



Expansion of the fern genus *Lecanopteris* to encompass some species previously included in *Microsorium* and *Colysis* (*Polypodiaceae*)

L.R. Perrie^{1,*}, A.R. Field², D.J. Ohlsen³, P.J. Brownsey¹

Key words

Bosmania
Colysis
Dendroconche
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microsoroid
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Zealandia

Abstract The fern genus *Microsorium* is not monophyletic, with previous phylogenetic analyses finding three lineages to group not with the type species, but to form a grade related to the 13 species of *Lecanopteris*. These three lineages have recently been recognised as separate genera: *Bosmania*, *Dendroconche*, and *Zealandia*. Here, we explore the morphological characterisation of *Lecanopteris* and these other three lecanopteroid genera. While the traditional circumscription of *Lecanopteris* has seemed sacrosanct, its defining morphological character states of rhizome cavities and ant brooding associations occur in other lecanopteroid ferns and elsewhere in the *Polypodiaceae*. Instead, we suggest that the morphological characterisation of an expanded *Lecanopteris* including the *Dendroconche* and *Zealandia* lineages is just as good, if not better, with the pertinent character states being the absence of sclerenchyma strands in the rhizome and at least some fronds having Nootboom's type 5 venation pattern. This wider circumscription is also better able to accommodate phylogenetic uncertainty, and it means that groups of species traditionally placed together in a single genus are not distributed across different genera. General users familiar with the narrower circumscription of *Lecanopteris* will not be significantly disrupted, because there is little geographic overlap with the lineages added to the genus. Consequently, we make new combinations in *Lecanopteris* for 11 species and one subspecies.

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INTRODUCTION

The *Polypodiaceae* is one of the largest families of ferns (PPG I 2016) and is renowned for morphological homoplasy (Hovenkamp 1996, Ranker et al. 2004, He et al. 2018, Zhao et al. 2019). This is reflected in frequent changes to the circumscriptions of its constituent genera. One such example is *Microsorium* Link, which has variously been separated or amalgamated with allied genera (Hennipman et al. 1990, Bosman 1991, Nootboom 1997, Bostock & Spokes 1998, Brownsey & Perrie 2014). The circumscription adopted by PPG I (2016) for *Microsorium* included *Dendroconche* Copel., *Kaulinia* B.K.Nayar, and *Phymatosorus* Pic.Serm., and encompassed 40 species, compared with the 49 accepted by Nootboom (1997). Most species occur in Malesia and southern and eastern Asia, but they also extend to Africa, Australasia, and the Pacific Islands. PPG I (2016) acknowledged that their circumscription of *Microsorium* was not monophyletic, something that had been known since at least Schneider et al. (2004), and later reinforced by subsequent studies (e.g., Schneider et al. 2006, Kreier et al. 2008, Testo et al. 2019, Chen et al. 2020a). The problem, as summarised in Fig. 1, is that species of *Microsorium* fall in two principal parts of the phylogenetic trees resulting from analyses of chloroplast DNA sequences, with six clades named by

Chen et al. (2020a) as MG1–MG5 and 'core' (which includes *M. punctatum* (L.) Copel., the accepted name for the type species of *Microsorium*, *M. irregulare* Link). The first of the two main groups of *Microsorium* species includes the core, MG4, and MG5 clades, and forms a strongly supported clade with *Leptochilus* Kaulf. This group of *Microsorium* may be monophyletic (Testo et al. 2019), or it could be paraphyletic, with Chen et al. (2020a) finding the MG5 clade of *Microsorium* to be more closely related to *Leptochilus* than to their core and MG4 clades of *Microsorium*. The clade containing *Leptochilus* and these three clades of *Microsorium* is in turn sister to a clade including *Lepisorus* (J.Sm.) Ching, *Lemmaphyllum* C.Presl, and several other genera (Testo et al. 2019, Chen et al. 2020a).

The second main group of *Microsorium* includes about 15 species, along with two Australian species previously attributed to *Colysis* C.Presl (with other species from that genus now placed in *Leptochilus*). This second group is strongly supported as related to *Lecanopteris* Reinw. (Testo et al. 2019, Chen et al. 2020a). However, these lecanopteroid *Microsorium* (and *Colysis*) species are paraphyletic with respect to *Lecanopteris*, forming three successive sister groups. While the MG1 clade of *Microsorium* is sister to the rest, there are conflicting phylogenetic results for whether the MG2 clade (Testo et al. 2019) or the MG3 clade (Chen et al. 2020a) is most closely related to *Lecanopteris*.

