ART. 43.—*Studies in the New Zealand Hymenophyllaceae: Part I—The Distribution of the Species in Westland, and their Growth-forms.*

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[*Read before the Philosophical Institute of Canterbury, 1st December, 1920; received by Editor, 5th December, 1921; issued separately, 8th June, 1923.*]

Plates 56–76.

ANALYSIS OF PAPER.

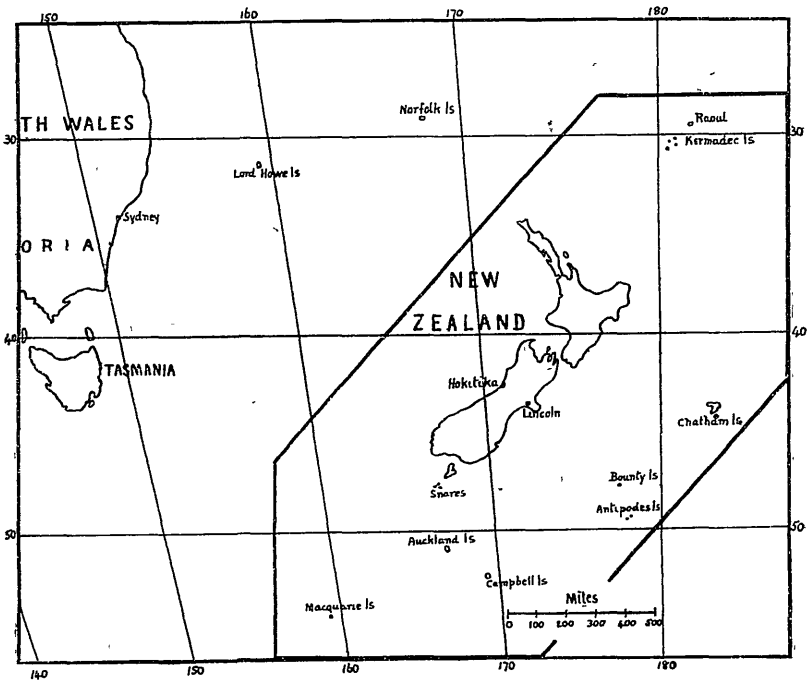
INTRODUCTORY.

THE Hymenophyllaceae constitute one of the most interesting of modern fern families, by reason of the fact that the family as a whole shows adaptation to hygrophytic conditions combined with a remarkable ability on the part of many of the species to flourish in more or less xerophytic situations. In the present and following papers I propose to set out the results of my studies in the New Zealand members of the family, basing my account of the distribution and of the growth-forms of the species upon what I learned as to their occurrence in the wet district of Westland, and in Part II comparing with these facts the ecology of the family as I have learned it in the drier parts of New Zealand. In the second paper I shall also bring together those facts concerning the general distribution of the species throughout New Zealand generally, and in the outlying islands belonging to the New Zealand Biological Region, which are contained in various botanical papers in the volumes of the *Transactions of the New Zealand Institute* and in other publications.

Two noteworthy publications dealing with the filmy fern as a living plant are those of Giesenhagen (12) and Forrest Shreve (26). The former of these authors gives a general biological survey of the gametophyte, and more especially of the sporophyte generation, basing his account upon herbarium material. Amongst other species, he discusses seven which occur in New Zealand. Forrest Shreve's paper is the outcome of his studies on the Hymenophyllaceae of Jamaica in their natural habitat. He deals with the vertical and the regional distribution of the greater number of these species, and he describes a number of illuminating physiological experiments conducted by him with the purpose of ascertaining the exact relation of the species to the water-supply and their ability to withstand drying.

New Zealand is well known to be a special centre of distribution of the Hymenophyllaceae. In actual number of species this family constitutes one-fifth of the entire fern flora of this country, embracing twenty-seven species, of which twenty belong to the genus *Hymenophyllum* and seven to *Trichomanes*. In the heavy taxad forests of the western districts, and more especially of Westland in the South Island, where the proximity of the high mountain-ranges to the coast-line causes the rainfall to be exceptionally heavy, the Hymenophyllaceae attain a notable luxuriance, and abound

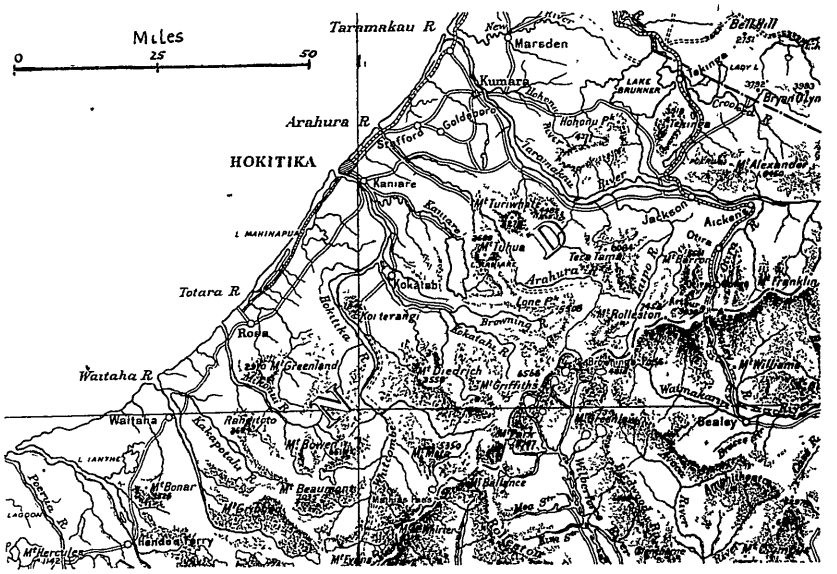
both in species and in individuals. In Westland they occur for the most part as epiphytes, clothing the trunks and overhanging boughs of the trees in sheets with their delicate drooping fronds, ranging from the forest-floor to the tops of the highest trees, and being distributed throughout the entire district from the coast-line to the subalpine zone. The suggestion to study the Hymenophyllaceae was made to me by Dr. L. Cockayne, F.R.S., some six or seven years ago, on my first going to live in Westland; and I have to thank him for many suggestions with regard to the scope of my work. Since then I have been able to examine thoroughly practically the whole of north Westland, as well as to see something of the forests farther south. My account of the Hymenophyllaceae as they here occur will be found, I think, to be fairly complete. I have also been able personally to study the family in the southern-beech and other forests of both Canterbury and Nelson at many selected places, and to trace its distribution in the Auckland District.



MAP 1.—The New Zealand Biological Region.

Of the four species of the family which do not seem to occur in Westland, two—viz., *Trichomanes elongatum* and *T. humile*—I have been able to study in North Auckland, while fresh material of *Hymenophyllum atrovirens* was kindly sent to me, with field-notes concerning it, by Mr. W. J. Williams, of the City Engineer's Office, Dunedin. Mr. H. Carse, of Kaiaka, North Auckland, early in my work sent me ample material of *T. humile*. I am glad to take this opportunity of thanking both these gentlemen. The fourth species, *H. ciliatum*, has never been rediscovered in New Zealand since it was first reported from Nelson over fifty years ago, but through the kindness of Mr. Cheeseman I have been able to examine material collected in the West Indies. It will thus be seen that all of the New Zealand species have been available for the purposes of this study.

