

NEW ZEALAND FERNS AND ALLIED PLANTS
- BEING A FURTHER CONTRIBUTION TO MAKING KNOWN THE
BOTANY OF NEW ZEALAND

(THE LUCY CRANWELL LECTURE 1990)

given by Dr Patrick Brownsey on 8 October 1990

at the University of Auckland

New Zealand Ferns and Allied Plants (Brownsey & Smith-Dodsworth 1989) was published in December 1989, and provides the first comprehensive account of the New Zealand fern flora including not only the native species but also the fern allies and adventive species. For each species there is a description, together with notes on distribution, habitat preferences, important field recognition characters, and a list of Latin, Maori and English names. Every one of the species is illustrated, almost all of them in colour. The book therefore breaks new ground in several respects and has been described as the definitive work on New Zealand ferns.

It is important, however, that it should not be regarded as the final word. Taxonomy, like other sciences, is a dynamic subject. People's ideas and interpretations change; new taxa are constantly being discovered; and new technologies are bringing new insights to the discipline. Hence, any Flora, whether aimed at the professional botanist or the lay person, is only a statement in time of the author's interpretation of the plants of one particular region, and it is a mistake to believe that such a work is ever going to be "the last word" on the subject.

A Flora should build on earlier work and hopefully make significant advances in critical areas. However, it shouldn't attempt to answer all the questions because it either won't get finished, or will provide only very superficial answers. It shouldn't be afraid to admit ignorance where the answer isn't known, but rather, should highlight areas of difficulty or uncertainty so that these can be picked up and worked on by others.

By the same token, taxonomists shouldn't be afraid to make mistakes, or to change their minds. I am not, of course, advocating sloppy work, but I think it is in everyone's interests for taxonomists to publish as frequently as possible so that their work is readily available to those working in other disciplines. It is much more efficient to get 80% of the answer after 5 years work, rather than waiting 20 years to get 95% of the answer. The feedback one gets from publishing the bulk of a revisionary work is far more beneficial than the diminishing returns that come from continuing to study a group for too long. It should always be remembered that the "final word" is a very elusive quality!

The corollary of this is that taxonomists shouldn't be too heavily criticised for changing their minds, providing, of course, that they make sound judgements based on the available evidence. Changing one's mind in the light of new information is, in my view, not a fault at all.

On the other hand, I do believe that taxonomists have an obligation to abide by the Rules of Botanical Nomenclature and should obey not only the letter of the law, but also the spirit. In particular, I am concerned about the proliferation of tag names. Informal publication of checklists, and lists of key characters for recognising undescribed taxa, have their place, but I am certain that the formal publication of tag names will cause us untold difficulties in the future. In saying this, I am aware that my own track record is not perfect, but, with a little more effort, we could often publish valid names rather than merely attach tag names to taxa identified by a list of diagnostic characters.

I also feel quite strongly that taxonomy should be essentially practical. If it is to serve the needs of biologists in other disciplines, it must be user-friendly. Unfortunately, nature is not always so benevolent, and often there is a conflict between what one can recognise in the field without the benefit of modern technology, and what one knows to be actual genetic entities. This is probably more of a problem in zoology where cryptic species are being recognised increasingly frequently, but there are also specific examples in the fern world which I will refer to later.

These views have influenced my approach to taxonomy, and they will be evident to the discerning reader of *New Zealand Ferns and Allied Plants*. However, my work has been much more influenced by the views of earlier botanists and, in the remainder of this talk, I want to provide an historical overview of the development of pteridology in New Zealand.

THE EARLY EXPLORATIVE PERIOD (1769-1867)

Carl Linnaeus

New Zealand pteridology really begins with the publication of *Species Plantarum* by Carl Linnaeus in 1753 where the binomial system, upon which our Code of Botanical Nomenclature is still based, was first proposed. The New Zealand flora includes several fern species first described by Linnaeus. However, in 1753 New Zealand was scarcely known to the European world and certainly no plant collections had been made from here. Linnaeus's names were based on specimens from other parts of the world; *Psilotum nudum*, *Lycopodium cernuum* and *Schizaea dichotoma*, for example, are all common tropical species. Others, such as *Botrychium lunaria*, *Anogramma leptophylla* and *Asplenium trichomanes*, are common European species, but the question today is whether our New Zealand representatives are really identical to their European counterparts, especially those which occupy rather different habitats.

Joseph Banks and Daniel Solander

The first European collections of New Zealand plants were made by Banks and Solander on Cook's first voyage to New Zealand in 1769. Hundreds of specimens were taken back to England and are now housed in the Natural History Museum, London, although duplicate sets have since been distributed to both the Auckland Museum and the National Museum in Wellington. Solander compiled fulsome descriptions of 57 species of ferns, and plates of 22 species were prepared by a variety of artists and engravers from Sydney Parkinson's sketches. Sadly, however, the proposed *Primitiae Florae Novae Zealandiae* was never published and has remained in manuscript form at the Natural History Museum ever since. This was a tragedy for New Zealand botany since the descriptions were excellent, the plates superb and the specimens well preserved and documented. Most of the species were eventually recognised and described by later authors but at least one fern, *Hypolepis lactea* (Fig. 1), remained un-named for over 200 years until the genus was revised by Brownsey & Chinnock (1984).

J.R. & J.G. Forster

The first published descriptions of New Zealand ferns appeared in two small books, *Florulae Insularum Australium Prodrromus* (Fig. 2) and *De Plantis Esculentis Insularum Oceani Australis*, both published in 1786 by George Forster, based on collections made during Cook's second voyage. In stark contrast to the work of Banks and Solander, Forster's two-line descriptions are totally inadequate, there are no illustrations, the locality details are frequently non-existent or wrong, and the specimens themselves are now widely dispersed, making the task of typification an exacting one. Some common and widespread species, (e.g. *Asplenium polyodon*), are unsupported by extant type specimens, and their identity is based solely on historical tradition.

