Lucy Cranwell Memorial Lecture, 1st September 2015

Ferns: what we've learnt in the last 25 years

Introduction

It was an honour to give the 2015 Lucy Cranwell Lecture for the Auckland Botanical Society. I am following in Lucy's footsteps as a museum botanist; she was with the Auckland Museum between 1929 and 1944.

She was known as a botanical 'allrounder', which is something to which I aspire. But, for me, it was this quote about Lucy that transcended the temporal distance: "...any outing which included any of these people [including Lucy] was everlastingly being held up, because of rare plants" (by Dennis Brown, in Cameron 2000). Like many people who belong to botanical societies, I too am forever being distracted by "rare" plants (or simply those I've not seen frequently before). As it was for Lucy, our fascination with plants means they can never be mere scenery for a journey; rather they *are* the journey.

My research specialty is ferns. As it happens, this was the subject of the 1990 Lucy Cranwell Lecture, given by Patrick Brownsey on 8th October. Pat's title for his talk was "New Zealand ferns and allied plants – being a further contribution to making known the botany of New Zealand". The corresponding article was published in the Auckland Botanical Society journal (Brownsey 1991). Pat's subtitle is borrowed from the many papers of William Colenso, a 19th century botanist whose collections are prominent in the WELT herbarium, where Pat was then, and still is, based. However, what was then the National Museum of New Zealand has become Museum of New Zealand Te Papa Tongarewa.

Pat's 1990 Lucy Cranwell Lecture coincided with the 1989 publication of the book New Zealand ferns and allied plants (Brownsey & Smith-Dodsworth 1989). Pat authored this book, which also included photographs by John Smith-Dodsworth and line drawings by Tim Galloway. The scope was comprehensive, including all native and naturalised species of ferns and "allied plants" in New Zealand. For each species, there was a short description of its appearance, along with distribution and ecological details. For genera with five or more species, there was a key to the species. Included in the book's introduction was a primer for fern jargon, and a key to genera. An updated second edition was published in 2000 (Brownsey &

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Smith-Dodsworth 2000). These have been the definitive resources for understanding New Zealand's ferns and lycophytes over the last 25 years.

Pat's lecture was "an historical overview of the development of pteridology [the study of ferns and allied plants] in New Zealand". It included: the Linnean approach to classification; the initial scientific documentation of New Zealand's ferns in the 18th century by Joseph Banks, Daniel Solander, Johann and Georg Forster, and others; the continuation of this work in the 19th century by Joseph Hooker and William Colenso; the Victorian fern craze; the publications in the early 20th century by Herbert Dobbie and Thomas Cheeseman; and HH Allan's 1961 Volume 1 of the Flora of New Zealand. Also included were the techniques that had or were understanding revolutionising the of fern relationships, such as electron microscopy, cytology, and chemical analysis (but this did not extend to DNA sequencing).

With Pat as my mentor, and with his 1989 book and 1990 lecture as a baseline, it seemed opportune to use my Lucy Cranwell Lecture in 2015 to examine how our understanding of ferns had changed in the intervening quarter-of-a-century.

What is a fern?

One of the biggest changes in our understanding of ferns is actually in the circumscription of the term Traditionally, and in the 1989 book, the "fern"! genera Lvcopodium. Isoetes, Selaginella. Tmesipteris, Psilotum, and Equisetum were treated as "fern allies" - not ferns, but allied to them, in being vascular and seedless plants. However, analyses of DNA sequences and sperm morphology have demonstrated that Tmesipteris, Psilotum, and Equisetum (Fig. 1) are actually more closely related to ferns (Pryer et al. 2004), and most practitioners now include them in the circumscription of ferns. For instance, the closest extant relatives of Tmesipteris and Psilotum are in the family including Botrychium and Ophioglossum (who, I would argue, are not particularly fern-like, despite their historical connection with ferns). These, along with Equisetum and Marattia and its relatives form a eusporangiate (the spore capsules are thickwalled and have no specialised opening structure) assemblage of ferns. Their relationships to one



Fig. 1. *Tmesipteris horomaka, Psilotum nudum,* and *Equisetum hyemale* make for odd-looking ferns, but they are more closely related to ferns than they are to lycophytes or seed plants.

another remain uncertain but they sit alongside the leptosporangiate ferns (the spore capsules are thin-walled and have an annulus for opening) that include most extant fern diversity.

The remaining "fern allies" of *Lycopodium*, *Isoetes*, *Selaginella* and their immediate relatives, are now commonly referred to as "lycophytes" (or "lycopods"). This gives three major groups of land plants that have specialised vascular tissue for internal transport of water and nutrients: lycophytes, ferns, and seed plants. Significantly, despite lycophytes and ferns both being seedless, ferns are actually more closely related to seed plants than they are to lycophytes.