The original photographs were the work of Mr. C. Beken, of Christchurch, and were taken from specimens in my own collections. These illustrations may be regarded as typically showing the species as they occur in Westland, with the exception, of course, of those which I have not been able to find there. Mr. T. F. Cheeseman, F.L.S., has informed me that they well represent also the form shown by the species in the deep ravines of the wet districts of the North Island, adding that he sees no indication of distinct geographical races. I am greatly indebted to Mr. Cheeseman, who has on many occasions generously placed at my disposal his knowledge of the distribution of the Hymenophyllaceae in many parts of New Zealand. I have to thank also the Director of the Government Meteorological Department for kindly supplying me with the rainfall and other meteorological data included in this paper. Finally, it gives me much pleasure to acknowledge the kind invitation extended to me by the Director and the Chief of the Biological Department of the Cawthron Institute at Nelson to carry on my work at the Institute during the six months that I was in that district, an invitation of which I fully availed myself.



MAP 2.—North Westland, N.Z.

I. LIST OF THE SPECIES.

The following is the complete list of twenty-seven species which occur in the New Zealand Biological Region (see map 1), all of which, it may be added, are present on the main islands of New Zealand. The ten which, so far as is known, are endemic are indicated in the list by asterisks. For this information I am indebted to Mr. Cheeseman. For the full systematic description of the species reference must be made to the *Manual of the New Zealand Flora* (6). With the exception of *H. ciliatum*, whose existence in New Zealand is doubtful, all are illustrated in the present paper from photographs, the numbers in square brackets in the list corresponding to the number of the plates on which each species will be found. In accordance with the rules of priority in nomenclature the specific names of four of the species will be found to differ from those given in the *Manual*. Other plants

mentioned in this paper are also referred to under their corrected nomenclature :—

Hymenophyllum rarum R. Br. [56]
H. sanguinolentum Hook. f. (= *H. polyanthos* var. *sanguinolentum* Hook.) [57]
**H. villosum* Col. [58, 59]
H. australe Willd. [60]
**H. atrovirens* Col. [60]
**H. pulcherrimum* Col. [61]
H. dilatatum Swartz [62]
H. demissum Swartz [63]
**H. scabrum* A. Rich. [64, 59]
H. flabellatum Lab. [65]
**H. rufescens* T. Kirk [65, 76]
H. ciliatum Swartz
H. ferrugineum Colla (= *H. subtillissimum* Kunze) [66, 76]
H. Malingii Metten [66, 76]
**H. Armstrongii* Bak. (= *H. Cheesemanii* Bak. and *Trichomanes Armstrongii* Bak.) [67]
H. minimum A. Rich. [67]
H. Tunbridgense Smith [68]
H. peltatum Bearne (= *H. unilaterale* Willd.) [68]
H. multifidum Swartz [69]
H. bvalve Swartz [70]
**Trichomanes reniforme* Forst. [71]
**T. Lyallii* Hook. & Bak. [72, 76]
T. humile Forst. [73]
T. venosum R. Br. [72]
**T. Colensoi* Hook. f. [73]
**T. strictum* Menz. [74]
T. elongatum A. Cunn. [75]

Illustrations of all of these species, with the exception of *H. ciliatum*, are given in Field's *Ferns of New Zealand* (11). I must, however, point out that *H. minimum* and *H. Armstrongii* are there incorrectly figured. Four species—namely, *H. atrovirens*, *H. Malingii*, *T. Lyallii*, and *T. Colensoi*—are figured in Cheeseman's *Illustrations of the New Zealand Flora*, vol. 2 (7), and *H. Malingii* also in a paper by L. Cockayne, published in *The Plant World*, entitled "Some Noteworthy New Zealand Ferns" (9). Three species are figured in the *Transactions of the New Zealand Institute*—viz., *H. rufescens* (vol. 11, p. 457), *H. Armstrongii*, and *H. atrovirens* (vol. 10, p. 394). *H. pulcherrimum* is illustrated in J. D. Hooker's *Flora Novae Zelandiae*, vol. 2 (15).

The following seven New Zealand species are found also in Tasmania (25) : *H. rarum*, *H. australe*, *H. flabellatum*, *H. Malingii*, *H. Tunbridgense*, *H. peltatum*, and *T. venosum*. Several of these, as well as *H. bivalve* and *T. humile*, occur also in New South Wales (20, 21). In his *Handbook* Rodway notes that *H. rarum*, *H. flabellatum*, and *T. venosum* occur commonly in Tasmania on the stems of tree-ferns, *H. australe* and *H. Tunbridgense* on mossy rocks, and *H. Malingii* on the bark of *Athrotaxis*† *selaginoides*, habitats which are closely similar to those adopted by these species in the less wet parts of New Zealand. Two additional species—viz., *H. multifidum* and *H. minimum*—are found on Lord Howe Island (23), whose flora gives evidence of both New Zealand and Australian affinities. Eight species are said by Cheesemen (6) to occur in Polynesia or Malaya—viz., *H. rarum*, *H. australe*, *H. flabellatum*, *H. dilatatum*, *H. demissum*, *H. multifidum*, *T. humle*, and *T. elongatum*. Two species—viz., *H. rarum* and *H. ferrugineum*—are found in South America, while *H. ciliatum* is well known from tropical America and tropical Africa. Two only, *H. Tunbridgense* and *H. peltatum*, are more or less cosmopolitan, although *H. rarum* is widely distributed throughout the Southern Hemisphere.

The New Zealand Biological Region includes, in addition to the three main islands of New Zealand, several outlying groups—viz., the Kermadec Islands to the north-east, the Chatham Islands to the east, and the Subantarctic Islands to the south. None of these outlying groups possesses species of Hymenophyllaceae which are absent from New Zealand itself. As is well known, the New Zealand flora as a whole is composed of several distinct elements additional to that peculiar to the country itself—namely,

† A common spelling of this genus is *Arthrotaxis*, but is is pointed out by Baker and Smith in their work entitled *A Research on the Pines of Australia* (Sydney, 1910) that the original spelling of Don, who established the genus, is *Athrotaxis*, and that this is in accordance with the derivation of the name.

H. rarum R. Br. Mesophytic and stunted forms. Nat. size.

Face p. 580.]

the Malayan, the Australian, the Fuegian, and the Cosmopolitan elements. It will be seen that these elements are represented in the New Zealand Hymenophyllaceae.

