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THE MODULAR GROWTH OF LYCOPODIUM ANNOTINUM

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ABSTRACT

Lycopodium annotinum L is a long-lived plant which consists of a series of annually produced segments which can be aged. This paper describes in detail the modular construction of the plant and analyses elements of deterministic and opportunistic growth by synthesizing a 20-year life cycle from historical records of the plant's growth.

By regarding a plant as a population of modules it is possible to use the methods of population biologists for discontinuous variables and the approach of growth analysis when studying continuous variables.

The balance between deterministic and opportunistic growth produces a foraging behaviour which enables the plant to harvest patchy resources, and to escape interspecific and intraclonal competition. The survival of the plant in its unfertile yet relatively predictable environment is enhanced by the recycling of nutrients between senescing tissues and growing points. This results in indefinite growth and the dominance of vegetative proliferation. Opportunistic colonization of new habitats is possible through the subsidized growth of pioneering horizontal modules and a constant production of airborne propagules which colonize open habitats outside existing locations. "Opportunistic escape" occurs when environmental adversity, such as hard substrate or prevented root formation, kills dominant growing points resulting in lateral branch proliferation and a great extension of the potential zone of exploitation.

The result is a plant which is successful in both colonizing and surviving in a spatially and temporally heterogenous habitat.

INTRODUCTION

The sporophyte of *Lycopodium annotinum* L. (Interrupted Club-moss) is a particularly useful tool for investigating population processes and modular growth due to its construction of repeated units (segments) within horizontal and vertical branches (modules). Seasonality in climate produces markers of annual growth (Callaghan & Collins 1976) which allow a plant to be divided into a series of annually produced units which, in cold climates, persist for a long time after death due to slow decomposition rates (Jenny et al. 1949). Roots and strobili can also be regarded as segments and, as the plant is long-lived, a time-specific investigation can yield data on growth, demography and physiology for a period of over 20 years.

The advantage of describing a plant as a population of defineable units (Prévost 1978; White 1979, 1984; Harper 1981) is that the methods used by population biologists are available. The growth of a plant can then be described in terms of numbers of units, the growth of these units and their death, survival and fecundity (Kays & Harper 1974; Callaghan 1976, 1984; Bazzaz & Harper 1977; Maillette 1982; McGraw & Antonovics 1983).

It is also possible to interpret interactions between the environment and growth, development and physiology of the repeated units in the long term context of the population of units within the whole plant (Callaghan 1984; Headley et al. 1985; Callaghan et al. 1986).

Populations of repeated growth units may be studied either by determining age class distributions and assuming a stable population to calculate rates of survival (Kawano et al. 1982) or by following a cohort throughout its life cycle (Deevey 1947; Merrell 1947; Harper 1967). The first method fails if the population is unstable (Callaghan & Emanuelsson 1985) whereas the second method is impractical with long-lived perennials. *Lycopodium annotinum* presents a plant in which patterns of survival can be recorded for a past period by identifying the dates and ages at which module death occurs.

This paper describes in detail the modular growth (or metameric growth, sensu White 1984) of this long-lived plant from a stressed environment. The paper serves as a basis for detailed investigations of the interactions between the plant and its microenvironment (Svensson & Callaghan unpubl.) and long-term age-based physiological processes (Headley et al. 1985; Callaghan et al. 1986).

MATERIALS AND METHODS

The study was carried out at the Abisko Scientific Research Station on the south shore of Lake Torneträsk in Swedish Lapland (68°23'N, 18°55'E). The site was situated in the boreal birch forest and was dominated by low density *Betula pubescens* ssp. *tortuosa* (Ledeb.) Nyman and the ground vegetation consisted mainly of *Vaccinium vitis-idaea* L., *V. uliginosum* L., *Empetrum hermaphroditum* Hagerup, *Linnaea borealis* L., and *Hylocomium splendens* B. & S. Climatic and micro-climatic characteristics of the site together with a more detailed description of the vegetation are presented in Callaghan et al. (1978) under the heading "*Hylocomium* site".

Observations were made in three years: 1975, 1980, and 1982. During 1975, 71 plants were excavated carefully in the field by tracing the prostrate stems back to a point where they were decomposing and their integrity had been destroyed. The plants were pressed dry and returned to the laboratory for analysis. In 1980 and 1982, two areas of vegetation $3.8 \times 4.2m$ were mapped in detail, including the exact positions of all the horizontal modules of *L. annotinum*. The plants were then excavated, and after measuring the length of each annual increment, and the location of each root, the plants were pressed dry for further analysis.

In the laboratory, each plant was divided into its component segments and the age of each was determined by counting successive morphological markers of annual growth (see Callaghan 1980). The relationship between every annual segment within a plant was recorded, as well as dry weight, and number of daughter segments. It was also recorded if the segments were dead (i.e. brown with detached microphylls) or alive. Of the individual segments analysed in 1975, 1980, and 1982, data from approximately 15,000 are presented here.

Correlations between mean monthly temperatures and annual growth were made. To reduce the effect of length variations between segments resulting from differences in module size, segment lengths were converted to a length index (I) using a method described by Fritts (1976). Variation between segments within modules due to positional effects was reduced by omitting the small first segment within each module from the analyses, although regressions were not required to remove further variation (Fritts 1976) as recognizable trends of segment length within modules were absent. The length index I was calculated as I = Lm/Be where Lm is the measured length of a segment and Be is the expected segment length estimated as mean segment length per module.

RESULTS

Organization of the plant and allocation of dry matter

The sporophyte of *L. annotinum* consists of a series of annually produced segments which are aggregated modules growing apically and senescing distally, as the plant moves across the ground. Arising from the horizontal segments are smaller, vertically orientated photosynthetic segments which are densely covered with microphylls. These vertical segments are aggregated into "vertical modules", which are terminated either by the death of the youngest vertical segment in the module or by the initiation of a spore-producing strobilus (Fig. 1). Horizontal segments may produce other horizontal segments, roots and vertical segments. In contrast, vertical segments can only usually produce other vertical segments and strobili.

The growth of a major plant unit, i.e. a horizontal module (without lateral modules) and all of the vertical modules, strobili and roots attached to it, shows a rapid accumulation of dry weight reaching a maximum of 3.8g in its seventh year (Fig. 2a). Thereafter, weight is lost gradually over a period of more than 17 years.

The survival of the horizontal module is theoretically indefinite (Fig. 1) but the probability of survival of an individual horizontal segment decreases as its age increases, which is a familiar biological pattern.

For the first 2 years, horizontal segments contribute most of the dry weight but vertical modules grow rapidly and are the major contributor of biomass for 10 years with a peak in year 6 (Fig. 2b). Living horizontal segments survive longer than vertical modules and after 13 years horizontal segments are again the major — and ultimately the only — contributor of biomass as the vertical modules decompose and become detached. The probability of survival of vertical segments varies from that described for horizontal segments (Fig. 1) and is described in detail below. Strobili are strictly annual structures and attain dry weights of 18mg (Callaghan 1980).

Roots contribute a maximum of 5% of the total biomass and reproductive effort in terms of dry weight of living strobili reaches only 5.1% of the total biomass (Fig. 2b).

Growth of horizontal modules

Differentiation of segments. When a new horizontal side-module is formed, the first segment to be produced within that module is always smaller in terms of dry weight and length than those subsequently produced. For example, the mean length of the first segment of modules collected in 1980 was 23.4 ± 1.8 (s.e.)mm (n = 223) compared with that of other segments which was 68.2 ± 1.7 (s.e.)mm (n = 558). The remaining segments show no recognizable differentiation in relation to their order within the module.

Apical dominance. The apex of a main horizontal module of *L. annotinum* is an active and fast growing organ which may photosynthesise (Callaghan 1980). Indeed, it is during the first year of growth when roots, vertical modules and other horizontal segments are formed (Fig. 1). Growth in this year may reach 170mm and 24mg dry weight. This active apex exerts a significant inhibition of the growth of daughtermodules such that the effect increases from the oldest to the youngest lateral module in a relationship described by: y = 71 - 3.88x (r = 0.64, p < .00), degrees of freedom = 224) where y = length of one year old segment as percentage of one year old segment of dominant branch, and x = order of branch initiation covering 13 orders of dominance (see Fig. 3 of Callaghan & Emanuelsson 1985).

At any one time, the population of apices consists of those surviving from the previous year, recently dead or dying apices, and newly initiated apices. The production of new apical meristems is strongly correlated with the death of dominant apices and varies from year to year (Fig. 3).

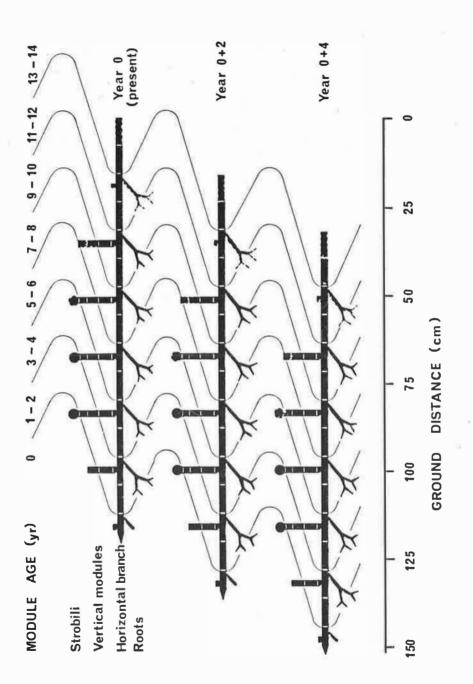


FIGURE 1. Diagrammatic representation of the growth and movement of an unbranched plant of *L. annotinum:* For simplicity vertical modules and roots are shown on alternate horizontal segments. The lighter hatched areas represent senescing tissues whereas the dotted lines contain decomposing tissues also represented by lighter hatching. White breaks represent annual markers of growth while the contours denote age classes for the segments.

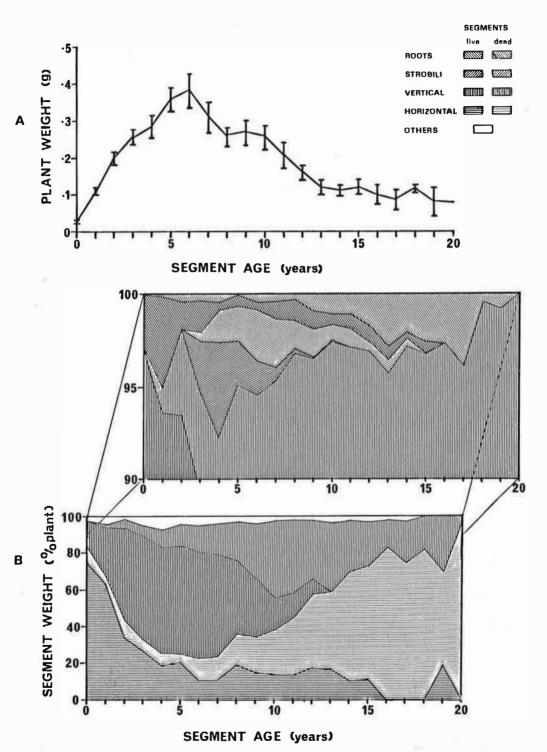


FIGURE 2. The dry weight trends (a) and dry weight partitioning (b) in an unbranched plant of L. *annotinum* over its life cycle. Bars represent standard errors. The data are based on samples collected in 1975 with a sample size of 1079 horizontal segments.

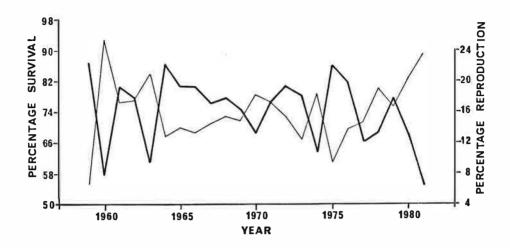


FIGURE 3. The relationship between the initiation of daughter-modules (reproduction, thick line) and the survival of existing horizontal modules (thin line) over a 22 year period. Data are presented for samples collected in 1975, 1980, and 1982. Correlation between annual means: r = -0.86 (*** with 21 d.f.).

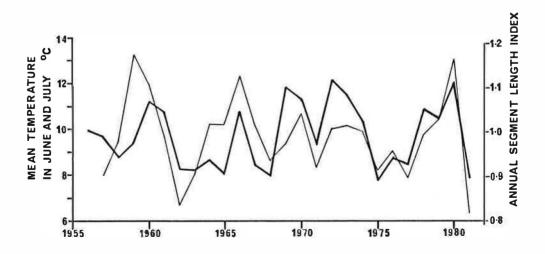


FIGURE 4. The relationship between the index of annual horizontal segment length (thin line) and the mean monthly temperature (thick line) for the summers of the years 1955 to 1981. Data are based on samples collected in 1975, 1980, and 1982 (n = 1698). See Table 1 for correlation analysis.

Climate. The final length of an horizontal segment is achieved within its year of initiation and length is therefore a useful variable to correlate with climate.

Relationships between mean monthly temperature and segment length show significant positive correlations for the summer months June and July and particularly for the combination of June plus July (Fig. 4). It would appear that 1975 was a particularly adverse season both for segment extension growth (Fig. 4) and survival (Fig. 3). No correlation was found between survival and precipitation nor between survival and temperature.

Growth of vertical modules

Differentiation of segments. There are great differences of growth between vertical segments according to their roles within the module. The first segment to be produced in a vertical module is the smallest whereas the second is the largest (Fig. 5). Segments produced after the second show a successive decrease in dry weight (Fig. 5). The differentiation mainly results from variations in growth rates during the first season of growth. Relative Growth Rates (RGR) of segments 1 to 3 were .021, .047, and .049g/g/day respectively (the strobilus had a RGR of .056g/g/day over the same period i.e. 17 June to 10 August).

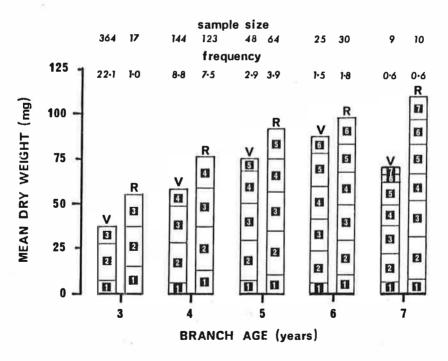


FIGURE 5. Comparison of the dry weights of segments of similar ages and position within vegetative (V) and reproductive (R) vertical modules. Numbers within black bars are the position of the segment within the module. The mean dry weight for segment 1 of vegetative and reproductive modules was 7 (n = 590) and 11.9mg (n = 244) respectively, t = 7.4 (***). The mean dry weight of all other segments for vegetative and reproductive modules was 19.8 (n = 941) and 21.4mg (n = 625) respectively (t = 1.86 N.S.), t for differences between segments 1 and the remaining segments of vegetative and reproductive modules = 19.5 (***) and 10.8 (***) respectively, Data from samples collected in 1975. The frequency of age classes 1 to 7 ofvertical modules (as percentage of 1644) is also given; the frequencies of age classes younger than 3 were 48.8% (vegetative) and 0.06% (reproductive). Those for age classes older than 7 yearswere 0.7% (vegetative) and 0.42% (reproductive).

TABLE 1. Branching in relation to segment position within reproductive vertical modules, and, strobilus weight in relation to age of reproductive modules (standard errors are given in brackets).

	51	li oblius).					
		2 3	4	5	6	7	> 7
Number of modules produced per vegetative segment for segment positions:	1: 2: 3: 4: 5: 6:	0 .294(.117) 118(.083) 	.309(.055) .423(.057) .041(.018) — —	.219(.079) .828(.116) .141(.05) 0 —	1.3(.13) .833(.162) .467(.117) .67(.047) 0	.3(.161) 1.4(.172) .7(.161) .2(.014) 0 0	11111
strobilus dry weight (mg):	no:	— 17.7(2.6) 1 17	17.0(.9) 123	16.7(1.3) 64	14.9(2.0) 30	12.6(3.4) 10	6.6(2.9) 5
Sample size:	%:	.4 6.8	49.2	25.6	12	4	2

Size of reproductive module (= numbers of vegetative segments plus strobilus):

TABLE 2. Comparison between segments on branches with living apices (n = 263) and dead apices (n = 336) of numbers of roots produced (n = 182 and 215, respectively) and the length supported by them. Means \pm standard errors are presented.

	BRANCHES WITH APICES		
	LIVING	DEAD	
Length of segment (mm) with: O roots / segment 1 root / segment 2 roots / segment 3 roots / segment	48.8 ± 2.6 71.2 ± 3.2 86.6 ± 3.2 131.0 ± 22.7	101.6 ± 4.9	
Overall length / segment (mm)	63.5	65.2	
Overall length of segments / root (mm)	91.8	101.9	
Percentage of segments with: O roots / segment 1 root / segment 2 roots / segment 3 roots / segment	46.8 38.4 13.7 1.1	50.6 36.0 12.2 1.2	
Overall number of roots / segment	0.69	0.64	
Number of roots / dm ²	0.4	3	
Longest distance between apex and root (mm)	275	5	

Associated with the differentiation of segments is a pattern of proliferation whereby daughter-modules are produced. In all vertical modules, vegetative reproductive capacity is minimal in the last segments to be produced independently of the ultimate size of the module (Tab. 1). In modules with 3 or more vertical segments, branching frequency is greatest in the second and largest module (Tab. 1). However, branching is not associated with size as the smallest segments (the first in a module) form more new segments than larger segments (i.e. the third, fourth etc.).

Production of strobili. The ultimate role of a vertical module is to support a strobilus but strobili may terminate vertical module growth at any stage. Large modules, i.e. those with greater numbers of vertical segments plus a strobilus, are common, and strobilus weight decreases as module size increases. Modules composed of 3 vertical segments and a strobilus clearly show the greatest frequency and largest strobili (Tab. 1).

The population of vertical modules. At a given point in time vertical modules attached to the same horizontal system may survive and remain vegetative, initiate a strobilus, or die. The frequency of strobilus-bearing modules is smaller than that of vegetative modules until age class 5 (Fig. 5). Branches consisting of vertical segments with high dry weights have a greater probability of producing a strobilus and this is even detectable in the small first segments of vegetative and reproductive modules (Fig. 5).

Vertical modules show an inverted pattern of age-based mortality since the first segment to die is the youngest and the last to die is the oldest first segment (Fig. 1). This is the opposite of that seen in horizontal modules.

Spore production

Spore production has been estimated by Plotnikov (1977) as 0.4×10^6 per strobilus and, with a strobilus density of 4.7 per dm² (0.23 ± 0.026 (s.e.)) as recorded in the present study, there would be an annual spore production of 1.88 × 10⁶ per dm² per year. The viability of spores is low, only 4% (Svensson unpubl.).

Root production

Roots are produced in a very regular way by *L. annotinum:* they are always initiated on year 0 horizontal segments and then grow and branch over a four year period. Thereafter, deterioration is slow but they may still be functional after 13 years (Headley et al. 1985). As the age of the roots increases, the dry weight increases relative to the fresh weight, probably due to suberization (Headley et al. 1985).

At least 1 root is initiated by each horizontal segment but root survival is uncertain so that a mean of 0.69 healthy roots per segment was recorded on healthy modules in which the apex was active (Tab. 2). Only a small percentage of segments possessed 2 or 3 healthy roots (Tab. 2). Root weight only reaches 5% oftotal plant dry weight which is at the lower end of the range for evergreens (Shaver & Cutler 1979, Miller et al. 1982) (Fig. 2b).

The average length of a horizontal module supported by a root is 91.8mm, and the longest distance found between apex and root was 275mm (Tab. 2).

DISCUSSION

The genus *Lycopodium* is primitive in terms of life cycle, morphology and anatomy, yet highly successful. *Lycopodium annotinum* and some other members of the genus *(L. selago, L. complanatum, L. clavatum* and *L. alpinum)* are successful even in severe environments and form an important component of upland boreal and tundra vegetation. Their success is based on an ecological strategy enabled by a particular balance between opportunistic and deterministic growth (Tomlinson 1982).

At the first level of organisation, growth of *L. annotinum* is deterministic in that the sporophyte is rigidly organized into a predictable pattern of horizontal modules, vertical modules, roots and strobili.

Horizontal module growth is strongly opportunistic; only the small first segment to be produced in a module shows any rigid genetic control although apical dominance controls the relative size of segments. Climate has a major effect on the actual size of horizontal segments. Survival of the horizontal apex is also opportunistic and is controlled by the ability of roots to function.

Water potential gradients are such that the horizontal apex has the lowest water potential and draws water and nutrients from roots as old as 12 years which may be 1m away (Headley unpubl.). This means that the growth of the apical part of the plant is subsidized and does not necessarily reflect its immediate environmental conditions.

Eventually, however, the subsidized growth of growing points appears to become impossible and they die. This then releases other sub-dominant apices from inhibition and thereby enables a flexible response by increasing the potential range of habitat exploitation (see Callaghan & Emanuelsson 1985, Fig. 6). This selection of apices by the environment helps to control the direction of the plant and when rooting becomes possible, a dominant apex extends the clone in a direction dictated mainly by micro-topography (Svensson & Callaghan unpubl.). Modules with dead apices had fewer roots per cm (Tab. 2) while the horizontal apex has been shown to have depressed water potentials on root excision or increased distance from the nearest viable root (Headley unpubl.). This lends some support to the hypothesis that a major cause of apical death is the inability of roots to grow.

The proliferation following apical death is most often a response to the microenvironment as correlations with climate were not significant. The result is opportunistic escape from this unsuitable microenvironment (Tomlinson 1982) and may be likened to the foraging behaviour of an animal. It may be argued that the "foraging" behaviour of *L. annotinum* is a successful strategy in a heterogeneous environment but that, when favourable microhabitats are found, the plant is at a disadvantage since it must grow away from them. However, if *L. annotinum* remained in such favourable microhabitats it would soon be over-grown by competitive plants, such as the different ericaceous species (Svensson unpubl.). The foraging behaviour is therefore successful in a heterogeneous environment and also avoids competition.