Lecanopteris, as currently construed, comprises 13 species largely confined to Malesia, with one widespread species extending to Taiwan, Thailand, Cambodia, Vietnam, Australia, Vanuatu, and the Solomon Islands (Gay et al. 1994). All species are

¹ Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; corresponding author e-mail: leon.perrie@tepapa.govt.nz.

² Queensland Herbarium, Department of Environmental Sciences; Australian Tropical Herbarium, James Cook University, Cairns, Australia.

³ Royal Botanic Gardens Victoria, Melbourne, Australia.

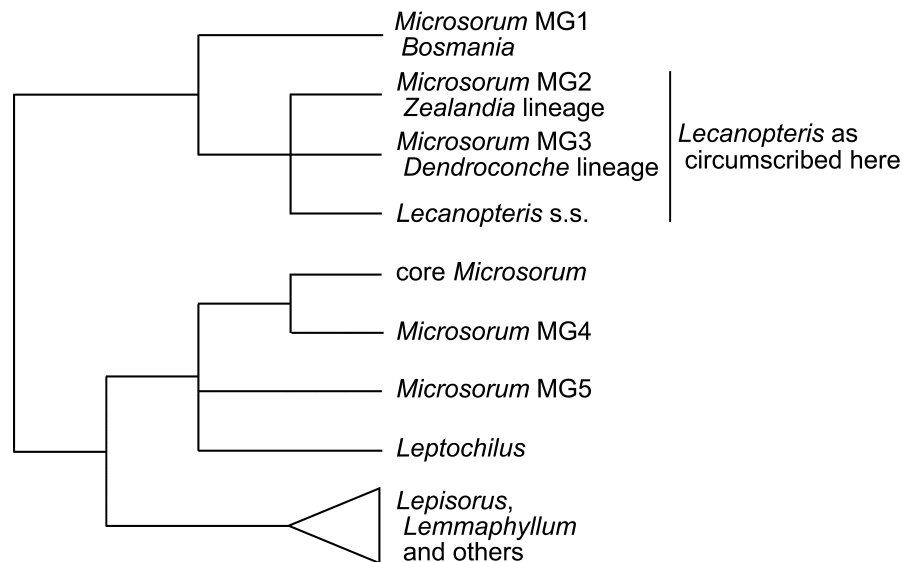


Fig. 1 Overview of phylogenetic relationships among *Microsorium* and its closest relatives, including *Lecanopteris*. Based on Testo et al. (2019) and Chen et al. (2020a). Only major branches that are well supported in both of these studies are shown as resolved.

associated with ant brooding. In *L. mirabilis* (C.Chr.) Copel., which is sister to the remainder of the species (Hauffer et al. 2003, Kreier et al. 2008, Testo et al. 2019), ants live under an expanded, arched rhizome. The other *Lecanopteris* species have hollow rhizomes in which ants live.

Producing a monophyletic classification for the lecanopteroid ferns can be achieved in several ways; Chen et al. (2020a) discussed three. Firstly, each of the four currently known lecanopteroid lineages could be treated as a genus, and this was implemented by Testo et al. (2019), who recognised *Bosmania* Testo (three species; the clade MG1 of Chen et al. 2020a), *Dendroconche* (eight species; MG3), and *Zealandia* Testo & A.R.Field (four species; MG2), alongside *Lecanopteris*. Secondly, the circumscription of *Lecanopteris* could be expanded to encompass the MG3 clade, since they are sisters in the analyses of Chen et al. (2020a), with separate generic names for each of MG1 and MG2. This, however, does not account for the uncertainty in the relationships among these clades, given the different results of Testo et al. (2019) and Chen et al. (2020a). Thirdly, *Lecanopteris* could be expanded to include both the MG2 and MG3 clades, with the MG1 clade treated as a separate genus (i.e., *Bosmania*). A fourth option would be to expand the circumscription of *Lecanopteris* to encompass all of the allied species formerly placed in *Microsorium* (i.e., the clades MG1, MG2, and MG3). Here we discuss the advantages and disadvantages for these different approaches, and provide the new combinations in *Lecanopteris* required for the third option.

DISCUSSION

Morphological characters

The phylogenies themselves do not provide a means to identify the best taxonomic option to deal with the polyphyly of *Microsorium* (other than the taxonomy needing to account for the uncertainty about which clade is sister to *Lecanopteris* sensu stricto (s.str.)). Other criteria are needed. From a morphological perspective, Testo et al. (2019) favoured the recognition of multiple genera because a broadly construed *Lecanopteris* would be 'morphologically incoherent'. Chen et al. (2020a) were cautious about an expanded *Lecanopteris* 'because it would be morphologically poorly defined'. However, while the current circumscription of *Lecanopteris* might seem sacrosanct, is it actually cohesive and well-defined?

