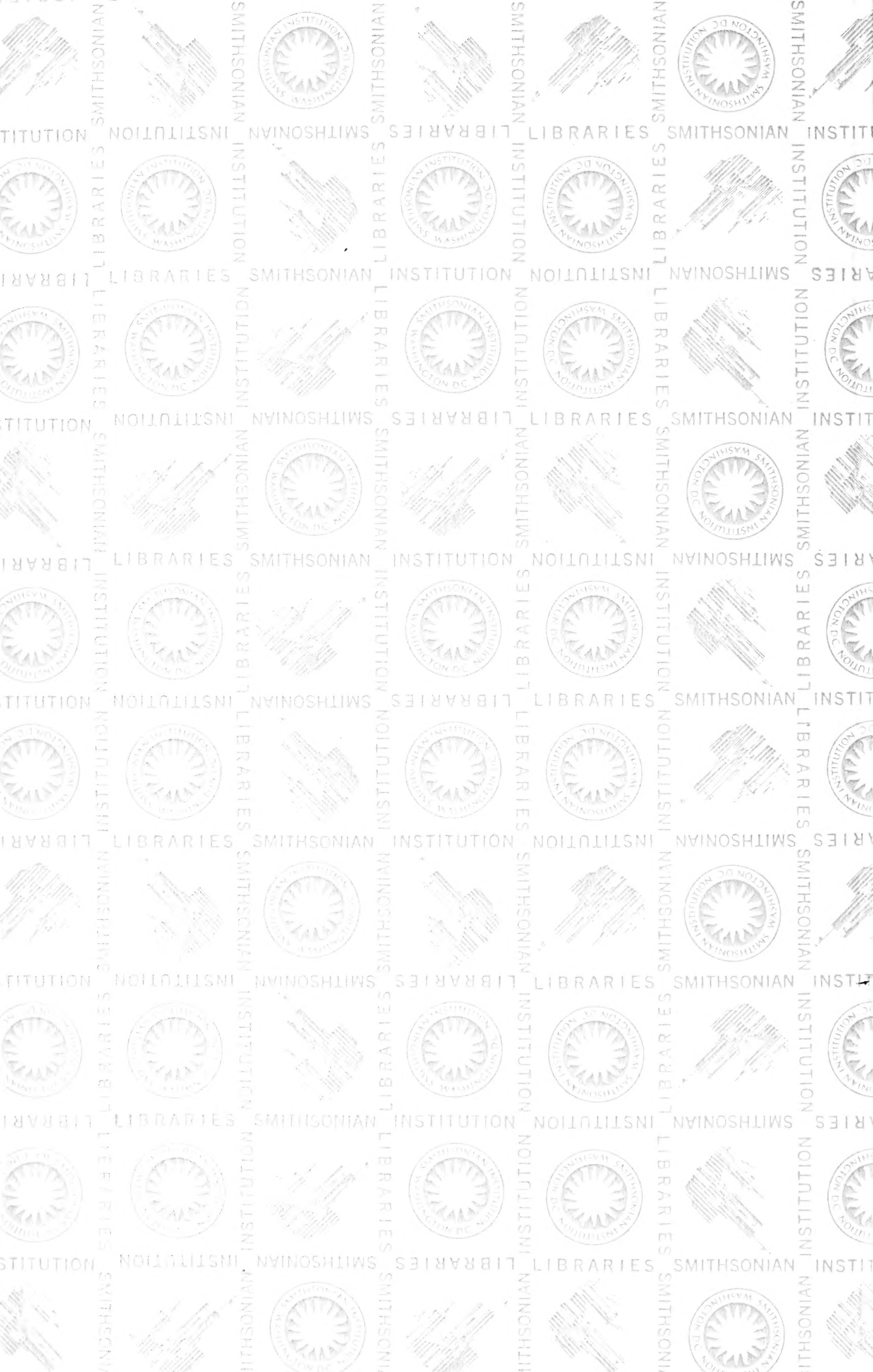

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BRITISH FERN GAZETTE

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Officers and Committee 1973 – 1974

The *Fern Gazette* and the *Bulletin* are the journals of the British Pteridological Society, published annually and sent free to members. The *Gazette* publishes matter chiefly specialist interest on international pteridology, the *Bulletin* topics of more general appeal.

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EXPLANATIONS 2: HOW THE BOOK CAME ABOUT

IRENE MANTON

In the first part of this serial story* I related some of the more amusing incidents which had led me, quite early in my professional life, to become involved with the cytology of ferns. For practical reasons the narrative was discontinued at the advent of World War Two and is resumed here to include the scientific events and pressures which led up to the publication of my book *Problems of cytology and evolution in the Pteridophyta* in 1950.

When the second world war broke out in September 1939 I had been for ten years a member of staff of the Botany Department at Manchester University, having been promoted from assistant lecturer to lecturer when a vacancy on the permanent staff arose. I was to remain in this position until the war ended, university teaching having been declared a reserved occupation, i.e. one could not be called up.

The invasion of Poland, with which active hostilities began, took place whilst I was attending an international genetics congress in Edinburgh which ended somewhat in disarray. Continental colleagues left precipitately for home with the news of impending cessation of cross-channel shipping (air services did not as yet exist). Some American colleagues did likewise, feeling momentarily relieved at having secured passages in the ill-fated Athenea which, in the event, was torpedoed off Northern Ireland as one of the first casualties of the war. As the congress ground sadly to its curtailed close two things stand out in my memory. One was meeting Emil Heitz for the second time, having seen him previously for a day in Hamburg in 1930 during which he had shown me how to make a preparation of liverwort chromosomes using acetocarmine and much violence. I should explain that this 'Kochmethode' (for details and earlier literature see Heitz 1928), though interesting, would never in my hands have developed into an effective squash method for spore mother cells such as I described in Manton 1937 & 1950 and which was essentially based not on Heitz but on McClintock 1929 to which I referred in part 1. The other, less personal, highlight of the Edinburgh Congress was the first verbal intimation of the use of acetocarmine on bone marrow cells for study of human chromosomes (see Slizyński 1945). An improved version of this method, involving tissue culture has since become standard practice in clinical medicine when accurate chromosomal information is needed.

New pressures dominating civilian life in the early years of the war, notably those occasioned by the black-out and the threat or reality of air-raids, had some unforeseen effects on me and my colleagues. While we all reacted positively to taking our fair share of extra-curricular duties in civil defence and the like, we collectively fell into two sharply distinct categories according to our previous psychological attitudes to our work for those whose lives had mainly revolved round teaching or administration, with research if carried out at all regarded as no more than an amusing hobby, such childish things were laid completely aside in order to concentrate attention on the national emergency. Those, on the other hand, for whom research was a vocation and indeed the most important reason for remaining in university life at all, could not so easily be stopped. We did indeed punctiliously pull our weight in civil defence and our

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* The Presidential address given in November 1972, part 1 of which appeared in the last number of the Gazette (vol 10: 285–292, 1973).

research was inevitably reduced in amount. We wrote fewer papers, feeling that some other things were more important, but when it came to the crunch concerning what should be eliminated completely, it was sleep, meals or recreation, but under no circumstances our last fragments of research. Time thus curtailed was nevertheless precious and, with the ever-present feeling that death for us or other people might be lurking just around the corner, we, or at least I, became much more selective in the type of research to which we clung. No longer could one feel free to explore amusing side-lines or easy material that other people could have handled as well or better. Instead it seemed necessary to concentrate attention on the most difficult type of problem with which one was in contact. For me this meant conquering the Pteridophyta.

Of course I had already begun to do this in a general way, guided by the problems and techniques that were already familiar (for details see part 1). Work on the cytology of apogamy in *Dryopteris remota* (Döpp 1932) had alerted me to the interest of apogamy and hybridity in ferns quite apart from my own accidental discovery of polyploidy and apogamy in other species of *Dryopteris.* Authentic material of continental *D. remota* was not available to me till much later (I saw it first in 1962 in Switzerland while visiting Professor Reichstein), but I already knew from Lang of the classic case of *Pteris cretica* and *Cyrtomium falcatum* which seemed likely to be other examples of the same phenomenon, and my last collecting journey abroad before outbreak of war had been to obtain *Pteris cretica* from the shores of Lake Maggiore. On my way I collected *Asplenium germanicum (= A.*x *alternifolium)* growing in a wall outside the railway station at Domodossola, and I also made a special detour to visit Les Plans sur Bex at the suggestion of a member of the University of Lausanne. Here I saw fern hybridization taking place with unique clarity under natural conditions, because this is a classic locality in which *Polystichum lonchitis* and *P. aculeatum* and their hybrid *P.* x *illyricum* grow together. I brought back living plants of all three, and it was not difficult to confirm hybridity in *P.* x *illyricum* by sectioning sporangia, while the demonstration of a polyploid series resembling that in the *D. filix-mas* complex came easily by sectioning roots. I also visited Roches in the Rhone Valley and brought back some polypodiums and other small ferns, taking fixings of *Lycopodium annotinum* cones in passing. Altogether a very useful journey.

At home I had begun to apply squashes to the spore mother cells of genera with relatively large sporangia. These included *Equisetum, Lycopodium, Ophioglossum* and *Isoetes.* I had visited Guernsey to collect *Isoetes hystrix* and *Ophioglossum lusitanicum,* having found *Isoetes echinospora* in Ireland and *I. lacustris* in Windermere. All these had been brought successfully into cultivation in Manchester where they remained alive for many years. My contacts with Lloyd Praeger had produced hybrid horsetails from Ireland *(Equisetum* x *trachyodon, E.* x *litorale* and *E.* x *moorei).* All these and some others were also established in culture, planted out in an unheated greenhouse in beds lined with concrete to prevent their rhizomes from straying. My association with Praeger had produced a contact with the botanic garden in Dublin (Glasnevin) famous among other things for its ability to maintain living *Tmesipteris,* an Australian epiphyte on tree-ferns, which eluded even Kew. This became important for a very special reason.

Early in 1939 Professor Lang had received a visit from Dr Holloway of New Zealand who had recently discovered prothalli of *Psilotum* on Rangitoto Island and had described his material in two papers (Holloway 1938, 1939). The prothalli were cylindrical subterranean saprophytes living by means of an endophytic fungus but remarkable for the presence of a discontinuous central strand of vascular tissue. This vascular tissue, which was unexpected in a gametophyte, was the reason why, after this visit, Lang entrusted the residual fixed material to me for cytological investigation. This material had been left by Holloway, I suppose for this purpose, the problem being whether some cytological departure from the normal had occurred to confuse the morphology of the two generations in a manner recalling without exactly imitating the phenomena associated with obligate apogamy.

By using my previous experience of nuclear structures (Manton 1935) and in other ways (see Manton 1942) I was able to show that Holloway's prothalli were diploid and associated with tetraploid sporophytes with meiotic abnormalities. These facts did not in themselves explain the anatomical peculiarities, although attention was necessarily drawn to the existence of polyploidy even in such a peculiar group of fern-allies, since a diploid sporophyte was located not only by a meiotic count from a plant at Kew, but also by a chromosome count in a wild rhizome from Ceylon that had been fixed by Professor Lang in absolute alcohol (!) in 1900 and handed to me for sectioning in 1940; this chromosome count is illustrated photographically in my paper of 1942.

Since I had qualified for sabbatical leave by 1939 I had applied for it according to the regulations, expecting such leave to take effect in 1940. With the advent of war invalidating all such plans, I turned to the cytological study of apogamy in *Pteris cretica* and *Cyrtomium falcatum,* using sporangial material from a local nursery where both species were for sale as decorative house-plants. All the nursery strains proved to be polyploid, *Cyrtomium falcatum* being triploid on the *Dryopteris-Polystichum* number while, in comparison with my own wild gathering of diploid *Pteris cretica* from Italy, the horticultural representatives of that taxon included triploids and tetraploids but no diploids. Somewhat to my relief the sporangia fixed beautifully (see for example chapter 10 of my book) thereby providing exciting new sources of information on the sporangial happenings in apogamous ferns. Somewhat unexpectedly both taxa also gave evidence of hybridity in their sporangial behaviour.

By this time I had obtained sufficient experience of British and other pteridophytes to aspire to greater completeness. Though foreign travel was no longer possible, I found *Polystichum, Athyrium, Scolopendrium, Polypodium* and several Aspleniums growing in or near my father's garden in Devon which I visited regularly in vacations. *Cystopteris* was common in Miller's Dale near Manchester, and so of course was *Pteridium. Blechnum* was everywhere in the Peak District, with the Oak Fern, Beech Fern and Limestone Polypody common in various other parts of the Pennines. The two Filmy Ferns *(Hymenophyllum)* came from Scotland and the Killarney Fern *(Trichomanes)* from Ireland. I soon had nearly the whole of the British fern flora in culture, and yet it was still the case that only *Osmunda* had as yet yielded to accurate numerical analysis, all the other counts being approximate only.

With *Cystopteris* and *Polypodium* I felt I had met more than my match, since I could not count either. They were worse even than the male fern which had depressed me so much as a beginner because sections were not only inaccurate but useless. Sectioned roots were too confused to be analysed, while meiosis which ought to have been easier (the number to be counted being halved) showed chromosomes in superimposed layers making numerical estimation impossible. I was also in considerable difficulty with some other genera notably *Asplenium.* In comparison with *Polystichum, Dryopteris* and *Athyrium,* which showed approximately 40 or multiples (the actual numbers in the first two are 41 and in *Athyrium* 40), *Asplenium* seemed to be slightly different (the actual base number is 36) though correct assessment of the degree of difference was hampered by the existence in the literature (see Andersson-Kottö & Gairdner 1938) of a much used but erroneous count of n=30 for *Scolopendrium.* The latter, as we now know, also possesses n=36, in agreement with its present inclusion within *Asplenium.*

At this point it became essential to explore other techniques. I had hitherto depended on sections for the polypodiaceous ferns because I thought the small sporangia and mixture of stages present in every sorus would make acetocarmine squashes, as used for large sporangia and Flowering Plants, impossible. I was nevertheless forced to try to revise this opinion and, by substituting manual pressure for the simpler form of coverslip pressure previously used, I succeeded with unexpected ease. I tried this first on a *Polypodium* growing on the wall of Wray Castle (Windermere) and at once I obtained an approximate count in the region of 112 chromosome pairs (we now know that the correct number is 111). In the attempt to establish this number more securely I visited Hull where I knew that the university greenhouse contained a good collection of ornamental ferns. I took fixings at random of several horticultural polypodiums which happened to have sporangia in the right condition expecting to find a high chromosome number, but instead I obtained with complete certainty well spread squashes showing respectively 74 and 37. *Polypodium vulgare* thus contained a polyploid series with at least three members (37, 74 and 111) though only one was as yet established from a wild plant. *Cystopteris fragilis* yielded to treatment in a similar manner giving two numbers (84 and 126), so here was another polyploid series.

I had reached the stage of seeing all too clearly that 'scratch a pteridophyte and find a cytological problem' was true. I also saw the painful necessity of retracing my steps through the whole of the British ferns to make squashes where before I had relied on sections. I had nevertheless at last a technique permitting complete numerical accuracy and I was still engaged upon this, the second round, when the war ended.

By this time, as you may imagine, I was somewhat choked with new information. I had published observations on spiral structure of chromosomes in *Osmunda* (Manton & Smiles 1943) and on Holloway's *Psilotum* prothalli (Manton 1942), because the first involved a new technique that I believed to be important (ultraviolet microscopy) and the second involved someone else's material which had been officially entrusted to me. Publication of everything else had been held back. I had nevertheless already written enough papers to know that it would take me the rest of my life to work off my findings if I had to do them species by species or even genus by genus in separate papers. I therefore consulted Professor V.H. Blackman, the editor of the Annals of Botany, as to whether he thought that book form might conceivably be used. He was encouraging and put me in touch with the Cambridge University Press for whom I prepared a sample chapter, on the male fern story now chapter 4 of the book. They in turn set up a sample page to indicate size, shape and format, in which illustrations could be included in the text. I then left Manchester.

My removal to the Chair of Botany at Leeds in January 1946, made vacant by the premature death of the previous holder, was a traumatic experience which I would not live through again for a king's ransom. Gone were the comfort, good fellowship and convenience of the Manchester department and in their place was virtually nothing except broken glassware with which to begin to build the postwar. There was not even a garden but only an almost derelict greenhouse on an exposed roof or alternatively a piece of a field 3 miles away with no gardener. It took me 17 years of the most gruelling hard work to conquer the worst defects consequent on the absence of a proper departmental building, and I retired six years later. I had nevertheless brought with me from Manchester some treasures. There were the polyploid osmundas and the first synthesized hybrids *(Dryopteris filix-mas* x *D. abbreviata* and *Polystichum aculeatum* x *P. setiferum)* still too young to bear sporangia. Other critical plants were added later. Fortunately I owned my own microscope and was able to buy second-hand some photographic equipment from various places including the army and University College, Aberystwyth. Cytology and photography could still be carried on, though I only attempted the quickest of the new methods, abandoning sections permanently, the need for them on this particular set of problems having passed. The purchase of a garden, the appointment of a gardener and the repair of a greenhouse with the aid of the local coffin-maker, permitted experimental work gradually to be resumed on a scale which increased with the years until at the time of my retirement we had three gardeners and a suite of greenhouses at all temperatures. These things nevertheless came slowly and for the first three years after my arrival in Leeds I had to concentrate on the job in hand — building the postwar including dealing with the demobilizing armed forces with minimal staff. The completion of the book had again to become a background activity.

Fortunately necessity is the mother of invention. It forced me to devise short cuts by mechanizing procedures that before would have been done by hand. I never again made drawings with a camera lucida (the 19th century way with which I started) but always on the basis of an enlarged photographic print on matt paper which could be bleached after the required information had been inked in with one's eyes to the microscope. I never at any time drew outlines of pinnae or fronds, since I found out how to use them as a means of obtaining a paper negative by photographic contact processes with the aid of a printing frame. Details of both methods will be found in the appendix to my book. They transformed the drudgery of recording cytology on a large scale with complete accuracy, and they added greatly to the decorative effect of the results. There are many examples of both methods on the pages of the Gazette and elsewhere (see especially the dedicatory issues for 1969 and 1970).

I do not need to repeat here what is written in the preface to Manton 1950. It is enough to say that in January 1949 the manuscript and illustrations were at last complete and ready to hand to a publisher. Two things then happened. I added a frontispiece of a fern spermatozoid taken with my ultraviolet microscope newly delivered that year, the earlier work of Manton & Smiles 1943 having been carried out in London at the National Institute for Medical Research. The purpose of this addition was mainly decorative but it did in fact contain an important scientific observation, namely the fibrillar disintegration of some of the cilia which led me subsequently into electron microscopy. The other event was a visit to Madeira together with two departmental colleagues in the Easter vacation of 1949. The object of this visit was intended to be recreational after completion of the manuscript of the book. Observational habits nevertheless die hard, and in three weeks we found ourselves with an almost complete collection of living ferns from the island, many of which had been fixed and examined in the field. Once established in cultivation in Leeds most species put up new fertile fronds within a few weeks until, by September and much to my surprise, we had cytological results from almost all. I was therefore able to rewrite the last chapter before it had been set up effectively in type to include the comparison between the floras of Britain and Madeira which now rounds off the book.

The publication then hibernated for nearly a year while a supply of paper was being manufactured. The book in the end came out in December 1950, by which time other events had overtaken the fern programme which must be told, if at all, on a later occasion.

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REVIEW

FERNS OF THE WITWATERSRAND by Florence D. Hancock and Annabelle Lucas. pp xiv, 94, 36 pls., 2 figs, 272 x 212 mm. Witwatersrand University Press, Johannesburg. 1973. Price R7.

This is an illustrated account of the thirty-two taxa of ferns and fern allies of the Witwatersrand Highveld. All however have a wider distribution in the summer-rainfall area of South Africa while some are even circumpolar. The descriptions are clear, although there is some unnecessary repetition. The illustrations are skilfully drawn and pleasantly presented. Species can be identified by an illustrated key which relies only on features seen with the naked eye or a x10 hand lens. More could however have been made of sporangia and spores for these are more distinctive than might be inferred from the rather scanty details and occasional drawings.

In an attempt to meet the requirements of both students and naturalists, the authors have included details of pteridophyte life cycles, general features of their classification and evolution and some ecological notes. Their usefulness is unfortunately marred by being too brief, while the sections on Classification and History and Evolution are rather outdated. The serious student would be well advised to look elsewhere for this information.

Nevertheless the book is useful and should appeal to those persons studying South African ferns, although it will be of limited interest to others.

B. A. THOMAS

ASPLENIUM CUNEIFOLIUM VIV. IN SCOTLAND

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ABSTRACT

Cytological examination of plants of the *Asplenium adiantum-nigrum* aggregate from two serpentine localities in Scotland has shown that they are diploid with a chromosome number of n=36.

Specimens from a number of other Scottish serpentine localities have been found to be morphologically identical with these diploid plants and reasons are given for referring all of them to *A. cuneifolium* Viv.

The known Scottish localities of this species are described and some aspects of its ecology are discussed.

INTRODUCTION

On the continent of Europe the *Asplenium adiantum-nigrum* complex consists of three closely related and morphologically similar species: *A. adiantum-nigrum* L., which is tetraploid, with n=72 chromosomes, and the two diploids, *A. onopteris* L. and *A. cuneifolium* Viv., each with n=36. Although *A. onopteris* has a southern European distribution centred on the Mediterranean region, it just reaches the British Isles, where it is only reliably recorded from the south and west of Ireland. *A. cuneifolium,* although occurring throughout central Europe (Crabbe, Jermy & Lovis 1964; Jalas & Suominen 1972) has a rather scattered and disjunct distribution, since it appears to be confined to serpentine rocks.

A. cuneifolium has hitherto not been accepted as a British plant although it has been pointed out on several occasions that it could be expected to occur on the serpentine outcrops in Scotland. As long ago as 1862, a fern was collected from serpentine rocks in the Cabrach district, on the borders of Banffshire and Aberdeenshire, by the Rev. Andrew Christie, and sent to Thomas Moore, who identified it as *A. adiantum-nigrum* var. *obtusum* Moore (syn. *A. cuneifolium* Viv.; *A. serpentini* Tausch) (Moore 1863). Further specimens were gathered a year later by Christie from the same area and also sent to Moore, who declared them to be indistinguishable from authentic specimens of *A. cuneifolium* which had been sent to him from the continent (Moore 1864).

G.C. Druce (1919) visited the Cabrach area in 1918 and examined these plants in the field. He concluded that this fern intergraded so completely with *A. adiantum-nigrum* that it did not even merit the subspecific rank to which some continental authorities (e.g. Milde and Christensen) had relegated it. Even so, by naming it *A. adiantum-nigrum* L. var. *cuneifolium* (Viv.) Druce [comb. nov.] (under which it was included in Druce's British Plant List, 2nd edition, 1928) he reaffirmed Moore's view that the Cabrach plants were identical with continental material of *A. cuneifolium.* Since that time this fern appears to have been largely overlooked by British botanists and no mention of it is made in any modern British flora or check list (e.g. Dandy 1958, Jermy 1960, Clapham Tutin & Warburg 1962, Hyde, Wade & Harrison 1969) although J.D. Lovis reported seeing "an unusual form of *A. adiantum-nigrum"* on the Cabrach serpentine (Lovis 1957), and J.W. Dyce gathered a

FIGURE 1 a—e: Silhouettes of fronds of *Asplenium cuneifolium.* a, and b, from Glendaruel, Argyll; c from Glen Lochay, Perthshire; a, and e, from Cabrach, Aberdeenshire.

fern from the same area which seemed, he said, "to agree with the description I had received of *A. cuneifolium*" (Dyce 1957). More recently Proctor & Woodell (1971), during a study of serpentine vegetation, noticed in Glendaruel, Argyll, an abundance of "a form of the fern *A. adiantum-nigrum* which resembles, in several respects, the continental serpentine species *A. cuneifolium* which is not recorded from Britain". Our own interest in this plant had already begun before we became aware of this reference.

MATERIAL AND METHODS

Living material of a fern resembling *A. adiantum-nigrum* was brought into cultivation from a number of Scottish serpentine localities. Young sporangia were fixed and examined by the aceto-carmine squash method described by Manton (1950). Suitable preparations were preserved for a few hours by ringing the cover-slip with paraffin wax. Spore mother cells showing countable chromosomes at meiosis were drawn under an oil-immersion objective and counts made from the drawings.

RESULTS AND DISCUSSION

Meiosis was observed in several cells in each of three plants: two from Glendaruel, Argyll, v.c. 98, and one from Glen Lochay, Perthshire, v.c. 88. In all of them meiosis was quite regular and a chromosome number of n=36 was observed. These plants are

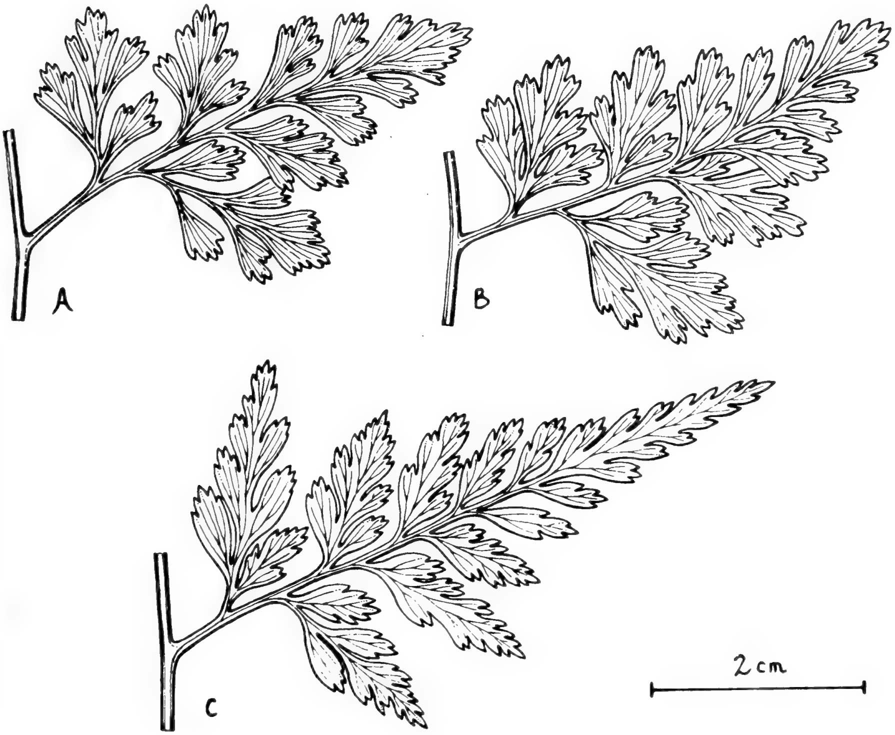

FIGURE 2 a–c: Lowest pinnae from fronds of a, *A. cuneifolium* from Glendaruel, Argyll; b, *A. cuneifolium* from Glen Lochay, Perthshire; c, *A. adiantum-nigrum* from Caernarvonshire.

thus clearly diploid, whereas *A. adiantum-nigrum* is tetraploid with n=72 (Manton 1950, Shivas 1969).

The plants from these two localities are remarkably uniform in their gross morphology and they can be distinguished from *A. adiantum-nigrum* with little difficulty. From their morphological resemblance to the Glendaruel and Glen Lochay plants there seems little doubt that our collections from other Scottish serpentine localities belong to the same taxon, and on the basis of their general morphology, close association with serpentine rock, and diploid chromosome number, we have no hesitation in referring all our plants to *Asplenium cuneifolium.*

A comparison of the Scottish plants with herbarium material of *A. cuneifolium* from the continent has shown that they cannot be separated on morphological grounds and they are clearly conspecific. *A. cuneifolium,* however, is a highly variable plant and there is some evidence of population differentiation, as may be expected in a species having such a disjunct distribution. Lovis (pers. comm.) has also found *A. cuneifolium* to be exceedingly variable in Austria.

Since it was first described by Viviani (1808), *A. cuneifolium* has been assigned to various taxonomic categories by different authors, but is now generally accepted as a good species, and our observations on the Scottish plants support this view. It is certainly a critical species, but the cytological work of M.G. Shivas (Mrs T.G. Walker) (1969) has shown that the artificial hybrid between *A. cuneifolium* and *A. adiantum-nigrum* is triploid and shows a highly irregular behaviour at meiosis. This hybrid has recently been found in the wild on serpentine rock above Verdasio, in Tessin canton, Switzerland, near the Italian border, and has been named *A.* x *centovallense* D.E. Meyer. It can be identified by having a combination of the frond characters of the putative parents, and by its high proportion of empty sporangia and completely abortive spores (Meyer 1968).

A. cuneifolium can be distinguished most readily by the shape of the ultimate leaf-segments. These segments vary from narrowly cuneate to broadly cuneate, but in all of them the margins at the base are either straight or recurved. This appears to be the most constant character of *A. cuneifolium.* In some plants the ultimate leaf-segments are broadly cuneate with a rounded or obtuse apex; only then do they display the flabellate character which, when present, is clearly diagnostic of this diploid species. These features may be seen in the silhouettes of fronds in fig. 1. In *A. adiantum-nigrum,* on the other hand, the ultimate leaf segments are ovate to lanceolate, with convex margins at the base (fig. 2c).

In *Flora Europaea* the ultimate leaf-segments of *A. cuneifolium* are described as flabellate with obtuse teeth, and these are, unfortunately, cited as key characters. In all the specimens of this species which we have seen, both from Scottish and continental sources, the teeth are most often acute, only rarely obtuse. They are, in fact, as variable in shape as those of *A. adiantum-nigrum,* and appear to have no taxonomic value.

A. cuneifolium also differs in general from *A. adiantum-nigrum* in its thinner, more broadly triangular-ovate frond blade, which is more often tripinnate than bipinnate; in its more slender stipe and rachis; and in the duller green upper surface of the frond which, in *A. adiantum-nigrum* is shiny green.

There is also a difference between the two species in the width of the basal stipe scales (fig. 3). A sample of twenty to twenty-five scales was taken from each of a number of plants and measured with a calibrated ocular micrometer, the

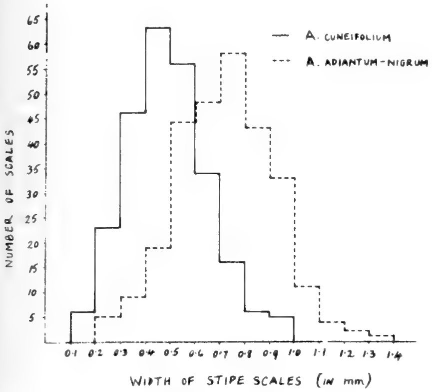

FIGURE 3: Histograms of stipe scale width in *A. cuneifolium* and *A. adiantum-nigrum.*

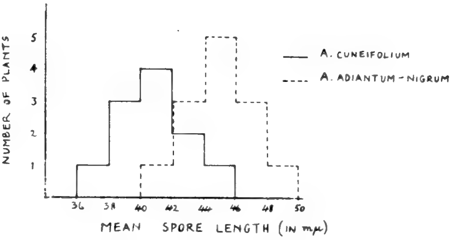

FIGURE 4: Histograms of mean spore length in *A. cuneifolium* and *A. adiantum-nigrum.* Each mean estimated from a sample of 50 spores.

measurements being made at the widest part of the scale near its base. The scales of *A. cuneifolium* are narrower (mean values 0.39 to 0.62 mm.) than those of *A. adiantum-nigrum* (mean values 0.65 to 0.86 mm.), and this character is sometimes useful in confirming the identification of *A. cuneifolium.*

Spore size was also studied in the two species. A random sample of fifty spores from each plant was measured, including the perispore. Mean spore length was found to have a lower range of values in the diploid than in the tetraploid, as may be seen from the histograms (fig. 4). However, the overlap, even in mean values, is so great that spore length has little taxonomic value. Other differences were noticed in the characters of the perispore. This is usually thinner in *A. cuneifolium* than in *A. adiantum-nigrum,* and frequently echinate in contrast to that of the latter which is raised into continuous ridges. However, perispore morphology in *A. cuneifolium* is very variable and is only occasionally useful in confirming the identification of the diploid species.

FIELD OBSERVATIONS

In all the Scottish localities where we have observed *A. cuneifolium,* it is closely associated with serpentine rock, growing in crevices and fissures, under boulders and overhangs, and sometimes also among scree where this has developed. The plants tend to be small and stunted in exposed positions, but can attain a large size in moist, sheltered situations. Fronds over a foot long, including stipe, were observed under a boulder near Cabrach, Aberdeenshire, and some of similar dimensions on sheltered rock outcrops in a wood near Colmonell, Ayrshire.

Interesting flowering plants which accompany *A. cuneifolium* in some of its Scottish sites include *Cardaminopsis petraea* (Argyll and Aberdeen), *Silene maritima* (Argyll, Perth and Aberdeen) and *Minuartia verna* (Aberdeen). The comparative richness of the vegetation on the serpentine is indicated by the almost constant presence of *Asplenium viride,* and, less frequently, *Selaginella selaginoides, Rubus saxatilis, Melica nutans* and *Helictotrichon pratense.* The lowest elevation at which *A. cuneifolium* has been observed in Scotland is 93 m near Colmonell, Ayrshire, and the highest at about 520 m at Craigs of Moniewhitt, Strathdon, and Coyles of Muick, Ballater, both Aberdeenshire.

The features which distinguish *A. cuneifolium* from *A. adiantum-nigrum* in the field are not easy to describe, but the difference between the two species is, nevertheless, readily apparent, at least to the eye of an experienced observer. Perhaps the most obvious features of the diploid are the more broadly triangular frond shape and the tendency for the frond to be tripinnate rather than bipinnate, giving it a distinctly more dissected appearance. The stipes of the fronds are often very long (up to twice the length of the blade), particularly when the plant is rooted in a deep earthy fissure, and they are of a characteristically brittle nature, being very easily broken when handled. This tendency often renders impossible the collection of frond specimens complete with the swollen, scaly base.

Rasbach *et al* (1968) mention the dying down of the fronds in autumn as a feature distinguishing *A. cuneifolium* from *A. adiantum-nigrum,* but this has not been observed to be the case in the Scottish sites. We have found the diploid in perfectly fresh condition at various times between October and March.

The most remarkable features of *A. cuneifolium* in its Scottish localities are its abundance in most of them, and its unique association with serpentine rock. In our experience *A. adiantum-nigrum* never occurs in such abundance on any kind of rock, and is quite rare on serpentine. We have observed the tetraploid species in only two of the sites mentioned in this account.

Although, as in its continental localities, this fern appears to be confined to serpentine rock, in many of its Scottish sites it is remarkably abundant, and it therefore seems rather surprising that this attractive species should have been neglected for so long in Britain. The following localities are known.

THE SCOTTISH LOCALITIES

Vice-County 75, Ayr: Serpentine rock occurs at about 100 m. altitude on the south side of Balhamie Hill, near Colmonell, both on the open hill-side and within a small plantation of Scots Pine near High Balhamie (NX 133859). *A cuneifolium* grows plentifully on a rock outcrop in the wood where, encouraged by the sheltered conditions, the plants are extremely large and strong-growing.

Vice-County 86, Stirling: A serpentine associated with the Highland Border Series outcrops at intervals between Balmaha, on the east shore of Loch Lomond, and Gartmore on the Perth border about seven miles to the north-east. The best exposures are at Conic Hill, Balmaha (NS 421917), and at Lime Hill in Loch Ard Forest (NS 473963). At Conic Hill the rock is rather dry with a limited vegetation, and *A. cuneifolium* is represented by only a few plants in fissures which afford some degree of shelter. At Lime Hill, however, much wetter conditions prevail and *A. cuneifolium* is abundant. At both sites the fern grows at between 150 and 170 m. altitude.

Vice-County 88, Mid Perth: An extensive mass of serpentine associated with the Highland schists lies just west of Corrycharmaig, Glen Lochay (NN 521358), reaching an elevation of about 250 m. *A. cuneifolium* is very abundant throughout the serpentine area on exposed rock and boulders and also in scree. Specimens labelled *A. adiantum-nigrum* var. *serpentini* have been collected from this locality by at least three collectors; J.A. Wheldon & A. Wilson, 1905, (NMW); P. Ewing, 1909, (GL), and D.A. Haggart, 1913, (E.).

Vice-County 90, Angus: A specimen named *A. adiantum-nigrum* var. *obtusum,* collected in Glen Prosen in 1874 by P. Ewing, is an excellent example of *A. cuneifolium,* and we have no hesitation in referring it to the latter species. It is not possible to say if this specimen was obtained from serpentine rock, and it has not yet been possible to search in the Glen Prosen area with a view to refinding the plant. However, Mrs H.A.P. Ingram (pers. comm.) reports having seen plants resembling the diploid in the upper part of the glen.

Vice-County 92, S. Aberdeen: We have not had the opportunity to visit all the serpentine localities mentioned by Proctor and Woodell (1971) as occurring in this division, but in the two localities we have investigated, Green Hill of Strathdon, and the Coyles of Muick, Ballater, we have found *A.*

cuneifolium. At Green Hill the fern occurs sparingly at over 500 m. on the Craigs of Moniewhitt (NJ 317138), and may be approaching its altitudinal limit at this elevation. It is more plentiful on serpentine by the Water of Nochty (NJ 326155) at about 300 m. On the extensive exposure at the Coyles of Muick (NO 328908) *A. cuneifolium* is abundant and probably occurs here also at over 500 m., both on rock and in scree.

Vice-County 93, N. Aberdeen: Serpentine is exposed in a number of localities in the Cabrach-Rhynie area near the Banffshire border. This is the area from which the earliest Scottish specimens of *A. cuneifolium* were obtained, and where most of the subsequent interest in this species as a British plant has been concentrated. The precise location where Christie obtained his specimens is not known, but Druce (1919), in August 1918, collected from "a serpentine hill to the east of the Buck of Cabrach", probably the Hill of Towanreef or Peddie's Hill. Our own observations in this vice-county have been confined to the vicinity of Red Craig, Craik, near Rhynie (NJ 453257), where the diploid is abundant.

Vice-County 94, Banff: *A. cuneifolium* occurs plentifully on both banks of a stream which forms a ravine in the serpentine on the county boundary between Aberdeenshire and Banffshire near Bridgend in the upper Deveron valley (NJ 400347). It also grows in limited quantity on Craig Dorney (NJ 403352) nearby. J.W. Dyce has collected specimens, which we refer to *A. cuneifolium,* from Craig Watch, 1½ miles further west and also on the county border (NJ 38-35-). Although most of these localities lie on the Aberdeenshire side of the county boundary they fall within the Watsonian vice-county 94. It is very likely that the diploid also occurs on the serpentine exposures on the Blackwater at Scorrs Burn (NJ 333228).

Vice-County 96, Easterness: On the serpentine outcrops which occur over a wide area just north of Polmailly, Glen Urquhart (NH 480323) *A. cuneifolium* is plentiful. In certain parts of this area the serpentine is very closely intermingled with limestone, and it is noteworthy that the diploid is found only on the former and never on the latter. A narrow-pinnuled form of *A. cuneifolium* occurs on a serpentine outcrop by the road junction just west of Milton, Glen Urquhart (NH 491303). This is almost certainly the plant mentioned by Moore (1859), collected by Miss McInnes in Glen Urquhart, and which he named *A. adiantum-nigrum* var. *leptorachis.*

Vice-County 98, Argyll: A substantial outcrop of serpentine reaches an elevation of about 370 m. near Kilbridemore, Glendaruel (NS 021904). It supports an interesting flora which includes Northern Rock-cress *(Cardaminopsis petraea).* In this locality one of the authors (A. McG. S.) noticed, in 1963, a curious form of *'A. adiantum-nigrum'* though it was only during the course of the present investigation, when these plants were found to be diploid, that the true identity of the population was realised. *A cuneifolium* is plentiful at this site.

Vice-County 99, Dunbarton: On the west side of Loch Lomond very limited exposures of the Highland Border serpentine occur on a ridge near Ben Bowie (NS 347831), about three miles east of Helensburgh. Here *A. cuneifolium* grows in the crevices of low outcrops where it is protected from sheep grazing. The altitude is about 275 m.

Vice-County 112, Shetland: From the examination of herbarium material it is evident that *A. cuneifolium* occurs on the serpentine of Unst. We have seen specimens collected by C.N. Peach at Muckle Heog in 1864 (E), by A. Craig Christie at Baltasound in 1868 (E), and by R.W.G. Dennis at Baltasound in 1952 (K). A specimen collected by G.C. Druce at Hoo Field, Cunningsburgh, Mainland, in 1921 (E) is also referable to *A. cuneifolium.* All of these specimens are labelled *A. adiantum-nigrum.*

ACKNOWLEDGEMENTS

We wish to record our thanks to the Regius Keeper, Royal Botanic Garden, Edinburgh and the Professor of Botany, University of Glasgow, for the generous loan of herbarium material; to the Director, Royal Botanic Gardens, Kew, and Miss Frances Jarrett, also of Kew, for kindly supplying a photograph of the herbarium specimens originally gathered in the Cabrach district by A. Christie; to Dr A. Sleep and Dr J.D. Lovis, both of the University of Leeds, for their valued interest and encouragement; and to Mrs H.A.P. Ingram, J.W. Dyce, J. Mitchell and R.C. Palmer, for information regarding some of the serpentine localities.

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REVIEW

THE FERNS AND OTHER PTERIDOPHYTES OF MONTANA, WYOMING AND THE BLACK HILLS OF SOUTH DAKOTA by Robert and Jane Dorn. 94 pp, illustr., photolithographed type-script, 1972, available from the authors at the Department of Botany, University of Wyoming, Laramie, Wyoming 82070. Price $ 1.00.

The illustrations are for the most part good and distribution maps are given for each species. The text is neatly laid out and the keys to the species work. It is interesting to note that a number of European species are found in this region e.g. *Asplenium septentrionale, Dryopteris filix-mas, Gymnocarpium dryopteris, Cryptogramma crispa, Cystopteris montana,* to mention a few. It is probably misleading to use the name *Dryopteris austriaca* as a portmanteau name when a more accurate determination could have been made. Thoroughly recommended and worth it at three times the price.

A. C. JERMY

THE FERN HABITATS OF MT WILHELM, NEW GUINEA

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ABSTRACT

The ferns present in the montane to alpine habitats of Mt Wilhelm, New Guinea are discussed, and their Malesian and Australasian relationships outlined.

INTRODUCTION

New Guinea has one of the world's richest fern floras, probably in excess of 2000 species, although many groups are still in need of revision. Mt Wilhelm (lat. 5°47'S, long. 145°01'E), in the Bismarck Range, is, at 4510 m, the highest mountain in Papua and New Guinea. It is also botanically one of the best studied areas in the country. Extensive collections have been made there particularly by the Department of Forests' Division of Botany, the Australian National University, the Commonwealth Scientific and Industrial Research Organisation (C.S.I.R.O.), and the 6th Archbold Expedition, while intensive work on the vegetation has been carried out by C.S.I.R.O. (Hoogland 1958; Robbins 1961, 1970) and the Australian National University (Walker 1968; Wade & McVean 1969). Johns & Stevens (1971) provide a checklist of the species collected, based on material held in the herbarium of the Division of Botany, Lae. Most work has been carried out in the Pindaunde Valley on the southeast slope of the mountain which is the most easily accessible area from Kundiawa, which is served by road and an air link with Lae and Goroka.

In December 1971 the author and J.P. Croxall spent four days in the Pindaunde Valley intensively collecting pteridophytes, especially Grammitidaceae. This account attempts to outline the ferns present in the various montane to alpine habitats on the mountain. It is based on the author's field observations and collections and to a limited extent on herbarium material examined at the Australian National University Research Station on Mt Wilhelm, Lae and Kew.

Duplicates of the author's collections are lodged in the herbarium of the Division of Botany, Department of Forests, Lae, New Guinea.

DESCRIPTION OF THE AREA

Mt Wilhelm is a block of Bismarck granodiorite uplifted during Pliocene-Pleistocene times. Its summit altitude is very near the present level of permanent snowfields in West Irian but, although snowfalls of up to 13 cm occur near the summit, they seldom last for more than a few days. During the Pleistocene glaciation the snowline was at c 3500–3600 m and the maximum extent of glaciation was at c 3500 m (Löffler 1972).

Soils on the mountain, even on steep slopes, are predominantly peaty (Walker 1968).

Annual rainfall (based on data from below Keglsugl, c 2300 m), calculated from four years data, is a total of 230 cm, with a February-March maximum and a June-July minimum (Brass 1964).

The lower limit for the area discussed here is at 2743 m. This is also the lower limit of the area studied by Wade & McVean (1969) as above this level no agriculture is practised by the Chimbu people, disturbance being restricted to hunting and foraging parties (Johns & Stevens 1971). Below this altitude the forest is likely to be modified

FIGURE 1: Lake Aunde, Pindaunde Valley, showing subalpine grassland in foreground and lower subalpine forest to left of and behind lake. The summit peak is invisible in this photograph. *(Photo A.C. Jermy).*

by the foraging of pigs and the establishment of native gardens. There is no forest in the area below c 2560 m (Brass 1964).

The habitat classification adopted here is based on the vegetation associations described by Wade & McVean (1969). They can be summarised thus:

1. Montane Forest (includes both lower and upper montane forest).
2. Lower and Upper Subalpine Forest (Subalpine Forest and Subalpine Scrub, respectively, of Robbins 1970).
3. Subalpine and Alpine Grasslands (the former is Tussock Grassland of Brass 1964).
4. Uppermost Rock Zone.

THE FERN HABITATS

1. Montane Forest

This occurs from the lower limit of the area considered to c 3300 m, in the base of Pindaunde Valley. Structurally it is of two types, although the ferns in each are not readily distinguishable. In the valley of Pengagl Creek the forest is moderately tall

FIGURE 2: *Cyathea macgregorii* in subalpine grassland. *(Photo A.C. Jermy).*

(18–30 m) (Brass 1964), with a fairly even canopy, scattered emergents and a reasonably distinguishable sub-canopy layer. Canopy trees include *Elaeocarpus, Decaspermum, Quintinia, Saurauia, Astronia, Timonius, Weinmannia, Dryadodaphne, Podocarpus* and *Papuacedrus.* On the steep slope from Pengagl Creek to the base of Pindaunde Valley the vegetation becomes reduced to a single tree layer 11–18 m tall and including species of *Decaspermum, Xanthomyrtus, Ilex, Quintinia, Podocarpus* and *Papuacedrus.*

Tree ferns (*Dicksonia sciurus* C. Chr., *Cyathea atrospinosa* Holttum, *C. hooglandii* Holttum, *C. pachyrrhachis* Copel., *C. rigens* Rosenst.) are notuncommon while large terrestrial ferns (*Marattia, Cyclosorus* sens. lat.), although more characteristic of the forest at lower altitudes, still occur. Smaller terrestrial ferns are present in undisturbed vegetation, but not in large numbers. They are, however, common by track margins, *Parathelypteris beddomei* (Baker) Ching., *Blechnum* spp. including *B. fraseri* (A. Cunn.) Luerss., *Plagiogyria glauca* (Bl.) Mett. and *Polystichum* spp. being notable. In clearings (perhaps due to fire) *Hypolepis papuana* Bailey and *Dennstaedtia* sp. form large colonies. Epiphytes are quite abundant, especially *Asplenium* spp., 6 spp. of *Hymenophyllum,* 2 spp. of *Trichomanes: T. (Pleuromanes)*

FIGURE 3: *Cyathae muelleri* in subalpine grassland near margin of lower subalpine forest. *(Photo A.C. Jermy).*

pallidum Bl. and *T. (Gonocormus) novoguineense* Brause, *Microsorium, Crypsinus, Belvisia, Selliguea* and *Loxogramme.* Grammitidaceae are represented by *Prosaptia contigua* (Forst.) Presl, *Ctenopteris denticulata* (Bl.) C. Chr. & Tard., *C. stellatosetosa* Copel. and several *Grammitis* species including *G. locellata* (Baker) Copel.

This forest is the upper limit for several genera common at lower altitudes, notably *Marattia, Cyclosorus* sens. lat., *Trichomanes* sens. lat., *Dennstaedtia, Hypolepis* and *Microsorium.*

In some genera, especially *Blechnum* and *Grammitis,* the same species occur also in lower subalpine forest.

2. Subalpine Forest

a. Lower Subalpine Forest

This occurs between c 3300 m and 3600 m. It is single-layered with a dense canopy 8–10 m high of, e.g., *Rapanea, Quintinia, Sericolea, Symplocos, Drimys, Olearia, Amaracarpus, Schefflera, Pittosporum* and *Podocarpus.*

FIGURE 4: *Cheilanthes papuana* in subalpine grassland, c. 3960 m. *(Photo J.P. Croxall).*

FIGURE 5: *Papuapteris linearis* in subalpine grassland, c. 4120 m. *(Photo J.P. Croxall).*

Within the forest *Cyathea* species, e.g. *C. percrassa* C. Chr. still occur. Large terrestrial ferns are absent, although smaller terrestrial ferns are still moderately common, especially by track margins. These include *Plagiogyria glauca, Pteris keysseri* Rosenst., *Blechnum fluviatile* (R. Br.) Salom., *Parathelypteris beddomei, Dryopteris wallichiana* (Spreng.) Hyl., *Stenolepia tristis* (Bl.) v.A.v.R., *Polystichum* spp. including *P. archboldii* Copel., *P. bolanicum* Rosenst. and *P. papuanum* C. Chr. Epiphytes are abundant. Small epiphytes are to be found at all levels within the forest, e.g. *Elaphoglossum angulatum* (Bl.) Moore, *Crypsinus* sp., *Lemmaphyllum novoguineense* (Rosenst.) C. Chr., *Loxogramme subselliguea* (Baker) Alston, *Selliguea* (2 spp.), *Ctenopteris sesquipinnata* Copel., *Prosaptia davalliacea* (F. Muell. & Baker) Copel. *Grammitis* is the dominant epiphytic genus in this forest, with at least 7 spp. occurring. These are *G. archboldii* (C. Chr.) Copel., *G. caricifolia* Copel., *G. locellata, G. novoguineensis* Copel., *G. scabristipes* (Baker) Copel., *G. stanleyana* (Baker) Copel. and *G. stomatocarpa* Copel. *Hymenophyllum (Meringium) foersteri* Rosenst. has its lower limit in this forest. Larger epiphytes, e.g. *Pteris brassii* C. Chr. and *Rumohra adiantiformis* (Forst.) Ching only occur low down on the trees.

In some parts of the lower subalpine forest, on steep slopes e.g. those on the side of Imbuka Ridge, landslips have occurred, leading to the removal of all tree cover. Scattered low shrubs e.g. *Rhododendron* may remain (or be regenerating) on small patches of peaty soil, otherwise the granodiorite outcrops at the surface. Often such areas are extremely wet, due to seepage. Species epiphytic elsewhere grow here on more or less bare rock, e.g. *Hymenophyllum (Meringium) melanosorum* (Copel.) Morton, *Flaphoglossum angulatum, Belvisia revoluta* (Bl.) Copel., *Crypsinus* sp., *Prosaptia davalliacea, P. contingua, Grammitis graminifolia* Copel., *G. scabristipes* and *Ctenopteris sesquipinnata.* In addition, some species were only found in this habitat e.g. *Amphipterum humatoides* Copel., *Elaphoglossum hellwigianum* Rosenst., *Xiphopteris subpinnatifida* (Bl.) Copel., *Ctenopteris nutans* J. Sm. var. *nutans, C. nutans* var. *trichocarpa* Rosenst., *C. subsecundodissecta* (Zoll.) Copel. and *C. whartoniana* (C. Chr.) Copel.

b. Upper Subalpine Forest

This occurs between 3600 m and 3900 m, i.e. to the upper limit of trees on the mountain, and covers a much smaller area than the lower subalpine forest. The canopy is lower (c 4.5–6 m) than that of the lower subalpine forest. The composition is basically that of the lower forest but with fewer species.

The fern flora is rather sparse in this upper forest. Some terrestrial species e.g. *Athyrium setiferum* C. Chr. and *Cyathea vandeuseni* Holttum were only collected in this community. Others, e.g. *Polystichum* spp., *Stenolepia tristis, Plagiogyria glauca* and *Hymenophyllum (Meringium) melanosorum* are also found in the lower subalpine forest and are less common in the upper forest. Epiphytes generally are fewer in numbers of both individuals and species and are also found in the lower subalpine forest e.g. *Hymenophyllum foersteri, Grammitis caricifolia, G. stanleyana* and *Loxogramme subselliguea. H. foersteri* is the most abundant epiphyte and is more common than at lower altitudes.

The margins of subalpine forest and subalpine grassland support a characteristic flora which includes species of *Olearia, Rhododendron, Dimorphanthera, Vaccinium, Coprosma, Eurya, Drimys, Amaracarpus, Polyosma* and *Symplocos,* some of which also occur as shrubs in the grassland. *Cyathea* spp., e.g. *C. aenifolia* (v.A.v.R.) Domin, *C. semiamplectens* Holttum and, to a lesser extent, *C. atrox* C. Chr., are a dominant feature. *Gleichenia bolanica* Rosenst. and *G. hooglandii* Holttum are common and form dense low thickets (especially the former species). *Plagiogyria papuana* C. Chr. and *Blechnum revolutum* (v.A.v.R.) C. Chr. may form small colonies.

The marginal flora is better developed at the edge of the lower subalpine forest than at the edge of the upper subalpine forest, and in the latter only *Gleichenia bolanica* is found in any abundance.

3. Grasslands

This occurs from 3300 to almost the highest part of the mountain. In its lower part it contains tussock grasses e.g. *Danthonia, Deschampia, Hierochloe* and *Poa,* although short grasses occur, especially in damper areas. Scattered shrubs may be common.

a. Subalpine Grassland

This occurs from 3300 to 3900 m. Tree ferns are a dominant feature of the grasslands, mainly pure stands of *Cyathea atrox* in the lower part of the area, with *C. muelleri* Baker and *C. macgregori* F. Muell. occurring further up the valley. *Elaphoglossum angulatum* and *Grammitis caricifolia* are very common epiphytes on the tree fern trunks. Fig 2 shows *C. macgregori* in subalpine grassland, while fig 3 shows *C. muelleri* in subalpine grassland near margin of lower subalpine forest. In drier areas where there are rocky outcrops *Belvisia revoluta* and a few other epiphytes grow in rock crevices in the lower part of the grassland, but there is not the same development of ferns as in the wetter landslip areas. *Asplenium trichomanes* L. and *Cheilanthes papuana* C. Chr. (fig 4) are of restricted occurrence in rock crevices in the higher parts while the monotypic genus *Papuapteris* (fig 5) is locally common in rocky areas of grassland in the upper part. *Schizaea fistulosa* Labill. Has also been recorded in the upper part of this community, on fine scree (Hoogland 1958). The few species of *Grammitis* growing on, or under, the rocky outcrops are, with two exceptions, both *G. aff. ornatissima* (Rosenst.) Copel., identical to those of the landslip areas. *Dryopteris wallichiana, Plagiogyria papuana, Blechnum revolutum, Gleichenia bolanica* and *G. hooglandii* are of scattered occurence. *G. vulcanica* Bl. forms quite dense colonies in wet low-lying areas.

b. Alpine Grassland

This association, is, not surprisingly, very poor in fern species and except for *Papuapteris linearis* C. Chr., those that do occur are usually in the shelter of rocks and shrubs. *Hymenophyllum (Mecodium) ooides* F. Muell. & Baker is very local terrestrially in the shelter of *Rhododendron* bushes, while *Gleichenia bolanica* and a few *Grammitis* species are found in sheltered sites.

4. Uppermost Rock Zone

Only one species, *Grammitis* sp., occurs in, and is largely restricted to, this habitat.

RELATIONSHIPS OF THE FERN FLORA

The majority of ferns on Mt Wilhelm have Malesian affinities but most of the species are endemic to New Guinea, e.g. *Gleichenia bolanica, G. hooglandii, Dicksonia sciurus,* all species of *Cyathea, Pteris, Polystichum, Grammitis* mentioned, all species of *Ctenopteris* (except *C. denticulata), Elaphoglossum hellwigianum, Blechnum revolutum, Hypolepis papuana* and *Cheilanthes papuana.* Several species are also found elsewhere in Malesia e.g. *Gleichenia vulcanica, Plagiogyria glauca, Elaphoglossum angulatum, Parathelypteris beddomei, Stenolepia tristis, Dryopteris wallichiana, Belvisia revoluta, Loxogramme subselliguea, Ctenopteris denticulata, Prosaptia contigua, P. davalliacea* and *Xiphopteris subpinnatifida.* In *Grammitis,* the species themselves are endemic, but most are closely related to other Malesian species, e.g. *G. graminifolia, G. stanleyana (G. fasciata* Bl. group); *G. locellata, G. stomatocarpa (G. stenocrypta* Copel. group); *G. novoguineensia, G. scabristipes (G. bulbotricha* Copel. – *G. limapes* Copel. group); *G.* spp. close to *G. ornatissima (G. fasciculata* Bl. group); *G. archboldii (G. setosa* Bl. group). Several other genera are centred in Malesia or South-east Asia, e.g. *Microsorium, Crypsinus, Selliguea, Lemmaphyllum* and *Loxogramme.*

A few species are common to New Guinea and Australasia e.g. *Schizaea fistulosa, Rumohra adiantiformis, Blechnum fluviatile* and *B. fraseri.*

Only one species, *Asplenium trichomanes,* is truly cosmopolitan.

For both higher plants (Wardle 1973) and pteridophytes there are many similarities in the New Guinea and New Zealand habitats of members of certain genera, e.g. *Gleichenia bolanica* and *G. cunninghamii* Hew. ex Hook. as marginal species in subalpine forest, *C. vulcanica* and *G. dicarpa* R. Br. var. *alpina* Hook. in boggy areas in subalpine grassland, *Grammitis* spp. in similar epiphytic and rupestral subalpine and alpine habitats, *Cyathea* and *Dicksonia* spp. in subalpine forests.

ACKNOWLEDGEMENTS

I am grateful to Dr N.M. Wace, Australian National University, Canberra, for permission to use the A.N.U. Research Station at Lake Aunde, Mt Wilhelm; Mr B. Maume, Assistant District Commissioner, Gembogl, for transport to Keglsugl; and to Mr J.S. Womersley and Mr E. Henty, Division of Botany, Department of Forests, Lae, for use of the herbarium and other facilities at Lae.

I should also like to thank Dr J.P. Croxall for assistance in the field, and for the use of colour transparencies from which R. Eudall and Miss M. Mitchell kindly prepared the black and white illustrations, and Mr A.C. Jermy for providing negatives.

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REVIEWS

POLLEN AND SPORE MORPHOLOGY/PLANT TAXONOMY: PTERIDOPHYTA by G. Erdtman and P. Sorsa. 302 pp. 1971 Price 40 Sv. kr.

This book is volume IV of an *Introduction to Palynology* and will take its place as a primary source book to spore morphology of Pteridophyta. The arrangement is alphabetical and the generic concept is that of Copeland, 282 genera being considered and the spores of some 1200 species are described in varying detail mostly from the authors's own observations. References are given to papers describing spores under each genus or species heading; the bibliography is extensive but some citations are difficult to track down (e.g. the Russian works). There are misspellings which, although easy to detect, lead one to suspect the volume and page numbers.

Spores for this enormous task were collected together by the senior author, the late Prof. Gunnar Erdtman, from herbaria throughout the world. This location of specimens is indicated under each species. What is not always certain is the authority of the determination. The spore illustrated (Pl. 6:4) as *Dryopteris carthusiana* is certainly not that tetraploid species which is (to quote Erdtman p 74) "densely spinulose granulate". It is most likely a spore of *D. assimilis* which being diploid has many fewer spines. The description part is illustrated by 60 SEM pictures which help but are not of very high standard.

The second part of the book (pp 227–295) is taken up by two very good papers on aspects of palynology. The first, by Dr John M. Pettitt, discusses some ultrastructural aspects of sporoderm formation in *Selaginella, Lycopodium Marsilea* and *Isoetes,* all of which are being studied further by that author. This paper is illustrated by 17 excellent electron micrographs, each of which is an essay in itself. In the second paper, Dr B.M. Gullvag discusses the fine structure of spores of *Equisetum, Lycopodium, Selaginella, Matteuccia, Polypodium vulgare* and *Blechnum spicant* before and during germination. One hopes that conclusions will not be drawn too rapidly on the observations of a few species but that the author, or her students, will continue this survey of plastid types and storage products. Both these papers contain fundamental data and add to the value of this very good book.

A.C. JERMY

UPLAND KENYA WILD FLOWERS by A.D.Q. Agnew. 827 pp, over 800 line-drawings, 255 x 200 mm (10 x 8 ins), Oxford University Press, 7 November 1974. Price £7.75.

This most carefully conceived and handsomely printed book is a pleasure, with its two-column layout, the concise yet explicit text (by the author and 19 contributors) with ample keys and line-drawings of diagnostic characters. Some plants (grasses, sedges, trees and woody shrubs) are not included because they are dealt with in separate currently available publications. *Upland* Kenya is its south-west third and includes dry thorn bushland, hot semi-desert, bush forest and alpine tundra, left by the Great Rift Valley. I quote the exact date of publcation because there are novelties (which need searching for as they are not distinguished or listed). New nomenclatural combinations I notice are two ferns *Blotiella stipitata* (Alston) Faden on p. 30, *Hymenophyllum capillare* Desv. var. *alternialatum* (Pic. Ser.) Faden on p. 28, and 14 Flowering Plants by Agnew on pages 466, 484, 635, 636, 638, 640, 643, 646; also there are *Ipomoea* "sp. nov." (p. 549), *"Saxymolbium* Bullock ined." (p. 374), and 176 species under review named A, B, etc. (gaps are not explained, e.g. *Xiphopteris* has sp. B but no sp. A); all are keyed out and treated in the general arrangement. There is hardly a spelling mistake or an inconsistency; among the ferns I notice *Didymochlaena "trunculata" (truncatula)* and *"Phanerophebia" (Phanerophlebia)* on p. 59. I'm all in favour of dichotomous keys but I find bracketed ones (as in this book) far less practical than yoked which, if indented, gives an even quicker visual image and, to save space, numbering can often be acceptably dispensed with.

The pteridophytes are dealt with by R.B. Faden who, regarding current discussion among pteridologists, has declined to give a key to, or descriptions of, families and has recommended us to consult Alston, Tardieu-Blot and "the most generally useful" Schelpe's Pteridophyta in *Flora Zambesiaca.* I wish page numbers were in the key, because the page headings do not give genus-numbers, only "Pteridophytes" (the Flowering Plants are better served with families and genus-numbers). Using key, text and pictures, I got into a muddle trying to understand *Asplenium* sp. B; it is placed no. 20, yet is supposed to be near nos. 9 & 10; 10 & 20 are figured, 9 says "gemmae", yet 10 is figured with a terminal gemma; 20 is "strictly epiphytic"; but my muddle is presumably due to my yoked versus bracketed thinking.

I heartily recommend this most useful book, particularly for anyone interested in nearly 3,000 species of wild plants growing at over 3,000 feet in Kenya and adjoining areas.

J.A. CRABBE

EQUISETUM SUBGENUS EQUISETUM IN THE SINO–HIMALAYAN REGION – A PRELIMINARY TAXONOMIC AND EVOLUTIONARY APPRAISAL

C.N. PAGE
The Herbarium, Royal Botanic Garden, Edinburgh

ABSTRACT

Evidence is presented from a study of both overall structure and micromorphology that specimens of *Equisetum* subgenus *Equisetum* in the Sino-Himalayan region show a wide range of morphological diversity and character-sharing atypical of the plants throughout the rest of their world ranges, and that the area also contains several endemic taxa. Four species, four varieties and one hybrid are recognised in the Sino-Himalayan region, a key to their identification provided and their geographic ranges plotted. The significance of the morphology of the Sino-Himalayan taxa is discussed in relation to the evolution of the subgenus. It is concluded that the Sino-Himalayan region has been a major centre of species-formation in this subgenus in the past and now contains some of the remnants of a former species complex, whilst many of the now distantly-spread taxa also show morphological affinities with the plants in this area indicative of their having evolved from the same complex. Thus, in contrast to currently established views of evolution in *Equisetum,* this survey suggests that the majority of species of subgenus *Equisetum* are palaeotemperate rather than neotropical in origin, and that the two subgenera *Equisetum* and *Hippochaete* have probably had relatively independent origins in the near geological past.

INTRODUCTION

The number of views concerning phylogeny and evolution among the living species of *Equisetum* are few and largely dominated by those put forward by Schaffner (1925, 1930 a & b) and more recently restated in the light of taxonomic modifications within subgenus *Hippochaete* by Hauke (1963).

Schaffner considered all living species of both subgenera of *Equisetum* to have evolved from a single common ancestral species which lived in the Cretaceous "somewhere in the region between Mexico and Chile". This hypothetical ancestral species is regarded by him as being most closely approached amongst living plants by *Equisetum giganteum* L., which still occurs in this area. From this starting point Schaffner postulated two separate evolutionary lines evolving and differentiating into the modern species, each in a phylogenetically more or less linear manner. These two lines became the modern subgenera, *Equisetum* and *Hippochaete**. Thus he viewed subgenus *Equisetum* as an early offshoot of the Central American stock, having *Equisetum fluviatile* as its "most primitive" species and *Equisetum arvense* as its "most advanced".

Schaffner further regarded the present day geography of *Equisetum* to be "in almost perfect accord" with his phylogenetic scheme, and it is probably because he thus painted such an apparently complete and simple picture of evolution of all modern species of horsetails from a single Central American ancestor that his overall picture of species formation in the genus has remained little challenged.

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* I have, in this account, used the term "subgenera" for the members of the *Equisetum* and *Hippochaete* groups of horsetails, to accord with general usage, without necessarily wishing to imply at this stage any final taxonomic opinions on the ultimate status which must be accorded to each.

In an earlier paper (Page 1972a) I first indicated that after a study of both macro- and micro-morphology of *Equisetum* there seemed little evidence to support the view that either subgenus *Equisetum* had necessarily evolved as an offshoot of subgenus *Hippochaete* as envisaged by Schaffner or that the species within subgenus *Equisetum* are related to one another in a linear manner.

Further study of the species concerned has indeed now substantiated this view.

MATERIALS AND METHODS

This study is based on examination of herbarium material of *Equisetum* from Indian herbaria together with that held at a number of European herbaria with large collections of Chinese-Himalayan origin. I would like to record my gratitude to the Directors of the Institutes named for kind co-operation in making available facilities for study and/or for loan of specimens. Holdings from the following herbaria have been examined:

Botanical Survey of India, Central National Herbarium, Howrah (CAL);
Botanical Survey of India, Northern Circle Herbarium, Dehra Dun (BSD);
Botanical Survey of India, Eastern Circle Herbarium, Shillong (ASSAM);
National Botanic Gardens, Lucknow (LWG);
Museum National d'Histoire Naturelle, Paris (P);
British Museum (Natural History), London (BM);
Royal Botanic Gardens, Kew (K);
Royal Botanic Garden, Edinburgh (E).

Near the centre of diversity of a species group, satisfactory taxonomic treatment of the plants involved becomes difficult but extremely necessary for an understanding of the entities concerned, and as a basis for satisfactory discussion of their inter-relationships.

I have here thus tried to delimit the taxa within *Equisetum* subgenus *Equisetum* in the Himalayan and Western China area on the basis of the collections I have seen — I have included with each, where possible, some indication of its range of morphological variation and where appropriate, in what ways it varies from its more widespread forms elsewhere.

In drawing morphological taxonomic comparisons in *Equisetum* subgenus *Equisetum* I have come to regard the detailed structure of the branches as seen externally with a low power hand lens (especially the internode ridge-and-furrow structure, the shape and proportions of the sheath and teeth) as providing particularly reliable taxonomic characters, showing relatively minimal variation in response to environment. The features of the main stem internodes and the sheath (its shape, relative proportions of free and fused parts, the shape of the teeth and their margins, and the ribbed structure of each segment) provide further valuable corroborative characters, whilst the overall habit and shape of the shoot (especially the length of the first internode of the branches), and the constancy of the monomorphic versus dimorphic character, when treated with appropriate caution, provide further features of taxonomic use (Page 1972a, b; 1973). All these can be seen readily in the field or in the external structure of a herbarium specimen.

Use of the scanning electron microscope to survey the fine surface structure of the plants has previously proved an especially valuable tool for providing further valuable data on which to base assessments of inter-specific relationships in *Equisetum* (Page 1972a). I have thus examined the structure of all the more critical Sino-Himalayan specimens by this means and used this as additional data in drawing phylogenetic conclusions.

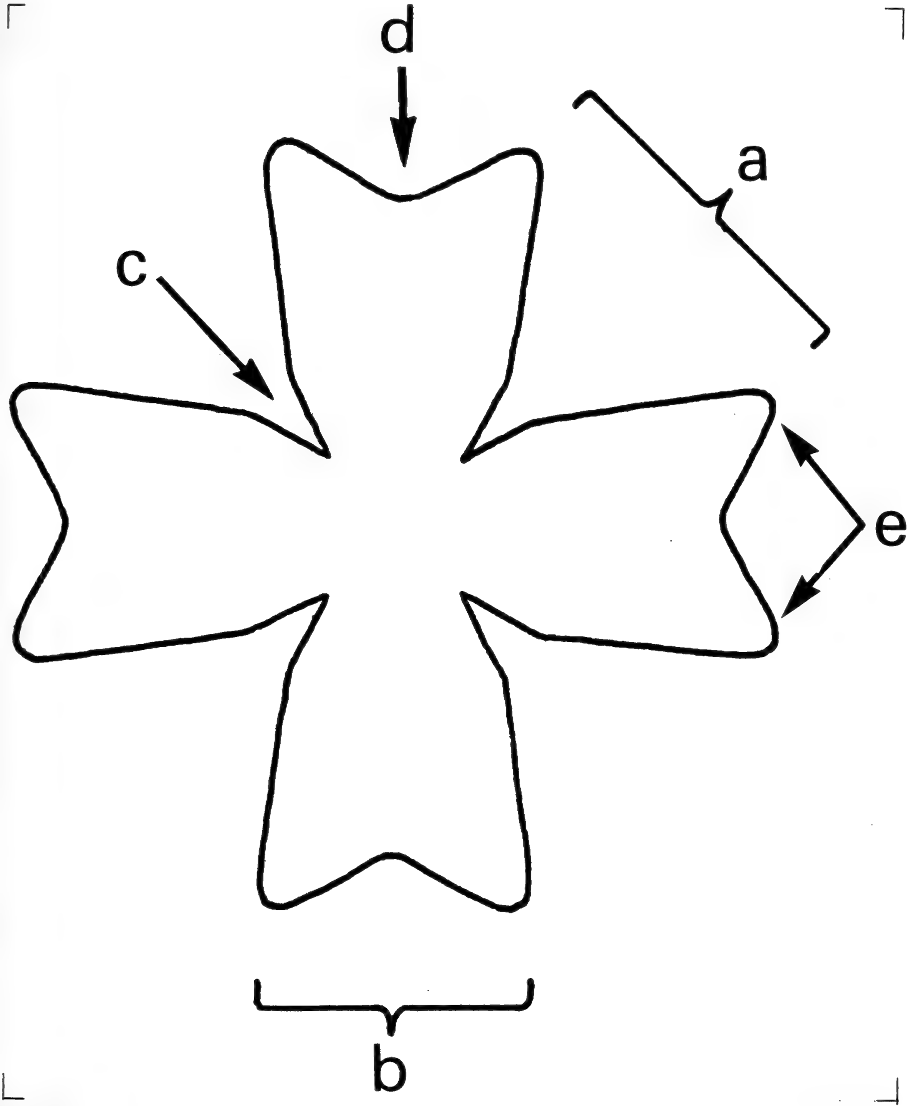

FIGURE 1: Diagram to illustrate the terminology adopted here for the description of branch morphology of *Equisetum:*
a, furrow (latin: vallecula); b, ridge (latin: carina); c, channel (latin: canaliculus); d, groove (latin: sulcus); e, angles (latin: angulae), here the specimen is biangulate.

KEY TO TAXA

Artificial Key to the Sino-Himalayan taxa of *Equisetum* subgenus *Equisetum* (See fig 1 for explanation of terminology).

Subgenus *Equisetum* has stomata on stem surface not sunken

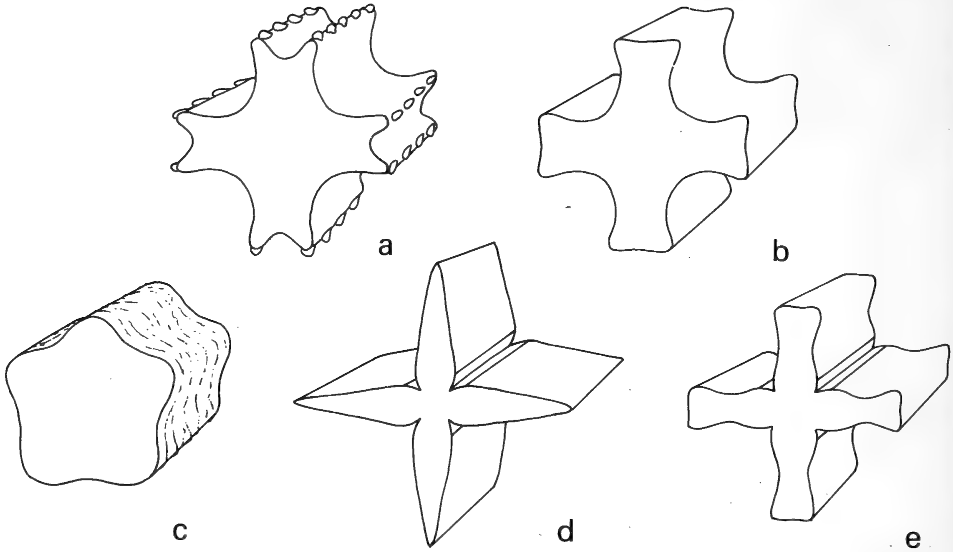

FIGURE 2: Block-diagrams to illustrate the characteristic types of branch-internode structure of Sino-Himalayan taxa of *Equisetum:* a, that of *E. diffusum* var. *diffsum* and *E. mekongense;* b, that of *E. diffusum* var. *paucidentatum;* c, that of *E. palustre* var. *palustre* and *E. palustre* var. *szechuanense;* d, that of *E. arvense;* e, that of *E.* x *wallichianum.*

1. Shoots distinctly dimorphic (cones normally borne on separate, morphologically distinct, short-lived non-photosynthetic shoots) 2

Shoots monomorphic (vegetative and cone-bearing shoots similar in general morphology) 3

2. Internodes of branches of vegetative shoot with simple, narrowly acute ridges, and V-shaped furrows with a narrow central longitudinal channel, visible with a hand lens (fig. 2d) . . . . . . *E. arvense*

Internodes of branch of vegetative shoot with distinctly biangulate ridges (having a narrow longitudinal groove along the apex of each ridge — fig. 2a) . . . . . . *E. mekongense*

3. Internodes of branches of all shoots with simple, rounded or acute angles 4

Internodes of branches with angles not simple, but either markedly truncated (flat-topped) in section (fig. 2b or 2e) or distinctly biangulate (having a narrow longitudinal groove along the apex of each ridge — fig. 2a) 6

4. Internodes of branches with narrowly acute ridges and V-shaped furrows, each furrow with a narrow central longitudinal channel, visible with a hand lens (fig. 2d) . . . . . . *E. arvense*

Internodes of branches with only low, rounded angles and shallow rounded furrows (fig. 2c) 5

5. Main shoot sheath-teeth short (less than 2/3 the length of the fused portion of the sheath), broad, with broad scarious margins and the fused portion of each segment without distinct keels . . . . . . *E. palustre* var. *palustre*

Main shoot sheath-teeth long (more than 2/3 the length of the fused portion of the sheath), narrow, with narrow scarious margins and the fused portion of each segment with distinct paired keels . . . . . . *E. palustre* var. *szechuanense*

6. Internodes of branches with truncated ridges or at least with only a very shallow ridge groove (fig. 2b or 2e) 7

Internodes of branches with distinctly biangulate ridges (having a narrow longitudinal groove along the apex of each ridge — fig 2a) . . . . . . *E. diffusum* var. *diffusum*

7. Internodes of branches with furrows rounded in section, each furrow without a central longitudinal channel (fig 2b) . . . . . . *E. diffusum* var. *paucidentatum*

Internodes of branches with furrows approximately V-shaped in section, each furrow with a narrow central longitudinal channel visible with a hand lens (fig 2e) . . . . . . *E.x wallichianum*

DESCRIPTION AND DIAGNOSIS OF TAXA

Equisetum diffusum D. Don, Prodr. Fl. Nepalensis: 19 (1825).

Long recognised as distinct from the more widespread species of *Equisetum,* this Himalayan endemic resembles *E. palustre* in general habit and size, having an invariably monomorphic type of shoot, the fertile ones of which terminate in typically long ovoid-cylindric cones. Most shoots bear regular whorls of long, green branches of spreading or ascending habit from all the nodes in the lower 1/3 to 2/3 of the shoot, although, as in *E. palustre,* occasional unbranched shoots occur (these often bear cones).

Distinctive from *E. palustre,* however, are the branch internode ridges, which are either truncated in section (fig 2b) or, most often, are conspicuously biangulate, (i.e. each ridge having a conspicuous narrow longitudinal groove along its apex, fig 2a). The biangulation of the ridge can be seen clearly even with a low power hand lens, and it continues into the branch leaf sheath to give each constituent leaf member a prominently 2-keeled appearance, the keels extending into, and usually more than half way along, the free portion of each leaf. Likewise, on the main stem the internodal ridges are shallowly biangulate, becoming almost flat-topped in specimens where biangulation in the branch internode is relatively poorly conspicuous. The biangulation persists into the main shoot sheaths to give each segment a prominently 2-ribbed appearance to at least ½–⅔ the way along the free portion of each tooth. On branches and main stems the free teeth of the sheaths are long (about ⅔ as long to often longer than the fused portion of the sheaths) with the free portions narrowly acute and lacking scarious margins. The first branch internode varies in length from a little shorter than, to up to twice as long as, the length of the adjacent stem sheath.

The biangulate branch internodes and 2-keeled sheaths, as well as the long first branch internode distinguish *E. diffusum* clearly from all specimens of *E. palustre. E. diffusum* can be distinguished from *E. arvense* especially by its biangulate branch ridges whilst its invariably monomorphic habit serves to separate it also from *E. mekongense* (described here). *E. diffusum* differs from all plants of the *E. telmateia* complex (which have similar biangulate branch ridges) chiefly by its relatively small size, green stem internodes with usually not more than 14 ridges, and ovoid cylindric cone.

Equisetum diffusum thus represents a good distinct entity in *Equisetum* subgenus *Equisetum* worthy of specific rank*.

Sub-specific variation: *Equisetum diffusum* shows wide variation in overall growth habit. Four varieties have been named by Milde (1867) (vars. *caespitosum, ramosum, nudum* and *polystachum*). All seem environmentally-induced growth habits of little taxonomic consequence.

In most plants of *E. diffusum* the biangulation of the branch internodes is conspicuous and each of the two angles of the branch ridge so formed is armed with a single row or more or less prominent dentate-serrate projections (fig 2a), the ridge-tubercles (Page 1972a: 359). The presence or absence of such ridge tubercles and their type is a relatively faithful feature of most species of subgenus *Equisetum.* I have,

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* Wallich used the manuscript names *Equisetum bicarinatum* Wall., *E. laeve* Wall., and *E. scoparium* Wall., for collections which were probably *E. diffusum,* although one sheet I have examined of *"Equisetum scoparium* Wallich 398" (K) is mixed and contains a specimen also of the hybrid *E. arvense* x *diffusum* (described here). None of these names is validly published and all are *nomina nuda.* Baker (1887) cites all three as synonyms of *E. diffusum* Don.

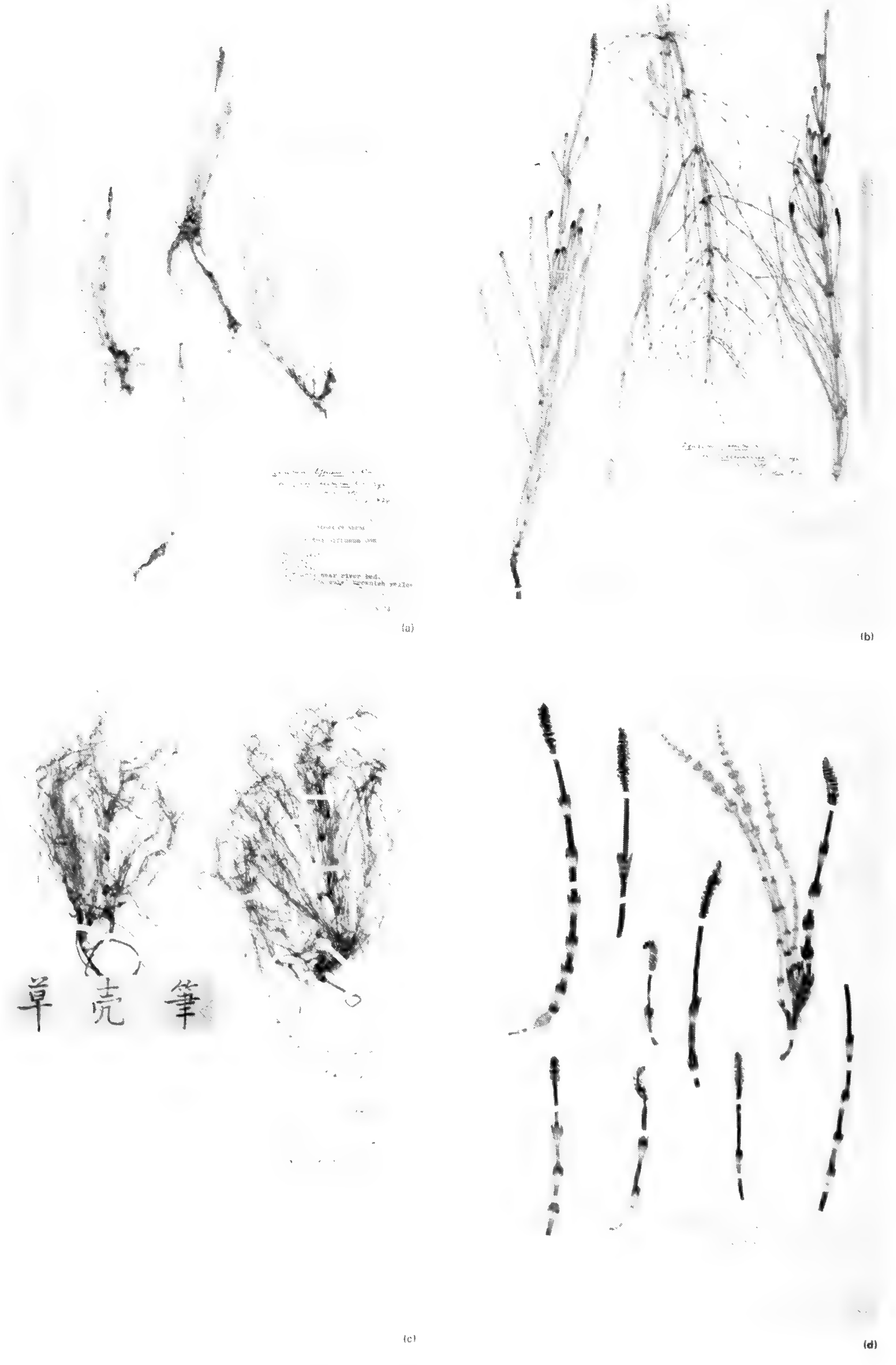

FIGURE 3: Type specimens of taxa of *Equisetum* described here: a, *Equisetum diffusum* var. *paucidentatum* (E); b, *E. palustre* var. *szechuanense* (E); c, *E.* x *wallichianum* (K); d, *E. mekongense* (P).

however, found a number of specimens of *E. diffusum* which have only flat-topped truncated angles to the branch internodes (fig 2b) and also largely or entirely lack the ridge tubercles (fig 2b). Most such specimens came from Central Nepal, and seem sufficiently distinct and constant in type to treat as a separable recognisable entity, *E. diffusum* var *paucidentatum.*

Equisetum diffusum D. Don var *diffusum.*

Characterised by ridges of branch internodes with a distinct longitudinal groove and dentate ridge tubercles.

Equisetum diffusum D. Don var *paucidentatum* C.N. Page *var. nov.*

Carinae internodiorum ramorum truncatae, et sulco et tuberculis absentibus vel fere absentibus.

Ridges of branch internodes truncated and lacking both the characteristic longitudinal groove and ridge tubercles, or nearly so.

Type: NEPAL: near Maikot, 7,500 ft. Moist area near river bed. *Stainton, Sykes & Williams 4734,* 8. Oct. 1954 (*E,* isotype *BM*).

Paratypes: NEPAL: Mardi Khola, on banks of paddy terraces, 4,000 ft, Stainton, Sykes & Williams, no. 7197, 13 Sept. 1954 (BM); NEPAL: Langtang-Syarpagon, damp swampy ground, 9,500 ft. O. Polunin, no. 1821, 23–31 August 1949 (BM); NEPAL: Bhragu, cultivated ground, 7,000 ft, O. Polunin, no. 096A, 1949 (BM); NEPAL: Mayangoli Khola, amongst sand on river bed, 3,500 ft. Stainton, Sykes & Williams, no. 4216, 5 Sept. 1954 (BM); INDIA: Garhwal. M.A. Rau no. 10045; INDIA: Simla, 7,000 ft. G. Watt 12 Sept. 1887.

Equisetum arvense L. Sp. Pl., ed. 1: 1061 (1753).

As in the rest of its range, *E. arvense* in the Sino-Himalayan area is characterised by having branch internodes with simple acute ridges and broad V-shaped furrows with flat flanks, and a narrow lengthwise basal channel interrupting the distribution of stomata across the furrow (fig 2b). In most plants the branch sheaths have free tips which are green and spreading. Branches are usually four-angled with the first branch internode generally up to 2–3 times the length of the adjacent stem sheath. The surfaces of shallow rhizomes are covered by a brownish tomentum, found elsewhere only in *E. diffusum.* Cones in this species, even when present on otherwise vegetative stems, are always markedly ovoid in shape (never ovoid-cylindric), mostly pale in colour, and generally borne on long pedicels.

The characters of the branch internodes serve to distinguish *E. arvense* from all other species and hybrids in *Equisetum.*

Sub-specific variation: Thus defined, plants of *Equisetum arvense* show considerable local variation in detailed taxonomic characters in the Sino-Himalayan area.

In material from Chefu, China, large and vigorous plants occur which nevertheless possess only predominantly 3-angled branches, although it has not been possible to determine whether this condition is general in the area. In other specimens from Kansu and Tibet, normal 4-sided branches are present but armed with prominent dentate-type tubercles similar to those of *E. diffusum,* whilst the same specimens also possess main stem sheaths with unusually long narrow acute blackish 2-ribbed teeth – features also more usually associated with *E. diffusum.* Throughout most of the Sino-Himalayan area, shoots of *E. arvense* are characteristically dimorphic, and in all specimens examined from China which are fertile this is a particularly distinct trait – the fertile shoots being totally devoid of developing whorled branches, white, with cones well exserted above the uppermost leaf-sheath on particularly long (3–4 cm) pedicels. By contrast several Tibetan specimens are relatively poorly dimorphic, having greenish cone-bearing shoots developing green branches from many of the lower nodes

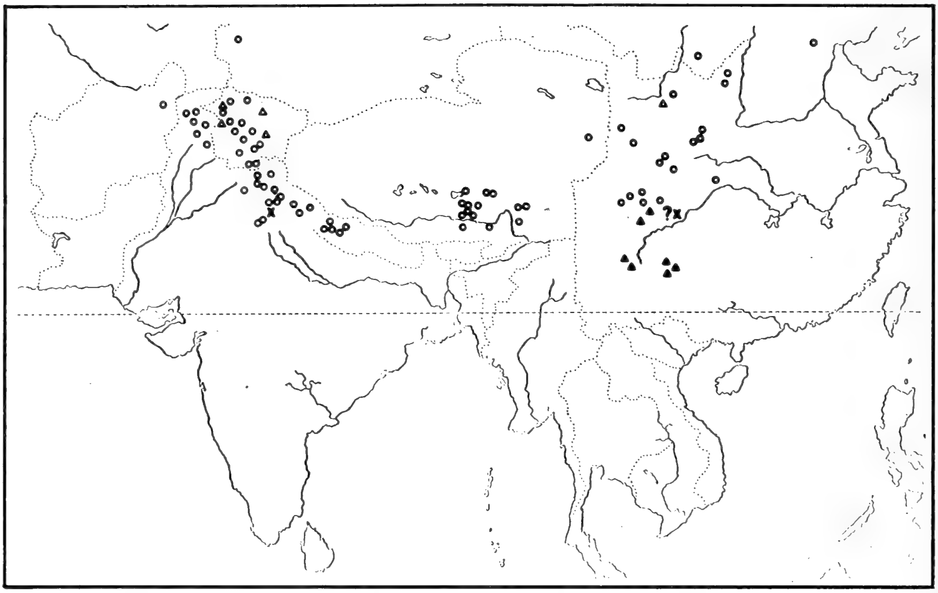

FIGURE 4: Natural distribution of Sino-Himalayan taxa of *Equisetum* subgenus *Equisetum* compiled from authenticated herbarium specimens: open circles (O) = *E. arvense;* open triangles (△) = *E. palustre* var. *palustre;* solid triangles (▲) = *E. palustre* var. *szechuanense;* crosses (X) = *E.* x *wallichianum* (? = approximate location only).

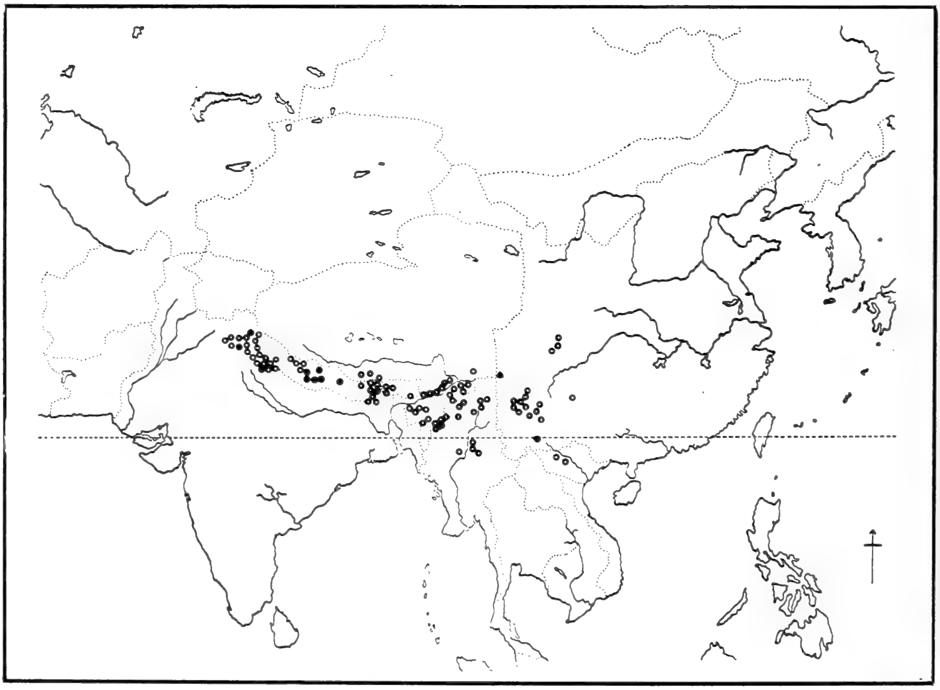

FIGURE 5: Natural distribution of Sino-Himalayan taxa of *Equisetum* subgenus *Equisetum* complied from authenticated herbarium specimens: open circles (O) = *E. diffusum* var. *diffusum;* solid circles (●) = *E. diffusum* var. *paucidentatum;* solid triangle (▲) = *E. mekongense.*

even before maturity of the cone. This trend is further accentuated in some specimens from the western Himalayas in which cones seem to be produced *only* on the tops of otherwise vegetative stems, although it is not known whether this is the general condition in plants in any part of this area. All such specimens however retain the characteristic cone-shape and pale colour of *E. arvense* and cones are borne on typically long pedicels.

Very many other small variations also occur even in good morphological characters in material of *E. arvense* from the Sino-Himalayan area, perhaps rather greater than that seen in the species over the whole of the rest of its range, suggesting the presence of a large polymorphic population. Despite this variation, however, *E. arvense* remains a distinct specific entity within the Sino-Himalayan area, and the virtual continuity of the intra-specific variation does not seem to justify segregation of the entities for recognition at a formal taxonomic level. This variation, however, remains worthy of note.

Equisetum palustre L. Sp. Pl., ed. 1: 1061 (1753)

Specimens of *Equisetum palustre* are characterised by having simple rounded angles and furrows to both the branch and stem internodes (fig 2c), very short first internode to the branch (usually less than ½ and often only ¼ the length of the adjacent stem sheath), stem with usually less than about 9 sides (often only 5 or 6 sides), long blackish cone distinctly ovoid-cylindric in shape usually borne on a relatively short pedicel rarely more than the length of the cone itself, and constantly monomorphic type of shoot. The internodes of the rhizome are blackish brown and shiny, always lacking any brownish tomentum.

The features of the branch internode morphology plus the distinctly ovoid-cylindric cone serve to distinguish *E. palustre* from all other species and hybrids in *Equisetum.*

Sub-specific variation: As elsewhere in Eurasia, specimens of *E. palustre* from both the western end of the Himalayas and from northern China (Kansu northwards) possess branch sheath-teeth which are broad, short, blackish, and typically more or less closely pressed to the stem; and main shoot sheath-teeth which are short (usually not more than ¼ the total length of the sheath), broadly triangular (often nearly equilateral) with conspicuous broad scarious margins). However, all specimens of *E. palustre* examined from south western China (Yunnan, Szechuan and Kweichow) have been consistent in differing substantially in these characters. All possess branch-sheaths which have relatively long free teeth which are often not closely appressed to the stem and may be partially spreading, whilst the main shoot sheaths are also long (up to 9 mm), each segment distinctly 2-keeled (not just shallowly 2-ribbed as in this species over much of its range) and the free portions of the leaves, which are up to ½ the overall length of the sheaths are long, narrow, acute, blackish, individual (i.e. not adhering in pairs) and more or less without broad scarious margins. In these features they approach closely the structure of the sheaths of *Equisetum diffusum.* These specimens are also exceptionally robust (with shoots to 65 cm), and frequently polystachious with each cone little, if at all, exserted from the uppermost sheath. In overall habit and sheath structure these plants thus approach closely the morphology of *E. diffusum* and I had at first thought that they might represent hybrids between *E.*

palustre and *E. diffusum* (the latter species is present in this area). However, all retain the typical branch and stem internode morphology of *E. palustre* (fig 2c) and in other general morphological features give no indication of intermediacy between *E. palustre* and *E. diffusum.* Nor is there any indication of reduced coning behaviour, and in the absence also of the typical form of *E. palustre* in this area I am forced to conclude that these south western chinese specimens represent a good geographical variant of *E. palustre* less strongly distinct from *E. diffusum* than is the species throughout the rest of its range.

I have thus given these plants formal taxonomic recognition, but in the lack of more extensive information about the biological and ecological relationship of this plant with *E. palustre,* with which it clearly has its strongest affinities, I have not felt justified at this stage in treating it at any higher rank than a variety, *Equisetum palustre* var. *szechuanense.*

Equisetum palustre L. var. *palustre*

Characterised by teeth of stem sheaths short, with broad scarious margins and without prominent paired keels on the sheath segments.

Equisetum palustre L. var. *szechuanense* C.N. Page *var. nov.*

Dentibus vaginarum caulium longis, augustis, acutis, angustius scarioso-marginati; segmenta vaginae distincte bicarinata.

Teeth of stem sheaths long, narrow, acute, with relatively narrow scarious margins; each sheath segment with distinct paired keels.

Type: CHINA: Kweichow: environs de Kouy-yang. Bord des ruisseaux (Kien Lin Chan). Emile Bodinier No. 2449, 26 Juillet 1898 (*E,* isotype *P*).

Paratypes: CHINA: Yunnan: Vicinity of Yun Nan Sen. E.P. Maire, no. 2933, received Nov 1906 (E); CHINA: Szechuan: Pao Hsing Hsien, 2700 m, K.L. Chu, no. 3412, 4 Aug 1936 (E): CHINA: Szechuan: Omei Hsien. S.S. Chien, no. 5405, 2 May 1936 (E); CHINA: Szechuan: Omei Hsien, by the stream 1500–2000 ft. W.P. Fang, no. 3379, 27 Aug 1928 (E); CHINA: Szechuan: Pao Hsing Hsien, river bank, 2000 m. K.L. Chu, no. 3932, 21 Sept. 1936 (E); CHINA: Kweichow: Environs de Kouy Yang. Bord des ruisseaux. Emile Bodinier, 26 Juillet 1898 (P); CHINA: Yunnan: Plaine de Tong Tchouan, terrains humides, 2900 m, E.E.M. Plantes du Yunnan — R.P. Maire, Reçu la 30 Juillet 1913 (P).

In var. *szechuanense* teeth of the stem sheaths are usually more than 3 times as long as wide and more than ⅔ the length of the fused portion of the sheath. Specimens are often robust and polystachious with cones little exserted from the uppermost sheath.

Equisetum x wallichianum C.N. Page *hybr. nov. (E. arvense* L. x *E. diffusum* Don var. *diffusum).*

Caules steriles 20–45 cm vel ultra alti, erecti, 1–2 mm diametro, virides, annui; valleculae 4–6 vel ultra, haud profundae, rotundatae; carinae plerumque truncatae, leves; vaginae (dentibus inclusis) 4.5–7 mm; lentes liberi trientem vel dimidium vaginae aequantes, augusti, acuti, virescentes vel nigrescentes; segmenta vaginae levites bicostata. Rami numerosi per inostrientes medios caulis, 8–12 cm, patentes vel suberecti, plus minusve regularites verticillati; simplices; internodium infirmum vagina proxima 1½–2 longius; internodia plerumque quadrangularia; valleculae late et haud profunde V-formes, canaliculo parvo medio inter stomata saepe praediti; carinae acutae sed saepe auguste truncatae et leviter sulcatae (fig 2e); vaginae ramorum pallidae, 1.5–2.0 mm, dentibus liberis trientem veldimidium vaginae aequantibus triangularibus acuminatis patentibus plerumque omnino veridibus; segmenta plerumque ad medium dentem minute bicostata costis saepe tuberculis minute dentato-serrulatis praeditis. Rhizoma tormento ferrugineo- brunneo indutum.

Vegetative shoots with stems 20–45 cm or more, erect, 1–2 mm diameter, green, annual; furrows 4–6 or more, shallow, rounded; ridges usually truncated, smooth; sheaths (including teeth) 4.5–7.0 mm; free teeth ⅓–½ length of sheaths, narrow, acute, greenish or blackish; *each sheath segment shallowly 2-ribbed.* Branches abundant throughout middle ⅔ of shoot, 8–12 cm, spreading

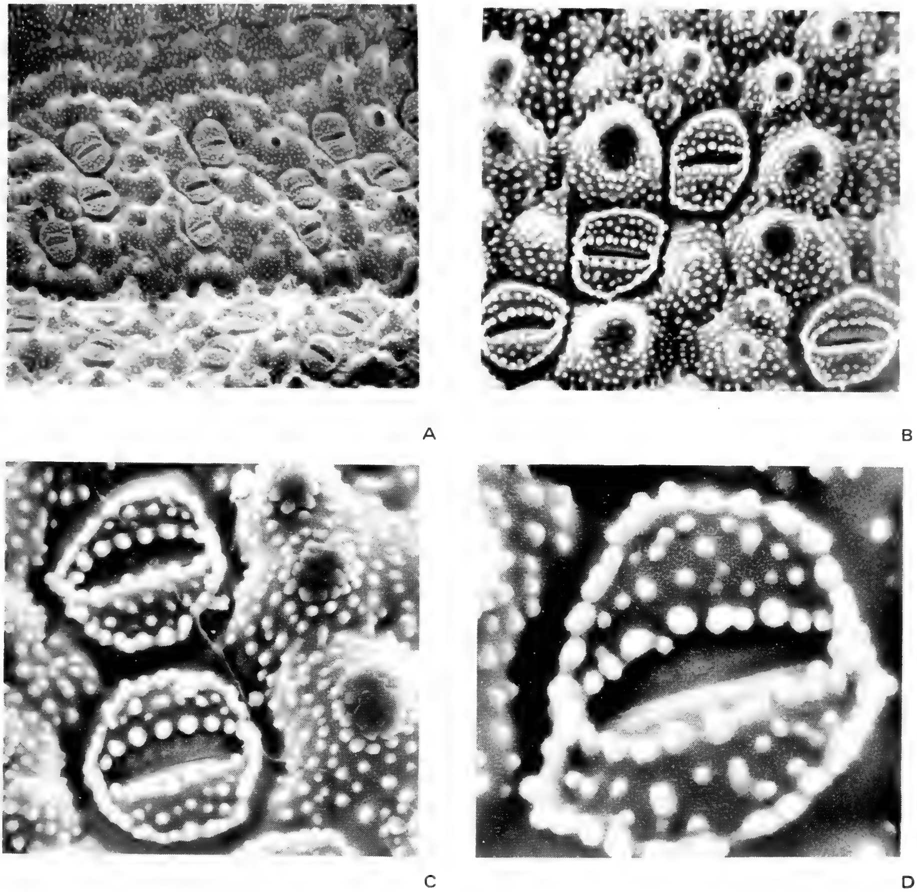

FIGURE 6 a–d: Scanning electron micrographs of the branch internode morphology of Sino-Himalayan *Equisetum arvense:* a, Tibet: 15 miles E of Lhasa, Kyi Chu Valley, H.J. Walton, Aug. 1904 (K), showing conical mamillae and scattered stomatal cell areas with inclined apertures, and clearly visible central channel to branch furrow (x 88); b-d, China: Eastern Szechuan, R.P. Farges No 1150 (E), showing relatively prominent thickly pilulate mamillae, and stomatal cell areas with elongate pilulae adjacent to the pore and around the outer periphery (x 208, x 404, x 820 respectively).

to suberect, in ± regular whorls, simple; the lowest internode 1½–2 times length of adjacent stem sheath; internodes mostly 4-angled, the furrows broad, *shallowly V-shaped, each often with a very shallow central channel interrupting the distribution of the stomata across the furrow, the ridges acute but often truncated by a narrow flat top with a shallow lengthwise groove* (fig 2e); branch sheaths pale, 1.5–2.0 mm, free teeth occupying 1/3–1/2 length of sheaths, trangular acuminate, *spreading, usually green throughout;* each segment usually minutely 2-ribbed to about half way along each free tooth, the ribs often with minutely dentate-serrulate tubercles.

Rhizome with rust brown tomentum.

Holotype: Com. F.S.A. Bourne, Chung-Ching. recd. 1/1886 [without detailed locality but probably collected in Western Szechuan] (K).

Paratypes: "Equisetum scoparium" Wallich 398. E. Ind. [without detailed locality but probably from Nepal] *; INDIA: Garhwal: Grohna, along lake margin. M.A. Rau, B.S.I. No. 10070, June 1959 (K).

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* *"Equisetum scoparium* Wall." is a *nomen nudum.*

Equisetum x *wallichianum* is distinctly intermediate in morphology between *E. arvense* and *E. diffusum* var. *diffusum.* It resembles *E. arvense* particularly in having broad furrows to the branch internodes with a shallow lengthwise central longitudinal channel separating the stomata on either flank; narrow acute ridges between the angles; and branch sheaths with spreading teeth. It resembles *E. diffusum* var. *diffusum* particularly in having truncated or biangulate ridges to the branch internodes and 2-ribbed segments to the branch and main stem sheaths.

E. x *wallichianum* can be distinguished from either parent by the combination of truncated branch ridges and branch furrows with a central channel, and from *E. diffusum* var. *paucidentatum* especially by the hybrid's broad V-shaped (versus shallowly rounded) branch internode furrows with central channel.

The direct morphological intermediacy of *E.* x *wallichianum* between local material of *E. arvense* and *E. diffusum* var. *diffusum,* its presence in areas where both parent taxa overlap, and sporadic occurrence in at least 3 widely separate localities within this area, leave little doubt that *E.* x *wallichianum* is the hybrid between them.

Equisetum mekongense C.N. Page *sp. nov.*

Caules valde dimorphici; steriles nempe 20 cm (fortasse 30–40 cm) alti, erecti, 2.5–3 mm diametro, ramosi, annui, virides; valleculae c. 11–15, haud profundae, rotundatae; carinae biangulatae, leves; vaginae (dentibus inclusis) 6–8 mm; dentes liberi trientem vaginae aequantes, angusti, acuti, fusco-brunnei saltem in dimidio superiore interdum peranguste scarioso marginati, saepe per paria cohaerentes, carina internodali biangulata in segmentum vaginae percurrente et costas duas planiusculas sulco angusto sejunctas formante. Rami numerosi per dimidium vel duos trientes superiores; internodia plerumque quandrangularia, carinis sulco conspicuo praeditis; vaginae ramorum pallidae, c. 2 mm; dentes liberi¼–⅓vaginae, late triangulares, appressi, virides, apice minuto patente nigro; segmenta prominenter carinata, carinis tuberculis conspicius dentato-serratis ad tertiam partem dentis percurrentitibus praeditis.

Caules coniferi 8–22 cm, erecti, 3–5 mm diametro, achlorophylli, simplices, ephemeri; sulci 10–12, haud profundi, rotundati; vaginae 12–16 mm laxae, segmentis conspicue 2-costatis per totam longitudinem; pedunculus 4–6 cm; strobilus 2–4 cm, ovoideo-ellipsoideus.

Rhizoma ferrugineo-tomentosum.

Fertile and sterile shoots strongly dimorphic. Vegetative shoots at least 20 cm (probably 30–40 cm in mature shoots), erect, 2.5–3.0 mm diameter, branched, annual, green; furrows circa 11–15, shallow, rounded; *ridges biangulate, smooth;* sheaths (including teeth) 6–8 mm; free teeth circa ⅓ length of the sheaths, narrow, acute, dark brown at least in upper halves sometimes with very narrow scarious margins, often cohering in pairs, the biangulate internodal ridge continuing into each sheath segment to form *two broad flattish ribs* with a narrow groove between. Branches abundant throughout most of the upper ½– of shoot, internodes mostly 4-sided, the *ridges with a conspicuous deep lengthwise groove;* branch sheaths pale, circa 2 mm, free teeth occupying¼–⅓ length of sheaths, broadly triangular, appressed, green, with a minute black spreading tip; *each segment prominently 2-keeled, the keels with conspicuous dentate serrate tubercles extending up to ¾ of the way along each free tooth.*

Cone-bearing shoots 8–22 cm, erect, 3–5 mm diameter, without chlorophyll, simple, ephemeral; furrows 10–12, shallow, rounded; sheaths 12–16 mm, loose; each segment conspicuously 2-ribbed throughout its length; peduncle 4–6 cm; cone 2–4 cm ovoid-ellipsoid.

Rhizome with rust brown tomentum.

Type: CHINA: NW Yunnan: Nekou (Haut Mekong); Vallee de ? Guiagatory, J. Lile No. 1496, 20 April–6 May 1899. *Plantes de Chine (Thibet oriental) of R.P. Soulie* (P). Known only from the type.

Equisetum mekongense is distinctive in having strongly dimorphic vegetative and fertile shoots, the vegetative ones with prominently 2-keeled branch sheaths, the fertile ones being ephemeral and bearing ovoid-ellipsoid cones. The combination of these features distinguishes *E. mekongense* from all other species of *Equisetum.*

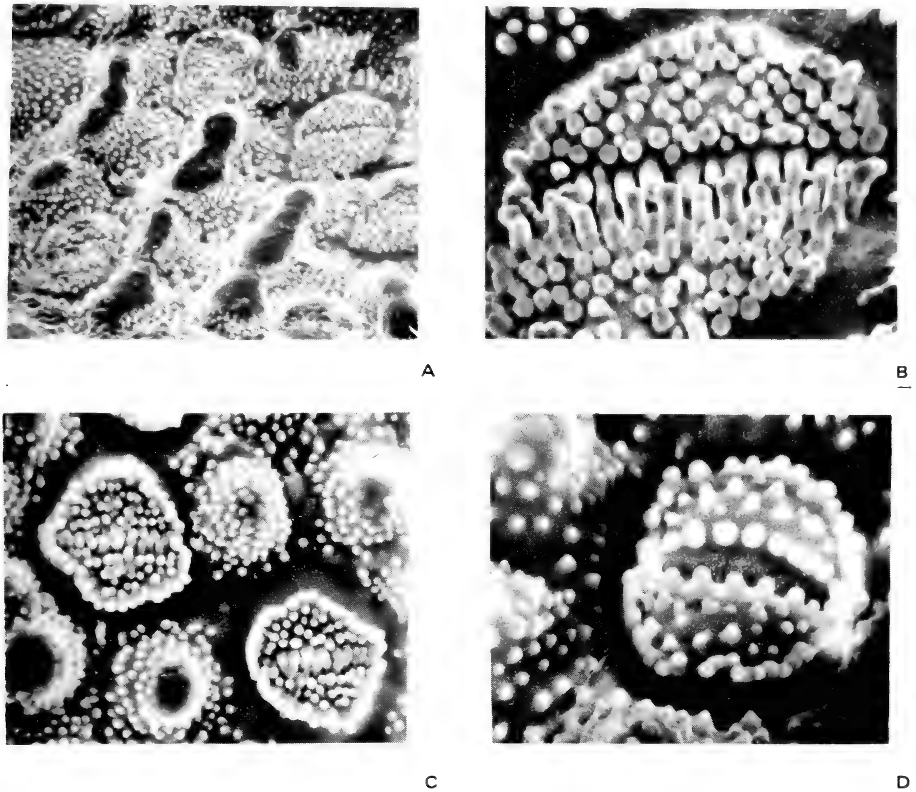

FIGURE 7 a–d: Scanning electron micrographs of the branch internode morphology of *Equisetum diffusum* var. *diffusum:* a-b, China: Yunnan, Forrest 28928 (BM), showing relatively low mamillae transversely aligned and partly fused, and flat-profile stomatal cell areas with exceptionally elongate pilulae adjacent to the pore (x 244, x 983 respectively); c-d, India: Kumaon: Nairu Tal, 6.500 ft., Strachey & Winterbottom No 2 (E), showing irregularly scattered conic mamillae and stomatal cell areas with rather high convex profile and circular plan (x 427, x 778 respectively).

I have seen only one collection of this unusual species, which superficially gives the appearance of young vegetative shoots of *E. diffusum* connected to ephemeral spring shoots of the *E. arvense* type. Because of the young state of the vegetative shoots, the mature dimensions of the stem and branch and internode lengths are unknown. Nevertheless its abundant cones and ephemeral spring shoots give no indication of hybridity (monomorphy is a dominant character in all known crosses between a monomorphic and a dimorphic species). Neither are any individual morphological characters intermediate in state between those of *E. arvense* and *E. diffusum* – *E. mekongense* thus differing significantly from *E.* x *wallichianum.*

In its unique combination of morphological features and geographical isolation from any material of *E. arvense* or *E. diffusum* I have seen, *E. mekongense* stands distinct as a good separate species, whilst retaining clear affinities with both *E. arvense* and *E. diffusum.*

GEOGRAPHY AND ECOLOGY

The total distribution of species of subgenus *Equisetum* in the Sino-Himalayan region as compiled from specimens (figs 4 & 5) is confined to a long narrow arc following the course of the Himalayan range eastwards from Kashmir to north Burma and western China. Species of subgenus *Equisetum* are absent south of a line following the southern foothills of the Himalayas. I have seen no specimens from far north of the Himalayan chain and the species may well be absent here. *Equisetum diffusum* var. *diffusum, E. diffusum* var. *paucidentatum, E. palustre* var. *szechuanense, E.* x *wallichianum,* and *E. mekongense* are entirely confined to this area. To the west of Kashmir *E. arvense* and *E. palustre* var. *palustre* continue westwards and north westwards into south west Asia; whilst to the east of the Himalayas these two taxa spread from China northwards and westwards to Manchuria, Korea and Japan.

Within the Sino-Himalayan region, *Equisetum arvense* (map fig 4) occurs, somewhat discontinuously, in three principal areas along, or to the north of the main range of the Himalayas. It is present in Kashmir, Punjab, Garhwal and central Nepal, in south-east Tibet and again in western Szechuan from where it seems continuous northwards into Sinkiang, Mongolia, north China, (Kansu, Shensi, Shansi, Hopei and Shantung) and Manchuria, although few specimens have been seen from this area. Within the Sino-Himalayan region *Equisetum arvense* occurs along sandy river and stream banks and on moist grassy slopes generally at altitudes of 9,000–13,000 ft (1750–4000 m), descending to 8,000 ft (2450 m) or less only in the north west Himalayas and northern China.

Equisetum palustre in the Sino-Himalayan region, appears to be confined to the extreme east and west ends of the Himalayan chain reaching from the west no further east than Kashmir whilst in the east occurring from south western China northward. I have seen no specimens from Nepal, Sikkim, Bhutan, Assam or Burma that have proved to be this species and the plant may well be absent from these areas, where it seems ecologically replaced by *E. diffusum.* In Kashmir, only *E. palustre* var. *palustre* has been found. In China both varieties occur, but var. *szechuanense* appears confined to south western China (Yunnan, Szechuan and Kweichow) whilst var. *palustre* occurs only to the north of this (Kansu northwards). Little information is available on the local ecology of this species or its varieties. Var. *palustre* in Kashmir is reported to be a relatively rare plant of damp grassland at altitudes of 8–12,000 ft (2450–3650 m), whilst in China var. *palustre* seems also a plant of damp alpine meadows at 9–10,000 ft (2750–3100 m). Var. *szechuanense,* which often adopts a polystachious habit even without apparent apical damage, has been collected mainly from river and stream banks at lower altitude of about 1500–6000 ft (450–1900 m). Whether this apparent ecological and altitudinal separation is real must await observation on a more extensive scale than the present material allows.

Equisetum diffusum (map fig 5) ranges from the extreme western end of the Himalayas in the Punjab along the Himalayan chain through Nepal, Sikkim, Bhutan to south eastern Tibet, is extensive in Assam, the mountains of North Burma (Northern Shan States) and Yunnan, from where it reaches northward into Szechuan, westward into Kweichow and southward into Northern Tonkin (North Vietnam). It thus spans nearly 2,000 miles (ca 3800 km) of the Himalayan chain, extends into Western China and reaches an extreme southerly latitude in both Burma and Tonkin at about 22°S. It is thus the only species of subgenus *Equisetum* in this area to enter the tropics. Var. *diffusum* is present over the whole of this range, whilst var. *paucidentatum* appears confined to the west and central Himalayas, occuring sporadically with the type in the

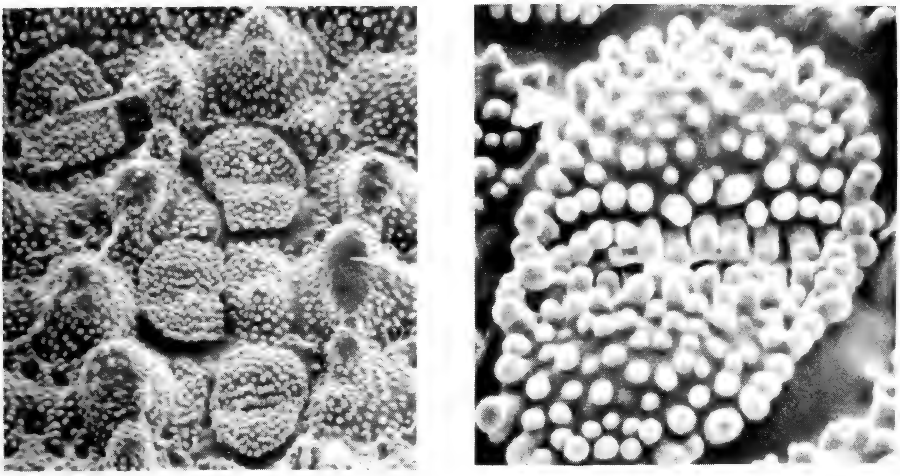

FIGURE 8 a—b: Scanning electron micrographs of the branch internode morphology of *Equisetum* x *wallichianum,* China: ? Western Szechuan, F.S.A. Bourne, Jan. 1886 (holotype, K), showing free conic mamillae weakly transversely aligned, and flat-profile stomatal cell areas with many closely-set low pilulae (x 224, x 904 respectively).

Punjab but apparently becoming the usual form in central Nepal. From herbarium sheet annotations, var. *diffusum* is a common plant throughout much of its range, often growing in quantity in sandy or rocky stream and river beds and banks and other damp sandy places. It occurs at relatively low altitudes of about 2,500—6,500 ft (ca 750—2000 m), though descending much lower than this (to 1,200 ft, 350 m) in Assam, whilst ascending to as much as 10,000 ft (ca 3050 m) in some of its southern most stations in Burma. Var. *paucidentatum* is also a plant of sandy river beds and banks, but generally at higher elevations (3,500—9,500 ft, 1050—2850 m, in central Nepal) than the type.

Equisetum x *wallichianum* (map fig 4) is known from three stations, one in Garhwal in the Western Himalayas and one probably in western Szechuan in the eastern Himalayas. The third, probably in Nepal, is not localisable. This hybrid is thus present in at least three areas where the ranges of its parent *E. arvense* and *E. diffusum* var. *diffusum* overlap, and the likelihood of its being more widespread than the present evidence suggests seems high, especially in areas such as Garhwal and the Punjab where both parents are abundant.

No information on the ecology of *E. mekongense* (map fig 4) is available but from its location at Nekou on the head-waters of the Mekong river in the extreme north-west of Yunnan Province, an altitude of 7—10,000 ft can probably be inferred.

MICROMORPHOLOGY

The value of the use of micromorphological data as seen with the scanning electron microscope in assessing inter-specific relationships in *Equisetum* and the general micromorphology of the species, has been discussed in detail elsewhere (Page 1972a). I have thus here described only those features which add to the already published information.

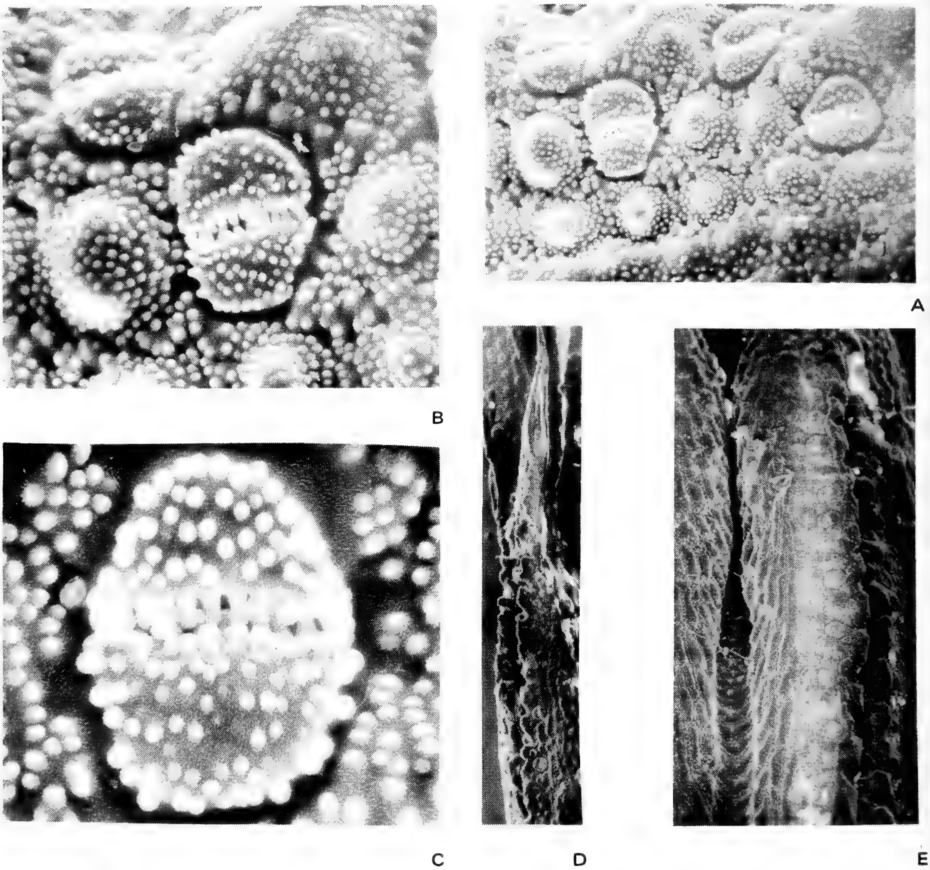

FIGURE 9 a–e: Scanning electron micrographs of the morphology of *Equisetum mekongense,* China: NW Yunnan: Nekou, J. Lile No 1496, 1889 (holotype, P), a-c internode morphology, showing relatively tall thickly pilulate conic mamillae, and stomatal cell areas mostly broader than long with elongate pilulae adjacent to the pore (x 204, x 410, x 816 respectively); d-e main-stem leaf-sheath, details showing conspicuous two-keeled segments and teeth (x 15, x 18 respectively).

Equisetum arvense (fig 6a–d) The micromorphological structure of most material examined from the Sino-Himalayan Region is closely similar to that described for plants from western Europe (Page 1972a). The principal difference seen in some material are a tendency for the stomatal cell areas to be of flatter (often nearly biconvex) profile (Page 1972a: 359); to have occasionally a more distinctive peripheral row of pilulae to the stomatal cell areas; and to occasionally have somewhat longer pilulae adjacent to the stomatal aperture. Each of these latter features is a character state more usually encountered in *E. diffusum,* and hence whilst *E. arvense* remains, on micromorphological grounds, a good distinct entity in the Sino-Himalayan area, a somewhat closer affinity with *E. diffusum* can be detected in material from this area than in material so-far examined from elsewhere.

E. diffusum (fig 7a–d) Some noteworthy variation has been encountered in samples of this species taken over its range, although insufficient material has so far been examined under the S.E.M. to know if any definitive geographical trends are involved. In general, material of var. *paucidentatum* usually corresponds closely with that described previously for *E. diffusum* (Page 1972a) and the exceptionally tall, slender pillar-like mamillae are particularly characteristic. Many specimens of var. *diffusum* are similar to var. *paucidentatum,* but in a number of specimens there seems to be trend for the mamillae to be shorter and more conic in shape and less frequently aligned into transverse rows than in var. *paucidentatum* (fig 7c). In var. *diffusum* stomatal cell areas occasionally occur which are of distinctly circular plan and have also a relatively high convex profile and sparsely scattered short pilulae, approaching the more typical condition of *E. arvense* (fig 7d). In material of Forrest 28928 from western China the pilulae adjacent to the stomatal pore are particularly long, the stomatal cell areas often longer than broad, and the mamillae transversely aligned and fused into low transverse bars (fig 7a–b) — features more typical of *E. palustre* var. *palustre.* Despite these variations, *E. diffusum* remains a good separable entity on micromorphological grounds, whilst specimens of var. *paucidentatum* often seem the most distinctive. It is significant to note that the presence of particularly prominent mamillae in the latter variety is associated with relatively poorly developed ridge tubercles — a correlation noted previously from other species to be a loose trend in the whole subgenus (Page 1972a: 359).

E. x *wallichianum* (fig 8a–b) Two specimens of *E.* x *wallichianum* have been examined under the S.E.M.: Bourne (1886) from Western China and Wallich 398, probably from Nepal. Both appear distinctly intermediate on micromorphological grounds between *E. arvense* and *E. diffusum* var. *diffusum.* In each the stomatal cell areas are usually scattered or only weakly transversely aligned, and their distribution across the furrow interrupted by a shallow central channel. These features seem strongly indicative of the involvement of *E. arvense* in its parentage. The stomatal cell areas are often broader than long, and have one or more rows of distinctly elongate pilulae adjacent to the stomatal pore, indicative of affinity with *E. diffusum.* The mamillae are, in both specimens, approximately intermediate in height between those of *E. arvense* and *E. diffusum.* In the Nepal material, although not in the western China plant, the stomatal pores are often inclined, as in *E. arvense*. In the Nepal plant an outer peripheral row of pilulae of the stomatal cell areas most closely resembles that of *E. diffusum* var. *diffusum* whilst in the Chinese material the stomatal cell areas are unusual in having closely-set low pilulae with an indistinct peripheral row. This latter condition has so far been seen elsewhere only in *E. bogotense* — a plant which, although South American in modern range, shows close affinities with *E. diffusum* also in many features of gross morphology. The micromorphological data thus support the conclusion that *E.* x *wallichianum* is intermediate in morphology between *E. arvense* and *E. diffusum* in most characters, and is probably the hybrid between them. The presence of *E. bogotense*-like features in Chinese material is intriguing, and is possibly indicative of the presence of such features in one of its parents in this area, not so far detected directly.

E. mekongense (fig 9a–e) This species shows strong indications of a relationship with *E. diffusum* in its micromorphology. The mamillae are scattered or irregularly transversely aligned, conic, relatively tall (more so than those of *E. arvense*), and thickly pilulate. The stomatal cell areas vary from approximately circular in plan to usually broader than long, with stomatal slits occasionally inclined. The arrangement of peripheral pilulae and distribution of pilulae along the stomatal aperture is similar to that of *E. diffusum.* The combination of these micromorphological features with

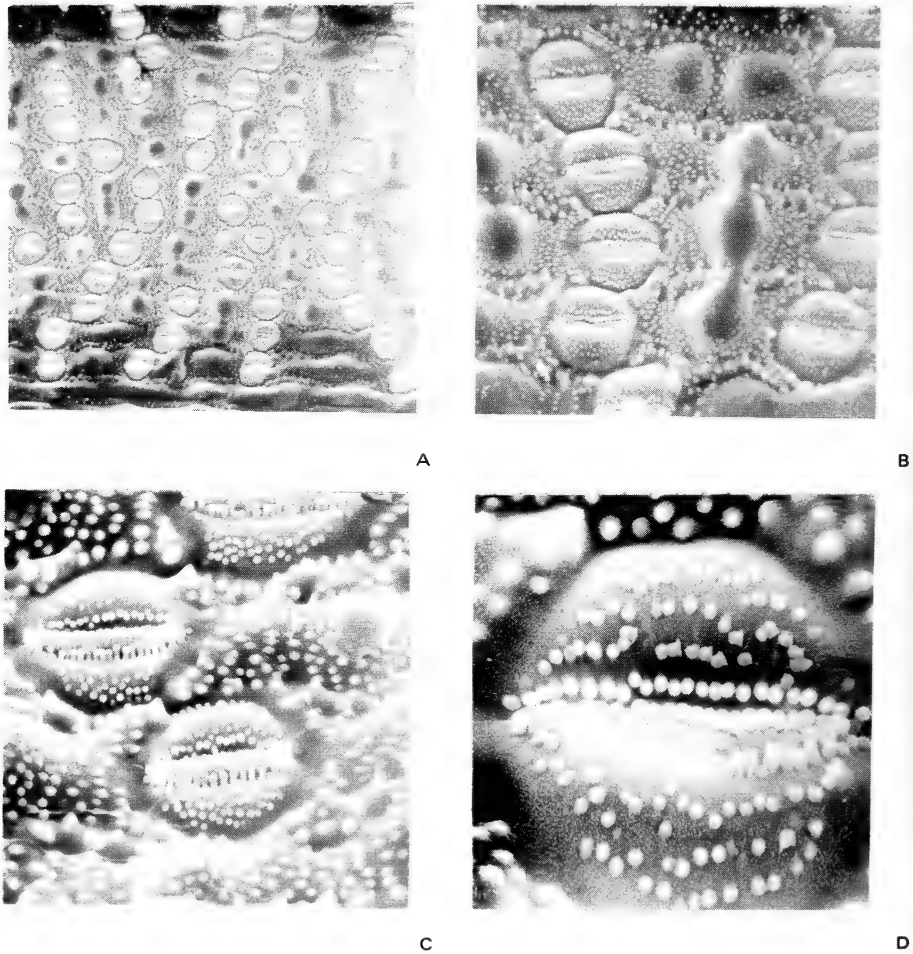

FIGURE 10 a–d: Scanning electron micrographs of the branch internode morphology of Sino-Himalayan *E. palustre* var. *palustre,* China: Western Kansou: Leou Chao Ling, 29th July 1918 (P), showing mamillae frequently transversely aligned and weakly fused, and stomatal cell areas with several rows of elongate pilulae intermeshing across the pore (x 86, x 240, x 490, x 916 respectively).

the presence of two-keeled sheath teeth (fig 9d–e) allow *E. mekongense* to be clearly distinguished from both *E. arvense* and *E. diffusum* even in the absence of information on the type of fertile shoot.

E. palustre (fig 10a–d, 11a–e) This species has a particularly interesting micromorphology, especially in the ornamentation of its stomatal cell areas. In both varieties there are several rows of pilulae along the stomatal pore modified into distinctive elongate rods, the tips of the rods intimately intermeshing with one another across the pore and apparently tightly sealing it. Away from the pore, pilulae become progressively more sparse, and in neither variety is there a distinct row of peripheral pilulae present. Stomatal cell areas are occasionally longer than wide, suggesting a distant affinity with *E. diffusum* var. *diffusum.* In both varieties the mamillae are of

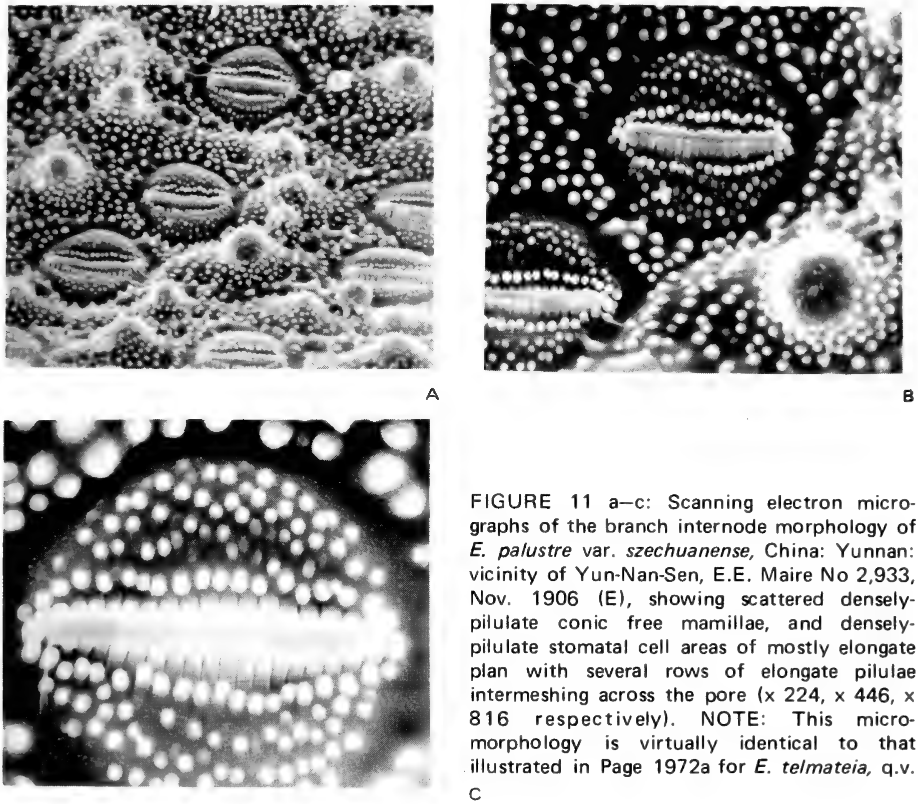

FIGURE 11 a–c: Scanning electron micrographs of the branch internode morphology of *E. palustre* var. *szechuanense,* China: Yunnan: vicinity of Yun-Nan-Sen, E.E. Maire No 2,933, Nov. 1906 (E), showing scattered densely-pilulate conic free mamillae, and densely-pilulate stomatal cell areas of mostly elongate plan with several rows of elongate pilulae intermeshing across the pore (x 224, x 446, x 816 respectively). NOTE: This micromorphology is virtually identical to that illustrated in Page 1972a for *E. telmateia,* q.v.

medium height and broadly conic, thickly studded with rather low pilulae. In northern Chinese material of var. *palustre* the mamillae are usually approximately transversely aligned, and weakly fused into irregular low transverse bars (fig 10a,b), but to a markedly lesser degree than that described in western European material (Page 1972a). In this feature, Chinese material of var. *palustre* differs less from the *E. telmateia* complex than does *E. palustre* material from the west European part of its range. This trend is taken to extreme in var. *szechuanense,* which differs significantly and consistently in its micromorphology from var. *palustre.* In var. *szechuanense,* mamillae invariably remain unfused and are seldom even transversely aligned (fig 11a). They thus not only appear distinctive from var. *palustre,* confirming the conclusions made on its gross morphology, but because of the similarity of the stomatal cell areas, scanning electron micrographs of the branch surfaces of Chinese *E. palustre* var. *szechuanense* are virtually indistinguishable from those of *E. telmateia.* This information now further underlines the view expressed in Page 1972a, formed on the basis of West European material of *E. palustre* var. *palustre* and *E. telmateia,* that these two species although superficially distinctive, are a very closely related pair with a relatively recent common evolutionary origin.

DISCUSSION

This survey reflects the taxonomic entities and their ranges established on the basis of authenticiated herbarium material, for which few previous details have been published.

With further collection in this area doubtless many more stations will be located both within and perhaps beyond the range yet known for each of the taxa, and further species may be discovered. Nevertheless sufficient material is already available to be able to give a preliminary taxonomic picture of the plants present and, more important, to indicate their phytogeographical, phylogenetic and evolutionary significance. Further gathering of material and study of the problem in this area, especially in the field, however, is to be greatly encouraged.

Morphological inter-relationships

The material examined shows that within the Sino-Himalayan region, various species of *Equisetum* subgenus *Equisetum* possess considerable variation in essential taxonomic characters, and that in many of the morphological traits, a close affinity can be detected both on evidence of macro- and micro-morphology between the species in this area, to a degree not so far found in any of the taxa elsewhere in their ranges. Moreover such character-sharing typically tends to involve character transposition between species (with different characters often transposed in different directions between species) rather than the occurrence of blended characters of intermediate expression.

The presence in both *E. arvense* and *E. palustre* of local Sino-Himalayan forms with main shoot sheath teeth which are narrowly acute (sometimes acicular) is a particularly noteworthy trait (especially so in *E. palustre* var. *szechuanense*) found elsewhere only in *E. diffusum* and, with slight modification, in the *E. telmateia* group. Both *E. arvense* and *E. palustre* also show a tendency in this area towards a generally more diffuse overall growth habit with often markedly longer branches than elsewhere, also features more typical of *E. diffusum,* whilst the high incidence of polystachy in shoots of *E. palustre* var. *szechuanense* (in more than half the specimens examined) is comparable only with that also seen in *E. diffusum* in this region. Another feature strongly linking *E. palustre* var. *szechuanense* with *E. diffusum* is the presence of only very short cone pedicels (and hence cones often only poorly exserted from the uppermost sheaths even at maturity). The tendency in the micromorphology of *E. palustre* var. *palustre* in this region to have mamillae transversely aligned but poorly fused is strongly similar to the condition in *E. diffusum* var. *diffusum,* whilst the striking similarity between the micromorphology of *E. palustre* var. *szechuanense* and *E. telmateia* clearly links the latter closer to the western Chinese material of *E. palustre* than to this species throughout the rest of its range. *E. palustre* var. *palustre* and var. *szechuanense* are themselves clearly closely interrelated in the western China area both in overall structure and micromorphology. The appearance of *E. bogotense* like micromorphological features in Chinese material of *E.* x *wallichianum* and the similarity between *E. bogotense* and *E. diffusum* in general morphology links *E. bogotense* also with the plants in this region. *E. diffusum* var. *diffusum* and *E. diffusum* var. *paucidentatum* are closely interrelated in the Himalayan area in both overall structure and micromorphology. Elsewhere, var. *diffusum* shows its strongest affinities with *E. palustre* var. *szechuanenese* in gross morphology, whilst some of its micromorphological traits link it also to *E. palustre* var. *palustre* and to *E. arvense,* and the particularly characteristic biangulate branch ridges armed with dentate tubercles and two-keeled branch sheaths are virtually identical to those found elsewhere only in *E. mekongense* and the *E. telmateia* complex. *E. diffusum* var. *paucidentatum,* which on geographical grounds seems confined to the general area of the west or central Himalayas, seems somewhat more regularly distinct in its micro-morphology from the other taxa than does the type variety. *E. mekongense,* whilst locally isolated from populations of both *E. arvense* and *E. diffusum* var. *diffusum,* shares close affinities in both micro- and macro-morphology with each of these taxa in different characters, whilst the combination of biangulate branch angles and a dimorphic shoot are found elsewhere only in the *E. telmateia* group, of which, in these respects, *E. mekongense* is the East Asiatic equivalent.

Phylogenetic interpretation

Although the horsetails are clearly an ancient group (cf. Page 1972b), many of the living species may well be relatively modern in their evolutionary origins, and the evidence from this survey showing inter-linking between the extant species in various morphological characters in a multiplicity of directions indicates that this may well be so. Furthermore, when considered over the whole of their modern ranges, the distinctive morphological traits and close mutual affinities between species in the Sino-Himalayan region, when compared with their more widespread counterparts, plus the presence of several endemics, suggests the Sino-Himalayan region to be one of special phylogenetic importance.

Two interpretations seem possible to explain this local morphological diversity in so many individuals and taxa. One is that the area concerned has been one of coming-together of several distinct taxa, with widespread hybridisation and introgression resulting in a local blending of species-characters. The other is that this region is the source from which several now-widespread species have evolved, there remaining within the region various relict forms many less distinct from one another than are their now-widespread derivatives. As such, this would be unlikely to be a primary area of speciation for such an old group, but might at least be a secondary centre of diversity and a centre of origin as far as the evolution of most of the now-living species is concerned.

Were the Sino-Himalayan area one of a relative recent meeting of several species of subgenus *Equisetum* followed by hybridisation and introgression, one might well expect to find in this region today a wide spectrum of plants of intermediate morphology between the parent species perhaps linked to the species by intergrading forms. Further, such plants might be expected to occur predominantly in the areas of overlap of the parental ranges perhaps as sporadic individuals, probably in ecologically more or less intermediate situations, and to possess no geographical ranges far beyond nor definitive ranges within the sympatric portions of the parental ranges. Furthermore the morphology of the local forms should be closely intermediate in most characters between the parental types (probably usually involving not more than two parents) and largely or entirely lacking in novel types of good morphological characters.

The majority of taxa of subgenus *Equisetum* in the Sino-Himalayan area are distinctive, and whilst having a number of features in common, linking them closely together, on the whole do not seem to blend with one another by intermediate forms. Further, the local endemics have mostly discrete geographical ranges whilst their ecological situation and/or altitudinal distribution often seems distinctive. In their morphology, whilst very strong links exist between taxa, these occur in a multiplicity of directions in different characters (both at the macro- and micro-morphological levels), and many features not present in the adjoining widespread species occur locally.

Of the taxa present in the Sino-Himalayan area today, only *E.* x *wallichianum* seems to have a sporadic distribution within the overlapping parts of the ranges of two species, between which it is directly intermediate in virtually all good morphological characters, and is in all probability likely to be a hybrid of recent origin. For the other taxa in the Sino-Himalayan area, the evidence seems consistent with the view that the plants are relatively old ones and not the result of recent meeting of widespread species. More likely the Sino-Himalayan plants are survivors from an area of past active evolution of species, centred either more generally in the far east of Asia or perhaps directly in the Sino-Himalayan region where the plants are still found today.

Although in so old a group of plants such an area can hardly be thought of as a primary centre of evolutionary diversity, the evidence does suggest that the region has been a major area of diversification and radiation probably for the majority of living species of subgenus *Equisetum. E. arvense* and *E. palustre* var. *palustre* are two of the widespread survivors of a complex of taxa whose immediate speciation appears to have been centred in this region. *E. palustre* var. *szechuanense, E. diffusum* var. *diffusum, E. diffusum* var. *paucidentatum* and *E. mekongense* are more local survivors also from such a complex, which further afield also appears to possess morphological links with the South American *E. bogotense,* and the West American and West European members of the *E. telmateia* complex, the predecessors of all of which may well have originated in this area.

By contrast, there seems no evidence that this region has any similar claim to be the centre of origin of any of the living species of subgenus *Hippochaete,* which, as indicated by Schaffner (1925, 1930a & b) and Hauke (1963) appear to have their centre of diversity in the central American region. If the views put forward here, as well as those of Schaffner and Hauke with respect to *Hippochaete,* are essentially correct, then the two subgenera of *Equisetum,* at least as represented by the living species, have relatively independent origins in the near geological past — *Hippochaete* being essentially neotropical and *Equisetum* essentially palaeotemperate in origin.

ACKNOWLEDGEMENTS

It is a pleasure to be able to record my thanks to Professor F.T. Last and Dr R. Warren of the Institute of Tree Biology at the University of Edinburgh for giving me access to their scanning electron microscope, and to Miss Vivienne Cowper and Miss Lynne Middlefell for their technical help and skill in operation of this machine. Mrs A.M. Ballantyne and Mr L.A. Lauener (R.B.G., Edinburgh) helped extensively with the geographical location of the specimens, Miss M.E. Mitchell prepared the photographs, Mr B.L. Burtt kindly prepared the latinisation of the descriptions, and he and Mr D.M. Henderson and Dr T.G. Walker (Newcastle upon Tyne) made many useful comments on the manuscript.

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RESEARCHES ON LIVING PTERIDOPHYTES IN INDIA, BURMA AND CEYLON. by N.P. Chowdhury. xii, 80 pp. 1971. Asia Publishing House, London. Price £2.50.

This is a review of some 300 papers on the pteridophytes of India, Burma and Ceylon, arranged systematically, and "compiled for postgraduate and research-level undertakings". Not all papers referred to are in the bibliography at the end (I could not find Chowdhury, 1954). *Marseleamajor* (Haines) Chowdhury, although said by the author to be a provisional name only is validly published on p 49. The reporting is not accurate and the conclusions are not always those of the original authors. The standard of typography is low which could be accepted if the numerous misspellings had been corrected, but those like *Tensipteris [Tmesipteris]* are confusing for students. Nevertheless as a list of references on Indian ferns, by Indian workers, this little book is useful.

A.C. JERMY

THE PHYLOGENY AND CLASSIFICATION OF THE FERNS. Edited by A.C. Jermy, J.A. Crabbe and B.A. Thomas. 284 pp, illustrated, supplement No 1 to the Botanical Journal of the Linnean Society, volume 67, 1973. Published for the Linnean Society by Academic Press, London. 19 x 26.5 cm. Price £9.00.

This book is the published record of the Symposium on the phylogeny and classification of the Filicopsida, held jointly by the British Pteridological Society and the Linnean Society of London, on 13–14 April 1972. It slightly enlarges on the papers read at the time, including also material resulting from demonstrations presented, plus bibliographies for all contributions. The book includes such approaches to fern taxonomy as a historical review, anatomy, morphology, cytology, biochemical systematics, scanning electron microscopy and gametophyte studies, whilst at a more theoretical level general problems are posed, and classification, taxonomic boundaries, phylogenetic and evolutionary relationships and future challenges of several major groups are discussed.

So wide a topic as fern phylogeny and classification involves a wide variety of approaches. The chapters dealing with cytology (T.G. Walker), biochemical systematics (T. Swain & G. Cooper-Driver) and scanning electron microscopy (C.C. Wood and R.M. & A.F. Tryon) can be especially recommended to scientists with an interest in these fields as showing their application to ferns and the growing importance in classification of the evidence to be gained by these means. In both the Thelypteridaceae and the cheilanthoid ferns it is interesting to note the good correlations between spore sculpture type and gross morphology of the plants, and in the Thelypteridaceae also with cytology.

To students in other branches of taxonomy, perhaps unfamiliar with ferns, the excellent historical review of fern systematics by R.E.G. Pichi-Sermolli and the opening and closing remarks to the Symposium by R.E. Holttum and I. Manton respectively lucidly convey the picture of fern systematics, past and present, and some of its likely problems and potential for the future. W.H. Wagner's exploratory view of future challenges raises further fields for study, amongst which he shows the need for an ecological approach. Here is perhaps an important aspect of pteridology today on which we are particularly ignorant — the need for good accurate observation, especially in the tropics, of fern ecology — and one in which amateur botanists, as well as professionals, can make a substantial contribution.

A novel approach towards classification in higher fern groups is taken by both W.R.J. van Cotthem in dealing with stomatal types and D.W. Bierhorst in dealing with what are termed non-appendicular fronds. Along more classical lines U. & T. Sen have used anatomical studies on the sporophyte to compare *Oleandra* and *Nephrolepis* groups, L.R. Atkinson has drawn attention to the potential value in taxonomic study of the much-neglected gametophyte, and T.M. Harris has given a brief survey of the almost equally neglected fossil ferns in considering the systematics of the living plants.

Other chapters in the book deal more especially with classification within specific major groups of the ferns, and reflect between them views evolved and matured over several decades. Especially notable here is the extensive contribution of R.E. Holttum on the old world Thelypteridaceae. The studies of W.A. Sledge and E.R. de la Sota are authoritative accounts of two of the other most complex problems in classification of the more advanced ferns, namely generic and family boundaries in the Aspideaceae-Athyriaceae group and phylogeny and classification in the Polypodiaceae. Finally J.D. Lovis has provided a particularly valuable contribution in stressing the potential value of biosystematic work in solving phylogenetic problems in ferns, exemplified by the intergeneric hybrids in the Aspleniaceae — still the only group in which such painstaking but rewarding work has so-far been extensively undertaken. It would indeed be valuable to see more of this type of approach applied to other fern groups in the future.

My chief critisicism of the book is that the large number of scientific (especially generic) names used in the text in several chapters will probably limit its value to some extent to existing pteridologists. To a large degree this is unavoidable in the interests of scientific accuracy, but one wonders if further exploration in the field of diagrammatic illustration of concepts, as well as illustration of some of the more important features of the plants themselves (one has to look very hard to find any whole fern illustrated) might well have been effective in broadening the audience which the book might reach.

However, these points should not detract from the great value of the book both as a summation of many existing ideas on pteridology and as a stimulus to future research. For, as pointed out by Professor Holttum, had there been a similar opportunity for meeting and exchange of ideas among some of the earlier pteridologists, many taxonomic mistakes may never have been made in the first place. The importance of this work to pteridology today is thus considerable, and the organisers of the Symposium as well as the editors of and contributors to this volume are clearly to be congratulated.

C.N. PAGE

GRAMMITIS JUNGERMANNIOIDES IN THE AZORES

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ABSTRACT

Grammitis jungermannioides is reported as new to the flora of the Azores. Its taxonomy and local geography and ecology are discussed.

INTRODUCTION

Wilmanns & Rasbach (1973) recently published an account of the pteridophytes of Sao Miguel. In Spring 1973 the authors, with Professor O. Wilmanns again visited the Azores, and as well as Sao Migeul spent a few days on Santa Maria, Faial and Pico. On the last island, a small fern, growing as epiphyte in mossy forest (fig 1) was detected by H. and K. Rasbach which we soon identified as a member of the genus *Grammitis.*

FIGURE 1: *Grammitis jungermannioides* in situ, epiphytic on stem of *Vaccinium cylindraceum.* Mossy forest on Pico ca. 850 m. leg. H. and K. Rasbach, 8.5 1973. Around and between the fronds of the *Grammitis* one can see *Hymenophyllum wilsonii, Parmelia* and *Usnea* sp. and *Frullania* sp. Photo: K. Rasbach

No member of the genus *Grammitis* is mentioned in the more recent botanical literature for the Azores (Tardieu-Blot, 1946; Dansereau, 1961; Palhinha, 1966; Carvalho e Vasconcellos, 1968; Ward, 1970; Hansen, 1971–73; Sjogren, 1973) and none is mentioned in Flora Europaea (Tutin et al 1964). Our plant thus seems to be the first collection of a *Grammitis* in Europe.

TAXONOMY

The plant showed some similarity to *G. dorsipila* (Christ) C.Chr. & Tard. (1939), native to eastern Asia. But A.C. Jermy in London and S. Serizawa in Tokyo kindly compared it with authentic material and found it to be different. Prof. H. Ito in Tokyo also sent us *G. dorsipila* from Japan (leg. S. Serizawa, Nr. 17182, Ryukyu Archipelago, 8.3.1973) with which to compare it. For geographical reasons we thought that our plant might be compared with species of *Grammitis* from the Caribbean and Central-American area. Dr David B. Lellinger in the Smithsonian Institution in Washington kindly undertook to do this and identified the plant.

. . . "I am very sure that this specimen is *G. jungermannioides* (Klotzsch) Ching. This species is known to occur in Jamaica, Hispaniola, Mexico, Guatemala, Honduras, Costa Rica, Panama, Venezuela, and Colombia. The specimen you submitted does not look like any species we have in our herbarium from Africa; besides that, almost all the

African species are from Madagascar on the "wrong" side of the continent. Your specimen agrees with *G. jungermannioides* in its frond size, details of the cilia of the frond, details of the venation of the fertile fronds, and in the lack of rhizome scales, which is an unusual character in *Grammitis.*" (Lellinger, in litt, 4 Mar. 1974).

In its original state the plant carried about 60 fertile fronds, each c. 4 cm long (see Fig. 3). A detailed description of *Grammitis jungermannioides* (sub *Polypodium jungermannioides* Klotsch) is given by Maxon (1938, p. 35–36), and some additional data by Morton (1967, p. 95). We have deposited a part of our plant in the herbarium of the Royal Botanical Gardens, Edinburgh (E) where Mrs B.S. Croxall is working on *Grammitis.*

Vouchers are to be deposited also at British Museum Natural History, (BM), and Botanisches Museum & Botanischer Garten, Berlin (B).

GEOGRAPHY AND ECOLOGY

The plant seems rare in the Azores, for despite many hours searching, no other specimen was found. One has of course to consider that the plant is not easy to find.

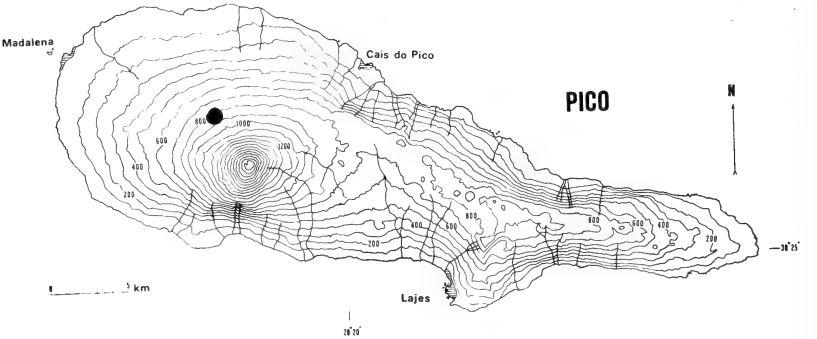

FIGURE 2: Locality of *Grammitis jungermannioides* on Pico.