The growth of vertical module segments, in contrast to that of horizontal modules, is deterministic. It is possible to predict which vertical segments will be terminated with a strobilus and which will remain vegetative while the production of daughter modules from the second vertical segment is regular. However, module size (i.e. the number of segments, including strobilus) is not predictable. Vertical modules initiated in the same year may carry strobili in different years. The decreasing size of the strobilus in relation to increasing module size and height may be related to the increasing costs of translocation of nutrients and water (Wallén 1983), and/or the lack of support tissues in this "primitive plant".

Perennials show a small allocation of dry weight to sexual reproduction compared with annuals and biennials. In *L. annotinum*, this allocation reaches a maximum of 5.1% of dry weight which is similar to values quoted by Chester and Shaver (1982) for evergreen and deciduous plants from Alaska and to tundra plants in general (Callaghan and Emanuelsson 1985). The probability of successful reproduction is reduced even further by a low spore viability of only 4%. However, low spore viability and the small allocation of dry matter are compensated for by the vast number of spores produced by a strobilus (0.4 × 10⁶) and the considerable longevity of reproducing clones of up to 250 years (Oinonen 1968). During 250 years, a clone may produce 1.5×10^{14} spores (Callaghan & Emanuelsson 1985). Successful reproduction from spores is probably related to the opportunistic colonization of disturbed areas as in *Viola* (Newell 1983).

The death of the apical parts of vertical modules before that of the lower segments, together with the greater longevity of the horizontal segments, allows the retranslocation of elements from senescing vertical segments into the horizontal axis and subsequently to new growing points. This transport may be between 63 and 90% efficient in terms of N, P and K (Callaghan 1980). Also, translocation of 14C (Callaghan 1980) was found to be extensive, as in stoloniferous *Viola blanda* (Newell 1982). Such efficient translocation allows the subsidized exploratory growth of the main axis when obstacles are encountered. However, should the obstacles be unsurmountable to the main axis, there is a flexible and opportunistic response whereby lateral axes are initiated and released from suppression with a consequent greatly enhanced zone of exploitation.

In conclusion, the sporophyte of *L. annotinum* shows a balance between deterministic and opportunistic growth which

- enables the plant to harvest patchy resources from a spatially heterogeneous environment via a foraging strategy,
- 2) reduces competition within the clone by controlling branching patterns,
- reduces competition with other species by producing roots and vertical modules in available niches along a constantly advancing axis,
- 4) allows survival in impoverished soils by recycling nutrients between segments,
- enables varying degress of environmental adversity to be overcome first by subsidized growth and then by opportunistic escape following lateral module proliferation,
- allows survival in a temporally predictable environment by indefinite growth associated with vegetative reproduction, and,
- enables opportunistic colonization outside existing locations (e.g. following forest fires) by constant production of vast numbers of airborne propagules.

It is not surprising therefore, that this primitive plant is so important ecologically throughout the northern latitudes.

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REFERENCES

- BAZZAZ, F.A. & HARPER, J.L. 1977. Demographic analysis of the growth of *Linum usitatissimum. New Phytol.* 78: 193-208.
- CALLAGHAN, T.V. 1976. Growth and population dynamics of *Carex bigelowii* in an alpine environment. Strategies of growth and population dynamics of tundra plants 3. *Oikos 27:* 402-13.
- CALLAGHAN, T.V. 1980. Age-related patterns of nutrient allocation in *Lycopodium annotinum* from Swedish Lapland. Strategies of growth and population dynamics of tundra plants 5. *Oikos 35:* 373-386.
- CALLAGHAN, T.V. 1984. Growth and translocation in a clonal southern hemisphere sedge, Uncinia meridensis. J. Ecol. 72: 529-546.

- CALLAGHAN, T.V. & COLLINS, N.J. 1976. Strategies of growth and population dynamics of tundra plants. 1. Introduction. *Oikos 27:* 383-388.
- CALLAGHAN, T.V., COLLINS, N.J. & CALLAGHAN, C.H. 1978. Photosynthesis, growth and reproduction of *Hylocomium splendens* and *Polytrichum commune* in Swedish Lapland. Strategies of growth and population dynamics of tundra plants 4. *Oikos 31*: 73-88.
- CALLAGHAN, T.V. & EMANUELSSON, U. 1985. Population structure and processes of tundra plants and vegetation. In: White, J. (ed.). Population structure of vegetation. Dr W. Junk Publishers, Dordrecht, pp. 399-439.
- CALLAGHAN, T.V., HEADLEY, A.D., SVENSSON, B.M., LI LIXIAN, LEE, J.A. & LINDLEY, D.K. 1986. Modular growth and function in the vascular cryptogram Lycopodium annotinum. Proc. Roy. Soc. Ser. B.: in press.
- CHESTER, A.L. & SHAVER, G.R. 1982. Reproductive effort in cottongrass tussock tundra. *Holarctic Ecol.* 5: 200-206.
- DEEVEY, E.S. 1947. Life tables for natural populations of animals. *Quart. Rev. Biol. 22(4):* 283-314.
- FRITTS, H.C. 1976. Tree Rings and Climate. Academic Press, London. 529 pp.
- HARPER, J.L. 1967. A Darwinian approach to plant ecology. J. Ecol. 55: 247-270.
- HARPER, J.L. 1981. The concept of Population in modular organisms. In: May, R.M. (ed.) *Theoretical Ecology. Principles and Applications.* 2nd. ed. Blackwell Scientific Publications, Oxford, London, Edinburgh, Boston, Melbourne, pp. 53-77.
- HEADLEY, A.D., CALLAGHAN, T.V. & LEE, J.A. 1985. The phosphorus economy of the evergreen tundra plant. *Lycopodium annotinum. Oikos 45:* 235-245.
- JENNY, H., GESSEL, S.R. & BINGHAM, F.T. 1949. Comparative study of decomposition rates of organic matter in temperate and tropical regions. *Soil Sci. 68:* 419-432.
- KAWANO, S., HIRATSUKA, A. & HAYASHI, K. 1982. Life history characteristics and survivorship of *Erythronium japonicum*. *Oikos* 38: 129-149.
- KAYS, S. & HARPER, J.L. 1974. The regulation of plant and tiller density in a grass sward. *J. Ecol.* 62: 97-105.
- McGRAW, J.B. & ANTONOVICS, J. 1983. Experimental ecology of *Dryas octopetala* ecotypes. 1. Ecotypic differentiation and life-cycle stages of selection. *J. Ecol.* 71: 879-897.
- MAILLETTE, L. 1982. Structural dynamics of silver birch. I. The fates of buds. J. Appl. Ecol. 19: 203-218.
- MERRELL, M. 1947. Time-specific life-tables contrasted within observed survivorship. *Biometrics 3(2):* 129-136.
- MILLER, P.C., MANGON, R. & KUMMEROW, J. 1982. Vertical distribution of organic matter in eight vegetation types near Eagle Summit, Alaska. *Holarctic Ecol. 5:* 117-124.
- NEWELL, S.J. 1982. Translocation of 14C-photoassimilate in two stoloniferous *Viola* species. *Bull. Torrey Bot. Club (USA) 109:*3:306-317.
- NEWELL, Ş.J. 1983. Demography of Newfoundland populations of three Viola species. Can. J. Bot. 61: 2581-2591.
- OINONEN, E. 1968. The size of Lycopodium clavatum L. and L. annotinum L. stands as compared to that of L. complanatum L. and Pteridium aquilinium (L.) Kuhn stands, the age of the tree stand and the dates of fire on the site. Acta For. Fenn. 87: 33-38. (Eng. summ.).
- PLOTNIKOV, V.V. 1977. Ontogenesis of the sporophyte of *Lycopodium annotinum* L. (Lycopodiaceae) and the structure of its population. *Bot. Zhurn.* (Leningrad) USSR 62(8): 1196-1200.
- PRÉVOST, M-F. 1978. Modular construction and its distribution in tropical woody plants. In: Tomlinson, P.B. & Zimmerman, M.H. (eds.) *Tropical trees as living systems*. The proceedings of the Fourth Cabot Symposium, Petersham, USA 1976. Cambridge University Press, Cambridge, London, New York, Melbourne, pp. 223-231.
- SARUKHAN, J. & GADGIL, M. 1974. Studies on plant demography: Ranunculus repens L., R. bulbosus L and R. acris L III A mathematical model incorporating multiple modes of reproduction. J. Ecol. 62: 921-936.
- SHAVER, G.R. & CUTLER, J.C. 1979. The vertical distribution of live vascular phytomass in cottongrass tussock tundra. *Arc. Alp. Res.* 11: 335-342.
- TOMLINSON, P.B. 1982. Chance and design in the construction of plants. *Acta Biotheor. 31A (1-3):* 162-183.
- WALLÉN, 8. 1983. Translocation of 14C in adventitiously rooting *Calluna vulgaris* on peat. *Oikos* 40: 241-248.
- WHITE, J. 1979. The plant as a metapopulation. Ann. Rev. Ecol. Syst. 10: 109-145.
- WHITE, J. 1984. Plant Metamerism. In: Dirzo, R. & Sarukhan, J. (eds.) *Principles of Plant Population Biology*. Sinauer Association. Mass. USA, pp. 15-47.

THE ECOLOGY OF PTERIDOPHYTES IN TASMANIAN COOL TEMPERATE RAINFOREST

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ABSTRACT

Forty nine pteridophytes from 17 families are reported from cool temperate rainforest in Tasmania. Epiphytes and terrestrial species are both well represented. Their occurrence is influenced by altitude and forest type, but on a regional basis most species are widespread. The biogeographical affinities of the rainforest fern flora are with New Zealand and southern parts of the eastern Australian mainland.

INTRODUCTION

The fern flora of Australia is considered small in relation to the area and latitude of the continent (Page & Clifford 1981), containing about 416 species in 118 genera (Jones & Clemesha 1981). Only four genera are endemic to Australia (all non-Tasmanian) and although six others have a predominantly southern hemisphere distribution most are widely dispersed on a global basis. Within Australia, the ferns attain their greatest richness in Queensland in tropical rainforests and cloud forests. Generic diversity decreases southwards towards Tasmania and also westwards from the coast to the drier parts of the continent (Page & Clifford 1981).

Within Tasmania, ferns and their allies are common but they show no pronounced specialisation to the Tasmanian environment with only two of approximately 90 species being endemic. The group is widespread in the state, occurring in most vegetation types but reaching its greatest diversity in rainforest, wetsclerophyll forest and moist gullies in drier areas. According to Page & Clifford (1981), the number of individuals in temperate rainforest and fern gullies in Tasmania and Victoria is very striking but their diversity is much lower than could be expected from analogous situations in the tropics. Furthermore, they comment that "almost every dominant species seems to have a much wider ecological range than its tropical counterpart, and consequently most occur virtually everywhere that appropriately moist forests and fern gullies are present".

Although the composition of Tasmania's fern flora is well-known (apart from a few taxonomic uncertainties), publications which deal directly with the ecology and distribution of species are scarce. This publication comprises an account of the ferns in Tasmanian cool temperate rainforest and is based mainly on information obtained during a broader examination of rainforest in Tasmania (see Jarman et al. 1984).

METHODS

The Environment — Cool Temperate Rainforest

Tasmania is a mountainous island situated approximately 240km south of the southeastern corner of mainland Australia, between latitudes 40° and 43°S. Its rainforest vegetation is classified as cool temperate rainforest and forms part of the island's Antarctic element (after Hooker 1860) or relict sub-element (after Nelson 1981).

Rainforest in Tasmania is defined as forests greater than 8m tall, dominated by *Nothofagus, Eucryphia, Phyllocladus, Athrotaxis, Lagarostrobos* or *Diselma* (Jarman & Brown 1983). It is widespread in the western half of the state with the largest unbroken tracts occurring in the northwest. Smaller patches of rainforest occur also in the northeast, with isolated pockets scattered elsewhere in the eastern half of the

state, usually in gullies. It occurs on both mineral and organic soils, and overlies a wide range of rock types from basalts, dolerite and granite to quartzites and sandstones. The rainfall requirements of rainforest in Tasmania have been given by Jackson (1968) as 1000mm per annum with a summer monthly minimum of 25mm. Rainforest extends from sea level to over 1200m in altitude.

On the basis of floristic and structural charactertistics, rainforest has been divided into four groups (Jarman et al. 1984). Group I (Callidendrous rainforest) is characterised by parklike forests with open understoreys, often with a layer of tree ferns. The main canopy trees are Nothofagus and Atherosperma, and the diversity of woody species in the forest is low. Group II (Thamnic rainforest) also includes forests with well-formed trees but they rarely appear parklike because of a shrubby understorey. The diversity of woody species is higher than in Group I and the main canopy trees are Nothofagus, Atherosperma, Eucryphia lucida, Phyllocladus, Lagarostrobos and/or Athrotaxis selaginoides. Group III (Implicate rainforest) is of lower stature and the trees are often of poor form. The understorey is dense with a tangled shrub layer from ground level to the canopy. Diversity of woody species is high. The main canopy dominants include Phyllocladus, Athrotaxis, Eucryphia and Nothofagus, but Leptospermum and Acacia species may also be present. Group IV (Open montane forest) is dominated by Athrotaxis cupressoides and comprises low open forests over grassy or low shrubby understoreys, the latter usually being less than half the height of the forest. The first three groups form the bulk of rainforest in Tasmania and they occur from lowland to highland areas. Thamnic and implicate rainforest reach their best development in western and southwestern Tasmania whereas callidendrous rainforest is best developed in northwestern, central and northeastern Tasmania. Open montane rainforest is confined to high altitudes and is found mostly on the Central Plateau.

Sampling

The survey of pteridophytes was part of a broader survey of rainforest in Tasmania (Jarman et al. 1984) involving both phanerogams and cryptogams. Cover and abundance data were collected from over 300 quadrats (20 × 20m) which sampled the broad geographic and altitudinal range of rainforest throughout the state. Supplementary data were used from Jarman and Crowden (1978). General comments relating to the occurrence of ferns in vegetation other than rainforest are derived from literature sources where indicated, from herbarium records or from unpublished observations.

"Mixed forest" (a rainforest understorey below eucalypts — see Gilbert 1959) was not systematically sampled during the survey. However, it is closely related to rainforest and is likely to exhibit the same general trends in its fern flora.

Nomenclature and Taxonomy

Nomenclature and classification of species follows that given in Jones and Clemesha (1981). For convenience throughout the text, the subspecific epithets of *Asplenium* trichomanes subsp. quadrivalens, Cystopteris filix-fragilis subsp. laetivirens and Grammitis magellanica subsp. nothofagetii are omitted.

The taxon referred to in this work as *Asplenium* cf. *terrestre* may be either an undescribed species or conspecific with *A. terrestre* from New Zealand (P. Brownsey, comments with herbarium material, Tasmanian Herbarium). It is widespread in Tasmania and has previously been confused with *A. flaccidum* or *A. bulbiferum* (Brownsey, *loc. cit.*).

Grammitis pseudociliata has been included in this paper but was not found during the survey. This species, previously considered a New Zealand endemic, has only

recently been collected in Tasmania (by M. Garrett). Although only found in "mixed forest" it has been included because it is epiphytic on *Eucryphia lucida*, a common rainforest dominant.

RESULTS AND DISCUSSION

Forty nine species of pteridophytes have been recorded from Tasmanian rainforest (see Table 1). These are contained within 15 families of Pteropsida (ferns), one family of Lycopsida (clubmosses) and one family of Psilopsida (fork-ferns). Three species, *Asplenium flabellifolium, Pteridium esculentum* and *Pteris tremula,* appear to be adventive and are considered doubtful rainforest species. The remaining 46 species represent just over half of the total number of pteridophytes recorded from Tasmania. The richest families in rainforest are the Blechnaceae (water ferns) and the Hymenophyllaceae (filmy ferns). Each is represented by eight species which includes all the Tasmanian species of filmy ferns and all but one of the water ferns. *Apteropteris applanata* is the only endemic fern known from Tasmanian rainforest.

Excluding adventive ferns, the rainforest pteridophytes include 27 terrestrial species (including two tree ferns) and 19 epiphytes although several species could be considered in either group, particularly some of those classified here as epiphytes. These two groups can be subdivided using some of the categories from Page's (1979) ecological classification of ferns in mesic and in xeric epiphytic environments in the tropics. Thus, three terrestrial habitats can be recognized: the forest floor, streamsides and rockfaces. Epiphytic habitats can be divided into two groups: the canopy and the understorey. The latter group comprises both crotch and main branch species (after Parris 1976) as well as those occurring below 2m. Low and high climbers, as described in Page (1979) for tropical forests, are not a feature of cool temperate rainforest in Tasmania with only one species, *Microsorium diversifolium*, occurring as a climber.

Terrestrial Ferns

Diversity among the ground ferns is usually low except in riverine situations, and in many forest communities only one or two species are present. Nevertheless, these are often abundant and may form a continuous cover up to 1m high. The most common ground ferns in undisturbed rainforest are Blechnum wattsii and Polystichum proliferum. They can occur intermixed but in many forests they are mutually exclusive or almost so. They are found throughout Tasmania although the best development of Blechnum wattsii is on the organic or infertile mineral soils of western and southwestern Tasmania whilst Polystichum proliferum is most charactertistic of fertile mineral soils in northwestern, central and northeastern Tasmania. Both species are found across a range of altitudes, from sea level to treeless alpine situations but in extreme highland sites they are confined to sheltered positions among rocks. The tree fern, Dicksonia antarctica, may accompany either species although its greatest abundance and most impressive growth is seen in communities where Polystichum is present. Dicksonia is particularly common along creek and river margins, and in moist gullies or water seepages. However, its occurrence in these situations is probably related as much to soil nutrients as to moisture availability since it also occurs in drier habitats, particularly on good soils.

In upland rainforests, particularly in central and northeastern Tasmania, two smaller species, *Blechnum penna-marina* and the facultative epiphyte, *Hymenophyllum peltatum*, may be more common on the ground than either *B. wattsii* or *Polystichum. Blechnum penna-marina* is an obligate soil-dwelling species and occurs as small scattered plants, often obscured by litter. *Hymenophyllum peltatum* forms low dense patches on mossy rocks, logs or exposed roots. A second facultative epiphyte, *Grammitis billardieri*, is often present as small scattered tufts and, like *Hymenophyllum peltatum,* shows an apparent predilection for mossy surfaces. As well as these species, small patches of *Lycopodium fastigiatum* are sometimes present on the forest floor in upland forests.

Two other ground ferns, *Histiopteris incisa* and *Hypolepis rugosula*, are widespread in rainforest but are most characteristic of disturbed sites. They are able to tolerate relatively high light intensities and form a dense cover in open situations below breaks in the canopy or along roadsides and tracks. In mature well-developed rainforest they occur as occasional plants, often weak and spindly, in local spots which are better lit than the surrounding forest. *Histiopteris* is one of only a few Tasmanian ferns which "die down" during the colder winter months.

Of the remaining forest floor ferns, most are patchy or rare in rainforest. Some of the more notable species include *Diplazium australe* and *Pteris comans* which are locally common on poorly drained soils but are mostly restricted to northwestern Tasmania. *Gleichenia microphylla* also occurs in poorly drained areas, mainly where the forest is disturbed, whilst *Lindsaea trichomanoides* is sporadic on peaty soil and on logs.

The narrow fringing band of rainforest which occurs along the edges of creeks, rivers and lakes represents a separate habitat from the forest floor and often supports an abundance of ferns. Many widespread species are present, e.g. *Dicksonia antarctica, Polystichum proliferum* and *Blechnum wattsii*, as well as several others which reach their best development in rainforest in this habitat. For example, *Blechnum vulcanicum* and *Sticherus tener* are particularly well-developed on the steep or overhanging banks of the larger streams although they are not confined to these sites. Within rainforest, *Blechnum nudum* is mostly confined to river edges, although outside of rainforest it is widespread in relatively open situations on the forest floor. *Blechnum fluviatile, B. minus* and *B. chambersii* are commonly associated with flowing water although occasionally they occur on rockfaces away from water. *B. chambersii* is particularly shade-loving and is rarely present where direct sunlight penetrates to the ground surface.

Rockfaces can also support a wide variety of ferns although at each individual site usually only a few species are present. The flora consists mainly of mixtures of terrestrial and epiphytic species. However, Cystopteris filix-fragilis, Asplenium trichomanes and A. flabellifolium appear to be restricted to this habitat and are considered characteristic of rockfaces. The most common terrestrial (including streamside) ferns are *Blechnum* spp. and these are usually represented by scattered plants on ledges or anchored in rock crevices. In open, often wet, conditions, Blechnum vulcanicum may form locally dense patches with many pendulous wedgeshaped fronds. Asplenium bulbiferum and several other less common ground ferns are also occasionally found on rockfaces. Epiphytic species present include Asplenium Microsorium diversifolium, Tmesipteris billardieri, Lycopodium cf. terrestre, myrtifolium, Grammitis billardieri and Hymenophyllum spp. Hymenophyllum flabellatum appears to be very drought tolerant and is often found on the dry roof below overhanging rocks. In high altitude situations in southwestern Tasmania the normally host-specific Apteropteris is sometimes abundant on rockfaces, forming a dense soft grey mat over the rock surface.

Epiphytic Ferns

Epiphytic ferns are widespread in rainforest but are usually smaller and less prominent than the ground ferns. The largest of the widespread species are *Rumohra adiantiformis, Asplenium* cf. *terrestre* and *Microsorium diversifolium*. Equally common but less conspicuous are members of the Hymenophyllaceae and Grammitidaceae, e.g. *Hymenophyllum rarum, H. peltatum* and *Grammitis billardieri*. Very few of the ferns included in this group are obligate epiphytes and most have been found (some rarely) on rocks or soil. Exceptions include *Asplenium flaccidum*, *Polyphlebium venosum* and *Grammitis pseudociliata*.