Lecanopteris already includes one species, *L. mirabilis*, without rhizome cavities. Furthermore, the *Dendroconche* MG3 lineage, which may (Chen et al. 2020a) or may not (Testo et al. 2019) be sister to *Lecanopteris* s.str., includes two species with rhizome cavities, albeit small ones (Testo et al. 2019). Additionally, one of these species, *Colysis ampla* (Benth.) Copel., can 'harbor colonies of ants under its rhizomes' (Testo et al. 2019), indicating that myrmecophily is not restricted to *Lecanopteris* s.str. Ant brooding associations also occur elsewhere in the *Polypodiaceae*, including *Platycterium* Desv. (Franken & Roos 1982, Hennipman & Roos 1982, Ashley Field pers. obs.), and *Microgramma* C.Presl, where one lineage has chambered rhizomes while another species, in a separate lineage, has domed rhizomes (Almeida 2018, Almeida et al. 2021). Multiple gains of ant brooding associations, often involving subsequent multiple losses from a particular gain, are typical of other plant groups, with breakdowns of mutualisms apparently common (Gutiérrez-Valencia et al. 2017, Chomicki & Renner 2017).

Thus the two character states, rhizome cavities and ant brooding associations, commonly associated with *Lecanopteris* s.str. are not strictly diagnostic. Moreover, an absence of ant associations in some of the other lecanopteroid lineages may simply reflect a lack of ants. This may apply particularly to the *Zealandia* lineage, in which two of the four species occur in New Zealand (one endemic and one shared with Australia). If New Zealand has been the setting for at least some of the diversification of this lineage (which it appears to have been for some other groups of ferns; e.g., Perrie & Brownsey 2005, Del Rio et al. 2017), then this would have occurred in the context of a globally-remarkable depauperate ant fauna (MacFarlane et al. 2010). This is consistent with the loss of ant associations following long distance trans-oceanic dispersal, and shifts to increasing latitude and elevation reported in other groups of ant-plants (Chomicki & Renner 2017).

Lecanopteris s.str. is also strikingly morphologically variable in that some species bear their sori on remarkable marginal lobes, whereas others are impressed into the lamina (Gay et al. 1994, Hovenkamp 2013). Similarly, the segregate genera of Testo et al. (2019) are not as morphologically cohesive as they might appear. For instance, *Dendroconche* and *Zealandia* were distinguished from *Bosmania* by being 'rarely terrestrial'. However, *Microsorium scandens* (G.Forst.) Tindale (of the *Dendroconche* lineage) and *M. pustulatum* (G.Forst.) Copel.

(*Zealandia*), which are both widespread and prominent in eastern Australia and New Zealand, are both frequently terrestrial (Leon Perrie, Ashley Field, Daniel Ohlsen, Patrick Brownsey, pers. obs.). That also impacts the characterisation by Testo et al. (2019) of *Dendroconche* as ‘hemi-epiphytes’ and *Zealandia* as ‘mostly holo-epiphytes’. Furthermore, *Zealandia* was distinguished as having ‘typically pruinose’ rhizomes, with *M. powellii* (Baker) Copel. being the exception, but Testo et al. (2019) noted that, in *Dendroconche*, *M. scandens* sometimes has pruinose rhizomes. According to Nootboom (1997), pruinose rhizomes also occur in some species of *Microsorium* sensu lato (s.lat.) outside the lecanopteroid clade, including *M. scolopendria* (Burm.f.) Copel. and *M. steerei* (Harr.) Ching, which are, according to Chen et al. (2020a), in the core *Microsorium* clade, and *M. hainanense* Noot. in the MG5 clade, as well as several phylogenetically unplaced species. *Zealandia* was characterised by Testo et al. (2019) as having sori that are deeply impressed into the lamina. However, this is also a characteristic of species that have been placed in *Lecanopteris* subg. *Myrmecopteris* (Gay et al. 1994, Hovenkamp 2013), as well as many *Microsorium* species outside the lecanopteroid clade.