The sole locality (38° 29.8' N, 28° 25.5' W; c. 850 m) is on the isle of Pico within the Misterio da Sta. Lucia (fig 2). The latter is a field of basaltic lava on the NW slope of Mount Pico (2351 m), a little above the road which leads east from Madalena (the "Estrada longitudinal"). The habitat is therefore within the "Azorean cloud zone vegetation", which according to Sjögren (1973) is situated between 500 and 1350 m alt., receiving much rain and possessing a constant high air humidity. The plant grew between mosses, lichens (*Parmelia* and *Usnea* sp.), a liverwort (*Frullania* sp.) and *Hymenophyllum wilsonii* at about 60 cm above ground level, on the north side of a c. 10 cm thick stem of a tree-like *Vaccinium cylindraceum.* The tree and shrub layer of the surrounding vegetation consisted, besides the *Vaccinium*, mainly of *Erica azorica* and *Juniperus brevifolia,* thus representing Juniperion brevifoliae Sjögren. These trees and shrubs were copiously covered with epiphytes, including *Elaphoglossum paleaceum.* The ground was covered with thick carpets of mosses with some sporadic *Blechnum spicant* and *Dryopteris aemula.*

For the flora of the Azores, *Grammitis jungermannioides* can be regarded as a caribbean-central american element, of which other representatives are known on the archipelago. For the Canary Islands, however, *Grammitis quaerenda* (fig 4) has been described by Bolle (1863: 324). Unfortunately he was not able to find out from which

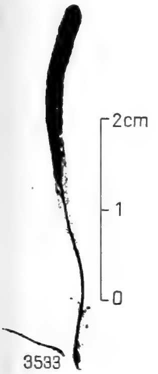

FIGURE 3 (left): Frond of *Grammitis jungermannioides* from Pico 2x. Cleared in ca. 40% acqueous chloral hydrate (3 days) and after passing through alcohol and xylol embedded in balsam.
Photo: Prof. L. Jenny, Basel.

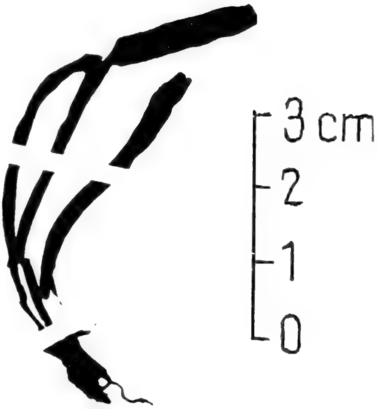

FIGURE 4 (right): *Grammitis quaerenda* Bolle. Type specimen (B). Mus. Bot. Berol. Film No. 1909.

of these islands it came and since the first collection it has never been found again. That plant is different from *G. jungermannioides.*

ACKNOWLEDGEMENTS

We would like to express our gratitude to the following: A.C. Jermy, London; Prof. H. Ito, Tokyo; S. Serizawa, Tokyo; and Dr D.B. Lellinger, Washington, for their help in our efforts to identify our plant; Mrs B.S. Croxall, Edinburgh, for further useful information; Dr E. Sjögren, Uppsala, for letting us have and use the map of Pico which he had made for his monograph (1973); Dr Lellinger and Prof. A. Fernandez, Coimbra, for valuable reprints; Prof. Th. Eckardt and Dr D.E. Meyer for the gift of the photograph of *Grammitis quaerenda* type specimen.

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INDEX HOLMENSIS – A WORLD PHYTOGEOGRAPHIC INDEX Vol 1 Equisetales, Isoetales, Lycopodiales, Psilotales, Filicales, Gymnospermae; 264 pp. 1969. Vol 2 Monocotyledons A–I. 224 pp. 1972. Vol 3 ibid. J–Z. 224 pp 1973. Price of Vols 2 & 3 140 SF. Edited by Hans Traleau. Publishers/distributors: The Scientific Publishers Ltd, Postfach, CH–8047, Zurich.

This is an index to books and papers containing distribution maps of plant species, based on Prof. Erik Hulten's indices collected for his arctic and boreal studies. It contains references to over 2300 taxa of pteridophytes: 178 to Equisetales; 82 to Isoetales; 356 to Lycopodiales; 2 to Psilotales; 1718 to Filicales. It is clearly produced in one type-face, two columns to a page in volume 1 three columns in vols 2 & 3, thus saving on paper. The geographical range covered by the citation is given in brackets. It includes references to fossil species also. There is one thing users must remember: entries are cited according to the names used by the publishing author which means a species may appear under several heads. The editor and his collaborators are to be congratulated; already in 1974 one Supplement is about to appear and I hope these will continue to come, together with the volumes on Dicotyledons.

CENSUS CATALOGUE OF THE FLORA OF IRELAND by M.J.P. Scannell and Donal M. Synnott. 127 pp, folded coloured map of vice-counties. 1972. Stationery Office, Dublin, available from Government Publications Sale Office, GPO Arcade, Dublin 1. Price 50p.

This is a concise conspectus of Irish Pteridophyta, Gymnospermae and Angiospermae including native and established aliens and giving the distribution in Ireland. Irish names are given for some common species, e.g. Raithineach gallda (*Osmunda*); Rathineach Mhadra for both the Lady and Male-fern? (cf. gaelic:- raineach Mhuire, Our Lady's Fern; Marc raineach, horse (or male) fern); Luibh na seacht ngabhadh (*A. ruta-muraria).* One is reminded how are *Gymnocarpium* species are, especially *G. robertianum* which one would expect on the limestone in some quantity. Hybrids are possibly under-recorded and *Polypodium australe* x *vulgare* I suspect to be more frequent. *Dryopteris remota* is given as *D. carthusiana* x *filix-mas* which is incorrect: cytological examination by Prof. Manton on Dalystown material sent to her by L. Praeger proved to be 3n and apogamous like the continental species suggesting *D. pseudomas* (2n) x *assimilis* or similar sexual diploid. *D. assimilis* has yet to be found in Ireland although common at sealevel in W. Scotland. The specimen quoted (from my own tentative record) for N Kerry by these authors was re-located in the field by the reviewer in 1973: it is undoubtedly *D. austriaca.* This is a well-produced and useful little book and at 50p can be on everyone's shelf.

A.C. JERMY

SHORT NOTES

POLYSTICHUM X ILLYRICUM IN SCOTLAND

Polystichum x *illyricum* (Borbás) Hayek, the hybrid between the Hard Shield Fern (*P. aculeatum)* and the Holly Fern *(P. lonchitis),* has only recently been shown to be a member of the British flora, having been identified from a herbarium specimen collected in Co Leitrim, Ireland in 1932 by R. LL. Praeger (Sleep & Synott, 1972) and refound in the field in 1972.

It seemed likely that this fern might occur in Scotland in a locality where the altitudinal ranges of the parent species overlap. This juxtaposition occurs only in comparatively few localities, and one which appeared to be most favourable was the area of Cambrian (Durness) limestone at Inchnadamph, West Sutherland, where both *P. aculeatum* and *P. lonchitis* grow in great profusion in limestone scree.

Inchnadamph was visited briefly by the author on 15th July 1973, and plants which appeared to be morphologically intermediate between the two parent species were sampled by taking ripe sporing frond specimens without damaging the plants. Fronds from three different stocks have proved to have abortive spores, and this feature, combined with the intermediate nature of their morphology, enabled Dr Anne Sleep, who examined them, to state that they are undoubtedly referable to *P.* x *illyricum.*

On 28th October 1973, the author again visited Inchnadamph, accompanied on this occasion by Dr Sleep. The area where the original specimens had been found was thoroughly searched, and no less than thirty-nine plants of the hybrid were discovered, scattered over an area of limestone scree approximately half a mile in length. Only mature sporing plants were counted.

The habitat of *P.* x *illyricum* at Inchnadamph is in limestone scree and rubble on a slope of approximately 35 degrees and at an altitude of about 140 m. Ferns predominate among the accompanying species and the following all occur: *Pteridium aquilinum, Blechnum spicant* (rare), *Phyllitis scolopendrium* (rare), *Asplenium adiantum-nigrum* (rare), *A. trichomanes* subsp. *quadrivalens, A. viride, Athyrium filix-femina, Cystopteris fragilis, Dryopteris filix-mas, D. dilatata, Polystichum aculeatum, P. lonchitis, Polypodium vulgare.* A colony of *Thelypteris robertiana* was growing not far away. Flowering plants noted included *Geranium robertianum, Dryas octopetala, Thymus drucei, Teucrium scorodonia, Carex flacca* and *Festuca rubra.* Calcicole mosses comprised the greater part of the bryophyte flora and the following were frequent: *Ditrichum flexicaule, Tortella tortuosa, Neckera crispa, Ctenidium molluscum* and *Camptothecium lutescens.*

This discovery constitutes the second record for the British Isles and the first for Scotland. Although it is difficult to imagine a more favourable site for the hybrid than that at Inchnadamph, *P.* x *illyricum* should continue to be sought wherever the parents grow in close association. This requirement is most likely to be met in the north-west Highlands where *P. lonchitis* descends to levels which are within the usual altitudinal range of *P. aculeatum.* In the central and eastern Highlands the Holly Fern rarely descends below about 750 m and the Hard Shield Fern seldom attains that elevation.

I am greatly indebted to Dr Anne Sleep, University of Leeds, for much helpful advice, criticism and assistance with field work, and to the Nature Conservancy for

permission to remove frond material from the Inchnadamph National Nature Reserve.

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SLEEP, A. & SYNNOTT, D.M. 1972. *Polystichum* x *illyricum:* a hybrid new to the British Isles. *Brit. Fern Gaz. 10* (5): 281–282.

A McG. STIRLING

THE DISTRIBUTION OF DRYOPTERIS AEMULA AND ITS DISCOVERY IN THE CANARIES AND TURKEY

Dryopteris aemula (Aiton) O. Kuntze, is a diploid species known from the Atlantic coast of Europe (Britain, Ireland, France and Spain) and also from the Atlantic islands (Azores and Madeira). It has not previously been recorded from the Canary Islands, but the present author has recently found it there on the island of La Gomera, which he visited with Mr D.J. MacCarthy on a field excursion from Charterhouse School in March 1974.

It was locally abundant on the NE side of the Montes del Cedro, on ascending Montana Quemada from El Carmine, at an latitude of c. 1100 m. The forests of *Erica* and *Ilex* are at their thickest in this area, with thick coatings of mosses and lichens on every branch, and ferns up to c. 2 metres in height. Growing with it were *Pteris vittata* L., *Dryopteris oligodonta* (Desv.) Pic. Ser., *Dryopteris pseudomas* (Woll.) Holub & Pouzar, and *Dryopteris austriaca* (Jacq.) Woynar agg. Specimens will be deposited at the British Museum (Natural History) (BM).

As well as the Atlantic coast of Europe, the present author has also found *Dryopteris aemula* growing abundantly in NE Turkey on the Black Sea coast, an area which seems to be a second enclave for some Atlantic species. Although it has been described from nearby in the U.S.S.R. as *Dryopteris liliana* Golicin, the author's Turkish collections and the type specimen of *Dryopteris liliana,* which he has seen at Tbilisi, are identical with western material, and have the same strong smell of hay on being dried. It seems that *Dryopteris liliana* is a synonym of *Dryopteris aemula.* Davis' specimen no. 32231 reported in the Flora of Turkey under *Dryopteris liliana* is not this taxon, but *Dryopteris assimillis* S. Walker. Specimens of *Dryopteris aemula* collected by the present author in Turkey are as follows:—

RIZE: 8 km. E. of Findikli, 30 m. alt., 25/8/1973, *4001* (BM, TBI).
Firna valley, Cat-Camlihemsin, S. of Ardesen, 1000 m. alt., 27/8/1973, *4021* (BM, TBI).

ARTVIN: Ciftek Koprin, near Kavak, S.E. of Arhavi, with *Hymenophyllum tunbrigense,* 200 m. alt., 26/8/1973, *4012* (BM, TBI).

Dryopteris aemula has not so far been found in the New World, nor on the Pacific Coast of Asia, and it may be that its closest relative from the latter is the quite distinct diploid species, *Dryopteris gymnophylla* (Bak.) C. Chr.

It would be of interest to attempt artificial hybridisation between the two species in order to see whether there is any degree of homology between their genomes.

C.R. FRASER–JENKINS

ASPLENIUM X TICINENSE D.E. MEYER FROM A FRENCH LOCALITY

Among herbarium sheets on loan from the National Museum of Wales, Cardiff, one has proved to be of considerable interest. On the sheet there are two large, mature fronds gathered at Vernet les Bains, Pyrenees Orientales, France, by Lt. Col. W.R. Roberts in March, 1960. They had been sent to the National Museum of Wales where they were identified by H.A. Hyde as *A. adiantum-nigrum,* but with the comment that they were unusually large for this species.

The two fronds are apparently from the same plant, the larger of them having a total length of over 38 cm (of which 21 cm is taken up by the blade) and a width of over 10 cm. The blade is tripinnate at the base, and both the blade and the pinnae have long, acuminate tips. The pinna-segments are broadly lanceolate with long, acuminate teeth as in *A. onopteris,* but the frond itself is coriaceous and its adaxial surface is a lighter green than is usual in *A. onopteris.* The stalk and rachis are thick, shiny and brownish-black almost to the apex on the abaxial side.

In both fronds the lower surface is completely covered with mature sori. However, microscopic examination of the contents of several sori showed that approximately 88% of the sporangia are abortive, and those which have developed contain only misshapen and defective spores. These vary considerably in shape and size, and are frequently seen adhering together in black, crumbly masses.

In all of these features the specimens agree completely with the description of the triploid hybrid between *A. adiantum-nigrum* and *A. onopteris,* which was first found in the wild by D.E. Meyer at Landeskrone in Oberlausitz, and which he named *A.* x *ticinense* (D.E. Meyer, 1960. Zur Zytologie der Asplenien Mitteleuropas. Ber. Deutsch Bot. Ges. 73: 386–394).

This interesting hybrid should be looked for in those localities in Ireland where *A. onopteris* and *A. adiantum-nigrum* both occur.

I am grateful to the Keeper of Botany, National Museum of Wales, Cardiff, for the loan of the herbarium specimens on which this note is based.

R.H. ROBERTS

THE ALTERNATIVE SPELLINGS ASPIDIUM TYLODES KZE AND A.XYLODES KZE

These alternative spellings for the name of a new species occur in Kunze's paper entitled *Filices nilagiricae* (Linnaea 24: 239–299; 1851). Subsequent authors have adopted different spellings, *xylodes* being preferred in more recent years, but I have seen no printed discussion of the subject. The species is widely distributed in India and southern China, extending south-wards to the mountains of Luzon in the Philippines.

Kunze died before his paper was published (a short obituary notice appears as a footnote to the title) and it is unlikely that he corrected proofs of it. At the beginning of the paper (pp 242–245) there is a list of the species described in it, one being no. 65 *Aspidium (Nephrodium) tylodes* Kze n. sp. But on p 281, at the head of the description, the name is printed *Aspidium xylodes.* However, on p 283, at the end of the description of *A. ochthodes,* the differences between the latter and *A. tylodes* are enumerated, a further indication that *tylodes* was the intended spelling.

The two species are closely related. Hooker placed *tylodes* as a variety of *ochthodes,* remarking that "they are clearly one and the same species" (Spec. Fil. 4: 110; 1862). But Beddome, while deferring to Hooker's opinion and ranking *tylodes* as a variety, expressed the opinion that "it is, I believe, quite entitled to rank as a species". A character the two species have in common is the presence of a swollen aerophore at the base of each pinna. This character was described by Kunze, and though he did not explain the derivation of his specific epithets it is clear that they both refer to the presence of aerophores *(tyle* = a swelling or lump; *ochthe* = a hill or mound). Thus the name *tylodes* has a descriptive significance; I can see no such significance in *xylodes.*

Hooker and Beddome both accepted the name *tylodes* without comment. Mettenius (Farngatt. IV: 82; 1858) wrote "*A. tylodes* Kze Linn. 24. 281 (*A. xylodes* l.c. 283 ex errore typogr.)" But Christensen, in his *Index Filicum* (pp 98, 280) accepted the spelling *xylodes,* adding (*tylodes* auctt.), and this practice has since been generally followed. It should be noted incidentally that Christensen (and some others who have copied him) wrongly cited p 283 for the description of *A. xylodes;* p 281 is correct.

From the foregoing it appears to me quite clear that *tylodes* was the spelling intended by Kunze, and I propose to revert to it.

R.E. HOLTTUM

DIPLOID ISOETES ECHINOSPORA IN BRITAIN

Relatively few chromosome counts have been made in the genus *Isoetes.* The counts that have been published for *I. echinospora* Durieu (*I. setacea* Lam.) are those made by Ekstrand (1920), Ehrenberg (1945), Manton (1950), Löve (1962) and Löve & Löve (1966). Ekstrand found 2n = 22, but Ehrenberg reported both 2n = 22 (-24) and 2n = c. 100 in plants from Sweden. Manton reported 2n = "more than 100" in root tips of material of *I. echinospora* from County Kerry, Ireland, and observed that it was cytologically indistinguishable from plants of *I. lacustris* from Windermere, Wicklow and Wales. The Windermere *I. lacustris* had n = 54—56. Löve (1962) and Löve & Löve (1966) found 2n = 22 in typical *I. echinospora* and its var. *muricata* from Sweden, Iceland and North America.

The basic number of x = 11 has been found in all the species that have been counted in recent years, and it thus seems likely that Manton's material of *I. echinospora* and *I. lacustris* was decaploid, with 2n = 110. A precise count of 2n = 110 has recently been made on material of *I. lacustris* from northern Poland (Rychlewski & Jakun 1972) but no counts of British material of either species have been published since 1950. Polyploidy has also been found in a group of Indian species of which at least one is apogamous (*I. coromandelina* L., with 2n = 22+1, 33, 33+1, 44; Abraham & Ninan 1958, Ninan 1958, Pant & Srivastara 1965) and in the American *I. piedmontata* Reed (2n = 22, 44; Matthews & Murdy 1969).

Plants of *I. echinospora* were collected from a large population in Llyn-fach, Glamorgan (NGR: SN 905 037) in June 1973. Mitotic chromosome preparations were obtained from root tips pre-treated for four hours in 0.1% colchicine solution, fixed in 1:3 acetic alcohol, and hydrolysed in 1N hydrochloric acid for five minutes before squashing in aceto-carmine. The two plants that were counted both had a chromosome number of 2n = 22, and were thus diploid. I am grateful to A.C. Jermy for confirming the identity of a voucher specimen of one of these plants, and of other specimens of *I. echinospora* from Llyn-fach.

I. echinospora has an extremely scattered and discontinuous distribution in the British Isles. Manton (1950) has drawn attention to the morphological variability of both *I. echinospora* and *I. lacustris,* and observed that "there are undoubtedly many true-breeding strains characteristic of different lakes". It seems possible that the morphological variability of the species may be accompanied by cytological variability. The Llyn-fach locality is an isolated oligotrophic montane lake at an altitude of 400m (1300 ft), in which abundant *I. echinospora* is associated with equally abundant *Lobelia dortmanna* L. and lesser quantities of *Sparganium angustifolium* Michx. The lake lies below north-facing cliffs which have an interesting montane flora including *Lycopodium selago* L., *Sedum rosea* (L.) Scop. and *Orthilia secunda* (L.) House; the last two species and *Lobelia dortmanna* reach their southern limit in the British Isles here, and Llyn-fach has a good claim to be regarded as the southernmost montane lake in the British Isles. *I. lacustris* has also been recorded from the area but has not been seen by the author.

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Q.O.N. KAY

EQUISETUM HYEMALE IN WEST NORFOLK

During February, 1974, I was sent a specimen of the Rough Horsetail or "Dutch rush", *Equisetum hyemale* L., found in a hedgerow at Stibbard, near Fakenham (v.c. 28). I subsequently visited the site to find the plant occupying a length of about 200 yards of a roadside hedge composed mainly of dogwood, hazel and hawthorn. Amongst the horsetail were *Galium aparine, Mercurialis perennis, Stellaria holosteum* and *Urtica dioica.* The evergreen stems of the *Equisetum* form dense thickets up to 4 feet high in places, but they have been very largely cut back in the course of hedge trimming. The soil is wet and black and appears to have had a woodland origin. There are some very ancient woods in that part of the county.

This is a quite astonishing find because the species had been thought extinct not only in East Anglia, but in all but two of its old haunts in southern and midland England. It was found in Arminghall Wood and at St Faiths Bogs near the end of the 18th century, (Turner & Dillwyn 1805) and at Hedenham a little later (Withering 1812), but it does not appear that later Norfolk botanists such as Trimmer, Geldart, Nicholson, and W.G. Clarke ever met with it; nor was it found by those recording for the B.S.B.1 "Atlas of the British Flora", published in 1962.

The only indication that it might have persisted after the middle of last century is a reference in F.W. Galpin's account of the *Flowering Plants of Harleston* (1888 which says that a Mr F. Spalding believed he had seen it growing at the Earsham end of the Bath Hills, Ditchingham. Unfortunately no-one seems to have confirmed that record. In Suffolk it used to grow in about eight localities but again there have been no recent finds.

H.C. Watson (1852) commented that "much suspicion attaches to several of the stations on record" for *E. hyemale* and he included Norfolk among the counties where early records more particularly required verification.

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E.A. ELLIS

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References in the text should be given in parenthesis, e.g. "Shivas (1962) points out. . ." or "It has been pointed out (Shivas 1962) that. . .". The reference list at the end of the paper with authors in alphabetical order and in the style of this number.

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Juliet Pannett.
1974.

This issue is dedicated
to
RICHARD ERIC HOLTTUM

Honorary Member and Past-President
of the British Pteridological Society,

Director of the Singapore Botanic Gardens 1925-1949

and

Professor of Botany,
University of Malaya, Singapore 1949-1954

on the occasion
of his
Eightieth Birthday
20th July 1975

A RE–DEFINITION OF THE GYMNOGRAMMOID GENUS AUSTROGRAMME FOURNIER

E. HENNIPMAN
Rijksherbarium, Leiden, Netherlands

ABSTRACT

The Gymnogrammoid genus *Austrogramme* is reinstated to accommodate five species formerly referred to *Aspleniopsis, Rheopteris,* and *Syngramma.* A key is included. The genus is divided into two sections including Section **Aspleniopsis** (Fournier) Hennipman. The following new combinations are proposed: **Austrogramme asplenioides** (Holttum) Hennipman, **A. boerlageana** (v.A.v.R.) Hennipman, **A. decipiens** (Mettenius) Hennipman and **A. francii** (Rosenstock) Hennipman. The now monotypic genus *Rheopteris* Alston is excluded from the Gymnogrammoid ferns. The relationship of *Austrogramme* to *Taenitis* and *Syngramma* is discussed.

INTRODUCTION

When making routine identifications at the Rijksherbarium I came across a specimen of *Rheopteris asplenioides* Holttum (New Guinea) which appeared to me as probably intimately related to *Aspleniopsis decipiens* (Mettenius) Kuhn, which is indigenous to New Caledonia, the New Hebrides, and possibly also New Ireland (Brownlie 1969). This aroused my interest, also as the real affinity of the monotypic genus *Aspleniopsis* was said to be unknown (Copeland 1947). In a correspondence, Prof. Holttum suggested that *Syngramma boerlageana* v.A.v.R. from the Moluccas, and the New Caledonian *Syngramma marginata* (Mettenius) Diels and *S. francii* Rosenstock, might be related to these as they did not fit into the genus *Syngramma* as presently construed by him. Detailed studies of the vascular organisation, the disposition of the sporangia, the spores, and the paraphyses, surprisingly showed conspicuous similarities in all of them. They further appeared to be different from *Syngramma* and *Taenitis* by the combination of leaf-shape and venation pattern. As a result, the genus *Austrogramme* Fournier, based on *A. marginata* is reinstated. The relationship of the Gymnogrammoid genus *Austrogramme* to *Syngramma* sensu Holttum (1954) (thus including *Craspedodictyum* Copeland), and to *Taenitis* sensu Holttum (1968) is discussed also in view of Walker (1968) and my own observations on representatives of the latter two genera.

Another finding of interest regards the identity of the now monotypic genus *Rheopteris* Alston. *Rheopteris cheesmaniae* Alston – the type species of the genus – appeared to be genetically different from *R. asplenioides* (here referred to *Austrogramme*). The genus which was formerly referred to the Gymnogrammoid ferns by Holttum (1962) shows several aberrant features. Its relationship will be discussed in detail later (Hennipman, in preparation).

MATERIAL AND METHODS

The present study is based on herbarium material present at the Rijksherbarium (L), as well as on additional collections of *Austrogramme asplenioides, A. decipiens, A. francii, A. marginata,* and *Rheopteris cheesmaniae* present at the British Museum (Natural History), London (BM); the Royal Botanic Gardens, Kew (K), and the Museum National d'Histoire Naturelle, Paris (P).

Spores were studied embedded in glycerine gelatine with the light microscope, and coated with gold in a Cambridge Stereoscan. The details of the spore-morphology are described from the electron micrographs. Paraphyses were studied after boiling in an aqueous solution of potassium hydroxide for one minute. Cross-sections of rhizome and petiole were made following routine procedures.

OBSERVATIONS

Vascular organisation

The vascular organisation of *Austrogramme* is uniform. The rhizome is solenostelic like in *Taenitis* and *Syngramma* species. The petiole of *Austrogramme* shows on cross-section two lateral vascular bundles. In *Taenitis* the number of vascular bundles in the petiole was found to be one (V-shaped) in *T. cordata* (Van Royen 5462) and two in the other species.

In *Syngramma* the number of vascular bundles is four in *S. luzonica,* three in *S. alismifolia,* and two in *S. borneensis.*

The observations on *Syngramma* and *Taenitis* are generally in accordance with Walker (1968).

Shape of the leaves and venation pattern

In *Austrogramme* compound leaves have a triangular terminal segment *(A. asplenioides, A. boerlageana, A. decipiens),* and a venation pattern which is either reticulate *(A. boerlageana)* or (largely) free *(A. asplenioides, A. decipiens).* The species with simple leaves *(A. francii, A. marginata)* have free veins. Compound leaves of *Taenitis* and *Syngramma* have the terminal segment ± conform to the pinnae. The venation pattern of all the species, thus including those with simple leaves, shows anastomosing veins at least towards the margin of the pinnae or the leaves. For illustrations of the venation patterns of *Syngramma* and *Taenitis* species see Holttum (1954) and Walker (1968).

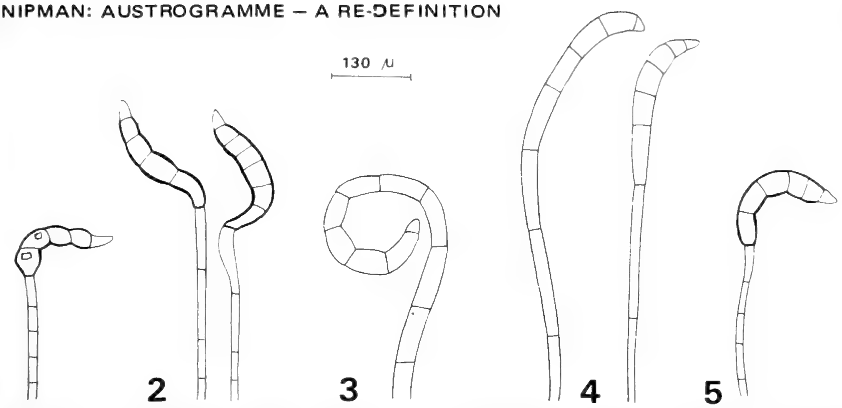
The disposition of the sporangia

In *Austrogramme* the sporangia are situated in ± orbicular to elongate sori, varying in size and generally situated, either mainly or exclusively along the distal parts of each vein or irregularly. In *Syngramma* the sporangia are generally inserted regularly all along each vein. Sporangia are variously situated in *Taenitis* (for details see Holttum 1968), a condition as found in *Austrogramme* is, however, not realised.

Paraphyses

In *Austrogramme* the paraphyses of the sori are mainly inserted either on the stalk of the sporangium (in groups of 2–8) or on the epidermis. They are uniseriate, unbranched, and vary in shape but usually have the upper part curved. They consist of a ± conical, small, hyaline or brownish, glandular (?), terminal cell, generally 4–7, ± spherical or elongate, yellowish to brownish, glandular subterminal cells, along with a varying number of non-glandular ± hyaline cells. The number of non-glandular cells is generally 1–3 when the paraphysis is inserted on the stalk of the sporangium. In mature glandular cells of the paraphyses of *A. asplenioides, A. boerlageana,* and *A. marginata,* small openings were observed (figs 1–5).

In *Taenitis* the paraphyses show a range of variation. In *T. blechnoides, T. interrupta,* and *T. marginata,* they are mainly inserted on the stalk of the sporangia. Their shape is almost similar to that of *Austrogramme* except for the terminal cell which is glandular and not deviating from the other glandular ones. Those of *T.*



FIGURES 1—5: Paraphyses of *Austrogramme*. 1, *A. asplenioides* (Henty & Foreman NGF 42542). 2, *A. boerlageana* (Buwalda 6175). 3, *A. decipiens* (Crookewit s.n., L. 339327). 4, *A. francii* (Compton 1480, BM). 5, *A. marginata* (Compton 1722, BM).

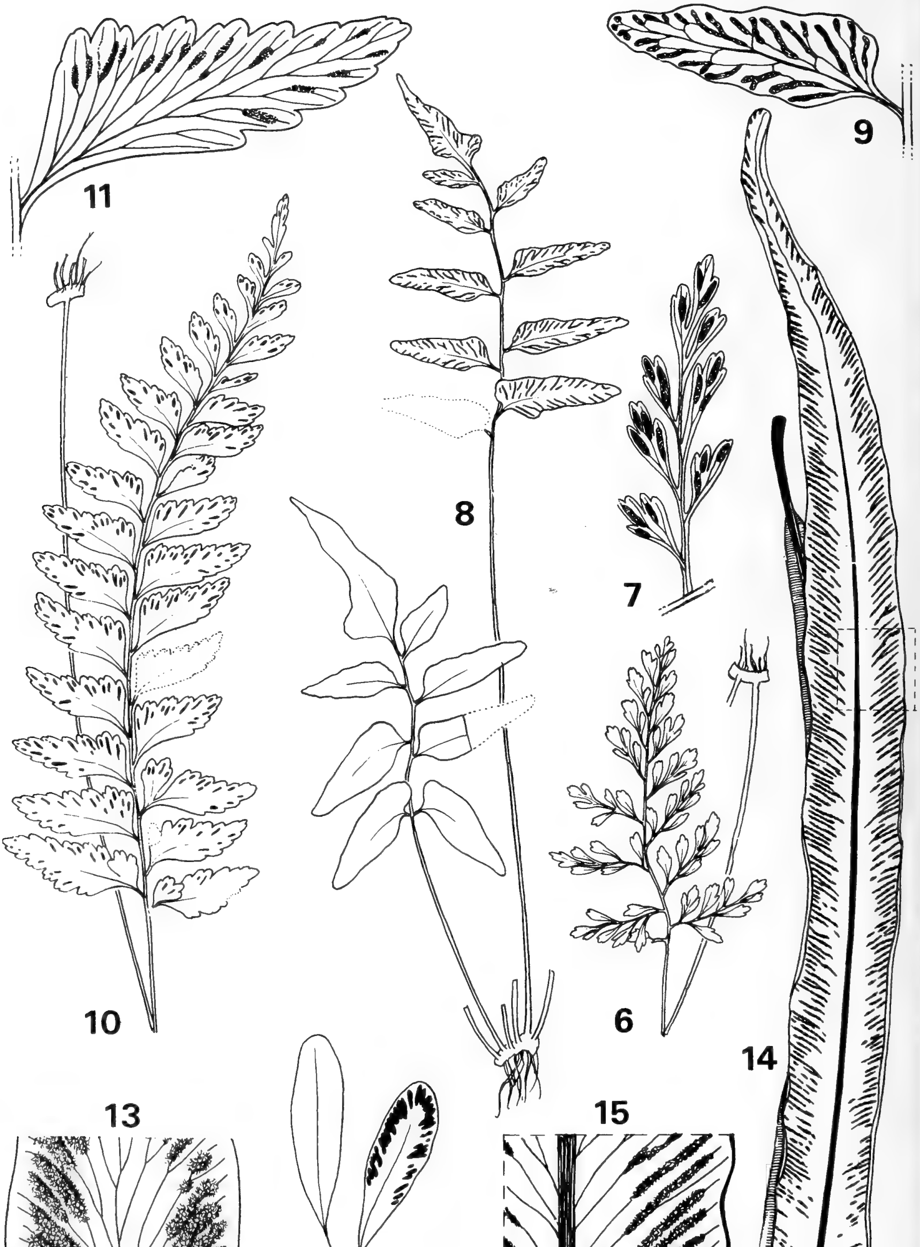
vittarioides and *T. flabellivenia* are essentially the same but are distinct because of the large number of glandular and non-glandular cells. In *T. requiniana* the paraphyses are mainly inserted on the epidermis; two different kinds were found. In BSIP 1987, 6329, 7292 (from the Solomon Islands), and LAE 53748 (from New Guinea) they are c. 375 μm long, straight, consist of 5—7 cells, of which the terminal cell is curved, brownish, presumably glandular, and has rather thick cell walls, the other, non-glandular cells are thin-walled and lighter coloured. Those found in NGF 29841 (from New Guinea) are 500—700 μm long, curved in the upper part, consist of 5—7 cells, and are all except for the lowermost one or two cells filled with a granular, obviously glandular substance. In *T. pinnata,* and *T. cordata* only the terminal cell of the paraphysis seems glandular. As regards *T. pinnata,* over 10 brownish paraphyses consisting of 6 or 7 cells are inserted on each stalk of the sporangia in A.C. Smith 6565 (Fiji), whereas in Carr 12144 (New Guinea) few paraphyses are present on each stalk which, moreover, consist of about 11 cells. The paraphyses of *T. lanceolata* (syn.: *Syngramma hookeri*), and *T. hosei* are very different from the above as they are exclusively seated on the stalk of the sporangia, generally one to each stalk, and consist of only 2—3 elongate cells of which the terminal cell is glandular.

Much variation of the paraphyses also occurs in *Syngramma*. Paraphyses are absent in *S. quinata,* whilst those of *S. alismifolia,* and *S. luzonica* appear to be mainly inserted on the stalk of the sporangium, generally one to each stalk. They consist of a somewhat swollen terminal cell which was often found surrounded by a ± spherical or pear-shaped yellowish to reddish glandular substance, and 2—5 hyaline cells. The paraphyses of *S. borneensis* are inserted in groups of 3—6 on the stalk of the sporangia, and are large, brownish, consisting of up to 10 cells of which the terminal cell only seems glandular.

Spores

The spores of *Austrogramme, Taenitis,* and *Syngramma* are trilete (figs 1—3). Spores of *Austrogramme* have a ± circular equatorial outline with a diameter of ± 35—40 μm. In equatorial view the distal part is ± globose, the proximal part ± depressed globose. The proximal side shows a labrum and a shorter suture. The outer surface is microverrucate with superimposed more or less distinct (clusters of) short irregular excrescences.

Spores of *Taenitis cordata, T. blechniodes, T. flabellivenis, T. interrupta, T. marginata, T. requiniana,* and *T. vittarioides* are characterised by a conspicuous



FIGURES 6–15: Leaf-shape and sporangial disposition in *Austrogramme*. 6, 7, *A. asplenioides* (Henty & Foreman NGF 42542). 8, 9, *A. boerlageana* (Kornassi 1241). 10, 11, *A. decipiens* (McGillivray 23, BM). 12, 13, *A. francii* (Compton 1480, BM) 14, 15, *A. marginata* (Franc 1424). Figs 6, 8, 10, 12, 14, x ½; figs 7, 9, 11, 13, 15: x 1½.

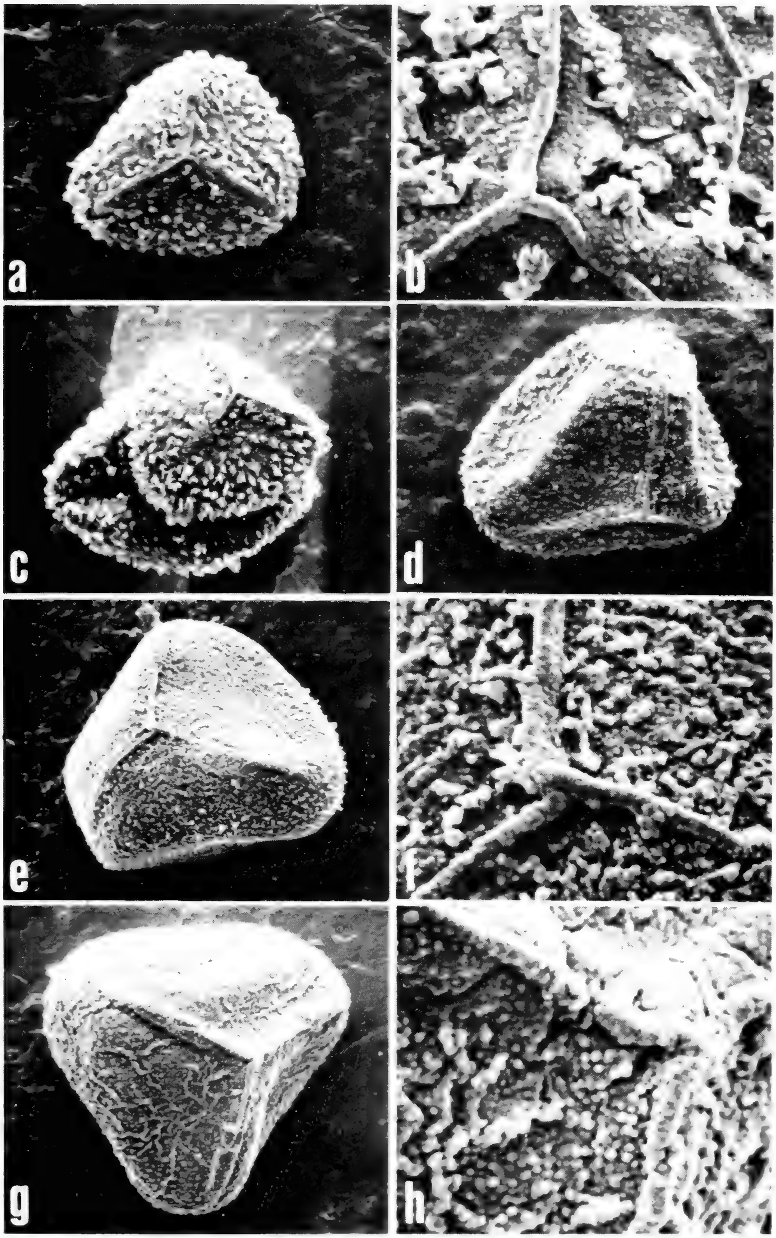


FIGURE 16: Spores of *Austrogramme* and *Syngramma:* a, b, *A. francii* (Le Rat 15, P); c, *A. decipiens* (Franc 336); d, *A. boerlageana* (Buwalda 6210); e, f, *A. asplenioides* (Henty & Foreman NGF 42542); g, h, *S. quinata* (Brass 3334); (a, c-e, g: x c. 1000; figs b, f, h: x c. 5000).

cingulum (equatorial flange) which is sometimes interrupted or reduced at the angles. The equatorial outline is (sub) triangular, its largest width 45–70 μm. In equatorial view the proximal part is more or less flattened or depressed globose, whereas the

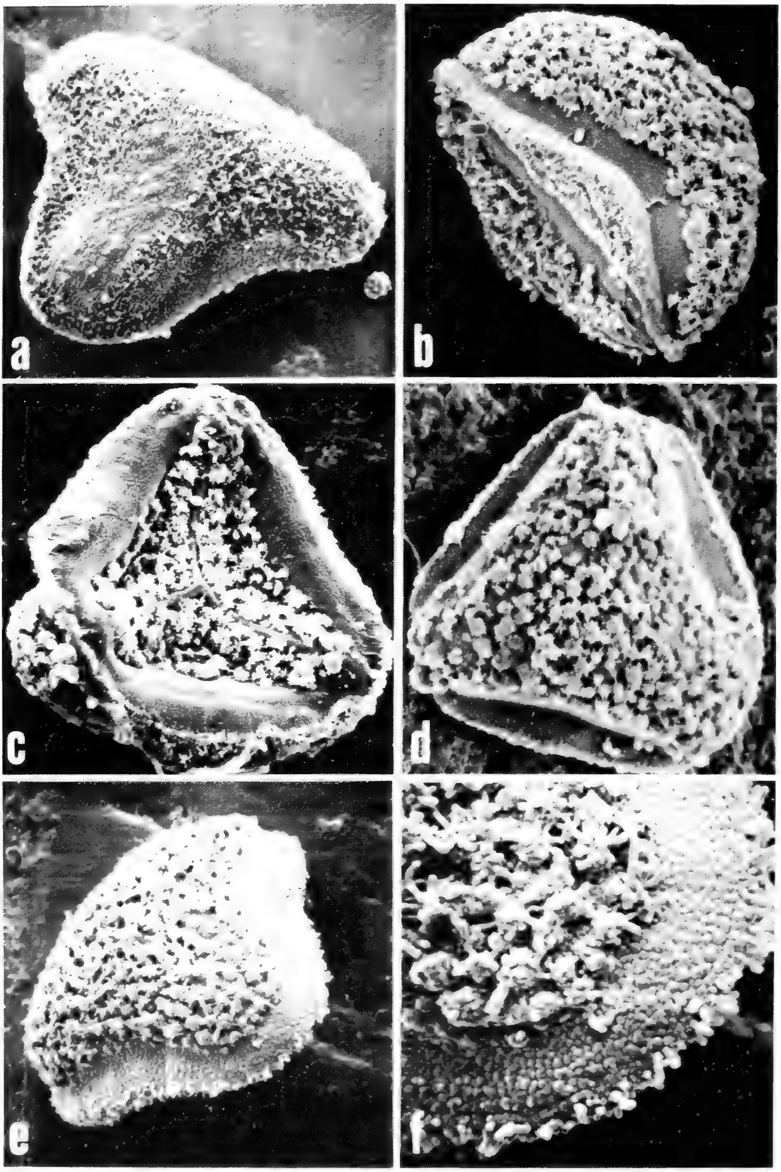


FIGURE 17: Spores of *Syngramma* and *Taenitis*. a, *S. luzonica* (Edano PNH 40526); b, c, d, *T. interrupta* (Schiffner s.n., L. 942. 123–124), e, f, *T. requiniana* (Coode & Katik NGF 29841), a-e: x c. 1000, f: x c. 2500).

distal part is globose or only occasionally depressed. The proximal part of the spores of *T. cordata* shows tori along the suture, the distal part has irregularly shaped, large, raised ridges; the surface is microverrucate, bearing spaced irregularly shaped granules of varying size all over the spore.

The spores of the other *Taenitis* species mentioned above are all more or less similar and of the same shape as those of *T. cordata*, but the proximal part without

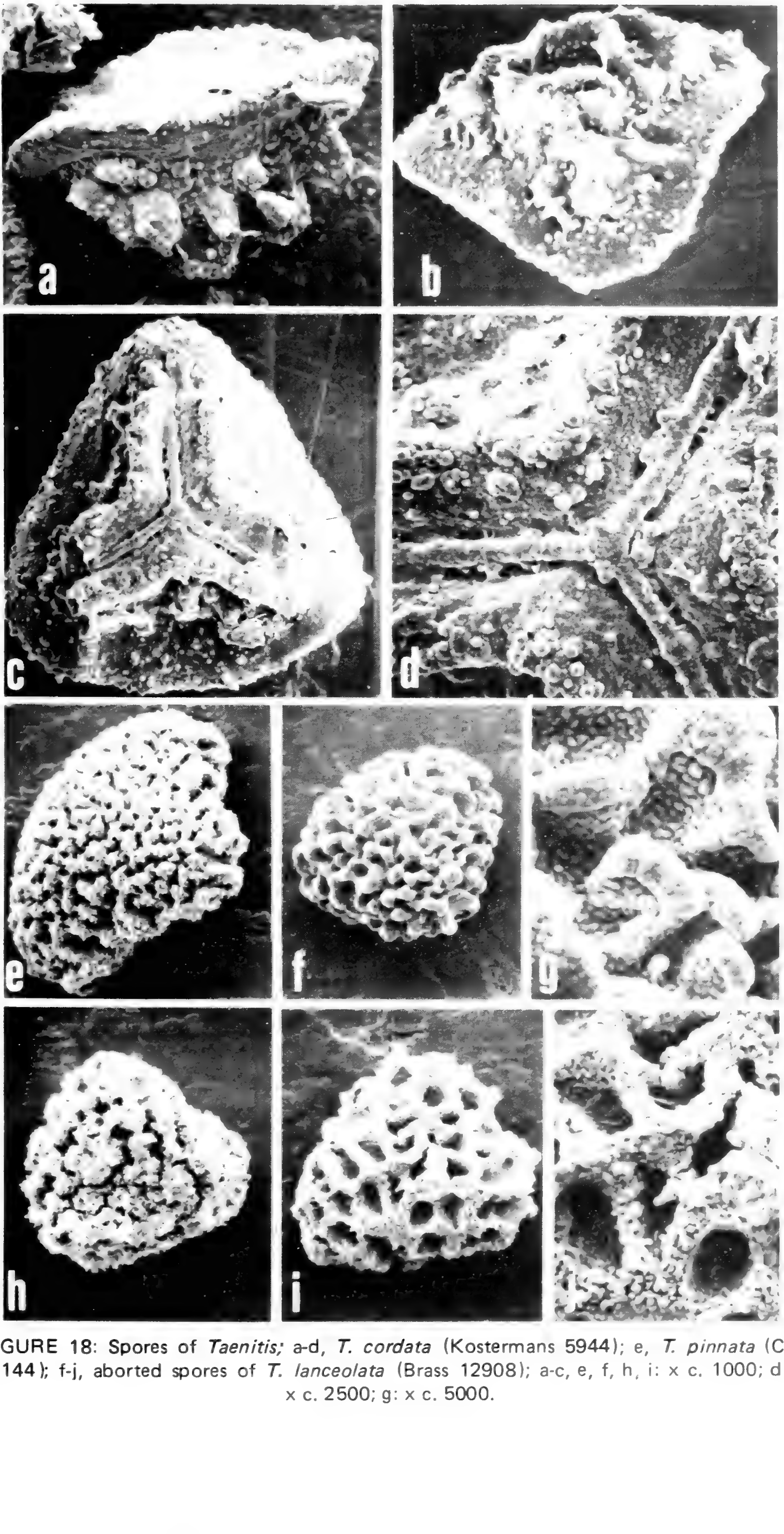


FIGURE 18: Spores of *Taenitis;* a-d, *T. cordata* (Kostermans 5944); e, *T. pinnata* (Carr 12144); f-j, aborted spores of *T. lanceolata* (Brass 12908); a-c, e, f, h, i: x c. 1000; d, j: x c. 2500; g: x c. 5000.

tori along the suture and the surface of a different shape. The upper and lower surface of the cingulum (and small adjoining parts) are microverrucate, laterally densely covered with irregularly shaped baculae and granules; the outside otherwise densely packed with ± globose raised ridges or ± globose clusters of variously shapped excrescences.

Spores of *Taenitis hosei, T. lanceolata,* and *T. pinnata* lack a cingulum. Those of *T. pinnata* show irregular, rather labyrinth-like ridges — but are in other respects quite like the spores of *T. interrupta.*

Spores of *T. lanceolata* were found to be aborted in several specimens, their outside rather differing in shape. Some spores lack a suture on their proximal side, though a weak indication of ridge-like tori may be present; otherwise the outside consists of somewhat reticulately arranged, rounded ridges. The surface of the spore is microverrucate, that of the ridges ± smooth. Other spores have a distinct suture and lack tori, their outside shows irregular reticulately arranged ridges of which the surface is densely packed with baculae and granules.

Spores of *Syngramma* have a ± circular to (sub)triangular equatorial outline with a diameter of 40–50 μm. Those of *S. alismifolia* and *S. quinata* are very similar in shape to the spores of *Austrogramme.* The proximal part bears a labrum and a shorter suture. The surface is microverrucate, and shows irregular, more or less densely placed, ridges. Spores of *S. luzonica* have a traingular equatorial outline, and have the distal and proximal part (strongly) depressed globose in equatorial view. The proximal part lacks a labrum, showing a long suture only. The surface is either covered with a dense felt of short excrescence throughout, or shows ± smooth parts.

DISCUSSION

The combination of leaf-shape, venation pattern, and disposition of the sporangia easily distinguish the genus *Austrogramme* from the genera *Taenitis* and *Syngramma.* The petiole anatomy of these three genera differs from that found in *Coniogramme* (Walker 1968).

The shape of the glandular paraphyses of part of *Austrogramme* resembles strongly that found in part of *Taenitis.* The glandular substance was found to be inside the cell. In other species of *Taenitis* different kinds of paraphyses were found. The paraphyses of *Syngramma,* if present at all, likewise show much variation. They apparently have a single terminal glandular cell surrounded by glandular substances. Variation in paraphyses of *Taenitis* and *Syngramma* has been noticed also by Walker (1968).

The spores of *Austrogramme* are proportionally small. Their shape resembles that of some *Syngramma* species. The information of the spores of *Austrogramme (Aspleniopsis) decipiens* given by Erdtman (1957) and Erdtman & Sorsa (1971) is rather poor. *S. alismifolia* and *S. (Craspedodictyum) quinata* and *S. (Craspedodictyum) schlechteri* (Erdtman & Sorsa 1971: pl 5, fig 1) have very similar spores which supports the inclusion of *Craspedodictyum* Copeland in *Syngramma* as proposed by Holttum (1954).

Spores of *Taenitis* are very different from those of *Austrogramme* and *Syngramma,* and are of two kinds either with or without a cingulum. These differences in spores are not correlated with differences in paraphyses. In *Taenitis* the cingulum was first reported by Tardieu-Blot (1963) for *T. ("Schizoloma") cordata.* From the publications of Erdtman (1957) and Nayar & Devi (1966, 1967), it becomes clear that a cingulum is also found in the spores of some other genera of the Pteridaceae sensu

Copeland. The occurrence of a cingulum also in *Taenitis* (and its American relative *Syngrammatopsis* — Hennipman, unpublished), seems of interest in view of the ambiguous systematic position of *Taenitis.* Mickel (1973) related *Taenitis* to the Lindsaoid ferns, whereas Holttum (1960) thought *Taenitis* more related to *Syngramma* than to *Lindsaea.* In both the Lindsaeoid ferns and *Syngramma* a cingulum is not known, however. A study of the spores seems promising when considering the relationships within Copeland's Pteridaceae.

The chromosome number of *Austrogramme decipiens* is n = c. 58 (Brownlie ex Fabbri 1963). That of *Syngramma* is n = 58 in *S. (Craspedodictyum) grandis* (Walker 1968) and in *S. alismifolia* (Holttum 1960), whereas it is n = 116 in *S. (Craspedodictyum) quinata* (Holttum 1960). These data suggest a base number of x = 29 for both *Syngramma* (Walker 1968) and *Austrogramme.* Chromosome numbers of *Taenitis* show more variation. *T. blechnoides* has n = 44 (Holttum 1960) and n = 110 (Walker 1968) which point to a base number of x = 22. *T. (Syngramma) lanceolata* has n = 114 (Walker 1968). Differences in chromosome number in *Taenitis* are associated with differences in the spores (presence or absence of a cingulum). But apart from the cingulum, the spores of the *Taenitis* species are very similar.

The properties of the spores, and the chromosome number indicate a relationship between *Austrogramme* and *Syngramma.* The relationship of *Austrogramme* to *Taenitis* seems less obvious, also in view of the variation of the paraphyses in the three genera studied.

Further, the present study supports the emendations of *Syngramma* and *Taenitis* as proposed by Holttum.

SYSTEMATIC TREATMENT

Austrogramme Fournier, Ann. Sc. Nat. V, 18: 278. (1873).

Lectotype (Copeland, Gen. Fil., 1947: 56): *A. marginata* (Mettenius) Fournier.

Aspleniopsis Mettenius ex Kuhn, *Chaetopt.:* 325 (1882); Diels in Engler & Prantl, *Nat. Pfl. Fam. 1, 4:* 272 (1899); Copeland, *Gen. Fil.:* 77 (1947); Brownlie, *Fl. Nouv.-Caled., Pterid.:* 161 (1969) — Type: *Aspleniopsis decipiens* (Mettenius) Kuhn.

Gymnogramme auct. p.p., non Desvaux.

Rheopteris auct., et sensu Holttum p.p., non Alston.

Rhizome short-creeping or suberect, solenostelic, clothed with inconspicuous bristles as least terminally; roots many, firm. Leaves tufted, in several rows, simple to tripinnatifid, 9—70 cm long; petiole dark reddish-brown, near the base or throughout *(A. marginata)* with inconspicuous bristles, with 2 vascular strands; lamina herbaceous, ± glabrous; veins free or variously anastomosed. Sporangia situated in (orbicular to) elongate sori, variously along the veins, with 16—20 indurated cells. Spores trilete, ± spherical, diameter of equatorial outline ± 35—40 μm, whitish, thin-walled, the outer surface ± smooth (when seen with the light microscope).
Chromosome number: n = c. 58 *(A. marginata).*

Distribution: Moluccas, New Guinea, New Ireland (?), New Hebrides, and New Caledonia.

Habitat: Usually terrestrial or rheophytic, rarely *(A. francii)* epiphytic. Altitude: 0—1000 m.

Notes: 1. On some petioles of *A. asplenioides* and *A. francii* I observed small buds situated just above the petiole base. In one leaf of *A. asplenioides* such a bud obviously had developed into an elongate rhizome bearing tufted roots and leaves terminally. 2. *Austrogramme deplanchei* (Baker) Fournier (bas.: *Polypodium deplanchei* Baker), the second species originally included in the genus, was transferred to *Grammitis* by Copeland (*Gen. Fil.* 1947: 211). 3. Stomata of *Austrogramme asplenioides* and *A. decipiens* are polycytic.

Because of difference in shape of the leaves two sections are recognised:

Sect. 1. **Austrogramme** Fournier, Ann. Sc. Nat. V, 18: 278 (1873). – Lectotype: *A. marginata* Fournier.
Leaves simple; veins free. Distribution: New Caledonia. Species 1–2.

Sect. 2. **Aspleniopsis** (Kuhn) Hennipman, *stat. et sect. nov.*

Aspleniopsis Mettenius ex Kuhn, *Chaetopt.*: 325 (1882). – Type *Gymnogramme decipiens* Mettenius.
Leaves pinnate to tripinnatifid; veins free or anastomosing. Distribution: as the genus. Species 3–5.

KEY TO SPECIES

1. Leaves simple. Veins free (sec. *Austrogramme*) 2
   Leaves compound. Veins either (almost) free or regularly anastomosing (sect. *Aspleniopsis*) 3
2. Leaves 30–70 by 2.5–4 cm. Petiole 2–7 by 0.20–0.25 cm. . . . . . . *A. marginata*
   Leaves 9–30 by 1–2.2 cm. Petiole 5–10 by 0.10–0.15 cm. . . . . . . *A. francii*
3. Leaves bipinnate to tripinnatifid. New Guinea . . . . *A. asplenioides*
   Leaves pinnate to bipinnatifid 4
4. Veins regularly anastomosing. Margin of pinnae entire. Terminal segment asymmetrical Moluccas. . . . . *A. boerlageana*
   Veins free. Margin of pinnae variously lobed. Terminal segment symmetrical. New Caledonia . . . . *A. decipiens*

Sect. 1. **Austrogramme**

1. **Austrogramme marginata** (Mett.) Fournier. – Fig. 14, 15, Ann. Sc. Nat. V, 18: 278 (1873). – *Gymnogramme marginata* Mett, *Ann. Sc. Nat. IV, 15*: 59 (1861) Fournier, *Bull. Soc. Bot. France 16*: 423 (1869); Compton, *J. Linn. Soc. Bot. 45*: 449 (1922). – *Syngramma marginata* Diels in Engler & Prantl, *Nat. Pfl. Fam. I, 4*: 257 (1899); Brownlie, *Fl. Nouv.-Caled. Pterid.*: 161 (1969). – Type: *Vieillard 1642* (iso in BM, P).

Leaves simple, 30–70 by 3.5–4 cm; petiole 2–7 cm long, 2–2.5 mm thick, lamina widest about the middle, long decurrent on the petiole, margin usually entire, sometimes the upper part irregularly crenate, apex acute to acuminate; veins free. Sori situated ± beyond the costa up to the margin, elongate, of varying length.
Chromosomes: n = c. 58 (Brownlie ex Fabbri, 1963).
Distribution: New Caledonia: *Compton 1722* (BM); *Franc 1424* (BM, P): *McKee 6405* (K); *Sarasin 64* (P); *Vieillard 1642* (BM, P).
Habitat: Primary forest. Terrestrial.

2. **Austrogramme francii** (Rosenst.) Hennipman, *comb. nov.* – Fig 12, 13.

Syngramma francii Rosenst., *Fedde Rep. 9*: 75 (1910); Compton, *J. Linn. Soc. Bot. 45*: 449 (1922); Brownlie, *Fl. Nouv.-Caled., Pterid.*: 160 (1969). – Type: *Franc 1427* (P, not seen; iso in BM).

Syngramma francii var. *intermedia* Rosenst., *Fedde Rep. 9*: 76 (1910). – Type: *Le Rat 15* (P, 2 sh.).

Leaves simple, 9–30 by 1–2.2 cm; petiole 5–10 cm long, 1–1.5 mm thick; lamina widest about the middle, decurrent on the petiole, margin entire, apex rounded to acuminate; veins free. Sori situated either ± beyond the costa up to the margin, or towards the margin only, (orbicular to) elongate, of varying length.
Distribution: New Caledonia: *Compton 1480* (BM); *Franc 1427* (BM); *Le Rat 15* (P).
Habitat: Along streams; terrestrial and epiphytic.

Sect. 2. **Aspleniopsis** (Kuhn) Hennipman

3. **Austrogramme asplenioides** (Holttum) Hennipman, *comb. nov.* – Fig. 6, 7.

Rheopteris asplenioides Holttum, *Blumea 11*: 531 (1962). – Type: *Kalkman BW 8528* (L).

Leaves bipinnate to tripinnatifid, up to 25 cm long; petiole 5–15 cm; lamina ± triangular, 1.5–2 times as long as wide, 7–9 by 4–5 cm; pinnae 10–20, alternate, the basal ones shortly stalked, 20–45 by 10–15 mm; pinnules 4–8, spaced, wedge-shaped, up to 17 mm long, distal margin ± entire or lobed to almost to costule; terminal segment of leaf and pinnae of ± similar shape as the pinnules; veins free, occasionally with a distal anastomosis. Sori elongate, of varying length.

Distribution: New Guinea. West. Div. South New Guinea, Subdiv. Muju, ± 5 km NE. from junction Iwur R. and East Digul: Kalkman BW 8528 (L). – East. West Sepik Distr., Telefomin subdistr., Prospect Creek near Frieda R.: *Henty & Foreman NGF 42542* (L).

Habitat: On rocks in stream-bed, inundated during high water.

Note: Many inconspicuous dark brown bristles are found at the apex of the rhizome. They were not studied by Holttum.

4. **Austrogramme boerlageana** (v.A.v.R.) Hennipman, *comb. nov.* – Fig. 8, 9.

Syngramma boerlageana v.A.v.R., Bull. Dept. Agric. Ind. Neerl. 18: 19 (1908), pl. 3. – Type: *Boerlage s.n.,* Ambon (BO, not seen; phot. K).

Leaves pinnate, up to 35 cm long; petiole 6–25 cm; lamina triangular, 7–15 by 6–10 cm; pinnae 5–11, alternate or opposite, the lowermost ones deflexed, shortly stalked, asymmetrical, up to 60 by 30 mm, the acroscopic side of the base truncate to cordate, its basiscopic side narrowly acute, margin entire, gradually narrowing from the base towards the acute apex; terminal segment ± triangular, asymmetrical, up to 50 by 20 mm, with 1 or 2 unequally-sized basal lobes, gradually narrowing towards the acute apex. Veins forming a regular network of elongate, angulate areoles. Sori situated along part of the veins, elongate, often ± curved, of varying size.

Distribution: Moluccas. Ambon: *Buwalda 6175 (L), 6210* (L); *Boerlage s.n.* (BO). *Brooks s.n.* (BM) – Ceram: *Kornassi* 1241 (L).

Habitat: Primary forest. Terrestrial.

5. **Austrogramme decipiens** (Mett.) Hennipman, *comb. nov.* – Fig. 10, 11.

Gymnogramme decipiens Mett., *Ann. Sc. Nat. IV, 15*: 60 (1861); Fournier, *Bull. Soc. Bot. France 16*: 422 (1869); *Ann. Sc. Nat. V, 18*: 279 (1873); Compton, *J. Linn. Soc. Bot. 45*: 448 (1922). – *Aspleniopsis decipiens* Kuhn, *Chaetopt.* 325 (1882); Diels in Engler & Prantl, *Nat. Pfl. Fam. I, 4*: 272 (1899); Copeland, *Gen. Fil.* 77 (1947); Brownlie, *Fl. Nouv.-Caled., Pterid.* 161 (1969). – Lectotype: *Vieillard 1648,* New Caledonia (P, not seen).

Gymnogramme decipiens var. *parva* Compton, *J. Linn. Soc. Bot. 45*: 449 (1922). – Type: *Compton 1781,* New Caledonia (BM).

Leaves pinnate or bipinnatifid, 15–45 cm long; petiole 2–20 cm; lamina 2–6 times as long as wide, widest about or below the middle, 9–25 by 1.5–9 cm; pinnae 30, alternate or opposite, ± sessile to shortly stalked, asymmetrical, the largest ones up to 45 by 10–15 (–20) mm, the acroscopic side of the base broadly acute to subcordate, its basiscopic side narrowly acute, margin shallowly lobed to lobed to almost the costa, apex acute; terminal segment inconspicuous, its shape similar to that of the pinnae. Veins free. Sori (orbicular to) elongate, of varying length.

Distribution: New Caledonia (common), New Hebrides, and possibly also in New Ireland (Brownlie 1969).

Habitat: In primary forest, terrestrial and rheophytic.

Note: The small rheophytic specimens were given varietal status by Compton. However, the size and shape of the plants seem largely determined by habitat conditions.

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THE BIOGEOGRAPHY OF ENDEMISM IN THE CYATHEACEAE

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ABSTRACT

One of the principal features of the biogeography of the Cyatheaceae is the strong development of local endemism. Closely related local endemics often occur in the same region. They are most frequent where pronounced environmental mosaics have been present for considerable periods of time. Local endemics are fewer in ecologically more uniform regions, and in areas subjected to climatic change. Data on local endemism in the Cyatheaceae support an hypothesis of local speciation based on the establishment and divergence of small peripheral populations. It is proposed that local endemics are ecologically specialised. In spite of high dispersibility, they are isolated through their adaptation to small environmental areas not duplicated within the range of dispersal.

The notable studies of Dr. R.E. Holttum on the systematics of the tree ferns (Cyatheaceae) merit recognition in this series of papers dedicated to him. His contributions to the systematics of this family include a revised generic classification and monographs of over 250 species of Indo-Asia, Malaysia, Australia and the Pacific islands.

INTRODUCTION

The scaly Cyatheaceae form a large evolutionary group of about 500 species. The scales are abundant on the stem apex and usually on the leaves, especially toward the base of the petiole. Holttum (1963) included these species in the genera *Cyathea* and *Cnemidaria,* while Tryon (1970a), recognising several evolutionary lines, treated them in the genera *Sphaeropteris, Alsophila, Nephelea, Trichipteris, Cyathea* and *Cnemidaria.* The Cyatheaceae are an excellent subject for biogeographic study because of the large number of species, the wide geographic distribution of the family, and the recent systematic work that provides sound geographic information. The strong development of endemism, especially local endemism, has become apparent from an analysis of the geographic ranges of the species. The nature of these endemics in the Cyatheaceae and the way they may have developed will be considered here. The data presented in this paper have been primarily obtained from publications by Holttum (1963, 1964, 1965) and Tardieu-Blot (1951, 1953) on the paleotropical species, and from papers and manuscripts on the neotropical species by Barrington (1974), Conant (1974), Gastony (1973), Riba (1969), Stolze (1974), Tryon (1971, 1972, 1974), and Windisch (1974). Some additional information has been obtained from other literature and collections in the Harvard University Herbaria.

BIOGEOGRAPHY

The scaly Cyatheaceae have a pantropical distribution, with a few extra-tropical extensions to the south in South America, South Africa, Australia, New Zealand, and the Pacific, and with an extension to the north in southeastern Asia to Japan and the Bonin Islands. The species are strongly concentrated in the major wet mountainous regions of the world (Fig. 1). Data on the number of species occuring in regions

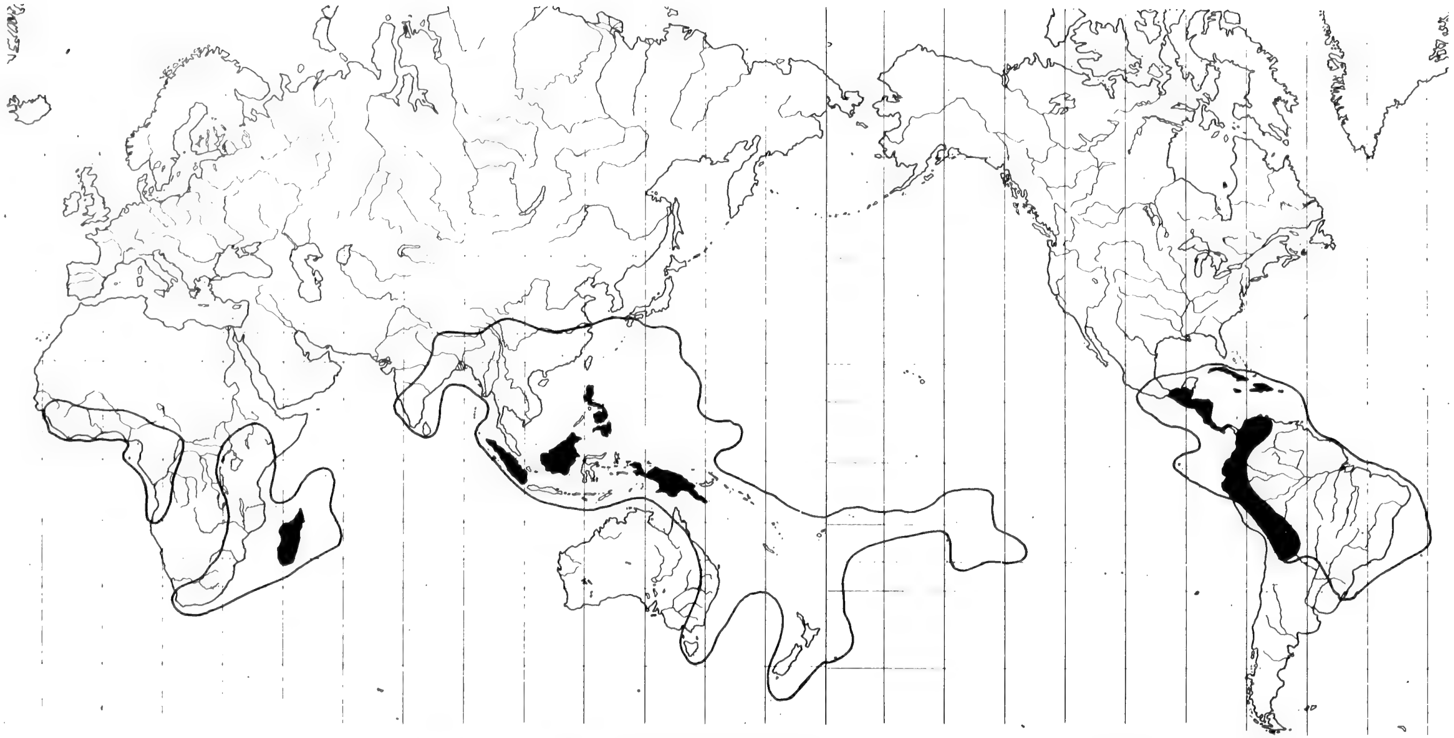

FIGURE 1: Generalized range of the scaly Cyatheaceae. The solid black areas are the major wet mountainous regions that are centres of species diversity.

included in Table 1 clearly indicate these centres of species diversity: the Greater Antilles, southern Mexico and Central America, the Andes, Madagascar, Sumatra, Borneo, Philippine Islands, and New Guinea. The altitudinal occurrence of species is shown in Table 2. Species grow from sea-level to 4200 m, and within this wide range they occur most frequently from 1000 to 1500 m. There is a progressive decrease in numbers of species below 1000 m, and the number also diminishes at altitudes from 1500 to 2500 m. Species are much less frequent above 2500 m. Two Andean species of *Cyathea* grow at 4200 m, which is the highest altitude reported for tree ferns.

Data on the number of endemics, the per cent of endemism and the number of local endemics are given in Table 1. Endemics are confined to a geographic area where they may occupy a considerable range or a very small one. It is important to distinguish between local endemics, those species with a limited distribution, and those endemics of wider distribution. The high dispersal capacity of fern spores requires a broader geographic definition of a local species than in the case of most seed plants. A range of about 300 miles (500 km) or less is considered a limited one in the ferns, and species with distributions of this size are regarded as local endemics. The 223 local endemics (Table 1) represent 44% of the species of Cyatheaceae. The strong development of local endemism in the family seems paradoxical when the high dispersal capacity of the spores is considered. The pantropical distribution of the whole group and of wide ranging species (Fig. 2), especially those species occurring on distant islands, such as *Sphaeropteris lunulata* and *S. medullaris,* clearly demonstrate effective dispersal capacity. However, local endemics suggest that other factors such as geographic isolation or ecological specialisation are involved in determining the extent of their distribution.

Geographic isolation may be the basis of local endemism in ferns if the distance is sufficient to prevent dispersal across extensive barriers to other areas of similar environment. Small and remote oceanic islands represent areas with strong geographic isolation. The distance between one island and another with a comparable environment may be so great that the chance of spores reaching it are slight. This is especially true when there is a small source area with a correspondingly small species population. The local endemics on small remote islands of the Pacific represent examples of this type of geographic isolation.

Local endemism in other regions may not be based on geographic isolation. Both local endemics and more widely distributed species occur in the wet forested mountains of the Andean area and of New Guinea. Wide ranging species are distributed along the Andes from Colombia south to Peru or Bolivia, and in New Guinea wide ranging species extend from the Milne Bay District west to the Weyland Mountain region or the Arfak Mountains. Within these extensive areas suitable for tree ferns, the local endemics are effectively isolated. The basis for their isolation seems to be adaptation to a local environment that is not duplicated in the region.

An explanation of the manner by which ecologically specialised local endemics can evolve must consider the events leading to speciation within an ecological-geographic framework. An ecological variant, generated from a population gene pool, that is adapted to a somewhat different environment in a peripheral area (one within easy dispersal distance) may become established there as a small population. This population will have unusual opportunities for speciation, as compared to the original one, through small population phenomena such as inbreeding and genetic drift that can rapidly alter the genetic basis for selection. In time the new population will become more closely adapted to the new local environment. A distant new species of limited range and narrow ecological adaptation may evolve when morphological

Region	Number of species[1]	Number of endemics	Percent endemism	Number of local endemics[2]
Greater Antilles	37	28	76%	22
Southern Mexico and Central America	50	30	60%	16
Andes[3]	75	57	76%	25
Brazil	24	9	37%	0
South America	127	101	79%	40
NEOTROPICS	197	196[4]		110
Africa	15	13	87%	7
Madagascar	39	35	90%	11
Southeast Asia (excl. Malay Peninsula)	23	17	74%	4
Sumatra	34	15	44%	9
Borneo	31	14	45%	10
Philippines	37	26	70%	13
New Guinea	79	58	73%	36
Malaysia (incl. Malay Peninsula)	186	175	94%	79
Pacific (east of Australia and New Guinea)	41	38	93%	18
PALEOTROPICS	314	313		113
TOTAL	510			223

1 Geographic subspecies and varieties are included as species.
2 With a range of about 300 miles (500 km) or less in extent.
3 State of Lara, Venezuela to Colombia, south through Bolivia to the Province of Salta, Argentina.
4 *Alsophila capensis* (L.f.) J. Sm. is in Africa and Brazil.

TABLE 1: Species and endemics of Cyatheaceae in selected regions.

divergence is linked with ecological specialisation. A local endemic, derived from a more widely distributed species, may in turn give rise to another species by the same process. Such a "second generation" endemic will be even more ecologically specialised and geographically limited as its genetic base becomes further restricted. Continuation of this mode of speciation will constantly increase the number of local endemics in a region providing that the climate remains equable. Such endemics would be highly vulnerable to extinction with a significant climatic change. The data on local endemism in the Cyatheaceae will be reviewed for its consistency with this hypothesis on the origin of local endemics.

Local endemics should be most numerous in topographically diverse terrain where a pronounced environmental mosaic provides many small areas that may be occupied by peripheral populations. The data in Table 1 show the concentration of 25 local endemics in the Andean area and 36 local endemics in New Guinea. In contrast, much larger regions having less topographic diversity have few local endemics. For example, there are only 7 in Africa and there are non in Brazil.

Related species should occur in areas within easy dispersal range of spores if they are derived by speciation of peripheral populations. All of the Greater Antilles are

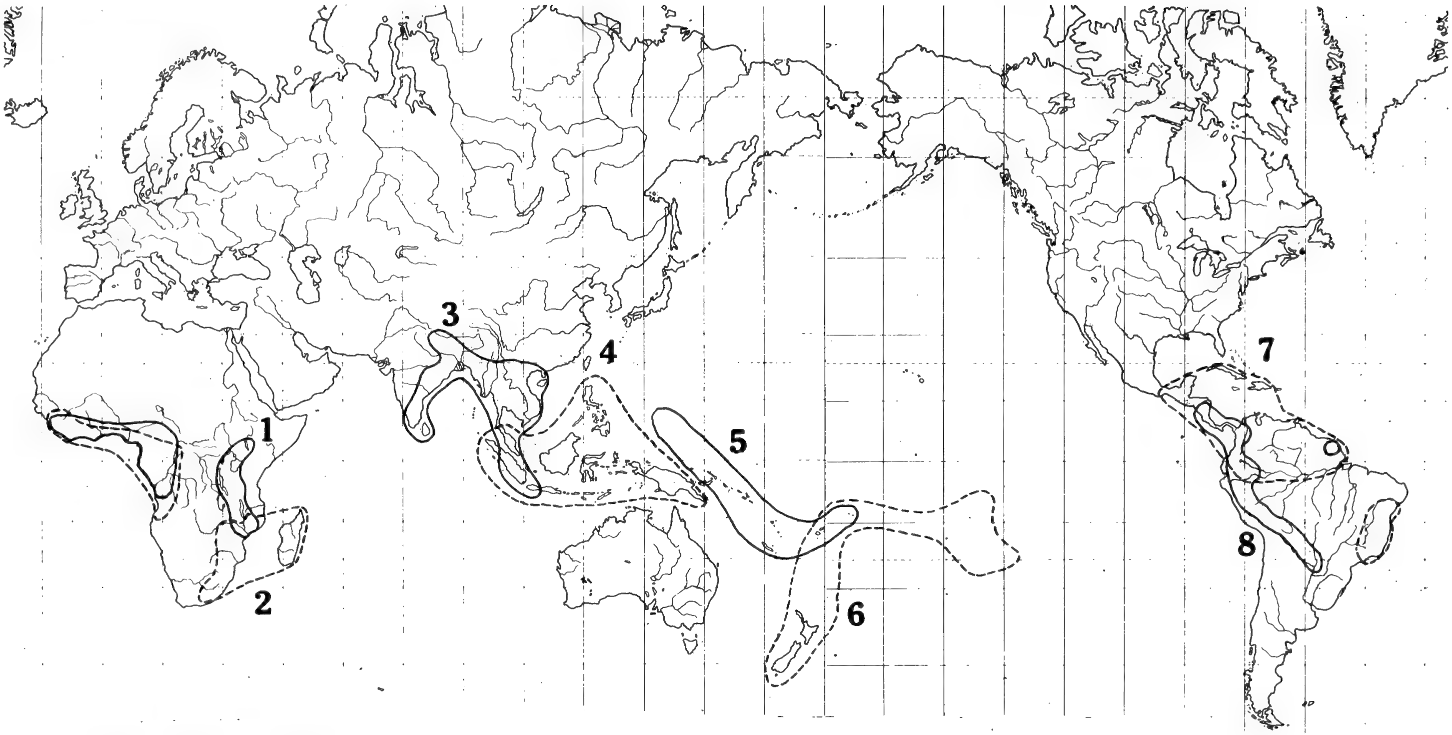

FIGURE 2: Widely ranging species of Cyatheaceae: 1. *Alsophila manniana* (Hook.) Tryon, 2. *A. dregei* (Kze.) Tryon, 3. *A. gigantea* Hook., 4. *Sphaeropteris glauca* (Bl.) Tryon [*Cyathea contaminans* (Hook.) Copel.], 5. *S. lunulata* (Forst.) Tryon, 6. *S. medullaris* (Forst.) Bernh., 7. *Trichipteris microdonta* (Desv.) Tryon, 8. *Nephelea cuspidata* (Kze.) Tryon.

sufficiently close so that there is no significant barrier of distance for spore dispersal between them. The mountainous areas of adjacent islands are about 150 miles (240 km) apart. Tryon (1970b) presents evidence that distances greater than 500 miles are required for isolation of an insular fern flora. In *Alsophila* there is a total of 9 species in the Greater Antilles, and in *Nephelea* there are also 9 species, one of them with three varieties. Seven of the species of *Alsophila* and all 11 of the taxa of *Nephelea* are endemic to single islands. In each of these genera the species are most closely related to others in the Greater Antilles. Thus these local endemics must have originated within the topographically diverse Greater Antilles and be maintained as endemics by environmental specialisation.

Altitude	**Number of species**	**Altitude**	**Number of species**
4000 m	2	2000 m	97
3500 m	8	1500 m	141
3000 m	22	1000 m	164
2500 m	52	500 m	98
		100 m	51

TABLE 2: Altitudinal occurrence of 391 species of Cyatheaceae. Species that occur only at altitudes between those listed are not included.

Altitudinal zones (in meters)	**New Guinea** 36 local endemics	43 other species	**Andes** [1] 25 local endemics	50 other species
4000–4200	0	0	0	2
3500–3900	2	6	0	4
3000–3400	7	10	2	9
2500–2900	9	14	3	18
Above 2400	*17*	*18*	*4*	*19*
2000–2400	12	19	8	30
1500–1900	9	21	8	35
1000–1400	8	21	4	39
500–900	4	18	6	28
0–100	2	11	5	12

[1] As delimited in Table 1.

TABLE 3: Occurrence of local endemics and other species of Cyatheaceae in altitudinal zones in New Guinea and in the Andes.

Local endemics would be expected to become extinct under environmental change. The mountainous regions of the Andean area and of New Guinea have had contrasting climatic histories. In the Andes, from Colombia to Bolivia (ca 10°N. Lat. to 20°S. Lat.), there are extensive areas above 3500 m and many mountains rise above 5000 m. In New Guinea, extending from the equator to 10°S. Lat., the area above 3500 m is much smaller and there are only a few peaks above 5000 m. Although information on the effects of Pleistocene climates in the two regions is limited, the influence must have been more extensive and severe in the Andes than in New Guinea. In both regions local endemics occur from sea level to above 3000 m (Table 3). Seventeen local endemics occur in New Guinea above 2400 m, and there are 19 species that are more wide ranging. In the Andes there are 4 local endemics above 2400 m and 19 more widely distributed species. The number of species at the higher altitudes that have moderate to wide ranges is similar in both regions, but the Andes have a reduced number of local endemics in comparison to New Guinea.

Local endemics can be derived by environmental restriction of a former larger range, as well as by local speciation. An interpretation of the local endemism as relict endemism, however, is not supported by the data on the species of the Andes and New Guinea. The occurrence of local endemics along with more widely distributed species throughout a wide altitudinal range (Table 3) is not a relictual pattern. In the Andes the local endemics are notably fewer at the higher altitudes where relict endemism should be pronounced.

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LUNATHYRIUM IN THE AZORES

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ABSTRACT

Evidence is presented that the plant known in the Azores as *Diplazium allorgei*, long considered to be an introduction, belongs to the *Lunathyrium japonicum* species-complex of eastern Asia, and is inseparable from *Diplazium lasiopteris* Kunze. Its great increase and spread to many islands of the Azores within a relatively short period is wholly consistent with its being an introduced species.

INTRODUCTION AND TAXONOMY

The fern currently known as *Diplazium allorgei* Tard.—Bl. was first recorded from the Azores by Christ (1907). He correctly recognised it as a *Diplazium* of the *D. japonicum* group and identified it, after comparison with Nilgiri examples, as *D. lasiopteris* Kunze. Christ's description and comments on this fern are given in a supplementary note on introduced species in which *Pityrogramma calomelanos* and *Adiantum hispidulum* are mentioned as other introductions. That the *Diplazium* was indeed introduced, either intentionally or accidentally, into its original locality at Feteiros (Sao Miguel) seems clear from the quoted remarks of Dr Carreiro whose collections formed the basis of Christ's papers. The quotation refers to the locality as a planted woodland on the estate of a rich landowner who was an enthusiastic gardener and who had imported many exotic trees, shrubs and ferns for stocking his gardens.

When Mme Tardieu-Blot (1938) described *D. allorgei* she was in no doubt that it was the same fern as that previously reported by Christ and since the collections of M & Mme Allorge on which her description was based, like those of Dr Carreito, also came from an artificial habitat — a *Cryptomeria* woodland — she was equally opposed to considering it an indigenous species. As regards the distinguishing features of *D. allorgei,* its author, whilst agreeing that it was "très voisine du *D. lasiopteris*", considered that it was specifically separable by "son pétiole et son rachis noir, son contour plus largement deltoide, ses lobes séparés par de plus larges sinus, ses sores plus longs et surtout, comme le fait remarquer Christensen *(in litt.)* son indusie ciliée-frangée".

The author's description of *D. allorgei* reads "stipite cum rachi ochraceo vel nigro": Christ's description makes no mention of black colouration but correctly refers to the stipes as "ochraceo". His description is applicable to all Azores specimens seen by me, none of which could properly be described as having black stipes though a variable degree of darkening in the lower part is not uncommon. This applies also to *D. lasiopteris.* I am unable to find any significant or constant difference between Azores specimens and Indian specimens in the supposed distinctions based on the width of the sinus between the lobes of the lamina or in the lengths of the sori, whilst a ciliate-fimbriate indusium is also typical of *D. lasiopteris* and indeed of the *D. japonicum* group as a whole. As regards the more deltoid outline of the fronds in Azores plants, a distinction to which both Christ and Tardieu-Blot refer, this is true of the original gatherings, which could well have been the product of one imported genotype, but it is certainly not true of many subsequent gatherings which show no difference from *D. lasiopteris* or *D. japonicum* in this respect. This is well shown in Wilmanns and Rasbach's illustration (1973, fig. 16) which depicts a typical plant.

None of the characters attributed to the Azores fern therefore in my opinion justify specific recognition. The extent to which some characters in the *Lunathyrium japonicum* species-complex are determined genetically or by environmental conditions as unknown and the range of variation between different individuals within populations of a single species is such that I do not believe Azores plants are distinct from all other described species.

As regards the correct name to be applied to the Azores fern the choice would seem to lie with one of the following three species.

1. **Lunathyrium japonicum** (Thunb.) Kurata, Journ. Geobot. 9: 99 (1961).

Asplenium japonicum Thunb., Fl.Jap. 334 (1784).

Thunberg described his species from mountains near Nagasaki. No authentic specimens are known to exist. There are none in Thunberg's herbarium and Swartz (1806) indicated that no specimen had been seen by him. The current interpretation of *Lunathyrium japonicum sensu stricto* is thus based on a traditional concept unsupported by any authentic example. In Serizawa's (1973) recent account of the *L. japonicum* complex in Japan 17 taxa are recognised — seven species, four varieties and six hybrids. Three species are cited as occurring in the Nagasaki area, the species construed as *L. japonicum s.s.* being separated from *L. petersenii* largely on the basis of its dimensions according more closely with those attributed by Thunberg to his species than with the form of *L. petersenii* which also occurs there. The larger *L. dimorphophyllum* also grows in the Nagasaki area.

The dimensions attributed by Thunberg to his species were equivalent to stipes 65 cm. long and pinnae 8 x 2.7 cm. In *L. petersenii* the stipes are cited as 13.5 cm long and the pinnae 5.4 x 1.35 cm. Such figures imply measurements based on individual specimens. That no distinction can be drawn between them on size alone is clear from Serizawa's own specimens (kindly sent by Prof. Reichstein). Serizawa 6246 of *L. japonicum s.s.* from Tokyo bears two fronds with stipes 27 cm and 35 cm and the largest pinnae are 6 x 1 cm. In Serizawa 11725 of *L. petersenii* from Ryukyu the stipe is 63 cm long and the largest pinnae are 12 x 2 cm. It is evident therefore that no reliance can be placed on size.

2. **Lunathyrium petersenii** (Kunze) H.Ohba, Sci.Rep.Yokosuka City Mus. 11: 53 (1965).

Athyrium petersenii Kunze, Anal.Pterid. 24 (1837).

This was described from specimens "ex insula prope Canton". Kunze states after his description that "There appears to be none akin to *A. petersenii* unless *A. japonicum* not seen by me and not recently recognised", adding that *Athyrium japonicum* would appear to be satisfactorily distinguished by its larger size.

Kunze's herbarium was destroyed during the Second World War and I have failed to trace any authentic specimen of his species in herbaria at London, Copenhagen, Leiden, Stockholm or Berlin. There are also no photographs either of this or *Lunathyrium japonicum* in the extensive collections of photographs of type specimens made in herbaria throughout Europe by Alston or Morton.

Since no type or authentic specimens of either *L. japonicum* or *L. petersenii* can now be traced I consider it unproved that the plants to which these names were originally applied belonged to distinct species. Christensen (1934) had already come to the same conclusion. The two species which Japanese botanists currently recognise under these names therefore require typification by the selection and designation of representative neotypes.

3. **Diplazium lasiopteris** Kunze, Linnaea 17: 568 (1843).

This was described from specimens sent to the Berlin Botanic Garden from the Birmingham Botanic Garden in England. Later, Kunze (1851) referred specimens from the Nilgiri Hills, S. India, to *D. lasiopteris.* There is an authentic Kunze specimen in Herb. Brit. Mus.

From specimens collected by Zollinger in Java, Kunze (1848) described another species under the name *Allantodia deflexa.* The type of this is at Geneva and Morton's photograph of it (kindly sent by D.B. Lellinger) shows a small plant with creeping rhizome and fronds up to 14 cm in length, the stipes and rhachises of which are hairy throughout and beset with scales. When Christensen (1906) treated *Allantodia deflexa* as synonymous with *Diplazium petersenii* he also included *Diplazium lasiopteris* as another synonym, but it seems to me that the very scaly and hairy axes of the Java plant accord better with small examples of S. Indian and Ceylon *D. lasiopteris* than with Japanese or Canton (or Hong Kong) plants. I have previously pointed out (Sledge 1962) that some plants from Java seem inseparable from *D. lasiopteris.*

Although Christ named the Azores fern *Diplazium lasiopteris* he had previously (1902) followed Baker (1874) in treating *D. lasiopteris* as synonymous with the earlier published *Asplenium petersenii* and Christensen (1906) also adopted this opinion. Later however Christensen (1934) rejected this view, unequivocally citing *Diplazium petersenii* as synonymous with Thunberg's *Asplenium japonicum.* The grounds for this change of view one must suppose to have been based on good reasons though I have not traced any published statement by Christensen in justification of his altered opinion.

In my account (Sledge 1962) of the athyrioid ferns of Ceylon, it was pointed out that the Ceylon *Diplazium thwaitesii* is the same as the Nilgiri *D. lasiopteris* and the latter name was used rather than the older *D. petersenii* partly on geographical grounds and partly on account of Christensen's statement as to the latter being equivalent to *D. japonicum s.s.* rather than to *D. lasiopteris.*

CYTOLOGY

The *Lunathyrium japonicum* species-complex includes diploid, tetraploid, pentaploid and hexaploid races based on a monoploid n = 20 as against n = 21 in *Diplazium.* Diploid, tetraploid and pentaploid races have all been recorded from near Darjeeling by Bir (1961), who also (1965) recorded tetraploid plants from S. India. Manton (1954) records a tetraploid *"D. japonicum"* from Malaya and (1954) a hexaploid *"D. thwaitesii"* from Ceylon. Serizawa *(in litt.ad* Reichstein) reports Japanese counts on *Lunathyrium japonicum* as hexaploid and on *L. petersenii* as diploid and tetraploid. The Azores fern is a tetraploid. Bir (1961) noted that in diploid plants of *"japonicum"* the fronds and spores were smaller than in tetraploid *"japonicum",* but Serizawa (1973) makes no mention of differences between diploid and tetraploid *L. petersenii.* It is clearly not possible at present to relate these chromosome counts to any clear-cut morphological differences between the plants which yielded them. Cytotaxonomic and experimental studies are urgently needed for a proper understanding of the taxa concerned since we do not know the extent to which characters are environmentally or genetically controlled. Until such an investigation has been made, identifications should conform with currently accepted names with the recognition that their validity is provisional only and subject to confirmation or rejection following experimental studies.

IDENTIFICATION

As regards the identity of the Azores fern, for the reasons stated above I reject the view that *D. allorgei* is a distinct species. Since no type specimens of *L. japonicum* or *L. petersenii* are available for comparison we can only compare Azores specimens with gatherings from the geographical areas whence the three species concerned were originally described. Such a comparison shows that Azores specimens match Kunze's own specimen of *D. lasiopteris* in the Brit.Mus. and other collections from South India and Ceylon more closely than those from Japan, Canton and Hong Kong. Eastern Asiatic gatherings, whilst far from uniform in size or in the clothing of the stipes and rhachises are less scaly along the frond axes and much more weakly clothed with multicellular hairs. I consider therefore that Christ's identification of the Azores fern was correct and that following the separation of *Lunathyrium* from *Diplazium* the proper name for it should be **Lunathyrium lasiopteris** (Kunze) *comb. nov.*

Basionym: *Diplazium lasiopteris* Kunze in Linnaea 17: 568 (1843).

Syn.: *Diplazium allorgei* Tardieu-Blot in Notul.Syst., Paris *7:* 150 (1938).

DISCUSSION

Although the source of the plants first introduced into Sao Miguel is unknown, probability is strongly in favour of an Indian origin. Portugal at that time had several territorial possessions around the coasts of India and trade between the two countries flourished. It is significant also that the two other ferns mentioned by Christ as introduced species are both widespread in India. Other species introduced into Azores which are widespread in India include *Cyrtomium falcatum* (L.f.) C.Presl, *Diplazium esculentum* (Retz.) Sw., *Pteris vittata* L. and *P. multifida* Poir., though these are too widespread in south-east Asia for any conclusion to be drawn as to the likely sources of their introduction. The number of introduced Japanese and east-Asiatic species, both flowering plants and ferns, is very few; in Dansereau's (1961) geographical analysis of Macaronesian Pteridophytes *Pteris multifida* is the only species cited from oriental Asia. Jermy's (1964) attribution of a possible South American origin for *D. allorgei* is incomprehensible, since regardless of whether Azores plants are, or are not taxonomically distinct, there can be no question as to their belonging to *L. japonicum sensu lato* and this is unknown in South America.

When Mme. Tardieu-Blot described *D. allorgei* she recognised that it was probably an introduction. Subsequent students of Azores ferns (e.g. Palhinha 1943, 1966 and Vasconcellos 1968) have seen no reason to question its adventive origin. Since this fern was first recorded on Sao Miguel it has been found in six other islands, viz. Faial, Flores, Santa Maria, Sao Jorge, Pico and Terceira (Ormonde & Paiva 1973). It is now "very common" on Sao Miguel and on Faial (Reichstein, pers.comm.), and Ormonde has sent me details of ten different localities on Sao Miguel and Terceira where he has collected specimens. Wilmanns and Rasbach (1973) also state that it is now a common plant on Sao Miguel and they indicate 13 different localities for it on their map of the island. This great increase and spread to other islands within a relatively short period is wholly consistent with its being an introduced species (as was recognised by Christ) and is incompatible with the endemic status which Jermy (1970) has claimed for it. Indeed any enquiry into the history of this fern in the Azores or consultation of Christ's paper would surely have precluded either of Jermy's claims being made and it is unfortunate that his statement as to endemism has now received wide circulation through quotation in the Atlas to Flora Europaea. Christ's original opinion that this fern is an introduced plant specifically indistinguishable from Nilgiri plants is in my view correct and I consider that subsequent statements relating to its identity and origin have raised a superstructure of errors on a foundation of truth.

ACKNOWLEDGEMENTS

My grateful thanks are due to Jorge Paiva and J. Ormonde, Instituto Botanico, Coimbra, who first drew my attention to this matter and supplied specimens. Although the specific status of *Diplazium allorgei* had been accepted by other students of Azores ferns they had already formed the opinion that it does differ significantly from Indian specimens but they asked me to look further into the problem of its status and correct name. They are also in no doubt that this fern is an introduced and not an indigenous species.

I wish to thank also Prof. T. Reichstein for the loan of Japanese specimens sent by Serizawa, Dr J. D. Lovis for cytological examination of Azores plants kindly supplied by A.C. Jermy and T. Reichstein, and J.A. Crabbe for much time and helpful assistance given.

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THE GAMETOPHYTE OF CHINGIA PSEUDOFEROX

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ABSTRACT

The gametophyte of *Chingia pseudoferox,* while conforming to the general thelypteroid gametophytic pattern, deviates from it by the frequent presence on margin and surface of a multicellular structure, tentatively interpreted as a hair and characterized by a reddish-brown terminal cell and simple glandular hairs borne laterally. These structures set apart the thallus of *C. pseudoferox* from other known thelypteroid gametophytes and support the views of those authors who propose taxonomic segregation.

INTRODUCTION

The fern *Chingia pseudoferox* Holttum, as the name implies, is very like the type species, *C. ferox* (Bl.) Holttum (Holttum 1971), a large fern of the mountains, usually near streams, with an erect caudex and reduced basal pinnae. The chromosome number is thought to be 36, based on a count for *C. atrospinosa* by T.G. Walker and another for the Phillipine fern *C. urea* by M.G. Price (Holttum 1974: 14).

The spores of this fern were collected in 1969 by Dr R.E. Holttum in the Cameron Highlands, Malaya, at 4000–6000 feet and sent to me under the name *Cyclosorus ferox* sensu Holttum (1954: 265) with the admonition that the Malayan plants are distinct from Blume's Java species and that this fern and its allies constitute a group not yet recognized and probably needs a new name. In 1971, Holttum segregated the group from *Cyclosorus* sensu Copeland (1947) under his new genus *Chingia,* named in honor of the Chinese pteridologist, R.C. Ching, whose application of the principles of Christensen (1913, 1920) to Old World sporophytic fern characteristics (Ching 1940) preceded the intensive study of Thelypteridaceae which has since taken place (Ching 1963; Morton 1963; Holttum 1969, 1971; Holttum, Senl & Mitra 1970; Iwatsuki 1962–1965; Smith 1971, 1973, 1974).

Relatively few gametophytes of the large assemblage known as the thelypteroid ferns have been described. Among those I know, I find a similarly recognizable basic pattern (Atkinson 1971; Atkinson & Stokey 1973): a rather thin cordate thallus, with colorless rhizoids, which has developed from the terminal cell of the germination filament (exceptions — *Coryphopteris arthrotricha* Holttum ined., *Thelypteris totta* (Thunb.) Schelpe =*Cyclosorus gongylodes* sensu Copeland, where the germination filament ends in a hair necessitating plate initiation from subterminal cells), marginal and simple surface hairs bearing a colorless or yellow secretion, a 4–5 cell thick midrib bulging on the ventral side, an advanced type of antheridium appearing usually on separate thalli after or before the archegonia. Superimposed on the basic pattern, and interpreted as of more recent development, are observed other gametophytic characteristics, notably additional types of hairs which have appeared among the Old World species where, judging by these differences and by the variety of sporophytic differences (Holttum 1971), the thelypteroid ferns are evolving rapidly. It seems therefore profitable to continue the search in the gametophyte for evidence of relationships which may add weight to that already expressed for the sporophyte generation.

OBSERVATIONS

The spore of *Chingia pseudoferox* is black and appears minutely spiny under the light microscope (fig 1). It measures about 40.9 (39–42.9) x 27.7 (27.3–31.2) µm. Germination takes place on agar within ten days (figs 2 & 3). The germination filament is composed usually of 4–5 but may be of as many as 9 cells (figs 4, 6). On a slightly more acid medium (pieces of crock over peat) germination and growth are slower. The filament may branch and the rhizoid is often delayed (figs 5, 9).

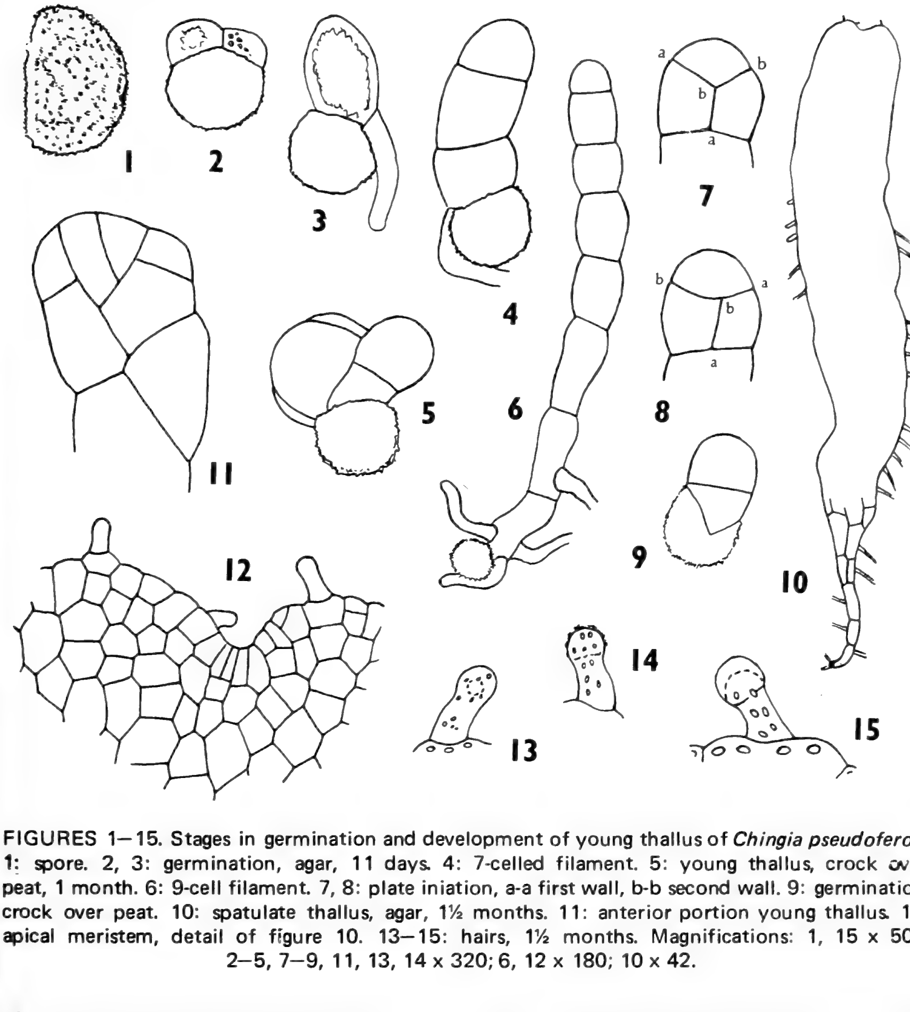
Development of a cordate thallus occurs along the lines of the basic pattern. The plate is initiated in the terminal cell of the germination filament by oblique walls (figs 7, 8). An apical cell, cutting off segments alternately to left and right, or right to left (fig 11) appears early and gives way to an apical meristem in our one and a half months (fig 12). Simple chlorophyllous hairs (fig 13) which become glandular (figs 14, 15) appear in about a month on the margin of the thallus and in six weeks also on the surface. Winter cultures in a north window when days are dark (December to February) were spatulate (fig 10) but cultures grown later in the year (March to August) or under artificial light were broadly cordate with a deep narrow notch or with slightly overlapping wings (figs 19, 21). The outside walls of the marginal cells are undulate (figs 17, 18). At 6 months the thallus is 4–5 cells thick (fig 39). The rhizoids are colorless.

In about 3 months, 3–4 celled hairs appeared, first on the anterior margins (fig 22), later on the surface near the notch of some thalli in agar culture (figs 26, 27). These hairs are not numerous in either location. They are much larger than the simple glandular hairs, and the first wall separating the hair from the mother cell is oblique, joining the posterior wall of the mother cell in such a way that the hair rests not only on the margin but also partly on the face of the mother cell. The basal and terminal cell of the hair are larger than the cells in between. Chloroplasts are very small and soon disappear (fig 23). As the hair increases in size the contents of the terminal cell become granular and of reddish-brown color. The terminal cell is easily broken and then the contents drain away (fig 24). The basal cell divides, accomodating to the expansion of the adjacent cells of the thallus proper (fig 24). The intervening cells in the majority of cases are 3 in number and one, or perhaps more, may divide (fig 29, 30). These cells may also bear laterally simple hairs with a colorless glandular secretion or with a granular reddish-brown head (fig 25). Such large multicellular branched hairs may perhaps be capable of continued growth as one example was observed of a long filament of 14 cells on the surface near the notch (fig 31). The terminal cell of this filament was granular and reddish-brown, and two short glandular hairs were borne on the 7th and 11th cells.

Antheridia appear at 2–2½ months on the surface of small meristematic thalli (fig 16) and from 3–6 months were observed infrequently at the posterior end of archegoniate thalli or on the wings (figs 20, 21). The antheridium (figs 33–35) is oval to globular with a funnel-shaped basal cell. On old thalli the antheridium is sometimes borne on a l-celled stalk. Dehiscence is by a pore (fig 36).

Archegonia appear in about 2 months and develop in the usual way. The mature archegonium is small in my cultures. It shows two basal cells in longitudinal section (fig 37) and a short neck projecting at right angles from the thallus or inclined slightly toward the posterior end of the thallus. The cells of the thallus surrounding the egg as well as the lower cells of the neck divide when the archegonium is mature and together with the basal cells form a jacket of small cells about the egg (fig 38).

Regeneration, a common characteristic among thelypteroid gametophytes, takes

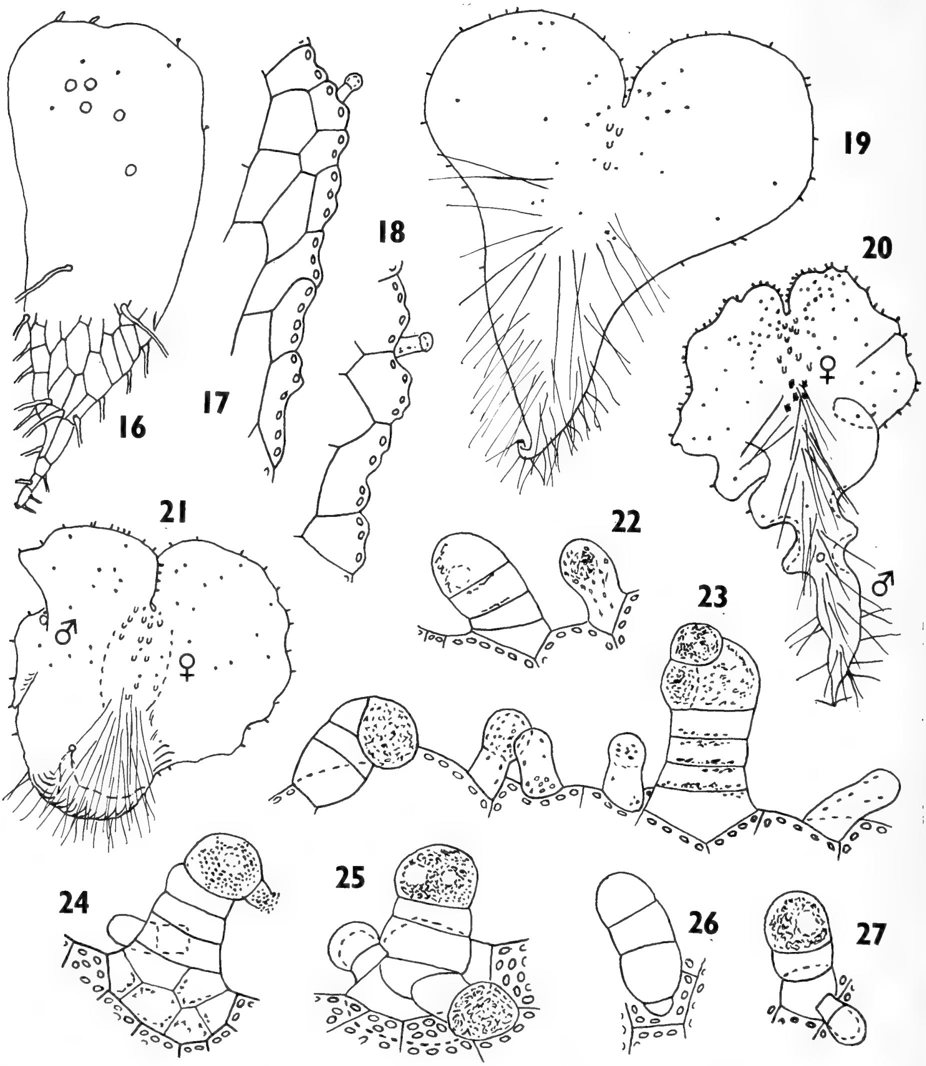


FIGURES 1—15. Stages in germination and development of young thallus of *Chingia pseudoferox.* 1: spore. 2, 3: germination, agar, 11 days. 4: 7-celled filament. 5: young thallus, crock over peat, 1 month. 6: 9-cell filament. 7, 8: plate iniation, a-a first wall, b-b second wall. 9: germination, crock over peat. 10: spatulate thallus, agar, 1½ months. 11: anterior portion young thallus. 12: apical meristem, detail of figure 10. 13—15: hairs, 1½ months. Magnifications: 1, 15 x 500; 2—5, 7—9, 11, 13, 14 x 320; 6, 12 x 180; 10 x 42.

place under adverse growing conditions. A thallus bearing simple glandular hairs and two multicellular branched hairs on the anterior margins was torn in mounting. On examination before discarding it sometime afterward, regenerative outgrowths were found on the surface of the thallus near the injury (fig 28). Rhizoids had not been developed on these outgrowths but two of them bore antheridia (fig 32).

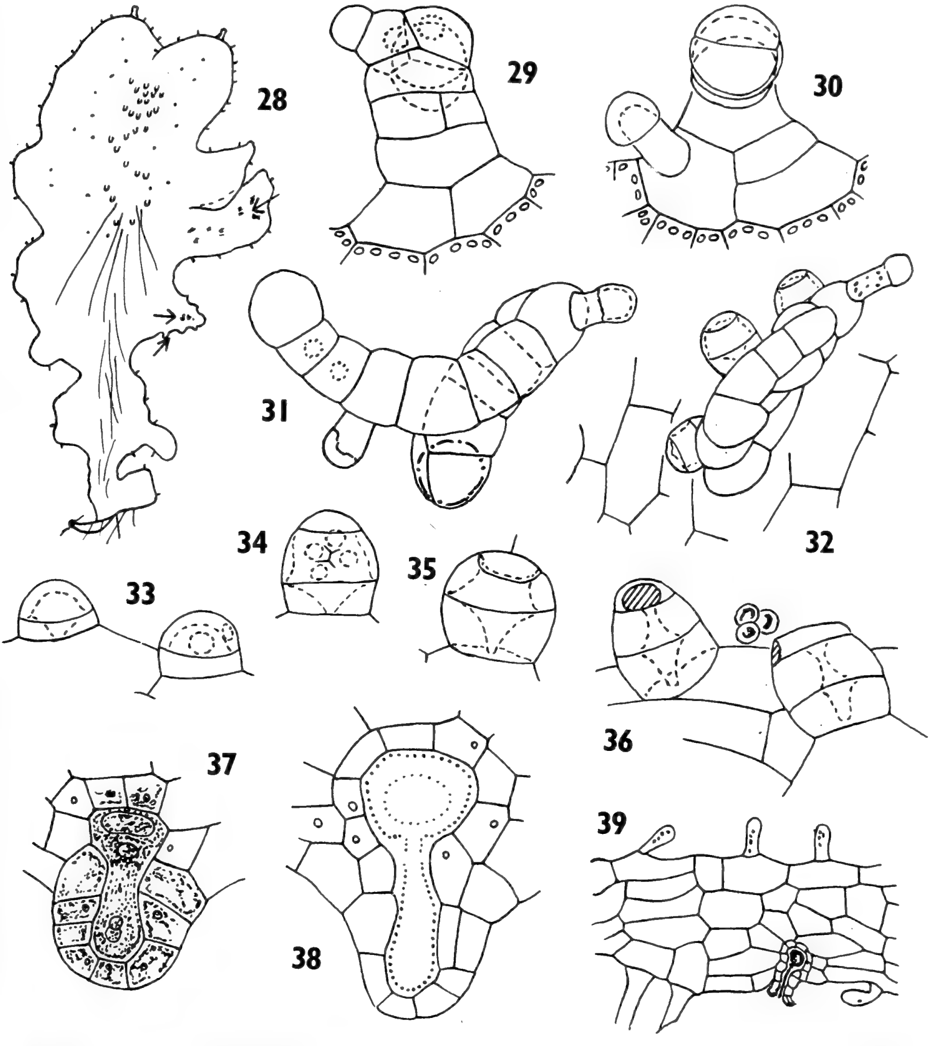
DISCUSSION AND CONCLUSIONS

The gametophyte of *Chingia pseudoferox* differs from that of other described thelypteroid ferns in its types of hair. The stout, red-tipped, multicellular structures here called hairs, set apart the gametophyte of *C. pseudoferox* from other gametophytes which show the basic pattern for thelypteroid ferns. Whether this is a variation characterizing the genus cannot be said since other gametophytes in the same genus are unknown, including that of *C. ferox,* the type species, which *C. pseudoferox* resembles so closely in the sporophyte.



FIGURES 16–27. Mature thallus of *Chingia pseudoferox*. 16: antheridial thallus, agar, 2 months. 17, 18: undulating marginal cells, details of figures 16 & 21 respectively. 19: archegonial thallus, agar, 2½ months. 20, 21: hermaphroditic thalli, 3 & 6 months respectively. 22: stages in development of marginal multicellular hairs at notch, agar 3½ months. 23: portion of anterior margin of thallus with simple and multicellular hairs, agar 3 months. 24, 25: marginal multicellular marginal multicellular hairs. 26, 27: stages in development of surface multicellular hairs, agar 3½ months. Magnifications: 16 x 42; 17, 18 x 180; 19 x 24; 20, 21 x 12; 22 – 27 x 320.

The evidence for calling the red-tipped gametophytic structure in *C. pseudoferox* a hair and not a regenerative outgrowth, rests on their differences when they are present on the same thallus. The cells of the red-tipped structure lose their chloroplasts or retain only very small ones, so that the subterminal cells appear colorless. This is a characteristic of many hairs. The red-tipped structure is borne on the anterior margin of the thallus or cushion near the notch on healthy-looking tissue and may bear other



FIGURES 28–39. Regeneration and sex organs in *Chingia pseudoferox.* 28: injured thallus, arrows indicate regenerated areas. 29, 30: multicellular hairs, anterior margins, detail of figure 28. 31: single specimen of multicellular structure, 3 month old thallus. 32: regenerative growth, detail of figure 28. 33, 34: development of antheridium. 35: mature globular antheridium. 36: dehiscence of antheridium. 37, 38: archegonium. 39: portion of thallus, l.s., 6 months. Magnifications: 28 x 12; 29–31, 33–34, 36 x 320; 32 x 180; 35, 37, 38 x 500; 39 x 115.

hairs. The regenerative outgrowths, on the other hand, are green, look like small thalli, appear near the injured tissue and bear not only hairs but also antheridia, a characteristic of thalli.

Among the thelypteroid gametophytes which I have seen, red-tipped gametophytic hairs are known in *Mesophlebion crassifolium* (Bl.) Holttum (Atkinson, in press) with a chromosome number also based on 36, but the hairs in *M. crassifolium* are quite different in form and abundance: they are simple or branched on a 2–3 celled stalk. They are numerous on margins and surfaces and are associated with acicular hairs which have not been observed in *C. pseudoferox.*

Holttum (1971: 30, 1974) finds sporophytic similarities between *Plesioneuron* and *Chingia* sufficient to suggest a relationship but the gametophytes do not wholly bear this out. Although the chromosome number may be 36, the spores spiny (light microscope), germination possible on both alkaline and acid media, marginal cells with undulating walls and an antheridium of similar form with a funnel-shaped basal cell, the gametophytes differ markedly in the hairs they bear. Hairs on margins and surfaces in *Plesioneuron marattioides* (Alston) Holttum are of one type: long slender, simple with an abundant yellow secretion (Holttum, 1975). The hairs in *Chingia pseudoferox* are of two types: either simple, short and stout with a colorless secretion, or, multicellular structures with a reddish-brown terminal cell and simple glandular hairs sometimes borne laterally.

Holttum (1971: 3l, 1974) also finds sporophytic similarities between *Chingia* and *Glaphyropteridopsis* but the mature gametophytes of my cultures of *C. pseudoferox* and of *G. erubescens* (Hook.) Ching the type species of the latter (Atkinson, 1971) are not similar, although the chromosome number is thought to be based on 36 and the spores are somewhat alike. Unlike *C. pseudoferox,* the margins of the mature thallus (3½ months) of *G. erubescens* were irregular (although the walls of individual marginal cells were not undulate) and the thallus bore only simple glandular hairs with a yellow secretion.

The large spore of *C. pseudoferox* suggests a polyploid condition in this fern. Thelypteroid ferns whose spores (according to my approximate measurements) are over 40 *µm* in length have been tetraploid (Atkinson & Stokey 1973, Atkinson, in press): these include Jamaican plants of *Thelypteris torresiana* (Gaud.) Ching, *T. totta* (Thunb.) Schelpe, *T. normalis* (C. Chr.) Small, *T. reticulata* (L.) Proctor and the Malayan *Metathelypteris singalanensis* (Bak.) Ching and *Mesophlebion crassifolium.* The spores of *C. atrospinosa* (C. Chr.) Holttum measure about 30.8 x 19.5 *µm.* This suggests a diploid plant, judging by my measurements of other thelypteroid fern spores from plants known to be diploid.

The gametophyte of *C. pseudoferox,* while conforming to the general thelypteroid gametophytic pattern deviates from it by the presence of a second type of hair not hitherto observed: a robust multicellular structure with a reddish-brown terminal cell and simple glandular hairs borne laterally. This characteristic must be looked for among other gametophytes of the *Chingia* group before its value can be assessed. The multicellular gametophytic hair borne by the *C. pseudoferox* thallus separates it from other known thelypteroid gametophytes but (beyond a similarity in the terminal cells of otherwise dissimilar gametophytic hairs borne by *Mesophlebion crassifolium* and by *C. pseudoferox)* does not suggest relationships. The gametophytic characteristics of *C. pseudoferox,* as interpreted here, do, however, support taxonomic segregation such as that proposed by Holttum on the basis of sporophytic characteristics and would seem to indicate a higher level of evolution among the thelypteroid species than those bearing only one type of hair.

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TAXONOMIC NOTES ON SOME AFRICAN SPECIES OF ELAPHOGLOSSUM

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ABSTRACT

The species of the group of *Elaphoglossum deckenii* s.l. in continental Africa are considered. Full descriptions are given for *E. deckenii* (Kuhn) C. Chr., *E. kuhnii* Hieron., *E. ruwenzorii* Pirrotta, and *E. tanganjicense* Krajina ex Pic.Ser., and a key to their identification provided.

INTRODUCTION

The treatment of the African species of *Elaphoglossum* in Schelpe's *Reviews of tropical African Pteridophyta, 1* (Schelpe 1969) has undoubtedly greatly contributed to our knowledge of the taxonomy of the African species of the genus, but some species need further consideration. This paper deals with the group of *Elaphoglossum deckenii* in continental Africa, and is intended as an addition to the treatment of that group in my account on the Elaphoglossaceae in the *Adumbratio Florae Aethiopicae* (Pichi Sermolli 1968).

GENERAL DESCRIPTION AND DISTRIBUTION OF GROUP

Elaphoglossum deckenii and related species belong to the group of species with flat, strongly ciliate and variously coloured scales and with sterile fronds densely paleaceous on the undersurface and at the edges. The group was named Chromatolepideae by Fée (1852).

The circumscription of the species of this group is rather confused; undoubtedly the species are not very sharply distinct, but the disagreement among authors about the taxonomical value of the various entities is mainly due to the fact that, in distinguishing them, some pteridologists dislike taking into consideration the structure and colour of the scales, which on the contrary offer us the best characteristics to distinguish one species from another. The study of many specimens belonging to both gerontogaean and neogaean species of the group has shown me that, besides the structure and colour of the scales of the rhizome, stripe and lamina, the best characteristics to distinguish the different species are the features of the rhizome, the size of the plant, the length of the sterile frond in comparison with the fertile one, the length of the stipe in comparison with the blade, the degree of toughness of the stipe, the shape of the blade, and the colour and the degree of covering of the lower and upper surfaces of the sterile blade.

The group is distributed throughout the tropics, particularly in America where we can enumerate many species, e.g. *E. muscosum* (Swartz) Moore, *E. perelegans* (Fée) Moore, *E. plumosum* (Fée) Moore, *E. elegans* Hieron., *E. meridense* (Klotz.) Moore, *E. orbignyanum* (Fée) Moore, *E. langsdorffii* (Hook. & Grev.) Moore, *E. laminarioides* (Bory) Moore, *E. chrysolepis* (Fée) Alston, *E. auricomum* (Kunze) Moore, and *E. vestitum* (Schlecht. & Cham.) Moore. It is only scarcely represented in the Old World and in the Pacific Islands. We may mention *E. paleaceum* (Hook. & Grev.) Sledge from Macaronesia, *E. nilgiricum* Krajina ex Sledge and *E. ceylanicum* Krajina ex Sledge from India and Ceylon, and *E. micans* (Mett. ex Kuhn) Pic.Ser. from Hawaii Islands.

As far as tropical Africa is concerned, the study of the types of all the described species from this continent and adjacent islands, and the revision of many specimens kept in the most important European herbaria have convinced me that the group is represented there by *E. deckenii* (Kuhn) C.Chr., *E. kuhnii* Hieron., *E. ruwenzorii* Pirotta, *E. tanganjicense* Krajina ex Pic.Ser., *E. splendens* (Bory ex Willd.) Brack., *E. rufidulum* (Willd. ex Kuhn) C.Chr., *E. leucolepis* (Bak.) Krajina ex Tardieu, *E. poolii* (Bak.) Christ and *E. multisquamosum* Bonap., the last five species being confined to Malagassia. Another undescribed species occurs in south tropical Africa. It has been often confused with *E. kuhnii.* Unfortunately I have examined few and incomplete specimens of it and I am not in the position to describe it here. Perhaps another species is present in west tropical Africa, but I have seen only two sterile and incomplete specimens. These latter two species are thus not included in the key.

Some of the Malagassian species of this group, for instance *E. splendens* and *E. rufidulum,* are closely related to the above-mentioned species from continental Africa. The former is endemic in Réunion, while the latter occurs in Madagascar, Comoro Is. and Réunion. Both are provided with paleae of the rhizome and phyllopodium with edges and cilia concolorous with the central portion of the surface; thus they appear nearer to *E. ruwenzorii* and *E. tanganjicense* than to the remaining two species. However they differ from them at first sight in the fertile fronds slightly longer than the sterile ones or as long as them, in the structure of the rhizome and in the size and shape of the fronds. Particularly good differences are found in the structure and size of the scales of the various parts of the plant.

KEY TO THE SPECIES

I give below a key and comparative description of each of the known species from continental Africa.

1. Paleae of rhizome and phyllopodium with cilia and often also edges manifestly darker than the central portion of their surface 2
   Paleae of rhizome and phyllopodium with edges and cilia con-colorous with the central portion of their surface 3
2. Paleae of rhizome and phyllopodium similar, subulate to narrowly triangular, 6–9.5 mm with a light castaneous central stripe and blackish-castaneous marginal band and cilia. Fertile fronds manifestly shorter than the sterile ones, the latter usually 70–90 cm with blade long linear. Rhizome long-creeping, stout . . . . *E. deckenii*
   Paleae of rhizome and phyllopodium different, those of rhizome very narrowly triangular, 3–4 mm, fulvous with castaneous cilia and sometimes margins; those of phyllopodium linear, 5–7 mm melleous to fulvous with dark castaneous broad-based spinules. Fertile fronds only slightly shorter to slightly longer than the sterile ones, the latter usually 15–22 cm with blade oblong-oblanceolate to linear-oblanceolate. Rhizome short-creeping, slender . . . . *E. kuhnii*
3. Paleae of stipe and midrib alike in fertile and sterile fronds; paleae of phyllopodium 6.5–9 mm, thin, light castaneous throughout, up to 6 mm irregularly spread. Sterile blade very narrowly oblanceolate, long tapering downwards, slightly paleaceous, rusty-green beneath. Fertile frond with lamina manifestly rounded at the base. Rhizome short-creeping . *E. ruwenzorii*
   Paleae of stipe and midrib different in fertile and sterile fronds; paleae of phyllopodium 3.5–5.5 mm reddish-castaneous, thick, with short straight cilia; paleae of the sterile stipe up to 11 mm melleous, squarrose, with very narrow castaneous marginal strip, apical part and cilia. Sterile blade narrowly linear to narrowly linear-elliptic or linear-lanceolate, cuneate at the base, densely melleous-paleaceous beneath. Fertile frond with lamina attenuate to cuneate, shortly decurrent. Rhizome erect . . . . *E. tanganjicense*

ELAPHOGLOSSUM DECKENII

E. deckenii (Kuhn) C.Chr. Ind. Fil. 305 (1905).

Basionym.: *Acrostichum deckenii* Kuhn, Fil. Deck. 16 (1867).

Holotypus: "Kilema ad radices montis Kilimandjaro (reg. Dschagga). 3–4000′. anno 1864". *Kersten 5* (B!).

Rhizome long-creeping, stout. Fronds borne in two rows on the upper portion of the rhizome. Sterile fronds (46) 70–90 (108) cm long; stipe about 2/3 to 3/5 as long as the lamina, slender; lamina chartaceous, long linear, usually long attenuate at the base and abruptly acuminate to shortly cuspidate at the apex, sparsely paleaceous and rusty-green above, densely ferrugineous-paleaceous beneath. Fertile fronds shorter than the sterile ones (4/7 to 3/5), [with stipe shorter than that of the sterile frond and] with lamina usually cuneate to rounded at the base. Paleae of the rhizome and phyllopodium alike, subulate to narrowly triangular, 6–9.5 mm long, with a light castaneous central stripe and with shiny, blackish-castaneous fairly broad marginal bands and cilia, the latter fairly long, more or less curved, irregular in length, direction and distance, arranged singly to 2–4 together. Paleae of the stipe of the sterile frond lanceolate, 6.5–8 mm long, fulvous, with long reddish-castaneous cilia and sometimes also with the apex and the edges irregularly and moderately reddish-castaneous. Paleae of the midrib fulvous with concolorous cilia. Paleae of the surface fulvous with long concolorous cilia and with a reflexed canaliculate, hemi-infundibuliform long base; some of them large, ovate-lanceolate, others small irregularly stellate, the two kinds nearly in the same proportion on the lower surface, the stellate ones predominant on the upper surface. Paleae of the stipe and midrib alike in the fertile and sterile fronds.

The species occurs in the mountains (2800–3500 m) of S. Ethiopia, Kenya, Uganda, NE Congo and Tanzania.

Schelpe (1969) records *E. deckenii* also in Malawi, Rhodesia and Comoro Is., but I have seen no specimen from these countries. I think that these records refer to *E. tanganjicense* which certainly occur in Malawi and Comoro Is. (cf. Pichi Sermolli 1968: 238, 241). Schelpe's remarks in *Fl. Zambesiaca* (1970: 215) that the specimens from Rhodesia and Malawi "have none or very few of the stipe scales with the black cilia usually seen in the E. African specimens" strongly support my supposition.

I cannot discuss here *E. hirtum* var. *giganteum* Bonap. (*Not. Pterid. 14:* 337; 1923) since I have not seen the type of this variety, *Bequaert 3851* from Ruwenzori; it may be related.

ELAPHOGLOSSUM KUHNII

E. kuhnii Hieron. Bot. Jahrb. Syst. *46:* 399 (1911).

Syntypi: "Trees. Mountains. Sierra Leone. N.E. 5.57" *Barter s.n.* Dupl. ex Herb. Kew 1133 (B! Type coll, in K! BM!)* – Kamerun: "Bipindi. Urwald bei Station Lolodorf. 600 m. ♃ Farn. An hohen Bäumen auf den grossen Aesten. Dec. 1901" *Zenker 2479* (B!) – "Kamerun. Aedf Bacdemm bei Moliwe. VIII. 1905". *Schlechter 15790* (B!).

Lectotypus: *Zenker 2479* (B!) – Schelpe (1969: 35) designates *Barter s.n.* as the lectotype of the species, but his selection cannot stand since the syntype in Berlin Herbarium studied by Hieronymus is sterile, while the latter describes also the fertile fronds in the protologue. Consequently one of the remaining syntypes, *Zenker 2479* and *Schlechter 15790,* both fertile, is better qualified as the lectotype of the species. I select as such the former, being more complete and better preserved than the latter.

Taxon. Syn.: *E. camerouniense* Tardieu in Tardieu, Nicklés & Jacq. Fél., *Etud.*

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*Hieronymus in the protologue gives "Barter n.6" as collection number and 1851 as the year of collection, but this is wrong. Probably he interpreted "N.E. 5. 57" (Niger Expedition May 1857) as "N. 6 May 1851".

Cameroun. 2. 92. t.3 (3–6) (1950). Holotypus: Cameroun: Makak, sur branches elevees. Oct. 1938. *Jacques-Felix 2331* (P!).

Rhizome short-creeping, slender. Fronds fascicled at the top of the rhizome. Sterile fronds (10) 15–22 (34) cm long; stipe 1/2 to 1/3 as long as the lamina, slender; lamina chartaceous, oblong-oblanceolate to linear-oblanceolate, attenuate at the base and subacute to sub-obtuse at the apex, sparsely paleaceous to nearly denudate and dark green above, densely fulvous-melleous paleaceous beneath. Fertile fronds shorter to slightly longer than the sterile ones, with stipe usually longer than that of the sterile frond, and with lamina rounded at the apex and long decurrent at the base. Paleae of the rhizome very narrowly triangular, 3–4 mm long, fulvous with castaneous cilia and sometimes also with castaneous narrow marginal borders cilia fairly short, rigid, irregular in arrangement but mainly ascending, arranged singly or sometimes 2–3 together. Paleae of the phyllopodium linear, 5–7 mm long, melleous to fulvous, sometimes with a very narrow castaneous edge, spinulose-ciliate with spinules dark castaneous, short, straight to falcate, rigid, thickened at the base, irregular in length. Paleae of the stipe of the sterile frond narrowly lanceolate, 3–5 mm long, melleous with long, thin, flexuose concolorous cilia. Paleae of the lamina melleous, opaque with long concolorous cilia and with a reflexed canaliculate hemi-infundibuliform long base; some of them large, lanceolate, others small, irregular stellate, the latter being more frequent. Paleae of the stipe and midrib alike in the fertile and sterile fronds.

The species is widely distributed in the mountains of west tropical Africa from Sierra Leone to Cameroon at an elevation of 600–2100 m.

E. kuhnii has been recorded in Rhodesia, Malawi and Madagascar (cf. Schelpe 1969: 35), but as far as I know it is not present there. Neither Christensen (1932), nor Tardieu-Blot (1960) record this species in Madagascar. The specimens from Rhodesia mentioned by Schelpe (1970) as *E. kuhnii* belong to the undescribed species from south tropical Africa mentioned above. Perhaps the latter occurs in Madagascar, too, but I have seen no specimen from there.

As mentioned above, two specimens from Cameroon and Fernando Po identified as *E. kuhnii* but with fronds of much larger size may be proved to be a distinct species; however, I cannot express any precise opinion on them since these specimens are poor and sterile.

ELAPHOGLOSSUM RUWENZORII

E. ruwenzorii Pirotta, Ann. di Bot. (Roma) *7:* 174 (1908)*

Syntypi: In the original paper devoted to the descriptions of the new species collected on the western side of Ruwenzori in 1906 by A. Roccati and A. Cavalli Molinelli, members of the expedition of the Duca degli Abruzzi, Luigi Amedeo di Savoia, Pirotta gives only the following information on the type: *"Hab.* Valle Mobuku". In a later publication on the results of the expedition (Savoia L.A., Il Ruwenzori. Relaz. Sc. *1* (Zool. Bot.). 1909), Pirotta, author of the account on the Pteridophytes, mentions (p. 483) that *E. ruwenzorii* is based on three specimens: "Valle Mobuku, epifita sulle Laurinee (?); Kiciuciu, scendendo da Kiciuciu a Nakitava, nella foresta di Nakitava; nella foresta di Nakitava a Kiciuciu, 8 Luglio 1906". Actually in the Turin herbarium among the collections of the Duca degli Abruzzi, we find three specimens identified by Pirotta as "Elaphoglossum Ruwenzorii". They bear no collection number or collector name; they are labelled as follows: "(1) Valle Mobuku. Epifita sulle laurinee. Kichuchu. 8 Luglio 1906" with the field label "Kiciuciu. 8 Luglio 1906". It consists of a sterile plant with rhizome (although incomplete). (2) "Valle Mobuku. Scendendo da Kichuchu a Nabitava. 9 Luglio 1906". It consists of seven sterile fronds without rhizome. (3) "Valle Mobuku. Nella foresta di Nabitava e Kichuchu. 8 Luglio 1906". It consists of a single sterile frond of *E. ruwenzorii* and five

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*Volume 7 of the Annali di Botanica bears 1909 as the date of publication, but pages 1–196 of it were published on 31 August 1908.

sterile fronds of *E. deckenii,* all without rhizome. Pirotta describes the fertile fronds in the protologue, but all the above-mentioned specimens are sterile and I have searched in vain for a fertile specimen in the Turin herbarium among the collections of the Duca degli Abruzzi. On the other hand also the duplicate in the Paris Herbarium is sterile. Probably the above-mentioned specimens bore only one fertile frond and it has been lost. In this situation I designate as the lectotype the first of the above-mentioned specimens being the only one provided with rhizome.

Lectotypus: Ruwenzori: "Valle Mobuku. Epifita sulle laurinee. Kichuchu. 8 Luglio 1906". *Roccati & Cavalli Molinelli* (Sped. Duca degli Abruzzi) *s.n.* (TO!).

Rhizome short-creeping, slender. Fronds fascicled on the distal part of the rhizome. Sterile fronds (20) 28–43 (51) cm long; stipe about 1/2 to 5/8 as long as the lamina, slender; lamina chartaceous, very narrowly oblanceolate, long tapering downwards into a long attenuate base, acuminate to long cuspidate at the apex, sparsely paleaceous becoming denudate and dark green above, paleaceous and rusty-green beneath. Fertile fronds usually shorter than the sterile ones, with stipe longer than that of the sterile frond, with lamina manifestly rounded at the base. Paleae of the rhizome triangular, 3–4 mm long, blackish-castaneous, becoming gradually paler towards the base, slightly folded in their distal part, with concolorous edges and cilia, the latter short, more or less falcate, irregular in length, direction and distance, mainly arranged singly. Paleae of the phyllopodium narrowly lanceolate-triangular, 6.5–9 mm long, thin, light castaneous in the lower half, becoming gradually darker and thicker to dark castaneous in the upper part, which is a little rolled, with concolorous, thin, flexuose, long cilia. Paleae of the stipe of the sterile fronds narrowly triangular, 3–6 mm long, spreading, light castaneous, with concolorous surface and cilia, the latter fairly long, thin, approximate and irregular. Paleae of the lamina of two kinds: some of them narrowly lanceolate to very narrowly triangular, with long concolorous cilia and with reflexed hemi-infundibuliform short base, others small, stellate, but very scarce. Paleae of the stipe and midrib alike in the fertile and sterile fronds.

E. ruwenzorii varies in the size of the fertile fronds in comparison with the sterile ones, and in the degree of the paleaceous covering of the stipe and blade, which, however, greatly depends on the age of the frond, but the structure of the paleae and the shape of the lamina are very characteristic and sharply distinguish this species from the others of the group.

E. ruwenzorii has been collected in the mountains (2100–3000 m) of Kenya (Meru, Fort Hall, Naivashs and Nakuru districts), Uganda (Ruwenzori) and NE Congo (Ruwenzori, Mt Kahuzi, Volcan Mikeno).

ELAPHOGLOSSUM TANGANJICENSE

E. tanganjicense Krajina ex Pic. Ser. Webbia 23: 239. f.5, 6. 1968.

Holotypus: Deutsch Ost Afrika (Tanganjika Terr.). Bezirk Morogoro: Ulugurugebirge. NW ca. 1480 m Nebelwald, Farn vereinzelt am Bäumen u. Felsen Kiluguru: Lussangasanga. 10. 12. 1932. *Schlieben 3071* (B!). Isotype in BM!, G!, P!, S!.

Paratypi: *Pichi Sermolli 7118* (PIC.SER.!) from Ethiopia, *Stolz 855* (B!) from Malawi, *Louis 5021* (EA!, PIC. SER.!) from Congo.

Rhizome erect, short, slender. Fronds fascicled at the top of the rhizome. Sterile fronds (20) 34–50 (73) cm long; stipe about 1/3 to 1/4 as long as the lamina, slender; lamina usually herbaceous to flaccid, narrowly linear to narrowly linear-elliptic or linear-lanceolate, usually cuneate at the base and acute to attenuate at the apex, sparsely paleaceous to nearly denudate and light green with midrib densely paleaceous above, densely melleous-paleaceous beneath, margins with dense, long and squarrose paleae. Fertile fronds shorter (1/2 to 3/4) than the sterile ones, with stipe longer and lamina much narrower (1/2 to 1/3) than those of the sterile frond, with lamina attenuate to cuneate, and gradually but shortly decurrent at the base. Paleae of the rhizome ovate-lanceolate, 3.2–4.3 mm long, reddish-castaneous, shining, flat on their distal part, with cilia, the latter short, straight, irregular in length and distance. Paleae of the phyllopodium narrowly lanceolate, 3.5–5.5 mm long, shining, reddish-castaneous but becoming fulvous towards the base, and dark castaneous towards the apex; cilia concolorous, short, slender, stiff, irregular, fairly close together. Paleae of the stipe of the sterile frond narrowly lanceolate-triangular, 6–11 mm long, squarrose, melleous but with castaneous edges, apical part and cilia, the latter relatively short, rigid, mainly straight. Paleae of the midrib melleous-fulvous with light castaneous apex and cilia. Paleae of the lamina melleous, shining with long concolorous cilia and with reflexed, canaliculate, hemi-infundibuliform base; some of them large, lanceolate, others small, irregularly stellate, the former being more frequent. Paleae of the stipe and midrib of fertile fronds different from those of the sterile fronds and darker in colour.

E. tanganjicense occurs in Ethiopia, Kenya, Tanzania, Ruanda, Congo, Malawi and Comoro Is. Probably it is present also in Rhodesia; in fact I think that the specimens identified by Schelpe (1970: 215) as *E. deckenii* belong here. In continental Africa it grows at an elevation of 1200–2300 m.

E. tanganjicense, E. ruwenzorii and *E. deckenii* occur in three different altitudinal belts, following each other, the first species growing at the lowest level, the third at the highest one. I think that *E. ruwenzorii* and *E. deckenii* may be interpreted as two altitudinal vicariants of *E. tanganjicense,* which is more widely distributed than the other two.

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OBSERVATIONS ON THE SPREAD OF THE AMERICAN FERN PITYROGRAMMA CALOMELANOS

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ABSTRACT

The spread of the Central and South American fern *Pityrogramma calomelanos* (L.) Link., and its var. *aureoflava* (Hook.) Weath. ex Bailey, through the Old World is traced. It appears that both varieties have become naturalised and spread from various centres of horticultural introduction.

INTRODUCTION

It is clear from the relevant literature, that the Central and South American *Pityrogramma calomelanos* (L.) Link., and its more temperate var. *aureoflava* (Hook.) Weath. ex Bailey, have become naturalised in the Old World and beyond, the former having become a weed in parts of the Old World tropics.

P. calomelanos was introduced to British horticulture from the West Indies in 1790 by Hinton East, Esq. (Aiton 1813) and the var. *aureoflava* was in cultivation in the Oxford Botanic Garden in 1862 (Hooker 1862). Both var. *calomelanos* and var. *aureoflava,* with their respective conspicuous silvery and golden yellow powder on the undersurface of the fronds, have made them both desirable horticultural subjects, and also once naturalised, not likely to escape the attention of plant collectors. Unfortunately the taxonomy of this genus was rather confused until Tryon's (1962) revision. The probable reasons for the ecological success of the var. *calomelanos* in West Africa were convincingly presented by Wardlaw (1962).

Although the present author has been interested in the spread of the var. *aureoflava* in Natal, South Africa, for many years (Alston & Schelpe 1952) a preliminary study of the spread of both varieties of *P. calomelanos* through the Old World and beyond became possible during a period of sabbatical leave at the Kew Herbarium during 1973 where most of the data presented here were obtained.

GEOGRAPHICAL SPREAD

The first appearance of *P. calomelanos* var. *calomelanos* outside the Americas was in the West African Islands, where it was collected on Principe by Barter in 1858 and on Fernando Po by Mann during the period 1859—1863. Its introduction to these islands was probably with tropical American nursery stock brought to these island "plantation colonies" which included coffee, cacao and chinchona (Cortesao 1962). Kuhn (1868) and Hooker and Baker, (1874) only record this taxon from the tropical West African islands outside the Americas and it seems that it only spread to the West African mainland after the turn of the century. There the earliest record seems to be from Sierra Leone in 1926, but by 1937 Deighton noted on an herbarium label that it was a "garden weed recently established here; it sows itself rapidly". According to available herbarium records it then appeared naturalised in Ghana in 1927, Cameroon Mountain in 1930, Liberia in 1939, Cabinda in 1958 and Côte d'Ivoire in 1959. By 1962, it had become a nuisance in Cameroons plantations (Wardlaw, 1962).

In East Africa, *P. calomelanos* was recorded from the Eastern Usambaras in Tanzania in 1914, possibly as an escape from the botanic gardens at Amani founded in 1903. It was found at Sese, Uganda, 1922, again possibly an escape from cultivation.

In 1962, isolated specimens were found in tea plantations on Namuli Mountain, Mozambique (Schelpe 1964).

The var. *calomelanos* was not recorded from the Seychelles by Baker (1877) but had been introduced by 1902, possibly with tropical nursery stock, followed by the var. *aureoflava* by 1961. The earliest record of the var. *calomelanos* in Madagascar found, was collected at Andevorante, Fanovana in 1912, but 20 years later, Christensen (1932) noted it as "very common". Neither varieties were recorded by Baker (1877) for Mauritius or by Cordemoy (1895) for Reunion. Tardieu-Blot (1960) regarded *P. calomelanos* as having been introduced to Mauritius and Reunion but dated specimens show that the var. *calomelanos* was definitely on Mauritius in 1967 and the var. *aureoflava* on both Mauritius and the Comoros in 1968. The most recent report from Reunion (Sauzier, 1973, pers. comm.) indicates that the var. *calomelanos* is present and the var. *aureoflava* abundant there.

As regards South Africa, the Transvaal record of *P. calomelanos* by Sim (1915) is doubtful and cannot be checked as the specimen was lost in the post. However, there is a definite record of the var. *aureoflava,* collected in Natal by Gerard in 1865, at Kew, most probably an escape from cultivation. By 1914, this variety had become naturalised in a railway cutting near Durban (Sim 1915) and has since spread to road cuttings as far south as Flagstaff and westwards to the foothills of the Drakensberg. Within the last decade this variety has also apparently escaped from cultivation in the vicinity of Kitwe, Zambia (Schelpe 1970).

As there is no mention of *P. calomelanos* by either Clarke (1880) or Beddome (1892) it is most probable that it had not become naturalised in India, Ceylon or Malaya at that time. The earliest available record of the var. *calomelanos* in this region is from the Terai in the foothills of the Sikkim Himalaya in 1898, to which it could have been introduced as a horticultural subject from the Royal Botanic Gardens in Calcutta. In 1913 it was recorded from the Tista Bridge and by 1933 had reached Kalimpong. Mehra (1932) reported that it had "run wild within recent times in Sikkim" and Verma (1966) noted its distribution from the Teesta to Kalimpong and Gangtok. In the meantime it had become naturalised in the states of Bihar and Orissa. As early as 1922, Blatter and D'Almeida (1922) reported that it had "run wild in and about Bombay" and also reported it from the Nilgiris and Ceylon. It had apparently become naturalised in the Agri-hort gardens in Madras at the turn of the century and appeared at Trivandrum in 1954. Meanwhile the var. *aureoflava* was reported by Blatter and D'Almeida (1922, as "var. *chrysophylla*") as "becoming naturalised in the Nilgiris".

In the Far East, the first available record of the var. *calomelanos* is in 1893 from Buitenzorg, Java, where the famous botanic garden was founded in 1817. Its presence there was recorded by Raciborski (1898) and a decade later Van Alderwerelt van Rosenburgh (1908) recorded both varieties as "much cultivated and escaped from gardens; very common in the neighbourhood of european settlements". According to Backer and Posthumus (1939), the var. *calomelanos* had become naturalised in the Javanese lowlands up to 1300 m and the var. *aureoflava* (cited as *P. tartarea* var. *ochracea*) naturalised from west to east Java between 800 m and 1600 m.

In the meantime the var. *calomelanos* had established itself by 1906 on the remnants of the island of Krakatoa, which exploded in 1883, almost certainly by wind dispersal of spores. By 1928, it had spread to northern Sumatra and to Bawean Island about 50 miles north of Java. An almost certain case of long distance wind dispersal of spores of the var. *calomelanos* in this region was its appearance as a single sporeling on Christmas Island in 1968, some 200 miles south of Java, in a locality inundated by salt spray for three months, and in which no other ferns were present.

In Malaya, the var. *calomelanos* appeared in a coffee plantation in Perak in 1900 and was later collected in Negri Sembilan in 1906, in Selangor in 1914, in Singapore in 1920, in Pahang in 1922, and in Kelantan in 1935. It apparently spread further north into southern Thailand about 1923 and reached north-western Thailand by 1958. In the meantime it was recorded from Cambodia in 1924, Hongkong in 1926, and Hainan in 1927. It was collected in Sabah in 1895 and had become a weed in Manila Hemp plantations there by 1962 (Wardlaw 1962), as well as appearing in Sarawak in 1922. After its apparent first record in the Philippines in Luzon in 1916, it seems to have spread to south-western Mindanao by 1961.

Eastwards from Java, the var. *calomelanos* was collected on Halmahera in 1951 and on Ceram in 1970, in the Moluccas. Further east, this variety apparently became naturalised in gardens at Wau, New Guinea, in 1963 and spread to logging roads by 1970. Another apparent example of long distance dispersal was the establishment of this variety in 1953 on lava flows on Mount Lamington, Papua, two years after its eruption. The latest phases of the spread of this taxon are its appearances at Rabaul, New Britain, in 1962 and in the Whitefield Range of northern Queensland, Australia, in 1964.

In conclusion it seems that typical *P. calomelanos* and its var. *aureoflava* have been introduced to new regions either accidentally together with tropical economic plants or intentionally as horticultural subjects. Their naturalisation and subsequent spread from such foci of introduction has clearly been encouraged by the establishment of plantations and by roadworks, the var. *calomelanos* spreading mainly in the wet tropics and the var. *aureoflava* in more temperate to subtropical environments.

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A PHYTOGEOGRAPHIC ANALYSIS OF CHOCÓ PTERIDOPHYTES

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ABSTRACT

The north western Pacific portion of Colombia (the Depto. del Chocó) is of crucial phytogeographic importance because it lies at the juncture of North and South America. The Chocó floristic region is bounded by the Pacific Ocean on the west and by drier areas and by the Andes (at about 1000 m altitude) in the east. To the north it intergrades with the lowland and lower montane areas of Panama and Costa Rica. To the south it intergrades with the lowland and lower montane areas of southern Colombia and Ecuador. Its boundaries can be set somewhat arbitrarily on the north at the Panama border and on the south at the Serranía Los Chancos north of Buenaventura. Considered as a whole, the pteridophytes of the Chocó floristic region are most like those of Costa Rica and Panama and secondarily like those of southern Pacific coastal Colombia and Ecuador.

INTRODUCTION

The Chocó region of north western Colombia is one of the biologically least known areas in the New World tropics. Botanical collecting has been hampered by the seasonally or continually wet climate, the permanently inundated and seasonally flooded areas, the scarcity of roads, and the absence of dependable means of transportation (Lellinger & de la Sota 1972). The region is important for distributional studies of both plants and animals, but data sufficient for such studies exists only for mammals and birds (Haffer 1970) and for pteridophytes.

The major features of the region (Fig. 1) are the river basins (Atrato, Baudó, San Juan, and León, the last of which drains part of the Depto. de Antioquia into the Golfo de Urbabá) and the mountain ranges (Cordillera Occidental of the Andes and its outlier Loma del Cuchillo, the Pacific coastal Serranía de Baudó, the Serranía del Darién, the Cerros de Quía, and the Cordillera de Jurado, the last three of which lie along the Panama border).

Daytime temperatures are high throughout the Chocó, although the cloud cover moderates them somewhat. From Bahía Solano and Riosucio northward a monsoon climate with a December to March dry season prevails because the northern tradewind belt shifts to the south and sends dry air south from the Golfo de Uraba towards the Pacific coast (Haffer 1970: 611). The remainder of the region is more or less constantly wet, with the most rainy area (8000–11000 mm annually) between the Rio San Juan and Rio Atrato basins (de la Sota 1972: 258).

In addition to the collections of Lellinger and de la Sota, specimens of the following collectors were studied: J. Duke from scattered sites in the northern Pacific and central portions of the Chocó, W.A. Archer from around Quibdó, O. Haught from Cupica on the Pacific coast, E.P. Killip from Bahía Solano, Quibdó, and other areas, José Cuatrecasas from the lower Río San Juan and the Río Calima, and H.P. Fuchs from the Río Baudó. Except for the Duke collections, which are at the New York Botanical Garden, all of the foregoing are deposited in the U.S. National Herbarium. The only other extensive collection of Chocó pteridophytes is at the Instituto de Ciencias Naturales in Bogotá; it includes Lellinger and de la Sota collections, plus those of R. Romero Castañeda and A. Fernández-Perez.

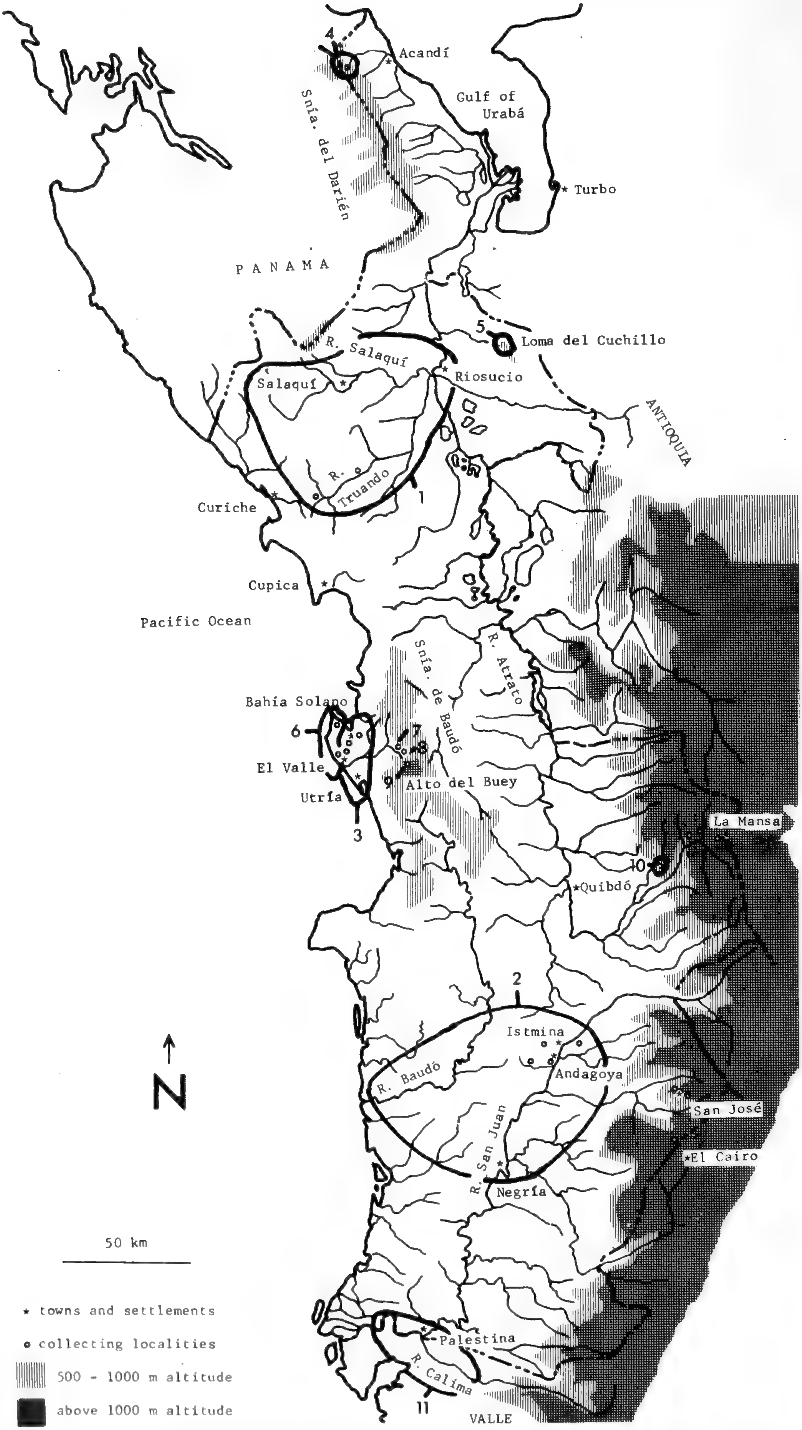

FIGURE 1. Map of the Departamento del Chocó with 11 lowland areas marked. The five upland areas lie near San José del Palmar and La Mansa.

GEOGRAPHICAL LIMITS OF THE CHOCÓ PTERIDOPHYTE FLORA

Unlike the political boundaries of the Depto. del Chocó, the borders of the Chocó floristic region are not precise, except where a discontinuity in geography, climate, or altitude occurs. In the north east, the Chocó floristic region includes roughly that portion of the Depto. de Antioquia south of the Golfo de Urabá which is drained by the Río León, beyond which the climate is much drier. The boundary in the east lies along the slope of the Andes. The altitude of this boundary was determined in the field by making observations of the ferns along the road near San José del Palmar. Species of *Nephrolepis* and *Cnemidaria* typical of the roadsides at and below 500 m altitude were not found much above 1000 m altitude. Also, the collections from behind the cemetery at San Jose del Palmar (altitude 1100 m) correlate slightly more with the Andean localities (r=0.033) than with the lowland Chocó ones (r=0.029). These roadside observations were confirmed along the road from Cuidad Bolívar to Quibdó, where again the boundary between the two fern floras was approximately at 1000 m altitude. Additional correlation data are discussed on p. 110.