II. The Climate and Forest-covering of Westland.

As this paper deals particularly with the distribution of the Hymenophyllaceae in Westland, certain details concerning the climate and forest-covering of this part of New Zealand must be given. The dominant feature in the topography of the South Island is the snow-clad ranges of the Southern Alps, which extend throughout almost the entire length of the Island in more or less close proximity to the western coast, forming a natural high barrier in the path of the prevailing westerly moisture-laden winds. On account of this the western districts receive by far the greater part of the rains, and carry from the coast-line back on to the ranges a continuous heavy mixed forest. The chief topographical features in Westland to be taken into consideration are the very narrow coastal flats, the river-plains, river-terraces, and morainic hills, the isolated outlying ridges and mountains, the flanks of the main ranges, and the gorges through which the rivers emerge on to the lowlands, practically the whole area being heavily forested. These features are indicated in map 2, on page 579. The lowlands are, in north Westland, not more than twenty miles in width, becoming narrower still farther south on account of the coastwards trend of the ranges.

The climate is characterized by a heavy rainfall, an infrequency of high and especially of drying winds, and an absence of extremes of heat and cold. In the latitudes in which New Zealand lies the prevailing winds are from the north-west and the south-west, and are heavily moisture-laden. An east wind is very occasionally experienced in the lowlands of Westland—more frequently, however, on the flanks of the ranges—and this is cold and more or less dry: it is the only wind which is able to wither the fern vegetation in exposed localities. The precipitation takes place mainly on the western side of the Island, and especially upon the ranges themselves. The eastern side of the Island, on the other hand, experiences a dry climate, the north-west wind arriving over the mountains for the most part bereft of all its moisture. These heavy dry winds undoubtedly here play a chief part in determining the nature of the plant-covering. The greater part of this eastern area is covered by tussock-grass, but the eastern flanks of the main ranges and also of the outlying mountains of Canterbury carry a more or less continuous covering of the southern-beech forest, whilst the latter mountains in South Canterbury show in places, on account of the added southerly precipitation, a true rain forest. In my next paper I hope to give a detailed account of the distribution of the Hymenophyllaceae throughout this Eastern Botanical District, comparing it with their occurrence in Westland under the different conditions of altitude and forest-covering, and of rainfall and wind. Carefully collected facts with regard to the relative abundance of the species, the presence or absence of individual species, and the particular station in the forest adopted by them, and as well the growth-form exhibited by the more plastic members of the family, undoubtedly may be regarded as reliable indications of the climate prevailing in the interior of a forest, and should prove of use in general forestry work.

The subjoined meterological data (Table A) are given with the object of showing, by means of a contrast drawn between the climates experienced at the west coast (Hokitika) and east coast (Lincoln) respectively of the South Island, the very favourable conditions prevailing in the forests of Westland for the Hymenophyllaceae. All the data given in this table were taken in

TABLE A.

Meteorological Data for Hokitika and Lincoln, situated on the West and East Coasts respectively of the South Island, New Zealand, giving the Means for the Period 1911–20 inclusive.

—	January.	February.	March.	April.	May.	June.	July.	August.	September.	October.	November.	December.	Year.
Rainfall, in inches—													
Hokitika	10·44	6·60	8·22	10·61	8·09	8·29	8·90	9·05	11·07	12·04	17·76	8·79	114·86
Lincoln	2·58	2·14	1·32	2·04	2·43	2·35	2·95	1·47	2·07	1·61	1·93	2·30	25·19
Rainy days—													
Hokitika	16·7	11·2	14·1	17·7	14·7	17·0	16·4	15·7	19·8	19·7	21·6	15·3	199·9
Lincoln	9·6	8·2	8·3	9·6	11·3	12·1	12·3	10·6	10·0	9·8	12·5	10·1	124·4
Mean humidity—													
Hokitika	77·0	77·6	76·5	76·3	73·2	75·9	73·1	72·9	75·5	77·7	79·6	79·5	76·3
Lincoln	68·2	70·8	69·3	71·9	74·5	76·5	76·7	74·9	71·6	69·6	69·5	68·2	71·7
Average daily velocity of wind, in miles—													
Hokitika (1911–19) ..	139·8	115·7	103·0	103·8	87·3	87·2	87·2	97·7	147·8	168·3	175·7	159·2	122·7
Lincoln	148·1	125·5	120·0	100·0	89·2	84·9	84·1	96·6	116·0	135·6	138·3	141·8	114·4
Sunshine, in hours and minutes—													
Hokitika (1913–20) ..	192 24	177 26	177 27	130 37	141 55	101 44	109 20	153 32	135 26	162 6	171 36	217 41	1871 14
Lincoln	217 85	188 12	197 5	152 45	137 55	113 40	124 73	153 50	176 5	218 5	208 32	213 65	2103 52
Shade temperature—													
Hokitika—													
Mean maximum ..	65·5	66·9	65·9	61·5	56·4	52·7	53·3	54·4	56·8	58·8	59·9	62·9	59·6
Mean minimum ..	51·5	52·6	51·1	47·5	40·3	38·2	37·6	37·9	42·6	45·4	47·0	49·1	45·0
Lincoln—													
Mean maximum ..	72·5	71·1	69·4	64·7	65·8	53·0	52·0	54·0	59·3	64·5	66·6	69·5	63·5
Mean minimum ..	50·6	54·4	49·3	44·7	39·3	36·2	36·0	36·6	40·5	43·8	45·7	47·5	43·7

the open, and do not, of course, refer to actual forest conditions. Moreover, the two stations mentioned are situated at sea-level, where the climate experienced will differ from that on the sides of the ranges. However, the general contrast will serve a useful purpose. The lack of drying winds in Westland—one of the most important facts for the present purpose, but one which cannot adequately be shown in a table—the low summer temperature and also daily range, the heavy rainfall and large number of rainy days evenly distributed over the whole year, all point to the fact that in its forests the humidity will be more or less consistently high, and that transpiration from frond and leaf surface will probably never be excessive. The fact that Hokitika lies in the path of the prevailing westerly moisture-laden winds is accountable for the greater average daily wind-velocity recorded there than at Lincoln, at which latter station the strong and exceedingly dry north-west winds are at certain times of the year frequently experienced.

The meteorological figures for Hokitika may be considered to represent fairly accurately the climate experienced throughout north Westland at the coast-line. Table B shows the amount of rainfall in inches and the number of rainy days at Hokitika for each month during the period 1911–20, from which it will be evident that Westland experiences neither seasonal dry periods nor even occasional periods of drought. This is, of course, an important fact to be noticed in connection with the distribution of the Hymenophyllaceae, since this family demands a constantly high atmospheric humidity which quite conceivably could be lacking notwithstanding a high annual rainfall.

TABLE B.

Detailed Meteorological Data for Hokitika, Westland, N.Z., showing Monthly Rainfall and Rainy Days for the Period 1911–20 inclusive.