An expanded *Lecanopteris* could be equally as well-characterised morphologically as each of *Bosmania*, *Dendroconche*, and *Zealandia* have been; in fact, it could be even better, with fewer exceptions. Testo et al. (2019) stated that the absence of sclerenchyma strands in the rhizome was “a synapomorphy for the lecanopteroid ferns, with a single exception [*Microsorium powellii*] that frequently possesses them”. However, Nootboom (1997) indicated that sclerenchyma strands were present in the rhizomes of *M. lastii* (Baker) Tardieu, *M. leandrianum* Tardieu, and *M. membranaceum*, the three species that make up the *Bosmania* MG1 lineage. Nevertheless, an expanded *Lecanopteris* encompassing the *Dendroconche* MG3 and *Zealandia* MG2 lineages would have the morphological synapomorphy of no sclerenchyma strands in the rhizome with a single reversal in *M. powellii*. However, it is important to note that Nootboom (1997) recorded an absence of sclerenchyma strands in the rhizome from several species outside the lecanopteroid ferns, including *M. rubidum* (Kunze) Copel. of the MG5 clade (according to Chen et al. 2020a) and *M. palmatopedatum* (Baker) Noot., now better placed in *Lepisorus*, as well as several species unplaced phylogenetically. There were also occasional

absences in *M. insigne* (Blume) Copel. of the MG4 clade, and *M. superficiale* (Bedd.) Ching, now better placed in *Lepidomicrosorium* Ching & K.H.Shing.

Schneider et al. (2006) noted that most species of the lecanopteroid clade shared a frond venation pattern, which is presumably derived. In particular, Nootboom (1997) characterised the species now attributed to the *Dendroconche* MG3 and *Zealandia* MG2 lineages (but not the *Bosmania* MG1 lineage) as having his 5a or 5b type of venation (Fig. 2a). In type 5a, “connecting veins forming one row of large areoles parallel to the costa, bordered by the first connecting vein between each pair of veins and bordered by several smaller areoles; included venation variously anastomosing...”, while type 5b was “as type 5a, but the [main?] areoles smaller, [with] mostly the areoles outside the main areoles smaller, but not very much so”, and “5a and 5b may merge in each other” (Nootboom 1997). In this type 5 venation, in addition to the largest row of areoles being against the costa, there is not a more-or-less continuous and straight vein extending from the costa to near the lamina margin. In the other venation types found in species that have been attributed to *Microsorium*, either the row of areoles closest to the costa is narrow and bordered by much larger main areoles, or there is a main vein that runs more-or-less continuously in a straight line from the costa to near the margin, with all or most main areoles of a similar size (Fig. 2). Of note, *M. pustulatum* from the *Zealandia* MG2 lineages only shows a type 5 pattern in fertile fronds, and type 5 patterns were recorded for several species currently unplaced phylogenetically but which may be lecanopteroids. Nootboom (1997) recorded type 3 venation for *M. powellii* from the *Zealandia* MG2 lineage, and the three species that make up the *Bosmania* MG1 lineage as having types 1 or 4 venation. *Leptochilus minor* Fée and *L. pteropus* (Blume) Fraser-Jenk. were also recorded with type 5 venation (Nootboom 1997), so this character state is not absolutely diagnostic for the clade comprising *Lecanopteris* s.str. and the *Dendroconche* MG3 and *Zealandia* MG2 lineages.

Microsorium powellii, which occurs from the Moluccas and New Guinea through to French Polynesia and Pitcairn Island (Testo et al. 2019), deserves particular mention. Placed in the *Zealandia* lineage by Testo et al. (2019) with chloroplast DNA sequence data, it differs from its apparent relatives in several characters