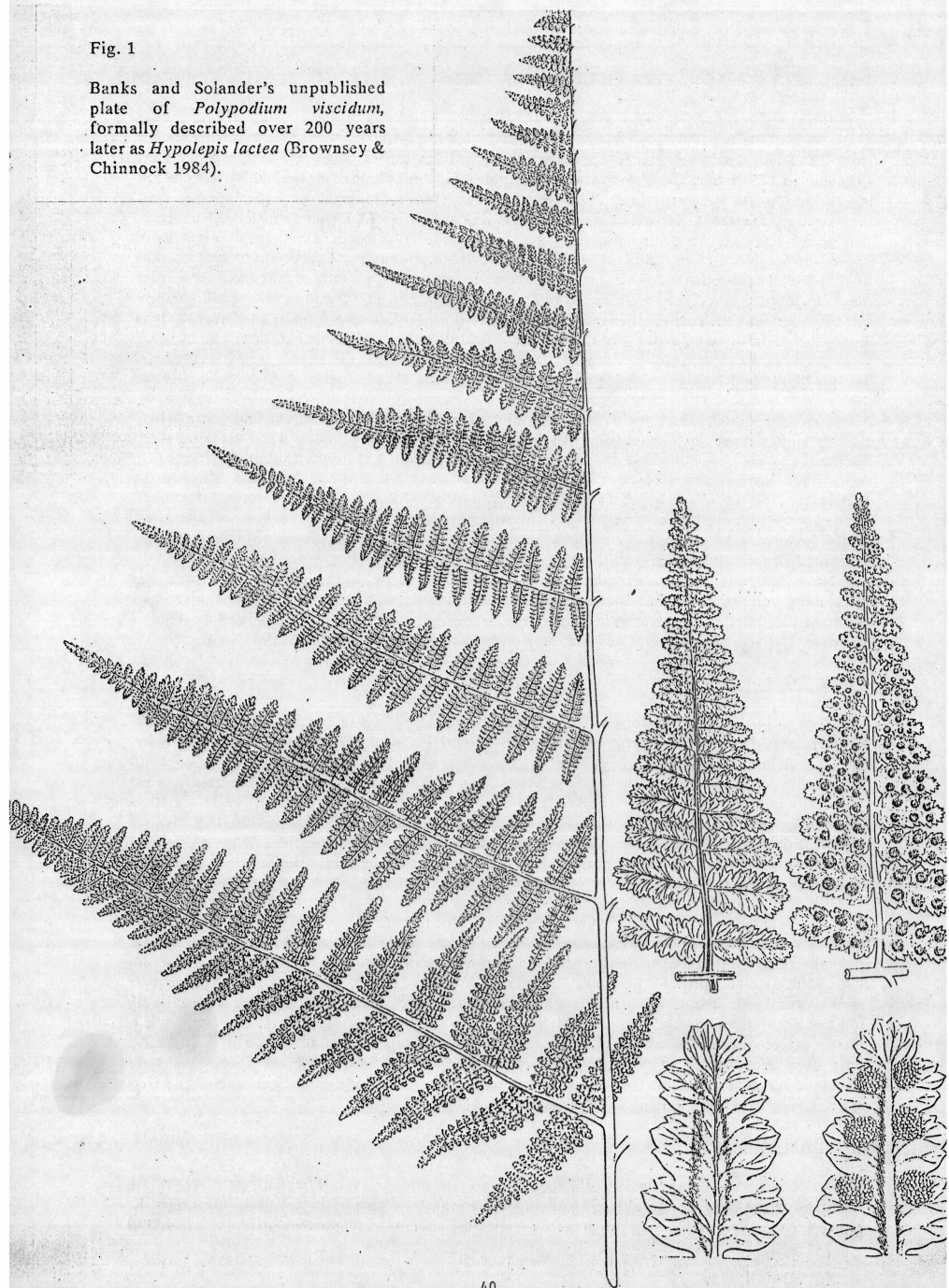
However, material collected by the Forsters did provide the basis for what is probably the first published illustration of a New Zealand pteridophyte (Fig. 3), the plate of *Tmesipteris tannensis* published in Schrader's *Journal für die Botanik* for 1800 (Bernhardi 1801). Ironically, the species was stated by the Forsters to have come from the island of Tanna in Vanuatu, from which the specific epithet is derived. However, Chinnock (1976a), has shown that *Tmesipteris* is only known on Tanna from higher parts of the volcanic peak, an area which was unlikely to have been visited by the Forsters because the volcano was erupting at the time of their visit. Furthermore, plants resembling *T. tannensis* have never been collected there since, and have only ever been found in New Zealand. It is much more likely that the specimens were collected by the Forsters at Dusky Sound where *T. tannensis* would have been one of the first species they saw after getting off the boat.

Archibald Menzies

Dusky Sound was also the main collecting ground for another early fern collector, Archibald Menzies, who visited the area in 1791 during Vancouver's voyage of exploration. Amongst the many ferns collected by Menzies were new species, such as *Trichomanes strictum*, as well as

Fig. 1

Banks and Solander's unpublished plate of *Polypodium viscidum*, formally described over 200 years later as *Hypolepis lactea* (Brownsey & Chinnock 1984).



FLORVLAE
INSVLARVM AVSTRALIVM
PRODROMVS

AUCTORE

GEORGIO FORSTER M. D.

SERENISSIMO REGI. POLONIAE A CONSILIIS INTIMIS
HISTORIAE NATVRAE ET BOTANICES IN ACADEMIA
VILNENSI. P. P. O. ACADEMIAE CAESARAE NATVRAE
CVRIOSORVM REGIAE MEDICAE MADRITENSIS
REGIAE SOCIETATVM SCIENTIARVM LONDINENSIS
ET HAVNIENSIS SOCIETATVM ANTIQVITATVM ET REI
AGRARIAE QVAE CASSELLIS SVNT REI AGRARIAE
CELLENENSIS ET NATVRAE SCRVTATOR. BEROLINENSIS
SODALI NEC NON REGIIS SOCIETATIB. GOTTINGENSI
SCIENTIARVM ET PARISIENAE REI AGRARIAE
LITTERARVM COMMERCIO CONIVNCTO.



GOTTINGAE

TYPIS JOANN. CHRISTIAN. DIETERICH.

•MDCCLXXXVI.

Fig. 2 The title page of Foster's *Prodromus* which contains the first published descriptions of New Zealand ferns.

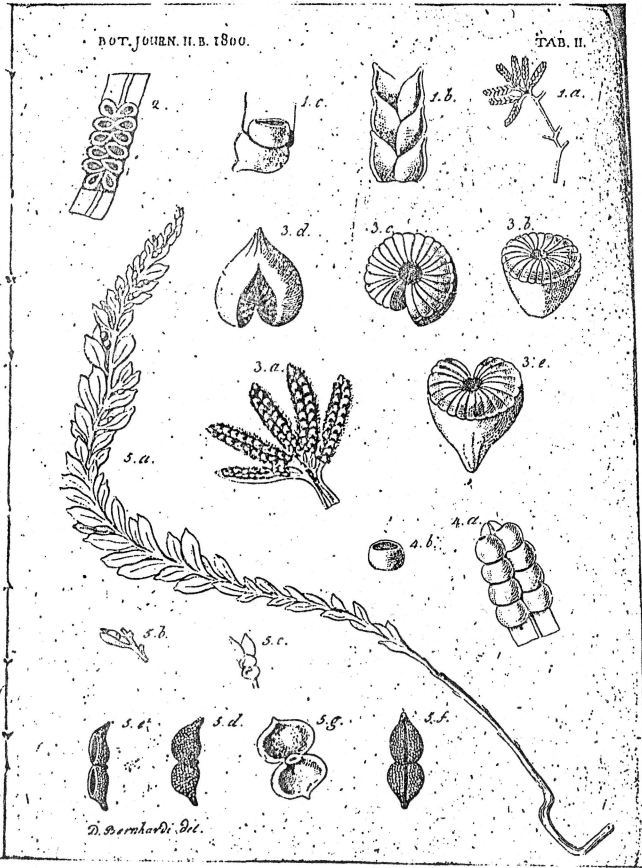


Fig. 3 Bernhardt's plate of *Tmesipteris tannensis*, probably the first published illustration of a New Zealand pteridophyte.

other more familiar species from Cook's voyages. These were written up in the lavishly produced *Icones Filicum* (Hooker & Greville 1831) where the first published illustration of the world-renowned kidney fern, *Cardiomanes reniforme*, can be found.