The number of species in New Zealand

The Brownsey & Smith-Dodsworth (1989) book listed 187 species of ferns and lycophytes indigenous to the New Zealand Botanical region. This included six species that were considered distinct but unnamed. For one of these, Nephrolepis flexuosa, an old name has been reinstated (de Lange et al. 2005), while four others have all been given new names: Blechnum novae-zelandiae, В. montanum, В. triangularifolium (Chambers & Farrant 1998a), and Pellaea calidirupium (Brownsey & Lovis 1990). The sixth, a putative species alongside Christella dentata, is no longer considered distinct (Brownsey & Perrie 2016a).

With ongoing investigation, the number of recognised species has continued to increase (Fig. 2). Brownsey and Perrie (2015) recognised 201 indigenous species of ferns and lycophytes for New

Zealand, comprising 188 fern species (89 endemic) and 13 lycophyte species (two endemic).

The change in species number between 1989 and 2015 included increases for several reasons. There described were newlv species: Asplenium *cimmeriorum* (Brownsey & de Lange 1997), (Perrie et al. Gleichenia inclusisora 2012), Hymenophyllum pluviatile (Perrie et al. 2013), Lastreopsis kermadecensis (Perrie & Brownsey 2012), and Tmesipteris horomaka (Perrie et al. 2010a). There were species first described from overseas but now accepted as also being indigenous to New Zealand: Notogrammitis gunnii (Parris 1998),

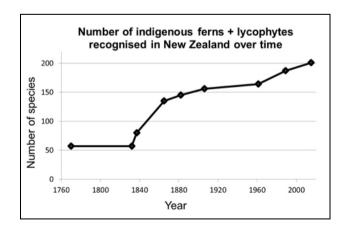


Fig. 2. The number of species of indigenous ferns and lycophytes recognised in New Zealand. Data from Solander (unpub.), Richard (1832), Cunningham (1837), Hooker (1867), Thomson (1882), Cheeseman (1906), Allan (1961), Brownsey & Smith-Dodsworth (1989), and Brownsey & Perrie (2015).

Sticherus tener, S. urceolatus (Brownsey et al. 2013), Trichomanes caudatum, Trichomanes humile, and Hymenophyllum polyanthos (Brownsey & Perrie 2016b); the latter two are known in New Zealand only from the Kermadec Islands. There were species with a revised status: Asplenium gracillimum, raised from *A. bulbiferum* subsp. *gracillimum*; *A. northlandicum*, raised from *A. obtusatum* subsp. northlandicum (Shepherd et al. 2008); Polystichum oculatum and P. wawranum reinstated from synonymy with what was called P. richardii (Perrie et al. 2003); and Gleichenia alpina reinstated from synonymy with G. dicarpa (Perrie et al. 2012). For those doing the sums, these increases in indigenous species have been offset by no longer considering the putative Christella as distinct and from no longer accepting Blechnum neohollandicum (was Doodia aspera) as being in New Zealand (Shepherd et al. 2007).

The discovery of additional indigenous species has not finished. For instance, the description of a new species of Asplenium is currently in press. We know or suspect that there are additional species in genera such as Asplenium, Gleichenia, Ophioglossum, and *Isoetes.* Some of these involve complexes that are difficult or even intractable with current analytical methods. And, while most of the recent increases in species numbers are the result of the resolution of long-standing taxonomic questions, it is also possible to find something completely unexpected. For instance, the recognition of Gleichenia inclusisora was completely novel (Perrie et al. 2012), even though its external appearance easily separates it (Fig. 3).

As an aside, there have also been two new subspecies in the last 25 years: *Davallia tasmanii* subsp. *cristata* (von Konrat et al. 2010), and *Dicksonia lanata* subsp. *hispida* which was raised from the varietal level (Brownsey & Perrie 2014).

Unfortunately, the number of naturalised or casual species has also increased from 22 species of ferns and lycophytes in Brownsey & Smith-Dodsworth (1989) to at least 52 species (Brownsey & Perrie 2015). Most of these exotics are only occasional escapes from cultivation, but continued observation is needed if we are to avoid the serious problems caused by the likes of *Selaginella kraussiana* and *Equisetum arvense*.

Name changes

Of the 201 indigenous species currently recognised, 145 (72%) had the same scientific name in New Zealand in 1989. Of the indigenous fern and lycophyte species recognised for New Zealand in 1989, 35 have experienced a change in either generic or specific epithet.

Change is a bane for users of scientific names. But change also reflects (1) a general desire to scientifically name organisms according to their relationships; and (2) that we are still learning how organisms are related to one another. For example, it seems that the kidney fern (Fig. 4) is actually more closely related to species of *Hymenophyllum* than it is to species of *Trichomanes* (meaning we prefer to call it *H. nephrophyllum* rather than *T. reniforme*). Because we do not know everything, change is inevitable as we learn more.



Fig. 3. From above, *Gleichenia inclusisora* resembles some of the other *Gleichenia* species in New Zealand. But look underneath and it is strikingly different, with large, orbicular scales (dark centres) and its sori (arrows) embedded in pits. Nevertheless, it was completely overlooked until recently. Scale bar = 1 mm.