Host specificity is poor and many vascular species can act as substrates including the forest dominants, lesser trees and some of the larger undershrubs. The thick fibrous trunks of the tree fern, *Dicksonia*, provide excellent substrates and may support all of the epiphytic ferns present at any one site. Ferns which appear to be confined to a particular host species include *Apteropteris applanata* which when epiphytic is found only on *Athrotaxis* trunks (either *A. selaginoides* or *A. cupressoides*). *Tmesipteris elongata* and *Polyphlebium venosum* have been recorded only on *Dicksonia* trunks in rainforest although the latter is also known from the trunks of *Cyathea cunninghamii* in wet sclerophyll forests. *Grammitis pseudociliata* is known in Tasmania from a single collection from *Eucryphia lucida*. *Ctenopteris heterophylla* has a wider range but when epiphytic shows a preference for *Eucryphia lucida* or *Olearia argophylla*. *Tmesipteris billardieri* is found most frequently on tree ferns but also occurs occasionally on the mossy buttresses and peaty litter cones of the larger tree species. The conifers, particularly *Phyllocladus aspleniifolius*, are poorly colonized by epiphytic ferns.

Differences in the fern flora between high and low epiphytic sites are manifest mainly in the poor development of the canopy flora. All epiphytes recorded from rainforest occur in the understorey but several appear to be very tolerant of a wide range of light and moisture conditions and extend into the canopy. However, the canopy flora is not characterized by any additional species and thus, in Tasmanian rainforest, there are no ferns which can be classed exclusively (or mainly) as high epiphytes (cf. Page 1979). Species present in the canopy are typically small ferns (Hymenophyllum rarum, H. peltatum, H. cupressiforme, Grammitis magellanica, Ctenopteris heterophylla) except for Microsorium diversifolium and occasional stunted plants of Rumohra adiantiformis.

Distribution

Very few ferns are restricted to rainforest in Tasmania. Exceptions include some of the uncommon species such as *Asplenium flaccidum* and *Lindsaea trichomanoides*. Many species are equally abundant in other vegetation types, particularly wet eucalypt forests and some, including *Asplenium bulbiferum*, *Lastreopsis acuminata*, *Gleichenia microphylla*, *Todea barbara* and *Cyathea australis* (possibly also *Sticherus lobatus* and *Blechnum patersonii*) are developed better outside of rainforest than within it.

Within rainforest, the distribution of ferns varies among the main rainforest groups. Callidendrous rainforest possesses the richest and most luxuriant fern flora (although this is not necessarily true at every site). It contains most of the common terrestrial and epiphytic ferns, but is especially typified by *Polystichum* and *Dicksonia* which dominate the understorey vegetation in many medium to low altitude forests. Two species are restricted to callidendrous forests, viz. the tree fern, *Cyathea australis* which, in rainforest, is confined to small relict patches mostly on the east coast, and *Tmesipteris elongata*. Several other species such as *Hymenophyllum cupressiforme* and species mainly epiphytic on tree ferns, e.g. *Hymenophyllum flabellatum*, *Polyphlebium venosum* and *Tmesipteris billardieri*, are found most commonly in callidendrous forest although they occur also in other rainforest groups.

Most fern species which are found in callidendrous forests occur also in thamnic rainforest but they rarely attain the same luxuriance. *Blechnum wattsii*, the main ground fern, is an exception and its leathery pinnate fronds may form a dense dark green cover up to 1m high, particularly where the canopy is broken. The most common epiphytes are *Hymenophyllum rarum* and *Grammitis billardieri*. The decline in

luxuriance of the fern flora compared with that in callidendrous forests may result, in part, from the scarcity of the "popular" epiphytic substrate, *Dicksonia*. However, it may also reflect some more fundamental habitat difference, possibly one associated with humidity.

In general, ferns are poorly developed in implicate rainforest although *Blechnum wattsii* is common in several communities. Many characteristic species from callidendrous and/or thamnic forests are absent or rare including *Dicksonia* (and its epiphytes), *Rumohra adiantiformis, Asplenium* cf. *terrestre, Microsorium diversifolium* and *Ctenopteris heterophylla*. However, *Grammitis billardieri, Hymeno-phyllum rarum* and *H. peltatum* are widespread and *H. australe* may be present in moister situations. *Hymenophyllum marginatum* reaches its best development in implicate rainforests although it is easily overlooked because of its small size and resemblance to some liverworts. It is absent from callidendrous forests and most thamnic forests (except riverine situations) but sometimes occurs in open montane forests.

Open montane rainforest contains an impoverished fern flora. *Grammitis* poeppigiana is restricted to this group and occurs in small patches usually in rock crevices. *Apteropteris applanata* (on *Athrotaxis* trunks) and *Hymenophyllum peltatum* (epiphytic or on mossy rockfaces) may be locally common. Other ferns are rarely present and are confined to the most sheltered, shaded microhabitats.

Although most ferns are widely dispersed throughout the state, several show restricted distributions. *Lindsaea trichomanoides* has been recorded only from south-western Tasmania and *Grammitis pseudociliata* is even rarer, being known from only one site in southern Tasmania. *Lastreopsis hispida, Tmesipteris elongata, Pteris comans, Diplazium australe and Sticherus lobatus* are local and are found mainly in northwestern Tasmania although rare occurrences are known elsewhere. *Blechnum patersonii* is found mostly in moist gullies in northern or eastern parts of the state and *Cystopteris filix-fragilis* occurs on shaded rockfaces in central and southwestern Tasmania. A number of other species show wider distributions but are constrained by specialised habitats. For example, the distribution of *Asplenium trichomanes* is contained within areas where limestone outcrops and the distribution of *Apteropteris applanata* (in its epiphytic form) is restricted to that of its host, *Athrotaxis*. Some species, although more widely dispersed in the state, are uncommon, e.g. *Asplenium flaccidum* and *Lycopodium myrtifolium*.

As a general trend, the abundance and luxuriance of ferns declines with increasing altitude with the most pronounced effect being apparent at 600-700m above sea level. Several of the larger ground ferns, e.g. *Polystichum proliferum* and *Blechnum wattsii*, may be present in rainforest above about 700m but they are represented by scattered, often small individuals which occur mostly in sheltered sites. A few species, including *Hymenophyllum peltatum, Grammitis billardieri, Blechnum penna-màrina* and *Lycopodium fastigiatum,* are well-adapted to high altitude situations although not necessarily restricted to them. In montane rainforests (above 1000m), *Grammitis billardieri* is replaced by *G. poeppigiana* which occurs in small dense mats in rock crevices. *Cystopteris filix-fragilis* also appears to be restricted to upland forests (altitudes above 800m).

A similar trend of altitudinal zonation is apparent in Victorian cool temperate rainforest (see Howard & Ashton 1973) although the altitude differences occur at lower elevations in Tasmania. One species, *Hymenophyllum peltatum*, which was found only in high altitude forests in Victoria (Howard & Ashton 1973) occurs across a wide range of altitudes in Tasmanian rainforest and may be present at sea level in some riverine communities in western parts of the state.

Biogeography

The geographical distribution of ferns found in Tasmanian rainforest, taken from Jones and Clemesha (1981), is shown in Table 1. Over two thirds of the rainforest ferns are confined to Tasmania-Australia, Tasmania-New Zealand or Tasmania-Australia-New Zealand. Several additional species occurring in these regions also extend their range into the Pacific Islands. Other biogeographical elements are poorly represented but include a few Cosmopolitan, Endemic, Old World Tropics and Austral species (after Parris 1976). A comparison between Tasmania and other land masses containing cool temperate rainforest indicates that 8% of Tasmanian rainforest ferns are shared with South America, 69% are shared with New Zealand and 92% are shared with mainland Australia.

The southern affinities of the Tasmanian rainforest ferns are borne out by their occurrence within Australia. Only 11 of the 49 species (22%) are found in tropical northern Queensland whereas 57% are found in southern Queensland. Eighty six per cent occur also in New South Wales and in Victoria, the most southerly part of the Australian mainland. These figures are reduced, at least with respect to Victoria, where the comparison is restricted to the same habitat in both states. Thus, of the 40 species listed by Howard and Ashton (1973) in cool temperaterainforest in Victoria, 31 were recorded in Tasmania during the present survey. Thus, 53% of species from rainforest habitats are shared between Tasmania and Victoria. The most notable Tasmanian species absent from Victorian rainforest include *Asplenium* cf. *terrestre, Sticherus tener, Hymenophyllum marginatum* and *Grammitis magellanica*.

SUMMARY

The fern flora in Tasmania's rainforest is small and comprises 40 species (including three species which may be adventive). A few ferns are confined to rainforest but most occur also in wet eucalypt forests or scrub. The most common ferns include *Polystichum proliferum, Blechnum wattsii, Dicksonia antarctica, Rumohra adiantiformis, Microsorium diversifolium, Asplenium* cf. *terrestre, Hymenophyllum rarum* and *Grammitis billardieri* but many other species are widespread or locally common in particular situations. Some of the rarer ferns include *Lindsaea trichomanoides, Cystopteris filix-fragilis, Grammitis pseudociliata* and *Lastreopsis hispida.* 80th epiphytic and ground species (including two tree ferns) are represented. In most communities, ground ferns account for the greatest biomass within the fern flora whilst epiphytes account for the greatest diversity. Only one endemic fern occurs in Tasmanian rainforest.

As a general trend, ferns decline in prominence and abundance from lowland situations to high altitudes. They also show differences in luxuriance and diversity among the four rainforest groups, with their best development in callidendrous rainforest. They are most impoverished in high altitude open montane rainforests.

Over two thirds of the ferns found in rainforest are confined to Australasia (Tasmania, Australia and New Zealand). Within Australia, the rainforest fern floras of Tasmania and Victoria are very similar with over thirty species being common to the rainforests of both states.

TABLE 1. Habitat and distribution of ferns recorded from Tasmanian rainforest. Distributions
outside of Tasmania are taken from Jones and Clemesha (1981). (Abbreviations: N = New South
Wales, NT = Northern Territory, NZ = New Zealand, Q = Queensland, SA = South Australia, SAf =
South Africa, SAm = South America, Tas = Tasmania, V = Victoria).

Species	Habitat and Distribution
Apteropteris applanata A.M. Gray & R.G. Williams	On rocks or epiphytic (on <i>Athrotaxis</i>), scattered throughout western, central and southwestern Tasmania; endemic.
<i>Asplenium bulbiferum</i> Forst.f.	Mostly on soil or rocks but uncommon in rainforest; more widespread in wet sclerophyll forest, particularly in northwestern, northern, and eastern parts of the state. Q, N, V, SA, NZ, Asia.
A. flabellifolium Cav.	Uncommon in rainforest and probably adventive; mostly found among rocks in drier forests. All states, NZ.
<i>A. flaccidum</i> Forst.f.	Epiphytic, scattered in rainforest throughout Tas. Q, N, V, NZ, Pacific Is.
A. trichomanes L. subsp. quadrivalens D.E. Meyer	Restricted to limestone rocks; present in several vegetation formations. All states except Q, NZ, Europe.
A. cf. terrestre	A widespread epiphyte in rainforest.
<i>Blechnum chambersii</i> Tindale	Ground species of shady situations in wet forests mostly along rivers or drainage channels but also on rockfaces. Q, N, SA, NZ, Fiji.
<i>B. fluviatile</i> (R.Br.) E.J. Lowe ex Salom.	Widespread ground species in wet forests near creeks but also on rockfaces. N, V, NZ.
B. minus (R.Br.) Ettingsh.	Common ground species along creeks. Q, N, V, SA, NZ.
<i>B. nudum</i> (Labill.) Mett. ex Luerss.	Widespread ground species; in rainforest, mostly along edges of creeks and rivers where the canopy is broken. Q, N, V, SA.
<i>B. patersonii</i> (R.Br.) Mett.	Ground species; local, near creeks in wet forests in northern and eastern Tasmania. Q, N, V, Fiji.
<i>B. penna-marina</i> (Poir.) Kuhn	Widespread ground species in high altitude situations in several vegetation formations; occasionally found to sea level. N, V, NZ, SAm, SubAntarctic Is.
<i>B. vulcanicum</i> (Bl.) Kuhn	Ground species, most common along the edges of creeks and rivers in western and southwestern Tasmania; also on rockfaces. NZ.
<i>B. wattsii</i> Tindale	Widespread ground species in wet forests. Q, N, V, SA.
<i>Ctenopteris heterophylla</i> (Labill.) Tindale	Epiphytic or on rocks; scattered in wet forests but also extending into drier vegetation. V, NZ.
<i>Cyathea australis</i> (R.Br.) Domin	Tree fern; occasional in rainforest but common in wet eucalypt gullies in eastern, northeastern and northern Tasmania. Q, N, V.
Cystopteris filix-fragilis (L.) Bernh. subsp. <i>laetivirens</i> (Prent.) C.Chr.	Occasional on rocks in central and southwestern Tasmania in high altitude forests. N, V, NZ. $\hfill \ $
<i>Dicksonia antarctica</i> Labill.	Tree fern; widespread in wet forests. Q, N, V, SA.
<i>Diplazium australe</i> (R.Br.) N.A. Wakefield	Ground fern; patchy in wet forests, mainly in northwestern Tasmania. Q, N, V, NZ.
Gleichenia microphylla R.Br.	Ground fern; occasional in rainforest, widespread in damp situations in other wet forests. All states, NZ.
Grammitis billardieri Willd.	Epiphytic or terrestrial; widespread in wet forests. N, V, NZ, SAf, SAm.
<i>G. magellanica</i> Desv. subsp. <i>nothofagetii</i> Parris	Scattered in wet forests, mainly epiphytic. NZ.

G. poeppigiana Scattered in high altitude vegetation, usually in sheltered rock crevices. N, V, NZ, SubAntarct. Is. (Mett.) Pic. Ser. G. pseudociliata Epiphyte known from one location only in Tasmania. NZ. Parris Histiopteris incisa Ground fern; widespread in wet forests. Q, N, V, SA, NT, Tropics & S. Hemisphere, (Thunb.) J.Sm. Hymenophyllum australe Common in wet forests, mostly on buttresses or mossy rocks Willd. where the humidity is high. Q, N, V, H. cupressiforme Labill, Usually epiphytic; widespread in wet forests. Q, N, V. H. flabellatum Labill. Mostly an epiphyte of Dicksonia, but also on logs or rocks. Q, N, V, NZ, Pacific Is. H. marginatum Hook. & Mostly epiphytic in western and southwestern Tasmania, in wet Grev. scrub and forests. Q. N. H. peltatum (Poir.) Desv. Widespread epiphytic or rock species in wet forests; common at high altitudes but also extending to sea level. Q, N, V, NZ, SAf, Mascarene Is. (Also in S. Chile -- Looser 1948). H. rarum R.Br. Widespread in wet forests; mainly epiphytic. N, V, NZ. Hypolepis rugosula Widespread ground fern in wet forests. Q, N, V, SA, NZ. (Labill.) J.Sm. Lastreopsis acuminata Ground fern; uncommon in rainforest but more widespread in (Houlston) Morton other wet forests, Q, N, V, SA. Ground fern: sporadic, mostly in northwestern Tasmania along L. hispida (Sw.) Tindale creeks, N. V. NZ. Lindsaea trichomanoides Localized in rainforests in southern and southwestern Tasmania, mostly along the larger rivers. N, V, NZ. Dryand. Widespread ground species in upland vegetation. Q, N, V, NZ. Lycopodium fastigiatum R.Br. 1. myrtifolium Forst.f. Occasional in wet forests; epiphytic or terrestrial, Q. N. V. NZ. Microsorium diversifolium Widespread across a range of vegetation types including dry (Willd.) Copel. forests; epiphytic or terrestrial. Q, N, V, NZ, Norfolk Is. Polyphlebium venosum Epiphyte: restricted to Dicksonia antarctica trunks in rainforest but (R.Br.) Copel. also on Cyathea cunninghamii trunks in wet eucalypt forests. Q, N, V, NZ. Polystichum proliferum Widespread ground fern in wet forests. N, V, SA. (R.Br.) Presl Pteridium esculentum Ground fern; adventive in rainforest, common in other wet and dry (Forst.f.) Cockayne lowland vegetation. All states, NZ, Pacific Is. Pteris comans Ground fern; patchy in rainforest, mainly found in northwestern Forst.f. Tasmania. Q, N, V, NZ, Pacific Is. P. tremula Uncommon ground fern in Tasmania, probably adventive in R.Br. rainforest. Q, N, V, SA, NT, NZ, Norfolk Is, Fiji. Rumohra adiantiformis Widespread terrestrial and epiphytic species. Q, N, V, NZ, SAm, SAf (Forst.f.) Ching Sticherus lobatus Ground fern; patchy in rainforest, mostly in forests from north-N.A. Wakefield western Tasmania. Q. N. V. Widespread ground fern in wet forests, often found along rivers or S. tener (R.Br.) Ching road cuttings. N, V. Tmesipteris billardieri Widespread in wet forests, usually epiphytic on Dicksonia Endl. antarctica but occasionally in peat or on logs. N, V. Recorded only from Dicksonia trunks; occasional in lowland T. elongata Dang. Tasmania but possibly overlooked. V, NZ. Todea barbara Ground fern; uncommon in rainforest, found elsewhere along (L.) T. Moore creeks and in gullies mostly in drier lowland parts of the state. Q, N, V, SA, NZ, SAf.

ACKNOWLEDGEMENTS

We wish to thank M. Garrett and M. Neyland for their comments on the manuscript and M. Garrett for permission to cite his unpublished record of *Grammitis pseudociliata*. The work was undertaken with a grant provided by the Forest Ecology Research Fund.

REFERENCES

- GILBERT, J.M. 1959. Forest succession in the Florentine Valley, Tasmania. Pap. Proc. Roy. Soc. Tas. 93, 129-151.
- HOOKER, J.D. 1860. Introductory Essay. In *Botany of the Antarctic Voyage of H.M. Discovery Ships "Erebus" and "Terror" in the years 1839-1843*, Vol. 3, *Flora Tasmaniae*, Reeve, London.
- HOWARD, T.M. & ASHTON, D.H. 1973. The distribution of *Nothofagus cunninghamii* rainforest. *Proc. Roy. Soc. Vic. 86:* 47-76.
- JACKSON, W.D. 1968. Fire, Air, Water and Earth an Elemental Ecology of Tasmania. *Proc. Ecol. Soc. Aust. 3.* 9-16.
- JARMAN, S.J. & BROWN, M.J. 1983. A definition of cool temperate rainforest in Tasmania. Search 14(3-4): 81-87.
- JARMAN, S.J., BROWN, M.J. & KANTVILAS, G. 1984. *Rainforest in Tasmania*. National Parks and Wildlife Service, Tasmania.
- JARMAN, S.J. & CROWDEN, R.K. 1978. *A Survey of Vegetation*. Lower Gordon Scientific Survey. Hydro Electric Commission, Tasmania.
- JONES, D.L. & CLEMESHA, S.C. 1981. Australian Ferns and Fern Allies. 2nd Edn. A.H. & A.W. Reed, Sydney.
- LOOSER, G. 1948. The ferns of southern Chile. American Fern Journal 38: 71-87.

NELSON, E.C. 1981. Phytogeography of southern Australia. In A. Keast (ed.), *Ecological biogeography of Australia.* W. Junk, The Hague.

- PAGE, C.N. 1979. The diversity of ferns. An ecological perspective. In A.F. Dyer (Ed.), The Experimental Biology of Ferns, Academic Press, London.
- PAGE, C.N. & CLIFFORD, H.T. 1981. Ecological Biogeography of Australian Conifers and Ferns. In A. Keast (Ed.), *Ecological Biogeography of Australia*. W. Junk, The Hague.
- PARRIS, B.S. 1976. Ecology and biogeography of New Zealand pteridophytes. *Fern Gaz. 11(4):* 231-245.

TMESIPTERIS IN VANUATU (NEW HEBRIDES)

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ABSTRACT

Cytological, anatomical and ecological observations on *Tmesipteris* from Vanuatu are presented and attention is drawn to the variation in stem anatomy and ecology in the genus as a whole. Three species are recognised in the archipelago: *T. oblongi-folia* sp. nov. (n = 104) from Tanna and Aneityum, *T. vanuatensis* sp. nov. (n = 104) from Espiritu Santo and *T. oblanceolata* (R.Br.) Desv. (n = 208) from Aneityum and Espiritu Santo.

INTRODUCTION

The genus *Tmesipteris* was based by Bernhardi (1801) on the species, *Lycopodium tannense*, which was described a year earlier by Sprengel (1800) from a Forster collection supposedly made on Tanna, Vanuatu. However, no Forster specimen from Tanna has ever been found and Sprengel's description is very brief and only sufficient to place the species in the genus. *Tmesipteris* was collected again in the archipelago by both Milne and Seeman in the middle of the last century but these collections came from Aneityum and differed from Bernhardi's description and illustration. Consequently the identity of the type species, *T. tannensis* (Spreng.) Bernh., remained for many years in doubt and our knowledge of the genus in the islands as a whole has been based on very few specimens and was inevitably incomplete.

Recently *Tmesipteris* has been found again on Tanna, Aneityum and, for the first time, on Espiritu Santo. The new material from Tanna has already clarified the typification and identity of *T. tannensis.* It differs from the species illustrated by Bernhardi (1801) and Chinnock (1976) has provided convincing evidence to show that the Forster specimen described and illustrated by Bernhardi in fact came from Dusky Sound, New Zealand, and has suggested that the reference to Tanna by Sprengel was probably an error. The Bernhardi illustration is, therefore, selected as the neotype of *L. tannense* Spreng. and the type species is now considered to be restricted to New Zealand.