J.J. de Labillardière and Robert Brown

The impetus for further work on the New Zealand fern flora during the early 19th Century came from the publication of two books on the plants of Australia, *Novae Hollandiae Plantarum Specimen* (Labillardière 1806) and *Prodromus Florae Novae Hollandiae* (Brown 1810). Based respectively on Australian collections made during the voyages of D'Entrecasteaux and Flinders, both books describe a great many ferns which are now known to be common to the two countries. A few species, such as *Schizaea fistulosa*, *Hymenophyllum cupressiforme* and *H. flabellatum* were illustrated for the first time by Labillardière (Fig. 4).

Achille Richard

The first attempt to produce a compilation of New Zealand ferns was made by a Frenchman, Achille Richard (1832), in his *Essai d'une Flore de la Nouvelle Zélande* (Fig. 5). Richard himself never visited New Zealand and his list of some 57 species of ferns was based on material collected by Dumont D'Urville and Lesson during the voyages of Duperrey in 1824 and Dumont D'Urville in 1827. It did not include all the species collected on the earlier British voyages and is therefore not a complete record of the known species at that time. Nevertheless it does provide beautiful illustrations of Richard's newly described *Hymenophyllum scabrum* and *H. minimum*.

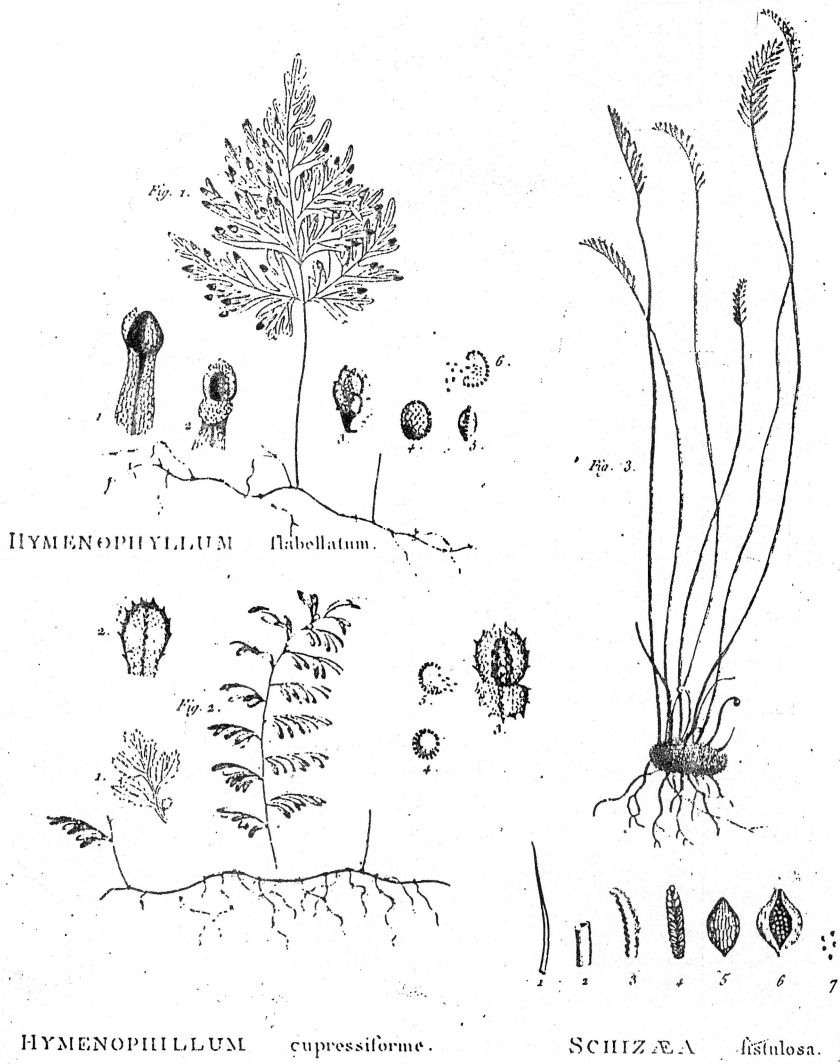
William Colenso

The first of the long-term resident botanists to contribute to an understanding of the New Zealand fern flora was the missionary, William Colenso. He described 33 new species in two papers in the short-lived *Tasmanian Journal of Natural Sciences* (Colenso 1842, 1846) from collections made during his remarkable journey from East Cape through the Ureweras to Rotorua, Auckland and the Bay of Islands. Many of his specimens were sent to W.J. Hooker at Kew and illustrated in *Icones Plantarum*. Colenso described a great many more fern species after his time as a missionary, but most of these have not stood the test of time.

Joseph Hooker

New Zealand botany in the middle of the 19th Century was unquestionably dominated by Joseph Hooker (Fig. 6), destined to succeed his father William Hooker as Director of Kew Gardens in London. He visited New Zealand during the Antarctic voyage of James Clark Ross (1839-1843) and met Colenso at the Bay of Islands in 1841. A whole series of publications resulted from this trip, including *Flora Antarctica* (Hooker 1844), *Flora Novae-Zelandiae* (Hooker 1855) and *Flora Tasmaniae* (Hooker 1860). A great many new species were described in these volumes based on Hooker's own collections, and on those of a number of resident botanists, including Colenso, Sinclair, Monro and many others. All the volumes are beautifully illustrated by Walter Fitch, but unfortunately include rather few ferns. Later, Hooker combined all the work on the New Zealand flora into a single volume, the *Handbook of the New Zealand Flora* (Hooker 1867), incorporating new information which had come to light in the intervening years.

Hooker's work really set New Zealand botany on its feet and rescued it from the shaky start that it had had following the non-publication of Banks' *Primitiae Florae Novae-Zelandiae* and the inadequate work of the Forsters. The value of his contribution was even recognised by the Government and influential colonists of the day who commissioned from an Auckland craftsman, Anton Seuffert, a magnificent escritoire decorated with a variety of inlaid marquetry designs utilising native timbers. Although it won an award at the Colonial and Indian Exhibition of 1886, the cabinet subsequently fell into a state of disrepair. It was bought at auction in London in 1987 by the National Museum, lovingly restored by another Auckland craftsman, Detlef Klein, and has recently been a major attraction in the Museum's *Treasures*



HYMENOPHYLLUM flabellatum.

HYMENOPHYLLUM cupressiforme.

SCHIZÆA fistulosa.

Wagner del.

Diels sculp.

Fig. 4 Illustrations of three trans-Tasman species from Labillardière's *Novae Hollandiae Plantarum Specimen*.

VOYAGE

DE DÉCOUVERTES

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PENDANT LES ANNÉES 1826-1827-1828-1829,

SOUS LE COMMANDEMENT

DE M. J. DUMONT D'URVILLE.

Botanique

PAR

MM: A. LESSON ET A. RICHARD.

PARIS.

J. TASTU, ÉDITEUR,

N. 4 519, RUE DES BEAUX-ARTS.

1832

ESSAI

D'UNE FLORE

DE

LA NOUVELLE-ZÉLANDE,

PAR

M. A. RICHARD.

and Landmarks Exhibition for 1990. The work of both Anton Seuffert and Detlef Klein have featured in an article in the *New Zealand Geographic* (Judd 1990) where a similar cabinet to the Hooker escritoire is illustrated.