Personally, I like to minimise taxonomic change while ensuring that the taxonomy reflects inferred relationships as closely as possible. I believe that each group formally recognised should include all of the species to which they are most closely related (the principle of monophyly). But deciding whether a particular monophyletic group should be ranked as, for example, a genus, subgenus, or family, is more contentious and, arguably, arbitrary. This is in part why we have not adopted suggestions that are about changing the rankings of groups. As examples, while we are comfortable with broadly-circumscribed Cyathea and Trichomanes, others prefer to divide them into multiple smaller segregates (Ebihara et al. 2006; Korall & Pryer 2014). Accepting these suggestions would have seen New Zealand's Cvathea species attributed to Alsophila or Sphaeropteris, and New Zealand's Trichomanes species attributed to Abrodictyum, Crepidomanes, and Polyphlebium.

Among the 35 species whose name has changed, the change for nine species involved the specific epithet (i.e., the second part of the scientific name). This was because:

1. New Zealand plants were found to be actually the same as a species from overseas: *Blechnum banksii* became *B. blechnoides* (Chambers & Farrant 1996), *Pilularia novae-zealandiae* became *P. novae-hollandiae* (Nagalingum et al. 2008), *Hymenophyllum atrovirens* became *H. australe* (Perrie et al. 2013); all three cases involved a loss of endemic status; or

2. New Zealand plants were determined to be actually different from a species overseas: *Hymenophyllum ferrugineum* became *H. frankliniae* (Ebihara et al. 2004), *Azolla filiculoides* became *A. rubra*; the former was a gain of an endemic species (Brownsey & Perrie 2013); or

3. An earlier name was found to apply: *Asplenium terrestre* became *A. appendiculatum* (Brownsey 1998), *Polystichum richardii* became *P. neozelandicum* (Perrie et al. 2003); or

4. There was a change in the species concept: *Cheilanthes humilis* became *C. sieberi* (Chambers & Farrant 1998), *Nephrolepis hirsutula* became *N. brownii* (Hovenkamp & Miyamoto 2005).

For a further 17 species, it was the generic epithet that changed. For example, when species moved genus from *Phymatosorus* to *Microsorum* (Nooteboom 1997), *Grammitis* and *Ctenopteris* to *Notogrammitis* (Perrie & Parris 2012), and *Lycopodium* to *Huperzia* or *Lycopodiella* (Chinnock 1998).

The remaining nine species had a change to both of their epithets! This included well known species such as *Doodia australis* becoming *Blechnum* *parrisiae* (Christenhusz et al. 2011), *Anarthropteris lanceolata* becoming *Loxogramme dictyopteris* (Kreier & Schneider 2006), and *Trichomanes reniforme* becoming *Hymenophyllum* nephrophyllum (Ebihara et al. 2006; Fig. 4). The reasons for these double-changes were often complicated. In the case of the latter example, the name *Hymenophyllum reniforme* is already in use for an American species, so the New Zealand kidney fern needed a new species epithet when it was transferred from *Trichomanes* to *Hymenophyllum*.



Fig. 4. The kidney fern is one of the species that has undergone a change in both its generic and specific epithets, from *Trichomanes reniforme* to *Hymenophyllum nephrophyllum*.

Above the species-level, New Zealand gained six genera with indigenous members. The newly (Murdock described Ptisana 2008) and Notogrammitis (Perrie & Parris 2012) include New Zealand species (previously attributed to Marattia, and to Ctenopteris and Grammitis, respectively), while Huperzia, Lycopodiella, Loxogramme, and Microsorum were accepted for New Zealand (for species previously attributed to Lycopodium, Lycopodium, Anarthropteris, and Phymatosorus, respectively; Chinnock 1998, Kreier & Schneider 2006, Nooteboom 1997). Conversely, six genera are no longer in use in New Zealand, with Marattia and Grammitis now used only for overseas species (Murdock 2008; Perrie & Parris 2012), while Phymatosorus, Ctenopteris, and Anarthropteris, *Doodia* are now treated as synonyms of Loxogramme, Microsorum, Prosaptia (which is not in New Zealand), and *Blechnum*, respectively (Kreier & Schneider 2006; Nooteboom 1997; Perrie & Parris 2012; Perrie et al. 2014).

Six additional families are recognised in New Zealand with indigenous members. This is not because of new species being discovered, but due to changes in the understanding of relationships, with Athyriaceae and Cystopteridaceae separated from Drvopteridaceae, Lindsaeaceae from Dennstaedtiaceae, Lomariopsidaceae and Tectariaceae from Davalliaceae, and Lygodiaceae from Schizaeaceae. Conversely, New Zealand lost a family, because Grammitidaceae is now treated as a synonym of Polypodiaceae (Smith et al. 2006; Rothfels et al. 2012).

That makes for a lot of change, and it might be asked whether it has finished or is slowing? The short answer is that more change is on the way, because there is still more to understand about the relationships of New Zealand's ferns and lycophytes. For example, for several species, including Asplenium polyodon, Hymenophyllum rarum, and Pellaea falcata, there are serious doubts about whether New Zealand populations are really the same species as overseas populations (and the name 'belongs' with the overseas populations, because that is where the name-bearing type specimen is from). Based on the rules of botanical nomenclature and the examination of the name-bearing type specimens, we have realised that the current applications of the names Asplenium northlandicum and A. richardii are wrong. We understand that the New Zealand species currently attributed to Microsorum do not belong there (Schneider et al. 2006), and the same goes for some of the New Zealand species currently attributed to Lastreopsis (Labiak et al. 2014), Hypolepis, and *Huperzia*. We think that *Leptolepia novae-zelandiae* should not be in a genus by itself, but it is currently unclear which genus is the best home for it (Perrie et al. 2015).