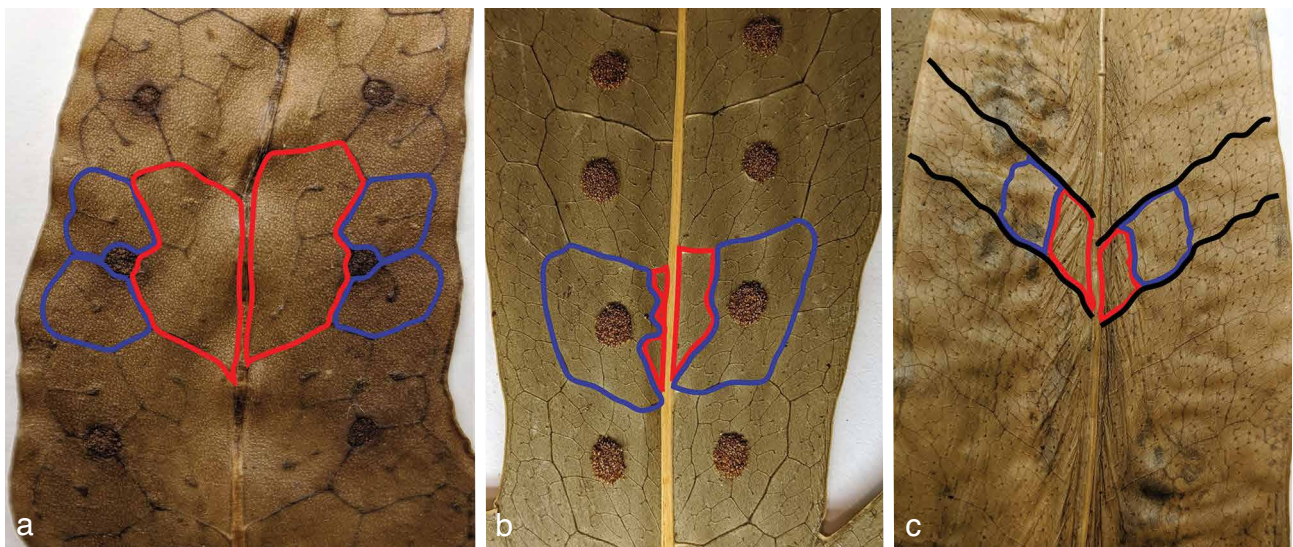


Fig. 2 Venation types in lecanopteroid and microsoroid ferns. a. *Lecanopteris pustulata* with the areole adjacent to costa (red outline) largest, bordered by smaller areoles (outlined in blue) toward the margin (= type 5 venation of Nootboom 1997); b. *Microsorium membranifolium* with the areole adjacent to costa (red outline) small and bordered by larger areoles (outlined in blue) toward the margin (= type 3 venation of Nootboom 1997); c. *Microsorium punctatum* with main veins running between the costa and margin (highlighted in black) forming a more or less straight line for most of its length (= type 1, 2 and 3 of Nootboom 1997) and with multiple similar sized areoles (e.g., those outlined in red and blue) formed within the main veins running between the costa and margin (= type 1 of Nootboom 1997).

as described above. However, with chloroplast DNA sequence data from a different sample, Chen et al. (2020b) recovered *M. powellii* as part of the core *Microsorium* clade which would reconcile these character differences. Nitta et al. (2018) recovered conflicting relationships for *M. powellii* among chloroplast loci and two nuclear loci. Testo et al. (2019) thought *M. powellii* might have a hybrid origin (i.e., between core *Microsorium* and the *Zealandia* lineage). They called for additional study (as did Chen et al. 2020b), but placed it in *Zealandia* 'for a lack of other appropriate options'. However, retaining it in *Microsorium* seems a viable provisional alternative, and this would leave the grouping of *Lecanopteris* s.str. and the *Dendroconche* MG3 and *Zealandia* MG2 lineages characterised by the venation and rhizome sclerenchyma states described above.

Morphology and identification

While an expanded *Lecanopteris* would be more heterogeneous, morphological heterogeneity per se is not a strong argument for one taxonomic option over another. As already mentioned, *Lecanopteris* s.str. and some of the segregate genera already exhibit considerable morphological diversity. A further example is the *Dendroconche* MG3 lineage that includes New Caledonia's *Microsorium latilobatum* Hennipman & Hett. and *M. varians* (Mett.) Hennipman & Hett. with reduced fertile fronds and acrostichoid sori. The morphological distinctiveness of this pair had them previously placed in *Christiopteris* Copel., until revised by Hennipman & Hetterscheid (1984). *Christiopteris* itself is now regarded as a synonym of *Drynaria* (Bory) J.Sm. The latter, now encompassing both *Christiopteris* s.str. and *Aglaomorpha* Schott (Christenhusz & Schneider 2012, Wilson 2016), well exemplifies the morphological diversity accepted in some *Polypodiaceae* genera for the sake of better reflecting phylogenetic relationships.

At a regional level, those familiar with *Lecanopteris* s.str. would experience very little change if it was expanded. Only four species from the *Bosmania* MG1, *Dendroconche* MG3, and *Zealandia* MG2 lineages overlap with the distribution of *Lecanopteris* s.str. These are *Microsorium membranaceum* (L.Don) Ching, *Dendroconche annabellae* (H.O.Forbes) Copel., *D. kingii* Copel., and *M. linguiforme* (Mett.) Copel., along with possibly some of the unplaced species below. Within the flora of a given country or region, these additional species should be able to be separated morphologically as easily as the cavity-less *L. mirabilis* already is. It is likely that this separation would be 'artificial', using characters that work locally but not necessarily globally, and appropriately pragmatic for providing means of identification that work efficiently at local scales. Moreover, regardless of the circumscription of *Lecanopteris* that is applied, because of the morphological homoplasy among this broader group of ferns, identification keys using practical field characters will have to deal with the likes of *Microsorium grossum* S.B.Andrews (of the core *Microsorium* clade) being superficially much more similar to the distantly related *M. pustulatum* than it is to the closely related but very different looking *M. punctatum*.