——	Jan.	Feb.	Mar.	April.	May.	June.	July.	Aug.	Sept.	Oct.	Nov.	Dec.	Year.
1911.													
Rainfall ..	14·08	1·03	8·33	7·94	6·94	6·29	2·42	5·66	10·00	14·10	14·84	13·26	104·89
Rainy days..	7	5	12	15	8	13	6	12	17	17	24	20	156
1912.													
Rainfall ..	10·86	8·24	7·98	11·87	6·48	14·38	4·44	9·14	18·66	11·12	9·50	2·94	115·61
Rainy days..	12	9	13	19	12	20	9	14	25	16	17	11	177
1913.													
Rainfall ..	8·85	4·74	10·68	4·29	7·64	9·13	12·73	7·49	11·49	9·62	10·04	4·27	100·97
Rainy days..	22	17	25	15	17	17	26	15	28	19	21	17	239
1914.													
Rainfall ..	13·74	5·97	3·30	11·65	9·81	5·75	7·98	6·00	7·64	6·59	19·16	14·73	112·32
Rainy days..	23	9	10	23	13	18	21	16	15	21	24	21	214
1915.													
Rainfall ..	13·93	15·61	6·65	6·29	9·93	7·50	14·11	7·78	12·66	11·93	15·21	12·72	134·32
Rainy days..	24	20	14	18	16	15	16	13	22	27	24	18	227
1916.													
Rainfall ..	7·81	6·29	10·96	13·52	9·01	6·00	10·02	11·27	7·20	10·34	13·11	2·04	107·57
Rainy days..	12	13	16	13	17	15	13	22	16	16	21	4	178
1917.													
Rainfall ..	2·22	9·42	12·54	11·11	10·24	8·49	9·06	7·64	17·98	18·52	1·40	10·54	119·16
Rainy days..	11	12	14	19	21	17	25	15	20	22	13	17	206
1918.													
Rainfall ..	9·37	6·95	8·86	10·26	9·69	7·74	7·99	13·52	10·33	15·51	14·00	10·28	124·50
Rainy days..	13	15	9	21	18	18	18	16	20	21	24	16	209
1919.													
Rainfall ..	14·26	2·64	5·24	7·89	2·59	12·09	9·85	8·65	7·72	9·15	13·18	6·27	99·53
Rainy days..	27	10	14	17	7	19	16	21	17	18	23	16	205
1920.													
Rainfall ..	9·26	5·15	7·67	21·32	8·62	5·53	10·42	13·39	6·98	13·59	17·17	10·86	129·96
Rainy days..	16	12	14	17	18	18	14	13	18	20	25	13	198

The total annual rainfall at the western coast-line of the South Island increases from north to south on account of the coastwards trend of the ranges in that direction. This is indicated in the following summarized figures for four coastal stations, from Westport in the north to Okuru in the south, which have been copied from the *New Zealand Geological Survey Bulletin No. 18*, 1917: Westport, 78·36 in. over a period of twenty-three years; Greymouth, 100·90 in. over twenty-five years; Hokitika, 116·23 in. over thirty-four years; Okuru, 148·16 in. over ten years.

The heaviest rainfall in Westland is experienced on the western flanks of the ranges, and especially in the river-gorges. For example, the average annual rainfall at Otira (see map 2, on page 579) for the period 1911–20 was 195·55 in., and the number of rainy days 176·5. This station lies at the western end of Arthur's Pass, at an altitude of 1,255 ft., and its rainfall and other meteorological features are probably fairly typical of those of similar localities along the west side of the dividing range. From the point of view of the fern flora it is important to note that both westerly and easterly winds at Otira are far heavier, and the latter wind more drying, than in the lowlands of Westland.

Although the timber-milling industry has been well established in Westland for some considerable time, the area still wholly untouched is comparatively large, while in south Westland the forest is practically altogether virgin. This is in striking contrast to the condition of the various isolated forests in eastern Canterbury, where the pines have largely been cut out, and where the only primitive forest is that contained in scenic or water-supply reserve blocks.

The extreme type of New Zealand rain forest is found most characteristically in Westland. Here the southern beech, which farther north is present along with the taxads, is absent except in the extreme south. The two species *Nothofagus fusca* and *N. Menziesii* extend down from the north as far as the Taramakau Valley, but do not cross it, except to a negligible extent in the upper portion of that valley. The mountain species *N. Cliffortioides* occurs as a continuous forest along the eastern flanks of the dividing range, but outside the Westland boundary. The principal tree members of the Westland mixed heavy forest are *Metrosideros lucida* (the southern rata), *Weinmannia racemosa* (kamahi), *Elaeocarpus Hookerianus*, and the taxads *Dacrydium cupressinum* (rimu, or red-pine), *Podocarpus kahikatea* (kahikatea, or white-pine), *P. spicatus* (matai, or black-pine) and *P. ferrugineus* (miro). Of the smaller trees, whose tops constitute the forest story beneath the canopy, those usually present along with small trees of the above-mentioned species are *Quintinia acutifolia* (locally misnamed "white-birch"), *Carpodetus serratus*, *Ascarina lucida*, *Griselinia lucida*, *Schefflera digitata*, and various species of *Nothopanax*. The tree-fern *Dicksonia squarrosa* is everywhere most abundant, and also, although to a less extent, *Cyathea Cunninghamii*. This may be described as the prevailing association or heavy mixed taxad forest. It covers the coastal flats, the lowland river-terraces and morainic hills, and the lower slopes of the mountains. Other particular associations are those of the river-flats and of the higher mountain-slopes. In the former of these the white and black pines are practically the only trees present, and the undergrowth is composed largely of such small-leaved shrubs as the various species of *Coprosma*. Another association prevails at altitudes of from 1,500 ft. to 3,000 ft., and consists of the southern rata, the mountain-totara (*Podocarpus Hallii*), and the kawhaka (*Libocedrus Bidwillii*), the other above-mentioned

taxads being absent. The kawhaka descends also in some localities into the lowlands, where it forms a very characteristic feature. The last association to be noted is that in which the small-growing *Dacrydium Colensoi* (the silver or Westland pine), and to a less extent *D. intermedium* (the yellow-pine) are present. These are found chiefly in swampy terrace-land, and in the sapling stage, along with *Phyllocladus alpinus* and various young taxads, are abundant on the " pakihis " or sphagnum bogs where older trees have been cut out. They also occur in open places at higher altitudes.

Throughout the heavy mixed forest where the canopy is more or less closed the Hymenophyllaceae are very abundant both in species and in individuals. Where the larger trees are more scattered, or where they have been partly cut out, the slender sapling-like *Quintinia*, with its erect stems, is the dominant tree of medium size, tree-ferns are largely absent, and the Hymenophyllaceae, along with other epiphytes, are more scantily represented. Generally speaking, however, the tree-ferns are a characteristic feature of the heavy mixed forest throughout the lowlands, and their fronds constitute a close story next above the floor, sheltering a luxuriant growth of filmy and other ferns, mosses, and liverworts on their stems and on the floor and fallen logs. The story next below the canopy is composed of the tops of the mixed assemblage of shrubby trees, several of which have comparatively large leaves, whose horizontally-spreading branches are thickly covered with epiphytic ferns, while some of the latter, including several species of *Hymenophyllum*, along with epiphytic orchids and species of *Astelia*, spread up the trunks of the tallest trees, and flourish even in the canopy. In short, on account of the uniformly high atmospheric humidity prevailing throughout Westland, there is a very general and abundant distribution of the Hymenophyllaceae, the main differentiating factor in their regional distribution being that of altitude, another operating more locally being that of the particular forest subassociation present.