Relationships

Many, but not, all of the changes to scientific names and classification have involved analyses of DNA, especially DNA sequencing. Some of this work has been done in New Zealand, and some of it has been done overseas. Short fragments of DNA sequence have now been obtained for almost all of New Zealand's ferns and lycophytes. Analyses of these DNA sequence have provided a much greater understanding of the relationships among species. This has in turn been reflected in the changes to taxonomic classification summarised above.

But we have also been able to use analyses of DNA to understand more about the evolution of New Zealand's ferns. The focal group for us has been the Aspleniaceae. With the exception of five species (Asplenium flabellifolium, A. pauperequitum, A. polyodon, A. trichomanes, and Pleurosorus rutifolius), the indigenous Aspleniaceae form hybrids with one another (Perrie & Brownsey 2005). The hybrids are recognisable by their abnormally-formed spores and usually intermediate morphology. DNA sequencing indicates that these hybridising species are relatively closely related to one another (Perrie & Brownsey 2005).

Moreover, the set of hybridising Asplenium species includes tetraploids and octoploids (four and eight sets of chromosomes, respectively). It seems that most of the octoploids are so-called allopolyploids, with their speciation involving both chromosomal doubling (polyploidy) and hybridisation (Shepherd et al. 2008). The exception is A. richardii which appears to have evolved from A. hookerianum by chromosomal doubling alone. Some of the hybrid origins were unexpected, such as the involvement of A. hookerianum with A. flaccidum in the polyploid speciation of A. appendiculatum. Other combinations are, from gross morphology, more intuitive, such as A. bulbiferum and A. hookerianum being both involved in the ancestry of *A. gracillimum*. What was surprising was evidence that A. gracillimum has originated at least four times, and that these lineages sometimes co-occur without appreciable gene-flow among them (Perrie et al. 2010b). Evolutionarily, these lineages within A. gracillimum are 'behaving' as distinct species, but we cannot distinguish them by their appearances. Outside Asplenium, allopolyploidy also seems to have occurred in New Zealand Polystichum (Perrie et al. 2003) and Pteris.

Origins of New Zealand's ferns

Globally, ferns are an ancient group. Overseas studies combining analyses of fossils and DNA sequences suggest that ferns (including *Equisetum*) had evolved by about 400 million years ago (mya), the leptosporangiate ferns c. 300 mya, filmy ferns c. 170 mya, Pteridaceae c. 110 mya, tree ferns c. 100 mya, Polypodiaceae c. 50 mya, Aspleniaceae c. 50 mya, and Blechnaceae c. 30 mya (Rothfels et al. 2015). At least for the groups whose evolution predates the geological separation of New Zealand from the rest of Gondwana some 55-80 mya, it is interesting to ponder whether the species living today in New Zealand belong to lineages that have been here since the separation from Gondwana.

If New Zealand's ferns and lycophytes had been geographically isolated for that long period of time, we would expect them to be quite different from those found elsewhere. But they are not particularly different (Brownsey 2001). In fact, 110 of the fern and lycophyte species indigenous to New Zealand are, according to current circumscriptions, also indigenous to somewhere else in the world. Most of



Fig. 5. *Hymenophyllum sanguinolentum* (left), *H. scabrum* (centre), and *H. villosum* (right) are each other's closest relatives and all are only found in New Zealand.

that sharing involves 93 species that also occur in Australia (particularly the colder, damper southeast), while smaller numbers are shared with the Pacific Islands and further afield, e.g., Norfolk Island (24 species), Lord Howe Island (18), New Caledonia (30), Fiji (23), and Solomon Islands (15). (The numbers total more than 110 because many species occur in multiple countries.)

Analyses of DNA sequences from species with populations in New Zealand and elsewhere generally supports the close relationship inferred from morphology. Furthermore, even the many species endemic to New Zealand are generally closely related to a species from elsewhere or a species that New Zealand shares with elsewhere (e.g., Perrie & Brownsey 2007; Perrie et al. 2014; Ohlsen et al. 2014). These comparatively high genetic similarities and close relationships are not consistent with a long isolated evolution in New Zealand since its separation from Gondwana. Similarly, it is of note that the biggest wholly endemic radiations of extant ferns in New Zealand are two groups that amount to a mere three species each: Adiantum cunninghamii, A. fulvum and A. viridescens; and Hymenophyllum sanguinolentum, H. scabrum and H. villosum (Fig. 5).