THE MIDDLE YEARS (1867-1961)

Hooker's work marks the end of the early explorative period of New Zealand botany during which most of the collecting was done by European expeditions, specimens went back to Europe, and the results were written up in European journals. From the 1860s onwards there were increasing numbers of botanists resident in New Zealand who came to know the flora well by virtue of constant contact with it. The names of Hector, Buchanan, Kirk, Cheeseman, Cockayne and Petrie stand out from a large number of people who made contributions to our understanding of the flora at this time.

Their work was assisted by the establishment of local herbaria so that specimens no longer disappeared out of the country; the Colonial Museum was founded in 1865 and the Auckland Museum herbarium in 1870. The *Transactions of the New Zealand Institute* were first published in 1865 and served as a local avenue of publication for the results of botanical research. Fern floras continued to appear, notably *Ferns and fern allies of New Zealand* by G.M. Thomson (1882) and *Ferns of New Zealand* by H.C. Field (1890), the latter with lithographic illustrations which were a novelty in their day.



J. D. HOOKER.

Fig. 6 Portrait of Joseph Hooker by George Richmond (1855).

The Victorian Fern Craze

Interest in ferns was also maintained by a tremendous wave of popular enthusiasm which began in England and, not surprisingly, quickly spread to New Zealand. Known as the Victorian fern craze, this was an era of Wardian cases for growing and transporting ferns, a time when popular books on the cultivation of ferns, such as Schneider's *Choice Ferns* of 1894, first recognised the potential of New Zealand species (Fig. 7), and a period when nature-printing reached its peak with the publication of Thomas Moore's *Nature-printed British ferns* (1859).

Supplying the material for this market became a lucrative business, and in New Zealand two Auckland dealers became pre-eminent in the field - Eric Craig, who had his Curiosity Shop in Princess Street, and Thomas Cranwell, who operated from Parnell (Goulding 1977). Advertisements from the time show that albums of pressed ferns were as popular then as books of scenic New Zealand are today, especially for mailing overseas, and that Joseph Hooker was used as a 19th Century equivalent of David Bellamy to promote their sale (Fig. 8). The more elaborate fern albums had mottled kauri covers, and inlaid marquetry designs were used in the de-luxe editions, whilst boxes of pressed specimens provided a variation on the same theme. For do-it-yourself enthusiasts, the raw materials, including pressed specimens, labels, pages, covers and even packets of spores, could be purchased individually and made up at home.

The blue-books

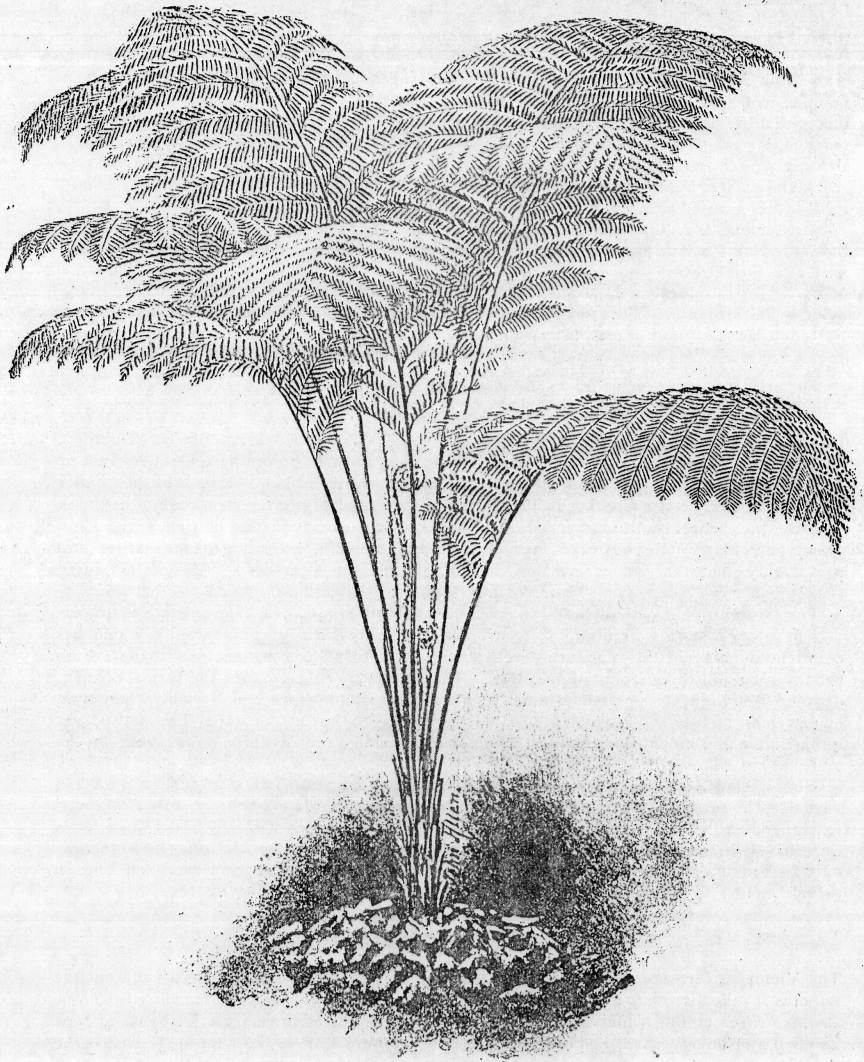
It is at this time that one of the great names of New Zealand pteridology - Herbert Dobbie - first appears. Generations of local botanists have been brought up on the several editions of his *New Zealand ferns* published between 1921 and the sixth and last edition published under the name of Marguerite Crookes in 1963. One of the minor mysteries surrounding this book was why the earliest traditional version (Dobbie 1921) was inscribed "2nd edition, revised and greatly enlarged". Nobody had been able to account satisfactorily for the earlier and presumably somewhat reduced version, until the matter was cleared up by Jeanne Goulding (1977) and, more recently, by Professor J.D. McCraw (1988, 1989).

The first edition is actually a so-called "blue-book" of cyanotypes. The cyanotype process was developed at this time and is regarded as an early form of photography which has culminated today in the blue-print. Originally it involved coating paper with potassium ferricyanide and ferric ammonium citrate. The paper was covered with the fern specimen, exposed to sunlight for a pre-determined length of time, and then washed in water, whereupon an extremely stable deep Prussian blue colour developed on the exposed parts. The method was quite simple and much used for illustrating flat specimens, such as ferns or seaweeds, in the same way as silhouettes are used today.

Dobbie (1990) produced two versions of his blue-book, the first in two parts with 145 varieties, the second in one part with 148 varieties. He then sold his plates to Eric Craig who rearranged and added to them, and published two more versions with 167 and 172 varieties respectively (Craig 1888, 1892). These books are now extremely rare. McCraw (1989) records only 14 known examples of which 11 are in New Zealand libraries, 1 is overseas and 2 are in private hands. Information about other copies would be of the greatest interest.