The boundaries on the north and south are not sharply defined by climate or geography. The distribution patterns of the pteridophytes that have at least one end of their range within the Chocó floristic region illustrate this. There are relatively few such species, and all that are known to me are listed below. Many more species do not terminate their range in the Chocó floristic region. Most of these extend well beyond the Depto. del Chocó in tropical South America, in Central America, or both. These illustrate the continuity of especially the lowland ferns of the New World tropics.

There are about 17 endemic species found only within the Depto. del Chocó (*Asplenium oblongatum* Mett., *Cnemidaria spectabilis* var. *colombiensis* Stolze, *Gleichenia gnidioides* Mett., *Oleandra archeri* Maxon, *Selaginella tanyclada* Alston ex Crabbe & Jermy, and about 12 new, undescribed species).

The following species range from the Chocó floristic region northward to Panama or Costa Rica. One species is known only from the Depto. del Chocó and from the Pcia. del Darién (*Trichopteris williamsii* (Maxon) Tryon). Two species extend farther in Panama (*Bolbitis killipii* (Maxon) Lellinger[1] and an undescribed species of *Dryopteris* subg. *Stigmatopteris*). Two species extend into Costa Rica only on the Atlantic side (*Elaphoglossum palmense* Christ and *Thelypteris turrialbae* (Rosenst.) Morton). Five species have been found both on the Atlantic and Pacific sides of Costa Rica or in the central mountains (*Adiantum seemannii* Hooker, *Cyathea frondosa* Karst., *Diplazium seemannii* Moore, *Elaphoglossum proliferans* Maxon & Morton, and *Grammitis alsophicola* (Christ) Lellinger[2]).

The following species range from the Chocó floristic region to southern Colombia or Ecuador. Twenty-two of these extend only to south western Colombia (*Cyathea columbiana* Domin, *C. decorata* (Maxon) Tryon, *Danaea serrulata* Baker, *Diplazium chocoense* (Triana ex Mett.) Hieron., *D. trianae* (Mett.) C. Chr., *Gleichenia*

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[1] **Bolbitis killipii** (Maxon) Lellinger, **comb. nov.** BÁSIONYM: *Leptochilus killipii* Maxon, Amer. Fern J. 21: 138. 1931. TYPE: Near Juan Díaz, Pcia. Panama, Panama, alt 75 m, *Killip 2778* (US).

[2] **Grammitis alsophicola** (Christ) * ~~**Lellinger, comb. nov**~~**.** BASIONYM: *Polypodium alsophicolum* Christ, Bull. Soc. Bot. Genève II, 1: 219. 1909. TYPE "Vallée du Copal", Pcia. Puntarenas, Costa Rica, *Pittier 10971* (P not seen).

Seymour, Phytologia [illegible]

maritima Hieron., *Grammitis rhizophorae* (Copel.) Morton, *Lycopodium trianae* Hieron., *Pteris daguensis* (Hieron.) Lellinger[3], *Selaginella longissima* Baker, *S. seemannii* Baker, *S. tomentosa* Spring, *Tectaria acutiloba* (Hieron.) Maxon, *Thelypteris insignis* (Mett.) Ching, *Trichomanes daguense* Weath., and seven new species. Nine other species extend southward into Ecuador (*Cnemidaria ewanii* (Alston) Tryon, *Ctenitis biserialis* (Baker) Lellinger[4]. *Elaphoglossum glossophyllum* Hieron., *E. setigerum* (Sodiro) Diels, *Grammitis alsopteris* Morton, *Polybotrya lechleriana* Mett., *Tectaria rivalis* (Mett.) C. Chr., *Thelypteris elegantula* (Sodiro) Alston, and *Trichopteris phalaenolepis* (C. Chr.) Tryon.

The distribution patterns cited above show that in species terminating at least one end of their range in the Chocó floristic region, 29% are Chocó endemics, 17% are distributed to the north, and 54% are distributed to the south. The north-to-south ratio is about 1:3. There is no marked difference in north or south distribution between coastal plain or lowland species and upland species.

The boundary of the Chocó floristic region on the north can be set at the Panama border because of the fewer species ranging north, compared to those ranging south. In addition, the Pcia. del Darién and areas to the west are drier than most of the Depto. del Chocó. Many Chocó species that are also found in Costa Rica are confined to the relatively wet areas of Panama, usually in the Atlantic side of the low mountains. Although more of the aforementioned species range to the south, Cuatrecases (pers. comm.) believes the limit of the Chocó floristic region on the south is the Serranía Los Chancos above the Río Calima in the Depto. del Valle north of Buenaventura. It is likely that the flowering plants, which tend to have narrower distributions than the pteridophytes, demonstrate the boundary better. Also, the rainfall pattern to the south is more even throughout the year, and the vegetation correspondingly more diverse.

INTRA-CHOCÓ PHYTOGEOGRAPHICAL RELATIONSHIPS

The Chocó pteridophyte flora is not entirely uniform, which is to be expected in an area some 475 km long. In order to understand the differences in the pteridophyte flora within the Depto. del Chocó, the distribution of species found in several scattered areas lying at various altitudes within the Depto. del Chocó was studied. For purposes of analyzing the variation, all specimens studied were grouped into 16 areas, 11 from the lowlands below 1000 m altitude or from the Serranía de Baudó and five from the Andean slopes of the Chocó lying above 1000 m altitude. Figure 1 shows the 11 lowland areas. The five upland areas are from nar San José del Palmar and La Mansa in the Cordillera Occidental.

The name of each pteridophyte taxon (species, subspecies, variety, of form) was

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[3] **Pteris daguensis** (Hieron.) Lellinger, **comb. nov.** BASIONYM: *Pteris orizabae* var. *daguensis* Hieron. Bot. Jahrb. Engler 34: 495. 1904. TYPE: Banks of the Río Dagua, Depto. del Valle, Colombia, alt 200–500 m, *Lehmann 8933* (B not seen; isotype US). This species is close to *P. orizabae* Mart. & Gal. in frond form, but differs in being less coriaceous, in having more pointed segments, and in lacking the indurated marginal teeth at the apex of each vein. The laminae are ca. 50–80 cm long and about the same distance wide. The basal pinnae are bipinnate or tripinnate, but the superior pinnae are only pinnatifid. The pinnae and pinnules are petioulate (5–10 mm), linear-lanceolate, cuneate or narrowly decurrent at the base, and caudate at the apex. This species is known to me only from the type, from the Santa Marta mountains, from Loma del Cuchillo in the Depto. Chocó, and from along the Río Cauca near Puerto de los Pobres in the Depto. de Antioquia.

[4] **Ctenitis biserialis** (Baker) Lellinger, **comb. nov.** BASIONYM: *Polypodium biseriale* Baker, Syn. Fil 309. 1867. TYPE: "Andes of Peru and Ecuador", *Spruce* (K not seen).

2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	area number and name		
360	324	247	153	216	181	200	073	055	082	021	020	034	016	030	1	northern Chocó	Chocó <1000 m
	348	162	158	287	170	250	152	145	119	017	043	052	035	039	2	upper Río San Juan	
		325	303	198	244	213	087	059	063	035	057	066	017	007	3	interior Bahía Solano & vic.	
			291	098	113	143	068	090	062	059	053	038	012	010	4	Serranía del Darién foothills	
				214	121	153	046	061	015	020	037	026	000	010	5	Loma del Cuchillo	
					125	176	120	081	091	021	000	057	026	022	6	coastal Bahía Solano & vic.	
						440	117	061	032	020	058	071	012	022	7	Río Mutatá	
							195	097	056	000	047	048	046	051	8	Alto del Buey montane forest	
								263	040	051	030	194	100	100	9	Alto del Buey mossy forest	
									036	050	095	045	060	050	10	Lower Quibdó--Bolívar Road	
										029	024	070	031	000	11	Lower Río San Juan & vicinity	
											038	043	000	050	12	San José del Palmar cemetery	Andes >1000 m
												018	078	100	13	Middle Bolívar--Quibdó Road	
													055	034	14	San José del Palmar ridge	
														183	15	La Mansa ridge	
															16	Serranía de Los Paraguas	

intra-Chocó ave. r = 0.156

Chocó--Andes ave. r = 0.040

intra-Andes ave. r = 0.060

FIGURE 2. Correlation coefficient matrix of 16 areas in the Departamento del Chocó. The decimal point is omitted before the numbers.

written on an edge-punched card and the 16 areas each assigned a position along the margin. These were notched for each area in which the taxon was known to occur, either as a herbarium specimen or as a sight record made by Lellinger and de la Sota.

The presence data were then compared for each pair of areas, using a familiar coefficient of association: (++)/(+–)+(–+), which is the number of taxa present in both areas divided by the number found in one or the other of the areas, but not both areas.

With respect to the limits of the Chocó floristic region in the Andes, the average of all the correlation coefficients linking the 11 localities lying below 1000 m altitude or in the Serranía de Baudó (Fig. 2) was r=0.156. The average of all the correlation coefficients linking the five localities lying above 1000 m altitude on the Andean slopes of the Departamento del Chocó was r=0.060. But the average of all the correlation coefficients linking the former with the latter was only r=0.040. This indicates that the lowland (Chocó) pteridophyte flora is distinct from the upland (Andean) pteridophyte flora.

The matrix of coefficients of association for the 11 non-Andean areas (Fig. 2) was used to produce a phenogram (Fig. 3) showing the relative similarity of the areas. An unweighted group method was used to calculate the values joining the branches of the phenogram, starting with the highest mutual coefficient (r=0.440) and working downward. The value of the coefficient joining a new area to the group of areas already placed on the diagram was the average of the coefficients between all pairs of members of the group, including the new one. An examination of the phenogram shows some interesting relationships among the various areas.

The Río Mutatá hillside and floodplain area (area 7) and the montane forest on the slopes at the base of Alto del Buey (area 8) are close geographically, and all are undisturbed, primary forest.

The mossy forest on the upper slopes towards the summit of Alto del Buey correlates most closely with the lower Andean slopes at 750 m altitude (area 10), more so than with the pteridophytes of the montane forest slopes at the base of Alto del Buey (area 8). Thus, the pteridophyte flora near the summit of Alto del Buey definitely belongs to the Chocó floristic region, even though it is above the 1000 m Chocó-Andean pteridophyte flora boundary. There are, however, some Andean species, like *Blechnum occidentale* L. and *Lophosoria quadripinnata* (Gmel.) C. Chr., that set it apart from lower altitudes in the Chocó. The Serranía de Baudó, being surrounded by lowlands, is probably warmer for its altitude than are the Andes, which rise much higher. The altitude of Alto del Buey is given on most maps as 1810 m, as Lellinger and de la Sota's specimen labels indicate that the mossy forest is at 1450-1810 m, but Haffer (1970, p. 608) suggests that 1342 m may be more nearly correct.

The lower Río San Juan (area 11), which is the southernmost study area in the Chocó, is least related to the other Chocó localities, probably because a few species typical of the Pacific Coast slopes farther south in Colombia or in northern Ecuador reach their northern limit there.

The Pacific coastal strip very close to the ocean (area 6) and Loma del Cuchillo (area 5) are divergent from most of the other localities in the central and northern parts of the Chocó. The Pacific coastal strip is much drier than the inland areas, and Loma del Cuchillo is isolated from the other study areas by many miles of lower Río Atrato swamps. The latter area has some affinity with the adjacent lowlands of the Depto. de Antioquia.

The remaining localities, from the Serranía del Darién foothills (area 4) through

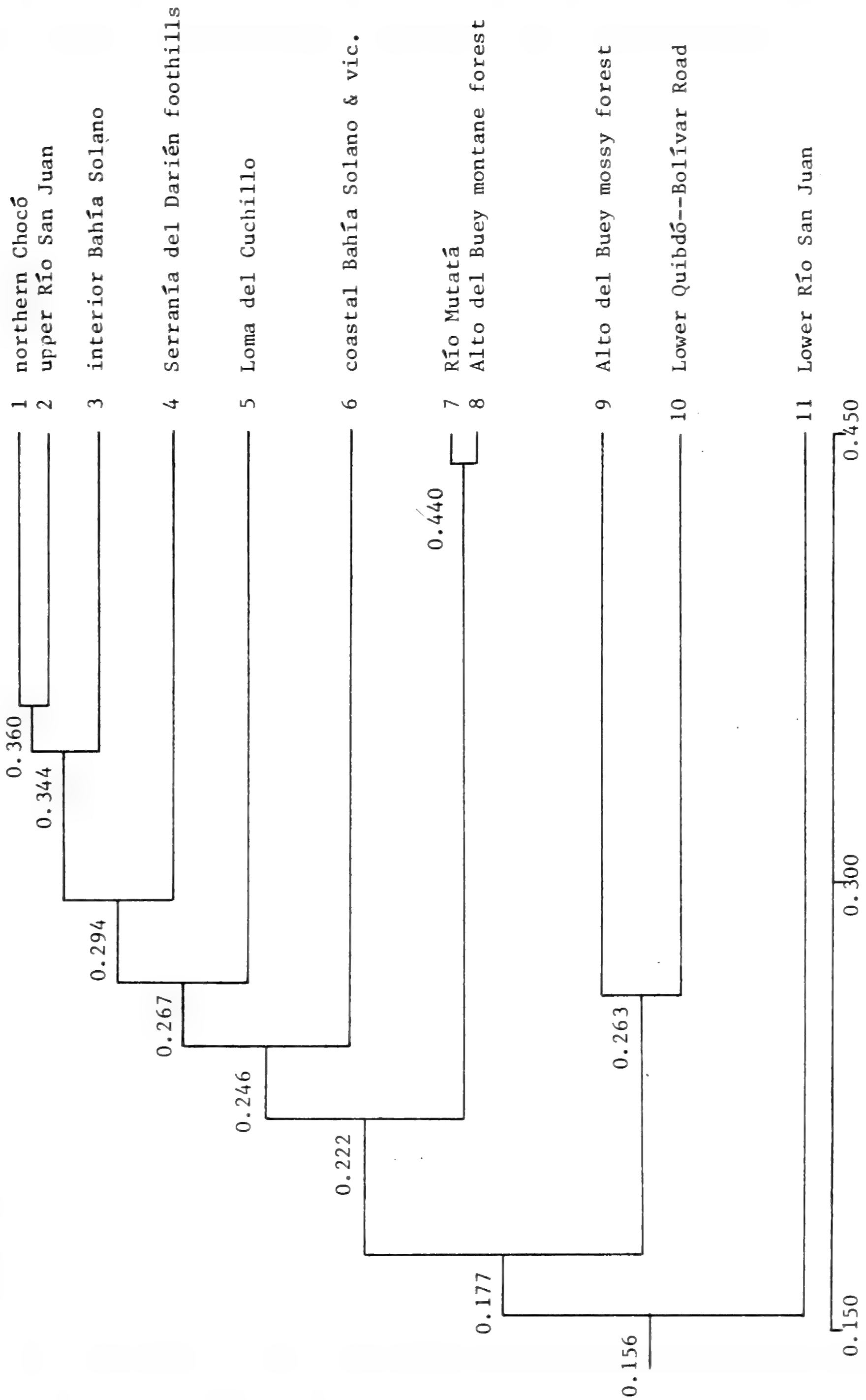

FIGURE 3. Phenogram of 11 areas in the Departamento del Chocó lying below 1000 m altitude.

the several northern Chocó localities (area 1) to interior Bahía Solano near the Pacific coast (area 3) and the upper Río San Juan (area 2), form a fairly coherent group, with more Panamanian-Costa Rican species present in the Serranía del Darién foothills than elsewhere in central and northern Chocó.

EXTRA-CHOCÓ PHYTOGEOGRAPHICAL RELATIONSHIPS

Evidence concerning the phytogeographic relationships of the lowland Chocó pteridophytes with the pteridophytes of other areas of tropical America is substantial, but not completely conclusive. Almost all the data on extra-Chocó distributions were taken from the U.S. National Herbarium collections, with some additions from the literature for the species of a few genera. The data are subject to collecting bias and representation in the herbarium, which probably accounts for the low percentage of Chocó pteridophytes recorded from El Salvador and, perhaps to a slighter extent, from Ecuador and Nicaragua.

To study the affinities of the Chocó pteridophyte flora, the New World was divided into 27 areas, each of which is a country or (in the Antilles) an island or a group of islands. Each Chocó taxon card was notched for each area in which it was found.

Figure 4 shows the results rounded off to the nearest percent. There is a decided drop-off in the percentage of affinity from Costa Rica to Nicaragua, from Guatemala to Mexico, from Venezuela to the Guianas, from Colombia to Brazil, and from Peru to southern South America. The highest percentages of pteridophyte taxa corresponding between the Chocó and the other areas are found in Colombia, Costa Rica, Panama, and Peru.

Although no numerical data have been collected, I estimate that about 85% of the Chocó pteridophyta are known in Colombia from departments other than the Chocó. Some extend only into parts of the departments of Antioquia and El Valle that lie within the Chocó floristic region, and so are not truly found in non-Chocó Colombia. Those that do extend to other parts of Colombia are mostly widespread species that also range beyond Costa Rica and Ecuador. Judging by the north or south distribution of near-endemic Chocó species discussed above, the affinities are with the Pacific Coastal phytogeographic areas, which are both adjacent to the Chocó geographically and also are more like it in climate. The average of the percentages found in Colombia (estimated at 85%), Ecuador (54%), and Peru (60%) is 66%. The 79% for Costa Rica and Panama is about 20% higher.

The affinity of the Chocó pteridophyte flora appears to be primarily with that of Costa Rica and Panama and secondarily with that of the Pacific coastal and submontane slopes from Colombia to Ecuador.

ACKNOWLEDGEMENTS

Most of the data for this paper came from specimens collected by the Smithsonian Institution-Museo de La Plata Botanical Exploration of the Chocó, which was made possible by grants from the National Geographic Society and the Smithsonian Research Foundation, plus financial support of the Comisión de Investigación Científica de la Provincia de Buenos Aires. The exploration was aided immeasurably by the staffs of the Instituto de Ciencias Naturales at Bogotá, the Departmento de Biología of the Universidad de Antioquia at Medellín, and the Instituto de Desarrollo de los Recursos Naturales Renovables (INDERENA) at Bogotá, Medellín, and Turbo. I wish to thank Drs. José Cuatrecasas, Helen Kennedy, and Harold Robinson for their valuable suggestions concerning this paper.

FIGURE 4. Map showing percentage of Chocó pteridophytes also known from other countries or Antillean island groups of the New World.

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STUDIES IN THE SYSTEMATICS OF FILMY FERNS: I. A NOTE ON THE IDENTITY OF MICROTRICHOMANES

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ABSTRACT

The features of the filmy fern genus *Microtrichomanes* are described. All the species referred to this genus are compared with each other from the viewpoint of alliance. Subdivision of the genus is proposed, and the relationship of each species is discussed, giving critical comments on the current conception that *Microtrichomanes* stands between *Trichomanes* s.lat. and *Hymenophyllum* s.lat.

INTRODUCTION

There are two alternative systems in the Hymenophyllaceae currently adopted by pteridologists: one is the classical two genera system, recognizing *Trichomanes* and *Hymenophyllum* in a broader sense, or sometimes separating a few distinct genera in addition to the above two (e.g. Morton 1968); the other is the system proposed by Copeland (1938 1947) distinguishing 34 genera. We have still insufficient information about the filmy ferns to conclude which system is natural and correct, and it is intended in this and following papers to elucidate the natural relationship among the species of the Hymenophyllaceae.

Microtrichomanes was first recognized as a group by Mettenius (1864) enumerating *Trichomanes digitatum, T. palmatifidum* and *T. dichotomum.* Subsequent authors added further species, increasing the number to 14 as listed by Morton (1968). Concerning the systematic position of this genus among the filmy ferns, there is general agreement that it is intermediate between *Trichomanes* s.lat. and *Hymenophyllum* s.lat., although Christensen (1906) included *Microtrichomanes* in *Trichomanes* sect. *Gonocormus.* This intermediate position of *Microtrichomanes* forms one of the reasons why Copeland could not maintain the above two genera in the broader sense. In his opinion (Copeland 1938: 36) the species of *Microtrichomanes* "present sufficient evidence of affinity to *Sphaerocionium* . . . so far as the marginal setae are present". Similarly, Holttum (1955: 87) discussed the hairs and sori of *Microtrichomanes* and states that "there is little doubt they are more nearly related to *Hymenophyllum*".

After detailed observation on most of the species belonging to *Microtrichomanes,* I am now inclined to have the same opinion as Morton (1968: 199) who says that "it is decidedly heterogeneous and would seem to be polyphyletic", though I have no evidence at hand to support his view that the genus "may have arisen anciently from hybridization between various species of *Trichomanes* and *Hymenophyllum,* perhaps belonging to quite different groups".

This is a preliminary report, for the true relationship will be elucidated only after detailed studies on the other "genera". Therefore, no new names are proposed here, and the specific names are used enumerating the species of *Microtrichomanes* under *Trichomanes* except in the case where no formal combination has ever been given in that way. The names of subdivisions of the filmy ferns are adopted in accordance with the Copeland's system, unless otherwise stated. These subdivisions are often referred to as genera, though they are not used here in the form of binary names.

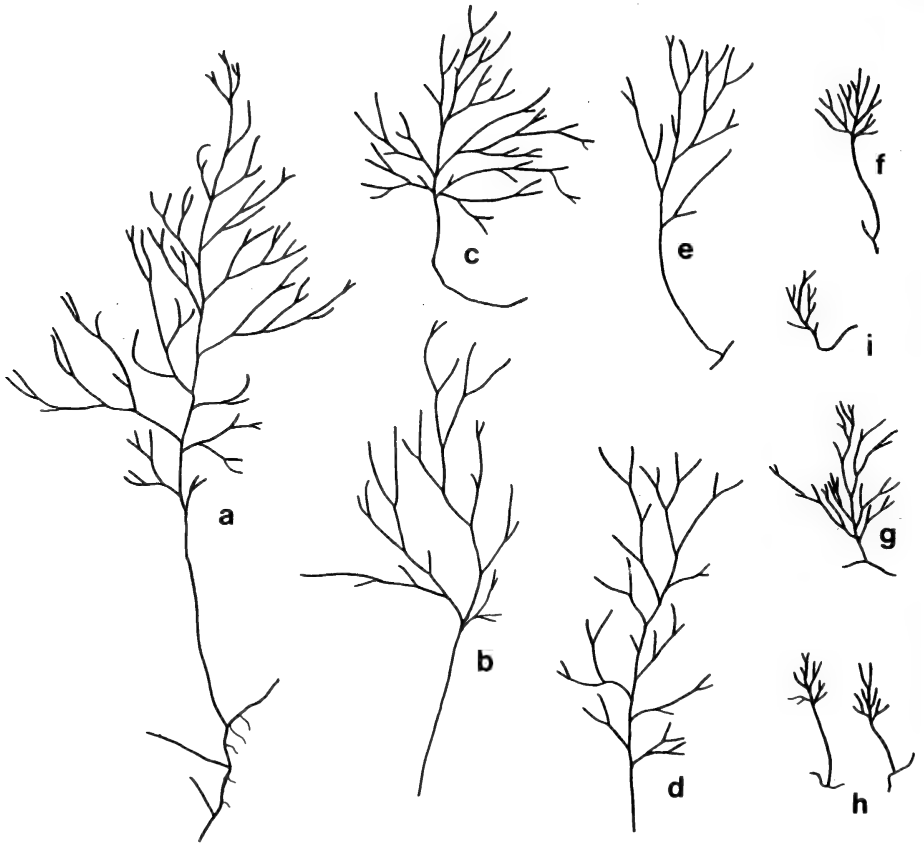

FIGURE 1: Pinnation in fronds in *Microtrichomanes,* all x 1/2. a, *T. dichotomum* (Sumatra, Iwatsuki et al. S—1127); b-f, *T. flabellatum* b, Sumatra, Iwatsuki et al. S—1163 bis; c, New Guinea, Kalkmann 5007; d, Borneo, Hotta 3854; e, Thailand, Tagawa et al. T—4823; f, Malaya, Iwatsuki et al. M—13234); g, *T. taeniatum* (Tahiti, Grant 3561); h, *T. nitidulum* (Malaya, Iwatsuki et al. M—13514); i, *T. lyallii* var. *neocaledonicum* (New Caledonia, Franc 828).

OBSERVATIONS ON TAXONOMIC FEATURES

The following taxonomic characters used to evaluate *Microtrichomanes* are described and discussed from the morphological and systematic point of view.

Rhizome

Most species of *Microtrichomanes* grow on tree trunks and boles and have a slender, more or less wiry rhizome less than 0.2 mm in diameter, brown, and sparsely bearing brown hairs usually about 1 mm in length. In *T. francii* the rhizome is wiry, about 0.3 mm in diameter, and nearly glabrous except in apical portion where brown hairs are found. In *T. vitiense* and *T. aswijkii,* the rhizome is not wiry, less than 0.2 mm in diameter, and quite densely covered with the blackish coarse hairs. The last type of rhizome is found also in *Microgonium,* while the first type is most frequently known in the filmy ferns especially common in *Hymenophyllum* s.lat.

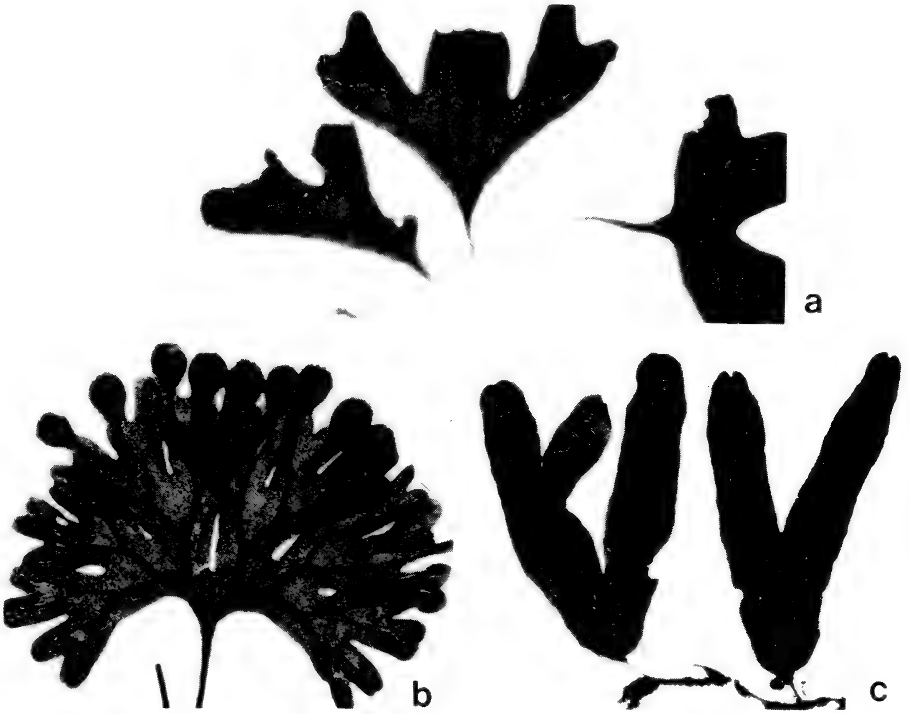

FIGURE 2: Fronds of *Microtrichomanes:* a, *T. francii* (New Caledonia, Franc s.n.), x 2; b, *T. vitiense* (Fiji, Degener 14607), x 2; c, *T. parvulum* (Madagascar, Forsyth-Major 203), x 2.

Pinnation

The pinnation in fronds is always described as dichotomous for *Microtrichomanes,* though this is not so in reality. Figs. 1 and 2 illustrate rather schematically the pinnation pattern of various forms referred to this genus. It is evident that *T. dichotomum* has pinnately divided fronds, and this is quite true for *T. flabellatum, T. taeniatum* and *T. lyallii* var. *neocaledonicum,* though their fronds are short and seemingly digitate. In *T. palmatifidum* and *T. nitidulum* the length of fronds is reduced, and the rachis is often very short usually giving the appearance of a dichotomously branched frond. It may be concluded that the apparently dichotomous fronds have resulted from the extreme shortening of the rachis by the reduction of the length of fronds. This does not necessarily mean that the larger species are primitive; as noted below, *T. dichotomum* is a specially elongate form of *T. flabellatum,* and can not be considered as the prototype of the latter. The same kind of variation in pinnation is seen in the various forms of *Gonocormus.*

The pinnately divided fronds have a definite rachis even when the length of fronds is extremely reduced, and typical dichotomy cannot be found even when the number of segments is extremely reduced. Contrary to these species, the fronds of glabrous species are simple to biforked or dichotomously branched when the number of segments is more than four. A similar pattern of branching in fronds is found in reduced species of *Microgonium,* and the simple frond may be referred to the most reduced form in this series.

Hairs

There are two types of hairs in *Microtrichomanes.* Setose marginal hairs are found on ultimate segments in *T. digitatum, T. flabellatum, T. dichotomum, T. taeniatum* and *T. lyallii* var. *neocaledonicum.* They are simple, short and rather thick, usually 0.2 mm long and up to 0.03 mm in diameter, and dark brown to blackish in colour. Hairs of this type are not found elsewhere in the filmy ferns except in the simple form of the marginal hairs of *Didymoglossum.*

The other type of hair is that found in *T. palmatifidum* and *T. ridleyi.* In *T. palmatifidum* they are found rather densely on the margin of segments and in some plants also on the veins. *T. nitidulum* is usually glabrous but occasionally bears the hairs of this type on the margin of segments. Hairs of this type are simple or forked, more or less downy, about 0.5 mm long, and pale brown in colour, and are similar to those found in *Sphaerocionium.* Various types of hairs in *Sphaerocionium* are summarized by Morton (1947) with diagrammatical illustration. In all the species of *Sphaerocionium,* the hairs are pale brown, long and slender, simple to stellate and no species have only simple hairs, e.g. the basally forked hairs are found mixed with the simple hairs as in Hawaiian *H. lanceolatum,* or many species have the forked and stellate hairs in addition to the simple hairs as in *H. microcarpum.* In *T. palmatifidum* no stellate hairs are observed, though we have no information to distinguish the hairs of this species from those of *Sphaerocionium.*

There are species quite glabrous and still referred to *Microtrichomanes.* They are *T. aswijkii, T. vitiense, T. francii* and *T. parvulum.*

Sorus

The structure of the involucre is obconic to campanulate or tubular; receptacles are long and usually extruded. In *T. nitidulum* and *T. palmatifidum,* the involucre is relatively short and obconic in appearance (fig. 3a), though relatively long and campanulate in *T. flabellatum* (fig. 3b) and the other species with setose marginal hairs. The variation in the form of involucre is not correlated with the breadth of the segments in general, except in *T. taeniatum* in which a tubular involucre is found in plants having narrower and longer segments and a campanulate one in plants with broader segments. The mouth is hardly bilabiate except in *T. nitidulum* and *T. palmatifidum,* in which the lips of the mouth are slightly extruded over and above the apex of the segments, though the form of lips is subtruncate to very moderately round. In *T. aswijkii* the involucre is tubular and the mouth is distinctly dilated as in the case of *Gonocormus* and *Microgonium.*

Generally the structure of the involucre is referable to that of *Trichomanes* s.lat. It is interesting in this connection that *H. borneense* Hook. is described under *Hymenophyllum,* though this is identical with *T. palmatifidum.*

COMMENTS ON THE SPECIES

Morton (1968) referred 14 species to *Trichomanes* sect. *Flabellata,* an equivalent of *Microtrichomanes.* All the species referred to *Microtrichomanes* are treated even when the same author separated the species from that genus in a later paper. A complete revisional treatment will be given in a future publication according to the genera defined there.

1. **Trichomanes lyallii** (Hook.f.) Hook.

This species was included in *Microtrichomanes* by Copeland in his 1933 paper but

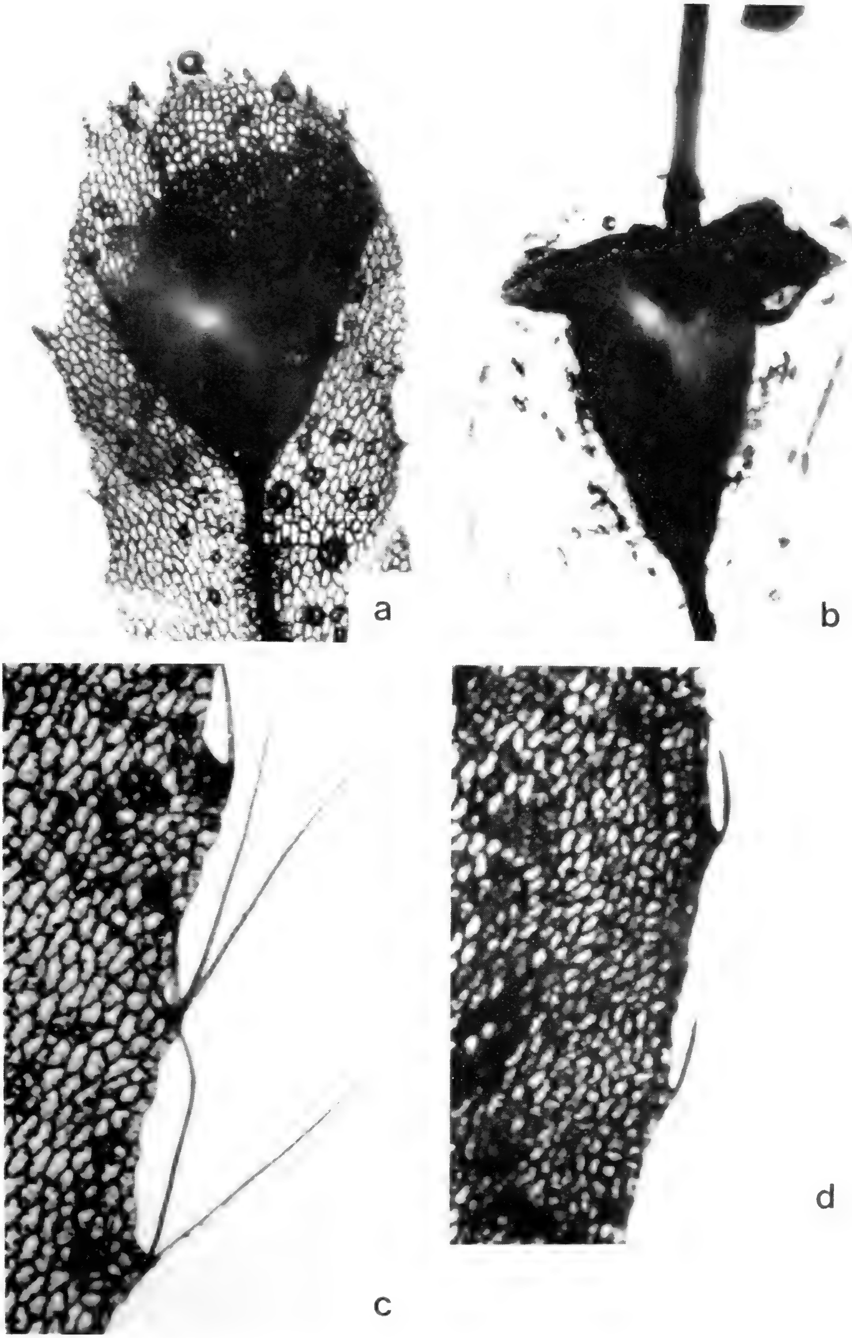

FIGURE 3: Sori and hairs of *Microtrichomanes:* a, sorus of *T. palmatifidum* (Sumatra, Iwatsuki et al. S–1163), x 20; b, sorus of *T. flabellatum* (Malaya, Togashi s.n.). x 15; c, hairs of *T. palmatifidum* (Sumatra, Iwatsuki et al. S–1163), x 30; d, hairs of *T. flabellatum* (Thailand, Iwatsuki et al. T–8359), x 30.

transferred to *Sphaerocionium* by himself in 1938. Morton (1968) placed this in his *Trichomanes* sect. *Flabellata* probably following Copeland (1933) without detailed study of the plants. This was placed in *Microtrichomanes* by Copeland on account of the reduced flabellate frond, though the marginal hairs are stellate, or d-type in Morton's scheme of 1947. Tindale (1963) made detailed observation on the size and form of fronds as well as the marginal hairs of this species. It is evident that this species belongs to *Sphaerocionium* indicated by the stellate marginal hairs and included cylindrical receptacles.

2. **Trichomanes palmatifidum** C. Müller

This species has always been treated as an ally of *T. digitatum* since Mettenius (1864) included this in his group *Microtrichomanes,* but the hairs on fronds of *T. palmatifidum* belonging to the types *a* and *b* in Morton's scheme are quite different from the marginal setose hairs of *T. digitatum* group and the same as the hairs found in *H. lanceolatum* and also in *H. microcarpum* mixed with types *c* and *d* by Morton.

The fronds of this species appear digitate and are commonly described as such, though this is pinnately compound with long segments and a short rachis. This frond construction is also found in *T. nitidulum,* and relates these species to *T. digitatum.* There is no example of reduced flabellate fronds in *Sphaerocionium* unless *T. lyallii* is included in that genus. The flabellate or digitate appearance of the fronds of *T. palmatifidum* is interpreted as the result of the reduction of length from more slender, pinnately compound fronds.

The involucre is obconic with somewhat bilabiate mouth (fig. 3a), and is somewhat similar to that of *T. flabellatum* with a campanulate to tubular involucre with a slightly dilated mouth. The extruded receptacle is distinct from that of *Sphaerocionium.* The morphology of the receptacles will be discussed in detail in a separate paper and here it is noted only that the receptacles of *T. palmatifidum* and *T. nitidulum* are not too long, and that receptacles can be extruded in various species of *Meringium. T. palmatifidum* can be referred to as an ally of *Sphaerocionium* in spite of having the extruded receptacles.

3. **Trichomanes nitidulum** van den Bosch

This species is usually described as glabrous, though the detailed observation of ample material shows that long downy hairs are sometimes found at the margin of ultimate segments. The morphology of these hairs is quite identical to those of *T. palmatifidum.* Except for this "glabrous" nature, *T. nitidulum* is the same as *T. palmatifidum,* and as the density as well as the occurrence of hairs are rather variable in that species, *T. nitidulum* seems to be better treated as a variety of *T. palmatifidum.*

4. **Trichomanes ridleyi** Copeland

This is distinguished from *T. palmatifidum* by long stipes and rather irregularly branched fronds with sparse hairs, and is known only from the type collection from G. Tahan in Malaya, where *T. palmatifidum* has repeatedly been collected. Some of the latter plants are similar to *T. ridleyi* (e.g. Wray & Robinson 5401 in SING). Holttum (1955) considers it "possibly a hybrid" between *T. digitatum* and *T. palmatifidum,* though by comparing the variation of pinnation pattern of *T. palmatifidum* and *T. nitifulum* it is suggested here that *T. ridleyi* is only a variant of the latter.

5. **Trichomanes digitatum** Sw.

T. digitatum in the most strict sense, excluding is *T. flabellatum* of Southeast Asia, is restricted to East African Islands, in Mauritius and Madagascar. The African form differs from *T. flabellatum* in its smaller size and the more simple aspect of fronds which have 1–5 segments digitate in appearance. In *T. flabellatum,* mature fronds with several segments are occasionally observed, although they are usually found on the same rhizome with the larger fronds with many segments.

6. **Trichomanes flabellatum** van den Bosch

Although I have insufficient data about the plants in East African Islands, I would agree partly with Christensen (1932) in distinguishing the African form from the East Asiatic form (including the type of *T. flabellatum*). The difference is found only in the degree of development of the fronds, and they might be better segregated in the rank of sub-species considering the difference in their distribution. Thus confined, *T. flabellatum* is recorded only in South-east Asia: in Sumatra, Peninsular Thailand, Malaya, Borneo, Philippines, Java and New Guinea.

I have not seen the type of *T. piliferum* v.A.v.R., and follow here Backer and Posthumus in reducing it to *T. flabellatum.*

7. **Trichomanes dichotomum** Kunze

In its largest form, this species is more than 20 cm in length and the digitate construction of fronds becomes elongate. As such it is distinct from *T. flabellatum,* though there are intermediate forms between the two extremes. It may be speculated that these long fronds are evolved from short fronds of *T. flabellatum,* and with the elongation of fronds the ultimate segments become longer with the tubular involucres bearing long extruded receptacles. This is not distinct specifically from *T. flabellatum* and is better treated as a variety of the latter.

8. **Trichomanes taeniatum** Copeland

This is similar to and possibly should be regarded as a subspecies of *T. flabellatum* which differs from it in usually having more numerous segments which are slender, green or rarely dark in dried specimens, with blackish and distinct veins. When the ultimate segments are slender, the involucre becomes longer and tubular in appearance.

Copeland (1933) noted the variation of this species; the Samoan plants referred by him to *T. digitatum* belong here, and its range includes the Society, Solomon and Marquisas Islands.

9. **Trichomanes lyallii** var. **neocaledonicum** C.Chr.

There are two taxa of *Microtrichomanes* represented in New Caledonia. One was described by Christ as *T. francii* (see below). The other belongs to a group of *T. digitatum* both in pinnation and setiferous margin of segments. It is similar to *T. flabellatum* but differs in having an obconic involucre and the smaller fronds usually of equal length and breadth. The hairs at the segment margins are rather slender and not so dark as typical *T. flabellatum.* The figure given by Brownlie (1969: pl. 12, fig. 6) is this setiferous form, not *T. francii* as stated. *T. lyallii* sensu Fournier (1873), *T. lyallii* var. *neocaledonicum* C.Chr. and *T. digitatum* sensu Compton (1922) are names given to this latter form, though I am not sure at present whether *T. cuneatum* Christ is also this taxon or not. Compton referred Rosenstock Exsicc. n. 51 to *T. cuneatum,* and that I have examined (in herb UC) is this taxon, but I have not so far seen Christ's type and his incomplete description is insufficient for determination. Anyway, this setiferous form is probably best treated as a variety or subspecies of *T. digitatum* and var. *neocaledonicum* is available as the correct name at varietal rank.

10. **Trichomanes francii** Christ

This is a completely glabrous form: rhizome wiry, nearly glabrous in older ones; segments 1 to 8, usually shorter than the breadth, each fork with wide sinus; involucre obconic, the mouth hardly dilated and with subtruncate apex. It is so far endemic to New Caledonia.

11. **Microtrichomanes zamboanganum** Copeland

I have not seen any material of this species, and place it at present close to *T. francii* only from the description and notes given by Copeland (1952, 1958).

12. **Trichomanes parvulum** Prior

I have not examined the type material of various names referred to this species, and so discuss here the affinities of this taxon but not the nomenclature. The dichotomous branching type of frond is found in this species and in *T. francii* (cf fig. 2a,c), though it is sometimes deformed in the latter, especially in the larger forms.

The frond pattern is similar to *Gonocormus* but the latter differs in its sorus and proliferous habit. The involucre of *Gonocormus* is usually campanulate with a dilated mouth, whereas that of *T. parvulum* is obconic with a bilabiate mouth bearing round and irregularly dentate lips.

13. **Trichomanes vitiense** Baker

Tindale (1963) gave a detailed description and notes on this species, and I have little to add. It differs decidedly from *T. digitatum* s.lat. in completely lacking hairs on the fronds. This is similar to *T. aswijkii* in having a slender rhizome densely covered with blackish hairs. The thin fronds remain green in the dried condition or eventually become pale brown. In these features as well as in general habit, this resembles species of *Microgonium,* and Tindale compared this actually with *T. motleyi.* I have no conclusive remark at present to this affinity, for the false veinlets in the filmy ferns are now under investigation and are still little known from the phylogenetic point of view. Besides *Microgonium,* this and the following species are comparable with *T. francii* and *T. parvulum* in some features. In the morphology of the involucre, *T. vitiense* and *T. aswijkii* resemble *Gonocormus.*

14. **Trichomanes aswijkii** Racib

This is similar to *T. vitiense* but differs from it in: stipes shorter, less than 1 mm long or sessile; the base of simple frond narrowly cuneate; the segments 1 to 4 (very rarely 6) 2.5–3 mm in breadth; the rhizome slender, bearing dense blackish hairs. Compared with *T. francii* the segments do not branch so widely and the involucre is tubular with a distinctly dilated mouth. This and the preceding seem to be closely allied and are compared with *Microgonium* tentatively; the alliance however, is obscure.

15-16 **Trichomanes barklianum** Baker and **Trichomanes liberiense** Copeland

Both of these African taxa were included by Copeland in *Microtrichomanes* in 1933 but referred to *Didymoglossum* in 1938. In the absence of false veinlets and presence of the marginal hairs, they seem to be similar to *T. digitatum,* but I cannot comment further at this stage.

SUMMARY

The species usually referred to *Microtrichomanes* may be grouped as follows:

1: Species included in, or compared with, *Sphaerocionium: T. lyallii, T. palmatifidum, T. ridleyi* and *T. nitidulum.*

2: *Microtrichomanes* s.str.: *T. digitatum, T. flabellatum, T. dichotomum, T. taeniatum* and *T. lyallii* var. *neocaledonicum.*

3: Species with dichotomous fronds comparable with *Gonocormus: T. francii, M. zamboanganum* (?) and *T. parvulum.*

4: Species close to *3* or comparable with *Microgonium: T. vitiense* and *T. aswijkii.*

5: Species probably belonging to *Didymoglossum: T. barklianum* and *T. liberiense.*

As summarized here, *Microtrichomanes* has usually been defined by the dwarfed frond construction and includes a variety of taxa, which may be regarded as belonging to various species groups or genera. It is quite natural that such a heterogenous "genus" relates both to *Trichomanes* s.lat. and to *Hymenophyllum* s.lat. However, if group 1 is removed, *Microtrichomanes* has no affinity with *Hymenophyllum* s.lat. and belongs wholly to *Trichomanes* s.lat. even if groups *2–5* are amalgamated into a single unit or genus. The real position of each species group will be elucidated by further studies, especially on the other groups of the filmy ferns, although I have shown that Copeland had little basis for segregating *Microtrichomanes* from the classical two-genera system of Hymenophyllaceae.

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A HYBRID POLYPODY FROM THE NEW WORLD TROPICS

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ABSTRACT

Polypodium leucosporum Klotz., from Jamaica is shown to be a hybrid between *P. lanceolatum* L., often placed in *Pleopeltis,* and *P. thyssanolepis* A. Br., a component of *Marginaria* or *Polypodium* s.s. The variation, especially of frond dissection and venation, is given and the hypothesis that there are genetically different forms of *P.* x *leucosporum* and that other species and/or cytotypes are involved in their origin is discussed.

INTRODUCTION

Most hybrid polypodies that have been found are crosses between sectors of the same species or between similar sibling species (e.g. Lang 1971). Wide hybrids (crosses between strongly distinctive elements) are very rare in polypodies, as they are in all groups of ferns. Such hybrids have special interest, however, in helping us assess systematic relationships and establish homologies. This is particularly true of those hybrids which combine characteristics of simple-leaved and divided-leaved taxa which have widely differing patterns of venation and soriation. In the Old World polypodioid genus *Colysis,* Lellinger (1968) discussed and figured *C. x shintensis* (Hayata) H. Ito, a plant morphologically intermediate between *C. wrightii* (Hook.) Ching, with simple blades, and *C. elliptica* (Thunb.) Ching, with pinnate blades. In *Polypodium* and its segregates in the New World, Weatherby (1935) described *P. bartlettii* as a possible hybrid between the simple-fronded *P. polylepis* Roem. (= *P. peltatum* Cav.) and the pinnatifid-fronded *P. polypodioides* (L.) Watt. He compared this fern with the South American and West Indian *P. leucosporum* Klotzsch, which Vareschi (1969) later interpreted as the cross between *P. lanceolatum* L. and *P. thyssanolepis* A. Br., plants frequently placed in different subgenera or genera.

All of these presumed hybrids exemplify what we have termed "hybrid irregularity" (Wagner 1962) in which the intermediate plant expresses the parental characteristics asymmetrically. Here we wish to discuss the morphology and cytology of one of those irregular ferns, basing our studies on both field-collected and greenhouse-grown specimens. We were especially interested in studying the intermediate characters and the extent or irregularity, emphasizing frond habit, venation, scales, sori, and chromosomes. Herein the plant involved will be given a new status, based upon the facts presented below; its name should now be as follows:

Polypodium x **leucosporum** Klotzsch, Linnaea 20: 404 (1847), *pro sp.*
Pleopeltis leucospora (Klotz.) T. Moore, *Index Filicum:* 77 (1857).
Lepicystis leucospora (Klotz.) Diels, in Engler & Prantl, *Die natürlichen Pflanzenfamilien 1 (4):* 324 (1899).

MATERIALS AND METHODS

We encountered a large colony of *P.* x *leucosporum* in Surrey Co., St Andrews Parish, Jamaica, about one-third of a mile from the Cinchona Gardens near the trail to New Haven Gap. Specimens were collected on 2 March 1970 (*Wagner 70100,* MICH), together with associated samples of *P. lanceolatum (70101)* and *P. thyssanolepis (70102)* growing in the same place. We found our specimens on rocks and at bases of small trees at the edge of a field. The habitat of *P.* x *leucosporum* and similar forms everywhere in the New World tropics seems to be terrestrial rather than epiphytic, usually on disturbed rocky ground with more or less shade, in mountainous regions at altitudes of 1300–3000 m. Statements gleaned from herbarium labels include such descriptions as the following: "on a wall", "on limestone rocks", "forest, on the ground", "dry rock wall", "on trunk of tree on hill", "on top of boulder", "on stump at border of cultivation", and "creeping on moss over boulders".

Living materials of all three polypodies were collected for cytological study. It turned out that *P.* x *leucosporum* flourishes under our greenhouse conditions and produces a vigorous potted plant. In culture it forms leaves over twice as large as those from the wild and variations appeared that are not yet known in herbarium collections. Hybrid fronds were consistently more robust than those of the parents, and some examples are shown in fig. 2 e-f.

MORPHOLOGY

Polypodium x *leucosporum* has consistently fewer lobes than *P. thyssanolepis* (fig 3). Furthermore, *P.* x *leucosporum* has numerous "mini-lobes", i.e. lobes only half or less the size of the adjacent ones. A majority of these miniature lobes are merely shallow concavities in the blade outline. Some herbarium collections (fig 1a) have only this type of lobing. The graph (fig 3) shows averages of many leaves grown in uniform culture; it shows that *P.* x *leucosporum* is intermediate in lobation between *P. thyssanolepis* represented by the upper line and *P. lanceolatum* the base line, in the last there being no lobation at all.

The major segments in *P.* x *leucosporum* tend to be longer and more pointed than in *P. thyssanolepis.* They are broadly adnate at base rather than contracted. They tend to be borne at a steeper angle and the vein departures at their bases have a different configuration. Rather than turning abruptly outward as in *P. thyssanolepis,* they run upwards for 4–10 mm and only then bow outwards. Related to this is the expansion of the laminar wing along the rachis, which is considerably wider in the hybrid than in *P. thyssanolepis.*

The most distinctive feature of frond structure in the hybrid is, of course, the asymmetrical outline. Irregularities may occur anywhere in the lower two-thirds of the blade, below the entire-margined tip, but two zones especially display extreme irregularity, namely the blade base at the transition between petiole and the lamina, and the transition between the lobed and unlobed blade sectors (indicated by arrows in fig 2e-f).

The vein patterns of the parents are different in a number of characters. The vascular system of the blade of *P. lanceolatum* is more complex than that of *P. thyssanolepis.* In the former (except in the narrow tip) there are multiple layers of areoles; in the latter, there is normally but a single costal layer, with only rare anastomoses distally (cf figs 4a and b). The costal areoles of *P. lanceolatum* are narrow and parallel to the midrib; the medial and submarginal areoles tend to be somewhat more oblique. Those of *P. thyssanolepis,* however, are not only broader but they run at angles of 40–50° from the midrib.

The marginal free veins in the entire-leaved species are projections from the outer circumferences of the marginal areoles and they are usually very short, less than 1 mm long. The marginal free veins in the pinnate species, on the other hand, are decidely longer, usually between 1–2.5 mm long. Also, the marginal vein tips in *P. lanceolatum* are only slightly expanded in contrast to those in *P. thyssanolepis* which

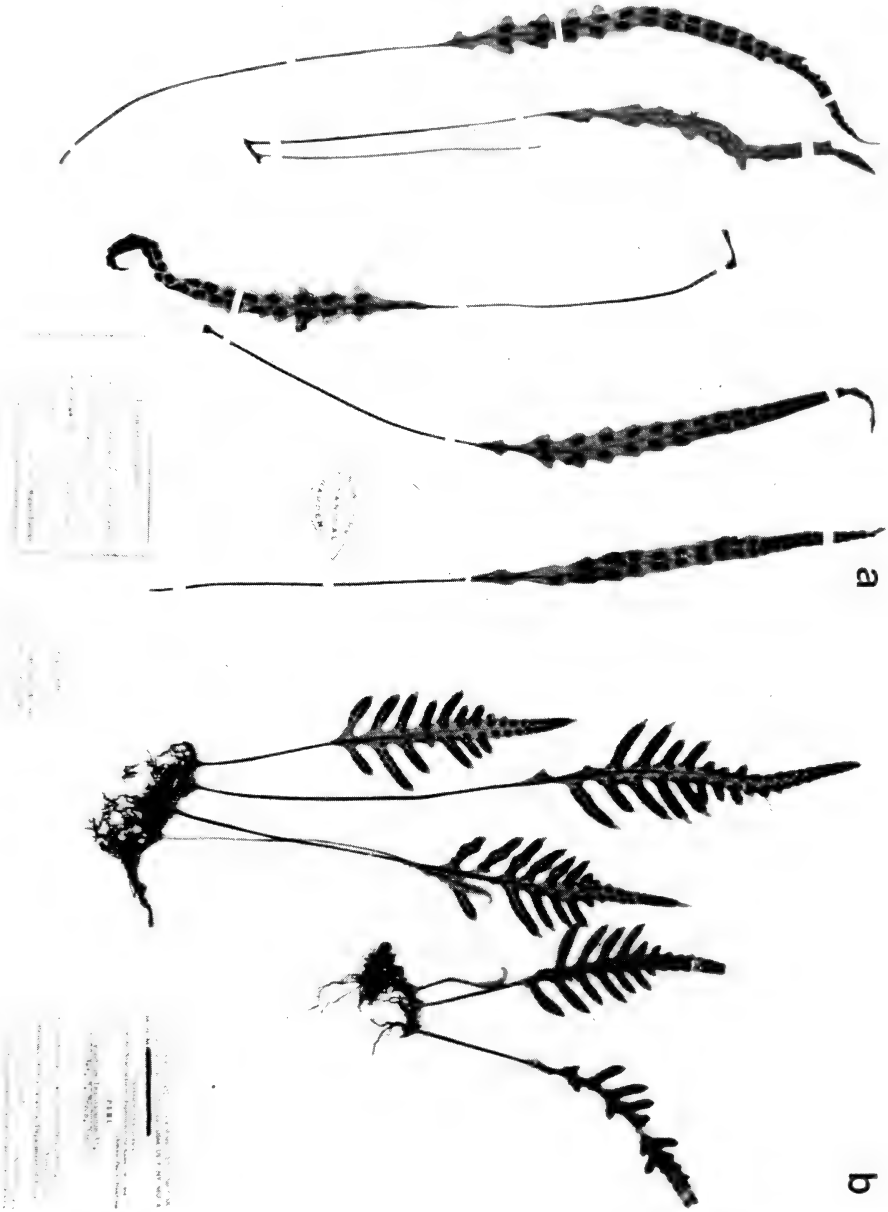

FIGURE 1. Forms of *Polypodium* x *leucosporum:* a, "Type 1" (hypothetical formula, LLT, see text), Santo Domingo, *Fuertes 1964* (NY). b, "Type 3" (formula, LTT), Peru, *Hutchinson & Wright 660* (F).

FIGURE 2. a, *Polypodium lanceolatum* (hypothetical formula LLLL, see text), Jamaica, field collection, *Wagner 70101* (MICH). b, *P. thyssanolepis* (TTTT), field collection, *70102*. c, *P.* x *leucosporum* "Type 2" (LLTT), Jamaica, field collection, *Wagner 70100*. d, the same, greenhouse-grown simple forms like *P. lanceolatum*. e, the same, greenhouse-grown forms like *P. thyssanolepis*. f, the same, greenhouse giant forms. Arrows point to zones of blade showing maximum variation.

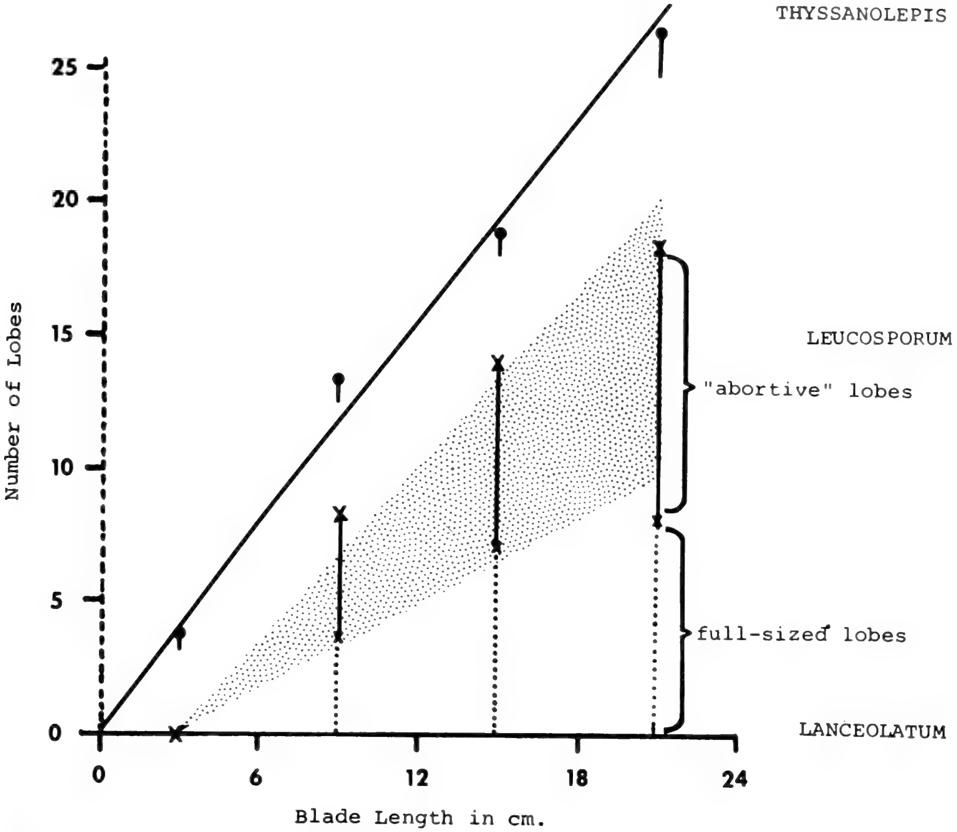

FIGURE 3. Lobation of leaf blades in relation to length of plants grown together under same greenhouse conditions. Base line: *P. lanceolatum* (no lobation at all). X—X: *P.* x *leucosporum* (numbers of lobes expressed as "full-sized" [dotted] and "abortive" [solid line]). ●—●: *P. thyssanolepis.*

are conspicuously clavate with the terminations broadly rounded or ovate and associated with well developed, pocket-like, hydathodes (cf figs 5a and b).

The fertile veins (i.e., the vein complexes subtending the soral receptacle) are also distinct in the parents. Under the sori of *P. lanceolatum* we find a complex reticulum, ovate in outline and composed of narrow bands of shortened tracheids. Subtending the sori of *P. thyssanolepis,* in contrast, there is usually a simple massive aggregation of shortened tracheids or at most a linear to lanceolate loop with a single cross-vein, as shown in figures 4 and 5. The sori of *P. lanceolatum* have a different location with respect to the over-all venation pattern. They are separated by 2–4 areoles from the midrib (except terminally), but in *P. thyssanolepis* they are contained in the costal areoles adjacent to the midrib.

In sterile and fertile vein characters, *P.* x *leucosporum* lies between its parents. From *P. lanceolatum* it receives the tendencies toward simplification of the blade, more numerous areoles, these more or less parallel to the midrib, and the more complex reticulate vein associated with the sori. From *P. thyssanolepis* it receives tendencies toward clavate hydathodal vein tips, as well as characteristics of the laminar scales to be described below. In all respects except one — the paraphyses — the hybrid appears to be a good intermediate.

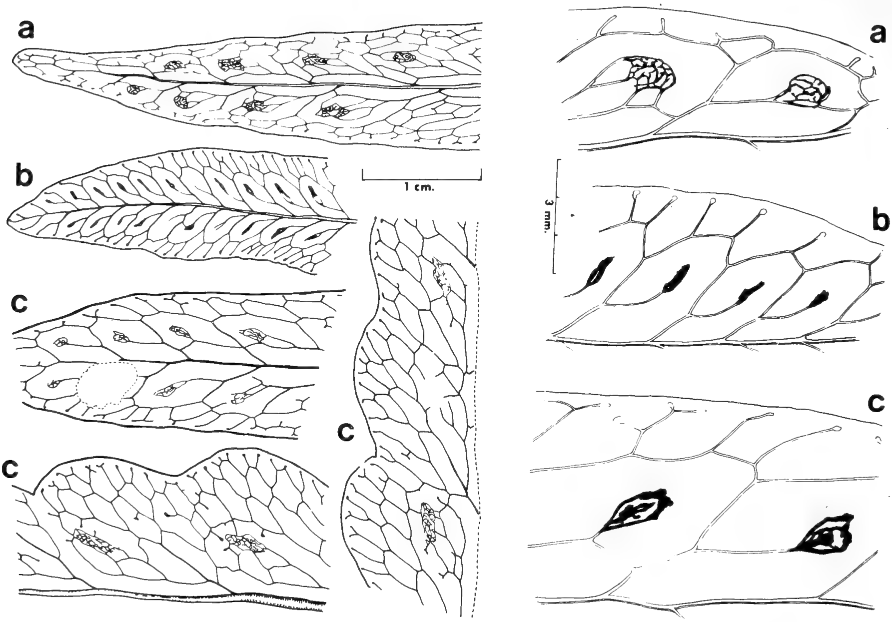

FIGURE 4. Tracings of venation patterns of Jamaican polypodies: a, *Polypodium lanceolatum;* b, *P. thyssanolepis;* c, *P.* x *leucosporum.* Right side: Fertile veins much enlarged to show simpler forms of each taxon.

The scales of the abaxial blade surface nicely distinguish the parents and the cross. In *P. lanceolatum* (fig 6a) the laminar scales are tiny, mostly 0.3–0.4 mm in diameter and round in outline. The "fringe" of thinner-walled, pale cells is relatively narrow, only about equal in width to the diameter of the dark central area of thick-walled cells. The scales are scattered remotely over the blade surfaces at distances averaging one or more millimeters. In *P. thyssanolepis* (fig 6b) the scales are much larger, being 2–5 times greater in over-all dimensions and mostly lanceolate in outline with an elongate tip. The "fringe" of pale cells is larger and the cells are elongated. Also the scale margin is conspicuously fimbriate. The scales are closer, covering between one-third and one-half of the blade surface and many of them overlap. The scales of *P.* x *leucosporum* (fig 6c-d) are transitional between these extremes in size, form, and distribution. This proves useful in identification: occasional simple fronds of *P.* x *leucosporum* (e.g., fig 2d) that might be confused with *P. lanceolatum* can be distinguished by their larger, more lanceolate and more densely distributed scales.

The sori of *P. lanceolatum* are distinguished by their large size, ovate outline, and presence of conspicuous peltate paraphyses. The paraphyses are trichomes like those of the lamina but they are borne on long stalks and appear above the young sporangia as a more or less continuous "roof". As the sorus becomes older, the paraphyses separate and fall off. The flattened terminal "umbrellas" have blackened centers with clathrate secondary walls and broad tan to white margins made up of cells with unmodified walls. Such paraphyses are absent in *P. thyssanolepis.* Remarkably they are also apparently absent in *P.* x *leucosporum.*

At first we thought that *P. thyssanolepis* and *P.* x *leucosporum* were without

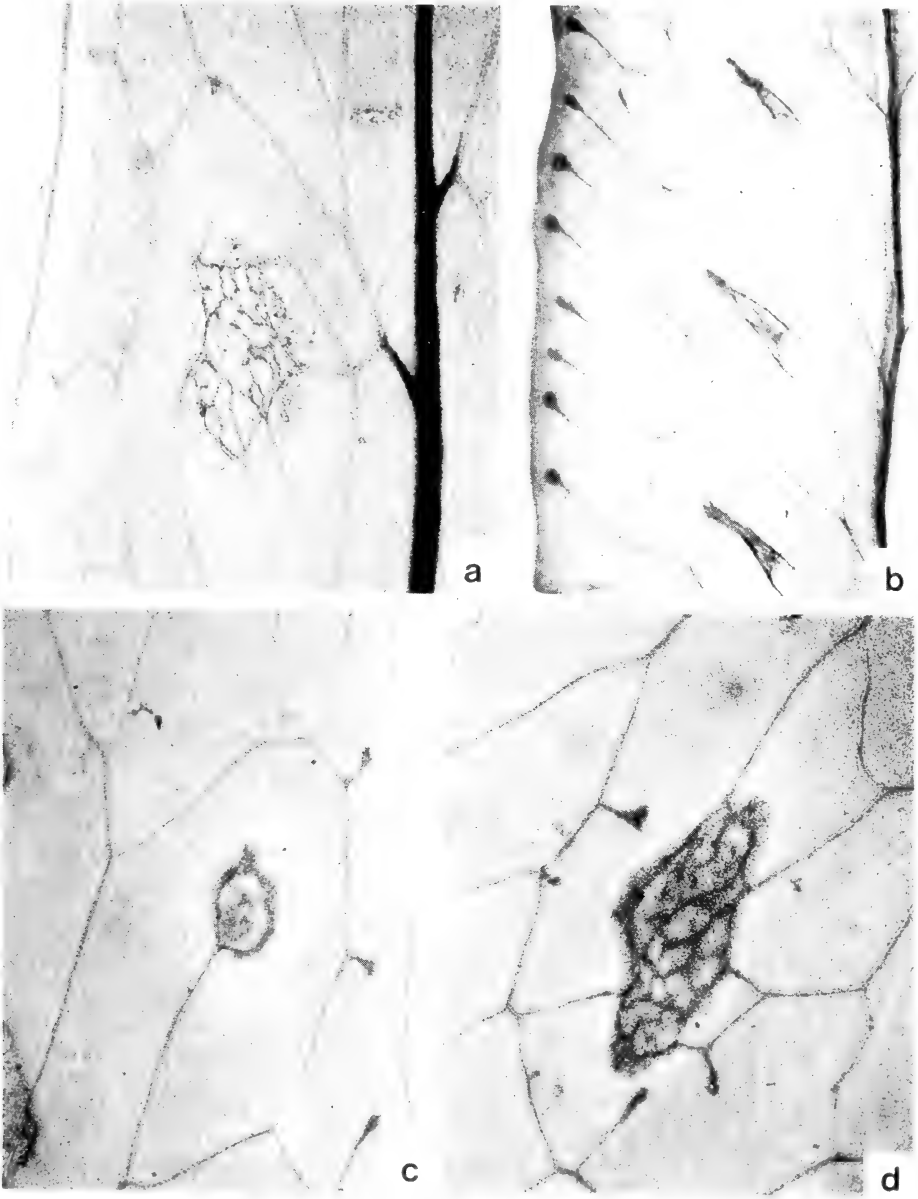

FIGURE 5. Photographs of cleared fertile veins: a, *P. lanceolatum,* b, *P. thyssanolepis;* c, *P.* x *leucosporum,* simple form on left, more complex on right.

paraphyses of any sort, but we later discovered that there are receptacular paraphyses among the sporangial stalks hidden below the sporangial capsules. They are very sparse and difficult to find in soral preparations. They were later discovered in *P. lanceolatum* as well. These paraphyses are narrow filaments of 2–9 cells in length. In *P. lanceolatum* and the hybrid they are normally between 150 and 300 μm long with

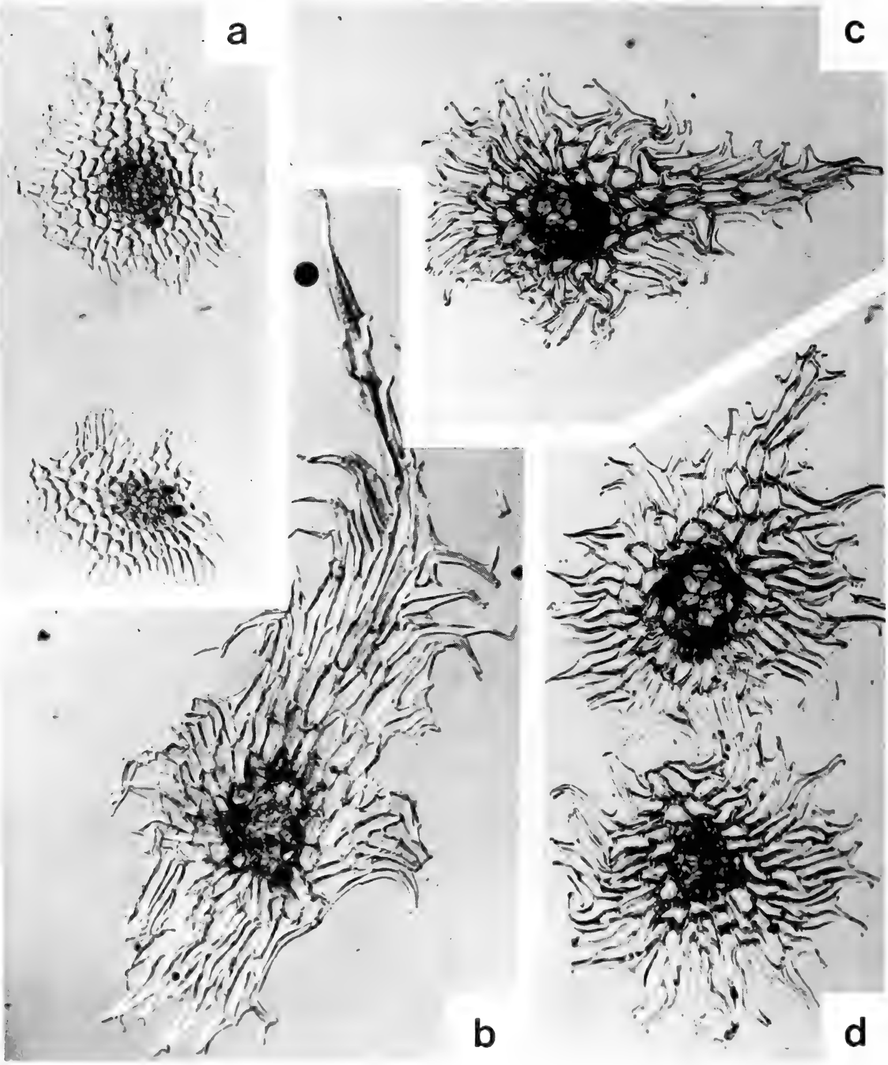

FIGURE 6. Laminar scales; a, *Polypodium lanceolatum;* b, *P. thyssanolepis;* c, *P.* x *leucosporum.*

3–5 cells; in *P. thyssanolepis* they are shorter, 100–150 μm, with only 2 cells.

CYTOLOGY

Studies of the chromosomes proved valuable in interpreting our material. In his discussion of *P. lanceolatum* in Jamaica, Walker (1973) noted tetraploid and pentaploid forms. The pentaploid had irregular meiosis, and two of the three tetraploids also had irregular meiosis. Presence of both 4x and 5x forms indicates the existence of 2x forms. Chromosome counts of our specimens from Jamaica gave 74 pairs and a somatic count of ca. 148. Our *P. thyssanolepis* also gave 74 pairs (fig 7c).

The hybrid polypody showed irregularity in meiosis, with uneven nucleus formation and excluded chromosomes. All figures contained, however, a high

FIGURE 7. Chromosomes squashes at meiotic metaphase. a, *Polypodium* x *leucosporum,* 59 II + 30I. b, the same, 63II + 22I. c, *P. thyssanolepis.*

incidence of pairs at meiotic metaphase, suggesting either compatibility between homoeologous chromosomes or autosyndesis or both. Five sporocytes examined in detail revealed the following patterns:

45 II + 58 I
51 II + 46 I
59 II + 30 I
63 II + 22 I
65 II + 18 I
Average 56.6 II + 34.8 I

From this evidence we conclude that at our locality in Jamaica, *P.* x *leucosporum* arose as a sterile cross of tetraploid forms of the parental species. By virtue of its vigorous creeping rhizome growth, the hybrid has formed a large colony. The spores are abortive, and presumably unable to reproduce the plant.

DISCUSSION

Hybrid polypodies more or less like the one described here have been taken sporadically from the Greater Antilles and Mexico to Peru. They seem to have been collected particularly often in Colombia and Venezuela. There are possibly genetically different forms of *P.* x *leucosporum* and indeed it is likely that some of the polypodies resembling it may have resulted from other species combinations (e.g., *P. bartlettii* Weatherby, 1935).

There seem to be three forms of *P.* x *leucosproum,* as was first suggested by Vareschi (1969: 193). We hereby designate these as follows: *"Type 1"* (fig 1a), closer to *P. lanceolatum,* the blade linear-lanceolate, remotely scaly, with shallow lobes or undulations; *"Type 2"* (fig 2c) intermediate, the blade broader, more scaly, with equal numbers of shallow lobes and long lobes, and a long tip (like the plants described herein); and *"Type 3"* fig 16), closer to *P. thyssanolepis,* the blade oblong-lanceolate, densely scaly, with many fully developed lobes, few shallow lobes, and a relatively shorter tip.* As both parents have diploid tetraploid forms (Walker 1973, Evans 1963, present paper), they can make different contributions to the hybrid. Perhaps, then, the following scheme may explain the variations where the superscripts are added to indicate pairing factors.

P. lanceolatum (L)		**P. thyssanolepis** (T)	**P.** x **leucosporum**
$L^1L^1L^2L^2$ (4*x*)	x	TT (2*x*) ——— L^1L^2T	(3*x*) "Type 1"
LL (2*x*)	x	TT (2*x*) ——— LT	(2*x*) "Type 2" Dip. form
$L^1L^1L^2L^2$ (4*x*)	x	$T^1T^1T^2T^2$ (4*x*) ——— $L^1L^1T^2T^2$	(4*x*) "Type 2" Tet. form
LL (2*x*)	x	$T^1T^1T^2T^2$ (4*x*) ——— LT^1T^2	(3*x*) "Type 3"

Of special interest is the fact that *P.* x *leucosporum* is the cross of a taxon commonly placed in subgenus or genus *Pleopeltis* and a taxon commonly placed simply in *Polypodium* or in subgenus or genus *Marginaria. Polypodium lanceolatum* clearly conforms to *Pleopeltis,* having peltate paraphyses and "veins anastomosing freely and irregularly with included veinlets; sori borne at the union of several veinlets" (from Copeland, 1947, p. 183). On the other hand, *P. thyssanolepis* fits Copeland's description (p. 180) of one of the common conditions in *Polypodium:* "The areolae usually form one row on each side of the costa, with always a single free vein in each areola. The sori are terminal on these free included veinlets" (l.c.). Without question, if these species can hybridize and combine so-called "generic" characters then there is room to doubt if they are taxonomically tenable.

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*Examples of *"Type 2"* are most common in herbaria. Of the others, the following seem to be good examples: *"Type 1"* – HAITI: Base of Guimbi Galata, *Holdridge 1770* (US); Massif de Cahos, *Ekman H.3478* (US). SANTO DOMINGO: Cordillera de Neyba, *Ekman H–13489* (US); Calo de Maco, *Fuertes 1964* (NY). VENEZUELA: State of Merida, Mucuruba, *Gehriger 304* (US, NY – this paper, fig. 1, left). *"Type 3"* – COLOMBIA: Dep. Antioguia, Medelliu, *Daniel 3310* (US); Auf Mauera in Tasto, *Lehmann 580* (US). PERU: Dep. Huanaco, Prov. Pachitea, La Molina, *Asplund 13662* (US); Dep. Piura, Prov. Huancabamba, *Hutchinson and Wright 6601* (F – Fig. 1, right, NY, US). We have also noticed several specimens labelled as *"P. leucosporum"* which we think may represent combinations of other species as parents, including the following: VENEZUELA: Monagas, Cerro Negro, *Steyermark 62109* (F, NY, US). COLOMBIA: Zipaquira, *Huertas and Camargo* in 1942 (US).

ACKNOWLEDGEMENTS

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ASPIDISTES THOMASII – A JURASSIC MEMBER OF THE THELYPTERIDACEAE

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Harris (1973) has drawn our attention to the neglect of late Mesozoic and Tertiary fern fossils, pointing out that these have usually received only rather superficial study and "glib determinations deserve and get little attention" (l.c., 43). The fault is however clearly mutual, insubstantial work by palaeobotanists being matched by disinterest and diffidence on the part of students of living ferns. To be able to suggest, as does Blasdell (1963: 30) in his monograph on *Cystopteris* that the disjunct distributional pattern of this genus can be explained if it is postulated that it evolved during the Carboniferous period is only possible if no note is taken of fossil evidence. A common and more understandable mistake is too ready an acceptance of palaeobotanical records at their face value, or even sometimes at rather more than their face value. For example, it is unfortunate that an otherwise excellent and valuable analysis of the Polypodiales by de la Sota (1973) is marred by the uncritical assumption that a Triassic record given the name *Polypodites* indicates the existence of Polypodiaceae (sensu stricto) at that time. In consequence, he suggests (l.c., 242) that "The Polypodiaceae would be at least as old as the Dipteridaceae", a conclusion which is certainly contrary to the actual fossil evidence.

The lack of liaison between palaeobotanists and pteridologists can thus lead the latter into regrettable error. However, Dr R.E. Holttum constitutes an extremely distinguished exception to the generally rather indifferent attitude of students of modern ferns towards palaeobotany. Some readers of the Fern Gazette may not know that more than fifty years ago, at the outset of his career, Holttum worked as a palaeobotanist with Seward, and published with him studies on Mesozoic and Tertiary floras, from Rhodesia, Ceylon and Mull (Seward & Holttum, 1921; 1922; 1924). Furthermore, he had the surely unforgettable experience of assisting Seward in the collection of Cretaceous plant fossils in Greenland (Holttum, 1922; Seward, 1926).

Stimulated by Prof. Harris's final comments in his address to the 1972 Symposium at the Linnean Society, and ignoring the warning of a well-known proverb about fools rushing in where angels fear to tread, I have recently (Lovis, in press) attempted to survey the fossil records of early "polypodiaceous" ferns. In consequence, I endorse Harris's opinion that very, very few Mesozoic fossils can be confidently accepted as "polypodiaceous" ferns. Only one such fossil is known from Jurassic rocks. This is *Aspidistes thomasii* Harris*. Holttum has discussed this fossil, albeit briefly, on three occasions (Holttum 1963: 65–67; 1971: 18; 1973b: 177). However, since his opinion of this fern appears to be as yet unappreciated by palaeobotanists (I have yet to see it mentioned in print outside his own publications), I take advantage of this very appropriate opportunity to draw attention here to his comments on this very significant fossil.

Aspidistes thomasii was very well described by Harris (1961) on the basis of material collected by Hamshaw Thomas from the famous Gristhorpe Bed in Cayton Bay, Yorkshire Harris placed it, albeit with reservations, in the family Aspideae (sic.)

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*Another species of *Aspidistes (A. beckerii* Lorch) has been described from Jurassic rocks in Israel (Lorch 1967) but this fossil is quite evidently entirely distinct from *A. thomasii,* and in my opinion is only very doubtfully of "polypodiaceous" character at all. (Lovis, in press).

However, Holttum states (1963: 67) that *"Aspidistes looks like an early Thelypteris".* Of course, Holttum is uniquely well qualified to pronounce on this particular subject, not merely by reason of his early experience as a palaeobotanist but because of his unrivalled knowledge of the Thelypteridaceae, derived from detailed and extensive studies on the family (Holttum, 1954; 1969; 1971; 1973b), in consequence of which he stands without equal as an authority on this group.

To those whose experience of Thelypteridaceae is limited to British taxa, the justification of associating with the Thelypteridaceae *Aspidistes thomasii,* possessing as it does "repeatedly pinnate" fronds with conspicuous and persistent round indusia, may appear rather less than obvious, since our three native species, *Phegopteris connectilis* (Michx.) Watt, *Oreopteris limbosperma* (All.) Holub and *Thelypteris palustris* Schott, all have fronds which are only bipinnatifid, and are either exindusiate, or bear very delicate evanescent indusia. The shape of the pinnules of *A. thomasii* resembles those of species of the tropical and sub-tropical genera *Pseudophegopteris* and *Macrothelypteris.* The total size of the frond of *A. thomasii* is not known, but it may have been large, since the fossil fragments can be well-matched by pinnae of the Malaysian species *M. polypodioides* (Hook.) Holttum (=*Thelypteris leucolepis* (Presl) Ching). They are also close in form to the better known and more widespread *M. torresiana* (Gaud.) Ching (=*T. uliginosa* Ching). In *Macrothelypteris,* the indusia are persistent but small, but large and persistent indusia, comparable to those of *A. thomasii,* are present in some species of *Coryphopteris,* a genus which includes forms which "may represent the most primitive extant members of the family" (Holttum, 1973b: 177). Furthermore, the lamina and indusia of *A. thomasii* bear unicellular glands which are very similar to the glands of *C. viscosa* (Bak.) Holttum. A notable feature of *A. thomasii* is the possession of trilete spores. Holttum has pointed out (1971: 29) that "If, as I believe, Thelypteridaceae have a relationship to *Cyathea,* trilete spores must have been primitive in the family". The spores of modern Thelypteridaceae are almost without exception monolete, but one small living genus, *Trigonospora,* does indeed possess trilete spores, even though it "in other respects is not evidently primitive". (Holttum, 1971: 29).

Thus, though no living thelypteroid possesses all the characteristics of *Aspidistes thomasii,* there is no character of this fossil which cannot be matched somewhere amongst modern Thelypteridaceae, and there appears to be no good reason why it should not itself be regarded as a member of this family. It follows that individual primitive thelypteroid characteristics (i.e., those seen in *A. thomasii*) have been conserved in certain different living genera, namely *Coryphopteris, Macrothelypteris* (and *Pseudophegopteris*) and *Trigonospora.*

Holttum has long since (1947, 1949) argued that the thelypteroids are quite distinct from the dryopteroid ferns, an opinion subsequently clearly endorsed by the cytological evidence (Manton & Sledge, 1954; Walker, 1973). More recently, with the re-unification of the tree-ferns within a single family (Holttum & Sen, 1961), it became evident that the thelypteroids and dryopteroids could not be as widely separate in their points of origin as Holttum had earlier supposed, but he has emphasised (Holttum 1969: 5, 6; 1973a: 5) that he still regards these two groups as having arisen from quite distinct sources within the Cyatheaceae, the Thelypteridaceae being related to *Cyathea,* whereas the origin of the dryopteroids is traced to the vicinity of the Thyrsopteridoideae†.

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†Following Holttum & Sen (1961), *Culcita* (with its possible fossil relatives, e.g. *Coniopteris* spp., cf. Harris, 1961; Holttum 1965: 63) is here included under Thyrsopteridoideae within Cyatheaceae, and therefore excluded from Dennstaedtiaceae, sensu. lato, contrary to Holttum 1947, 1949).

It follows that the detection of a thelypteroid fern in the Jurassic can tell us nothing regarding the emergence of the main radiations of ferns with superficial and indusiate sori. There is in my opinion as yet no convincing fossil example of Dennstaedtiaceae (sensu lato, and therefore including the dryopteroids, e.g., Holttum 1947, 1949) known from the Mesozoic period. The earliest fossil known to me acceptable as a dryopteroid fern is *Dryopteris meeteeseana* Brown, of Palaeocene age (Brown, 1962), though even this example is perhaps more likely to be a tectarioid (Lovis, in press). The evidence is as yet far too fragmentary for conclusions to be drawn, but it is possible that the distinctness of the Thelypteridaceae, already attested by cytology, may in time be further confirmed by this family proving to be of significantly greater age than the dryopteroid ferns.

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A NEW GENERIC SEQUENCE FOR THE PTERIDOPHYTE HERBARIUM

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ABSTRACT

In a preamble to Index Filicum, Christensen (1906) listed a classification scheme of 136 genera which was based on that of Engler & Prantl (1898—1902) and which he considered worthy of recognition. This arrangement, already accepted in principle by the older herbaria, was accepted and adopted for the next 30 to 40 years wherever curators required a systematic (phylogenetic) order for the ferns. In 1938 Christensen revised his 1906 classification and there followed at least ten other proposals by other workers putting foward phylogenetic schemes. The scheme presented here is the result of discussions with a large number of pteridologists in the course of rearranging the pteridophytes at the British Museum and New York Botanical Garden.

INTRODUCTION

The diversity of opinion and lack of consensus on a taxonomic treatment of the ferns causes problems for all devising a useable herbarium arrangement or for that matter for those wishing to arrange fern data systematically in any other data bank, e.g., a computer, visual card index, etc. The authors have been wrestling with the problem of the most suitable arrangement for the large fern collections at their institutions and had to answer the following questions: should the herbarium curator follow a traditional treatment until the dust of disagreement settles; or is consensus just around the corner and can we devise a new arrangement.

The history of fern classification from that of Smith (1793, 1810) onwards has been reviewed by Pichi Sermolli (1973). Whilst some early curators used Presl (1836, 1845), possibly the most widely accepted, if not the most important classification, was that used by Engler & Prantl (1898—1902). The Polypodiaceae s.l. account (pp 139—339) was written by Diels who devised a classification of nine tribes based on sorus structure. The Engler and Prantl system was adopted by Christensen in the preamble to his *Index Filicum* (Christensen 1906). For the next thirty years writers and curators alike followed this arrangement in spite of its unnatural sequence of families and misconception and incorrect systematic position of some genera. Diels attempted to show fern relationships as he saw them, but in light of our present knowledge, his is now quite misleading. For example, the genera *Dennstaedtia, Hypolepis* and *Pteridium* are situated far apart in the Diels scheme yet today we know that they are closely related; *Dryopteris* includes most of the thelypterids along with *Ctenitis* and other genera generally recognised as distinct today; the woodsioid ferns are apart from other athyrioids and are placed near the tree ferns; *Nephrolepis* is separated from the other davallioids. In 1938 Christensen revised his 1906 outline (slightly changed by him in 1934) in view particularly of the work of Bower (1923—28). Since 1940 no fewer than ten botanists have proposed phylogenetic schemes for the ferns (Ching 1940, Dickason 1946, Copeland 1947, Holttum 1947, 1949, 1973a, Pichi Sermolli 1958, Mehra 1961, Sporne 1962, Wagner 1969, Nayar 1970, Mickel 1973, 1974). As in any group involving the activity of many workers, there results a great diversity of opinion on the taxonomic arrangement within that group. This wide assortment of treatments includes examples of strong taxonomic amalgamation to extreme fragmentation. The most severe disagreement at the family level centres around the Polypodiaceae which has been maintained traditionally as a single family or divided into as many as 33 families (Ching 1940). A significant contribution to a phylogenetic arrangement of the Polypodiaceae was made by Holttum (1947, 1949). At the same time Copeland (1947) produced his *Genera Filicum,* again presenting a new arrangement in places misleading with unnatural groupings. Furthermore, the past 25 years have been marked by intensive research on the ferns and fern allies. Much of this was triggered by Manton's classic cytological work (1950), but studies have proceeded in many other directions, including anatomy, chemistry, genetics, physiology, development and palynology. Some of these studies have merely used ferns as research tools (Mickel 1971) but others have contributed substantially to a better understanding of the relationships of ferns. These advances have been well summarised in three recent symposia (Tryon 1971, Jermy, Crabbe & Thomas 1973, Taylor & Mickel 1974).

We should like to suggest that an arrangement of taxa in an herbarium might take any form, and selection of a system should be dictated by its primary users. Thus, a small regional herbarium where all the genera are known might find it most practical to maintain the ferns alphabetically by genus or according to a local Flora or monograph; other herbaria may wish to keep a well-established arrangement simple because the primary users of the herbarium know where everything is placed. It is our feeling that a large collection that is used daily for identification, floristic, or monographic purposes should be arranged to reflect relationships in the best way possible. Proximity of related plants is essential to facilitate consultation during identification. It enables a floristician or monographer to better see the boundaries between genera and to find valuable materials filed in related groups.

An alternative to a phylogenetic scheme is an alphabetical system. It has the advantage of ease of filing by untrained personnel and the ease of finding genera by visitors to the herbarium. However, the system is fixed in a most awkward manner. Generic names cannot be readily brought up-to-date without major reorganisation to the herbarium or an elaborate cross-reference system. Related genera cannot readily be compared since the alphabetical system separates without bias all genera from their relatives. Such a system may be useful in certain herbaria where there is no pteridologist or, as suggested above, where the collection is very small.

In preparing the following system we have tried to incorporate the most recent evidence bearing on phylogeny, including gross morphology, cytology, anatomy, gametophytes, palynology, and chemistry. We have conferred with specialists of as many groups as possible to get their opinions on particular problems and with leading pteridologists throughout the world. We wish to thank all who have provided us with valuable information and suggestions but emphasise that we alone are responsible for any errors or misconceptions that time may show to have crept in.

We feel that the family concept is still in a state of flux and requires considerable monographic work at the species and genus level before further conclusions should be drawn. Family and subfamily headings are given solely to indicate the general systematic layout. As Christensen (1938: 525) pointed out "the linear sequence of families and genera moreover gives no clear idea of the highly interwoven phylogeny of recent ferns and it is perhaps impossible to demonstrate to others the reticulated phylum as it appears to the trained taxonomist". It is appreciated that the sequence of these major units can vary according to the phylogenetic route taken. We have done our best to place related groups of genera in justaposition.

Numbering and layout of the list

Mostly we have followed the concepts of higher taxa generally agreed by pteridologists but feel that a hierachical layout as proposed here shows relationships more clearly. For this reason we have adopted the oldest family name available, as demanded by the *Code,* and have formalised certain subfamily names where necessary.

Each family and subfamily unit is separated by a solid line. Where we think such units could be divided, a broken line has been inserted. As the emphasis in this treatment is on the genus, the families and subfamilies are not numbered. The numbers are thus consecutive throughout the list; new genera or curatorial units may be added as a number following a point, i.e. using an extended decimal system.

Certain of the generic names are indented. These are (i) genera which have been segregated, often on a regional basis (e.g. Ching 1954) and with an incomplete knowledge of the group, and which we feel are in need of revision; (ii) genera now regarded as giving a more constructive picture of the classification of a major group hitherto (and by some pteridologists, still) regarded under a single genus (e.g. *Thelypteris, Cyathea*); (iii) genera morphologically distinct and traditionally accepted as separate but which recent studies have shown to be genetically close (e.g. *Asplenium*); or (iv) where we feel further studies will reveal closer associations or new generic limits within the group. The indented names have been given a full number in the sequence of genera to avoid complicating the system. Should certain indented (or non-indented for that matter) genera be not accepted in a system the numbers can be omitted or placed in brackets (e.g. 288 (289–294) *Asplenium*) or, if the species group (genus) is accepted at a curatorial level (as subgenus or section) within the aggregate genus, the number may follow in brackets e.g. 288 (289) *Asplenium* (sect. *Camptosorus*). It should be noted that these names are legitimate generic names and *not* subgeneric and if the latter rank is used there may be a prior name at that rank; e.g. in the case of *Ctenopteris* if placed as a subgenus of *Grammitis* the name *Cryptosorus* must be used.

We have listed the genera in the following assemblages:

1. Fern allies.
2. Eusporangiate ferns (Ophioglossales, Marattiales, Osmundales) and Plagiogyriales.
3. Schizaeoid ferns ⟶ adiantoid ferns

   Note: Initially we tried to place all the traditional Polypodiaceae *sens. lat.* together for those curators who do not wish to make sweeping changes. However we believe — and there is an increasing opinion accepting — the adiantoid ferns to be a distinct group arising from schizaeaceous stock.
4. The filmy ferns and related groups

   Note: generic concepts in the Hymenophyllaceae will remain in a state of flux until a large-scale monograph is carried out. We have followed Morton (1968) in arrangement and taxonomy excepting that we have accepted his Sections at generic rank for those wishing to break down the large umbrella genera of *Trichomanes* and *Hymenophyllum.* In those five cases where no generic name exists we have used the Sectional name followed by *(pro sectione)* rather than make a new combination and status for a Section which may on further study remain at that, or even be reduced in, rank.
5. Gleichenioid ferns ⟶ polypodioids and grammitid ferns, by way of *Matonia, Cheiropleuria* and *Dipteris.*

6. Proto-cyatheoid and cyatheoid ferns → dennstaedtioid → thelypterid → asplenioid ferns, the "Aspidiales" and the blechnoid ferns.
7. Hydropterides
   Note: We place the water ferns here not because we feel they are related to each other, but out of convenience. They are quite distinct and there is no firm data to justify placing them elsewhere.

SYSTEMATIC LIST OF PTERIDOPHYTE GENERA

Psilotaceae	001	Psilotum
	002	Tmesipteris
Lycopodiaceae	003	Lycopodium
	004	Lycopodiella
	005	Diphasium
	006	Huperzia
	007	Phylloglossum
Selaginellaceae	008	Selaginella
Isoetaceae	009	Isoetes
	010	Stylites
Equisetaceae	011	Equisetum
Ophioglossaceae	012	Botrychium
	013	Botrypus
	014	Sceptridium
	015	Helminthostachys
	016	Ophioglossum
	017	Cheiroglossum
	018	Rhizoglossum
Marattiaceae	019	Angiopteris
	020	Archangiopteris
	021	Protomarattia
	022	Marattia
	023	Macroglossum
	024	Danaea
	025	Christensenia
Osmundaceae	026	Osmunda
	027	Osmundastrum
	028	Plenasium
	029	Todea
	030	Leptopteris
Plagiogyriaceae	031	Plagiogyria
Schizaeaceae	032	Schizaea
	033	Actinostachys
	034	Lygodium
	035	Anemia
	036	Mohria
Parkeriaceae	037	Ceratopteris
Platyzomataceae	038	Platyzoma
Adiantaceae: Adiantoideae	039	Actiniopteris

Adiantaceae: Adiantoideae *(continued)*

- 040 Afropteris
- 041 Ochropteris
- 042 Anopteris

- 043 Onychium
- 044 Cryptogramma
- 045 Llavea

- 046 Neurosoria

- 047 Cheilanthes
  - 048 Adiantopsis
  - 049 Aleuritopteris
  - 050 Aspidotis
  - 051 Cheiloplecton
  - 052 Mildella
- 053 Notholaena
  - 054 Argyrochosma (pro sectione)
- 055 Sinopteris
- 056 Negripteris

- 057 Pellaea
- 058 Doryopteris
- 059 Ormopteris
- 060 Saffordia

- 061 Trachypteris

- 062 Anogramma
- 063 Pityrogramma
  - 064 Trismeria
- 065 Pleurosoriopsis

- 066 Hemionitis
  - 067 Gymnopteris
- 068 Bommeria
- 069 Paraceterach

- 070 Pterozonium
  - 071 Syngrammatopteris
- 072 Jamesonia
- 073 Eriosorus
- 074 Nephopteris

- 075 Syngramma
  - 076 Craspedodictyum
  - 077 Toxopteris
- 078 Austrogramme

- 079 Taenitis
  - 080 Platytaenia
  - 081 Holttumiella

- 082 Coniogramme

- 083 Aspleniopsis
- 084 Rheopteris
- 085 Cerosora

- 086 Adiantum

Adiantaceae:	Vittarioideae	087	Antrophyum	
		088		Polytaenium
		089		Scoliosorus
		090	Anetium	
		091	Hecistopteris	
		092	Ananthacorus	
		093	Vittaria	
		094	Monogramma	
		095	Vaginularia	
	Pteridoideae	096	Pteris	
		097	Idiopteris	
		098	Copelandiopteris	
		099	Neurocallis	
		100	Acrostichum	
Loxsomaceae		101	Loxsoma	
		102	Loxsomopsis	
Hymenophyllaceae		103	Hymenoglossum	
		104	Serpyllopsis	
		105	Rosenstockia	
		106	Hymenophyllum	
		107		Buesia
		108		Meringium
		109		Eupectinum (pro sectione)
		110		Myriodon
		111		Sphaerocionium
		112		Apteropteris
		113		Craspedophyllum
		114		Hemicyatheon
		115		Mecodium
		116	Cardiomanes	
		117	Trichomanes	
		118		Lacosteopsis (pro sectione)
		119		Crepidomanes
		120		Polyphlebium
		121		Reediella
		122		Abrodictyum
		123		Pleuromanes
		124		Gonocormus
		125		Selenodesmium
		126		Davalliopsis
		127		Cephalomanes
		128		Callistopteris
		129		Nesopteris
		130		Didymoglossum
		131		Microgonium
		132		Lecanolepis
		133		Achomanes (pro sectione)
		134		Neuromanes
		135		Odontomanes
		136		Lacostea
		137		Trigonophyllum (pro sectione)
		138		Homoeotes
		139		Feea
		140		Ragatelus

Hymenosphyllaceae *(continued)*		141		Acarpacrium (pro sectione)
Hymenophyllopsidaceae		142	Hymenophyllopsis	
Stromatopteridaceae		143	Stromatopteris	
Gleicheniaceae		144	Gleichenia	
		145	Diplopterygium	
		146	Sticherus	
		147	Dicranopteris	
		148		Acropterygium
Matoniaceae		149	Matonia	
		150	Phanerosorus	
Cheiropleuriaceae		151	Cheiropleuria	
Dipteridaceae		152	Dipteris	
Polypodiaceae:	Drynarioideae	153	Drynaria	
		154	Photinopteris	
		155	Merinthosorus	
		156	Aglaomorpha	
		157		Dryostachyum
		158		Holostachyum
		159		Drynariopsis
		160		Pseudodrynaria
		161	Thayeria	
	Platycerioideae	162	Platycerium	
		163	Pyrrosia	
		164	Saxiglossum	
		165	Drymoglossum	
	Microsorioideae	166	Microsorum	
		167		Dendroconche
		168		Phymatosorus
		169		Lecanopteris
		170		Colysis
		171	Podosorus	
		172	Diblemma	
		173	Leptochilus	
		174		Paraleptochilus
		175		Dendroglossa
		176	Christiopteris	
		177	Pycnoloma	
		178	Grammatopteridium	
		179	Oleandropsis	
		180	Holcosorus	
		181	Crypsinus	
		182	Selliguea	
		183	Arthromeris	
		184	Polypodiopteris	
	Pleopeltoideae	185	Pleopeltis	
		186		Microgramma
		187		Anapeltis
		188		Craspedaria
		189	Solanopteris	
		190	Marginariopsis	

Polypodiaceae:	Pleopeltoideae *(continued)*	191	Neurodium	
		192	Neolepisorus	
		193	Lemmaphyllum	
		194	Drymotaenium	
		195	Paragramma	
		196	Belvisia	
		197	Dicranoglossum	
		198	Neocheiropteris	
	Polypodioideae	199	Niphidium	
		200		Pessopteris
		201	Campyloneurum	
		202	Anapausia	
		203	Dictymia	
		204	Phlebodium	
		205	Synammia	
		206	Polypodium	
		207		Goniophlebium
		208		Thylacopteris
		209		Marginaria
Grammitidaceae		210	Grammitis	
		211		Xiphopteris
		212		Ctenopteris
		213	Calymmodon	
		214	Acrosorus	
		215	Amphoradenium	
		216	Prosaptia	
		217	Glyphotaenium	
		218	Oreogrammitis	
		219	Nematopteris	
		220	Scleroglossum	
		221	Cochlidium	
		222	Hyalotricha	
		223	Loxogramme	
		224	Anarthropteris	
Metaxyaceae		225	Metaxya	
Lophosoriaceae		226	Lophosoria	
Cyatheaceae		227	Cnemidaria	
		228	Cyathea	
		229		Trichopteris
		230		Nephelea
		231		Alsophila
		232		Sphaeropteris
		233	Dicksonia	
		234	Cystodium	
Thyrsopteridaceae		235	Thyrsopteris	
		236	Culcita	
		237	Cibotium	
Dennstaedtiaceae:	Dennstaedtioideae	238	Dennstaedtia	
		239	Microlepia	
		240		Oenotrichia
		241		Leptolepia

Dennstaedtiaceae:	Dennstaedtioideae *(continued)*	242	Hypolepis	
		243	Paesia	
		244	Pteridium	
		245	Histiopteris	
		246		Lepidocaulon
		247	Lonchitis	
		248	Blotiella	
		249	Saccoloma	
		250		Orthiopteris
	Monachosoroideae	251	Monachosorum	
	Lindsaeoideae	252	Lindsaea	
		253		Humblotiella
		254		Sambirania
		255	Ormoloma	
		256	Sphenomeris	
		257	Odontosoria	
		258	Tapeinidium	
		259	Xyropteris	
Thelypteridaceae		260	Thelypteris	
		261		Amauropelta
		262		Phegopteris
		263		Pseudophegopteris
		264		Cyclogramma
		265		Parathelypteris
		266		Coryphopteris
		267		Macrothelypteris
		268		Oreopteris
		269		Metathelypteris
		270		Cyclosorus
		271		Trigonospora
		272		Pronephrium
		273		Mesophlebion
		274		Plesioneuron
		275		Glaphyropteridopsis
		276		Chingia
		277		Haplodictyum
		278		Nannothelypteris
		279		Stegnogramma
		280		Steiropteris
		281		Sphaerostephanos
		282		Ampelopteris
		283		Goniopteris
		284		Meniscium
		285		Pneumatopteris
		286		Christella
		287		Amphineuron
Aspleniaceae:	Asplenioideae	288	Asplenium	
		289		Camptosorus
		290		Phyllitis
		291		Ceterach
		292		Ceterachopsis
		293		Pleurosorus
		294		Loxoscaphe
		295	Diellia	
		296	Holodictyum	
		297	Antigramma	

Aspleniaceae: Asplenioideae *(continued)*	298	Diplora	
	299	Schaffneria	
	300	Boniniella	
Athyrioideae	301	Matteuccia	
	302	Onoclea	
	303	Onocleopsis	
	304	Athyrium	
	305	Cornopteris	
	306	Rhachidosorus	
	307	Diplazium	
	308		Monomelangium
	309		Callipteris
	310		Allantodia
	311		Diplaziopsis
	312		Dictyodroma
	313	Anisocampium	
	314	Hemidictyum	
	315	Gymnocarpium	
	316	Cystopteris	
	317		Acystopteris
	318		Cystoathyrium
	319	Woodsia	
	320	Lunathyrium	
	321		Dryoathyrium
	322		Athyriopsis
	323	Adenoderris	
	324	Cheilanthopsis	
	325	Hypodematium	
	326	Kuniwatsukia	
Tectarioideae	327	Trichoneuron	
	328	Ctenitis	
	329	Ctenitopsis	
	330	Lastreopsis	
	331	Psomiocarpa	
	332	Atalopteris	
	333	Pleocnemia	
	334	Arcypteris	
	335	Pteridrys	
	336	Dryopolystichum	
	337	Tectaria	
	338		Luerssenia
	339	Pseudotectaria	
	340	Hemigramma	
	341	Quercifilix	
	342	Cionidium	
	343	Tectaridium	
	344	Fadyenia	
	345	Pleuroderris	
	346	Hypoderris	
	347	Amphiblestra	
	348	Dictyoxiphium	
	349	Camptodium	
	350	Stenosemia	

Aspleniaceae:	Tectarioideae *(continued)*	351	Heterogonium
		352	Cyclopeltis
		353	Didymochlaena
	Dryopteridoideae	354	Peranema
		355	Diacalpe
		356	Polystichum
		357	Papuapteris
		358	Plecosorus
		359	Cyclodium
		360	Cyrtomium
		361	Cyrtomidictyum
		362	Cyrtogonellum
		363	Phanerophlebia
		364	Arachniodes
		365	Polystichopsis
		366	Lithostegia
		367	Polybotrya
		368	Maxonia
		369	Dryopteris
		370	Nothoperanema
		371	Stigmatopteris
		372	Acrophorus
		373	Stenolepia
	Lomariopsidoideae	374	Bolbitis
		375	Egenolfia
		376	Thysanosoria
		377	Arthrobotrya
		378	Teratophyllum
		379	Lomagramma
		380	Lomariopsis
	Elaphoglossoideae	381	Elaphoglossum
		382	Peltapteris
		383	Microstaphyla
Davalliaceae:	Davallioideae	384	Humata
		385	Trogostolon
		386	Scyphularia
		387	Parasorus
		388	Davallia
		389	Davallodes
		390	Paradavallodes
		391	Araiostegia
		392	Leucostegia
		393	Gymnogrammitis
		394	Rumohra
	Oleandroideae	395	Oleandra
		396	Arthropteris
		397	Psammiosorus
		398	Nephrolepis
Blechnaceae		399	Blechnum
		400	Salpichlaena
		401	Doodia

Blechnaceae *(continued)*	402	Brainea
	403	Sadleria
	404	Woodwardia
	405	Anchistea
	406	Chieniopteris
	407	Lorinseria
	408	Pteridoblechnum
	409	Stenochlaena
Marsileaceae	410	Marsilea
	411	Regnellidium
	412	Pilularia
Salviniaceae	413	Salvinia
Azollaceae	414	Azolla

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APPENDIX I

Summary of the families and sub-families used in this paper

Adiantaceae (C. Presl) Ching in *Sunyatsenia 5:* 229 (1940). Bas. Filicineae trib. Adiantaceae C. Presl, *Tent. Pterid.* 139 (1836).

Subfam. Adiantoideae

Subfam. **Pteridoideae** C. Chr. ex Crabbe, Jermy & Mickel **subfam. nov.**

Syn.: *Polypodiaceae* subfam. *Pteridoideae* C. Chr. in Verdoorn, *Man. Pterid.* 536 (1938) pro parte; sine descr. lat.

Filices terrestres, rhizomate erecto vel repente plerumque solenostelico saepe perforato vel vere dictyostelico paleis induto. Frondes homomorphae tripartitaeque vel dimorphae pinnataeque, venis liberis vel anastomosantibus sine venulis inclusis. Sori marginales coenosori facientes, portati in commissura vasculare (qua extremitates venarum conjuncta sunt), margine folii membranaceo reflexo obtecti; vel sori faciens coenosorum super totam paginam sine receptaculo extendentem vel in receptaculo intramarginali inter venas positum. Sporae triletae raro monoletae perispora praeditae. Chromosomata $x = 29, 30$.

Typus: *Pteris* L., *Sp. Pl.* 2: 1073 (1753).

Subfam. **Vittarioideae** (C. Presl) Crabbe, Jermy & Mickel **stat. nov.**

Basionym: *Filicaceae* tribus *Vittariaceae* C. Presl, *Tent. Pterid.* 164 (1836) pro parte.

Syn.: *Polypodiaceae* subfam. *Vittarioideae* C. Chr. in Verdoorn, *Man. Pterid.* 539 (1938) sine descr. lat.; *Vittariaceae* (C. Presl) Ching emend. in *Sunyatsenia 5:* 232 (1940).

Aspleniaceae Mett. ex Frank in Leunis, *Syn. Pflanzenk.*, ed. 2, *3:* 1465 (1877).

Subfam. Asplenioideae.

Subfam. Athyrioideae Holttum ex Nayar in *Taxon 19:* 235 (1970) sub *Dryopteridaceae.*

Subfam. Dryopteridoideae Holttum ex Nayar in *Taxon 19:* 235 (1970) pro parte, sub *Dryopteridaceae.*

Subfam. **Elaphoglossoideae** (Pichi Serm.) Crabbe, Jermy & Mickel **stat. nov.**

Basionym: *Elaphoglossaceae* Pichi Serm. in *Webbia 23:* 209 (1968).

Syn.: *Polypodiaceae* subfam. *Elaphoglossoideae* C. Chr. in Verdoorn, *Man. Pterid.:* 549 (1938), sine descr. lat.

Subfam. **Lomariopsidoideae** (Alston) Crabbe, Jermy & Mickel **stat. nov.**

Basionym: *Lomariopsidaceae* Alston in *Taxon 5:* 25 (1956), excl. *Elaphoglossum.*

Syn.: *Dennstaedtiaceae* subfam. *Lomariopsidoideae* Holttum in *J. Linn. Soc. Lond., Bot., 53:* 146 (1947), sine descr. lat., excl. *Elaphoglossum.*

Subfam. Tectarioideae Holttum ex Nayar in *Taxon 19:* 235 (1970) sub *Dryopteridaceae.*

Azollaceae Wettstein, *Handb. Syst. Bot. 2:* 77 (1903).

Blechnaceae (C. Presl) Copeland, *Gen. Fil.* 155 (1947).

Cheiropleuriaceae Nakai, in *Bot. Mag., Tokyo 42:* 210 (1928).

Cyatheaceae Kaulfuss, *Wesen Farrenkr.* 119 (1827).

Davalliaceae Mett. ex Frank in Leunis, *Syn. Pflanzenk.*, ed. 2, *3:* 1474 (1877).

Subfam. Davallioideae.

Subfam. **Oleandroideae** (Ching ex Pichi Serm.) Crabbe, Jermy & Mickel, **stat. nov.**

Basionym: *Oleandraceae* Ching ex Pichi Serm. in *Webbia 20:* 745 (1965).

Syn.: *Polypodiaceae* subfam. *Oleandroideae* C. Chr. in Verdoorn, *Man. Pterid.* 365 (1938), sine descr. lat.; *Oleandraceae* Ching in *Sunyatsenia 5:* 221 (1940), sine descr. lat.; *Dennstaedtiaceae* subfam. *Oleandroideae* Holttum in *J. Linn. Soc. Lond., Bot. 53:* 137 (1947), sine descr. lat.; *Davalliaceae* subfam. *Oleandroideae* (C. Chr.) Tindale in *Contr. N.S. Wales Nat. Herb., Fl. Ser. 208:* 7 (1961), comb. illeg.

Dennstaedtiaceae Pichi Serm. in *Webbia 24:* 704 (1970).

Subfam. Dennstaedtioideae

Subfam. **Lindsaeoideae** (Pichi Serm.) Crabbe, Jermy & Mickel, **stat. nov.**

Basionym: *Lindsaeaceae* Pichi Serm. in *Webbia 24:* 707 (1970).

Syn.: *Polypodiaceae* subfam. *Lindsayoideae* C. Chr. in Verdoorn, *Man. Pterid:* 535 (1938), sine descr. lat.; *Dennstaedtiaceae* subfam. *Lindsayoideae* Holttum in *J. Linn. Soc. Lond., Bot. 53:* 134 (1947), sine descr. lat.

Subfam. **Monachosoroideae** Crabbe, Jermy & Mickel, **subfam. nov.**

Filices terrestres, rhizomate ascendenti vel erecto dictyostelico, sine paleis sed frondibus caulibusque juvenilibus muco et pilis minutissimis indutis. Frondes pinnatae ad quadripinnatae, homomorphae, non articulatae; stipes mucilaginus hirsutus, duobus fasciculis vasorum ut in *Athyrio;* lamina tenuis in statu vivo fere pellucida sed in siccitate impellucida, venis liberis. Sori superficiales, ad apices venarum terminales saepe ex sporangiis paucis constantes, exindusiati. Sporae triletae perispora praeditae. Chromosomata $x = 56$.

Typus: *Monachosorum* Kunze in Bot. Zeit. 6: 119 (1848).

Syn.: *Monachosoraceae* Ching in Sunyatsenia 5: 241 (1940), sine descr. lat.

Dipteridaceae (Diels in Engler & Prantl) Seward & Dale in *Philos. Trans. Roy. Soc. Lond. ser. B. 194:* 487, 499, 502 (1901).

Bas. *Polypodiaceae* trib. *Aspidieae* subtrib. *Dipteridinae* Diels in Engler & Prantl, *Nat. Pflanzenfam. 1(4):* 167, 202 (1899).

Equisetaceae Rich. ex DC. in Lam. & D.C., *Fl. Franc. ed. 3. 2:* 580 (1805).

Gleicheniaceae (R. Br.) C. Presl, *Rel. Haenk. 1(1):* 70 (1825).

Grammitidaceae (C. Presl) Ching, *Sunyatsenia 5:* 264 (1940) ("Grammitaceae").

Bas. Filicaceae trib. Grammitaceae Presl, *Tent. Pterid.* 205 (1836).

Hymenophyllaceae Link, *Handb. Erken. Gew. 3:* 36 (1833) ("Hymenophylleae").

Hymenophyllopsidaceae Pichi Serm. in *Webbia 24:* 712 (1970).

Isoetaceae Dumontier, *Anal. Fam. Pl.* 67 (1829) ("Isoetineae").

Lophosoriaceae Pichi Serm. in *Webbia 24:* 700 (1970).

Loxsomaceae C. Presl, *Gefassb. Stip. Farrn.* 31 (1847).

Lycopodiaceae P. Beauv. ex Mirbel in Lamarck & Mirbel, *Hist. Nat. Veg. 4:* 293 (1802) ("Lycopodia").

Marattiaceae Berchtold & J.S. Presl, *Prirozen. Rostl. 1:* 272 (1820) ("Marattiae").

Marsileaceae Mirbel in Lamarck & Mirbel, *Hist. Nat. Veg. 5:* 126 (1802) ("Marsileae").

Matoniaceae C. Presl, *Gefassb. Stip. Farrn* 32 (1847).

Metaxyaceae Pichi Serm. in *Webbia 24:* 701 (1970).

Ophioglossaceae (R. Br.) Agardh, *Aphor. Bot. 8:* 113 (1822).

Bas. Filices trib. Ophioglosseae R. Br., *Prodr. Fl. Nov. Holl.* 163 (1810).

Osmundaceae Berchtold & J.S. Presl, *Prirozen Rostl. 1:* 272 (1820).

Parkeriaceae Hooker, *Exot. Fl. 2(20):* t. 147 (1825).

Plagiogyriaceae Bower, *Ann. Bot. 40:* 484 (1926).

Platyzomataceae Nakai, *Bull. natn. Sci. Mus. Tokyo 29:* 4 (1950).

Polypodiaceae Berchtold & J.S. Presl, *Prirozen Rostl. 1:* 272 (1820).

Subfam. Polypodioideae

Subfam. **Drynarioideae** Crabbe, Jermy & Mickel, **subfam. nov.**

Filices epiphyticae; rhizoma saepe crassum, carnosum, lepidotum, raro tenue glabrescensque. Frondes glanduliferae, cum rhizomate non vere articulatae, saepe eimorphae vel basibus frondium scariosis per humi collectionem praesertim mutatis (quamobrem frondes nidi vel cornucopiae faciunt); pinnae vel segmenta frondium normalium (i.e. frondium foliacearum) semper ab rhachide caducae, textura coriacea herbaceave, venis conspicuis reticulatis areolatis venulis inclusis. Sori ad compitum venarum punctati vel coenosori facientes; parphyses desunt. Sporae monoletae; plerumque perisporae desunt. Chromosomata *x* 36, 37.

Typus: *Drynaria* (Bory, *pro sectione Polypodii* in *Ann. Sci. nat. 5:* 464) J. Smith in *J. Bot. Lond.* 4: 60 (1841).

Subfam. *Microsorioideae* Nayar in *Taxon 19:* 233 (1970).

Subfam. *Platycerioideae* Nayar in *Taxon 19:* 233 (1970).

Subfam. *Pleopeltoideae* Nayar in *Taxon 19:* 234 (1970).

Psilotaceae Kanitz, *Novenyrends. Attek.* 43 (1887).

Salviniaceae Dumortier, *Anal. Fam. Pl.* 67 (1829).

Schizaeaceae Kaulfuss, *Wesen Farrenkr.* 119 (1829).

Selaginellaceae Willkomm in Willkomm & Lange, *Prodr. Fl. Hisp. 1(1):* 14 (1861).

Stromatopteridaceae (Nakai) Bierhorst in *Phytomorphology 18:* 263 (1968).

Bas. Gleicheniaceae subfam. Stromatopteridoideae Nakai in *Bull. natn. Sci. Mus. Tokyo 29:* 32 (1950).

Thelypteridaceae Ching ex Pichi Serm. in *Webbia:* 709 (1970).

Thyrsopteridaceae C. Presl, *Gefassb. Stip. Farrn,* 38 (1847) [*Abh. K. Bohm. Ges. Wiss., ser 5, 5:* 346 (1848)].

APPENDIX 2

Generic names. This list is based on Holttum (1966, 1973b) and in the majority of cases we have accepted the concepts of Holttum with regard to the synonymy. Some names of minimal importance (e.g. orthographic variants) have not been included because this list is primarily a working list for herbarium curators. Those genera asterisked are nomina conservanda.

Abacopteris Fée = 272
Abrodictyum Presl 122
Aconiopteris Presl = 381
Acropelta Nakai = 356
Acrophorus Presl 372
Acropteris Link = 288
Acropterygium (Diels)Nakai 148
Acrorumohra (H.Itô)H.Itô = 369
Acrosorus Copel. 214
Acrostichum L. 1010
Actiniopteris Link 039
Actinophlebia Presl = 227
Actinostachys Wall. 033
Acystopteris Nakai 318
Adectum Link = 238
Adenoderris J.Smith 323
Adenophorus Gaud. = 215
Adiantopsis Fée 048
Adiantum L. 087
Aetopteron Ehrh. = 356
Afropteris Alston 040
Aglaomorpha Schott 156
Alcicornium Gaud. = 162
Aleuritopteris Fée 049
Allantodia R.Br.(1810) = 307
Allantodia Wall.(1830) = 311
Allosorus Bernh. = 047
Allosorus auctt. = 044
Allostelites Börner = 011

Alsophila R.Br. 231
Amauropelta Kunze 261
Amblia Presl = 363
Amesium Newm. = 288
Ampelopteris Kunze 282
Amphiblestra Presl 347
Amphicosmia Gardn. = 231
Amphidesmium J.Smith = 225
Amphineuron Holtt. 287
Amphipterum Presl = 115
Amphisoria Trev. = 331
Amphoradenium Desv. 215
Ananthacorus Underw. & Maxon 092
Anapausia Presl 202
Anapeltis J.Smith = 186
Anarthropteris Copel. 224
Anaxetum Schott = 200
Anchistea Presl 405
Aneimia Sw.corr.Kaulf. = 035
Aneimiaebotrys Fée = 035
Aneimidictyon J.Smith corr.C.Chr.= 034
*Anemia Sw. 035
Anemidictyon J.Smith = 035
Anemirhiza J.Smith = 035
Anetium (Kunze)Splitg. 091
Angiopteris Adans. (1763) = 302
*Angiopteris Hoffm.(1796) 019
Anisocampium Presl 313
Anisogonium Presl 307

Anisosorus Trev.(nomen) = 247
Anogramma Link 062
Anopteris (Prantl)Diels 042
Antigramma Presl 297
Antiosorus Roemer 247
Antrophyum Kaulf. 087
Apalophlebia Presl = 163
Aphyllocalpa Cav. 026
Apteropteris (Copel.)Copel. 112
Arachniodes Blume 363
*Araiostegia Copel. 391
Archangiopteris Christ & Giesenhagen 020
Arcypteris Underw. 334
Argyrochosma (J.Smith)Pic.Ser. 054
Aropteris Alston (sphalm.) = 040
Arthrobotrya J.Smith 377
Arthrobotrys Wall.(nomen) = 369
Arthromeris (Moore)J.Smith 183
Arthropteris J.Smith 306
Aspidotis (Nutt.)Copel. 050
Aspidium Sw. = 337
Asplenicystopteris P.Fourn. = 316
Asplenidictyum J.Smith = 288
Aspleniopsis Mett. 083
Asplenium L. 288
Asplenoceterach D.E.Meyer 288 × 291
Asplenophyllitis Alston 288 × 290
Asplenosorus Wherry 288 × 289
Asteroglossum J.Smith (nomen) = 165
Atalopteris Maxon & C.Chr. 332
Athyriopsis Ching 322
Athyrium Roth 304
Austrogramme Fourn. 078
Azolla Lam. 414

Bakeriopteris O.Ktze = 058
Balantium Kaulf. = 233
Balantium auctt. = 236
Bathmium Link = 337
Belvisia Mirbel 196
Bernhardia Willd. = 001
Blechnidium Moore = 399
Blechnopsis Presl = 399
Blechnopteris Trev.(nomen) = 399
Blechnum L. 399
Blotiella Tryon 248
Bolbitis Schott 374
Bommeria Fourn. 068
Boniniella Hayata 300
Boschia Copel. (nom.prov) = 115?
Botrychium Sw. 012
Botryogramme Fée = 045
Botryopteris Presl = 015
Botrypus Richard 013
Bowringia Hooker = 402
Brachysorus Presl = 304
Brainea J.Smith 402
Buesia (Morton)Copel. 107
Byrsopteris Morton = 364

Caenopteris Bergius = 288
Calamaria Boehm. = 009
Calamistrum O.Ktze = 412
Callipteris Bory 309
Callistopteris Copel. 128
Callogramme Fée = 075
Calymella Presl = 144
Calymmodon Presl 213
Calypterium Bernh. = 302
Campium Presl = 374
Campteria Presl = 096
Camptodium Fée 349
Camptosorus Link 289
Campyloneurum Presl 201
Campylogramma v.A.v.R. = 166
Candollea Mirbel = 163
Cardiochlaena Fée = 337
Cardiomanes Presl 116
Carpanthus Rafin. = 414
Carpogymnia Löve & Löve = 315
Cassebeera Kaulf. = 059
Cephaloceraton Genn. = 009
Cephalomanes Presl 127
Ceratodactylis J.Smith = 045
Ceratopteris A.Brongn. 037
Ceropteris Link = 063
Cerosora Bak. 085
Ceterac Adans. = 288
*Ceterach Lam. & DC. 291
Ceterachopsis (J.Smith)Ching 292
Chamaeclinis Mart.(nomen) = 003
Chamaefilix Hill = 292
*Cheilanthes Sw. 047
Cheilanthopsis Hieron. 324
Cheilogramma (Bl.)Maxon = 191
Cheilolepton Fée = 379
Cheiloplecton Fée 051
Cheilosoria Trev. = 047
Cheiroglossa Presl 017
Cheiropleuria Presl 151
Cheiropteris Christ = 198
Chieniopteris Ching 406
Chingia Holtt. 276
Chnoophora Kaulf. = 229
Choristosoria Mett. = 057
Chorizopteris Moore = 379
Christella Lév.emend.Holtt. 286
Christensenia Maxon 025
Christiopteris Copel. 176
Chrysochosma (J.Smith)Kümm. = 049
Chrysodium Fée = 101
Chrysopteris Link = 204
Cibotium Kaulfuss 237
Cincinalis Gled.(1764) = 047
Cincinalis Desv.(1811) = 244
Cionidium Moore 342
Clementea Cav. = 019
Clopodium Rafin.(nomen) = 003
Cnemidaria Presl 227
Cnemidopteris Reichenb. = 227
Cochlidium Kaulfuss 221
Colina E.L.Greene = 036
Colysis Presl 170
Coniodictyogramme Nakai = 082
*Coniogramme Fée 082
Copelandiopteris B.C.Stone 098
Copodium Rafin. = 003
Coptidipteris Nakai & Momose = 252?
Coptophyllum Gardner = 035
Cormophyllum Newm. 228
Cornopteris Nakai 305
Coryphopteris Holtt. 266
Cosentinia Todaro = 047
Costaricia Christ = 238?
Craspedaria Link 188
Craspedodictyum Copel. 076
Craspedoneuron v.d.Bosch = 123
Craspedophyllum (Presl)Copel. 113
Crepidium Presl = 121
Crepidomanes (Presl)Presl (1851) 119
Crepidomanes v.d.Bosch (1861) = 121
Crepidophyllum Reed = 121
Crepidopteris Copel. = 121
Crypsinus Presl 181
Cryptogramma R.Br. 044
Cryptosorus Fée = 212
Cteisium Michx = 034
Ctenitis (C.Chr.)C.Chr. 328
Ctenitopsis Ching 329

Platyloma J.Smith = 057
Platytaenia Kuhn 080
Platyzoma R.Br. 038
Plecosorus Fée 358
Plectopteris Fée = 213
Plenasium Presl 028
Pleocnemia Presl 333
Pleopeltis Humb. & Bonpl. 185
Plesioneuron (Holtt.)Holtt. 274
Pleuridium (Presl) Fée = 200
Pleuroderris Maxon 344
Pleurofossa Nakai = 094
Pleurogramme (Bl.) Presl = 094
Pleuromanes Presl 123
Pleurosoriopsis Fomin 065
Pleurosorus Fée 293
Pneumatopteris Nakai 285
Podopeltis Fée = 337
Podosorus Holtt. 17~~6~~ 1
Poecilopteris Eschw. = 374
Polybotrya Humb. & Bonpl. 367
Polycampium Presl = 163
Polycocca Hill = 088
Polydictyum Presl = 337
Polyphlebium Copel. 120
Polypodiopsis Copel. = 184
Polypodiopteris Reed 184
Polypodium L. 206 C. Chr. et Christen
Polystichopsis (J.Smith)~~Holtt~~. 365
Polystichum Roth 356
Polytaenium Desv. 088
Pomataphytum Jones = 047
Proferea Presl = 270?
Pronephrium Presl 272
Prosaptia Presl 216
Protangiopteris Hayata = 020
Protolindsaya Copel. = 258
Protomarattia Hayata 021
Protowoodsia Ching = 319
Psammiosorus C.Chr. 397
Pseudathyrium Newm. = 304
Pseudocyclosorus Ching = 285
Pseudocystopteris Ching = 304
Pseudodrynaria C.Chr. 160
Pseudophegopteris Ching 263
Pseudotectaria Tard. 339
Psilodochea Presl = 019
Psilogramme Kuhn emend. Underw. = 073
Psilotum Sw. 001
Psomiocarpa Presl 331
Psygmium Presl = 156
Pteretis Rafin. = 301
Pteridanetium Copel. = 090
Pteridella Mett. = 057
*Pteridium Gled. ex Scop.(1760) 244
Pteridium Rafin.(1814) = 096
Pteridoblechnum Hennipman 408
Pteridrys C.Chr. & Ching 335
Pteriglyphis Fée = 307
Pterilis Rafin. (1819) = 301
Pterilis Rafin.(1830) = 096
Pterinodes O.Ktze = 301
Pteris L.(1753) 096
Pteris Scop.(1760) = 369
Pteroneuron Fée = 384
Pteropsis Desv. = 165
Pterozonium Fée 070
Ptilophyllum v.d.Bosch = 140
Ptilopteris Hance = 251
Ptychophyllum Presl = 108
Pycnodoria Presl = 096
Pycnoloma C.Chr. 177
Pycnopteris Moore = 369
Pyrrosia Mirbel 163
Pyxidaria Gled. = 117

Quercifilix Copel. 341

Ragatelus Presl 140
Ragiopteris Presl = 302
Ramondia Mirbel = 034
Reediella Pic.Ser. 121
Regnellidium Lindman 411
Rhachidosorus Ching 306
Rheopteris Alston 084
Rhipidopteris Schott = 382
Rhizoglossum Presl 018
Rhizosperma Meyen = 414
Riedlea Mirbel = 302
Ripidium Bernh. = 032
Rosenstockia Copel. 105
Rumohra Raddi 394
Rumohra auctt. = 356
Rutamuraria Ort. = 288

Saccoloma Kaulf. 249
Sadleria Kaulf. 403
Saffordia Maxon 060
Sagenia Presl = 337
Salpichlaena J.Smith 400
Sambirania Tard. 254
Salvinia Séguier 413
Saxiglossum Ching 164
Sceptridium Lyon 014
Schaffneria Fée 299
Schellolepis J.Smith = 207
*Schizaea Smith 032
Schizocaena J.Smith = 232
Schizogramma Link (gen.dub.) = 066?
Schizolegnia Alston = 252
Schizolepton Fée = 079
Schizoloma Gaud. = 252
Schizoloma sensu Copel. = 079
Schizostege Hilleb. = 096
Schizostegeopsis Copel.(sphalm.) = 098
Schizostegopsis Copel. = 098
Scleroglossum v.A.v.R. 220
Scoliosorus Moore 089
Scolopendrium Adans. = 290
Scyphofilix Thouars (gen.dub.) = 239?
Scypholepia J.Smith = 239
Scyphopteris Rafin.(gen.dub.) = 239?
Scyphularia Fée 386
Scytopteris Presl = 163
*Selaginella P.Beauv. 008
Selaginoides Séguier (1754) = 008
Selaginoides Boehm.(1760) = 008
Selago P.Br.(1756) = 008
Selago Hill(1757) = 006
Selago Boehm.(1760) = 006
Selago Schur (1866) = 006
Selenodesmium (Prantl)Copel. 125
Selliguea Bory 182
Serpyllopsis v.d.Bosch 104
Sinopteris C.Chr. & Ching 055
Sitobolium Desv.(sphalm.) = 238
Sitolobium Desv. corr. J.Smith = 238
Sivetes Rafin. = 009
Solanopteris Copel. 189
Solenopteris Copel.(sphalm.) = 189
Sorolepidium Christ = 356
Soromanes Fée = 367
Spathepteris Presl = 035
Sphaerocionium Presl 111
Sphaeropteris Bernh.(1801) 232
Sphaeropteris Wall.(1830) = 354
Sphaerostephanos J.Smith 281
Sphaerostichum Presl = 163
*Sphenomeris Maxon 256
Spheroidea Dulac = 410
Spicanta Presl = 399

A NOTE ON THE DISTRIBUTION OF ISOETES IN THE CADIZ PROVINCE, SPAIN

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ABSTRACT

Brief notes on the ecology, and distribution in Cadiz Province of *Isoetes histrix, I. durieui* and *I. velata* are given. *I. durieui,* although frequent in southern Portugal, has not been hitherto recorded for southern Spain.

When Clive Jermy suggested that I look for *Isoetes* in my area of the Cadiz province, it stimulated my waning interest in ferns. I had not really bothered about this easily overlooked genus but when I did, an interesting picture unfolded.

First, it appeared that *I. histrix* Bory is an extremely common plant in most parts of this south west corner of Spain, especially in the low hills. Also that it does not seem to be very selective about its habitat, growing in seasonally damp places by streamsides, on mossy rocks in the lowland corkwoods, on grassy slopes often much trampled by cattle; in heavy clay soil in open fields where slight depressions hold water during the winter, and in the firm sand and soft soil behind salt marshes or estuaries (especially near Cadiz). In the hills, too, at 500 m where it becomes a little more selective, this species is common in seepages and in humus-filled crevices between the large rock outcrops which dominate most of the hilltops.

Sometimes *I. histrix* is abundant over a wide area, and on an open hilltop not far from San Roque, at about 240 m, it forms sward-like patches often mixed with *Ophioglossum lusitanicum, Cicendia filiformis* and *Crassula tillaea.* The soil is a sandy loam and the surrounding vegetation consists of short windswept *Lavandula stoechas, Genista triacanthos, Lithodora diffusa. Cistus salvifolius, C. crispus, Satureja salzmannii, Chamaespartium tridentatum, Erodium cicutarium* and *Ulex parviflorus.* All this area is continually damp from about October/November until at least early March, and about May the leaves of *I. histrix* start disappearing.

Practically all the above habitats become very dry and hot during the summer, but occasionally *I. histrix* grows where the seepage remains damp. This is common just above small streams of Rhodendron or Oleander in light corkwoods. The leaves of these *Isoetes* are usually much longer (to 28 cm) and more flaccid than normal, but die back for the summer. The megaspores appear to be developed later than those growing in the wet/dry cycle. This habitat is more where one would expect to find *I. durieui.*

A second species, *I. durieui* Bory is not nearly so common here as the former and seems to be more frequently found on sloping grassy ground in seepages where there is more shade, again in ground well broken by cattle hooves. The distribution seems to be imperfectly known for in the Atlas Florae Europaeae (1. Pteridophyta, p. 31), *I. durieui* is shown for Spain only in the east near the Pyrenees, although it occurs in southwest Portugal not far from the Spanish border. In the Cadiz province (see Allen, 1975) I have found it from 750 m on the summit of a ridge above Algeciras down to about 170 m, but sporadically; also from near the Malaga border at 680 m altitude. It would appear to require more permanent moisture, shade and possibly higher altitudes on the whole than *I. histrix,* and most of these areas are damp all through the year, although some have shade for only part of the day. On the summits of the Algeciras hills, mist lies frequently throughout the summer, and it was here that

I found some plants of *I. durieui* on a moss-covered rock which was flat and thinly covered with soil. Over this water was seeping and with it were some short grasses, including *Poa inferma,* and also *Moenchia erecta, Spergularia* sp., *Campanula erinus, Plantago serraria* whilst *Teesdalia nudicaulis* grew alongside in a drier place. Other areas are in small openings in mixed forest of *Quercus suber* and *Q. faginea* mostly on sloping grassy, cattle-trodden ground. Occasionally it grows fairly near *I. histrix* but so far I have not found them actually growing side by side. The most distant locality within this province, near the Cerro de Jovati, is towards Cortes de la Frontera. These plants were in a fairly open place, again in a seepage but in base-poor soil, and with them were the "indicator plants" (for *I. histrix*) *Cicendia filiformis, Pinguicula lusitanica, Anagallis crassula* and a few small grasses. Just above the seepage was heathland of short *Erica umbellata, E. australis, Calluna vulgaris* and *Cistus* spp. etc.

It suggests that *I. durieui* may occur more frequently than is generally supposed, especially from 300 or 400 m upwards, in this province anyway. Cattle, deer and goats almost certainly play an important part in the distribution of this species as well of *I. histrix,* the megaspores becoming imbedded in the cloven hooves.

Have the hard, black leaf-bases which are present in these two terrestial species some function in protecting the resting stems from damage? A species of *Triglochin (T. barrelieri)* which grows here in salt marshes as well as inland, and commonly together with *I. histrix,* has similar black and hardened leafbases and it also rests during the summer.

The other species which I have seen here is *I. velata* A.Br. is much rarer and I know of only two places in one locality where it grows. This is an aquatic species, but this locality dries out in the summer; it was growing in a pool on the flat top of a large and isolated rock in full sun. According to the watermark on the side of the pool, the normal water depth would be about 60–80 cm and when full, the leaves of *I. velata* are submerged and spread more or less in a star-shape. When the water is lower, and this seems to be the more usual state now that the climate appears to be becoming drier, the leaves lie across the top of the water and are flaccid and bright green. Normally they should be submerged from about November or December to May, exceptionally from September, when the new growth would be in danger of drying out again in December, which is mainly a dry month. Last year the megaspores were becoming mature in February, probably as there had been little rain in January; in April they were quite mature and greyish. They start to die down as the water dries up, which it does rapidly in May. Mixed with the *Isoetes* was *Callitriche brutia,* and on the edge of the flat side of the pool, in black earth was *I. histrix* forming a dense fringe with leaves longer than usual. There were a few plants of *Ophioglossum lusticanicum* on the outer edge, *Serapias* probably *parviflora, Lythrum portula, Allium triquetrum* and one plant of *Lavandula stoechas.* The earth at the base of the pool was not deep and in July and August the heat thrown off into this depression, from the vast white surrounding stone, must be intense. As I write this however, a widespread fire has already burnt the surrounding vegetation and for hundreds of acres surrounding this area, and so it remains to be seen what the result will be to this plant, and whether the *I. histrix* and *Ophioglossum* which were so common amongst the vegetation below, will appear this year after the autumn rains.

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LECANOPTERIS SPINOSA — A NEW ANT-FERN FROM INDONESIA

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ABSTRACT

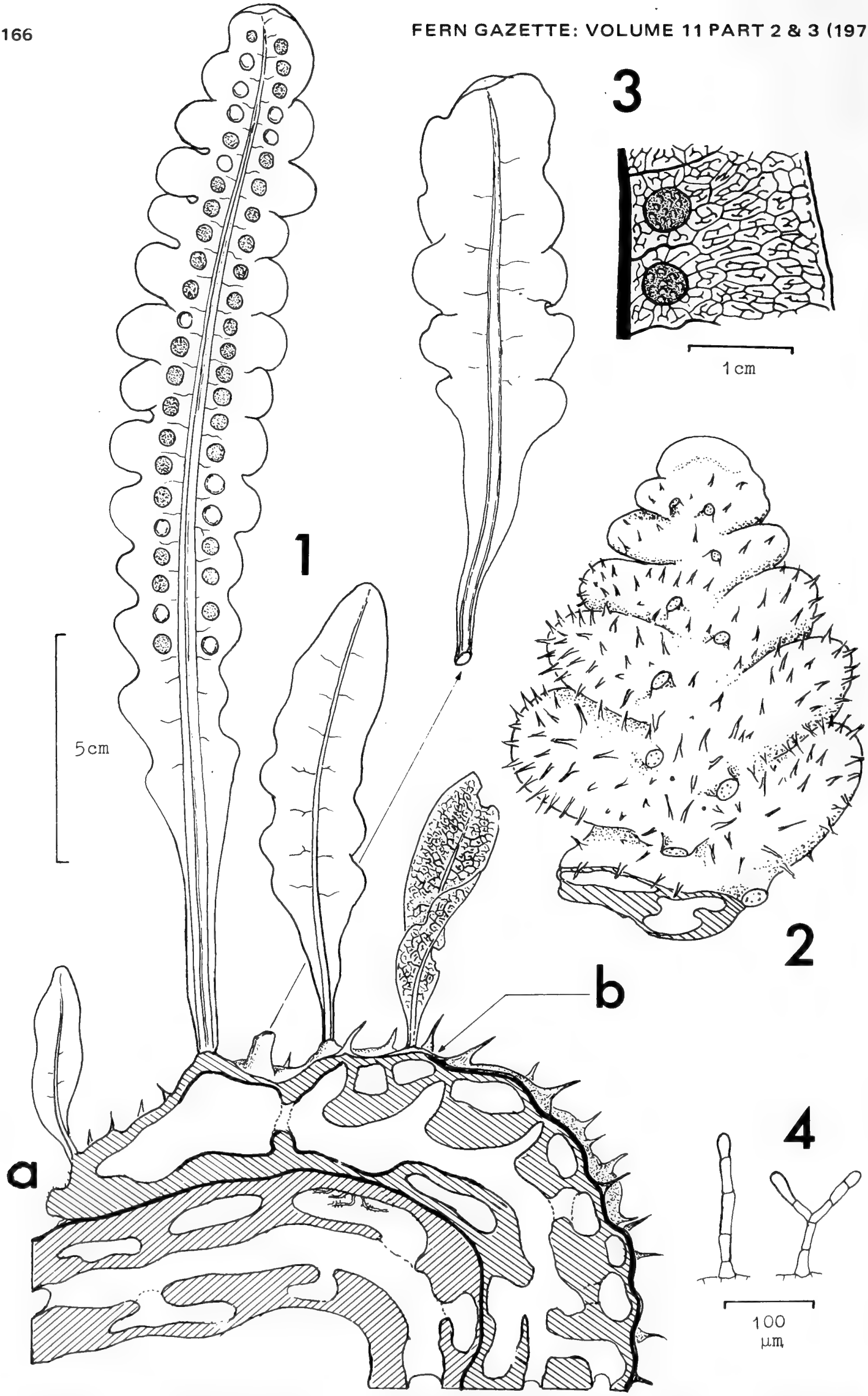
Whilst collecting plants in the Latimojong Mnts., Sulawesi (Celebes) the authors found a new species of ant-inhabited fern here described as **Lecanopteris spinosa** sp. nov. An account of the morphology and anatomy is given and comparisons are made with other species variously placed in the genera *Lecanopteris* Reinw. and *Myrmecophila* (Christ) Nakai. On grounds of anatomy and rhizome morphology it is argued that the new species is intermediate between these genera thus supporting Copeland's view that they should be united. The highly developed rhizome structure is discussed in relation to the ants that inhabit it.

INTRODUCTION

In 1824 Reinwardt described a fern which he called *Onychium carnosum,* unaware that Kaulfuss (1820) had already used the generic name for another totally different species. No sooner than the name was published Reinwardt became aware of his mistake and in 1825 published a substitute generic name, *Lecanopteris.* Blume (1828a) elaborated the description emphasizing that the species was distinct from any other *Polypodium* in having a peculiar habit with a swollen rhizome and sori immersed at the reflexed tips of the pinnae segments. Later (1828b) he figured *L.carnosa* together with a variant which he called *L.pumila* although the text description of this new species never appeared.

The genus was upheld by some pteridologists (e.g., Presl 1836, Fee 1852) whilst others (e.g. Mettenius 1856; Hooker & Baker 1868, 1874) still preferred to treat it under a large and variable *Polypodium.* Cesati (1876) described a related species (now *L. deparioides* (Ces.) Bak.) under *Davallia* believing the reflexed leaf tip to be similar to the indusium of that genus. In 1881 however Baker accepted *Lecanopteris* and described a fourth species *(L. incurvata)* from Sumatra placing it here on account of its soral structure alone, as his specimen (*Curtis 24:* K) was without a rhizome. Later collections of what is undoubtedly the same species (e.g. Benkoelen, *Brooks, s.n.* 1920—23; BM) show a typical swollen and naked rhizome.

Christ (1897), whilst not accepting the generic rank, did however accept the taxonomic concept of Baker (et alia) and he went further and grouped together four other species of *Polypodium* which had similar swollen ant-inhabited rhizomes, under the section *Myrmecophila,* a name legally instated at generic rank by Nakai (1929). Whilst the rhizomes of *Myrmecophila* were ant inhabited and often massive they were not naked but covered with distinct clathrate, dark-centred scales. The sori were superficial, although sometimes deeply immersed lying close to the rachis or costa. This taxonomy was maintained although some (e.g. van Alderwelt van Rosenburgh 1909) went further and included *Lecanopteris* as a subsection within section *Myrmecophila,* when others (e.g. Ching 1940) accepted both as genera. Copeland (1905) maintained *Lecanopteris* (pro gen.) but placed *Myrmecophila* as a section of *Polypodium.* In 1929 he pointed out the affinity of the former to *Microsorium* sect. *Phymatodes* and its relationship to *Myrmecophila* which he proposed (1929: 122) should be united under *Lecanopteris,* a position he maintained in 1947 and 1960.



FIGURES 1–4, *Lecanopteris spinosa:* 1, diagrammatic sketch of whole plant, (a, growing point; b, advancing front of black pigment zone); 2, portion of rhizome; 3, enlargement of portion of frond showing venation; 4, hairs from rhizome apex.

Holttum (1954) placed the two species of section *Myrmecophila* found in Malaya in *Phymatodes* Presl. [*P. sinuosa* (Wall. ex Hook.) J. Sm.; *P. crustacea* (Copel.) Holtt.] on the grounds that they "have all the characters . . . [of *Phymatodes*] apart from the swollen rhizome". They do not however have the characteristic knobbly, branched paraphyses amongst the sporangia as the other species of this genus, e.g. *P. scolopendria* (Burm.) Ching. *Lecanopteris,* with its distinct sori and clathrate scales, Holttum keeps as a separate genus.

The finding of an ant-fern in Sulawesi with a swollen, naked rhizome but with fronds with the texture and sori of *L. sinuosa* places it intermediate between sections *Lecanopteris* and *Myrmecophila.* Although in the two genera the position of the sori varies and this is correlated with the dissection of the frond, the vascular supply to it and its general structure is similar. The species examined by us are listed under the two sections in Table 1. In all, the maturing fertile sporangia are immersed in a mat of long setae topped by an abortive sporangium which often breaks away leaving a curious cup-shaped head and which, although possibly homologous with the branched paraphyses of other Microsorioid genera, should not be confused with them. The rhizome architecture varies from the more massive irregular growth pattern in *L. crustacea* through *L. spinosa,* both without scales, to the regular *L. sinuosa* with scales; *L. mirabilis* is irregular and expansive with often an almost naked upper surface; according to Copeland (1929) *L. sinuosa* has a Papuan form (not seen by us) with a glabrescent rhizome. Except for *L. davallioides* and *L. nieuwenhuisii,* where we have seen no rhizome material, all the species in section *Lecanopteris* have uniseriate, occasionally branched, trichomes on the epidermis of the young rhizome. In anatomical structure both the rhizome and frond of *L. spinosa* are similar to *L. carnosa* and *L. sinuosa* (cf. Yapp 1902).

TABLE 1: Species of *Lecanopteris* discussed in this paper.

Rhizome naked; sorus only slightly immersed at pinnae or segment ends which are ± reflexed (= **section Lecanopteris**)	Rhizome with clathrate scales; sorus immersed close to costa of ± simple fronds or close to costule of pinnae (= **section Myrmecophila**)
L. carnosa (Reinw.) Bl.	L. lomarioides (Brause) Baker (incl. L. crustacea Copel)
L. davallioides v.A.v.R.	L. mirabilis (C. Chr.) Ching
L. deparioides (Ces.) Bak. (incl. L. curtisii Bak.)	L. sarcopus de Vr. & van Teyss.
L. incurvata Bak.	L. sinuosa (Wall.) Copel. (incl. L. pumila Bl. ex Copel.)
L. nieuwenhuisii Christ*	
L. philippensis v.A.v.R.*	
L spinosa Jermy & T.G. Walker	

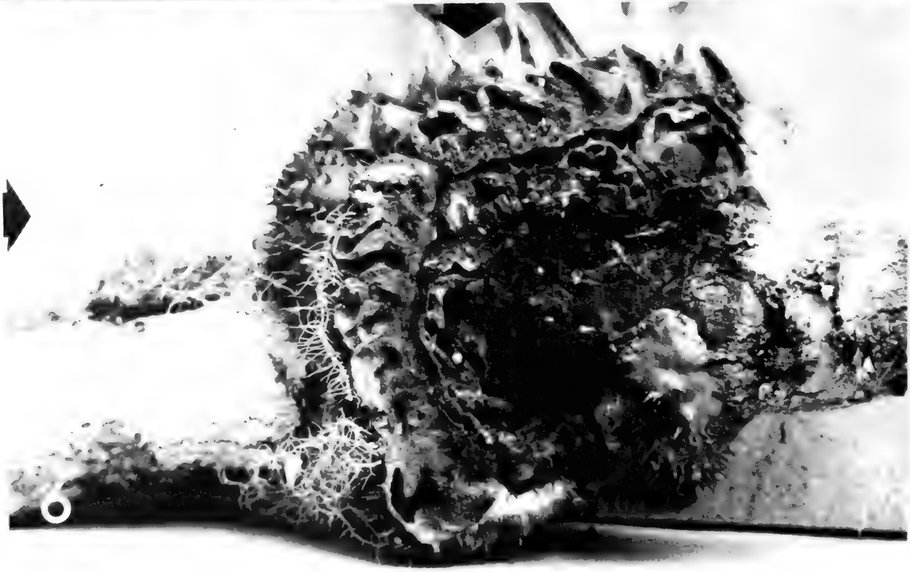
* rhizome not seen

It is seen that *L. spinosa* is intermediate between the two sections as hitherto defined and is further proof in support of Copeland to unite *Myrmecophila* and *Lecanopteris* under the latter. If the degree of organisation and adaption of the rhizome is significant, *L. spinosa* would be the most advanced member of section *Lecanopteris.*

DIAGNOSIS AND DESCRIPTION

Lecanopteris spinosa Jermy & Walker **sp. nov.** (fig 1 et sequ.)

Planta myrmecophila epiphytica. *Rhizoma* glabrum ventricosum 2.5–4 cm crassum, ramis brevibus



FIGURES 5–6, *Lecanopteris spinosa:* 5, plant in situ x ½; 6, sectioned rhizome showing galleries (arrow intersection indicates ants removing pupae).

lateralibus, porticus ad apicem capiens, initio subviride pruinosum, demum nigrum coriaceum, spinis ad 6 mm conicis attenuatis. *Frondes* exstipitatae, bifariae, usque ad 30 x 5 cm (frondes steriles saepe 6–8 cm longae); rhachis flavovirens; *lamina* frondum sterilium simplex, frondum fertilium pinnatifida lobata, apices loborum rotundatis; venae anastomosantes, areolae venulis liberis clavatis includentibus. *Sori* immersi uniseriati prope rhachidem, sporangia initio sporangibus sterilibus elongatis obtecta at sine paraphysibus ut in speciebus nonnullis *Microsorii*. *Sporae* monoletes (56–) 69–(82.5) μm longae luteolae laeves.

Typus Indonesia, Sulawesi, Latimojong Mnts, SW slopes of Mnt. Rantemario, below Buta Jakke above base camp; on *Platea latifolia* Bl. in mixed oak-podocarp forest, at 1950 m alt., 10 November 1969, *A.C. Jermy 7609;* holotypus in BM; isotypi in BO, GH, L.

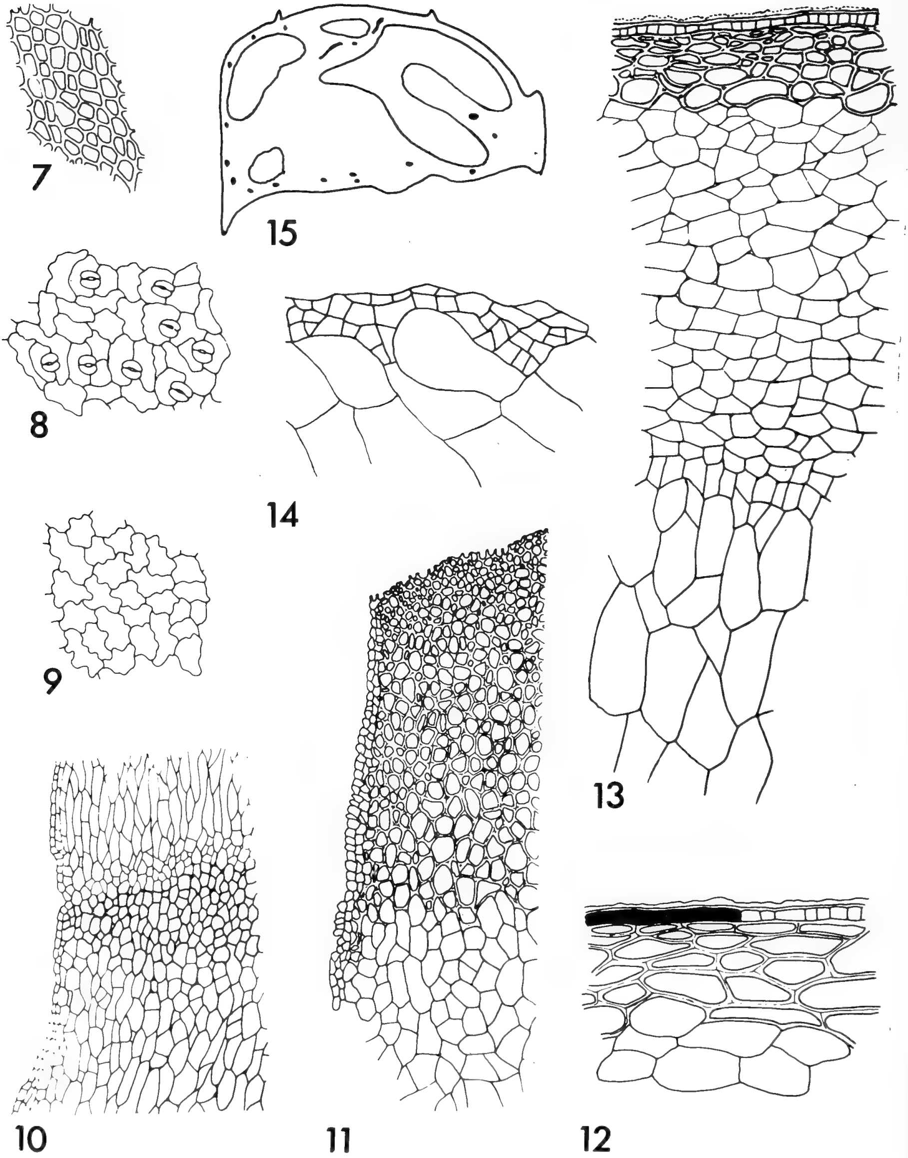
Paratypus: Loco citato, *T. G. Walker T12179* (in herb Walker).