My preferred explanation for the origins of New Zealand's ferns and lycophytes is that there has been a lot of interchange between the floras of New Zealand and elsewhere, with species regularly (on a geological scale) blowing into New Zealand (and out of New Zealand; more below). Fern spores are tiny (c. 0.04 mm long for an *Asplenium*), making them comparatively great dispersers and colonisers. This means that I think ferns and lycophytes have always

been present in New Zealand (because wherever there is unfrozen land, they will almost certainly reach it), but that the lineages present here 80 million years ago have not, for the most part, had an unbroken New Zealand-based genealogical connection to those here today.

It is important to appreciate that the interchange is bidirectional; species have also emigrated from New Zealand. For example, genetic analyses indicate that *Asplenium hookerianum* has twice dispersed westward from Australia (as well as twice eastward to the Chatham Islands; Shepherd et al. 2009; Perrie et al. 2010c). Long-distance dispersal can be relatively frequent. According to unpublished data of Daniel Ohlsen, *Asplenium flabellifolium* has dispersed across the Tasman Sea at least five times, with the pattern being too complicated to infer the directionality.

Hymenophyllum deserves special mention. It may have originated in New Zealand (and possibly the surrounding southwest Pacific) before dispersing more or less throughout the world, with some 250 species in 10 subgenera. This hypothesis is based on New Zealand being home to more subgenera – nine – than anywhere else. Two subgenera are endemic to New Zealand (both represented by a single species each, *H. nephrophyllum* and *H. dilatatum*). The only subgenus not in New Zealand comprises three species in South America and Madagascar (Ebihara et al. 2006).

Another lineage that may have had a long presence in New Zealand is that of *Loxsoma cunninghamii*. *Loxsoma* is the only fern genus

endemic to New Zealand (*Anarthropteris* has been synonymised with the widespread *Loxogramme*, *Cardiomanes* with the widespread *Hymenophyllum*, while *Leptolepia* belongs with a group presently attributed to *Dennstaedtia*; Kreier & Schneider 2006; Ebihara et al. 2006; Perrie et al. 2015). The single species, *Loxsoma cunninghamii*, is found only in the northern North Island. Its closest extant relative is in South America, and is separated by several tens of millions of years of evolutionary divergence (Pryer et al. 2004).

Nevertheless, most ferns and lycophytes in New Zealand clearly have close relatives overseas, with divergences post-dating New their Zealand's separation from Gondwana. Additionally, analyses indicate that for most families and genera of ferns and lycophytes, within each of these groups, the extant New Zealand species are evolutionarily subsets of the world's diversity. Combining these two observations means that most of New Zealand's extant ferns and lycophytes originate from immigrants arriving after New Zealand's separation from Gondwana (and this does not preclude some of these immigrants subsequently giving rise to emigrants that colonised elsewhere).

The Online Revolution

A huge societal change in the last 25 years has been the advent of the internet. Disseminating information online is relatively efficient, in terms of both production and access. Information about New Zealand's plants is now available from many online resources. The website of the New Zealand Plant Conservation Network (www.nzpcn.org.nz) is popular, with its illustrated species profiles as well as it holding digitised "species lists" for many areas. Distribution maps for species can be obtained from Zealand Virtual the New Herbarium (www.virtualherbarium.org.nz). These are assembled from databased specimens in New Zealand's herbaria. It is hoped that the current rudimentary implementation will be greatly improved.

A recent undertaking has been to revise the Flora of New Zealand series and publish it electronically (the so-called "eFloraNZ") – www.nzflora.info. Δ Flora is the definitive account of the vegetation in an area. Alongside the text expected in a Flora (e.g., nomenclature, description, habitat), the eFloraNZ includes distribution maps based on specimens whose identification has been verified bv experts, and colour images showina the important characteristics. Revisions are usually done on a family-by-family basis, and are published in two formats: webpages and pdfs. The latter are the definitive version, and are easily printed. I am helping Pat Brownsey to author eFloraNZ chapters for New Zealand's ferns. Visit

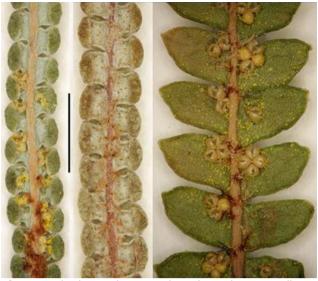


Fig. 6. *Gleichenia dicarpa* with scales only proximally on the alpha axes (left) and with scales extending along the alpha axes (centre; the scales are pale and may be hard to see, but they are obscuring the axis), and *G. microphylla* (right). Scale bar = 2 mm.

the following webpage to see what is currently available: www.nzflora.info/publications.html.

Another exciting online development are citizen science websites like NatureWatchNZ www.naturewatch.org.nz. If you would like help with identifying a plant (or anything living), you can upload photos to the website and see what the online community thinks. Participants are a mix of beginners and experts, and avocational or professional. If you upload photos of a fern to NatureWatchNZ, there is a good chance I will identify it for you (unless someone beats me to it). Expert users often provide identification tips, so it can be a good way to extend your botanical knowledge. Because observations are associated with locality details, NatureWatchNZ is also a good way of recording the presence of plants. In this regard, it offers advantages over traditional, written species lists because the photos allow for subsequent verification.