Stability and general users

A considerable advantage of an expanded *Lecanopteris* is that it is better able to accommodate phylogenetic uncertainty. There are many species that have been attributed to *Microsorium*, whose relationships have not actually been determined by phylogenetic analysis (Nootboom 1997, cf. Chen et al. 2020a). Testo et al. (2019) listed *M. cinctum* Bosman, *M. egregium* (Brause) Bosman, *M. longissimum* Fée, *M. rampans* (Baker) Parris, *M. rubidum* (Kunze) Copel., *M. samarense* (J.Sm.) Bosman, and *M. sibomense* Copel., all of Malesia, as unplaced but potentially related to the *Dendroconche* or *Zealandia* lineages. Chen et al. (2020a) showed that *M. rubidum* belonged to the MG5 clade

(i.e., not lecanopteroid), which agrees with the type 3 venation reported for this species (Nootboom 1997). Nootboom (1997) noted that *M. sibomense* had sclerenchyma strands in its rhizome and type 3 venation, suggesting that it too is not lecanopteroid. Of the others listed by Testo et al. (2019), plus a few more species of *Microsorium* s.lat. that have type 5 venation and no sclerenchyma strands (Nootboom 1997), if they are shown to indeed be lecanopteroid ferns, then they could easily be accommodated within an expanded *Lecanopteris*. Even then the number of species would be far from unwieldy. But in what is arguably a significant problem with the segregate classification, if any of the unplaced species did not fall within the already-identified lineages (as happened within this geographic region for some New Caledonian *Lastreopsis*; Gardner et al. 2017), then additional genera would be required. These too would inevitably be very small, alongside the current three species for *Bosmania*, eight for *Dendroconche*, and four for *Zealandia*.

Another advantage of an expanded *Lecanopteris* is that it may be better for general users of botanical names. While an expanded *Lecanopteris* would have little impact on present users of *Lecanopteris*, it would for the taxa needing transfer from *Microsorium* maintain a taxonomic connection between species that have traditionally been associated with one another. Given that a classification accepting only monophyletic genera requires name changes for the lecanopteroid ferns previously placed in *Microsorium*, it is probably better for general users of plant names that these be transferred to one genus (i.e., *Lecanopteris*) rather than dispersed across several. Especially pertinent examples are *M. pustulatum* (of the *Zealandia* MG2 lineage) and *M. scandens* (*Dendroconche* MG3) that are common, widespread, and often co-occur in south-eastern Australia and New Zealand, and New Caledonia's *M. latilobatum*, *M. varians* (both *Dendroconche* MG3) and *M. vieillardii* (*Zealandia* MG2).

Because of the merits of expanding the circumscription of *Lecanopteris*, we provide below the necessary new combinations for the lecanopteroid species previously placed in *Microsorium* or *Colysis* that have been shown to be part of the *Dendroconche* MG3 and *Zealandia* MG2 lineages. This broader circumscription of *Lecanopteris* is delimited by two character states documented by Nootboom (1997) and Schneider et al. (2006): the absence of sclerenchyma strands in the rhizome and at least some fronds with the type 5 venation pattern.

TAXONOMY

Lecanopteris Reinw.

Lecanopteris Reinw. (1825a) 48. — Type: *Lecanopteris carnososa* (Reinw.) Blume.

Onychium Reinw. (1825b) 2, nom. illeg., non Kaulf. (1820). — Type: *Onychium carnososa* Reinw. (= *Lecanopteris carnososa* (Reinw.) Blume).

Dendroconche Copel. (1911) 91. — Type: *Dendroconche annabellae* (H.O.Forbes) Copel. (= *Lecanopteris annabellae* (H.O.Forbes) Perrie & Brownsey, see below for new combination).

Myrmecopteris Pic.Serm. (1977) 239. — Type: *Myrmecopteris sinuosa* (Wall. ex Hook.) Pic.Serm. (= *Lecanopteris sinuosa* (Wall. ex Hook.) Copel.).

Zealandia Testo & A.R.Field in Testo et al. (2019) 749. — Type: *Zealandia pustulata* (G.Forst.) Testo & A.R.Field (= *Lecanopteris pustulata* (G.Forst.) Perrie & Brownsey, see below for new combination).

Epiphytic, rupestral or terrestrial ferns. *Rhizomes* long-creeping, terete or slightly dorsiventrally flattened, either lacking cavities or with hollow spaces inside or below often associated with ants, lacking sclerenchyma strands, pruinose or not, scaly or without scales or nearly so and spiny, sometimes also glandular hairy. *Rhizome scales* peltate, clathrate and occasionally marginally hyaline, orbicular to narrowly ovate, squarrose or appressed. *Fronds* monomorphic or occasionally dimorphic, articulated on short phyllopodia along the rhizome. *Laminae* undivided, variously lobed, or deeply 1-pinnatifid, herbaceous to coriaceous,

glabrous. *Veins* reticulate, in type 5a or 5b pattern (Nootboom 1997), forming one to several series of areoles between costa and lamina margin, lacking main lateral veins that extend in a more or less continuous and straight line from costa to near the margin; largest areoles adjacent to costa, with free included veinlets, ending in hydathodes. *Sori* round or slightly elongate, or rarely the sporangia acrostichoid; superficial, or immersed in the lamina and often bulging on the upper surface; arranged in one row at either side of the costa, or deeply immersed in marginal semi-circular projections; paraphyses present or rarely absent; exindusiate. *Spores* monolete, bilaterally symmetrical, finely rugulate to tuberculate, sometimes with twisted strands around the spore.