Plants epiphytic, found on the upper branches (3–6 cm thick) of trees 15–20 m high. Primary rhizome 2.5–4 cm thick, the advancing front somewhat flattened and adpressed to the substrate and budding off lobes which develop into lateral branches 2.5–5 cm long, 1–3 cm thick, and which on maturity swell to press against each other (see fig 2). In all the plants studied the main axis of the rhizome soon orientated itself across the branch and gradually encircled it. When the first complete turn has been achieved the main rhizome continues to grow in the same direction on top of the old dead, leathery rhizome. Thus a "ball" of rhizome would result often three or four stems thick, each growing epiphytically on itself and in which there would be usually only one advancing apex although occasionally a side branch would continue growth for a time. It is possible that such "balls", found up to 25 cm across, could contain more than one plant but this seems unlikely.

Living rhizomes are pale green with a pronounced glaucous bloom on the younger parts which dries as flat, plate-like scales of white wax. Scales absent but the very young epidermis is sparsely covered with simple, very rarely branched, caducous trichomes of four to eight cells uniseriately arranged, the terminal cell of which is not obviously glandular. Epidermis minutely papillate with scattered multicellular spines, 4–6 mm long, narrowly conical, or cylindrical and tapered with a swollen conical base, occasionally consisting of this only, green and flexuous often turning black before the rest of the epidermal tissue. Green rhizome becoming black (see para. on anatomy) as fronds absciss; the tissue eventually dying as the outer layers become horny or leathery. The meristematic tissues of the lateral branches die at this stage and the invaginated apex is often perforated as the tissues shrink (see below).

Fronds, in two ranks on the main rhizome, not normally seen on the lateral branches although some are initiated there; for the most part initiated on the meristematic front of the rhizome which develops, as the leaf ages, into a conical phyllopodium, stipe virtually absent, articulate to rhizome, the fronds falling as the rhizome blackens. Lamina up to 30 x 5 cm (often only 6–8 cm long in sterile fronds), linear-oblanceolate tapering below to form in the lower 2–5 cms a wing along the rachis, apex rounded, often imperfect and emarginate, margin entire in small sterile fronds to undulate or ± regularly lobed $\frac{1}{3}$ to the rachis in fertile fronds (see fig 1); texture coriaceous, dull, pale green, midrib distinct, yellowish green, raised on the adaxial side and with a narrow ridge on the abaxial surface, the veins conspicuous on drying, anastomosing to form areolae with included free veinlets (see fig 3).

Sori in one row close to and either side of the rachis usually in the upper $\frac{2}{3}$ of the leaf only; circular on flat immersed receptacles which cause projections on the upper surface; sporangia protected in the early stages by long-stalked abortive sporangia which overtop them and whose heads touch one another to form a compact layer (see fig 25). Spores monolete, pale yellow (56–) 69 (–82.5) μm long (in a sample of 50), sporoderm smooth under the SEM with only the occasional papilla in the region of the suture.



FIGURES 7–15, *Lecanopteris spinosa* anatomy: 7, epidermis of rhizome (x 65); 8, lower epidermis of frond (x 65); 9, upper epidermis of frond (x 65); 10, LS young dehiscence region of frond base (x 45); 11, LS old frond base (x 45); 12, LS old rhizome at junction of green and black areas (x 65); 13, LS young rhizome, boundary between lower water storage tissue and upper parenchyma arrowed (x 55); 14, delimiting region arrowed in fig 13 at later stage just prior to breakdown of water storage tissue of rhizome (x 70); 15, TS rhizome showing galleries (cross hatched) and vascular system.

ANATOMY

1. The root

The roots are short, black and wiry and cling to the substrate and when developed in the chambers produce copious root-hairs. The xylem is diarch and there is a particularly well defined pericycle (fig 26). Abutting onto the endodermis is a ring of cells with heavily thickened walls about seven cells in depth, except opposite the protoxylem points where it is interrupted. This is identical to the root structure of *L. carnosa* as described by Yapp (1902).

2. The rhizome

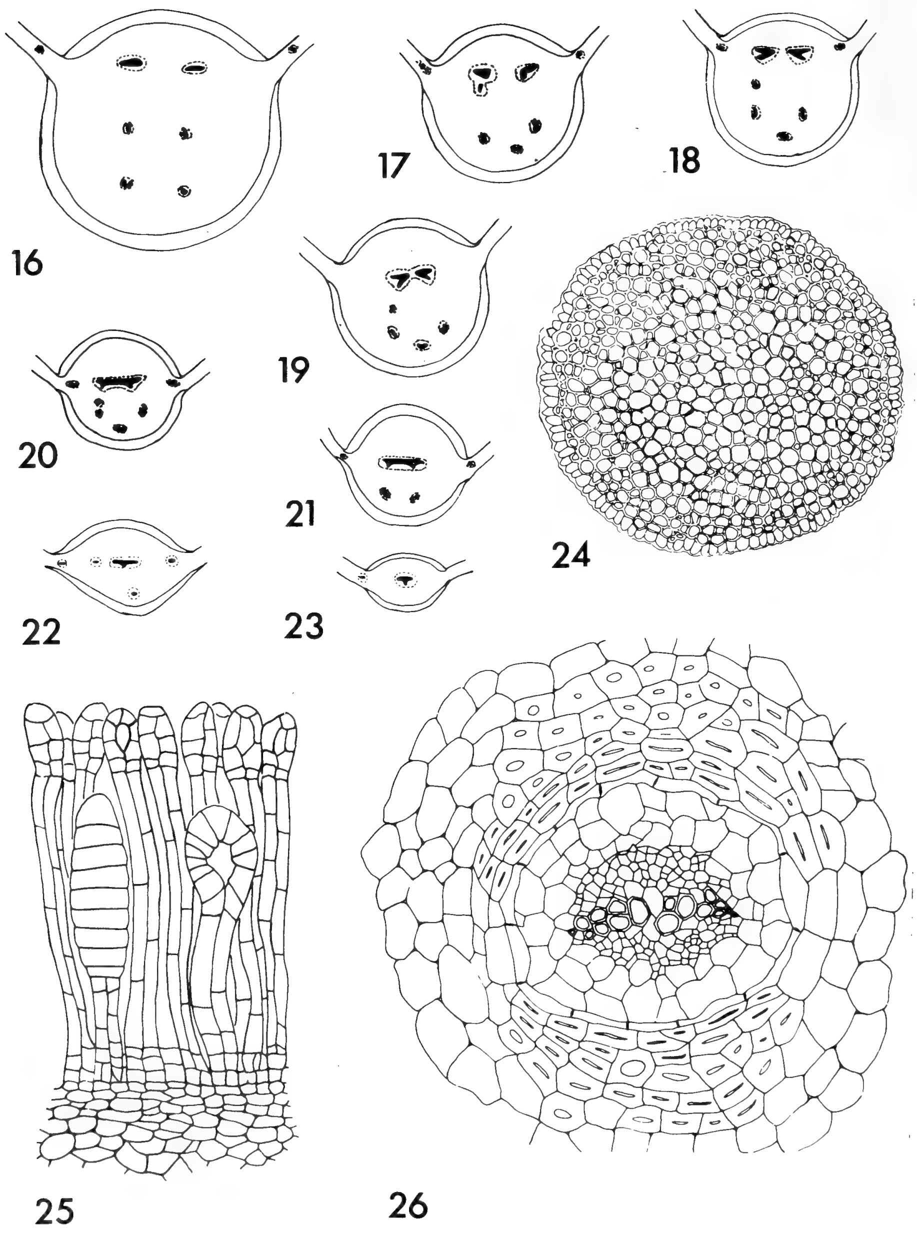
In the young parts the spines, which are such a conspicuous and permanent feature of this plant are green and flexible when young, consisting of cells with living contents and having lignified walls. As they age the cells lose their contents (fig 24) and the spines become rigid. They first blacken at the tip and then ultimately throughout, this blackening frequently preceding that of the rhizome discussed later.

The rhizome epidermis consists of thick walled cells and is devoid of stomata (fig 7). Overlying the cuticle is a very thick transparent, wax, becoming white on drying seen under the SEM as irregular flakes which harden to the surface when the rhizome blackens. As in some other species of *Lecanopteris* e.g. *L. carnosa,* the rhizome blackens with age and a curious feature in *L. spinosa* is that frequently the boundary between green and black areas is absolutely sharp as if drawn by a pen. Although, as ageing occurs, there is a gradual browning of the underlying tissues, the black appearance is entirely caused by the deposition of dense melanic substances in the epidermal layer only (fig 12).

Immediately beneath the epidermis there is a layer a few cells deep which is lignified and internal to this is parenchyma. In the centre of the young parts of the rhizome the parenchyma forms a very distinctive water storage tissue which can be distinguished by the naked eye by its lighter colour. In this tissue the cells are much larger than those of the surrounding parenchyma, are elongated vertically and have a glistening translucent appearance due to their high water content. It is the breakdown of this tissue which leads to the formation of the cavities.

The water storage tissue is of short duration, rarely being found intact more than about two centimetres behind the apex of the main stem of the branches. This agrees with the situation as described for *L. carnosa* by Yapp but although he described some of the anatomical details their possible importance in the formation of the cavities appears to have eluded him as he believed that only very young plants (which he did not possess) would provide the answer.

The innermost one or two layers of the parenchyma bordering onto the water storage tissue are not especially prominent at first, being thin walled and tending to be aligned with their long axes in the same plane as the cells of the water storage tissue (arrowed in fig 13). Later on, however, these parenchyma cells divide to form a very conspicuous delimiting layer from which finger-like processes project between the outermost cells of the water storage tissue (fig 14). This later stage is illustrated by Yapp (1902). The cells of this delimiting layer become rapidly and progressively more suberized and when this process has reached a certain stage the water storage tissue also develops a very small amount of suberization. At this point the delimiting layer apparently cuts off the once more or less intimate contact between the water storage tissue and the ground parenchyma of the rhizome, with the subsequent disintegration of the water storage tissue and the resultant space forming a chamber lined by a layer



FIGURES 16–26, *Lecanopteris spinosa* anatomy: 16–23, TS rachis from base towards apex, xylem as solid black, endodermis as broken line (x 5.75); 24, TS mature spine of rhizome (x 55); 25, LS young sorus (x 90); 26, TS stele and inner cortex of root (x 400).

of dark suberized cells. If a young apex is sectioned the development of the delimiting layer, its progressive suberization and the breakdown of the water storage tissue can be seen as a continuous process occurring over a distance of 0.5–1 cm. Hence the chambers or galleries are constantly being extended, keeping pace with the elongation of the rhizome.

The apices of young rhizome lobes or of the lateral branches are frequently invaginated and have the appearance of a "pore". On dying the parenchymatous cells at the base of this pore shrink and break down thus linking the chamber with the exterior. It is through such natural openings that ants gain entrance to the galleries. The cells lining these openings are similar to those in the galleries suggesting that the opening has been formed in much the same way as the galleries themselves.

In actively growing portions of the rhizome there is a "lip" on the leading edge which consists of young dividing cells forming the meristem. It is in this region that the leaf primordia and the spines arise (marked a in fig 1). This extends along the growing margin and no single apical cell was detected, although it would be exceedingly difficult to find if it did exist without microtoming a considerable number of sections. Toward the sides as the rhizome matures, or in the lateral branches of limited growth, the edges tend to be more or less rounded, the parenchyma comprising the bulk of the rhizome being fully expanded and enclosed in a layer of lignified cells on both upper and lower surfaces and bounded by the epidermis. Further back in the blackened areas, all the cells become orange-yellow and spongy in texture.

The rhizome is permeated with a network of vascular strands which are embedded in the parenchyma above and below the galleries (see fig 15) but which are absent from the water storage tissue where this is present. The individual strands are very similar in structure to the vascular supply of the root (fig 26) except that immediately outside the endodermis there is at most a single layer of thickened cells.

The pattern of the galleries tends to be rather more complex in this species than in most others of *Lecanopteris*. Here they tend to be on three levels with a major gallery running along the entire length of the rhizome and giving off frequent chambers above and below which interconnect with one another. The layout is not so clear as in some other species such as *L carnosa* and *L. deparioides* where the rhizome can be likened to a series of flasks joined together, each bearing a frond and having one or more chambers within. In *L. spinosa* the fronds tend to be somewhat sparse and the rhizome not organised into units joined together, other than the lateral branches. According to the position of the cut, at any part of an opened rhizome there may be seen three lines of chambers or else large irregular spaces where all the chambers meet (see fig 1). Thus there is a continuous network of galleries and chambers throughout the plant as in all of the Asiatic ant-ferns. This is in contrast to the New World species of *Solanopteris,* described in detail recently by Hagemann (1969) and Wagner (1972), in which the rhizome is dimorphic and the inflated areas are produced on short shoots.

3. The frond

The upper surface of the lamina is devoid of stomata unlike the lower epidermis which is richly provided with them (figs 8–9) the mean length of the guard cells being 46 μm (range 41–52 μm in a sample of 50). The photosynthetic region consists of several layers of cells which are densely filled with chloroplasts and form a spongy mesophyll. Yapp (1902) reports the presence in *L. carnosa* of a single layer of large colourless cells immediately beneath the upper epidermis which possibly forms a hypodermal water reservoir but in *L. spinosa* the situation is somewhat variable, even in the same section. In some areas the layer is clearly present, containing conspicuous cells which completely lack chloroplasts, whilst in other areas these cells are less obvious and contain some chloroplasts, although fewer in number than in the spongy mesophyll.

The fronds are initiated at the edge of the rhizome and are completely naked throughout life. Each is borne on a prominent cone-shaped leaf base (phyllopodium) and there is a well-defined dehiscence region present from the beginning which results in the old fronds being shed cleanly. This region consists of a layer of rather irregularly shaped, but more or less isodiametric cells some 12 rows deep, which contrast with the more elongated cells on either side, i.e. in the base of the stipe and in the top of the phyllopodium. The cell walls of the dehiscence layer, with the exception of the uppermost 2 or 3 rows, start to thicken early in development and can be seen even when the young frond has just unfurled (fig 10). Lignification proceeds and ultimately a layer some 20 or more cells thick caps an old leaf base from which the frond has been shed (fig 11). Dehiscence occurs by tearing along the uppermost two or three rows of unlignified cells, and their torn remains may be seen in section. This behaviour contrasts with that reported by Phillips & White (1967) for representatives of several genera belonging to the Polypodiaceae in which a specialised dehiscence layer was by no means so conspicuous.

Six or seven vascular strands are present in the leaf base and traverse the dehiscence layer into the bottom of the rachis, where they become orientated into two vertical rows (fig 16). The upper two strands nearest the adaxial side of the rachis tend to be more conspicuous than the others and are elongated transversely. They approach one another more closely at successive levels up the rachis and quickly fuse to form a very prominent trace which then persists through the remaining length of the rachis. This behaviour is in contrast to that of the other strands which gradually decrease in number by a process of fusion and finally disappear near the tip, leaving only the conspicuous trace noted above (figs 16–23).

The sori are produced in a single row on either side of the rachis and are deeply impressed (fig 1). The base of the sorus is richly supplied by vascular tissue which is delimited from the other tissues of the lamina by a single continuous layer of very thick walled cells on the under side only and abutting on to the endodermis. One might speculate as to whether or not this is a device whereby the supplies carried in the vascular strands are diverted to supplying the sorus rather than the underlying tissues of the lamina. There is no mention of this structure in Yapp's account of *L. carnosa* and we failed to find it in our sections of *L. sinuosa* and *L. deparioides.*

ANT-FERN RELATIONSHIP

The rhizome galleries of *L. spinosa* were inhabited by a species of *Crematogaster.* Specimens have been deposited in the Department of Entomology, British Museum (Natural History). It is possible that other genera or species of ants were commensal in the rhizome but we have no evidence of this; Gomez (1974) found at least three genera coexisting in *Solanopteris brunei* (Werkle ex Christ) Wagner. Ants gain access to the chambers through the apical cavities of the lateral branches and we have no evidence that the ants eat their way into the chambers as do *Azteca* sp. into *Solanopteris* (Gomez, l.c.) although they may physically remove dead cells and other detritus that accumulates in the aperture. A full discussion on the evolution of the interaction of *Iridomyrmex myrmecodiae* with *Lecanopteris sinuosa* and other mymecophytes in Sarawak is given by Janzen (1974). The following observations are given in support of his ideas.

The affect of the plant on the ant

Apart from shelter ants may absorb moisture from the living tissue either directly or indirectly. The outer epidermis of *L. spinosa* is hard and impervious to water but rain water could perculate through open phyllopodia or apical "pores" and become absorbed on the spongy dead parenchyma thus maintaining a moist atmosphere within the chambers. To what extent the *Lecanopteris* attracts other arthropods which in turn are captured by *Crematogaster,* by being a source of food or shelter was not observed but little evidence of such is seen on dried material now before us. On analysis, the heaps of debris found rarely at the ends of the galleries consisted mainly of heads (and leg and mouth-parts) of *Crematogaster* and no other specifically recognisable remains except coleopteran (?) larva/castes and elytra and many fragments of insect wing and limbs.

That the fern offers food in the way of highly nutritious spores or young or abortive sporangia has been suggested by several workers (Holttum 1954a, b,; Janzen 1974). Certainly in many cases the whole sorus is removed, presumably by some grazing animal and often the lamina beneath the sorus is also eaten away. As Holttum (1954b) reports for *L. sinuosa,* the paraphysis-like abortive sporangia are full of globules that have the appearance of oil bodies, although we found these difficult to stain with Sudan blue/red. In all the species of *Lecanopteris* studied by us most of the abortive sporangial heads had been lost at the time of sporangial dehiscence leaving a characteristic broken cell at the top of the seta. This may be due to natural fall off or to grazing by ants but it must be admitted that this type of "paraphysis" is seen in many *Microsorium* species not associated with ants. We have not investigated the chemistry of the rhizome tissue and it is possible that the large parenchymatous cells described above contain sugars similar to those in *Solanopteris* (Gomez, l.c.). Ants are certainly found in the green succulent rhizome.

The effect of the ant on the plant

Holttum speculates that in return for shelter provided by the plant the ants bring in mineral substances from the ground and also some nitrogen in their excreta. No evidence of the former was found in *L. spinosa* and no mineral carton was seen associated with the species as is often the case with other myrmecophytes, e.g. *Hydnophytum* and *Myrmecodia* (Janzen 1974). Fern roots were seen to penetrate the cavities, usually through broken down phyllopodia, and once inside developed copious root hairs; whether they absorb anything other than water has yet to be proved.

Another hypothesis is that frequently put forward, and with good evidence, in connection with some flowering plants which also show an association with ants, namely that the ants protect the plant from attack by insects. Our limited observations suggest that first, the ants tended to flee rather than attack when the plant was touched and second, fronds and sori showed signs of being eaten presumably by a herbivorous insect other than the ants themselves. In *L. spinosa* and in the genus as a whole the young fleshy parts of the rhizome are devoid of scales or very poorly furnished with them whilst at the same time occupying an exposed position in the tree canopy. Certain parallels exist between this situation and that discussed in some detail by Janzen (1966) for the "swollen thorn" acacias of Central America. It is certain that in cultivation, slugs will seek out *Lecanopteris* rhizomes in preference to other fern species. This was demonstrated at Newcastle when 39 sporelings of *L. mirabilis* were raised, in the absence of ants, dispersed among several propagating frames and intermixed at random among several hundred sporelings belonging to a large number of genera. In every case the *Lecanopteris* sporelings were irrevocably damaged by slugs whilst those of the surrounding species had hardly been affected. It is unlikely however that slugs would be predators in nature but the observation establishes the palatability of the rhizome tissue which in nature is untouched.

Although the rhizome is green, little or no CO_2 exchange can take place through the waxy cuticle. The presence of actively respiring ants in the chambers of the green rhizome could then be an advantage.

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DRYOPTERIS TYRRHENA NOM. NOV. – A MISUNDERSTOOD WESTERN MEDITERRANEAN SPECIES

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ABSTRACT

A rare west mediterranean fern first found on the Sierra Nevada (southern Spain), and described as *Aspidium nevadense* Boissier (1938) has since been reduced by most botanists to a subsp. or var. of different representatives of either the *Dryopteris filix-mas* or *D. villarii* complexes. In our opinion it should be recognised as a good species, and as *D. nevadensis* is unfortunately no longer available we propose the name *D. tyrrhena*. In its morphology it is intermediate between members of the *D. filix-mas* and *D. villarii* complexes and we assume that it may once have arisen by chromosome doubling from a diploid hybrid of *D. abbreviata* x *D. villarii* subsp. *pallida*. Chemical results agree well with this hypothesis but final cytological proof must await further experimental work. We also describe two important back crosses: *D.* x *sardoa*, a natural triploid hybrid of *D. abbreviata* x *tyrrhena* and an experimental triploid of *D. tyrrhena* x *D. villarii* subsp. *pallida*. The latter showing c. 40 bivalents in meiosis in agreement with the above hypothesis.

We have collected or seen specimens of *D. tyrrhena* from the Sierra Nevada, the Tyrrhenian Islands (Corsica, Sardinia, Elba, Capraia) and from Italy (Riomaggiore, Liguria) from altitudes near sea level to c. 2500 m. Its disjunct distribution in isolated places, often in caves or deep crevices in silicate rock, suggests that it is an old relict species.

INTRODUCTION

Many species of the genus *Dryopteris* are critical taxa, often difficult to differentiate. In Europe (excluding the Azores) three complexes are known, and only after the introduction of cytology to fern taxonomy by Manton (1950), was a better understanding of their classification possible. Today the following species are accepted as members of these complexes.

A. The **D. carthusiana-dilatata** complex (formerly known as *D. spinulosa* complex) comprising: *D. aemula* (Ait.) O. Kuntze, *D. assimilis* S. Walker, *D. carthusiana* (Vill.) H.P. Fuchs, *D. cristata* (L.) A. Gray and *D. dilatata* (Hoffm.) A. Gray.* This is not involved in this study.

B. The **D. filix-mas** complex comprising 1. *D. abbreviata* (DC.) Newm.,* diploid; 2. *D. caucasica* (A.Br.) Fraser-Jenkins & Corley (1972), diploid, known so far only from the Caucasus, Turkey and Persia; 3. *D. filix-mas* (L.) Schott, allotetraploid and 4. *D. borreri* Newm.,* apogamous with diploid and triploid cytotypes. Manton (1950) has shown that *D. filix-mas* contains two genomes of *D. abbreviata* and according to

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*In this article we use Heywood's nomenclature of Flora Europaea (1964) despite the fact that some names are illegitimate. This is true for *D. abbreviata* (DC.) Newm. (see Fraser-Jenkins & Jermy, in press), *D. borreri* Newm. (see Holub 1967), and *D. dilatata* (Hoffm.) A. Gray (see Jermy 1969).

Fraser-Jenkins & Corley (1972) the two other ones most probably come from *D. caucasica.* As these two diploid ancestors are morphologically somewhat similar it is understandable that all these three species can sometimes be very difficult to tell apart.

C. The **D. villarii** complex, growing nearly exclusively on limestone. This is today treated as one species, following Heywood (1964) and divided as follows: 1. *D. villarii* (Bell.) Woynar subsp. *villarii,* the alpine diploid; 2. *D. villarii* subsp. *pallida* (Bory) Heywood, a diploid, morphologically rather variable taxon from low altitudes around the Mediterranean Sea which can further be separated into different varieties of which we mention for the present study only var. *balearica,* originally described as *D. rigida* (Sw.) A. Gray subsp. *australis* (Ten.) C. Chr. var. *balearica* by R. Litardière (1911: 23, see also Knoche 1921: 252). 3. *"The tetraploid taxon"* (Widén et al. 1971). This is the only form of *D. villarii* found so far in Great Britain (Manton 1950; Gilbert 1966). It is also distributed on the European Continent from Spain to the Balkans (Vida 1969) mainly above 800 m. It is probably an allotetraploid derived from the two mentioned diploids (Manton 1950, 1961; Panigraphi 1965) but final proof for the degree of affinity between the three subspecies is still missing. The morphology of the tetraploid is more or less intermediate between the two diploids but nearer to subsp. *pallida.* Its unequivocal differentiation from the two diploids is difficult and without cytological analysis, sometimes impossible.

METHODS

For meiotic counts pinnae with unripe sporangia were fixed in freshly mixed absolute alcohol: glacial acetic acid (3:1) either in the field or from cultivated plants. After 24 hours the liquid was replaced by new mixture kept (wherever possible) at 0°C and the fixings sent to Budapest by air-mail. If this was not possible the fixings were transferred to 70% aqueous alcohol and kept at room temperature. The samples were kept at Budapest at −15°C until examination. Staining, squashing and the making of permanent preparations was done following Manton (1950: 293–299).

Root tips for meiotic counts were treated in 0.1% aqueous colchicine for 8 hours at 4°C (if this was not possible 2 hours at 20°C), dried quickly on blotting paper and fixed as mentioned above. Before staining the root tips were softened with snail enzyme (Fabergé 1945, Roy & Manton 1965) or commercial "cellulase 50,000" (a preparation from *Aspergillus* spec. by courtesy of "Schweizerische Ferment AG.", Basel), c. 2% in 1% aqueous acetic acid. Root tips which had been stored in 70% alcohol were first transferred for 1 hour to 1% aqueous acetic acid before treatment with any of the enzymes to eliminate the alcohol which otherwise inhibits the action.

THE TAXONOMIC POSITION AND RANK OF *ASPIDIUM NEVADENSE* BOISS.

We now report on a European fern whose morphology is intermediate between the members of the *D. filix-mas* and the *D. villarii* groups. It is therefore understandable that its proper classification caused difficulties even to expert pteridologists for more than 130 years. We refer to *Aspidium nevadense* Boissier (1838) found by that author in the Sierra Nevada (Southern Spain at c 8000′ (=c 2600 m)[1]). We were able to see the type (in G, see fig 2–3) and to also collect consepecific living material (plants and spores) from different localities (see below and fig 1), now in cultivation for detailed studies including cytological control. From this it is evident that Boissier was right in

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[1] Provided Boissier used French feet (pied de Roi 1′ = 32.4 cm: we thank Mr F. Badré, Paris, for information) as did Linnaeus (see Stearn 1966: 112–113).

FIGURE 1. ***Dryopteris tyrrhena*** **in situ, Corsica, Calanche de Piana: The** colony from which TR–3562 was collected. In the left lower corner are leaves of *Cyclamen neapolitanum. (Photo. H. & K. Rasbach 4.5.1971).*

describing the plant as a distinct species but, due to its intermediate morphology, later botanists reduced it to a subspecies, variety or forma of either *D. villarii* (e.g. Mettenius 1856–8, Moore 1858, Milde 1867, 1868) or of *D. filix-mas* (see synonymy). It was also a reason why Litardière (1924: 122–126) suggested the treatment of *D. villarii* as subsp. of *D. filix-mas,* a suggestion obviously not accepted by later authors.

Nomenclature

According to current nomenclature *Aspidium nevadense* Boiss. is a member of the genus *Dryopteris* Adanson. But according to the *Code* (Stafleu et al. 1972) it is unfortunately not possible to use the combination *D. nevadensis* (Boiss.) as Eaton (1878) described a different (American) species as *Aspidium nevadense.* This was of course an illegitimate name but Baker (1891) published for this plant the legitimate new name *Nephrodium nevadense* which was transferred to *Dryopteris* by Underwood (1893). The valid name for the American species under *Dryopteris* is therefore *D. nevadensis* (Baker) Underw. It is true that Christensen (1905: 281) suggested the name *D. oregana* C. Chr. for it, but this must be considered illegitimate for the above reasons. Despite the fact that the plant in the meantime has been transferred to another genus as *Thelypteris nevadensis* (Baker) Clute (see Morton 1958), we had to choose a new name for *Aspidium nevadense* Boiss.

TAXONOMIC TREATMENT

Synonymy and typification[2]

Dryopteris tyrrhena Fraser-Jenkins et Reichstein, **nom. nov.**

≡ *Aspidium nevadense* Boiss. (1838: 93–94) non *Dryopteris nevadensis* (Baker) Underw. (1893: 113).

≡ *Aspidium rigidum* "forma pinnatisecta" Milde (1867: 127), nomen invalidum.

≡ *A. rigidum* var. *pinnatisectum* Milde (1868: 362).

≡ *A. rigidum* var. *nevadense* (Boiss.) Luersen (1889: 408, 410 fig 150a, a pinna).

≡ *A. rigidum* "Rasse" *nevadense* (Boiss.) Ascherson in Ascherson & Graebner (1896: 30, 1913: 44).

≡ *Dryopteris rigida* var. *nevadense* (Boiss.) C. Christensen (1906: 84).

≡ *Nephrodium rigidum* subsp. *nevadense* (Boiss.) Rouy (1913: 409, footnote).

≡ *Dryopteris filix-mas* subsp. *rigida* var. *nevadensis* (Boiss.) Litardière (1924: 123).

≡ *D. villarii* var. *nevadensis* (Boiss.) Fiori (1943: 113 gives a good description but wrong figure with petiolated pinnules, corresponding to subsp. *pallida*).

— *Aspidium filix-mas* var. *glandulosum* auct. non Milde (1867: 123); see below.

— *Dryopteris filix-mas* var. *glandulosa* auct. pro parte, non (Milde) Briquet (1910: 10–11).

— *Nephrodium filix-mas* "race" *rigidoformis* auct. parte, non Rouy (1913: 408).

— *Dryopteris litardierei* sensu Rothmaler (1945: 94–95, pro hybr. *D. paleacea* x *pallida*) partim, excluso typo.

Type: *Aspidium nevadense* Boiss. (1838) Sierra Nevada, southern Spain, c. 8000' leg. Boissier April, 1837 (G), see figs 2 and 3.

Description of **D. tyrrhena**

Both Boissier's (1838) diagnosis and Milde's (1868: 362) description are excellent. Nevertheless the plant has frequently been confused since and we therefore give a detailed description, listing some characters in Table 1 which can be used to distinguish *D. abbreviata, D. filix-mas* and *D. villarii* subsp. *pallida* from *D. tyrrhena;* these also show the intermediate position of *D. tyrrhena* in some of these characters.

Diagnosis: A D. filix-mas differt: 1. lamina ad basim versus saepissime minus angustata; 2. segmentis secundariis (minoribus ad fines frondis pinnarumque exemptis) ± ovalibus, saepe magis distantibus, basi saepe paulum angustatis minusque confluentibus, apice ± rotundatis 0.5–1 mm longe acute denticulatis; 3. lamina indusiis rachidique inclusis utraque pagina pilis glanduliferis brevibus dense vestita.

Perennial plant, ± evergreen if not completely damaged by frost. Rhizome ascendent up to c. 2 cm thick, covered with scales at the apex, slowly branching, thus sometimes forming colonies up to 1 m diameter in suitable places. Ripe fronds similar to *D. filix-mas* but only c. 10–50 (–60) cm long and 4–10 (–16) cm wide. Petiole c. 1/4–3/4 as long as the lamina. Petiole and rachis like the rhizome densely covered with pale strawcoloured or light reddish brown, finely striped scales. Scales at the base of the petiole up to c. 1–2 cm long and 4–6 mm wide (fig 9). Lamina 1–2 pinnate, deltoid-lanceolate in outline (figs 2 & 4). Lowest pair of pinnae rarely the longest, usually a little shorter than the following ones, broadest part of the lamina usually just below the middle. Pinnae usually symmetrical (with acroscopic and basiscopic segments ± the same length) and

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[2] The following abbreviations are used: ≡ for homotypic synonyms, = for heterotypic synonyms, — for misapplied names (see below).

FIGURE 2. *Aspidium nevadense* Boiss. Original specimen in G.

divided in the manner of *D. filix-mas,* i.e. only the basal pair of segments completely separated from the next. Basal segments ± oval, often slightly auriculated but not or only scarcely petiolate; further segments similar but sessile and contracted at the base which becomes increasingly broader and decurrent higher up the pinna. Extreme forms of very big fronds have the largest basiscopic pinnules of the lowest pair of pinnae deeply dissect (as in *D. villarii* subsp. *pallida)* and c. 1.5–2 times as long as the acroscopic, thus making these lowest pinnae strongly asymmetric (fig 8). All pinna segments (except the very small ones) are usually more distinctly separated from each other and less fused at the base than in normal forms of *D. filix-mas,* their apex is ± circular, and finaly serrate with acute teeth, separated c. 0.5–1 mm from each other and tending to splay out after the manner of *D. abbreviata* but often curving inward at the tips (figs 3 and 6), the margins are more coarsely and partly twice dentate. Sori c. 1 mm diameter, 1–12 per segment crowded at the base of the segments, leaving the upper 1/3–1/2 bare. Indusia similar to those of *D. abbreviata* but slightly less convex and covered with glands over the whole surface, becoming lifted at the margin when the sporangia are ripening. Whole lamina on both sides including rachis, densely covered with shortly stalked glands, easily visible with a lens even after pressing. Spores bean shaped with distinct ridges similar to *D. villarii* in appearance (32–) 40–42 (–46) μm long (fig 10). Tetraploid (2n = 164), sexual, with 64 spores per sporangium.

TABLE 1. Some characters which usefully distinguish the four critical *Dryopteris* species, not including extreme forms.

	D. villarii subsp.[1] pallida	**D. tyrrhena** [2]	**D. filix-mas** [3]	**D. abbreviata** [4]
Length of ripe fronds, in cm	(10–) 30–70	10–50 (–60)	30–80 (–120)	20–70 (–90)
Relative length of pinnae versus base	not or scarcely reduced	usually a little reduced	usually distinctly reduced	tapering markedly often from as as far up as the the middle
Longest pairs of pinnae (counted from base)	number 1–5	number (1–) 3–6	number (4–) 6–14	number (6–) 8–16
Widest part of lamina	Much below the middle	Just a little below the middle	Just a little above the middle	Distinctly above the middle

(footnotes 1–4, see p 183)

continued on following page

	D. villarii subsp. pallida 1	**D. tyrrhena** 2	**D. filix-mas** 3	**D. abbreviata** 4
Base of the larger pinna segments (on lowest part of pinnae)	petiolate, usually with a stalk of 1–2 mm	The lowest pair separate from the next but not petiolate, the next pairs sessile but *not* fused	The lowest pair separate from the next but not petiolate the next pairs sessile ± *fused*	The lowest pair separate from the next but not petiolate the next pairs *not* fused
Apex of the pinna segments	narrow ± pointed with acute teeth	± circular with acute teeth often curving inward	usually narrow but not acute, sometimes round with acute teeth	usually round ± circular with obtuse-tipped spreading teeth
Margins of the pinna segments	coarsely and deeply lobate, lobes with acute teeth	partly distinctly lobate, lobes with acute teeth	usually shallowly lobate with acute teeth	usually shallowly lobate, with obtuse teeth
Sori: diameter(mm)	c.1 (–1.5)	c.1 (–1.5)	c. 1.2–2	c.1 (–1.5)
Amount of segment covered by sori	nearly to apex	c.1/2–2/3 (–3/4) of basal part	c.1/2–2/3 (–3/4) of basal part	c.1/2–2/3 (–3/4) of basal part
Indusium	convex at first, ± flat later, strongly glandular	convex at first, ± flat later, strongly glandular	usually ± flat, though somewhat convex when growing on dry or exposed conditions, glabrous	convex, glabrous except for glands on the margin occasionally.
Av. length of spores in μm^5	(28–) 30–34	(35–) 38–42	(36–) 40–46	(30–) 32–36 (–40)
Glandulosity of lamina and rhachis	both sides usually strong	both sides very strong	both sides ± glabrous	usually ± glandular particularly on the lower side, less so in Northern Europe
Scales on stipe	straw coloured or light reddish brown	straw coloured or light reddish brown	yellowish or reddish brown	reddish brown
Persistence of fronds through winter	always	nearly always	only in rare cases	never
Favoured habitats	limestone rocks, walls screes, sunny ± bushy places	N-exposed silicate rocks, caves, rocks, crevices, edged of screes	humus, woods but also in rocks, walls screes and road-sides	N-exp. silicate rocks, boulders, screes, near water courses, sometimes road-sides
Favoured altitudes	0–800 m	0–2000 m	0–2000 m	800–2000 m
Ploidy	2n = 82	2n = 164	2n = 164	2n = 82

(footnote 5, see p 183)

Footnotes to Table 1.

1 Common on Sardinia, absent or very rare on Corsica (see below).
2 Rather rare everywhere.
3 Rare on Sardinia more frequent on Corsica.
4 Often growing in big colonies on the higher mountains of Sardinia, Mt Gennargentu and Mt Limbara (CRFJ & TR 1974) but more frequent on Corsica.
5 Exospore measured without perispore, in balsam. Only good spores measured and not stunted or damaged ones. Contents of complete sporangia examined, having been collected from fronds that are just ripe, not residues from herbarium specimens.

INTERPRETATION AND TREATMENT OF *DRYOPTERIS TYRRHENA* BY FORMER AUTHORS

The identity of **Aspidium filix-mas** Sw. var. **glandulosum** Milde as **Dryopteris abbreviata**

D. tyrrhena is often found in many herbaria under names based on *Aspidium filix-mas* var. *glandulosum* Milde. It was therefore advisable to examine Milde's type even if for our purpose (to select a valid name for *Aspidium nevadense*) it was not strictly necessary. Milde quotes for his var. *glandulosum* the following two specimens "In Monte Gennargentu Siciliae[3] . *(Ascherson)*. Corsica (*Requien*)". We hesitate to select one as lectotype as the identity of the specimens is not completely certain. We do not know for certain whether Milde's first specimen still exists though it would seem to be identical with the specimen of *Ascherson* & *Reinhardt* in (B): "Steinige Abhange des Xuxu, Gennargentu Sardoa 1863" determined by Milde as var. *glandulosum* and mentioned in Fiori (1943: 100, translated into italian). CRFJ identified this specimen in (B) as *D. abbreviata.* He also saw three specimens of the second origin: "*Requien,* âout 1847 Forêt d'Aitone" (see Briquet 1910: 10) deposited in (B), (P) and (G) and identified all three as *D. abbreviata.* This species is rather common in the Forêt d'Aitone but in spite of careful search we (CRFJ & TR, July 1974) could not find *D. tyrrhena* there. Further arguments supporting the synomyny of *Aspidium filix-mas* var. *glandulosum* with *Dryopteris abbreviata* are:

1. Milde's description of var. *glandulosum* fits *D. abbreviata* much better than *D. tyrrhena* (except for glandular indusia, though *D. abbreviata* often has minute glands on the margins of the indusia).
2. We do not believe that such a careful worker as Milde would publish one and

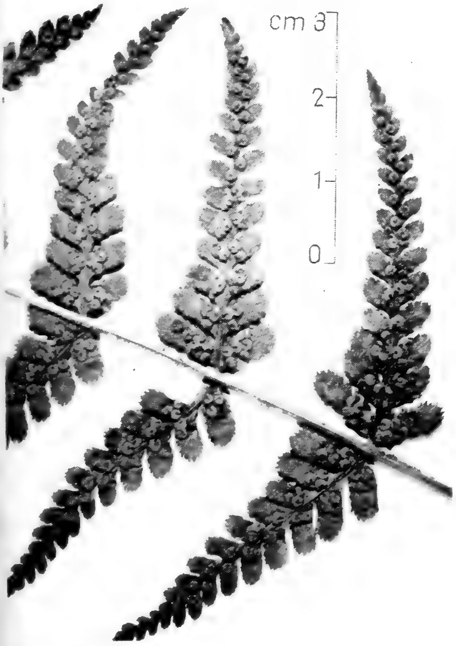

FIGURE 3. ***Aspidium nevadense*** **Boiss.** Single pinnae of original specimen (G) corresponding to fig 2. *(Photo. L. Jenny).*

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[3] This must be an error because Mt Gennargentu is in Sardinia, not in Sicily.

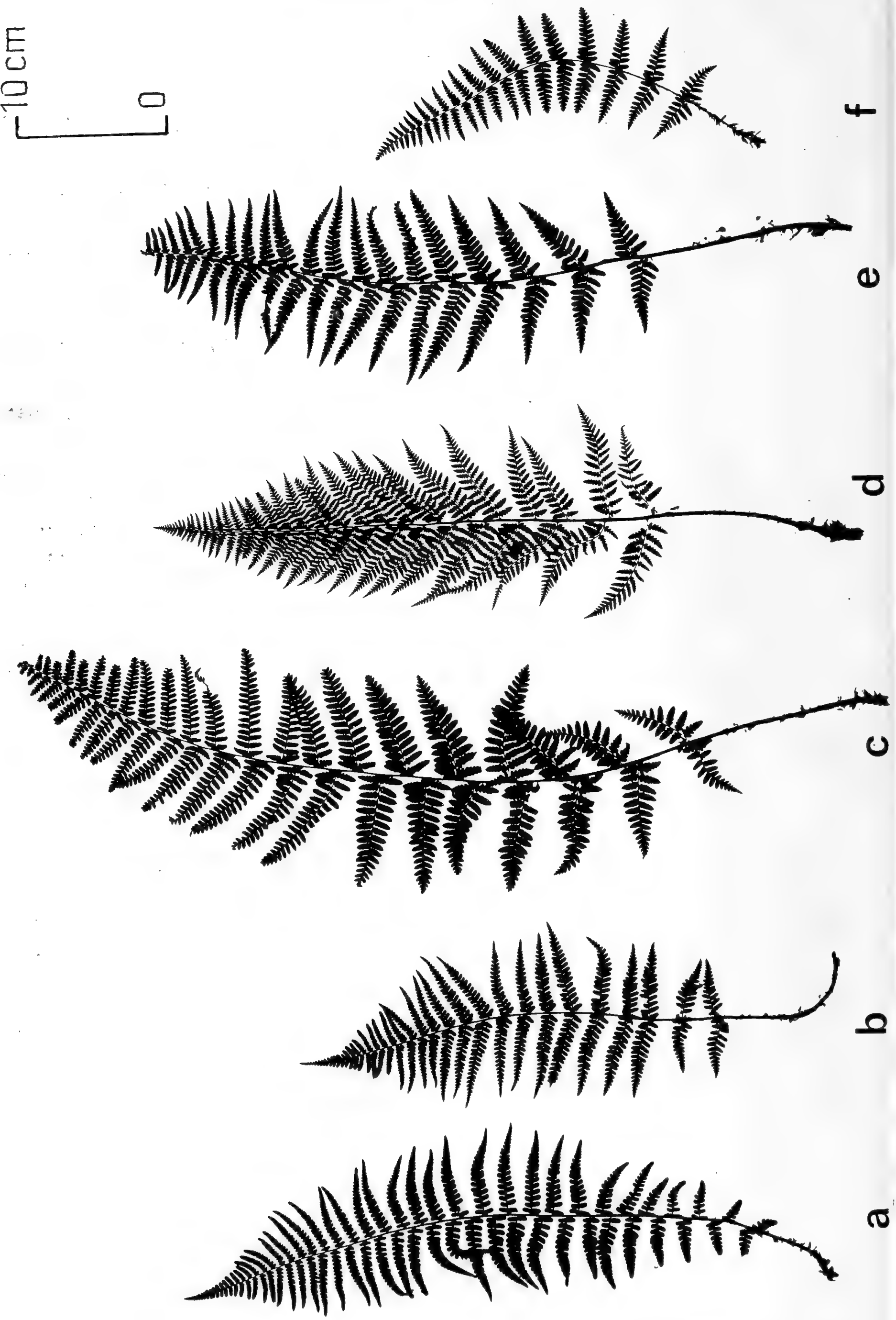

FIGURE 4. Silhouettes of fronds x c. 1/5. a, *D. abbreviata* 3558; b, *D. tyrrhena* 3562; c, *D. tyrrhena* hybrid 3789(4); d, *D. villarii* 4x 3568; e, *D.* x *sardoa* 3775; f, exp. hybr. GV579.

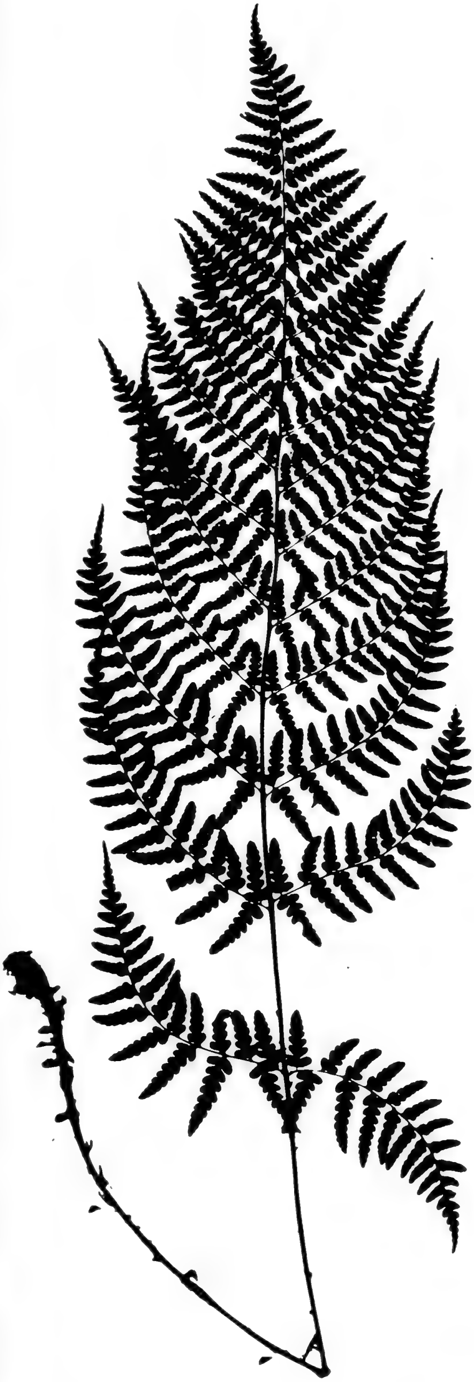

FIGURE 5. Silhouette of frond of *D. villarii* subsp. *pallida* CRFJ 2126, x c. $\frac{1}{5}$.

the same taxon *(D. tyrrhena)* under two different names *(Aspdium rigidum* forma *pinnatisecta* and *A. filix-mas* var. *glandulosum)* in the same publication.

3. *D. abbreviata* is much more frequent on Mt Gennargentu (Sardinia) than *D. tyrrhena*[4].

We are therefore confident, that Milde's *A. filix-mas* var. *glandulosum* is indeed what we call today *D. abbreviata* and that Milde did intend and was able to separate it well from *Aspidium nevadense* Boiss.

The identity of **Dryopteris litardierei** Rothmaler pro hybr.

Under this name we have seen only one specimen of *D. tyrrhena,* but it was an important one and we therefore discuss this taxon:

Dryopteris litardierei Rothm. was originally interpreted as a hybrid *D. paleacea* x *pallida* by Rothmaler (1945: 94–95), who cites: "Korsika, Evisa, Forêt d'Aitone, 1'100 m. *Sagorski* = Typus". This specimen (JE) was identified by CRFJ as *D. abbreviata.* The name *D.* x *litardierei* is therefore a synonym of the latter species. Rothmaler equates his putative hybrid with Milde's var. *glandulosum* and states that he has seen Milde's type. The three following specimens (in B), identified by Rothmaler as *D.* x *litardierei,* seen by CRFJ, were all *D. abbreviata:* 1. Forêt d'Aitone, Corsica *(Requien),* det. by Milde (1867: 123) as *Aspidium filix-mas* var. *glandulosum;* 2. Steinige Abhänge des Xuxu, Gennargentu, Sardoa *(Ascherson* & *Reinhardt* 1863) det. by Milde as var. *glandulosum;* 3.

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[4] The authors saw (July 1974) a big colony of *D. abbreviata* (more than 100 plants) on the N side of Bruncu Spina, beside a stream W of the new road at c. 1500 m alt. and only c. 0.5 km N of the lower ski-lift station.

Mte. Renoso, Corsica *(Requien).* But another specimen: Liguria, Riomaggiore, leg. *Bornmuller* (B), designated by Rothmaler as *"D. paleacea* x *pallida* Rothm. (Hybr. nova) Typus! (Original)" was identified by CRFJ as *D. tyrrhena.* Had Rothmaler selected this specimen as type in his publication (as he probably originally intended to do) we would have to use the name *D. litarierei* Rothm. for *Aspidium nevadense* Boiss.

Other attempts to distinguish the critical taxa

As mentioned above, Milde was able to distinguish his *Aspidium filix-mas* var. *glandulosum* (=*D. abbreviata*) from *A. rigidum* "forma pinnatisecta" (=*D. tyrrhena*). Some, but not all of his successors were able to do the same, to mention Litardière, Briquet, Rouy and Fiori.

Litardière (partly together with v. Tavel) has in his later publications (1924, 1928 and the three following not dated) probably distinguished "var. *nevadensis*" from "var. *glandulosa*". Of the many specimens he quoted (1924) for "var. *nevadensis*" we have so far examined only the 4 mentioned below (sub Corsica), all correct *D. tyrrhena.* Those he lists under "var. *glandulosa*" are probably all *D. abbreviata.* CRFJ examined several correctly determined collections of 1908 (P, CLF & BR) and the following, quoted in Litadière (1924: 125): "Corse, Massif du Rotondo: forêt de Polverella, ravin de la Tasseta. N.W. de Corte, 1,070–1.120 m. (*Litadière* 31. aout 1919)" (P), which was again correct *D. abbreviata.* The bulk of Litadière's herbarium, however, is owned by his family and has not been seen by us.

Briquet (1910: 10) does not mention *Aspidium nevadense,* but gives sub *D. filix-mas* var. *glandulosa* (Milde) Briq. the specimen of *D. tyrrhena* mentioned below (see p. 189) and eight other specimens, of which the five following have been seen by CRFJ and were all identified by him as *D. abbreviata: Requien* 1847 Forêt d'Aitone, Corse (G, B & P); *Lit.* (see Litardière 1908) Monte Grosso (CLF) Mt. d'Oro (P& BR); *Briquet* 1906 Mt. Rotondo, rocher a 2600 m, 6 aout (G); and 1908 Monte Asto, creux des roches, 1500 m. 1. juill. (G). These other localities given are: *Lit.* Vallon de Taita; Lac du Capo Felo; and Lago Maggiore sous le Capo al Berdate. However although these are mostly *D. abbreviata,* from notes written by Briquet on specimens in Geneva, it seems that *D. tyrrhena* was the nearest to his concept of var. *glandulosa,* being more glandular.

Rouy (1913: 408–409) does distinguish, theoretically, between *Aspidium nevadense* Boiss. and his *Nephrodium filix-mas* race *rigidoformis* (based on *A. filix-mas* var. *glandulosum* Milde) but quotes 4 specimens under the second name, of which the first *(Requien)* is *D. abbreviata,* the next (Forêt 'Asco) real *D. tyrrhena,* and the last two (Rotondo & Asto) again *D. abbreviata.* These specimens were determined by CRFJ at (G).

Fiori (1943: 100 & 113–114) distinguishes between *D. filix-mas* var. *glandulosa* and *D. villarii* var. *nevadensis.* One of the specimens he quotes sub var. *glandulosa* for Corsica (Foresta d'Asco) is *D. tyrrhena,* but most of the other ones are *D. abbreviata,* except "Piem.–Alpi Mar. fra Trappa e Garessio e pr. Ormea a Chioraira (Burn. ex Christ). CRFJ could find Burnat's specimens (in P), they were 3 *D. borreri* (with glands). Chioraira was also visited in June 1974 by H.L. and T. Reichstein, *D. filix-max* and *D. borreri* with hybrids are abundant but no other *Dryopteris* was seen.

Among the 7 specimens which Fiori (1943: 114) quotes for var. *nevadensis* only those from Elba and Capraia are correct *D. tyrrhena;* we have not seen "Is. d'Ischia (*Bolle* ex Bég.)", but "Laz. al M. Circeo, tra S. Felice ed il Faro (*Somm.*); "Sard. tra Ulassai e la V. del Tarquisara (*Somm.,* det Christ)" and "V. del Tarquisara (*Biondi*)", (all in FI) are *D. villarii,* most probably subsp. *pallida.* We have visited the two last mentioned localities (CRFJ & TR in July 1974). The altitude is from c. 740–800 m with limestone rocks. *D. villarii* is abundant, probably as subsp. *pallida* (but we cannot exclude some tetraploids, this will be checked when our living plants grown from spores can be counted). Among plants from these localities were a few which produced single fronds simulating *D. tyrrhena* rather well. Without careful control such fronds can easily be confused. But additional fronds from the same plant usually make identification much easier.

DISTRIBUTION OF *D. TYRRHENA*

We have unequivocal material of *D. tyrrhena,* including living plants or viable spores collected by ourselves or obtained from friends and have seen specimens in different herbaria, from the following places:

Southern Spain

Besides the three type specimens (in G) we have seen the following:

N-exposed silicate rocks above scree on southern side of upper Dilar valley, Western Sierra Nevada, at c. 2300 m alt. 6 Aug. 1974 leg *Fraser-Jenkins 4369* (BM). The species has already been collected in the same area by Spanish botanists, e.g. by *Clemente* "Bajolas peñas en las Lagunillas de Sierra Nevada" (MA). When identifying herbarium specimens it is important to remember that *D. filix-mas* and *D. villarii* (the tetraploid taxon) also grow on the Sierra Nevada the latter at slightly lower elevations and exclusively on limestone. Both *D. tyrrhena* and *D. villarii* are rare there (see below).

Sardinia

Massif of Mt Gennargentu: Mt Spada, silicate rocks on E face but near the NW ridge, mostly in crevicess or under overhanging rocks between c. 1400–1500 m alt. leg. *Fraser-Jenkins 4310* & *Reichstein 3776,* 25 July 1974; sporadic single plants or small groups, sometimes together with a few *D. abbreviata* and one hybrid (see below).

Sardinia, no exact locality, leg. *J. Bornmüller* (B; det. as var. *glandulosa* by Rothmaler). This is *D. tyrrhena.*

Corsica

1. La Trinite, WNW of Bonifacio: between granite boulders in a cave below a slight overhang at the base of the N facing cliff of the western peak at c. 150 m alt., huge, obviously very old colony, leg *H.L. & T. Reichstein TR–3088,* 16 June 1970. We found the place with a description and sketch obtained from J. Prudhomme, who had sent us in July 1967 a frond with spores from which progeny, *TR–2047,* were raised in Basel for cytological control. It was tetraploid, 2n = c. 164 (G.V. 1 June 1969; fig 11). Specimens of this plant (in BR, G and P) have been collected by *Stefani* 1912 at the same spot. The place was rediscovered independently by J. Vivant on 28 March 1967 who informed Prudhomme. *D. tyrrhena* (CRFJ 4345; TR–3789–5, 6, 10, 11, 13) grows there with fronds up to 60 cm long, some with strongly asymmetric basal pinnae (fig 8) together with a hybrid producing fronds up to 85 cm long (see 3789–4 in fig 4) and abortive spores, leg. *Fraser-Jenkins CRFJ–4346* and *Reichstein TR–3789–1, 2, 3, 4, 7, 8, 9, 12,* 31 July 1974. This hybrid may be *D. filix-mas* x *D. tyrrhena* and is being examined further.

2. Calanche de Piana: N-exposed scree with granite boulders c. 50 m below the road N–199 from Porto to Piana, c. 350 m west of the Auberge: "Les Roches Bleus"

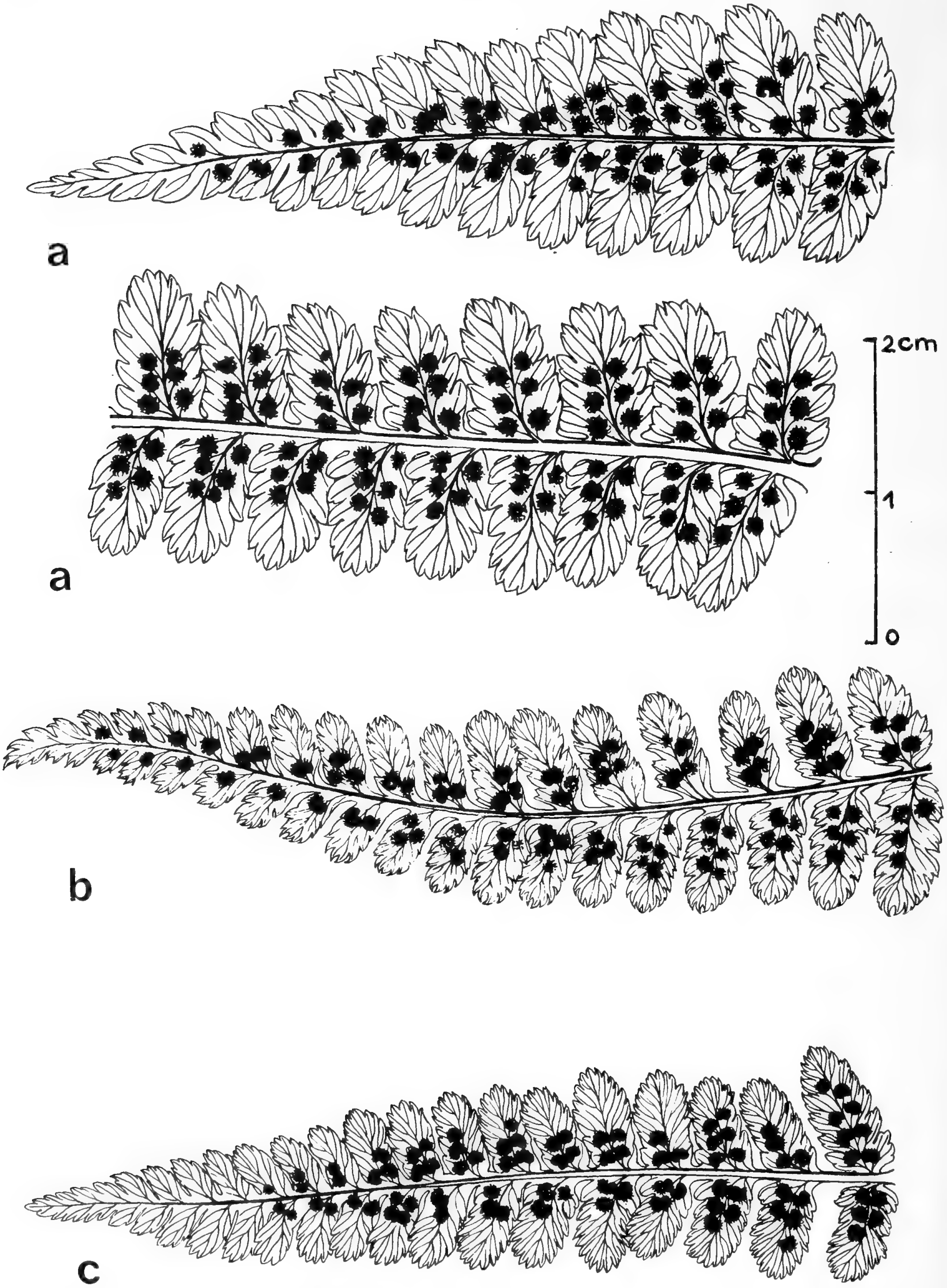

FIGURE 6. Pinnae from ± widest part of fronds cleared in c. 70% chloral hydrate to show venation; indusia are lost in this procedure. x 2, drawn by R. Hirzel. a, *D. filix-mas;* b, *D. tyrrhena* (CRFJ–4350), the inward curving of the segment teeth is somewhat exaggerated (this character is not always present but if visible is highly significant and only rarely present in a and c), detail x 4; c, *D. abbreviata* (3628).

c. 400 m. alt. 3 colonies, leg. *H.L. & T. Reichstein TR–3562,* 26 June 1973 following indications of H. & K. Rasbach who found this place, 4 May 1971 (see fig 1). Some other good plants were also found c. 80 m higher, i.e. above and south of the road in the rocks at c. 480 m alt. leg. *Fraser-Jenkins CRFJ–4350* and *Reichstein TR–3812,* 1 Aug. 1974.

3. Mt Renoso, près sommet. leg. *R. Deschatres* 1967.

4. Mt Renoso, Rocher près d'une pozzine sous le lac de Bastani al. 2050 m env. leg. *R. Deschatres* 8. août 1974.

5. South of Mt Cinto: Silicate rocks at the junction of the rivers Viro and Golo ("rives droites de chaque rivière"), c. 1 km SW of Albertacce, c. 820 m alt. leg. *R. Deschatres* 21 juillet et 9 août 1974; together with *D. abbreviata* and hybrids (see below).

6. Massif du Cinto (bassin sup. de l'Asco): Rochers sur la rive gauche de l'Asco près de la Résinerie de la forêt d'Asco 1200 m, leg. *Burnat, Briquet, St. Yves, Cavillier* et *Abrezol,* 20 juill. 1906 (G) sub *D. fillix-mas* var. *glandulosa* (Briquet 1910: 10).

7. Asco, Rochers au Pinzalone, au-dessous des bergeries d'Entrata, 1050 m env., *Litardière* 28 juill. 1921 (CLF) sub *D. filix-mas* subsp. *rigida* var. *nevadensis* (Litardière, 1924: 124).

8. Asco, Vallée de Violini, rochers 1100 m env. *Litardière* 25 juill. 1921 (CLF) sub same name.

9. Environs d'Asco, au Fornello di Grosso, rochers porphyriques, 1060 m env., *Litardière,* 22 juill. 1921 (P) sub *D. filix-mas* subsp. *rigida* var. *nevadensis* forma *rotundata* Lit. et Tavel, (Litardière, 1924: 124 et figs 2 & 4).

10. Asco, route de Stagno, Forêt de la Carozzica. leg. *J. Callé* & *R. Deschatres,* 10 août 1967.

11. Cap Corse: Southern slope of Mt Stello, near the small path from Pozzo to the Bocca di Santa Maria at the little shepherd's hut above a spring, c. 900 m. alt. between silicate rocks and boulders, localy abundant, leg. *H.L. & T. Reichstein TR–3551,* 22 June 1973 now cult. in Basel. Tetraploid n = c. 80 (G.V. 5.2.1974). We visited this place because of a specimen of *Jaquet* 1921 sub. *D. filix-mas* var. *glandulosa* (Milde) Briq. in (G) which was *D. tyrrhena.*

12. Cap Corse: Mt Canneto, versant SE rocher 1220 m env. *Litardière* 17 juillet 1921 (P) sub *D. filix-mas* subsp. *rigida* var. *nevadensis* (Litardière, 1924: 124).

Italy, mainland

Liguria, Riomaggiore (W of La Spezia) leg. *Bornmüller.* Specimen (B) designated by Rothmaler as "*D. paleacea x pallida* Rothm. (Hybr. nova) Typus! (Original)", discussed above.

Capraia

Fiori (1943: 113–114) gives for his *D. villarii* var. *nevadensis* apart from Elba (see below) the Is. Capraia, a Cala della Mortala. This specimen, *Sommier* 1896 sub. *Aspid. filix-mas* (FI) is *D. tyrrhena.*

Elba

Vineyard walls (silicate) and transverse ditch c. 50 cm deep, near Ripa Baretta W of Marciana Marina c. 110 m alt. 6 plants with fronds 13–45 cm long all fertile leg. *F. Mokry,* 24 May 1974. Spores sown in Basel *(TR–3730).* Fiori (1943: 113–114) gives this place correctly under his *Dryopteris villarii* var. *nevadensis* mentioning a specimen of *Sommier* (1900) sub. *Aspidium fil-mas* var. *glandulosum*. This specimen (in FI) has been confirmed as *D. tyrrhena.*

Obviously this list does not claim to be complete and we suspect that other specimens of *D. tyrrhena* may be found in different herbaria under different names. On the other hand other species, particularly *D. villarii, D. abbreviata* and *D. filix-mas* are often deposited in herbaria under some of the names used for *D. tyrrhena.*

DRYOPTERIS VILLARII ON CORSICA

As *D. tyrrhena* can be confused with abnormal forms of *D. villarii* and also when considering its possible parentage we were interested to know the distribution of *D. villarii* on Corsica. The result was unexpected.

Briquet (1910: 11–12) gives for his *D. rigida* Underw. var. *meridionalis* Briq. three localities: 1. Mt Cinto 2000–24000 m. (Briq. Rech. Corse 107 et exsicc. Burn. ann. 1900, n. 129); 2. col de Tavoria, 1600 m (Rotgès in litt.); 3. Pointe de la Monte, au-dessus du col de Verde, vernaies du versant W, 1600–1700 m (20 juill. 1906). We were able to see the first and third specimens in (G) (CRFJ–1973), these being *D. abbreviata:* The two last mentioned places were also visited by H. & K. Rasbach and H.L. & T. Reichstein on 26 and 27 July 1973. In both places *D. abbreviata* was growing abundantly. A living specimen (TR–3624) was collected at the Col de Taoria (c. 1600 m) and turned out to be diploid (2n = c. 80 det. G.V.). Both places consisted of granitic scree and boulders, the second with *Alnus viridis,* completely unlikely habitats for *D. villarii.* CRFJ has also seen specimens (in P) of Rotgès "Corse, Ghisoni, Col de Tavoria, 1400 m, 1 Sept. 1899", sub *Polystichum rigidum,* which were again *D. abbreviata.*

For his var. *australis* Briq. (= subsp. *pallida*) he also gives three places: 1. Châtaigneraies près de Bocognano, 600 m *(Briq.);* 2. forêt d'Ospedale (*Seraf.* ap. Viv. l.c.) and 3. Cime de la Chapelle de S. Angelo, rochers et balmes, 1100–1180 m. calc. 15 juill. 1906 et 13 mai 1907. The specimen from Bocognano is in (G) and is *D. abbreviata.* In summer 1970 CRFJ visited the place and found a few plants of *D. abbreviâta,* an extremely low altitude for this species in Corsica. In the forêt d'Ospedale we searched in vain for *D. villarii,* the rocks there are silicate and the soil acid, it is extremely unlikely that *D. villarii* would grow there. We have not yet found the original specimen *(Seraf.)*.

The only unequivocal specimens of *D. villarii* from Corsica we have seen (in G examined by CRFJ) came from the Cime de la Chapelle de S. Angelo. They are either subsp. *pallida* or the *tetraploid taxon.* A final identification is difficult without cytological control and curiously the plant has not so far been found again. The place is given with great precision and cannot be missed. The whole area (1100–1180 m) which corresponds with the top of the hill contains many shallow and deep cracks in the white karstic limestone pavement and is exposed in all directions. It is not a very large area and is an ideal habitat for *D. villarii.* The place was searched independently and rather carefully by Fraser-Jenkins on 13 July 1970 and again on 29 June 1973 by H.L. & T. Reichstein. No trace of *D. villarii* could be found. R. Deschatres, who has an excellent knowledge of the Island, told us that he had the same experience and also that he had never seen *D. villarii* in any other place in Corsica. The specimens in (G) show, however, that it must once have grown there but as a great rarity. In Sardinia, on the other hand, the species is rather common in most of the limestone areas (e.g. de Joncheere 1963), we have the diploid subsp. *pallida* from the east coast *(TR–117,*

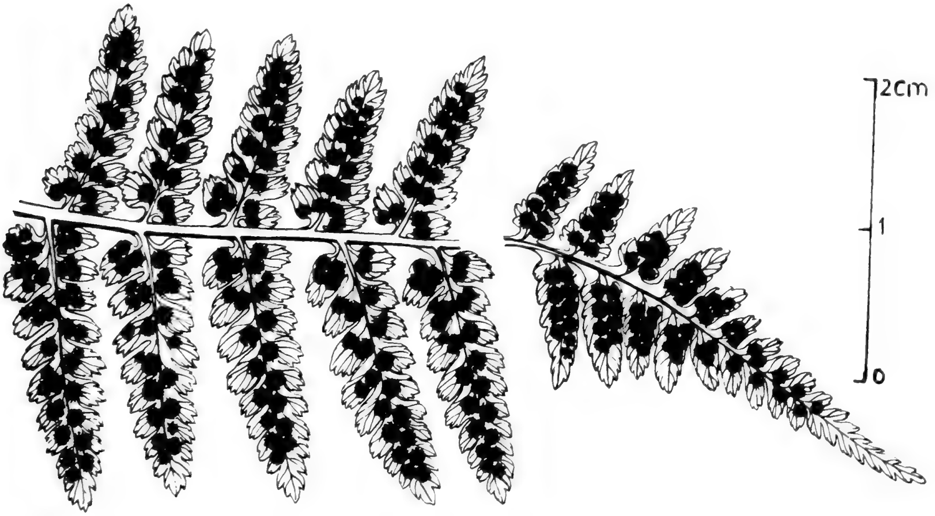

FIGURE 7. Base and apex of fertile pinna of *D. villarii* subsp. *pallida* TR–3588, cleared as in fig 5.

1.10.1959; n = 41 det. G.V.) but are not yet sure whether the tetraploid also grows on the island; the alpine diploid is very unlikely to be there and we have not seen any specimens of it from Sardinia.

POSSIBLE ORIGIN OF *D. TYRRHENA*

As pointed out in the introduction *D. tyrrhena* is intermediate in morphology between the members of the *D. filix-mas* and *D. villarii* groups and we suspect that it once arose from a diploid hybrid between a representative of each of these groups, with subsequent doubling of its chromosomes. Provided that the putative ancestors are still living and grow in Europe or not far from it, the most suitable candidates would be *D. abbreviata* and *D. villarii* subsp. *pallida.* Both are diploids and both are distinctly glandular albeit not usually as pronounced as in *D. tyrrhena.* But it is known that certain characters may be not only suppressed but sometimes enhanced by hybridisation. We suspect that subsp. *pallida* rather than the alpine dipl. subsp. *villarii* is the second ancestor because in *D. tyrrhena* the frond tapers only slightly towards the base, or sometimes not at all. The chances of finding a diploid hybrid of *D. abbreviata* x *D. villarii* subsp. *pallida* in nature are not very great because normally these species grow in quite different habitats. But it could be formed under special conditions, as when granite or schists and limestone meet near a water course and we have already seen single plants of *D. pallida* on granite in rare cases. Under present conditions it could perhaps form on Sardinia but not on Corsica.

Provided our hypothesis is correct it would be another example of how an alpine species *(D. abbreviata)* and a lowland one *(D. villarii* subsp. *pallida)* form an allopolyploid plant *(D. tyrrhena)* which grows from the lowland to high alpine level. An other example which is known is *Polystichum aculeatum* (L.) Roth. (growing from lowland to alpine level) which according to Manton (1950, see also Manton & Reichstein 1961) has arisen by chromosome doubling from a hybrid of the alpine *P. lonchitis* (L.) Roth., and the lowland *P. setiferum* (Forskål) Woynar. The relict type of distribution (rare and scattered with big gaps between different localities, partly in caves) suggests that *D. tyrrhena* is an old allotetraploid, perhaps formed at a time when

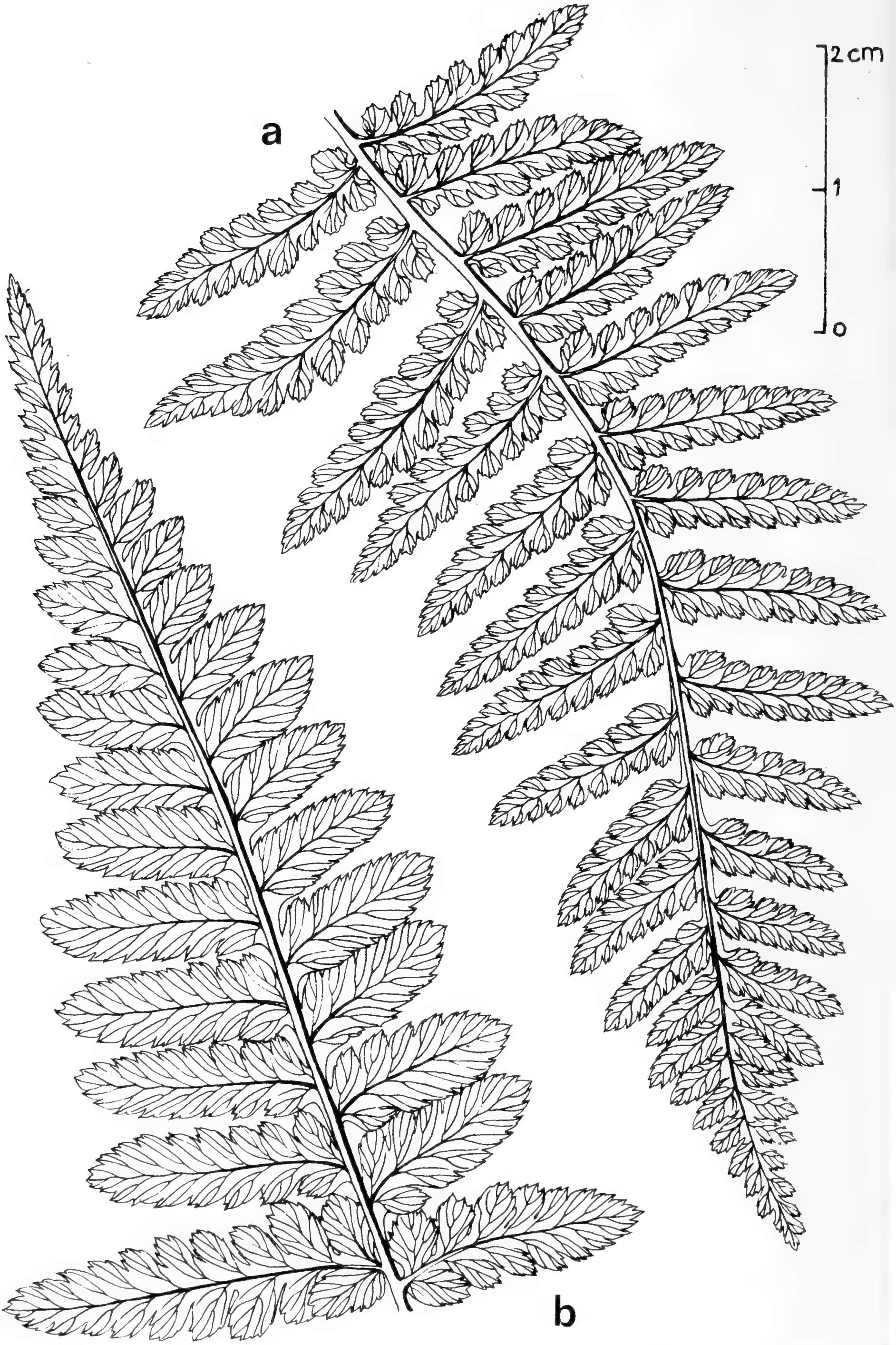

FIGURE 8. Lowest pinnae, cleared as in fig 5. a, *D. villarii* subsp. *pallida* (3588); b, extreme form of *D. tyrrhena,* strongly asymmetric (3789—10).

the putative parents were slightly different from the present representatives of the mentioned species.

To test this hypothesis we intend to examine the cytology of suitable hybrids. particularly their behaviour in meiosis. These experiments have only been recently started and need much time but we already have two important hybrids, a natural and an artificial one, which represent exactly the putative backcrosses which we need.

HYBRIDS

Dryopteris x **sardoa** Fraser-Jenkins & Reichstein, **hybr. nova** *(D. abbreviata* x *D. tyrrhena)*

Diagnosis: Planta hybrida media inter parentes praesumptos *D. abbreviatam* et *D. tyrrhenam* sed illi similior. Frondes validae ad 55 cm longae, eis D. abbreviatae similes. Ab hac distinguitur: 1. lamina ad basim versus minus angustata; 2. squamis latioribus (ad 8 mm); 3. sporis abortivis; 4. numero chromosomatum somaticorum c. 123.

Type: Sardinia, Massif of Mte Gennargentu, in crevices of the silicate rocks at the east face of Mt Spada near the NW ridge at c. 1500 m alt., close to a plant of *D. tyrrhena* and with a plant of *D. abbreviata* c. 10 m away, 25 July 1974. *Fraser-Jenkins* & *Reichstein 3775.* Holotype G; Isotypes B, BM, FI, K, P (fig 4). We took 2 pieces of rhizome, one (TR–3775) is cultivated in Basel and one (CRFJ–4309) in Abingdon.

Two or three plants of the same hybrid have been found by *R. Deschatres* in Corsica: south of Mt Cinto at the junction of the rivers Viro and Golo c. 1 km SW of Albertacce, c. 820 m alt. between the parents, 21 July and 9 August 1974.

The hybrid has characters intermediate between the two putative parents *D. abbreviata* and *D. tyrrhena* but is more similar to the former. The fronds are no more glandular than in *D. abbreviata* but in outline taper slightly less towards the base, the scales at the base of the stipe are a little wider (up to 8 mm, fig 9). For final determination it is essential to examine the content of ripe sporangia showing abortive

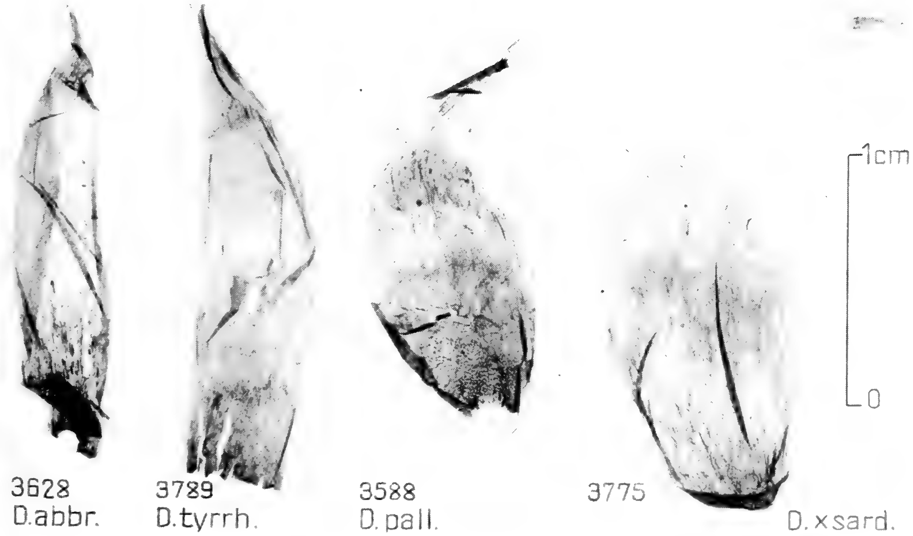

FIGURE 9. Scales from petiole bases. Left to right: *D. abbreviata; D. tyrrhena; D. villarii* subsp. *pallida; D. x sardoa. (Photo. L. Jenny).*

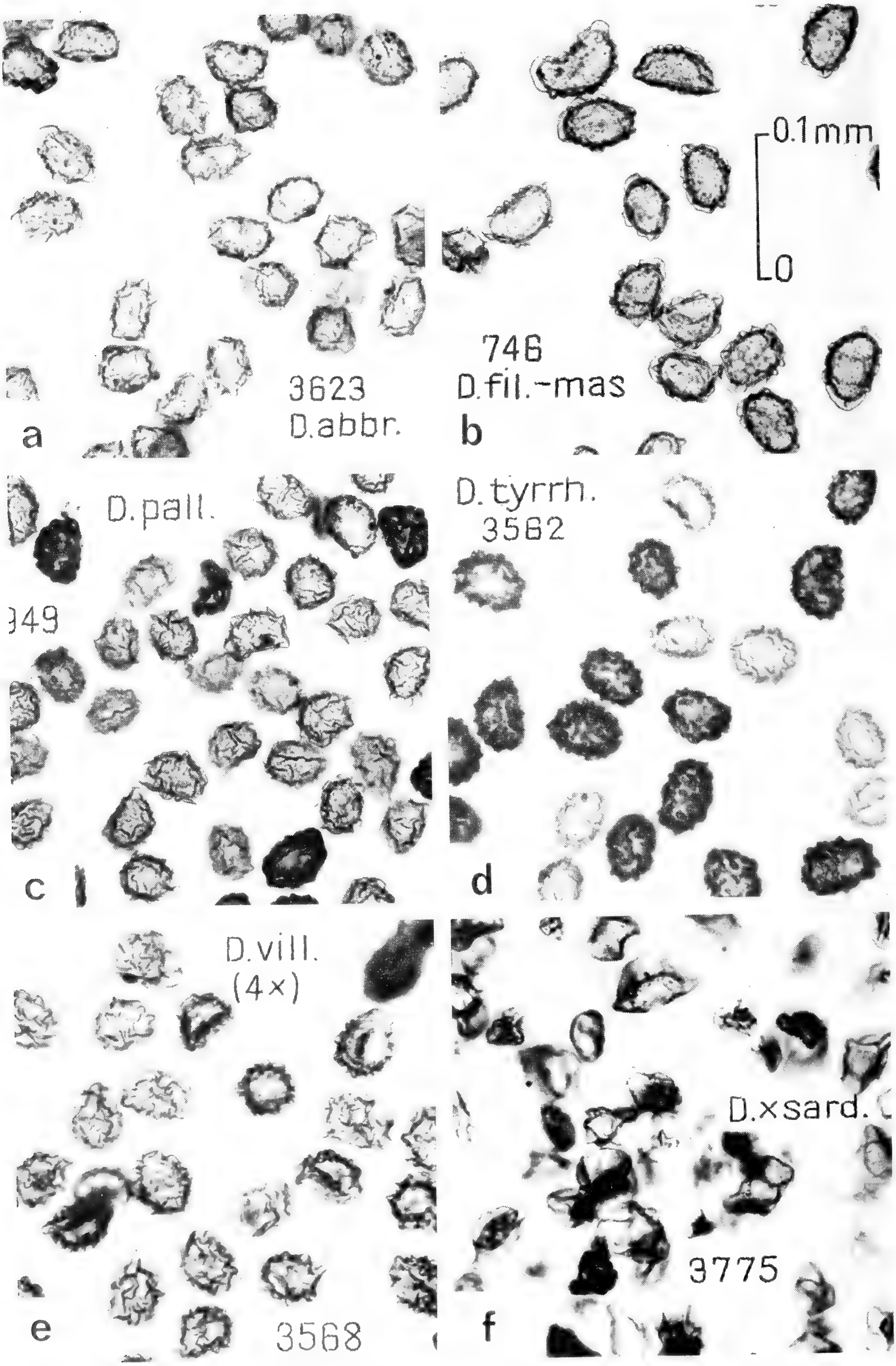

FIGURE 10. Contents of ripe sporangia x 200: a, *D. abbreviata;* b, *D. filix-mas;* c, *D. villarii* subsp. *pallida;* d, *D. tyrrhena;* e, *D. villarii* subsp. *villarii;* f, *D.* x *sardoa. (Photo. L. Jenny).*

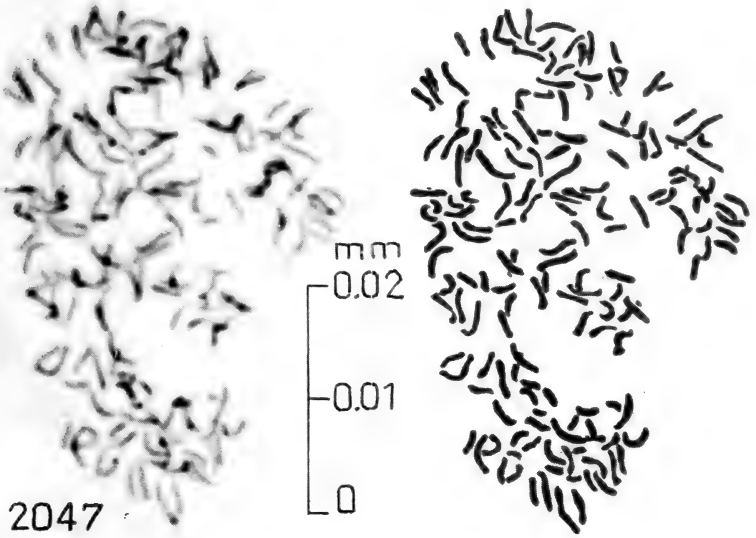

FIGURE 11. Mitosis of *D. tyrrhena*, showing c. 164 chromosomes, x c. 1500.

spores (fig 10). So far only mitosis has been examined. This shows that *D.* x *sardoa* is a triploid hybrid, as expected with c. 123 chromosomes. Further results will be published later.

Experimental hybrid GV–579 of **Dryopteris tyrrhena** x **D. villarii** subsp. **pallida**

This was produced by Vida in Budapest using methods similar to those described earlier by Lovis (1968). Prothalli of *D. tyrrhena* (TR–3088) were used as ♀ and of *D. villarii* subsp. *pallida* (TR–949) as ♂. The latter was raised in Basel from spores collected by E. Hauser on limestone rocks on Mt Bondone (N Italy, near Trento) c. 400–700 m alt. where it is rare; diploid (n = 41, det. G.V. 17 June 1969). Hybridisation was done on the 12 March 1971; 23 ♀ prothalli gave 2 hybrids. Fig 4 shows a frond and fig 12 the contents of ripe sporangia. Cytological examination showed that the plant is a triploid hybrid producing at

FIGURE 12. Sporangial content (abortive spores) of exper. hybrid GV–579, x c. 200. *(Photo. L. Jenny).*

meiosis c. 40 bivalents, the other chromosomes were present as univalents. Details will be given later.

CONCLUSION AND DISCUSSION

The above preliminary cytological results are compatible with the assumption that *Dryopteris tyrrhena* is an allotetraploid species formed originally from a diploid hybrid of *D. abbreviata* (genomic formula AA) with *D. villarii* subsp. *pallida* (PP) and therefore should possess the genomic formula AAPP. The back cross with *D. abbreviata* should be a triploid hybrid with the genomic formula AAP and should show at meiosis c. 41 pairs and c. 41 univalent chromosomes. Whether or not *D.* x *sardoa* will show this behaviour we hope to ascertain next summer. But the fact that this hybrid was found twice in nature at places where both parents grow together but are represented only by few plants makes it probable that this hybrid is formed easily. In the genus *Dryopteris* ready hybridisation has so far been observed only in those cases in which both parents contain a common genome (e.g. *D. abbreviata* x *D. filix-mas; D. assimilis* x *D. dilatata; D. carthusiana* x *D. dilatata* etc.). The relationship between *D. borreri* and *D. filix-mas,* which also hybridise readily, is not quite clear.

In a similar way the experimental hybrid of *D. tyrrhena* x *pallida* which should possess the formula APP, also shows the expected behaviour (c. 40 pairs). The proof in still missing so far that *D. tyrrhena* is an allo- and not an autotetraploid. Other hybrids will be necessary to prove this.

D. tyrrhena (sub. *D. filix-mas* var. *rigidoformis*) has also been subjected to chemical analysis (Widén et al. 1971). It contains in its rhizomes seven phloroglucides of which two, albaspidin and trispara-aspidin (together with traces of two others) are not present in *D. abbreviata* nor in *D. filix-mas* or *D. caucasica,* (see Widén et al. 1973) while desaspidin was absent in *D. tyrrhena* and in *D. abbreviata,* but present in *D. filix-mas* and in higher concentration in *D. caucasica.* These results fit very well with the fact that albaspidin and trispara-aspidin are found in relatively high concentration in *D. pallida* while only little desaspidin is present. This would be expected if the phloroglucides of *D. tyrrhena* are ± the sum of those present in its putative parents provided we assume that formation of para-aspidin (present in high concentration in subsp. *pallida* but lacking in *D. abbreviata* and *D. tyrrhena*) is inhibited in *D. tyrrhena* by the *D. abbreviata* genomes. Although chemical analysis can only be regarded as supplying one more character, these results are highly compatible with the assumption that *D. tyrrhena* contains two genomes each of *D. abbreviata* and *D. villarii* subsp. *pallida* and they also correlate well with the assumption that *D. filix-mas* contains two genomes each of *D. abbreviata* and *D. caucasica.* Final proof must come from cytological analysis of all the necessary hybrids.

Acknowledgements

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APPENDIX

Origin of plants used in the figures if not mentioned before:

TR– 746=*Dryopteris filix-mas,* Germany, Black Forest, Wiesental, between Zell and Schonau, c. 480 m alt., common, leg T. Reichstein, 7.10.1962.

TR– 949=*Dryopteris villarii* subsp. *pallida,* Italy Mt. Bondone, N of Trento, bushy place above limestone c. 400–700 m alt. rare, leg E. Hauser, 1962 cult. in Basel since 12.9.1963. n=41 (G.V. 17.6.1969).

TR–3558=*Dryopteris abbreviata,* Corsica, Forêt d'Aitone, along the road, c. 1330 m alt. common, leg H.L. & T. Reichstein, 25.6.1973, since then cult. in Basel.

TR–3568=*Dryopteris villarii* tetraploid taxon, France, Caussols, N of Grasse, deep cracks in limestone pavement, c. 1150 m alt. leg H.L. & T. Reichstein, 1.7.1973 since then cult. in Basel. 2n=c. 160 (G.V. 26.10.1973).

TR–3588=*Dryopteris villarii* subsp. *pallida,* Italy Abruzzi, Gole del Sagittario bushy place above limestone rock, c. 750 m alt. leg P. Brownsey, H. & K. Rasbach & T. Reichstein, 18.7.1973, since then cult. in Basel.

TR–3623=*Dryopteris abbreviata,* Corsica, Col de Taoria (N of Col de Verde) granitic block scree c. 1600 m alt. leg. H. & K. Rasbach, H.L. & T. Reichstein, 27.9.1973, since then cult. in Basel. 2n=c. 80 (G.V., 27.10.1973).

TR–3628=*Dryopteris abbreviata,* Corsica, Pointe de la Monte, E of Col de Verde grantic block scree with *Alnus viridis* c. 1700 m alt. H. & K. Rasbach and H.L. & T. Reichstein, 28.9.1973.

CRFJ–2126=*Dryopteris villarii* subsp. *pallida,* Turkey, Antalya, Irmasan Pass N of Akseki, c. 1500 m. alt. leg. C.R. Fraser-Jenkins, 21.8.1970. n=41 (CRFJ 1.6.1974).

No number in fig 6=*Dryopteris filix-mas,* wild collection cult. in Basel.

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Original papers, articles, or notes of any length on any aspect of pteridology will be welcomed from members and non-members and considered for publication. Manuscripts should be in English, and headed with a title, the surname(s) and initials of the author(s) (female authors may use one given name in full, if so wishing) and address, as appropriate.

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NOTES ON SOME MASCARENE SPECIES OF ELAPHOGLOSSUM (LOMARIOPSIDOIDEAE SENSU HOLTTUM)

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ABSTRACT

The preparation of an account of the fern genus *Elaphoglossum* in the Mascarene area has brought to light certain problems. This article deals with the taxonomy of *Elaphoglossum lanatum,* the leptotypification and taxonomy of *E. lepervanchii* and the leptotypification of *E. sieberi.*

INTRODUCTION

The preparation of an account of the fern genus *Elaphoglossum* for the forthcoming "Flore des Mascareignes" has brought to light certain problems which are dealt with in the following notes. Abbreviations used herein are in accordance with those found in the "Index Herbariorum" ed. 5, with the exception of REU, which is used as an abbreviation for the "Herbier du Centre d'Enseignment Supérieur Scientifique (Ile de la Réunion)".

THE TAXONOMY OF ELAPHOGLOSSUM LANATUM

Elaphoglossum lanatum (Bojer ex Baker) Lorence, *comb.* & *stat. nov.*

Basionym: *Acrostichum viscosum* Sw. var. *lanatum* Bojer ex Baker, Fl. Maurit. & Seych.: 512 (1877).
Holotype: Mauritius, *Bojer* s.n., "Acrostichum lanatum nob. Hab. in rupibus, et ad rivulorum ripas in ins. Mauritii au quart. *Moka,* juxta Bois Chéri" (four left-hand collections, excluding two right-hand fertile fronds, Herb. Hook. K!).

Elaphoglossum lanatum was originally collected in Mauritius by Bojer who considered it to be a new and distinct species, a fact which he noted on several of his gatherings. The plant was subsequently described by Baker (1877) and treated as a variety of *Acrostichum viscosum* Sw., for which he gives *A. salicifolium* Willd. ex Kaulf. as a synomym.

The latter species, *A. salicifolium,* was transferred to the genus *Elaphoglossum* by Hieronymus as a variety of *E. viscosum.* More recently Schelpe (1969) has considered it to be a subspecies of *E. petiolatum* (Sw.) Urban *E. petiolatum* ssp. *salicifolium* occurs in Africa and the adjacent islands, and, according to Schelpe, forms "a reasonably distinct segregate of a world-wide *E. petiolatum* complex with small, variously shaped laminar species". Furthermore, it is a strictly free-veined species, bears scattered acicular, substellate laminar scales and occurs as an epiphyte on trees and rotting logs.

On the other hand, *Acrostichum viscosum* var. *lanatum* has not, to my knowledge, been transferred to the genus *Elaphoglossum* to which it belongs. Although it shows certain affinities with *E. petiolatum* ssp. *salicifolium,* the following differences are sufficient for it to merit specific status. It is unique in being the only Mauritian *Elaphoglossum* that is rupicolous and grows exclusively on vertical river banks and cliff faces composed of decaying lava, a fact noted by Bojer on his type specimen ("in rupibus et ad rivulorum ripas"). Apparently endemic to Mauritius, it is a viable species forming large but localized colonies, and there is also evidence that it hybridises with other species of the genus. It possesses arachnoid laminar scales with long, more or less tangled cilia (fig. 1g) which are quite dense and matted on young fronds (fig. 1b), thus imparting a characteristic lanate appearance not found in *E. petiolatum* ssp. *salicifolium.* Finally, in *E. lanatum* a certain percentage of the veins reunite into simple intramarginal arcs, the rest being free. This trait is quite variable, some specimens being predominantly free-veined, others not. Both the extremes and the intermediates may, in fact, occur on the same plant as they do in Bojer's type specimen.

Material Studied

MAURITIUS. *Bojer* s.n., Bois Chéri (K-holo); *Bojer* s.n., ex ins. Mauritii (K); *Bojer* s.n., Bourbon, *pro parte* (K, mixed collection, origin probably Mauritius); *Anon.* in MAU 16849 (MAU); Mare Longue Plateau, *Lorence* in MAU 15014 (MAU, P); ibid., *Lorence* in MAU 15243 (MAU, K, P. REU); Cascade 500 pieds, *Lorence* in MAU 15241 (MAU); Tamarin Falls Reservoir, *Lorence* in MAU 15823C (MAU); Black River Gorges, *Lorence* in MAU 15533 (MAU, REU); Le Pouce Mt., *Lorence* 21.1 in MAU 16280 (MAU); Perrier Nature Reserve, *Lorence* 17.2 in MAU 15830 (MAU); Bel Ombre forest, *Lorence* 1406A in MAU 17542 (MAU).

THE LECTOTYPIFICATION AND TAXONOMY OF ELAPHOGLOSSUM LEPERVANCHII

Elaphoglossum lepervanchii (Fée) Moore, Ind. Fil.: 11 (1857); Tard. in Notul. Syst. 15 (4): 428, pl. 2, fig. 8–11 (1959). Type: Réunion, *collector?* (Herb. Bory no. 27, 14 right-hand specimen, P-lecto!)

> *Acrostichum lepervanchii* Fée, Mém. Fam. Foug. 2: 37, pl. 9, fig. 1 (1845).
> *Acrostichum conforme* sensu Bojer, Hort. Maurit.: 412 (1837); sensu Baker, Fl. Maurit. & Seych.: 511 (1877); sensu Cordemoy, Fl. Reun.: 93 (1895), *non* Sw.
> *Acrostichum ovalifolium* Bojer, Hort. Maurit.: 414 (1837), *nom. nud.* Type: Mauritius, *Bojer* s.n. (K!)
> *Acrostichum didynameum* Fée, Mém. Fam. Foug. 2: 37, pl. 16, fig. 2 (1845). Type: Réunion, *Lepervanche-Mézière* s.n. (Herb. Bory no. 27, 13–P!).
> *Elaphoglossum didynameum* (Fée) Moore, Ind. Fil.: 8 (1857); Tard. in Humbert, Fl. Mad. 5^e Fam. 2: 26, pl. 11, fig. 1–2 (excluding pl. 11, fig. 3)4) (1960) *pro parte; synon. nov.*
> *Acrostichum latifolium* sensu Baker, Fl. Maurit. & Seych.: 511 (1877) *non* Sw.
> *Acrostichum curtisii* Baker in Ann. Bot. 5: 489 (1891). Type: Madagascar, *Curtis* 121 (K!).
> *Acrostichum borbonicum* Baker in Ann. Sot. 5: 491 (1891). Type: Réunion (Bourbon), *Balfour* 27 (K!).
> *Elaphoglossum borbonicum* (Baker) C.Chr., Ind. Fil.: 303 (1905).
> *Elaphoglossum curtisii* (Baker) C.Chr., Ind. Fil.: 305 (1905); Dansk. Bot. Ark. 7: 165 (1932); Tard. in Humbert, Fl. Mad. 5^e Fam. 2: 36, pl. 11, fig. 5–6 (1960); *synon. nov.*
> *Elaphoglossum latifolium* sensu C.Chr. in Trans. Linn. Soc., ser. 2, Bot. 7: 420 (1912), *non* (Sw.) J.Sm.
> *Elaphoglossum conforme* sensu C.Chr. in Trans. Linn. Soc. ser. 2, Bot. 7: 420 (1912), sensu Tard. in Humbert, Fl. Mad. 5^e Fam. 2: 35 (1960) *pro parte, non* (Sw.) Schott.
> *Elaphoglossum angustatum* sensu Tard. in Humbert, Fl. Mad. 5^e Fam. 2: 38, (including pl. 10, fig. 1–3) (1960) *pro parte, non* (Schrad.) Hieron.

Elaphoglossum lepervanchii (Fée) Moore is an extremely polymorphic species and there is evidence to suggest that this variability, as expressed primarily in size and shape of lamina and stipe: 1 lamina length, is to a large degree a function of age and response to environmental factors. *Elaphoglossum lepervanchii* and *E. didynameum* were both described concurrently under the genus *Acrostichum* by Fée (1845). It is accordingly decided to retain the epithet *lepervanchii* because Fée's type and description are most representative of the species as a whole.

The holotype specimen of *E. lepervanchii* (Réunion, *Lepervanche-Mézière* 1834, in herb. Bory) was not located at the Muséum National d'Histoire Naturelle, Paris in 1972, nor was it found during a further search in 1975 (Badré, pers, comm.). As a result, the specimen figured by Fée (op. cit.: 37, pl. 9, fig. 1) that is, Réunion *collector?* (Herb. Bory no. 27, 14 P) and bearing in his manuscript the annotation "Acrostichum lepervanchii, F. mém, sur les acrostich.

ERRATUM in Fern Gaz.11:201 (1976): Amend caption to read:

> . . . (d, fertile frond;) e, scale from rhizome x 25; f, scale from stipe x 50; g, scale from sterile lamina x 50.

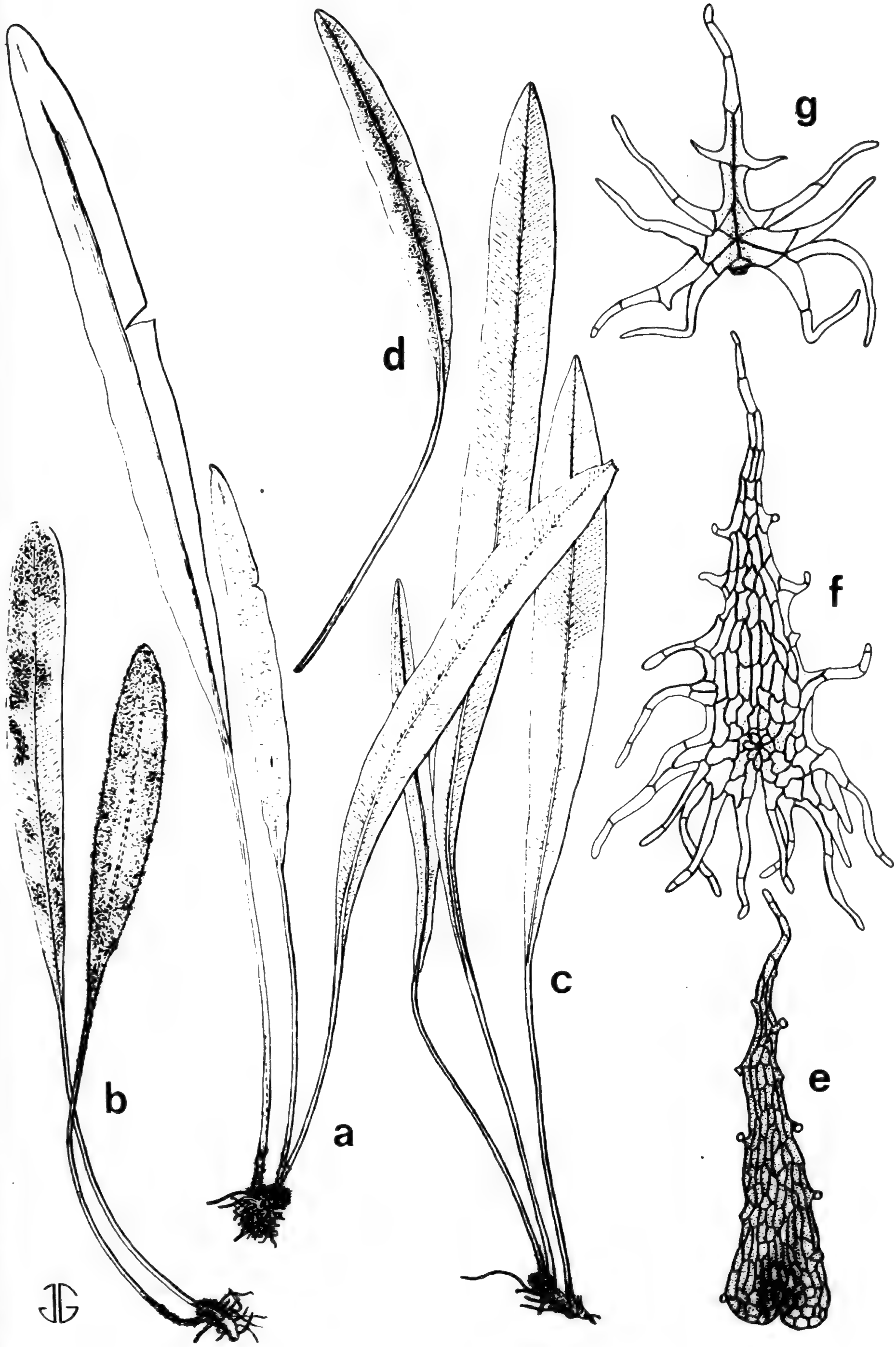

FIGURE 1: *Elaphoglossum lanatum* (*Bojer* s.n. "Bois Chéri", holotype): a, c, fertile plants; b, sterile plant showing densely scaly young fronds; d, fertile frond; e, scale from rhizome x 25; f, scale from stipe x 50; g, scale from sterile.

Tab. 9. C'est là le specimen lithographié dans l'ouvrage cité (signed) Fée", is hereby chosen as lectotype. This is in accordance with the International Code of Botanical Nomenclature (1966 ed.). The lectotype collection consists of two fertile fronds with attached rhizomes mounted to the left (not figured by Fée), and to the right is a plant bearing four clustered sterile fronds and one fertile (although Fée's illustration shows only two of the sterile fronds). The sterile lamina are elliptic to slightly ovate-elliptic, 9–13.5 x 3.5–4.5 cm, and borne on stipes 2.5–4.5 cm long. The fertile lamina is anguste-elliptic, 8 x 1.6 cm, on a stipe 8 cm long. The sterile lamina has free veins with thickened tips, revolute margins with a distinct brown and cartilaginous border, and the lower surface bears scattered tiny, brown, irregularly substellate scales with glandular-tipped cilia. Somewhat larger and darker scales, subulate with a stellate base, are scattered along the lower surface of the midrib. The fertile frond is much narrower than the sterile, and on a stipe two to three times as long.

The rhizome scales are pale brown to rufous, curling, ovate to linear, 2–5 x 0.5–1.5 mm, with often involute margins bearing more or less long and tortuous glandular-tipped cilia. The scale are composed of a network of thin-walled rectangular cells arranged in rows, often with transverse bands of shorter, squarrish cells. Similar scales are also present on the lower part of the stipe. The rhizome is 4–5 mm thick and bears two dorsal rows of fronds.

Suboptimal environmental conditions appear to cause arrested frond development in *E. lepervanchii.* Mascarene plants growing under more or less exposed conditions subject to repeated drying in *Philippia-Phylica* heath formations or in clearings, for example, are characterized by having fronds resembling those found on juvenile plants. The lamina is usually xeromorphic, elliptic to ovate-elliptic with obtuse apex and strongly decurrent base, margins somewhat inrolled, texture coriaceous, the stipes are short, 1/4 to 1/3 as long as the lamina and the rhizomes are short-creeping. The type of *Acrostichum ovalifolium* (Mauritius, *Bojer* s.n. (K)) is representative of this form.

Under growing conditions protected from drying, e.g. in moist, shady *Sideroxylon* formations, *E. lepervanchii* may attain a maximum frond size of 60 x 6 cm, the stipes being 1–1.5 times the laminar length, lamina elliptic to anguste-elliptic, apex acute to acuminate, base anguste-cuneate and decurrent as low ridges or lines along the upper 1/2 to 2/3 of the stipe, texture subcoriaceous, the rhizome moderately long-creeping with fronds up to 1 cm or more distant (Mauritius, *Lorence* in MAU 15826 (MAU, K, P, REU); Mauritius, *Vaughan* in MAU 12511 (MAU, K, P)). One of the author's collections (Mauritius, *Lorence* in MAU 15828 a-h (MAU)) consists of plants growing on a dry, exposed top of a tree stump (including a fertile individual with sterile fronds only 3–4 cm long), ranging to those rooting in moist humus in shade at the base of the stump (including plants with sterile fronds 28 cm long). This shows well how the plant's growth habit is influenced by the habitat. Transplant experiments were also carried out showing that these depauperate forms gradually progressed into robust mature plants.

Two other species subsequently described by Baker obviously only represent forms of *E. lepervanchii.* The type of *E. borbonicum* Baker (Bourbon (= Réunion), *Balfour* 27 (K)) is a juvenile plant of *E. lepervanchii* possessing rhomboid-ovate to rhomboid-elliptic obtuse fronds strongly decurrent at the base, stipes shorter than or equalling the lamina, and a short-creeping rhizome with clustered fronds. *E. lepervanchii* is often precociously fertile and individuals possessing sterile fronds only 4–6 cm long may produce fertile fronds, as seen in the type collection of *E. curtisii* Baker, upper right hand plant (Madagascar, *Curtis* 121 (K)). Larger plants on the same collection show increased stipe length (1–2 times laminar length) and larger, rhomboid-ovate to rhomboid-elliptic lamina. The fertile frond is narrower and on a stipe 1.5 times that of the sterile. Similarly, the type of *E. didynameum* (Fée) Moore (Réunion, *Lepervanche-Mézière* s.n., in Herb Bory 27, 13 (P)) as shown in Fée's illustration (op. cit.: 37, pl. 16, fig. 2) is a form exhibiting short stipes, narrowly elliptic sterile fronds with acuminate apex and attenuate, decurrent base. The fertile frond has a long stipe, 1.5–2 times that of the sterile, hence the specific name "didynameum".

As in *Elaphoglossum lepervanchii,* the types of *E. borbonicum, E. didynameum* and *E. curtisii* all possess lamina with free veins, bearing scattered tiny glandular-ciliate scales on the lower surface, and characteristic pale brown to rufous, soft, curling rhizome scales with glandular-tipped marginal cilia. When numerous specimens are examined all are seen to possess similar frond and rhizome scales, the differences in size and frond shape intergrade, and it becomes apparent that we are dealing with a single extremely polymorphic species.

In the Mascarenes, *E. lepervanchii* is allied to *E. sieberi* (Hook. & Grev.) Moore in Mauritius and to *E. macropodium* (Fée) Moore in Réunion. The latter two species are distinguishable by their veins which reunite into simple arcs or a commisure along the margin (the Aconiopteroid condition), their extremely thick and short-creeping rhizomes with large scales that are in *E. sieberi* dark brown, 1.0–1.5 cm long with filiform tips and more or less entire margins, and in *E. macropodium* yellowish-brown, 1–2 cm long with entire margins. *E. lepervanchii* also occurs in Madagascar and the Seychelles.

Material Studied

MADAGASCAR. Paralima, *Boiteau* 3006 & 3009 (P); vallée de la Mandraka, *Corréard* s.n. (P); district d'Ambatondrazaka, *Cours* 126 = ANK 100 (P); *Curtis* 121 (K-types of *Acrostichum curtisii*); forêt d'Ambohitantely, *Decary* 7476 (P); province de Mananjary, *Geay* 95 (P), ibid., *Geay* 8300 (P); *Hildebrandt* s.n. (K); central plateau, *Hodgkin & Stansfield* s.n. (K); massif de l'Andrangovalo, *Humbert* 17676 (P); massif de Anjanaharibe, *Humbert* 24657 (K, P); massif de Ankarata, *Humbert* 30265, 30266 (P); vallée du Mandraka, *Humbert* 20501 (P); massif de Marojejy, *Humbert* 22506 (P); montagne au nord de Mangindrano, *Humbert* 24930 (P, K); 25186 (P); forêt d'Analamazoutra, *Perrier de la Bâthie* 6128 (P, centre and right-hand collections), ibid., 6150 (P), ibid., 11914 (P); massif de Manongarivo, *Perrier de la Bâthie* 78608 & 7860E (P); Antananarivo, *Poole* 4/76 (K); Ambohimanza, Raharijaona 12 (P).

MAURITIUS. *coll.?,* in MAU 16927 (MAU); *Bojer* s.n. (K-type of *Acrostichum ovalifolium*); *Bojer* s.n. (K); *coll?* ex Herb. Dorfler 1137 (P, two sheets); Crown Land Declerc, *Julien* in MAU 13318 (MAU); Plaine Champagne/Chamarel road, *Julien* in MAU 14640 (MAU); Piton Grand Bassin, *Lorence* in MAU 14589 (MAU); Macabé/Brise Fer road, *Lorence* in MAU 14588 (MAU); Pétrin Nature Reserve, *Lorence* in MAU 14590 (MAU); ibid., *Lorence* in MAU 14600 (MAU); ibid., *Lorence* 18.3 in MAU 15812 (MAU, K, P, REU); ibid., *Lorence* 1.8 in MAU 15820 (MAU); ibid., *Lorence* 12.1 in MAU 15822 (MAU, K, P, REU); ibid., *Lorence* 2.1 in MAU 15826 (MAU, K, P, REU); ibid., *Lorence* 1.6 in MAU 15827 (MAU); ibid., *Lorence* 1.9 a-h in MAU 15828 (MAU); ibid., *Lorence* 2.8 in MAU 15829 (MAU, K, P, REU); Bassin Blanc, *Lorence* in MAU 14607 (MAU); ibid., *Lorence* in MAU 14610 (MAU); ibid., *Lorence* in MAU 14611 (MAU); ibid., *Lorence* 828 in MAU 16319 (MAU); Plaine Champagne/Chamarel road, *Lorence* in MAU 14722 (MAU); ibid., *Lorence* in MAU 15103 (MAU); ibid., *Lorence* 14.1 in MAU 15811 (MAU, K, P, REU); Black River Gorges, *Lorence* in MAU 14880 (MAU, K, P); Plaine Champagne, *Lorence* in MAU 15010 (MAU, K, P); ibid., *Lorence* 2.3 in MAU 15831 (MAU); Mare Longue Plateau, *Lorence* in MAU 15242 (MAU, REU); Pétrin/Macabé road, *Vaughan* in MAU 12551 (MAU, K, P); *Wallich* s.n. (K).

REUNION (BOURBON). Brûlé, *Bedier* 52 (P, right-hand specimen); *Boivin* s.n. (P, three sheets); *Collector?,* ex Herb. Bory 27, 13 (P); ibid., 27, 14 (P-lectotype of *E. lepervanchii*); Brûlé de St. Denis, *Cadet* 2950 (REU); Cilaos, *Coode* 4938 (K); *Frappier* s.n. (P);

Gaudichaud s.n. (P); *Gaudichaud* A.9 (P); *Lepervanche-Mézière* 1 (P); *Lepervanche-Mézière* & *Richard,* ex Herb. Bory 27, 14 (P); forêt de Béhour near Rivière des Marsouins, *Lorence* in MAU 15617 (MAU, two sheets); ibid., *Lorence* in MAU 15642 (MAU); ibid., *Lorence* in MAU 15643 (MAU, two sheets); *Potier* s.n. (P); *Schlieben* s.n. in MAU 12451 (MAU).

SEYCHELLES. Mahé, *Gardiner* s.n. (K); Silhouette, *Gardiner* x.8 (K); Mahé, Congo Rouge Mossy forest, *Guého* in MAU; Mahe, *Jeffrey* 451 (K).

THE LECTOTYPIFICATION OF ELAPHOGLOSSUM SIEBERI

Elaphoglossum sieberi (Hook. & Grev.) Moore, Ind. Fil.: 14 (1857); excluding C.Chr. in Dansk. Bot. Arkiv. 7: 165 (1932) and Tard. in Humbert, Fl. Mad. 5^{e} fam. 2: 34 (1960) as to Madagascan and Comoran plants.

> *Acrostichum sieberi* Hook. & Grev., Ic. Fil. 10: t. 237 (1830); Bojer, Hort. Maurit.: 413 (1837); Baker, Fl. Maurit. & Seych.: 511 (1877).
> Lectotype: Mauritius, *Bojer* s.n. "very near Acr. longif. from W. Indies Acr. Latifolium Sieber non Sw. Acr. Sieberi Ic. Fil. t. 237" (left-hand specimen, Herb. Hook. K!).
> *Olfersia sieberi* (Hook. & Grev.) Presl, Tent. Pter.: 235 (1836).
> *Acrostichum ellipticum* Fée, Mém. Fam. Foug. 2: 30, t. 4, fig. 2 (1845) (type not seen).

In their type description of *Acrostichum sieberi,* Hooker and Greville indicate both Sieber and Bojer as collectors for this species from Mauritius. According to the International Code of Botanical Nomenclature, 1966 ed., these constitute syntypes and a lectotype must be chosen from amongst them.

There is, in the Herbarium Hookerianum at Kew, a sheet bearing on the left hand side a detached sterile and fertile frond of *E. sieberi* without rhizome, annotated "Mauritius, Sieber". Although obviously not the plant illustrated in plate 237 of *Icones Filicum,* it is apparently the Sieber specimen cited by Hooker and Greville in their text, thus representing one of the syntypes. Mounted adjacently to the right is a plant with rhizome and one fertile frond and one sterile frond collected in Mauritius by Telfair; this also does not correspond to plate 237.

Also to be found in Herb. Hook. is a Bojer sheet with two collections, the left hand one of which consists of a plant with a sterile and a fertile frond exhibiting their abaxial surfaces with attached rhizome and annotated "Mauritius, Bojer. very near Acr. longif. from W. Indies Acr. latifolium Sieber non Sw. Acr. Sieberi Ic. Fil. t. 237"; the specimen corresponds exactly with plate 237 in *Icones Fillicum.* On the right hand side of the same sheet is a large fertile lamina, with a portion of the attached stipe, which is not illustrated by Hooker and Greville. Consequently, the left hand Bojer collection obviously represents the most suitable choice for the lectotype of *Elaphoglossum sieberi* and it is hereby so designated.

Although there has been some confusion as to the actual distribution of the species, various authors having cited it from the Comoro Islands, Madagascar and Réunion Island, *Elaphoglossum sieberi* is apparently endemic to Mauritius. De Cordemoy (1895), in his Flore de l'île de la Réunion, wrongly applies the name *Acrostichum sieberi* Hook. & Grev. to what is actually *Elaphoglossum macropodium* (Fée) Moore, a rather common species on that island. Examination of specimens from Madagascar and the Comoro Islands cited by Madame Tardieu-Blot (1960) has revealed that they represent a different species characterized by having a thinner and longer-creeping rhizome bearing smaller, thinner and sparser scales than are found in *E. sieberi.* Finally, a Commerson specimen supposedly from Madagascar is apparently the result of a mixture in herbarium tickets, for he collected a number of specimens of *E. sieberi* in Mauritius, and the author has seen no recent authentic material from Madagascar.

In Mauritius, *E. sieberi* is one of the commonest species of the genus, generally occuring as an epiphyte on tree trunks from ground level to 10—12 metres high, but is also casually terrestrial on humus tussocks or mossy rocks, usually in the shade of *Philippia* heath, *Sideroxylon* or climax formations ranging from 200 to 900 metres altitude.

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REVIEWS

FERN GROWERS MANUAL by Barbara Joe Hoshizaki, 1975. Alfred A. Knopf, New York. 256 pages, 285 x 220 mm. (10¼ x 8¾ ins). 315 photographs and drawings. Price US $15.00.

The author, a member of our Society, is Professor of Botany at Los Angeles City College, Curator of Pteridophyta at the University of California in Los Angeles, and President of the Los Angeles International Fern Society. She has done much field work on ferns in the Western Hemisphere but in addition to being a well-known botanist she is a keen and knowledgeable grower of ferns and this book is intended as a handbook or reference book for anyone cultivating these plants. It is, of course, aimed at the American grower but we in this country can profitably study its pages and learn a lot.

The introductory chapters give general information on ferns, their structure, how to obtain them by collecting or purchase, and how to grow them, with information on planting and cultural needs, soils and fertilisers, propagation from spores and vegetatively, and also how to deal with pests, disease and poor culture. There is a chapter on landscaping with ferns with lists of the best ones for particular uses, another dealing with the growing of special ferns indoors, in glass terrariums and out of doors, and an interesting one on how ferns get their names.

A long chapter taking about half the book (116 pages) deals with the species and many of their varieties, as well as fern allies, in cultivation in the United States. There is an imposing list, all described and illustrated, each with concise tabloid information on height, form, temperature requirements, light needed, soil, watering, easy or difficult to grow, and evergreen or deciduous. A tremendous amount of work has gone into compiling this information and as so many of the ferns mentioned are grown in this country the book will prove most valuable to the grower over here as well as in the United States. At the end is a glossary, instructions on how to measure light, a list of fern societies and nurseries, where to get special information, a bibliography, and for the botanically inclined a classification of ferns and fern allies. The abundance of drawings and black and white photographs are all excellent, clear and informative, and 8 pages of coloured plates are beautifully produced.

Altogether the book is a magnificent one excellently produced and finished. The author is an expert in her subject and is to be highly complimented on a production which I am greatly delighted to place on my fern bookshelves where it most certainly will not be left in repose to gather dust. At the present rate of exchange the cost is about £7.50 in this country, very cheap for a book of this calibre.

J.W. DYCE

ENUMERATIO PTERIDOPHYTARUM JAPONICARUM: FILICALES by Toshiyuki Nakaike. xiii + 375 pp. 10.5 x 7.5 ins. (263 x 186 mm). University of Tokyo Press, March 1975. Price 8000 Yen.

"Enumeratio" is the clue to this book (in English) by "a fern lover", one of whose wishes "has been to observe and to collect all the (about 800 taxa of) Japanese pteridophytes in the field", thereby needing to "arrange information on each taxon . . . [including] subspecies, variety, form and monstrosity", and to produce a "System of Filicales . . . newly proposed here". Genera are indexed under their botanical (Latin) names. Species are not indexed, except under their vernacular Japanese (transliterated to Latin alphabet) names, but they appear alphabetically in the text under their genera. One purpose the book claims is to "clarify taxonomic status", but the only diagnostic statement is the "System" where the family names form a sequence from Osmundaceae to Azollaceae; but groups and genera are alphabetical and there are no keys. Each entry adds synonyms, the Japanese name and the distribution (Japanese island and world countries). Apart from basionyms being given first, synonyms seem to be cited randomly date-wise and alphabet-wise.

There are many new nomenclatural combinations (un-indexed), mostly at infraspecific level and often to "monstr.". His *Lunathyrium lasiopteris* (p. 175) ante-dates that of Sledge (Gazette 11: 84) but Ching's *Nothoperanema* (Act. Phytotax. Sin. 11: 25) ante-dates his (p. 239).

The main value of the book is as an index to places of publication and to treatments in other works. It is a pity that entries for these other works are not complete and that they could not have been quoted in some shortened code system.

The author must have spent a considerable part of his "several years" in making this compilation which serves a valuable purpose in providing a multitude of references.

J.A. CRABBE

STUDYING FERNS IN THE CAMEROONS. I. THE LAVA FERNS AND THEIR OCCURRENCE ON CAMEROON MOUNTAIN

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ABSTRACT

The author gives an account of lava ferns and their occurrence on Cameroon Mt, with particular reference to the lava flows above Mapanja, at Bibundi, and near Ekona. The conspicuous prevalence of the pumice-fern, *Nephrolepis pumicicola* Ballard, is stressed and elucidated.

INTRODUCTION

The re-establishment of plant growth exterminated by volcanic activity has been the subject for scientific research since the well known Krakatau catastrophe in August 1883, the vegetation of which island had been devastated by volcanic cinders piled up to 60 m in places. It was scarcely three years after this explosion that a new vegetation had reappeared consisting almost entirely of ferns: eleven species were collected by Treub in the interior of the island. In the course of the following 47 years no fewer than 61 species of ferns and fern-allies could be observed (Leeuwen 1936: 323–345), mostly coming by abundant spore-dissemination from the neighbouring islands of Sumatra (at a distance of 37 km in the NNE) and Java (41 km in the E). A thin film of cyanophyceae completely covering the cinders provided the substrate for germination of the fern spores. A similar process might once have taken place in Juan Fernandez and in Ascension. According to Schimper (1898: 201) ferns belonged to the first colonizers of the lava also on the Mt Goentoer in West Java (Pijl 1938: 141).

> "Après qu'une île — ou une partie d'un continent — a été ravagée par une éruption et recouverte de matières volcaniques, les Cryptogames vasculaires — et notamment les Fougères — jouent encore atuellement par exception un rôle qui leur revenait très souvent dans les périodes lointaines où ils avaient la prédominance sur la surface terrestre" (Treub 1888: 223).

OBSERVATIONS IN AFRICA AND THE CAMEROONS

In Africa, Robyns (1932: 14, 28) was the first to study the repopulation of volcanic deposits 14 years after the 1912 eruption of the Rumoka volcano (Kateruzi) — one of the adventive craters of the Nyamuragira (or Nyamlagira) volcano (3056 m), belonging to the Virunga mountain group N of the Kivu lake. Besides 22 species of phanerogams only 4 fern species were recorded by him. but when Lebrun examined the flora and vegetation of the same region in 1937–1938, he mentioned 15 fern taxa, i.e. 20.5% of the various vascular plants, growing in lava crevices: "Les Ptéridophytes jouent un rôle fort important et très actif dans la colonisation des fentes, fissures et crevasses" (1960 288). The total number of pteridophytes all over the lava fields explored by Lebrun was 33.

Like him Léonard (1959: 250–258) ascertained the "classic" process of colonization on various lava streams (emitted between 1912 and 1956) of the Nyamuragira volcano. At the beginning lichens only established, together with some mosses. Ferns then followed before higher plants appeared, thanks to the moisture-retentive capacity of the cryptogamic pioneers. This scheme of plant succession could vary according to conditions of environment, but the ferns always ranked among the first plants in lava field colonization due to their modest ecological requirements and their physiological adaptability to poor soils. Among them *Nephrolepis biserrata* (Swartz) Schott — replaced by *N. exaltata* (L.) Schott in Hawaiian volcanoes, or by *N. abrupta* (Bory) Mett. in Grand Comoro Island — prevailed; it was accompanied by *Pteris vittata* L., *Phymatosorus scolopendria* (N.L. Burm.) Pic. Ser., *Arthropteris orientalis* (J.F. Gmelin) Posth. and *A. monocarpa* (Cordemoy) C.Chr., *Pellaea calomelanos* (Swartz) Link and *P. schweinfurthii* (Hieron.) Diels, *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf., and *Psilotum nudum* (L.) Beauv.

Concerning the speed at which lava flow colonization takes place, Guillaume (1966) in his brief description of Cameroon Mountain remarked: "The 1959 lava already carries some plant life in the form of ferns, small creeping plants, mosses and lichens. This is all the more remarkable when one realises that, last year, parts of this flow were still warm and steamed during the rainy season".

The first historic outbreak of Cameroon Mountain, the only active volcano in West Africa, is presumed to have occured between 1800 and 1815 (Gèze 1943: 156). In the course of this eruption lava broke forth from a small subsidiary cone, called "Black Crater", streaming in SSE direction towards Mapanja, a Bakweri village famous for Mann's first ascent of the mountain in December 1861. (Gustav Mann was a German botanist of repute, in the service of the British Government). Burton (1862: 242) who described this ascent gives a vivid picture of the scenery: "Bush and forest suddenly ceased as if felled with the axe . . . Nothing met the eye but a broad green slope of small moss and larger fern, all of it the *F. nephrolapis* (sic), based upon a rugged bed of old and degraded lava." In February 1861 G. Mann had collected some of these plants (no 1396, K) not very tall at that time. On 16 February 1895 Preuss — no 1373. *Nephrolepis cordifolia* (L.) Presl (B) — met with the same fern in the same place: "Im Urwald nordwestlich von Mapanja, in größter Menge, aber nur an einer Stelle, darunter Baumchen von *Ericinella mannii,* sonst fast keine Bäume".

We searched for that place on 10 February 1975, and on the track from Mapanja (770 m above sea-level) to Mann's Spring* we met with a lava flow at an altitude of 1430 to 1460 m. Surrounded by dense forest it represents a unique area of *Nephrolepis pumicicola* Ballard (fig. 1), up to 1.31 m in frond length. Of course since 1895 some trees, such as the Ericaceous *Agauria salicifolia* Hooker f. and the Liliaceous *Dracaena fragrans* Ker-Gawler, in part bearded with lichens, as well as some flowering shrubs (e.g. *Begonia poculifera* Hooker f., det. F.N. Hepper) have been interspersed. But in vain did we look for an additional fern growing on the lava surface! The rain forest having advanced more and more from both sides into the decomposed lava, scanty specimens of the pumice-fern are now growing in the forest itself; we even observed it as an "ephemeral" epiphyte on a *Ficus.*

Some more lava ferns may be seen between Isobi (just one house in ruins left!) and the village of Bibundi, on a lava produced from the Waldau—craters over a period of six months amidst the forest belt on the SW flank (1365 m, Gèze 1943: 139). Gèze (1943) stated: "Sur les coulées de laves récentes (coulées de 1922) qui ont coupé la prairie alpine et la forêt, il s'est établi une florule très spéciale comportant deux *Senecio* dont *S. cf. ruwenzoricus,* des *Plectranthus* et *Nephrolepis serrata*" (p. 74), and: "Coulées actuelles (1909 et 1922), commençant seulement à se recouvrir d'une flore spéciale dans la zone d'altération active proche de la mer" (p. 154). The volcanic activity of 1922 began on 3 February near the centre of the mountain, the later Mateer Cone (3540 m), the lava of which did not reach the forest; it was followed by

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* Richards had discovered here *Xiphopteris flabelliformis* (Poiret) Schelpe "on bare lava". *Asplenium adiantum-nigrum* L. had been collected by Mann "on lava fields" (no 1373, K) and by Brenan "on sides of crater near Mann's Spring" (no 4244; BM, K).

FIGURE 1: *Nephrolepis pumicicola,* growing on the lave flow above Mapanja, 1430 m. *(Photo G. Benl).*

eruptions of the later Waldau—craters beginning on 21 February. Maitland had made gatherings of the pumice-fern from the inside wall of one of the 1922 craters at 1320 m (no 1091, K) and, in 1930, even from an old lava flow of the Robert Meyer—craters at an elevation of 2280 m (no 961, K). In August 1922 the flow had finally reached the sea by three partial streams (Semmelhack 1929). Later, various plants were collected there by Mildbread in 1928, by Rosevear in 1936 and 1937, and by Keay in 1951; among these plants eight species of ferns were represented according to Keay (1959: 27): *"Arthropteris cameroonensis, Microgramma owariensis, Microsorium punctatum, Nephrolepis biserrata, N. pumicicola, N. undulata, Pityrogramma calomelanos, Phymatodes scolopendria".*

On 3 February 1975 we entered the southernmost lava tongue, not easily accessible from the coast, and then advanced towards the mountain after crossing the motor road Victoria-Idenau (about 30 m above sea-level). Immediately at the shore the black pahoehoe lava is still kept free from vegetation by the surf (fig. 2). A few metres behind it the decomposition of the basalt lava has proceeded (due to the amply moist conditions caused by the water-laden sea winds and to a uniformly high temperature*) to such an extent that, within a tropical rain forest climate, an almost impenetrable jungle has re-appeared, containing characteristic secondary forest species,

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* "The weathering potency of the water increases 4- or 6-fold with an increase in temperature from 10° to 25 or 30°" (Mohr & v. Baren 1954: 349).

some of which, like *Alstonia boonei* De Wildeman and some *Ficus* species, have already reached heights of 8 to 10 m here. Amongst the ferns, *Nephrolepis biserrata* predominates at the lava base between the coast and the road. The two shade-loving *Asplenium barteri* Hooker and *A. vagans* Baker were not only found growing as epiphytes on *Ficus* buttresses – beside small specimens of *Asplenium dregeanum* Kunze – but also as terrestrial plants, after having fallen from their trees. *Phymatosorus scolopendria* with its slightly fleshy fronds occurs as an epi- and geophyte, as is usual in secondary evergreen forests. Only towards the western road border, where vegetation becomes sparser, may small specimens of *Arthropteris cameroonensis* Alston with their crenate pinnae be seen in limited quantity.

East of the road (1 km from the coast) where the lava is less weathered because of decrease in humidity, there are no tall trees, only bushes. But in this lighter ground *A. cameroonensis* increases considerably in numbers and size (above 80 cm). In addition we observed (at 40 m altitude) *Phymatosorus scolopendria,* rather less numerous *Nephrolepis biserrata,* and *Pityrogramma calomelanos* (L.) Link, as well as some meagre examples of scattered *Asplenium barteri* and of *Microsorium punctatum* (L.) Copel., both growing terrestrially. At 50 m elevation *Microgramma owariensis* (Desv.) Alston [*M. lycopodioides* (L.) Copel.] with dimorphic fronds and the sparingly occurring *Nephrolepis undulata* (Afz. ex Swartz) J.Sm. joined them, the latter as a geophyte, too, its leaves not being adapted to stand a hot dry season. At 60 m, a few individuals of scanty *Pteris atrovirens* Willd. appeared and then the expected *Nephrolepis pumicicola* cropped up in abundance. *Pteris manniana* Mett. ex Kuhn had been collected in this region by Mildbraed (no 10657, B; "häufig in Bachbetten auf Lava"). In other places of this field the pumice-fern descends to 45 m or lower. According to our present knowledge its general occurrence is restricted to the South West Province of Cameroon* and to the Guinea Islands of Fernando Póo and São Tomé, almost exclusively on lava flows.

A real attraction is the lava bed emitted in February 1959 from two subsidiary vents of the multipartite Cameroon volcano into dense forest on its NE slope, at 1100 m above the Ekona-Lisoka area. The process of this eruption was described in an interesting day-to-day record by Hasselo & Swarbrick (1960). The lava had flowed partly over previous volcanic deposits, partly it had burnt a new track through the forest.

We went to see this stream of lava (fig. 3) – the natives appropriately call such a stream "fire-born" – leaving the Victoria-Kumba highway at Ekona Mbenge (395 m) and continuing our journey on the road to Lisoka. After a drive of 3.5 km we faced the tip of a lava tongue towering up to a front height of 6 to 10 metres into a banana plantation. In September 1959, Swarbrick had taken photographs of a small specimen of an unrecognizable fern in this spot; now, on 17 and 19 February 1975, we saw, in the same spot, the virtually pantropical *Pityrogramma calomelanos,* having many xerophytic features and "appearing everywhere in newly cleared ground" (Holttum 1966: 594), *Phymatosorus scolopendria,* usually preferring slightly shaded places, and *Nephrolepis biserrata* usually in more or less sunny positions. Nearby, in open shade, were luxuriant specimens of *Microsorium punctatum.* All representatives bore fertile fronds.

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* The collection of Deistel (Bot. Mus. Berlin) comprises some specimens of this fern gathered by him on 3 March 1900 (no 611) in the top region of the mountain (3700 m): "einfallende Felsspalten, aus denen warme Wasserdämpfe aufsteigen, die sich beständig zu Tropfen an den Rändern dieser Felsspalten verdichten. Diese Ränder sind überzogen mit Moosen 605, 606. Dazwischen dieser Farn mit Sporen. Wedel dunkelgrün. Nur an diesen tiefen, engen senkrechten Felsspalten der höchsten Spitzen, die beständig solch warmen Wasserdampf ausströmen".

FIGURE 2: Front of the lava flow 1922 near Bibundi. Behind the margin being swept by the surf the re-establishment of the rain forest quickly advances.

FIGURE 3: Lava flow of 1959 above Ekona (400 m) showing its colonization by ferns. *(Photos G. Benl).*

Higher up, the arid surface of the "fire-born" is heavily broken, thus looking like a big coke bed, and the scoriaceous masses are piled high above the level of the surrounding land (Hasselo 1961: 19). About 7 m behind the lava front, *Nephrolepis pumicicola* begins to spread (fig. 4), sprouting from crevices, with a vertical rhizome up to 10 cm in length, and a rather extensive root system. We counted roughly 60 plants within an area of four square metres, each with 2–7 fronds, the larger ones with sori. At 410 m altitude we counted 15 distinct patches of this charming fern. Its usual companion, *Arthropteris cameroonensis,* is very sparse here, but it increases in number at higher altitude: at 430 m we counted 17 plants (maximum frond length of 60 cm) within two square metres, though all sterile.

In altitudes above 430 m, one is surprised to find the epiphyte *Platycerium stemaria* (Beauv.) Desv., the elk's-horn fern, growing amidst specific lava ferns, pressing its pergamentaceous sterile leaves closely to lava blocks (fig. 5). But it is known that epiphytic ferns and orchids, forming the principal part of the epiphytic flora in Africa, can become established on lava (Schimper 1898: 202). The inconspicuous *Pyrrosia mechowii* (Brause & Hieron.) Alston, another representative of the Polypodiaceae, is more or less hidden in cracks of fractured lava and on the lower side of projecting rocks. In the hot dry season its fronds are reflexed upward against desiccation, showing only their scaly lower sides. At about 432 m altitude fern growth on the *Ekona lava flow* reaches an optimum, with *Nephrolepis pumicicola* dominating the whole vegetation. At about 500 m another specimen of the leathery-leaved *Microsorium punctatum* was found, showing again, that random distribution plays an important part in the beginning of the re-establishment of plant vegetation.

Among the orchids already established here, and flowering at the time of our excursions, *Bulbophyllum lupulinum* Lindley and *Polystachya dolichophylla* Schlechter (det. Dr. P.J. Cribb) might be regarded as the most remarkable ones. As far as we know, the flora of this lava field has not yet been studied.

DISCUSSION

Let us return to the ferns and compare the respective situations on the lava fields above Mapanja and above Ekona. In both cases the flow penetrated into an evergreen forest; one flow took place about 160 years ago, the other 16 years ago. On the younger flow we recorded eight species of ferns. It might be possible to find still more in the wet season. The considerably older lava (by no means "unrecognizable in the general forest growth", as alleged by Boughey 1955: 147, who did not visit the slopes to the sea-shore in person) bears a single species, as notified by Burton 115 years ago.

There is one plausible interpretation of this seeming discrepancy. As may be inferred from the horizontal position of its numerous pinnules (we counted up to 175 pairs!), *Nephrolepis pumicicola* is a fern demanding much light. Growing plentifully into a bushy plant with stiff vertical fronds more than one metre tall (the longest was 131 cm, above Mapanja), this species produces dense swards in which any other competitor will succumb in the struggle for light.

Doubtless, because of its lesser frond length the pumice-fern will initially be exceeded by *N. biserrata;* but in the long run the latter plant, thriving essentially in the shade and frequently forming a dense vegetation in light forests, will be overcome in this open lava habitat. A similar picture is probably also true for the epiphytic *Platycerium stemaria* and *Microsorium punctatum,* which certainly originate from the adjacent rain forest, where they normally occupy the sunnier and drier sections of emergent trees. (The immediate origin of *N. pumicicola* remains a puzzle!)

The leathery-leaved *Arthropteris cameroonensis* ought to be equal to the ecological conditions of a barren and widely unshaded lava bed; but it will be excluded

FIGURE 4: Prime colonizer in this lava ground is the pumice-fern, *Nephrolepis pumicicola*. *(Photo G. Benl).*

FIGURE 5: *Platycerium stemaria* establishing on the lava flow of 1959. *(Photo G. Benl).*

by an intense competition with the preponderant *Nephrolepis pumicicola,* the latter being superior in frond length and in its denser bushy growth. The same goes for *Pityrogramma calomelanos,* a fern which usually forms the dominant vegetation in exposed areas. Without human interference the distinct young colonies of the pumice-fern on the 1959 flow may be united to a single large population within less than 50 years. This opinion is justified by the facts stated in the Mapanja area as well as by our corresponding observations in the Southern Uplands of Fernando Po where vast lava flows of prehistoric ages are densely colonized and exclusively occupied by the pumice-fern, the immense masses of which are just sporadically intermingled with some specimens of *Arthropteris cameroonensis* (Benl 1975: 29). The lower temperature and a lower precipitation in the Moka Highland had retarded the decomposition of the lava so that apparently no woody plant could have become established before our fern had completely taken possession of the flow. The necessary moisture will be guaranteed in the dry season by patches of thick moss layers retaining the nightly dew. The populations of *N. pumicicola* there show about the same luxurious growth as the vigorous colony above Mapanja.

If we keep an eye on the fact that primarily the pumice-fern is a light-demanding geophyte, we realize why on the 1922 lava this fern is only seen now in the more open parts providing a larger amount of light.

We looked in vain for the lava from the 1909 outbreak of the Okoli—craters (side vents on the NE flank of the mountain, at 2400 m altitude). This stream is said to have stopped just short of the "road from Muyuka to Ikata between mile 4 and mile 5" (Guillaume 1966: 4), but in that place we only observed a scanty "farm" of coco-yams and bananas among old lava blocks; unfortunately we failed in penetrating to the area above Mokona-Likoko.

The 1954 discharges of Cameroon Mt were caused by a summit cone; there was no flow of lava.

ACKNOWLEDGEMENTS

A lot of people assisted me in my Cameroon fieldwork in December 1970/January 1971, in February/March 1974 and January/March 1975. Among others I am very grateful to Mr James K. Wilkie (Estate Manager, Idenau), M. E.-A. Essono (Chief of Dept. Waters, Forests and Wild Life, Fako Division), Mr R.M. Ngute (Executive Secretary, Mbonge). Most of all I am indebted to Mr N. St. Ekema (Herbarium Assistant, Victoria), my constant helpful companion in February 1975.

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REVIEWS

HYBRIDIZATION AND THE FLORA OF THE BRITISH ISLES by C.A. Stace (Ed.). 626 pp., 9 x 6 ins. (230 x 155 mm.). London, New York, San Francisco: Academic Press and Botanical Society of the British Isles. 25 July 1975. Price £14.80.

Here is not only a magnificent essay (pp. 1–90) on hybrids and hybridization, backed up by over 300 literature references, but also 488 pages wherein 86 specialists enumerate and elaborate on the hybrid vascular plants of Britain, together with exotic examples which are relevant because of their parentage. Non-vascular plants are not given, though "much needed", because of "relative lack of information" and "the rather different principles which can be applied to them". The title says "Flora" which is either a titling result or it links us with CTW; I would prefer it as "flora".

One becomes increasingly aware how many species are of hybrid origin so that on the one hand it seems an almost unending task to try to unscramble the biology, while on the other hand such knowledge helps immensely to comprehend many seemingly illogical phenomena.

Pteridophytes are treated in the following genera: *Asplenium, Ceterach, Cystopteris, Dryopteris, Equisetum, Gymnocarpium, Hymenophyllum, Phyllitis, Polypodium, Polystichum, Pteridium, Woodsia.*

J.A. CRABBE

BRITISH BOTANICAL AND HORTICULTURAL LITERATURE BEFORE 1800, COMPRISING A HISTORY AND BIBLIOGRAPHY OF BOTANICAL AND HORTICULTURAL BOOKS PRINTED IN ENGLAND, SCOTLAND, AND IRELAND FROM THE EARLIEST TIMES UNTIL 1800 by Blanche Henrey. 1128 pp, 32 col. pls, 162 pp. of b & w illustr., 10.9 x 7.3 ins. (275 x 185 mm). Oxford University Press, 4 December 1975. Price £70.

This magnificent work, three volumes weighing eleven pounds in a slipcase, is the result of innumerable diggings and delvings over many years into this huge spectrum. All kinds of printed and manuscript records have been sought, all aspects of horticulture and its personalities have been considered, and the bibliographies contain more than 1500 entries. The three volumes comprise: I 16th and 17th centuries, II and III 18th century. James Bolton's Filices Britannicae is the only British fern book before 1800 and we are given reproductions of his pictures of *Adiantum capillus-veneris, Asplenium ruta-muraria* and *Polystichum lonchitis.* Petiver's Pterigraphia Americana is included, with a reproduction of the 16 woodcuts on Table III.

If, like me, you feel you will not afford to buy this book, every effort should be made to make it available at libraries.

J.A. CRABBE

THE POSITION OF THE MEGAPROTHALLUS OF SALVINIA NATANS

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ABSTRACT

The archegonia of the megaprothalli of *Salvinia natans* (L.) All. are, not as previously reported, directed upwards but are submerged in water and directed downwards; it is usual in the ferns that the archegonia are on the lower surface of the prothallus. The flat, usually archegonium-free part of the megaprothallus lies above the surface of the water. It looks like a small floating leaf and maintains a stable position. The earlier described twisting of the young sporophyte during the development of the scutellum was not observed.

INTRODUCTION

Particularly during the second half of the last century *Salvinia* was the object of many investigations; most work was concerned with its alternation of generations (Hofmeister 1851, Pringsheim 1863, Prantl 1879, Belajeff 1898); later studies on the gametophyte have been made by Arnoldi (1910), Yasui (1911) and Lasser (1924). The majority of modern textbooks (for example Eames 1936, Sculthorpe 1967, Bierhorst 1971, Mägdefrau 1971) are based on the results of Pringsheim (1863) and particularly on the detailed account of Lasser (1924). My observations do not agree with these earlier accounts and are thus worth reporting.

MATERIAL

Material of *Salvinia natans* (L.) All. was collected in Autumn 1974, near Prarolo, Prov. Vercelli, N. Italy. During the winter, even in greenhouse cultivation at University of Zurich Botanic Garden plants became weak, but produced many sporocarps. In January and February 1975 many megaspores and microspores germinated.

OBSERVATIONS

Prantl (1879) reported that the archegonia may be directed upwards or downwards. However, Lasser (1924) said that the normal position is with the archegonia and bulge-like swelling of the megaprothallus directed upwards (figs. 1a-c). His explanations of the further development of the sporophyte are based on this statement (figs. 1d-f). I must agree with Prantl (1879) that the position is not always constant. However, nearly all megaprothalli had the flat, archegonium-free part upwards and the bulge and archegonia downwards (figs. 1g-i). The flat upper part is normally dry and lies slightly above the surface of the water (fig. 1i). Prothalli that are reversed (with the flat side downwards) have most of their tissue submerged and showed poor growth and most of them soon died. These prothalli were never seen to produce sporophytes. When the flat side is above the water surface the wings develop as soon as the embryo is formed. As soon as the scutellum has developed it becomes bouyant and floats while the rest of the megaprothallus becomes submerged in water (figs. 1j, k).

DISCUSSION

In my opinion there are several arguments which can be used to show the advantages of having the flat surface above the water. In the opinion of Lasser (1924) the flat part

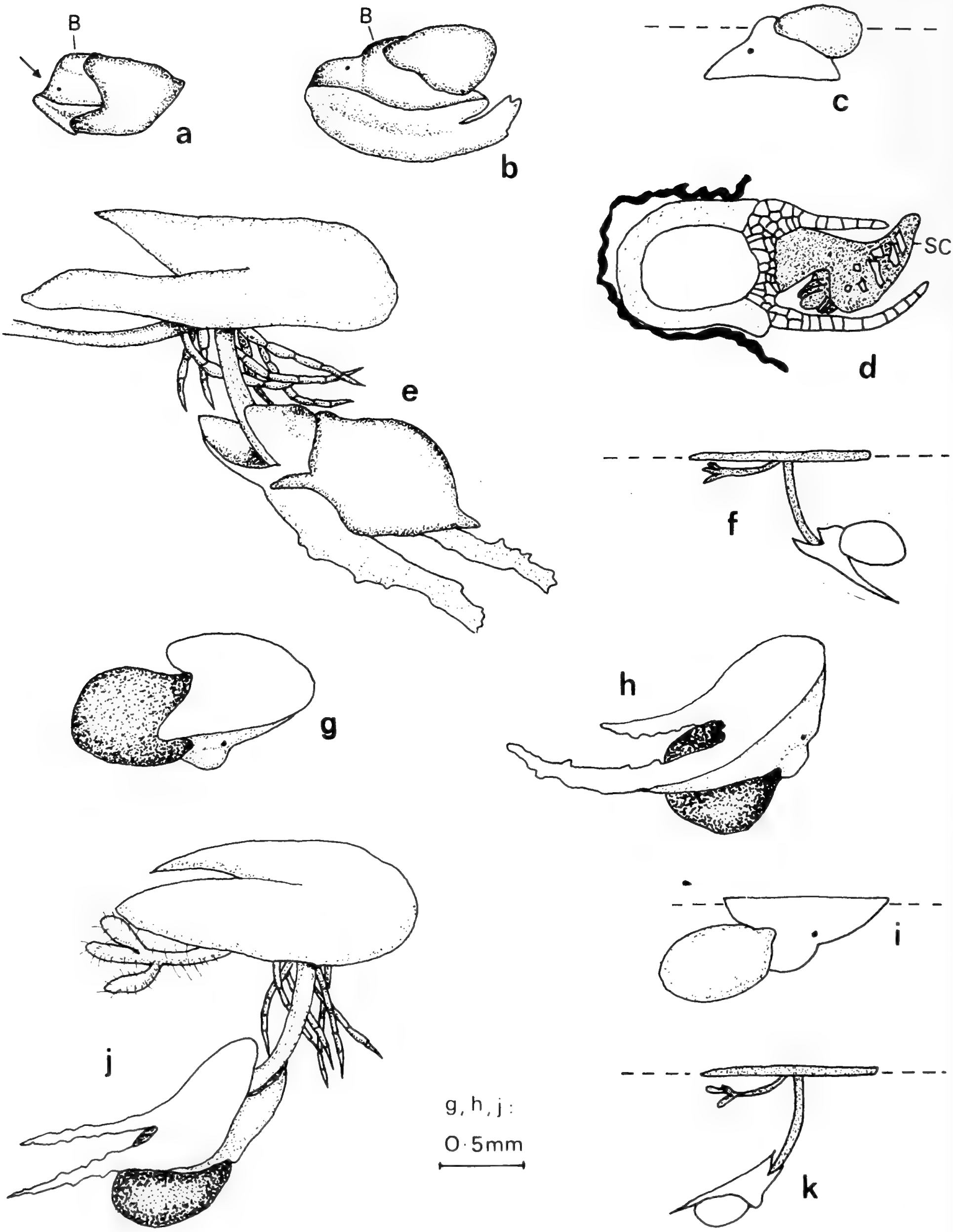

FIGURE 1: *Salvinia natans* (L.) All. (a-f after Lasser 1924, c, f, i, k schematic): a, young megaprothallus emerging from spore (arrow points to an archegonium, also bulge "B" is seen); b, megaprothallus of later stage with developing wings; c, position of megaprothallus in water (broken line indicates water surface); d, section of spore, prothallus and embryo with developing scutellum "SC"; e, gametophyte and sporophyte with well-developed scutellum; f, position of gametophyte and sporophyte in water; g, young megaprothallus of material in Zurich Botanic Garden (flat surface on the upper side); h, megaprothallus of later stage with well-developed wings; i, position of spore and prothallus in water as seen in culture; j, gametophyte and well-developed scutellum (first leaf of sporophyte) — no twisting of scutellum is observed; k, observed position of the gametophyte and the sporophyte in water.

of the gametophyte and its wings remain submerged (figs. 1a-c). If one accepts that the wings have a stabilizing function, then in the submerged state they are exposed to all currents and local turbulences and can hardly fulfill their function. If the flat part and the wings occupy the air-water interface with upper surface exposed to the air (figs. 1g-i), then the whole gametophyte is more stable. Also in this position the development of the sporophyte is not disturbed by changes in position.

The direct contact of the flat (upper) side with the air also allows for a constant exposure to light and presumably has a more effective gas exchange. Gametophytes that are left upside down have been observed to be very weak and die before the sporophyte develops; perhaps because of poor gas exchange.

Lasser (1924) described a twisting of the young sporophyte during the development of the scutellum (figs. 1d-f). When the flat side is uppermost this twisting is not necessary and was not observed (figs. 1j, k).

The floating megaprothallus can be compared to a small floating leaf or frond. From an ecological point of view it occupies the air-water interface with other free floating plants or leaves. From Lasser's description the prothalli are more likely to occupy a position below the inhabitants of the air-water surface and thus come into poor light conditions. The bulge-like swelling on the lower surface of the megaprothallus is surrounded by archegonia and could have a keel-like function.

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REVIEWS

FLORA OF TAIWAN VOLUME 1 PTERIDOPHYTA AND GYMNOSPERMAE. Edited by Hui-lin Li et al. 158 x 235 mm. 562 pp. Taipei, 1975. Price $ 18.00 US from Epoch Publ. Co. Ltd, P.O. Box 1642, Taipei, Taiwan.

This is the first of six volumes on the Taiwan flora, the whole, some 4,300 pages, scheduled to be completed in 1976. There is a readable account of the environmental background at the beginning of this volume. The bulk of the ferns and allies have been tackled by a well-known name in Taiwan pteridology, Prof. Charles E. De Vol; Drs Kuo Chen-meng and Shieh Wang-chueng have also contributed several families. Apart from the Chinese names for genus and species all data are in English. Keys and descriptions are clear and concise; full geographical distribution, both in Taiwan and the rest of the world is given as are relevant references in other regional floristic accounts. There are 169 very fine plates of line drawings of whole plants and close-ups of critical organs. Although I expect every major institute to get this series, this is not a book that everyone will buy but I can see pteridologists with teaching responsibilities wanting their own personal copy.

A.C. JERMY

CYTOGEOGRAPHIC STUDIES ON DRYOPTERIS OF JAPAN by Haruk Hirabayashi, 186 x 261 mm, 176 pp. Tokyo 1974. Harashobo Co. Ltd., 1-25-13 Shinjuku, Shinjuku-ku, Tokyo.