In this context, one of the fern questions I invite assistance with is understanding the morphological variation in Auckland's *Gleichenia dicarpa*. As detailed in the Gleicheniaceae chapter for the eFloraNZ (Perrie & Brownsey 2015), I think there are two entities within Auckland's *G. dicarpa*, along with hybrids with *G. microphylla* (Fig. 6). Photos uploaded to NatureWatchNZ that show clearly the underside of the fronds from *Gleichenia* plants in the northern North Island are welcomed.

Summary

The previous 25 years have seen a considerable increase in the understanding of New Zealand's ferns and lycophytes. Some of this has emanated

from work done overseas, and some in New Zealand. A substantial contribution has come from studies using analyses of DNA, a field of inquiry that was only in its infancy when Pat Brownsey gave his Lucy Cranwell Lecture in 1990.

My current research focus is on helping Pat Brownsey complete the eFloraNZ accounts for New Zealand's ferns and lycophytes. However, even when this is done, hopefully within the next several years, the understanding of New Zealand's ferns and lycophytes will not be complete; some taxonomic problems will remain, and name changes will be ongoing. This is in part because understanding New Zealand's species also requires understanding biodiversity elsewhere, especially the Pacific, and current resources are inadequate for that. Secondly, some taxonomic problems are intractable with current approaches (or effectively so, without enormous resourcing), and their resolution awaits methodological breakthroughs akin to that provided by the relativelysimple DNA analyses of the last quarter-of-a-century. In the meantime, there are plenty of opportunities for anyone interested to contribute to the further documentation of New Zealand's ferns and lycophytes.

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References

- Allan, H.H. 1961: *Flora of New Zealand*. Vol. 1. Indigenous Tracheophyta: Psilopsida, Lycopsida, Filicopsida, Gymnospermae, Dicotyledones. Government Printer Wellington.
- Brownsey, P.J. 1991: New Zealand ferns and allied plants being a further contribution to making known the botany of New Zealand. Auckland Botanical Society Journal 46: 38-60
- Brownsey, P.J. 1998: Aspleniaceae. Flora of Australia 48: 295-327.
- Brownsey, P.J. 2001: New Zealand's pteridophyte flora plants of ancient lineage but recent arrival? *Brittonia* 53: 284-303.
- Brownsey, P.J.; Lovis, J.D. 1990: Pellaea calidirupium a new fern species from New Zealand. New Zealand Journal of Botany 28: 197-205.
- Brownsey, P.J.; de Lange, P.J. 1997: Asplenium cimmeriorum, a new fern species from New Zealand. New Zealand Journal of Botany 35: 283-292.
- Brownsey, P.J.; Perrie, L.R. 2013: Azolla rubra revisited. New Zealand Botanical Society Newsletter 111: 6-7.
- Brownsey, P.J.; Perrie, L.R. 2014: Taxonomic notes on the New Zealand flora: recognition of two subspecies in *Dicksonia lanata. New Zealand Journal of Botany* 52: 343-351.
- Brownsey, P.J.; Perrie, L.R. 2015: *Te Papa's list of New Zealand ferns and lycophytes*. Updated 21 April 2015. Latest version available from http://collections.tepapa.govt.nz/Topic/3003
- Brownsey, P.J.; Perrie, L.R. 2016a: Re-evaluation of the taxonomic status of *Christella dentata* (Thelypteridaceae) supports recognition of one species in New Zealand. *Tuhinga* 27: 50-55.
- Brownsey, P.J., Perrie, L.R. 2016b: Hymenophyllaceae. In: Breitwieser, I.; Heenan, P.; Wilton, A. eds. *Flora of New Zealand Ferns and Lycophytes*. Fascicle 15. Manaaki Whenua Press, Lincoln
- Brownsey, P.J.; Smith-Dodsworth, J.C. 1989: New Zealand ferns and allied plants. David Bateman, Auckland.
- Brownsey, P.J.; Smith-Dodsworth, J.C. 2000: New Zealand ferns and allied plants. Edition 2. David Bateman, Auckland.
- Brownsey, P.J.; Ewans, R.; Rance, B.; Walls, S.; Perrie, L.R. 2013: A review of the fern genus *Sticherus* (Gleicheniaceae) in New Zealand with confirmation of two new species records. *New Zealand Journal of Botany* 51: 104-115.
- Cameron, E.K. 2000: Obituary. Lucy May Cranwell, MA, DSc, DSc(Hon), FLS(Lond.), FRSNZ, 1907-2000. New Zealand Journal of Botany 38: 527-535.
- Chambers, T.C.; Farrant, P.A. 1996: *Blechnum blechnoides* (Bory) Keys. (Blechnaceae), formerly *B. banksii* (Hook.f.) Mett. ex Diels, a fern from salt-spray habitats of New Zealand and Chile. *New Zealand Journal of Botany* 34: 441-445.
- Chambers, T.C.; Farrant, P.A. 1998a: The *Blechnum procerum* (*"capense"*) (Blechnaceae) complex in New Zealand. *New Zealand Journal of Botany* 36: 1-19.
- Chambers, T.C.; Farrant, P.A. 1998b: Cheilanthes. Flora of Australia 48: 271-286.
- Cheeseman, T.F. 1906: Manual of the New Zealand Flora. Government Printer, Wellington.
- Chinnock, R.J. 1998: Lycopodiaceae. *Flora of Australia* 48: 66-85.
- Christenhusz, M.; Zhang, X-C.; Schneider, H. 2011: A linear sequence of extant families and genera of lycophytes and ferns. *Phytotaxa* 19: 7-54.
- Cunningham, A. 1837: Florae insularum Novae Zelandiae precursor, or a specimen of the botany of the islands of New Zealand. *Companion to the Botanical Magazine* 2: 222-233, 327-336, 358-378.
- de Lange, P.J.; Gardner, R.O.; Sykes, W.R.; Crowcroft, G.M.; Cameron, E.K.; Stalker, F.; Christian, M.L.; Braggins, J.E. 2005: Vascular flora of Norfolk Island: some additions and taxonomic notes. *New Zealand Journal of Botany* 43: 563-596.
- Ebihara, A.; Hennequin, S.; Iwatsuki, K.; Bostock, P.D.; Matsumoto, S.; Jaman, R.; Dubuisson, J-Y.; Ito, M. 2004: Polyphyletic origin of *Microtrichomanes* (Prantl) Copel. (Hymenophyllaceae), with a revision of the species. *Taxon* 53: 935-948.
- Ebihara, A.; Dubuisson, J-Y.; Iwatsuki, K.; Hennequin, S.; Ito, M. 2006: A taxonomic revision of Hymenophyllaceae. Blumea 51: 221-280.
- Hooker, J.D. 1867: Handbook of the New Zealand flora. Reeve, London.
- Hovenkamp, P.H.; Miyamoto, F. 2005. A conspectus of the native and naturalized species of *Nephrolepis* (Nephrolepidaceae) in the world. *Blumea* 50: 279-322.
- Korall, P.; Pryer, K.M. 2014: Global biogeography of scaly tree ferns (Cyatheaceae): evidence for Gondwanan vicariance and limited transoceanic dispersal. *Journal of Biogeography* 41: 402-413.
- Kreier, H.P.; Schneider, H. 2006: Reinstatement of *Loxogramme dictyopteris*, based on phylogenetic evidence, for the New Zealand endemic fern, *Anarthropteris lanceolata* (Polypodiaceae, Polypodiidae). *Australian Systematic Botany* 19: 309-314.