T.F. Cheeseman

The Victorian fern craze had petered out by the turn of the century and with it went the impetus for the discovery of new species. The publication of Cheeseman's *Manual of the New Zealand Flora* (1906), which lists 156 species, marks the end of the descriptive phase of New Zealand pteridology. As is graphically illustrated in Figure 9, there was a rapid increase in the number of known species in the 35 years between Richard's *Essai* (1832) and Hooker's *Handbook* (1867), a slower period of discovery in the succeeding 40 years to Cheeseman's *Manual* (1906), and then a period of consolidation in the following 50 years to Allan's *Flora* when very few new species were described. Nevertheless, important work was being done in pteridology at this time, notably investigation of the anatomy and gametophyte generations of the Psilotaceae, Lycopodiaceae and Hymenophyllaceae by John Holloway, but further progress in systematics awaited the development of new techniques.



Cyathea medullaris
(much reduced).

Fig. 7 An illustration from Schneider's *Choice Ferns* which includes reference to the cultivation of many New Zealand species.

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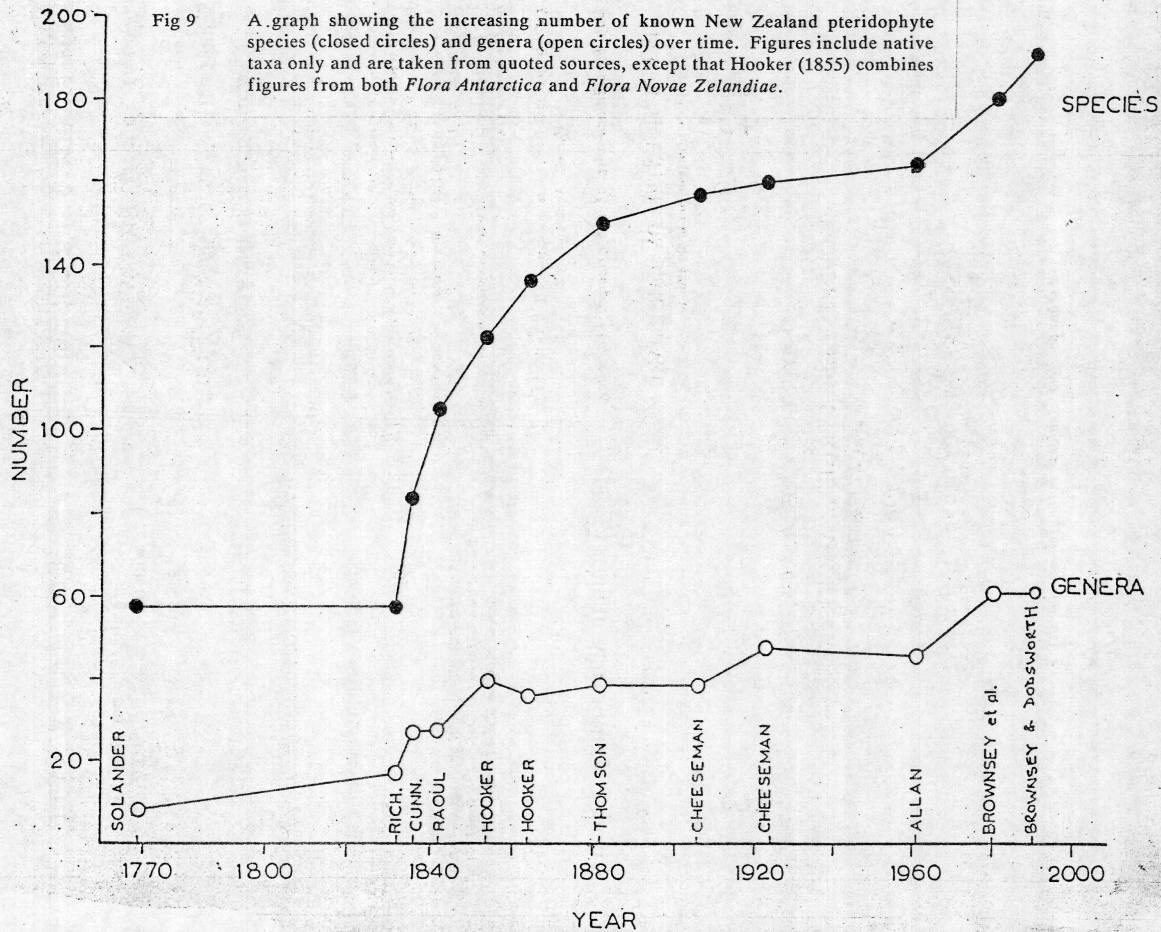
100, QUEEN STREET, AUCKLAND.

3

Fig. 8 Advertisements for fern albums from three different Auckland dealers - note the use of Joseph Hooker's name to promote sales. (Reproduced from Goulding 1977).

Fig 9

A graph showing the increasing number of known New Zealand pteridophyte species (closed circles) and genera (open circles) over time. Figures include native taxa only and are taken from quoted sources, except that Hooker (1855) combines figures from both *Flora Antarctica* and *Flora Novae Zelandiae*.



MODERN FERN SYSTEMATICS (1961 - present)

The long wait for the renaissance of interest in fern systematics following the initial descriptive phase was largely due to the lack of good taxonomic characters in ferns. The best characters are those associated with the reproductive parts of the plant, and, in angiosperms, there is a wealth of taxonomic and phylogenetic information to be gleaned from the flower. In ferns, however, the reproductive organs occur on the prothalli which are almost never collected. Some information can be obtained from characters associated with the sorus - for example, its shape, position and nature of the indusial covering - as well as from the sporangia and spores, but thereafter one is heavily reliant on vegetative features. This accounts for why we still have an imperfect higher level classification for ferns, and why fern families are still poorly defined compared to those of the angiosperms (e.g. there is a much better popular understanding of, say, the Ranunculaceae, than the Dryopteridaceae). The situation is better at the sub-family level but generic limits within, for example, the Polypodiaceae, and species limits within genera such as *Ophioglossum* and *Nephrolepis* are still very ill-defined. The resolution of these problems, and relationships within other critical groups, is only now being worked out with modern techniques supplementing the purely morphological approach.

Nevertheless, since the publication of Allan's *Flora*, there have been several excellent generic revisions based purely on morphological work. These include *Lastreopsis* (Tindale 1965), *Doodia* (Parris 1972), *Tmesipteris* (Chinnock 1975), *Grammitis* (Parris & Given 1976) and *Lindsaea* (Kramer & Tindale 1976), with significant numbers of new species being recognised in the revisions of *Doodia*, *Tmesipteris* and *Grammitis* (Fig. 10).