This well-produced little book is based upon a thesis submitted to Tokyo Educational University for the degree of DSc. A summary of the cytological work and chromosome numbers counted in some 62 species of *Dryopteris* in Japan is given: 36 are apogamous, mostly triploid, and 22 are diploid and sexual. Only 15 hybrids were detected and only 6 sexual tetraploids. One cannot help thinking that with 22 diploid species there should be more hybridization with the resulting allopolyploids, if the state of the genus in Europe and N. America is anything to go by. A chart is given showing relationships of the 15 hybrids with their putative parents but no analysis of meiosis is reported. There are 14 plates of photographs each with 6-8 pictures of on the whole, good, chromosome preparations, and the bulk of the work (80 plates) give detailed maps of the distribution of these species in Japan. The author has obviously looked at a great specimens; he has also shown what an enormous task it would be to tackle the biosystematics of Japanese *Dryopteris,* but what a challenge!

A.C. JERMY

A SCANNING ELECTRON MICROSCOPIC INVESTIGATION OF THE SPORES OF THE GENUS CYSTOPTERIS*

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ABSTRACT

An investigation of spore architecture of several species of the fern genus *Cystopteris* Bernh. using scanning electron microscopy was undertaken in order to determine possible taxonomic significance. Distinct morphological differences at the subgeneric and specific levels within the genus are reported. Five spore types are described including types which have not been described previously. Results indicate that spore ornamentation is useful in the taxonomy of the genus.

INTRODUCTION

With the development of the scanning electron microscope (SEM), a strong tool for the taxonomic study of spores has appeared. The limitations in resolution and depth of field of the light microscope have precluded thorough observations of the ultramicroscopic morphological structure of spores and thus, the fine detail of their structure has not been available for taxonomic use to the extent which is now present with the SEM. Works which rely heavily on the systematic use of scanning electron microscopy of fern spores are beginning to appear with increased frequency in the literature. Papers by Tryon (1971, 1972), Wilce (1972), Britton (1972), Crabbe, *et al.*, (1970), Brownsey and Jermy (1973) and Mickel (1974) have shown the potentialities of the SEM.

The present study is concerned with the examination of the spores of the genus *Cystopteris* Bernh. in order to determine possible taxonomic significance. The species studied are from a wide variety of geographic areas throughout the world and cut across species groups within the genus. *Cystopteris* is cosmopolitan in distribution although primarily restricted to temperate regions. According to the latest treatment by Blasdell (1963), the genus consists of ten species and six hybrids.

METHODS AND MATERIALS

Spores for this study were taken directly from herbarium sheets and transferred to double-faced Scotch tape, which had been mounted on standard ¾ inch aluminium SEM studs. These were coated *in vacuo* with vaporized carbon and gold using a Denton vacuum coater with a random rotating head. The random rotating head ensures even distribution of charge in the microscope. The specimens were then viewed on an AMR model 900 Scanning Electron Microscope, made available by the Department of Chemical and Metallurgical Engineering at the University of Tennessee, Knoxville.

The photos selected are representative spores from a larger sample of plant specimens examined and are not the result of the study of single spores or of single specimens. The actual size of the spores studied is in the range of 27—53 microns.

RESULTS

Until now, three basic spore types have been described in the genus (Blasdell, 1963). The echinate, or spiny, spore (fig. 1) is the most common type. Variations, such as

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* Contributions from the Botanical Laboratory of the University of Tennessee, Knoxville, N. Ser. *442.*

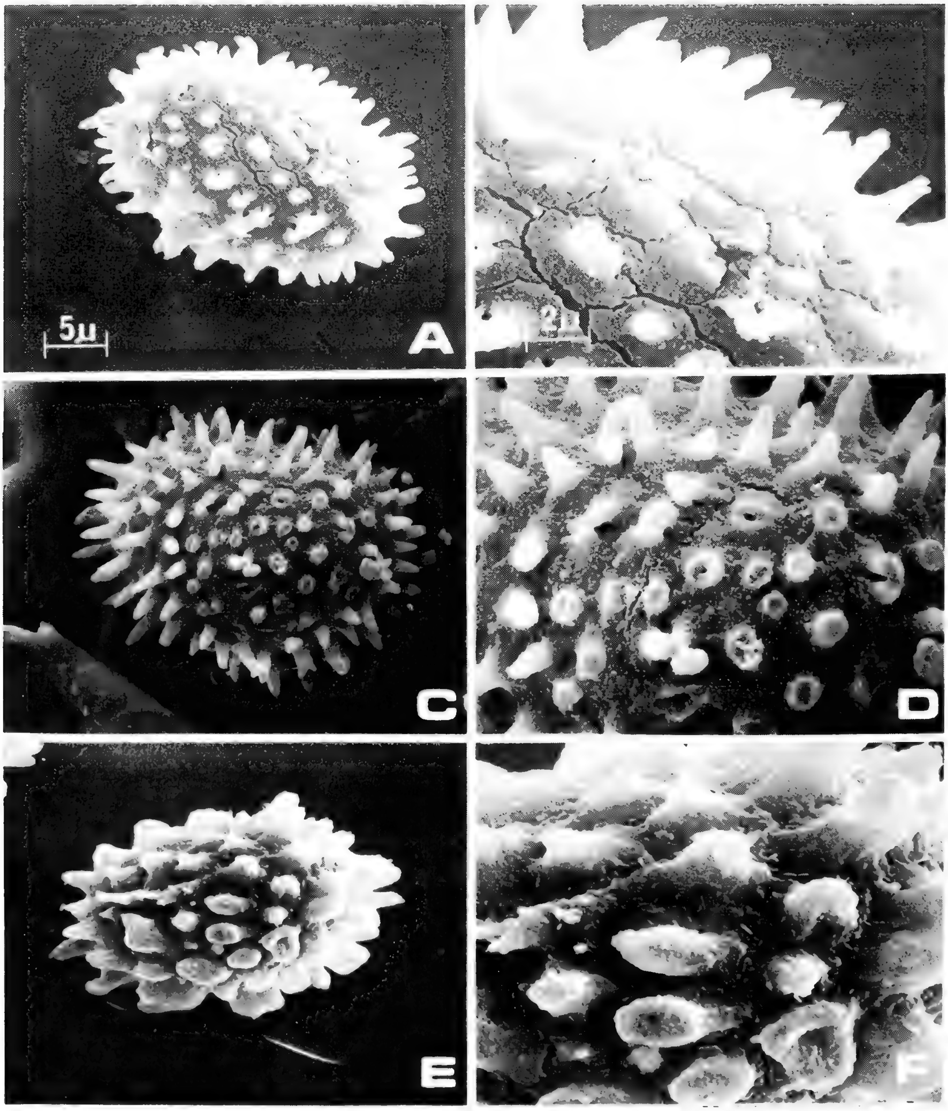

FIGURE 1: Echinate spore types: A-B, *C. protrusa,* Knoxville, Tenn., USA, Pearman 45282 (TENN); C-D, *C. tennesseensis,* Smith Co., Tenn., USA, Pearman 45290 (Type locality, TENN); E-F, *C. bulbifera,* Montgomery Co., Tenn., USA, Pearman 45284 (TENN).

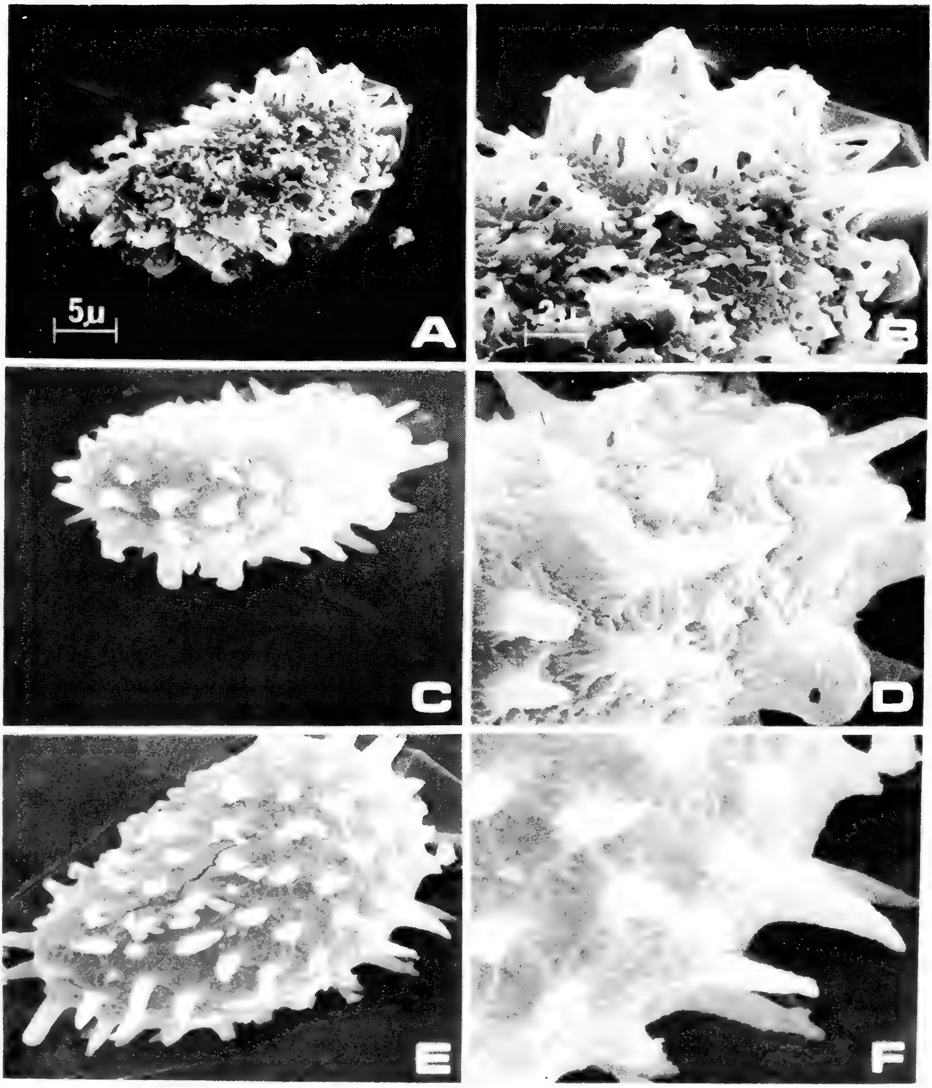

FIGURE 2: Conical-lacunar and echinate spore types: A-B, *C. montana,* Abisko, Lappland, Sweden, Samuelson 39 (NCU); C-D, *C. sudetica,* Silesia, Poland, Milde s.n. (US); E-F, *C. douglasii,* Hawaii, USA, Baldwin s.n. (US)

those with sharp spines (fig. 2, E—F), occur but the basic type is the same. The second type is the saccate or warty type (fig. 3) and is known from only two taxa within the genus. The third type, the rugose or wrinkled spore (fig. 4, E—F) is known from scattered populations of the *C. fragilis* aggregate. As a result of this study, two other types, which will be referred to as the spiny-lacunar type (fig. 5) and the conical-lacunar type (fig. 2, A—B) will be described.

The following are descriptions of the spores of the species included in this study.

Spiny Spores

Cystopteris protrusa (Weath.) Blasdell (fig. 1, A—B). The spores are the basic echinate type. The spines are relatively short and sharp and the surface of the spores has an irregular granular texture. These spores are relatively small in comparison to the other spores in the genus, averaging 27—32 microns.

Cystopteris bulbifera (L.) Bernh. (fig. 1, E—F). The spores are of the echinate type but the spines are extremely blunt and irregular as well as being larger than most echinate types, thus creating a spore type which is characteristic of only this species. The surface texture is rough and irregular.

Cystopteris tennesseensis Shaver (fig, 1, C—D). These spores were varied in morphology but in most cases they approached the spores of *C. protrusa* in appearance. However, in some specimens examined, the spores had the general appearance of *C. bulbifera.* The usual case was that the spores were intermediate between *C. protrusa* and *C. bulbifera.* The surface texture is almost always more granular than *C. protrusa* and not as irregular as *C. bulbifera.*

Cystopteris douglasii Hooker (fig 2, E—F). This species possessses echinate type spores with thin, sharp spines. They are of particular interest because they are the only spores having a very fine grainy surface around the base of the spines and even on the spines. This surface is quite different from the coarser and flatter granular texture found on the spores of *C. protrusa* and *C. tennesseensis.*

Cystopteris sudetica A. Br. et Milde (fig. 2, C—D). The spores are echinate with rough, irregular spines. The surface texture is also very rough and the most irregular found in the echinate type.

Cystopteris fragilis (L.) Bernh. (fig. 4, A—D). These echinate types are variable depending on which geographical area they are found. They vary from small, blunt spines to longer, sharp spines. The spore surface also varies from an irregular surface, approaching *C. sudetica,* to a smooth surface as in fig. 4, A—B.

Warty Spores

Cystopteris tenuisecta (Bl.) Mett. (fig. 3, A—B). The spores are the warty or saccate type. The individual "warts" are made up of clustered columns, each cluster with a common, irregular, dilated, flat-topped apex. The "warts" are so close together that the surface of the spore is out of view.

Cystopteris japonica Luerssen (fig. 3, C—D). The spores are virtually identical in size and morphology to *C. tenuisecta.*

Rugose Spores

Cystopteris fragilis var. *dickieana* (Sim) Lindberg (fig. 4, E—F). The rugose type spore has numerous folds in the outer wall and the surface is covered with small papillate projections. The occurrence of the folds is variable with some spores having none at all.

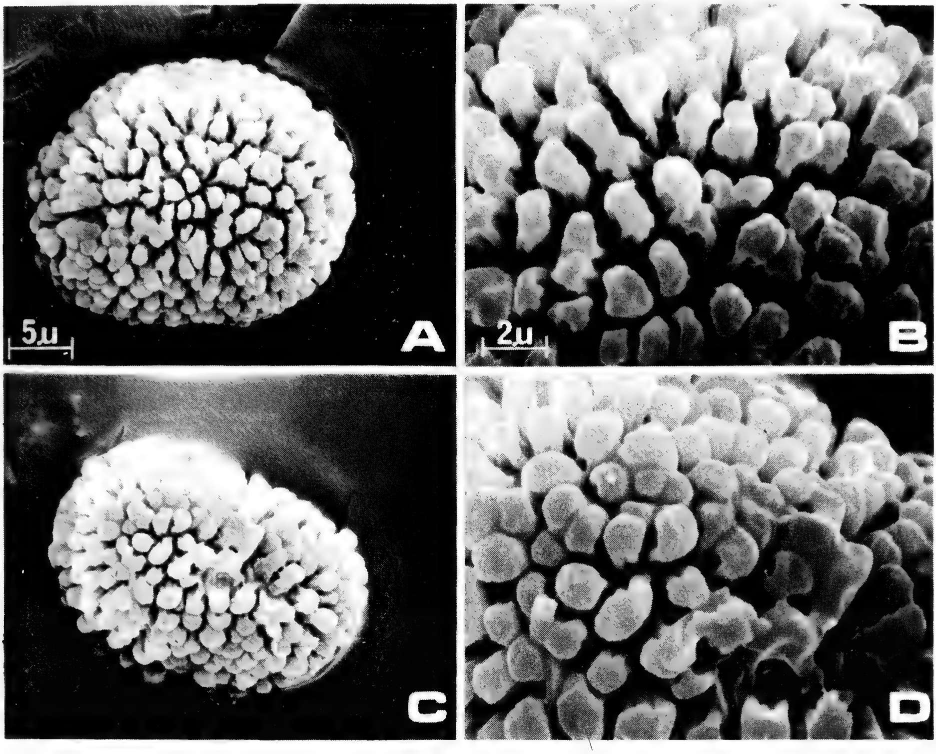

FIGURE 3: Warty type spores: A-B, *C. tenuisecta,* Pahang, Malaya, Molesworth-Allen 2875 (US); C-D, *C. japonica,* Kyushu, Japan, Kido 2006 (NCU).

Conical-lacunar Spores

Cystopteris montana (Lam.) Bernh. (fig. 2, A—B). These spores are a rather radical modification of the echinate type. They are so different that they have been described as a separate type. The spores have large spines with wide and irregular spaces. The surface is irregular and covered with numerous small papillate projections.

Spiny-lacunar Spores

Cystopteris fragilis (L.) Bernh. (fig. 5). The spiny-lacunar type spore has spines which are made up of several small projections of the spore wall which unite at the tip to form one spine. There are two basic variations, one from the Canary Islands (fig. 5, A—B) in which the spines are far apart enough to be distinct and the second from Costa Rica (fig. 5, C—D) in which the spines seem to form an open network across the spore.

DISCUSSION

Cystopteris tennesseensis is a species proposed by Shaver (1950) as a hybrid derived from a cross between *C. protrusa* and *C. bulbifera,* based only on morphological characters. In cytological studies, Blasdell (1963) reported the chromosome number of *C. tennesseensis* as n = 84 and each of the presumed parents as n = 42. The present study shows that *C. tennesseensis* produces good spores in all specimens examined and that they are intermediate between the presumed parents. In spore germination studies

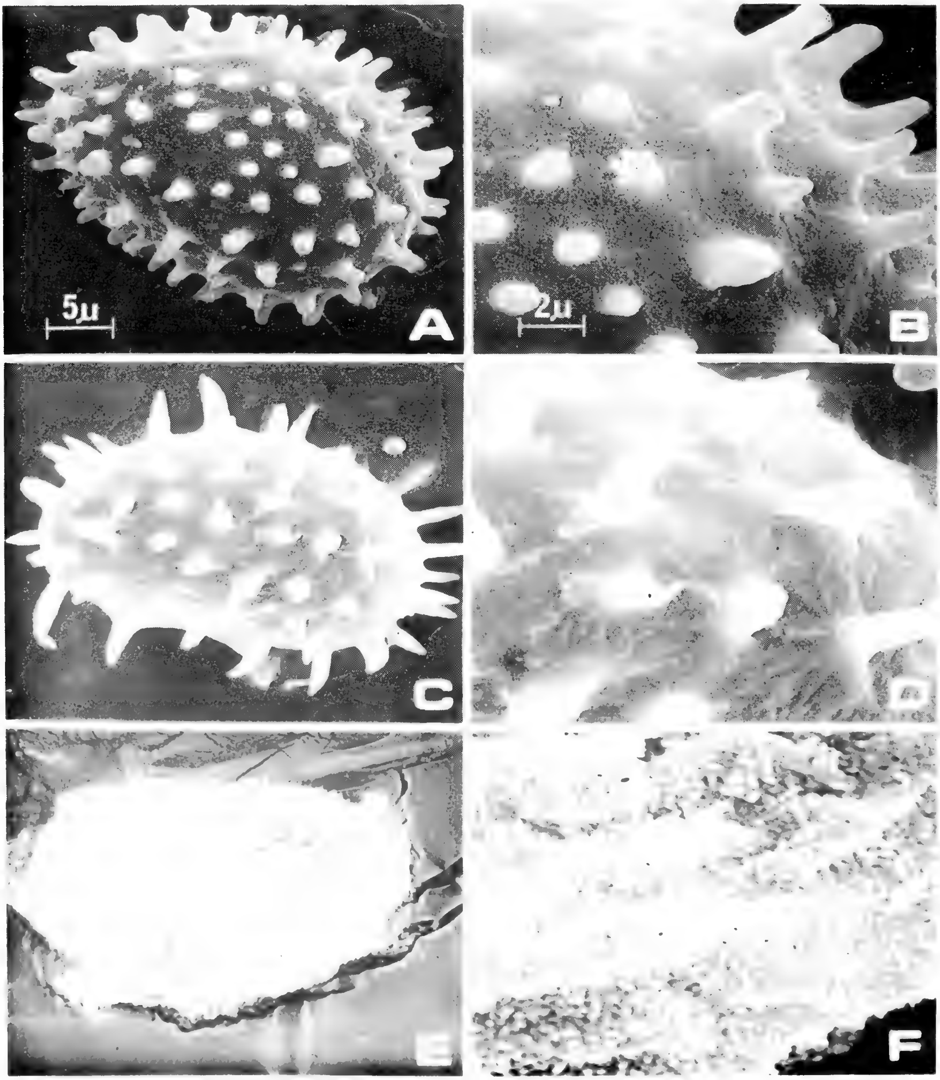

FIGURE 4: Echinate and rugose spores: A-B, *C. fragilis,* Lermatt, Switzerland, Churchill s.n. (US); C-D, *C. fragilis,* Arakamtehetchene Island, USSR, Wright s.n. (US); E-F, *C. fragilis* var. *dickieana,* Harney Co., Ore., USA, Train s.n. (TENN).

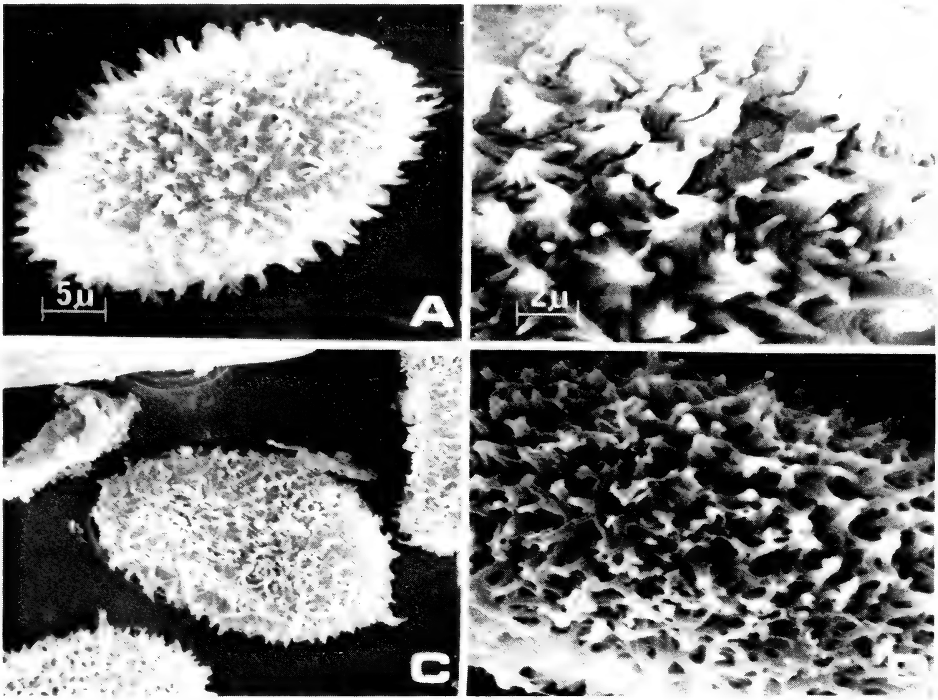

FIGURE 5: Spiny-lacunar spores of *C. fragilis:* A-B, Canary Islands, Knoche 1113 (US); C-D, San Jose, Costa Rica, Evans and Lellinger 100 (TENN).

C. tennesseensis spores germinate normally, produce both archegonia and antheridia and normal sporophytes. All these data indicate that *C. tennesseensis* is an allotetraploid which is able to reproduce itself by sexual means as a good species. Biosystematic studies are continuing to further characterize the assumed hybrid origin of *C. tennesseensis.*

Cystopteris montana produces a unique spore type which possibly reflects the uniqueness of the plant itself. The spines were previously thought to be solid in this species, but are actually hollow. No other spore type duplicates the overall morphology of this type, although the spiny-lacunar type of *C. fragilis* and the warty spores of *C. tenuisecta* and *C. japonica* approach it in different ways. The term *conical-lacunar* has been coined to describe this type.

The sporophyte of *C. sudetica* is very similar in overall appearance to *C. montana* but they are characterized by two distinctly different spore types. The broad, cone-shaped, open spines and the papillate surface of *C. montana* is drastically different from the long, irregular spines and rough surface of *C. sudetica.* The spores of *C. sudetica* are much like those of *C. bulbifera,* which is not as close morphologically to *C. sudetica* as *C. montana.* The usefulness of spore characters should be emphasized here since this single character may be used to easily distinguish *C. sudetica* from *C. montana.*

Often morphological similarities in the plants are reflected by similarities in the spore types. *Cystopteris japonica* and *C. tenuisecta* are good examples. The plants are very close morphologically, and the spores are virtually identical. Using light microscopy, the spores of the warty type appear to have solid projections, but when viewed with the SEM, definite spaces beneath the warts are evident.

Cystopteris douglasii offers another unique spore type with its distinctive fine grainy surface on and around the spines. The overall appearance of the spore is very close to *C. fragilis* and once again the morphology of the two species is similar. *Cystopteris douglasii* is endemic to the Hawaiian Islands and is probably distinctive due to geographic isolation.

By far the biggest problem within the genus lies with the *C. fragilis* complex. This species is one of the most widespread of all ferns, and it has been impossible so far to sample specimens from every geographic area where it is found. The species is still poorly understood and research is continuing in all areas in order to provide greater insight into the complex.

Within *C. fragilis* three spore types were found. The normal echinate type (fig. 4, A–D) is the most widespread. Variations occur in the length of spines and in surface ornamentation where North American material has a rougher, striate surface compared to the smooth surfaced spores found in European material. Blasdell (1963) reported different spore sizes from tetraploid, hexaploid and octoploid cytotypes of *C. fragilis* and Jermy and Harper (1971) have found an increase in density of spines with increase in ploidy level.

The rugose type (fig. 4, E–F) has been reported from scattered locations in Northern Europe and North America and, as a result of this study, from one location in Costa Rica (San Jose Prov., Cerro Chirripo. *Evans and Lellinger* 101 [TENN]). It has long been thought by the present author and reported recently by others (Jermy and Harper, 1971) that the rugosity of these spores is due to shrinkage of the outer wall during drying. The papillate surface alone is unlike any other spore type in the genus even if the rugose surface is not considered. The rugose type has been described by other authors variously as a variety of *C. fragilis*, as *C. dickieana* Sim or as *C. baenitzii* Dorfler based only on spore morphology for its taxonomic treatment.

The spiny-lacunar spore type (fig. 5) is described for the first time in this paper. It has been suggested that the variation with the open network (fig. 5, C–D) may represent an abortive spore from a hybrid. However, in checking the specimens, it was found that 64 normal spores are produced in every sporangium examined. There is absolutely no evidence of abortive spores and both types are representative of normal functional spores. A recent thorough examination of numerous specimens from the Canary Islands and South America using light and scanning electron microscopy show the two spore types are restricted to their respective geographic regions. The Canary Island specimens are always of the type in figure 5, A–B while Central and South American material are either the normal echinate or the spiny-lacunar type of figure 5, C–D.

In the analysis of the spiny-lacunar type, the remainder of the genus must be considered. Most members of the genus produce spores which are more or less distinct at the specific level. Those taxa which are closely related produce spores which are very similar in structure. This is reinforced by current studies of the North American taxa of *Cystopteris* which produce virtually identical spores in varieties of *C. fragilis*. It is concluded that these two spiny-lacunar types represent two taxa other than *C. fragilis*. Blasdell (1963) reported the rather ill-defined taxon, *C. diaphana* (Bory) Blasdell, from the Canary Islands. The Canary Island spore type is possibly *C. diaphana*, however, this will not be known until the type can be studied. Blasdell also showed a considerably expanded range for this taxon into Central and South America but present data indicate that this is not true. Canary Island type spores were not found among Central or South

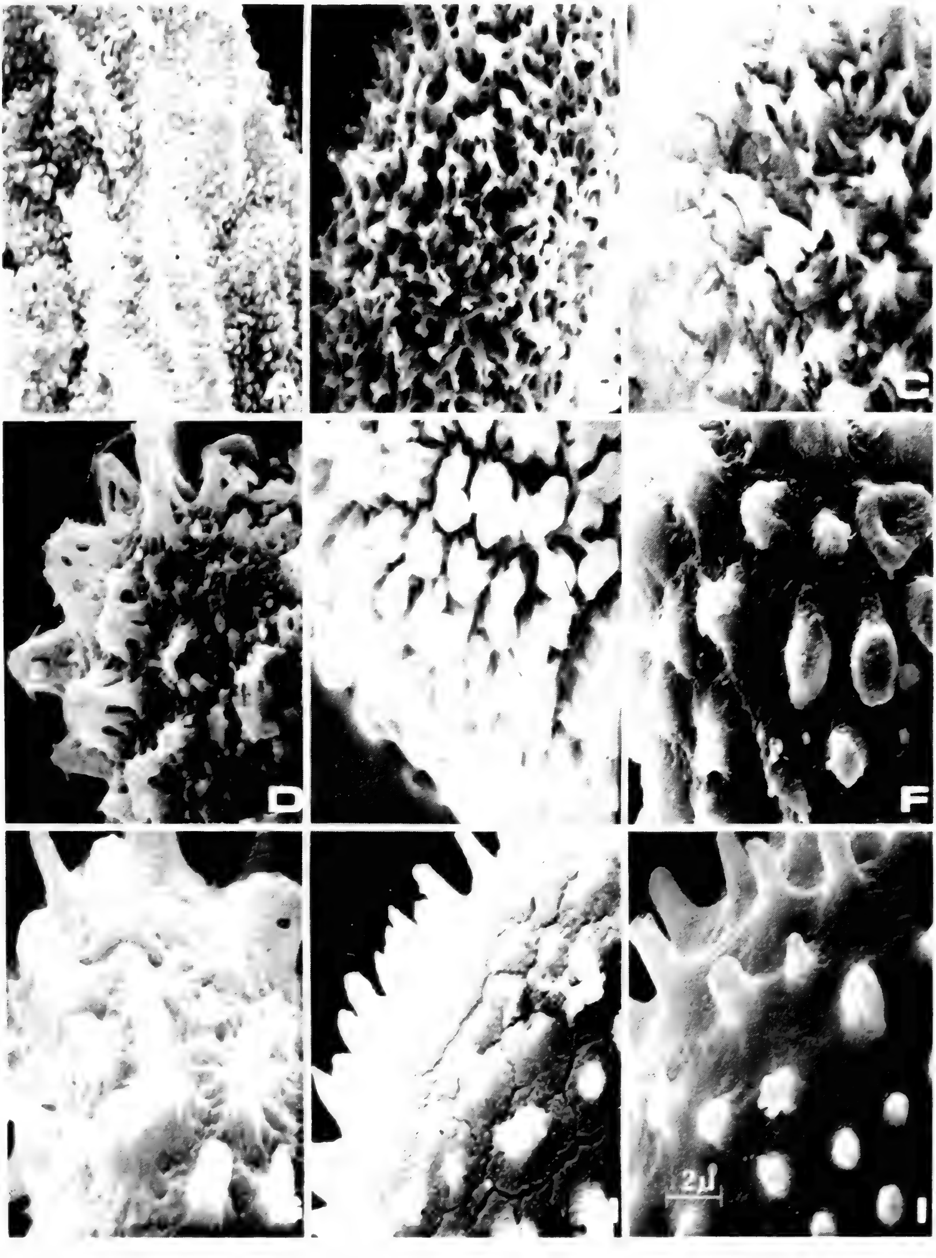

FIGURE 6: Summary of spore types: A, rugose *C. fragilis* var. *dickieana;* B-C, spiny-lacunar *C. fragilis;* D, conical-lacunar *C. montana;* E, warty *C. tenuisecta;* F, *C. bulbifera;* G, *C. sudetica;* H, *C. protrusa;* I, echinate *C. fragilis.*

South American material. Since the overall morphology of the ferns are similar to *C. fragilis,* final determinations are here deferred until such a time as a more definitive understanding of these taxa and their relation to *C. fragilis* can be made.

Figure 6 shows a summary of the different spore types found in the study, arranged in a possible evolutionary progression of perispore development (although not necessarily implying the same evolutionary arrangement of the taxa). 'A' is the rugose type with papillate projections of the perispore of *C. fragilis* var. *dickieana;* 'B' and 'C' are the spiny-lacunar type of *C. fragilis;* 'D' is the conical-lacunar type of *C. bulbifera* and 'G', 'H', and 'I' are echinate types of *C. sudetica, C. protrusa* and *C. fragilis* respectively, showing a progression from a rough surface to a smooth spore surface.

Spore ornamentation as shown by scanning electron microscopy, in conjunction with other traditional morphological studies, can be used to separate taxa within the genus *Cystopteris* and be a guide to possible evolutionary relationships. As with any other morphological unit, spores cannot stand alone in providing systematic answers to biological questions, but these data are presented to further enrich the understanding of the genus *Cystopteris.*

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ECOLOGY AND BIOGEOGRAPHY OF NEW ZEALAND PTERIDOPHYTES

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ABSTRACT

The main New Zealand pteridophyte habitats are outlined and the component species discussed in relation to their ecology. The biogeographical affinities of the pteridophytes are described and the contribution of each biogeographical element to the above habitats and to the intra-New Zealand distribution zones discussed.

INTRODUCTION

The New Zealand pteridophyte flora contains about 171 species of ferns and 19 species of fern allies which are native; in addition there are 11 adventive ferns and 2 adventive fern allies. The main islands of New Zealand extend from a subtropical climate north of lat. 35°S to the cool temperate zone south to lat. 47°S. Pteridophytes form a ubiquitous and important element in the New Zealand flora, occurring from sea-level up to 2560 metres altitude, in a wide variety of habitats and situations. The largest genera are *Asplenium* (17 species), *Blechnum* (17 species), *Lycopodium* (12 species), *Mecodium* (12 species) and *Grammitis* (9 species). In this account the native species are briefly discussed in relation to their ecology and the habitats in which they occur. In addition, the biogeographical relationships of the pteridophyte flora are outlined with reference to the contribution each element makes, not only to the separate habitats but also to the internal distribution zones which are chiefly latitudinal in basis.

The ecological data which form the foundation of the account were compiled by the author over a period of 14 years of field observations, mainly in the North Island, but including a number of expeditions to the South Island. Botanical nomenclature follows Allan (1961), except for species whose authority is given after their first mention in the text.

BIOGEOGRAPHY

The relationships of the New Zealand pteridophyte flora are inevitably complex, and are outlined in Table 1. As would be expected, the greatest affinity lies with Australia, but relatively few species are restricted to Australia and New Zealand, many having a wider distribution throughout South-east Asia and/or the Pacific. Indeed, most of the species common to Australia, New Zealand and Polynesia also occur widely throughout South-east Asia.

The pteridophytes can usefully be assigned to one of the following biogeographic elements.

1. Cosmopolitan; 6 species

This comprises species such as *Anogramma leptophylla, Cystopteris fragilis* and *Asplenium trichomanes* which have a bipolar distribution or which also occur on high mountains in the tropics. It is the smallest element in the New Zealand fern flora.

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TABLE 1

Relationships of the New Zealand pteridophyte flora in decreasing order of importance

	No. of species	*Percentage*
Shared between Australia and New Zealand	97	51.1
Restricted to Australia and N.Z.	34	17.9
Endemic to New Zealand	83	43.7
Shared between Polynesia and New Zealand	35	18.4
Not also in Australia	5	2.6
Shared between New Caledonia and N.Z. (and Australia)	35	18.4
Shared between New Guinea and New Zealand	32	16.3
Not also in Australia	3	1.6
Shared between South America and N.Z.	21	11.1
Not also in Australia	2	1.1
Shared between South Africa and N.Z.	18	9.4
Not also in Australia	1	0.5

2. Old World Tropics; 24 species.

Species with a wide distribution extending through Australia and/or Malesia to Polynesia (sometimes even further afield to Africa) are included here, e.g. *Lycopodium cernuum, Dicranopteris linearis, Adiantum hispidulum, Cyclosorus interruptus* (Willd.) Ito *(Thelypteris gongylodes)* (all in Australia, Malesia, New Caledonia, Melanesia, Polynesia, South Africa), *Schizaea dichotoma, Cheilanthes tenuifolia, Adiantum diaphanum, Lunathyrium japonicum* (Thunb.) Kurata, *Blechnum vulcanicum* (all in Australia, New Caledonia, Malesia, Melanesia, Polynesia), *Thelypteris confluens* (Thunb.) Morton (*T. palustris* var. *squamigera*) (New Guinea, South Africa).

3. Polynesia; 16 species

The species of this element are those of Melanesia and/or Polynesia, most of which occur also in Australia and sometimes in New Caledonia and/or New Guinea, e.g. *Lycopodium volubile* (Australia, New Caledonia, Polynesia), *Marattia salicina* (Australia, Polynesia), *Mecodium flabellatum* (Labill.) Copel. (Australia, Melanesia, Polynesia), *Cyathea medullaris, Asplenium shuttleworthianum* (Melanesia, Polynesia), *Reediella endlicheriana* (Presl) Pic.-Ser. (Australia, New Guinea, Melanesia, Polynesia).

4. Australia, New Caledonia (and New Guinea); 11 species

These species are largely restricted to Australia and New Caledonia but a few have also reached southeastern New Guinea, e.g. *Lycopodium deuterodensum, Schizaea bifida, Sphaerocionium lyallii* (Hook. f.) Copel., *Lindsaea linearis, Cheilanthes distans, C. sieberi* (Australia, New Caledonia), *Gleichenia dicarpa* R. Br. *(G. circinata), G. flabellata* (Australia, New Caledonia, New Guinea).

5. Austral; 16 species

This includes species with a purely circum-antarctic distribution, found in at least two of the three southern continents and/or their associated islands, e.g. *Lycopodium scariosum, Botrychium australe, Blechnum penna-marina, Grammitis magellanica* Desv. (Australia, South America), *Sphaerocionium ferrugineum* (Colla) Copel., *Grammitis patagonica* (C.Chr.) Parris (South America), *Hymenophyllum peltatum, Grammitis armstrongii* Tindale (Australia, South America, South Africa).

6. Australia; 34 species

These are species confined to Australia and New Zealand, e.g. *Tmesipteris*

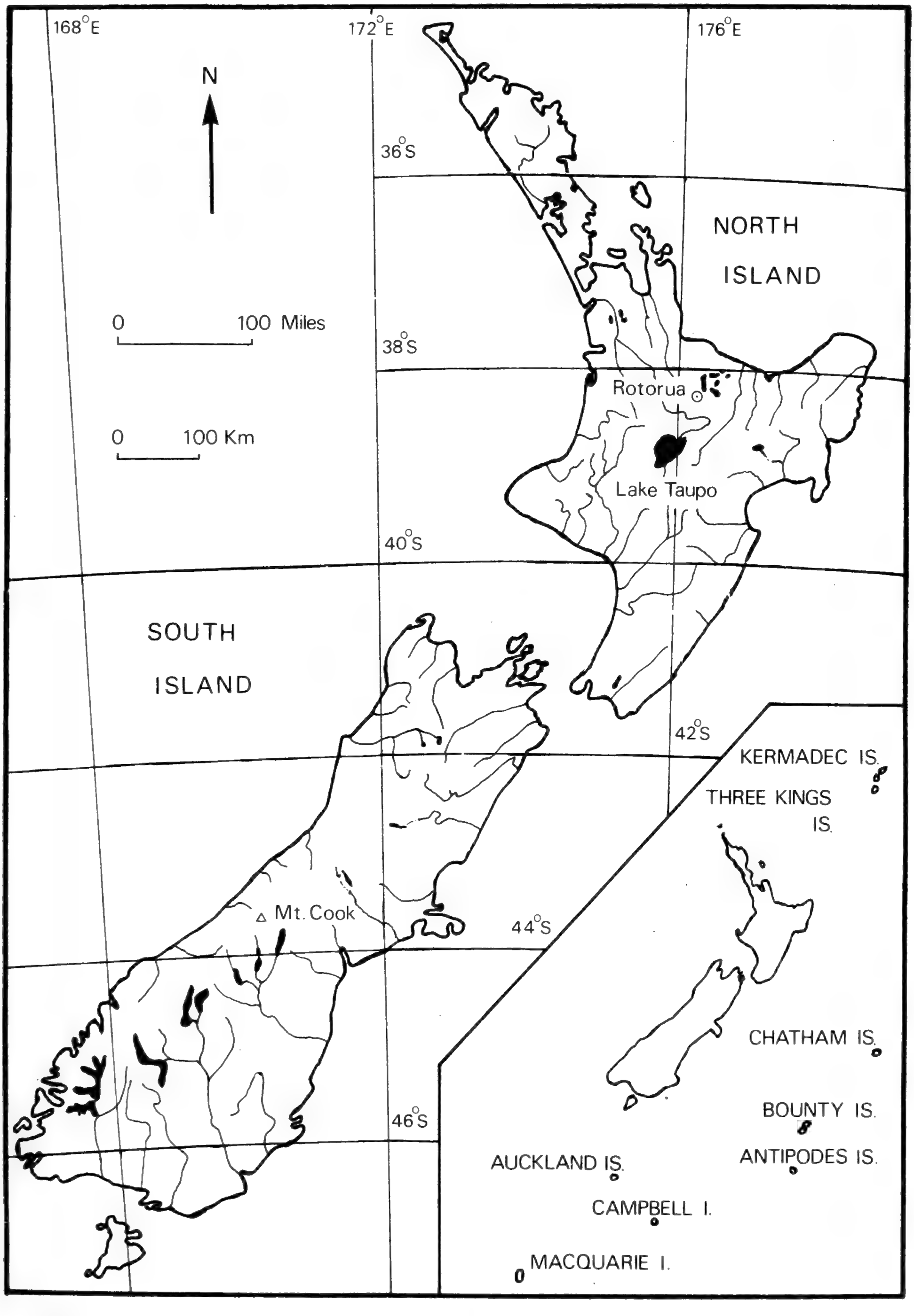

FIGURE 1: New Zealand: map showing latitudes, outlying islands and principal localities mentioned in the text.

elongata Dang., *Phylloglossum drummondii, Lycopodium fastigiatum, Gleichenia microphylla, Mecodium rarum* (R.Br.) Copel., *Hymenophyllum cupressiforme* Labill., *Lindsaea trichomanoides, Pellaea rotundifolia, Cyathea cunninghamii, Arthropteris tenella, Lastreopsis hispida* (Sw.) Tindale, *Pneumatopteris penniger* (Forst. f.) Holttum, *Athyrium australe, Asplenium flabellifolium, Pleurosorus rutifolius, Microsorum diversifolium* (Willd.) Copel., *Grammitis billardieri, Ctenopteris heterophylla* (Labill.) Tindale. This is, after the endemic species, the largest element in the pteridophyte flora.

7. Endemic; 83 species

Species found only in New Zealand represent several different levels of endemism. They may be monotypic genera of isolated taxonomic position, e.g. *Loxoma, Cardiomanes,* or monotypic genera with recognisable relatives elsewhere, e.g. *Leptolepia, Anarthropteris,* or be rather distinct and isolated species in their genera, e.g. *Meringium minimum* (A. Rich.) Copel., *Mecodium pulcherrimum* (Col.) Copel., *Lindsaea viridis, Blechnum filiforme.* Alternatively they may have more or less close relatives outside New Zealand, e.g. *Mecodium dilatatum* (Forst. f.) Copel., *Craspedophyllum armstrongii* (Baker) Copel., *Vandenboschia colensoi* (Hook. f.) Copel., *Paesia scaberula, Adiantum viridescens* Col., *Cyathea dealbata, Blechnum discolor, Pyrrosia serpens,* or be most closely related to other New Zealand species, e.g. *Lycopodium novae-zelandicum, Mecodium rufescens* (Kirk) Copel., *Pteris macilenta, Blechnum durum, B. membranaceum, Asplenium anomodum, A. hookeranum, Microsorum novae-zelandiae* (Baker) Copel., *Grammitis ciliata, G. pseudociliata* Parris.

HABITATS

The habitats described below, although broadly based on the categories recognised by Cockayne (1958), do not follow any single published system as they are modified to reflect more precisely the characteristics of the fern floras. The pteridophytes in each habitat are usually divided into terrestrial, low epiphytes (to 2 m up the main trunks of trees), crotch and main branch epiphytes, and high epiphytes. These last have various modifications for life in an extremely dry and often strongly insolated environment; they may adopt a mat form, such as various small filmy ferns, have a dense frond covering of hairs, or have thickened fronds, to prevent desiccation. Most high epiphytes have creeping, rather than tufted rhizomes. The main branch and crotch epiphytes are less xeromorphic, and more species in this micro-habitat have tufted rhizomes, especially those which grow in association with the large humus-collecting perching lilies, *Astelia* and *Collospermum.* The environment of the main trunk is more humid than higher up in the canopy and consequently a greater variety of species is found here, both creeping and tufted rhizomes being common. With decreased rainfall or humidity, as in more open forest, epiphytes grow lower down on the trees until, in extremely dry forest habitats, the high epiphytes of wet forest may occur rupestrally, as a rock substrate can give the same free drainage as do tree trunks and branches. In microhabitats marginal to forest such as open tracksides and roadside banks the more light-demanding species such as *Hypolepis tenuifolia, Paesia scaberula, Pteridium esculentum* (Forst. f.) Diels, *Cyathea dealbata, C. medullaris, Pellaea rotundifolia* and *Blechnum procerum* (Forst. f.) Sw. are frequent, while *Pteris* species and *Adiantum* species are more common here in the north, especially at low altitudes.

1. Coastal Cliffs; c. 21 species

This comprises both completely exposed sites and those under the protection of a coastal scrub or tree canopy. Although it intergrades with coastal forest at the cliff

FIGURE 2: Exterior of lowland forest with *Cyathea medullaris* at margin, Piha Valley, North Island. *(Photo. J.P. Croxall).*

top, this habitat is characterised by exposure to both sun and salt spray, and extremely free drainage. The ferns growing here are either specialised and restricted to this habitat, or are very hardy sun and salt spray tolerant species which occur in other habitats, sometimes as epiphytes. *Asplenium obtusatum* (a vicariate of the northern hemisphere *A. marinum* L.), *Blechnum banksii* and *B. durum* grow nearest to the high tide mark and are subjected to considerable amounts of salt spray. All are able to produce raw humus from their dead fronds (Cockayne 1958) and thus can colonise open rock surfaces. They are more common in the south of the country than in the north, which may be due to the need for a moist climate to prevent desiccation in an extremely free-draining habitat. *Blechnum banksii* is alone restricted to this habitat, as the other two species are common in coastal forest in the far south of the South Island and on the Subantarctic islands. Higher on the exposed cliffs grow *Cheilanthes distans, C. sieberi* and, south of c. lat. 38°S, *C. tenuifolia.* These three species also grow on equivalent sites in inland localities. At a similar level, where grasses and shrubs are able to establish, *Asplenium flaccidum* is common. It has a number of locally distinct terrestrial coastal forms which differ markedly from the epiphytic ones of inland forests. The widespread epiphytes *Pyrrosia serpens* and *Microsorum diversifolium* grow rupestrally at this level. Underneath the protection of a tree or shrub layer a few of the hardier species of coastal forest can establish, particularly on sheltered or eastern coasts. North of lat. 38°S *Pteris comans* is local on warm north-facing sites on the mainland but is far more common on the climatically milder offshore islands. *Pteris macilenta, P. saxatilis* (Carse) Carse and *P. tremula* are widespread in the North Island, particularly north of lat. 38°S. *Adiantum cunninghamii, Polystichum richardii, Blechnum procerum* and *Asplenium lucidum* are common throughout the country, as are the treeferns *Cyathea dealbata* and *C. medullaris* in particularly sheltered sites.

2. Coastal Forest; c. 77 species

Forest extending from above high tide mark and cliff tops to a few miles inland is subject both to varying amounts of salt spray and the ameliorating effect of a coastal climate. Generally it is more open in character and with fewer epiphytes than lowland forest with which it merges on its landward side. A few species are restricted to cliff and coastal forest and several species are far more common in coastal forest than in other habitats. Terrestrial species predominate in coastal forest. All the species of cliff forest are common on the forest floor, with the addition of *Lastreopsis glabella* (A. Cunn.) Tindale, *L. microsora* (Endl.) Tindale and *L. velutina* (A. Rich.) Tindale, *Blechnum chambersii* Tindale *(B. lanceolatum), B. membranaceum, Asplenium bulbiferum, A. lucidum* and the treefern *Dicksonia squarrosa. Adiantum aethiopicum, A. hispidulum, Doodia media* and *Asplenium lamprophyllum* are more common north of lat. 38°S, Whilst *Blechnum durum, Asplenium obtusatum* and *A. scleroprium* Homb. & Jacq. are common on the Subantarctic islands. On shaded banks and streamsides the more hygrophilic species such as *Mecodium demissum* (Forst. f.) Copel. and *M. sanguinolentum* (Forst. f.) Copel. occur throughout the country. In the north, *Reediella endlicheriana, Adiantum diaphanum, Lunathyrium japonicum* and *Doodia caudata* are restricted to this microhabitat in coastal forest, while in the south *Meringium minimum* is apparently found in similar situations. Epiphytes are not abundant in coastal forest. *Pyrrosia serpens* and *Microsorum diversifolium* can occur at all levels on trees from the main trunk to high branches but *Mecodium rarum, M. sanguinolentum, Arthropteris tenella* and *Microsorum scandens* (Forst. f.) Tindale are restricted to the main trunks, usually no more than 2 m above ground, and *Asplenium flaccidum, A. lucidum* and *A. polyodon* Forst. f. *(A. falcatum)* are usually only in crotches and on main branches. The climbing fern *Blechnum filiforme,* which is ground-rooting and hence not dependent on moisture retention in its epiphytic habitat, can be very common in coastal forest.

The species apparently restricted to cliff and/or coastal forest are *Pteris comans, Lastreopsis velutina, Davallia tasmani, Blechnum durum, Asplenium obtusatum* and *A. scleroprium.*

3. Lowland Forest; c.126 species

This replaces coastal forest within a few miles of the sea and may extend up to 300 m in the North Island and c. 200 m in the South Island, where it merges into upland forest. Structurally it is more dense than coastal forest and the resulting higher humidity favours a greater number of epiphytes. Figures 2 & 3 show respectively the exterior and interior of lowland forest. Lowland forest covers a large area of the country and thus contains more species than any other habitat. Only two species, *Marattia salicina* and *Adiantum formosum,* are restricted to it. Nearly all species are shared with coastal and/or upland forest but many are more common in lowland forest. The ground ferns include those of cliff and coastal forest with the exception of those listed above, but *Pteris* and *Adiantum* species are less common than in coastal forest. Other common ground ferns are *Lindsaea trichomanoides, Lastreopsis hispida, Pneumatopteris penniger* and, in damper places, *Leptopteris hymenophylloides* (A.

FIGURE 3: Interior of wet lowland forest showing dense development of epiphytes, Fox Glacier, South Island. *(Photo J.P. Croxall).*

Rich.) Presl and the filmy ferns *Mecodium demissum* and *Meringium multifidum* (Forst. f.) Copel. The principal low epiphytes, in addition to the two terrestrial filmy ferns, are *Mecodium flexuosum* (A. Cunn.) Copel., *M. flabellatum, M. rarum, M. sanguinolentum, Cardiomanes reniforme* (Forst. f.) Presl (fig. 4) and *Microsorum scandens.* Higher up, in crotches and on main branches, grow *Lycopodium billardieri, Asplenium lucidum, A. flaccidum* and *A. polyodon,* all the low epiphytic species of *Mecodium* except *M. flexuosum, Meringium multifidum, Cardiomanes reniforme, Ctenopteris heterophylla, Pyrrosia serpens* and *Microsorum diversifolium. Anarthropteris lanceolata,* however, is absent from southern forests. High epiphytes include *Mecodium flabellatum, M. rarum, M. sanguinolentum, Asplenium flaccidum, Ctenopteris heterophylla, Pyrrosia serpens* and *Microsorum diversifolium.* A few species are particularly common on treefern trunks; *Tmesipteris elongata* and *Polyphlebium venosum* (R.Br.) Copel. occur throughout New Zealand but *Tmesipteris lanceolata* Dang. is restricted to north of lat. 39°S.

4. Upland Forest; c. 104 species

This extends from c. 300 m to c. 850 m in the North Island, and from c. 200 m to c. 550 m in the South Island. At its lower limits it merges into lowland forest and at its upper level intergrades with montane forest. Structurally it is very similar to lowland forest and also contains relatively high numbers of epiphytes. Rainfall is somewhat higher than in lowland forest and the climate is cooler, hence the epiphytes are even more common. There are no species restricted to upland forest and all are shared with lowland and/or montane forest, but rather few of the common coastal forest ferns are important in upland forest. With the exception of lowland forest, it contains more species than any other habitat. Ground ferns are very numerous and include *Meringium bivalve* (Forst. f.) Copel., *Leptolepia novae-zelandiae, Blechnum discolor, B. fluviatile, B. "minus", B. vulcanicum* and the treeferns *Dicksonia lanata,* and *Cyathea smithii.* The miniature treefern *Blechnum fraseri* is common in the northern kauri *(Agathis australis)* forests, while *Polystichum silvaticum* is local in upland forest south of lat. c.38°S. *Leptopteris superba* (Col.) Presl (south of lat. 38°S), *Mecodium atrovirens* (Col.) Copel. (throughout), *Selenodesmium elongatum* (A. Cunn.) Copel. (mainly north of lat. 38°S), *Blechnum nigrum* (throughout) and *B. colensoi* (Hook f.) Wakefield (south of lat. 37°S) are usually restricted to dark wet streambanks, while the treeferns *Dicksonia squarrosa, Cyathea dealbata* and *C. medullaris* prefer the more open banks of wider streams. The low epiphytes include those of lowland forest together with *Mecodium scabrum* (A. Rich.) Copel., *Sphaerocionium ferrugineum, Hymenophyllum peltatum* and *Grammitis billardieri,* while the epiphytes of crotches and main branches are identical of those of lowland forest, with the addition of *Mecodium scabrum* and *Rumohra adiantiformis. Microsorium novae-zelandiae* is fairly common in this microhabitat, although restricted to the forests of the central North Island. The high epiphytes and climbing ferns are those occurring also in lowland forest, as are the treefern epiphytes, with the addition of *Sphaerocionium lyallii.*

5. Montane and Subalpine Forests; c. 67 species

These include all the forests at higher altitudes than upland forest, up to the treeline where beech is absent and to the lower limits of beech forest where it is present. They occur mainly south of lat. 38°S, tend to be simpler in structure than upland forest, especially at higher altitudes, but still support many epiphytes, although species are fewer than in lowland and upland forests. Rainfall is higher than at lower altitudes, and extensive frequent cloud cover can be very important in reducing the light within the forests. This, together with the colder climate, is doubtless responsible for the reduction in numbers of species compared with the lower forests. No species is restricted entirely to this habitat but several occur only here and in beech forest. Others are shared with lowland and/or upland forest, and a few species common to coastal, lowland and upland forests are still found here. Typical terrestrial species are *Leptopteris hymenophylloides, L. superba, Mecodium villosum* (Col.) Copel., *Meringium multifidum, Polystichum vestitum, Blechnum colensoi, B. "minus"* and the treeferns *Cyathea smithii* and *C. colensoi,* with *Asplenium richardii* and *A. trichomanes* common in the South Island in this habitat. Due to the moist climate, hygrophilic species are not restricted to dark streambanks in this habitat. Filmy ferns are the dominant low epiphytes *(Mecodium rarum, M. dilatatum, M. scabrum, M. flabellatum, M. demissum, M. villosum, Apteropteris malingii* (Hook. f.) Copel. (virtually confined to the trunks of the conifer *Libocedrus bidwillii), Hymenophyllum peltatum, Meringium bivalve, M. multifidum, Cardiomanes reniforme)* together with *Grammitis billardieri* and *G. magellanica* subsp. *nothofageti* Parris. The above filmy ferns, with the exception of *Hymenophyllum peltatum* and *Meringium bivalve* and the inclusion of *Mecodium pulcherrimum* and *Craspedophyllum armstrongii* together with the two *Grammitis* species above, *Asplenium flaccidum* and *Microsorum diversifolium* occur in crotches and on main branches. Higher in the canopy the number of epiphytes is reduced, with *Mecodium flabellatum, M. rarum, M. villosum, Meringium multifidum, Asplenium flaccidum, Microsorum diversifolium* and *Grammitis* species typically present. Most of the treefern epiphytes characteristic of lower altitude forest habitats are, with the exception of *Polyphlebium venosum,* no longer present at

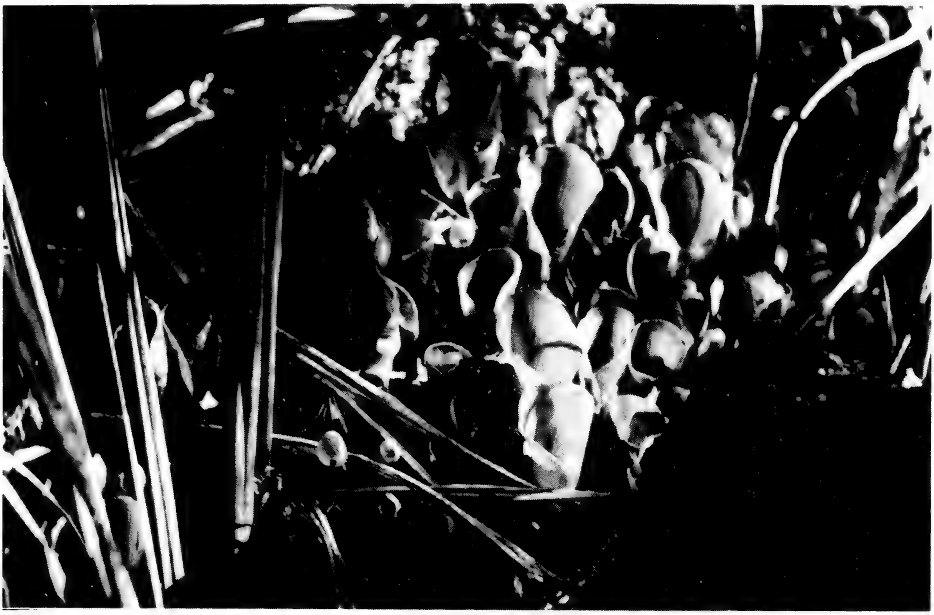

FIGURE 4: *Cardiomanes reniforme,* a common low epiphyte of lowland and upland forest, can also grow on rocks, as here on Rangitoto Island, North Island. *(Photo J.P. Croxall).*

these altitudes, and climbing species are also absent.

6. Beech Forest; c. 61 species

Both pure beech forest at low altitudes in the South Island and mountain beech forest are included here. The vegetation type is only found south of lat. 38°S. Structurally it is a fairly open forest and in the drier parts of the country may completely lack an understory. This leads to free air movement and rapid drying after rain, which markedly restricts the development of epiphytes. Although beech forest contains nearly as many species as montane-subalpine forest, they are, on the whole, far less abundant numerically. No species are restricted to this habitat, all being shared with subalpine-alpine scrub and/or montane-subalpine forest. In very wet beech forest the fern flora is nearly identical to that described for montaine-subalpine forest but in the much drier forests east of the main divide in the South Island the ground ferns may be restricted to *Polystichum vestitum* and *Blechnum penna-marina,* with the more drought-resistant species of filmy ferns, e.g. *Mecodium villosum* and *Meringium multifidum,* growing rupestrally or as low epiphytes, together with the *Grammitis* species of montane-subalpine forest.

7. Subalpine and Alpine Scrub; c. 29 species

Shrubland above the timberline (which occasionally forms mosaics with subalpine forest) mainly occurs south of lat. 38°S. It is essentially a single-story habitat but because it occurs in areas of high rainfall and frequent cloud cover there is usually some development of epiphytes, especially *Mecodium villosum, Craspedophyllum armstrongii, Meringium multifidum* and *Grammitis magellanica.* The climate is cool and snowfalls are frequent in winter, while on fine days the insolation can be intense. No pteridophytes are found solely in this habitat, all being shared with subalpine-alpine non-scrub communities and/or beech forest. *Lycopodium australianum, L. fastigiatum, L. varium, Mecodium villosum, Meringium multifidum, Hypolepis millefolium, Blechnum penna-marina, B. "capense"* and *Asplenium richardii* are terrestrial, while *Polystichum cystostegia* favours the more exposed and free-draining microhabitat of rocky debris and stabilised screes. *Cystopteris fragilis* is chiefly found in fairly open rock crevices. *Grammitis armstrongii, G. givenii* Parris and *G. patagonica* are frequently mat-forming on steep or overhanging rock-faces, a habit which with their coriaceous fronds enables them to withstand desiccating conditions.

8. Subalpine and Alpine Non-scrub Communities; c. 21 species

Subalpine and alpine grassland, herbfield and fellfield are characterised by their lack of woody shrub growth; hence epiphytes are absent. The climate is similar to that of subalpine-alpine scrub in the lower part of this habitat, with cool summers, much cloud cover and high precipitation, falling as snow in winter, but becomes more severe with increasing altitude. Insolation is more intense than in subalpine-alpine scrub. Most species are shared with the previous habitat, with others occurring in open areas at lower altitudes. The species of *Lycopodium* discussed under subalpine-alpine scrub together with *L. scariosum, Mecodium villosum, Meringium multifidum, Ophioglossum coriaceum, Blechnum penna-marina* and *Asplenium richardii* may all be found here more or less in the shelter of taller vegetation, while *Gleichenia alpina* R.Br. is often dominant in damper areas. *Polystichum cystostegia,* together with *Blechnum penna-marina,* is a pioneer of rock debris slopes and, as in subalpine-alpine scrub, *Grammitis* species are frequent on rock faces and overhangs; indeed, *Grammitis armstrongii* reaches higher altitudes than any other fern in New Zealand.

9. Open Areas; c. 12 species

This is essentially an artifically circumscribed habitat as it lacks the relatively definable altitude boundaries of the coastal to montane-subalpine forest habitats, but it includes all parts of these habitats where the canopy is broken and admits much light. Subclimax dune vegetation, open rocky areas and inland cliffs, and margins of swamps where the pteridophyte flora is in marked contrast to that of surrounding forest are included in this habitat, but land cleared from forest for agricultural use which often maintains (in marginal areas) a residual terrestrial forest fern flora of species resistant to high light intensity, grazing and trampling is excluded. All ferns of open areas are light-demanding and tolerant of higher temperatures and lower humidity than those in neighbouring forest areas. Three species, *Ophioglossum pedunculosum* (in fairly level grassy places), the annual *Anogramma leptophylla* (steeper and more rocky grassy sites) and *Pleurosorus rutifolius* (north-facing rock crevices, south of lat. 38°S) seem restricted to this habitat while the majority of the others e.g. *Cheilanthes distans, C. sieberi* (both extremely resistant to drought), *Pellaea rotundifolia, P. falcata* (both more shade tolerant than the other species) and *Asplenium flabellifolium* occur more or less throughout the country.

10. Scrub; c. 31 species

This includes the communities of *Leptospermum scoparium* and *L. ericoides* in lowland to montane habitats (but not subalpine scrub), which are largely seral following forest clearing or burning, and which regenerate in time to the primary forest of the area, so the ferns of mature scrub include the hardy pioneer species of forest. Scrub tends to be quite open in character underneath a fairly dense canopy, so epiphytes are absent. Frequently the ground is covered with a dry layer of dead *Leptospermum* leaves and there may be open areas, particularly on ridges in North

FIGURE 5: *Nephrolepis cordifolia* on banks of warm stream, Otumakokori, North Island. *(Photo J.P. Croxall).*

Auckland province where kauri forest has been destroyed, where the soil is a sterile bare grey or white clay. The pteridophytes of this habitat are usually particularly tolerant of dry conditions. Three species are entirely restricted to this habitat *(Phylloglossum drummondii, Schizaea bifida* and *Lindsaea linearis)* while others, e.g. *Gleichenia* species, are far more common here than in other habitats, where they occur only as marginal species. *Schizaea fistulosa, Gleichenia microphylla, Lindsaea linearis* and *Pteridium esculentum* are widespread, while *Lycopodium laterale, Gleichenia dicarpa* and *Blechnum procerum* are more common in damp areas. Species found only north of lat. 38°S are *Phylloglossum drummondii, Lycopodium cernuum, L. deuterodensum* and *Schizaea bifida,* with *Loxoma cunninghamii* and *Gleichenia flabellata* quite common on streambanks in the far north of the country.

11. Cold Water and Cold Water Swamps; c. 13 species

This ranges from still open water where pteridophytes are free-floating or bottom-rooting, to swamps and bogs which will intergrade at their margins with scrub or forest communities. Six species are restricted to this habitat while the others are also found in damper parts of scrubland. *Azolla filiculoides* Lam. *(A. rubra)* is the only native free-floating fern but in the north of the North Island the recent immigrant *Azolla pinnata* R.Br., a common Australian fern, and the adventive *Salvinia hertzogii* de la Sota may occasionally occur. *Isoetes alpina* (above 300 m), *I. kirkii* (throughout but scattered), *Thelypteris confluens* (north of lat. 39°S) and *Pilularia novae-zelandiae* (throughout) grow fixed to the bottom at lake and pool margins. *Thelypteris confluens* can also grow in very wet areas of swamps in open water and *Cyclosorus interruptus* occupies a similar habitat north of lat. 35°S. *Lycopodium laterale, Gleichenia dicarpa* and *Blechnum procerum* are common swamp pteridophytes but none grow actually in water.

12. Thermal Areas; c.34 species

The hot water swamps, streamsides and steam-heated ground in this habitat are mostly dominated by *Leptospermum ericoides,* but when heat and fumes are less intense a depauperate forest may develop. These communities are best developed in the Rotorua – Taupo district of the North Island. The pteridophytes are tolerant of varying degrees of soil heat, sulphur-laden fumes and mineral-rich warm water. Two species *(Dicranopteris linearis* and *Nephrolepis cordifolia)* are found only in this habitat while some others are more common here than elsewhere (e.g. *Christella dentata* (Forssk.) Brownsey & Jermy, and *Cyclosorus interruptus)* but the remainder are typical of the normal vegetation of the district. *Lycopodium cernuum, Gleichenia microphylla, Dicranopteris linearis, Hypolepis tenuifolia, Pteridium esculentum, Histiopteris incisa* and *Doodia media* grow in heated ground and on the banks of warm streams, while *Nephrolepis cordifolia* (fig. 5) and *Christella dentata* grow almost at water level by the streams, and *Cyclosorus interruptus* is usually restricted to warm water swamps. In the depauperate forest and well-developed *Leptospermum* scrub of the thermal areas, ground ferns include the treeferns *Dicksonia fibrosa, D. squarrosa* and *Cyathea medullaris, Pteris tremula, Adiantum cunninghamii, Polystichum vestitum, Pneumatopteris penniger* and *Blechnum fluviatile* while hardier epiphytes may also occur, e.g. *Mecodium rarum, M. sanguinolentum* and *Meringium multifidum,* together with *Asplenium lucidum, A. polyodon, Pyrrosia serpens, Microsorum diversifolium* and *Ctenopteris heterophylla.*

LATITUDE-BASED ZONES

In addition to the predominantly altitudinal and higher plant community-based habitat classification of the pteridophyte flora, a geographical division based primarily on latitudinal distribution within New Zealand is also possible, and a comparison of this with biogeographical elements is instructive. This classification recognises certain well-defined limits of distribution for both pteridophytes and higher plants.

1. Northern Islands only

Nine species are found only on the Kermadec group in the New Zealand region and one *(Davallia tasmani)* is endemic on the Three Kings Islands off the extreme north of the North Island.

2. North of lat. 36–38°S

24 species including those just reaching the north of the North Island (e.g. *Todea barbara, Doodia aspera* R.Br.) are not found south of this limit.

3. North Island and to the north of South Island, to lat. c. 42°S

27 species have their southern limit here.

4. Predominantly south of lat. 36–38°S (and usually over 300 m altitude, especially in the North Island)

43 species are not found north of this latitude.

5. Wide New Zealand Distribution

82 species occur more or less throughout New Zealand.

6. Thermal Areas

These are distinct in having a much warmer climate than is normal at their latitude. Two species are entirely confined to these areas and another two are found rarely north of lat. 35°S.

DISCUSSION

Table 2 shows the percentage of the pteridophyte flora in each latitude zone attributable to each biogeographic element. From this it can be seen that the cosmopolitan element is relatively unimportant and contributes a small number of the widely distributed and the southern species only. The fern flora of the thermal areas is completely derived from the Old World Tropics element which also provides many of the Northern Islands restricted species, quite a few species restricted to north of lat. 36–38°S and lat. 42°S, but very few of the widely distributed species and those confined to south of lat. 36–38°S. The Polynesian element makes a moderate contribution to both the widely distributed species and those occurring north of lat. 36–38°S, and smaller contributions to the species confined to the Northern Islands and north of lat. 42°S. The Australian-New Caledonian (–New Guinea) species form a moderate proportion of those north of lat. 36–38°S and 42°S, and a smaller proportion of those widely distributed throughout New Zealand. The Austral element provides a fair proportion of the species of more southern distribution and a smaller number of those restricted to north of lat. 36–38°S. The Australian element makes approximately equal contributions to four zones: north of lat. 36–38°S, north of lat. 42°S, wide, and southern distributions. The endemic element forms a large percentage of Northern Islands, north of lat. 42°S restricted, wide, and southern confined species and a considerable percentage of species restricted to north of lat. 36–38°S.

It is interesting now to compare the percentage contribution of the biogeographical elements to each of the previously discussed habitats. The basic data

TABLE 2

Percentage contribution of each biogeographic element to each latitude zone

	Element						
Latitude Zones	Cosmopolitan 6 spp.	Old World Tropics 24 spp.	Polynesia 16 spp.	Australia—New Caledonia (—New Guinea) 11 spp.	Austral 16 spp.	Australia 34 spp.	Endemic 83 spp.
Northern Islands 10 spp.	—	40	10	—	—	—	50
North of lat. 36–38°S 24 spp.	—	20.8	12.5	12.5	4.2	25	25
North of lat. 42°S 27 spp.	—	18.5	7.5	11.1	—	18.5	44.4
South of lat. 36–38°S 43 spp.	9.3	9.3	—	—	16.3	18.6	46.5
Wide distribution 82 spp.	2.4	2.4	12.2	6.1	9.7	18.2	48.9
Thermal Areas 4 spp.	—	100	—	—	—	—	—

are shown in Table 3. From this it can be seen that the cosmopolitan element is most important in open areas, subalpine-alpine non-scrub communities and cold water-cold water swamps, and is absent from the relatively low altitude habitats of coastal and lowland forest, scrub and thermal areas. The Old World Tropics species are most important in thermal areas, less so in cold water-cold water swamps, scrub, coastal and lowland forest and are absent from subalpine-alpine non-scrub communities. The Polynesian element contributes most to coastal cliffs, somewhat less to coastal forest, scrub and thermal areas, and is absent from subalpine-alpine non-scrub, open and thermal areas. The Australian-New Caledonian (—New Guinea) species are important in scrub, open areas and cold water-cold water swamps, and are absent from montane-subalpine and beech forest, and subalpine-alpine scrub and non-scrub communities. The Austral element contributes most to the subalpine-alpine scrub and non-scrub communities, somewhat less to montane-subalpine and beech forest and scrub, and is absent from open areas and cold water-cold water swamps. The endemic species are most important in coastal cliffs, coastal, lowland, upland, montane-subalpine and beech forest and last important in open areas.

In summarising the contribution of the various biogeographical elements several points are significant.

1. The high proportion of endemic species in all latitude-based zones and in all forest habitats, in coastal cliffs and subalpine-alpine scrub, and the reduced importance of this element in the more open and seral habitats. Numerically, endemic species are most common in lowland forest, have a wide distribution throughout New Zealand, and are least common in open areas and on the Northern Islands.
2. The fairly uniform contribution of Australian-New Zealand restricted species to each habitat and to the mainland latitude-based zones. The greatest numbers of species in this element occur in lowland forest and have a wide distribution in New Zealand.
3. The increased proportion of Austral species in the higher altitude habitats and the higher latitude zone. Numerically this element is most common in upland forest and the majority of the species are distributed throughout New Zealand or

TABLE 3

Percentage contribution of each biogeographic element to each habitat.

Habitat	Cosmopolitan 6 spp.	Old World Tropics 24 spp.	Polynesia 16 spp.	Aust.-N. Cal. (–N. Guinea) 11 spp.	Austral 16 spp.	Aust. 34 spp.	Endemic 83 spp.
Coastal cliff c.21 spp.	–	4.8	23.8	9.5	4.8	9.5	52.4
Coastal forest c.77 spp.	–	14.3	14.3	1.3	3.9	19.5	48.0
Lowland forest c.126 spp.	–	11.9	9.5	4.0	4.8	20.6	50.0
Upland forest c.104 spp.	1.0	8.7	8.7	1.9	6.3	18.3	55.8
Montane-subalpine forest c.67 spp.	1.5	7.5	9.0	–	7.5	17.9	58.2
Beech forest c.61 spp.	1.6	6.6	9.8	–	8.2	24.6	52.5
Subalpine-alpine scrub c.29 spp.	3.4	3.4	6.9	–	13.8	24.1	48.2
Subalpine-alpine non-scrub c.21 spp.	14.3	–	–	–	19.0	33.3	33.3
Open areas c.12 spp.	33.3	16.6	–	16.7	–	25.0	8.3
Scrub c.31 spp.	–	12.9	12.9	22.6	9.4	9.4	29.0
Cold water-cold water swamps c.13 spp.	15.4	15.4	–	15.4	–	15.4	38.5
Thermal areas c.34 spp.	–	35.3	14.7	5.9	2.9	14.7	26.5

are confined to the south of lat. 36–38°S.

4. The complete absence of the Australia-New Caledonia (–New Guinea) element at high altitudes and its relatively large contribution to the open and seral, compared with the closed, habitats. The greatest number of species is found in scrub and most are distributed throughout New Zealand.
5. The predominantly forest, coastal cliff and scrub-centred Polynesian contribution and the absence of this element from open habitats (except coastal cliff and thermal areas). Most species are found in lowland forest, north of lat. 36–38°S and 42°S.
6. The cosmopolitan element contributes mainly to open habitats and to the closed habitats of high altitudes and high latitudes. Numerically the cosmopolitan element is highest in open areas and south of lat. 36–38°S.

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REVIEWS

COMMON FERNS OF LUQUILLO FOREST, PUERTO RICO by Angela Kay Kepler 215 x 278 mm, vii + 125 pp. San Juan 1975. Price $ 15 US ($ 5 paperback) Spanish editions in both bindings available at same prices. From Inter American University Press, GPO Box 3255, San Juan, Puerto Rico 00936.

"This book is for the casual nature lover, interested amateur or professional biologist" is Mrs. Kepler's claim and I am always suspicious of such claims; but I think this book is excellent for many reasons, not the least being that in my opinion it lives up to it's aim in being an identification book for the interested layman. The drawings that accompany the text throughout are clear in detail and get the "feel" of the plant in habit sketches. Descriptions are readable for the uninitiated yet scientific, as are the ecological notes and geographical distributions; differences from similar species are given. The key looks as if it would work for a layman too, it certainly does for me. Specialists may criticise small points. I wonder about the common names which are so much a personal matter: I would have associated *Hernidictyum marginatum* for instance with *Heliconia* for which I almost mistook it when I first saw it in the forest, by calling it the Wild-plantain Fern, and even for the layman I do not like the use of Latin names without their authorities. We hope some who use this book will turn to other Floras, and Mrs. Kepler should have introduced us to the idiosyncrasies of nomenclature. Nevertheless this is a book worth having — it contains much of use to the indoor fern grower, and even if it had been reprinted at twice the price it would still be a very cheap buy.

A.C. JERMY

MORPHOLOGY OF THE SPOROPHYTE OF THE VITTARIOID FERN ANANTHACORUS

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ABSTRACT

The present studies have revealed that the monotypic genus *Ananthacorus* Und. et Maxon shows all the characters of the Vittariaceae and has several characters in common with those of *Vittaria.* Perhaps the most interesting and unique morphological feature of *Ananthacorus* is the nature of the vascular cylinder of the rhizome with its regular arrangement of leaf gaps representing suppressed leaves. On the basis of morphological comparisons, it is suggested that *Ananthacorus* is probably allied to *Vittaria* and possibly derived from it.

INTRODUCTION

Ananthacorus Und. et Maxon is a monotypic genus of vittarioid fern, the sole species *A. angustifolius* (Sw.) Und. et Max. being restricted in distribution to Jamaica and Tropical America. Goebel (1896) pointed out its relationship to the Vittariaceae on the basis of its spicular cells but did not give it a generic name. Christensen (1938), following Diels (1902), included it with *Vittaria* because of its two-lined sporangial arrangement. Benedict (1911) and Copeland (1947) separated it as a distinct genus. *Ananthacorus* is here considered to be a well marked genus of herbaceous epiphytic fern. The plant is rather inconspicuous because of the grass-like appearance of the fronds. Hitherto, the morphology of the genus has been almost unknown, except for the shape and size of the leaf, nature of the venation pattern and the shape of the sori and paraphyses (Benedict 1911, Copeland 1947).

MATERIAL AND METHODS

The present study of sporophyte morphology is based on material from Jamaica (S.C. Sinha, 63072, LWG), fixed in F.A.A. and stored in 70% alcohol. Anatomical observations recorded here are based on microtome sections stained with safranin and fast green. Stelar organisation has been studied mainly from serial sections (cut at 100 μ) and reconstructions based on camera lucida tracing of the outline of the vascular cylinder in serial section. Spore morphology is based on acetolysed spore samples mounted in glycerine jelly (Erdtman 1952). The spore descriptions are based on Nayar (1964).

OBSERVATIONS

Rhizome

The rhizome is creeping (c 3—4mm thick) and tufted, covered with dark brown basally attached, narrowly lanceolate paleae. The palea are clathrate (i.e. the internal lateral walls of the cells of the paleae thickened and all other walls thin) with a broad base, gradually tapering to an uniseriate apex terminated by a slightly swollen, ovoid, thin walled gladular cell (fig. 1 b, c-g). The stalk is 2—4 cells thick, the margin of the palea dentate, and the marginal teeth are formed by protruding ends of marginal cells (fig. 1 i). Some of the small paleae are hair-like, being uniseriate except at the base where they are two to four cells broad (fig. 1d, e). The thickening of the walls gradually progresses from the apex downwards. Mixed with the paleae on the rhizome, are found usually yellowish brown, long unicellular and septate hairs, some of which are gland tipped and branched (fig. 1 f-h). Structurally the rhizome is soft, parenchymatous and contains dense starch deposits. A characteristic feature of the rhizome is the thickening of the walls of the central cells of the ground tissue (both pith and cortex), the thickening being progressively less conspicuous from the centre towards the periphery of the rhizome. Cells of the inner ground tissue possess silvery, pitted walls. Often the corners of the parenchyma cells of the ground tissue are thickened in a collenchyma-like manner, as is also reported in *Vittaria remota* by Benedict (1914). The epidermis is thin walled. Sclerenchyma is absent.

The vascular cylinder of the rhizome is solenostelic, dissected by two rows of dorsally placed small elliptic leaf gaps (fig. 1a). These gaps are in paired groups. Within each group the members are close to each other but between groups there are wide separations. However, in contrast to other vittarioid ferns all gaps are not associated with leaves. Both gaps of each pair lie one in front of the other and not laterally as reported in other vittarioid ferns. The anterior gap (fig. 1 a "VG") of each pair is not associated with any leaf. Each leaf associated gap (i.e. the posterior one of each pair, fig. 1 a "LG") is similar to the leaf gap of other vittarioid ferns, although these gaps are more prominent.

The leaf traces are paired ribbon-shaped bundles and the leaf gap extends markedly on the posterior side between the leaf trace bundles so that the traces are attached one to either margin of the leaf gap near its middle plane. In each anterior gap a pair of ribbon-like vascular strands (fig. 1 a "V"), similar in shape and size to the leaf trace bundles are given off from each margin, the gap extending on the posterior side between these bundles. These two bundles curve out in the cortex of the rhizome like the leaf trace bundles and end blindly in the cortex well below the periphery of the rhizome. There is no indication of a reduced leaf externally on the rhizome but these gaps, associated with paired blind ending vascular strands, apparently represent suppressed leaves (fig. 1 a "V"). The suppression of this anterior member of each pair of leaves is characteristically regular. The suppressed anterior leaves (fig. 1 a "V"), directly in front of the well developed posterior ones (fig. 1 a "L"), contrasts with other vittarioid ferns where individual gaps alternate and pairs of gaps form two alternate rows.

Branching of the vascular cylinder is dichotomous as in other vittarioid ferns, the branching having no correlation with the leaves. However, each branch (fig. 1 a "B") is associated with a prominent gap in the vascular cylinder which extends to the base of the branch trace.

Roots are found in two irregularly lateral rows. There is no correlation between roots and either leaf or branch. Root traces (fig. 1 a "R") originate as superficial solitary vascular strands from the outer surface of the vascular cylinder.

The xylem tissue of the vascular cylinder is very much reduced and usually consists of only a single layer of tracheids, though at places it may become two layered (fig. 2). It consists entirely of tracheids having scalariform thickenings and there is no admixture of xylem parenchyma within them. The surface of the xylem band is irregular. Protoxylem points are situated at the free ends of the xylem band and also distributed on the outer surface (facing cortex) of the xylem cylinder and occupy an exarch position. A thin sheath of small xylem parenchyma cells envelops the xylem tissue except at the free ends of the xylem band. Phloem tissue is also very much reduced and usually consists of a thin (1–2 row) layer of small cells interrupted especially at the regions of the leaf gaps. The pericycle consists of 2–3 layers of large thin-walled parenchyma cells, becoming one layer towards the free ends of the vascular cylinder. Both the inner and outer endodermis are poorly-differentiated from the cells of the ground tissue.

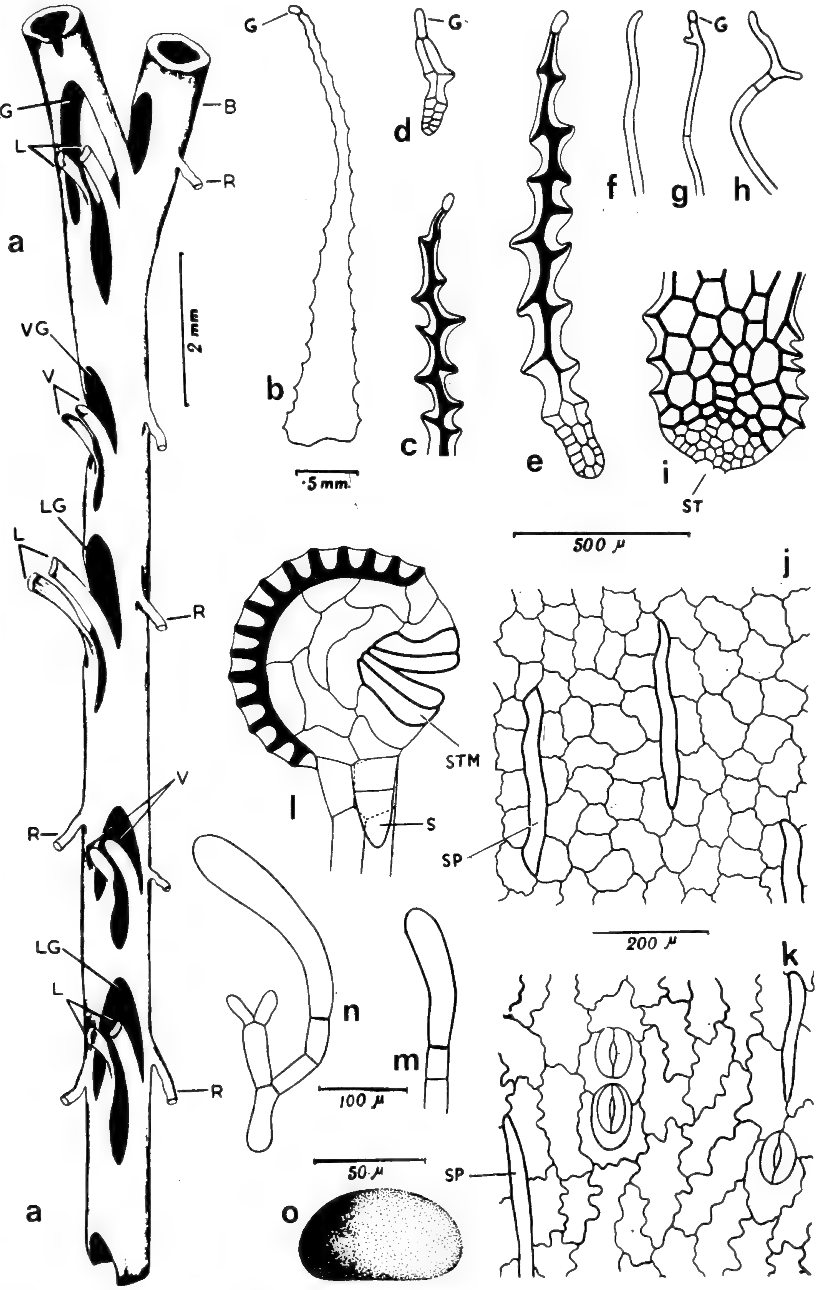

FIGURE 1: Morphology of *Ananthacorus angustifolius* (Sw.) Und. et Max.: a, portion of stelar cylinder of the rhizome; b, mature palea; c, apex of mature palea; d-e, young paleae; f-h, hairs mixed with paleae; i, base of mature palea showing margin and attachement of the stalk; j-k, upper and lower foliar epidermis; l, mature sporangium; m-n, paraphyses; o, lateral view of spore. ("B" = branch trace; "G" = glandular cell; "L" = leaf trace; "LG" = leaf gap; "R" = root trace; "S" = third row of stalk cells; "ST" = stalk; "STM" = stomium; "SP" = spicular cell; "V" = vascular strand representing suppressed leaf; "VG" = suppressed leaf gap).

Leaf

Leaves are simple, narrowly linear, stipitate (fig. 3) and non-articulated to the rhizome. They are arranged alternately in two rows along the upper surface of the creeping rhizome. The stipe and rachis are cylindrical and grooved on the dorsal side. The vascular supply to the stipe consists of a pair of ribbon-shaped strands, the xylem tissue of which is of 2–3 layers of cells, exarch and protostelic. The phloem usually consists of 2–3 layers of cells surrounding the xylem exept on the protoxylem points. The pericycle is of 2–3 layers of large-sized parenchyma cells, and the endodermis is poorly-differentiated.

The lamina is soft, thin and ribbon-like, gradually attenuated at both ends, with an entire margin. The venation is reticulate, with a prominent midrib, and a series of 4–5 rows of polygonal elongated areolae. These areolae are smaller towards the margin of the lamina than near the midrib and devoid of included veinlets. This type of venation, termed "pluriseriate" by Benedict (1911), is also found in the vittarioid ferns *Anetium, Antrophyum* and *Polytaenium.*

The foliar epidermis, on both surfaces, usually has copious long thickened epidermal cells, the so called "spicular" cells (fig. 1 j, k "SP"). The walls of these spicular cells are thicker than the other epidermal cells and have, by contrast, almost smooth margins. The presence of spicular cells along with the polygonal irregular epidermal cells has been reported in other vittarioid ferns by Goebel (1924), Benedict (1911), Bower (1928), Ogura (1938), Christensen (1938), Copeland (1947) and Holttum (1954). In *Ananthacorus* both the upper and lower epidermis are composed of cells with irregular sinuous outlines in surface view. The cells of the upper epidermis (fig. 1 j) are broad and polygonal with a faintly wavy outline. Those of the lower epidermis (fig. 1 k) are larger than the upper, narrow, elongated with their long axis parallel to the long axis of the leaf, and have more sinuous walls with more irregular outlines. Stomata are scattered all over the lower epidermis with their long axis parallel to the long axis of the leaf. The guard cells are elongated and oblong. The subsidiary cell of the stoma differs in shape from other epidermal cells and is broader than long. It surrounds nearly half to two third the circumference of the guard cells at the posterior end, whilst at the anterior end it dovetails into the corners of 2–3 cells or it completely surrounds the guard cells (fig. 1 k). In the latter case the stoma is at the anterior end of the encircling cell where the walls of the two are attached. Rarely a stoma is encircled by two rings of subsidiary cells; while the inner cell is narrow, small and with smooth outline, the outer one is similar to those described above (fig. 1 k). Both the upper and lower epidermis are chlorophyllous.

Sporangia

Fertile leaves are similar to the sterile ones. The exindusiate coenosori are present in two submarginal rows on each side of the midrib, in shallow grooves formed by the veins. Sporangia are borne in an elongated marginal sorus along the outermost veinlets on either side. The sorus usually extends all along the margin. The sporangia are of the common leptosporangiate type (fig. 1 l) with a large pear-shaped capsule borne on a short stalk of two cells thick, except at the capsule base where there is a short third row of cells (fig. 1 l "S") which is formed secondarily during sporangial development as a downward protrusion of the basal wall cell on one side of the sporangial capsule. The wall of the sporangial capsule is thin and composed of one layer of 10–12 flattened wall cells. The annular ring is well demarked with a region of 14–20 highly indurated thick walled cells protruding prominently from the surface of the capsule. As in all other vittarioid ferns, the stomium is of four cells (fig. 1l "STM") with thin walled accessory cells above and below it. Sporangia are usually protected by simple

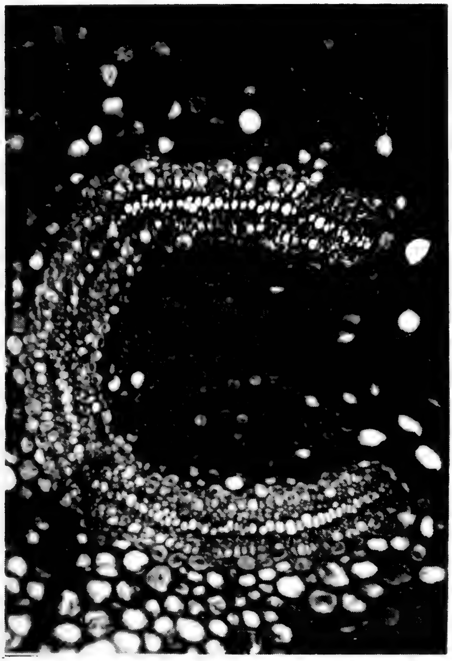

FIGURE 2: *Ananthacorus angustifolius* (Sw.) Und. et Max., transverse section of the stelar portion of the rhizome.

FIGURE 3: *Ananthacorus angustifolius* (Sw.) Und. et Max., habit of frond.

slender paraphyses (Benedict 1911, Copeland 1947) and rarely with branched paraphyses (fig. 1 m, n). The terminal cell of each type of paraphysis is large, swollen, elongated, club-shaped and dark brown. Branched paraphyses have not been previously described in *Ananthacorus,* but have been reported in several species of *Vittaria* (Benedict 1911, 1914; Holttum 1954), *Antrophyum semicostatum* (Holttum 1954) and *A. plantagineum* (Rao and Srivastava 1968).

Spores

The spores of *Ananthacorus* are of monolete-bilateral type, plano-convex or concavo-convex in lateral view (fig. 1 o), elongated oblong in polar view and measure on an average 44 x 80μ (polar diameter x longest equatorial diameter). The laesura is 58μ long. The exine is 2–2.5μ tick; the sexine slightly thicker than nexine and smooth. Perine is absent. The fresh spores are bright greenish yellow in colour, with many small plastids and dense contents including one or two large nearly colourless oil globules.

DISCUSSION

The morphology of the plant described in this paper shows all the characters of the Vittariaceae referred to by Benedict (1911), Bower (1928), Christensen (1938), Ching (1940), Copeland (1947) and Holttum (1954). The present studies have revealed that *Ananthacorus* has several characters in common with those of *Vittaria* as reported by Benedict (1911, 1914), Copeland (1947), Bir & Devi (1971). These include a rhizome with two rows of leaves, basally attached clathrate paleae, solenostelic vascular cylinder, binary leaf trace, xylem tract of the rhizome without admixture of xylem parenchyma; leaf lamina with sori in two submarginal rows along the outermost veinlets; simple and branched paraphyses; and bilateral, non-perinate spores. *Ananthacorus* differs however from *Vittaria* in having a pluriseriate venation pattern; distantly placed leaves over the rhizome; leaf gaps with suppressed leaves; xylem tissue of the rhizome with a single layer of tracheids; thickened ground tissue cells with silvery, pitted walls; and the pair of gaps alternating together to form two rows instead of individual alternating gaps as in other vittarioid ferns. Thus comparative morphology supports the earlier view of Benedict (1911) and Copeland (1947), who segregated *Ananthacorus* from its nearest relative *Vittaria* because of its pluriseriate venation pattern.

On the basis of similar venation in *Ananthacorus* and *Polytaenium,* Copeland (1947) suggested a close relationship of these genera. But the present studies have shown that *Ananthacorus* differs from *Polytaenium* in having a solenostelic vascular cylinder; origin of leaf trace bundles from either margins of the gap; paraphysate sori; two sporangial lines; and typical bilateral spores. However, in contrast to *Ananthacorus, Polytaenium* possesses a dictyostelic vascular cylinder; both leaf trace bundles originating from the same margin; sporangia usually in more than two lines; and typical tetrahedral spores.

Perhaps the most interesting and unique morphological feature of this monotypic genus is the nature of the vascular cylinder of the rhizome: its regular arrangement of leaf gaps representing suppressed leaves, where instead of individual gaps alternating, the paired gaps alternate, forming two rows on the dorsal surface of the rhizome. Thus the vascular cylinder of this genus does not resemble that of other known members of the vittarioid group. The vascular cylinder of the rhizome also presents some advanced features compared with *Vittaria:* namely the less dissected solenostele; xylem tissue reduced to only a thin layer of tracheids; suppressed leaf gaps; thickened cells of the ground tissue; and branches with prominent adaxial gaps.

The sum of these characters, together with the specialised venation pattern (Benedict 1911), point to a comparatively advanced position of the genus *Ananthacorus,* and suggest, on balance, that *Ananthacorus* is probably allied to *Vittaria* and possibly derived from it.

ACKNOWLEDGEMENTS

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REVIEW

COMPANION TO BEDDOME'S HANDBOOK TO THE FERNS OF BRITISH INDIA by B.K. Nayar and S. Kaur. 244 pp. Pama Primlane, The Chronica Botanica, Post Box 123, New Delhi-1, India. 1974. $14.00, Rs. 55.00.

Beddome's *Handbook* was first published in 1883 shortly after its author's retirement from Government service. He had spent over 30 years in India and published a bulky illustrated volume on the ferns of Southern India followed by another dealing with all the other ferns of British India known to him and not covered by his first work. The *Handbook* represented a more compact and up-dated distillation of this knowledge and it remained for more than 60 years a pteridologist's *vade mecum,* for few botanists if any have had Beddome's long and intimate field knowledge of Indian ferns. The last 30 years have seen a strong revival of interest in these plants and rapid advances have been made in our ideas about relationships and classification. One consequence of these advances is that Beddome's *Handbook* has lost some of its former value; most of the ferns described in it are now known by different names and often related species are very different from those assigned by Beddome.

The present volume is an attempt to correct the nomenclature of all the species included in the *Handbook* and its *Supplement* and to indicate modern views as to relationships. The book is divided into three parts. The first part entitled "Nomenclatural Changes" consists of a species by species list in the sequence of the *Handbook* with Beddome's name followed by the corrected name in bold-face type. The second part is devoted to Professor Nayar's proposed system of classification of ferns. This is an elaboration of the scheme published in *Taxon* in 1970. The third part consists of a revised list of names of Thelypteroid ferns following Holttum's subdivision of this group. A surprising feature of this section is the large number of new combinations which are made in Holttum's name.

The most important part of this "Companion" – indeed the *raison d'être* of the work – is the first part wherein the authors aim to give the corrected nomenclature for all species in the *Handbook.* It is on the success or failure therefore with which it achieves this aim that the book must be judged. In the opinion of the present reviewer the book fails in this respect to do what it sets out to do.

One of the features of the nomenclatural list is the provision of alternative names. These cover splinter genera in, for example, the Thelypteridaceae and also cases where specific epithets have been linked with several different genera by different authors. The alternative names are given in such cases on the grounds that "there is some difference of opinion among taxonomists regarding the genera to which they properly belong". This is a reasonable approach to a troublesome problem, but there are surely instances where the choice of name is heavily weighted in favour of one combination. The opinions of a taxonomist who has studied and monographed a genus on a world basis transcend in importance the views of those with a more restricted geographical knowledge of the same genus. Dr. Kramer has for many years made the lindsaeoid ferns his special study and no other living pteridologist could claim a comparably wide and deep knowledge of these ferns. One would have expected therefore that Kramer's views would have been reflected in the present list and that his choice of name would have been given priority where alternative names are cited. Yet *Schizoloma* and *Isoloma* which Kramer rejects as distinct genera, are used as the "correct" names in the case of *Schizoloma heterophylla, S. walkerae, S. orbicularis* and *Isoloma divergens* with Kramer's nomenclature cited under alternative names.

A more serious criticism however concerns the numerous errors in this and other groups throughout the list. The correct name for the fern cited by Nayar and Kaur as *Lindsaea lancea* (L.) Bedd. is *L. caudata* Hook. The Linnaean epithet was given to a South American fern. The correct name for the fern Beddome called *L. scandens* – a name which is repeated by Nayar and Kaur – is *L. parasitica* (Roxb. ex Griff.) Hieron. As described in the *Handbook, L. repens* covers two species viz. *Lindsaea repens* (Bory) Thwaites and *L. glandulifera* v.A.v.R. The latter is nowhere mentioned by Nayar and Kaur who do however cite *L. pectinata* Bl. as a second species though this has been reduced by Kramer to varietal status. The correct name for *L. orbiculata* var. *tenera* is not *Schizoloma tenerum* but *L. orbiculata* var. *commixta* (Tagawa) Kramer. The plant to which Beddome refers under the name *Schizoloma lobata* is the fern to which the name *Lindsaea cultrata* (Willd.) Sw. properly belongs and also includes *L. venusta* Kaulf. ex Kuhn (not mentioned by Nayar and Kaur) to which Beddome's illustration, F.S.I.t.27, of *Schizoloma recurvatum* belongs. Poiret's *Lindsaea lobata* which is here used as the corrected name for the Indian fern, is native to Sumatra, Java and eastwards to the Philippine and Caroline Islands but not known in India or Ceylon. Since the paper in which Kramer pointed these facts out is quoted by Nayar and Kaur their errors are inexcusable. Kramer also showed many years ago that the type of the species which had previously been known universally as *L. cultrata* (Willd.) Sw. – a name regrettably once again repeated here for the wrong species – belongs to the fern commonly called *L. decomposita* Willd. and the correct name for *"L. cultrata"* is *L. odorata* Roxb. It is particularly unfortunate that these avoidable errors should have been made since they reintroduce nomenclatural confusion and disorder into a group of ferns the systematics of which has been so carefully clarified by its monographer.

The errors noted above all fall within three pages of the nomenclatural list. The list runs to 106 pages. Other mistakes occur all too frequently. Some of these are due to the authors' having overlooked relevant literature, Dr. T.G. Walker's papers on *Pteris* being one example. The cause of some errors is difficult to understand. How can one reconcile the citation of a taxonomic paper with the fact that its contents are disregarded? My revision of the athyrioid ferns of Ceylon is quoted on p. 40 yet the nomenclature relating to *Diplazium* as given in that paper is ignored and incorrect names are perpetuated.

This is a work which might have been of considerable value to Indian and other pteridologists, but the standard of accuracy falls so far short of what is required in such a list that great care will need to be exercised by those using it. It is to be hoped that a corrected edition will be issued in due course.

W.A. SLEDGE

SIX NEW SPECIES OF SELAGINELLA FROM TROPICAL SOUTH AMERICA

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ABSTRACT

Six new tropical American species of *Selaginella (anisoclada, asplundii, cruciformis, euclimax, glossophylla, leucoloma)* are described on, respectively, pages 255, 257, 257, 259, 259, 262. They should be cited as Alston ex Crabbe & Jermy in Fern Gaz. 11 (1974).

Following our presentation of seven new species (Amer. Fern J. 63: 135–144, 1973) we now present six further new species recognized by A.H.G. Alston and based on his manuscript. We are indebted to Michael Mullin of our Section for help with the photography of the illustrations.

Selaginella anisoclada Alston ex Crabbe & Jermy, *sp. nov.* (Fig. 3a and b)
Species heterophylla inter fere omnes ramulis minutifoliatis distinguenda, ex affinitate *S. porphyrosporae* A. Br. sed foliis lateralibus ovatis (non lanceolatis) obtusioribusque distinguitur.

Stems glabrous, ascending, 4–10 cm high; 0.3 mm in diam. at the base, branched from the base; rhizophores restricted to the basal third; primary branch-system ovate to oblong, with secondary branches about 5–8 mm apart, pinnate, up to 2 cm long, and tertiary branches 2–3 mm long, fertile and simple, or sterile and branched, sometimes appearing swollen at the tips. Leaves heteromorphic becoming isomorphic in the ultimate branchlets; lateral leaves distant, ovate, 0.5–2.0 x 0.25–1.0 mm, subacute, the inner half-leaf* semi-ovate, rotundate at the base and distantly serrulate, the outer half-leaf semi-ovate-oblong, rotundate-truncate at the base and entire; axillary leaves ± the same as the lateral leaves; median leaves ovate or ovate-elliptic, 1.25–0.5 x 0.3–0.8 mm, entire, acute. Strobili single at the apex of or forming the entire ultimate lateral branches, sometimes continuing growth vegetatively at the apex, subtetrastichous, c. 3 x 2 mm. Mega- and microsporophylls similar, 1.25 x 0.5 mm, obliquely lanceolate, carinate, white-margined, serrulate, with acute apices. Megaspores 220–280 μm, yellow, minutely scabrate with a reticulum of low rounded ridges. Microspores c 22–32 μm, yellow, ± smooth.

Type: Venezuela, Aragua, above Guamitas, Parque National, 900 m, on rock in forest stream, bright green, 30 December 1938, *Alston 5814* (holotype BM; isotypes US, VEN).

Paratypes: Colombia, Magdalena, Sierra del Libano, Santa Marta, 1675 m, common locally on open or shady wet rocks in a ravine, pale gray green, 1898–99, *H.H. Smith 2242* (BM, NY, US); Santa Marta, 1898–1901, *H.H. Smith 2567* (BM).

Geographical range: confined to E coastal ranges of Venezuela and Colombia.

This species is distinct in its distant arrangement of both median and lateral leaves which are almost isomorphic on the ultimate branchlets. It varies, in the limited

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* We first, in Amer. Fern J. 63: 135, 1973, used the term "half-leaf" for each of the two parts of the leaf blade divided by the midrib, the "inner" being on the acroscopic side, the "outer" on the basiscopic.

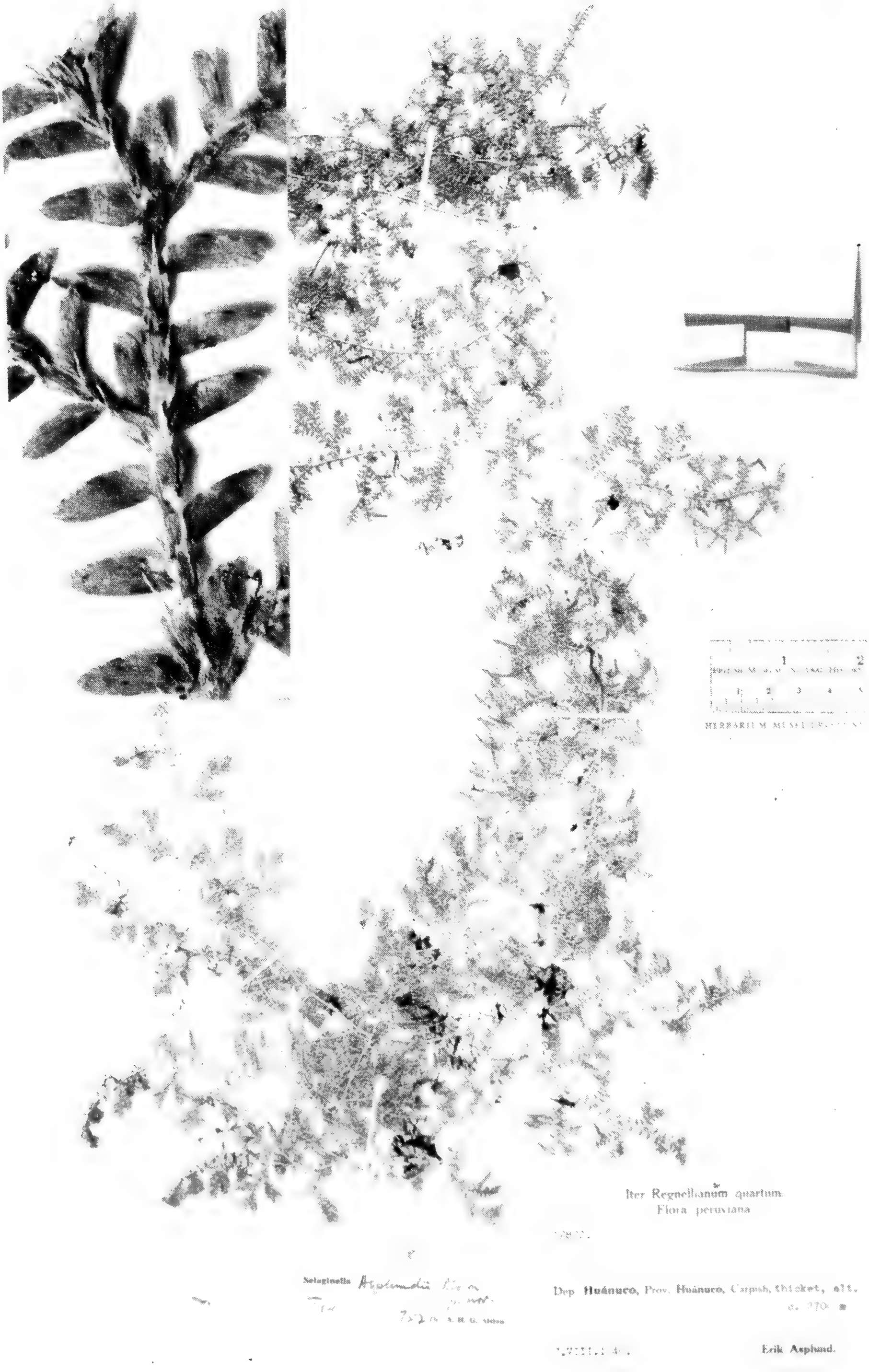

FIGURE 1: Type specimen of *Selaginella asplundii* inset: close-up of dorsal surface x 9.

material seen, in stature of plant and degree of branching, a character obviously affected by the moistness of and competition in the habitat. It is most similar to *S. porphyrospora* A. Br. from Mexico to Panama (type: Mexico, Vera Cruz, *C. Sartorius 1896,* B, isotype BM) but in that species the lateral leaves are large, lanceolate and acute, and there is a tendency for them to show a false nerve when dry. In Venezuela and Colombia *S. lychnuchus* Spring can be similar in habit, but that species has dimorphic sporophylls and large, oblong lateral leaves and long aristate median leaves.

Selaginella asplundii Alston ex Crabbe & Jermy, *sp. nov.* (Fig. 1).
Species heterophylla ex affinitate *S. arenariae* Bak., sed habitu caulibus multo longioribus repentibus (nec habitu compacto) et foliis intermediis valde aristatis (nec acutis) differt.

Stems glabrous, up to 1 m long or more, creeping, prostrate, obscurely articulate, monostelic, pale green-straw coloured, alternately pinnate or irregularly branched with lateral branches, 2- or 3-pinnate, spreading, ovate or irregular in outline; rhizophores dorsal in origin, distant. Leaves heteromorphic throughout; lateral leaves spreading, up to 5 mm apart, but more crowded on the branches, 2.25 x 1.0 mm, with obtuse apices, the inner half-leaf semi-oblong-lanceolate, denticulate towards and gradually rotundate at the base, abruptly cuneate at the apex, the outer half-leaf semi-oblong, shortly rotundate at the base, abruptly cuneate at the apex; axillary leaves oblong-lanceolate, obtuse; median leaves distant, elliptic, denticulate, 1.5 x 0.75 mm, long-aristate at the apex, the outer half-leaf rotund-auriculate at the base. Strobili tetrastichous, c 10 x 1.25 mm, single at the apices of ultimate branches. Megasporophylls 2.0 x 1.2 mm, at the base of the strobili; megaspores c 550 μm, pale brown-yellow, with an irregular crested white reticulum. Microsporophylls 1.5 x 0.9 mm, ovate, denticulate; microspores c 40 μm, hyaline, strongly spiny.

Type: Peru, Huánuco, Carpish, in thicket, 2700 m, 7 Aug 1940. *E. Asplund 12822* (S-P, isotype BM).

Paratype: Peru, Huánuco, Carpish, on shore of rivulet, 2650 m, 7 Aug 1940, *E. Asplund 12843* (S-P).

Geographical range: confined to Peru.

This species is named in honour of the late Erik Asplund, curator of the Regnell Herbarium at Stockholm and a world-famous authority on the flora of South America.

Selaginella cruciformis Alston ex Crabbe & Jermy, *sp. nov.* (Fig. 2).
Species heterophylla ex affinitate *S. chrysoleucae* Spring, sed foliis intermediis ovato-oblongis (nec elliptico-falcatis), brevissime acuminatis (nec longe aristatis), plerumque distantibus (nec crebre imbricatis), et textura flaccidiora differt.

Stems glabrous, suberect from an ascending base, 20–40 cm high, 2 mm in diam. at the base; rhizophores restricted to the basal quarter; branch system pinnate throughout, secondary branches initially perpendicular to main stem (i.e. cruciform), and those towards the base often continuing growth and becoming the primary branch system, sporulation simultaneous on any one primary branch system, colour generally blue green. Leaves everywhere heteromorphic; lateral leaves spreading, subcontiguous or slightly imbricate, oblong, 5.0 x 2.5 mm, obtuse, inner half-leaf semi-oblong-lanceolate, broadly rotundate and distantly serrulate at the base, outer half-leaf semi-oblong, rotundate-cuneate and serrate at the base, serrulate towards the apex, otherwise entire; axillary leaves unequal-sided and ± similar to the lateral leaves;

FIGURE 2: Type specimen of *Selaginella cruciformis* inset: close-up of dorsal surface x **9**.

median leaves elliptic-oblong, 2.5 x 1.75 mm, minutely apiculate, serrulate. Strobili tetrastichous, 8.0 x 1.5 mm, single as lateral spurs on secondary or tertiary branches. Sporophylls 1.5 x 0.75 mm, ovate-deltate, carinate, serrate, acute. Megaspores c 280 μm, pale brown when moist, minutely granular, cristo-reticulate with prominent proximal ridges. Microspores c 23μm, pale yellowish when moist, with close elongate papillae.

Type: Venezuela, Carabobo, R. Aguada, by stream in forest, 1800 m, *Alston 6240* (BM).

Paratypes: Venezuela, Aragua, Rancho Grande, 1400 m, *Box 3879* (BM); Colonia Tovar, 915 m, *Fendler 487* (BM); Yaracuy, Cerro La Chapa, N of Nirgua, 120–1400 m, 9/10 Nov 1967, *Steyermark, Bunting & Wessels-Boer 10025* (BM, US).

Geographical range: confined to Venezuela.

This species resembles *S. chrysoleuca* Spring in the lateral strobili and the basal rhizophores. It might also be confused with *S. truncata* A. Br., but that species is prostrate and rooting throughout and has terminal strobili.

Selginella euclimax Alston ex Crabbe & Jermy, *sp. nov.* (Fig. 3c, d and e).

Species heterophylla ex affinitate *S. huehuetenangensis* Hieron., sed foliis intermediis et lateralibus serratis (nec valde ciliatis, praesertim semifacie lateralium superiore) differt.

Stems glabrous, ascending from a creeping base, c 15 cm high, 1 mm in diam. at the base, with a small but characteristic tubercle at the insertion of the superior margin of the lateral leaf; branching throughout, branch-system ovate-elliptic, branches c 6 mm apart, pinnate or bipinnate, up to 3.5 cm long. Leaves heteromorphic throughout; lateral leaves spreading, closely spaced, oblong, 3.0 x 1.3 mm, obtuse, the inner half-leaf semi-oblong-lanceolate, serrate, gradually rotundate-cuneate at the base, thickened at the point of insertion with the stem, the outer half-leaf semi-oblong, almost entire; axillary leaves ± similar to lateral leaves but less unequal-sided; median leaves elliptic-oblong, 1.5 x 1.0 mm, serrate, aristate at the apex, aristae up to almost half the length of the lamina. Stobili tetrastichous, 4.0 x 1.5 mm, single or paired at the apex of short lateral branches. Sporophylls c 1.4 x 0.9 mm, narrowly ovate--deltate, carinate, serrulate, acute. Megaspores c 300μm, pale yellow-brown when moist, verrucose. Microspores c 30μm, yellow when moist, papillate with elongate papillae.

Type: Colombia, Cauca, W of Tambo, 2300 m, *Haught 5220* (BM, isotype US).

Paratype: Colombia, Antioquia, Rio Guatope, 5–6000 m, *Kalbreyer 1457* (B).

Geographical range: confined to Colombia.

This species also resembles *S. tarapotensis* Bak. which is prostrate (instead of suberect) and with a longer arista. *S. pearcei* Bak. is also very similar but it has broader lateral leaves with acute apices, very short aristae, and is usually less branched below.

Selaginella glossophylla Alston ex Crabbe & Jermy, *sp. nov.* (Fig. 4a and b).

Species heterophylla ex affinitate *S. popayanensis* Hieron., sed foliis lateralibus oblanceolatis, obtusis (nec ovatis, acutis), foliisque intermediis acutis (nec acuminatis) differt.

Stems glabrous from ± creeping base, c 7 cm long, filiform, branched from the base, whitish straw-coloured when dry; rhizophores restricted to the basal part; branch-system irregular, branches c 8 mm apart, simple or pinnate, 1–3 cm long. Leaves heteromorphic throughout; lateral leaves spreading, distant, entire or with a few teeth, 2 x 1 mm, obtuse, round cuneate, sometimes symmetrical, oblong-elliptic, or asymmetrical, the inner half-leaf semi-oblanceolate-oblong, the outer half-leaf semi-oblong-elliptic; axillary leaves broadly oblong-elliptic, slightly oblique; median leaves obovate, mostly 1.0 x 0.5 mm, distant, entire, or with a few teeth, acute. Strobili lax with few sporophylls, 4 x 3 mm, single at the apex of lateral branches. Sporophylls 1.5 x 0.7 mm, of one kind, varying slightly in width and colour, oblong-lanceolate or oblong-elliptic to ovate, acute or slightly acuminate, serrate from a hyaline margin. Megaspores c 330μm, golden yellow, cristate-reticulate, granulate. Microspores c 34μm, golden yellow when moist, smooth or minutely pitted.

Type: Bolivia, Cochabamba, Chaparé, Incachaca (lat. 17°14'S, long. 65°49'W, 130 kms NE of Cochabamba), 3000 m, 22 Aug 1950, *Winifred M.A. Brooke 6783* (BM).

Paratype: Chile, without exact locality, 1848, *Mercier s.n.* (P).

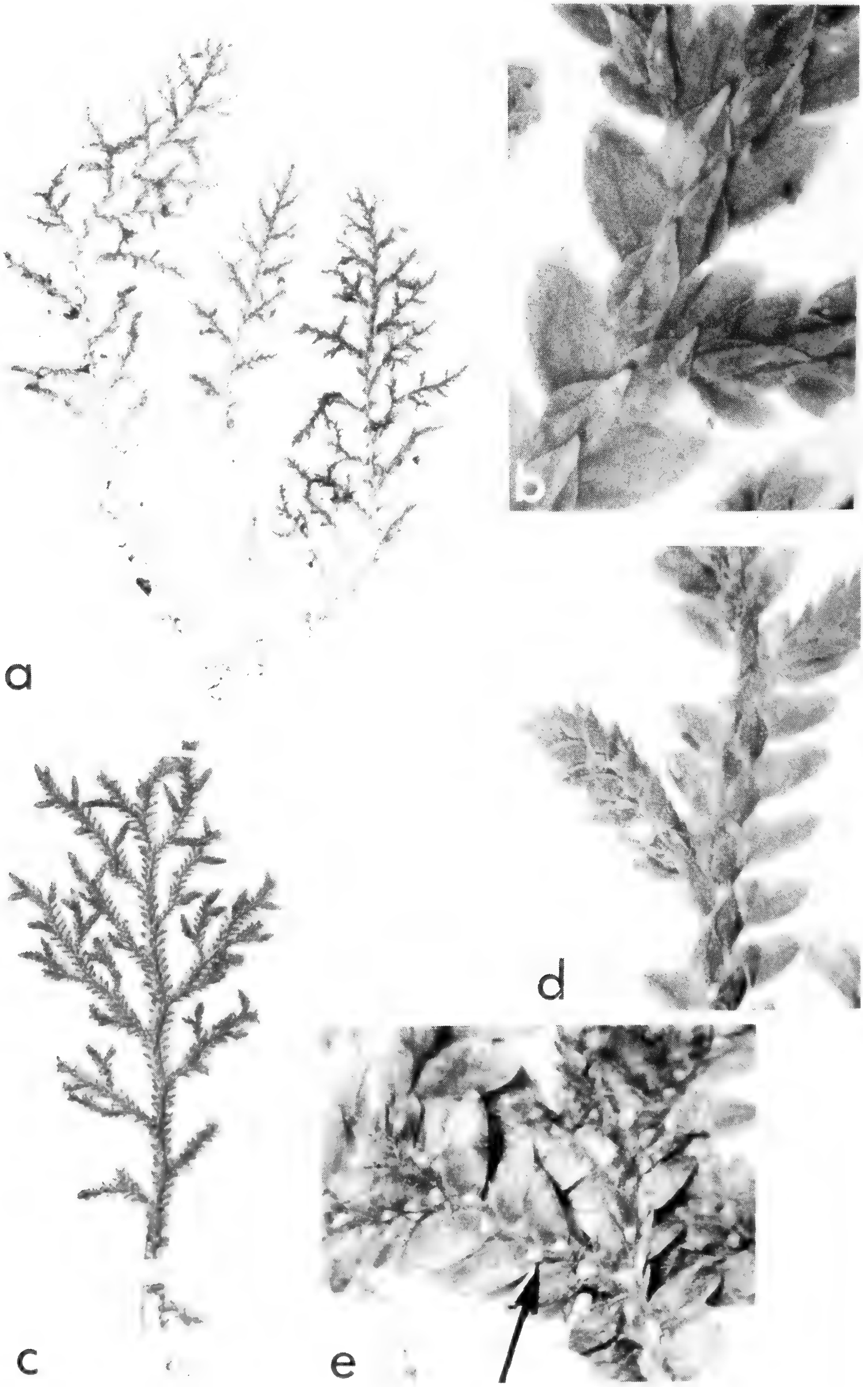

FIGURE 3: a and b, Type specimen of *Selaginella anisoclada;* a, whole plant x 1; b, dorsal surface of main stem x 18; c, d and e, Type specimen of *Selaginella euclimax;* c, whole plant x 1; d, dorsal surface of branch with cone x 9; e, ventral surface showing characteristic tubercles (arrowed) x 9.

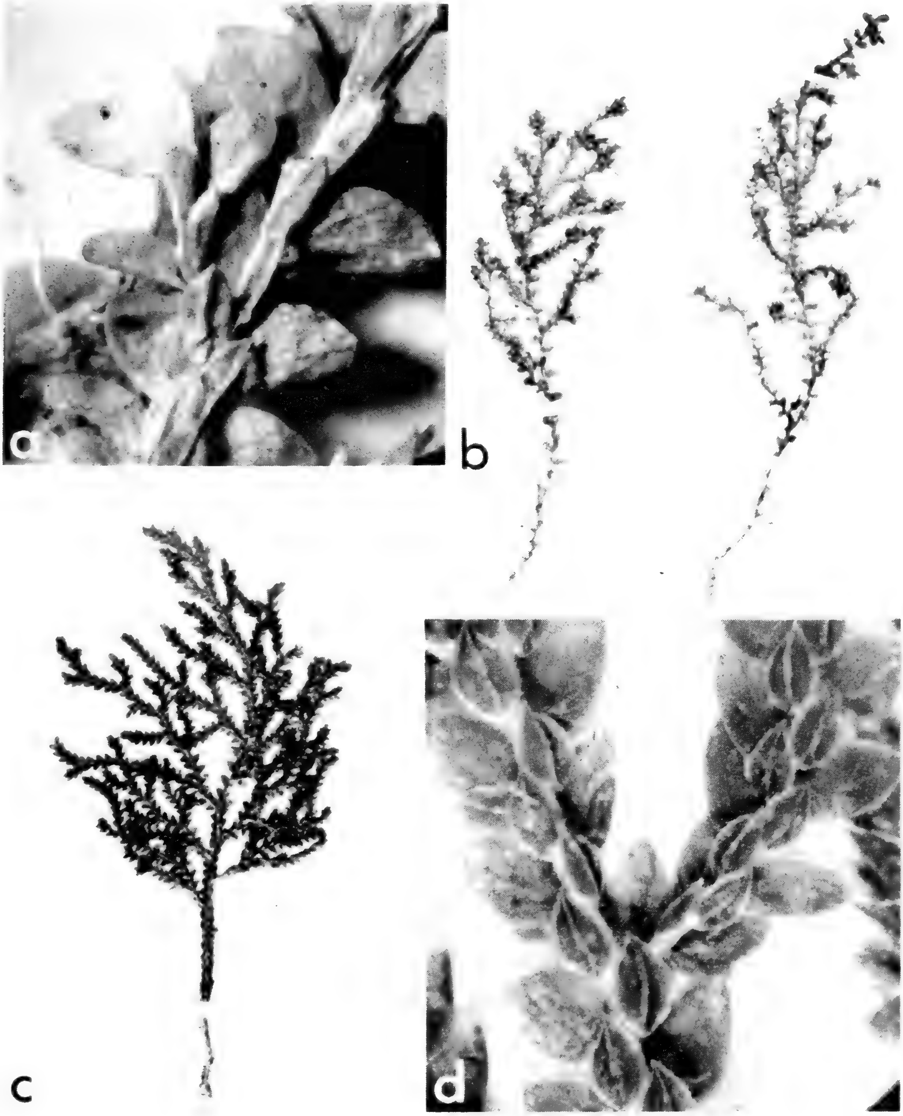

FIGURE 4: a and b, Type specimen of *Selaginella glossophylla;* a, dorsal surface x 18; b, two plants from type sheet (BM); x 1; c and d, Type specimen of *Selaginella leucoloma;* c, whole plant x 1; d, dorsal surface of main branch x 18.

Selaginella leucoloma Alston ex Crabbe & Jermy, *sp. nov.* (Fig. 4c and d).

Species heterophylla ex affinitate *S. novae-hollandiae* (Sw.) Spring, sed foliis intermediis acutis (nec aristatis), albo-marginatis et exauriculatis differt.

Stems glabrous, erect from a very short creeping base, up to 10 cm high, 0.5 mm in diam. at the base, the lower part simple, 1.5—4.0 cm long, pale green-straw coloured when dry; rhizophores restricted to the base; branch-system ovate-oblong, branches up to 5 mm apart, bipinnate, irregular, up to 3 x 1 cm, occasionally a lower primary branch-system developing and becoming dominant. Leaves heteromorphic throughout; lateral leaves spreading, contiguous or distant, broadly ovate-oblong, 1.75 x 1.30 mm, obtuse, rounded at the base, with white margins; inner half-leaf broadly semi-ovate-oblong, ciliate in the lower half, serrate at the apex; outer half-leaf semi-oblong, entire; axillary leaves ovate or ovate-oblong, mostly equilateral, 1.5 mm long, ciliolate at the base; median leaves broadly elliptic, with hyaline white margins (best seen by transmitted light), the lower ones long-ciliate, the higher ones short-ciliate, 1.0 x 0.7 mm, distant or imbricate, acute. Strobili subtetrastichous, lax with few sporophylls, 3 x 1 mm, single at the apex of short lateral branches. Sporophylls 1.2 x 0.6 mm, ovate, carinate, serrate, acute. Megaspores c 200μm, pale brown, minutely warted. Microspores c 37.5μm, pale yellowish when moist, papillose.

Type: Bolivia, La Paz, Hacienda Simaco, on the road to Tipuani, Larecaja, 1400 m, Feb 1920, *Buchtien 5280* (BM, isotype US).

Paratypes: Bolivia, La Paz, Hacienda Simaco, on the road to Tipuani, Larecaja, 1400 m, Feb 1920 *Buchtien 5278[A]* (BM, isoparatype US) — this gathering is a mixture of *S. novae-hollandiae* and *S. leucoloma,* and specimens of the latter at BM & US have been labelled 5278*[A]*; Bolivia, ravin de Pelechuco, 1843—48 or 1851, *Weddell 4779* (P).

In habit this species resembles *S. popyanensis* Hieron., but its branches are denser and its lateral leaves are ciliate (not entire).

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ERRATA—CORRIGE

On p. 96, 9 lines from bottom, after "light castaneous" insert "in lower half and blackish castaneous upwards, with long flexuous cilia; paleae of stipe castaneous".

On p. 98, line 12, after "melleous to fulvous" insert "concoloroas throughout or"; line 14, after "irregular in length" insert, "direction and distance".

On p. 99, 3 lines from bottom, after "distal part, with" insert, "concolorous edges and".

DRYOPTERIS CAUCASICA, AND THE CYTOLOGY OF ITS HYBRIDS

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ABSTRACT

Meiosis in wild collected plants of *Dryopteris* x *initialis* (= *D. abbreviata* x *D. caucasica*) and *D.* x *euxinensis* (= *D. caucasica* x *D. filix-mas*) has been studied; the results adding much weight to the hypothesis that *D. caucasica* represents the hitherto unknown diploid ancestor of *D. filix-mas.* The cytological results show there to be a certain degree of homology (c 5—23 bivalents) between the two diploid genomes presumably contributed by *D. caucasica* and *D. abbreviata* — which casts doubt on the traditional amphidiploid nature of *D. filix-mas.* Some other diploid species possibly not far removed are also mentioned, and the question of *D. filix-mas* in North America is raised. New localities for *D.* x *euxinensis* (one in Europe) are given, and *D. caucasica* is reported from European Turkey and European Russia along with a diagnostic description of the Flora Europaea format.

INTRODUCTION

Tentative identification of the diploid species *Dryopteris caucasica* (A.Br.) Fraser-Jenkins and Corley as a parent of the tetraploid species *D. filix-mas* has recently been proposed (Fraser-Jenkins and Corley 1973); and the chemical constituents of *D. caucasica* have been investigated with a view to testing out its suitability as a parent of *D. filix-mas* (Widen *et al.* 1973). The other parent of *D. filix-mas* was shown nearly twenty-five years ago by Professor Manton to be *D. abbreviata* (DC) Newman (Manton 1950). However only fragmentary cytological evidence was available to support the position of *D. caucasica,* and further investigation remained to be done.

The present paper gives the results of recent cytological work carried out on cultivated plants of wild hybrids of *D. caucasica.* These hybrids were collected in Turkey and the Caucasus in 1971 and are:

1. *Dryopteris* x *initialis* Fraser-Jenkins & Corley (*D. caucasica* x *D. abbreviata*) — diploid.
2. *Dryopteris* x *euxinensis* Fraser-Jenkins & Corley (*D. caucasica* x *D. filix-mas*) — triploid.

The third hybrid in the group, *D.* x *mantoniae* Fraser-Jenkins & Corley (= *D. abbreviata* x *D. filix-mas*) has already been thoroughly investigated cytologically by Manton in artificially produced plants (Manton 1950) and by Dr. S. Walker in wild plants (Fraser-Jenkins & Corley 1973), both finding it to be triploid with approximately 41 bivalents and 41 univalents at meiosis.

CYTOLOGY

D. x initialis

The plant used for this study was the one from which the holotype and isotypes were taken in the wild. This was found in 1971 growing with *D. abbreviata* and *D. caucasica* in the Caucasus — the upper Teberda valley below the Klukhurskiy Pass at c 2,100 m alt., in mixed forest, CRFJ 3210 (BM, LE and G). Fixed material was prepared from a clonal offset of this plant in May 1974 and meiosis was examined using the standard acetocarmine squash technique (Manton 1950). The results consistently show this hybrid to be diploid (2n = 82) with a number of bivalents ranging from 5 to 23 (mean: 14) and the corresponding number of univalents (fig. 1).

FIGURE 1: Diagram of Meiosis in *D.* x *initialis,* type plant: CRFJ 3210, cult. Radley, May 1974. 17 bivalents, 48 univalents, diploid.

D. x euxinensis

The plants used for this study again came from the Caucasus — the Teberda valley, below the Klukhurskiy pass at c 2000 m alt. (not 2,300 m alt., as stated in Fraser-Jenkins & Corley, 1973) CRFJ 3209 (BM); and also from the Black Sea Coast of Turkey — Bolu province, above Kaynasli on Bolu Dagi at c 900 m alt. CRFJ 2080 (BM), where they were both growing with *D. caucasica* and *D. filix-mas.* Fixed material of clonal offsets of these plants was prepared in May 1974 and meiotic preparations consistently show these hybrids to be triploid (2n = 123) with 41 bivalents and 41 univalents.

Interpretation

Up until now many difficulties have arisen in the interpretation of the cytological evidence that was available. Bivalent formation could perhaps have been the autosyndetic pairing of an autopolyploid, along with suppression of multivalent formation by a genetic mechanism — as has been shown to exist by Riley (1960) and suggested in *Asplenium* and *Adiantum* by Vida and others (Manton, Sinha & Vida 1970; Vida 1970 & Lovis, Sleep and Reichstein 1969). Indeed *Dryopteris marginalis* x *D. filix-mas* found wild in Ontario, Canada and Michigan, U.S.A. has been investigated cytologically and chemically (Wagner 1971; Widen & Britton 1971) and a range of from c 5 to 41 bivalents has been found which is more or less compatible with the result now obtained from *D.* x *initialis.* However, although this has been interpreted by Wagner (1971) as showing *D. filix-mas* to be an autopolyploid there is considerable morphological difference between European *D. filix-mas* and that of the Eastern U.S.A. and the present author strongly suspects that the two are quite different species, which is also suggested by the chemical analyses carried out by Widen & Britton (1971). Stereoscan studies of the spores of these taxa are reported in Britton & Jermy (1974). Against the possibility of autopolyploidy is the presence of artificially induced diploid plants of *D. filix-mas* made independently by Manton & Walker (1954) and Döpp (1961) which show a high number of univalents at meiosis, for example Manton & Walker report between 2 and 5 bivalents which is also a lower number than in most *D.* x *initialis.* More confusing is the possibility of partial homology between the genomes, in particular if both *D. abbreviata* and *D. caucasica* have subsequently evolved away from the original genome or genomes which gave rise to *D. filix-mas.* It is clearly most important to hybridise *D. filix-mas* with a quite unrelated species such as *D. assimilis,* which should not show any genomic homology, and observe the meiotic pairing behaviour in the hybrid, as being representative of the two genomes of *D. filix-mas.*

However the present results on *D.* x *euxinensis* and *D.* x *initialis* throw much light on the situation which has in fact turned out to be most interesting. The two diploid species are clearly not entirely representative of the same genome, otherwise c 41 bivalents would be expected at meiosis. The inability of most of the chromosomes to form bivalents at meiotic metaphase, along with the 41 bivalents present in *D.* x *euxinensis* confirms the identity of *D. caucasica* as genome "C" of *D. filix-mas* – the second hitherto unknown parental diploid, different from *D. abbreviata.* However, the rather high number of bivalents (from 5 to 23), is of interest because it suggests a certain degree of homology between the genomes of the two diploid species; so *D. caucasica,* though quite distinct, is fairly closely related to *D. abbreviata.* This might well be expected on the basis of the very general morphological similarities between them and they would probably both be put into the same group even if the morphologically intermediate *D. filix-mas* did not exist. This also means that the nature of *D. filix-mas* may not be the straightforward amphidiploid that has sometimes been suggested, e.g. Stace (1975: 47), but rather nearer to a segmental allopolyploid.

It is of interest to point out that several other diploid species are superficially similar to this group and might also show a certain degree of genome homology if the diploid hybrids between them and the *D. filix-mas* aggregate could be synthesised – the triploid hybrids between these species and *D. filix-mas* would be less informative as one could not be sure which genomes were responsible for pairing behaviour; this is part of the problem which besets the interpretation of the hybrids mentioned above between *D. marginalis* and *D. filix-mas.* Examples of taxa which might be somewhat related are *Dryopteris fragrans* (L.) Schott, *D. pallida* (Bory) Fomin and its subspecies (including *D. arguta* (Kaulf.) Watt and *D. raddeana* Fomin); *D. villarii* (Bell.) Woynar, *D. barbigera* (Moore) O. Ktze., *D. monticola* (Makino) Christ and *D. goldiana* (Hook) A. Gray. Indeed closeness of *D. villarii* to *D. caucasica* is suggested even more by their having the same chemical constituents (Widen *et al.* 1973), and Vida has already suggested that the *D. villarii* aggregate has a central position in the evolution of most species of European *Dryopteris* (Vida 1969), an opinion which the present author also endorses.

The proposed origin of *D. filix-mas* supposes that it arose spontaneously from *D.* x *initialis* by doubling of chromosomes, a situation similar to the case with *Asplenium adulterinum* (Lovis 1968). This might be confirmed by sowing pure samples of the spores of *D.* x *initialis,* an operation which the author has not yet carried out, to see if some of them are fertile and diploid despite their highly abortive appearance, thus probably giving rise to tetraploid plants. If this is so, one might also expect *D. filix-mas* to be forming *in situ* in the Caucasus and Turkey at the present day, and as *D. caucasica* and *D. abbreviata* show a wealth of minor variation in those areas, so should *D. filix-mas.* More collections from the Caucasus would therefore be highly desirable.

NEW LOCALITIES FOR DRYOPTERIS x EUXINENSIS, D. x INITIALIS and D. CAUCASICA

On an expedition to Turkey and Iran in 1973, three new sites for *D.* x *euxinensis* were discovered though the identity of all these plants has not yet been cytologically confirmed:

IRAN: Gilan, Ardabil-Astara, Tavalesh, 1490 m alt., growing with *D. caucasica,* 14/8/1973, CRFJ 3924 (BM).

TURKEY (Asia): Artvin, S.W. side of Yalnizcam Dag, 1,800 m alt., growing with both parents, 22/8/1973, CRFJ 3988 (BM).

TURKEY (Europe): Kirklarelli, nr. top of Mahya Dag, Istranca Daglari, 1000 m alt., with *D. filix-mas,* 31/7/1973, CRFJ 3899 (BM) and 28/7/1975, CRFJ 4567–8 (BM).

These last specimens represent the first discovery of *D.* x *euxinensis* in Europe; and the author was also able to find a very few plants of *D. caucasica* there in 1975, CRFJ 4566 (BM), though most of the population consisted of hybrids. This therefore represents a species new to Europe and an amended key and diagnostic description follow below to allow it to be inserted in Flora Europaea.

Further specimens of all three *D. filix-mas* group hybrids from the Caucasus were seen by the author in the herbarium at LE in January 1976 and specimens of *D. caucasica* were seen there from the Crimea (Alexeenko 1894; Kotov, Rishakov and Svetev 1955; Busch 1905; Grigoryev; and Wulff 1916) and from the vicinity of Kalarash in Soviet Moldavia (Igoshina 1948; Opatskaya 1958; and Borisova and Kapustina 1949).

(1–4) *D. filix-mas* group

2 Large plant with 1 or only a few crowns; acute pinnule-teeth; non-inflected indusia.
3 Shortly acute pinnule-teeth; rounded lobes at the sides of the pinnules usually bearing teeth singly. Spores greater than 36μm long. **1. D. filix-mas**
3 Long acute pinnule-teeth; square lobes at the sides of the pinnules usually bearing teeth in pairs. Spores up to 37μm long. **1/1. D. caucasica**
2 Small plant with several crowns; obtuse pinnule-teeth; inflected indusia. **3. D. abbreviata**

1/1 D. caucasica (A.Br.) Fraser-Jenkins & Corley, Brit. Fern Gaz. 10(5): 221–31 (1973). Like 1 but distinguished by the thinner texture and paler colour of the fronds which usually have a long stipe and a markedly truncate base to the lamina. Pinnae noticeably wider towards the middle and often asymmetric with longer segments on the basiscopic side. Pinna segments with square lobes at the side and with acute tips bearing long very acute teeth usually in pairs. Sori with wide flat caducous indusia, and spores small (31–37μm long) with distinctive short ridges or verrucae. $2n = 82$. *Montane forest in South West Russia, Krym and North West Turkey* Tu, Rs (W, K), ?RM. (Caucasus, N. Turkey and the Caspian area of Iran).

It may be that *D. caucasica* has retreated from most of Europe due to climatic changes but it might be expected to have survived in some suitable relict habitats and it would be well worth looking for in such places as the eastern mountain ranges of Bulgaria and Romania. It also survives on Ulu Dag in Bursa province, Turkey, CRFJ 3904 (BM) along with *D. filix-mas.*

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SHORT NOTES

SELAGINELLA IN RAJASTHAN, INDIA

Despite its wide occurrence in India (Alston 1945, Panigrahi 1967), *Selaginella* has not been previously recorded from any locality in Rajasthan (Mital 1969a). One of us (O.P. Sharma) discovered an isolated patch of *Selaginella* at Gwaparnath – about 20 km from Kota in south east Rajasthan – during a botanical excursion. The same patch was again located by a colleague (C.B. Gena) in 1974. Further study has revealed it to be *S. rependa* (Desv.) Spring, a species reported earlier from Khandwa (Madhya Pradesh) about 360 km south and Mirzapur and Dudi (Uttar Pradesh) about 600 km north east of the present locality (Panigrahi 1967). This material, however, shows some interesting differences from the description of *S. rependa* by Panigrahi (1967). Firstly, the spikes are mostly megasporangiate in this material and it is only in the terminal part of a plant that a spike may also contain 2 or 3 microsporangia. Secondly, both the micro- and megaspores are larger in size (microspores 35–52μ; megaspores 268–315μ) than those of *S. rependa* (where these measure 25–30μ and 150–180μ respectively – Panigrahi 1967). The segregation of the Rajasthan material as a separate species from *S. rependa* on these features alone may not be justified however. The preponderance of megasporangia in this *Selaginella* corresponds to the pattern of the other heterosporous pteridophytes of the state, *Marsilea* and *Isoetes*, where arid conditions prevalent in Rajasthan seem to induce an increase in the megaspore/microspore ratio (Bhardwaja 1959, Gena et al., in press). This material seems to differ from *S. rependa* studied by Mital (1969b) also in features of stomatal distribution. In our specimens stomata have not been found on the adaxial surface of the dorsal leaves, but are reportedly present here in Mital's material. Moreover, stomata, though few in number, have been found on the rest of the lamina besides the midrib region on the abaxial surface of the ventro-lateral leaves of this material, whereas according to Mital the stomata on this surface are confined to the midrib region only.

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ECOLOGICAL NOTES

FERNS IN CANAL NAVIGATIONS IN BIRMINGHAM

In an industrial city, the canals and railways provide an environment which does not suffer from frequent redevelopment and change. Consequently the flora of industrial canal banks and bridges has had considerable time to develop (nearly 150 years in Birmingham, for the Birmingham Canal Navigation was built between 1770 and 1830).

Within a single 100 km grid square in the City of Birmingham no less than 25 miles (c. 40 km) of such canals exist, presenting a wide range of habitats in the form of banks and embankments, canal paths, fragments of woodland and the mortar of old walls and bridges. The following notes show that, even within such an industrial British city and even against the long background of heavy industrial pollution, a significant number of native fern species have succeeded in establishing and persisting.

Equisetum arvense L. Present throughout the area, often forming enormous tangled colonies along canal sides. Colonies invading poor ash-like substrate have abundant cone-shoots in April; those in richer grassy areas appear purely vegetative.

Pteridium aquilinum (L.) Kuhn. Frequent on exposed or wooded banks and embankments and frequent the base of old walls of factories and warehouses. Occasional in cinders of towpath and occasional in the mortar of old walls and between brickwork of aqueduct. Plants remain stunted and sterile on mortar.

Asplenium scolopendrium L. Specimens seen at two localities, one plant somewhat stunted, both in old brickwork mortar of old bridges crossing canals.

Asplenium trichomanes L. Single specimen in crumbling mortar of railway bridge; another in mortar of old road bridge over canal.

Asplenium ruta-muraria L. Several thriving colonies on mortar of one bridge. Of particular interest because the species seems totally absent elsewhere in the Birmingham area.

Athyrium filix-femina (L.) Roth. Surviving in large colonies (perhaps originally planted) in abandoned gardens amongst bramble and invading bracken, established naturally along canal banks and embankments and a single stunted (but fertile) plant amongst brickwork of aqueduct.

Polystichum aculeatum (L.) Roth. Solitary plant on mortar of low retaining wall with young *Dryopteris.*

Dryopteris filix-mas (L.) Schott. Frequent on wooded banks and amongst bracken on canal embankments, occasional amongst bracken at bases of old walls (often sterile). Also amongst brickwork of aqueduct and bridge. Juvenile plants, probably this species, in mortar of low retaining wall.

Dryopteris pseudomas (Will.) Holub & Pouzar. Occasional amongst bracken at bases of old walls (often sterile).

Dryopteris austriaca (Jacq.) Woynar. Occasional with *Athyrium* on embankment in shade of beech trees.

A.R. BUSBY
Department of Biological Sciences, University of Aston, Birmingham.

[A longer account of fern surveying along the Birmingham Canals will appear in the forthcoming edition of the Bulletin. Notes on the prevalence and habitats of ferns in other cities and elsewhere would be welcomed for the Gazette — Ed.]

REVIEW

BEDFORDSHIRE PLANT ATLAS by John G. Dony 242 x 178 mm. 132 pages. Borough of Luton Museum and Art Gallery. 1976. Price £3.00.

This is the result of another meticulous recording exercise by a doyen of county-flora writers and an elder statesman of British botany. It is a neat, attractive presentation of maps showing the tetrad distribution, as a presence or absence, of some 500 species of vascular plants, 15 of which are ferns. Maps are not provided for the following species, but their distributions are as follows:—

Lycopodium inundatum; wet heaths (93G).
Dryopteris pseudomas; woods (92J, 96Q, 01C, 11J).
Thelypsteris (=Oreopteris) limbosperma; heathy woods (93G).
Gymnocarpium robertianum; walls (02S, 03I).
Azolla filiculoides; "introduced into ponds" (02S, 04E).

The figures in brackets refer to some of the 249 tetrads in the County (see map on p. 15). The following have not been refound:—

Lycopodium clavatum — last recorded 1907;
Equisetum hymale, E. sylvaticum, Thelypteris palustris and *Botrychium lunaria* — none of which have been recorded since 1798.

These maps will obviously provide a format for botanical bingo and any new records — and there will surely be many in spite of Dr. Dony's hard work — should be communicated to Luton Museum and Art Gallery. I will recommend anyone finding one of the five last-mentioned species naturally occurring alive in Bedfordshire today for a free year's membership to the B.P.S.

A.C. JERMY

THE FERN GAZETTE

Original papers, articles, or notes of any length on any aspect of pteridology will be considered for publication. Contributions will be particularly welcomed on floristic, biogeographical and ecological aspects of ferns and their allies, worldwide. Members are especially encouraged to make use of short notes for reporting pteridophyte field observations and records. All may be illustrated with black and white photographs of good technical quality and line drawings.

Contributions should be sent to:

C.N. Page, Royal Botanic Garden, Edinburgh, U.K.

The *last date* for receiving notes and articles to make the following early summer number is:

30 November each year

Authors should follow the general style of this number. Close adherence to the following notes is *not essential,* but will help to speed the publication of contributions.

NOTES FOR CONTRIBUTORS

Manuscripts should be in English, and headed with a title, the name(s) of the author(s) and address, as appropriate.

Copy should preferably be submitted in double-spaced type with adequate margins, on one side of the paper only. For all papers, other than short notes, the inclusion of a short abstract is asked for, indicating the topic and main conclusions.

The use of sub-headings often improves layout. Footnotes should be used only if absolutely necessary. Latin names should be underlined, and the authority given (usually) at the first mention only.

References in the text should be given in parenthesis, e.g. "Shivas (1962) points out . . ." or "It has been pointed out (Shivas 1962) that . . .". The reference list at the end of the paper with authors in alphabetical order and in the style of this number.

Any number and combination of line and half-tone illustrations (original drawings or diagrams in ink, or black and white photographs of good technical quality) can be included with a manuscript where these help to augment or amplify the text. Drawings and diagrams should be of black ink on white paper (or card) or photo-silhouettes, as appropriate, preferably not more than twice their final size. Photographs should be of the required magnification or larger and need not be made up into full page plates. Each drawing or photograph should be clearly marked on the back with details of author and figure number, and the top edge clearly marked "top". All diagrams, drawings and photographs should be referred to consecutively as figures, e.g. fig. 2, fig. 3, etc., except where it is more appropriate to group them, when the system fig 1a, fig. 1b, fig. 2a, fig. 2b, etc., should be preferred. All lettering on photographs, drawings, etc, should be added lightly in pencil or indicated on a transparent overlay. Captions must be typed on a separate sheet from the manuscript, and should include any necessary details of magnification as submitted (the editors will apply any necessary correction for reduction).

Twenty-five reprints are supplied free of charge to authors, who may order in advance further reprints which will be supplied at cost (plus postage) if requested at time of returning the first proofs.

BOOKS FOR REVIEW

Books for review should be sent to A.C. Jermy, Botany Department, British Museum (Natural History), Cromwell Road, London SW7 5BD.

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See inside back cover for notes to contributors.

The British Pteridological Society is open to all interested in ferns and fern-allies. Contact Secretary for details.

Back numbers of the *Gazette* and the *Bulletin* are available for purchase either as complete sets or single issues. Full details can be obtained from the Secretary.

ECOLOGICAL NOTES

OBSERVATIONS ON SOME RARE SPANISH FERNS IN CADIZ PROVINCE, SPAIN

PTERIS SERRULATA Forskal. In an earlier paper, when I published the finding of one plant of this fern, I rather doubted its native status here in southwest Spain as it had not been recorded previously (Molesworth Allen 1967). Later when I found four more plants in another mountain range some kilometers from the first, and in a much less disturbed area I felt that perhaps it was a representative of the vestigial remains of a macaronesian flora that was probably common in these hills and valleys in the past (Molesworth Allen 1971).

Recently, whilst in search of an easier access to a high mist-laden valley in the Los Barrios/Algeciras mountain complex, I crossed a stream which no doubt flows from this valley and near it found more *Pteris serrulata.* I counted 98 plants, mostly adult, within a small area, and with my field glasses, could see others higher up, but did not get to these. Some distance to the left, in a shallow *Rhododendron*-clad arroyo, were a few large adults. Then, near (but not in), a large rocky stream about 100 metres to the north-west, I found a large, dense patch of possibly hundreds of plants of *Pteris*, growing within a narrow strip.

So I now have no doubt that this graceful fern is indeed native to southwest Spain, and this, especially the second place, was a glimpse of what it must have looked like previously in many more of the valleys in these hills. This area is still in a rather inaccessible part of the foothills. Cattle and goats have helped to keep the *status quo* over the centuries, so that bracken and bramble have not yet taken over. The goats however have gone and trees, especially alder, are being cut. Since fencing is now obligatory where cattle graze, alders are cut for posts, and so it looks as though a new cycle is about to start. There are more openings in these arroyos where the water may dry out more quickly. In the absence of goats, bracken and bramble may become dense, and one can only hope that these rare ferns, like *Pteris, Diplazium* and *Culcita,* will be able to survive.

In this area the fronds of *Pteris serrulata* are large (fonds to 147cm (including stipes to 25cm) x 47cm) compared with those described in *Flora Europaea* (Walker 1964), although many were within this range. The rhizome was immensely thick and long, about 25 x 10cm. The pinnae are distinctly caudate. Most fronds have 7-9 and a very few 10 pairs of pinnae.

In the second area, some of the fronds had 11 pairs. The basioscopic pinnae of the lowest pair usually have three pairs of well developed pinnules; the basioscopic of these being the largest and sometimes its lowest segment is either lobed as a minature pinna or crenate. The acroscopic pinnule may also be enlarged and deeply lobed or crenate. Often the next pair of pinnae have their basioscopic lobes shallowly lobed or crenate or even pinnatifid, but this is less common.

P. serrulata certainly requires a special environment here, for it does not appear to grow in or at the sides of the rocky streams so common in the hill forest, but where there is a permanent seepage or underground water. These places would probably be flooded every winter for at least a short time. The rocks amongst which they grow are white, sharply angled and moss-covered, and all these localities have a nearby rocky stream which would help to keep up the high humidity. *Trichomanes speciosum* often grows at their bases, and *Diplazium caudatum* occasionally. Sometimes the seepage is stagnant, but usually the water which is always shallow, moves slowly.

As these areas may well be destroyed in the future, for new roads are constantly being built, it may be of interest to record some of the other plants which grow in this environment.

Most of the first locality is similar to that above Algeciras (Molesworth Allen 1971): tall saplings of *Alnus glutinosas*, and large, very dense *Rhododendron ponticum* ssp. *baeticum* covered with liane-like creepers. Most of it had undoubtedly been damaged in the past as large alders had been removed and some trunks of each *Rhododendron* cut, but apparently never cleared enough to allow bracken to establish — the greatest enemy of these rare ferns. *Frangula alnus* and *Ilex aquifolium* L. are mixed with the alders in the upper storey and on the dryer slopes immediately above, large cork oaks no doubt help to shade the *Pteris* area. In the damper rocky ground on the edges are large trees of *Quercus faginea* ('Quehigo'). Shrubs include *Rhamnus alaternus* as well as young holly, *Frangula* and occasional *Laurus nobilis.* The creepers are mainly *Smilax mauritanica, Rubia peregrina,* long free-hanging stems of *Hedera helix* which also cover the alder trunks, and long shoots of bramble *(Rubus ulmifolius).* Ground plants are comparatively sparse: one metre tall *Ruscus hypophyllus*; a few *Osmunda regalis* and *Athyrium filix-femina,* occasional *Blechnum spicant* and *Lamium flexuosum. Carex pendula* is frequent, with a few tree seedlings and *Iris foetidissimma, Sibthorpia europaea* and the ubiquitous *Arisarum proboscidium* are here. (The latter is perhaps the commonest ground plant in the wet or seasonally damp areas of the oak woods here, from about 30 to at least 670 m altitude and apparently halted only by direct sunlight).

The water which collects from the seepages forms a shallow swamp on flat, more open land in three localities. Here lady fern is abundant, also *Carex pendula* and *Callitriche stagnalis* with small sedges including *Scirpus cernuus* Vahl and *Juncus* spp. Mosses on the rocks and on the ground amongst the *Pteris serrulata* include *Thamnium alopecurum, Mnium hornum, M.affine, Fissidens serrulatus* and others. *Sphagnum* was absent, although it would seem to be a suitable habitat, but this genus is extremely rare in southwest Spain. The rocky stream, less than 10 m away, with swiftly flowing water, have similar moss-covered rocks, plenty of *Athyrium* and *Osmunda*, but no *Pteris*.

The other main locality about 100 m away from the above one, is in a similar habitat, but the alders are large and cast ample shade together with two mature *Quercus faginea.* The *Pteris* plants dominate a rocky strip. Between them are scattered rhododendrons, and towards the back *Frangula*, laurel, and alder saplings and a few young figs *(Ficus carica).* The forest has been completely cut to within 20 m, and a dense border of rhodendrons keeps the secondary growth from encroaching. No plants grow beneath them. Beyond the dense stand of *Pteris,* the habitat is open, with scattered *Pteris,* a few *Diplazium,* and a single young plant of *Trichomanes speciosum* was wedged between two rocks above underground water.

POLYSTICHUM SETIFERUM (Forskal) Woynar was collected in the Cadiz province during last century, but not recently. It has not been known from the Algeciras/Los Barrios districts unless the *Polystichum spinulosum* (L.) Sw. recorded by Allorge (1934) from the Miel valley was this.