The present paper gives a more complete account, including cytological and anatomical studies, of *Tmesipteris* in Vanuatu. The material from Tanna belongs to the *T. lanceolata* group and is described as a new species, *T. oblongifolia*, which is also found on Aneityum. Two further species are also recognised in the archipelago, namely, *T. vanuatensis* A.Braith. a new species proposed for material from Espiritu Santo, and *T. oblanceolata* (R.Br.) Desv. from Aneityum and Espiritu Santo.

MATERIALS AND METHODS

The material was collected by the author during the 1971 Royal Society and Percy Sladen Expedition to the New Hebrides. The details of the localities of the collections are given in Table 1. At each locality plants were collected for herbarium specimens and preserved in 70% alcohol for anatomical studies. When available, sporangial material was also fixed in the field in 1:3 acetic-alcohol and despatched by air to the U.K. where it was stored in a deep freeze. Meiotic preparations for chromosome counts were subsequently made using the acetocarmine squash method. The material for anatomical studies was embedded in paraffin wax and the sections stained in safranin and light green or aniline blue. Spore samples were taken from dried herbarium specimens and mounted in gum chloral for measurement. Herbarium material of each species is deposited in the Herbarium, Royal Botanic Gardens, Kew.

CYTOLOGY

The results of the chromosome counts are summarised in Table 1 and representative cells are illustrated in Figs. 1 & 2. It is difficult to produce absolutely unequivocal counts in the genus because of a) the high chromosome numbers, b) variation in the size of chromosomes and c) the sometimes peculiar shapes of the bivalents. The latter has generally been attributed to a laxity in the spiral structure (Manton 1950, Lovis 1977). Nevertheless the counts listed in Table 1 are accurate to within one or two chromosomes except where indicated, and even in these cases the order of the chromosome number is not in doubt.

Species	Locality	Chromosome number	Spore length* (µm)	Length of Stomata* (µm)
T. oblongifolia	RSNH 2146, Woptiabo, Aneityum	n = 104	62.7 ± 4.2	96.0
	RSNH 2204, Mt. Toukosmeru, Tanna	n = 104	57,5 ± 3.3	92.5
	RSNH 2211, Mt. Toukosmeru, Tanna	n = 104	57.4 ± 3.8	-
T. vanuatensis	RSNH 2354, Apouna Valley, Espiritu Santo	n = 104	62.0 ± 3.6	93.2
	RSNH 2382, Mt. Tabwemasana, Espiritu Santo	n = c.104	58.6 ± 3.6	92.3
T. oblanceolata	RSNH 2112, Inrero, Aneityum	n = 208	82.8 ± 4.1	133.4
	RSNH 2152, Nezwon Nelgon, Aneityum	n = c.208	81.5 ± 4.3	123.6

TABLE 1. Chromosome Numbers in Tmesipteris from Vanuatu

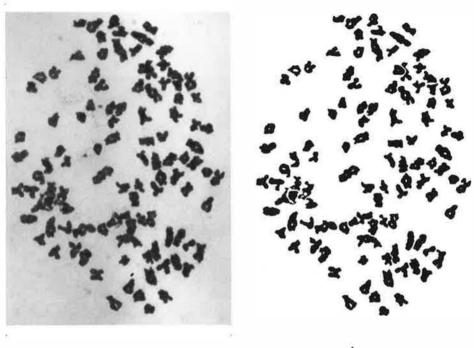
* Data based on 100 measurements from one specimen from each collection.

The numbers recorded here fall into the cytological pattern already established for the genus by Barber (1957) from Australian material of two groups with n = 104 and n = 208 respectively. These relatively high numbers have in the past been designated as various levels of polyploidy but are here interpreted in terms of the lowest extant number known in the Psilotales, which is n = 52 (Lovis 1977). Thus *T. oblongifolia* and *T. vanuatensis* are tetraploids and *T. oblanceolata* is an octoploid.

The mean length of spores and stomata are also given in Table 1. It is clear from this data that the spores and stomata of the octoploid, *T. oblanceolata*, are considerably larger than those of the tetraploids, *T. oblongifolia* and *T. vanuatensis*. Although the samples are small, the data do suggest that these microcharacters are potentially useful in Vanuatu as polyploid indicators.

ANATOMY

The species from Vanuatu show the basic vascular pattern described from other *Tmesipteris* species (Sykes 1908, Sahni 1925). Thus the solid core of tracheids in the rhizome becomes medullated and breaks up in the transition region to form a variable number of groups of tracheids arranged around a central pith. The representative sections illustrated in Fig. 3 show the typical arrangement of the stele at the top of the transition region. In all three species groups of tracheids can be seen surrounding a well defined pith. There are, however, differences in the nature of the pith cells and two basic types can be recognised.



а



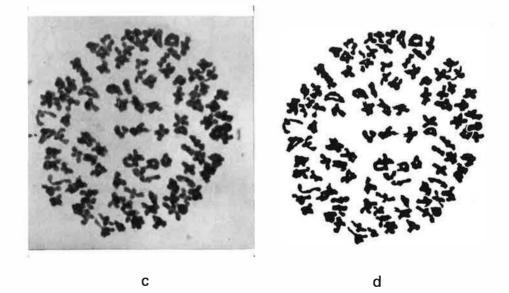


FIGURE 1. Permanent acetocarmine preparations for meiosis. X 750. a) *T. oblongifolia* RSNH 2204. b) Explanatory diagram showing 104 bivalents. c) *T. vanuatensis* RSNH 2354. d) Explanatory diagram showing 104 bivalents.

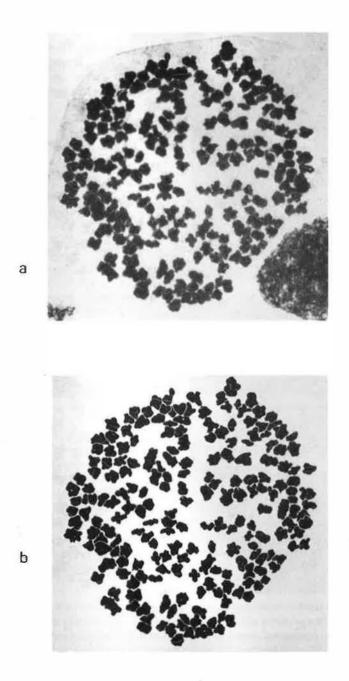


FIGURE 2. Permanent acetocarmine preparation of meiosis. X 750. a) *T. oblanceolata* RSNH 2112. b) Explanatory diagram showing 208 bivelents.

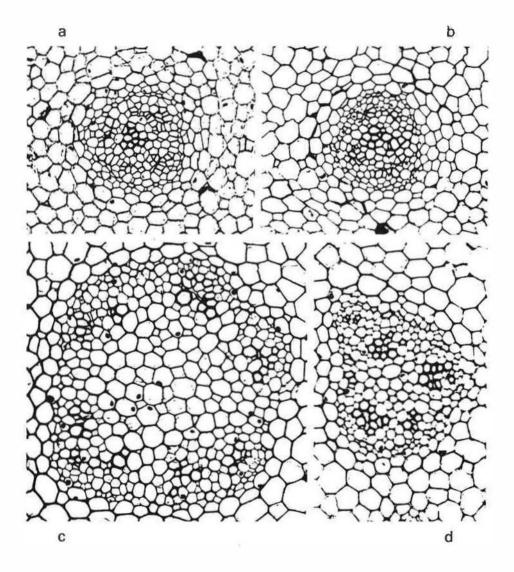


FIGURE 3. Transverse sections of aerial shoots of *Tresipteris* species from Vanuatu. X 100. a) 7. *oblongifolia* RSNH 2204. b) 7. *vanuatensis* RSNH 2382. c) & d) 7. *oblanceolata* RSNH 2112. a, b & c from top of transition region; d from distal part of aerial shoot. The first type is illustrated by *T. oblongifolia* (Fig. 3a) and *T. vanuatensis* (Fig. 3b). In these species the pith is small and made up of narrow thick walled, lignified cells which in transverse sections have the same appearance as fibres or sclerenchyma. The tracheids around the pith are by contrast thinner walled and the tracheid bundles can be located in the sections by their mesarch protoxylem. The second type of pith is characteristic of *T. oblanceolata* (Fig. 3c,d). Here the groups of tracheids surround a relatively large pith made up of thin walled parenchymatous or slightly collenchymatous cells. Even in the distal parts of the leafy shoot, where the number of tracheid bundles and pith are much reduced, the pith cells are still essentially parenchymatous (Fig. 3d). Medullary xylem has been found associated with this type of pith in *T. vieillardii* (Sahni 1925) from New Caledonia and *T. oblanceolata* (Braithwaite 1973) from the Solomon Islands, but none has been found in the material from Vanuatu. On present evidence the pith type appears to be constant for each species.

Variations in the pith cells in the stems of other *Tmesipteris* species have been reported by a number of previous investigators, notably Dangeard (1890-91), Sahni (1925) and Braithwaite (1973). In all cases two types of pith composed of either parenchymatous cells or sclerenchymatous cells have been recognised. The consistency of the observations so far suggests that this recently rather neglected anatomical character perhaps merits further investigation to establish whether it may be useful as a taxonomic indicator, either at the species level or for the grouping of species.

ECOLOGY AND DISTRIBUTION

During the 1971 Royal Society and Percy Sladen Expedition to the New Hebrides *Tmesipteris* was encountered only sporadically in montane forest at altitudes of 475-745m on Aneityum and Tanna in the south and 900-1650m on Espiritu Santo in the north. However, many of the other larger islands in the group attain altitudes in excess of 500m so that it can perhaps be anticipated that further collecting will extend its distribution within the islands.

T. oblongifolia and *T. vanuatensis* were confined almost exclusively to the lower parts of the tree fern trunks belonging to the genus *Cyathea*. Both species were recorded from *C. lunulata*, but they were also collected from other *Cyathea* species so that they do not appear to be confined to any particular species.

Unlike the other two species, *T. oblanceolata* was never found on tree ferns. It grew among mosses and filmy ferns on the trunks of angiospermous trees such as *Metrosideros* and *Weinmannia* (see Fig. 1b in Braithwaite 1975) or out of organic accumulations beneath epiphytic ferns such as *Asplenium nidus. T. oblanceolata* has also been recorded on decayed wood on the forest floor (Milne 272K). Non-tree-fern substrates have been reported for *Tmesipteris* species elsewhere; notably *T. vieillardii* of New Caledonia (Sahni 1925), *T. tannensis* (Spreng.) Bernh. s strict. in New Zealand (Chinnock 1976) and *T. oblanceolata* from the Solomon Islands (Braithwaite 1973).

It is becoming increasingly clear that speciation within the genus has been accompanied by some ecological differentiation, although the extent to which the latter may be useful in delimiting species or determining species relationships is at present not clear.

KEY TO THE SPECIES

Aerial shoots 6-16cm long, leaves ovate-oblong or narrowly oblong to elliptic.

Leaves ovate-oblong with obtuse apices, I/b ratio <3, distichously arranged beyond the sporophylls.

Leaves narrowly oblong to elliptic with acute apices, 1/b ratio > 3, spirally arranged beyond the sporophylls.

Aerial shoots 15-38cm, leaves narrowly rectangular to narrowly obovate with truncate or rounded apices.

T. vanuatensis

T. oblongifolia

T. oblanceolata

Tmesipteris oblongifolia A. Braith. sp. nov.

Planta epiphytica in truncis filicum arborum. Surculis aerius simplex, pendulus, (6-)8-14(-16)cm longus, per unum crescentem maturescens, folio magno terminati. Folia infra sporophylla spiraliter disposita, supra sporophylla disticha disposita, subcoriacea, (7-)9-13(-15)mm longa, (3-)3.5-4.5(-5)mm lata, ovato-oblonga, apicibus rotundatis obtusis mucronatis. Sporophylla spiraliter disposita, medianum caulis foliosi occupantes, longitudine folia aequantia. Synangium 2-4mm longum, sporangiis lobiis aequalibus. Sporae bilaterales, monoletae, concavo-convexae, (51-)57-62(-73)µm longae, (18-)21-22(-25)µm latae. Chromosomatum numerus gametophyticae 104.

Holotype: Tanna, W ridge of Mt. Toukosmeru (19°33'S 169°21'E), 500m, epiphyte on *Cyathea* trunk (same sp. as RSNH 2184), 28 Jul. 1971, A.F. Braithwaite RSNH 2204 (K).

Plant epiphytic on trunks of tree ferns. Aerial shoots simple, pendulous, (6-)8-14(-16)cm long, maturing in one growing season and terminating in large leaf-like appendage. Leaves spirally arranged below the sporophylls, distichously arranged in portion of leafy shoot distal to the sporophylls, 3-4 per cm stem, subcoriaceous, (7-)9-13(-15)mm long, (3-)3,5-4.5(-5)mm wide, ovate-oblong with rounded obtuse mucronate apex. Sporophylls pirally arranged, 5 per cm stem, occupying the middle of the leafy part of the shoot or throughout the upper two thirds, \pm equal in length or slightly shorter than the leaves. Synangia 2-4mm long, 1-1.5mm high, with lobes of sporangia approximately equal, \pm globular. Spores bilateral, monolete, concavo-convex, (51-)57-62(-73)µm long, (18-)21-22(-25)µm broad. Chromosome number n = 104.

T. oblongifolia is closely allied to *T. lanceolata* from New Caledonia and New Zealand. The two species are similar in size and share a distichous arrangement of leaves in that portion of the leafy shoot distal to the sporophylls. The two species also possess the same pith type in the stem and chromosome number. Dangeard (1890-91) describes and illustrates the pith cells of *T. lanceolata* as "fibres medullaires" and unpublished chromosome counts by the author show it to be a tetraploid. *T. oblongifolia* can however be distinguished by its thinner texture, ovate-oblong leaves with an obtuse apex and by the position of the sporophylls, which are found in the middle or upper two thirds of the leafy shoot and never only at the base or in the lower half as in *T. lanceolata*.

Distribution: Philippines, Vanuatu and the Marquesas.

Specimens examined:

VANUATU. Aneityum, ridge leading to Woptiabo, c.5km ENE of Anelcauhat (20°13'S 169°49'E), 487m, epiphytic on *Cyathea lunulata* in ridge side forest, 23 Jul, 1971, Braithwaite RSNH 2146 (K). Tanna, W ridge of Mt. Toukosmeru (19°33'S 169°21'E), 644m, epiphytic on base of large *Cyathea lunulata*, 28 Jul, 1971, Braithwaite RSNH 2211 (K).

MARQUESAS. Feani, vieux sentrer 'Atuona à Hanamenu, haute vallée côte Hanamenu, 850m, brousse fougeres arborescentes et *Freycinetia*, épiphyte sur les bases de fougeres arborescentes, assay rare, 5 Mar. 1975, Schafer & Oline 5272 (K); Chemin d'Omoa à Hanavave, crête principale, mont Moratina (Mt. Bóise de la carte), 670m, brousse assay humide avec *Cyathea, Crossostylis,* sur bases de *Cyathea,* assay rare, 18 Sept. 1975, Schafer 5758 (K); Feani, montagnes entre la haute vallée de Hanamenu et la crête de Temetiu, 900m, petit haut vallée à foret très humide: *Crossostylis, Cyathea, Pandanaceae, Weinmannia, Myrsine,* sur troncs de *Cyathea,* assay rare, 23 Oct. 1975, Schafer 5914 (K); Nukuhiva, Quayle 1305 (K). PHILIPPINES. Mindanao, Davao Dist: Mt. Apo 6000ft, epiphyte always on trunks of tree

PHILIPPINES. Mindanao, Davao Dist: Mt. Apo 6000ft, epiphyte always on trunks of tree ferns, Oct. 1904, Copeland 1433 (K); Mt. Apo, May 1909, Elmer 10600 (BM, K); Mt. Apo, 9000ft, Feb. 1929, Hachisaka s.n. (BM); Mt. Apo, 1800m, 1932, Copeland 203 (BM).

Tmesipteris vanuatensis A. Braith. sp. nov.

Planta epiphytica in truncis filicum arborum. Surculis aerius simplex, pendulus, (6-)8-15(-16)cm longus, foliis et sporophyllis spiraliter dispositis et folio magno terminatis. Folia subcoriacea, 8-14mm longa, 2.5-3.5mm lata, anguste oblonga vel anguste elliptica, apicibus acutis et mucrone setaceo 0.5-1.0mm longo. Sporophylla medianum caulis foliosi occupantes, longitudine folia subaequantia. Synangium parvum, 3-3.5mm longum, globosum, sporangiis lobis aequantibus. Sporae monoletae, concavoconvexae, (50-)59-62(-67)µm longae, (18-)21(-25)µm latae. Chromosomatum numerus gametophyticae 104.

Holotype. Espiritu Santo, crest of NW ridge of Mt.Tabwemasana, c. 1600m, epiphyte on *Cyathea* sp. in ridge top *Metrosideros-Weinmannia* forest, 2 Sept. 1971, A.F. Braithwaite RSNH 2382 (K).

Plant epiphytic on the trunks of tree ferns. Aerial shoots simple, pendulous, (6-)8-15(-16)cm long, maturing in one growing season, with leaves and sporophylls spirally arranged and terminating in a large leaf-like appendage. Leaves subcoriaceous, 8-14mm long, 2.5-3.5mm, narrowly oblong or ovate-oblong to narrowly elliptical with acute apices and bristle-like mucro 0.5-1.0mm long. Sporophylls occupying the middle or throughout leafy part of shoot, equal to or slightly shorter than the leaves. Synangia 3-3.5mm long, globose, persistent, with two equal sporangial lobes. Spores monolete, concavo-convex, $(50-)59-62(-67)\mu m long$, $(18-)21(-25)\mu m broad$. Chromosome number n = 104.

T. vanuatensis can be distinguished from *T. oblongifolia* by its spirally arranged narrowly oblong to almost elliptical leaves with a larger length/breadth ratio and generally acute apices. The leaves are also more widely spaced and arise from the stem at a more acute angle giving the plant a generally more lax and slender appearance than *T. oblongifolia* (Fig. 4).

Known only from Mt. Tabwemasana, Espiritu Santo.

Other specimen examined:

Espiritu Santo. Camp site no. 4, Nokovula Village, 23k SSW of Malau, Big Bay (15°20'S 166°44'E), disturbed forest area below village, c. 900m, epiphyte on *Cyathea lunulata*, 1 Sept. 1971, Braithwaite RSNH 2354 (K).

Tmesipteris oblanceolata Copel., Philip. J. Sci. 60: 99 (1936); A. Braith., Brit. Fern Gaz. 10: 296 (1973).

Type: Solomon Islands, Guadalcanal, Tutuve Mt, 1700m, Kajewski 2632 (A).

Plants epiphytic on angiospermous tree trunks or growing on moss covered decaying wood on forest floor. Aerial shoots simple, pendulous or occasionally sub-erect, (15-)20-30(-38)cm long, maturing in a single growing season and terminated by a small leaf-like appendage; transition region (4-)5-10(-11)cm long; leaves and sporophylls spirally arranged and often tending to decrease in size towards the apex. Leaves (10-)11-14(-16)mm long, 2.5-3.5mm broad, coriaceous to subcoriaceous, (4-)5(-6) per cm stem, narrowly oblong or rectangular but narrowing towards the base to narrowly obovate, \pm falcate, apex truncate and sometimes bilobed to rounded, mucronate; mucro stiff, 1-2mm long. Sporophylls developed in mid region or throughout upper two thirds of leafy shoot, equal in length to leaves; synangia 3-4mm long, 1.5-2mm high, persistent, bilocular, sporangial lobes \pm equal. Spores monolete, concavo-convex, (73-)81-83(-94)µm long, (25-)31(-36)µm broad. Chromosome number n = 208.

TMESIPTERIS IN VANUATU

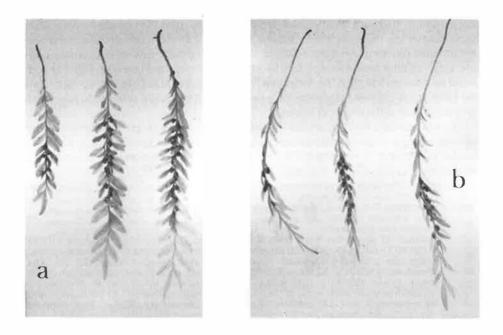


FIGURE 4. a) *T. oblongifolia* RSNH 2204. b) *T. vanuatensis* RSNH 2382. Specimens preserved in alcohol. X 1/2.

T. oblanceolata in Vanuatu is rather variable with respect to length of the aerial shoot and in size and shape of the leaves. The plants from Espiritu Santo with aerial shoots up to 26cm long bearing short narrowly obovate leaves with rounded apices, are virtually indistinguishable from *T. oblanceolata* Copel. from the Solomon Islands, except that medullary xylem found in specimens from the Solomon Islands (Braithwaite 1973) was not found in the single specimen available for sectioning from Espiritu Santo. The pith is otherwise of a similar parenchymatous type. The more extensive collections from Aneityum have aerial shoots up to 38cm long, some possessing narrow slightly obovate leaves with rounded apices. Similar variation is evident in material attributed here to *T. oblanceolata* from New Caledonia and Samoa.

The plants from Aneityum, with leaves with markedly truncate sometimes almost bilobed apices, are very similar to the Australian species *T. truncata* (R.Br.) Desv. They also share the same chromosome number. Barber (1957) reported a chromosome number of n = 201-211 for *T. truncata* from several different localities in New South Wales and n = 208 has been found here in material from Aneityum. There are however some ecological and anatomical differences. The plants from Aneityum are either epiphytic on angiospermous trees or terrestrial on decayed wood while *T. truncata* from Australia is generally, though not exclusively, epiphytic on tree ferns. There are two specimens from Australia at Kew collected from non-tree-fern substrates; one with typical truncate leaves labelled "Macquarie Harbour, humid rocky banks B mountains in shaded woods, 1825, Cunningham 92"; and the other with more oblanceolate leaves labelled "Head of Clyde River, 25 miles SSW of Howra, 2000ft, on mossy ledge of sandstone cliff, 2May 1937, Rodway 2369". The anatomical difference concerns the pith type in the stem. Dangeard (1890-91) reported a sclerenchymatous

pith type in *T. truncata* from Australia which differs from the parenchymatous pith found here in the material from Vanuatu. However Dangeard (in contrast to the often very detailed drawings from the stems of the other species he examined) shows only a very small outline tissue sketch for the stem of *T. truncata* (Plate XIV, Fig. 11) and it would be desirable to have the detail confirmed for material both from tree-fern trunks and from non-tree-fern substrates. It is possible that variation in the pith type may be correlated with differences in ecology.