Another area where the purely morphological approach has been successful is in the critical comparison of New Zealand and Australian taxa. Previously many species had been thought to occur in both countries but when looked at carefully, some have proved to be quite distinct in the two areas. Norman Wakefield in Australia was one of the first to consider trans-Tasman affinities and, as a result of his work, *Blechnum colensoi* and *Hypolepis rufobarbata* were recognised as New Zealand endemics quite different to the Australian *Blechnum patersonii* and *Hypolepis rugosula* (Wakefield 1956). Subsequently, it has been shown that the Australian *Blechnum watsii* is distinct from our *B. procerum* (Tindale 1963), *Doodia mollis* is a new Zealand endemic distinct from the Australian *Doodia caudata* (Parris 1980), and that Tasmanian plants previously referred to *Apteropteris malingii* are a separate species, *A. applanata* (Gray & Williams 1979). Other trans-Tasman species, such as *Hymenophyllum rarum* and *H. flabellatum*, have populations of rather different appearance in the two areas, but require further investigation to establish their exact relationships. A few Australian species have been detected only relatively recently in New Zealand, e.g. *Hymenophyllum cupressiforme* (Parris & Croxall 1972), *Doodia aspera* (Parris 1972) and two adventive species, *Polystichum proliferum* and *Marsilea mutica* (Brownsey 1989). Conversely, so-called New Zealand "endemics" such as *Hypolepis distans* (Chinnock 1976b), *Asplenium terrestre* (Brownsey 1983) and *Grammitis pseudociliata* (Duncan & Isaac 1986) have been found in Tasmania. The identity of Tasmanian populations of *Asplenium terrestre* should have been resolved much earlier but, despite the very similar appearance of plants in the two areas, their ecological preferences are rather different. As the name suggests, New Zealand *Asplenium terrestre* is a ground fern, quite different to the epiphytic *A. flaccidum* with which it had earlier been confused (Brownsey 1977). However, in Tasmania both of these species grow as epiphytes in rain forest, and although the Tasmanians had distinguished the two as different, they had not recognised the second one as being *Asplenium terrestre* because my New Zealand description referred to it as a terrestrial species. This only goes to show that one should see plants in the wild throughout their range of distribution before describing them!

Scanning electron microscopy

One of the most useful pieces of new technology has been the scanning electron microscope (SEM) which has been used extensively to study fern spores. SEM images provide much greater resolution of the fine detail on the surface of the spores than is possible from light microscopy, and also display the information in a way which can be more readily assimilated by the eye.

Recently, Mark Large has completed a comprehensive survey of the spores of New Zealand

GRAMMITIDACEAE

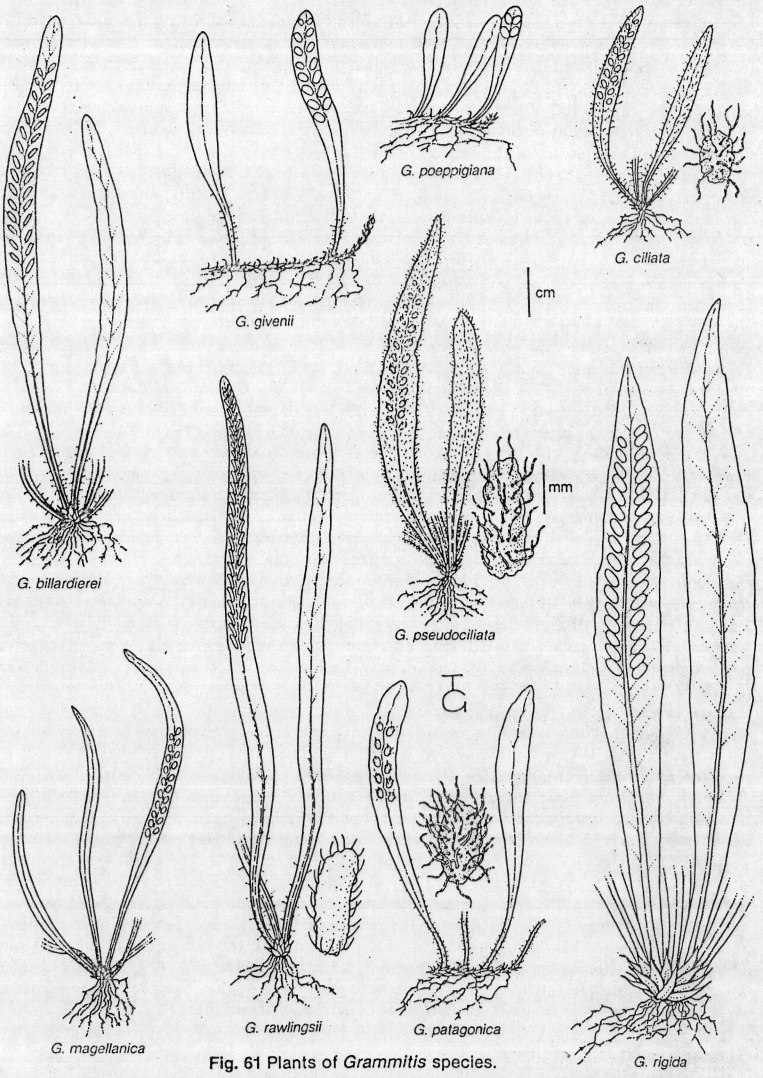


Fig. 61 Plants of *Grammitis* species.

Fig. 10 A plate by Tim Galloway from Brownsey & Smith-Dodsworth's *New Zealand ferns and allied plants* showing the species of *Grammitis* now recognised in New Zealand.

pteridophytes for a Ph.D. thesis at the University of Auckland (Large 1989). He has taken photographs of spores of all species under both the SEM and the light microscope - information which I hope will soon be published in the form of an *Atlas of fern spores*, and which will be an invaluable resource for all future fern systematists.

He has shown that the range of variation in some groups is of critical importance. Two examples will suffice to demonstrate the point (with due acknowledgement to Mark Large for allowing me to use these unpublished results).

Lycopodium is a large and varied genus which has been subdivided in a number of different ways in recent years without any satisfactory consensus having been arrived at. Photographs of the spores taken by Mark Large show four very different types:-

foveolate	(e.g. <i>L. australianum</i> , <i>L. varium</i>)
rugate	(e.g. <i>L. serpentinum</i> , <i>L. laterale</i> / <i>ramulosum</i> , <i>L. cernuum</i>)
reticulate	(e.g. <i>L. scariosum</i> , <i>L. fastigiatum</i> , <i>L. volubile</i>)
baculate	(e.g. <i>L. deuterodensum</i>).

A recent revision by Ollgard (1987) has assigned the first three of these groups to the genera *Huperzia*, *Lycopodiella* and *Lycopodium* respectively on the basis of morphological and chemotaxonomic study. Large's spore study supports these groupings, suggesting that they are taxa in which we can have some confidence. The only point of difference concerns the very distinctive spores of *L. deuterodensum* which may indicate that this species should be in a separate genus rather than in *Lycopodium sensu stricto* as proposed by Ollgard.

The second example where Large's work has proved helpful is in finally determining the identity of the type specimen of *Polypodium pustulatum* Forst. f. (Large, Braggins & Green, in prep.). This specimen clearly belongs to the genus *Phymatosorus*. In New Zealand, this is represented by three species, *P. diversifolius*, *P. scandens* and *P. novae-zelandiae*, which can be distinguished easily on the basis of their rhizome characters. Borster (1786a) described two species, *Polypodium scandens* and *P. pustulatum*, collected during Cook's second voyage. There is no doubt about the identity of *P. scandens*, which is clearly the plant we now know as *Phymatosorus scandens*, but the identity of the other has always been unclear. The specimen is poor and lacks a rhizome, and the name has been regarded as a *nomen ambiguum*. Large, however, has shown unequivocally that the spores from the type specimen are referable to the species currently known as *P. diversifolius*, and not to *P. novae-zelandiae* as suggested by Pichi-Sermolli (1951). However, although it is satisfying to resolve this issue once and for all, it has the unhappy consequence of necessitating yet another name change to a common species!