III. The Distribution of the Species in Westland.

It is, of course, apparent that the study of the forest flora of any particular district involves the close comparison of gullies with hillsides and ridges, and also the detailed observation of the epiphytic flora from the tree-bases to the canopy, as well as the more general comparison of the lowland with the upland and subalpine floras. In studying the high epiphytes in Westland I have been greatly assisted by the sawmilling which is at work in many different localities, being thereby able to examine thoroughly the tops of large numbers of newly felled trees throughout the district. Wind-felled trees also were examined at every opportunity. With respect to the Hymenophyllaceae in the forests of Jamaica, Forrest Shreve (26) has drawn attention to the facts regarding the relative occurrence of the species on the mountain-slopes and ridges and in the ravines. He there found (*ibid.*, bottom of p. 189), with regard to both the Hymenophyllaceae and the epiphytes generally, that " the trees of the upper slopes have the same epiphytic flora that would be found in the upper two-thirds of the [height of the] trees of the ravines, while the trees of ridges and peaks have only those that are characteristic of the uppermost third, and the mid-height species are restricted in these habitats to the sides of prostrate trunks or fallen logs." I may state briefly that the present study bears out this statement in a general way with regard to the more widely ranging members of the New Zealand Hymenophyllaceae, but that since certain species are confined altogether to lower altitudes and others to higher,

and some again are altogether terrestrial or low epiphytic plants, a really satisfactory description of the distribution can only be gained by going into the question in much greater detail.

The only published information dealing with the occurrence of the Hymenophyllaceae in Westland is contained in a list of plants collected by A. Hamilton in the district of Okarito, south Westland. He there records (13) the presence of twenty species, omitting the four which I also have been unable to find, and also *H. australe*, *H. Malingii*, and *H. bivalve*. Hamilton was not able to explore the flanks of the ranges. In the same volume T. Kirk published some brief notes on a few of the species collected by Hamilton.

I have found that in Westland the species occur to a great extent in groups according to their habits. It will be convenient to refer to them as far as possible in these groups.

A. *The Groups of Species and their Occurrence.*

(a.) *H. dilatatum*, *H. scabrum*, *T. reniforme*. (Plates 62, 64, 59, 71.)

Beginning with those species which are more or less confined to the lowlands, there is first the group *H. dilatatum*, *H. scabrum*, and *T. reniforme*. Throughout the lowlands of Westland these three species are found in abundance, and almost invariably in close association. Up to an altitude of 1,200 ft. they occur as low and middle epiphytes, and at somewhat higher altitudes on mossy boulders and in a low epiphytic station, in gorgy streams on the mountains. In these last-named localities the prothalli and young sporeling plants of all three species can usually be found in abundance both on tree-trunks and on boulders, this showing that the humidity conditions are here especially favourable. All three species, however, are absent from the forests on the flanks of the ranges. *T. reniforme*, with its erect fronds, prefers large surfaces on which to grow, such as are afforded by the trunks of trees, but the two others keep to horizontally-growing boughs, from which they are pendulous. In various places in the lowlands where the larger trees have been cut out I have noticed these three species growing, though somewhat scantily, upon the floor, but in the heavier forest they are not to be found in this station. Their fronds show a comparatively very large extent of lamina. *T. reniforme* possesses a peculiar unsegmented form of frond, and the margin of the lamina is strongly thickened. The lamina of the frond-segments of *H. dilatatum* is very broad, and the segments tend to be confluent; the rhachis is also broadly winged. The fronds of this latter species and of *H. scabrum*, when pendulous, are as much as 2 ft. or more in length. A characteristic feature of *H. scabrum* is the clothing of reddish jointed hairs on the stipe (see Plate 59).

Apart from the fact that the fronds of *H. dilatatum* and *H. scabrum* assume a shorter and more deltoid form when growing erect on rocks, the species of this group are unable to modify the frond-form by stunting and imbrication after the manner of certain other mid-epiphytic species of the family. The fronds of *T. reniforme*, however, inroll closely under dry atmospheric conditions, and it is no doubt the possession of this character, combined with its short stiff frond-form, that enables this species to climb higher than the two others, and to endure a mid-epiphytic station in localities too exposed for the latter.

It is well known that these three species, contrary to what is the case in the family as a whole, possess in the adult frond a lamina which is several cells in thickness, and with respect to this character they have

been looked upon as the least-specialized members of the family. I may state briefly that from an examination of the sporeling plants of all three species I have found that the multi-layered condition is developed secondarily in the ontogeny and from the vein outwards towards the margins. The first-formed frond in all three species is of a simple linear form with an unbranched vein. The lamina is one cell in thickness, except immediately adjoining the vein, where it is three-layered, the outer dorsal and ventral cell-layers extending over the vein. Sections of succeeding fronds of young sporelings show that the next stage toward the multi-layered condition is attained by the development of a second and inner layer of small cells overlying the vein both dorsally and ventrally, at the same time the two or three interior cells of the lamina laterally adjoining the vein increasing in number by subdivision, and also in size, so that this multi-layered zone begins to extend outwards into the lamina proper. The further development of this zone results from indiscriminate periclinal and anticlinal divisions of the cells of both the outer and the inner layers of the lamina, so that in progressively older fronds both its gradual outward extension towards the margin and also the further increase in width of the inner layer of the lamina in the same direction can clearly be traced. In these young sporeling plants, and even to a much later stage in their development, there is a broad zone of lamina extending inwards from the margin which remains in the original one-layered condition, and the irregular edge of the multi-layered portion of the lamina where it adjoins the outer one-layered portion can easily be seen by the naked eye. In all three species the cells of the inner layer of the lamina are comparatively large, and probably function as a water-reservoir. In young sporelings of *T. reniforme* progressively older fronds show a repeated forking of the vein and of the lamina, so that the young frond becomes somewhat digitate in form. The lamina soon extends and webs the segments together, although the margin of still older fronds remains more or less crenate. The lamina of the adult composite frond of this species is multi-layered to the margin, but whereas it is five cells thick in the oldest basal parts of the frond, it becomes four and finally only three cells thick towards the margin. It must be added that in well-grown plants all new fronds are reniform from the first.

In the case of *H. scabrum* the multi-layered condition is attained much later than in the two other species, appearing first in the oldest parts of the developing frond. In this species the segments of the mature fronds and the wings of the rhachis permanently remain one cell in thickness for some distance in from the margins.