T. oblanceolata and *T. truncata* are clearly very closely related and they probably represent forms of the same species. However on present evidence it is difficult to assess the extent or taxonomic significance of their ecological and anatomical differences. Future studies may well confirm their conspecificity but it is considered preferable for the time being to segregate the Pacific material under *T. oblanceolata*.

Distribution: New Caledonia, Vanuatu, Solomon Islands, Fiji, Samoa.

Specimens examined:

VANUATU. Aneityum: ridge crest N of Woptiabo, S end of Nithuon Nelvau (20°13'S 169°49'E), 640m, ridge top forest with *Metrosideros*, epiphyticon large leaning tree on ridge top growing underneath a large plant of *Asplenium nidus*, 23 Jul. 1971, Braithwaite RSNH 2152 (K); c. 5km NE by N of Anelcauhaut, on crest of ridgerunning S from Inrero (20°11'S 169°47'E), 745m, epiphytic on trunk of *Metrosideros*, occasionally on forest floor, 21 Jul. 1971, Braithwaite RSNH 2112 (K); high grounds, decayed trees, Nov. 1853, Milne 272 (K); 1854, Seeman s.n. (BM); crěte S de l'Inrero, alt. 750m, epiphyte au bas de troncs, fronde portee ± horizontalement, 23 Jul. 1971, Raynal RSNH 16147 (K). Espiritu Santo: northern ridge of Mt. Tabwemasana (15°22'S 166°45'E), 1650m, low forest on ridge crest, *Weinmannia* dominant, 4 Sept. 1971 Raynal RSNH 16386 (P).

SOLOMON ISLANDS. Guadalcanal, Mt. Popomanaseu, halfway between upper camp and Vunuvelakama, c. 5000ft, growing erect in moss around base of trees in ridge top moss forest, 3 Nov. 1965, Braithwaite RSS 4782 (K).

NEW CALEDONIA. Mt. Koghi, kauri ft. 1000ft, on prostrate decaying trunk covered with liverworts, 13 Jun. 1914, Compton 764 (BM).

LORD HOWE ISLAND. Epiphyte on the top of Mt. Gower in mist forest, 2600ft, Aug. 1965, Game 65/1/SN (K).

SAMOA. May 1876, Whitmee s.n. (K).

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REFERENCES

BARBER, H.N. 1957. Polyploidy in the Psilotales. Proc. Lin. Soc. N.S. W. 82: 201-208.

BERNHARDI, J.J. 1801. Tentamen alterum filices in genera redigendi. Schrad. J. Bot. 1800(2): 131, t.2, f.5.

BRAITHWAITE, A.F. 1973. Tmesipteris in the Solomon Islands. Brit. Fern Gaz. 10: 293-303.

BRAITHWAITE, A.F. 1975. The phytogeographical relationships and origin of the New Hebrides fern flora. *Phil. Trans. R. Soc. Lond. B.* 272: 293-313.

CHINNOCK, R.J. 1976. The identification, typification and origin of *Tmesipteris tannensis* (Psilotaceae). *Taxon.* 25: 115-121.

DANGEARD, P.A. 1890-91. Memoire sur la morphologie & l'anatomie des *Tmesipteris. Le Botaniste, Series II:* 163-222.

LOVIS, J.D. 1977. Evolutionary patterns and processes in ferns. Adv. Bot. Res. 4: 229-419.

MANTON, I. 1950. Problems of cytology and evolution in the Pteridophyta. Cambridge University Press.

SAHNI, B. 1925. On *Tmesipteris vieillardii* Dangeard, an erect terrestrial species from New Caledonia. *Phil. Trans Roy. Soc. B. 213:* 143-170.

SPRENGEL, K. 1800. Bemerkungen uber einige kryptogamische Pflanzen. Schrad. J. Bot. 1799(2): 267.

SYKES, M.G. 1908. The anatomy and morphology of Tmesipteris. Ann. Bot. 22: 63-89.

EFFECTS OF SALINITY ON GAMETOPHYTE GROWTH OF ACROSTICHUM AUREUM AND A. DANAEIFOLIUM

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ABSTRACT

Spore germination and gametophyte growth under salinity regimes varying from 0.0 to 3.0% NaCl was studied to determine the stress tolerance of the gametophyte generation. Responses of both New World species of *Acrostichum* are similar to those of other mangrove species which have been studied. *A. aureum* has slightly greater tolerance to increased salinity than *A. danaeifolium*. Growth responses of *A. aureum* suggest it can be classified as a true halophyte, whereas those of *A. danaeifolium* suggest it is a semi-halophyte. The response of the gametophyte generation of these species to salinity parallels the natural habitats of the sporophyte generation.

INTRODUCTION

Halophytes are notably rare in pteridophytes. The most well known example is the mangrove fern genus *Acrostichum*. There are three species circumscribed in this genus, each with different apparent tolerance to salinity. The observed habitat variation of the species forms a continuum from fresh water to inundation by tides and sea water. The most widely distributed species is *A. aureum* L., circumtropical in distribution and frequently forming large colonies in mangrove swamps, salt- and brackish-marshes, and low hammocks near sea water (Holttum 1955; Small 1938; Walsh 1974). The remaining two species are much more restricted in distribution. In tropical Asia and Australia, *A. speciosum* Willd. occurs in mangroves (Walsh 1974) frequently inundated by tides and has a greater tolerance for sea water than *A. aureum* (Holttum 1955). *Acrostichum danaeifolium* Langsd. & Fisch. is distributed in the New World tropics and subtropics in fresh or brackish water swamps, lakes, and ditches and along canal margins (Adams and Tomlinson 1979). This species is frequently found inland from coastal regions, sometimes associated with pines and palms or other glycophytes.

One of the primary factors determining the growth and distribution of plants in salt marsh habitats is the level of soil salinity (Jefferies *et al.* 1979). Other factors include both intraspecific and interspecific competition, especially when species may be only facultative halophytes. Barbour (1970) has questioned whether all halophytes are just facultative halophytes and has suggested that the ability to reproduce under "halophytic" conditions should be the ultimate criterion of salt tolerance. In halophytic pteridophytes, for sexual reproduction to be successful the gametophytic and sporophytic generation must succeed. Therefore, both generations should exhibit parallel tolerances to stress under soil salinity, assuming that the soil salinity conditions of the gametophytic and sporophytic habitats parallel one another. However, Ungar (1978) has reported that surface soils may have salinities from two to 100 times that of subsoils. Thus, the gametophytic stage may be critical if a species is to successfully inhabit a saline environment.

In the New World, collections have been made of both *Acrostichum* species. Gametophytes originating from spores of these plants as well as from the fresh water aquatic, *Ceratopteris thalictroides* (L.) Tod., have been grown under a variety of salinity conditions to test the hypothesis that tolerance to salinity by the gametophytic generation will parallel the habitat conditions in which the sporophytes occur.

MATERIALS AND METHODS

Spores utilized in this study were collected from the following locations: *A. aureum:* culture 190, Jamaica, Westmoreland Parish, 0.25 mile east of Negril on road to Savana la Mar. Plants occur densely in a large population in a lowland coastal swamp which is periodically inundated by tides; culture 193, Panama (Canal Zone), very large population of over 3000 individuals in mangrove swamp about 0.2 mile from road to Colon on road to Coco Solo; culture 150, Florida, Dade Co., 30.5 miles southwest of entrance of Everglades National Park, at road to Westlake, growing in Rhizophoraswamp; *A. danaeifolium:* culture 204, Florida, open marsh with about 40 individuals, Collier Co., 0.7 mile south of state route 92 on U.S. Highway 41, about 3.5 miles inland from coast; *Ceratopteris thalictroides:* culture 174, Guyana, two miles east of Georgetown on main coastal public road, in wet marsh with *Nymphaea* next to gasoline station; culture Hawaii, taro patches, Hawaiian Islands, inundated weekly with fresh water. Adscript numbers and letters designate spore progenies from different individual sporophytes collected at each location.

Spores were sown and gametophytes grown on inorganic nutrient medium solidified with 1% agar (see Klekowski 1969, for composition) in 100 x 15mm petri dishes under continuous illumination from fluorescent and incandescent lamps at about 23°C. Nutrient media were supplemented with NaCl prior to the addition of agar, yielding concentrations of 0.5 to 3.0%. NaCl concentration was ascertained by conductivity measurements (from 0.8mmhos/cm at 25°C in control to 44mmhos/cm in 3.0% NaCl.) Conductivity was measured with a Radiometer CDM2 conductivity meter. Data for 190-D/193-B (Table 4) represent gametophytes of both progenies transferred on to single petri dishes.

TABLE 1

Percent spore germination in *Acrostichum* (15 days following sowing) and *Ceratopteris* (12 days following sowing) at salinity regimes varying from 0.0% to 3.0% NaCl. (Sample size = 100).

	A. aureum			A. danaeifolium		C. thalictroides		
NaCI (%)	190-D	193-B	193-K	204-2	204-8	174-A	Hawaii- A	Hawaii- B
0.0 0.5 1.0 1.25 1.5 1.75 2.0 2.25 2.5 2.75	69(100*) 55(80) 51(74) 19(28) 11(16) 3(4) 1(1.4) 2(3) 0 0	66(96) 69(100) 60(87) 44(64) 43(62) 19(28) 8(12) 2(3) 1(1.4) 0	76(100) 61(80) 47(62) 54(71) 56(74) 17(22) 17(22) 5(7) 4(5) 1(1.3)	99 99 92 72 24 28 18 3 0	89(100) 67(75) 72(81) 54(61) 21(24) 8(9) 1(1) 0 0	86(96) 90(100) 85(94) 84(93) 19(21) 11(12) 2(2.2) 0 0 0	95(100) 50(52) 30(32) 0 0 0 0 0 0 0 0 0 0	90(100) 20(22) 0 0 0 0 0 0 0 0 0 0
3.0	0	1(1.4)	1(1.3)	õ	0	õ	ŏ	0

Species and Culture Number

*Values given in () are adjusted to 100% to adjust for variation in intersporophytic spore viability.

RESULTS

Spore germination in all three species initially occurred five to six days following sowing and was highest in the control and the lowest NaCl concentration. There was a differential response of spore progenies from individual sporophytes of each species to each of the culture regimes. In *Acrostichum*, germination rates differ slightly at the higher NaCl concentrations (Table 1). Spore progenies of both species exhibited consistent but decreasing levels of germination up to 1.25% NaCl. At salinities above 1.25 and 1.5%, respectively, in *A. danaeifolium* and *A. aureum*, there are significant decreases in germination. At NaCl concentrations between 2.25 and 3.0%, spore progenies of *A. aureum* exhibited low levels of germination, whereas in the other species germination did not occur. There are indications of bimodality (stress pulses) in three of the five dose response curves (193-K, 204-2, 204-8 at salinities of 1.25-1.5%, 1.75%, and 1.0% respectively). If this pattern is real it could result from the operation of two physiological processes whose reaction optima occur at different levels of salinity.

In *Ceratopteris*, germination was greatly inhibited in Hawaiian spore progenies at all NaCl concentrations and did not occur above 1.0%. The Guyana sample is of potential interest, however, as germination responses were similar to those of *A*. *danaeifolium*.

The fraction of gametophytes to attain two-dimensional growth within 15 days of sowing was determined in order to evaluate the effect of salinity on developmental rates (Table 2). There is no appreciable difference in the two species of *Acrostichum* at the lower salinities with almost all gametophytes reaching the two-dimensional stage. The reaction curves for developmental rate versus salinity are markedly bimodal for the spore progenies of *A. aureum* tested. Developmental rates decreased synchronously for all four samples from both species between 1.0 and 1.25% NaCl. The second range of salinities (1.25 to 1.75%) which resulted in rapid gametophyte development for *A. aureum* produced reduced development in culture 204-2 and severely inhibited development at 1.75% NaCl in culture 204-8 of *A. danaeifolium*. The phenomenon responsible for the higher developmental rate in higher salinities for *A. aureum* appears to extend this species' maximum salinity tolerance beyond that of *A. danaeifolium*. However, it was not determined what proportion of 15 day old one-dimensional gametophytes later attained the two-dimensional stage under hypersalinity conditions.

TABLE 2

Mean percent attainment of two-dimensional morphology in gametophytes of *Acrostichum* grown under varying salinity regimes 15 days following sowing.

Species and Culture Number

	A. aureum		A. danaeifolium		
NaCI (%)	193-B	193-К	204-2	204-8	
0.0	100	97	100	100	
0.5	100	96	100	100	
1.0	100	97	97	98	
1.25	90	84	85	93	
1.5	97	90	80	87	
1.75	97	86	83	14	
2.0	75	54	0	0	
2.25	0	0	0	0	

Sample size variable and dependent upon number of available gametophytes: 30-45 in 0.0% to 1.75%; (1)10-29 in 2.00%; 11-14 in 2.25%; less than 5 in remaining regimes.

TABLE 3

Maximum and (mean) gametophyte size (in sq. mm) attained in cultures of Acrostichum at salinity regimes varying from 0.0% to 2.25%. Sample size = 10.

	A. aureum			A. danaeifolium		
NaCI (%)	190-D*	193-B*	193-K**	204-2***	204-8***	
0.0 0.5 1.0 1.25	2,8(1.4) 1.9(1.0) 2.0(0.9) 0.4(0.3)	10.9(3.8) 5.9(2.8) 4.0(1.8) 2.5(1.2)	4.1(2.4) 13.9(2.0) 4.5(2.0) 1.8(0.8)	11.8(5.1) 6.0(3.1) 4.0(2.1) 2.4(1.2)	6.3(4.3) 8.5(3.2) 2.8(1.2) 1.9(0.9)	
1.5 1,75 2.0 2.25	1.1(0.6)	1.2(0.7) 0.6(0.4) 0.1(0.1) 0.2(0.1)	0,4(0.2) 0,4(0,4) 0,2(0,1) 0,09(0,07)	0.7(0.4)	0.8(0.4) 0.09(0.08) 	

Species and Culture Number

sampled 19 days following sowing.
sampled 18 days following sowing.

TABLE 4

Mean percent non-chlorotic tissue in gametophytes of A. aureum grown 70 days in nutrient control medium and then transferred to variable salinity regimes.

	150-B: Days from transfer			190-D/193-B: Days from transfer		
NaCI (%)	3	14	21	4	7	15
0.0	99	91	91	100	100	100
1.0	100	99	99	100	100	100
1.25	94	86	94	100	99	92
1.75	91	80	83	97	91	69
2.0	71	74	75	97	90	72
2.25	73	62	58	87	74	69
2.5	40	27	0	76	81	39
2.75	45	31	0	38	25	13
3.0	40	30	0	32	23	0

Maximum and mean gametophyte area was measured 18 to 21 days following sowing to evaluate the effect of salinity on growth rates (Table 3). The growth rate of A. danaeifolium appears to be greatest in the 0% NaCl controls and then decreases linearly with increasing levels of salinity. Low NaCl concentrations (0.5 and 1.0%) reduced growth rates of A. danaeifolium to a greater extent than those of A. aureum. For example, reduction of mean gametophyte size (compared to 0.0% NaCl) of A. aureum progenies varies from 16.7 to 52.7%, whereas reduction in size of A. danaeifolium progenies is 58.9 to 72.1%.

Salt stress and development of chlorotic tissue was measured in gametophytes of A. aureum (Table 4). These gametophytes were grown to maturity for 70 days on control media and then transferred to various salinity regimes. In culture 150B, below 2.0% NaCl there is no apparent difference over time but only with salinity concentration. The effect appears to be initial and then persistent. There is some indication of a stress pulse at 1.25 to 2.0% NaCl with gametophytic tissue recovery after 21 days. Above 2.25%, the salinity effects are progressive over time. In culture 190/193, effects appear to be absent below 1.25% NaCl. At levels of 1.25% and above, there is a progressive increase in chlorotic gametophytic tissue with both time and NaCl concentration.

DISCUSSION

The tolerance to salinity of gametophytes of both species of *Acrostichum* appears to be significantly greater than two of the three progenies of the glycophyte *Ceratopteris thalictroides.* Warne and Hickok (pers. comm.) have also studied NaCl effects on spore progenies of *C. thalictroides.* They analyzed spore germination and gametophyte survival of progenies from ten sporophytes from various parts of the World. These progenies exhibit a wide range of tolerance to NaCl. At 0.8% NaCl, spore germination in six of the ten progenies was reduced by 4.0 to 15.9 (mean = 7.53%) compared to the controls (0.0% NaCl). In the remaining four progenies, germination was reduced 48.8 to 97.3 (mean = 77.7)%. Twenty-one days following sowing, gametophytes, whereas gametophytes of the latter group failed to survive. These results indicate that some populations of *Ceratopteris* may have salinity tolerance approaching that exhibited by *A. danaeifolium.* Recently, Petersen (1985) reported that spores of *A. danaeifolium* were capable of germinating in up to 2.5% NaCl whereas spores of the glycophytic species *Osmunda* spp. and *Onoclea sensibilis* ceased germination at 0.6% NaCl.

In Acrostichum, there is a wide range of tolerance to salinity, although A. aureum consistently shows a slightly greater tolerance at slightly higher NaCl levels. In spore germination, two of the three progeny samples of A. aureum show 50% germination at NaCl concentrations of 1.5 and 1.75%. In A. danaeifolium, 50% germination occurs between 1.25 and 1.5%. Similarly, the critical salinity level for attainment of two-dimensional morphology is 1.75 to 2.0% NaCl in A. aureum and 1.5 to 1.75% in A. danaeifolium. In addition, some progenies of mature gametophytes of A. aureum can tolerate prolonged exposure to salinities of 2.0 to 2.25%. These results suggest that the critical soil salinity which will limit gametophyte survival of A. danaeifolium will be about 1.5% and of some plants of A. aureum, about 1.75 to 2.0%. However, due to the extremely large number of spores produced by individual sporophytes of these species, even very low percentages of survival at higher salinities could result in millions of successful gametophytes.

Germination and growth in *Acrostichum* parallels that of other mangrove species which have been studied and have optimal growth between 0.6 and 1.5% NaCl (Connor 1969; Pannier 1959; Patil 1964).

The spore germination and gametophyte growth patterns of *A. danaeifolium* are similar to those described for semi-halophytes by Waisel (1972). Semi-halophytes show a slow decrease in growth at initial stages of salinity increase, followed by a steady decrease with increasing salinity. On the other hand, in *A. aureum*, the stress-pulse growth phases followed by a steady decrease in growth with increasing salinities is similar to the pattern of true halophytes. These studies indicate, therefore, that species of *Acrostichum* can be considered to be semi-halophytes or halophytes and that the salinity tolerance by the gametophyte generation is an integral part of their life-history.

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REFERENCES

ADAMS, D.C. & TOMLINSON, P.B. 1979. *Acrostichum* in Florida. *Amer. Fern J.* 69: 42-46. BARBOUR, M.G. 1970. Is any angiosperm an obligate halophyte? *Amer. Midl. Nat.* 84: 105-120. CONNOR, D.J. 1969. Growth of grey mangrove (*Avicennia marina*) in nutrient culture. *Biotropica* 1: 36-40. HOLTTUM, R.E. 1955. *Flora of Malaya*, Vol. II, *Ferns of Malaya*. Gov't. Printing Office, Singapore. JEFFERIES, R.L., DAVY, A.J. & RUDMIK, T. 1979. The growth strategies of coastal halophytes. In

R.L. Jefferies & A.J. Davy (eds.) *Ecological Processes in Coastal Environments*. Blackwell Scientific Publ., Oxford, 243-268.

KLEKOWSKI, E.J. JR. 1969. Reproductive biology of the Pteridophyta. III. A study of the Blechnaceae. Bot. J. Linn. Soc. 62: 361-377.

PANNIER, P. 1959. El efecto de distintas concentrationes sotenas sobre el desarrolo de *Rhizophora mangle* L. *Acta cient. Venez.* 10: 68-78.

- PATIL, R.P. 1964. Cultivation of mangrove seedlings in pots at Allahabad. U. P. Sci. Cult. 30: 43-44.
- PETERSEN, R.L. 1985. Use of fern spores and gametophytes in toxicity assessments. *Proc. Roy. Acad. Edin.* 86B: 453.
- SMALL, J.K. 1938. Ferns of the Southeastern States. Facsimile Ed. (1964), Hafner Publ. Co., New York.

UNGAR, I.A. 1978. Halophyte seed germination. Bot. Rev. 44: 233-264.

WAISEL, Y. 1972. The Biology of Halophytes. Academic Press, New York and London.

WALSH, G.E. 1974. Mangroves: A review. In R.J. Reimold & W.H. Queen (eds.), Ecology of Halophytes, Academic Press, New York and London.

THE ECOLOGY OF PTERIDOPHYTES IN THE MWANIHANA FOREST RESERVE, TANZANIA

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ABSTRACT

A collection of pteridophytes made in the Mwanihana Forest Reserve, Tanzania is described and related to the ecology of the forest. In all 78 species were collected, demonstrating the richness of the area in comparison with the total number of 500 species estimated for the whole of tropical Africa.