I found this fern growing on sloping ground in the Sierra de Ojen, facing roughly north-east, the highest being at 570 m. Here the fronds are slightly longer and wider than given in *Flora Europaea* by Valentine (1964) and resemble the form from the Azores. Although a few of the adults are near streams, the majority are not, and grow in rather loose soil in an area that remains wet during winter, but dry in summer. Scattered around here are 17 plants, mostly adult and fertile and young plants were found establishing by small rocks. The habitat is a small patch of sapling forest mainly of tall *Frangula, Rhamnus alaternus,* Holly, very tall *Erica arborea* and *Cytisus striatus,* young cork oaks, *Arbutus unedo* and laurel trees. Paths had been hacked as the undergrowth was dense. Ivy and *Lonicera periclymenum* L. hang in festoons; *Daphne laureola* is common as a small (1-1.5m) shrub; and in what must have been a seepage during the wet months, some very large *Diplazium caudatum* grow. *Asplenium onopteris* L. is common throughout, but *Athyrium* and *Osmunda* were absent. Some distance below this, under very tall *Quercus faginea,* are more, large *Polystichum setiferum* in damper places.

TRICHOMANES SPECIOSUM Willd. now appears to be locally abundant in a number of arroyos in some of the hill valleys in the Algeciras, Los Barrios and less frequently, Tarifa districts, where the forest has not been cleared or burnt, and rocky streams never dry out during summer. It is surprising to find it growing also on exposed rocks in small streams at altitudes over 500m in the hills above Algeciras. Here the forest has been burnt, probably long ago, and now short windswept secondary growth covers the shallow valleys. The plants are in bright sunlight and all have small, tough fronds, and seem to survive in this habitat year after year. The two-metre tall secondary growth *('monte bajo')* is mainly of *Arbutus unedo,* very small *Quercus suber* and *Rhododendron, Cytisus villosus* and C. *striatus* and dense brambles and bracken. The streams although very small, always have water in them, and mist over these hills is very common, providing high humidity.

Trichomanes is usually found here in streams with a northerly or easterly aspect, never, I think southerly. Patches of over a metre long or wide with fertile fronds still persist in the well shaded valleys with arroyos of swiftly flowing water. Perhaps the best examples are seen on small vertical rocks, for those which grow on the ceiling of overhangs are frequently damaged by frequent flash floods. Clumps accessible to collectors deteriorate rapidly, especially if the rhizome is disturbed. I now understand how the Irish localities disappeared, for its growth seems to be halted, and no new fronds produced for perhaps a year or more, or they lose their firm hold and are washed away during the rainy season, and so indeed resent the attentions of collectors. Luckily *Trichomanes* seems to be holding its own here in some of the more distant places, yet of the 40 to 50 distinct plants or patches that I know, I have seen only a few with fertile fronds. The clumps apparently have to become large and dense before this happens.

DIPLAZIUM CAUDATUM (Cav.) Jermy is locally common, but less widely distributed than *Trichomanes,* occuring in the valley behind Algeciras from where I first recorded it in an east-facing situation. On the hills beyond this, with an approximately northerly aspect, and as far west as the Sierra de Ojen, are some fine examples in private property which should be safe for the time being. They grow in damp rocky arroyos between 350 and 540 m, associated with *Trichomanes, Pteris serrulata, Polystichum setiferum* (and more rarely, near *Culcita macrocarpa).* In some of the localities, especially near the *Polystichum,* the plants were about 2 metres tall, and abundantly fertile, but very young plants were rare. I think it is slow to develop mature fronds, and the site with the few plants behind Algeciras may have suffered from collectors, for there were few fertile fronds last time I saw them.

CULCITA MACROCARPA C.Presl is a strikingly beautiful fern, long known to be in a locality in southwest Spain, from where it was first collected by Col. White on "rocks near Gibraltar" in 1869. There are few records this century. The only ones appear to be those of Allorge (19 4), who carefully described its habitat in a valley behind Algeciras, and Nieschalk & Nieschalk (1965). It is not mentioned by Wilkomm & Lange 1861, 1893 or by Caballero (1940).

In the Miel valley behind Algeciras, (which has an easterly aspect) one or two patches still survive. The *Culcita* now commences at about 200 metres where there are large plants at the side of the Miel river, which is just a large rocky stream. These are fertile, but bracken is encroaching rather rapidly. Further upstream a few more plants of *Culcita* occur at about 300m, but after that I found only a small adult plant, not fertile at 450 m. At 670 m. there is one plant in a rocky stream. It is tall, about the height of the dense secondary growth which surrounds it, adequately shading its rhizome. So it would appear that *Culcita* is still scattered through this wooded valley and upper slopes of the Sierra del Algarrobo up to the Tajo del Espino.

On the northwest slope of the Sierra la Palma, about 350 m altitude are patches of *Culcita* in at least three short streams more or less adjacent to each other. The whole of this area has been greatly disturbed and I was surprised to see this fern here. Although there are *Alnus glutinossa, Frangula alnus,* and fairly dense *Rhodedendron,* none is tall and the remainder consist of dryish cork woods, which are periodically cleared for de-corking. The streams have little water in them, but the growth is dense enough to keep the brambles and bracken out. One of these small arroyos has 17 plants (7 adult and mainly fertile, the remainder small); the next has 12 of varying size but none very large and only two fertile. The smallest and almost dry stream has one very large and fertile plant with its huge rootstock firmly wedged between large boulders. So in this small area there are at least 30 plants of *Culcita.* Other ferns present include a few *Blechnum spicant,* many very large *Athyrium filix-femina* and *Osmunda regalis* but no *Diplazium* or *Trichomanes* (which suggests that this locality has been almost cleared in the past, *Culcita* being the only vestigal survivor).

In part of the large complex of the Sierra de Ojen and facing roughly north, there is a small arroyo well shaded by large *Quercus faginea,* tall alders and *Frangula,* with *Rhododendrons* making a tall and dense screen. Here at 540 m are perhaps the finest examples of *Culcita* that I have seen. I counted over 100 plants, mostly adult, of which the tallest were about 2.75 m and there were many fertile. It is a most beautiful and graceful fern when well grown with its bright green glossy fronds and long smooth stipes which are covered at the base with reddish hairs. The rhizome is very large and thick, and the fertile laminae are weighed down by the dense soral portion.

In this place there were several plants of *Trichomanes speciosum* and a few *Diplazium caudatum,* one of which was fertile, but oddly enough, although these two ferns are common in nearby streams, there is no more *Culcita.*

In another large range of hills, the Sierra del Nino, which is further inland, more *Culcita* grows in a deep arroyo at 350 m. The forest here has been mainly cleared except for this small area on one slope above the stream. There are 3-4 small tributaries and under the *Rhododendron* there is a fine stand. In 1969 I counted 97 plants and they did not seem greatly altered when I saw them last year when showing them to the sympathetic owner. Because of this, the *Culcita* has a good chance of preservation. The land-owner, has told his keeper that the locality must not be touched, and as visitors are not encouraged, there should be less danger of fire. The plants are tall, again about 2.75 m and in a similar habitat to those above except that there was neither *Diplazium* nor *Trichomanes* present. Trichomanes does grow downstream in a rather exposed position, about half a Km away. On the mossy rocks are young plants of *Culcita* with *Asplenium onopteris,* whilst *Blechnum,Osmunda* and *Athyrium* are common, and on the upper part of the rocks are *Davallia canariensis* and *Polypodium australe. Frangula* and alders are present shaded by Cork Oaks.

My gardener, an ex-cork-cutter has told me of yet another place where *Culcita* grows, and this is near the Sierra Blanquilla, but we are both too old to go there now!

If it still exists, this would add yet another distinct and more easterly locality. Amongst these species there is some confusion of local names. The rhizome of *Culcita* was used medicinally by the country people here, and until quite recently was sold in Los Barrios (25pts. for a small piece of dried rhizome). It was used in the same way as the rhizome of *Davallia canariensis*, and is of much the same colour. In this area, in the districts of Tarifa, Los Barrios and Algeciras at least, *Cuicita* is called *"Helecho macho"*, the Male Fern, and is known to most country people here even if they have not seen it. *Davallia* is called *Calaguala* or *Cabrina*. In most parts of Spain, "Helecho macho" certainly refers to *Dryopteris filix-mas* (L.) Schott and this leads me to the question of presence of the latter plant in the above districts. I have looked for it in many places in this damp wooded corner of the Cadiz province, and am convinced that if it is not extinct, it is now extremely rare. There are plenty of places that would be very suitable and also it should have a better chance of survival than some of the above rare ferns. So I can see no reason why it is not represented in this fern flora.

In the *Atlas Flora Europaea, Dryopteris filix-mas* is shown for this extreme southwest corner, below the original Alcala citing, but I have not seen any specimens in herbaria. Wolley-Dod (1914) gives two localities which are recorded from the Algeciras hills. He apparently did not see the fern himself nor specimens from here, yet both these localities are where I have seen Helecho macho *(Culcita)* growing. Surely such a striking and tall fern would not have been overlooked in these localities, where it may well have once been more common than it is today.

I think *Dryopteris filix-mas* was first recorded by Clemente, who lived earlier, then was possibly cited later by the other two in their publications, and then the three names included by Wolley-Dod. Until one sees *D. filix-mas* specimens collected from this area it is impossible to get much further.

Perhaps the mystery deepens, for Allorge (1934) who gives such an excellent ecological account of the *Culcita* habitat in the Miel valley, lists amongst the ferns, *Dryopteris carthusiana* (Vill.) H.P.Fuchs (as *spinulosum*(L.) Sw.), growing together with *Carex pendula* (with which *Diplazium caudatum* is also associated here). It was surprising how little this area had changed over the 40 years since Allorge saw it (until a disastrous fire last year, 1973), yet I am almost sure that no *Polystichum* is there now. In fact the nearest Aspidiaceae I know of is *P. setiferum,* several kilometers away in another mountain complex. *Dryopteris carthusiana* is not a fern one would expect to see in southern Europe except at a much higher altitude. I rather hesitantly suggest, that if the original specimen had been infertile, could Allorge have seen a small plant of *Diplazium* there, and not collected it? If there is no specimen, we may never know.

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B. MOLESWORTH-ALLEN
Los Barrios,
Spain.

UNBRANCHED PLANTS OF EQUISETUM PALUSTRE L.

The variation in branching shown by *Equisetum palustre* L. is well known and is referred to in most Floras. Bergdolt (1937), for example, lists nine forma based primarily on the degree of branching. Of these, *f.simplicissimum* A.Br. is described as almost or entirely unbranched. Slender, unbranched plants can be puzzling in the field and may lead to confusion with *E.variegatum* in areas where both species occur.

This note is concerned with observations on unbranched and sparingly branched plants which were found during a brief visit to Alaska in the summer of 1975. The site was on gently sloping tundra on the south side of the Atigun River 'gorge' immediately to the north-east of Galbraith Lake (69° 27'N, 149° 20°W), on the north side of the Brooks Range. Herbarium specimens (Halliday, A468/75) are in ALA, BM, C, E, LANC. The plants were conspicuous by their bright green colour and occupied a shallow peaty depression running down towards the river. Lack of time prevented detailed notes of the habitat being taken but *Carex atrofusca* was a conspicuous associated species.

It was noticed that the central part of the depression was occupied by unbranched plants, that *E.pratense* occurred along the sides and that sparingly branched plants were in between. Since the only species of *Equisetum* which I had encountered in the area were *E.pratense, E.variegatum* and *E.scirpoides,* I assumed that the unbranched plants were slender specimens of *E.variegatum* and that the sparingly branched plants were hybrids with *E.pratense,* but careful examination revealed that this was not the case. The unbranched plants lacked the black ring around the top of the stem-sheaths and also the grooved ribs which are characteristic of *E.variegatum.* They were, in fact, unbranched specimens of *E.palustre* as also were the sparingly branched individuals.

Subsequent study of the herbarium material showed a few more or less typically branched specimens. It was also apparent that the unbranched shoots occurred in dense clusters of up to 15 and arising over a short distance (1-2cm) of the rhizome just below ground level. Usually the rhizome produces only one or two shoots per node, with the internodes being 1-2cm. The contrast in the origin of the unbranched and sparingly branched shoots is well shown in Fig. 1. It is evident that the clusters of unbranched shoots arise from a rhizome showing reduced internodal extension and a tendency for one or more whorls of lateral buds to produce shoots directly rather than to continue growth of the rhizome. It is to be expected that such shoots would be intermediate in morphology between normal aerial shoots and branches. It is not possible to tell whether this development of the lateral buds is associated with damage to the main shoot primordium and one can only speculate as to the cause of the failure of the internodes to elongate. Since the degree of branching increases from the centre of the depression outwards it seems likely that it is the result of soil frost damage, or solifuction, probably occurring every year in this particular habitat.

FIGURE 1. Unbranched, sparingly branched and normal stems of *Equisetum palustre.* Galbraith Lake, Brooks Range, Alaska, *Halliday, A 468/75* (LANC).

ACKNOWLEDGMENTS

I should like to express my indebtedness to Alyeska Pipeline Service Co. for logistic support while in Alaska, to Dr C. Page for suggesting and commenting on this note, and to Mr K. Oates for assistance with the Figure.

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CYRTOMIUM FALCATUM NATURALISED ON RHUM

During April 1976 I noticed an unfamiliar fern growing high up in an old mortar filled crevice on the wall of the derelict greenhouse belonging to Kinloch Castle on the Isle of Rhum, Western Scotland. I collected a fertile frond which was identified by staff at the Royal Botanic Gardens Edinburgh as a species of the genus *Cyrtomium,* almost certainly *C. falcatum.*

This species is widespread in E. Asia and frequently cultivated as a pot plant in Britain but is not known to have become naturalised before in Scotland. A closer inspection of the greenhouse wall at Kinloch revealed 4 plants growing on the south face of the wall and two more on the north side. None of the plants were very large having between 3 and 6 fresh green fronds per plant, each 6 to 12 inches long. All the plants were growing in similar situations, in crevices 8 to 10 feet above ground level. Although the greenhouse wall is in a sheltered situation surrounded by trees, all traces of the glass roof have long since disappeared.

Several other greenhouse escapes are recorded at Kinloch and still survive ie. *Selaginella kraussiana, Polystichum setiferum,* and I have recently found *Saxifraga stolonifera* growing under an old grating in the same greenhouse.

Lousley J.E. 1971 'The Flora of the Isles of Scilly' records *C. falcatum* as a very rare established alien on St Mary's where he saw two clumps in 1956 growing under boulders on the shore near Porth Minick. In May 1976 I was shown another clump on St Mary's by P.Z. Mackenzie, growing in semi shade in grazed rough pasture near Porth Hellick. Lousley says *C. falcatum* has also been recorded as an escape in Alabama, Florida, Hawaii and the Azores. It has been recorded also in Holland at two localities (van Ooststroom in Ned. Kruidk. Archf., 57, 217-8, 1950).

P. CORKHILL
Chief Warden.
Nature Conservancy Council.
Isle of Rhum.

REVIEW

DIE FARNPFLANZEN ZENTRALEUROPAS, Gestalt, Geschichte, Lebensraum, by O. Wilmans (text) and K. & H. Rasbach (photographs), 2nd revised edition, 304 pp., 154 illustrations (mostly half-tone photographs). 24 x 31.5 cms. Gustav Fischer, Stuttgart 1976. Price DM79 (about £19.60).

The aim of this book is an introduction to modern botanical research exemplified by pteridophytes. The authors emphasise that this group is especially suited for this purpose, not only because of its multitude of different forms and great variety of habitat but also because of its richly documented fossil history. The first eighty-five pages are devoted to a broad general survey of pteridophyta in the widest sense. The reader is instructed about their fundamental difference from the thallophytes and their position in relation to the spermophytes with which they are grouped as cormophytes. The significance of the alteration of generation in the life-cycle of a fern plant is discussed in detail and demonstrated by a fine line drawing. This is experimental morphology and physiology. Much space is devoted to a review of fern systematics with concise descriptions of higher taxa; the information is by no means confined to morphological descriptions and geographical distribution but includes cytological data as well as speculations pertaining to their phylogeny. Although one is aware from the title that the work is confined to the pteridophyta of Central Europe, the reader might expect a little more statistical information on the size of each group e.g. the number of genera and species. Most instructive is the chapter on the phylogeny of pteridophytes, and it is this section, together with the following one on hybridisation, which justifies the claim made that here we have a text book. The general part is concluded by chapters on various aspects of fesbotany with special emphasis on the chorology and sociology of fern. The main part of the book is given to "biographies" of Central European ferns grouped according to their habitats. Out of the 95 main species no less than 84 are illustrated by photographs. For each species the scientific and the most common vernacular name is given. The extensive description includes chromosome number, ecology, distribution and differences from related species. By adopting this method the authors have dispensed with the traditional one of using keys for determining species. In view of the limited amount of species which are treated in this book and considering the clarity of the Pteridophytes however, with their relative outward simplicity of structure and uniformily of colour lend themselves readily to the former medium, and the illustrations in this book, some of them extremely beautiful (e.g. 58 and 66) may be regarded as an unqualified success. The work is concluded by a substantial list of references, an index which actually works and a geological time table. The design of the book is satisfactory on the whole although the borders around the photographs give it a rather old fashioned thirties look. Nevertheless it has to be said that the receiver has not come across such a generally pleasing work as this for a long time now and one wonders why it has not already appeared in translation.

E. LAUNERT

[NOTE – For a review of edn.1 of this book, see Brit Fern Gaz. vol. 10 pages 96 & 105, 1969 – Ed.]

A PTERIDOPHYTE FLORA OF THE DERBYSHIRE DALES NATIONAL NATURE RESERVE

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ABSTRACT

A systematic list of the pteridophytes of the Derbyshire Dales National Nature Reserve, an area of Carboniferous Limestone in the English Midlands, is given, along with details of the habitats in which the species occur. The flora is briefly compared with those of adjacent areas; and a number of interesting habitat preferences shown by species in the reserve are commented on in relation to the habitat preferences of the species in the British Isles.

INTRODUCTION

North Derbyshire is famous botanically for its dales, which are narrow, steep-sided valleys with small streams in a Carboniferous Limestone plateau (Waters 1969). To conserve some of the best examples of the plant communities that occur in these dales, the Nature Conservancy Council is establishing the Derbyshire Dales National Nature Reserve. It has declared since 1974 an area of about 150 acres in Lathkill Dale; and two areas in Monk's Dale which together are about 150 acres. It is also about to declare further areas in Lathkill Dale which add up to about 110 acres and an area in Cressbrook Dale of about 20 acres (Fig. 1). This survey, which was carried out during the summer of 1975, covers all of the areas declared and to be declared, except one of about 80 acres in Lathkill Dale whose acquisition was not sufficiently advanced in 1975 to allow a visit. The exact areas surveyed were given in Willmot (1976). The survey was carried out at the request of the Council as part of their programme to assess the biological value and conservation needs of the new reserve.

The main habitats present in the reserve areas are as follows: outcrops, screes and drystone walls of Carboniferous Limestone: deciduous woodlands mostly dominated by *Fraxinus excelsior;* scrub communities mostly dominated by *Corylus avellana;* small areas of heathland on the shoulders of the dales; and a variety of tall herb communities and of calcareous grasslands. All of these habitats occur in each dale, except that there are no heath areas in Cressbrook Dale, and all habitats are better represented in the Lathkill and Monk's Dale parts of the reserve due to the greater size of these areas.

The survey was carried out by visiting examples of each of the major habitats present in each one kilometer square of the national grid in the reserve areas. Results were given on this basis in Willmot (1976) but are given in a more general manner here. In the systematic list reference is also made to pteridophyte records in Clapham (1969) for the reserve areas and their immediate vicinity; and to some of my own field records for the same area made between 1971 and 1974, where the survey of 1975 failed to relocate the specimens. The nomenclature for pteridophytes used here is as used in the British Museum Herbarium (BM) in 1975 from a list supplied by A.C. Jermy (Anon. undated) and for other plants as in Clapham, *et al.* (1962).

SYSTEMATIC LIST OF TAXA

The mention of outcrops and scree in this section always refers to Carboniferous Limestone.

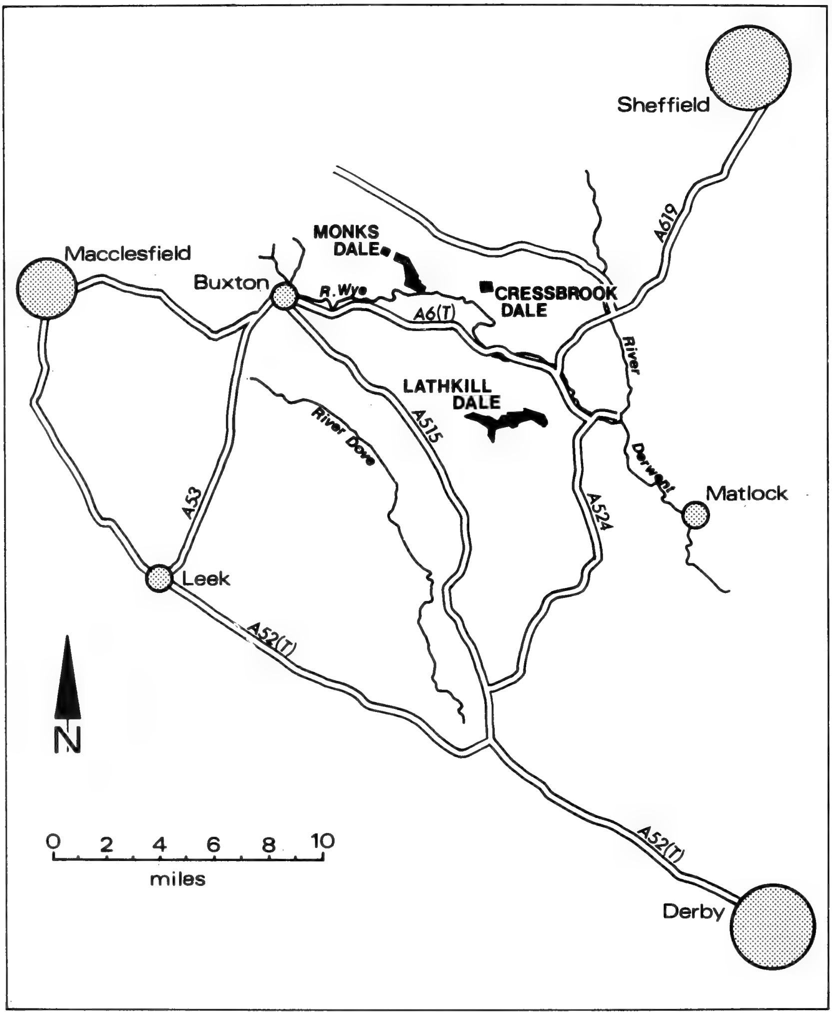

FIGURE 1: The location of the various areas of the Derbyshire Dales National Nature Reserve examined in the survey described here.

Huperzia selago (L.) Bernh. ex Schrank & Mart. was recorded for short, limestone grassland amongst rock outcrops on the dale side, between the two areas of the Monk's Dale part of the reserve in Clapham (1969) but was not found in this survey in the reserve or in the locality given above.

Equisetum fluviatile L. occurs in the southern end of the Monk's Dale part of the reserve, where it grows in damp, calcareous grassland in the base of the dale. This damp grassland merges into calcareous marsh in places. Here the species is occasional to frequent, growing as scattered stems amongst the grasses and sedges that dominate the vegetation.

E. arvense L. occurs in the same part of the reserve and habitats as *E. fluviatile,* although it occurs over a wider area extending into rather drier regions of grassland. It varies in abundance from frequent to occasional.

Botrychium lunaria (L.) Swartz is a wide-spread but local species of short grassland on the Carboniferous Limestone in Derbyshire (Clapham 1969). It was not found in the reserve in this survey, although it is likely that it occurs, as there are many, apparently suitable localities. However, it has been found by me in Lathkill Dale just to the west of the reserve area in short calcareous grassland amongst limestone outcrops on the dale side. It was also recorded by Clapham (1969) at Youlgreave Moor which is just south of Lathkill Dale.

Hymenophyllum wilsonii Hook. has been recorded for only one site in Derbyshire (Clapham 1969), this site was just to the south of the Cressbrook Dale part of the reserve. This locality is apparently very suitable for the species, being a humid, narrow, shaded limestone gorge, however, searches of the gorge by myself and other local botanists have failed to confirm the original record.

Pteridium aquilinum (L.) Kuhn occurs in both the Lathkill Dale and Monk's Dale parts of the reserve, but only on the deeper, and therefore leached and acidic, soils on the shoulders of the Dales or less-steep dale sides. In one place on the shoulders of Lathkill Dale it is dominant, and invading and replacing heathland dominated by a mixture of calcifuge species including *Calluna vulgaris* and *Vaccinium myrtillus.* On the slopes of Lathkill Dale and the shoulders of Monk's Dale it occurs occasionally amongst acidic, tall-herb vegetation with such species as *Chamaenerion angustifolium.* The patch on the shoulder of Monk's Dale is apparently spreading into the *Corylus avellana* scrub just below the shoulder.

Asplenium scolopendrium L. occurs in all three parts of the reserve mostly on shaded outcrops. It becomes increasingly abundant and luxuriant as the degree of dampness of the outcrops increases, and reaches its maximum growth on the shaded rocks near the rivers in Lathkill and Cressbrook Dales. It also occurs rarely on the floor of the *Fraxinus excelsior* woods near the river in Lathkill Dale.

A. adiantum-nigrum L. occurs in the Cressbrook Dale part of the reserve but only two small plants were seen on an outcrop shaded by *Corylus avellana* scrub. It has also been seen by me on two shaded outcrops in Lathkill Dale outside of the reserve area.

A. trichomanes L. occurs throughout all three parts of the reserve on shaded and unshaded outcrops. It is rare to occasional on unshaded outcrops and frequent to occasional on shaded or damper outcrops. It also occurs rarely in damper crevices of partially-stabilised scree in Monk's Dale.

A. virde Huds. was recorded for Monk's Dale in Clapham (1969) but was not refound during this survey, although there are many apparently suitable sites for the species, as judged by its occurrence elsewhere in the Derbyshire Dales.

A. ruta-muraria L. occurs throughout all three parts of the reserve on outcrops. It is frequent to occasional on unshaded outcrops, where it is often the only fern present, but only rare to occasional on shaded outcrops.

A. ceterach L. only occurs in the Lathkill Dale part of the reserve and is rare there, growing in only one locality in the reserve area visited and one further which is in the reserve area which is to be declared but which was not visited. At both localities it is on south-facing, unshaded outcrops and each population consists of about 10 to 12 individuals.

Athyrium filix-femina (L.) Roth occurs in the Cressbrook Dale and Monk's Dale parts of the reserve and in Lathkill Dale just outside the reserve area. It grows only in the shade of trees or shrubs and avoids areas where there are abundant particles of limestone in the upper layers of the soil. In Monk's Dale only one individual was seen in a patch of scrub on level ground but in Cressbrook Dale a number were seen amongst willow scrub in an area of impeded drainage. Both these localities are in the bottom of dales near streams. In Lathkill Dale the species is occasional on the floor of a mixed deciduous/coniferous plantation on the side of the Dale, just to the east of the reserve area.

Gymnocarpium robertianum (Hoffm.) Newm. occurs in the Lathkill Dale and Monk's Dale parts of the reserve. In Monk's Dale it grows abundantly, throughout large areas of dry, unshaded scree on the east side of the Dale. It also occurs rarely in three other habitats, namely shaded scree, and shaded and unshaded limestone outcrops. In these habitats the populations are always much smaller than those on the unshaded scree. In Lathkill Dale there is one small population on a shaded outcrop.

Cystopteris fragilis (L.) Bernh. occurs throughout all three parts of the reserve on outcrops of limestone. It is rare on unshaded outcrops but becomes frequent on shaded or damp outcrops. It occasionally occurs in unshaded screes in Lathkill Dale and Monk's Dale but never in large amounts. However, it is locally abundant on unshaded limestone waste resulting from lead mining in one area in Lathkill Dale. It is also occasional on the floor of *Acer pseudoplatanus/Fraxinus excelsior* woodland in Monk's Dale in one area.

Polystichum aculeatum (L.) Roth occurs in the Lathkill Dale and Monk's Dale parts of the reserve and in Cressbrook Dale just outside of the reserve area. Its two main habitats are on the floor of *Fraxinus excelsior* woods, where it may be locally frequent in the damper areas; and shaded outcrops, again particularly where these are damp. In Monk's Dale it occurs in a wider range of habitats than Lathkill Dale: growing on unshaded outcrops; in *Corylus avellana* scrub; and in unshaded scree. It is, however, only rare in these habitats.

Dryopteris filix-mas (L.) Schott occurs throughout all three parts of the reserve. It is most abundant in the *Fraxinus excelsior* woods where particularly in the damper parts, it forms the dominant species over large areas in the tall herb layer. It is frequent on shaded outcrops; in block screes; in the acidic, leached areas of tall herb vegetation on the shoulders of the dales in Lathkill Dale and Monk's Dale; and in the *Corylus avellana* scrub in Monk's Dale. It is rare on unshaded outcrops and has a tendency in this habitat to occur as small, sterile plants.

D. pseudomas (Wollaston) J. Holub and Pouzar is included in this list on the basis of one small, fertile plant from an unshaded outcrop in south-facing, calcareous grassland in Lathkill Dale, however, this specimen was determined by A.C. Jermy and J.A. Crabbe. A number of Male Fern plants from the *Fraxinus excelsior* woods in this dale show a tendency to have the more square-cut pinnules which are characteristic of *D. pseudomas.* However, two plants with this character were examined by A.C. Jermy and J.A. Crabbe and determined as *D. filix-mas.*

D. austriaca (Jacq.) Woynar occurs in all three parts of the reserve, it is widespread but local. The habitat it is most abundant in is *Fraxinus excelsior* woodland where the pH of the surface layers of the soil are less alkaline than elsewhere and probably acidic. In this habitat it is locally abundant in a few places but more usually it is only frequent to occasional. The presumed acidity of these areas is due to either a deeper, and hence more leached soil, or a more acidic leaf litter produced by conifers. The species also has a marked affinity for rotting tree stumps and logs in these woods and very rarely occurs as an epiphyte on old, large *Fraxinus excelsior* trees. In Monk's Dale it occurs occasionally in *Corylus avellana* scrub.

In Lathkill Dale it grows rarely on shaded outcrops but the plants are never large; and in the heathland on the shoulder of the dale in one place.

Polypodium vulgare agg. occurs throughout all three parts of the reserve but is rather local. Only a few plants were critically examined by A.C. Jermy and J.A. Crabbe to determine to which species of the aggregate they belong: these records are given below. The description of habitats given here refers to the aggregate. It occurs on shaded and unshaded outcrops, being occasional to locally frequent, especially where damp, on the former and rare to occasional on the latter. It has a marked preference for the shallow soil cappings on the upper edges of the shaded outcrops; such that, when viewed from below, its fronds often form a fringe along the top of outcrops. It also occurs on shaded and unshaded screes in Monk's Dale being commoner in the former.

P. vulgare L. occurs in the Lathkill Dale part of the reserve.

P. interjectum Shivas occurs in the Cressbrook Dale part of the reserve.

P. x mantoniae Rothm. occurs in the Monk's Dale part of the reserve. This is believed to be the first record of this hybrid in Derbyshire. Only two small clumps of the hybrid are known to occur in the Dale, these are both on shaded outcrops.

SUMMARY OF FLORA

Eighteen species of pteridophyte and one hybrid are known from the reserve. This represents the majority of the pteridophytes that occur in northern Derbyshire in the types of habitats represented in the reserve. (Clapham 1969). The only obvious absences are *Equisetum palustre* L. and *Ophioglossum vulgatum* L., as these are the only species that are common locally in habitats that occur in the reserve. There are also a number of less-common species that occur locally in habitats that occur in the reserve. These species should be looked for in the reserve but because of their local rarity no importance can be attached to their absence. These include *Equisetum telmateia* Ehrh. *Huperzie selago* and *Botrychium lunaria* of which the last two have been recorded for areas only just outside of the reserve. There is one further species whose absence is worth noting, although it does not grow in the vicinity of the reserve, and that is *Dryopteris villarii* (Bellardi) Woynar ex Schinz and Thell. This a local species of clefts in limestone pavement in north Wales and northern England (Clapham, *et al* 1962) and its absence from the carboniferous limestone of Derbyshire has always seemed strange to me. In fact it has been recently found on this limestone in the county (Patrick and Hollick 1974) which increases the probability that it might occur in the area of the reserve. However, it should be pointed out that this new locality is in a man-made habitat and so it may represent a new addition to the Derbyshire flora rather than a truely-native species.

SUMMARY OF HABITATS

The majority of the species recorded in the reserve occur in the types of habitats that they occur in generally in the British Isles and these will not be commented on further. However, a number of species either occur in unusual habitats or are absent from their usual ones: these cases are outlined below.

One noticeable absence is of the wall ferns *Asplenium trichomanes, A. ruta-muraria* and *A. ceterach* (Clapham, *et al.* 1962 and Hyde, *et al.* 1969) on the drystone walls of the reserve. These species do occur on walls in the Peak District of Derbyshire (Clapham 1969) and in the surrounding counties of Nottinghamshire (Howitt and Howitt 1963) and Staffordshire (Edees 1972). These species, however, are much less frequent on the drystone walls of the Derbyshire Peak District than they are on walls elsewhere in the British Isles. This is probably due to the lack of soil between the stones of the walls in the area.

Gymnocarpium robertianum in Derbyshire (Clapham 1969) and in the British Isles (Clapham, *et al.* 1962) is a plant of limestone rocks and screes, and it does occur in these habitats in the reserve. However, although it is very common in screes in the Monk's Dale part of the reserve, it is apparently absent from very similar screes in the Lathkill Dale part of the reserve. In its other major habitat of limestone outcrops, it is rare in the reserve but it is very abundant, although only on a local scale, in this habitat elsewhere in the Peak District. There is no obvious explanation for this apparently haphazard occurrence of the species.

The presence of *Dryopteris pseudomas* in the reserve on limestone, albeit in very small amounts, is of interest as the species is generally considered a species of acidic soils (Clapham, *et al.* 1962) and is only rarely, if ever, recorded on basic rocks. Clapham (1969) recorded the species as "usually on acid soils" in Derbyshire and provided one locality where the species might have been growing on a calcareous soil, Bakewell, although he did not specifically state that it was. I have found this species on numerous occasions in Derbyshire recently and in the great majority of cases the species was growing on acid soil in woodland. I know of only two other localities in the county where the species occurs on limestone, in both cases it is Carboniferous Limestone and there were only a few plants at each site. Hyde, *et al* (1969) record the species as being very variable with numerous forms and varieties, it would be interesting to see if these Derbyshire limestone plants belong to any particular taxon.

Polypodium vulgare agg. is the only British vascular plant with claims to being an epiphyte (Rose 1974), although it does grow on rocks, walls and the ground as well (Clapham, *et al.* 1962). This species is noticeably absent from trees in the reserve and it has not been recorded as an epiphyte for the adjacent counties of Nottinghamshire (Howitt and Howitt 1963) or Staffordshire (Edees 1972). However, Clapham (1969) recorded the species on old trees in Derbyshire but I have seen the species on numberous occasions in the county and never seen it as an epiphyte. The species may then occur as an epiphyte in the area but it does so much less commonly than it does in the south and west of the British Isles. The reason for this is probably the lack of an epiphytic moss carpet on trees which in its turn may be due to a drier climate or higher level of aerial pollution than elsewhere, as suggested by Rose (1974).

ACKNOWLEDGEMENTS

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FERNS IN THE CAMEROONS. II.
THE PTERIDOPHYTES OF THE EVERGREEN FORESTS

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ABSTRACT

This account describes the ferns collected by the author in evergreen forests on Cameroon Mountain, ascending on four different routes. Indications of some notable fern localities north of the mountain are presented, along with some new fern records.

INTRODUCTION

Most of the localities attractive for a botanist studying ferns in the "United Republic of Cameroon" are found in the South West Province, i.e. in the southern half of the late West Cameroon. One of the wettest places in the world is situated in this part of the country (Benl 1976 b). It includes the famous "mist forests" of Cameroon Mt, with which only Mt Oku (North West Province) can compete in wealth of ferns. Both old and recent lava flows are found comparatively close together in that region; their fern flora and vegetation have been the main topic of a previous account (Benl 1976 c).

Cameroon Mountain regions

Cameroon Mt. (fig 1) was built up by a successive series of gigantic eruptions to a stratified mass of 4070 m, its highest summit called "Fáko". With a basal surface of 2000 km^2 and a volume of roughly 1400 km^3, this isolated massif forms the highest elevation in West Africa. Probably the eruptions began in the Upper Cretaceous with basaltic tuffs and continued in the Lower Tertiary with basaltic lavas. In the Miocene a second active phase occurred with trachytes and phonolites; a third phase followed in the Pliopleistocene, consisting of the "upper basalts" (Bederman 1966: 115). The visible whale-backed mass of the strato-volcano is anyway of post-Cretaceous origin.

Old lava flows of unknown ages form the typical feature of the desolate and inhospitable upper regions, but are often well recognizable within the forest belt too. In the lower zones they are in part heavily decomposed; the weathered and accumulated material, sometimes extending upwards to 900 m, provides fertile soils for both native food plants and for rubber and oil palm plantations. Younger flows poured out from dozens of secondary vents mostly lying in the upper part of the mountain, but some of them arose in 1922 and 1959 (Benl 1976c: 208-212) amidst the forest. Their flows cut deep openings into the forest or they enclosed clumps of verdure, if a stream divided and united again — thus intersecting the fringe of the forest belt to a high degree. Originating from these events and the local topographic situations the upper edge of the evergreen forest forms a most irregular line.

Violent dry NE winds with temperatures below 5°C sweep the mountain top above 3000 m level and may even cause snowstorms in August. They meet the heated moisture in lower levels (particularly between 1500 and 2000 m), causing an almost constant presence of cloud and dense mist generally encircling and veiling the upper forest belt — a phenomenon shown up all the year round, but reinforced at the height of the rainy season (June to October), when mist comes down to 900 metres.

The French phytogeographer R. Letouzey who was engaged for 22 years in the

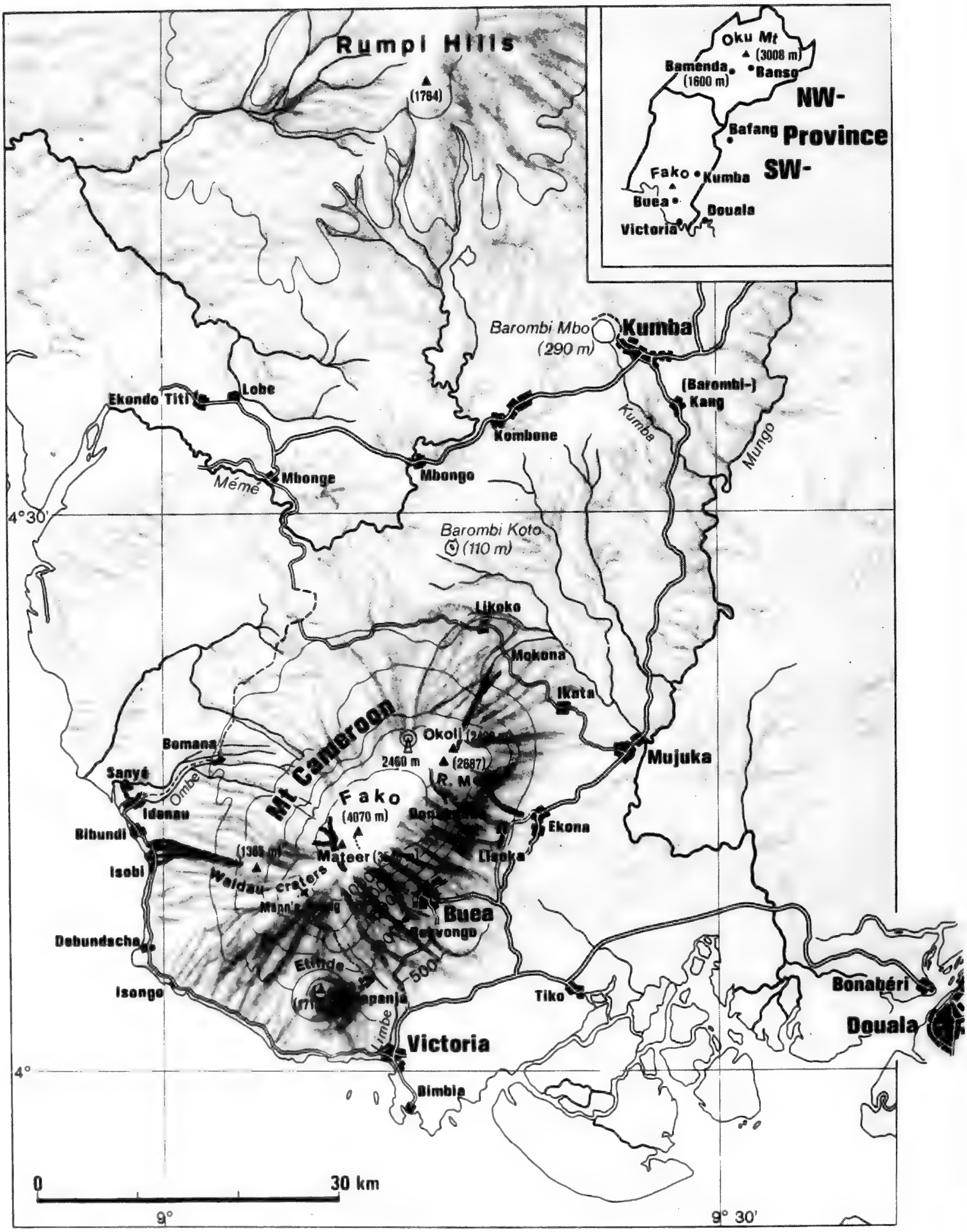

FIGURE 1. Mt Cameroon and its environs (South West Province of the United Republic of Cameroon). *(Map, A. Böhm).*

research of Cameroon forests, actually distinguishes three altitudinal zones above the lowland tropical rain forest, adapted to the nomenclature used for East African mountains: a submontane zone from 1000-1200 to 1600-1800 m, a montane zone from 1600-1800 to 2200-2500 m, and an afrosubalpine zone from 2200-2500 to 4070 metres. But 'a definitive nomenclature for the zones on Cameroons Mountain is perhaps not yet in sight' (Richards 1963: 552). Whilst 'the flora of the zones above the forest in Mt Cameroon is ... comparatively well known' (Keay 1955: 140). the submontane forest is characterized by Letouzey as 'very poorly known' (Letouzey 1968: 461).

Areas from which we collected ferns form part of the lowland tropical rain forest as well as of the rainy submontane zone, both of primary and secondary character, but all belonging to the 'climax' of evergreen forest.

Since the beginning of this century the ascent of the mountain has usually been started from the SE or E side (the 'Buea side'), whether directly from the elevated 'town' of Buea (965 m) or from Bonakanda, from where a road leads up to 2430 m, passable for a landrover. Concerning pteridology, the ascent beginning at Buea via Upper Farm is the more recommendable: It passes the eastern edge of the Mosole ravine, the slopes of which are fairly abundant in *Asplenium unilaterale* Lam. (the dimidiate pinnae often looking curved), *A.variabile* Hooker, *Ctenitis securidiformis* (Hooker) Copel. var. *securidiformis* (fig 2) – var.*nana* (Bonap.) Tardieu was listed by us N of Debundscha, 50 m above sea-level – *Dryopteris pentheri* (Krasser) C. Chr. (stipe scales entire, no hair-like scales on pinna costules), *Nephrolepis undulata, Pteris linearis* Poiret, *P.manniana* and *P.togoensis* Hieron. *[P. quadriaurita* Retz. ssp. *togoensis* (Hieron.) Schelpe], *Tectaria angelicifolia* (Schum.) Copel. (fig 3) -creeping rhizome, no indusia!-, *Trichomanes borbonicum* v.d. Bosch (indusia very long), *T.radicans* Swartz [*T. giganteum* sensu Alston], *T.rigidum* Swartz (stout erect rhizome), and some *Selaginella* species *(S. kalbreyeri* Baker, *S. soyauxii* Hieron., *S. versicolor* Spring, *S. vogelii* Spring); down to the more or less dry but always shaded stream bed, at about 1100 m altitude, *Asplenium paucijugum* Ballard -with an apical bud or an adventitious plant usually on every pinna!- and *Coniogramme africana* Hieron. may still be found today. The long-stiped *Antrophyum mannianum* Hooker and *Bolbitis fluviatilis* (Hooker) Ching had been observed by us in January 1971 but no longer in February 1975. Much has been 'cleared out', since Alice F. Tryon (1965: 52) described that interesting site, where she had her richest collecting of Cameroon ferns. Moreover, considerable parts of the western ravine slope, bearing the handsome *Alsophila camerooniana* (Hooker) Tryon, have been destroyed.

If you follow a path leading immediately above the dam banking up the Mosole River for supplying Buea with the necessary water, you will come -at about 1200 m elevation- to some humid places with delicate filmy-ferns like *Hymenophyllum polyanthos* Swartz in Schrader var.*kuhnii* (C.Chr.) Schelpe -fronds glabrous-, *H.capillare* Desv. -fronds with stellate hairs; stipe and rachis unwinged-, associated with *Xiphopteris villosissima* (Hooker) Alston var. *laticellulata* Benl (1976 a), *Trichomanes pyxidiferum* L. var. *melanotrichum* (Schlecht.) Schelpe, *T.clarenceanum* Ballard -false veinlets-, upon upright and fallen tree trunks. Additional epiphytes are *Asplenium hemitomum* Hieron. (pinnae subtrapezoid) and *Loxogramme lanceolata* (Swartz) C. Presl.

The usual road runs farther eastward, formerly bordering, at 1270 m, a large and very pretty grove of the common tree-fern *Alsophila manniana* (Hooker) Tryon, demolished during the past two years in favour of new 'chop-farms'. Before you enter the forest proper (1350 m), you pass a dense bush comprising *Hypolepis sparsisora*

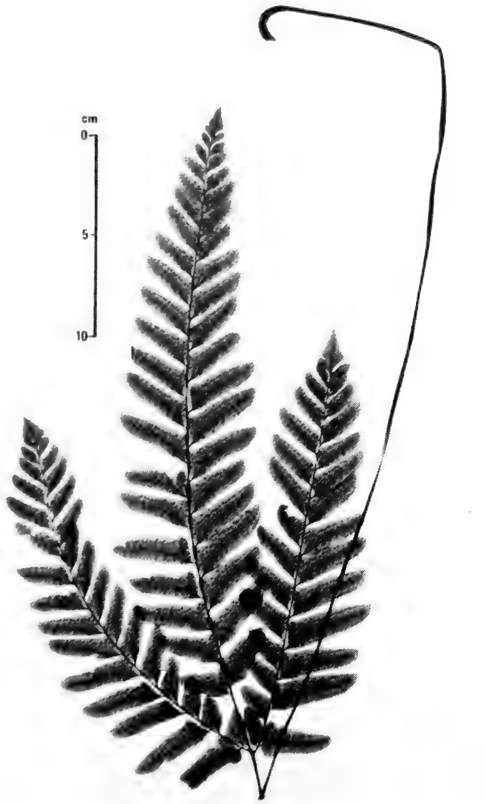

FIGURE 2. *Ctenitis securidiformis* (Hooker) Copel., well recognizable by its trapezoid pinnules with oblique costae. *(Photo K. Liedl).*

FIGURE 3. *Tectaria angelicifolia* (Schum.) Copel., an aspidiaceous fern with a wide-creeping rhizome, anastomosing veins and exindusiate sori. *(Photo K. Liedl).*

(Schrader) Kuhn and *Diplazium velaminosum* (Diels) Pic.Ser., each 1.5 to 2 m tall, with finely dissected leaves. Furthermore *Lonchitis occidentalis* Baker (a member of the Hypolepidaceae with marginal sori between the lobes of frond segments), *Tectaria fernandensis* (Baker) C.Chr., *Amauropelta oppositiformis* (C.Chr.) Holttum -pinnae deeply lobed, veins all free- and *Pneumatopteris afra* (Christ) Holttum -pinnae crenate, 4-6 pairs of veins anastomosing- are notable, the latter being the most frequent representative of the *Thelypteris* group in this area; it will accompany you up to altitudes of 1400 metres.

Besides numerous terrestrial ferns, e.g. *Pteris pteridioides* (Hooker) Ballard, *Asplenium erectum* Bory ex Willd. var. *usambarense* (Hieron.) Schelpe and the proliferous *A.preussii* Hieron., a lot of epiphytes were noted by us in the forest itself. These include *Drynaria volkensii* Hieron., on an isolated tree with its big base fronds (you may see this fern even nestling on a roadside-tree in Buea), some Elaphoglossaceae -*Elaphoglossum cinnamomeum* (Baker) Diels, *E.isabelense* Brause, *E. salicifolium* (Willd. ex Kaulf.) Alston-, *Asplenium aethiopicum* (N.L.Burm.) Becherer, a very variable species throughout its range, *A.biafranum* Alston & Ballard (the sharply serrate pinnae are broadest towards the middle), the crowded *A.dregeanum* G. Kunze with strongly asymmetric lobed pinnae (fig 4), *A.theciferum* (Kunth) Mett. var.

FIGURE 4. *Asplenium dregeanum* G. Kunze is reported as a terrestrial plant, but in the mist forest we found it growing always as an epiphyte. *(Photo K. Liedl).*

cornutum (Alston) Benl (1975: 40). Other species here are the locally frequent *Arthropteris orientalis* (J.F. Gmelin) Posth., readily distinguishable by its white dots on the upper pinna surface from *A.monocarpa* (Cordemoy) C.Chr., which we had found in 1971 as a climber on tree-fern stems above Bokvongo (Bukuangu, 1100 m), near a track to Mann's Spring. Here we had listed among others *Asplenium theciferum* var. *concinnum* (Schrader) Schelpe, *Microlepia speluncae* (L.) Moore, the polypodiaceous *Pleopeltis macrocarpa* (Bory ex Willd.) Kaulf., and *Pteris preussii.*

At 2040 m altitude the path emerges most abruptly ("as through a doorway") from the forest which is then replaced by open mountain grassland, the 'savannah'.

If one chooses the more convenient ascent starting at Bonakanda (810 m), the 'savannah' will be reached at 1430 m. A black, slaggy lava flow (of 1868?) probably emitted from the Robert Meyer – craters (2687 m) has extended down to this level, breaking an opening into the forest quickly colonized by grasses and fair amounts of the ubiquitous *Pteridium aquilinum* (L.) Kuhn. The mountain grasslands, up to roughly 3300 m are more or less regularly burnt down for hunting pursuits in every part of the mountain at the beginning of the dry period – another reason for the varying altitude of the present forest occasionally involved by its fire, primarily above the 'mist zone'. But the grassfires cannot seriously damage the bracken because of its deeply buried rootstocks, and on 14 February 1975 its fronds had reached a height of 1.5 m again, in the locality cited.

Above Bonakanda the pathway is bordered with small coverings of *Selaginella kraussiana* (G. Kunze) A.Br. Clumps of tree-ferns, always dependent on a humid atmosphere, appear at an altitude of about 1000 m; the forest begins at 1170 m. In that region we met with *Marattia fraxinea* J.Sm ex J.F.Gmelin, the clubmoss *Huperzia brachystachys* (Baker) Pic.Ser., and with peculiarly large specimens of *Tectaria camerooniana* (Hooker) Alston growing from rootstocks, the height of which can amount to 60 cm! At 1220 m we had an ample gathering of the proliferous filmy-fern *Trichomanes manii* Hooker. The forest district between 1320 and 1430 m is of particular pteridological interest for its unusual abundance of the gemmiferous *Pteris preussii,* the fronds of which grow like twining plants amongst shrubs; we measured lengths up to 2.2 m here, i.e. by far more than had ever been recorded.

In respect to fern richness neither the short but sharp ascent to the summit above Buea (first described by Mary H.Kingsley in 1897) nor the convenient road from Bonakanda to the Robert Meyer-craters can be compared with the 'classic' though much longer way of Mann and Burton, who started for "Mann's Spring" (2260 m) on 22 December 1861. 'The characteristic of the scenery now was the fern – fern, fern, everywhere', writes Burton (1862: 241): 'Some were like palm-trees, 10 to 20 feet high, surpassingly fair to look at; others were dwarfed epiphytes, springing moss-like from the arms of their parent trees. There were beds of ferns upon the ground, and others running creeper-like up the trunks. Never had I seen a more beautiful fernery, set off as it is by the huge tropical growth around it. The path, however, was vile.'

At Mapanja village we asked permission to pass the farmland, and engaged a capable guide and a porter. We were accompanied for about one hour by *Selaginella kraussiana* fringing the road with its patches, and then by *Tectaria fernandensis,* already forming a well-established colony at 500 m near Lower Bonjongo. This species resembling *T.camerooniana* in many respects, bears a lot of easily dropping buds (sitting on the upper frond surface only, in this area) and arises from considerably smaller rootstocks.

Clumps of beautiful tree-ferns *(Alsophila manniana,* fronds tripinnatifid to tripinnate, stipe bases very spiny, costae hairy above), in community with *Marattia* *fraxinea,* showed up the scene at a height of 990 m more numerously than on the Buea side. At 1120 to 1150 m and again at 1190 m tree-ferns are the constituent of the vegetation, forming a real fern-forest and giving us 'a blurred picture of one of the most ancient types of vegetation' (Warming 1909: 339). Many of them are draped with the rhizome-climbers *Blechnum attenuatum* (Swartz) Mett. and *Asplenium hypomelas* Kuhn with its multipartite arching fronds.

As regards Burton's moss-like ferns in that sublime scenery, surely he meant the graceful filmy-ferns *Trichomanes borbonicum* and especially *Hymenophyllum splendidum* v.d.Bosch (leaf-surfaces completely covered with stellate hairs; stipe and rachis winged), which often cover the branches of a *Ficus,* along with the bushy, gemmiferous *Asplenium dregeanum* (fig 4). The high degree of humidity in that part of the forest belt is manifested by an unusual epiphytic growth of *Selaginella versicolor* at 1320 m and by *Lomariopsis mannii* (Underw.) Alston, a rain forest climber with a length of (31-jugate) fronds up to 95 cm here.

The "beds of ferns" in the deeply shaded forest floor are formed by *Selaginella vogelii, Asplenium preussii, A.unilaterale, Dryopteris manniana* (Hooker) C.Chr. -mostly proliferous-, *Pteris manniana* and other species of this genus, especially *P.togoensis.* We were lucky to find a new *Pteris* species in this region, described later-on as *P.ekemae* Benl (1976 a). The "fernery" growing above 1180 m is composed of *Athyrium ammifolium* (Mett.) C.Chr., *Coniogramme africana* -with exindusiate parallel sori along lateral veins-, *Didymochlaena truncatula* (Swartz) J.Sm. (fig 5), *Diplazium velaminosum, Hypolepis sparsisora* etc. etc., which seem to have found a veritable paradise here. To us it appeared a paradise too, the silence of which was only interrupted by strange voices of the many birds, by rare calls of chimpanzees and the frightening noise of an elephant sufficiently distant not to upset my companions.

FIGURE 5. *Didymochlaena truncatula* (Swartz) J.Sm. — Only two pinnae of this handsome fern are shown here. The whole fronds may reach a length of more than three metres. *(Photo: K. Liedl).*

Above 1350 m the faintly-indicated trail through a real fern-jungle became absolutely overgrown, and it was only possible to make headway by the help of machetes. Further 80 metres up, the view was opened to the impressive pumice-fern lava flow, described previously (Benl 1976 c).

The nearer we come to the seaward side of the mountain the higher is the precipitation. The warm water-laden monsoon-like W and SW winds from the Gulf of Guinea are forced to ascend the Cameroon massif: they are cooled in the upper atmospheric strata and subsequently deprived of their moisture by condensation. That means heavy rains and extreme humidity in this wettest sector, rain-shadow on the opposite side of the mountain (fig 6). At sea-level Cameroon's west coast enjoys the heaviest rainfall of the globe.

On 3 March 1974 we took the opportunity of following a gradually rising bush-path leading from Idenau to Bomana. After a one hour's walk across the Idenau oil palm plantations -with their 'hanging gardens' mainly consisting of epiphytic ferns (Benl 1976 b)- we entered a primary forest without any transition and ascended the W face of the mountain up to 500 m. That path was used by elephants (their tracks could not be overlooked), which did much damage to the crops of the Bomana people. Even in the driest months heavy rain or fine drizzle will come nearly every afternoon and night, keeping the stony path slippery. For the pteridologist this region scarcely ever disturbed by human interference with its moist habitats on various substrates, is of high interest. ("The northern and western sides have always been, and still are, very little known botanically" Richards 1963: 529). It is not surprising that masses of filmy-ferns are found thriving, ferns which can take up water in the same manner as mosses: *Trichomanes chamaedrys* Taton [*T.erosum* var. *aerugineum* (v.d.Bosch) Bonap.] covers the rocks, *T.pyxidiferum* var. *melanotrichum* and especially *T.erosum* Willd. are frequent on tree-trunks, *T.africanum* Christ was found on both substrates, and unexpectedly *T.borbonicum,* usually occurring at over 800 m on trees, showed too. Moreover *Alsophila camerooniana* (fronds bipinnatifid to bipinnate) already appeared 340 m above sea-level, certainly because of the most favourable growth conditions presented by an exceptional humidity in this tropical rain forest proper, extending upwards to about 1000 metres.

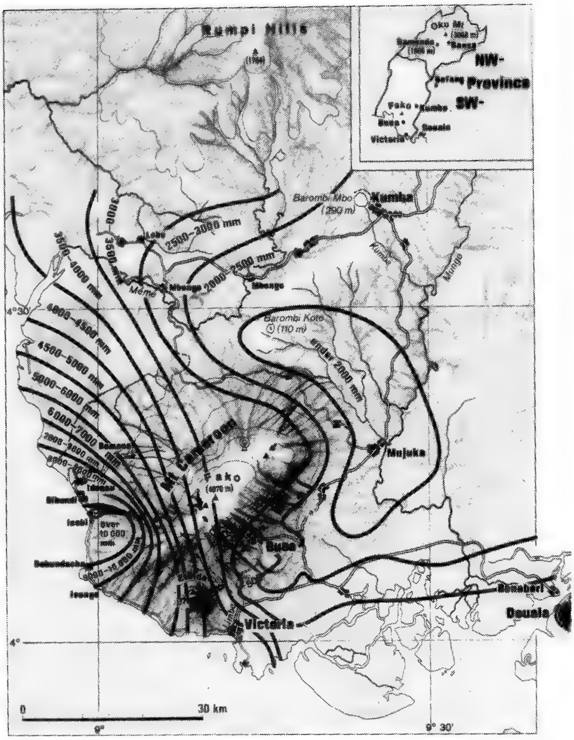

FIGURE 6: Isohyetes covering the respective part of the South West Province demonstrate the enormous difference of precipitations within this region. *By A. Böhm, after Semmelhack 1942, Eisentraut 1963).*

Among our further collections from this district *Selaginella molliceps* Spring and two representatives of the family Lomariopsidaceae may be cited: the geophytic *Bolbitis acrostichoides* (Afz. ex Swartz) Ching -veins anastomosing- at 140 and 170 m and the epiphytic *Lomariopsis guineensis* (Underw.) Alston -veins free- at 260 m, climbing by the rootlets of its flattened rhizome like ivy (Alston 1959: 67).

According to Tardieu-Blot (1964) the total of fern taxa collected on Cameroon Mt amounted to 111. It was increased by 4 more species in consequence of Tryon's report in 1965. We must emphazise on this occasion that it is not satisfactory to compare the Cameroon Mountain with the island of Fernando Po as a whole, as regards their wealth in ferns. ('The slightly richer pteridophyte flora of Fernando Po includes several species that are not on Cameroon Mountain, such as *Osmunda regalis...',* Tryon 1965: 55). Any one who knows Fernando Po merely by seeing it from the continent, may erroneously identify the peak (Pico de Malabo, 3007 m) with the whole island. In reality this mountain (closely comparable with Cameroon Mt in its structure, climate, and altitudinal zones, though of lower height and smaller size) scarcely covers half of the area; the central and southern parts of the island being an upland of from 800 to 1300 m, though including a caldera and some volcanic cones, in part with lakes. Furthermore there are coastal districts with a special vegetation. You cannot expect to meet with a mangrove fern (*Acrostichum aureum* L.) on a mountain slope, nor with an aquatic pteridophyte like *Isoëtes biafrana* Alston, a climber on ***Raphia*** (*Stenochlaena mildbraedii* Brause), a fern preferring banks of a lake or of an even-flowing stream (*Osmunda regalis* L.). In Fernando Po all those plants grow at a greater or lesser distance from the Pico; and the same species do occur in Cameroon too, but of course not on the mountain. About 25 different pteridophytes are common to West Cameroon and to the island, growing neither on Cameroon Mt nor on the Pico de Malabo. A number of species well known from Cameroon Mt. (e.g. the 3- to 4 pinnate *Adiantum thalictroides* Willd. ex Schlecht. *[A.poiretii* Wikström], *Asplenium adamsii* Alston, *A. adiantum-nigrum* L., *Aleuritopteris farinosa* (Forssk.) Fée [*Cheilanthes farinosa* (Forssk.) Kaulf.], *Huperzia saururus* (Lam.) Rothm.) were never met with on the Pico. If, on the other hand, you confine yourself to the respective mountain vegetation of the two regions, you will find 110 taxa in Alston's list (1959) for Cameroon Mt, i.e. 60% of his total for West Cameroon. Adams (1957) recorded 91 valid taxa for the Pico and 80 exclusively for other parts of the island, the first figure being 53% of his total.

Regions north of Cameroon Mountain

In marked contrast to the western side of Cameroon Mt with its excessive precipitation and its damp atmosphere the eastern and the northern regions lying in the rain-shadow have a fairly well defined dry period. The average annual rainfall amounts to 4150 mm in Victoria, to 2900 mm in Buea, to 2350 mm at Kumba; the lowest rainfall being approximately 20% of its maximum on the west coast, at a direct distance of 50 km (fig 6) — a unique phenomenon in the world. Our observations on the amphibian fern *Bolbitis heudelotii* (Bory ex Fee) Alston — see Brit.Fern Gaz.10:152 — showed that this fern displays a luxuriant growth of only sterile emergent leaves in the moist climate of Victoria, but produces also fertile fronds in the drier climate at Kumba, with more sunshine favouring sporulation. On 14 February 1974 we obtained sterile leaves of up to 1.1 m (with pinnae up to 22 cm) from ample colonies on rocks on the Limbe River bordering the Botanical Garden in Victoria; according to Mr Ekema's notes fertile fronds had not been observed here. On 26 February 1975 we found a clump of smaller plants on rocks in the Kumba River, each stock with fertile fronds.

Amidst the northern region there are some evergreen forests we thought worth looking at for ferns, in particular the surroundings of the two crater-lakes of Barombi Mbo and Barombi Koto. The deep Lake Barombi Mbo or Elephant Lake (altitude 290 m, max.depth 111 m), with its surface of 453 ha the largest lake in Cameroon, is easy to reach from Kumba (260 m). Its steep banks, the walls of a former crater, are clothed in dense forest, in part of primitive nature. The area on the SE side of the lake (near the former 'Barombi Station', 385 m; see Hutter 1904), is the *locus classicus* of *Pteris barombiensis* Hieron., once collected by Preuss and described on the evidence of a single imperfect frond. But only some plants looking like meagre specimens of *P. mildbraedii* Hieron. were present here, associated with the locally common *Tectaria camerooniana,* on the SE bank of the lake at an altitude of 310 m. On a row around the lake we met with *Pyrrosia lanceolata* (L.) Farwell -rhizome scales ciliate-, settling on a rock towering up in the water. After a landing on the flat NW shore we moved on to Barombi village. On the road to and near by this village we found on somewhat marshy ground magnificent colonies of *Christella hispidula* (Decaisne) Holttum [syn. *Thelypteris quadrangularis* (Fée) Schelpe] -ca 8 pairs of veins per pinna lobe- and especially of *Cyclosorus striatus* (Schum.) Ching -ca 20 pairs of veins per lobe- with extreme frond lengths up to 4.1 m (Tardieu-Blot: 1.1 m; Schelpe: 1.67 m; Holttum:

1.6 m or more).

The romantic lake Barombi Koto (alt. 110 m, max.depth 6.2 m; surface 330 ha) was in our reach from Kumba via Kombone-Kwakwa-Bay Panya only. It had been discovered in 1877 by Comber who baptized it 'Lake Rickards'. In its centre there is a small volcanic island of more recent age with a village upon it. This crater-lake with its steep banks is interesting for an abundance in fish (see Trewawas 1962), turtles and water-birds, but fairly disappointing as to ferns. On our row in the shallow lake and on our walk around the island we looked in vain for a noteworthy fern, most of the representatives being *Nephrolepis biserrata.* The annual rainfall in that area is below 2000 mm (fig 6).

We were luckier in our excursions (on 24 and 25 February 1975) towards the mouth of the Mémé River, which passes the broad valley between Mt Cameroon and the Rumpi Hills (fig 1). Judging from some outcrops it was possible to infer that most of the soils in that valley were deposited by the sea at a rather recent geological age (Hasselo 1961: 35). Crossing the river near Mbongo we found, on its loamy bank, young specimens of the regularly bipinnate *Adiantum vogelii* Mett. ex Keys., of *Pteris linearis* (veins anastomosing along pinna costa), *P.atrovirens* Willd. (united veins throughout the lamina), and *P.togoensis* (veins free) occurring fairly close together.

In the area of the Lobe Estate Palms (100 m above sea-level) with prevailing wetter conditions provided by the western sea we found plenty of *Ctenitis lanigera* (Mett. ex Kuhn) Tardieu and the gemmiferous *Lastreopsis subsimilis* (Hooker) Tindale with oblong reddish sori, in strong-growing specimens in the undergrowth of the plantations. The annual rainfall here is 3000-3500 mm; we had a rainy morning on 25 February 1975.

Finally we mounted one of the volcanic rock hills in that region, the 'Munya Hill' ('Fire-Hill'), between the villages of Bogongo I and Bogongo II, SE of Lobe. Up to its top (220 m) it is covered with virgin high forest of relict character; from its black rich humus soil we took up some fronds of *Ctenitis buchholzii* (Kuhn) Alston -veins forming isolated areoles!- and of *Diplazium welwitschii* (Hooker) Diels (det. Pic.Ser.). Finally vigorous individuals of *Pteris barombiensis* Hieron. appeared with striking spiny frond stipes, a fern eagerly expected by us.

At the foot of this hill, at an elevation of 60 m, *Diplazium proliferum* (Lam.) Kaulf. [syn. *Callipteris prolifera* (Lam.) Bory] with a regularly reticulate venation, and *Cyclosorus striatus* are favoured by the drainage of a warm saline swamp (called 'Ndimo') in the neighbourhood. The whole area is far from being sufficiently investigated.

On our way back to Victoria we saw *Lycopodiella cernua* (L.) Pic. Ser., the 'Christmas-tree clubmoss', with erect stems 85 cm tall, on the exposed roadside banks near (Barombi-) Kang, 190 m altitude. Richards (1963: 136) points out that this clubmoss, in community with the sun fern *Dicranopteris linearis* (N.L.Burm.) Underw., 'occurs in such habitats throughout the lowland tropical rain forest region of Africa', but we observed this community in considerably greater quantities at 1100 m elevation, e.g. between Kekem and Bafang, and higher up. On our ride to Bamenda (1600 m), where we had a week's stay at the turn of 1970, we furthermore met with *Alsophila dregei* (Kunze) Tryon (near Geondanko, 1540 m), unknown from Cameroon Mt, but not uncommon in the environs of Bamenda, e.g. between Bamessing and Bambili (1750 m); from *A. manniana* it is at once distinguished by the stipe bases only muriculate and its costae glabrous above. Near Bamenda in addition we collected *Christella hispidula* and *C.microbasis* (Baker) Holttum — yellow glands on lower surface —, *Doryopteris concolor* (Langsd. & Fischer) Kuhn var. *kirkii* (Hooker) Fries, ample individuals of the 'grassland species' *Dryopteris athamantica* (G.Kunze) O.Kuntze, beside the slightly fleshy *Loxogramme lanceolata, Pyrrosia mechowii* (Brause & Hieron.) Alston -rhizome scales entire-, etc.

In a small ravine above Bamenda we unearthed *Asplenium inaequilaterale* Willd. (pinnae toothed, subdimidiate), not recorded to Cameroon so far, yet found by the 'Mission Botanique Camerounaise' on Cameroon Mt at 1800 m too (MC 222 A, 4 February 1962; K). In the same locality there was an abnormal form of *Bolbitis acrostichoides* with a large number of lateral pinnae (up to 21 pairs in its sterile, up to 23 in its fertile fronds) and a narrowly triangular terminal segment with a regular gemma on its base. According to Dr.E.Hennipman the specimens of *B.acrostichoides* 'are markedly heterogenous'; he expects 'hybridisation to be one of the agents causing this' (litt. 7 December 1971).

Between Bamenda and Bafut large areas of *Osmunda regalis* are occupying bank-sides and small islands of the 'Ngomirgham Water'. We also came across the royal fern near Banso on a trip to Oku Mountain (3008 m), which Dr.Letouzey had advised me to visit because of its rich fern flora hitherto rather unknown. Near Sanyere (2050 m) a vigorous colony of *Amauropelta bergiana* (Schlecht.) Holttum could be admired. It was interesting to state, that *Lycopodium clavatum* L. var. *borbonicum* Bory not yet cited from the western provinces of the United Republic, and the white-backed *Aleuritopteris farinosa,* known from the grasslands and the lava fields of Cameroon Mt, were growing here not infrequently on the lower treeless E and NE slopes of Oku Mt, with its misty atmosphere even during the dry period. The same is the case with *Polystichum fuscopaleaceum* Alston [*P.setiferum* (Forssk.) Moore ex Woynar var. *fuscopaleaceum* (Alston) Schelpe], hitherto unknown from this area.

At an altitude of about 2100 m there is an astonishing wealth of ferns in the evergreen montane woodlands and its edges: *Adiantum thalictroides* (frond length more than 60 cm), various asplenia — *Asplenium abyssinicum* Fée with 2- to 3 pinnate fragile leaves, *A. aethiopicum, A. erectum* var. *usambarense* (the strongly decrescent lamina with up to 70 pairs of auriculate pinnae), *A.friesiorum* C.Chr. (sori subcostal), *A.gemmiferum* Schrader (the one metre fronds often without a gemma), *A.preussii* with its decorative laminae (base of pinnae almost equal) up to 38 cm tall —, *Dryopteris inaequalis* (Schlecht.) O.Kuntze (stipe scales with numerous lateral processes, pinna scales hairlike) are present in abundance; furthermore *Pellaea quadripinnata* (Forssk.) Prantl, known from the lava of the Robert Meyer — craters (Maitland), and *Huperzia mildbraedii* (Herter) Pic.Ser. The fronds of *Dryoathyrium boryanum* (Willd.) Ching attain lengths of more than two metres, those of *Hypolepis sparsisora* (pseudo-indusia subentire) more than three metres. Most of these species had not been reported from Oku Mt before. Yet our top-find was *Asplenium elliottii* C.H.Wright, new to West Tropical Africa entirely.

ACKNOWLEDGEMENTS

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Voucher specimens of my own collections are deposited in the Botanische Staatssammlung München; duplicates of various specimens are lodged in BM, K, VICT

(nos. HNC/V 441-510), and in the herbarium of Prof. R.E.G. Pichi Sermolli, who very kindly checked and corrected my determinations and discussed doubtful specimens with me.

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AN ECOLOGICAL SURVEY OF THE FERNS OF THE CANARY ISLANDS

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ABSTRACT

This survey attempts to define the principal native fern communities to be found in the Canary Islands, the main physical features of their environment, and give an outline of the ecology of the fern species concerned. Some areas in need of further research are indicated. By careful selection and conservation of a relatively small number of types of habitats a large percentage of the common ferns could be preserved, and the urgency and value of taking adequate conservation measures to achieve this end is stressed.

INTRODUCTION

Ferns form an integral and scientifically important part of the vegetation of the Canary Islands, especially of the mid-mountain forest communities. Their scientific importance stems not only from the high percentage of macaronesian endemic or near-endemic species, but especially from the unique phytogeographical and evolutionary position in the world's vegetation of these ferns, as surviving insular fragments of former more widespread evolutionarily important species (Page 1973 and in press).

The importance of the Canarian ferns and the vegetation which contains them has attracted the serious attention of many scientists since the 19th century, amongst whom Webb & Berthelot (1836), Bolle (1863, 1864, 1866 a & b), Schenck (1907), Pitard & Proust (1908), Burchard (1920), Lindinger (1926), Borgesen (1924), Ceballos & Ortuno (1951), Lems (1960), and Dansereau (1961) have made notable contributions.

In recent years various excellent notes on the Canarian ferns in specific areas, their taxonomy and their importance have also been made by G. Benl and G. Kunkel (e.g. Kunkel 1966 a & b, 1967 a & b, 1969 a & b, 1971; Benl 1964, 1965, 1966 a, b & c, 1967 a & b; Benl & Kunkel 1967; Benl & Sventenius 1970). This account draws on this literature and on personal observations to outline something of the native ecology of at least all the more abundant and vegetationally significant ferns of the Canary Islands. During visits to the Canary Islands in the summers of 1963 and 1964 and spring 1973, I had opportunity to make observations at some length on the ecology of the Canarian ferns in untouched forest areas of the more remote western islands of La Palma, Hierro and Gomera, with shorter visits to Teneriffe and Gran Canaria (fig. 1). These visits left an overwhelming impression of the endangered ecological position of the fern species in the face of widespread destruction of the habitats which contain them, especially of the evergreen forests. I have tried to indicate the types of community and habitats which are characteristic of each, and which would be necessary to conserve in order to ensure their survival, in the hope that this may help stimulate local conservation measures to this end.

PHYSICAL ENVIRONMENT

Geography and topography

The seven main islands of the Canary archipelago lie some 200 miles off the adjacent West African coast, 4½ degrees outside the tropics (lat. 28°N – fig. 1). The islands are

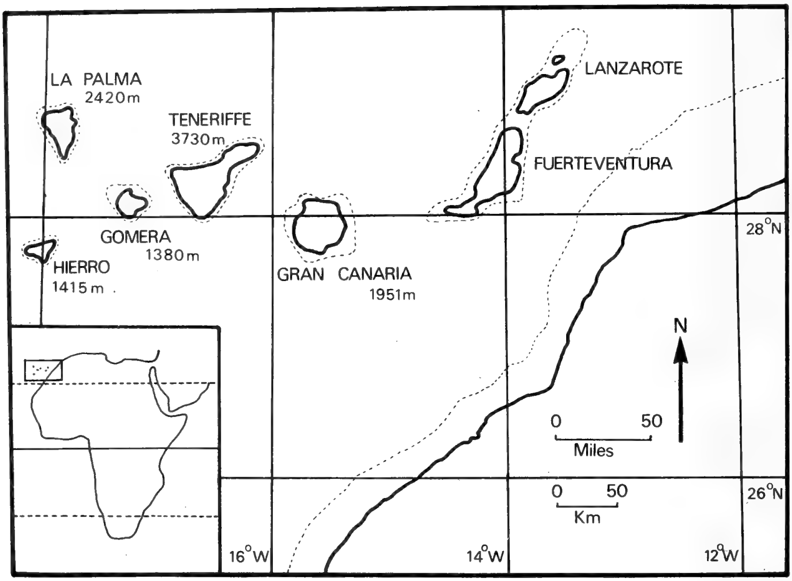

FIGURE 1. Map of the Canary Islands showing position of the archipelago with respect to continental Africa.

all of volcanic origin, and whilst more or less continental in position, have originated from a deep ocean bed. At least all the western islands of the group seem to have had no land connection with adjacent Africa during the arrival and establishment of their flora (from the mid-Tertiary period onward). In this they compare closely with Madeira and the far more oceanic and isolated Azores archipelago.

With the exception of the islands of Lanzarote and Furteventura nearest to the African coast, the five remaining Canary Islands rise steeply from the sea to great heights, and one, Teneriffe, exceeds in height all other islands of the North Atlantic Ocean. Of the three western islands with which this survey is chiefly concerned, *La Palma,* about 130 km (c. 80 miles) ENE of Teneriffe is the largest, approximately 50 x 25 km (c. 30 x 15 miles) and the second highest of the Canaries. The highest points at 2424 m (8080 ft) lie on the rim of the large central caldera, from where the land falls rapidly for about 8 km (c. 5 miles) at an average gradient of about 1 in 4 to sea level on all sides but the south, where an actively volcanic ridge extends to the southernmost tip (fig. 2). *Gomera* is an approximately circular island, dome-shaped in profile, about 25 km (c. 15 miles) in diameter and 1380 m (over 4000 feet) in height. It is due west of Teneriffe and a channel of about 30 km (c. 20 miles) separates the two. Gomera has long been inactive volcanically, and erosion has carved a rugged landscape of ridges and ravines, dotted with the outcropping pinnacles of old volcanic cores (fig 3). *Hierro,* the smallest of the islands, lies at the extreme south-west of the group, about 145 km (90 miles) WSW of Teneriffe. Although it is only about 20 km (c. 12 miles) across, it nevertheless reaches 1415 m (4710 ft) in height. The island is the surviving fragment (the southernmost quarter) of a large volcanic caldera, and what was formerly the inside wall of this crater form the steep northerly slopes ("El Golfo") of the island today.

The present physical structure of the Canaries is the result of many volcanic outpourings of lava, 'ash' and 'cinders', and later, intrusive basalt dykes and sills, which over long periods of time have built up the steep conical, often slightly concave profile

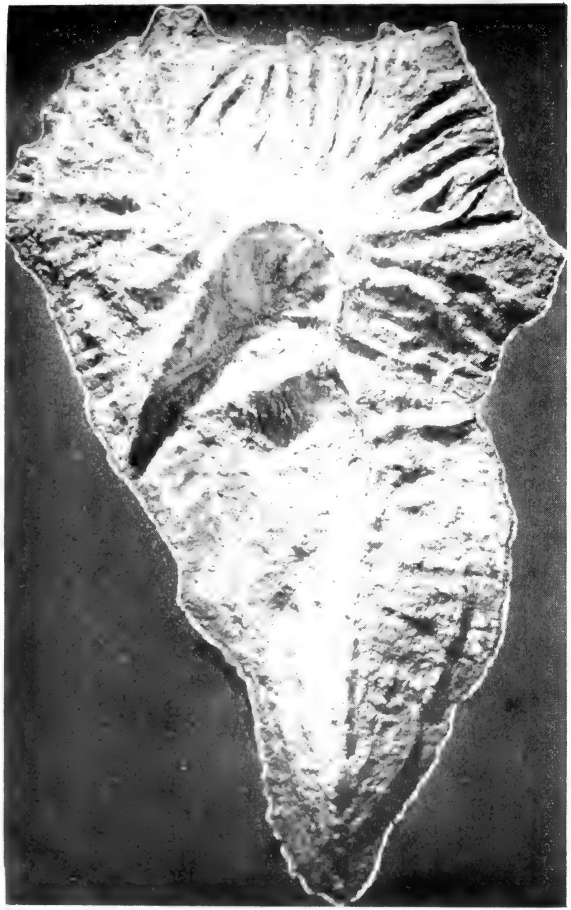

FIGURE 2. Relief map of La Palma, showing the typical steep, deeply incised topography and radiating drainage pattern typical of many parts of the Canaries.

FIGURE 3. North slopes of the island of Gomera (El Cedro area) on a rare clear day (with cloud dispersed) showing the forest blanket at cloud-belt altitude, with laurel forest in the ravines, heath forest on the ridges between, and the close juxtaposition of forest and steep rocky outcrops.

of the western islands. Superimposed on this are the effects of powerful erosion. Around most sides of the islands, fierce seas have carved impressive cliffs. On land, the rapid run-off of heavy winter rains down the steep slopes has sculptured the older parts of the islands into a series of radiating deep steep-sided ravines (the *barrancos)* which discharge their winter torrents through precipitous gulleys and long cascades to the sea. Between these barrancos, which are often over 300 metres (more than a thousand feet) in depth, narrow ridges are left standing which may come to knife-like crests. Weathering of the steep barranco sides has often exposed numerous walls and ledges of old volcanic dykes and sills and has added long scree slopes of loose rock. This deeply inscised barranco-type radiating drainage pattern is a particularly characteristic feature of northern La Palma, Gomera, and many areas of Gran Canaria and Teneriffe (fig 2).

Climate

Because of the small size of the islands in relation to the large mass of surrounding ocean water, mean temperatures in the group vary little throughout the year. But as a result of the great altitude to which the islands rise, and the constancy of the prevailing wind direction, (NW to NE) there are constant marked differences of climate with aspect and altitude, resulting in three distinctive altitudinally-banded vegetation zones on the windward slopes of each island.

The xerophyte zone from sea level to about 760 m (c. 2500 ft) has a dry subtropical climate. It receives the bulk of its rainfall over a short winter period whilst the rest of the year is almost rain-free. The summers are hot and dusty, although there may be appreciable dew-fall at night. The sparse vegetation is characterised by winter annuals and a large number of xerophytes (mainly woody succulents) amongst which Crassulaceae, Compositae and Euphorbiaceae dominate. This vegetation gives way sharply as the base of the cloud is reached.

The cloud zone from about 760 to 1250 m (c. 2500-4000 ft) has a moist warm temperate oceanic climate. Here, on the windward (north and north-east) aspects of the islands, the climate is kept continually damp by the almost perpetually-impinging belt of cloud produced as the trade-wind breezes rise and cool over the steep topography. At the altitude of the cloud zone, the passing moisture-laden cloud produces frequent light precipitation. This either falls as light rain or, most usually, condenses directly and abundantly from the moving air on to the leaves and twigs of the vegetation through which it is passing. Consequently, the vegetation intercepting this cloud runs and drips freely with such condensed moisture ('cloud-drip'), even though no rain is falling. The climate at this altitude is thus continually mild, damp and uniform, and by contrast with the basal region, the vegetation of the cloud zone consists of a lush evergreen forest (the "Monte-verde") dominated by arborescent heaths and tall laurels.

The upper dry zone above about 1250 m (c. 4000 ft) (extensive on La Palma, Teneriffe and Gran Canaria only) has a dry warm temperate climate in its lower reaches, becoming cooler and more severe at higher altitudes. The upper part of the cloud zone has a much more gradual cut-off than the abrupt transition at its base, and consequently intermittent amounts of cloud pass through the lower part of this zone, with some cloud-drip from the trees. In general, temperature extremes are much greater than in the cloud zone, the sun more frequent and intense by day, and the skies clearer and cooler at night. *Pinus canariensis* forest dominates the lower part of

FIGURE 4. North coast of La Palma looking ENE from 1250m showing the early morning impinging cloud-belt bringing light rain and mist to windward slopes, here between 700-1100m.

this zone, merging gradually at higher altitudes (about 1800 m or 6000 feet) into a dry legume scrub and finally (Teneriffe only), to a barren subalpine zone with winter snow.

The leeward (southern) slopes of all the Canary islands gain less benefit from the cloud belt, and hence are relatively dry at all altitudes. These aspects of the islands are dominated chiefly by xerophyte scrub at low altitudes merging into *Pinus canariensis* forest at higher levels.

FOREST VEGETATION OF THE CLOUD ZONE

The evergreen cloud zone vegetation, in its virgin state, is typically dense and luxuriant throughout. It varies in species composition according to its degree of exposure to the moisture-laden winds and the water-retentive capacity of the underlying rock, from a woodland of arborescent heaths to a hygrophilous laurel forest.

The more exposed situations (particularly the ridges between barrancos) and all the areas where the water-retentive capacity of the ground is low (such as the soft, porous pumice-like rocks of relatively recent volcanics) are generally dominated by heath vegetation of varying development. In some of the more exposed areas, shrubs of *Erica arborea* form no more than a dense waist-high thicket. More typically, throughout much of this vegetation on all the western islands, the heath forms a dense 10-12 m high woodland, dominated by tall gnarled old trees of *Erica arborea* and *Myrica faya* with *Ilex canariensis* in damper pockets.

In more sheltered situations (especially in all the deep barrancos) and where the water-retentive capacity of the rock is high (usually where older, more massive, volcanic rocks outcrop), the heath forests give way to laurel forests. These vary in type from low gnarled woodland in areas of most exposure but good ground water, dominated by *Laurus azorica* and *Ilex canariensis,* to the most hygrophilous forests of the sheltered ravine bottoms, with tall straight trunks and a leafy canopy at around 30 m, dominated by *Persea indica,* sometimes with *Ocotea foetens.*

The contrast between heath and laurel vegetation is particularly distinctive in northern La Palma. Here, heath forests dominate the barranco ridges, whilst laurel forests reach their most luxuriant development in the Canaries in the depths of the sheltered ravines, the two types of vegetation occuring in surprisingly close proximity. By contrast, on Hierro virtually all the land in the cloud-belt is of recent porous volcanics, with barrancos poorly developed, and the vegetation is dominated by old mature heath forests, and good laurel forests are lacking. On Gomera, much of the land in the cloud-zone is of older, harder rocks with a high water-table evident in summer-flowing streams. Here laurel forest occurs over extensive areas.

Throughout virtually all these forests, abruptly outcropping cliff-faces provide distinctive habitats of their own with local enclaves of exposure-resistant plants close by the more hygrophilous habitats of the forests themselves — a contrast which is particularly emphasised by their ferns.

THE FERN COMMUNITIES

Each of the main cloud zone habitats is characterised by distinctive communities of ferns. The *laurel forests* contain communities of the most shade-tolerant, shelter and moisture-demanding (hygrophilous) species, most of which are of large size and all of which are terrestrial or grow on moss-covered rocks. These form a dense community over the forest floor and on the sides of the ravines within it. The *heath forests* contain more scattered communities composed of more light-demanding species, of smaller size and able to tolerate some degree of exposure and intermittent periods of drought. These are terrestrial, rock inhabiting or epiphytic. The communities of *dry outcropping rocks* are composed of particularly small-sized light-demanding species each able to withstand considerable degrees of exposure to desiccating conditions at all stages, and long periods of drought. Few, if any, however, thrive in continual exposure to full sun, and most exist within the partial shelter of rock crevices.

With destruction of the forests, as has happened widely on Gran Canaria and Teneriffe, the fern species of the laurel forest readily disappear, except locally in occasional sheltered ravines. Those of the heath community mostly diminish in numbers and luxuriance, but persist longer, the epiphytes often surviving in rupicolous habitats (where their morphology is invariably different from that of their former forest form). The species of the rock communities, already frequent around the natural forest margins and extending to some extent both above and below the original forests, usually survive and may even extend their range with the loss of the forests. These species, therefore, tend to be much more abundant today on Gran Canaria and Teneriffe than on the three western islands.

Laurel forest fern community

Most of the floor of the laurel forests is of gently or steeply sloping ground, dissected with innumerable rock outcrops and steep or sheer-sided rocky ravines. The soils, which vary from thin coverings over rocks to deep accumulations are dark, perpetually moist and mostly well-drained. The ravine bottoms are typically rocky and boulder-strewn, with frequent ledges and waterfalls. In Teneriffe and La Palma, the streams usually cease flowing in summer, and dry or leave a series of disconnected pools. On Gomera many remain flowing throughout the summer. In virgin forest the canopy is largely continuous and even in sunny spells only dappled light reaches the forest floor. Further, except for brief periods around the middle of each day, sun is cut off from the depths of the deep ravines by the height of many of the barranco sides. The ravine bases thus often continuously enjoy cloudy skies or screened sunlight, with frequent light precipitation, sheltered both from wind and from temperature extremes, perpetually good ground moisture and high humidity, augmented at least in winter by cascading streams. The laurel forest interior, at its best development can be thus an extremely constant and hygrophilous one.

Almost the whole of the forest floor, in its virgin state, carries a fern community varying from a sparse covering (in drier laurel forests and southerly slopes) to, more usually, a dense covering breaking only in more exposed spots and along the stream beds. In many of the deep ravines of La Palma and parts of Gomera, the fern covering is nearly continuous, and undoubtedly forms an important and integral part of the forest community as a whole.

Predominant amongst the ferns in size and numbers of individuals throughout the laurel forests everywhere is *Dryopteris oligodonta* (Desv.) Pic. Ser. with fronds up to 1½ metres and massive ascending or erect rhizomes. Nearly as large, and usually codominant or dominant in the more hygrophilous situations is *Diplazium caudatum* (Cav.) Jermy *(Athyrium umbrosum* (Ait.) C. Presl*)* the two species forming a close association and a dense waist-high sward over most of the sloping ground. Another large *Dryopteris, D. guanchica* Gibby & Jermy joins the association in the most sheltered areas of Gomera and Teneriffe (Gibby *et al,* 1977). *Dryopteris aemula* (Ait.) O.Kuntz also occurs sparsely in this habitat on Gomera. Neither has been found on the other islands, but on La Palma, a species superficially similar in morphology to *D.guanchica* joins the forest floor association in more hygrophilous areas; this taxon needs further investigation. Elsewhere in the Canaries, *Culcita macrocarpa* C. Presl occurs in this habitat on Teneriffe. This *Dryopteris/Diplazium* forest-floor community gives way on the very steepest and most sheltered damp slopes, earth banks and rocky faces, especially alongside streamcourses, to stands of *Woodwardia radicans* (L.) J. Sm. Here, *Woodwardia* often dominates exclusively, its fronds, up to about 4 metres, hanging down in dense curtains (fig 5). *Woodwardia* is virtually confined to such habitats, and its ecology seems associated with areas of moving groundwater. This fern reproduces extensively by vegetative rooting of the single large distal bud at the end of each frond (a behaviour it readily repeats in cultivation) and in the laurel forest whole colonies of *Woodwardia* doubtless establish in this way. Complete shelter from wind is clearly essential if the tip of the long frond is to take root, and *Woodwardia* is thus virtually confined to sheltered situations. *Woodwardia* is most abundant along the banks of the steep rocky barranco-base ravines of La Palma and particularly large plants are frequent alongside streambanks in the El Cedro region of Gomera. By contrast, where streams are not deeply incisced and the banks sheltered but shallow (notably on Gomera), *Athyrium filix-femina* (L.) Roth may succeed well, often accompanied by *Cystopteris diaphana* (L.) Blasdell and large plants of *Pteris serrulata* (L.) Forsk. At lower altitudes, the *Pteris* is the more frequent of these becoming to some extent ecologically replaced by *Athyrium* in the upper part of the cloud zone, although there is a very wide range of altitudinal overlap. Unlike *Woodwardia,* both *Athyrium* and *Pteris* usually occur as scattered individuals along streamsides. They lack the extensive vegetative reproductive capacity of *Woodwardia,* but in cultivation *Pteris* and *Athyrium* succeed much better and quicker from spores than does the slow-growing and massive *Woodwardia,* a behaviour doubtless also found in the wild. Both *Athyrium* and *Pteris serrulata* are absent from Hierro, but by contrast, *Cystopteris diaphana* succeeds well on all the western islands, displaying a very wide

FIGURE 5. *Woodwardia radicans* with fronds exceeding 3 metres, dominating the steep side of a rocky ravine in the depths of the laurel forest (with a single plant of *Diplazium caudatum* at lower left centre), Northern La Palma: Barranco del Rio, c. 1000 m.

and adaptable ecology. On La Palma and Gomera, *C.diaphana* is a laurel-forest species, present on shaded faces of wet rock, below waterfalls and on shaded rocks around springs and beside streams, demanding continually good ground water and shelter and tolerant of low light levels. Occurring only above about 760 m. (c. 2500 ft) *Cystopteris* ecologically replaces *Adiantum Capillus-veneris* L. in similar habitats below this altitude. On La Palma and Gomera, *Cystopteris* seems not to occur outside laurel forest, but on Hierro is present in habitats with more ephemeral moisture in the heath forests (see later).

In the darkest and most humid locations in the laurel forests, plants of *Trichomanes speciosum* Willd. occur occasionally in pockets of soil beside streams and on the boles of large trees. *Hymenophyllum tunbrigense* (L.) J.E.Smith is present occasionally on boulders, especially in the splash zones of waterfalls, and epiphytically in areas of laurel forest more directly exposed to impinging cloud. Throughout the laurel forests and also around the forest margins on mossy rocks and tree boles, and sometimes on damp earth banks, are the striking, entire palmate-fronded plants of *Asplenium hemionitis* L. In their more juvenile stages, the fronds of this plant look much like leaves of ivy *(Hedera),* with which it often grows. *Asplenium hemionitis* seldom occurs in quantity, but in cultivation (fig.7) has been found to re-establish freely on moss-covered rocks. Also on moss-covered boulders within the laurel forests and forest margins, *Asplenium trichomanes* L. ssp. *quadrivalens* D.E. Meyer emend. Lovis and *Asplenium anceps* von Buch occur sparsely but widely (Page 1967) and *Asplenium monanthes* L. (not found by me) is reprotedly a plant of similar situations. *Selaginella denticulata* (L.) Link is often abundant in these habitats, also colonising tree boles and succeeding even in areas of the forest margins receiving considerable summer drought. The latter species seems tolerant of a very wide range of light intensities, though does not succeed well in permanently exposed situations. Another species of mossy boulders as well as earth banks throughout the laurel forests and laurel-forest margins is *Anogramme leptophylla* (L.) Link. In these partly or fully shaded situations, plants are green in summer (a second annual generation?), and this species, like *Cystopteris diaphana,* also succeeds well in the heath forests of Hierro (see later).

As the laurel forest floor community approaches the heath-forest transition, the *Dryopteris/Diplazium* association becomes more sparse and eventually consists of *Dryopteris obligodonta* alone. The more hygrophilous and shade-demanding *Diplazium caudatum* and *Dryopteris* species are replaced by scattered plants of *Polystichum setiferum* (Forsk.) Woynar and (on Gomera only) *Dryopteris pseudomas* (Woll.) Holub & Pouzar. With increasingly lighter, more exposed and extreme conditions, these ferns become replaced by *Asplenium onopteris* L., and this point marks the transition to the heath forests.

Heath forest fern community

As one ascends the steep barranco sides (such as those of northern La Palma), the laurel forests, confined markedly to the barranco bottoms, give way quickly to the heath forest vegetation, dominated by *Erica arborea* with *Myrica faya* as a constant associate and scattered *Ilex canariensis.* In the most exposed situations on the barranco crests, the vegetation may form only a dense waist-high sward, but with only slightly more shelter, a thick woodland is present with dense shade beneath the trees, and exposed patches between them. In brief cloudless periods, insolation in these forests is much more intense than in the laurel forests, and is not cut-off for such long periods by the barranco sides. The large *Erica* trees however, usually cast a dense shadow on the ground beneath them. During periods of passing cloud the trees run with abundant moisture, which irrigates the ground below each tree, although patches of bare ground between trees receive much less benefit. Environmental extremes are thus much greater in the heath forests than in the laurel forests. Frequent shifts in cloud density continually cause conditions to fluctuate between dense drifting mist and brief bright sunshine.

The soils are less humus-rich than those of the laurel forests, well drained and generally drier, and the surface is frequently tightly bound by the abundant surface rootlets of the heaths (which obtain maximum benefit from the cloud-drip and the falls of dew at night) and by a frequently present covering of mosses.

With the more extreme conditions within heath forests the ferns of this community are fewer in species than those of the laurel forest but each much wider in ecological and altitudinal range. Hence the most abundant and characteristic ferns of this vegetation — *Asplenium onopteris, Davallia canariensis* J.E. Smith and *Polypodium macaronesicum* A. Bobrov — all show a particularly wide (sometimes confusing) array of morphology through an extensive altitudinal range of about 400-1400 m (c.1400-4700 ft). Cultivation experiments show some of this variation to be genetic, whilst most is environmental, and that despite the range of morphology, probably only single variable species are chiefly involved.

Asplenium onopteris is the most abundant fern of the heath forests of La Palma, and has (I think rightly) been used by Sunding (1972) as a plant species by which the whole *Erica* association can be characterised. It is tolerant of a wide range of well-drained edaphic habitats, water availability, and exposure. It usually grows on earth banks and rocky slopes, on moss-covered boulders, or around the boles of large *Erica* and *Myrica* trees, and occasionally as a low epiphyte on large exposed moss-covered tree roots. More characteristically epiphytic in their habitats are the other two principal ferns of this community: *Davallia canariensis* and *Polypodium macaronesicum*. Both these species show ecological adaptations which parallel one another, differing chiefly in the ability of *Polypodium* to withstand greater shade and humidity, and *Davallia* somewhat greater exposure, but there is an extremely wide range of ecological overlap. Within the heath forests both occur widely, often originating in crevices or soil-filled pockets, their long scale-clad rhizomes rambling extensively over rock or moss-covered boulders, along the mossy forest floor, upon trunks of fallen trees, along exposed roots or along large branches of mature tree heaths, or over exposed rock faces and cliffs. Both plants remain evergreen in lightly shaded situations, but adapt readily to habitats which are summer-dry by abscissing fronds and persisting only as long, thick creeping scale-clad rhizomes during the dry summer months.

These three characteristic heath fern species show some variation in their frequency in different types of heath forest on different islands. In the particularly exposed barranco-ridge heath vegetation of La Palma, the rocks and soils over the steep terrain are frequently of poor stability. *Davallia* and *Polypodium* here are of very scattered occurrence and are usually confined to large trees or out-cropping hard rock shoulders. By contrast, *Asplenium onopteris* is particularly abundant in this vegetation. On Hierro, where there are a larger number of firm rocky outcrops, shallow dry ravines and solid fissured rock faces, *Davallia* and especially *Polypodium* are more abundant; both demand well-drained but firmly fixed edaphic situations and thrive best amongst mossy footings lightly shaded from full sun. With the removal of the forest cover, as has happened widely on Gran Canaria, *Davallia* and *Polypodium* often successfuly persist in the rocky habitats so-exposed, including those in areas which formerly bore laurel forest. With the further activities of man, these species also establish on firm substrates such as dry walls and the man-made retaining walls of earth terraces. Such situations, present sufficient local shelter and moisture between the stonework for the plant to establish, and an adjacent firm rocky substrate. The plants successfully survive even at considerably lower altitudes than they are normally found in the wild, their rhizomes emerging from between the stonework and spreading over the bare rock. *Asplenium onopteris* may also succeed in establishing deeply in amongst such stonework.

As in the laurel forest margins, *Selaginella denticulata* occurs frequently, spreading over soil banks and lightly shaded mossy boulders in the more sheltered parts of the heath forests. In many areas of the heath forests, *Pteridium aquilinum* (L.) Kuhn is widely spread, ascending to the very uppermost limits of summer cloud in the Canary Pine forests. Amongst shrubby *Erica* scattered fronds of *Pteridium* may reach over 4 metres in height. In undisturbed areas of forest it seldom dominates. In the lower pine forests, hower, *Pteridium* may become extensive after forest fires, where it dominates during the early stages of re-establishment of the forest. *Pteridium* may extensively invade the deep dry rocky solid of scree slopes, where it establishes well, its pioneering ability providing the habitat with stability and shade as it does in other parts of the world (Page 1976). Re-establishment from spores and rhizome fragments appears obvious only in such open habitats and sporelings of *Pteridium* can occassionally also be found establishing in the bare walls of dry caves down to 200 m. In the mature heath forests of the crest of Hierro, two ferns elsewhere more typical of laurel forest — *Anogramma leptophylla* and *Cystopteris diaphana* — here occupy unusual and ephemeral habitats. *Anogramma* is scattered widely and frequently through the upper parts of the heath forests along the crest of El Golfo. Here it may be locally abundant on summer-dry cliffs, frequent on earth banks and tree boles especially along winter watercourses, frequent around outcropping boulders and cave mouths, especially where lightly shaded, and is often accompanied in such habitats by succulent xerophytes of *Aeonium* and *Greenovia.* In these situations, plants are apparently dead by July, and re-establishment is presumably annual for the complete life-cycle of both generations. Its local abundance may perhaps be associated with the frequency of lightly-shaded vesicular lava outcrops and earth banks kept open by occasional heavy winter rains and long summer droughts. Doubtless, after such rain, the habitats may hold a sufficient reservior of water to ensure a rapid completion of the annual life cycle of these small, fast-growing ferns. *Cystopteris* is less frequent, but widely spread in sheltered shade pockets and summer-dry earth banks in the heath forests along the El Golfo crest of Hierro. Here it is perhaps also annual in summer-dry situations, becoming perennial only in a few rare more permanently damp localities. Again, openness of the habitat appears an important factor in determining its success. The local ecology of *Anogramma* and *Cystopteris* in such situations should be further investigated, and year-round observations are much needed.

Two more pteridophytes, confined to unusually damp habitats in the heath vegetation, are extremely local in their occurrence and confined to relatively high altitudes. Both are species of cool-temperate northerly (circum-boreal) distribution and in each case the Canary Islands form a southerly outpost. *Selaginella selaginoides* (L.) Link is known only from one deep, damp cool shaded fissure in the steep north-facing cliffside beneath the north face of the peak of Malpaso, c. 1250 m. 4170 ft) on Hierro (Page 1971). The other, *Blechnum spicant* (L.) Roth I have seen very locally but in large patches on a wet north-facing exposed cliff and bank, c 800 m (2890 ft) in N E Teneriffe, and is also present on north-facing roadside banks on El Cedro, Gomera (M. Gibby, pers. comm.).

FIGURE 6. *Cheilanthes maderensis* in a typical rock-fissure habitat, NE Gran Canaria, c. 700m.

Fern communities of outcropping rocks

The habitats of the abruptly outcropping rock faces which occur throughout the forests of all the islands frequently bear little resemblance to the forest floor habitats from which they arise. Most are more exposed to extremes of conditions than any of the forest environments and offer only relatively small rock crevices and fissures with little or no soil in which plants can establish. Most are dry for long summer periods, some may receive impinging cloud and at the other extreme some receive constantly dripping water from cliffsides above, providing very local exceptionally wet rock-face habitats. In contrast to the species of the forest floor, all the ferns of these rock habitats seem remarkably tolerant of exposure and intense light, and most also of long periods of drought at all stages. Experiments in culture suggest that even at the vunerable stage of prothalli carrying young sporophytes the species of these habitats are able to withstand total desiccation for many weeks with the majority recovering on receiving fresh water).

Such rock outcrops are extensive both above and below the cloud-zone forests, as well as within them. The species composition of the rock-fern communities varies with altitude being richest within the cloud-zone and progressively poorer with increasing distance both above and below it. In addition to *Polypodium* and *Davallia* which invade these habitats from the heath forests, the fern species more typical of outcropping rocks are plants of small size with summer-persistent fronds and many with various strongly xeromorphic adaptations (leathery frond texture, hairy or scaly coverings, in-rolling laminas, etc). They are able to thrive in pockets of soil (sometimes with mosses) in small rock fissures which may shelter their rhizomes from sun and from which often only their fronds emerge.

Confined to relatively low altitudes is the Canary Island representative of the *Asplenium aethiopicum* aggregate. This is a scarce plant of dry outcropping lava rocks within and below the lower forest margins. In summer the pinnae fold tightly each in a fan-like manner, substantially reducing the area of exposed surface. In cultivation, such plants fully re-open within hours of return of moisture, and presumably behave in the same manner in the wild. Confined also chiefly to low altitudes although on wet rock faces, is *Adiantum capillus-veneris.* This more desiccation-sensitive species is particularly frequent on La Palma on summer-wet dripping cliff faces, on rocks around springs and hanging from damp cave mouths and roofs, usually in lightly-shaded situations (the size of the plants diminishing with increasing shade), up to the lowermost limits of the forest at around 650 m (c. 2170 ft). Above this altitude it is ecologically replaced by *Cystopteris diaphana* (q.v.). It is also abundant as an adventive of damp calcareous places, especially of concrete irrigation channels, tunnels and reservoirs within its natural altitudinal range, usually in lightly-shaded permanently humid situations. In extremely exposed but normally wet situations, colonies adopt a low (2-5 cm high) cushion-like habit, and in this form can tolerate periods of drought.

Christella dentata (Forsk.) Brownsey & Jermy *(Cyclosorus dentatus* (Forsk.) Ching*)* is a rare low-altitude species of damp rocky banks beside streams, seen on only one occasion by me.

Adiantum reniforme L., is by contrast, a plant of usually dry rocky situations (although in cultivation thrives well under damper conditions provided the air is not stagnant and light is good). It occurs in scattered localities, occasionally in local abundance, on dry, porous well-drained cliffsides, mouths of dry caves and hanging from the undersides of dry rock ledges and sills (fig 8). It is present throughout the lower part of the cloud zone and in patches of more open forest, occasionally descending to lower levels than the forests in barrancos. It is absent above about 1100 m (c. 3700 ft). It is most usual in lightly-shaded to slightly exposed situations, and clearly intolerant of dense shade. The fronds are leathery, evergreen and persistent, often remaining erect when dead, the old fronds providing some shelter for emerging ones.

Asplenium aureum Cav. *(Ceterach aureum* (Cav.) von Buch*)* and *Notholaena marantae* L. (R.Br.) *(Cheilanthes marantae* (L.) Domin*)* share an essentially similar ecology to one another. Both occur sparsely and widely scattered in crevices and on ledges in dry lava cliffs from the lower margins of the forest upwards, but particularly towards the upper most limits of the cloud zone. Here each succeeds in lightly shaded, sheltered or partially exposed situations and each seems also able to invade areas of full sun. Both frequently grow together. In both there is a leathery upper surface to the frond and a thickly scale-clad lower surface, and in the dry summer months and the fronds become tightly inrolled, exposing in each only the scaly lower surface to the dry atmosphere. Like *Adiantum reniforme* the dead dry fronds of *Notholaena* remain erect. *Notholaena vellea* (Ait.) Desv. *(Cheilanthes catanensis* (Cos.) H.P. Fuchs*)* shares an essentially similar ecology, but is more frequent at lower altitudes and on the eastern islands of the Canaries. The lower surface of the frond is covered with a dense mass of woolly hairs and the fronds inroll tightly in summer.

Cheilanthes pulchella Bory, *Cheilanthes sventenii* Benl and *C. maderensis* Lowe (fig 6) are a trio of closely inter-related species (Vida et al 1970). They occur in shallow rock fissures throughout a particularly wide range of altitude, *C. maderensis* perhaps succeeding better at lower elevations and the others higher, but with a very wide range of overlap, although the different taxa are seldom together. Further field investigation of the ecology of these taxa is much required.

Of the remaining rock ferns, plants of the *Asplenium billottii* group are confined to scattered occurrences in lava rock at high altitude, apparently in areas directly receiving frequent cloud and moisture. These seem more common on the eastern islands and interesting possible allies of this species have been reported by Kunkel

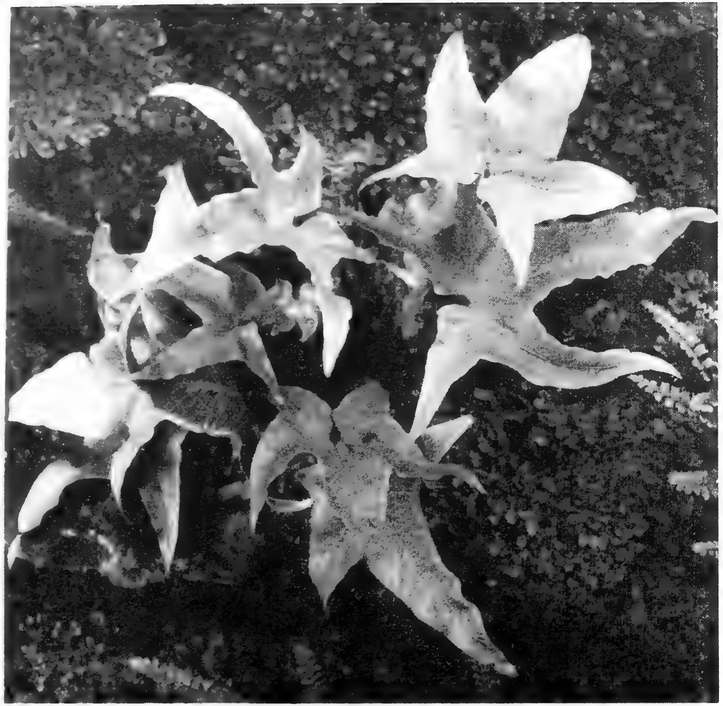

FIGURE 7. *Asplenium hemionitis,* 4 years old from spores. Cultivation shows it will re-establish freely on moist shaded rocks (Royal Botanic Garden, Edinburgh).

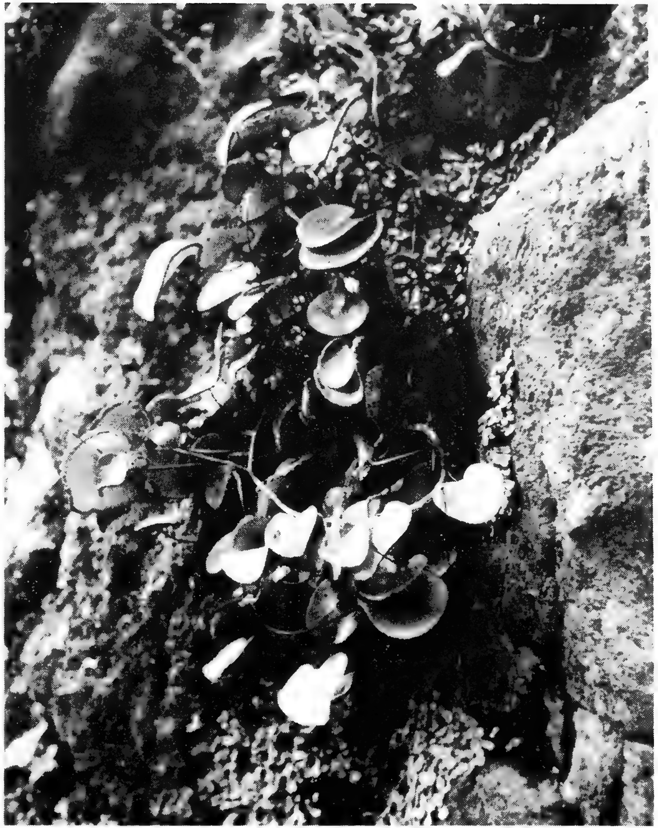

FIGURE 8. *Adiantum reniforme* in a typical habitat of cliffs emerging from the forest, N W Gran Canaria, c. 850 m.

(1966b, 1971) from Gran Canaria and their cytology and taxonomy should be further investigated. Elsewhere, *Asplenium septentrionale* (L.) Hoffm, is reportedly seen in similar habitats at high altitudes, but known only from La Palma and Teneriffe (Kunkel 1971).

CONCLUSIONS

With the exception of a very few other pteridophytes which are present exclusively in habitats distantly outside the cloud belt (e.g. *Asplenium marinum* L., *Equisetum ramosissimum* (Desf.) a very large proportion of the Canarian ferns and fern-allies have their principal ranges within the cloud belt of the islands, and a high percentage are confined to this region. Within the cloud belt the three distinctive types of fern communities described occur in close association with one another and together form an integral and significant part of the forest vegetation as a whole. The ferns are related to the whole forest community not only is their ecology but almost certainly also in their origin and history. For the history of many of the Canary Island flowering plants of the cloud zone vegetation, as well as the Canary pines (Page 1974) and ferns (Page 1973 and in press) is one which suggests them to be fragments of a more widespread flora and vegetation of the Tertiary Period, which have survived as insular relicts on the macaronesian archipelagos. Study of the fern component of this vegetation can give particularly exact evolutionary data of relevance of the community as a whole.

The Canarian mountains thus harbour unique plant communities of international significance and an irreplaceable genetic resource, and the fern habitats illustrate well some of the types of habitats which should be included in any forest conservation scheme. These show clearly that adequate samples of laurel forest, heath forest and rock outcrop are required to conserve a cross-section of species, ideally where each occurs near together, and preferably with comparable samples on the windward aspects of each of the different islands (as component species may vary between them). Study of the ecology of these unique forests and that of the ferns and other plants within them seem scarcely yet begun. It would thus be a particularly significant loss to science if adequate samples of the Canarian cloud-forest vegetation were not preserved in a permanently protected condition. Such conservation schemes must be urgently sought in the Canary Islands today, in the face of rapid commercial development.

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A NEW RECORD OF SYNCHYTRIUM ATHYRII ON ATHYRIUM FILIX-FEMINA

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ABSTRACT

The fungal fern parasite *Synchytrium athyrii* Lagerheim ap. Minden has been found for the first time in Central Europe (Vals-Valé, Grison, and Beatenberg, Berne, Swiss Alps) and its occurence could be also reported for Turkey (Soganli, prov. Trabzon). A description of the fungus and some morphological details are presented.

Fungal fern parasites belonging to the genus *Synchytrium* de Bary (Chytridiomycetes) are rare. Only two species are described so far: *Synchytrium athyrii* Lagerheim on *Athyrium filix-femina* (L.) Roth from Northern Norway and *Synchytrium phegopteridis* Juel on *Gymoncarpium dryopteris* (L.) Newman and *Thelypteris phegopteris* (L.) Slosson from Northern Norway and Sweden. We know only of a single collection of a *Synchytrium* from outside Scandinavia: from *Cystopteris fragilis* (L.) Bernh. found in British Columbia which — with some reservation — has been determined as *S. athyrii* (Karling 1956). In 1975 we collected *Synchytrium athyrii* on *Athyrium filix-femina* in the Swiss Alps (above Vals -Valé, Grison, near the road to Zervreila in a *Picea* forest, 1380 m.s.m., 24.8. and 10.9. 1975, coordinates 732450/163040, map Vals (1234), 1 : 25). *Athyrium filix-femina* was the dominant fern but only few plants were infected. The infected plants were covered with small, brown, erect resting-spore galls but did not seem to be much influenced in growth and fertility. Our specimen agrees in every respect with iso-type material distributed in "Vestergren; Micromycetes rariores selecti, n. 909 (1905)" from Trom district in Northern Norway. It represents the second collection on *Athyrium* and the third record if one includes the questionable find in *Cystopteris.*

Difficulties arise about the present citation of the fungus name (Karling 1964). G. Lagerheim, the collector of the Norwegian material, is indicated to be the author on the printed label. Unfortunately, Lagerheim omitted to describe the fungus and therefore *Synchytrium athyrii* remained a "nomen nudum" until v. Minden (1911) included it in his monograph on chytrids and gave a description. However he did not mention the missing description and assigned the fungus name to Lagerheim. Considering the retarded appearance of a valid publication the correct citation is *Synchytrium athyrii* Lagerheim ap. Minden (1911).

Our specimen offers a good opportunity to give some additional morphological information. The brown resting-spore galls, the only fructification observed so far, are scattered or grouped on both surfaces of the leaves, where they prefer the veins. They may also be found within the sori. Every gall originates in an epidermal cell. Infected host cells are induced to enlarge more than ten times in length and up to four times in width and are thus considerably raised above the surface of the leaf. The young galls are hyaline and thin-walled but gradually become brown and thick-walled and therefore flexible (fig. 1). A certain number of infected cells do not form galls, these are only slightly enlarged but their walls also become thick and brown.

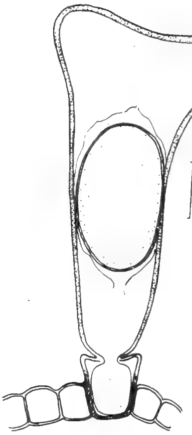

FIGURE 1. *Synchytrium athyrii.* Section of a young resting-spore gall with the included resting-spore.

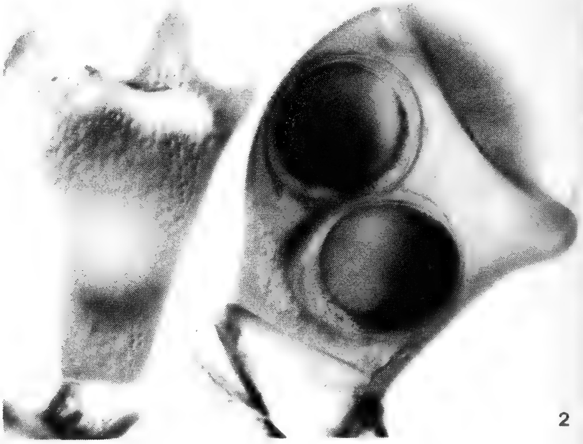

FIGURE 2. *Synchytrium athyrii.* Microphotographs of resting-spore galls. Left: surface with the light pits and the basal portion representing the original epidermal cell. Right: microscopic section: two thick-walled resting-spores are included. Magnification ca x 500.

The resting-spore galls are variable in shape and size. They often become wider at the apex and may also have small but distinct tubercules (fig. 2). They may reach a length up to 300 u and a width up to 180 u as indicated by Karling (1964). Of the 200 galls observed we found 155 with one, 40 with two, 4 with three and 1 with four resting-spores. The resting-spores are spherical, elliptical or somewhat irregular; they have a diameter of 45 - 75 u or are 60 - 100 u long and 50 - 70 u wide. Younger stages of resting-spores are hyaline, later they become gray brown; their walls are comparatively thick (6 - 8 u) and show two distinct layers (fig. 2).

Karling includes *Synchytrium athyrii* in the subgenus *Pyconochytrium* which is characterised by the absence of haploid summer sporangial sori. *Pycnochytrium* is the largest of seven subgenera of *Synchytrium* and therefore divided into two sections differing in the colouration of resting-spores. Karling (1964) believed *S. athyrii* to have hyaline resting-spores and put it in *Leucochytrium* Our observation shows that it is not a typical *Leucochytrium* as the resting-spores are gray-brown when they are mature.

Athyrium filix-femina is widely distributed over Eurasia, North Africa and America, and invaded Scandinavia after the last glaciation. New records for this fungal parasite are to be expected. We are lucky to report on two further records, both on *Athyrium filix-femina:*

Switzerland, Kt. Bern, south-western portion of the Wichelmooswald, above Waldegg, Beatenberg, 1290 m.s.m., 22.7.1976, coordinates 628730/172960, map Beatenberg (1208), 1:25000, leg. E. Urmi (Z, ZT).

Turkey, prov. Trabzon, N. slope of Soganli dag above Caykara, rocky igneous slope in Picea-Rhododendron shrub, 1700 m.s.m., 4.8.1957, coll. Davis and Hedge (K, sub D. 32195).

We hope that this note may enable pteridologists to recognise this parasite and contribute records of any further finds.

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FURTHER CYTOGENETIC STUDIES AND A REAPPRAISAL OF THE DIPLOID ANCESTRY IN THE DRYOPTERIS CARTHUSIANA COMPLEX

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ABSTRACT

The synthesis of two diploid hybrids, *D. assimilis x intermedia* and *D. assimilis x azorica,* is reported. New hybrids have also been synthesised between *D. azorica* and the tetraploid species *D. austriaca* and *D. carthusiana.* The analysis of chromosome pairing at meiosis in these hybrids, together with further investigation of meiosis in the wild hybrid *D. assimilis x carthusiana* from Finland, provide new insight into the diploid ancestry of the *D. carthusiana* complex. Three of the four diploid parental species are now recognised, namely *D. ludoviciana,* the *D. intermedia* aggregate and *D. assimilis.*

INTRODUCTION

The inter-relationships of species within the *Dryopteris carthusiana* complex were investigated (referred to as the *Dryopteris spinulosa* complex) by Walker (1955, 1961), following the study of chromosome pairing during meiosis in both wild and synthesised hybrids. Since then many other workers have studied the morphology, cytology and chemotaxonomy of representatives of the complex from wild specimens in different countries of the northern hemisphere (a selection of the most relevant papers from all those published are referred to later in the text).

Within the *D. carthusiana* complex in Europe there are three tetraploid species : *D. cristata* (L) A.Gray, *D. carthusiana* (Villars) H.P. Fuchs (=*D. spinulosa* (O.F.Muell.) Watt) and *D. austriaca* (Jacq.) Woynar (=*D. dilatata* (Hoffm.) A.Gray), *D. cristata* and *D. carthusiana* are found in Europe and also in North America. *D. austriaca,* however, was not considered present in N.America unless it be represented by the tetraploid species *D. campyloptera* (Kunze) Clarkson. This has recently been shown to be so following cytogenetic studies by Gibby (1977).

Evidence for the allopolyploid origin of *D. cristata* is provided by the hybrids *D. x boottii* (Tuckerm.) Underw. (=*D. cristata* x *intermedia* (Muhl.) A.Gray) and *D. x slossonae* (Hahne) Wherry (=*D. cristata* x *marginalis* (L) A.Gray). Both *D. intermedia* and *D. marginalis* are diploid species. These triploid hybrids show almost complete lack of chromosome pairing during meiosis indicating that the two genomes present in *D. cristata* are unrelated (Manton and Walker, 1953; Walker, 1955, 1959). *D. austriaca* was shown to be allopolyploid by the investigation of an induced apogamous sporophyte in this species (Manton and Walker, 1954), which exhibited complete lack of chromosome pairing of the 82 chromosomes present in meiosis and indicated lack of homology between the two genomes involved. Evidence suggesting that *D. carthusiana* is allopolyploid is obtained from three sources. Wagner and Wagner (1965) reported wild hybrids from Rochester area, New York, which they considered were most probably *D. carthusiana* x *celsa* (Palmer) Knowlton, Palmer and Pollard (referred to as *D. celsa* x *spinulosa).* Both of these species are tetraploid and investigation of meiosis in the putative hybrid showed mostly unpaired chromosomes (1-11 bivalents). Wagner (1971) also reported cytogenetic findings in the wild triploid hybrid from Michigan, identified as *D. marginalis* x *carthusiana* (referred to as *D. marginalis* x *spinulosa)* in which were seen from 0 - 8 bivalents and 123-107 univalents. Further evidence comes from the wild hybrid *Lastrea remota* sensu Moore* which was found to be tetraploid by Manton (1950) and given the putative parentage *D. carthusiana* x *filix-mas* (L.) Schott, both species being tetraploid. In a recent re-investigation by Fraser-Jenkins, Reichstein and Vida (personal communication, 1976) of an offset from the original hybrid from Windermere, Vida found only 8 or 9 bivalents in meiosis, the remainder of the 164 chromosomes present being unpaired. If the putative parentage for these hybrids is correct this evidence indicates *D. carthusiana* contains two unrelated genomes and is allopolyploid. Chemical results from chromatographic studies (Widén et al., 1976) on *Lastrea remota Moore,* under the name of *D. x brathaica* Fraser-Jenkins & Reichst., are in accordance with the parentage *D. carthusiana* x *filix-mas*.

Investigation of meiosis (Walker, 1955) in the tetraploid hybrids *D. x uliginosa* A.Br.exDoell (= *D. carthusiana* x *cristata*) and *D. x deweveri* (Jansen) Jansen & Wachter (=*D. austriaca* x *carthusiana*) indicated that *D. cristata, D. carthusiana* and *D. austriaca,* assuming them to be allotetraploids, are inter-related by common diploid ancestors. With this and additional cytogenetic evidence from wild and synthesised hybrids, Walker (1955) proposed that at least four ancestral diploids were required to account for the origin of the three allotetraploids as follows:

D. cristata: A + B
D. carthusiana: B + C
D. austriaca: C + D

where A, B, C and D represented ancestral diploid genomes, with B common to *D. cristata* and *D. carthusiana* and C common to *D. carthusiana* and *D. austriaca.*

D. ludoviciana (Kunze) Small, a diploid species with a restricted distribution in N. America, from Florida to N. Carolina, has been shown to be an ancestral parent of *D. cristata* (Walker, 1969). The synthesised triploid hybrid between the two species showed during meiosis 36-37 bivalents together with 51-49 univalents, indicating a common genome. Which genome, A or B, in *D. cristata* is represented by *D. ludoviciana* is however not certain. *D. ludoviciana* also represents an ancestral genome in the tetraploid species *D. celsa* (Walker, 1962) and an investigation of meiosis in the wild hybrids identified most probably as *D. carthusiana* x *celsa* (Wagner and Wagner, 1965) suggests that *D. ludoviciana* represents genome A (Walker, 1969).

Cytogenetic analysis of synthesised hybrids (Walker, 1955, 1961) indicated that each of the diploid species, *D. assimilis* S.Walker which is circumboreal in the northern hemisphere, *D. maderensis* Alston from Madeira and *D. intermedia* (Muhl.) A.Gray from N. America, represented the common genome C between *D. carthusiana* and *D. austriaca.*

The triploid hybrids gave a degree of chromosome pairing in meiosis ranging from 33-39 pairs together with 57-45 univalents. The similarities in frond and spore morphology of *D. maderensis* and *D. intermedia* suggested they were conspecific (Walker, 1961) but the differences in the same characteristics between these two species and *D. assimilis* were striking even though they apparently represented the same genome. Walker (1961) also reported two possible hybrids between *D. assimilis* and *D. maderensis* which exhibited normal meiotic pairing, but approximately 40% spore abortion. This report was however not regarded as conclusive for it was stated that more hybrids were necessary to establish these observations.

Chemical studies of *D. intermedia* and *D. maderensis* show them to contain practically the same range of phloroglucinols, this same spectrum being found also in the diploid *D. azorica* (Christ) Alston from the Azores (Widén & Britton, 1969; Widén et al., 1970; Widén et al., 1975). *D. assimilis* was found to have a variable

*non A.Br., and found to be tetraploid.

phloroglucinol spectrum, but it differs considerably from *D. intermedia, D. maderensis* and *D. azorica* (Widén & Britton, 1969; Widén & Sorsa, 1969; Widén et al., 1970).

Wagner and Hagenah (1962) reported a putative hybrid between *D. intermedia* and *"D. dilatata"* from Lake Superior. Both parental taxa are diploid and the hybrid exhibited 82 chromosomes unpaired, indicating no relationship between the parental genomes. The morphology of this *"D. dilatata"* is very similar to that of *D. campyloptera* and not unlike *D. assimilis.* The phloroglucinol content of the Lake Superior *"D. dilatata"* was found to be distinct from *D. assimilis* by Widén and Britton (1969) but this finding has been negated by their later work showing it to be a highly variable character in this taxon (Britton & Widén, 1974). They conclude that Lake Superior *"D. dilatata"* and *D. assimilis* are con-specific. Only once has a wild putative hybrid between *D. assimilis* and *D. carthusiana* been found. This hybrid (referred to as *D. assimilis* x *spinulosa* and morphologically and chemically in agreement with this) was from Nylandia, Espoo, Finland (Widén et al, 1967; Sorsa and Widén 1968) where the proposed parents are the only representative species of the *D. carthusiana* complex in or near that locality; *D. austriaca* is confined to the extreme south-west of Finland. The chromosome behaviour in the hybrid was reported to be "a varying number of univalents (60-70) and bivalents (15-20) and even a few multivalents (5-8) visible at diakinesis". Even allowing for possible chromosome stickiness, evident in the published photograph (Sorsa & Widén, 1968) the result was very different from that reported in the synthesised hybrid *D. assimilis* x *carthusiana* (Walker, 1955) which had 38 bivalents and 47 univalents.

Because of the conflicting evidence available it became essential to re-investigate the relationship of *D. assimilis* with *D. intermedia, D. maderensis* and with *D. carthusiana.* A programme of experimental hybridisation was initiated in 1971 and the results are now presented.

MATERIALS AND METHODS

The material used in the hybridisation experiments was collected by several people, and is listed below. Voucher specimens are deposited at the British Museum (Natural History), London.

D. assimilis S. Walker (2*x*)

Plant collected by T.M.C. Taylor, Vancouver [Island], Canada, 1953.

D. austriaca (Jacq.) Woynar (4*x*)

Plant collected by A.C. Jermy, No. 9399, Ramscombe, Somerset, 1971.

D. carthusiana (Villars) H.P. Fuchs (4*x*)

Herbarium material with spores collected by J.D. Lovis, Brathay, Ambleside, Cumbria, 1971.

Plant collected by A.C. Jermy, No. 8425, Aros Park, Isle of Mull, 1970.

D. azorica (Christ) Alston (2*x*)

Spores collected by T. Reichstein, No. 3503, Azores 1972.

D. intermedia (Muhl.) A. Gray (2*x*)

Plant collected by A.C. Jermy, No. 8412, Ithaca, New York State, 1970.

D. maderensis Alston (2*x*)

Spores collected by C.R. Fraser-Jenkins from a plant from Madeira in cultivation at University of Leicester Botanic Garden.

D. assimilis x carthusiana (3x)

Fixings of sporangia from an offset, No. TR 3380, of the wild putative hybrid from Nylandia, Finland, were sent to Liverpool by T. Reichstein for analysis. (We are particularly grateful for this plant being made available for investigation by Drs J. Sarvela and C.J. Widén, who gave an offset of this unique hybrid to Professor T. Reichstein for his own cultivation).

Hybridisations were carried out at the University of Liverpool Botanic Gardens, using the technique described in detail by Lovis (1968). Cytological preparations from sporangia were made according to the method of Manton (1950) and slides were made permanent by the freezing method (Conger & Fairchild, 1953).

RESULTS

Of the species involved in the hybridisation programme *D. assimilis, D.azorica, D. intermedia* and *D. maderensis* are diploids with a regular meiosis showing 41 bivalents, and *D. austriaca* and *D. carthusiana* are tetraploids, having 82 bivalents at meiosis. The hybrids synthesised successfully are listed in Table 1 together with an analysis of pairing behaviour at meiosis (See also Figs 1 & 2). The meiotic behaviour of the wild putative hybrid TR 3380, *D. assimilis* x *carthusiana,* is also included. Attempts to synthesise this hybrid were unsuccessful in either direction. In all, 81 attempts were made using 447 prothalli but no hybrids were obtained.

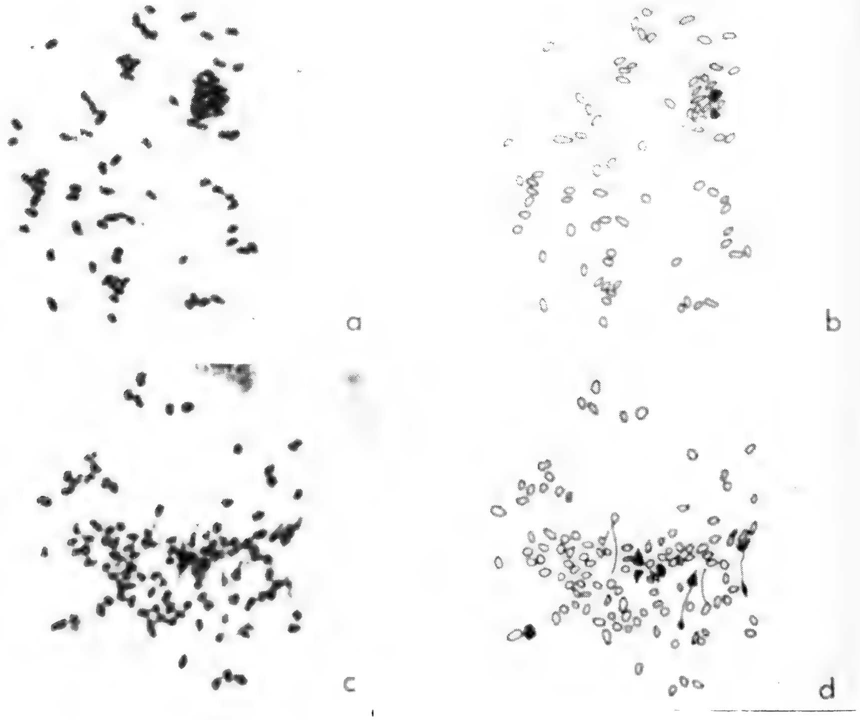

FIGURE 1. Meiosis in hybrids. Magnification x 1000. a. *D. intermedia x assimilis.* b. Explanatory diagram of 1a showing 2 bivalents (in black) and 78 univalents (outlined). c. *D. assimilis x carthusiana* TR 3380. d. Explanatory diagram of 1c showing 6 bivalents and 111 univalents.

TABLE 1: Chromosome pairing in hybrid *Dryopteris*

Synthetic Hybrids			Prothalli	Selfs	Hybrids	Ploidy of hybrid	Meiotic pairing behaviour in hybrid
♀		♂					
D.intermedia	x	assimilis	95	5	2	2*x*	1 – 6 bivalents 80 – 70 univalents
D.azorica	x	assimilis	26	1	1	2*x*	2 – 4 bivalents 78 – 74 univalents
D.azorica	x	austriaca	4	2	2	3*x*	40 – 41 bivalents 43 – 41 univalents
D.azorica	x	carthusiana	33	3	3	3*x*	39 – 41 bivalents 45 – 41 univalents
D.carthusiana	x	azorica	39	20	6	3*x*	38 – 41 bivalents 47 – 41 univalents
D.intermedia	x	carthusiana	10	3	2	3*x*	36 – 37 bivalents 51 – 49 univalents
D.carthusiana	x	maderensis	32	5	13	3*x*	34 – 40 bivalents 55 – 43 univalents
Wild Hybrid : D. assimilis x carthusiana (TR 3380)					1	3*x*	0 – 8 bivalents 123 – 107 univalents

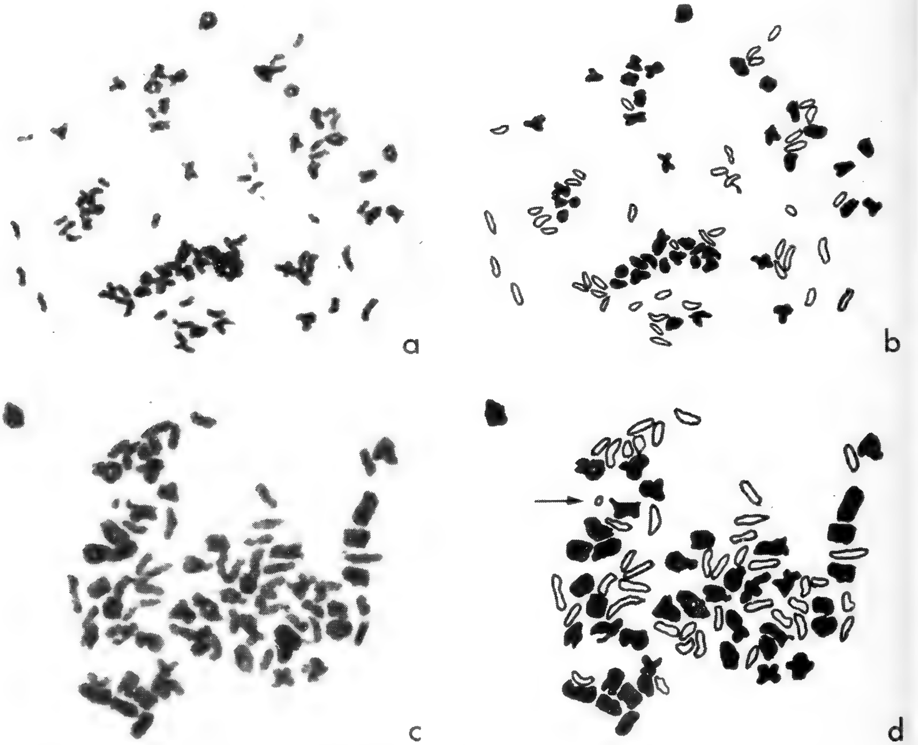

FIGURE 2. Meiosis in hybrids. Magnification x 1000. a. *D. carthusiana* x *azorica.* b. Explanatory diagram of 2a showing 40 bivalents and 43 univalents. c. *D. azorica x austriaca.* d. Explanatory diagram of 2c showing 41 bivalents and 41 univalents plus one chromosome fragment arrowed.

DISCUSSION

The low degree of chromosome pairing seen at meiosis in the synthesised hybrids *D. assimilis* x *intermedia* (See Table 1 and Figs. 1a & b) indicates a lack of homology in the genomes involved. As *D. intermedia* and *D. maderensis* have been shown to have a common genome (Walker, 1961), then the above finding is different from that in the two plants reported by Walker (1961) as possible hybrids between *D. assimilis* and *D. maderensis.* Our present results therefore indicate that the meiotic chromosome pairing between *D. assimilis* and *D. intermedia* is minimal, and that the two plants tentatively reported by Walker (1961) were not hybrids between *D. assimilis* and *D. maderensis.*

They also indicate that *D. assimilis* and *D. intermedia* are not descendants from a common ancestral genome. These results agree with the wild hybrid reported as a *"D. dilatata* x *intermedia"* from Lake Superior (Wagner and Hagenah, 1962). They also support the evidence of different phloroglucinol spectra in the two species (Widén & Britton, 1969; Widén & Sorsa, 1969; Widén et al., 1970).

The synthesised diploid hybrid *D. assimilis* x *azorica* again shows very little association of the chromosomes at meiosis (see Table 1). Clearly *D. assimilis* and *D. azorica* are not conspecific. In its hybrids with *D. austriaca* and *D. carthusiana* (see Table 1 and Fig 2) *D. azorica* shows approximately 41 bivalents and 41 univalents at meiosis. In all the hybrids synthesised involving *D. azorica,* it behaves in the same way chromosomally as *D. intermedia* and *D. maderensis* (Walker, 1955; 1961 and see Table

1); this finding, together with the similarities in morphology and chemistry of all three species, would suggest that they have all arisen from a common ancestral genome. For the sake of brevity they will be referred to below as the *D. intermedia* aggregate.

The allotetraploid nature of *D. austriaca* has been established conclusively (Manton and Walker, 1954); bivalents seen in the triploid hybrids involving this tetraploid with species of the *D. intermedia* aggregate can be interpreted as being allosyndetic. Thus all three species of the *Dryopteris intermedia* aggregate represent one of the parental species of *Dryopteris austriaca*. Since both wild and synthesised triploid hybrids between *D. austriaca* and *D. assimilis* show about equal numbers of bivalents and univalents in meiosis (Walker, 1955), *D. assimilis* also represents a parent of *D. austriaca. D. assimilis* has now been shown to be unrelated to the *D. intermedia* aggregate and hence the evidence suggests that *D. austriaca* has arisen by chromosome doubling in a hybrid between *D. assimilis* and a species of the *D. intermedia* aggregate. Morphological comparison of the synthesised diploid hybrids *(D. assimilis* x *intermedia* and *D. assimilis* x *azorica)* shows them to be similar to *D. austriaca* in frond shape, pinnation and toothing (see Fig 3). The scales at the base of the stipe in the hybrids have the dark line which is diagnostic for *D. austriaca.* Attempts to resynthesise *D. austriaca* from the diploid hybrids have been made by sowing sporangial material. Diploid *Asplenium* hybrids give rise to tetraploid progeny by the production of abundant diplospores; these germinate to give prothalli with the unreduced chromosome number and subsequent self fertilisation results in germination of tetraploid sporophytes (Lovis and Reichstein, 1968). However, examination of the sporangial contents of *D. assimilis* x *intermedia* and *D. assimilis* x *azorica* reveals mostly debris, with few spores, and any germination seems unlikely.

The evidence for an allopolyploid origin of *D. carthusiana* stems from wild hybrids whose parentage can only be surmised (see earlier), but this evidence is now strong following the recent work on *D. x brathaica* (Widén et al., 1976; Fraser-Jenkins, Reichstein & Vida, 1976, personal communication) and the additional information derived from the triploid hybrid *D. assimilis* x *carthusiana* from Finland which shows very few (0-8) bivalents present at meiosis (See Fig 1c & d). The report of multivalents and bivalents in this hybrid by Sorsa and Widén (1968) appears to have been in error, and the result of chromosome "stickiness". In both wild and synthesised triploid hybrids involving *D. carthusiana* and the *D. intermedia* aggregate approximately 41 bivalents and 41 univalents are seen at meiosis (see Table 1). Assuming *D. carthusiana* to be allotetraploid, this is interpreted as allosyndetic pairing, with the *D. intermedia* aggregate representing one of its parents.

Walker's report (1955) of about equal numbers of bivalents and univalents at meiosis in synthesised *D. assimilis* x *carthusiana* does not agree with the results from the wild putative hybrid of this cross from Finland. Although synthesised hybrids are usually taken to be more reliable than wild hybrids whose parentage can be derived only by comparative morphological studies, it seems that the hybrid plants synthesised as *D. assimilis* x *carthusiana* by Walker (1955) were in fact not of this parentage and *D. assimilis* is not related to *D. carthusiana.* Examination of herbarium material of the hybrids synthesised in 1955 shows that the plants could also have been *D. assimilis* x *austriaca* (This could be accounted for by possible contamination of either the *D. carthusiana* spore collection or the pot-grown prothalli, at the time of sowing, by spores from *D. austriaca*). Repeated attempts to resynthesise the hybrid *D. assimilis* x *carthusiana* have been as yet unsuccessful. Probably one reason for this difficulty and for the rarity of the wild hybrid, even where both parents are found, is that the two species are unrelated.

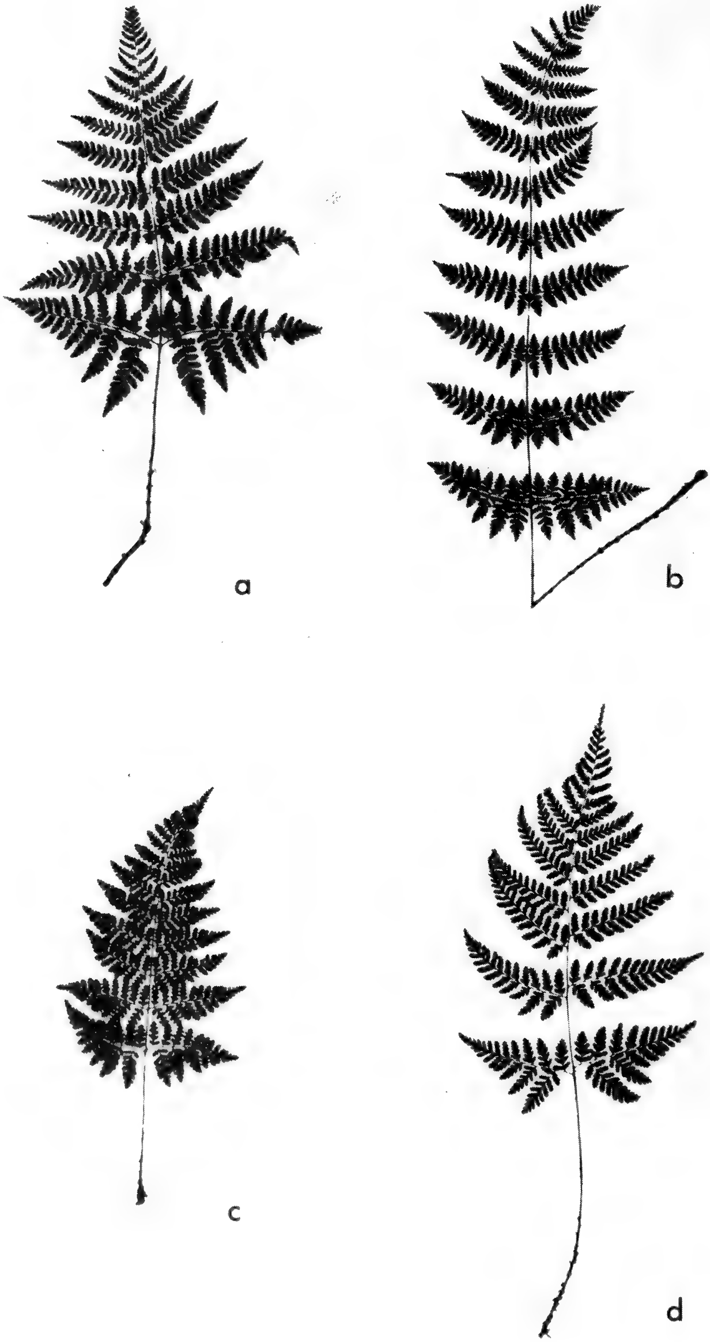

FIGURE 3. Silhouettes of fronds, 1/4 natural size, all from cultivation at Liverpool a. *D. assimilis,* Vancouver. b. *D. intermedia.* c. *D. intermedia x assimilis.* d. *D. austriaca.*

Our findings now indicate that three of the original four ancestral diploids postulated by Walker (1955) for the origin of *D. cristata* (A + B), *D. carthusiana* (B + C) and *D. austriaca* (C + D) are known. *D. ludoviciana* represents either genome A or B, the latter being common to both *D. cristata* and *D. carthusiana.* Evidence (Walker, 1969) is in favour of it being genome A but this is by no means conclusive and relevant experimental hybridisation is in progress. The *D. intermedia* aggregate represents genome C, that common to both *D. carthusiana* and *D. austriaca. D. assimilis* represents genome D. (See Fig 4).

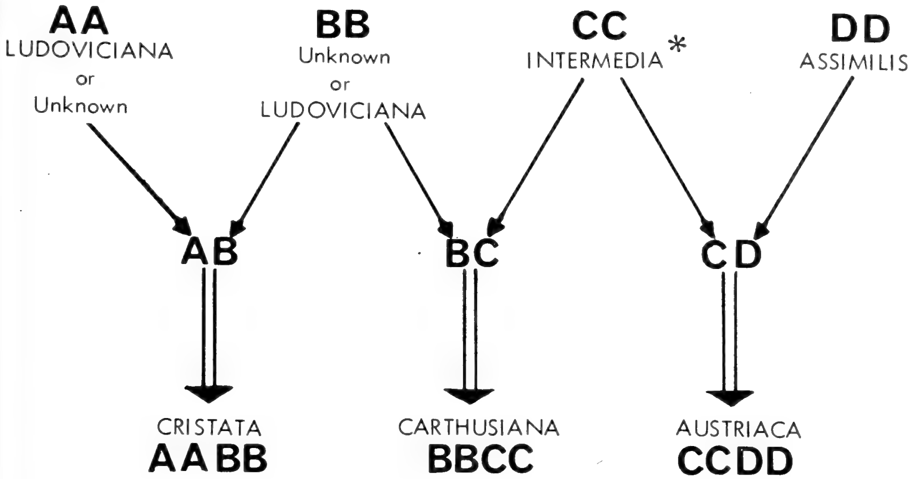

FIGURE 4. Evolutionary relationships within *D. carthusiana* complex, indicating the allopolyplord origin of the three tetraploid species (see text). *Represents the species aggregate including *D. intermedia, D. maderensis* and *D. azorica.*

Acknowledgements

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CYTOLOGY AND REPRODUCTION OF CHEILANTHES FARINOSA FROM YEMEN

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ABSTRACT

Cheilanthes farinosa is a well known species complex. The type of *Pteris farinosa* Forsk. originated from Yemen. It is shown that the Yemen material is triploid and apogamous, and differs both morphologically and cytologically from the so-called *C. farinosa* from India, which is diploid and sexual.

INTRODUCTION

Of all the Indian species of *Cheilanthes* which are farinose on the undersurface, *C. farinosa* (sensu Beddome, 1883) is the most common and it is also the least understood taxonomically. Balnford (1886) analysed the 'Silver Ferns', as they are called owing to farina, from Simla hills (western Himalayas), and segregated three species in the *C. farinosa* group. He identified the very common fern of the foot-hills as *C. farinosa* (Forsk.) Kaulf., and the two others were named by him as *C. anceps* Blanford and *C. grisea* Blanford. The three species are easily distinguishable following Blanford (1886), although both *C. farinosa* and *C. anceps* are polymorphic. Subsequent workers on Indian ferns till recently followed Blanford in naming the common farinose species of lower altitudes (fig. 1) as *C. farinosa* (Forsk.) Kaulf. (see Verma and Khullar, 1965; Mehra and Dhir, 1969). Throughout the Himalayas, this species is sexual diploid (n=29 and n=30, the latter cytotype far more common, Verma and Khullar, 1965; Verma, unpublished). Manton, Roy and Jarrett (1966) confirmed that the so-called *C. farinosa* from northern India was diploid (Dehra Dun form, n=30), and pointed out that it was unlike *C. farinosa* from Africa both in morphology and cytology. The African form from Kenya and Eritrea was triploid and apogamous, and it matched the type of *Pteris farinosa* Forsk. (=*C. farinosa*) from Yemen (Fl. Aeg.- Arab.:187, 1775). They concluded that the African triploid was *C. farinosa, sensu stricto,* and that the Indian diploid was without a name, owing to its earlier confusion with *C. farinosa* (Forsk.) Kaulf.

Since the type of *C. farinosa* was described from Yemen, it was, therefore, desirable to study the material originating from Yemen before a new name was introduced for the Indian *C. farinosa.* The observations on the cytology and reproduction of one collection from Yemen are reported here, and emphasise the conclusion that the Indian diploid is a distinct, as yet un-named, species.

MATERIAL AND METHOD

Ripe spores of *C. farinosa* from Yemen were obtained (14-9-1973) from J.R.I. Woods's specimen No. 72/127, dated 11-10-1972 (BM) collected from a damp crevice of a rock hill on the Wadi side (loc. Wadi Banna, above Saddah, c. 8500 ft. alt., fig. 2). The spores were sown in November 1973, at Chandigarh, on Parker and Thompson's nutrient solution (for composition, see Klekowski, 1969). Chromosome counts were made from aceto-lacmoid squashes of filamentous prothalli, pretreated with 0.004 M aq. 8-hydroxyquinoline for six hours and fixed in 1:3 acetic alcohol. The fixed material was heated in 9:1 mixture of lacmoid — N-HC1 and squashed in 1 per cent. aceto-lacmoid.

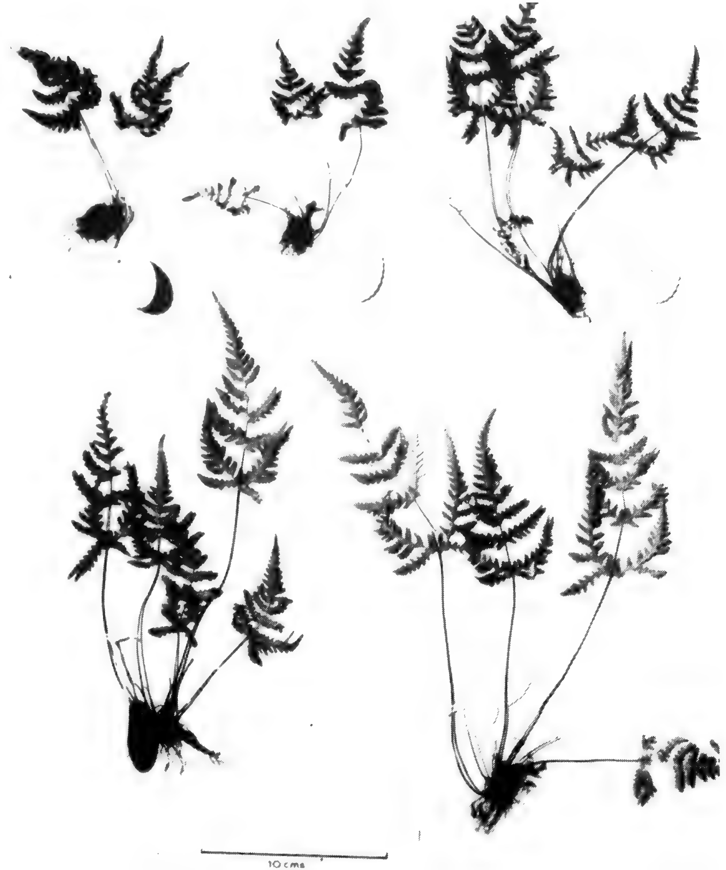

FIGURE 1. Some variants of the Common Indian diploid (n=30), identified as *C. farinosa,* following Blanford (1886).

FIGURE 2. Specimen of *C. farinosa* from Yemen (J.R.I. Wood No. 72/127, British Museum, source of spores).