Cytology

This is a discipline that was pioneered in New Zealand by Garth Brownlie at Canterbury University and continued more recently by both myself and John Lovis. It is a technique that is of the utmost importance in fern systematics and yields information in three main categories - chromosome number, chromosome size and chromosome pairing.

Chromosome number is the most basic information that can be obtained from cytology and, although ferns tend to have rather high numbers, the information has been useful at all taxonomic levels. For example, in earlier times the families Aspleniaceae and Athyriaceae were frequently confused because both have their sori elongated along the veins. However, cytology has shown the fundamental difference between them with a base number of 36 in Aspleniaceae and 40 or 41 in Athyriaceae.

At the generic level, cytology has been helpful in resolving the subdivision of the Gleicheniaceae. At one time, only the single genus *Gleichenia* was recognised, but cytology has shown that there are five distinct lineages with base numbers of 20-22 in *Gleichenia sensu stricto*, 34 in *Sticherus*, 39 in *Dicranopteris*, 43 in *Acropterygium*, and 56 in *Diplopterygium*. These differences are supported by morphology (Fig. 11) and, today, most classifications recognise these five groups as separate genera (e.g. Brownsey, Given & Lovis 1985).

Chromosome number can be useful, too, at the species level. *Blechnum* is an excellent example, with numbers of $n = 28, 29, 31, 33, 34, 36$ and 37 having been recorded from species in different parts of its southern hemisphere range. Clearly this represents evolution based either on fusion or fraction of individual chromosomes (aneuploidy), but further evidence is needed

GLEICHENIACEAE

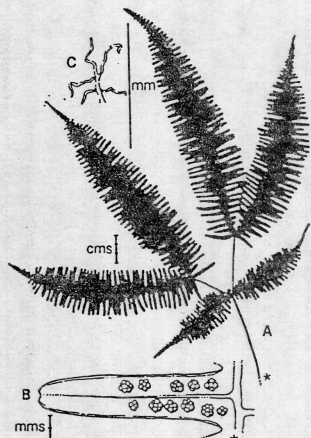


Fig. 55 *Dicranopteris linearis*. A portion of a frond with pinnae on ultimate rachis branches only; B pinna with notched apex, and sori of 6-10 unprotected sporangia; C irregularly branched hair from the rachis.

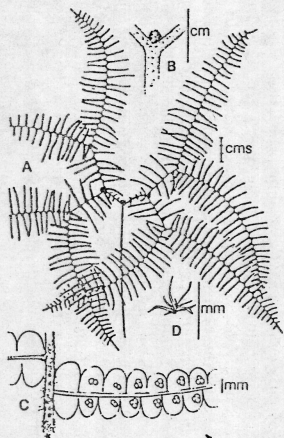


Fig. 56 *Gleichenia microphylla*. A frond showing the rachis branching at wide angles with pinnae on all branches; B bud at a fork of the rachis; C pinna with ultimate segments bearing sori of 2-3 unprotected sporangia; D stellate hair from the rachis.

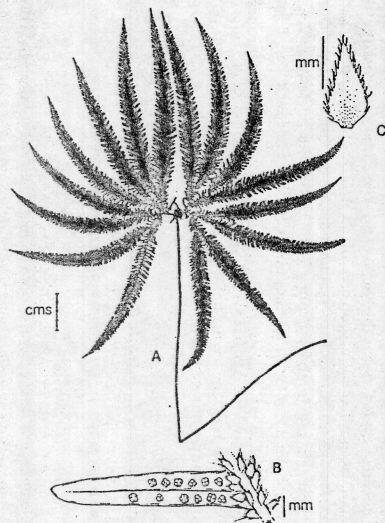


Fig. 57 *Sticherus cunninghamii*. A frond; B pinna bearing sori of 3-5 unprotected sporangia; C fringed scale from the rachis.

Fig. 11. Drawings by Tim Galloway from Brownsey & Smith-Dodsworth's *New Zealand ferns and allied plants* showing differences between genera of the Gleicheniaceae.

to determine which way the series runs. In addition, some species show multiplication of their entire chromosome sets (polyploidy), with different populations showing different numbers. In New Zealand, $n = 33$ and $n = 66$ have been recorded for *B. fluviatile*, whilst, in Tasmania, $n = 99$ has also been reported. It remains to be determined whether these cytotypes are indicative of separate taxa, but casual observation suggests that *B. fluviatile* in Tasmania is quite distinct.

Fern chromosomes are often rather small. In a few groups, however, marked differences in size are apparent, and this is nowhere more evident than in the filmy ferns. Subdivision of the Hymenophyllaceae has always been a contentious issue and, although there is universal agreement about the basic separation of *Trichomanes* and *Hymenophyllum*, there is a wide range of views about their further subdivision, with as many as 42 separate genera having been proposed (Pichi Sermolli 1977). The evidence from cytology is conflicting. Genera like *Craspedophyllum* are clearly well-defined, having not only a distinctive morphology but also an unusually low chromosome number of $n = 13$ (Lovis, unpub.). Others, such as *Meringium* with toothed margins, or *Mecodium* with entire margins, appear to be morphologically clear cut, but are cytologically heterogeneous with base numbers ranging from 21 to 36. It is in such areas that chromosome size may come to the rescue because there is a marked difference between even quite closely related groups. This has been graphically illustrated by Braithwaite (1975) in his study of Pacific filmy ferns, but is equally true of the New Zealand representatives.

The study of chromosome pairing and hybridisation is a more complex subject and can be mentioned only briefly here. To date it is in *Asplenium* that results have been most rewarding. A good example is the common Hen and Chickens fern, *A. bulbiferum*, which has been shown to have two chromosome races in New Zealand, one with $n = 72$ and the other with $n = 144$. Because these two forms are difficult to tell apart in the field, being distinguished with certainty only by their chromosome number and spore size, I referred them to subspecies of *A. bulbiferum*, as subsp. *bulbiferum* and subsp. *gracillimum* respectively (Brownsey 1977a). However, the two forms are ecologically separated, with subsp. *bulbiferum* preferring damper valley bottoms, and subsp. *gracillimum* usually occupying drier ridges. When they meet, the two forms hybridise and the resulting hybrids invariably produce aborted spores and are quite sterile. This is due to the inability of the chromosomes from the two parents to pair at meiosis, and indicates that the forms are genetically distinct and should really be regarded as good species, despite the difficulty of recognising them in the field. Here, then, is a classic case of the conflict between genetic reality and practical taxonomy.

Over 20 different hybrid combinations of *Asplenium* species have been recorded in New Zealand (Brownsey 1977b). In every one of these combinations the spores show some degree of abortion and are effectively sterile. This indicates that the chromosomes from even quite closely related species will fail to pair satisfactorily at meiosis, resulting in a sterile hybrid. On the other hand, polymorphic forms, such as var. *hookerianum* and var. *colensoi* of *A. hookerianum*, although strikingly different in morphology, have never been found to give rise to hybrids that produce sterile spores, suggesting that they are only forms of the one species and not genetically isolated entities. Interestingly, despite the propensity for most species to cross, there are two species, *A. trichomanes* and *A. polyodon*, which have not been found to hybridise with any other species, suggesting that they may be of fundamentally different origin. *Asplenium polyodon* is a widespread tropical species, and *A. trichomanes* a northern hemisphere plant, whereas all the others are probably of southern derivation.