Distribution — 24 species, one with two subspecies, occurring mainly in Malesia and Australasia, but extending to Thailand, Cambodia, Vietnam, and some western Pacific Islands as eastward as Fiji.

Species accepted by Hennisman & Hovenkamp (1998) (specimens seen only as online images are indicated by *):

***Lecanopteris balgooyi* Hennisman**

Lecanopteris balgooyi Hennisman (1986) 783. — Type: *Hennisman 5650* (holo L 0051786*), Indonesia, C. Sulawesi, Sopo Valley, 27 May 1979.

***Lecanopteris carnosa* (Reinw.) Blume**

Lecanopteris carnosa (Reinw.) Blume (1828) 120. — *Onychium carnosum* Reinw. (1825b) 3. — Lectotype (designated by Hennisman & Hovenkamp 1998): *Reinwardt s.n.* (lecto L 0051788*), Indonesia, Celebes [Sulawesi].

***Lecanopteris celebica* Hennisman**

Lecanopteris celebica Hennisman in Hennisman & Verduyn (1987) 316. — Type: *Hennisman 5665* (holo L 0051790*), Indonesia, C. Sulawesi, Sopo Valley, 28 May 1979.

***Lecanopteris crustacea* Copel.**

Lecanopteris crustacea Copel. (1931) 406. — Type: *Burchard 158* (holo UC 391610*), Indonesia, Sumatra.

***Lecanopteris darnaedii* Hennisman**

Lecanopteris darnaedii Hennisman (1986) 785. — Type: *Hennisman 5322* (holo L, not seen; iso K 000638016*), Indonesia, C. Sulawesi, Mt Roroka Timbu, 13 May 1979.

***Lecanopteris deparioides* (Ces.) Baker**

Lecanopteris deparioides (Ces.) Baker (1881) 366. — *Davallia deparioides* Ces. (1876) 13, t. 4, f. 8. — Type: *Beccari s.n.* (FI 013631*), Sarawak, Mattang, 1866.

***Lecanopteris holttumii* Hennisman**

Lecanopteris holttumii Hennisman in Hennisman & Verduyn (1987) 317. — Type: *Lack & Grimes 1743* (holo K 000638152*), Indonesia, Sulawesi, Morgwali Province, Mt Tambusisi, 29 Mar. 1980.

***Lecanopteris lomarioides* (Kunze ex Mett.) Copel.**

Lecanopteris lomarioides (Kunze ex Mett.) Copel. (1929) 123. — *Polypodium lomarioides* Kunze ex Mett. (1856) 102, n. 192, t. 2, f. 18. — Lectotype (designated by Hennisman & Hovenkamp 1998): *Cuming 242* (lecto K 000638706*), Philippines, Luzon.

***Lecanopteris luzonensis* Hennisman**

Lecanopteris luzonensis Hennisman (1987) 311. — Type: *Hernaez (Hennisman 7820)* (U, not seen), Philippines, Luzon, Quezon Province, near Real.

***Lecanopteris mirabilis* (C. Chr.) Copel.**

Lecanopteris mirabilis (C. Chr.) Copel. (1929) 123 ('*mirabile*'). — *Polypodium mirabile* C. Chr. (1906) 545. — Type: *Karsten s.n.* (not viewed), Ambon.

***Lecanopteris pumila* Blume**

Lecanopteris pumila Blume (1851) pl. 94b. — Lectotype (designated by Hennisman & Hovenkamp 1998): pl. 94b in Blume (1851).

***Lecanopteris sinuosa* (Wall. ex Hook.) Copel.**

Lecanopteris sinuosa (Wall. ex Hook.) Copel. (1929) 123. — *Polypodium sinuosum* Wall. ex Hook. (1864) 61, t. 284. — Type: *Wallich 2231* (holo K-W K000637629*), Peninsular Malaya, Malacca.