OBSERVATIONS AND COMMENTS

Two medium-density cultures were raised on sterilized Parker and Thompson's nutrient solution in petri dishes of six inches diameter, kept against south-facing glass window under diurnal conditions of temperature and day length. In both the cultures germination was fast, and bilobed prothalli appeared by the 50th day from sowing. On examination it was found that only about 33 per cent. of the spores had actually germinated (table 1). This is not surprising, for spores one year old from a species which might be expected to produce some abortive spores (see below).

Table 1

Data on Gametophyte Cultures of *C. farinosa* from Yemen 65 days from sowing

Item	Culture 1	Culture 2	Per cent. (of total)
Total spores	c. 300	c. 300	
Gametophytes recovered	94	106	33.3
Mature gametophytes (bilobed)	49	44	15.5
Gametophytes bearing apogamous sporophytes	16	15	5.2

Complete data were scored on the 65th day from sowing. Approximately 45 per cent. of the germinated spores had reached maturity as judged from the characteristic bilobed structure of prothalli, and practically one-third of the bilobed prothalli, which were larger, had produced by the 65th day baby sporphytes apogamously on the lower surface behind the notch meristem (fig. 3a-c, table 1). By the 80th day from sowing, all the bilobed prothalli bore apogamous sporophytes, and hence reproduction was entirely apogamous.

The Bilobed prothalli completely lacked both archegonia and antheridia, and even the filamentous prothalli lacked antheridia. This is unusual amongst apogamous ferns, which generally produce functional antheridia. The possibility of cultural conditions affecting antheridial production needs to be verified. It should be noted that the African triploid apogamous plant, considered as *C. farinosa* s.s., also lacked archegonia on the gametophyte, but antheridia were present as evidenced by the recovery of few hybrids with the African sexual tetraploid from Victoria Falls (Manton, Roy and Jarrett, 1966).

Aceto-lacmoid squashes of prothallial cells revealed 90 chromosomes (fig. 4), showing that the Yemen material is triploid (x=30) like the African samples which matched the type of *C. farinosa* from Yemen (see Manton, Roy and Jarrett, 1966).

In comparison, *C. farinosa* from northern India is sexual and diploid, the gametophytes become larger and typically cordate (see Verma and Kapur, 1972). It is, therefore, to be concluded that all *C. farinosa* from the type locality (Yemen) is probably also triploid and apogamous. The specimen of *C. farinosa* from Yemen (Wood No. 127, fig. 2) nearly resembles the description provided by Manton, Roy and Jarrett (1966) for the African triploid, expecting the spores, which are not smooth but are finely granulate-reticulated. As well as the extreme variability in form, the Indian diploid differs consistently from the Yemen triploid in at least four features, namely (1)

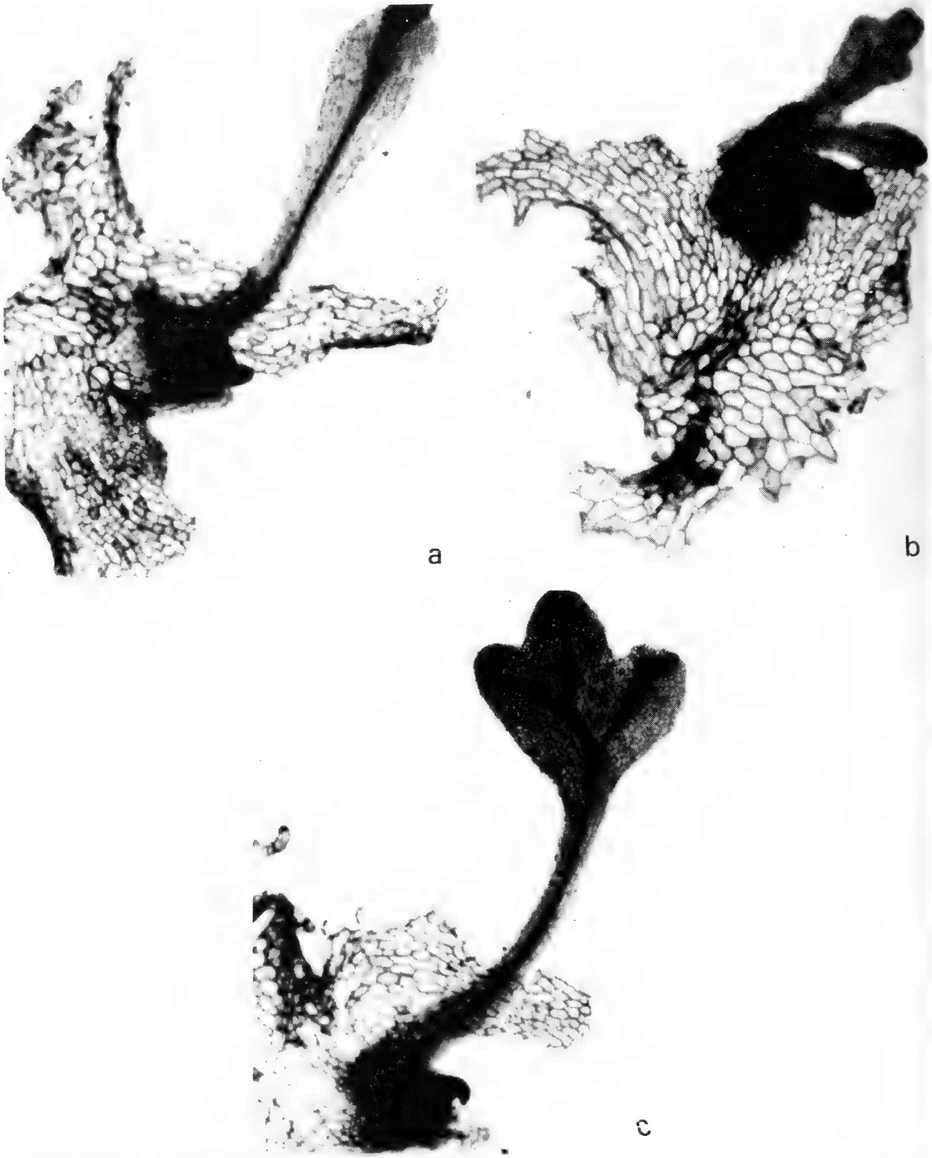

FIGURE 3a-c. Bilobed gametophytes of *C. farinosa* (Yemen) bearing apogamous baby sporophytes, x 10. Note the absence of archegonia and antheridia. The characteristic central cushion of sexual species is missing.

lanceolate-pentagonal or deltoidly-lanceolate lamina, generally distinctly shorter than the stipe, (2) lowermost pinnae are the longest, usually ascending, and with the proximal basiscopic pinnule strongly developed and divergent, (3) nearly bicolourous scales, limited to rhizome and base of stipe, and (4) spores with bold flap-like ridges.

The Indian material considered thus far under *C. farinosa* is then without a name. The nomenclature will be proposed after analysing the range of variability in the species from India, particularly the Himalayas.

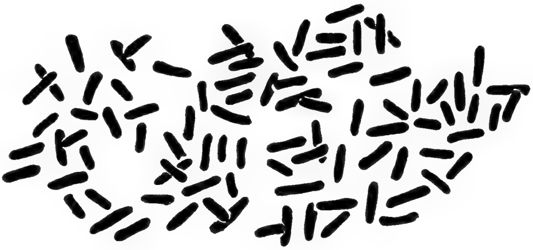

FIGURE 4. Drawing of mitosis in a prothallial cell showing 90 chromosomes, x 1500.

ACKNOWLEDGEMENTS

I am grateful to the British Council and the Commonwealth Universities Association for the award of Academic Staff Fellowship which enabled me to visit U.K. for one year (1972-1973). I have to thank Mr. Parvesh Kumar Dewan for helping in raising of cultures and in getting the photographs. Grateful thanks are due to Prof. P.N. Mehra, head of the department, for facilities and encouragement. I thank A. Clive Jermy of the British Museum for the photograph of the Yemen specimen, and for permission to obtain spores from the herbarium specimen quoted.

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REVIEW

CYTOTAXONOMICAL ATLAS OF THE PTERIDOPHYTA by A. Löve, D. Löve and R.E.G. Pichi Sermolli, 1977. J. Cramer. 23 x 15cm, 398 + xviiipp. Subs. Price 120 DM (about £29.75), Regular 150 DM (about £37.20).

The explosive growth of fern cytology since 1950 made the appearance of the accurate Tavole Chromosomiche delle Pteridophyta of Chiarugi in 1960, followed by Fabbri's two Supplements in 1963 and 1965, most welcome events. The chromosome numbers (often published in rather obscure journals) have continued to increase apace and another compilation was overdue. This has now materialized in the Cytotaxonomical Atlas of the Pteridophyta which purports to list the chromosome numbers, using the correct nomenclature irrespective of the names used by the original cytological authors. The numerous, some may feel excessive, number of genera are arranged in accordance with a new classification which it is stated will be published in Webbia and the new names and combinations validated in Taxon.

Despite the fact that most authors quote the majority of fern chromosome numbers as the gametophytic (n or "n") number, in the Atlas they are all converted to the sporophytic number (2n). Since an appreciable proportion of ferns are apomicts and have the same chromosome number in both phases of the life cycle such a conversion inevitably simply will not be true in those cases where apomixis has not been detected and is a totally unjustified practice despite the reasons advanced by the authors for this course of action. Furthermore there is no attempt to distinguish between sexual and apomictic taxa — a most valuable piece of information from a taxonomic viewpoint.

Under the generic headings supposed basic chromosome numbers are quoted, which in the majority of cases appear to be founded on simple and arbitrary arithmetic division and results in such absurdities as *Ophioglossum* with its chromosomes numbered by the hundreds being quoted as x = 15(45). *Equisetum* which has an unvarying n = 108 or 2n = 216 is assigned a basic number of 9 — why 9 in preference to one of the many other factors of 108 is not clear. In *Lygodium* where monoploid numbers of 28, 29 and 30 exist, this genus is given the base numbers 7, 8, 15 and 29! In yet other cases it appears that the choice of a base number has been capricious with little regard being paid to the evidence available e.g. 29 is the only base number quoted for *Hypolepis* despite the fact that only *H.nigrescens* has been reported as having n = 29 whilst the other 6 species quoted all have chromosome numbers which are multiples of 26 (or 52). In *Woodsia* with base numbers of 38, 39 and 41 recorded in the literature these are given as "x = 39, 41?" Under *W.ilvensis* is "2n = 78" although only one record of this number is noted, the other 8 records for this species being given as 2n = 82. Similarly, *W.polystichoides* is headed "2n = 78?" despite all four independent counts being quoted as exactly 2n = 82!

In many cases where an author has not been able to determine a precise number but has given the maximum and minimum numbers possible these are not quoted directly but transmuted to a single figure preceded by c. (circa). This sometimes results in quite unwarranted assumptions e.g. in Jermy, Jones and Colden on p.150 of J.Linn.Soc.(Bot.) vol. 60, 1967, the original entry for *Selaginella stenophylla* is 2n = 50-60 and the authors have deliberately not given a base number because of uncertainty. This count appears in the Atlas as "2n = 48?" and the actual count given as "c.50".

In any large compilation a few errors are almost unavoidable but the scale of them in this book is inexcusable. In a check on a more or less random sample of five papers by different authors from various countries and quoted in the Atlas out of a total of approximately 750 eligible entries there were over 90 errors or ommissions. This, together with the quoting of all numbers at the 2n level means that not a single entry can be taken for granted without checking against the original paper and consequently the practical value of the work is entirely lost. When this is also combined with the capricious assignment of base numbers with all their implications for phylogeny it makes the Atlas full of pitfalls for the unwary. In brief, the publication of this book has done a great disservice to the whole subject of fern cytology and is likely to lead to a proliferation of errors. The very high price, however, may help to place it beyond the means of most students.

T.G. WALKER

LUNATHYRIUM IN THE AZORES; A POSTSCRIPT

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ABSTRACT

Three sheets from Copenhagen Museum of the gathering by C.W. Petersen from Canton on which Kunze based his *Asplenium petersenii* have been compared with Kunze's isotype of *Diplazium lasiopteris* in Herb. BM. These are considered to be taxonomically inseparable. The correct name for the Azores *Lunathyrium* and for all gatherings previously called *D. lasiopteris* therefore becomes *Lunathyrium petersenii* (Kunze) H. Ohba.

In my paper on *Lunathyrium* in the Azores (Sledge 1975) I gave reasons for regarding *Diplazium allorgei* Tard.-Bl. as an introduced species which had been correctly identified by Christ as *Diplazium lasiopteris* when first he recorded it for these islands. None of the claims made for it during its subsequent history when it was successively created a distinct species and then credited with a possible South American origin and later with endemic status, would bear close scrutiny and I advocated a return to Christ's original identification at the species level. Modern views on generic boundaries require its transference either to *Lunathyrium* or *Athyriopsis* according to the authority followed. The choice of a specific epithet was difficult since no authentic specimens of *Asplenium japonicum* Thunb. or *A. petersenii* Kunze could be traced for comparison with the Azores fern and only one frond of authentic *Diplazium lasiopteris* Kunze is known to exist.

For the reasons given in my paper it was concluded that *Lunathyrium lasiopteris** was the correct name for the Azores fern which it is virtually certain was originally introduced from eastern or south-eastern Asia and has become widespread since its introduction.

Some weeks after the publication of my paper I received a letter from Mr Alfred Hansen of the Copenhagen Museum stating that there were three sheets of the original gathering on which Kunze had based his *Asplenium petersenii,* in their collections. One of the Copenhagen sheets, here designated as lectotype (see fig 1,3), bears the signature C.W. Petersen and the locality and date — Canton, 1827 — written by him on the reverse side of the sheet. The second sheet, bearing a single fertile frond 34 cm long, also bears the identifications and other data on the reverse side whilst the third sheet with a single small frond 12 cm long carries the locality "Ad Canton, China" but no collector's name. This sheet has been identified by Mettenius *"Asplenium lasiopteris* Kze. (sub Dipl.)." The other two sheets have also been named *Aspl. lasiopteris* (Kze.) Mett., the identifications being in the handwriting of H.Kjaerskou (Curator, Copenhagen Museum 1883-1900). No doubt the fact that none of these sheets carries the name *Asplenium petersenii* and much of the information, including Petersen's signature, is written on the backs of the sheets, accounts for the reply I had earlier received that no isotypes of Kunze's species could be found in the Copenhagen herbarium.

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* This combination was made by Nakaike in *Enum.Pterid.Jap.:* 175, March 1975, the publication date preceding by a few weeks my own publication of the same combination. As used by Nakaike however the name refers to a fern quite different from Kunze's species, for he copies Serizawa's (1973) synonymy under *L.dimorphophyllum* where *D.lasiopteris* was mistakenly listed, though ***with a query,*** as a possible synonym. Nakaike, ignoring the query, adopts Kunze's basionym as the "corrected" name for the Japanese *L.dimorphophyllum.*

There can be no doubt that these specimens represent part of the original collection, some of which was sent to Kunze who described his new species *Asplenium petersenii* from them, for this was said to have come "Ex insula prope Canton...... retulit C.W.Petersen, Danus". Kunze states that he received his material from Lehmann and I am informed by Mr Hansen that the Director of the Copenhagen Museum at that time was Prof. J.W.Hornemann and that he and Prof. J.G.C.Lehmann of Hamburg knew each other very well and doubtless exchanged specimens. It would seem (*fide* Hansen *in litt.*) that C.W.Petersen was probably a sailor, perhaps with natural history interests and acquainted, if not with the Director, then with some other employee at the Copenhagen Museum to which he gave these and some other specimens collected in the proximity of ports likely to be visited on trading voyages to the Far East.

Petersen's Canton specimens are clothed with chaffy scales and copious multicellular hairs on the stipe and rhachis (fig 3). The lamina is hairy above and below and the margins of the indusia are fimbriate. In these characters they agree with Kunze's description and also come very much closer to Indian specimens of *D.lasiopteris* than to specimens which Japanese botanists construe as *L.japonicum sensu stricto.* Having compared Petersen's specimens with Kunze's specimen of *D.lasiopteris* (fig 2,4) in Herb. BM. and with sheets of John Smith's *D.decussatum* which Kunze stated was identical with his *D.lasiopteris,* I have no doubt that *A.petersenii* and *D.lasiopteris* are forms of the same species; they are indeed so closely similar that a separation even at varietal rank would scarcely be practicable.

The correct name and synonymy for the Azores fern and for all gatherings previously called *D.lasiopteris* therefore becomes:—

Lunathyrium petersenii (Kunze) H. Ohba in Sci.Rep.Yokosuka City Mus. 11 : 53 (1965).
Asplenium petersenii Kunze, Anal.Pterid. : 24 (1837). Type from Canton.
Diplazium lasiopteris Kunze, Linnaea 17 : 568 (1843) — Bedd., Ferns S. Ind.: 53, t.160 (1864). Type from Berlin Bot.Gard. ex Birmingham. Later cited from Nilgiri Hills.
Allantodia deflexa Kunze, Bot.Zeit.: 191 (1848). Type from Java.
Diplazium decussatum J.Sm. (Bot.Mag. 72 Comp.28 (1846) *nom.nud.*) ex Moore & Houlst., Gard.Mag.Bot.3 : 231 (1851). Type from Nepal.
Asplenium lasiopteris (Kunze) Mett., Fil.Hort.Bot.Lips. : 78 (1856).
Asplenium deflexum (Kunze) Moore, Index Fil. : 43, 123 (1859).
Asplenium thwaitesii A.Braun ex Mett. in Abhandl.Senckenb.Naturforsch. Ges.3 : 227 (1859) — Hook., Sp.Fil.3 : 250 (1860) — Hook. & Bak., Synops.Fil. : 235 (1867). Type from Ceylon.
Diplazium thwaitesii (A.Braun ex Mett.) Klotzsch ex Moore, Index Fil. : 339 (1862). Bedd., Ferns Brit.Ind. : t.291 (1868).
Athyrium thwaitesii (A.Braun ex Mett.) Milde in Bot.Zeit. : 354 (1870).
Diplazium japonicum sensu Bedd., Handb.Ferns Brit.Ind. : 180 (1883) pro parte — Brownlie, Fl.Nouv.-Caled. 3 Pterid. : 204 (1969) non *Asplenium japonicum* Thunb.
Diplazium petersenii (Kunze) Christ in Bull.Acad.Geogr.Bot.Mans : 245 (1902) — C.Chr., Index Fil. : 237 (1905) — C.Chr., in B.P.Bish.Mus.Bull. 177 : 73 (1943).
Athyrium japonicum sensu Copel. in Philip.Journ.Sci.3C : 290 (1908) — Holtt., Fl.Malaya II : 551 (1954) — Copel. Fern Fl. Philip. : 385 (1960) non *Asplenium japonicum* Thunb., Fl.Jap. : 334 (1784).
Diplazium allorgei Tard.-Bl., Notul.Syst. Paris 7 : 150 (1938). Type from Azores.
Athyriopsis lasiopteris (Kunze) Ching in Acta Phytotax.Sinica 9 : 65 (1964) excl. syn. *D.dimorphophyllum* Koidz.
Athyriopsis petersenii (Kunze) Ching, *loc.cit.* : 66, as *peterseni.*
Athyriopsis thwaitesii (A.Braun ex Mett.) Ching, *loc.cit.*
Lunathyrium lasiopteris (Kunze) Nakaike, Enum.Pterid.Jap. : 175 (1975) excl. syn. *D. dimorphophyllum* Koidz. — Sledge in Fern Gaz.11 : 84 (1975).

A.petersenii and *D.lasiopteris* were treated as synonyms by Moore (1859), Baker (1874) and Christensen (1906). According to Baker *(loc.cit.)* they were first united by Kuhn : I have failed to trace where Kuhn made this union, but earlier still Mettenius

FIGURE 1. *Asplenium petersenii* Kunze Coll. C.W. Petersen : Canton 1827. Lectotype C.

FIGURE 2. *Diplazium lasiopteris* Kunze Isotype BM.

(1859) had united specimens from Java and the Nilgiri Hills with Petersen's Canton fern and, as stated above, one of the three Canton sheets in Herb. Copenhagen has been seen by Mettenius and identified as *Aspl. lasiopteris.* In the Third Supplement to *Index Filicum,* Christensen (1934) reversed this long held view and transferred *A.petersenii* to synonymy under *D.japonicum sensu stricto.* He does not appear ever to have published a statement in justification for this change and since no authentic specimen of Thunberg's species was available to him for examination, it seems most likely that Christensen's changed ideas regarding the identity of *A.petersenii* were based on the geographical probability that the plant from Canton was more likely to be the same as one from Japan than one from India. It is evident moreover that his revised view should be regarded as an intuitive belief rather than a proven fact since, despite his entry in Ind.Fil.Suppl.3, in a later work on the ferns of Samoa (1943) – the manuscript of which was completed in 1938 – he did not use the name *D.japonicum* but retained the binomial *D.petersenii* (Kunze) Christ with the comment that "It seems to me by no means different from East Asiatic and Malayan specimens usually called *D.Petersenii* to which *Asplenium lasiopteris* Kunze was referred in my Index, but perhaps wrongly because I suspect the genuine *A.Petersenii* from Canton to be *D.japonicum.*" In view of the words "perhaps" and "I suspect," it is somewhat surprising that Christensen's citation in Ind. Fil.Suppl. 3 was not accompanied by any indication of uncertainty as to the correctness of this citation.

The generic standing of *Lunathyrium* is itself not accepted by all pteridologists. In his paper on the evolution and inter-relationship of athyrioid and diplazioid genera, Bir (1973) rejects all of Ching's (1964) splinter groups and considers that *Lunathyrium* is best treated as a subgenus of *Athyrium.* Of the numerous genera proposed by Ching *(loc.cit.)* the species of *Lunathyrium* are said to have erect rhizomes and spores with a broadly winged perispore in contrast to the creeping rhizomes and "coarsely verrucose" perispores of *Athyriopsis* species. Ching states *(loc.cit.*: 70) that "*Lunathyrium* is typified by *Athyrium pycnosorum* Christ from north-eastern Asia, a species closely related to *Athyrium acrostichoides* (Sw.) Diels of the eastern North America and the same region." Yet *Lunathyrium acrostichoides* (Sw.) Ching has a creeping rhizome and winged spores whilst *L.pycnosorum* (Christ) Koidz. combines an erect rhizome with spiny spores. Since the distinctions between these groups are far

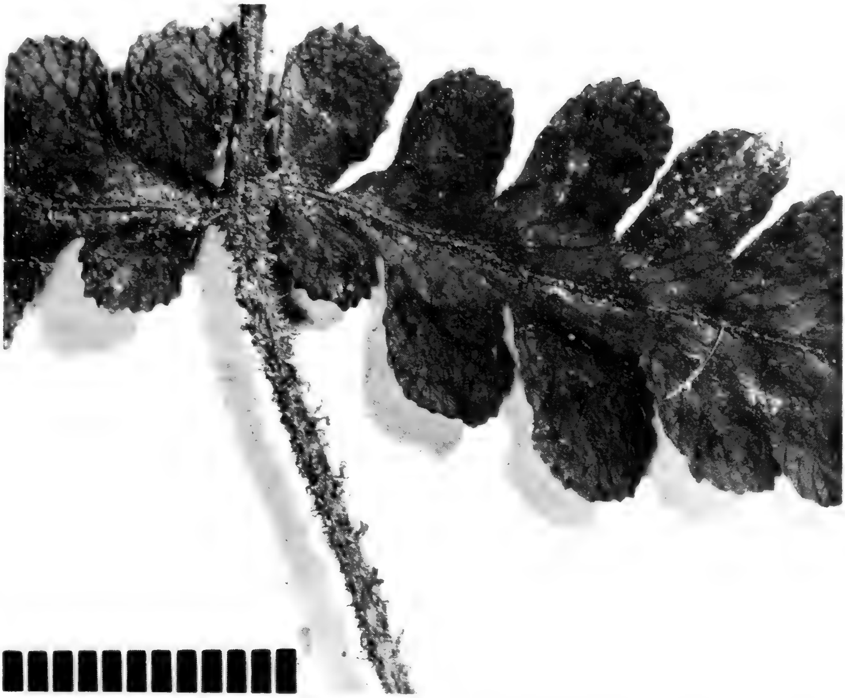

FIGURE 3: *A. petersenii* Kunze. Part of pinnae and frond axis enlarged (Scale in mm).

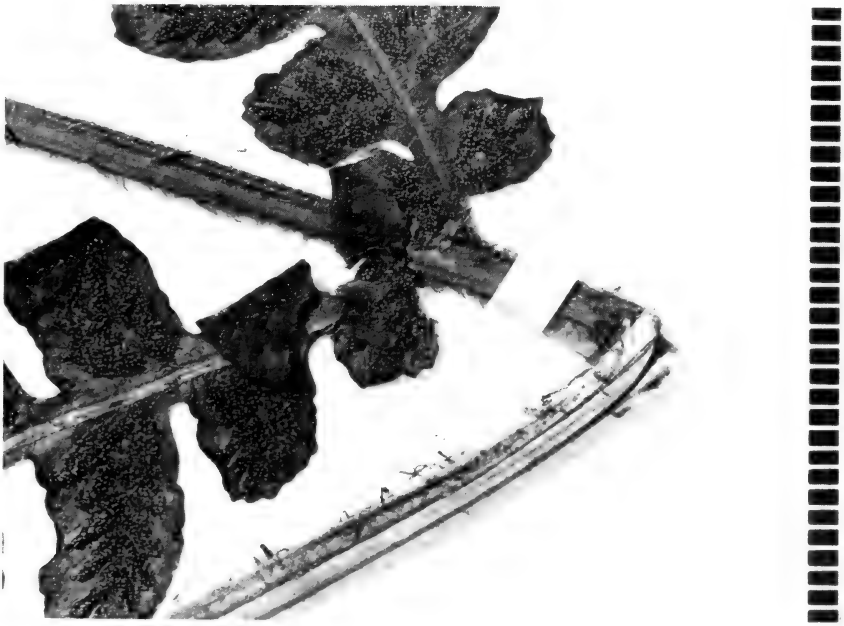

FIGURE 4: *D. lasiopteris* Kunze. Part of pinnae and frond axis enlarged (Scale in mm).

less clear-cut than Ching's paper implies and, indeed, break down in some of the species cited by him, I consider Ohba's (1965) arrangement in which *Lunathyrium* and *Athyriopsis* are combined, to be a more realistic and workable treatment.

The need for experimental work in resolving the *Lunathyrium japonicum* species complex was referred to in my previous paper. Satisfactory qualitative differences between taxa are few : distinctions hinge largely on differences of a quantitative nature which may or may not be of real systematic significance, for the extent to which such differences are determined genetically or are environmentally controlled is unknown. The degree of hairyness and scalyness of the frond axes may be a response to environmental factors or it may be determined by the level of ploidy. Observations on plants brought into cultivation should reveal the degree of plasticity inherent in each taxon within this group. Only by combining such observations with cytological investigations will a clear understanding be reached of the number of valid taxa to be recognised within the *L.japonicum* complex, of the boundaries between these taxa and of the systematic rank to be accorded to them.

My grateful thanks are due to Mr Alfred Hansen for drawing my attention to the extistence of the Petersen specimens in the Copenhagen Museum and for arranging to have them sent to me for study; also for identifying the handwritings of Petersen, Hornemann and Kjaerskou on the sheets and for the information kindly supplied about them.

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SHORT NOTES

DRYOPTERIS x BRATHAICA FRASER-JENKINS & REICHSTEIN HYBR. NOV., THE PUTATIVE HYBRID OF D. CARTHUSIANA x D. FILIX-MAS

As pointed out by Manton (1938, 1950) two different ferns have been referred to under the name Dryopteris remota (A.Br.) Druce: (1) a triploid apomictic species distributed from Spain to the Caucasus, although relatively rare throughout its whole range, and (2) a sterile tetraploid hybrid probably *D. carthusiana* x *D. filix-mas* found only once, in England (see Clowes, 1860), but since then cultivated in different gardens and still living in some. Both taxa are rather similar in gross morphology and until recently there has been no agreement as to which of them Braun's name has to be attached (see Benl & Eschelmüller, 1973). Chemical analysis (Widén et al., 1976) combined with a careful study of the range of morphological variation in a great number of cytologically checked plants of the triploid taxon, has made it possible to prove that Braun's type (in B) of *Aspidium remotum* was indeed the triploid species (Fraser-Jenkins, Reichstein & Vida, in preparation). We therefore give the following new name to the tetraploid hybrid:— *D.* x *remota* sensu Druce non Lowe nec (A. Br)

Dryopteris x brathaica Fraser-Jenkins & Reichstein *hybr. nov.* = *Lastrea remota* sensu Moore partim et auct. brit. *Icon.* Hooker, W.J. (1868, *Brit. Ferns, t.22);* Lowe, E.J. (1864, *Nat. Hist. New & Rare Ferns, t.22).*

Diagnosis: Recedit a *D. remota*: numero chromosomatum 2n = 164; sporis omnibus abortivis; pinnula prima basiscopica pinnae basalis semper quam 2.8 cm breviore; et squamis petiolos rhachidisque plerumque pallide ochraceis, raro rufescentibus, minorius minus capillari protractis.

Lectotype: [Brathay wood], Windermere, Westmorland, England, 1859, *F. Clowes* ex Herb. T. Moore (K); syntype BM. **Paratypes:** pressed fronds from the same clone presently cult. in Basel as TR-3330 will be sent to B, BM, BR, E, FR, G, K, M, P, Z, ZT. Similar fronds already to be found in OXF, P, S, WU, and BM, deposited this century by Druce, Stansfield, CRF-J and others who have had it in cultivation.

ACKNOWLEDGEMENTS

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NOMENCLATURAL NOTES ON DRYOPTERIS : 2

AN EARLIER NAME FOR DRYOPTERIS ASSIMILIS

Dryopteris assimilis S. Walker was described (Walker, 1961) from cytologically determined material (2n = 82) from Ben Lawers, Scotland and based on *Lastrea dilatata* (Hoffm.) Presl var. *alpina* T. Moore (see Jermy & Walker, 1964). During the latter part of 1976 our attention was drawn by David Wagner, of the University of Oregon, to the plant called *Nephrodium expansum* C. Presl collected by Thaddaeus Haenke at Nootka Sound, in what is now British Columbia, Canada. In his description Presl (p.38) states "Habitus Aspidii spinulosi et dilatati" and says the pinnules are deeply cut. A diploid taxon in this complex has been shown to be present in the Vancouver region (Walker, 1955) and therefore Presl's name needed investigation.

Type material of *N. expansum* was sent on loan by both Charles University (PRC) and the National Museum of Prague (PR); that in PR was designated lectotype and the material, a mature frond with good spores, was undoubtedly *D. assimilis*. The epithet *expansa* must therefore have priority; the synonymy is as follows:

Dryopteris expansa (C.Presl) Fraser-Jenkins & Jermy *comb.nov.*

Nephrodium expansum C. Presl, Rel. Haenk.:38 (1825); non Desv. (1827)
Lastrea expansum (C.Presl) C. Presl, Tent. Pterid.:76 (1836).
Lastrea dilatata (Hoffm.) C. Presl var. *alpina* T.Moore, Nat. print. ferns Gt. Brit. Irel., sub tab.22 (sine figura) (1856).
Dryopteris siranensis Nakai, in Bull. Nat. Mus. Tokyo, 33:3 (1953).
Dryopteris assimilis S. Walker, in Amer J. Bot., 48:607 adnot. (1961).
Dryopteris spinulosa (Müll.) Watt subsp. *assimilis* (S. Walker) Schidlay, *Fl. Slovensk.* 2:217 (1966).

TWO HITHERTO UNNAMED HYBRIDS OF DRYOPTERIS EXPANSA

The following two hybrids have been recorded in the wild and are here given names and validating descriptions.

Dryopteris x **ambroseae** Fraser-Jenkins & Jermy *hybr.nov. (D. austriaca* (Jacq.) Woynar x *expansa)*

Planta triploidea hybrida, intermedia inter parentes, *D.austriacam* et *D. expansam. D.austriacae* similis colorae frondis at plerumque paleis fuscata linea, sed lamina plana pinnulaque longa basiscopica in pinna infirma.. Sporae abortivae. Numerum somaticus chromosomatum 123. **Holotype:** Johnny's Wood, Barrowdale, Cumbria.NGR 35/253145, growing with parents; alt. 120m. 22 Aug. 1972, *Mary Gibby & F. Jackson M37* (BM, two sheets). *Icones:* Widén C.J., Sarvela J.,& Ahti, T. 1967. Acta. Bot. Fenn. 77: tab 3 & 5c. Named after Mary Gibby (née Ambrose) who has collected and studied the cytology of the above plants.

This hybrid is difficult to distinguish from the parent species except by its abortive spores. It is similar to *D. austriaca* in its frond colour and the dark centre line of the scales; the flattened lamina and long basiscopic pinnule on the lowermost pinna is characteristic of *D.expansa*. It could also be confused with the tetraploid hybrid *D. x deweveri* (Jansen) Jansen & Wachter (*D.austriaca* x *carthusiana* (Vill.) H.P. Fuchs) which also has abortive spores. The fronds of *D. x deweveri* are erect, lighter green, and the lowest innermost basiscopic pinnule is about equal in length to its neighbour; the pinnule segments have acute teeth with a distinct arista as in *D. carthusiana*. The rhizome may be more or less creeping or erect as in *D. x ambroseae*. *D. x ambroseae* has been synthesised (Walker, 1955) and, with those cytologically investigated from the wild, shows approximately 41 bivalents and 41 univalents at meiosis.

This hybrid is found in Britain where the parents grow together and usually below 200m (Arnold et al., in press). It has also been recorded for Bavaria (Benl & Eschelmüller, 1970; Walker 1955), Switzerland (Döpp & Gätzi, 1964) Finland (Widén, Sarvela & Ahti, 1967; Sorsa & Widén, 1968) Poland (Piekoś, 1974) and Spain (H. MacAllister, comm. M. Gibby).

Dryopteris x sarvelii Fraser-Jenkins & Jermy *hybr. nov. (D. carthusiana* x *expansa)*

Planta hybrida intermedia inter parentes, *D.carthusiam* et *D.expansam.* Rhizoma crassum horizontale crescens. Frons glandulifera and 75 cm; stipes paleis fuscis pallidis cum linea media obscuriore praedita. Indusia trichomatibus glandulifere tibus fimbriata; sporae abortive. Planta triploidea, numerus somaticus chromosomatum 123. **Holotype** Finland, Nylandia, Espoo, Luukki, NE of Lake Vääralampi. In *Betula-Populus-Picea* wet woodland with *Ledum palustre, Andromeda* sp., *Dryopteris carthusiana* and *D. expansa.* 4 Aug. 1966, *J. Sarvela 19* (H; isotype BM). *Icones:* Widén C.J., Sarvela, J. & Ahti, T. 1967. Acta Bot Fenn., 77: tab.4B & 6C. This hybrid is named in honour of Jaakko Sarvela who discovered this population (Widén C.J., Sarvela J & Ahti, T., 1967).

In the type locality this hybrid stands out in being intermediate between the parent species having the frond texture of *D.carthusiana* and the habit of *D.expansa.* The fronds do not overwinter but die down later than *D.expansa.*. The rhizome grows almost horizontally, the fronds often reaching 75 cm. The scales on the stipe are pale brown with a diffuse darker median stripe, and the lamina intermediate in dissection between that of the parents and densely glandular. The indusium is fringed with glandular hairs and the spores are abortive. The plant is triploid (2n = 123), with 0-8 bivalents at meiosis (Gibby & Walker, 1977).

So far this hybrid has only been collected in the type locality and would be very difficult to separate where the above species grow with *D.austriaca* and there is a possibility of *D* x *deweveri* being present.

THE TETRAPLOID SUBSPECIES OF DRYOPTERIS VILLARII

Dryopteris villarii (Bell.) Woynar ex Schinz & Thellung subsp. **submontana** Fraser-Jenkins & Jermy *subsp.nov.*

Syn: *Polystichum rigidum* (Hoffm.) DC.var. *bertolonii* Trev., Syll. Spor. Ital. Atti. Soc. It Sci. Nat: 230 (1874); *Aspidium rigidum* (Hoffm) Sw. var. *cuneilobum* Borbás ex Luerss., Farnpfl., in Rabenhorst, Krypt. Fl. : 411 (1889); *Dryopteris villarii* var. *nevadensis* sensu Heywood, Feddes Rep. 64:27 (1961) non *Aspidium nevadense* Boiss. (1838); *Dryopteris villarii* auctt. brit. et Dandy, List of British Vascular Plants: 5 (1958).

Frondes erecta, ad 50 cm; petiolus plerumque c.½ laminae aequans; lamina triangulo-lanceolata, 2-pinnata, griseo-lazulina impolita, utrimque dense glandulis ornata, pinnis infimis dimensionem maximam plerumque habent, pinnulis lobatis ± profunde, dentes acutos anguste plerumque marginem acroscopicem ferens, dentes ad apicem pinnulam longiorescentes acutiorescentesque. Planta tetraploidea numerus somaticus chromosomatum 164.
Holotype Mid West York, v.c. 64, Ingleborough, on limestone outcrop. *I. Manton* Ex Leeds University Botanic Garden (BM).

The fronds are upright, 50cm with the stipe usually half the length of the lamina. The lamina is triangular-lanceolate, usually widest at the base, 2-pinnate, dull blue-green, glandular on both surfaces, sometimes very densely so. The pinnules are more or less deeply lobed with narrowly acute teeth mainly on the acroscopic side of each lobe, the teeth becoming longer and more acute towards the pinnule apex. This is a tetraploid taxon (2n = 164) which has been investigated chemically (Widén et al., 1971) and cytologically (Manton, 1950; Panigrahi, 1965; Vida, 1969) and the results suggest it is probably an allotetraploid resulting from the hybridization of diploid *D.villarii* subsp. *villarii* with *D.pallida* (Bory) Fomin. It has been recorded from Al, Br, Ga, Gr, Hs, It, Ju, Ru and outside Europe from N. central Algeria and western

Caucasus. The detailed distribution and ecology in Britain is given by Gilbert (1966; 1970) and Arnold et al. (in press).

ACKNOWLEDGEMENT

We should like to thank Mary Gibby for cytological data on the hybrids and for discussion and Dr. N. Robson for help with the latin descriptions.

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REVIEWS

A MONOGRAPH OF THE FERN GENUS BOLBITIS (LOMARIOPSIDACEAE) by E. Hennipman. Leiden University Press (Leiden Botanical Series, 2), 1977. Dfl. 92 (about £21.65).

This significant Monograph is the result of over ten years investigation, including field expeditions, study of plants under cultivation, detailed morphological analysis, chromosomal cytology, spore structure and development, and an extensive survey of material available in major herbaria. The considerable body of biological information is collected together in the general part of the publication (the first 118 pages) which is then synthesized into the taxonomic part (just over 200 pages) in a scholarly survey that must surely make this one of the most thoroughly documented of the leptosporangiate fern genera.

It is in this taxonomic section of the monograph that Hennipman, having recognized the problems posed by homoplasy and neoteny in the evolution of a group of species, applies this understanding to the problem of delimiting the genus *Bolbitis.* The complexity of this problem becomes obvious when one realises that species of this genus as previously defined have been variously referred to 23 different genera, leading to "a somewhat intricate synonomy."

Many of the species of *Bolbitis* have, at some stage, been included in *Leptochilus,* the study of which we are told is still in progress. The genus *Bolbitis* as amended includes the genera *Egenolfia* and *Edanyoa.* Dr. Hennipman recognizes 44 species, 13 hybrids and 12 species of doubtful status. Thirty four of the species he divides into 10 series, the remainder are grouped as "species incertae sedis" and are probably mostly of hybrid origin. The series groupings are based on characters of the adult plants especially venation pattern, perispore and rhizomes. It would have been easier to follow the logic of this work if the author had supplied us with a conspectus, or even better, a key to the series. For the species however, three separate keys are provided — Africa and Madagascar; America; Asia and the Pacific. Additional keys to subspecific taxa are also provided under the relevant species.

A most welcome feature of the monograph is a clear schematic diagram explaining the application of terminology to the frond morphology. For each species, as well as full synonomy, description and distribution maps, line drawings of the salient characters are supplied which are simple, clear and of excellent quality and in many cases these illustrate not only the typical but also the range of variation.

One realises as does Dr. Hennipman that this is not the last word on many aspects of this group of tropical ferns. This model Monograph now needs testing by use. Only then will the questions he raises and no doubt others be answered.

T.C. CHAMBERS

AUSTRALIAN FERNS AND FERN ALLIES by D.L. Jones and S.C. Clemisha. 294 pp., numerous illustrations including 61 in colour. 19 x 25.5 cms., A.H. & A.W. Reed, Sydney, Wellington & London, 1976. Price $A 12.95 (about £8.30).*

This is the first comprehensive guide to the ferns of the whole of the Australian continent, and it thus represents a distinct pteridological milestone. It is well-researched and excellently produced, and for its size and value by no means over-expensive.

For each species, a short but sound description is given, its geographical distribution (both within and outside Australia) indicated and species with which its identification might be confused are mentioned. For each there are useful ecological notes and comments on cultivation. Species are illustrated adjacent to their descriptions with helpful frond-outline drawings, and for some there are superb full-colour field photographs. Nomenclature used throughout is well up-to-date and accurate, with authorities quoted. Where available and appropriate, Australian common names are also given, and botanical synonyms are listed in one of the several useful appendices. Where genera are at present under study and taxonomic changes might result, this is stated in the text, and where taxa have been found to be lacking botanical names, with commendable Australian frankness, these are nevertheless included under their appropriate genera, and so-indicated.

In such a vast continent with so few pteridologists and so under-collected and botanically under-explored, sheer comprehensiveness of coverage of taxa is a daunting task. Nevertheless, this is done excellently, with certainly the vast majority of Australia's 350 or more ferns (at a very conservative estimate) included, embracing almost everything pteridological likely to be encountered by most readers. Unfortunately, there are no generic or specific keys — perhaps these could be included in a future edition?

It is difficult for a book to be both of popular appeal and also to contain enough 'meat' to satisfy the more discerning devotee. This book undoubtedly provides both, with a high standard of accuracy. There is a lot in it for the student, general naturalist, scientist and gardener alike. As such, one hopes it may stimulate a sounder popular appreciation of the diversity and significance of pteridophytes 'down-under'. The authors and publishers are to be congratulated.

C.N. PAGE

FERNS AND FERN ALLIES OF NEW ZEALAND by Eric Heath (illustrations) and R.J. Chinnock (text). 48 pp., 106 coloured illustrations. 18.5 x 24.5 cms., A.H. & A.W. Reed, Wellington, Sydney & London, 1974. Price $NZ 4.95 (about £2.80).*

This book covers 88 out of about 152 ferns and 19 fern-allies known in New Zealand. For each included it gives a brief description of the plant with outline notes on its ecology and distribution in New Zealand. Each has a hand-painted illustration in colour of a single or part frond (or two in dimorphic species), and the book ends with a brief account of cultivation and propagation.

The illustrations are clearly the main feature of the book. As well as being pleasing in appearance, they seem generally scientifically accurate and give a good idea of the form and colour of each plant. The text augments this, although it is very brief and botanical names are quoted without authorities.

Nevertheless, this is a pleasing book to own, and my main regret is that it is not more comprehensive. But it helps further awareness and conservation of ferns in a country which must once have had these plants virtually everywhere (including in Maori designs and its National Emblem), it will perform a valuable purpose.

C.N. PAGE

** [Prices not printed in book, but the prices at which I found copies being sold in bookshops in Hobart (Dec. 1976) and Christchurch (Jan. 1977) respectively — Ed.]*

THE FERN GAZETTE

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A TETRAPLOID CYTOTYPE OF ASPLENIUM CUNEIFOLIUM VIV. IN CORSICA.

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ABSTRACT

A tetraploid, morphologically similar to *Asplenium cuneifolium* Viv., is reported for the first time.

INTRODUCTION

Asplenium cuneifolium Viv. is a small fern of the *Asplenium adiantum-nigrum* group so far known to extend from Portugal (Pinto da Silva. 1968), throughout most of Europe (Crabbe, Jermy & Lovis, 1964; Jalas & Suominen, 1972, map 92) to Turkey (Henderson, 1965). It grows exclusively on ultrabasic rocks (serpentine; peridotite, magnesite) or mixed rocks and screes containing these materials. As in all other members of this group (*A. adiantum-nigrum* L., *A. onopteris* L., *A. balearicum* Shivas and *A. pseudolanceolatum* Fomin), it is morphologically a rather variable species and single fronds cannot always be identified with confidence from herbarium material. If more ample material is available, or if populations can be seen in the field, correct identification is usually easy.

All plants of *A. cuneifolium* from central and eastern Europe which have been checked so far (Löve, Löve & Pichi-Sermolli, 1977, p. 241) have been found to be diploid and sexual (n = 36, 2n = 72) and *A. cuneifolium* has been shown to be an ancestor of the allotetraploid *Asplenium adiantum-nigrum* (Shivas, 1969). In 1974, a population growing on serpentine s.l. (green schists) in Corsica was detected by one of us (R.D.). Progeny raised from spores in Basel (TR-3839) proved to be tetraploid. On the basis of gross morphology we are unable to distinguish these plants with confidence from the hitherto known diploids, although they do have bigger spores and possibly other differences in micro-characters. We assume that they represent a tetraploid cytotype of essentially autotetraploid origin, which is not uncommon among other members of *Asplenium* (Lovis, 1964; Sleep, 1966), *Phyllitis* (Emmott, 1964) and *Ceterach* (Vida, 1963). Such essentially autopolyploid cytotypes have frequently been distinguished from their diploid ancestors as subspecies, and we intend to follow this procedure. This treatment, however, is not entirely satisfactory since the category of subspecies was created for other purposes.

We refrain from suggesting any new subspecific name until we can establish to which cytotype Viviani's type of *A. cuneifolium* can be referred. Documentation with figures will be published elsewhere. The spores used for raising the plants which have been counted were collected by R. Deschatres in Corsica, between Sermano and Bustanico, 9th July 1974. A tetraploid cytotype has also been found in Scotland and Ireland (Sleep et al., 1978)* and may occur in other localities. We are willing to accept well pressed fronds with spores for identification.

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*See p.345 of this issue

ACKNOWLEDGEMENT

We thank Dr. Anne Sleep and Mr. A. McG. Stirling for their kind co-operation.

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FURTHER INVESTIGATIONS ON ASPLENIUM CUNEIFOLIUM IN THE BRITISH ISLES

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ABSTRACT

Chromosome counts have been made from twenty collections of putative *Asplenium cuneifolium* from Scottish serpentine localities and all have proved to be uniformly tetraploid, with n = 72. It is thought that these plants are identical with a tetraploid cytotype of *Asplenium cuneifolium* which has recently been described from Corsica.*

The discovery of a fern believed to be morphologically identical with the continental *Asplenium cuneifolium* Viv. was described by Roberts & Stirling (1974) from several different serpentine localities in Scotland. Three plants from two of these localities (Glen Lochay and Glendaruel, Argyll) were counted and gave diploid chromosome counts. Subsequently chromosome counts of plants from three more of the Scottish serpentine localities were made in order to check the distribution of putative *Asplenium cuneifolium* for the Atlas of Ferns of the British Isles (Jermy et al., 1978), which was, at that time, in preparation. Surprisingly, every plant examined proved to be tetraploid, with n = 72. A similar result was obtained from a plant of putative *A. cuneifolium* which was collected from serpentine rocks at Dawross, Connemara, Ireland, by A. Rutherford, M. Scannell and A. McG. Stirling in July 1975. Following these rather unexpected results, the Scottish localities from which the original collections came were re-sampled during the summer of 1977; sporangial fixings were taken by A. McG. S. from the sites enumerated in Table I, and were sent to Leeds for cytological examination. In this re-investigation, some twenty plants from eight localities have been examined cytologically, and all have proved to be tetraploid (see Table I). No diploids have been recorded. In view of the uniformity of these results, it seems that these populations of putative *Asplenium cuneifolium* from serpentine rocks in Scotland and Ireland may generally prove to be tetraploid.

As has been shown by Roberts & Stirling (1974), these Scottish *Asplenium* populations are morphologically distinct from *Asplenium adiantum-nigrum* L. and are very similar to the continental *A. cuneifolium* Viv., a central European species characteristic of serpentine and other ultrabasic rocks. The specimens of *A. cuneifolium* which have been examined cytologically have been found to be diploid, with n = 36 (Löve, Löve & Pichi- Sermolli, 1977). In addition, Shivas (1956, 1969) has shown this species to be one of the ancestors of *A. adiantum-nigrum* L. Recently, a plant from Corsica, which one would, on morphological grounds, have no hesitation in referring to *A. cuneifolium* Viv., was counted, and proved to be tetraploid (Deschatres, Schneller & Reichstein, 1978). This plant could be an autotetraploid derivative of the diploid cytotype of *A. cuneifolium* Viv. The spores of this tetraploid

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*See p.343 of this issue.

TABLE 1

LOCALITY	COLLECTOR AND NUMBER	RESULT	NO. CELLS OBSERVED
Near Ben Bowie (NS 347831). Helensburgh. vc 99. Dunbarton.	AMS/1/77	n = c.70	2
Lime HILL (NS 473963). Loch Ard Forest. vc 86. Stirling.	AMS/2/77	n = 72	7+ *
"	AMS/3/77	n = c.70	10
"	4/75	n = c.70	2
Glendaruel (NS 021904). vc 98. Argyll.	AMS/4/77	n = 72	7
"	AMS/5/77	n = 72	6
"	AMS/6/77	n = 72	10
"	AMS/7/77	n = 72	4
Corrycharmaig. Glen Lochay (NN 521358). vc 88. Mid Perth.	AMS/8/77	n = 72	4
"	AMS/9/77	n = 72	7
"	AMS/10/77	n = c.70	3
"	AMS/11/77	Tetraploid	6
Balhamie Hill. near Colmonell (NX 133859). vc 75. Ayr.	6/75	Tetraploid	9
Craigs of Succouth. Upper Deveron Valley. Bridgend (NJ 400347). vc 94. Banff.	7/75	n = 72	6
"	JIS/76/8	n = 72	8
"	JIS/76/11	Probably tetraploid	4
"	JIS/76/12	Tetraploid	4
"	JIS/76/16	Tetraploid	3
Fetlar. vc 112. Shetland.	R.C. Palmer	Tetraploid	8
Dawross. Connemara. vc H16. West Galway. Ireland.	2/75	Tetraploid	5

FOOTNOTES TO TABLE I

* 7+ indicates that unequivocal counts of n = 72 were obtained from 7 cells, but that other cells seen gave counts of a similar order.

n = 72. Precise and unequivocal counts were obtained from the cells listed.

Tetraploid indicates that all cells observed gave counts of tetraploid order.

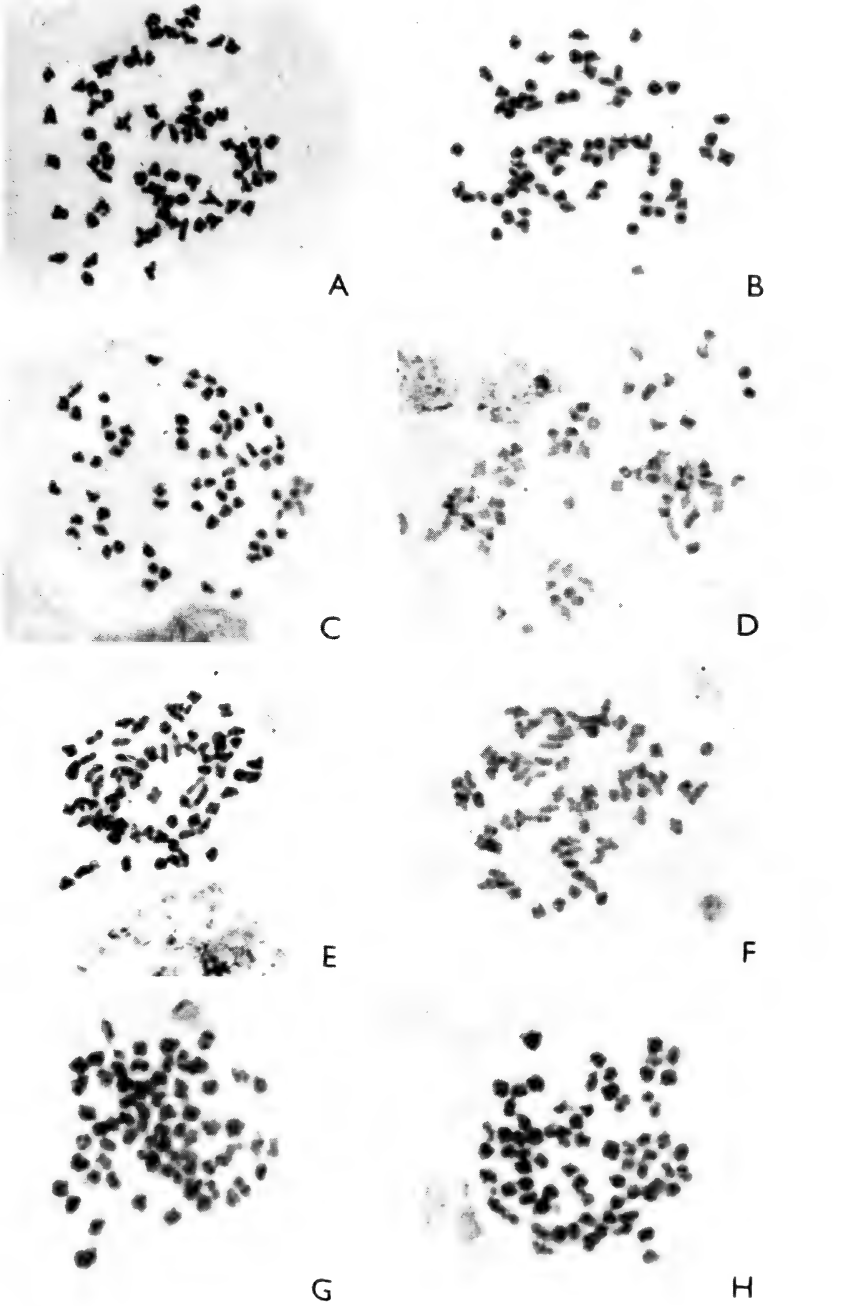

FIGURE 1. Photomicrographs of spore mother cells in meiosis of putative *Asplenium cuneifolium* from different Scottish localities. A-B, AMS/6/77 (Glendaruel, Argyll) diakinesis, both showing n = 72; C, AMS/5/77 (Glendaruel, Argyll) first metaphase showing 72 bivalents; D, AMS/9/77 (Glen Lochay, Mid Perth) diakinesis showing 72 bivalents; E-F, AMS/2/77 (Lime Hill, Stirling) diakinesis, both showing n = 72; G-H, 7/75 (Bridgend, Banff) first metaphase, both showing n = 72 (all from permanent acetocarmine preparations, A-F x 800, G-H x 1500).

cytotype are significantly larger than those of known diploid plants of *A. cuneifolium* (Reichstein, pers. comm.). In a preliminary investigation (which will be reported in full elsewhere), spore measurements were made using material from one Irish and ten Scottish localities. It was found that in these plants the spore size was larger than in central European material of *A. cuneifolium*, but agreed closely with that recorded for the Corsican tetraploid. The plants from the British Isles thus correspond well with the newly-described tetraploid from Corsica in gross morphology, spore size and chromosome number. We believe that these collections are identical, and that they possibly represent a tetraploid cytotype of *A. cuneifolium* Viv.

The question of the nature of this tetraploid now arises. We consider it very likely that, as suggested by Deschatres, Schneller & Reichstein (1978), these plants are indeed the autotetraploid derivative of diploid *A. cuneifolium* Viv., but further work is necessary to confirm this hypothesis. Another possibility is that *Asplenium adiantum-nigrum*, when growing on serpentine, can produce a certain type of morphology which resembles *A. cuneifolium*. This, however, is unlikely in view of the fact that *A. adiantum-nigrum* and *A. cuneifolium* grow together on mixed rocks which contain serpentine in both Italy and southern Switzerland. In such places not only can they be distinguished morphologically, but the triploid hybrid between them is known (*A. x centovallense* D. E. Meyer) (Meyer, 1968). A hybridization programme is at present in progress at Leeds, the aim of which is to elucidate the nature and origins of material of tetraploid *Asplenium cuneifolium* from Corsica, Scotland and Ireland.

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THE PTERIDOPHYTES OF RÉUNION ISLAND *

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ABSTRACT

The pteridophytes of the island of Réunion and their habitats are described.

INTRODUCTION

The pteridophyte flora of Réunion Island is characterized by a high number of species (about 240) in relation to its small surface area. This holds true for the entire Mascarene archipelago where the total number of species is known to be about 265, or about one-half the number occurring in Madagascar and the Seychelles.

One of the authors (T.C.) has been actively investigating the botany of Réunion Island during the last ten years. His field observations, together with the results of many botanical missions carried out by the other author (F.B.) and those of J. Bosser and F. Friedmann have permitted a general outline of the island's present day pteridophyte vegetation to be established. The collections are housed at the Paris Herbarium and/or at Centre Universitaire de La Réunion.

In the past, ecological observations regarding the island's pteridophytes have been rare; Cordemoy (1895), Baker (1877) and Bory de Saint Vincent (1804) usually give only vague indications consisting of the localities without any mention of the biotope (habitat). The island's vegetation was studied by Rivals (1952) but he scarcely mentions the pteridophytes.

Until the last few years the study of tropical floras undertaken by large european institutions has been almost exclusively oriented towards a purely descriptive and systematic outlook.

Recently some ecological observations have been published for Africa by Tardieu-Blot, Nicklès & Jacques-Félix (1949), Tardieu-Blot, Jaeger & Adam (1971) & Adams (1954). Concerning the Mascarenes, most of the collections were made by Bory de Saint-Vincent, Boivin, Commerson, Sieber, Gaudichaud and Lepervanche-Mézière. These ancient collections are often very imprecise as to the locality and the biotope (which are generally not indicated), the collector merely stating "Mascarenes" or "Bourbon" (the island's previous name to 1848).

GEOGRAPHY AND RELIEF OF THE ISLAND

Réunion Island, Mauritius and Rodrigues form the Mascarene archipelago. Réunion (55°30'E, 21°00'S) lies 800 km east of Madagascar. Mauritius lies closest to Réunion at 170 km ENE. Rodrigues, on the other hand, is more isolated and is located 600 km ENE of Mauritius (fig. 1).

Réunion is oriented NW-SE and has a roughly elliptic contour, about 70 km long and 50 km wide, with a surface area of 2,500 km^2. A geologically young island (about 3 million years old) of volcanic origin, it was formed from two volcanic complexes, in the middle of which is a vast expanse occupied by the Plaine des Cafres and the Plaine

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* English translation by D. Lorence, Mauritius Herbarium, MSIRI, Reduit, Mauritius. (Present address: Missouri Botanical Garden, 2345 Tower Grove Avenue, St. Louis No. 63110, U.S.A.).

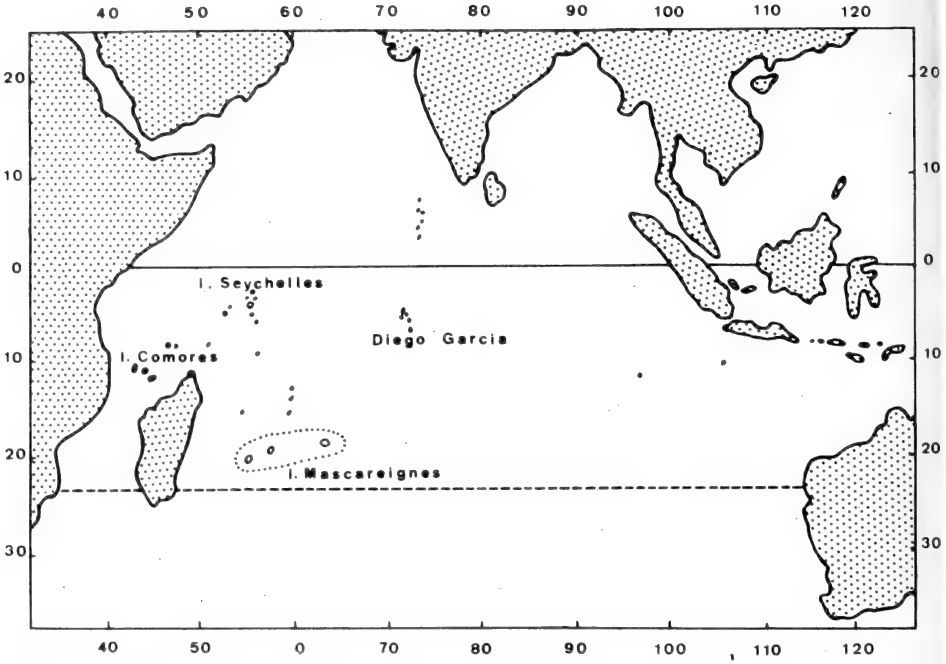

FIGURE 1. Position of the Mascarene Archipelago (Réunion Island, Mauritius, Rodrigues) in the Indian Ocean, with respect to other island groups.

des Palmistes (Fig. 2). The massif du Piton des Neiges, representing the NE two-thirds of the island, reaches 3,069 m. In the SE, the massif de la Fournaise has a crater which is still active, rising to 2,630 m. Each of these two massifs is the result of successive volcanic eruptions subsequently acted upon by erosion. As a result, the topography is extremely rugged and is characterised by "cirques" and radiating valleys with steep flanks bordering the remains of more or less extended expanses of somewhat regular slopes of about 10° inclination. The material detached by the still active erosion has formed several rather limited littoral plains extending from the mouths of some of the major rivers.

PHYSICAL AND CLIMATIC DATA

As a result of its geographical situation, the island enjoys a tropical climate with an insular character due to the influences of the trade winds and its accentuated relief which modify an otherwise truly tropical climate. Two more or less well marked seasons exist. The warm and rainy season (summer) lasts from December to April. It is marked by the passage of cyclonic disturbances over or near the island which bring very heavy rains. The cooler and relatively drier season (winter) extends from May to November.

The temperatures are not excessive. Along the coast the mean maximum temperature for the warmest month (February) is 32.4°C at St. Leu and 30.2°C at St. Benoit. The mean minimum temperature for the coldest month (August) is 18°C at St. Leu and 16.4°C at St. Benoît. The temperature decreases with altitude and the higher parts of the island (above 1800-2000m) are subject to frequent frosts at night. The temperature may reach –5°C at soil level on the Massif de la Fournaise.

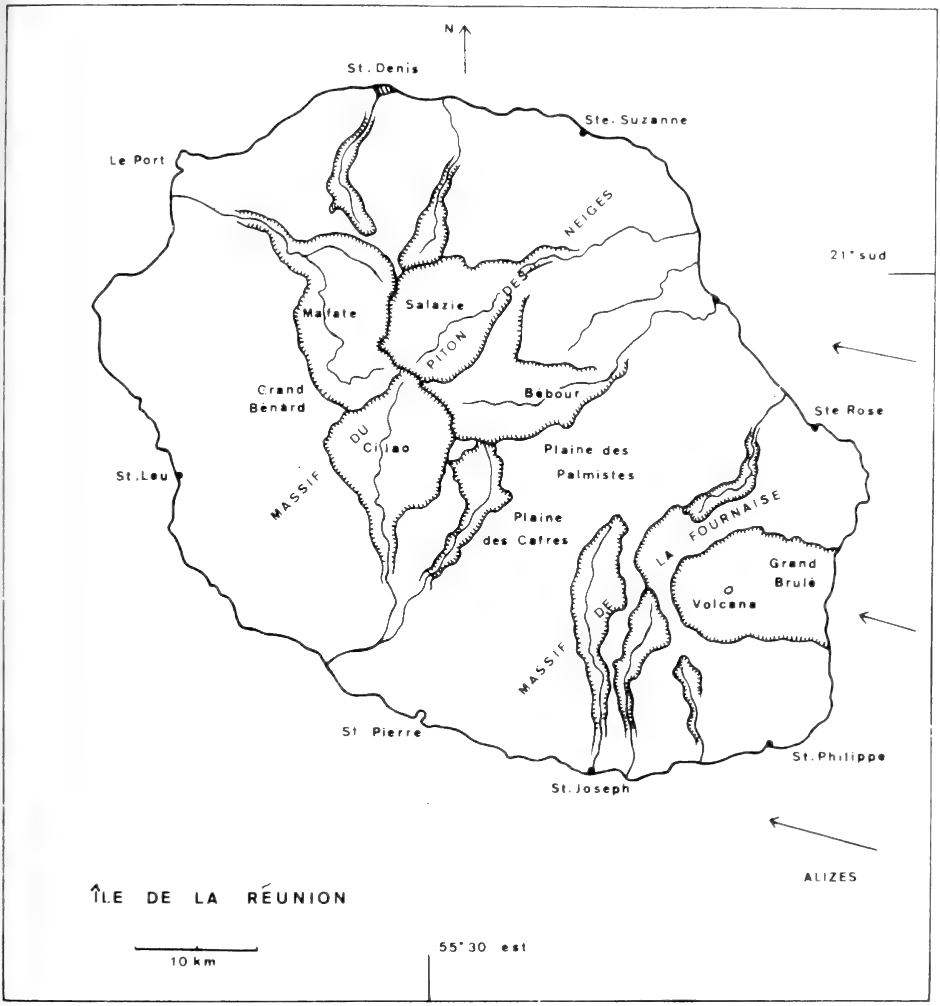

FIGURE 2. Map of Réunion Island showing chief volcanic areas, drainage and prevailing wind direction.

The mountain range results in markedly different climates between the windward and leeward regions. The ESE slopes, exposed to the direct force of the trade winds, experience a heavy rainfall (3m at St. Benoît) and have no ecologically dry season (the precipitation is more than 110 mm at St. Benoît for each of the months of August, September and October). In the leeward rain-shadow of the mountainous screen, a rather marked dry season prevails from May to November and the total yearly rainfall is much lower (less than 800 mm east of the port of St. Louis). In spite of this, most of the island receives more than 1500 mm of rain yearly, without any ecologically dry periods. The regions at low altitudes along the leeward zone are exceptional and the yearly total is frequently less than 1 m with a dry season that can be rather marked.

VEGETATION

As one goes from low to high altitude, the general aspect of the plant communities varies following more or less horizontal bands. This altitudinal succession of stages of vegetation depends on various factors among which are the decrease in temperature with altitude and the situation in relation to the ESE trade winds. The main zones of vegetation are as follows:

Littoral Vegetation

The original littoral vegetation has totally disappeared and has been replaced by secondary formations composed of numerous exotics with a few rare indigenous halophiles (*Scaevola taccada* (Gaertn.) Roxb., *Lysimachia mauritiana* Kam. and *Zoysia tenuifolia* Willd. ex Thiele).

Marsh Vegetation

Behind the littoral strands along certain coastal areas (St. André, St. Paul, Le Gol), marshes have developed which are flooded periodically. These have been colonized by large heliophytes among which the Cyperaceae are prevalent (*Cyperus papyrus* L. var. *madagascariensis* (Willd.) Kunth, *C. articulatus* L., *Eleocharis equisetina* Presl. and *Typha angustifolia* L.)

Megathermic Dry Sector Vegetation

This formerly occupied the zone occuring between the littoral and altitudes of 600 - 700 m in the leeward regions. Degraded remnants of this vegetation still exist along the vertical walls enclosing some of the large rivers (Riviére de St. Denis, Ravine de la Grande Chaloupe, Riviére des Galets, Bras de Cilaos and Bras de la Plaine). Species characteristic of this vegetation type may often be encountered in the form of a few isolated individuals. Some examples are : *Foetidia mauritiana* Lam., *Erythroxylum hypericifolium* Lam., *Olea chrysophylla* Lam., and *Cossignia pinnata* Lam. This formation probably occupied, at least in part, what today consists of lowland savanna of *Heteropogon contortus* Beauv. ex Roem. & Schult. and *Bothriochloa pertusa* (L.) Camus which have developed from the Massif de la Montagne (between 0 and 300 m) to the Plaine du Gol (near sea level at St. Louis).

Low Altitude Hygrothermic Forest or Lowland "Bois de Couleur" Forest

This formation formerly covered the lower slopes of the eastern region between 0 - 800 m, and in addition a narrow band in the west above the megathermic dry sector vegetation, between 700 and 1000-1100m. Today only more or less degraded vestiges remain at the Massif de la Montagne, the Plaine des Makes and above 600 m in the windward region. Some few remnants may also be seen in the region of St. Philippe and Grand Brulé below 400 m.

This type of vegetation consists of three characteristic strata : arborescent (average height of 10 - 15 m), understory shrubs, and herbs with the presence of numerous epiphytes (ferns and orchids). The most characteristic species are : *Sideroxylon majus* (Gaertn. f.) Baehni, *Mimusops maxima* (Lam.) Vaughan, *Labourdonnaisia callophylloides* Bojer, *Mallotus integrifolius* Mull. Arg., *Calophyllum inophyllum* L., *Hyophorbe indica* Gaertn., *Ochrosia borbonica* Gmel., *Eugenia cymosa,* Lam., *Eugenia paniculata* Lam., and *Diospyros melanida* Poir.

FIGURE 3. *Nephrolepis abrupta*, the first vascular plant on 1961 lava flow covered with the lichen *Stereocaulon vulcani*. Grand Brulé, 100 m.

High Altitude Hygrophylic Formations

These formations represent the best preserved stands of primary vegetation in Réunion today. The lower limits rise progressively from 700-800 m in the southeast and east to 1000 – 1100 m in the West and the upper limits extend from 1500 – 1600 m to about 2000 m. The floristic composition and physiognomy can be subdivided as follows:

1) The hygrophilic *Dombeya* or "Bois de couleur des Hauts" forest. In this type of forest the canopy trees rarely exceed ten metres. Epiphytes abound from ground level to the highest branches (e.g. at Plateau de Bébour and Plaine des Chicots). The most characteristic woody species are : *Dombeya reclinata* Cordem., *D. punctata* Cav., *Eugenia cotinifolia* Jacq., *Bertiera rufa* A. Rich and *Cladoxylon glandulosun* Baill.

2) The "Tamarin des hauts" forest (*Acacia heterophylla* (Lam.) Willd.). In the west at about 1300-1400 m the *Dombeya* forest passes progressively into a formation where *Acacia heterophylla* and *Nastus borbonicus* Gmel. are dominant. The latter species, a bamboo, forms an extremely dense but discontinuous lower stratum at Plaine des Chicots for example. The *Nastus borbonicus* stratum is inexistent on the east of Massif du Piton des Neiges (North of Plaines des Cafres, Bébour and Bélouve). Here it is replaced either by ericoid shrubs (*Philippia, Senecio, Stoebe* and *Phylica*) or by species found in the *Dombeya* forest.

3) Hygrophilous thickets of *Pandanus montanus* Bory. This formation type occurs on the eastern and northern slopes of the Massif de la Fournaise in a region receiving 5-6 m of rain yearly. Numerous tree ferns (*Cyathea* spp.) and *Acanthophoenix* palms impart a characteristic physiognomy to this formation.

High Altitude Ericoid Vegetation

This formation begins at 1600-1700 m in the windward and at 2000 m in the leeward

FIGURE 4. A group of *Dicranopteris linearis* (broad frond) and *Sticherus falgellaris* (narrow frond) in a pioneer shrubby vegetation along the road from St-Benoit to Plaine des Palmistes, 700 m.

FIGURE 5. A typical thermophilic and skiophilous species, the epiphytic fern *Antrophyum giganteum*. La Mare Longue forest near St-Philippe, 300 m.

FIGURE 6. Another typical fern species of the hygrophilous and thermophilic forest, the epiphytic *Asplenium nidus* with very large fronds attaining 2 m.

region. It consists of more or less dense thickets of ericoid shrubs (*Philippia montana* (Willd.) Klotzsch, *Stoebe passerinoides* (Lam.) Willd., *Senecio hubertia* Pers. and *Phylica leucocephala* (Bory) Cordem.) and also herbaceous or bushy montane species (*Faujasia pinifolia* (Bory) Cass., *Eriothrix lycopodioides* (Lam.) D.C., *Psiadia* spp. and *Heterochaenia rivalsii* Badré & Cadet).

Although the predominance of *Philippia montana* imparts a uniform appearance to this formation, variations in climatic and edaphic factors result in a number of subgroups; two of these are as follows:

1) Along its lower limits and in windward areas of very high rainfall the ericoid vegetation forms a very dense heath scrub of *Philippia* sheltering a herbaceous stratum rich in ferns. Beneath this primary vegetation, locally called "voune" or "avoune", there exists a thick cushion of raw humus which may exceed one metre in depth.

2) High mountain prairies. These are edaphic in origin, and develop over fine soil and débris which has accumulated in depressions. These prairies are rich in composites, *Cyperaceae* and *Graminae* (e.g. *Helichrysum arnieoides* (Lam.) Cordem., *Psiadia aspera* (Bory) Cordem., *Festuca borbonica* Spreng.) and also harbour two lycopods : *Lycopodiella affinis* (Bory) Pich.Serm. and *Huperzia saururus* (Lam.) Rothm.

DEFINITION OF THE PRINCIPAL ECOLOGICAL GROUPS

The distribution of pteridophytes on the island according to geography and station appears to depend upon three principal factors: temperature, light and humidity. The latter factor is the least decisive because of the high rainfall that most of the island receives.

The island's pteridophytes can be divided into two principal groups: those of forest formations including the pioneers (pioneer vegetation of *Nephrolepis abrupta* (Bory) St. John, pre-forest *Sideroxylon* association and *Philippia* scrub); and those which are associated with marsh vegetation, savanna, abandoned fields or have a more or less ruderal character.

Amongst the forest species, variation in temperature with altitude enable three categories of species to be defined:

- Thermophilic species of low to medium altitudes, 0 to 700-800 m, but extending to 1000-1100 m in the leeward zone, or even to 1200-1300 m in the cirque de Mafate and cirque de Cilaos where the altitude-temperature gradient differs from the usual one.
- Oligothermophilic species of extremely hygrophilic high altitude forests and ericoid vegetation of upper regions above 1000-1100 m.
- Eurythermophilic species occurring with the same frequency from sea level to the highest altitudes. Within the limits of the island, these species appear to be indifferent to temperature.

In each of the above three categories the light factor enables a further breakdown into:

- Heliophilic to hemi-skiophilous species. These are species of pioneer shrub formations, secondary scrubs occupying old abandoned fields or of forest clearings.
- Skiophilous terrestrial species growing beneath dense forests.
- Skiophilous epiphytes.

A group of species apparently restricted to remnants of forest in the warmer and drier regions of the west (the dry megathermic sector of RIVALS, 1952) is

FIGURE 7. ***Blechnum tabulare***, anoligothermic and pioneer species of fern with a cycad-like habit. *Philippia* thicket on recent lava flow at Basse Vallée, St-Philippe, 900 m.

FIGURE 8. *Vittaria isoetifolia*, with its long and very narrow fronds in tuft on the lower face of bowed trunks. Hygrophilous forest of Bébour, 1350 m.

FIGURE 9. The very commun ***Antrophyum boryanum***, an epiphytic, lithophytic or even terrestrial fern. Bébour, forest, 1350 m.

characterized equally by numerous species of phanerogams which, like certain pteridophytes, are no longer to be found on the island (thermophilic and more or less xerophilic species).

Amongst the non-forest species which are for the most part thermophilic heliophiles, there are:

- Saxicolic, more or less xerophilic species.
- Hygrophilic species of marshes, edges of water courses and seepage.
- Terrestrial species, some of which are more or less ruderal.

FOREST FERN SPECIES

These constitute the majority of the island's pteridophyte flora including more than 80% of the species.

Thermophilic forest species

The thermophilic species are associated with forests at the lower stage of vegetation occupying certain of the lower slopes of the island between 0 and 700-800 m altitude on the windward and 1000-1100 m on the leeward aspects.

These species are all more or less hygrophylic. More precisely, the humidity is quite sufficient here to assure their optimal development as a whole without much variation into sub-categories, except for those species of the "dry megathermic sector" as defined above.

Heliophilous or hemi-skiophilous species

These are essentially pioneer species colonizing lava flows. Some of these also occur in abandoned fields, others prefer forest clearings. *Nephrolepis abrupta* (Bory) Mett., *Sticherus flagellaris* (Bory) St. John, and *Dicranopteris linearis* (Burm. f.) Underwood are the three species which colonize recent volcanic flows (less than a century old) before the shrubs and trees have created a continuous canopy, at Grand Brule, for example. The latter two species are also encountered in considerable abundance in more or less degraded formations on mountain crests in all the low, humid regions of the island, particularly in the East (Hauts de St. Benoît and of St. André).

Sphaerostephanos elatus (Boj.) Holtt. (*Cyclosorus mauritianus* (Fée) Tard.) is a large, relatively hygrophilic fern very common in clearings, often along forest paths and roads, where it forms dense colonies. *Ochropteris pallens* (Sw.) J. Sm., *Lindsaea ensifolia* Sw. (*Schizoloma ensifolium* (Sw.) J. Sm.), and *Sphaerostephanos arbuscula* (Willd.) Holtt. (*Cyclosorus arbusculus* (Willd.) Ching), are less frequent, and the latter often grows in semi-shade, occupying rock fissures in stream beds. *Sphenomeris chinensis* (L.) Maxon is most frequently encountered in shrub formations occupying abandoned fields or along forest borders, paths and roads.

Skiophilous terrestrial species

The species in this category are not very numerous. The authors can cite *Angiopteris madagascariensis* De Vriese which had never before been recorded from Réunion, and is known only from the forest of Brûlé de Takamaka in the southeast. Also belonging to this group are species of *Ctenitis* (Nos. 3572 and 4371), *Selaginella obtusa* (Beauv.) Spring, of which there exists a form (or variety?) restricted to the rocky littoral of the southeast, and *Selaginella falcata* (Beauv.) Spring, which ranges up to 1100-1200 m altitude.

FIGURE 10. *Elaphoglossum splendens*, a typical epiphytic and skiophilous fern of the high altitude forest growing with the filmy fern *Hymenophyllum inaequale* on an horizontal trunk. Bébour forest, 1350 m.

Skiophilous epiphytic species

Certain of these can develop on rocks, at the bases of large tree trunks or on a substrate of still intact lava and constitute an essential part of the berbaceous stratum, but disappear where there is a true soil. Such is the case with ***Nephrolepis biserrata*** (Sw.) Schott and *Phymatodes scolopendria* (Burm. f.) Ching, both very abundant in forests occupying modern volcanic flows (100-200 years) in the southeast (St. Philippe region).

The true epiphytes in this group are numerous, certain of them are frequent and abundant: *Hymenophyllum sibthorpioides* (Bory ex Willd.) Mett. ex Kuhn, *Hymenophyllum hirsutum* (L.) Sw., *Trichomanes bipunctatum* Poir., *Trichomanes giganteum* Bory, *Ophioglossum pendulum* L., *Humata repens* (L.f.) Diels, *Vittaria ensiformis* Sw., *Asplenium pellucidum* Lam. (3404, 3388, 3595), *Asplenium nidus* L. (with immense fronds attaining 2m), *Microsorium punctatum* (L.) Copel, *Belvisia spicata* (L.f.) Mirb., *Arthropteris boutoniana* (Hook.) Pich. Serm., and *A. giganteum* Bory (fig. 5).

The remaining species are not particularly rare, but are represented by fewer individuals: *Antrophyum immersum* (Bory ex Willd.) Mett., *Elaphoglossum lepervanchei* (Fée) Moore, *Lomariopsis pollicina* (Willem.) Mett. ex Kuhn., *Vittaria scolopendrina* (Bory) Thwait., *Vittaria elongata* Sw., *Xiphopteris serrulata* (Sw.) Kaulf., *Trichomanes bonapartei* C. Chr. (Cadet 3333 and 3764).

Forest species within the dry megathermic sector

These tend to be more or less xerophilic. They can sustain a dry period sometimes exceeding two months (August-September). Their leaves are able to remain in a shrivelled state or tolerate the dryness because of their coriaceous lamina.

The more characteristic terrestrial species are: *Schizaea dichotoma* Sm., *Tectaria puberula* (Desv.) C. Chr. (3711 and 4117), *Asplenium adiantoides* (L.) C. Chr., *Asplenium viviparum* (L.F.) Presl., *Asplenium pellucidum* Lam. var. *dareaefolium* (Bory) Tard., *Adiantum reniforme* L. var. *asarifolium* (Willd.) Sim, and *Adiantum hispidulum* Sw. The latter two species have never been observed by the authors on the more humid side of the island (with the exception of a single station for *Adiantum hispidulum*) and apparently cannot tolerate a high and constant humidity.

Epiphytes are rare in this group. *Arthropteris orientalis* (J.F. Gmel.) Posth. thrives at the base of trunks and on rocks in open understories. It can also tolerate exposure to full sun and its fronds shrivel completely during the dry season. *Trichomanes pyxidiferum* L. var. *melanotrichum* (Schlechttend.) Schelpe is of rare occurrence. The commonest epiphytes are in fact those species with a large ecological amplitude for water. Abundant principally in the humid region, they persist equally in the dry sector, but develop less copiously .This is the case with *Nephrolepis biserrata* (Sw.) Schott and *Phymatodes* scolopendria (Burm. f.) Ching.

Oligothermic forest species

These may be encountered beginning at 800-900 m altitude in the east and about 1000 m in the west. Strongly hygrophilic, they are restricted to humid *Dombeya* forests and ericoid vegetation of high altitudes.

Heliophilic to hemi-skiophilous species

Certain of these demand a fairly high light intensity and grow in rather open tree formations along forest borders, ravines and roads, or in natural clearings. *Blechnum tabulare* (Thunb.) Kuhn, a large fern with a cycad-like habit, prefers *Philippia* thickets over intact lava flows for its habitat and occurs principally on the Massif de la Fournaise around the active volcano. Bory de Saint-Vincent named the Plaine des Osmondes after this impressive fern. *Blechnum montbrisonis* C. Chr. has more or less the same biotope and abounds beneath *Philippia* thickets covering intact lava flows between about 1500-2000 m altitude. This species also commonly grows inside ravines in dense rain forests. Certain other species are restricted to clearings, particularly in the "Tamarin des Hauts" forests: *Hypolepis villoso-viscida* (Thouars) Tard., *Histiopteris incisa* (Thunb.) J. Smith, *Athyrium scandicinum* (Willd.) C. Presl, *Pseudophegopteris aubertii* (Desv.) Holtt. (*Thelypteris cruciata* (Willd.) Tard.), *Ophioglossum ovatum* Bory and *O. reticulatum* L. may even grow in clearings within *Casuarina, Eucalyptus* or *Acacia* plantations.

The remaining species tend to occupy the lower stratum of pioneer ericoid formations: *Lycopodium clavatum* L. var. *borbonicum* Bory, *Mohria caffrorum* (L.) Desv., *Gleichenia boryi* Kze., *Amauropelta salazica* (Holtt.) Holtt., *Huperzia saururus* (Lam.) Rothm., *Lycopodiella affinis* (Bory) Pichi Sermolli. The latter two species are characteristic of high mountain prairies. *Huperzia selago* (L.) Bernh. ex Schrank & Mart. is known only from a single station at Petit Matarum in the Cirque de Cilaos. *Cyathea glauca* Bory is a component of the upper stratum in pre-forest formations and imparts a characteristic physiognomy to these.

Skiophilous terrestrial, more or less humilolous species

There are many species which are constant and highly characteristic components of the ground flora of high altitude rain forest : *Blotiella pubescens* (Kaulf.) Tryon, *Athyrium arborescens* (Bory) Milde, *Polystichum ammifolium* (Poir.) C. Chr.,

FIGURES 11 and 12. The obligothermic tree fern *Cyathea glauca*. Hygrophilous forest on the ridge between Cirque de Mafate and Cirque de Salazie, 1600 m.

FIGURE 13: An eurythermic terrestrial and skiophilous fern : *Marattia fraxinea.* La Mare Longue forest near St-Philippe 300 m.

Amauropelta heteroptera (Desv.) Holtt. (*Thelypteris heteroptera* (Desv.) Tard.), *Amaurolpelta strigosa* (Willd.) Holtt. (*Thelypteris tomentosa* (Thouars) Ching), *Dryopteris aquilinoides* (Desv.) C. Chr., *Ctenitis subglandulosa* (Mett.) Tard., *Ctenitis crinita* (Poir.) Tard., *Ctenitis mascarhenarum* – *lanuginosa* group, and *Ctenitis* sp. (Cadet 4154 and 4360). Other less abundant species include: *Selaginella cataphracta* (Willd.) Spring, *Ctenitis* sp. (Cadet 4155) and *Pteris croesus* Bory.

In the latter category we can also include *Asplenium unilaterale* Lam., an extremely hygrophilic species which thrives on humid soil and is particularly fond of humid rocks in shady stream beds and *Pityrogramma argentea* (Willd.) Domin. which favors old fallen trunks or humus tussocks especially in old *Acacia heterophylla* forests.

Skiophilous epiphytes

These species occur on tree trunks at various levels but always in the shade of the canopy. Certain of them are particularly common : *Pleopeltis excavata* (Bory ex Willd.) Schelpe, *Vittaria isoetifolia* Bory (with long and narrow pendant fronds), *Asplenium aethiopicum* (Burm.f.) Bech. (Cadet 3187, 3512 and 4114), *Asplenium boltonii* Hook. ex Schelpe, *Elaphoglossum aubertii* (Desv.) Tard., *Elaphoglossum splendens* (Bory ex Willd.) Brack., and *Elaphoglossum hybridum* (Bory) Brack. Others are less common and include: *Huperzia verticillata* (L.f.) Rothm., *Huperzia obtusifolia* (Sw.) Rothm., *Hymenophyllum peltatum* Desv., *Asplenium protensum* Schrad., *Asplenium rutifolium* (Berg.) Kze., *Asplenium theciferum* (Kunth) Mett., *Ctenopteris leucosora* (Boj.) Tard., and *Ctenopteris parvula* (Bory ex Willd.) J. Smith.

Some species, although consistently found growing on the lower and middle levels of trunks, tolerate increased light and may also become established on high and exposed branches. They may even be encountered within dense *Philippia* thickets at bases of shrubs or rooting in carpets of moss. They include the following species: *Blotiella glabra* (Bory) Tryon, *Elaphoglossum angulatum* (Bl.) Moore (*E. alstonii* Tard.), *Elaphoglossum* sp., *Ctenopteris rigescens* (Bory ex Willd.) J. Sm., *Ctenopteris torulosa* (Bak.) Tard., , *Pleopeltis macrocarpa* (Bory ex Willd.). The latter species is particularly abundant on the trunks and branches of *Acacia heterophylla*.

Cavernicolous species

A certain number of species favour rocky walls of grottos, fissures in cliffs, or rock concavities at high altitudes. These include : *Asplenium kassneri* Hieron., *Asplenium erectum* Bory ex Willd., *Asplenium stoloniferum* Bory, *Cystopteris fragilis* (L.) Bernh., *Ctenitis* sp. (1942, 1974, 2047, 1532, 1553), *Elaphoglossum deckenii* (Kuhn) C. Chr. var.rufidulum (Willd.) Tard., *Elaphoglossum hybridum* (Bory) Brack.var. *vulcanii* Lepervanche ex Fée, and *Elaphoglossum stipitatum* (Bory ex Fée) Moore. *Grammitis barbatula* (Bak.) Copel. is consistently found in this biotope, but may also occur in forests in extremely sheltered sites, e.g. on the lower surface of inclined trunks. *Cheilanthes farinosa* (Forsk.) Kaulf. is more or less heliophilic and occurs at the mouths of caverns or on the edges of cliffs.

Eurythermic forest species

In view of their geographic distribution over the island, these species have a wide tolerance for temperature. They are just as common in forests of low altitude as they are in those of the uplands.

In terms of biomass they are without equal amongst the pteridophyte flora.

The tree ferns

The tree ferns have a special appearance which imparts a characterised physiognomy to much of the island's forested expanses, so we shall give it special consideration. Two of the component species are truly polyaltitudinal. The first, *Cyathea borbonica* Desv. (*C. canaliculata* Willd.), has a fairly slender stem which often becomes ramified at higher altitudes. It is generally a component of the canopy where the trees exceed 7-8 m. *Cyathea excelsa* Sw. is, on the other hand, a large tree fern attaining 10-12 m. Its fronds are a component of and often transcend the canopy. The base, which is thickened by a dense network of adventitious roots, is used for the construction of planters ("fanjans") or support plaques well suited for orchid culture.

Cyathea glauca Bory is much more oligothermic and is never found below 1000-1100 m altitude. A pioneer species in ericoid formations, it dominates the upper stratum of preforest shrub vegetation for quite some time. During the hot and humid period its leaves dry up, after which new growth is initiated. The base of the stem of this species is used in the same way as that of *Cyathea excelsa*.

A fourth species of *Cyathea*, probably introduced, is cultivated in humid regions of low altitudes (Ste. Rose, St. Benoit, Plaine des Palmistes), where it now appears to be naturalized.

Heliophilic species

These species are not very numerous and three can be cited. *Lycopodiella cernua* (L.) Pich. Serm. is common within pioneer shrub formations and also in fallow land, particularly those of very humid regions. *Pteridium aquilinum* (L.) Kuhn is almost ubiquitous in fields on poor soil, fallow land, gravelly areas, secondary scrub and even more or less degraded forests. This incredible fern sometimes exceeds four metres in height. *Elaphoglossum spatulatum* (Bory) Moore is a tiny fern which grows exclusively on exposed and humid boulders in sheltered streambed. This species could be considered to be a heliophilic saxicole.

Skiophilous terrestrial species

At times these constitute the greater part of the forest ground flora. Examples include: *Selaginella sinuosa* (Desv.) Alston, *Selaginella surculosa* Spring, *Marattia fraxinea* Sm, ex J.F. Gmel., *Pteris scabra* Bory ex Willd., *Asplenium viviparum* (L.f.) Pr. var. *lineatum* (Sw.) Tard. and *Ctenitis* sp. (Cadet 1674 3399, 3472, 3378, 3544, 3555). The remaining species are much less frequent : *Trichomanes meifolium* Bory, *Trichomanes parviflorum* Poir., *Nephrolepis tuberosa* Bory, *Pteris cretica* L., *Pteris woodwardioides* Bory ex Willd., and *Blechnum australe* L.

Eurythermic, skiophilous epiphytes

Most species of this group are generally quite frequent. Certain are strict skiophile: *Huperzia squarrosa* (G. Forst.) Trev., *Huperzia gnidioides* (L.f.) Rothm., *Huperzia ophioglossoides* (Lam.) Rothm., *Asplenium petiolulatum* Mett., *Hymenophyllum hygrometricum* Desv., *Hymenophyllum inaequale* Desv., and *Hymenophyllum capillare* Desv. which is very exacting as far as shade is concerned, and is always found on the lower surfaces of inclined trunks or at base of trees.

Trichomanes erosum Willd. (probably synonymous with *T. cuspidatum* Willd.) is also extremely hygrophilic and has the same habitat as the preceding species but also grows closer to or even on the soil. The tiny fronds shrivel readily with the slightest decrease in humidity. *Trichomanes tamarisciforme* Poir. and *Elaphoglossum* *tomentosum* (Bory ex Willd) Christ are also present. *Antrophyum boryanum* (Willd) Kaulf. is often lithophytic or even terrestrial. *Blechnum attenuatum* (Sw.) Mett. occasionally forms a complete collar around trunks, especially those of Cyathea. At middle altitudes the species may acquire a terrestrial habitat and even constitute a dominant part of the herbaceous stratum. *Loxogramma lanceolata* (Sw.) C. Presl. quite often lithophytic, can withstand short periods of dessication. It also occurs in the Eastern dry zone inside ravines.

Certain other species are encounted less frequently : *Psilotum nudum* (L.) Beauv. (in crevices of more or less shaded rocks), *Trichomanes borbonicum* Bory, *Trichomanes digitatum* Sw., *Cheiroglossa malagassica* (C. Chr.) Pich. Serm. (*C. palmata* Presl var. *madagascariensis* C. Chr.), *Elaphoglossum richardii* (Bory) Christ, and *Monogramma graminea* (Poir.) Schkuhr.

Although indeed very abundant on trunks in the shade, another group of species is equally at home on high branches exposed to full sun. These include : *Rumohra adiantiformis* (Forst.) Ching, *Oleandra distenta* Kunze, *Elaphoglossum macropodium* (Fee) Moore, *Elaphoglossum petiolatum* (Sw.) Urban ssp. *salicifolium* (Willd. ex Kaulf.) Schelpe, *Ctenopteris argyrata* (Bory) Tard., and *Grammitis obtusa* Willd.

NON FOREST FERN SPECIES

The pteridophyte flora outside of the forest is poorly represented, probably because the biotopes are not very diverse. All thermophilic, these species can be divided into three ecologic categories.

Saxicolious, heliophilous more or less xerophilic species

Not very numerous, these species are highly characteristic of the "dry megathermic sector". They live in small cracks and fissures of the most exposed rocks and their fronds dehydrate completely during the dry season. *Actiniopteris australis* (L.f.) Link and *Actiniopteris radiata* (Sw.) L. are characteristic. The latter species can also be found between rocks of walls along roads. *Adiantum rhizophorum* Sw. prefers a more protected habitat and retains its leaves year round. We can add to this group *Pyrrosia lanceolata* (L.) Farw. which is found equally in the very humid eastern zone. It grows on isolated tree trunks and can withstand fairly prolonged dessication during the dry season.

Terrestrial, heliophilous, more or less ruderal species

A number of species have an ecology sometimes difficult to define. They commonly occur along roads, in fields at the base of dry stone walls, in gravel and sometimes in fallow land.

Plants of such situations include : *Pellaea viridis* (Forsk.) Prant. var. *viridis* and *Asplenium adiantum-nigrum* L. *Equisetum ramosissimum* Desf. is almost always encountered on the moist alluvium deposited in torrent beds or on their banks but also occurs on impermeable soil within the "cirques", where it attains 1600-1700 m altitude. *Ophioglossum lancifolium* C. Presl and *O. nudicaule* L.f. are diminutive ferns allied encountered in *Heteropogon* savannahs in the west. Their fronds appear just after the first rains marking the end of the dry season. This species has the same ecology in Madagascar. *Pteris linearis* Poir. occurs at the foot of walls in the dry western region. *Pityrogramma calomelanos* (L.) Link. var. *calomelanos* grows between rocks in stream beds that are almost always dry and also along roadsides. *Pityrogramma calemelanos* var. *aureoflava* (Hook.) Weath. ex. Bailey is commonly situated along roadsides. *Sphaerostephanos unitus* (L.) Holtt. (*Cyclosorus unitus* (L.) Ching) is extremely frequent in abandoned fields and along roads. *Macrothelypteris torresiana* (Gaud.) Ching (*Thelypteris uliginosa* (Kunze) Ching) may occur between rocks of torrent beds which are for the most part dry.

Certain species are extremely localized, being restricted to one or two "cirques". *Cheilanthes hirta* Sw., *Pellaea calomelanos* (Sw.) Link. var. *calomelanos* and *Pellaea dura* (Willd.) Hook. are known only from the Cirque de Cilaos and Cirque de Mafate. Two other species are known exclusively from the Cirque de Cilaos : *Doryopteris pedatoides* (Desv.) Kuhn. and *Doryopteris pilosa* (Poir.) Kuhn. All of these species are absent from the Cirque de Salazie, which is much more humid. They can be considered as species which are thermophilic but scarcely hygrophilic.

Hygrophilic and heliophilic species of marshes, water courses and seepage

Not many species grow in this biotope. *Cyclosorus interruptus* (Willd.) H.Ito (*Thelypteris totta* (Thunb.) Schelpe) is abundant around marshes at low to medium altitudes. *Osmunda regalis* L. grows in areas of marshy prairie below the village of Plaine des Palmistes, the only known station. *Athyrium accedens* (Bl.) Milde (*Diplazium proliferum* (Lam.) Kaulf.) and *Pteris pseudolonchitis* Bory are most frequently encountered amongst rocks along permanent streams or springs, or on talus slopes along irrigation canals at low altitudes.

The flora of waterfalls and seepage at low altitudes is characterised by *Adiantum capillus-veneris* L., and *Pteris vittata* L. the latter of which is not exclusively found in this habitat and occasionaly occurs along streams on humid alluvials. *Christella hilsenbergii* (Presl) Holtt. is a sun loving species which is not very particular in its water requirements. It is also found on seepage areas as well as on the almost permanently dry silty banks of streams and in the undergrowth of forests of the hot dry parts of the island.

CONCLUSIONS

Most of the 240 or so species of native pteridophytes are still abundant in Réunion because they occupy habitats which are presently quite extensive and they do not have ecological requirements that are highly exacting. Many hygroskiophilous species of low altitudes, for example, may thrive in secondary formations (*Eugenia jambos* L. forests) which have taken the place of the indigenous forests. Other species, notably those belonging to the genera *Hymenophyllum*, *Trichomanes* and *Humata*, even grow on old fruit trees in orchards. On the other hand, as a consequence of the reduction of the areas once occupied by the forests in the dry megathermic sector, certain species restricted to this formation have become rare, for example *Asplenium adiantoides* (L.) C. Chr., *Actiniopteris radiata* (Sw.) Link, and especially *Actiniopteris australis* (L.f.) Link which is confined to emergent rock faces in the *Heteropogon* savanna of the leeward region. These species are infrequent and more importantly, are menaced by fires. *Pellaea calomelanos* (L.) Link var. *calomelanos*, *Doryopteris pedatoides* (Desv.) Kuhn, and *D. pilosa* (Poir) Kuhn are only encountered at rare stations, principally in the Cirque de Cilaos, in areas alternatively cultivated and left fallow. *Asplenium nidus* L. is also in danger because it is often collected for its attractive fronds.

Various other species such as *Vittaria scolopendrina* (Bory) Thwait. and *Angiopteris madagascariensis* De Vriese are limited to areas of low altitude humid forest which have become established on lava flows about 200 years old. Their restricted distribution can only be explained by man's destruction of this type of formation. These species are thus threatened by extinction.

ACKNOWLEDGEMENTS

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REVIEWS

FERNS OF HONG KONG by Harry H. Edie XVIII + 285 pp., 15 pl. Hong Kong University Press, 1978. 214 x 140 mm. Price not quoted.

This is a flora of the island of Hong Kong and that part of the China mainland and offshore islands that make up the New Territories. Harry Edie has written this book "out of necessity" for his undergraduate students and the first 23 pages therefore are devoted to notes on life-cycle, ecology, classification morphology and evolution. These are clear and concise and will be easily understood by amateurs and sixth-form students alike. That on classification is weakest and I feel the higher taxa could have been discussed more fully or, at least, references given to up to date work on the subject. In that on morphology, the variation of spore shape and wall structure and ornamentation is not mentioned nor is its importance as a taxonomic character. I would have liked a paragraph on geographical affinities to emphasise that some 50% of the species are south-east Asian ranging from India to S.E. China and often to Philippines and Malesia; 12% are Chinese reaching Formosa and Japan, and only 17% are confined to SE China. Two or three species are doubtfully endemic.

There is a checklist to the 180 or so species covered, arranged according to R.E. Holttum's account of genera for *Flora Malesiana*. One new combination (*Lunathyrium zeylanicum* (Hook.) H. Edie) is made there. Keys and descriptions are good, illustrated with clear thumbnail sketches by the author. Standard of binding (soft but durable) and printing are good. I detected only one printing error *Arachnoides* instead of *Arachniodes* and perhaps 'deltoid' (p.18) should be 'deltate' but these are minor points. This is a nice book to possess as an introduction to the fern flora of mainland east Asia and will, I feel sure, encourage the study of ferns generally in that part of the world.

A.C. JERMY

THE PTERIDOPHYTE FLORA OF FIJI by G. Brownlie. 397 pp. 44 plates. 175 x 250 mm. (Beihefte 55 zur Nova Hedwigia). J. Cramer, Vaduz, 1977. Price DM 200 (about £51.00) Subscription price DM 160 (about £41.25).

The main body of this work is given over to description of families (25), genera (89) and species (296) of the pteridophytes found on the Fiji island Group. Full place of publication is given for each taxon but few details are given on types. The author, Garth Brownlie, on the staff of the University of Christchurch, Canterbury, NZ, has already one other fern Flora to his credit, namely that of New Caledonia. This reviewer would have wished for a biogeographical discussion on the flora of Fiji and more about the environment of those islands; only seven pages are given over to introductory matter.

Eighteen of the species are described here for the first time (in *Belvisia, Bolbitis, Ctenitis, Ctenopteris, Elaphoglossum, Grammitis, Hypolepis, Lycopodium, Microlepia, Pteris, Tectaria* and *Trichomanes*). The following new combinations are also made: *Dicksonia moluccana* Bl. var. **inermis** Baker is transferred to *Dennstaedtia*; *Microlepia* **tenuis** Brack. to *Orthiopteris*; *Ctenitis* **gordonii** (Baker) Copel. and *Athyrium* **gillespiei** to *Lunathyrium; Dryopteris* **maxima** (Baker) C.Chr. to *Arachnoides; D.* **waiwaiensis** C.Chr. to *Ctenitis; Lomaria* **coriacea** Brack., *L.* **doodioides** Brack. and *L.* **pilosa** Brack. to *Blechnum;* and *Microsorium* **parksii** Copel. to *Phymatosorus*.

The book is of the technical standard we have come to expect from J. Cramer; clear typography and the plates by Hélène Mulder are exceptionally good and show useful diagnostic features. However, one must ask the question: "For whom do we write such Floras?" For the professional botanist, the student or keen amateur who wishes to identify ferns of Fiji the meat of this book could have been produced for one quarter the price.

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A NEW SPECIES OF LOMARIOPSIS FROM MAURITIUS

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ABSTRACT

A new species of *Lomariopsis, L. mauritiensis* Lorence, is described from Mauritius, and its ecology discussed.

INTRODUCTION

During the preparation of an account of *Lomariopsis* for the forthcoming 'Flore des Mascareignes', examination of material of the genus from the Mascarene Islands has revealed the existence of a new species. The genus is represented in the Mascarenes by four indigenous species restricted to the islands of Mauritius and Réunion, none occurring on Rodrigues. The gregarious *Lomariopsis pollicina* (Willem.) Mett. is undoubtely the most frequently encountered species on both islands. It is particularly common on Mauritius in lower montane wet and cloud forest formations. Young Mascarene specimens tenatively assigned to *L. buxifolia* (Kuntze) Fée (type from Madagascar) by Holttum (1939) appear to represent extreme variants of *L. pollicina*, which is quite plastic in its juvenile form. The other three species of *Lomariopsis* are much more localized in distribution. Three collections of *L. cordata* (Bonap.) Alston, a Madagascan species, were made by Commerson (herb. Paris) on Réunion almost 200 years ago and represent the only known occurrence of the species in the Mascarenes. *L. variabilis* (Willd.) Fée, with its remarkably polymorphic juvenile fronds, is presently known only from a single station on Mauritius. Its present status on Réunion is uncertain, having been last collected there over one hundred years ago. Finally, *L. mauritiensis* is apparently restricted to Mauritius where it is likewise known from a single locality at present (Lorence 1978).

Lomariopsis mauritiensis Lorence, sp. nov. (Figs 1 & 2)

Affinis *Lomariopsis pollicina* (Willem.) Mett., differt bathyphyllis 2-jugis dispositis, acrophyllis 3-6-jugatis bis latioribus, rhachidi alata, squamis rhizomatis obscurius brunneis minoribus (0.5-0.8 x 7-8mm) et habitatione riparia. Frons fertilis ignota.

TYPE: MAURITIUS, eastern flank of Mt. Lagrave, *Lorence 821* in MAU 16293 (MAU-holo). PARATYPES: MAURITIUS, Curepipe, Kanaka, *Emmerez s.n.,* Aout 1907 (P); Mt. Lagrave, eastern flank, *Gueho & Lorence 1638* (MO).

Riparian fern, rhizome dorsiventral, long-creeping, fronds two-ranked, 2-3cm distant, apex covered with soft, curling, glossy medium brown scales intermixed with smaller glandular scales and hairs. Rhizome scales (Fig. 2A) linear-ovate to subulate, to 0.5-0.8 x 7-8mm, base truncate to rounded, apex filiform or sinuate with glandular tip cell, margins subentire, bearing scattered multicellular cilia 0.1-0.5mm long, cells long-rectangular, seriate, walls dark brown, lumina pale brown. ACROPHYLLS: Sterile frond 16-35cm long. Stipe 12-17cm long, 1.5-2.0mm diam., dull pale brown to stramineate, winged in upper half, wings continuing as dark lines to rhizome, adaxial surface sulcate. Stipe bearing at its base a few scales like those of the rhizome but paler brown and wider (to 1mm wide) with cordate base (Fig. 2B). Entire length of stipe bearing sparse, scattered small brown multicellular glandular scales or hairs. Lamina ovate to ovate-elliptic, 15.5-22.5 x 10.0-0.18.0 cm, imparipinnate, lateral pinnae 3-6-jugate, articulate, subsessile, subopposite to alternate, spaced 2.5-3.0cm on each side, the basal ones slightly reduced. Rachis winged, slightly zig-zag, adaxial surface sulcate, abaxial surface rounded and stramineate, bearing sparse small brown multicellular-glandular hairs scattered along its length. Largest lateral pinnae ovate-elliptic to linear elliptic, slightly falcate, 7.0-10.5 x 2.0-3.0cm, apex obtuse or usually bluntly acuminate, basiscopic side of base oblique and narrowly cuneate, acroscopic side broadly cuneate. Costula raised, stramineate, adaxial surface grooved, abaxial surface rounded. Veins raised on both surfaces, simple or usually forking 1-2 times, tips free, thickened into hydathodes. Margin slightly revolute, entire, slightly sinuate, narrow, brown and cartilaginous. Lower surface of pinnae bearing scattered, adpressed brown septate glandular-tipped hairs ca 1mm long, entire or branched (Fig 2C). Drying dark olive brown on adaxial surface, much paler beneath. Terminal pinna not articulated, similar to laterals but larger, to 10-14 x 2.5-3.2cm, apex usually acuminate. Fertile frond unknown.

BATHYPHYLLS ca 10cm long, stipe 5cm long x 1mm diam. Lamina with 2-jugate pinnae 1.0-1.2cm distant, subsessile, ovate-elliptic, lateral pinnae 1.8-2.8 x 1.1-1.5cm, base narrowly cuneate, apex obtuse, terminal pinna larger, rachis winged.

ECOLOGY

Presently known only from the type locality on the eastern flank of Mt. Lagrave, (alt. ca 600m), in low cloud forest invaded by exotics, the new species was found to be extremely localized. A few plants were seen creeping over mossy rocks in the bed of a small stream in the deep shade of a forested ravine. Fertile material should be sought in order to complete our knowledge of the species. The type locality is extremely rich in pteridophytes, some 40% of the island's species occurring there (Lorence, 1978). The collection made by D.D. Emmerez de Charmoy in 1907 unfortunately gives no precise collection data, merely stating "Curepipe, Kanaka." However, these two upland localities are separated by about 10km, the whole of which has been more or less completely deforested, so that chances of relocating the species there are almost nil. Preservation of the habitat at Mt. Lagrave is therefore essential in order to ensure the survival of this species.

ACKNOWLEDGEMENTS

I am grateful to the curators of the herbaria at Kew, Mauritius and Paris for the loan of specimens used in this study. Warmest thanks are extended to Professor R.E. Holttum for encouragement and advice.

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A NEW SPECIES OF ASPLENIUM FROM MAURITIUS

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ABSTRACT

A new species of *Asplenium, A. mauritiegsis* Lorence, is described from Mauritius, and its ecology discussed.

INTRODUCTION

Asplenium is the largest fern genus to occur on Mauritius (SW Indian Ocean), constituting eleven species and four varieties of the 163 pteridophytes presently known from the island (Lorence, 1978). Although Mauritius has been well botanized since the 18th century by French, British, Mauritian and other collectors, recent intensive collecting for the forthcoming 'Flore des Mascareignes' continues to yield occasional new species and new records for the island.

While on Mauritius, I encountered an undescribed species of *Asplenium* on the summit of Piton du Fouge. Examination of specimens at the Royal Botanic Gardens, Kew, Museum National d Histoire Naturelle, Paris and Missouri Botanical Garden herbaria failed to reveal a comparable species.

DESCRIPTION

Asplenium mauritiensis Lorence, sp. nov.

Species *Asplenium angolense* Baker affinis; gemmis 2-10 lateralibus utroque costa pinnis lateralibus terminalibus praesentibus, venis proximioribus ca 1 mm distantibus, squamis rhizomatis stipitisque maioribus integris 8-12 x 0.5-0.8 mm differt.

TYPE: MAURITIUS. Piton du Fouge, crest near summit, *Lorence 1602* (holotype MO; isotypes K, MAU, P). PARATYPE: MAURITIUS, Piton du Fouge, *Lorence 1019* (MAU) (Fig. 1).

Terrestrial fern, rhizome prostrate, short-creeping, 6-7 mm diam. (excluding scales), apex densely paleaceous, fronds caespitose, ca 5 mm distant. Scales of rhizome narrowly- to linear-ovate, falcate, 8-12 x 0.5-0.8 mm, clathrate, cells rectangular, cell walls dark reddish-brown, lumina transparent, base truncate, slightly constricted, margins entire, apex long, filiform, tip cell glandular. Stipe 11-22 (-28) cm long, 1.5-2.5 mm diam., slightly swollen and stramineate at base, pale greenish-gray above, adaxial surface sulcate with low, lateral decurrent ridges, when young bearing at base linear-ovate scales 8 x 1 mm, clathrate, base peltate, margins entire, apex filiform; upper part of stipe bearing smaller curling or sinuate scales, the peltate, substellate base bearing glandular-tipped cilia. Lamina ovate to elliptic, 18-21 (-24) x 9-14 cm, imparipinnate, pinnae 2-4 (-5) pairs, opposite to sub-opposite, 3.5-5.5 cm distant, ascendant at 70-80° angle, subequal, the lowest pair slightly reduced, borne on petiolules 1-2 mm long. Rachis flattened, winged, shallowly sulcate near the base, when young bearing scattered scales 1-2 mm long with tortuous, filiform glandular tip, the substellate base clathrate, ovate, bearing 1-3 pairs of glandular cilia. Largest pinnae 4.5-8.5 x 2.0-3.3 cm, narrowly angular-ovate, trullate to trapezoidal, slightly falcate; basiscopic side of base narrowly cuneate, acroscopic side broadly cuneate to truncate or auriculate, auricle not detached; apex bluntly acute to acuminate; margin shallowly dentate-serrate, teeth 1 mm long, 5-6 per cm. Drying pallid chalky green; texture flexible, herbaceous. Apical pinna similar to laterals but longer and more deeply serrate or even incised. Veins forking 1-2 times, at an angle of 30-40° with costa, tips free, ending in elliptic hydathodes on adaxial surface of lamina 1 mm diatant. Both surfaces of pinnae when young bearing tiny scattered scales 1.0-1.5 mm long with tortuous, filiform glandular tips, cell walls dark, base 0.5 mm wide, clathrate, substellate with 1-3 pairs of glandular-tipped cilia. Scales on upper surface soon caducous. Sori 10-20 pairs on alternate veins, often alternately long and short, 3-10 mm long, situated midway between costa and margin, indusium 0.5-0.6 mm wide, linear, falcate, white, membranous, not reflexed at maturity. Mature plants gemmiferous, adaxial surface of pinnae each bearing 2-10 gemmae along either side of costa.

FIGURE 1. Paratype of *Asplenium mauritiensis* Lorence from Piton du Fouge, Mauritius (alt.ca 650 m). Note abundance of gemmae and their lateral position along costa on both terminal and lateral pinnae.

AFFINITIES

The new species is most closely allied to and indeed strongly resembles *Asplenium angolense* Baker from Kenya and Uganda in terms of gross morphology. In fact, I was at first inclined to regard the two as conspecific, differing at an infraspecific level. However, closer examination has revealed a number of more important differences. Most striking are the differences in scales. In *A. mauritiensis* scales from the rhizome and base of stipe are much larger (8-12 x 0.5 -0.8 mm), narrowly to linear-ovate, with entire margins and long-rectangular cells, but in *A. angolense* they are tiny (1-2 x 0.5 mm) ovate-deltoid with glandular-ciliate margins and short, squarish cells. Both species are gemmiferous, but Faden (1973 and pers. comm.) notes that *A. angolense* produces only a single gemma medially on the upper surface of the terminal pinna, while in *A. mauritiensis* from two to ten gemmae are produced on both sides of the costa on the terminal and frequently the lateral pinnae as well The veins on *A. angolense* are spaced about 2 mm distant but are only about 1 mm apart in *A. mauritiensis.* Although closely allied to *A. angolense,* these differences are sufficiently important for the Mauritian plants to merit specific status. Fern scales provide excellent diagnostic features and are critical to the taxonomy of the group.

ECOLOGY

Piton du Fouge is one of the highest peaks of the southernmost flanking mountain range, ca 650 m, and is the only known locality for *A. mauritiensis*. The peak represents an ecologically unique situation for the island. Its extreme southwestern position provides it with rainfall of 1800 mm per year carried by the southeast trade winds, significantly higher than that received by adjacent mountains, and subjects it to comparably high temperatures

A single extremely localized colony of about 20-25 plants of *A. mauritiensis* measuring about 30 x 10 m was found growing along the crest just below the summit in moderate shade of a low montane evergreen forest dominated by *Diospyros tesellaria* Poiret, *Securinega durissima* Gmelin and *Nuxia verticillata* Lam. *Asplenium auritum* Sw., *A. nitens* Sw. and *A. viviparum* (L.f.) Presl var. *viviparum* were also locally common as ground ferns or growing at bases of trees.

The presence of this unique colony of *A. mauritiensis* on Mauritius seems to indicate extreme ecological specificity. Reproduction in the small colony may be exclusively vegetative; the occurrence of plantlets growing from fallen gemmae around mother plants was common. Although the colony appears to be in no immediate danger, preservation of the habitat at Piton du Fouge is imperative in order to ensure survival of the species.

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REVIEW

THE BIOLOGY OF BRACKEN – Edited by F.M. Perring and B.G. Gardiner for the Linnean Society of London. Bot. J. Linn. Soc. Vol. 73 nos. 1, 2 & 3 (1976) pp. viii + 302. Academic Press. London. 257 x 180 mm. £13.20

This substantial volume is the result of a Symposium on the biology of *Pteridium aquilinum* (L.) Kuhn held in London on 3rd and 4th September 1974. It is well edited and nicely executed to the standard we except from the Linnean Society and Academic Press.

The most significant papers for the pteridologist are those on the Taxonomy and phytogeography by C.N. Page (pp. 1–34), and on Chemotaxonomy and phytochemical ecology by G. Cooper-Driver (35–46). Page reviews morophological and cytological evidence for the phylogenetic affinities of the genus and concludes that although related possibly to Dennstaedtiaceae it should perhaps be placed with *Paesia* and *Hypolepis* in a separate family, the Hypolepidaceae. Unfortunately due to the restricted amount of work on other genera this could not be substantiated chemically by Copper-Driver. The infra-specific taxonomy discussed by Page is based predominantly on R. Tryon *(Rhodora,* 43: 1–31, 36–67; 1941) and whilst the geography of each of the twelve varieties is fully discussed the morphology and distinctions of each are not. This could, of course, have been boring in a delivered paper but the reviewer would have found a key to varieties very useful indeed in this printed account.

Peter Bell and J.G. Duckett give a detailed account of (pp. 47–78) the principal events in spermatogenesis and oogenesis and point out the parallels of the spermatozoid with the motile cells of chaetophoralean algae. The chemistry of bracken is discussed a great length in five papers. The reason why bracken is so well studied in this field is I suspect because of its abundance and also because it is an economically importance pest. H.J. Duncan and M.C. Jarvis (pp 78–85) discussed the role of sugar nucleotides; G.H. Williams and A. Foley (pp 87–93) showed that a knowledge of seasonal variation in carbohydrate content is important for controlling by cutting and herbicide-application; S.R. Gliessman showed (pp 95–104) how toxins released by dead bracken frond allow the plant to assert its dominance over associated plants. An enzyme, thiaminase, which destroys thiamine is the main contributor to the poisonous effect of bracken on animals according to W.C. Evans (pp. 113–131); other substance, among them shikimic acid, are shown by I.A. Evans (pp 105–112) to cause cancer and the possibility of an environmental human hazard must not be ruled out.

Four papers discuss the ecological role of bracken. The most important is that by Alex Watt (pp 217–239) who has spent a lifetime studying the species – and it is mainly thanks to him that this symposium contains the contributions it does. He points out that where litter formed in the bracken stand exceeds loss through natural decomposition, bracken may become the victim of its own success through having to recycle the nutrients of its own tissues. S.A. Hutchinson showed (pp 145–150) the effects of Fungi on bracken and J.C. Frankland (pp 133–143) showed that whilst readily leached components (Na, K and P) may be removed from dead fronds within a few months the main body of stipes and rhachides took 11 – 23 years – hence the value of bracken peat to the horticulturist and bracken straw to the farmer as bedding for animals. The latter reminded the reviewer of being shown a stand of bracken on an estate in the Island of Mull which was conserved for its use in the cow-shed, there being little other on the estate of 200 ha! J.H. Lawton described (pp 187–216) the one important animal community, namely the arthropods and their relation to seasonal change.

The control of bracken is briefly discussed by D.J. Martin (pp 241–246). P. Veerasekaran, R.C. Kirkwood and W.W. Fletcher describe (247–268) the mode of action of *Asulam,* the herbicide which the agriculturist believes spells salvation and which the pteridologist fears bodes ill for the conservation of other species of ferns which are also killed regardless. I.A. Nicholson and I.S. Patterson discuss (pp 269–283) the ecological implications of bracken control to plant/animal systems. They estimate that bracken herbicide is unlikely to be used on more than 25% of Scotland's bracken coverage because of the cost of the produce and its application, and that wild vertebrate populations are not in jeopardy. In a paper on the botanical implications of bracken control (pp 285–294) C.J. Cadbury considers Asulam to be a useful aid to the management of nature reserves where bracken needs to be controlled but emphasies that indiscriminate aerial spraying can be detrimental.

Lastly two papers were presented on the history of the occurrence and use of bracken. M.R.D. Seaward reported (pp 177–185) the occurrence of bracken in the pre-Hadrianic deposits at Vindolanda, Northumberland and L. Rymer, in a very readable and interesting paper (pp 151–176), reviewed the uses and ethnobotany of this fern we now come to know as a pest.

The volume reviewed above is a compendium on *Pteridium acquilinum* and all biological and agricultural research institutes and libraries should, if they are not subscribers of the Linnean Society of London, obtain it.

A.C. JERMY

FIRE-RESISTANCE IN THE PTERIDOPHYTES OF ZAMBIA

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ABSTRACT

Observations have been made on the incidence of burning in various types of habitats occupied by the pteridophytes in the savanna woodland zone of Zambia, and the relevant herbarium collections have been checked for fire-scars. No less than one fifth of all pteridophyte species in the study area proved to be able to survive repeated burning, and some of them possess morphological and biological features of advanced pyrophytes. Problems of origin and evolution of the pyrophytic habit in the pteridophytes are briefly discussed.

INTRODUCTION

Fire is commonly recognized as a master factor shaping the vegetation in seasonally dry parts of tropical Africa. Various types of savannas and savanna woodlands of this immense area are believed to be fire-climaxes (Fanshawe 1971, Hopkins 1963, Knapp 1973, Phillips 1974, West 1972), and many plant species occurring there possess peculiar morphological and biological features which enable them to persist under recurrent burning (Cole 1974, Exell and Stace 1972, Jackson 1974, West 1972). Such pyrophytic adaptations, however, have been studied so far only in the phanerogams, and almost nothing is known about the effects of burning upon the pteridophytes growing in fire-affected habitats in tropical Africa and elsewhere. The scope of the present paper is to contribute towards filling this gap and to present an evidence as to the importance of the fire factor in the life of ferns and fern-allies in Zambia.

STUDY AREA

Zambia is situated in the very heart of the Zambezian Domain of the Sudano-Zambezian Phytogeographical Region (White 1965, Chapman and White 1970). It has a typical tropical savanna climate (type Aw in Köppen's system, type II in Walter's classification), with a warm rainy season between November and April, and a long dry season, cool at the beginning (May-July), but becoming more and more hot towards the end (August-October). The annual rainfall is more than 1200 mm in the north decreasing gradually to 800 mm or less in the south, in the Zambezi and Luangwa valleys. The dry season is the burning time for vegetation and most of the country, except for farmland and land with permanently wet soils, falls prey to fire before the new rains start.

The main vegetation types occurring in Zambia have been recently described by White (1969) and Fanshawe (1971). Savanna woodlands occupy the majority of the territory, especially on the vast expanse of the Central African Plateau. Savannas and flood-plain grasslands are also fairly common, while other vegetation types are confined to small areas with unusual conditions of moisture and soils.

The Zambian flora is rather poor in ferns and fern-allies. Only 144 species have been found to occur there (Schelpe 1970, Kornaś 1974, 1976), many of them very rare and strictly limited to the higher rainfall areas in the northern part of the country. Many species show a decided preference for rare extrazonal communities of special habitats (e.g. evergreen forest patches) or for the earlier successional stages in both xeroseres (on rocks) and hydroseres. Very few pteridophytes occur in mature stands of near-climax woodland communities.

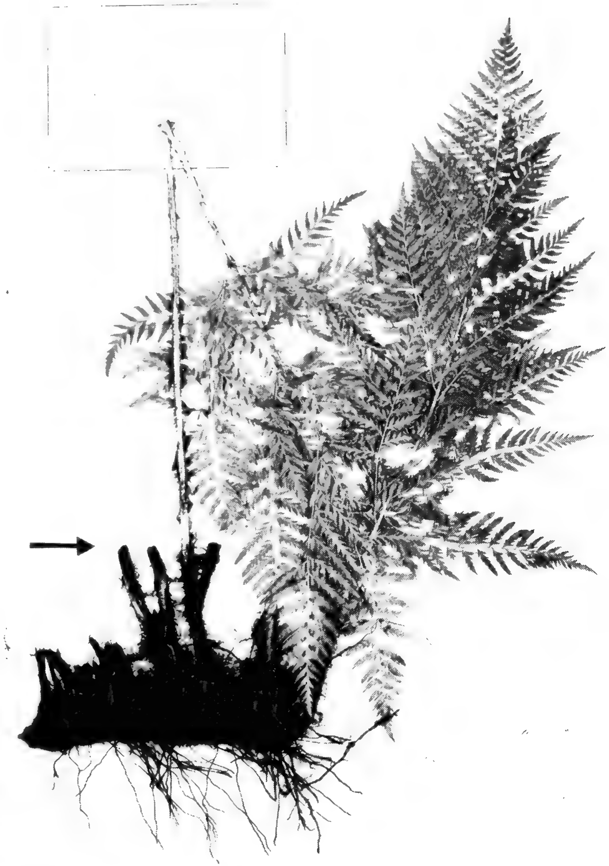

FIGURE 1. *Cheilanthes angustifrondosa* with fire-scars on stipes of the previous year. Zambia, Northern Province, Kalambo Falls, 7 April 1973. J. Kornaś Pl. Afr. 3662 (KRA).

FIGURE 2. *Dryopteris athamantica* with fire-scars on stipes of the previous year. Zambia, Central Province, near Serenje, 3 February 1973. J. Kornaś Pl. Afr. 3141 (KRA).

MATERIALS AND METHODS

Field data on the incidence of fires in various types of habitat and on the effects of burning upon the pteridophytes have been collected between August 1971 and July 1973 during extensive trips throughout Zambia (except the Western and Luapula Provinces – fig. 16 A). These observations have been subsequently confirmed and supplemented through the study of herbarium specimens from Zambia in the author's collection deposited at the Institute of Botany of the Jagellonian University of Kraków (KRA*, duplicates in AAU, BR, EGR, G, K, MO, NDO, NSW, and the University of Zambia Herbarium, Lusaka), as well as in the herbaria of the Royal Botanic Gardens, Kew (K), British Museum (Natural History), London (BM), Commonwealth Forestry Institute, Oxford (FHO), and the East African Herbarium, Nairobi (EA). Every complete specimen of a pteridophyte with its underground parts properly preserved has been carefully checked under the binocular microscope for fire-scars. This is a very simple and reliable test for detecting burning marks from the previous season which usually appear very clearly as charred remnants of old stipes, more or less evenly cut near the ground-level (figs. 1-15). There is, however, one serious limitation to this test: it is applicable only to those plants in which some living or dead above-ground organs normally persist through the dry season of the year. Plants with their perenating organs hidden under the ground (geophytes) do not usually bear any fire-scars even when growing in places evidently burnt in the last dry season. Therefore the real number of species which survive the fires is certainly higher than that confirmed through the study of herbarium specimens.

The species limits and nomenclature adopted in the present paper are those proposed by Schelpe (1970).

RESULTS

Numerical data concerning fire-scarred specimens found in the herbarium collections of pteridophytes from Zambia are presented in table 1. All in all 23 species (22 ferns and 1 club-moss) are listed, i.e. almost 16% of the total number of 144 species of ferns and fern-allies known to occur in that country. According to the field notes, half a dozen or so further species, mostly geophytes (*Pteridium aquilinum* (L.) Kuhn, *Nephrolepis undulata* (Afz. ex Sw.) J.Sm. in Curt., *Ophioglossum* spp., etc.) have also been observed to persist in recently burnt places. Thus, a surprisingly high number of Zambian pteridophytes prove to be able to survive burning, either at annual intervals or at least occasionally. The majority of them belong to the species most widely distributed and most abundant throughout the country, a fact which strongly suggests a very high importance of fire as a limiting factor for pteridophytes in the study area.

The species listed in table 1 occur only in a small number of habitat types: rock crevices, savanna woodlands, forest edges and "dambos" (i e. grasslands of flat depressions, wet at least in the rainy season). The incidence of fires is very high in all these places but there are essential differences between them in the ecological effects of burning.

The savanna woodlands of the "miombo" type, which are the dominant vegetation over most parts of upland Zambia, are usually burnt each year in the dry season. The fires are rather light, sweep fast over the ground, and consume only the ground layer of vegetation leaving the trees and shrubs more or less undamaged. In the ground layer, however, all dry plant material, including grass, tree leaves and twigs, is burnt fairly completely. Herbaceous plants occurring in such places have to survive

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* The herbarium abbreviations are those proposed by Holmgren and Keuken (1974).

Species	Collections examined			Habitats
	total number	with fire scars		
		number	%	
Actiniopteris dimorpha P.Serm.	7	4	57.1	rocks
Actiniopteris pauciloba P.Serm.	13	9	77.8	rocky miombo
Actiniopteris radiata (Sw.) Link.	12	1	8.3	rocks
Actiniopteris sp. indet. (mainly hybrids)	12	7	58.3	rocks, rocky miombo
Adiantum incisum Forsk.	21	3	14.3	rocks
Anemia angolensis Alston	16	12	75.0	rocky miombo
Arthropteris orientalis (J.F.Gmel.) Posthumus	37	4	10.8	rocky miombo
Aspidotis schimperi (Kunze) P.Serm.	20	8	40.0	rocky miombo
Asplenium buettneri Hieron.	14	2	14.3	rocks
Athyrium schimperi Moug. ex Fée	9	2	22.2	forest edges
Cheilanthes angustifrondosa Alston	2	2	100.0	rocky miombo
Cheilanthes inaequalis (Kunze) Mett. var. *inaequalis*	25	9	36.0	rocks
Cheilanthes multifida (Sw.) Sw.	14	2	14.3	forests, rocks
Cheilanthes similis Ballard	4	2	50.0	rocks
Dryopteris athamantica (Kunze) Kuntze	12	4	33.3	miombo (ditches)
Dryopteris inaequalis (Schlechtend.) Kuntze	7	1	14.3	forest edges
Lycopodium carolinianum L. var. *tuberosum* (Welw. et A.Braun ex Kuhn) Nessel	4	1	25.0	dambos
Mohria caffrorum (L.) Desv.	2	2	100.0	rocky miombo
Mohria lepigera (Bak.) Bak.	17	9	52.9	rocks
Pellaea calomelanos (Sw.) Link.	4	2	50.0	rocks
Pellaea longipilosa Bonap.	38	33	86.8	rocky miombo
Pellaea pectiniformis Bak. in Hook.	27	10	37.0	rocks
Pellaea viridis (Forsk.) Prantl in Engl. var. *glauca* (Sim) Sim	5	1	20.0	rocks
Pellaea viridis (Forsk.) Prantl in Engl. var. *involuta* (Sw.) Schelpe	1	1	100.0	rocks
Thelypteris confluens (Thunb.) Morton	30	1	3.3	dambos
Total	353	132	37.4	

TABLE 1: Fire scars in fern specimens collected in Zambia

burning every year. Miombo woodlands on deeper soils are usually completely devoid of pteridophytes, most probably because of the presence of a dense cover of highly competitive grasses. In the moister regions of the country however, especially at higher altitudes, *Pteridium aquilinum* (a rhizome geophyte) may be abundant or even subdominant in this type of environment. The bracken seems to be perfectly fire-resistant there, as elsewhere in the world (Tardieu-Blot et al. 1971: 127, Tryon 1941: 20, 29, 45, 50). Another large terrestrial fern occasionally found in the miombo stands on deeper soils is *Dryopteris athamantica* (fig. 2). It grows there, however, almost always in ditches or holes, its rhizome several centimeters below the level of the surrounding woodland-floor. This seems to assure both bare humid soil for developing gametophytes and additional fire protection for perenating organs of the mature sporophyte.

On shallow soils of steep slopes and rocky ridges the miombo woodlands become more open and their grass cover more scarce. In such places small xerophytic ferns are commonly found which represent the life form of hemicryptophytes (*Aspidotis schimperi* – fig. 3, *Pellaea longipilosa* – fig. 4, *Anemia angolensis* – fig. 5) or an intermediate type between hemicryptophytes and geophytes with the perenating buds hidden under a thin layer of soil (*Arthropteris orientalis* – fig. 6). They are the most regularly subject to annual burning of all the Zambian ferns and, accordingly, fire-scars are found in more than half of the herbarium collections of this group (fig. 17 A) (the lower share of scarred specimens in *Arthropteris orientalis* being obviously due to the nearly-geophytic habit of this species). Rarely the following hemicryptophytic ferns may also be encountered in this type of habitat: *Cheilanthes angustifrondosa* (fig. 1), *Actiniopteris pauciloba* (fig. 7), and *Mohria caffrorum* (fig. 8).

Rock outcrops outside woodland may also be burnt each year. However, their vegetation is usually scarce enough to make the fire very patchy and irregular. Consequently, numerous small spots in the burnt areas are left untouched. Therefore there is always the likelihood that a number of individual plants will not catch fire every year. This is clearly reflected in Table 1 in that the rock-inhabiting species are characterized by the presence of fire-scars in only one tenth to one third of collections (fig. 17 B). All the fern species found in rock crevices are typically xeromorphic and represent the life form of hemicryptophytes (*Actiniopteris dimorpha, A. radiata, Cheilanthes inaequalis* – fig. 9, *Mohria lepigera* – fig. 10, *Pellaea calomelanos* – fig. 11, *P. pectiniformis* – fig. 12, *P. viridis* agg., etc.).

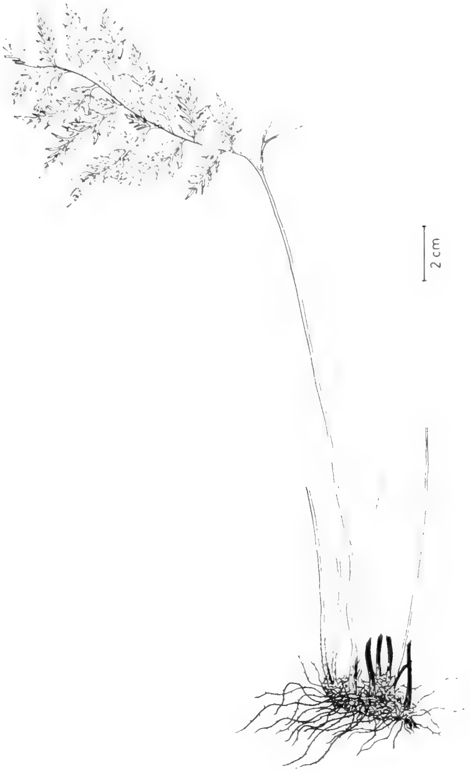
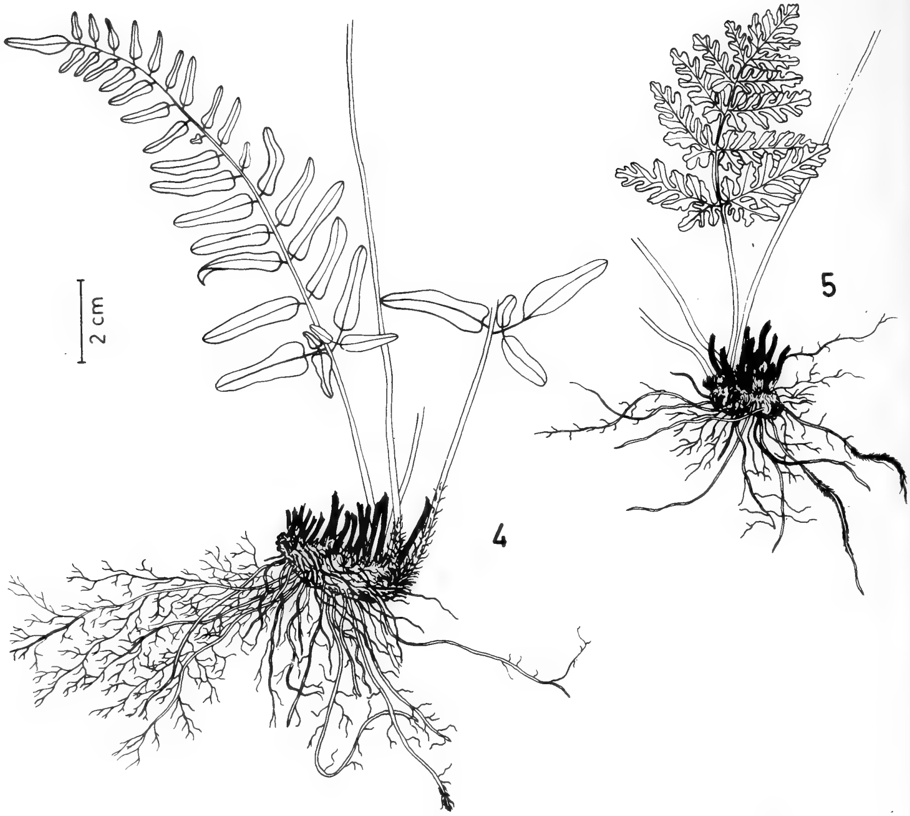


FIGURE 3. Basal parts of a specimen of *Aspidotis schimperi* collected in the rainy season and bearing fire-scars on stipes of the previous year. Zaïre, Shaba, Kipopo, 7 December 1970. S. Lisowski 10064 (KRA).

The dambo grasslands are usually completely burnt each year. However the only pteridophytes found there belong to the geophytes (*Thelypteris confluens*, an obligate geophyte – fig. 14, *Lycopodium carolinianum* var. *tuberosum*, a facultative geophyte – Kornaś 1975, figs. 1-6) and therefore only exceptionally retain the fire-scarred parts until the next rainy season.

The mesic habitats of forest edges are normally situated just on the border-line between burnt and unburnt areas. That is why the ferns growing in these places (*Athyrium schimperi* – fig. 15, *Dryopteris inaequalis*, etc.) only seldom catch fire. Between one tenth and one fifth of their collections have been found with scars.

It is highly significant that no fire-scars have ever been found in species growing in other habitats than those already discussed. True forest ferns, both terrestrial and epiphytic, which occur in evergreen montane forests, riverside forests, "mushitu" swamp forests, etc., never show even the slightest evidence of fire-damage. This is also true of epiphytes (*Pleopeltis excavata* (Bory ex Willd.) Sledge, *P. macrocarpa* (Bory ex Willd.) Kaulf.) in the mist-affected miombo patches on hill tops, although these stands

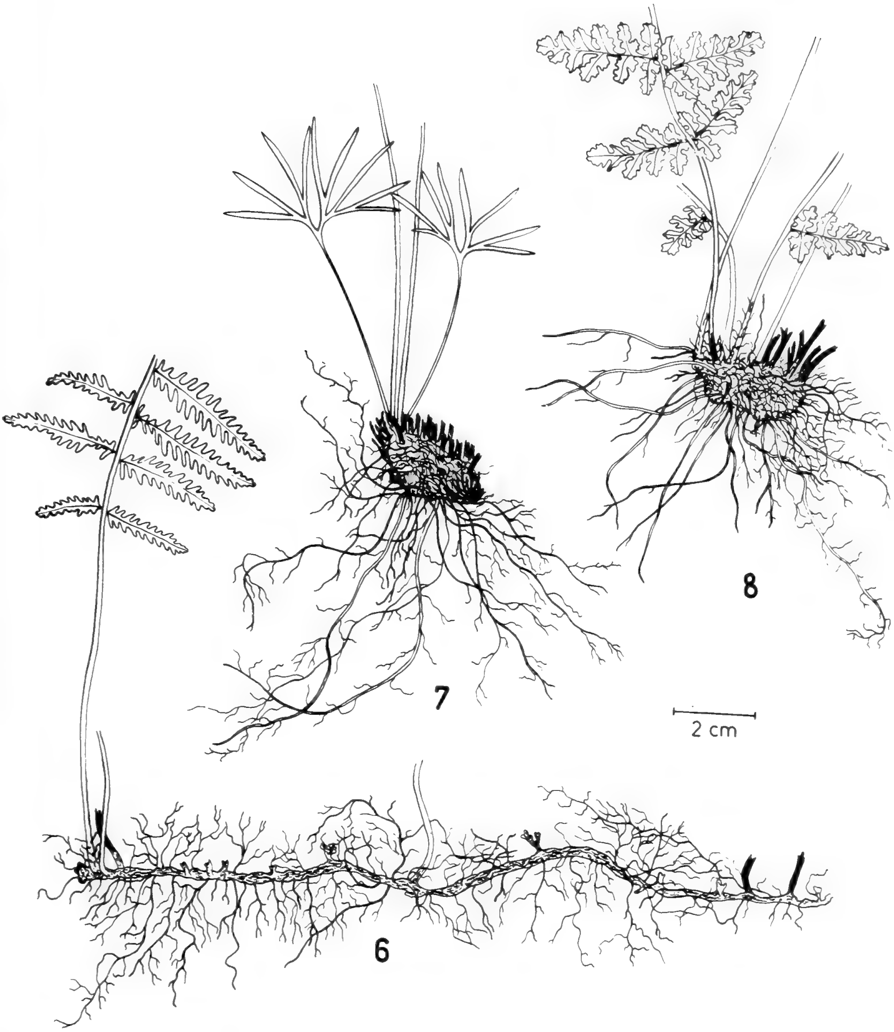


FIGURES 4 & 5. Basal parts of fern specimens from Zambia, collected in the rainy season and bearing fire-scars on stipes of the previous year (all specimens housed in KRA). 4, *longipilosa*. Central Province, Lake Mulungushi, 27 December 1971. J.Kornaś Pl. Afr. 0725. 5, *Pellaea Anemia angolensis*. Central Province, near Lusaka, 4 March 1972. J. Kornaś Pl. Afr. 1326.

are burnt regularly at annual intervals. Obviously, the surface fires have no influence on the epiphytes growing in the tree crowns two metres and more above the ground. Neither have fire-traces been detected in species of humid rocks (e.g. near waterfalls), and rocky river banks (and, of course, in true water ferns growing in lakes, pools, sluggish river arms, etc.). All species confined to such habitats are apparently more or less fire-tender. This is certainly the case with ferns of the evergreen forest which inevitably perish after burning, along with other components of this ecosystem. All in all fire-tender species certainly form the vast majority of the Zambian fern flora.

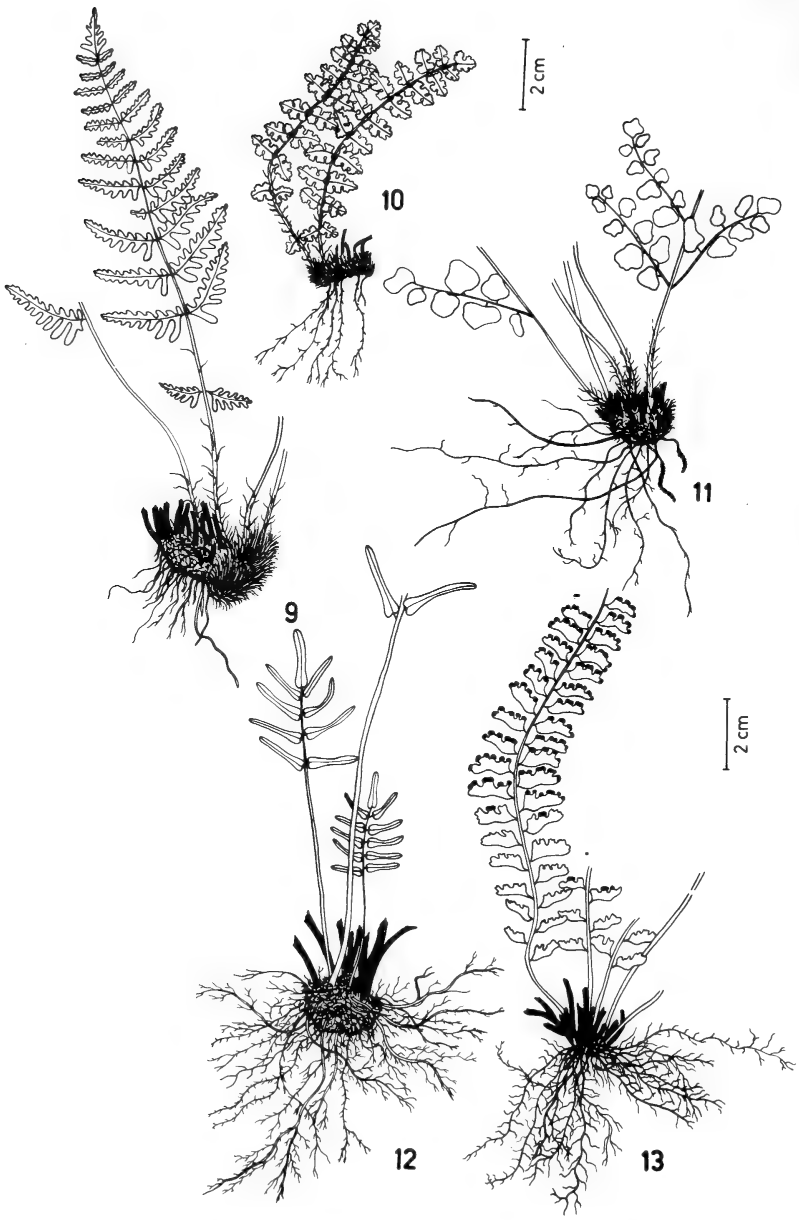
DISCUSSION

The fire-resistance characteristic of a number of ferns in Zambia is based on various morphological and biological features of these species. All of them are more or less typical xerophytes and display a strict seasonal periodicity, with a long and very pronounced dormancy period during the dry season. The renovating buds are produced either below the ground (in true geophytes e.g. *Pteridium aquilinum*, *Nephrolepis undulata*, etc.) or just at the ground-level (in hemicryptophytes e.g. *Actiniopteris* spp., *Cheilanthes* spp., *Pellaea* spp., etc.). In the latter group the buds are

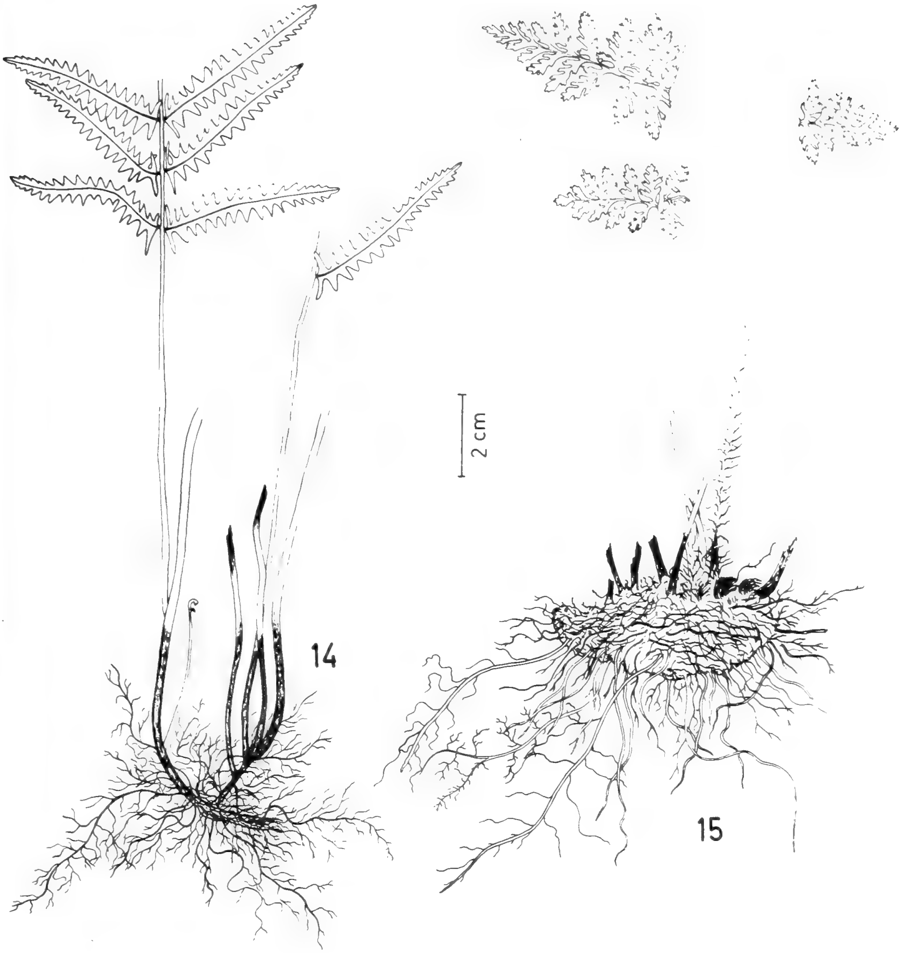


FIGURES 6–8. Basal parts of fern specimens from Zambia, collected in the rainy season and bearing fire-scars on stipes of the previous year (all specimens housed in KRA). 6, *Arthropteris orientalis*. Central Province, Kundalila Falls, 17 January 1972. J. Kornas Pl. Afr 0888. 7, *Actiniopteris pauciloba*. Eastern Province, Kachalola, 4 March 1973. J. Kornaś Pl. Afr. 3412. 8, *Mohria caffrorum*. Central Province, Kundalila Falls, 5 May 1972. J.Kornaś Pl. Afr. 1666.

always deeply hidden between old stipe bases, and usually covered with a dense, thick coat of scales (particularly conspicuous in *Cheilanthes inaequalis* – fig. 9, and *Dryopteris athamantica* – fig. 2). Sometimes, e.g. in *Anemia anglensis* (fig. 5) and *Actiniopteris pauciloba* (fig. 7), a tunic-like structure results, similar to that in the South American *Anemia* species mentioned by Eiten (1972: 303) All these characters may have originated as adaptive responses to severe seasonal drought and only subsequently have become also effective as means of protection against fire. We cannot, however, exclude the possibility that fire has also been directly acting as an



FIGURES 9-13. Basal parts of fern specimens from Zambia, collected in the rainy season and bearing fire-scars on stipes of the previous year (all specimens housed in KRA) 9, ***Cheilanthes inaequalis*** var. *inaequalis*. Northern Province, Bwingi Mfumu Hills, 18 January 1972. J. Kornaś Pl. Afr. 0934. 10, *Mohria lepigera*. Northern Province, Mt. Sunzu, 6 April 1973. J. Kornaś Pl. Afr. 3635. 11, ***Pellaea*** *calomelanos*. Southern Province, Changa, 13 February 1973. J. Kornaś Pl. Afr. 3278. 12, ***Pellaea*** *pectiniformis*. Copperbelt Province, N of Kapiri Mposhi, 30 March 1972. J. Kornaś Pl. Afr. 1486. 13, *Adiantum incisum*. Central Province, Sanje, 9 March 1972. J. Kornaś Pl. Afr. 1359.



FIGURES 14 & 15. Basal parts of fern specimens from Zambia, collected in the rainy season and bearing fire-scars on stipes of the previous year (all specimens housed in KRA). 14, *Thelypteris confluens.* Central Province, between Undaunda and Rufunsa, 2 January 1972. J. Kornaś Pl. Afr. 0779. 15, *Athyrium schimperi.* Central Province, Kundalila Falls, 17 January 1972. J. Kornas Pl. Afr. 0890.

evolutionary factor, stimulating mutation and eliminating fire-tender plants from places regularly affected by burning. At present it certainly excerts an extremely strong selective pressure on the vegetation of the upland habitats of savanna woodlands. Very few ferns are able to persist in such habitats, but those which manage it, e.g. *Pellaea longipilosa*, *Anemia angolensis*, *Actiniopteris pauciloba*, *Pteridium aquilinum*, *Arthropteris orientalis*, etc., may be regarded with every reason as true pyrophytes.

In two genera of Zambian ferns, pyrophytic species exist which closely resemble those without pyrophytic habit: *Arthropteris orientalis* is a counterpart of *A. monocarpa* (Cordem.) C. Chr., and *Cheilanthes inaequalis* is apparently very near to *Ch. laechii* Schelpe. This gives the opportunity to make interesting comparisons.

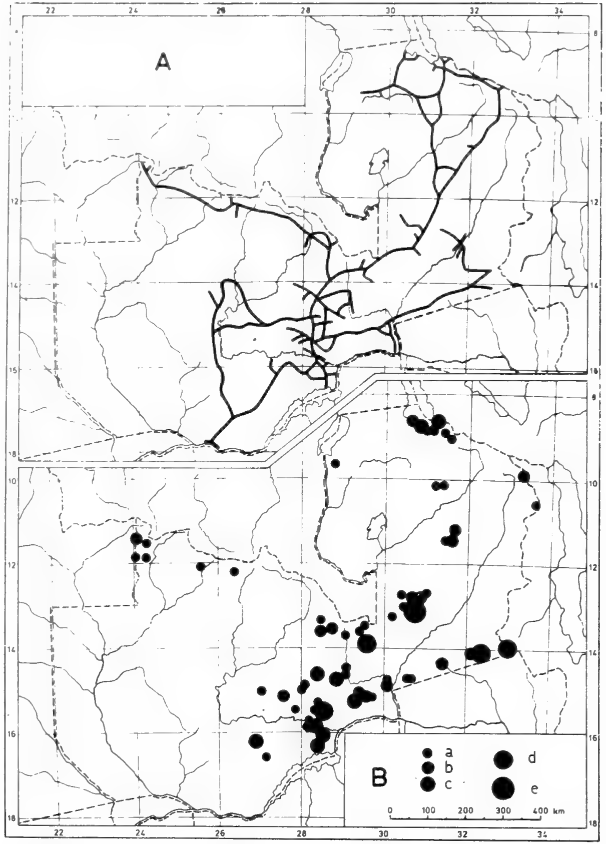


FIGURE 16. A — Routes of the author's collecting trips in Zambia. B — Localities in which fire-scarred specimens of pteridophytes have been collected in Zambia: a — 1 collection, b — 2 collections, c — 3 collections, d — 4 collections, e — 5 collections.