INTRODUCTION

The Mwanihana Forest Reserve (7°50'S 36°55'E) is located on the steep east facing escarpment of the Uzungwa Mts, overlooking the Kilombero Valley and Selous Game Reserve. These mountains are composed of Pre-Cambrian crystalline gneiss, and have probably been in existence since the Cretaceous. The rainfall is relatively high for Tanzania, being estimated to be 2,000-2,500mm a year with one wet season receiving greater than 100mm of rain a month between November and May on average, which has a peak in March and April (DHV, 1982). The dry season, between July and October, receives less than 50mm of monthly rain on average, with months of no rain common.

Despite the marked dry season the escarpment is covered by continuous closed moist forest from an altitude of 450m to 1,800m, and in the past extended into the Kilombero flood plain where it has now been replaced by sugar plantation. These forests are part of the Eastern Arc group (Lovett, in press) which are notable for the high degree of endemism they contain, and it is now hoped that the Mwanihana Forest Reserve will become a National Park in order to protect many rare plants and animals.

During the course of surveying the Reserve as part of the 1984 Uzungwa expedition supported by the National Geographic Society and World Wildlife Fund, a substantial collection of plants was made. This collection included some 78 species of pteridophytes from the Mwanihana and nearby forest reserves which are presented here divided into various ecological categories, and as a check-list. The collections made were far from exhaustive, and there are probably something in the region of 100 species of pteridophyte in the area. This is high for Tropical Africa, which is estimated to contain only 500 species altogether (Parris, 1985). Thus the small area of the Mwanihana Forest Reserve may contain as much as 20% of the total Tropical African pteriodophyte flora.

Despite the incompleteness of the collections and the brief nature of the ecological observations it was thought necessary to publish them in order to draw attention to the high species richness of the Mwanihana Forest Reserve in the hope that further work may be stimulated.

ECOLOGY

The vegetation of Africa has been divided into a number of phytochoria based on plant species distribution and physiognomic types which are described by White (1983). Although the broad scope of this work renders it inaccurate at the small scale, it is useful as a general pattern within which to designate arbitrary ecological boundaries. Five types of forest can be recognised in the Mwanihana Forest Reserve according to this system, and they are briefly described below for the forest reserve using White's terminology. Ten examples of tree species which occur in each forest type in the reserve are also given. Within each forest type the pteridophyte habitat is divided into terrestrial, lithophytic, and epiphytic. Additional notes on the habitat follow the species name in parenthesis when necessary. All pteridophytes were growing in forest shade unless noted. These notes are self explanatory except for the following: an exposed habitat is one in partial shade; a stream habitat is on rocks in streams and river beds flowing through the forest. A "C" in parenthesis indicates that the species was collected at Chita (8° 30' S 35° 55' E), a locality to the south of the reserve, but also in the Uzungwa mountains. All other species were collected in the reserve.

Zanzibar-Inhambane Lowland Forest

Altitudinal range 450-750m, canopy height 25-30m with emergents to 40m. Large trees include: Afrosersalisia cerasifera; Albizia adianthifolia; Aningeria pseudoracemosa; Chlorophora excelsa; Dialium holtzii; Erythrophleum suaveolens; Funtumia africana; Lettowianthus stellatus; Newtonia paucijuga; Terminalia sambesica. Terrestrial: Bolbitis acrostichoides, (C)*; Christella hispidula, (C); Microlepia speluncae; Pellaea doniana, (exposed).

Lithophytic: *Adiantum capillus-veneris*, (exposed); *Bolbitis* sp. aff. *acrostichoides*, (C); *Nephrolepis biserrata*, (C).

Zanzibar-Inhambane Intermediate Forest

Altitudinal range 750-1,200m, canopy height 25-30m with emergents to 40m. Large trees include; Anisophylla obtusifolia; Cassia angolensis; Cephalosphaera usambarensis; Ochna holstii; Octoknema orientalis; Sibangea pleioneura; Syzygium guineense; Tabernaemontana holstii; Trichilia dregeana; Uapaca pallidosa. Terrestrial: Amphineuron opulentum; Asplenium blastophorum; A. obscurum, (C); Bolbitis auriculata; B. gemmifera; Christella gueintziana, (C) (swamp); Lonchitis occidentalis; Pteris sp. aff. mildbraedii; P. sp. aff. prolifera; P. quadriaurita subsp. friesii; Tectaria gemmifera.

Lithophytic: Antrophyum mannianum, (C) (stream); Asplenium formosum, (stream); A. inaequilaterale; A. unilaterale; Bolbitis sp. aff. acrostichoides; Christella sp. aff. gueintziana, (stream); Elaphoglossum spathulatum, (stream); Menisorus pauciflorus, (stream); Sphaerostephanos arbuscula subsp. africanus, (stream). Epiphytic: Lycopodium phlegmaria, (canopy).

Epiphytic: Lycopodium phiegmaria, (can

Afromontane Rain-Forest

Altitudinal range 1,200-1,700m, canopy height 25-30m, with emergents to 35m. Large trees include: Allanblackia stuhlmannii; Beilschmiedia kweo; Cassipourea gummiflua; Cleistanthus polystachyus; Chrysophyllum gorungosanum; Myrianthus holstii; Newtonia buchananii; Ocotea kenyensis; Parinari excelsa; Strombosia scheffleri.

Terrestrial: Asplenium christii; A. sp. aff. gilpinae; A. hypomelas; A. monanthes; A. ?volkensii; Athyrium scandicinum; Blechnum attenuatum; B. ivohibense; Blotiella natalensis; Ctenitis languinosa; Cyathea humilis, (ravine); Cyathea mossambicensis; Didymochlaena trunculata; Diplazium nemorale; D. pseudoporrectum; Dryopteris inaequalis; D. kilemensis; Histiopteris incisa; Microlepia fadenii; Polystichum zambesiacum; Pneumatopteris usambarensis; Pteris buchananii; P. preussii; P. pteridioides; Tectaria gemmifera; Trichomanes cupressiodes; T. giganteum.

Lithophytic: Asplenium boltonii, (damp, exposed); Elaphoglossum phanerophlebium; Hymenophyllum splendidum; Pellaea angulosa; Trichomanes borbonicum.

Epiphytic: Asplenium aethiopicum; A. dregeanum; A. rutifolium; Belvisia spicata; Elaphoglossum acrostichoides; Hymenophyllum polyanthos var. kuhnii; H. sibthorpioides; H. splendidum; Lomariopsis warneckei; Lycopodium verticillatum; Trichomanes giganteum.

* = collected at Chita (see text above).

Afromontane Undifferentiated Forest

Altitudinal range 1,200-1,800m, canopy height 15-25m. This forest type represents a drier or more exposed type of Afromonate Rain-Forest. Large trees include: *Aphloia theriformis; Bequaetiodendron magalismontanum; Cryptocaria liebertiana; Ficalhoa laurifolia; Hirtella megacarpa; Isoberlinia scheffleri; Psydrax vulgare* subsp. *rubrocristatum; Rapanea melanophloeos; Xylopia aethiopica; Xymalos monospora.* Terrestrial: *Schizaea dichotoma; Dicranopteris linearis,* (exposed).

Afromontane evergreen bushland and thicket

Altitudinal range 1,700-1,800m, canopy height 5-10m. In the reserve this forest type is better referred to as Elfin Forest, and has been described for the nearby Uluguru mountains by Pocs (1976). It is a variant of Afromontane undifferentiated forest but is distinguished by the low canopy and rich cover of epiphytic bryophytes, indicating that a great deal of moisture must come from mist. Large trees include: *Allanblackia ulugurensis; Apodytes dimidiata; Faurea saligna; Maytenus acuminata; Ocotea usambarensis; Olinia rochetiana; Podocarpus latifolius; Syzygium cordatum; Ternstroemia polypetala; Trichocladus goetzei.*

Terrestrial: Blechnum punctulatum.

Lithophytic: Elaphoglossum macropodium.

Epiphytic: Ctenopteris sp. aff. villosissima; Elaphoglossum macropodium; Grammitis kyimbilensis; G. nanodes; Lycopodium ophioglossoides; L. dacrydioides; Pleopeltis excavata; Xiphopteris strangeana.

Collection List

The following is a list of the pteridophyte collections made in the Mwanihana Forest Reserve and Chita forests of the Uzungwa scarp. The numbers are those of D.W. Thomas' collections. The collection is at MO, with duplicates at DSM and K. All the species mentioned in this list are also cited in the ecology section of this paper.

Pteridophyta

Filicopsida

Adiantaceae Adiantum capillus-veneris L., 3933 Pellaea angulosa (Bory ex Willd.) Bak., 3861 P. doniana J. Sm. ex Hook., 3934

Aspidiaceae Ctenitis Ianuginosa (Willd. ex Kaulf.) Copel., 3862 Didymochlaena trunculata (Sw.) J. Sm., 3918 Dryopteris inaequalis (Schlechtend.) Kuntze var. inaequalis, 3802, 3881 D. kilemensis (Kuhn) Kuntze, 3880 Tectaria gemmifera (Fée) Alston, 3685, 3895 Polystichum zambesiacum Schelpe, 3801, 3925

Aspleniaceae Asplenium aethiopicum (Burm. f.) Becherer, 3923 A. blastophorum Hieron., 3688 A. boltonii Hook. ex Schelpe, 3878 A. christii Hieron., 3676 A. dregeanum Kunze, 3856 A. formosum Willd., 3696 A. hypomelas Kuhn, 3885 A. inaequilaterale Willd., 3697 A. monanthes L., 3855, 3858 A. obscurum Bl., 3955

A. rutifolium (Berg.) Kunze, 3854

A. unilaterale Lam., 3686 A. Pvolkensii Hieron., 3883 A. sp. aff. gilpinae Bak., 3919 Athyriaceae Athyrium scandicinum (Willd.) C. Presl. 3864 Diplazium nemorale (Bak.) Schelpe, 3863, 3917 D. pseudoporrectum Hieron., 3857 Blechnaceae Blechnum attenuatum (Sw.) Mett., 3891 B. ivohibense C. Chr., 3884 B. punctulatum Sw., 3813 Cvatheaceae Cvathea humilis Hieron., 3886 C. mossambicensis Bak., 3889 Davalliaceae Nephrolepis biserrata (Sw.) Schott, 3974 Dennstaedtiaceae Blotiella natalensis (Hook.) Tryon, 3675 Histiopteris incisa (Thunb.) J. Sm., 3859 Lonchitis occidentalis Bak., 3683 Microlepia fadenii Pic. Ser., 3869 M. speluncae (L.) Moore, 3932 Gleicheniaceae Dicranopteris linearis (Burm. f.) Underw., 3709 Grammitidaceae Ctenopteris sp. aff. villosissima (Hook.) Harley, 3815 Grammitis kvimbilensis (Brause) Copel., 3817A G. nanodes (A. Peter) Ching, 3817 Xiphopteris strangeana Pic. Ser., 3818, 3847A Hymenophyllaceae Hymenophyllum polyanthos Sw. var. kuhnii (C. Chr.) Schelpe, 3866 H. sibthorpioides (Borv ex Willd.) Mett. ex Kuhn, 3865 H. splendidum v.d. Bosch, 3867 Trichomanes borbonicum v.d. Bosch, 3868 T. cupressoides Desv., 3681 T. giganteum Bory ex Willd., 3682 Lomariopsidaceae Bolbitis acrostichoides (Swartz) Ching, 3972 B. auriculata (Lam.) Alston, 3661 B. gemmifera (Hieron.) C. Chr., 3742A B. sp. aff. acrostichoides (Swartz) Ching, 3658, 3659, 3973 Elaphoglossum acrostichoides (Hook. & Grev.) Schelpe, 3821 E. macropodium (Fée) Moore, 3814 E. phanerophlebium C. Chr., 3849 E. spathulatum (Bory) Moore, 3659A Lomariopsis warneckei (Hieron.) Alston, 3890 Polypodiaceae Belvisia spicata (L.f.) Mirb., 3814A Pleopeltis excavata (Bory ex Willd.) Sledge, 3816 Pteridaceae Pteris buchananii Bak. ex Sim, 3887 P. preussii Hieron., 3888

P. pteridioides (Hook.) Ballard, 3860

P. quadriaurita Retz. spp. friesii (Hieron.) Schelpe, 3689

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P. sp. aff. mildbraedii/atrovirens, 3695 P. sp. aff. prolifera Hieron, 3742

Schizaeaceae Schizaea dichotoma (L.) Smith, 3699

Thelypteridaceae Amphineuron opulentum (Kaulf.) Holtt., 3743 Christella gueintziana (Mett.) Holtt., 3946 C. hispidula (Decne) Holtt., 3971 C. sp. aff. gueintziana (Mett.) Holtt., 3694 Menisorus pauciflorus (Hook.) Alston, 3655 Sphaerostephanos arbuscula (Willd.) Holtt. ssp. africanus Holtt., 3693 Pneumatopteris usambarensis Holtt., 3920

Vittariaceae Antrophyum mannianum Hook., 3945

Lycopsida

Lycopodiaceae

- L. dacrydioides Bak., 3807
- L. ophioglossoides Lam., 3765
- L. phlegmaria L., 3654
- L. verticillatum L.f., 3808

ACKNOWLEDGEMENTS

We gratefully acknowledge the assistance of Dr B.S. Parris of the Royal Botanic Gardens, Kew, in naming the fern collection. The Tanzanian National Scientific Research Council and Ministry of Natural Resources and Tourism very kindly gave us permission to work in the Mwanihana Forest Reserve. The National Geographic Society and World Wildlife Fund generously supported the field work. Langson Kusoma and Henry provided much needed assistance in the field.

REFERENCES

DHV. 1982. Water supply survey: Southern Morogoro Region. DHV Consulting Engineers.

LOVETT, J.C. (in press). Endemism and affinities of the Tanzanian montane forest flora. *Ann. Miss. Bot. Gard.*

PARRIS, B.S. 1985. Ecological aspects of distribution and speciation in Old World tropical ferns. *Proc. Roy. Soc. Edin. 86B:* 341-346.

- POCS, T. 1976. Vegetation mapping in the Uluguru mountains (Tanzania, East Africa). *Boissiera* 24: 477-498.
- WHITE, F. 1983. The Vegetation of Africa. UNESCO.

REVIEW

INDEX FILICUM – SUPPLEMENTUM QUINTUM PRO ANNIS 1961-1975 by F.M. Jarrett, with T.A. Bence, J.W. Grimes, B.S. Parris and J.L.M. Pinner. Pp. 245. Clarendon Press, Oxford. 1985. ISBN 0-19-854579-7. Price £25.00.

Fern taxonomists have been well served by the provision of Indices giving the details of the publication of names. *Index Filicum* (1905-1906) was compiled by Carl Christensen who updated it by producing Supplements in 1913, 1917 and 1934. This valuable work was continued by a committee of I.A.P.T. who published in 1965 the Fourth Supplement covering the period from 1934 to 1960.

The present Fifth Supplement has been compiled at Kew under the direction of Dr Frances Jarrett who undertook the onerous task of extracting names from the literature from 1961 to 1970, this being continued by her collaborators to complete the period covered by this work.

The Supplement lists new names at all ranks between family and species but does not make taxonomic judgements as did Christensen's work. Infra-specific categories are not included as a general rule although they are quoted where they form the basionym for a new name. Where hybrids have been named their parentage is given and cross-referenced, for example *Dryopteris x gotenbaensis* Nakaike is quoted in full together with the information that it is the hybrid of *D. hondoensis x uniformis*. A further entry for *D. hondoensis x uniformis* refers the reader to the name *D. x gotenbaensis*. Thus, having either the name of the hybrid or its parentage the other can be found — a very useful feature when it increasingly is becoming common practice to give formal names to hybrids.

All previous parts of the *Index* have dealt exclusively with ferns, a somewhat restrictive practice as fern workers are usually involved with the pteridophytes as a whole. Compilations of names for the fern allies have appeared in a variety of places at different times and it is a great convenience for them to be included along with the ferns as has been done in this Fifth Supplement for the first time.

Users of the *Index* owe a great debt to the compilers for the meticulous way in which the work has been carried out. The publishers are also to be congratulated on the overall presentation and the quality of the type face.

T.G. WALKER

GEORGE GARDNER'S PTERIDOPHYTE HERBARIUM AND LECTOTYPES OF GARDNER'S NEW FERN SPECIES

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ABSTRACT

George Gardner's original pteridophyte collections are at CGE and not with his phanerogam material (Brazilian specimens at BM, Ceylon specimens at K).

INTRODUCTION

George Gardner (1812-1849) is well-known as a botanical explorer in Brazil who later became superintendent of the Peradeniya Botanic Garden in Ceylon. His collections from both countries are large and important. The originals of his Brazilian material are stated to be in the British Museum (Natural History) (BM), while those of his Ceylon plants are said to be in the herbarium of the Royal Botanic Gardens, Kew (K) (Stafleu & Cowan 1976). These were presumably part of the herbarium offered for sale by Samuel Stevens and described in the Gardeners' Chronicle of 31st May 1851 (Anon. 1851). The disposition of Gardner's higher plants is undoubtedly as given above, but it is not so for the pteridophytes. Although both BM and K hold good sets of his pteridophyte numbers they are all duplicates and the original collections are held in the herbarium of the Botany School, University of Cambridge (CGE).

A clue to how this may have come about is provided by a small printed label attached to some of the sheets which reads "Presented by Dr Churchill Babington". Dr Babington is known to have had an interest in cryptogams and presumably purchased the pteridophyte part of Gardner's collections either directly or indirectly from Samuel Stevens for his own use. In 1865 he became Professor of Archaeology at the University of Cambridge At that time his cousin Charles Cardale Babington was Professor of Botany at Cambridge (Desmond 1977) and was acquiring duplicates of the major plant collections then available for the University Herbarium; doubtless Churchill Babington presented them to the Botany School as a gift to the herbarium which was rapidly expanding under his cousin's administration.

The c. 1990 sheets of Gardner's material are mounted on a distinctive blue lined paper and include not only his own gatherings but also duplicates from a variety of other collectors. I propose to document the latter in a subsequent paper. His own numbered original collections are represented, together with many un-numbered sheets which were presumably unicates or plants collected in too small a quantity to be numbered and distributed as duplicates. These are from Brazil, British Isles, Ceylon, India and Mauritius. None of the sheets of his own collections bear his name, but the handwriting is undoubtedly Gardner's and matches exactly that on his duplicates and in his notebooks kept at CGE, and the names and numbers on the duplicates (of which there are four incomplete sets in CGE) always correspond with those of the originals. The duplicates are widespread in herbaria (Stafleu & Cowan 1976) and usually have the plant name and number written in Gardner's hand; sometimes locality and date of collection is indicated, but ecological information is lacking. This is often present on the originals and is usually quoted verbatim in his descriptions of new species.

Gardner described 16 new species of fern and now that his original pteridophyte collections have come to light (with the exception of one type) it seems expedient to choose lectotypes for them.

The lectotypes of George Gardner's fern species at CGE.

Information in quotation marks is written in Gardner's hand on the herbarium sheets.

Acrostichum alpestre Gardner in Fielding & Gardner, Sert.Pl. t.25 (1844). [Gardner] "5924. On shady rocks near the summit of the Organ Mountains. March 1841. Acrostichum alpestre. Gardn." Lectotype chosen here.

Adiantum filiforme Gardner in Hooker, *Ic.Pl.* t.503 (1843). [Gardner] "2391. Shady cliffs of sandstone rocks. Oeiras, Piauhý. 1839. Adiantum filiforme, Gardn." Lectotype and 3 isolectotypes chosen here.

Adiantum sinuosum Gardner in Hooker, *Ic.Pl.* t.504 (1843). [Gardner] ''3552. Serra de Natividade. Goyaz, Brazil. Jany. 1839. Adiantum sinuosum, Gardn.'' Lectotype and 3 isolectotypes chosen here.

Anemia dentata Gardner in Fielding & Gardner, Sert.Pl. ad t.70 (1844). [Gardner] "2387. Between Canabrava & Tranquiera, Province of Piauhý, Brazil. 1839. Anemia dentata, Gardn." Lectotype and 3 isolectotypes chosen here.

Anemia glareosa Gardner in Fielding & Gardner, Sert.Pl. t.70 (1844). [Gardner] "4086. Dry open campos, Goyaz, Brazil. Near Natividade and Arrayas. 1840. Anemia glareosa, Gardn." Lectotype and 2 isolectotoypes chosen here.

Anemia pallida Gardner in Fielding & Gardner, Sert. Pl. ad t. 70 (1844). [Gardner] ''3560 bis. On rocks in woods. Natividade, Goyaz. Jany. 1840. Anemia pallida, Gardn.'' Lectotype and 2 isolectotypes chosen here.

Anemia wightiana Gardner in Calcutta Jour.Nat.Hist. 7:10, t.1-2 (1847). [Gardner s.n.] "Open rocky places on the Malabar slopes of the Neelgherries. Feby. 1845. Anemia wightiana. Gardner in Calcutta Journ." Lectotype and isolectotype chosen here.

Asplenium woodwardioideum Gardner in Lond.Jour.Bot.(Hooker) 1:547 (1842). [Gardner] ''43. Corcovado, Rio de Janeiro. 1836. Asplenium woodwardioideum, Gardn.'' Lectotype chosen here.

Cassebeera gleichenioides Gardner in Hooker, Ic.Pl. t.507 (1843). [Gardner] "5295. Bushy rocky places. Diamond district. Aug. 1840. Cassebeera gleichenioides, Gardn." Lectotype and 2 isolectotypes chosen here.

Cheilanthes monticola Gardner in Hooker, Ic.Pl. t.487 (1842). [Gardner] ''3557. Summit of the Serra de Natividade. Province of Goyaz. Brazil. Jany. 1840. Cheilanthes monticola, Gardn.'' Lectotype and 3 isolectotypes chosen here. Coptophyllum buniifolium Gardner in Lond.Jour.Bot.(Hooker) 1:133 (Jan. 1842). [Gardner] "4084. Serra de Natividade, Goyaz, Brazil, 1840. Coptophyllum buniifolium, Gardn." Lectotype and 3 isolectotypes chosen here.