Labiak, P.H.; Sundue, M.; Rouhan, G.; Moran, R.C. 2014: New combinations in *Lastreopsis* and *Parapolystichum* (Dryopteridaceae). *Brittonia* 67: 79-86.

Murdock, A. 2008: A taxonomic revision of the eusporangiate fern family Marattiaceae, with description of a new genus *Ptisana. Taxon* 57: 737-755.

Nagalingum, N.S.; Nowak, M.D.; Pryer, K.M. 2008: Assessing phylogenetic relationships in extant heterosporous ferns (Salviniales), with a focus on *Pilularia* and *Salvinia. Botanical Journal of the Linnean Society* 157: 673-685.

Nooteboom, H.P. 1997: The microsoroid ferns (Polypodiceae). *Blumea* 42: 261-395.

Ohlsen, D.J.; Perrie, L.R.; Shepherd, L.D.; Brownsey, P.J.; Bayly, M.J. 2014: Phylogeny of the fern family Aspleniaceae in Australasia and the south-west Pacific. *Australian Systematic Botany* 27: 355-371

Parris, B.S. 1998: Grammitidaceae. Flora of Australia 48: 450-468.

- Perrie, L.R.; Brownsey, P.J. 2005: Insights into the Biogeography and Polyploid Evolution of New Zealand *Asplenium* from Chloroplast DNA Sequence Data. *American Fern Journal* 95: 1-21.
- Perrie, L.R.; Brownsey, P.J. 2007: Molecular evidence for long-distance dispersal in the New Zealand pteridophyte flora. *Journal of Biogeography* 34: 2028-2038.
- Perrie, L.R.; Brownsey, P.J. 2012: *Lastreopsis kermadecensis*, a new fern species from Raoul Island in the Kermadec Islands, New Zealand, with notes on *L. pacifica. New Zealand Journal of Botany* 50: 29-36.
- Perrie LR Brownsey PJ. 2015: Gleicheniaceae. In: Breitwieser I, Heenan P, Wilton A, eds. *Flora of New Zealand Ferns and Lycophytes.* Fascicle 12. Manaaki Whenua Press, Lincoln.
- Perrie, L.R.; Parris, B.S. 2012: Chloroplast DNA sequences indicate the grammitid ferns (Polypodiaceae) in New Zealand belong to a single clade, *Notogrammitis* gen. nov. *New Zealand Journal of Botany* 50: 457-472.
- Perrie, L.R.; Brownsey, P.J.; Lockhart, P.J.; Large, M.F. 2003: Evidence for an allopolyploid complex in New Zealand *Polystichum* (Dryopteridaceae). *New Zealand Journal of Botany* 41: 189-215.
- Perrie, L.R.; Brownsey, P.J.; Lovis, J.D. 2010a: *Tmesipteris horomaka*, a new octoploid species from Banks Peninsula. *New Zealand Journal of Botany* 48: 15-29.
- Perrie, L.R.; Shepherd, L.D.; de Lange, P.J.; Brownsey, P.J. 2010b: Parallel polyploid speciation: distinct sympatric gene-pools of recurrently derived allo-octoploid Asplenium ferns. *Molecular Ecology* 19: 2916-2932
- Perrie, L.R.; Ohlsen, D.J.; Shepherd, L.D.; Garrett, M.; Brownsey, P.J.; Bayly, M.J. 2010c: Tasmanian and Victorian populations of the Australasian fern *Asplenium hookerianum* result from independent dispersals from New Zealand. *Australian Systematic Botany* 23:387-392.
- Perrie, L.R.; Shepherd, L.D.; Brownsey, P.J. 2012: *Gleichenia inclusisora*, a new and uncommon tangle fern from New Zealand. New Zealand Journal of Botany 50: 401-410.