It is to be noted in this connection that in the case of *T. elongatum*, in which species also the frond-lamina is particularly extensive, the lamina is two or three cells in thickness in those parts of the pinnae where the larger veins converge, but only in the immediate vicinity of the veins—*i.e.*, the multi-layered condition does not extend outwards very far towards the margins. The pinnules of *H. demissum* show a circle of parenchyma one cell thick completely surrounding the veins, but in most of the New Zealand species even this is absent. Further details concerning the frond-anatomy of the New Zealand species cannot here be given, but the above facts have been mentioned to indicate that the multi-layered condition of the lamina in the three species of the group under consideration may, after all, be a specialized and not a primitive feature. This point will again be referred to.

No doubt the multi-layered condition of the lamina in these three species assists them, even in the absence of the ability to modify the frond-form, to endure the mid-epiphytic station, by ensuring a supply of water within the frond.

(b.) *H. ferrugineum* and *T. venosum.* (Plates 66, 76, 72.)

These two species form a very characteristic group, which also is confined to the lowlands. Along with *Tmesipteris* and *Lycopodium Billardieri* var. *gracile* they occur very commonly on the stems of tree-ferns, and more especially upon *Dicksonia squarrosa.* In the heavy forest of the lowlands these two species are rarely to be found on other than tree-fern stems, but at the foot of the ranges *T. venosum* occasionally occurs also on the bases of large forest-trees. In deep narrow ravines in the same localities *H. ferrugineum* not infrequently may be found on dripping mossy rock-walls, its fronds being here actually bathed in water to a far greater extent than most Hymenophyllaceae naturally seek. In such stations the fronds are apt to become very attenuated in form, some which were measured being 1½ ft. in length and only from ¼ in. to 1 in. in width. These two species are always low epiphytes, and are evidently strongly hygrophilous.

T. venosum is a small delicate species, and occurs in close mats, its fronds pendulous and overlapping. *H. ferrugineum* also occurs in more or less close overlapping colonies with pendulous fronds, but is less mat-like. The latter species is reddish-brown in colour, whence its name, being clothed on the surface and on the margins of the lamina with short stellate hairs (Plate 76). These two species have a range practically identical with that of the *Dicksonia*—*i.e.*, up to about 1,400 ft.—but this tree-fern in the Westland climate will flourish alongside forest-roads and in clearings where the humidity is not consistently high enough for the filmies. *H. ferrugineum* is rather more restricted in its regional distribution than *T. venosum.* In not a few localities on the lower slopes and at the base of the ranges where tree-ferns are abundant the latter filmy fern is present but not the former. The tree-fern fronds seem to give the close shelter needed, and the trunks afford a substratum more constantly damp than the bark of trees. The favourable nature of such a station for pteridophytic growth is attested by the fact that the prothalli and sporeling plants of both *Tmesipteris* and the *Lycopodium,* as also of various species of ferns, occur abundantly along with many small liverworts on the stems of *Dicksonia. T. venosum, H. rarum,* and *H. flabellatum* are said to occur commonly in Tasmania on tree-fern stems (25), and in rather drier parts of New Zealand, also. the two latter species frequently adopt this station along with the two which usually occur there. It will be noted that all these tree-fern-loving Hymenophyllaceae possess a filiform stipe.

T. venosum probably affords an example of reduction. The margins of the frond-segments are irregularly sinuate in outline, and the veins give rise to secondary and tertiary veinlets which end in spurious venules. Individuals can occasionally be found in which the pinnae are further divided, bearing from two to four sori.

(c.) *H. sanguinolentum, H. multifidum,* and *H. villosum.* (Plates 57, 69, 58, 59.)

Taken individually, these three species are the most abundant in the New Zealand family, not only in Westland but throughout the North and South Islands generally, although the last-named towards the north becomes more and more restricted to higher altitudes. In the middle lowlands of Westland they are to be found usually together, but whereas *H. multifidum* occurs from sea-level to the highest altitudes attained by the Hymenophyllaceae, and is an invariable member of this group, the two other species are more or less complementary in their distribution. *H. villosum* is absent from the coastal forest and is properly a mountain plant, while. on the other hand, *H. sanguinolentum* is abundant at sea-level but does not

H. sanguinolentum Hook. f. Mesophytic (upper half of frond) and stunted forms. Nat. size.

Face p. 588.]

H. villosum Col. Mesophytic and stunted forms. Nat. size.

H. villosum Col. Young frond showing hairs. × 1½.
H. scabrum A. Rich. Stipe showing hairs. × 1½.

H. australe Willd. (centre). × $\frac{7}{9}$.
H. atrovirens Col., showing two forms. × $\frac{7}{9}$.

ascend much above 1,200 ft. As will be shown later, intermediate forms may sometimes be found at intermediate altitudes, which may equally well be referred to either of these species. Cheeseman notes (6, p. 932) that Hooker originally placed *H. villosum* as a variety of *H. sanguinolentum*, and remarks that the two are closely allied. The two species are very distinct, however, in the forms in which they usually occur, and in these forms, from the middle lowlands to the base of the ranges, occur commonly together, but the presence of intermediate forms undoubtedly gives added significance to the fact of their more or less complementary distribution. In the lowland forests *H. multifidum* and *H. sanguinolentum* are middle epiphytes, but they also occur here in the tops of the forest-trees in a stunted form along with several other species. In favourable places in the forest, where their fronds can hang from the undersides of horizontally growing boughs, they attain as middle epiphytes a most luxuriant growth. *H. villosum* descends as far as the middle lowlands, and it there occurs commonly with the two other members of this group in the tops of the rimu and other forest-trees, but not as a mid-epiphyte.

On the lower parts of the ranges *H. multifidum* and *H. villosum* occur commonly together both in the gullies as high epiphytes, and on the spurs and valley-sides on the lower branches of the trees, *H. sanguinolentum* being here absent. At still higher altitudes *H. multifidum* descends to the floor in moss, but *H. villosum* retains for the most part a low epiphytic station on the stunted trees. This difference in behaviour between the two species is found to hold also in other parts of New Zealand. When growing terrestrially *H. multifidum* adopts a very characteristic "mountain form" (Plate 69), in which the segments of the small strictly deltoid frond are more or less inrolled and overlap one another, and the frond as a whole is decurved and lies close to the moss in which the plants are growing. The short segments on which the sori are borne then bend sharply upward, so that the sori stand erect although the frond is practically horizontal. This mountain form is very distinct, and is found wherever the species occurs on the ground at altitudes above 1,500 ft. Occasionally fronds on terrestrially-growing individuals of the mountain plant may be found intermediate in form between the pendulous epiphytic and the deltoid terrestrial form, but this seems to be always when the fronds are able to hang freely. This species, along with *H. villosum*, is found also at altitudes above the subalpine forest, *H. multifidum* in sheets on moss or damp rock-faces and in other specially favourable places, and *H. villosum* in close mats on rocks and boulders and in other extremely xerophytic situations, as well as epiphytic on the shrubs. In sheltered gullies at lower altitudes the fronds of *H. villosum*, though generally deltoid in form and erect-growing, attain an extreme length of 6–9 in. and become pendulous, but in exposed situations at higher altitudes they are exceedingly stunted and imbricated. Moreover, in these latter situations the hairy clothing of the frond, from which this species derives its name, is well developed, not only the rhizome and young fronds but also the mature fronds, which in more mesophytic situations are bare of hairs, being strongly villous.