Coptophyllum millefolium Gardner in Lond.Jour.Bot.(Hooker) 1: 133 (Jan. 1842). [Gardner] ''4083. Villa de Arrayas, Goyaz, Brazil, 1840. Coptophyllum millefolium, Gardn.'' Lectotype and 4 isolectotypes chosen here.

Grammitis organensis Gardner in Hooker, *Ic.Pl.* t.509 (1843). [Gardner] "5913. On rocks and on the stems of trees near the summit of the Organ Mountains, March. 1841. Grammitis organensis, Gardn." Lectotype and 2 isolectotypes chosen here.

Polystichum pallidum Gardner in Lond.Jour.Bot.(Hooker): 1:547 (1842). [Gardner] "54. Woods, Corcovado, Rio de Janeiro, 1836. Polystichum pallidum, Gardn." Lectotype chosen here.

Trochopteris elegans Gardner in *Lond.Jour.Bot.(Hooker)* 1:74 (Jan. 1842). [Gardner] "4085. Serra de Natividade, Goyaz, Brazil. Feby. 1840. Trochopteris elegans, Gardn." Lectotype and 3 isolectotypes chosen here.

Only one species described by Gardner is not lectotypified here. Adiantum calcareum Gardner in Hooker, Ic.Pl. t.467 (1842) was based on Gardner no. 3551, but there is no original material of this number at present in CGE. Although duplicates exist (two of them in CGE) it is possible that the original may yet be found at CGE and typification should ideally wait until then.

ACKNOWLEDGEMENTS

I am grateful to Peter Sell, Assistant Curator of the herbarium, Botany School, Cambridge, for his advice and encouragement during my studies on the pteridophyte collections in CGE.

REFERENCES

ANON. 1851. Miscellaneous section. The Gardnerian Herbarium. *Gardeners' Chronicle* 1851: 343-344.

DESMOND, R. 1977. *Dictionary of British and Irish Botanists and Horticulturalists.* Taylor & Francis: London.

STAFLEU, F.A. & COWAN, R.S. 1976. *Taxonomic Literature* (2nd ed.) Volume 1: A-G. Bohn, Scheltema & Holkema: Utrecht.

REVIEW

ILLUSTRIERTE FLORA VON MITTELEUROPA/GUSTAV HEGI Bd I Teil I PTERIDOPHYTA, 3rd fully revised edition by Karl U. Kramer. 309 pp., 11 coloured plates, 275 figs. 200 x 268mm. Paul Parey, Berlin & Hamburg. ISBN 3-489-500020-2. Price DM 228. (1984). (Publ. 1983).

Our concepts in species delimitations, distribution and general systematic relationships in Pteridophyta have changed considerably over the last 35 years and so this completely rewritten work (by J. Dostal, T. Reichstein, C. R. Fraser-Jenkins & K.U. Kramer) of this classic regional Flora, previously produced in 1935, is long overdue and greatly welcomed. Geographically the area of the Flora (shown in map-form on the end papers) is difficult to equate with present-day political bounderies, being originally based on the German and Austrian Empires with the addition of Switzerland. Thus Alsace-Lorraine (France), Slovenija (Yugoslavia), Bohemia/Moravia (Czechoslovakia), Posen and Prussia (Poland) are included. This is hardly a floristic zone and one could ask why not include the whole of Poland and Czechoslovakia — and also Hungary?

After a brief but concise general account of the group the book describes 39 genera in 23 families. Comprehensive and detailed descriptions of genera and species are illustrated with line drawings and/or silhouettes and photographs of the plants in situ. Most species are shown in the eleven excellent coloured plates. At the taxonomic level, full synonymy, with references, and infra-specific variation is given; ecology, with associated species and both general (with maps) and detailed (in the area of the Flora) distribution is discussed. Vernacular names, including English, are also listed as are many relevant references to all chapters and subheads. Hybrids are treated less fully but still in considerable detail.

A comprehensive work such as this, written by experts and edited with such thoroughness by Karl Kramer is, of course, a mile-stone in regional Floras. It will also be used as a reference book in a wider context e.g. for guidance to family names and classification. At this level it would have been useful to give synonymy of family names and a little discussion. In the reviewer's opinion the names and concepts used are sound and I hope that they will be taken up by other forthcoming European Floras.

One cannot fault a book like this except on minor points. The illustrations vary: some are precise and pertinent e.g. in *Polystichum*; others not so helpful, e.g. the line drawings of *Diphasiastrum* do not show as much as the photographs and could have shown the important differences in lower leaves. Professor Kramer's eagle eye has eliminated even small errors but I noticed, under *Ophioglossum azoricum*, *O. vulgatum* subsp. *ambiguum* (Cross. et Germ.) E.F. Warburg being quoted as published in C.T.W. Fl. Brit. Isles (1962). Warburg published the combination in *Watsonia 4:* 41 (1957). Much more unfortunate is the use of often unclear light microscope photographs of spores when surely SEM pictures would have said everything, and on Plate 5 the individual figures are incorrectly labelled in relation to the key on p.160. A.C. JERMY

A NEW DRYOPTERIS HYBRID FROM SPAIN

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ABSTRACT

A new *Dryopteris* hybrid, *D. x asturiensis* Fraser-Jenkins & Gibby, is described, and the cytology of this hybrid and *D. corleyi* Fraser-Jenkins is discussed.

The northern coastal region of Spain is particularly rich in Dryopteris species, including the recently described endemic D. corlevi Fraser-Jenkins (1983) and D. guanchica Gibby & Jermy, known only from the Iberian peninsula and the Canary Islands, and thus provides opportunities for hybridization. A recently discovered hybrid from this area is D. x fraser-jenkinsii Gibby & Widén (1983), the hybrid between D. affinis (Lowe) Fraser-Jenkins subsp. affinis and probably D. guanchica, although the second parent could possibly be D. dilatata (Hoffm.) Gray. A second hybrid involving D. affinis has been found in N Spain recently, and although similar in morphology to D. x fraser-jenkinsii, differs in certain characters, and particularly in its cytology. Both hybrids are tetraploid, and produce some 8-celled sporangia with 164 bivalents at meiosis, and are capable of limited reproduction by spores, this apomictic character being inherited from D. affinis. However, D. x fraser-jenkinsii shows no chromosome pairing at meiosis in 16-celled sporangia, whereas the new hybrid has 41 bivalents and 82 univalents at first metaphase in 16-celled sporangia (Fig. 1). Morphological comparison suggests that the new hybrid may be D. affinis subsp. affinis x D. corleyi, with which it grows. D. corleyi is a tetraploid species (Fig. 2) that may have originated from the diploid species D. oreades Fomin and D. aemula (Ait.) O. Ktze. (this is at present under investigation). Such a parentage could be compatible with the pairing seen in the hybrid, the bivalents being formed between the two 'oreades' genomes, one from D. affinis subsp. affinis and one from D. corlevi,

Dryopteris x asturiensis Fraser-Jenkins & Gibby hybr. nov.

(= D. affinis subsp. affinis x D. corleyi)

Planta hybrida morphologia intermedia inter parentes. Stipes et rhachis crassiores quam in *D. corleyi* paleis fulvis basibus valde densioribus vestitis. Frons deltatolanceolata, pinnata; pinnae sessiles, infimae e pinnulis basalibus longis gradatim decrescentes; pinnulae infernae valde sed non profunde lobatae usque ad dimidium latitudinis inter costam et marginem, lobi lati rectangulares, superi non-lobati vel lobis minoribus rotundatioribus; apices pinnularum late rotundati vel in plantis minoribus rotundato-truncati, lobi et apices pinnularum aliquot crenas veldentes non manifestos ferentes, velut saepe apicibus acutis. Indusia valde decurvata ad margines eorum, aliquantum crassae et persistentia. Sporae abortivae, sed aliquot sporae magnae non-abortivae praesentiae.

Holotype: Dryopteris x asturiensis Fraser-Jenkins & Gibby. c. 100m, in wood on sandstone 2km below Puron, c. 7km SE of Llanes, Oviedo to Santander, Oviedo (Asturias), Spain. C.R. Fraser-Jenkins 10835, 5 Oct. 1981 (BM) Fig. 3.

Isotypes: Ditto (MA; Herb. T. Reichstein, Basel).

Paratypes: c. 50m, in wood on sandstone above main Oviedo to Santander road, above Pendueles village, c. 2km E of Vidiago, E of Llanes, Oviedo to Santander, Oviedo (Asturias), Spain. C.R. Fraser-Jenkins 10778 (BMI KI MAI PI), 10779 (BMI), 10780 (BMI), 10781 (BMI), 10798 (BMI Herb. M. Laínz, Gijón University!).

Plants occurring with both parents and also *D. dilatata, D. affinis* subsp. *borreri* (Newm.) Fraser-Jenkins and *D. filix-mas* (L.) Schott. Morphology intermediate



FIGURE 3 Dryopteris x asturiensis CRFJ 10835 holotype.

A NEW DRYOPTERIS HYBRID FROM SPAIN

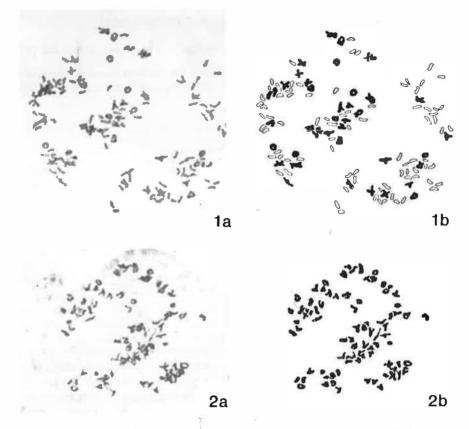


FIGURE 1a *Dryopteris x asturiensis* CRFJ 10835 spore mother cell from 16-celled sporangium at diakinesis showing 41 bivalents and 82 univalents; b explanatory diagram with bivalents in black, univalents outlined, x 750.

FIGURE 2a *Dryopteris corleyi* CRFJ 10782 spore mother cell at diakinesis showing 82 bivalents; b explanatory diagram, x 750.

between the parents. Stipe and rhachis thicker than in D. corleyi and markedly more densely clothed in light brown scales with dark bases. Frond deltate-lanceolate, once pinnate; pinnae sessile, the lowest ones gradually tapering from long basal pinnules; lower pinnules markedly but shallowly lobed up to half the width between the midrib and margin with wide, rectangular lobes, upper pinnules unlobed or with smaller, more rounded lobes; pinnule apices broadly rounded, or in smaller plants, roundedtruncate, the lobes and pinnule apices bearing a few insignificant crenations or obtuse teeth, though often with pointed apices. Indusia strongly curved down at their margins, somewhat thick and persistent. Spores abortive but with a few large, good spores present. Differs from D. affinis in its long stipe, deltate-lanceolate frond, long lowest opposite pair of pinnules on the lower few pairs of pinnae, much more deeply lobed pinnules, the lower ones with narrower apices, and mostly abortive spores. Differs from D. corleyi in its denser and browner scales, many with dark bases, its thicker stipe and rhachis, more sessile pinnae and pinnules, less lobed lobes or divided pinnules, markedly broader pinnule apices, thicker indusia and mostly abortive spores. Differs from D. x fraser-jenkinsii in its slightly paler stipe scales, markedly broader, less pointed pinnule apices, more rounded pinnule lobes with shorter, less acute teeth, and a generally flatter lamina with less twisted segments.

REFERENCES

FRASER-JENKINS, C.R. 1982. Dryopteris in Spain, Portugal and Macaronesia. Bol. Soc. Brot., Ser. 2a. 55: 175-336.

GIBBY, M. & WIDEN, C.-J. 1983. Three new *Dryopteris* hybrids from Spain and the Canary Islands. *Fern Gaz.* 12: 267-270.

REVIEWS

MED-CHECKLIST 1 PTERIDOPHYTA (ed. 2) GYMNOSPERMAE DICOTYLEDONES (ACANTHACEAE-CNEORACEAE) edited by W. Greuter, H.M. Burdet & G. Long. 330+ C pp. 312 x 210mm. Published by Conservatoire et Jardin botaniques, Ville de Genève, Med-Checklist Trust of OPTIMA, Genève ISBN 2-8277-0151-0, ISBN 2-8279-0004-1, 1984.

This is a checklist of vascular plants from all the countries that border on the Mediterranean, plus Portugal, Bulgaria, the Crimea and Jordan. The taxonomic advisers for pteridophytes are C.R. Fraser-Jenkins, A.C. Jermy and T. Reichstein, and the book includes over 150 fern species. For each species the name, authority and source is given and synonyms, and the distribution (by country) within the Mediterranean region. For recent or doubtful records the reference is given in the appendix. Unfortunately some of the names used in this checklist are not those found in Hegi's Illustrierte Flora von Mitteleuropa (Kramer 1983; see review p.112) which was published in the same year, and this must reflect an editorial decision, since C.R. Fraser-Jenkins and T. Reichstein were pteridophyte advisers for Hegi. For example, the Med-Checklist uses *Lycopodium* for all the Lycopodiaceae, whereas Hegi uses *Lycopodiella*, *Diphasiastrum* etc., and such disagreement is frustrating for all pteridologists. However, the Med-Checklist, which uses a computerized system for information processing, formating etc. and thus minimizing typographical errors, provides a valuable reference source.

M. GIBBY

EVOLUTIONARY CLADISTICS OF MARATTIALEAN FERNS by Christopher R. Hill & Josephine M. Camus. Bulletin of the British Museum (Natural History), Botany series Vol. 14 No. 4. 27 February 1986. Price £14.50.

The application of cladistic methods to problems of fern taxonomy has not, as yet, been widespread. It is encouraging, therefore, to read this paper on the classification of Marattiales which relies on cladistics to resolve relationships within the order. The concepts and terminology of the method are given, which is useful for those readers unfamiliar with cladistics. All species of the order have not been included, but the 23 species selected cover the range of variation in each of the extant genera; 73 characters are used ranging from the stelar anatomy of the adult stem to the shape of the exine spines of the spores. The resulting cladogram indicates the distinctness of both *Christensenia* and *Danaea*, and the paraphyletic nature of *Marattia*, *Macroglossum*, *Angiopteris* and *Archangiopteris*. As a check on the taxonomic relationships defined by the cladogram the authors have used stratigraphy, phytogeography and ontogeny, and present a convincing case for their conclusions. I look forward very much to seeing their further work on revising the genera and species of Marattiaceae.

SUBGENERIC NAMES IN SELAGINELLA

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ABSTRACT

In an account of Selaginellaceae to be published in The Families and Genera of Plants: Pteridophyta (ed. Kramer et al.) the author proposes five subgenera in the sole genus *Selaginella: Selaginella, Ericetorum Jermy, Tetragonostachys Jermy, Stachygynandrum* (P. Beauv.) Baker and *Heterostachys* Baker. In this brief synopsis the names *Ericetorum Jermy* and *Tetragonostachys* Jermy are described and validated.

INTRODUCTION

The genus *Selaginella* contains approximately 700 species for the most part concentrated in the tropical areas of the world. Botanists of the late eighteenth century (e.g. Adanson, Boehmer, Palisot de Beauvoir) describing the relatively small number of species available to them at that time saw generic distinctions that cannot be upheld today. Kuntze (1891), in the belief that *Lycopodioides* Boehmer was the earliest name for the genus, published some 320 new combinations in that genus. Rothmaler (1944) proposed acceptance of these earlier generic names but large-scale nomenclatural changes have not been published without the broad revision of the classification of the family that is needed. The present author, having studied *Selaginella* in some detail throughout its range, has proposed in a forthcoming book (The Families and Genera of Plants: Pteridophyta, ed. K.U. Kramer et al.) the following infrageneric classification which is published here in synopsis only in order to validate two of the names used. A full account of the morphology and relationships of these taxa is in preparation.

SELAGINELLA P. Beauv.

Palisot de Beauvoir, Magasin Encycl. 5: 478 (1804); Prod. fam. Aetheog. 101 (1805), em. Spring in Flora (Regensb.) 21: 148 (1838); nomen conserv.

Subgenus *Selaginella*. Type-species *Selaginella spinosa* P. Beauv. = *Selaginella selaginoides* (L.) Link.

Syn.: Subgen. *Homoeophyllum* (Spring) Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanz. 1 (4): 669 (1902) p.p.

Stems erect, new primary shoots arising from the base upon maturation of the single terminal strobilus, rooting from a basal hypocotular node; leaves and sporophylls spirally arranged, uniform and herbaceous.

Two species: *S. selaginoides* — circumboreal in the Northern Hemisphere, south to the Canary Islands; *S. deflexa* Brackenridge — endemic to Hawaiian Islands.

Subgenus Ericetorum Jermy subgen. nov.

Syn.: Subgen. *Homoeophyllum* (Spring) Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanz. 1 (4): 669 (1902) p.p.

Rami erecti, aut ramosi aut rarius simplices, e caule repenti solenostelam continenti procumbente, exorientes; folia aequabilia, saltem ad basin decussata, plus minusve herbacea, lamina ovata vel ovato-lanceolata; sporophylla tetrasticha. Type-species *Selaginella uliginosa* (Labill.) Spring, Bull. Acad. R. Belg. 10: 136 (1843). Stems erect, either unbranched or more compound, arising from a creeping solenostelic stem; leaves uniform, decussately arranged at least below, more or less herbaceous with an ovate or ovate-lanceolate lamina; sporophylls tetrastichous. Three species: *S. uliginosa* — Australia and Tasmania; *S. gracillima* (Kunze) Spring — SE Australia; *S. pygmaea* (Kaulf.) Alston — southern Africa.

Subgenus Tetragonostachys Jermy subgen. nov.

Syn.: Subgen, Homoeophyllum (Spring) Hieron, & Sadeb, in Engler & Prantl, Nat. Pflanz. 1 (4): 669 (1902) p.p.

> Planta repens, caulibus pleuriramosis, per totam longitudinem radices emittentibus, prostrata et saepe tegetes formans, vel humilis ramis erectis; folia spiraliter disposita, aequabilia vel in ramis prostratis dimorphescentia, plerumque coriacea, linearilanceolata, apice aliquando acicularia vel apice pilum praedita; sporophylla tetrasticha. Type-species Selaginella rupestris (L.) Spring, Flora 21: 149 and 182 (1838).

> Plants creeping, stems much-branched, rooting throughout their length, prostrate and often mat-forming or with short erect branches; leaves spirally arranged, similar, or on prostrate branches slightly dimorphic, usually coriaceous, linear-lanceolate, apex sharp or bearing a hair; sporophylls tetrastichous.

> About 50 species ranging from southern North America through the tropics of South America, Africa and the Indian subcontinent to N China and Japan.

Subgenus Stachygynandrum (P. Beauv.) Baker, J. Bot., Lond. 21:3 (1883) emend. Jermy, Fern Gaz. 13:118 (1986), Basionym: Stachvoynandrum P. Beauv, ex Mirbel in Lam. & Mirbel, Hist. Nat. Veg. 3: 477 (1802). Type-species Lycopodium flabellatum L.= Selaginella flabellata (L.) Spring.

Syn.: Subgen. Heterophyllum Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanz. 1 (4): 673 (1902); subgen. Homostachys Baker, J. Bot., Lond. 21: 4 (1883).

> Stems either creeping with prostrate branches, or erect with various and often complex branching systems, leaves dimorphic, at least on the secondary branches, in four distinct rows, those of the upper rows being distinctly smaller; sporophylls uniform, or in a few cases showing slight dimorphism, tetrastichous.

> Baker's concept is enlarged to include those species (S. ciliaris (Retz.) Spring; S. pallidissima Spring) he separated as being in his fourth subgen., Homostachys, Those species and others, such as those included in that subgenus by Walton & Alston (1938), have loose strobili with sporophylls that begin to show some dimorphism. In my opinion, and in that of N. Quansah (pers. comm.) who has studied the African species in detail these can rightly be included in subgen. Stachygynandrum.

About 600 species ranging throughout the tropics of all continents.

Subgenus Heterostachys Baker, J. Bot., Lond. 21: 4 (1883). Lectotype-species Selaginella heterostachys Baker, J. Bot., Lond. 23:177 (1885).

Syn. subgen. Heterophyllum Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanz. 1 (4): 673 (1902).

> Stems creeping and much-branched, or secondary branches erect and suffruticose, rooting in branch axils; leaves as in subgen. Stachygynandrum, strobili complanate. sporophylls dimorphic, tetrastichous, those on the ventral side smaller than those on the upper side of the shoot.

> About 60 species with a distribution range similar to that of subgen. Stachygynandrum.

REFERENCES

KUNTZE, O. 1891. Revisio Generum Plantarum, 1: 824-827. PALISOT DE BEAUVOIR. 1805. Prodromus de la famille Aetheogamie. Pp. 112. Paris. ROTHMALER, W. 1944. Pteridophyten-Studien | Feddes Repert. 54: 55-82. WALTON, J. & ALSTON, A.H.G. 1938. Lycopodiinae. Chap. XVII in Manual of Pteridology (ed. F. Verdoorn), Nijhoff, The Hague.

SHORT NOTES

THE OCCURRENCE OF SCHIZAEA DICHOTOMA IN TANZANIA

The curious and primitive fern *Schizaea dichotoma* (L.) Smith has been discovered recently in the Uzungwa mountains of Tanzania in the Mwanihana Forest Reserve above Sanje village at latitude 7°50'S and longitude 36°55'E. It is now known from three collections, which represent the first records of the species in continental Africa. Its previous known range was Madagascar to Polynesia and Australia (Holttum, 1968), where it is widespread and frequently collected.

In Tanzania it grows on the forest floor in leaf litter under a canopy of *Albizia gummifera, Filicum decipiens, Funtumia africana,* and *Parinari excelsa,* with the saprophytic herb *Seychellaria africana,* at an altitude of between 900-1200m. The forests themselves occur on the east facing slopes of the ancient crystalline Uzungwa mountains in an annual rainfall of 2000-2500mm, and are well known for the high degree of endemism they contain (Lovett, in press).

