosmania

1. Sori present in costal areoles, plants of southern and southeastern Asia ......................................................... B. membranacea

2. Sori absent in costal areoles, plants restricted to Madagascar. ................................................................. B. lastii

3. 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. Sori prominent, anastomosing, forming regular areoles. Spores yellow, ellipsoid, monolete, verrucate. Figure 3. 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.—ANTANARIVO PROVINCE: Crensers 3688 (MO); Rosolodyer 160 (MO).—TOLIARA PROVINCE: DaPuy MB758 (MO).

**Bosmania membranacea** (D. Don) Testo comb. nov., Polypodium membranaceum D. Don, Prodr. Fl. Nepal. 2. 1825. Plants terrestrial. Rhizome long-growing, 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. Sori round to slightly elongate, absent from costal areoles. Spores yellow, ellipsoid, monolete, verrucate.

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 Microsorum.

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.
Species distributions.

Georeferenced herbarium collections; dotted lines indicated approximate Dendroconche.

C. diam.

Rhizome scales creeping, terete dorsiventrally slightly flattened, 3–10 mm in diam.

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.


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 Microsorum linguiforme, and Dendroconche was relegated to synonymy under Microsorum. Later studies (Schneider et al. 2006; Kreier et al. 2008; Testo and Sundue 2014) indicated that Microsorum 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

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

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

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cavities, laterally inserted clasper roots, and non-glaucescent rhizomes (Fig. 4). The flattened rhizomes and clasper roots found in the genus correspond closely to the “hemiepiphyte syndrome” proposed by Testo and Sundue (2014) in a study on *Dendroconche ampha* (as *Colysis ampla*); indeed, it appears that all *Dendroconche* species are at least facultative hemiepiphytes. The genus is represented in Melanesia, 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 reflect 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 *Microsorum cinctum* Bosman, *Microsorum egregium* (Brause) Bosman, *Microsorum longissimum*, *Microsorum rampans* (Baker) Parris, and *Microsorum samarensis* (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*
3. Fertile leaves unguiculate, with conspicuous rounded base ........................................... *D. lingii*

#### 2. Fertile leaves unguiculate

4. Apical portion of fertile leaves lanceolate, 2–5 cm wide ........................................... *D. annabeliae*
5. Apical portion of fertile leaves ciliate, < 1.5 cm wide ........................................... *D. varians*

#### 4. Fertile leaves with two rows of areoles between the costa and leaf margin

6. Mature leaves typically with one row of areoles between the costa and leaf margin; sori round ........................................... *D. sanderi*
7. Mature leaves typically with two rows of areoles between the costa and leaf margin; sori elongate ........................................... *D. ampla*

#### 3. Fertile leaves lanceolate

8. Sori elongate ........................................... *D. varians*
9. Sori round ........................................... *D. sanderi*

#### 6. Mature leaves typically with one row of areoles between the costa and leaf margin

10. Fertile and sterile fronds monomorphic or weakly dimorphic, fertile fronds with segments < 1 cm wide; plants from New Caledonia ........................................... *D. annabeliae*

#### 7. Petioles typically not winged near base

11. Sori mostly extending from near costa almost to the leaf margin; spores generally 45–60 μm long ........................................... *D. ampla*
12. Sori mostly extending from near costa almost to the leaf margin; spores generally 28–30 μm long ........................................... *D. linguiforme"


**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: Rockingham Bay, 18 Aug. 1866, J.Dallachy s.n. (lectotype, designated here: MEL, barcode MEL12169912 image!; isolecotypes: MEL, barcode MEL1061215 image!; MEL, barcode MEL12166916 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 claspering, 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. sanderi* 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.

**Polypodium cyclobasis** Baker, Keru 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 claspering, 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. *Dendroconche linguliforme* comb. nov., *Polypodium linguiforme* (as *linguaeformis*).—Melville Bay Province: P01545165, image!.

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.