Along with the changes which take place in this association as we proceed from lower to higher altitudes it is found that even in the middle lowlands, in localities where for some particular reason the humidity is liable to unusual fluctuations, *H. villosum* is the member most consistently present and *H. sanguinolentum* the one most likely to be absent. For example, in the small-leaved totara-coprosma scrub which commonly occurs on the river-valley flats under the white and black pines, or still higher

up the flats where the latter are absent, the three species occur abundantly and together as low epiphytes wherever the thicket is tall and close. Even *T. reniforme*, and sometimes also *H. dilatatum* and *H. scabrum*, may occur here, though somewhat scantily, whenever a greater variety of shrubby trees is present. But where the thickets are more open *H. villosum* alone is present, though still as an abundant epiphyte. These river-flats are more open to the effects of the infrequent but drying east winds off the mountains than are the closer forests of the terraces and coastal flats, and the moss and epiphytes on the shrubs are at these times liable to be shrivelled for several days together. It is noticeable that *H. villosum* can recover from such shrivelling to a more marked degree than either *H. sanguinolentum* or the ordinary mesophytic form of *H. multifidum*.

(d.) *H. flabellatum*, *H. rarum*, *H. rufescens*, and *T. Lyallii*. (Plates 65, 56, 72, 76.)

The next group to be considered consists of four species whose characteristic habit is that of occurring in close colonies in large crevices and other overhung places on the bases of large trees, and also, in the case of the two first-named, on the underside of leaning tree-trunks and stout branches. *H. rufescens* does not descend into the lowlands, and *T. Lyallii* also prefers the mountain-flanks, although it descends occasionally to sea-level; but the other two species are more wide-ranging. They all agree in the slender capillary nature of the stem and rhizome. The two larger-growing species, *H. flabellatum* and *H. rarum*, are characteristically pendulous in habit.

H. flabellatum and *H. rarum* are abundant throughout the lowlands as middle epiphytes on large-stemmed trees, where they adopt the overhanging station. Here they frequently grow most luxuriantly, the fronds of both species attaining an extreme length of 9–12 in. It is noticeable how rapidly these two species respond to changes in the environment, on the same tree-trunk the growth-form being open with elongated fronds, or, again, mat-like with fronds stunted and pinnae closely imbricating, according to some change in the surroundings which cannot always be discerned. On account of the ease with which they can thus modify the growth-form, they are able to occupy in their stunted form comparatively xerophytic stations, being found commonly in the lowlands as high epiphytes in mats in the canopies of the forest-trees, although *H. flabellatum* to a less degree than the other. In the gullies on the ranges they ascend half-way up the largest trees, but it is to be observed that *H. villosum* and *H. multifidum* overtop them in such localities.

On the sides of the mountain-valleys, and on the ridges and flanks generally, all four species occur abundantly as low epiphytes on the large bases of the rata and mountain-totara. *H. rufescens* and *T. Lyallii* attain here their optimum development. The fronds of these two species are hairy (Plate 76), the hairs in the case of the latter being branched and confined to the margins of the lamina, and in the former being long and silky and of a simple form, thickly clothing the stipe and rhachis and the costae on both sides of the frond. These two small-fronded species are practically fixed with respect to the frond-form, and do not stunt or imbricate. They never vary from the low epiphytic station, and always preserve the mat growth-form with more or less overlapping fronds. In accordance with the fact that in the lowlands *H. rarum* is a somewhat more pronounced high epiphyte than *H. flabellatum*, it is found that on the mountain-sides the former invariably occupies a slightly higher position

on the tree-trunks than does the latter, these two species overtopping the other two smaller species. *H. rarum* is occasionally to be found also in close mats on the perpendicular damp rock-walls of open ravines from which *H. flabellatum* is absent.

I have rarely found the fronds of any of these four species wilted. In the gorges on the main ranges, after some unusual period of drying east winds, when practically all the epiphytic ferns and mosses show signs of drought, it is to be observed that even the large-sized fronds of *H. rarum* and *H. flabellatum* in a mid-epiphytic station are generally quite unaffected. It is to be noted that both these species are unusually coloured, *H. rarum* being a pale grey-green or even sometimes grey-blue colour, and *H. flabellatum* having a somewhat yellowish tinge. It may be that the colour acts as a protection, enabling the protoplasm in the frond-cells to withstand greater degrees of insolation and drying. The strap-shaped prothalli of *H. rarum*, and also the first-formed fronds in the sporeling plants, are of exactly the same colour as the adult fronds, and I have found the prothalli of this species, as well as both young and older plants, altogether unaffected by drought when the moss in which they were growing was dry and shrivelled. *H. rufescens* and *T. Lyallii* are clearly more hygrophilous than are the other two species, and in their sheltered station are less exposed to the danger of shrivelling.

Intermediate forms can sometimes be found at mountain altitudes which seem to link up *H. flabellatum* with *H. rufescens*, although these two species for the most part occur side by side in their usual distinctive forms. With regard to specimens of *H. flabellatum* collected on the subantarctic Auckland Island, Cheeseman says (22, p. 436) "they belong to a curious form intermediate between *H. flabellatum* and *H. rufescens* . . . which could almost be referred to either species." I may add that I have collected such intermediate forms also on Mount Hope, in the Nelson District. As Cheeseman indicates (*loc. cit.*), however, the stipe and rhachis of *H. flabellatum*, especially in its most stunted rufous form, never become quite so slender as are those of *H. rufescens*, and the frond of the latter always preserves the more delicate form characteristic of it.

(e.) *H. Tunbridgense, H. peltatum, H. Armstrongii, H. minimum.* (Plates 68, 67.)

These four species are among the smallest in the New Zealand family, showing typically the close mat growth-form, and may for this reason conveniently be grouped together. Of these the two latter are quite diminutive in size. *H. Armstrongii* is, in Westland, the most widely distributed of these species, occurring very commonly both as a low and as a high epiphyte, and ranging from the sea-coast to the upper limit of forest on the ranges. On account of its small size it is liable to be overlooked, especially as it usually grows in moss. In the lowlands it occurs quite commonly as a low epiphyte on the smooth sapling-like stems of *Quintinia* and young kamahi, on which a very thin, scanty moss covering, a most suitable substratum for such a small plant, is often present. In this station the individual plants are usually long-drawn-out and not aggregated into mats. It also occurs commonly in a more mat-like form in the tops of the tall taxads throughout the lowlands along with the other high epiphytic filmy ferns mentioned already. It is abundant on the mountain-flanks also up to an altitude of 3,000 ft., both on the stems of *Quintinia* and occasionally also in mats on mossy stones. I have also found this species in the neighbourhood of Otira, growing in dense mats

on the wet rocky walls of open ravines, situations which lie outside the shelter of the forest altogether. In such exposed localities as that last named extreme and rapid fluctuations in the atmospheric humidity will undoubtedly be frequent, and it is to be noted that the only Hymenophyllaceae which can endure these conditions are those which can adopt most typically the mat growth-form—viz., *H. villosum*, *H. multifidum*, *H. rarum*, *H. Armstrongii*, and *H. minimum*.