Although hybrids in *Asplenium* are almost always sterile, it would be a mistake to think of them as having no evolutionary importance, as there is good evidence that at least some of them have given rise to new species by the process of allopolyploidy. This involves doubling of the chromosome number, usually during the formation of the spores, to produce a plant in which the doubled chromosomes can pair with each other and fertility is restored. The new plant is morphologically intermediate between the two parents species, has twice the chromosome number, is highly fertile and must therefore be regarded as a distinct species. *Asplenium scleroprium* is a good example which has almost certainly originated in this way from a hybrid between *A. flaccidum* and *A. obtusatum* (Fig. 12).

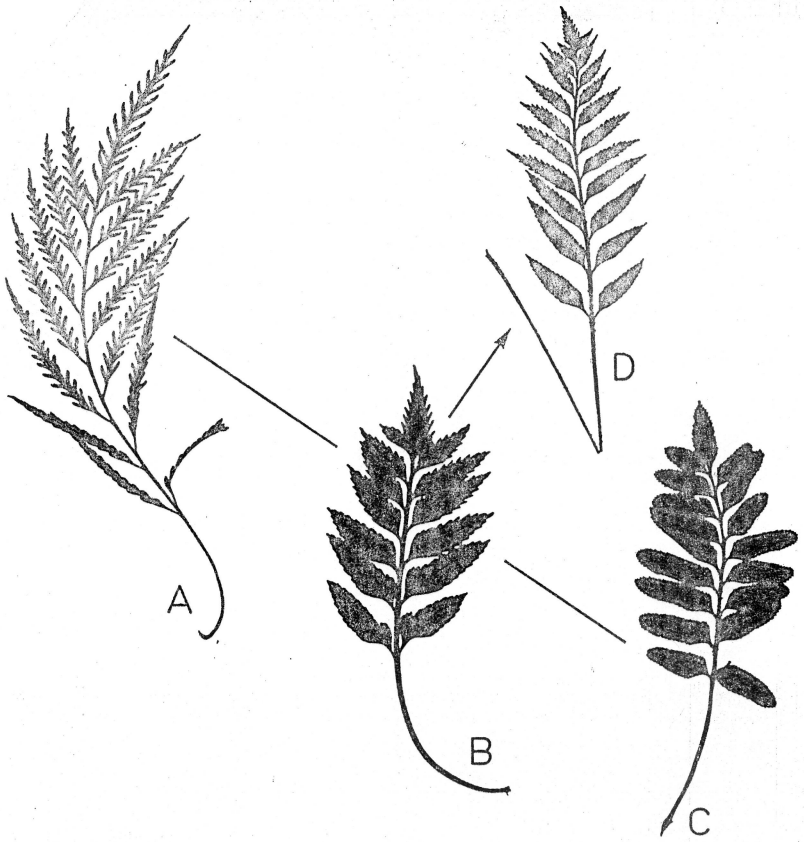


Fig. 12 The postulated origin of *Asplenium scleroprium* (D) from a hybrid (B) between *A. flacidium* (A) and *A. obtusatum* (C). From Brownsey (1977b).

Apomixis

Further evolutionary potential, or taxonomic confusion, depending upon one's point of view, can result from hybridisation involving apomictic species. These are species in which reproduction occurs without fertilisation of male and female gametes, and in which reduction of the chromosome number is avoided at meiosis. In general, an incomplete meiosis results in the production of spores with the same chromosome number as the parent fern. Fertilisation does not occur, but instead, new sporophyte plants develop directly from the prothallial tissue. The advantage of this type of life cycle for ferns is that there is no need for moisture at the fertilisation stage, allowing them to grow in habitats which would otherwise be too dry. It also results in the production of a large number of genetically identical individuals, which may or may not be beneficial in the long term.

The disadvantage from a taxonomist's point of view is that apomictic species can occasionally produce male gametes which may fertilise female gametes from closely related sexual species. Some species may even alternate between a sexual and an apomictic life cycle, giving rise to a range of subtly different populations which are virtually impossible to sort out taxonomically. Fortunately New Zealand has an unusually small number of apomictic species; it is known for certain in *Asplenium flabellifolium*, and strongly suspected in both *Adiantum hispidulum* and *Cheilanthes sieberi*. In other species, such as *Adiantum diaphanum* and *Pellaea rotundifolia*, a number of distinctive populations are known which could be the result of hybridisation and/or apomixis.

Chemotaxonomy

This is a technique which has not been widely applied in New Zealand, being confined largely to flavonoid chemistry and practised effectively only at Ken Markham's laboratory in DSIR Chemistry. However, one example will suffice to show its potential. The Psilotales, including *Tmesipteris* and *Psilotum*, have traditionally been regarded as extremely primitive pteridophytes more closely allied to the earliest land plants than to any living ferns. This view was challenged by David Bierhorst who suggested in a long series of articles that they were really highly reduced ferns related perhaps to *Stromatopteris*, a New Caledonian fern belonging to the Gleicheniaceae, and not fern allies at all (see Bierhorst 1977 for full bibliography). This prompted a thorough review of the affinities of the Psilotales. In the end, one of the most critical pieces of evidence came from chemical analysis which showed that the Psilotales have biflavonols (biflavone and amentoflavone) which are absent from all true ferns, but lack entirely both flavonols (kaempferol and quercetin) and proanthocyanidins (procyanidin and prodelphinidin) which are characteristic of primitive ferns (Wallace & Markham 1978). This, along with evidence from many other sources, strongly supports the traditional view of the Psilotales as an isolated group of ancient lineage.

FUTURE DIRECTIONS

Today a whole new range of chemical and molecular techniques are opening up, none of which has yet been applied seriously to New Zealand ferns but which are in use elsewhere. Of these, potentially the most valuable is probably isozyme analysis. The principle of this technique is that in any one population of plants there may be a range of enzymes (isozymes) which carry out the same function but differ slightly in their structure. Since enzyme structure is coded for by DNA, any differences in the enzymes relate ultimately to changes in the genetic code caused by mutations.

Enzymes can be separated electrophoretically and visualized as a series of bands on a starch gel. Analysis of the bands gives an indication of the genetic variability of a single enzyme, and this can be used to assess systematic relationships (Haufler 1985). For example, one would expect more isozyme variation in polyploid species because of the duplicated gene loci, and ferns have high chromosome numbers which are thought to have resulted from ancestral polyploidy. However, isozyme analysis does not show higher levels of variation in ferns than in flowering plants, and one therefore has to conclude that ferns either have high base numbers or that they have become effectively diploidised by "turning off" of the duplicated chromosomes. Whichever is the case, there are significant implications for our thinking about

polyploidy in ferns.

An even more recent technique is DNA analysis. This involves comparing DNA (or RNA) from related species by electrophoresis, and takes isozyme analysis a stage further down to the basic genetic code. The actual process is complicated in ferns by tannins which have a contaminating effect. Nevertheless, it is a powerful tool which will ultimately yield valuable information in a group where traditional morphological characters are thin on the ground.

These techniques show that we have come a long way in the 230 years since Banks and Solander first collected ferns in New Zealand - from the macro-morphological approach right down to the molecular level. Every new technique opens up new possibilities and quite clearly there is a great deal still to be achieved in our understanding of this fascinating group of plants.

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