Plants hemiepiphytes. Rhizome long-creeping, dorsiventrally flattened, with occasional cavities, not pruinose. Rhizome scales brown, spreading, lanceolate, 2–8 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. Petrole 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, 2.5–6 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 lecaniopterid ferns 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—Papua New Guinea. *Dendroconche linguiforme* (Mett.) Testo, Sundew, & A.R. Field comb. nov., *Polypodium linguiforme* (as *linguaeformis*).—Northern Province: Monotrouzier 250 (P, image!).—South Province: Guillain et al. 10415 (US); Macke 196 (P, image!).—Unknown Province: Cribs 453 (P, image!); Franc 656 (US); Germain s.n. (P, image!); Hennecart 4 (P, image!); Le Rat 74 (P, image!).


Plants hemiepiphytic, less commonly terrestrial or holoepphytic. 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. Petrole 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.”


Gymnogramma baileyi Baker, Kew Bull. 64: 86. 1892. Colysis baileyi (Baker) Ching, Sunyatsenia 5: 261. 1940. Type: AUSTRALIA. Queensland, Bellenden Ker Range, 5200 ft, 1887, Sayer & Davidson 72 (K, barcode: K000959615, image!).

Plants hemiepiphytic or rarely terrestrial. Rhizome long-crawling, dorsiventrally flattened, with occasional cavities, not 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 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).


Plants hemiepiphytic or rarely terrestrial. Rhizome long-crawling, 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 & Vicker s.n. (US).—QUEENSLAND: Forster 7347 (CANB); Gray 2271 (CANB, image!); Jones 11621 (CANB).—NEW ZEALAND.—NORTH ISLAND: Forster 5048 (US); Walker 4394 (US); Walker 5175 (US).—SOUTH ISLAND: Brass 1845 (US); Brass 1849 (US).—WAIKATO: Wright 13450 (AK, image!).


Plants hemiepiphytic or rarely terrestrial. Rhizome long-crawling, 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 Hetterscheid (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**—Guillaumin & Baumann-Bodheim 8787 (US); Schmid 3413 (P, image!).—**South Province**—Baumann 5441 (US); El Raal 63 (P, image!); Mackee 12141 (P, image!); Veillon 7642 (P, image!). Unknown: Franc 1081 (P, image!); Veillon 1529 (P, image!); Veillard 1528 (B, image!).


**Plants** terrestrial, epiphytic, 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* novae-zealandiae
3. Plants from New Caledonia, sori submarginal, lamina of fertile leaves strongly contracted relative to sterile leaves ........ *Z. veillardi* novae-zealandiae
4. Plants from Australia, sori intramarginal, lamina of fertile leaves not or only weakly contracted relative to sterile leaves ........ *Z. pustulata* novae-zealandiae


**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); Braine s.n. (US); Cheeseman s.n. (US); Gardner 878 (CBG); Grace 1022 (US); Hutchinson s.n. (US); Sledge 176 (US).


**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, 2.5–5 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 lecaniopterid 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.
**Microsorum rubidium** (J. Sm.) Copel. and *Microsorum 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.**—RAUQONGA: 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.**—MOLUCAS: 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 & Jourdan 11465 (L, image!).—VaupeL 350 (AK, image!). **Solomon Islands.**—GUADALCANAL: Braithwaite 4720 (CBG). Vanuatu. Braithwaite 2397 (K, image!).


**Plants** terrestrial, epiphytic, or epiphyllous. **Rhizome** long-creeping, 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).


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

**Plants** epiphytic, rarely epiphyllous. **Rhizome** long-creeping, 5–10 mm in diameter, not 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** 15–30 cm long, not winged. **Leaves** simple or lobed on young plants and pinnatifid on mature plants, 30–75 cm long, 15–40 mm 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.—ILE OF PINES: Bernardi 9713 (US).—PROVINCE NOORD: Pigmal 5178 (P, image); Pigmal 5305 (P, image!).—PROVINCE SUD: Baumann 8274 (US); Francisco 330 (US); Guillaumin 7621 (US); Guillaumin 10335 (US); Guillaumin & Baumann 7735 (US).—UNKNOWN PROVINCE: Pancher 119 (US).

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Author Contributions

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

Literature Cited


Rambaut, A. 2009. FigTree, version 1.4.3. Computer program distributed by the author.


Appendix

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.