***Lecanopteris spinosa* Jermy & T.G. Walker**

Lecanopteris spinosa Jermy & T.G. Walker (1975) 167. — Type: *Jermy 7609* (holo BM 001038419*), Indonesia, Sulawesi, Latimojong Mts, Mt Rantemario, 10 Nov. 1969.

New combinations:

Lecanopteris ampla* (F. Muell. ex Benth.) Perrie & Brownsey, *comb. nov.

Grammitis ampla F. Muell. ex Benth., Fl. Austral. 7 (1878) 777. — Lectotype (designated by Testo et al. 2019): *Dallachy s.n.* (lecto MEL 2166912*), Australia, Queensland, Rockingham Bay, 18 Aug. 1866.

Lecanopteris annabellae* (H.O. Forbes) Perrie & Brownsey, *comb. nov.

Polypodium annabellae H.O. Forbes, J. Bot. 26 (1888) 33, t. 280. — Lectotype (designated by Testo et al. 2019): *Hartmann 86* (lecto BM 000036777*), New Guinea, 1887.

Lecanopteris kingii* (Copel.) Perrie & Brownsey, *comb. nov.

Dendroconche kingii Copel., Univ. Calif. Publ. Bot. 12 (1931) 407. — Lectotype (designated by Testo et al. 2019): *King 387* (lecto MICH 1003428A*), Papua New Guinea, Mt Tuan, 1911.

Lecanopteris latilobata* (Hennisman & Hett.) Perrie & Brownsey, *comb. nov.

Acrostichum varians Mett. forma *major* Mett., Ann. Sci. Nat., Bot. Sér. 4, 15 (1861) 57. — *Microsorium latilobatum* Hennisman & Hett., Bot. Jahrb. Syst. 105 (1984) 6. — Type: *Vieillard 1528* (holo B 20-0054328*), New Caledonia, Poila.

Lecanopteris linguiformis* (Mett.) Perrie & Brownsey, *comb. nov.

Polypodium linguiforme Mett., Ann. Mus. Bot. Lugduno-Batavi 2 (1866) 228 ('*linguaeforme*'). — Lectotype (designated by Bosman 1991): *Zippelius s.n.* (lecto L 0051905*), New Guinea.

Lecanopteris novae-zealandiae* (Baker) Perrie & Brownsey, *comb. nov.

Polypodium novae-zealandiae Baker in Hooker, Icon. Pl. 17 (1886) t. 1674. — Lectotype (designated by Brownsey & Perrie 2012): *Cheeseman 361*, rec'd 5/77 (lecto K 000959805), New Zealand, Pirongia Mt, Upper Waikato District.

Lecanopteris pustulata* (G. Forst.) Perrie & Brownsey, *comb. nov.

Polypodium pustulatum G. Forst., Fl. Ins. Austr. (1786) 81. — Lectotype (designated by Pichi Sermolli 1951): *G. Forster s.n.* (lecto BM 000066256), New Zealand.

Lecanopteris pustulata (G.Forst.) Perrie & Brownsey subsp. ***howensis*** (Tindale & P.S.Green) Perrie & Brownsey, *comb. nov.*

Phymatosorus pustulatus (G.Forst.) Large, Braggins & P.S.Green subsp. *howensis* Tindale & P.S.Green in Green, Fl. Australia 49 (1994) 617. — Type: *Hoogland 8673* (holo NSW 536359*), Australia, Lord Howe Island, Transit Hill, 28 Oct. 1963.

Lecanopteris sayeri (F.Muell. & Baker) Perrie & Brownsey, *comb. nov.*

Gymnogramma sayeri F.Muell. & Baker, J. Bot. 25 (1887) 163. — Type: *Sayer & Davidson 72* (holo K 000959615*), Australia, Queensland, Bellenden Ker Range, 1887.

Lecanopteris scandens (G.Forst.) Perrie & Brownsey, *comb. nov.*

Polypodium scandens G.Forst., Fl. Ins. Austr. (1786) 81. — Lectotype (designated by Pichi Sermolli 1951): *G. Forster s.n.* (lecto BM 000066255), labelled Society Islands, but probably from New Zealand.

Lecanopteris varians (Mett.) Perrie & Brownsey, *comb. nov.*

Acrostichum varians Mett., Ann. Sci. Nat., Bot. Sér. 4, 15 (1861) 56. — Type: *Viellard 1526* (holo B, not seen, likely destroyed; isotype P 01545167*), New Caledonia, Poila.

Lecanopteris vieillardii (Mett.) Perrie & Brownsey, *comb. nov.*

Polypodium vieillardii Mett., Ann. Sci. Nat., Bot. Sér. 4, 15 (1861) 77. — Lectotype (designated by Brownlie 1969): *Viellard 1598* (P 0062684), New Caledonia, Balade, 1855–60.

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