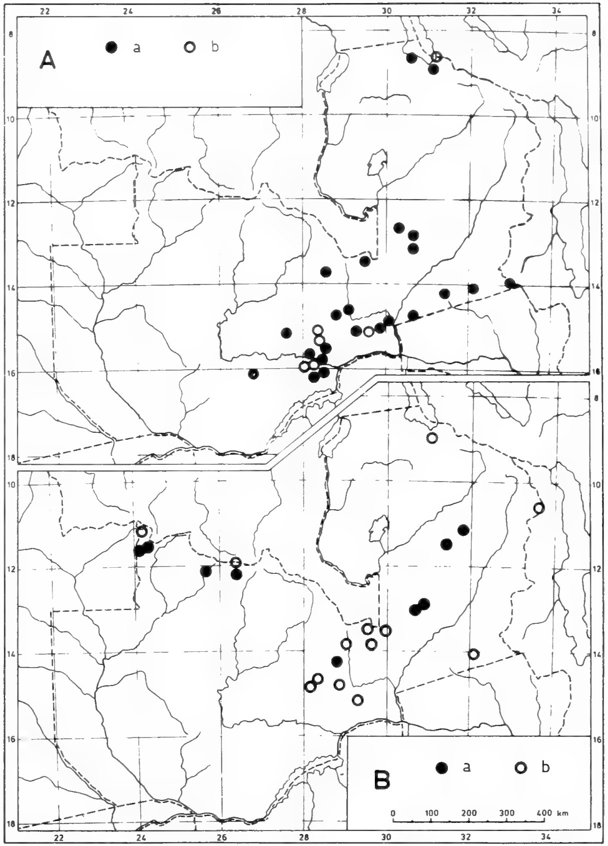


FIGURE 17. Distributions of *Pellaea longipilosa*, a fern of open miombo woodland (A) and *Cheilanthes inaequalis*, a fern of rock crevices (B) in Zambia: a — localities in which fire-scarred specimens have been collected, b — other localities. Records from literature, field notes and herbarium specimens without underground parts have been disregarded

Arthropteris monocarpa is an epiphyte of the evergreen forests, with more or less continuous growth throughout the year. It produces renovating buds, without special protective structures, on the tops of long rhizomes creeping widely on the surfaces of tree trunks. Thus it represents the life form of a phanerophyte. Its leaves are larger and much more delicate than those of *A. orientalis*. *Cheilanthes leachii* occurs in shaded rock crevices, usually in places where, in the rainy season at least, some water is constantly dripping. It has a pronounced dormancy period during the dry months, but does not produce tunica-like structures around the perenating buds. Its leaves are much thinner and less hairy than in *Ch. inaequalis* and it is reproducing freely by gemmae arising in the apical parts of the leaves. This way of vegetative reproduction is known only in ferns of humid habitats and certainly would be a complete failure in fire-affected places. Thus, the differences between closely similar pyrophytic and non-pyrophytic fern species turn out to be those between the xerophytes and the mesophytes. It seems that a detailed comparative morphological and ecological study of both pairs of species discussed above as well as of other similar cases from outside the flora of Zambia, could be especially helpful for an understanding of the nature and origin of the pyrophytic habitat in ferns.

Fire-scarred pteridophytes have been found all over the territory of Zambia (figs. 16 and 17). They are, however, especially frequent in the drier areas of the southern and central parts of the country. The species with most advanced pyrophytic features (e.g. those from the genera *Actiniopteris, Cheilanthes, Mohria*, and *Pellaea*) seem all to belong to the same geographical and ecological element of the "afrikanische Süd- und Randflora" as defined by Christ (1910: 259).

In the present paper the problem of fire-resistance and pyrophytic adaptation in ferns has been discussed only in relation to mature sporophytes. However, the gametophytic phase is certainly the most critical stage in the life history of every pteridophyte. No sexual reproduction is possible, even in the most extreme xerophytes, in the absence of liquid water. The prothallia are generally more delicate and more susceptible to adverse environmental conditions than the sporophytes. (However, many xerophytic ferns, e.g. from the genera *Cheilanthes* and *Pellaea*, are able to produce sporophytes apogamously, and this is believed to be an adaptive feature particularly important in dry environments (Hevly 1963)). It certainly would be an exciting task to study the germination of spores and the survival of gametophytes, as well as their reproductive biology, in pyrophytic ferns growing under natural conditions and subject to repeated burning.

ACKNOWLEDGEMENTS

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SPORE CHARACTERS OF THE GENUS CHEILANTHES WITH PARTICULAR REFERENCE TO SOUTHERN AUSTRALIA

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ABSTRACT

Spores of five of the species of *Cheilanthes* found in Australia are examined using the scanning electron microscope. All differ markedly from each other in spore ornamentation, and one species, *C. tenuifolia* Sw., shows two distinct spore types associated with distinct geographical distribution patterns. Spores of the Mediterranean species *C. catanensis* (Cosent.) H.P. Fuchs are compared with those of *C. vellea* (R.Br.) F. Muell. of Australia, and found to be very different from one another.

INTRODUCTION

The fern genus *Cheilanthes* Sw. is a complex group of approximately 150 species, found throughout the world, but primarily in dry, exposed, rocky areas. Preliminary study indicates that 11 or 12 species are present in Australia, but accurate taxonomic delimitation of some of these requires more detailed investigation.

The high degree of intraspecific variability within the widespread species *C. tenuifolia* Sw. and the lesser known and more restricted species of Queensland and northern Australia, present many taxonomic difficulties.

The best known Australian species are widely distributed, and at least three (*C. sieberi* Kze., *C. distans* (R. Br.) Mett. and *C. tenuifolia*) are also found outside Australia. Varying distribution patterns from species to species suggests that they differ significantly from each other in their tolerance to aridity.

Pichi Sermolli (1951) demonstrated the distinctness of *C. vellea*, *C. lasiophylla* and *C. distans*, species which previously had been confused by a number of writers. The distinction between *C. tenuifolia* and *C. sieberi* has also been subject to controversy; for example, Willis (1970) referred to *C. sieberi* as a variety of *C. tenuifolia* but was doubtful even of its varietal status.

Previous studies of spore morphology in the genus *Cheilanthes* have been reported by Tryon and Tryon (1973), Knobloch, Spink and Fulfs (1970), Devi, Nayar and Knobloch (1971) Nayar and Devi (1967) and Welman (1970). Spore morphology of only one Australian species, *C. tenuifolia*, has previously been described.

The present study is concerned with the examination of the spores of five of the species of *Cheilanthes* found in Australia, in order to provide some additional characters and to determine their possible taxonomic usefulness. These species are *C. tenuifolia*, *C. sieberi*, *C. distans*, *C. lasiophylla* Pic. Ser. and *C. vellea* (R.Br.) F. Muell.

MATERIALS AND METHODS

Spores from both herbarium and fresh material were used. The specimens studied are listed after the description of the spores of each species.

Spores from fresh material were obtained by picking a few pinnules which bore ripe, black sporangia. These were washed under running water, folded in clean paper and left for 1-2 days, after which time spores had been shed. Those from herbarium specimens were selected from sori which appeared mature, and in which a significant number of the sporangia had already dehisced. Spores were mounted on standard aluminium stubs, either on double-sided sticky tape, or in a small drop of glue prepared in acetone from double-sided sticky tape (Chambers and Godwin 1971).

Stubs were coated with carbon, then gold palladium, while being rotated in the vacuum unit on a planetary attachment. The specimens were studied on a Cambridge S4-10 scanning electron microscope.

In order to determine the presence of a perine, the spores were treated with 1N NaOH, according to the method devised by Erdtman (1960) and modified by Gastony (1974) and as used by Gastony and Tryon (1976).

CHARACTERISTICS AND NOMENCLATURE USED TO DESCRIBE THE SPORE COAT

Almost every study in recent years of fern spore coat characteristics has tended to create yet another set of definitions, both for the spore coat layers and the spore coat ornamentation. Clearly, a great deal more information, particularly from developmental studies, will be necessary before any really meaningful set of generalisations may be made on the true nature and homologies of these layers. For this reason we have chosen to follow the significant recent account of spores of cheilanthoid ferns by Tryon and Tryon (1973).

The term sporoderm is used for the spore wall, when referring to it generally. The outer layer of the sporoderm is regarded as a perine, and presumably originates from the tapetum.

Spores of all species studied were treated with 1N NaOH (following Gastony 1974). This caused significant swelling and even disruption of the outer sporoderm layer, and, following Gastony and Tryon (1976), this layer is therefore interpreted as perine, and the surface below as exine. Fig. 1 shows spores of *C. distans*, *C. tenuifolia* and *C. sieberi* before and after treatment with 1N NaOH.

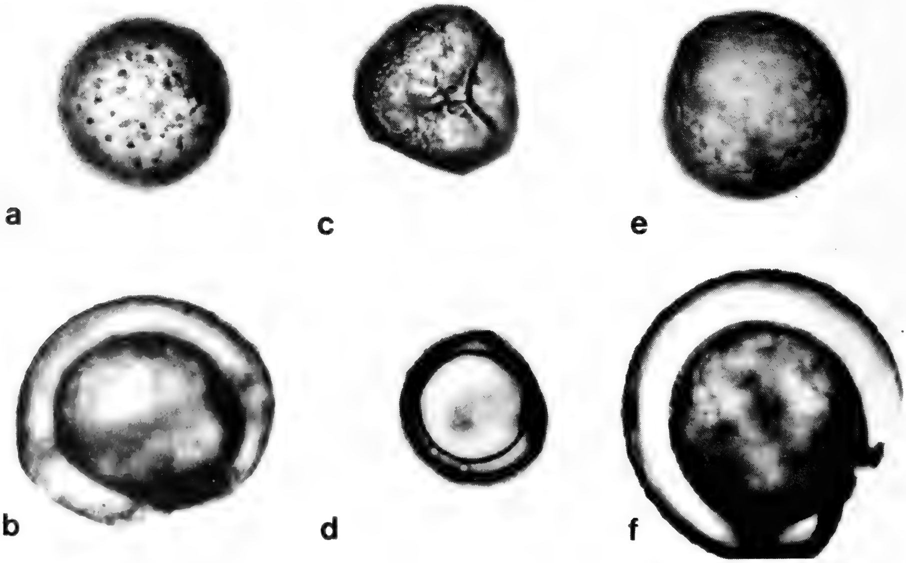

FIGURE 1 a–f. Light micrographs of spores, before and after treatment with 1N sodium hydroxide, to expand and thereby demonstrate the presence of a perine layer. All x 500. a, b, *C distans* MEL 515005, Dargo, Victoria; c, d, *C. tenuifolia* MEL 515001, You Yangs, Victoria; e, f, *C. sieberi* MEL 514993, You Yangs, Victoria.

Perine may be of one or more layers, the outer usually ornamented, and also often with contours created by the triradiate scar of the exine showing. The exine is regarded as the layer of the sporoderm immediately below the perine. The outer surface of the exine may, in some cases, also be ornamented.

Descriptive terms used by Tryon and Tryon (1973) are used here to describe the surfaces of the sporoderm. These are : *smooth, cristate, verrucate, reticulate, echinate* and *granulose*.

RESULTS

C. tenuifolia

Mapping of collection localities of herbarium specimens has shown that there is a definite disjunction in the distribution of *Cheilanthes tenuifolia* between (i) southern Australia and (ii) northern Australia and south-east Asia. There is a corresponding disjunction in spore sculpturing characteristics of northern and southern specimens (see fig. 2).

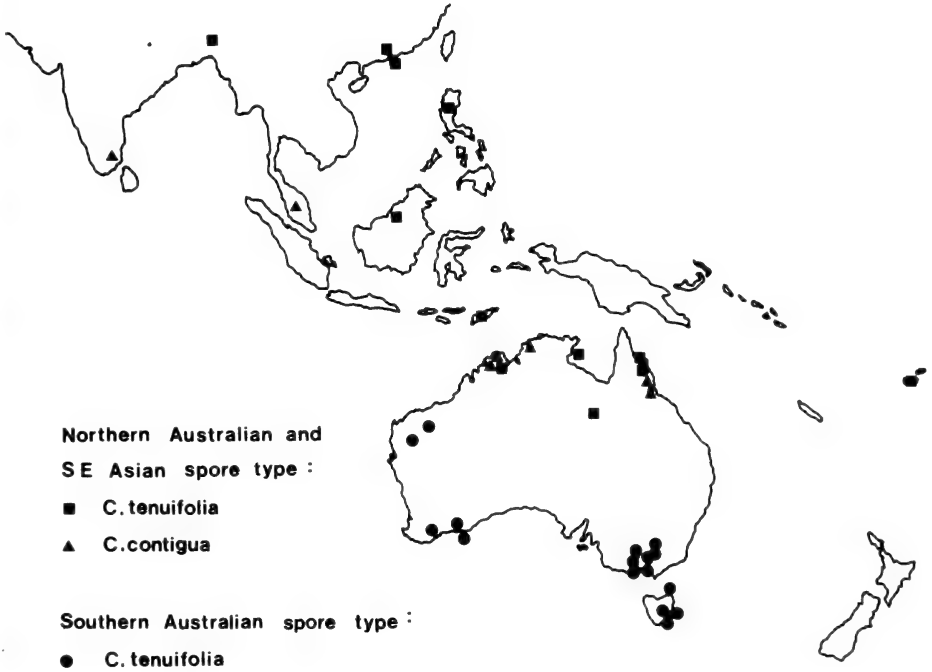

FIGURE 2. Map showing the distributions of the two spore types of *C. tenuifolia*. For the northern Australian and S.E. Asian spore type, distinction is made as to whether spores are from typical *C. tenuifolia* specimens or from specimens of *C. contigua*.

Southern Australia. Spores of plants from southern Australia identified as *C. tenuifolia* are spherical, or nearly so, 40-50 µm in diameter, have a cristate *perine*, and disconnected, irregular ridges forming a trilete mark (fig. 4 a, b). The perine is a distinct outer layer, which can break off entirely, to reveal the outer surface of the *exine* with its finely granulose texture and prominent trilete mark (fig. 4 c, d).

FIGURE 3. Herbarium specimens of *C. tenuifolia* from southern and northern Australia, and of *C. contigua* showing longer, less finely divided frond of *C. contigua*: a. *C. tenuifolia*, MEL 514999, Springhurst, Victoria; b. *C. tenuifolia*, MEL 504703, Bellenden Ker Range, Queensland; c. *C. contigua*, MEL 504704, Port Darwin, Northern Territory.

Northern Australia, South-east Asia and the Pacific. A problem arises when considering the northern specimens of *C. tenuifolia*, because the sporophyte, although often indistinguishable from southern specimens in general appearance (fig. 3 a, b), also appears, at least superficially, to grade into a less finely divided form. This form has very elongated ultimate pinnules, and in extreme cases may be no more than bipinnate for much of its length (fig. 3 c). After careful examination of many specimens of this form, it has been assigned to *Cheilanthes contigua* Baker, a species with both frond division pattern and scale cover distinct from those of *C. tenuifolia*.

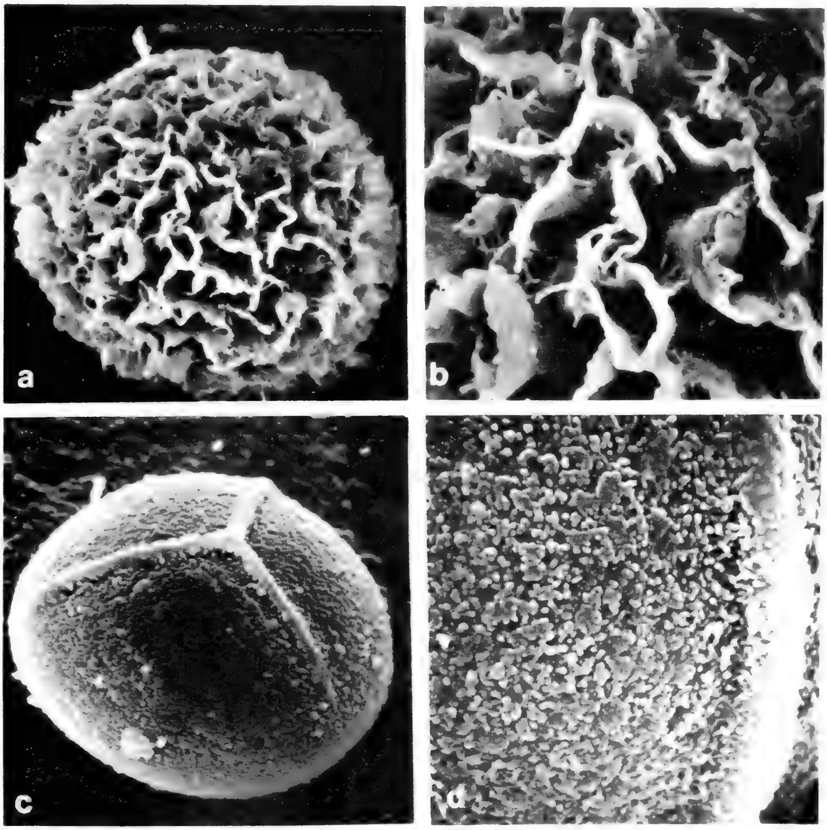

FIGURE 4. Spores of *C. tenuifolia* in southern Australia : a, *C. tenuifolia,* MEL 14995, Eildon, Victoria, spore showing cristate perine, X 810; b, surface detail, X 1940; c, *C. tenuifolia,* MEL 504716, Recherche Archipelago, Western Australia, whole spore showing exine, X 950, d, Surface detail, X 1940.

However, both the northern Australian and northern extra-Australian material of *C. tenuifolia* and *C. contigua* have identical sporoderm sculpturing, and the spores are quite distinct from those of southern *C. tenuifolia*. They are distinctively triangular in shape, and 40-55 um across. The sporoderm has a prominent trilete mark and is reticulate-echinate, consisting of ribbed spikes protruding from the finely granulose surface (fig. 5 a-d). These spikes may wear off and the outer sporoderm break away to reveal the smooth inner sporoderm (fig. 5 e, f).

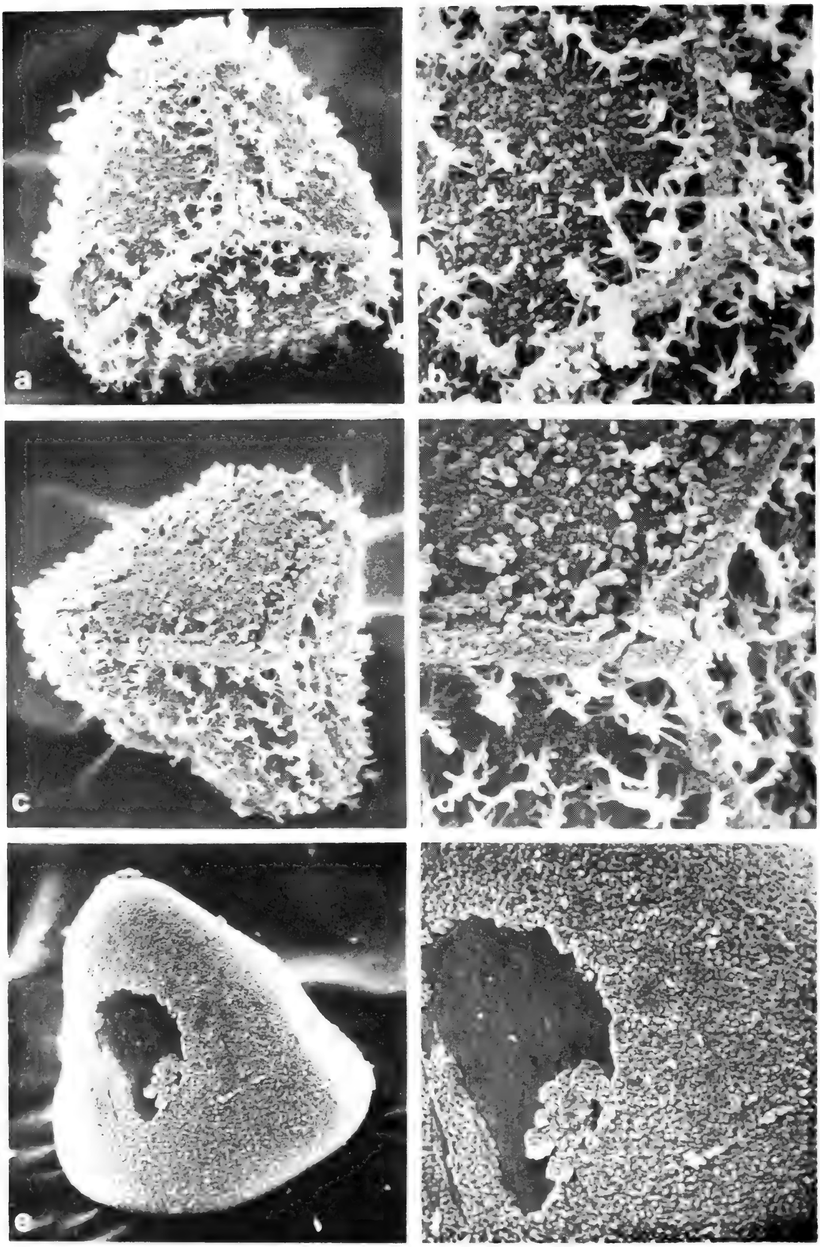

FIGURE 5. Spores of *C. tenuifolia* and *C. contigua* in northern Australia and S.E. Asia : a, *C. contigua*, BM, Shevaroy Hills, Southern India, whole spore showing sporoderm, X 840, b, Surface detail, X 1940; c, *C. tenuifolia*, BM, Luzon, Philippines, whole spore showing sporoderm, X 750, d, Surface detail, X 1850; e, *C. tenuifolia*, BM Timor; whole spore from which spines of sporoderm have worn away, and part has worn off entirely, to reveal the smooth inner sporoderm, X 820, f, Surface detail, X 1850.

Specimens studied:

Southern *C. tenuifolia* spore type:

Collector	**Location**	**Date**	**Herbarium**
R.D. Joyce 6609	Barlee Ra., Henry R., W.A.	August 1961	PERTH
A. Morrison	Ellen's Peak, Stirling Ra., W.A.	Oct. 1962	PERTH
E.N.S. Jackson 1239	Eucla Division, Esperance Dist., W.A.	Sept. 1968	PERTH
J.V. Blockley 307	Duck Ck. to Fortescue R. Hammersley Ra.	July 1966	PERTH
J. Somerville	Bellerive, Tasmania	Nov. 1940	HO2221
A.V. Giblin	7-Mile Beach, Tasmania	Nov. 1920	HO2230
L. Rodway	Schouten Is., Tasmania	April 1925	HO2228
J. Somerville	Buckland Tasmania	Jan. 1940	HO2224
Aust. Geographic Soc.	Sandy Hook Is., Recherche Arch., W.A.	Nov. 1950	MEL504716
T.C. Chambers	Snobb's Ck. Rd., near Eildon, Vic.	Sept. 1975	MEL514995
H. Quirk No.20	You Yangs Forest Park, Victoria	April 1975	MEL514996
H. Quirk No.87	You Yangs Forest Park, Victoria	Aug. 1975	MEL515000
H. Quirk No.79	You Yangs Forest Park, Victoria	April 1975	MEL515001
H. Quirk No.112	Big Hill, south of Bendigo, Victoria	Sept. 1975	MEL514998
H. Quirk No. 12	Warby Ra., N.E. Vic.	Feb. 1975	MEL515003
E. Canning EMC 4014B	Springhurst, N.E.Vic.	May 1975	MEL514999
T.C. Chambers	Mt. Alexandra, Vic.	Sept. 1975	MEL514997
H. Quirk No.93	Arthur's Seat, Vic	Aug 1975	MEL515002

Northern *C. tenuifolia* spore type (i) *C. tenuifolia:*

P.R. Messmer	West Cairns Ra., Qld.	July 1954	MEL504700
Karsteio	Trinity Bay, Qld.	1881	MEL504701
S. Johnson	Bellenden Ker Ra., Qld.	1891	MEL504703
H.O. Forbes 3445	Fawnaba Hills, Timor	1883	B M
B. Seeman	Fiji Islands	1860	B M
C.J. Brooks	Sarawak, Borneo	1909	B M
Cuming No.62, 281	Luzon, Philippines	1841	B M
C.J. Simons	Khasi Hills, India	1932	B M
Hance	Whampoa, China	–	B M
J. Lamont No. 1006	West Pt Victoria, Hong Kong	1873	B M

Collector	Location	Date	Herbarium
Bradshaw & Allen	Prince Regent R., West Kimberleys, W.A.	1891	MEL504719
R.L. Specht	South Bay, Bickerton Is., N.T.	June 1948	MEL504711

Northern *C. tenuifolia* spore type : (ii) *C. contigua*

Collector	Location	Date	Herbarium
J.S. Beard 7017	Mitchell Plateau, N. Kimberley, W.A.	June 1974	PERTH
C.A. Gardiner	Prince Regent R., Kimberleys W.A.	June 1921	PERTH
A.S. George 12827	Prince Regent R., W.A.	–	PERTH
Dallachy	Rockingham Bay, Qld.	–	MEL504705
Schultz 207	Port Darwin, N.T.	–	MEL504704
R. Brown	'North Coast' Aust.	1802-5	B M
L. Faucheux	Shevaroy Hills Southern India	Oct. 1939	B M
F.B. Forbes 570	Malaya	–	B M
Banks & Solander	Endeavour R., Qld.	1770	B M

C. sieberi

Spores of *C. sieberi* are spherical, and either 40-50 or 60-75 μm in diameter. The perine is verrucate — that is, with small, low, rounded tubercles over the entire surface. The fine texture of the perine is granulose. The surface of the perine may be clean, except for a few small globules of loose sporoderm material (fig. 6 a, b), or may be coated with a random, open, irregularly branched material, presumably of tapetal origin and laid down in the final stages of spore formation just before dehiscence of the sporangium (fig. 6 c, d). The exine surface is more finely verrucate (fig. 6 e).

Almost all plants examined have spores lacking a trilete mark, but those from two localities studied have spores of identical sculpturing, but with a conspicuous trilete mark (fig. 6 f).

Specimens studied:

Collector	Location	Date	Herbarium
J.W. Stalker	Rockhampton, Qld.	1876	B M
P. Hynes	Wairakei Thermal District. N.Z	1953	B M
Sayer	Golden Valley, W.A.	1888	PERTH
M. Koch IX	Watheroo Rabbit Fence, W.A.	1905	PERTH
G. Chippendale	Todd R , N.T.	Nov. 1954	MEL504712
R.A. Saffrey No.435	Pallarup Rocks, S.E. of Lake King, W.A.	Aug. 1968	PERTH
L. Norton	Between the Upper Bogan and the Lachlan Rivers, N.S.W.		MEL504708

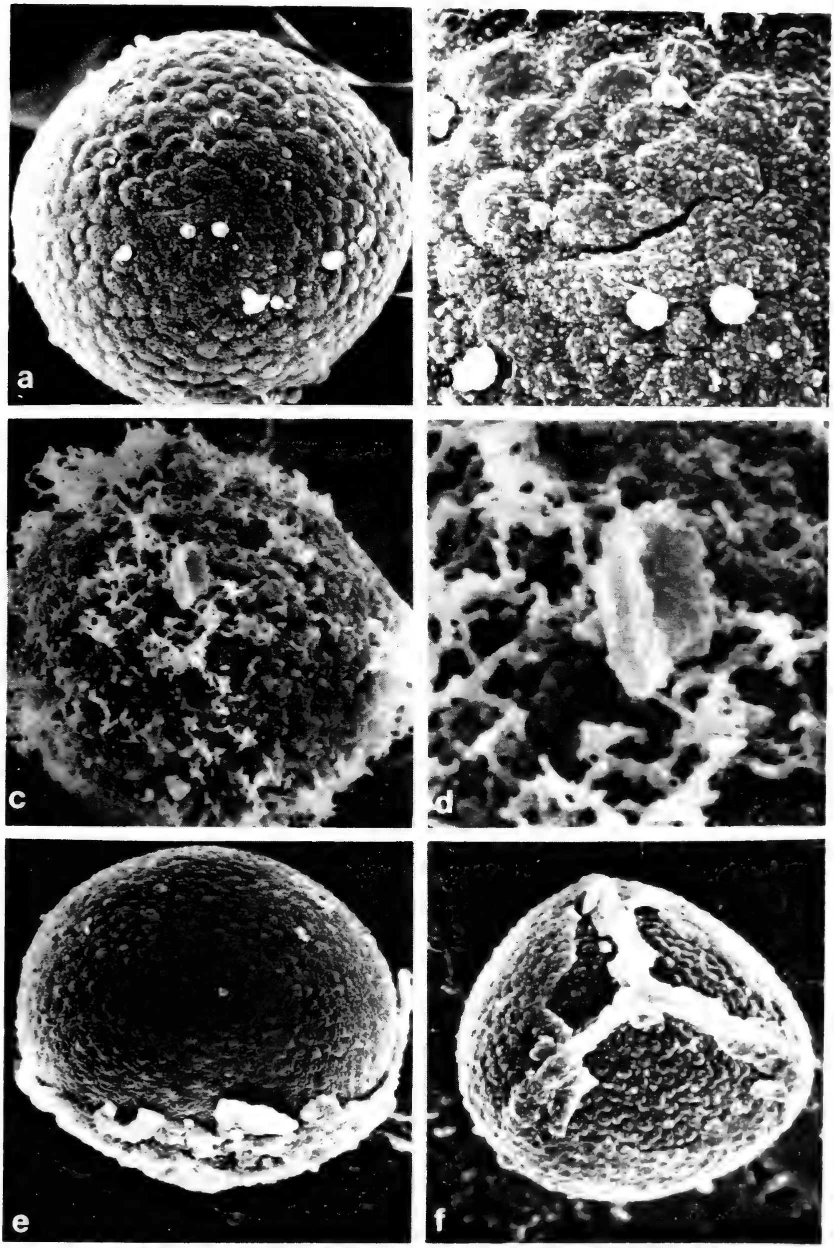

FIGURE 6. Spores of *C. sieberi* : a, *C. sieberi,* BM, Wairakei, New Zealand, whole spore showing verrucate perine, X 760, b, surface detail, X 1940; c, *C. sieberi,* MEL 514991, Wycheproof, Victoria, spore with irregular network overlying verrucae of perine, X 672, d, surface detail, X 2000; e, *C. sieberi,* PERTH, Watheroo, Western Australia, spore showing verrucate exine, X 760; f, *C. sieberi,* MEL 504706, Mudgee, New South Wales, spore with prominent trilete mark, and verrucate perine and exine, X 880.

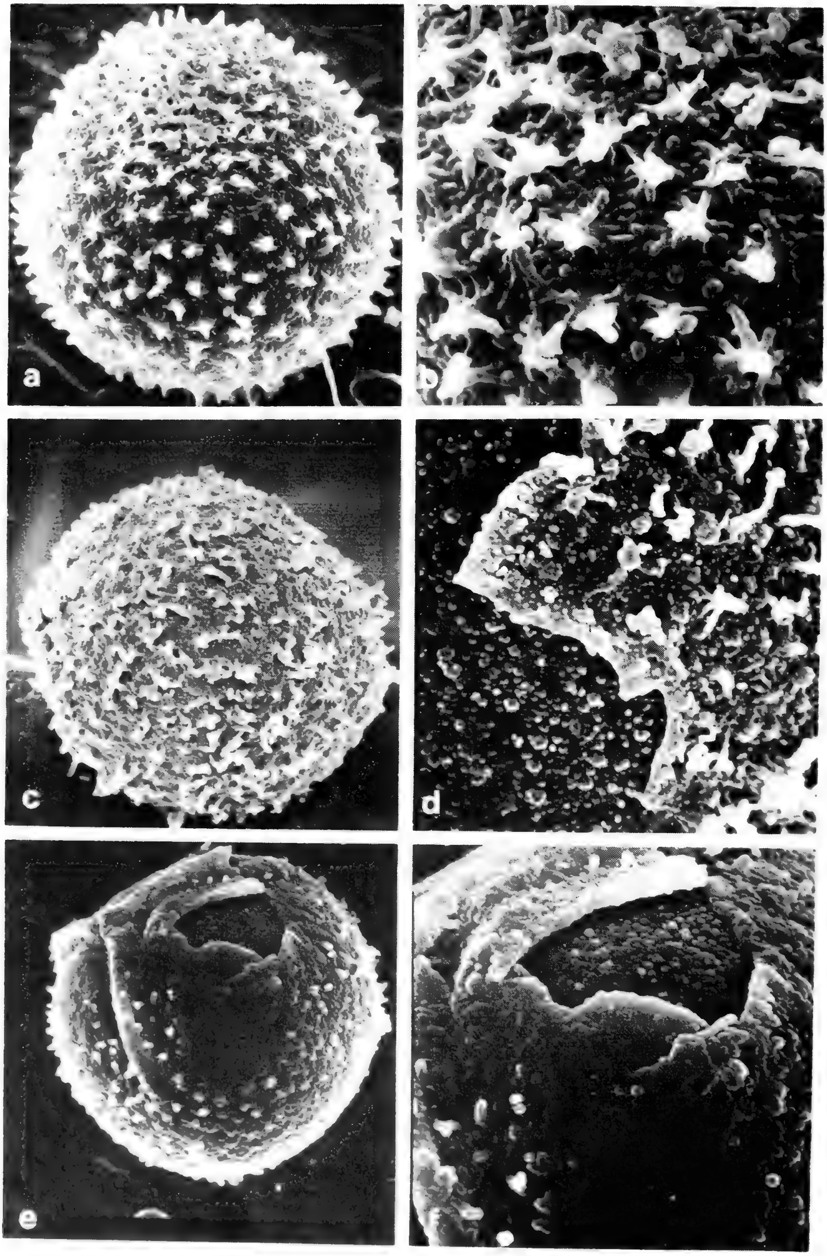

FIGURE 7. Spores of *C. distans* : a, *C. distans,* MEL 515005. Dargo, Victoria, whole spore with echinate-reticulate perine, X 780, b, Surface detail, X 1920; c, *C. distans,* type specimen, BM, R. Brown 4, Port Jackson, New South Wales, whole spore, X 680; d, *C. distans,* MEL 504710, Cocopara Reserve, New South Wales, surface detail showing granulose exine X 1940; e, *C. distans,* MEL 504713, Clermont Queensland, spore with prominent trilete mark, X 910, f, surface detail, X 1920.

Collector	Location	Date	Herbarium
Taylor	Mudgee, N.S.W.	1870	MEL504706
R. Thorn	Wagga Wagga, N.S.W.	March 1885	MEL504702
H. Quirk No.111	Big Desert, Vic.	Sept. 1975	MEL514990
I.G. Stone	Wycheproof, Vic.	Sept. 1975	MEL514991
H. Quirk No. 21	You Yangs Forest Park, Vic.	April 1975	MEL514992
H. Quirk No. 19	You Yangs Forest Park, Vic.	April 1975	MEL514993
I.G. Stone	Pyramid Hill, N.W. Vic.	Sept. 1975	MEL514994

C. distans

Spores of *C. distans* are spherical in shape, 40-80 µm in diameter, with an echinate-reticulate perine of groups of 4-5 protuberances coming together to form single spines (fig. 7 a, b). Spores of the type specimen are also of this pattern (fig. 7 c). The perine forms a distinct outer layer, covering a finely granulose exine (fig. 7 d). Spores of plants from all but one locality lack a trilete mark, but those of a specimen from Queensland (MEL504713) show identical patterning of both perine and exine, but with a prominent trilete mark (fig. 7 e, f). These were also the smallest of the spores studied, being only 40-50 µm in diameter.

Specimens studied:

Collector	Location	Date	Herbarium
R. Brown	Port Jackson, N.S.W.	1802-5	B M Type Specimen
Christensen	Laudes, Noumea, New Caledonia	1922	B M
C. Andrews	Toodyay, W A.	Aug. 1904	PERTH
Fullager	Lord Howe Is	—	MEL
S. Johnston	Clermont, Qld.	Oct. 1897	MEL504713
J.H. Willis	Cocopara Nature Reserve, N.S.W.	Oct. 1969	MEL504710
H. Quirk No.1	Nr. Dargo, Vic.	Feb. 1975	MEL515005

C. lasiophylla

Spores of *C. lasiophylla* are spherical, 60-70 µm in diameter, and have a reticulate perine of strongly anastomosing muri (fig. 8 a, b). The perine is a distinct outer layer, overlying a granulose exine (fig. 8 c, d). No trilete mark is present.

Specimens studied:

Collector	Location	Date	Herbarium
R. Brown	Memory Cove, Eyre Peninsula, S.A.	1802-5	B M
A.S. George 4215	Victoria Rocks, S.W. of Coolgardie, W.A.	Sept. 1962	PERTH
G. Chippendale	Mt. Olga, N.T.	Sept. 1956	MEL502446

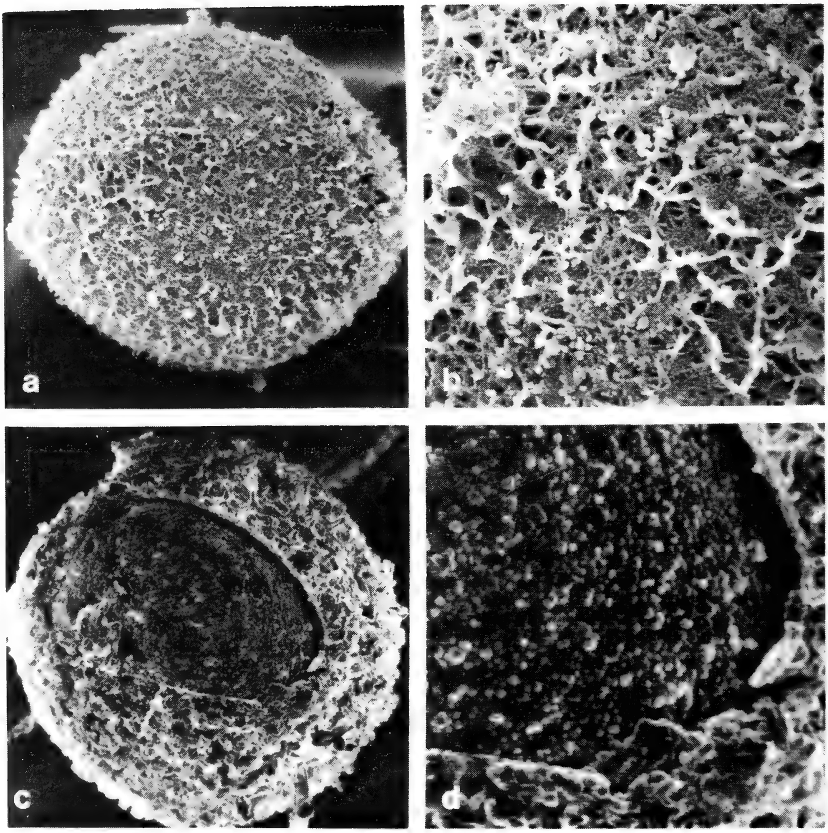

FIGURE 8. Spores of *C. lasiophylla:* a, *C. lasiophylla,* BM, Eyre Peninsula, South Australia, whole spore showing reticulate perine, X 680, b, surface detail, X 1850; c, *C. lasiophylla,* MEL 502446, Mt. Olga, Northern Territory, spore with perine broken away to reveal granulose exine, X 700, d, surface detail of exine, X 2000.

Collector	Location	Date	Herbarium
T.S. Henshall 170	Mt. Fraser, N.T.	April 1974	MEL504720
J.H. Willis	Mt. Liebig, N.T.	July 1966	MEL504709
H. Quirk No.107	Big Desert, Vic.	Sept. 1975	MEL515004

C. vellea

The outer sporoderm of spores of *C. vellea* has a finer and smoother patterning than that of the other species examined (fig. 9 a, b). The granular outer coat is often creased on one line, but a trilete mark is not present. The outer sporoderm is closely appressed to the smooth inner surface. Spores are c.60 um in diameter.

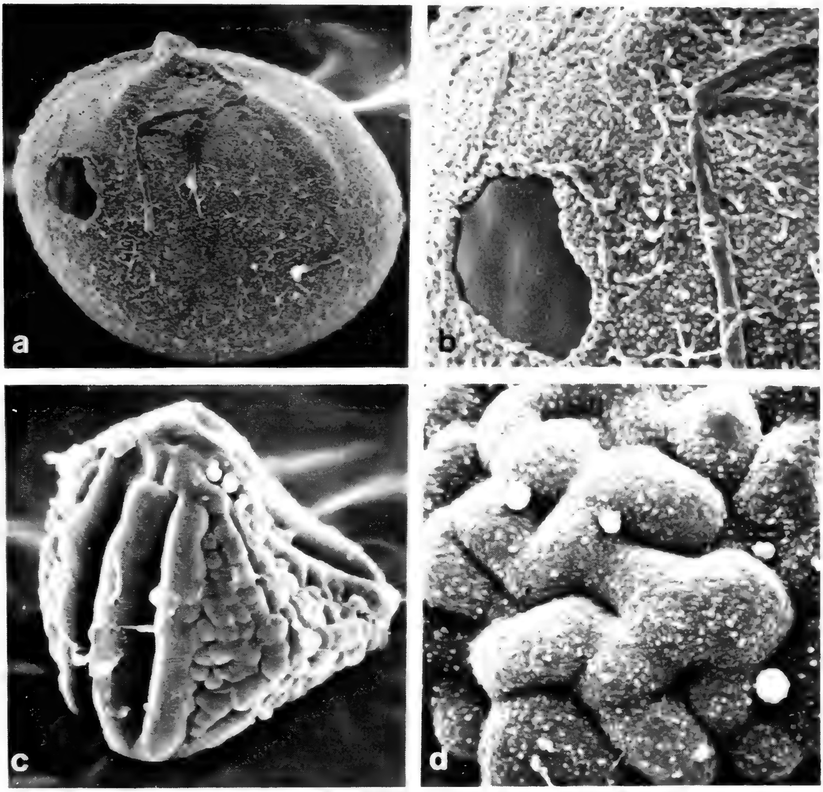

FIGURE 9. Spores of *C. vellea* and *C. catanensis* : a, *C. vellea,* type specimen, BM, R. Brown,5, Caledon Bay, Northern Territory, whole spore showing granulose perine X 660, b, surface detail, X 1850; c, *C. catanensis*, BM, Lake Hula, Palestine, spore with verrucate sporoderm, X 760, d, Surface detail, X 1850.

Specimens studied:

Collector	**Location**	**Date**	**Herbarium**
R. Brown	Caledon Bay, N T.	Feb. 1803	BM (Type specimen)
W.R. Eaton	Calder R., West Kimberly, W.A.	Sept. 1923	PERTH
E. Giles	Kimberley District, W.A.	1888	MEL503612
Persich	Endeavour R., Qld.	May 1887	MEL504718

A member of the genus, *C. catanensis* (Cosent.) H.P. Fuchs, found in the Mediterranean region, has been confused with *C. vellea* on the grounds of its superficial vegetative morphology, and especially its fronds densely covered with white hairs. Scanning electron microscopy of the spores of this Mediterranean fern (taken from herbarium specimens at the British Museum — R.F. Jones No. 350, Lake Hula, Palestine, Dec. 1935; and F.M. Norris Elijah's Tomb, Bauiges, Syria, 1945) clearly indicated a marked difference from any Australian material we have encountered (fig.

9 c, d). Spores are c.65 μm in diameter and tetrahedral, with a rounded distal surface and flatter proximal surface, a faint trilete mark and two deep equatorial slits on either side. They are strongly verrucate, with a finely granular texture.

DISCUSSION

Examination of spore morphology of these Australian species of *Cheilanthes* strongly supports the existing boundaries between them, and points to a possible new division within the species *C. tenuifolia*. All five have distinct patterns of sporoderm sculpturing, and each fits into one of the general kinds of sporoderm of cheilanthoid fern described by Tryon and Tryon (1973).

The citation accompanying the original description of *C. tenuifolia* in Swartz (1806) is "India Orientalis"*. Unfortunately we have not seen spores of the type, but the striking difference between the two kinds of spores of *C. tenuifolia* reported in this study, and the corresponding separation in their distribution patterns, suggests that the ferns of southern Australia thought to be *C. tenuifolia* may, in fact, be a different species, or perhaps subspecies. This possibility points to the need for more critical morphological and cytological study of the plants themselves. The gradation in degree of division of the fronds in *C. tenuifolia* in northern areas, and the existence of identical spores in both *C. tenuifolia* and *C. contigua*, further emphasises the need for detailed re-examination. It is possible that there may also be more than one species in this complex in northern Australia and south-east Asia.

Spore morphology also clearly demonstrates the distinctness of the previously confused *C. tenuifolia* and *C. sieberi*.

Most of the specimens of *C. sieberi* have spores which lack a trilete mark, and this reflects their apogamy.

Cytological investigation of Australian material has shown that the sporophyte of *C. sieberi* is a triploid of n = c.84, and that only 16 spores are formed, by mitosis, in the sporangium. Brownlie (1957) has reported a similar chromosome number for New Zealand populations.

Most specimens of *C. distans* also have spores which lack a trilete mark, and they too are formed by mitosis. The existence within these two species of some plants with well formed spores of identical sculpturing, but which do show a prominent trilete mark, suggests that these may be allopolyploids not separable on gross morphological characters, but capable of meiosis, and possibly of sexual reproduction.

The reticulate structure of the sporoderm of *C. lasiophylla* varies in its degree of complexity, but is clearly distinguishable from the smooth, granulose sporoderm of *C. vellea*, with which species it has often previously been confused. *C. lasiophylla* is apogamous, and the absence of a trilete mark in spores of *C. vellea* suggests that it, too, reproduces apogamously.

This study has also demonstrated the distinction between spores of *C. catanensis* and *C. vellea;* their differences suggest that they are probably only distantly related.

Spore characteristics clearly offer an important tool for the taxonomic delineation of species of *Cheilanthes* in Australia. These spore characters lend weight to existing species boundaries, and also point to exciting new areas of research on possible intraspecific boundaries not discernible from gross morphological study.

ACKNOWLEDGEMENTS

We wish to thank the following for making herbarium specimens available to us, and for allowing spore samples to be taken from them: Mr A.C. Jermy and Mr J.A.

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* Swartz, Syn. Fil. p. 332: Habitat in India orientali: China: Ins. philippinis.

Crabbe of the Department of Botany, British Museum (Natural History), London; Dr D.M. Churchill and Mr T.B. Muir of the National Herbarium, Royal Botanic Gardens, Melbourne; Mr J. Parham of the Botany Department, University of Tasmania; Mr J. Green of the Western Australian Herbarium, Perth. We are especially indebted to Messrs Jermy and Crabbe for their interest and support in this project.

This study was done with the assistance of a Melbourne University Postgraduate Scholarship to one of us (H.M.Q.).

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REVIEW

ALTAS OF FERNS OF THE BRITISH ISLES by A.C. Jermy, H.R. Arnold, Lynne Farrell & F.H. Perring. 101 pp 21 x 29.5 cm. Published jointly by The Botanical Society of the British Isles and The British Pteridological Society, London, 1978. Available from F. & M. Perring, Oundle Lodge, Oundle, Peterborough PE8 5TN, England. Price (paperback) £3.50 (including postage).

This book is a tribute to British botanists, and especially to British pteridologists, and as much to amateurs as to professionals. For there can be few who have had an interest in British pteridophytes in the field who have not in some small way contributed to the information contained within it. Some (not mentioned in the authorship), who have been regular participants of field meetings and collected very many of the records, have certainly contributed much.

This Atlas attempts to collate and present in map form all the many changes in our knowledge of pteridophyte occurrence in the British flora that have developed since (and been stimulated by ?) the publication of the original *Atlas of the British Flora,* now 16 years ago. In this it certainly succeeds.

The present known ranges are given for 80 pteridophyte species or subspeices (including 24 fern allies) and 29 hybrids (including 7 fern allies) in 95 clear, large format (17.5 x 19.5 cm.), black and white dot maps. The maps appear one per page, and their large size makes them easily inspected in detail Species are recorded on the now-familiar 10-km British grid squares used for the original *Atlas of the British Flora.*

Readers might like to annotate their copies of the new Atlas to note, however, that in general open circles in the new Atlas indicate *pre-1950* records and solid dots *post-1950* records (not pre and post 1930 as in the old *Atlas of the British Flora),* for mention of this point has been inadvertently omitted. As yet there are no transparent overlays provided to the new map scale (the ones from the old Atlas no longer fit), although to do this would presumably have increased the price (perhaps these could be made available separately at a later date?). A helpful point is, however, that this pteridophyte-only volume, does have its own index, which is necessary to quickly locate species amongst the surprisingly large number of pages.

The maps are accompanied by textual comments on the taxa by A.C. Jermy. These include reference to some of the more significant taxonomic or ecological points about the plants concerned, although are not, and are probably not intended to be, complete synopses or bibliographies for each. More extensive accounts are given for the identification of *Asplenium trichomanes* in Britain and for the species of the *Dryopteris filix-mas* complex.

For the sheer amount of manpower that has gone into the making of this volume, a high standard of presentation might be expected. This seems largely achieved. Doubtless small errors of fact or omission have been included, however, which will become apparent through usage, and if these are notified to the Biological Records Centre they can presumably be corrected in a future edition. One error that readers might like to correct in their own copies, however, is the spelling throughout p.95 (also mentions on p.87 and index) of *"Dryopteris x ambrosiae"* to its correct spelling as *Dryopteris x ambroseae,* as this was not intended, I understand, to be a proposal for an orthographic change.

The inclusion of maps of critical taxa (especially hybrids) shows how widely some of these are now becoming recognised in the British Isles. It seems likely that several of these remain yet considerably under-recorded: particularly perhaps *Polypodium interjectum,* the subspecies of *Asplenium trichomanes, Dryopteris x tavelii, D. x deweveri, Equisetum x litorale, Polypodium x mantoniae* and possibly *Asplenium onopteris* and hybrid *Polystichum.* Here there is clearly room for more work to be done.

Pteridophytes, in the nature of things, tend to appear amongst the first in such projects as these maps, and hence tend to be ahead of other groups and thus set trends and standards to be followed. The completion of this useful volume now begs the question: where do we go in British plant recording from here? Some suggest mapping on a finer grid scale. I would prefer to suggest that pteridology will need to harness the enthusiasm and ability that this Atlas has shown to be present amongst B.P.S. and B.S.B.I. members for the collection of much more thorough ecological data on pteridophytes throughout their ranges in the British Isles. Such information, once gathered, — the "how" and "why" of plant distributions and not just the "where" — will become even more important as pressures on conservation and land use increase.

In the meantime, the present Atlas will clearly stand as a pteridological milestone, and a valuable foundation on which developing further recording can be based. Botanists will probably find that like me, they really need two copies of this useful volume — one for the bookshelf and one for the car!

C.N. PAGE

PRELIMINARY NOTE ON A FOSSIL EQUISETUM FROM COSTA RICA

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ABSTRACT

A brief description of two sections from the aerial shoots of an unknown species of *Equisetum* subg. *Hippochaete* found in travertine deposits of Upper Tertiary of Costa Rica is presented.

INTRODUCTION

In the palaeobotanical literature there are numerous records of fossil Sphenophyta which have been traditionally placed into five orders: Hyeniales, Pseudoborniales, Sphenophyllales, Calamitales and Equisetales (Arnold 1947, Hirmer 1927, Smith 1955) the latter comprising the one family Equisetaceae which differs from all other sphenophytes in the lack of secondary growth, having smaller leaves and no sterile bracts in the strobilus. The family includes two genera: *Equisetites* Sternb. the oldest known member described from the Rhaetic of Germany and ranging from Devonian to Tertiary, with several records for the United States, Mexico, Peru, Brazil and Argentina (Reed, 1971). The other genus is *Equisetum* whose fossil record extends from the Caenozoic to the Recent and is the only extant genus of this old family of vascular plants. Jongmans (1922) listed 143 fossil species ascribed to *Equisetum* and for the

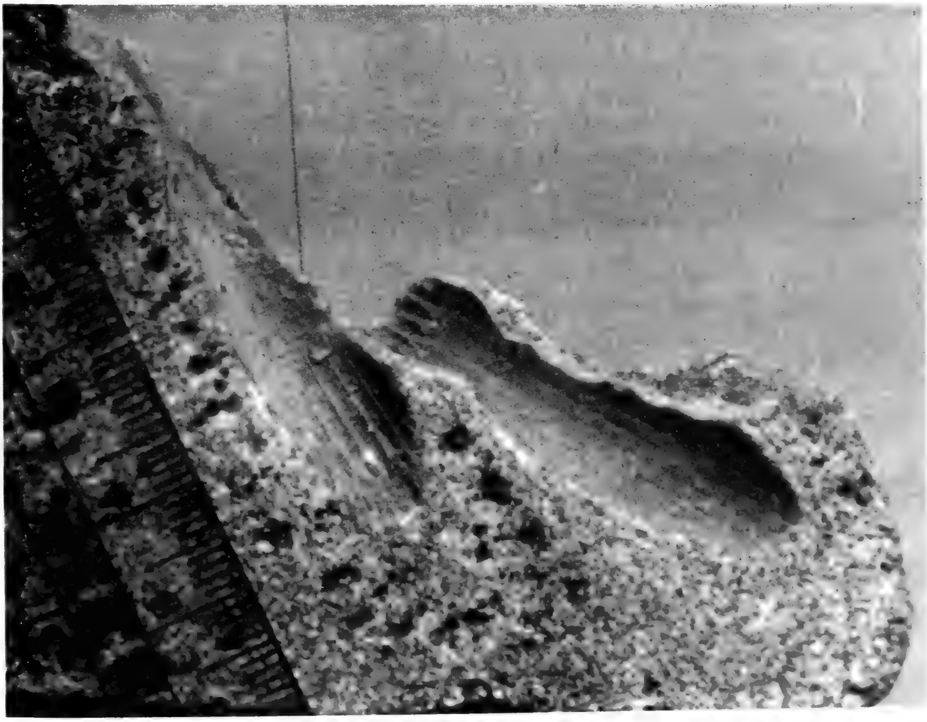

FIGURE 1. Travertine slab and imprints of two stems of the Costa Rica fossil *Equisetum* sp. (scale in cm.)

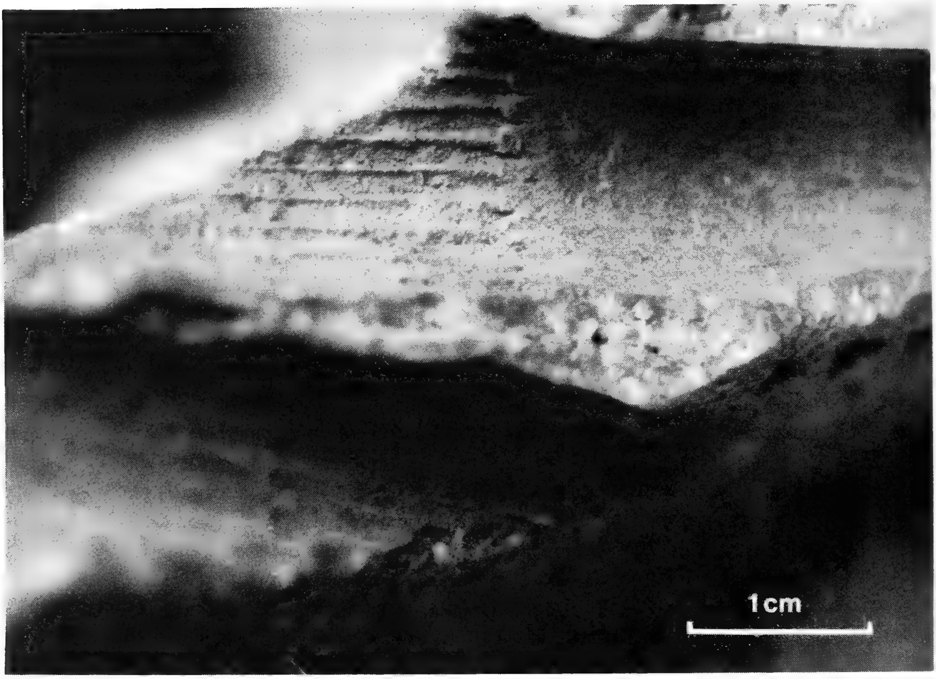

FIGURE 2. Close-up of imprint of fossil Equisetum showing ridges and nodal sheath.

subgenus *Hippochaete* the fossil evidence is enumerated by Hauke (1963). There are no records of fossil Equiseta for Central America.

THE COSTA RICA FOSSIL

Recently, a fragment of a slab of a concretionary limestone of the type known as Travertine or Spring Tuff from the quarries of the River Navarro, Province of Cartago, Costa Rica, was found to contain the moulds of two stems undoubtedly belonging to *Equisetum*. The impressions are of one node and an internode and show well-defined, longitudinal ridges and part of the whorl of scale-like leaves that make the nodal sheath (figs. 1,2). The impressions are quite rounded, suggesting a slow and gentle deposition of the calcareous particles suspended in water which enabled the matrix to concresce without crushing and flattening the brittle aerial shoots of the horsetail. Thus, it may be safely assumed that both moulds include more than half of the circumference of each of the stems and that their diameter, number of ridges and nodal sheath leaves can be estimated for the living plants. Acetate peels after cleansing with 1% aqueous solution of HCl reveal nothing of the epidermal features, the finer particles of the embedding carbonates having filled the sunken stomatal apparatus and obliterated the cuticular interstices along cellular walls. A silicone cast was obtained to count the number or ridges as well as to determine their configuration (convex, bituberculate, etc) and the possible pattern of the silica incrustations along them.

The stems are 1.6 cm in diameter, had ± 32 slightly convex ridges, 1.2-1.4 mm wide. Length of internode was underfermined. The nodal sheath was 1.7-2 cm long and had also ± 32 leaves, the apical teeth or segments were ± 4 mm long. From the meristic information at hand it is possible to ascribe this material to the giant horsetails of subgenus Hippochaete represented in Costa Rica by *E. giganteum* L., *E. myriochaetum* Cham & Schlecht., and their putative hybrid *E. x schaffneri* (Milde) Hauke. Nevertheless, the lack of data on the number of rows of sunken stomata, the silica incrustation pattern of the ridges etc. makes assignment to one of the cited species difficult and must await the discovery of more material in better preservation.

The region of the eastern Central Valley of Costa Rica where the fossil comes from is generally considered as an undifferentiated Miocene-Pliocene locality on the evidence of nearby clastic and paraclitic marine sediments. The travertine quarries of the River Navarro are surrounded by lava flows of Upper Tertiary age and the tuff bears numerous imprints of angiosperm foliage and stems representing Melastomataceae, Lauraceae and Annonaceae. To date, this is the only report of a vascular cryptogam from these calcareous deposits and the first record of a fossil *Equisetum* for Central America.

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REVIEW

TRAITE DE PALEOBOTANIQUE, by E. Boureau, S. Jovet-Ast, O.A. Hoeg, & W.G. Chaloner. Vol. 2: Bryophyta, Psilophyta, Lycophyta. 845 pp. Price NF580.00 (about £69.05). Vol. 3: Sphenophyta, Noeggerathiophyta. 544 pp. Price NF400.00 (about £47.62). Vol. 4(1): Filicophyta. 519 pp. Price NF365.00 (about 43.45). Vol. 4(2): Pteridophyta. Part 1. 768 pp. Price NF850.00 (about £101.19). Masson et Cie. Paris.

Fossil ferns and fern-allies are often only of passing interest to people interested in living plants. This is partially due to difficulties encountered when one attempts to search the literature. The larger texts are often out of date, and the modern scientific papers have been published in a wide range of journals not normally used by people studying extant material. This series, however, goes a long way towards filling this gap in the literature by compiling an almost complete catalogue of fossil pteridophytes. Anyone interested in the past history of ferns and their allies will find these books of immense value. They are the only parts yet published of a series planned to encompass all fossil plants. Various specialist authors have all succeeded in giving comprehensive compilations which should provide the basis for many years of future research. Volume 2 deals with the psilophytes and lycopods and also includes the bryophytes; Volume 3 the horsetails and their relations; while Volume 4 is devoted to the ferns. They are beautifully produced and lavishly illustrated with excellent photographs, enabling one to simply browse. The series is obviously produced for the specialist and their price will effectively stop any casual purchase. Research workers will definitely need access to them but non-specialists should see a copy if at all possible. Volume 4 part 3 is eagerly awaited, for it will complete the ferns and it is promised to contain ideas of fern evolution.

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THE SOUTHERN FERN GUIDE: SOUTHEASTERN AND SOUTH-MIDLAND UNITED STATES, by Edgar T. Wherry, illustrated by Jame C.W. Chen and Keith C.Y. Chen. Edition one, reprinted with corrections by John T. Mickel, 1978. Doubleday/AFS 117 x 110 mm. Price S4.50

Most readers of the *Gazette* will know of this useful companion volume to Prof. Wherry's *Fern Guide to NE and Midland U.S. and adjacent Canada,* first published in 1964 in the Doubleday Nature Guide Series. It has now been reprinted by the New York Chapter of the American Fern Society and is available from them, care-of the New York Botanical Garden, Bronx, New York, 10458.

This edition is photo-copied and the corrections and additions are confined to one page (p.8). Most are corrections to nomenclature but *Thelypteris thelypteroides* Michx (1803) which should replace *T. palustris Schott.,* (1834) (pp. 44 and 102) has not been included. This is a case where the earlier name must be used however much the later one is loved and used. The first correction transfers *Hypolepis* from Dennstaedtiaceae to Hypolepidaceae "to join *Pteridium.'* This is in order but Wherry put the latter genus in "Pteridaceae" and this should have been corrected. It is said *Hymenophyllum tunbrigense* (wrongly spelt in the original and correction as *tunbridgense)* is now found elsewhere. The range, if not the exact location could perhaps have been given. Likewise we are told to add *Trichomanes holopterum* Kunze (p. 232) and *Lygodium microphyllum* R. Br (p. 238) but no localities are given.

This little book, not only broadens our knowledge of warm temperate ferns, it also has many facets of knowledge e.g. on the culture of each species, epithets and their significance, authors of fern latin name etc. If you do not have it already you should take the chance of getting it now it is again available.

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SPORODERM ARCHITECTURE IN MODERN AZOLLA

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ABSTRACT

The morphology of the megaspore apparatus in extant *Azolla* is reconsidered and certain terms clarified. Examination of the sporoderm, by means of scanning electron microscopy and thin sectioning of *A. pinnata, A. nilotica, A. microphylla* and *A. filiculoides,* indicates the occurrence of five distinct morphological types, though the 3-layered sporoderm is common to all species studied. Sporoderm structure in *A. filiculoides* var. *rubra* suggests that this variety may be considered as a distinct species.

INTRODUCTION

Mettenius (1847) described the morphology of the megaspore apparatus within the section Azolla, but it was Strasburger (1873) who provided the first illustrations of sporoderm sculpture and structure in *A. pinnata, A. nilotica, A. microphylla* (described as *A. caroliniana* by Strasburger) and *A. filiculoides.* Svenson (1944) considered sporoderm features to be of taxonomic importance, but excluded sporoderm structure in his study of the New World species. More recent contributions on the sporoderm in modern *Azolla* are:— *A. pinnata* (Kempf 1969a, Sweet and Hills 1971, Martin 1976), *A. nilotica* (Demalsy 1954, Martin 1976), *A. filiculoides* (Bonnet 1957, Bertelsen 1972, Martin 1976). Much of the developmental organisation of the megaspore apparatus, particularly sporoderm differentiation, is still poorly understood.

In recent years, the attention focused on fossil species of *Azolla* has undoubtedly provided more information on architecture of the megaspore apparatus than that obtained from modern species. Kempf (1969a, 1969b), not only provided the basis of our understanding of the morphology of the megaspore apparatus, but also demonstrated that interspecific variability of sporoderm structure provides a useful means of taxonomic separation and identification of both fossil and modern species.

The purpose of the present work is to provide preliminary illustrated descriptions of the sporoderm in *A. pinnata, A. nilotica, A. microphylla* and *A. filiculoides.* A more extensive comparative treatment of sporoderm architecture in modern species of *Azolla,* including sporoderm elaboration at the proximal surface and its relationship to taxonomy within the genus, will be described elsewhere; as will the significance of the sporoderm in the evolutionary development of the megaspore apparatus (Fowler and Stennett-Willson, in press).

MATERIALS AND METHODS

Herbarium material investigated was obtained from the British Museum (Nat. Hist.) and the Royal Botanic Gardens, Kew. Specimens were examined and photographed with a Cambridge Instruments Company Stereoscan. Thin sections, approximate thickness 1.5 μm, were cut with a LKB Ultratome III and glass knife, examined and photographed with a Wild-Heerbrugg M20 light microscope with Photoautomat. Measurements given are based on median longitudinal sections taken from two to three specimens of each species investigated.

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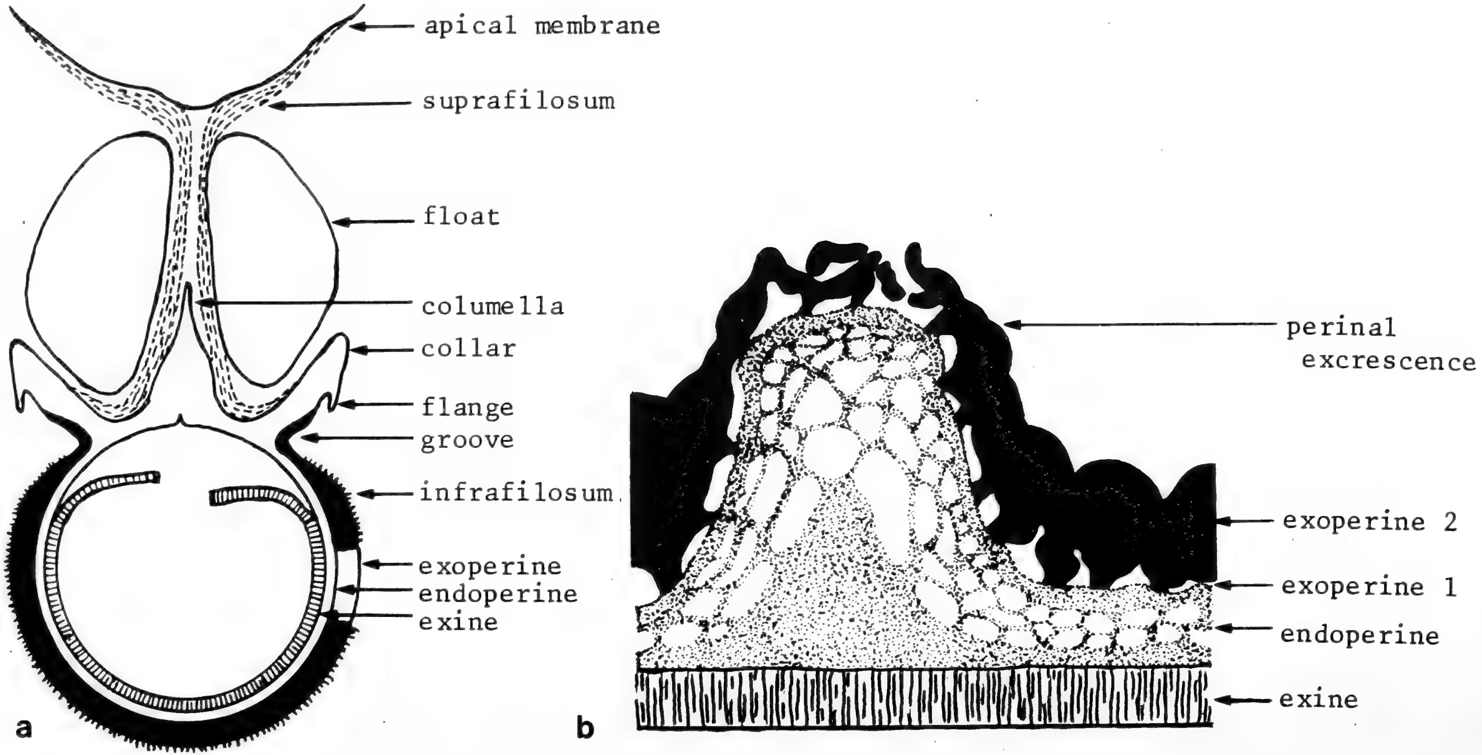

FIGURE 1. a, diagrammatic median L.S. through megaspore apparatus of a member of section *Azolla,* showing its organisation and terminology used; b, diagrammatic representation of sporoderm structure of *A. filiculoides* var. *rubra,* with terminology used.

TERMINOLOGY

It is hoped that the following list of terms (illustrated in fig. 1) may form the basis for a standardised, simplified terminology, at the same time offering some clarification of certain terms. Though re-defined in some cases, many of the terms have been used by previous authors (Sweet and Chandrasekharam 1973, Sweet and Hills 1976).

Megaspore apparatus: essentially a thick-walled megaspore from which hairs arise to enmesh the floats. The proximal sporoderm often becomes elaborated to form a collar and columella, the hairs originating in this region forming a superstructure accommodating the proximally positioned floats.

Megaspore: consists of the megaspore proper bounded by the exine, surrounded by the sculptured hairy perine.

Collar: delimits periphery of the proximal surface of megaspore, appearing raised and contoured due to increased thickness and vacuolation of the endoperine. In extant members of section *Azolla* it is tricuspid, with cusps extending between and supporting the floats, and with a downwardly directed flange on the outer face.

Columella (*syn.* gula, acrolamella, labrum, column): conical, triseptate, centrally placed elaboration of the proximal sporoderm composed mainly of vacuolate endoperine. The septa divide the proximal surface into three equal sectors, and partially support the floats. Previous confusion over this term has surrounded its use for both the triseptate structure and the superstructure of hairs on the proximal surface. As interpreted here, the term does not include the hairs.

Filosum: hairs on the sporoderm. The definition given by Sweet and Chandrasekharam (1973) can be applied to a megaspore apparatus showing little polarity. With distinct polarity, it is necessary to distinguish between the proximal hairy superstructure and the hairs on the remaining megaspore surface.

Infrafilosum (new term): hairs originating outside the collar region, forming a mat on the perine surface.

Suprafilosum (new term): proximally positioned superstructure of hairs arising from the collar region and columella, and which houses the floats. Basically cylindrical, but apically inverted to become umbrella-shaped. On removal of the megaspore apparatus from the megasporocarp, the suprafilosum becomes erect and funnel-shaped (fig.2a). This basic structure is further modified by float development, resulting in a triseptate form between the floats.

Apical membrane: remnant of megasporangial wall attached to apex of suprafilosum.

Float: vacuolate, pseudocellular structure often with hairs on inner faces and at apex which serve as a means of attachment to the suprafilosum.

Sporoderm: megaspore wall, consisting of innermost exine and 2-layered perine.

Exine: wall surrounding megaspore proper. A thin basement layer, the endoexine, may often be delimited from a thicker, radially striated exoexine.

Perine: 2-layered wall outside exine which gives rise to the filosum.

Endoperine: innermost homogeneous or vacuolate layer of the perine located adjacent, and loosely attached, to the exine. Extensive development of this layer is significant in the formation of collar, columella and sculptural features.

Exoperine: outermost sculptured layer of perine with 2 — 3 zones usually recognisable, excluding the filosum.

Perinal excrescence: large protuberance from perine surface composed of both exoperine and endoperine.

Use of the terms exine and perine is becoming increasingly acceptable to describe the sporoderm of both fossil and modern species of *Azolla* (Fowler 1975, Sweet and Hills 1976, Martin 1976). Erdtman (1952) defines the perine as an extra-exinous layer formed by the activity of a tapetal plasmodium. Though use of these terms for *Azolla* implies a knowledge of sporoderm development which does not exist, its use seems justified in view of the structural similarity between floats and massulae, usually accepted as perinous, and the endoperine.

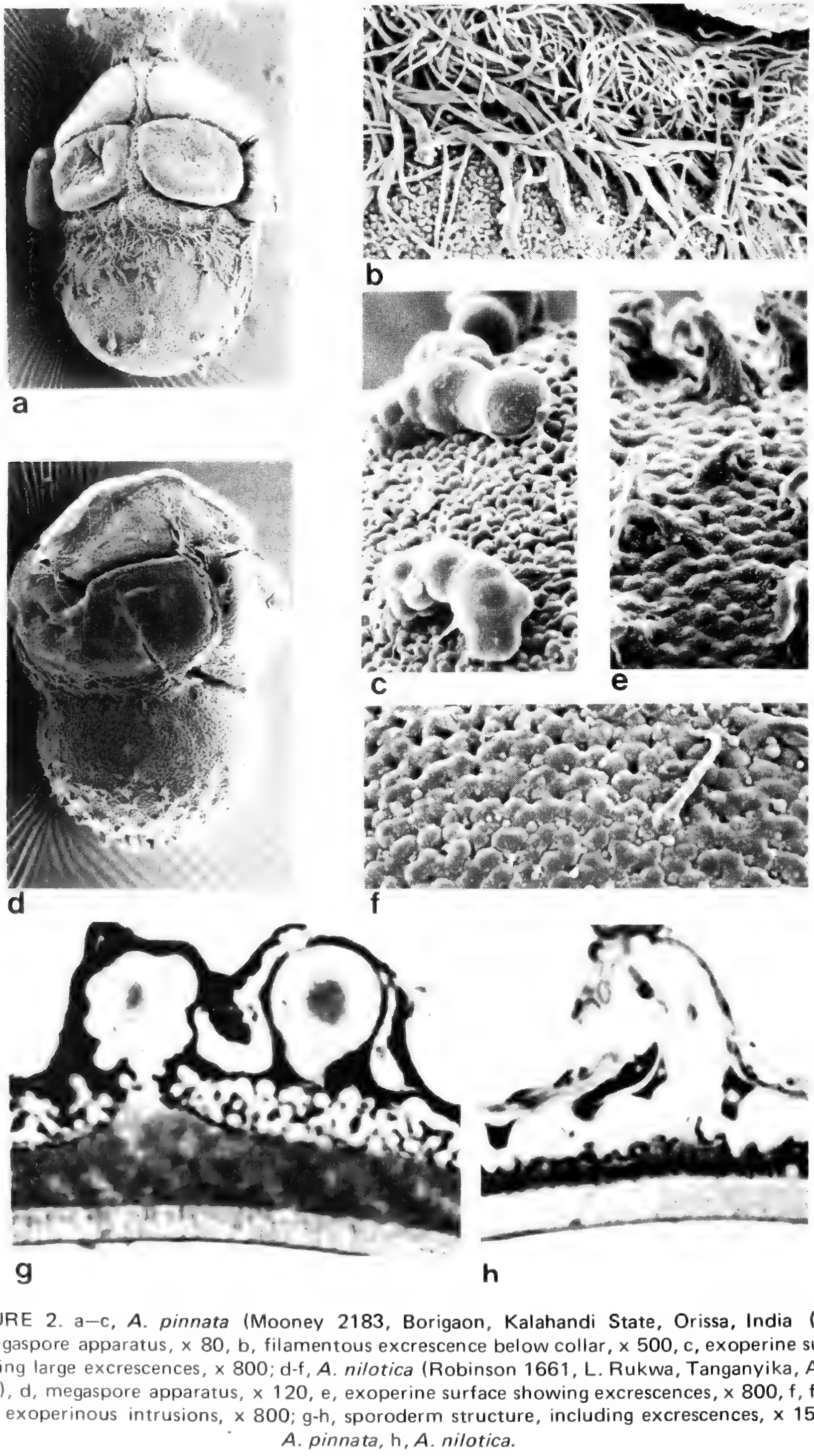

FIGURE 2. a–c, *A. pinnata* (Mooney 2183, Borigaon, Kalahandi State, Orissa, India (K)), a, megaspore apparatus, x 80, b, filamentous excrescence below collar, x 500, c, exoperine surface showing large excrescences, x 800; d-f, *A. nilotica* (Robinson 1661, L. Rukwa, Tanganyika, Africa, (BM)), d, megaspore apparatus, x 120, e, exoperine surface showing excrescences, x 800, f, foveae with exoperinous intrusions, x 800; g-h, sporoderm structure, including excrescences, x 1500, g, *A. pinnata*, h, *A. nilotica*.

SPORODERM ARCHITECTURE

Section RHIZOSPERMA – megaspore apparatus 9-floated.

A. pinnata

Sculpture: Distinct ornamentation of large, cylindrical, elongated prostrate perinal excrescences forming the exoperine 3 zone (fig. 2a). Excrescences immediately beneath collar are filamentous, attaining 75.0 μm length but of uniform diameter ca. 5.0 um (fig. 2b). More prominent excrescences occur on the remaining sporoderm, being larger (diameter ca. 15.0 um, length ca. 16 – 40.0 um), with constrictions at irregular intervals, and fused directly, or by elongated baculae, to the surface below (fig. 2c). The exoperine 2, constititing most of the perine surface, is composed of anastomosing baculae of uniform diameter ca. 2.0 μm, with rounded free ends at, or near, the surface. Sporoderm devoid of hair-like filaments except in the collar region and on the proximal surface.

Structure (fig. 2g): Sporoderm thickness ca. 32.0 um including perinal excrescences which can attain ca. 15.0 um in height. Exine (ca. 3.8 μm) characterised (as in all extant species examined) by radial striations and thin basement zone. Endoperine (ca. 6.8 μm) homogeneous, composed of elements smaller than those of the exine. Exoperine 1 (<0.5 μm) composed of both large and small baculae, represents the transitional zone at the base of the exoperine 2 layer. The anastomosing baculae of the exoperine 2 layer (ca. 5.5 μm) occur throughout its thickness. Occasional enlarged hollow baculae connect the endoperine with overlying excrescences, and sections clearly indicate that endoperinous material, as well as exoperinous, is involved in the composition of these structures.

A. nilotica

Sculpture: Numerous large spiny perinal excrescences occur distally (length usually ca. 16.0 μm, though some attain 40.0 μm), often with a recurved and blunt apex (fig. 2d). Perine surface otherwise foveolate with regularly arranged foveae (ca. 2.0 μm in diameter, 4 – 5.0 μm apart) situated in depressions demarcating areas between fused clavae of the exoperine. Spines are compound, appearing to be formed by fusion of prolongations of adjacent clavae. Perine surface, including spines, finely granulate (fig. 2e). Intrusion of exoperinous material into foveae from below appears to be a secondary feature in wall development (fig. 2f). This feature may have formed the basis for the term 'inperinal prolongation' (Sweet and Chandrasekharam 1973), though there is no evidence supporting the view that such structures are endoperinous, as suggested by those authors. No hair-like filaments present.

Structure (fig. 2h): Sporoderm thickness ca. 29.0 μm including perinal excrescences. A coarsely granular endoperine (ca. 3.0 μm) surrounds the exine (ca. 4.5 um). Base of exoperine forms a zone of short tapering columellae, here designated the exoperine 1 (ca. 1.0 μm). Exoperine 2 (ca. 4.8 μm) forms the general perine surface and is composed of a dense layer of fused clavae with intervening foveae. The exoperine 3 zone consists of perinal excrescences into which the endoperine extends, as in *A. pinnata*.

Section AZOLLA – megaspore apparatus 3-floated.

A. microphylla

Sculpture: Rugulate-verrucate with irregularly arranged foveae of varying size. Numerous hair-like filaments (diameter ca. 0.5 – 1.0μm) often emerge from smaller foveae (diameter ca. 2 – 5.0μm) (fig. 3b) Large rounded foveae (diameter ca. 6 – 8.0 um) impart a distinctly pitted appearance at a low magnification, the largest cavities occuring toward the distal surface (fig. 3a).

Structure (fig. 3c): Sporoderm thickness ca. 22.0 μm, excluding infrafilosum. Exine ca. 4.2 um. Endoperine (ca. 3.8 μm) coarsely granular with a low degree of vacuolation. Transition from endoperine to exoperine gradual, with fusion and thickening of elements toward the upper endoperine surface, passing into an anastomosing network of predominantly tangentially arranged baculae (diameter ca. 0.5 μm) in the exoperine 1 zone (ca. 3.0 μm). Exoperine 2 (ca. 11.0 μm) with baculae extending upward, branching and fusing at their apices to support a thick, loosely arranged, perforated 'tectum-like' layer, forming the rugulate-verrucate surface sculpture. Hairs appear to arise from the exoperine 1 zone.

A. filiculoides

Sculpture: Raised angular areas interconnected by narrow ridges surround closely placed rounded

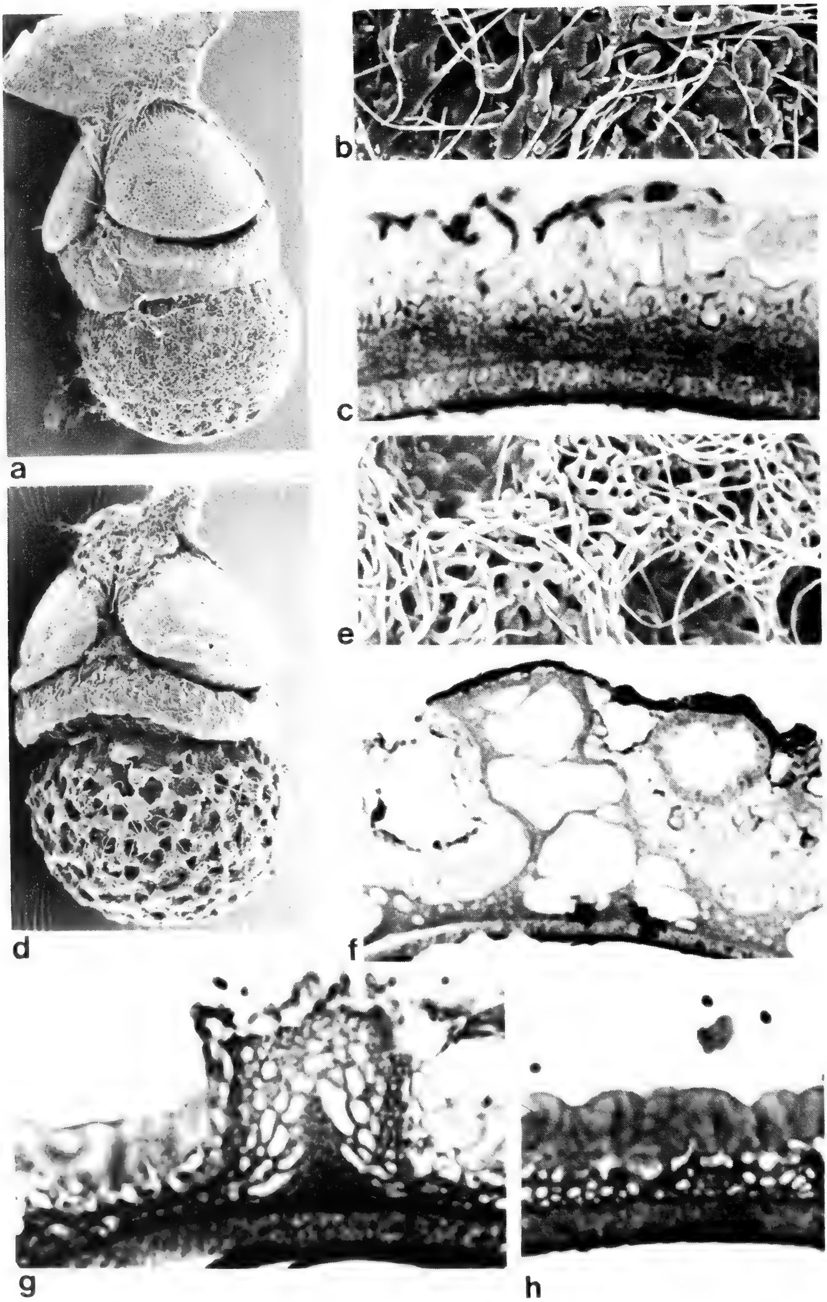

FIGURE 3. a–c, *A. microphylla* (Molina 3962, En el Rio, Orillas del Rio Lizapa, Llano Lizapa, Honduras (BM)), a, megaspore apparatus, x 110, b, exoperine surface, x 800, c, sporoderm structure, x 1500; d, e, g, h. *A. filiculoides* var. *rubra,* (Byrne 8310, Oura Road, Wagga Wagga, N.S.W., Australia (BM)), d, megaspore apparatus, x 110, e, exoperine surface, x 800, g, sporoderm structure at eruption, x 1500, h, sporoderm structure in depression, x 1500; f, sporoderm structure of *A. filiculoides,* x 1100 (collected by authors from Greywell, England).

depressions uniformly distributed over the perine surface (fig. 3d). Raised areas prominently ornamented with anastomosing baculae in lateral continuity with the relatively smooth, though undulating, exoperine surface of the adjoining depressions. Hair-like filaments (diameter ca. 0.5 – 1.0 um) originate beneath the angular areas, emerging between the baculate elements (fig. 3e). A less pronounced rugulate-verrucate sculpture, pierced by foveae through which hairs penetrate, may be seen in certain areas, possibly representing a later developmental stage of the sporoderm.

The above description can be applied both to *A. filiculoides* and *A. filiculoides* var. *rubra.*

A. filiculoides var. *rubra*

Structure (fig. 3f): Sporoderm thickness varies from ca. 15.0 µm beneath depressions to ca. 42.0 µm in raised areas. Raised areas are large interconnecting excrescences formed by eruptions of the vacuolate endoperine and superposed by exoperine. Below depressions, sporoderm composed of exine (ca. 3.0 µm), endoperine (ca. 3.0 µm), exoperine 1 (0.5 – 1.0 µm) and exoperine 2 (ca. 8.0 µm). Within an excrescence, endoperine can attain a thickness of ca. 37.0 µm, exoperine to the outside being reduced to ca. 2.0 µm. Endoperine granular, with occasional small, centrally positioned, rounded alveolae except in excrescences which are composed almost entirely of large rounded alveolae, some exceeding 20.0 µm in diameter. Exoperine 1 composed of short columellae. Exoperine 2 forms a thick dense layer beneath depressions, thinning out on the flanks of eruptions, and becoming modified as an anastomosing network of baculae at the apex of an eruption.

Sporoderm structure in *A. filiculoides* var. *rubra* is sufficiently different from that of *A. filiculoides,* particularly in the nature of the endoperine, as to merit separate description (see fig. 3 g-h).

Sporoderm thickness ca. 16.0 µm beneath depressions, reaching ca. 30.0 µm in raised areas. Below depressions, sporoderm composed of exine (ca 4.2 um), endoperine (ca. 3.8 um), exoperine 1 (0.5 – 1.0 µm) and exoperine 2 (ca. 7.0 µm). Within an excrescence, endoperine can attain a thickness of ca. 23.0 µm. Endoperine conspicuously vacuolate, appearing reticulate in section, with a thick, coarsely granular mesh. Elongated alveolae (maximum diameter ca. 1.0 µm, except within excrescence) are arranged in a central zone between dense, narrow peripheral zones. Endoperine zonation is conspicuous within an excrescence where the basal dense zone projects upward and is separated by the vacuolate zone from the upper dense zone. The exoperine 1 is constructed as in *A. filiculoides,* but with more numerous, strongly developed columellae. Exoperine 2 is similar to that of *A. filiculoides,* including modification at the sites of eruptions.

CONCLUSIONS

Many specimens in herbarium collections of *Azolla* do not possess sporocarps, resulting in only a limited collection of each of the species being available for study. However, five distinct sporoderm types are recognised, though the 3 - layered sporoderm is common to all species investigated. Sporoderm structure in *A. filiculoides* var. *rubra* is sufficiently distinct to suggest that this variety may possibly be considered as a separate species.

In the past, too much reliance may have been placed on the use of vegetative features for the identification of *Azolla* species, leading to incorrect determination. For example, during this investigation, collections attributed to *A. africana,* long regarded as a variety of *A. pinnata* (Baker 1886, Sweet and Hills 1971), were found to possess megaspore apparatuses of the *A. nilotica* type. This might suggest that *A. pinnata* and *A. nilotica* are not easily separable using vegetative morphology.

The megaspore apparatus is believed to offer the best means of defining *Azolla* species at the present time, at least initially, meaningful vegetative differences may then be established from species collections over a wide geographical area.

ACKNOWLEDGEMENTS

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MORPHOLOGY, ANATOMY AND TAXONOMY OF LYCOPODIACEAE OF THE DARJEELING HIMALAYAS

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ABSTRACT

This paper deals with the anatomy, morphology, palynology and taxonomy of lycopods of Darjeeing Himalaya. A total of 5 genera and 13 species are described, illustrated and critically circumscribed from the area for the first time, and 6 new combinations are established. The altitudinal distribution of all the taxa in different forest types in Darjeeling Himalaya are noted and a key for their identification is proposed.

INTRODUCTION

The Lycopodiaceae as conceived here includes the following genera : *Lycopodium, Diphasium, Huperzia, Palhinhaea,* and *Phlegmariurus.* Most of these plants are small, herbaceous or shrubby in nature. Some of them are epiphytic and have erect or pendent sporophytes; others are terrestrial and may become horizontal or erect. They have eligulate microphyllous leaves and sporangia occurring singly on the adaxial surface of the sporophyll.

These plants grow in different parts of the world from the tropics to the polar regions. In India they are generally restricted to the Himalayas, Andaman-Nicobar Islands, and on the mountains of South India. The only important account of the living lycopods of India is contained in the 'Notes on Indian species of *Lycopodium* with remarks on the distribution of the genus in India, Burma and Ceylon' (Chowdhury 1937). Unfortunately, in this work no attempt was made to describe and circumscribe the individual species, and no keys were designed to facilitate their identification. Moreover during the last three decades new lines of thought and understanding have developed and have changed the earlier generic concepts of the lycopods. The purpose of the present treatment is to consider the morphology, anatomy, palynology and delimitation of all the lycopodioid taxa of Darjeeling in the Himalayas.

The district of Darjeeling lies between 26.31' and 27.13' north latitude and 87.93' and 88.53' east longitude. It contains a total area of 1,873 square kilometres. The principal town of the district, Darjeeling is situated at an average altitude of 2,044 metres. The soil is mainly composed of alluvium of light loamy texture; it is commonly known as black, red and white soil. Among these white soil is the poorest, while the black one is very rich and contains organic matters. The soil is covered by a layer of humus, 2.5-10 cm deep. The nitrogen content of the soil is low, while the calcium content is high. The rainfall is minimum during the months from November to March, while it is maximum during the monsoon. Darjeeling receives on an average 306.5 cm of rain within a year. Heavy rains caused by monsoons and humus work together for the development and growth of forests and vegetations of all kinds on the mountains of the Darjeeling district. The humidity is also less during the winter, but gradually it increases during the monsoon and becomes highest in the month of July (above 90%). The temperature rises to about 24 C during the months of May to October but decreases sharply during the winter, almost at a freezing point.

KEY TO GENERA

A. Plants isodichotomous, roots restricted to the base of the stem, sporangia cauline or axillary, spores pitted.
  B. Vegetative leaves and fertile leaves similar, no definite formation of strobili . *Huperzia*
  BB. Vegetative leaves and fertile leaves dissimilar, formation of definite strobili . . . . *Phlegmariurus*

AA. Plants monopodial, roots scattered throughout the stem, sporangia foliar, spores without pits
  C. Vegetative leaves di- or trimorphic, ultimate branchlets flat with tetrastichous leaves . . . . *Diphasium*
  CC. Vegetative leaves isomorphic, ultimate branchlets round with spiral leaves
    D. Branches erect and tree-like in habit, valves of the sporangium unequal, strobili sessile . . . . *Palhinhaea*
    DD. Branches ascending and unlike the trees, valves of the sporangium equal, strobili peduncled . . . . *Lycopodium*

GENUS HUPERZIA

HUPERZIA BERNHARDI (in Schrad, Journ.Bot.1800(2) : 126, 1801). The plants are terrestrial or epiphytic in habit, and are isodichotomously branched. All the branches are functionally alike and grow indefinitely. The vascular cylinder of the stem may be actinostelic or plectostelic; frequently, however, both types of the stelar structure may occur at different regions of the adult plant. The vegetative and reproductive leaves are similar in shape and the latter are never aggregated into definite cones. Sporangia are borne directly on the stem or in the axils of the sporophylls. The ektexine of the spore is pitted. The roots occur only at the base of the stem; in transverse section the xylem mass of the root is cresent shaped with pholem situated in the bay.

Gametophytes are dorsiventral, flattened and possess a distinct or indistinct rim on the dorsal side (Bruchmann, 1885; Boivin, 1950). Rhizoids develop only at the undersurface of the prothallus. Sex organs are scattered and restricted within the rim.

Ghatak (1965) suggests that the basic chromosome number may be x = 11 within the genus, while Pichi Sermolli (1958) remarks that the chromosomes of this genus were derived from a hypothetical basic number 17, and that the present numbers are characterized by a high polyploidy.

Type : *Huperzia selago* (L.) Bernh. ex Schrank et Mart. Hort. Monac. 3, 1829.

Key to the Species

A. Plants terrestrial, erect or suberect, sporophylls scattered throughout the stem; walls of the guard cells without any lignified ray-like thickenings; spores with truncate corners and concave or straight side walls; pits on the spores free, never coalescent
  B. Leaves and sporophylls oblanceolate, not uniform in size; hypostomatic; walls of the guard cells around the stomatal pore thick
    C. Leaves and sporophylls thin, strongly and remotely serrated, never in small alternating homogeneous groups; sporangia cauline . . . . . *H. serrata*
    CC. Leaves and sporophylls very minutely or obscurely dentate towards the apices, always in small alternating homogeneous groups; sporangia axillary . . . . *H. herteriana*
  BB. Leaves and sporophylls lens-subulate, entire or minutely serrated, uniform in size; amphistomatic; walls of the guard cells uniformly thin. . . . . *H. selago*

AA. Plants epiphytic, pendulous at maturity; sporophylls more corwded near branch tips; walls of the guard cells with ray-like lignified thickenings; spores with rounded corners and convex sides; at least a few pits on the spores coalescent
  D. Leaves and sprophylls spreading; midrib distinct, sporangia cauline; pits on spores uniformly distributed both on proximal and distal surfaces

E. Stem slender, 1-2 mm in diameter; leaves and sporophylls oblong, tips of which never drawn into a sharp point; glossy on dryness, hypostomatic . *H. hamiltonii*

EE. Stem thick, never less than 3 mm in diameter; leaves and sporophylls linear, long, tips of which drawn into a sharp point; amphistomatic . . *H. squarrosa*

DD. Leaves and sporophylls ascending (only occasionally basal ones spreading); midrib obscure; sporangia axillary; pits on spores almost lacking on the proximal surface

F. Plants usually short; leaves and sporophylls soft, linear, uniform in size throughout, never appressed to the stem; rays of the guard cells extending the entire lumina of the cells strongly lignified.

G. Plants never tufted; leaves setaceous, never incurved at sides or twisted at the base; amphistomatic; foliar epidermal cells without any pits; pits on spores mostly coalescent, rarely free . . . . . . *H. subulifolia*

GG. Plants tufted, leaves always incurved at the margins and often twisted at the base; hypostomatic; foliar epidermal cells pitted; pits on the spores free, only occasionally coalescent . . . . . . *H. pulcherrima*

FF. Plants long; leaves rigid, strongly appressed, lanceolate, gradually smaller merging into sporophylls; rays of the guard cells extending half the cells' lumina faintly lignified; foliar epidermal cells strongly pitted; pits on the spores free, rarely coalescent . . . . *H. laxa*

HUPERZIA SELAGO (L.) Bernh.ex Schrank et Mart. Hort. Monac.3, 1829

Lycopodium selago L.Sp.Pl.2:1102, 1753; Chowdhury in Trans.nat. Inst. Sci., India, 1 : 190, 1937. (Fig. 1 a-j)

Plants are terrestrial, and usually grow on shady rocks. They are small, generally about 2-10 cm long, but under favourable conditions grow upto 20 cm, erect or sometimes become suberct. The stem is about 1.5-3 mm in diameter, actinostelic at the basal and the distal parts while in the middle region it becomes almost pectostelic, and exarch. The xylem rays are expanded at the periphery, and their numbers vary at different regions of the same plant. The tracheids of the first formed protoxylem are long, narrow, and possess delicate, unlignified primary wall with a series of thickened annular rings on the inside. Often adjacent rings are connected by one or two vertically or obliquely oriented bands, but more frequently they are free from one another. The later-formed protoxylem elements possess a delicate unlignified primary wall, internal to which there occurs a discontinuous system of thickening in the form of a net. The metaxylem elements develop bordered pits, the pits being circular, oval or elongated. The cottex is composed of thin walled parenchymatous cells filled with starch grains. The branches are isodichotomous and are of indefinite growth. Leaves are crowded, 8-ranked, lens-subulate, gradually acuminate towards the apex, and narrow towards the base, minutely serrated or very rarely entire, glossy and moderately thick. They are about 1 cm long and 1.5 mm broad. The vein is raised on both the surfaces in fresh material but becomes obscure in dried specimens. The epidermal cells of the leaves are thin walled, elongate and wavy. Stomata are numerous and occur on both the surfaces of the vegetative and reproductive leaves. The walls of the guard cells are uniformly thin and do not show additional thickenings. The mespophyll cells are not differentiated into palisade and spongy tissues. Mesophyll cells are hexagonal in outline. A few irregular shaped air-cavities occur between the mesophyll cells. The leaftrace is composed of a few tracheids surrounded by parenchymatous cells.

The sporophylls are very numerous and may be distributed from the apex down towards the base of the stem. They neither form a definite strobilus, nor the sterile and the fertile zones are clearly differentiated. The basal region of the stem is, however, often sterile. Occasionally isolated sporophylls occur among the vegetative leaves. The sporangia are broadly reniform, shortly stalked and attached in the axils of the sprophylls. The sporangia split into two equal valves. A very interesting feature is the production of bulbils in the axils of the leaves. The roots are basal, clustered and dichotomously forked. The spores are tetrahedral, sub-triangular, about 41 u in diameter and have slightly concave sides and truncate corners. The trilete mark extends upto 2/3 of the spore's radius. Exospores are distinctly pitted; pits being numerous on both the surfaces and never coalescent (i.e. foveolate).

HUPERZIA HERTERIANA (Kumm.) Sen et Sen, *comb. nov.*

Lycopodium herterianum Kumm. in Magyar Bot.Lap.26:99, 1928, a substitute name

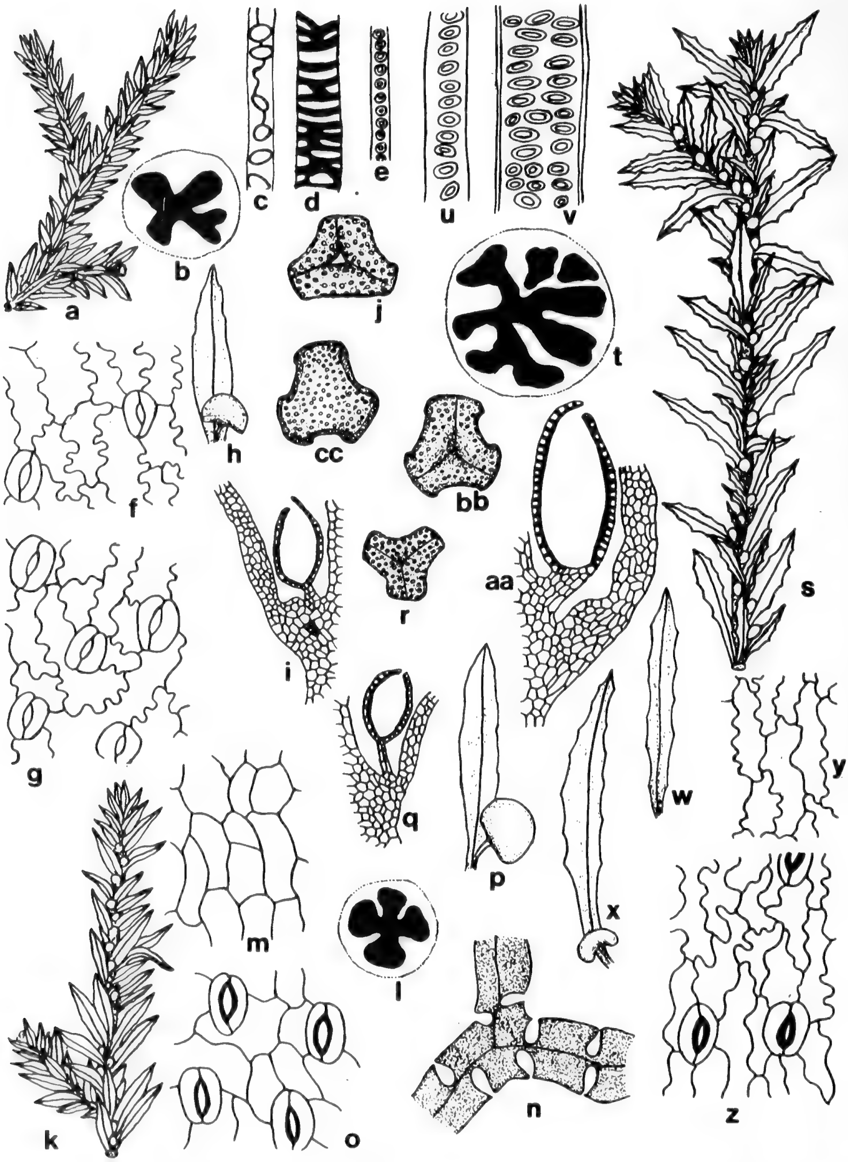

FIGURE 1. a-j, *Huperzia selago;* k-r, *Huperzia herteriana;* s-z, aa-cc, *Huperzia serrata.* a, part of a plant (X 1); b, T.S. of cauline stele near the base of plant (X 87); c-e, tracheary elements of stem (X 435); f-g, epidermal cells from adaxial and abaxial surfaces of lamina respectively showing stomata, (X 140); h, sporophyll (X 3); i, V.S. through a sporangium showing axillary attachment (X 25); j, spore (X 435); k, part of plant (X 1); l, T.S. of stele near the basal region of plant (X 87); m, epidermal cells from the adaxial surface of lamina (X 140); n, epidermal cells with pits on walls (X 1000); o, epidermal cells from the abaxial surface of the lamina showing stomata (X 140); p, sporophyll (X 3); q, V.S. through sporangium showing axillary attachment (X 25); r, spore (X 435); s, part of plant (X 1); t, T.S. of stele at basal region of plant (X 87); u-v, tracheary elements of stem (X 435); w, vegetative leaf (X 3); x, sporophyll (X 3); y, epidermal cells from the adaxial surface of lamina (X 130); z, epidermal cells from the abaxial surface of lamina showing stomata (X 130); aa, V.S. through sporangium showing cauline attachment (X 25); bb-cc, spores (X 435).

based on *L. sikkimense* Hert. *L. sikkemense* Hert. in Bot. Jahrb. 43 : Beibl nr. 98,42, 1909; non K. Muell, 1861. *L. lucidulum* sensu Clarke in Trans. Linn. Soc.II. Bot.1 : 589, 1880. (Fig. 1 k-r).

The plants grow on rocks in shady forests. They are small about 15-20 cm long, suberect, three or more times isodichotomously branched. Branches are spreading and about 1.5-2 mm in diameter. The cauline vascular cylinder is actinostelic; its protoxylem elements occur in continuous bands at the peripheral margins of the xylem arms. Tracheids of the metaxylem have bordered pits, which may be round or elongate and uni- or bi-seriate.

The leaves are moderately crowded, mostly 6-ranked, spreading or deflexed, oblanceolate and usually minutely toothed or wavy above the middle. They are of various sizes and a large leaf is about 10 mm long and 1.5 mm broad. All the leaves are sessile and have prominent midribs. Epidermal cells are rectangular in outline and have prominently pitted walls. Stomata are confined to the abaxial surface only. The guard cells are large and have slightly thick walls. The mesophyll cells of the lamina are undifferentiated, but are mostly rectangular in cross section. The airspaces between the mesophyll cells are large but few in number. The sporophylls resemble the vegetative leaves in shape but are usually shorter in size. They usually occur in small groups alternating with the zones of sterile leaves. However, isolated sporophylls may occur among sterile leaves. The sporangia are borne on short stalks, and are attached in the axils of the leaves; they dehisce by apical suture, which divides the jacket into two equal valves. The spores are tetrahedral, subtriangular, about 26 u in diameter, and have many circular pits, which are never coalescent. The pits occur both on the distal and the proximal face. The trilete mark is extended upto the margin. The side walls are concave, and the corners are truncate.

The roots both morphologically and anatomically resemble those of *H. selago.*

HUPERZIA SERRATA (Thunb.) Rothm. Feddes Repart. 54 : 58-, 62, 1944.
Lycopodium serratum Thunb. Fl. Jap., 341, 1784; Clarke in Trans. Linn. Soc. Lond., II. Bot 1 : 591, 1880. (Fig. 1 s-z, aa-cc).

Plants are terrestrial and grow in moist and deep shady places on humus rich soil. They are suberect, about 15-40 cm long, and 3-4 times isodichotomously forked. The branches are spreading, and about 2-3 mm in diameter. The vascular cylinder is actinostelic at the basal retion but higher up gradually changes into a plectostelic condition. At the distal end of a branch the vascular cylinder regains its actinostelic state. The tracheids of the proto-and metaxylem are similar to those of ***H. selago.*** The leaves are large or small, thin, oblanceolate, crowded, sessile and characteristically serrated. They have a prominent midrib, narrowed base and an acute apex. A large leaf is about 3 cm long and 3-5 mm wide. The small and large leaves are intermixed with one another. The small leaves usually bear sporangia, but often sporangia occur on large leaves. The epidermal cells of the leaves are elongate, sinuous, and bear stomata only on the abaxial surface. The wall of the guard cells adjacent to the stomatal pore is heavily and uniformly thickened. The mesophyll cells are not differentiated into spongy and palisade cells and are of irregular shape and size. The sporophylls may be borne all along the stem excepting the base. Occasionally the sprophylls and the vegetative leaves form alternate fertile and sterile zones. The sporangia are cauline, reniform but without any sinus on the proximal wall, larger than the base of the sporophyll, and are borne on a massive stalk. The jacket of the sporangium is composed of cells with wavy walls and splits into two equal valves. The spores are about 31 u in diameter, triangular, but appear hexagonal due to truncate corners. The side walls are concave. Ektexine is thick and pitted. The pits are round, non-coalescent, closely spread excepting around the tetrad scar where only a few of them occur. The trilete mark extends up to the margin.

HUPERZIA SUBULIFOLIA (Wall. ex Hook et Grev.) Sen et Sen, *Comb. Nov.*
Lycopodium subulifolium Wall. ex Hook. et Grev. Icon. Fil. 1 : t. 49, 1827. *L. setaceum* Ham. ex D. Don. var subulifolium Wall. apud Clarke in Trans. Linn.Soc.II. Bot. 1 : 590, 1880. (Fig. 2 a-k).

Plants grow as epiphytes usually in dark shady forests. They are weak, pendulous, non spreading and fork isodichotomously two or three times. Usually a plant attains a height of 10-25 cm, but under favourable conditions of growth it may be more than 50 cm long. The stem is 1-2 mm in diameter, actinostelic but often the radiating xylem arms become separated from one another, showing a tendency towards formation of irregular plates. The protoxylem elements have

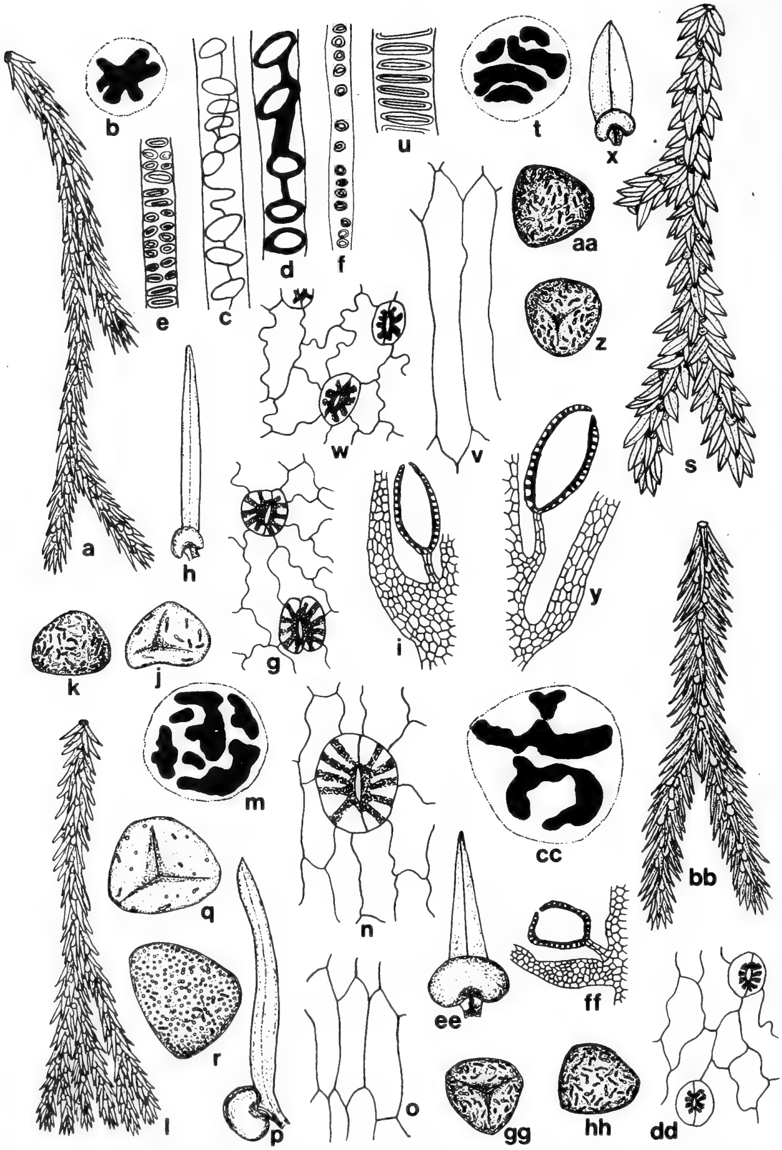

FIGURE 2. a-k, *Huperzia subulifolia;* l-r, *Huperzia pulcherrima;* s-z, aa, *Huperzia hamiltonii;* bb-hh, *Huperzia squarrosa.* a, part of plant (X 1); b, T.S. of stele near proximal end of plant (X 87); c-f, tracheary elements of stem (X 435); g, epidermal cells from abaxial surface of lamina showing stomata (X 130); h, sporophyll (X 3); i, V.S. through a sporangium showing its axillary attachment (X 25); j-k, spores (X 435); l, part of plant (X 1); m, T.S. of stele near proximal end of plant (X 140); n, epidermal cells from abaxial surface of lamina showing a stoma (X 300); o, epidermal cells from the adaxial surface of lamina (X 140), p, sporophyll (X 7); q-r, spores (X 640); s, part of plant (X 1); t, T.S. of cauline stele near middle region of plant (X 87); u, tracheid from stem (X 435); v, epidermal cells from adaxial surface of lamina (X 130); w, epidermal cells from abaxial surface of lamina (X 130); x, sporophyll (X 3); y, V.S. through a sporangium showing cauline attachment (X 25); z, aa, spores (X 435); bb, part of plant (X 1); cc, T.S. of cauline stele just above base of plant (X 87); dd, epidermal cells from abaxial surface of lamina showing stomata (X 140); ee, sporophyll (X 5); ff, V.S. through a sporangium showing its cauline attachment (X 25); gg-hh, spores (X 435).

annular or annular-helical hybrid type of thickening. The vertical bands connecting two adjacent rings are mostly thin but often become considerably thickened extending up to ¾ of the thickness of the tracheids. The rings are of various sizes; some are well fitted within the surrounding wall, while others are attached only at one side of the wall. There are also rings which are very small and are attached to one another by the vertical bands only. The metaxylem elements have bordered pits; the pits are round, oval or elongate.

The leaves are linear-subulate, thin, setaceous, entire ascending and crowded. They have a flat base and a gradually narrowed acute apex. There is no incurving or twisting of the lamina. The midrib is inconspicuous. Foliar epidermal cells are short and without any pits. Stomata develop on both the surfaces. The guard cells are with conspicuous ray like thickenings, radiating from the wall encircling the stomatal pore to the peripheral wall of guard cells. The mesophyll cells are oval to elongate. The sporophylls are usually crowded towards the distal region but occasionally develop in the basal region of the plant. The sporangia are axillary, long stalked, larger than the base of the sporophyll, reniform and are without any sinus at the proximal margin. The sporangial jacket is composed of wavy walled cells and shows apical dehiscence. Spores are subtriangular and have convex or flat sides and rounded corners. They are tetrahedral and pitted. The pits are closely distributed excepting around the tetrad scar where they are few in number. They are generally united with one another and only occasionally free. The trilete mark extends upto the margin. The spores measure about 34 u in diameter.

HUPERZIA PULCHERRIMA (Wall.) Sen et Sen, *~~Comb.~~ Nov.*

Lycopodium pulcherrimum Wallich List n.115, 1828; Hook. et Grev. Icon. Fil. t. 38, 1929. (Fig. 2 l-r).

Plants are epiphytic, pendent, 15-20 cm long and grow in shady forests. Branches are isodichotomous, 2-5 times forked at short intervals, especially near the distal region and become tufted.

The cauline vascular cylinder is plectostelic and is composed of tracheids very similar to those of *Huperzia subulifolia.* The leaves are crowded, linear, upto 8 mm long and 0.5 mm wide, never appressed to the stem, generally ascending and only occasionally spreading at the basal region. They are sessile, having a flat base and typically inrolled entire margins. The foliar tip is often curved inward and the midrib is inconspicuous. The epidermal cells of the leaf are elongate and have almost straight and pitted walls. Stomata are scattered on the abaxial surface and have 5-6 rays extending the entire width of the guard cells. On the adaxial surface of the leaf they occur only at the basal region. The mesophyll cells are almost circular and have large air spaces between them. The sporophylls resemble the vegetative leaves. Sporangia are axillary and exceed the width of the sporophylls. They have a broad but shallow sinus and a slender stalk. Sporangial wall is sinuous and splits into two equal halves. Spores are tetrahedral, pitted, subtriangular and have convex margins and rounded corners. Pits are usually free and only occasionally coalescent. They occur in large numbers on the distal surface but few on the proximal surface. The trilete mark extends to the margin. The spores are about 30.5 u in diameter.

HUPERZIA HAMILTONII (Spring) Sen et Sen, *Comb. Nov.*

Lycopodium hamiltonii Spring ex Hook.et Grev. in Hook., Bot. Misc.,2 : 366, 1831. Clarke in Trans.Linn.Soc.Lond., II Bot. I : 590, 1880. (Fig. 2 s-z, aa).

Plants grow as epiphytes in shady places and rarely as lithophytes in rather exposed situations. They are usually weak, pendulous and generally attain a height of 10-25 cm. The stem is slender, about 1-2 mm in diameter and isodichotomously forks 2-4 times. Vascular cylinder is plectostelic and the peripheral protoxylem points often touch the single layered pericycle. Tracheids are bordered pitted, the pits being uniseriate, round or elongated. The leaves are thick, glossy when dry, firm, sessile, crowded, oblong, spreading, 7-15 mm long and about 5 mm wide. They have a narrow base, an entire margin, and a distinct midrib. Foliar epidermal cells are highly thickened and are without any pittings. The adaxial epidermal cells are larger in size and are without any stomata. The guard cells of the stomata, which are numerous on the abaxial surface, have ray like thickening extending upto the middle of the guard cells. The leaf in transverse section is rather thick and shows many layers of mesophyll cells hexagonal in outline. The mesophyll cells lying immediately below the upper epidermis are more compact and smaller than those situated on the abaxial surface of the leaf.

The sporophylls resemble the vegetative leaves. They are usually aggregated in the apical part of the plant and often occupy the entire apical half of a branch. Occasionally an isolated sporophyll may occur among the vegetative leaves in the basal region of the plant. The sporangia are large, reniform, and are borne on long stalks, attached directly on the stem. The spores are subtriangular, tetrahedral, and have rounded corners and convex sides. Ektexine is thin and pits are dense and laterally united with each other. The spores are about 33 u in diameter.

HUPERZIA SQUARROSA (Forst.) Rothm. Feddes Repert. 54 : 58-62, 1944.

Lycopodium squarrosum Forst., Prodr. Fl. Austral, 86, 1786. Clarke in Trans. Linn. Soc.II. Bot.1 : 591, 1880. (Fig. 2 bb-hh).

Plants are epiphytic and hang from the bark of the trees. They are deep green in colour, 10-70 cm long and never less than 3 mm in diameter at the base. They branch 3-5 times mainly towards the distal region. Stem is actinostelic at the basal and distal regions, elsewhere it is plectostelic. The radial xylem arms of the actinostele are broadened at the periphery. Tracheids have bordered pits; the pits are round, oval or elongate, uniseriate but show a tendency towards biseriate form.

The leaves are linear, though, crowded, spreading and twisted at the base when dry. Their tips are drawn into sharp spines. The margin of the leaf is entire, and the midrib is distinct. A leaf is about 20 mm long and 2 mm wide. The foliar epidermal cells have highly cuticularised thickened walls but no pits. They are rather rectangular in shape, and have minutely wavy walls. Stomata occur on both the surfaces of the leaf. The guard cells have 5-6 inconspicuous ray like thickenings extending from the wall adjacent to the stomatal pore and ending blindly long before reaching the periphery of the guard cells. The mesophyll cells are angular in cross section and the intercellular spaces between them are conspicuously small. Sporophylls are either aggregated at the tips of the branches or occur among the vegetative leaves. The sporangia are reniform, larger than the base of the sporophyll and are borne on short stalks attached directly on the stem.

The spores are tetrahedral, subtriangular and have convex sides and rounded corners. The ektexine is thin and pitted. The pits are minute, and coalescent; they occur in large numbers over the distal surface. The trilete mark extends upto 2/3rds of the spore's diameter. The spores are about 39 u in diameter.

HUPERZIA LAXA (Presl) Sen et Sen, *Comb Nov.*

Lycopodium laxum Presl in Reliquiae Haenkeanae, Vol. 1 : 83, 1825. (Fig. 3 a-j).

Plants are epiphytic, and usually grow on large trees in dark forests. They are slender, pendulous, non-spreading, and 3-4 times isodichotomously forked, the successive points of forking being widely apart. A mature plant is about 80 cm long, and about 4 mm in diameter near the proximal end. The stem near the basal region is tough, actinostelic and characteristically develops 5-7 protoxylem points; it, however, becomes plectostelic towards the distal part. Early formed protoxylem elements are long, narrow and possess a thin delicate unlignified primary wall with a series of annular thickenings on their inside. The later formed elements are broad and exhibit reticulate type of pittings. Metaxylem tracheids possess circular to oval unseriate simple and bordered pits.

The leaves are lanceolate, thick, rigid, ascending, always pointing towards the apex, strongly appressed, decreasing in size towards the apex and merging into the sporophylls. A mature leaf is entire, convex on the abaxial surface, and 4-7 mm long; about half of its proximal part forms the sheathing base. Foliar epidermal cells are short, pitted and rectangular to hexagonal in surface view. Stomata develop on both the surfaces, but they are lesser in number on the abaxial surface. The guard cells have 6-7 faintly lignified rays extending half way between the margin of the stomatal pore and their peripheral walls. Sporophylls resemble the vegetative leaves and do not form distinct strobili. The sporangia are axillary and have a deep sinus accommodating the slender stalk. The sporangial jacket is composed of wavy walled cells. Spores are subtriangular, about 33.5 u in diameter and pitted. The pits are few on the proximal surface but are numerous on the distal side. The tetrad scar extends to the spore's margin.

GENUS PHLEGMARIURUS

PHLEGMARIURUS (HERTER) HOLUB (in Preslia, 36 : 17, 21, 1964). Plants are epiphytic and pendulous in habit. The branches are regularly dichotomous and bear strongly differentiated strobili at the tips of the ultimate branches. The strobili are

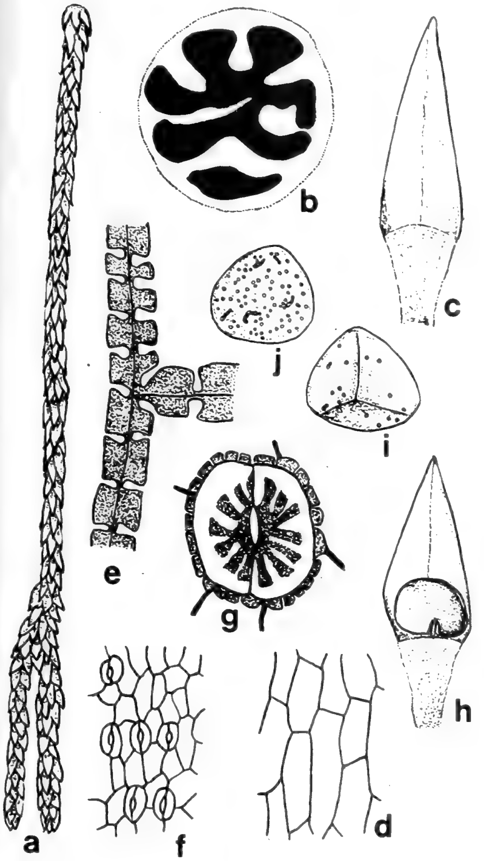

FIGURE 3. a-j. *Huperzia laxa*. a, part of plant (X 1); b, T.S. of stele near middle of plant (X 87); c, vegetative leaf with sheathing base (X 7); d, epidermal cells from abaxial surface of lamina (X 87); e, epidermal cells with numerous pits (X 640); f, epidermal cells from adaxial surface of lamina showing numerous stomata (X 53); g. stoma (X 640); h, sporophyll (X 7); i-j, spores (X 435).

slender, repeatedly dichotomously forked and rarely the tips of the cone axes proliferate into vegetative branches. Ray-like thickening occur around the stomatal pore. The sporophylls are small and different from the vegetative leaves. Sporangia are borne on slender stalks and are attached at the axils of the sporophylls. The spores are pitted.

Roots are aggregated at the base of the stem.

The gametophytes are subterranean, ramified, cylindrical, elongate and saprophytic in habit. The sex organs occur between the scattered rhizoids (Bruchmann, 1885; Boivin, 1950). Ghatak (1965) suggests that basic chrosome number of the genus is n = 17.

Type : *Phlegmariurus phlegmaria* (L.) Sen et Sen, comb. nov (Hoblu *l.c.* designated the species *phlegmaria* as the type of *Phlegmariurus,* but did not transfer any epithet to the new genus.)

PHLEGMARIURUS PHLEGMARIA (L.) Sen et Sen, **Comb. nov.**

Lycopodium phlegmarium L. Sp. Pl. 2 : 1101, 1753. (Fig. 4 a-j).

Plants are epiphytic, weak and pendulous; they usually occur on the bark of the trees, and are about 30-50 cm long. The stem is isodichotomously forked, and is rooted at the base only. The vascular cylinder of the stem is a plectostele. The xylem is exarch and the tracheids have elongate, oval or round, uniseriate or multiseriate bordered pits. Vegetative leaves are spreading, ovate-lanceolate and are closely arranged. They have a prominent midrib, herbaceous acute apex and a broad base. The margin of the leaf is entire. The epidermal cells of the lamina on both the surfaces are sinuous and they bear stomata only on the abaxial surface. The wall of the guard cells surrounding the stomatal pore is thickened and have rays traversing about half the way between the inner and outer walls of the guard cells. The mesophyll cells are of variable shapes and sizes; numerous air spaces occur between the cells of the mesophyll.

The sporophylls are very distinct from the vegetative leaves, 1.5 mm long and 1 mm wide, and form well organised, slender, repeatedly dichotomously branched strobili. The strobili are spreading, slender and sessile. The sporophylls are very small and bract like in appearance. They are wrinkled on the back but are not cuspidate. The sporangia are shortly stalked, large, cauline, and have apical dehiscence. Sterile bracts often occur at the basal region of a strobilus. The spores are small, subtriangular and have straight or convex sides. They are pitted and foveolate, the pits being minute, numerous and equally distributed on distal sides. Spores are about 35 u in diameter.

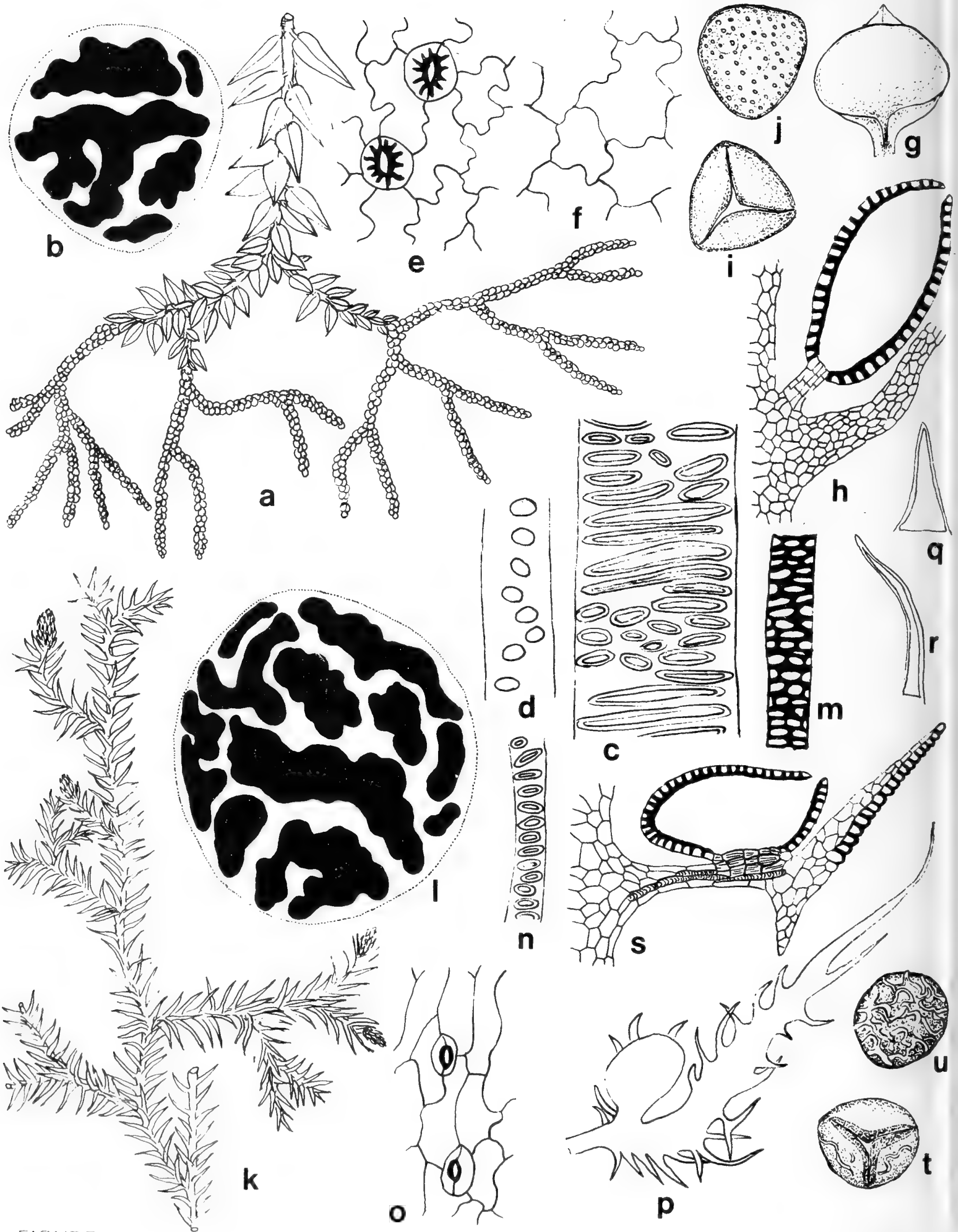

FIGURE 4. a-j, *Phlegmariurus phlegmaria;* k-u, *Palhinhaea cernua.* a, part of a plant with dichotomously branched strobilus (X 1); b, T.S. of stele near middle region of stem (X 53); c-d, tracheary elements of stem (X 435); e, epidermal cells from abaxial surface of lamina showing stomata (X 140); f, epidermal cells from adaxial surface of lamina (X 140); g, sporophyll (X 18); h, V.S. through a sporangium showing axillary attachment (X 53); i-i, spores (X 435); k, part of stem (X 1); l, T.S. of stele near middle region of stem (X 87); m-n, tracheary elements of stem (X 435); o, epidermal cells from abaxial surface of lamina showing stomata (X 140); p, sporophyll (X 18); q-r, minute hairs from base of leaf (X 87); s, V.S. through a sporangium showing folia attachment (X 53); t-u, spores (X 435).

GENUS PALHINHAEA

PALHINHAEA FRANCO ET VASC. (in Vasconcellos et Franco, Bol. Soc. Broter. ser.2, 41:25, 1967). Plants are terrestrial and with tree-like lateral shoots spreading from the creeping stem. The erect lateral branches are unbranched towards the base and the ultimate tips of the branchlets are terete. Vascular cylinder of the stem is usually a mixed haplostele. The creeping stem roots at intervals. The vegetative leaves are isomorphic and bear hairs. The sporophylls are aggregated into cones and the penduncles of the cones are wanting. The sporangia are foliar and divides into two unequal valves. Spores are rugulate.

Gametophytes are more or less conical with tapered and pointing downwards; their truncate ends bear numerous lobes. Antheridia and archegonia are located between the bases of the lobes (Bruchmann, 1885; Boivin, 1950).

Pichi Sermolli (1959) and Ghatak (1965) state that the chromosome of this genus had an origin from a hypothetical base number 13.

Type : *Palhinhaea cernua* (L.) Franco et Vasc. in Vasc. et Franco, Bol. Soc.Broter.Ser. 2, 41 J 25, 1967.

PALHINHAEA CERNUA (L.) Franco et Vasc.

Lycopodium cernuum L. Sp. Pl 2 : 1103, 1753. (Fig. 4 k-u)

Plants are with tree-like branches, spreading from a creeping stem which roots at intervals. The stem is mixed haplostelic. Metaxylem tracheids have scalariform, bordered or simple pits. The pits may be in one or two rows.

The leaves are linear, membranous, sessile, densely crowded and spreading on ultimate branches. They have a distinct midrib and bear hairs at the basal region of the lamina. Foliar epidermal cells are very long and narrow, slightly wavy and without any pit on their walls. Stomata occur on both the surfaces. The wall of the guard cells surrounding the stomatal pore are slightly thickened. The sporophylls are broad, ovate, ascending and are densely ciliated. They are aggregated into definite sessile, strobili. There may be over one hundred strobili in a plant. An important feature is the presence of some cells in sporangial stalk resembling the transfusion tissue.

The sporangia always dehisce into two unequal valves. Spores are rugulate on the distal side; their proximal surface is unornamented and the triradiate scar is obscured in a groove. The diameter of the spores is about 29 u.

GENUS DIPHASIUM

DIPHASIUM PRESL EX ROTHMALER (in Feddes Repert. 54:64, 1944). The plants are always tetrahedral and monopodially branched. The main stem is prostrate and grows indefinitely. Tips of the ultimate branches are always flat and bear tetrastichous leaves. Vegetative leaves are di- or trimorphic. Vascular cylinder is plectostelic. The vegetative and reproductive leaves are dissimilar in shape, and the latter are aggregated into definite cones. Sporangia are foliar, dehisce into two equal valves. Ektexine of the spore is reticulately thickened.

Roots are scattered throughout the main stem.

The gametophyte is an upright steep sided cone. It is subterranean, radially symmetrical and has a cuspidate upper end. The subterranean portion of the gametophyte is composed of different types of tissues. Antheridia and archegonia are produced on the broad cuspidate upper end (Boivin, 1950).

The basic chromosome number x = 12 has been suggested by Ghatak (1965) but Löve and Löve (1958) state that the basic number is x = 8.

Type : *Diphasiumjussiaei* (Desv.ex Poir in Lam.et Poir; *Lycopodium jussiaei*) Presl ex Roth., Feddes Repert. 54:64, 1944.

KEY TO THE SPECIES

A. Branches of short aerial stems never flabelloid; strobili peduncled, terminal, 1-5 on a peduncle, 4-5 cm long. Sporangium borne on a massive stalk. No thickening in the guard cells around the stomatal pore . . . . *D complanatum*

AA. Branches of short aerial stems always flabelloid, strobili mostly sessile, 1, rarely 2 on a branch tip, about 2 cm long. Sporangium borne on a slender stalk. Wall of the guard cells around the stomatal pore thickened . . . . *D. alpinum*

DIPHASIUM COMPLANATUM (L.) Rothm. Feddes Repert. 54 J64, 1944.

Lycopodium complanatum L. Sp.Pl. 2 J 1104, 1753. (Fig. 5 a-j).

The plants are terrestrial and prostrate; they are either shallowly buried in surface litter or superficial on soil. The trailing horizontal stems are 1-2 mm thick and produce widely separated reduced leaves. Aerial stems are ascending, small, much branched and becomes flattened at the apices. These branches are limited in growth and never flabelloid. Stems are plectostelic and have the protoxylem points at the ends of the xylem plates. The pericycle is one layered and is surrounded by a single layered endodermis. The endodermal cells are large, barrel shaped, thin walled.

Roots are adventitious, terete and are scattered throughout the stem.

Leaves on the creeping stems are isomorphic; they are nearly linear to narrowly lanceolate and have acute apices. On the buried stems the leaves are spatulate. Leaves on the ultimate branchlets are 4-ranked; they are scale like and may be trimorphic. Such leaves are pouch-like, lanceolate or narrowly deltoid. The epidermal cells are highly corrugated nad have conspicuous pits on their walls. Stomata are present on both the surfaces. The wall of the guard cells around the stomatal pore is thin. Transverse section of a leaf shows loosely differentiated thin-walled, roundish or irregularly shaped parenchymatous cells with conspicuous air spaces. The mesophyll cells on the upper side are large and have a tendency towards forming palisade cells.

The sporophylls are aggregated into strobili, borne on short lateral branches. The peduncle is slender, dichotomously branched, not very long and bears alternately arranged leaves. The sporophylls are broader and larger than the vegetative leaves, and have broad base and gradually narrowed apex. Their margins are scarious. The sporangia are borne on massive stalks, foliar, and dehisce into two equal valves. The spores are tetrahedral and subtriangular. The tetrad scar extends to the margin. The ektexine is reticulate on the distal side and the lamellae project out at the periphery. The spores are about 37 μ in diameter.

DIPHASIUM ALPINUM (L.) Rothm. Feddes Repert. 54 : 64, 1944.

Lycopodium alpinum L.Sp. Pl 1104, 1753. (Fig. 5 k-r)

Plants are terrestrial, dwarf and trail over or just beneath humus or mossy stones. The short lateral branches are erect, 2-3 times dichotomously forked, flabelloid and are determinate in growth. The ultimate tips of these branches are flattened, while the remaining part of the stem is usually terete. The vascular cylinder is plectostelic. Tracheids of the metaxylem have scalariform and bordered pits. The pits are small round, oval, elongate or mixed; they may be uniseriate or multiseriate.

The vegetative leaves on the main axis are spirally arranged. They are lanceolate with narrow base and acute apex. The margins of the leaves are slightly serrated towards the tip. Leaves of the ultimate branchlets are heteromorphic and arranged in 4 rows; they may have well developed blades and decurrent bases, or they may be broad, lanceolate with rounded or acute apices. Some of these leaves are strongly divergent and have rolled margins, while others are flat and spreading. The epidermal cells of both the surfaces of the leaf. The wall of the guard cells around the stomatal pore is uniformly thickened.

Sporophylls are arranged into strobili, which are borne singly or in pairs at the tip of each fertile branch. The strobili are generally sessile. The sporophylls are deltoid to subcordate; they have entire to faintly erose, rounded margins and tapering apex. The sporangium is foliar, smaller than the basal broad portion of the sporophyll. It is borne on a slender stalk with a flat base, and dehisces into equal valves. Spores are tetrahedral, subtriangular to round with convex sides. Ektexine is lopho-reticulate. The reticulation is more conspicuous on the distal side than on the proximal surface. Spores are about 36 μ in diameter including the reticulum, which often tends to break around the tetrad scar.

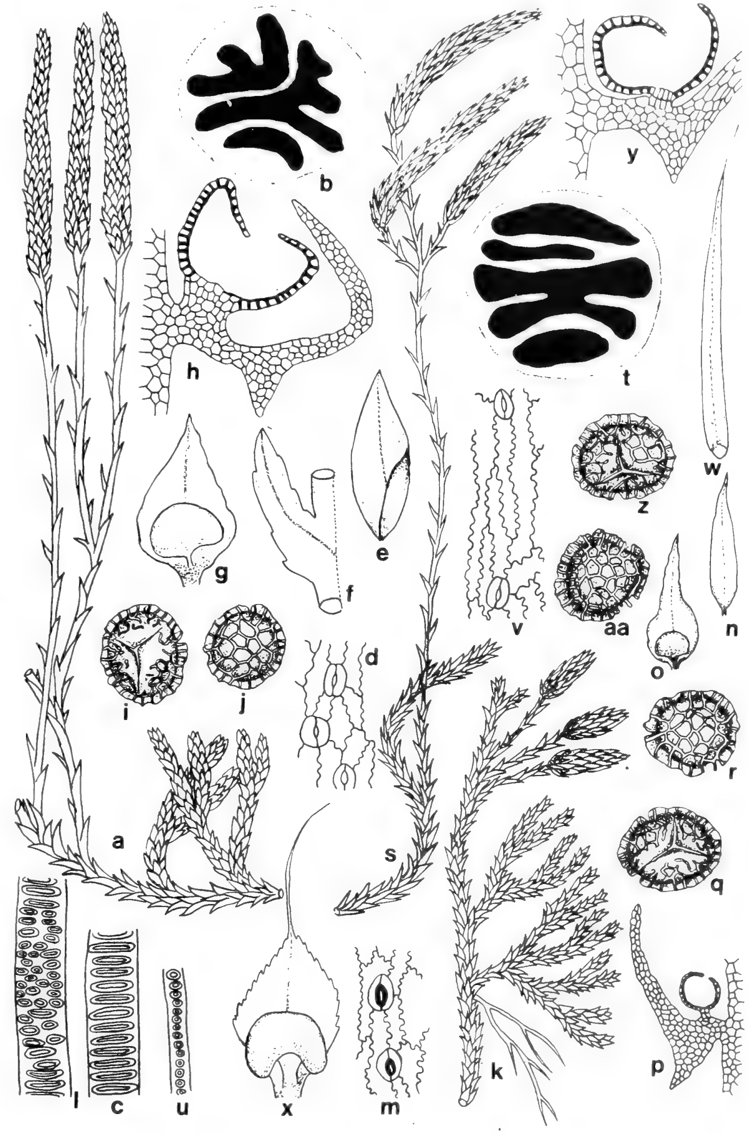

FIGURE 5. a-j, *Diphasium complanatum;* k-r, *Diphasium alpinum;* s-z, aa, *Lycopodium clavatum.* a, part of plant (X 1) b, T.S. of stele near the middle region of plant (X 87); c, tracheid with elongated bordered pits (X 435); d, epidermal cells from abaxial surface of lamina (X 87); e-f vegetative leaves (X 6); g, sporophyll (X 6); h, V.S through the sporangium showing foliar attachment (X 25); i-j, spores (X 435); k, part of plant (X 1); l, tracheid from stem (X 435); m, epidermal cells from abaxial surface of lamina showing stomata (X 130); n, vegetative leaf (X 6); o, sporophyll (X 6); p, V.S. through a sporangium showing foliar attachment (X 25); q r, spores (X 435); s, part of plant (X 1); t, T.S. of stele near middle region of plant (X 87); u, tracheid with circular bordered pits (X 435); v, epidermal cells from abaxial surface of lamina (X 140); w, vegetative leaf (X 6); x, sporophyl (X 10); y, V.S. through a sporangium showing foliar attachment (X 25); Z, aa, spores (X 435).

GENUS LYCOPODIUM

LYCOPODIUM LINNAEUS (in Sp.Pl.2 : 1100, 1753). Plants are terrestrial, creeping and have shallowly to deeply buried rhizome. The vegetative leaves are isomorphic, spirally arranged, and are sharply distinct from the sporophylls. The sporophylls are aggregated into cones. The cones are terminal and usually peduncled. The sporangia are foliar and divides into two equal valves. Gametophytes are subterranean, short, conical or bilobed. There is no internal differentiation of cells. The upper flattened end of the gametophyte bears a distinct and continuous rim (Boivin, 1950).

Pichi Sermolli (1959) and Ghatak (1965) state that the chromosome in this genus is referable to the hypothetical basic number 17.

Type : *Lycopodium Clavatum* L. Sp. Pl 2 : 1101, 1753.

LYCOPODIUM CLAVATUM L. Sp. Pl. 2 : 1101, 1753. Clarke in Trans. Linn. Soc. Lond., II, Bot., 1 : 592, 1880. (Fig. 5 s-z, aa)

Plants are terrestrial and prostrate. The rhizome is superficial or shallowly buried, long and indefinite in growth. It produces small several times dichotomously forked lateral branches of definite growth. The lateral branches are soft round and shiny, and bear dense leaves. The stem is plectostelic and tracheids are bordered pitted. The leaves are small about 7 mm long, linear and are drawn into long pointed almost hyaline hair-like structures. The bases of the leaves are broad and rounded and the margins are entire. The epidermal cells of the leaves are narrow, elongate, and densely pitted. Amphistomatic guard cells have unifromly thickened walls. Three or more strobili are grouped on a peduncle. The peduncle is slender, about 15 cm long, and bears bracts. The sporophylls are broadest in the middle, and abruptly narrowed to a long pointed hyaline hair-like structure. Their margin is serrated. The sporangia are reniform, stalked, foliar and almost cover the lower portion of the sporophyll. The stalk is broader than long. The jacket of the sporangium dehisces into two equal valves.

The spores are roundish to subtriangular, lophoreticulate; the reticulum on the ektexine projects out at the periphery and breaks up irregularly around the tetrad scar. The trilete mark extends upto the margin. The spores are yellow and 37 u in diameter.

COMMENTS ON DISTRIBUTION IN THE DISTRICT

Most of the taxa featured in this article were widely distributed in the district even some twenty years ago, but unfortunately many of them are in imminent danger of at least local extinction through the actions of mankind. The awesome fact is that once a species becomes extinct, no amount of human ingenuity can resurrect it again. But it is not at all difficult to conserve a species if some determination is employed by man for its defence.

The following is the list of places of known continued occurrence of different taxa :

Huperzia selago : Senchal (2448 m), Tiger hill (2550 m), Bijanbari (1820 m)

H. serrata : Darjeeling Cart Road (2250 m) Bijanbari (1820 m), Senchal (2448 m), Takedah (1800 m), Bhutia Basti (200 m), Palmajua-Rimbick (2300-2200 m)

H. herteriana : Senchal (2448 m), Bijanbari (1820 m), Jalapahar (2285 m), Sandakphu (3500 m)

H. hamiltonii : Senchal (2448 m), Darjeeling Cart Road (2044m), Kurseong (1350 m)

H. pulcherrima : Kalimpong (1182 m), Lolagaon (1520 m)

H. subulifolia : Lebong forest (1500 m)

H. squarrosa : Kalimpong (1182 m)

H. laxa : Lolagaon (1520 m)

Phlegmariurus phlegmaria : Sukhna forest (100 m)

Palhinhaea cernua : Birch hill (2300 m), Lebong (1970 m)

Diphasium complanatum : Sandakphu (3400 m)

D. alpinum : Tonglu (3100 m), Chiabanjan (3300 m)

Lycopodium clavatum : Lebong (1700 m), Lolagaon (1520 m), Takedah (1800 m), Kalimpong (1300 m), Birch bill (2300 m), Peshok (2400 m), Chiabanjan (3300 m), Sandakphu (3400 m), Tonglu (3100 m)

The altitudinal distribution of 13 species of lycopods occurring in different types of forests in Darjeeling District is presented in the following table :

Alpine forest (above 3,900 m)	
Cold temperate-subalpine forest (2,700 – 3,900 m)	*Huperzia herteriana, Diphasium complanatum, D. alpinum, Lycopodium clavatum*
Warm temperate forest (1,500 – 2,700 m)	*Huperzia laxa, H. selago, H. serrata, H. harteriana, H. hamiltonii, H. squarrosa, Lycopodium clavatum, Palhinhaea cernua*
Tropical-subtropical forest (upto 1,500 m)	*Huperzia serrata, H. hamiltonii, H. pulcherrima, H. subulifolia, H. squarrosa, Phlegmariurus phlegmaria, Lycopodium clavatum*

It can be seen that although lycopods grow prolifically in the tropical-subtropical to warm temperate forests, none of the species ascend above the subalpine forest.

ACKNOWLEDGEMENTS

We are very grateful to Professor R.E. Holttum who guided many of our thoughts in the many hours of discussion; however, the taxonomic and nomenclatural conclusions here presented are those of the present authors. We are particularly indebted to Professor S.P. Sen for his interest in the work.

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SHORT NOTES

RANGE EXTENSION OF THE GENUS CIBOTIUM TO NEW GUINEA

The taxonomy and distribution of the genus *Cibotium* Kaulfuss (Cyatheaceae) in Malesia was revised by Holttum (1963). There are three species in the area: *C. barometz* (L.) J.Sm. (N.E. India to S. China and Formosa, south to Malay Peninsula, Sumatra and Java), *C. cumingii* Kunze (Philippines) and *C. arachnoideum* (C.Chr.) Holttum (Sumatra, Borneo). In May 1977 *C. barometz* was collected in eastern New Guinea, thus considerably extending the eastward range both of this species and of the genus. It was an uncommon floor species on steep slopes in *Lithocarpus/Castanopsis* forest at 800 m on Oomsis ridge on the north side of the Herzog Range, Morobe district. Voucher specimens are lodged in the herbarium of the Department of Botany, Division of Forests, Lae, in the Rijksherbarium, Leiden and in the author's private herbarium, no. 5962.

ACKNOWLEDGEMENTS

I wish to thank my husband, John Croxall, and David Symon and family, for assistance in the field; and Nigel Cluny for organising this collecting trip.

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NOTES ON SOIL TYPES ON A FERN-RICH TROPICAL MOUNTAIN SUMMIT IN MALAYA

Gunong Ulu Kali is a forested mountain peak (101° 47.5′ E, 3° 25.7′ N;5,814 ft. (c. 1772m)) in the southern part of the Main Range of Peninsular Malaysia, 20 miles (c. 32.2 km) NNE of Kuala Lumpur. Annual rainfall is estimated at 100 inches (c. 2500 mm), with most of this falling between October and December (Dale 1960, 1963, 1964). Dry, sunny mornings are usually followed by mist or rain, with temperatures frequently below 18° C.

The natural vegetation at around 5,000 feet is montane oak forest, nearing its upper limit, and growing in lithosols, podsols and shallow yellow latersols derived from the granite core of the mountain (Panton 1964). Above this it a montane ericaceous forest, with scrub forest in very exposed situations (Wyatt-Smith 1964, Burgess 1969). The flora of the summit and ridge is, however rich in ferns, with over 100 species and varieties recorded, about half of which are terrestrial (Piggott 1977).

Amongst the most commonly encountered ferns are *Plagiogyria tuberculata* Copel. and *Blechnum vestitum* (Bl.) Kuhn, which are abundant in the wetter areas of dwarf forest. *Coryphopteris gymnopoda* (Bak.) Holtt. and *Acrophorus blumei* Ching are common in sheltered hollows. *Cyathea hymenodes* Mett. and *C. lurida* (Bl.) Copel. are found along the ridge, and *C. contaminans* (Hook.) Copel. in the larger valleys.

The recent opening of a hotel complex near the summit, with access by road, has given opportunity for soil types and an exposed roadside soil profile to be examined. The paucity of such observations in localities so rich in ferns has prompted the following brief observations to be recorded.

Surface soil types consist chiefly of thick, fibrous root mats overlying varying depths of peat. Both the soil and the run-off water have proved to be very acidic. Two samples of orange-brown run-off water collected in steep montane ericaceous forest with abundant *Pandanus*, which were tested, gave pH readings of 4.10 and 4.18 respectively. A sample of dark-brown fibrous root mat peat from a very exposed remnant of scrub forest on a ridge gave a field pH reading of 4.0 and consisted of 99.4% organic matter. A sample of dark-brown *Sphagnum* root-mat from scrub forest with *Rhododendron* and *Nepenthes* on a ridge gave a field pH reading of 3.90 and contained 99.1% organic matter. A sample of dark chocolate-brown soil obtained from a road cutting 0.7miles (1 km) from the summit in montane ericaceous forest with *Pandanus* and palms gave a field pH reading of 3.92 and contained 88.2% organic matter. A sample of medium-brown subsoil from the same locality gave a field pH reading of 4.30, although the content of organic matter was only 11.9%.

At this latter station, the road cutting enabled a clear idea of the soil profile to be obtained. From this it could be seen that only the top 2 inches (c. 5.0 cm) consisted of forest litter. Below this, the dark-brown highly acidic fibrous peat formed an 8-inch (c. 20 cm) thick layer, overlying the acidic sandy loam, which formed a layer 14 inches (c. 35.5 cm) deep. The bottom of this layer followed the contour of an approximately 1 inch (c. 2.5 cm) thick red-brown iron-stained layer of compact weathered rock, immediately overlying the bedrock, which is granitic.

Analysis of the bedrock showed it to consist of about 80% free quartz and about 20% ferromagnesian compounds.

The soils and run-off near the summit of this mountain are clearly strongly acidic, and compare with, although are even more acidic than, those reported at a similar altitude (5,250 ft. (c. 1600 m)) by Dames (1955) in East Central Java.

ACKNOWLEDGEMENT

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ISOETES IN RAJASTHAN, INDIA

Isoetes is known, so far, from Mt. Abu in south west Rajasthan (Mital, 1969) and Atru, Kota in south east Rajasthan (Gena *et al.,* 1976). We now record its occurrence about 175 km away north of the latter locality. A luxuriant patch spread over an area of approximately 500 sq ft was observed by one of us (SM) in November 1975 near Dausa, Jaipur along the Dausa-Rajgarh Road. The plants were growing along the margin of rain water collected in a wide depression beside the road near the 5 km stone. This *Isoetes* was found to resemble the bigger form from Atru in habit, size of plants and the ornamentation of megaspore wall. However, the rhizomorph here invariably contains 3 lobes as against the equal frequency of 2 and 3 lobed rhizomorphs of Atru material. More important the elongated megasporangia in this form contain fused megaspores frequently and are of four types. The circular megasporangia of the Atru material in contrast rarely contain fused megaspores and are trimorphic. Although at Atru a smaller form of *Isoetes* also occurs intermixed with the bigger form (Gena *et al.,* 1976) we found no other form at Dausa, though the locality was visited again in June 1976 during the dry spell to ascertain if there is any late appearing smaller form (cf *I. coromandeliana, I. indica* and *I. panchananii;* Pant & Srivastava, 1962). Thus Rajasthan state may contain four different taxa of *Isoetes* – a bigger form at Dausa, a smaller form at Mt. Abu and intermixed bigger and smaller forms at Atru. The cyto-taxonomy of all these taxa is currently being studied.

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PARIS HERBARIUM PTERIDOPHYTES

The large and important collections of Pteridophytes in the herbarium of the Museum d'Histoire Naturelle, Paris, have recently been reorganised from an alphabetical sequence to the generic sequence of Crabbe, Jermy and Mickel (1975), which has made it more easy to find types and other important specimens.

Pteridologist are welcome to visit the herbarium and are requested to write in advance to the Director, 16 rue de Buffon 75005 Paris, France. The collection is under the supervision of Mr F. Badré.

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Museum National D'Historie Naturelle, Paris

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