In view of the previous known range of *Schizaea dichotoma*, the question arises as to whether its distribution pattern is a relict which predates the break up of Gondwanaland and the separation of Madagascar from continental Africa, or whether its occurrence in Tanzania is a result of later long distance dispersal from Madagascar. The former idea has been suggested to explain the distribution of the bryophyte family Rutenbergiaceae which also occurs on the ancient crystalline East African mountains and Madagascar (Pocs, 1975). However, for *Schizaea dichotoma*, long distance dispersal is perhaps more likely in view of its limited distribution in Tanzania, and its spores might be carried by the prevailing winds from Madagascar to Tanzania.

Interestingly enough the associate of *Schizaea dichotoma, Seychellaria africana,* which is currently only known from the Uzungwa mountains, belongs to a genus which is otherwise only found on Madagascar and adjacent islands (Vollesen, 1980). Perhaps it too reached Tanzania by long distance dispersal of its small seeds. The association of *Schizaea* and *Seychellaria* is even more curious in that it has been noted in the Neotropics that *Schizaea* is found in association with saprophytic plants in the same family as *Seychellaria*, the Triuridaceae (Maas, 1979), and the fact that this condition is also found in Tanzania may suggest that *Schizaea* is also saprophytic to some degree.

I am grateful for the assistance of Barbara Parris in the identification of Tanzanian ferns, and the Tanzania National Scientific Research Council who very kindly gave me permission to conduct field work in Tanzania. The National Geographic Society and World Wildlife Fund generously provided the support for the field work.

Collection numbers from the Tanzanian locality are: Lovett 244, (K, DSM) Stuart & Rodgers 838 (K, DSM), Thomas 3699 (K, MO).

REFERENCES

HOLTTUM, R.E. 1968. Ferns of Malaya. Flora of Malaya Vol. II, Ed. 2.

- LOVETT, J.C. (In press). Endemism and affinities of the Tanzanian montae forest flora. *Ann. Miss.* Bot. Gard.
- MAAS, P.J.M. 1979. Neotropical saprophytes. In: Tropical Botany. Ed. Kai Larsen & Lauritz B. Holm-Nielsen. Academic Press.
- POCS, T. 1975. Affinities between the bryoflora of East Africa and Madagascar. *Boissiera 24:* 125-128.
- VOLLESEN, K. 1980. A new species of *Seychellaria* (Triuridaceae) from Tanzania. *Kew Bull. 36:* 733-736.

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A CHROMOSOME COUNT FOR ANOGRAMMA LEPTOPHYLLA IN MADFIRA

A comprehensive study of the cytology of the native ferns of Madeira has recently been completed (Manton et al. 1986). However, for one fern, Anogramma leptophylla (L.) Link, a definitive count proved difficult, owing in part to a tendency for clumping of the chromosomes but also to the annual habit of the fern, In early Spring of this year J.F.M. and M.J. Cannon made fixings in the wild (Madeira: Levada from Boco do Risco east to Canical tunnel entrance. Cannon & Cannon 5169, 10 March 1986. BM), and a chromosome count of 26 bivalents at meiosis has now been confirmed (Fig. 1). This is in agreement with Fabbri (1963) quoting Tutin as 'n = 26?' for material from Jersey, and Kurita (1971) who gives n = 26 for material from Europe without giving a precise locality, and contrasts with counts of n = 29 for this species from New Zealand (Brownlie 1958) and South Africa (Baroutsis & Gastony 1978), and n=56-7 (Mehra & Verma 1960) and n=58 (Verma, quoted by Manton et al. 1986) from India.

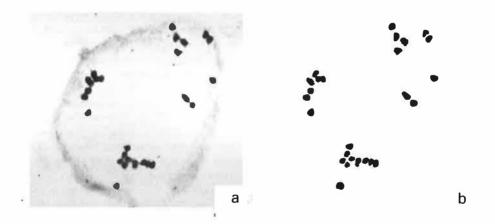


FIGURE 1a Spore mother cell of Anogramma leptophylla at metaphase 1 showing 26 bivalents; b explanatory diagram, x 1000.

REFERENCES

BAROUTSIS, J.G. & GASTONY, C.J. 1978. Chromosome numbers in the genus Anogramma. II. Am. Fern J. 68: 3-6.

BROWNLIE, G. 1958, Chromosome numbers in New Zealand ferns. Trans. R. Soc. N.Z. 85: 213-216

FABBRI, F. 1963. Primo supplemento alle Tavole cromosomiche delle Pteridophyta di Alberto Chiarugi. *Caryologia*, 16: 237-335.

KURITA, S. 1971. Chromosome study of four species of leptosporangiate ferns Ann. Rep. Foreign Students' Coll., Chiba Univ. 6: 41-43.

MANTON, I., LOVIS, J.D., VIDA, G. & GIBBY, M. 1986. Cytology of the fern flora of Madeira. Bull.

Br. Mus. nat. Hist. (Bot.) 15: in press.
MEHRA, P.N. & VERMA, S.C. 1960. Cytological observations on some west Himalayan Pteridaceae. Caryologia 13: 613-650.

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CYSTOPTERIS IN THE CAPE VERDE AND CANARY ISLANDS

The specimens of *Cystopteris* which I collected in the Cape Verde Islands have been published by me as *C. fragilis* sens. lat. (Lobin, 1982).

Now, using the vein character of Rocha Afonsa (1982) and the spore characters I myself have observed, I can say that the Fogo (Cape Verde Islands) specimens are *C. fragilis* (L.) Bernh. and that the specimens which I collected on Tenerife (Canary Islands) are *C. viridula* (Desv.) Desv. The key characters I used are:

Veins ending in the apex of the teeth; spores echinate, loosely covered with spines ± equal in size and shape *C. fragilis* Veins ending in the sinus between two teeth; spores spiny-lacunar, so densely covered with spines unequal in size and shape and connected at their base, that they obscure the surface *C. viridula*

C. fragilis was discovered in the Cape Verde Islands in 1863 by A. Stübel (Bolle, 1866). A second collection of this rare fern was made by Chevalier (1935) and the third by Barbosa (Nogueira, 1975). I found the species growing at Fogo in the walls of small shady humid valleys (ribeiras) at about 800 to 1200m alt. and apart from one specimen in the southwest, all on the north side.

REFERENCES

BOLLE, C. 1866. Die Standorte der Farrn auf den Canarischen Inseln III. Z. ges. Erdk., 1: 209-238; Berlin.

CHEVALIER, A. 1935. Les îles du Cap Vert. Flore de l'Archipel. Rev. int. Bot. appl. Agric. trop., 15: 733-1090: Paris.

LOBIN W. 1982. Untersuchung über Flora, Vegetation und biogeographische Beziehungen der Kapverdischen Inseln. Cour. Forsch.-Inst. Senckenberg, 53: 112 pp.; Frankfurt.

NOGUEIRA, I. 1975. Plantas colhidas pelo Eng.º L.A. Grandvaux Barbosa no arquipélago de Cabo Verde I. Pteridophyta. *Garcia Orta, (Bot.) 2 (2):* 79-84; Lisbon.

ROCHA AFONSA, M. 1982. Contribuição para o estudo do género *Cystopteris* Bernh. em Portugal continental e insular. *Bol. Soc. Brot., (2) 55:* 337-352; Coimbra.

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CYSTOPTERIS VIRIDULA IN MAINLAND AFRICA

Although known from the Cape Verdes, Macaronesia, south-west Europe, west Mediterranean Europe, Morocco and Algeria, *Cystopteris viridula* (Desv.) Desv. has not so far been reported from mainland Africa (in the floristic sense). My father and I recently found it on Mount Oku in North-West Province, Cameroon: above road on NE side of Mt. Oku, c. 4km SE of Oku on Kumbo road, NE of Bamenda, c. 2300m alt., on moss-covered boulder in dense natural forest by stream, above encroaching potato fields. Coll: CDFJ & CRFJ 11489, 6 June 1985 (BM, H).

This suggests that this species could be yet another example of the African affinity of much of the Macronesian and Atlantic European floristic element in ferns, which I see as secondarily invading south-western Europe in many cases, though often with presumed more ancient Asian connections, sometimes via Africa. I have not yet been able to investigate other west or central African populations of the *Cystopteris fragilis* (L.) Bernh. group from the Tibesti, Hoggar etc.

ACKNOWLEDGEMENTS

The author would like to thank his father, C.D. Fraser Jenkins of Bridgend, the Botanical Museum, University of Helsinki and Professor T. Reichstein for their generous financial help. C.R. FRASER-JENKINS

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FIRST RECORD OF EQUISETUM x DYCEI IN CONTINENTAL EUROPE

During a botanical survey of plants growing in the "Maximilianpark" in the vicinity of Hamm (North Rhine-Westphalia, Federal Republic of Germany) one of us (U.P.) collected a strange looking horsetail which at first was thought to represent *Equisetum x litorale* Kühlew. ex Rupr. Further studies revealed, however, that the plants showed closer relationships to *E. palustre* L. than to *E. arvense* L. Our tentative determination as *E. x dycei* C.N. Page was subsequently confirmed by C.N. Pageto whom we sent our plants for examination. As far as we know this is the first record of *E. x dycei* outside the British Isles and the first for continental Europe. Diagnostic features of this hybrid are given by Page (1982).

The environmental conditions of the E. x dycei stand in Hamm are similar to those described by Page (1985) for the British and Irish localities. It is a wet habitat being permanently flooded by shallow water and has been disturbed or at least modified in some degree by man. This occurred recently during the development of the whole area for the "Landesgartenschau", an open air display of ornamental flowers exhibiting modern trends and features of garden architecture, which took place in 1984. In the course of the work the site where E. x dycei grows was covered with loamy soil and an artificial water regime installed to keep the site flooded. Additionally, several species of macrophytes (e.g. Lythrum salicaria, Typha angustifolia, Carex acutiformis) were planted to re-create a vegetation cover. Both parental species of E. x dycei, E. palustre and E. fluviatile L., are present, but only a small number of shoots; these have not been planted. The vegetation is still very scarce and open, and this is another common feature with the Scottish and Irish localities. Here the rather few (about 20), small and weakly growing shoots of E. x dycei persist. This hybrid appears to be a weak competitor and disappears as soon as other plants start to grow more vigorously and vegetation becomes more dense. This is very much in contrast to E. x litorale which can form large colonies and seems to compete quite successfully with many other plant species. The whole circumstances suggest that the E. x dycei stand in Hamm originated there only a few years ago.

Although it is difficult to make any predictions on the future development of the population we are inclined to believe that the plants will not survive for a very long time. The stand could be adversely affected by both enhanced growth of other macrophytes and possible disturbance of the habitat by recreational activities.

Regarding the distribution of *E. x dycei* we fully agree with the statement of Page (1985) that *E. x dycei* can very easily be overlooked and it may well turn out that it is more frequent on the European continent than this one reported locality suggests.

ACKNOWLEDGEMENTS

We thank Dr C.N. Page, Edinburgh, for his kind support and for examining our *Equisetum* specimens and Mr Ralph David, Witten, for improving our English.

REFERENCES

PAGE, C.N. 1982. The ferns of Britain and Ireland. Cambridge University Press. PAGE, C.N. 1985. The distribution and habitats of *Equisetum x dycei*. *Pteridologist* 1:60.

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AN ANOMALY OF BOTRYCHIUM MATRICARIIFOLIUM

In August 1985 the author found one specimen of *Botrychium matricariifolium* A.Br. ex Koch in the hills of the Českomoravská Vrchovina about 70km northwest of Brno (Czechoslovakia). It was surprising to see that it bore sporangia on the sterile part of its frond.

Since this specimen was rather old when it was found it was impossible to determine the correct species at once so it was sent to Prof. Dr. Follmann (Köln) for detailed analysis. He ascertained the abnormal sporangia to be stunted and the number of chromosomes to be about 180. As *B. virginianum* (L.) Sw. must be eliminated because of its very different habit the specimen can only be *B. matricariifolium*.

For further details the author may be contacted. Special thanks are due to Prof. Dr. Follmann for his efforts.

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CORRECTIONS TO INDEX FILICUM

Index filicum is now produced by the Royal Botanic Gardens, Kew, and as the new editor I am keen to correct the errors in the original and subsequent supplements. I am aware of a number of these but am sure that others are as yet undetected. I very much welcome information on any omissions and mistakes known to my colleagues. Infraspecific names are to be included in the next supplement, which will run from 1976-1985. From 1986, new names of pteridophytes will be published annually, as an appendix of an annual *Index Kewensis*, but *Index Filicum* will continue to be published at 5 or 10 year intervals.

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OBITUARY

PROFESSOR E.A.C.L.E. SCHELPE

Professor Edmund André Charles Lois Eloi ('Ted') Schelpe died after a sudden heart attack at his home on Saturday 12th October 1985. Professor Schelpe was born in Durban on 27th July 1924. He completed a BSc with distinction in Botany at Natal University in 1943 and at the same University obtained an MSc (Class I) in 1946. He obtained the DPhil degree of Oxford University (Wadham College) in 1952. He held the following posts at the University of Cape Town: Lecturer in Botany, 1953-1954; Senior Lecturer and Curator of the Bolus Herbarium, 1954-1958; Associate Professor and Curator of the Bolus Herbarium, 1968-1973, the title Curator being changed to Director from 1970; Professor (ad hominem) and Director of the Bolus Herbarium, 1973-1985. Professor Schelpe was an elected Fellow of the Royal Society of South Africa, the Linnean Society of London, and the University of Cape Town, From 1964 he had been a Member of the Committee on Pteridophyta of the International Association of Plant Taxonomists. Professor Schelpe has made major contributions to the systematics of Pteridophyta in southern Africa. A few days before he passed away he finished checking the final proofs of the Pteridophyta volume for the Flora of Southern Africa. This was a culmination of studies in the course of which he published the accounts of the Pteridophyta for the Flora Zambesiaca, the Flora de Mocambique and the Conspectus Florae Angolensis. He published over 100scientific papers and books, which besides Pteridophyta covered topics in orchids, bryophytes, plant ecology and phytogeography. Professor Schelpe was a distinguished and internationally wellknown botanist and his passing away is a sad loss to the scientific community.

> Information supplied by A.V. HALL Bolus Herbarium, Rondebosch, 7700 South Africa

REVIEWS

FERNS OF JAMAICA by G.R. Proctor. 631 pp., 135 figures, 22 maps, 175 x 250mm. British Museum (Natural History), London. ISBN: 0-565-00895-1. 1985. Price £50.00.

Jamaica is an island especially rich in ferns for which no adequate modern handbook was available. The defect has now been remedied in a very authoritative manner by the publication of this book. All groups of pteridophytes are covered and some idea of the richness of the flora and the techical problems facing the author can be gained from the fact that 579 species and a further 30 clear varieties are described.

A very valuable feature of the short Introduction is the listing of the 178 collectors known to have gathered ferns in Jamaica, together with their collecting dates and herbaria where the author has seen their specimens.

The main text is easy to read and well laid-out — thus for each family there is a general account and a note on any special literature, followed by clear keys to the genera. The species entries are concise and informative, giving the detailed authority, the type specimen, basionym and synonyms, species description, general range and Jamaican distribution and a short entry on habitat, together with comment as to relative abundance in Jamaica.

The specific descriptions average some 10-12 lines and are clear proof of Dr Proctor's familiarity with the plants in the field. Use has been made of published cytological evidence where this has thrown light on a particular taxonomic aspect such as the separation of taxa and the recognition of hybrids, etc.

In taking a wide view of such genera as *Thelypteris, Polypodium, Grammitis, Cyathea,* etc., and by maintaining a hierarchy based on the subgenus, Proctor is of the opinion that the ends of classification are thus best served. All the keys are clear and well-constructed and avoid the use of comparative terms which are an unfortunate feature of some works and are of little use unless the student has both taxa to examine. The acid test of any key is how easy and accurate it is in use and I selected eight of the largest genera and from these pulled out at random folders of 20 species, all of which keyed out satisfactorily. There was one discrepancy, namely in the key leading to *Polypodium loriceum* where the rhizome was said to be "bearing a few scattered appressed scales, otherwise naked" whilst the specific description (p.529) describes the rhizome as bearing numerous appressed scales. Indeed, in the same folder of *P. loriceum* that I examined, some specimens had numerous rhizome scales whilst others had very few. Nevertheless despite this difficulty the keying process still gave the right answer because of the other alternatives.

A delightful feature of the book is in the illustrations. Seventy five of the 83 native genera are delineated and a very skilful choice has been made to demonstrate a range of artistic styles and printing methods — some old such as those from Rovirosa, Hooker, Schkuhr, etc., and others modern from Small, Stolze and A.R. Smith for example. In a number of cases excellent original drawings by P.J. Edwards are included.

In summary, this is an invaluable work written by the leading authority on Jamaican ferns who has built up an intimate knowledge of these plants in the field over many years and who has put this to use in a very clear and concise manner. No one who has an interest in these ferns can afford to be without this book, although the price is somewhat daunting. I hope that we may look forward to sequels covering the history of plant collecting in Jamaica and an account of the ecology and behaviour of these ferns.

It may be somewhat churlish to adversely comment on a feature of such an excellent book, especially as it is not the responsibility of the author, but mention must be made of the binding Books of this type which are going to be used extensively both in the laboratory and the field will be subject to quite heavy wear and tear. A first essential is to provide covers which will stand up to this and which preferably should be waterproof or wipeable. In the short time I have had my copy (which has only been used in the laboratory) the cover is showing dirty marks and on attempting to wipe them off the red dye has come away. In addition the corners are fraying. Surely more thought could be put by publishers to the use to which a book is going to be put and provide more appropriate covers, particularly in view of the high price of books in general.

T.G. WALKER

GAMETOPHYTES OF OPHIOGLOSSACEAE by D.D. Pant, D.D. Nautiyal and D.R. Misra, Phyta Monograph 1: 1-111. 1984. 180 x 250mm. Published by the Society of Indian Plant Taxonomists, Allahabad, 211002. India. Price not given.

This is a thorough descriptive account of the gametophytes of six species of *Ophioglossum*, four of *Botrychium* and *Helminthostachys zeylanica*, and an historical review of work on the subject. The gametophytes of Ophioglossaceae are geophilous, cylindrical, fleshy and tuberous, and for the most part monoecious. Xylem stands are shown to be present in the centre of the prothallus of *H. zeylanicum* and comparisons are suggested with the fossil *Rhynia gwynnevaughanii*, thought by someto be a highly organised prothallus. The book is well illustrated both with photomicrographs and well executed line drawings.

A.C. JERMY

BRITISH PTERIDOPHYTE RECORDS

Compiled by A.J. Worland

Since the appearance of the 'Atlas of Ferns', an annual list of additions and corrections has been compiled from information supplied by the Biological Records Centre, BSBI vice-county recorders and members of the BPS and BSBI. Lists have been published in the BPS 'Bulletin' up to and including 1982 and subsequently annually in the *Fern Gazette.*

The records are presented thus: 100km square (letters are used for Irish grid squares to avoid confusion)/10km square followed by the recorder's name. Nomenclature follows the Atlas. The following additions have been received up to the end of March 1986.

POST 1980

- 2.1 Lycopodiella inundata E Cumberland, R.W.M. Corner
- 5.2 Selaginella kraussiana 36/67 E.P. Beattie
- 7.1 Equisetum hyemale 37/41 N.F. Stewart
- 7.1x2 E. x trachyodon 35/37 G. Halliday, 35/78 G.A. Swan
- 7.2 E. variegatum H12/37 F. Bonham
- 7.3 E. fluviatile 53/04 N.J. Hards
- 8.1 Botrychium lunaria 25/67 V. McClive
- 14.1 Hymenophyllum tunbrigense 26/25 B. Simpson
- 16.1 Polypodium vulgare 52/94 E.M. Hyde, 62/13 E.M. Hyde
- 16.2 P. interjectum 53/05 N.J. Hards
- 16.2x1 P. x mantoniae 52/94, 62/03, 62/13 E.M. Hyde
- 17.1 Pteridium aquilinum 53/24 N.J. Hards
- 18.1 Thelypteris thelypteroides 22/93 R.G. Woods, H12/27 F. Bonham
- 20.1 Oreopteris limbosperma 34/86 N.J. Hards, 51/04 M.D. Reed
- 21.1 Asplenium scolopendrium 53/04 N.J. Hards
- 21.2 A. adiantum-nigrum 43/97, 53/04, 53/14 N.J. Hards
- 21.6 A. marinum 36/68 M. McAffer
- 21.7a A. trichomanes subsp. trichomanes 22/72 R.N. Stringer & I.K. Morgan
- 21.11 A. ceterach 26/40 B. Simpson
- 22.1 Athyrium filix-femina 48/02 A.O. Chater, 53/34 N.J. Hards
- 26.2x3 Polystichum x bicknellii 18/52 M. Barron, 22/40 I.K. Morgan
- 26.3 P. setiferum 43/97, 53/34 N.J. Hards
- 27.2 Dryopteris filix-mas 53/24 N.J. Hards
- 27.3 D. affinis subsp. affinis 22/40 I.K. Morgan
- 27.3 D. affinis subsp. borreri 22/40 I.K. Morgan
- 27.3 D. affinis subsp. stillupensis 22/72 I.K. Morgan
- 27.5 D. aemula 41/22 F. Rose & R.J. Hornby
- 27.6 D. villarii subsp. submontana 35/90 R.G. Jefferson
- 27.8 D. carthusiana 34/85 N.J. Hards
- 27.9x8 D. deweveri 22/63 I.K. Morgan, 34/85 N.J. Hards
- 30.1 Azolla filiculoides 33/10 C.J. Harris, 33/20 M. Wainwright & E.D. Pugh. 44/63 E. Chicken