- Perrie, L.R.; Shepherd, L.D.; de Lange, P.J.; Batty, E.L.; Ohlsen, D.J.; Bayly, M.J.; Brownsey, P.J. 2013: *Hymenophyllum pluviatile*, a new and uncommon fern from New Zealand. *New Zealand Journal of Botany* 51: 308-320.
- Perrie, L.R.; Wilson, R.K.; Shepherd, L.D.; Ohlsen, D.J.; Batty, E.L.; Brownsey, P.J.; Bayly, M.J. 2014: Molecular phylogenetics and generic taxonomy of Blechnaceae ferns. *Taxon* 63: 745-758.
- Perrie, L.R.; Shepherd, L.D.; Brownsey, P.J. 2015: An expanded phylogeny of the Dennstaedtiaceae ferns: *Oenotrichia* falls within a nonmonophyletic Dennstaedtia, and *Saccoloma* is polyphyletic. *Australian Systematic Botany* 28: 256-264.
- Pryer, K.M.; Schuettpelz, E.; Wolf, P.G.; Schneider, H.; Smith, A.R.; Cranfill, R. 2004: Phylogeny and evolution of ferns (monilophytes) with a focus on the early leptosporangiate divergences. *American Journal of Botany* 91: 1582-1598.
- Richard, A. 1832: *Essai d'une Flora de la Nouvelle Zélande*. In: Lesson, A.; Richard, A. *Botanique*. In: Dumont d'Urville, J. *Voyage de Découvertes de l'Astrolabe*. Tastu, Paris. Pp. [1]-376.
- Rothfels, C.J.; Sundue, M.A.; Kuo, L-Y.; Larsson, A.; Kato, M.; Schuettpelz, E.; Pryer, K.M. 2012. A revised family-level classification for eupolypod II ferns (Polypodiidae: Polypodiales). *Taxon* 61: 515-533.
- Rothfels, C.J.; Li, F-W.; Sigel, E.M.; Hiet, L.; Larsson, A.; et al. 2015: The evolutionary history of ferns inferred from 25 low-copy nuclear genes. *American Journal of Botany* 102: 1089-1107.
- Schneider, H.; Kreier, H-P.; Perrie, L.R.; Brownsey, P.J. 2006: The relationships of *Microsorum* (Polypodiaceae) species occurring in New Zealand. *New Zealand Journal of Botany* 44: 121-127.
- Shepherd, L.D.; Perrie, L.R.; Parris, B.S.; Brownsey, P.J. 2007: A molecular phylogeny for the New Zealand Blechnaceae ferns from analyses of chloroplast trnL-trnF DNA sequences. *New Zealand Journal of Botany* 45: 67-80
- Shepherd, L.D.; Perrie, L.R.; Brownsey, P.J. 2008: Low-copy nuclear DNA sequences reveal a predominance of allopolyploids in a New Zealand *Asplenium* fern complex. *Molecular Phylogenetics and Evolution* 49: 240-248
- Shepherd, L.D.; de Lange, P.J.; Perrie, L.R. 2009: Multiple colonizations of a remote oceanic archipelago by one species: how common is long-distance dispersal? *Journal of Biogeography* 36: 1972-1977.
- Smith, A.R.; Pryer, K.M.; Schuettpelz, E.; Korall, P.; Schneider, H.; Wolf, P.G. 2006: A classification for extant ferns. Taxon 55: 705-731.
- Solander, D.C. *Primitiae Florae Novae Zelandiae*. Unpublished manuscript based on collections made in New Zealand 1769-1770, held at Natural History Museum, London (photocopy at Museum of New Zealand Te Papa Tongarewa).

Thomson, G.M. 1882: The ferns and fern allies of New Zealand. Robertson, Melbourne.

von Konrat, M.J.; Braggins, J.E.; de Lange, P.J. 2010: *Davallia* (Pteridophyta) in New Zealand, including description of a new subspecies of *D. tasmanii. New Zealand Journal of Botany* 37: 579-593.