The frond of *H. Armstrongii* sometimes possesses a strong, dark, thickened margin, and this character was at one time interpreted as an evidence of reduction. It was also supposed to constitute a distinct form, which was accordingly given specific rank under the original name *H. Armstrongii*, the name *H. Cheesemanii* being kept for the form which lacked the marginal thickening. It has long been recognized, however, that the marginal thickening is a very variable character, and for many years the name *H. Armstrongii* has not been used. The latter name has lately been applied again to this plant instead of the other, on the ground of priority. I have found fronds of this species showing every stage in the development of the marginal thickening. This begins at the tips of the strong marginal teeth, and shows itself clearly as a brown coloration extending to the base of a tooth, and being continued along the margin of the frond to the tooth next below. It would seem to be best interpreted —as has been done by Giesenhagen (12, p. 440)—as a means for keeping the little frond flat and rigid, and for preventing curling and tearing of the lamina.

Cheeseman notes (6, p. 939) that *H. minimum* "appears to be a littoral plant, never found far from the sea." I have found it in Westland in only three, yet widely separated, localities, in each case far from the sea-coast. These three localities are the scrub-covered terminal moraine of the Franz Josef Glacier, in south Westland; low shrubby trees on the Koiterangi Plain, in the Hokitika River valley; and damp rocky walls in the lower part of the Otira Gorge.* I may add that Mr. G. Anderson, of West Oxford, Canterbury, has recently forwarded me specimens of the same species collected by him from a rock-face in Gamman's Creek, near Mount Oxford, Canterbury. It is evident, therefore, that this species is by no means a littoral plant; but it certainly appears to have a somewhat discontinuous distribution. Owing to its diminutive size, however, it is, like the preceding species, liable to be overlooked. Judging from the few localities in which I observed it, *H. minimum* is a low epiphyte or rupestral plant, which, like *H. Armstrongii*, grows in mats in short moss, and in exposed situations at higher altitudes adopts a very close mat growth-form. The sori, which, relatively to the size of the plant, are large, are borne terminally, one on each frond. Occasionally instances may be found in which a frond bears two sori.

Judging from their occurrence in Westland, *H. Tunbridgense* and *H. peltatum* are complementary in their distribution, and a comparison with the distributional data from other parts of the South Island shows that this is undoubtedly the case. The former species is extremely abundant throughout the lowland forests of Westland as a low epiphyte, and

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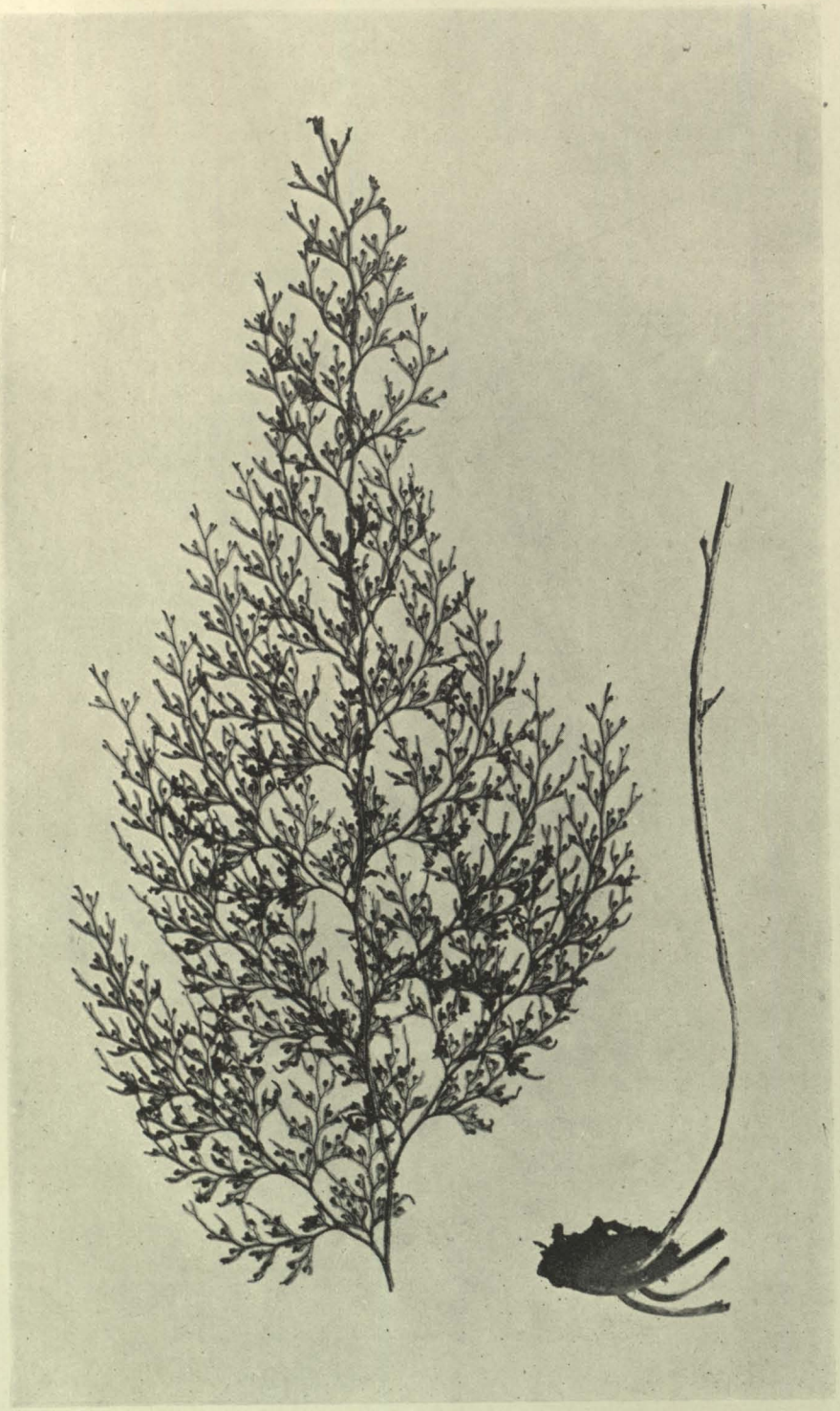
*Since writing the above I have found *H. minimum* growing abundantly in thick mats, on boulders and on the ground in moss, in damp wooded situations, along a considerable length of the Taramakau River terrace, five miles below Otira, at an altitude of about 900 ft. From its notable abundance in this locality it seems probable that this species is by no means scanty in its distribution.



H. pulcherrimum Col. Upper third of frond, and also the complete stock and the stipe. × ⅔.

Face p. 592.]

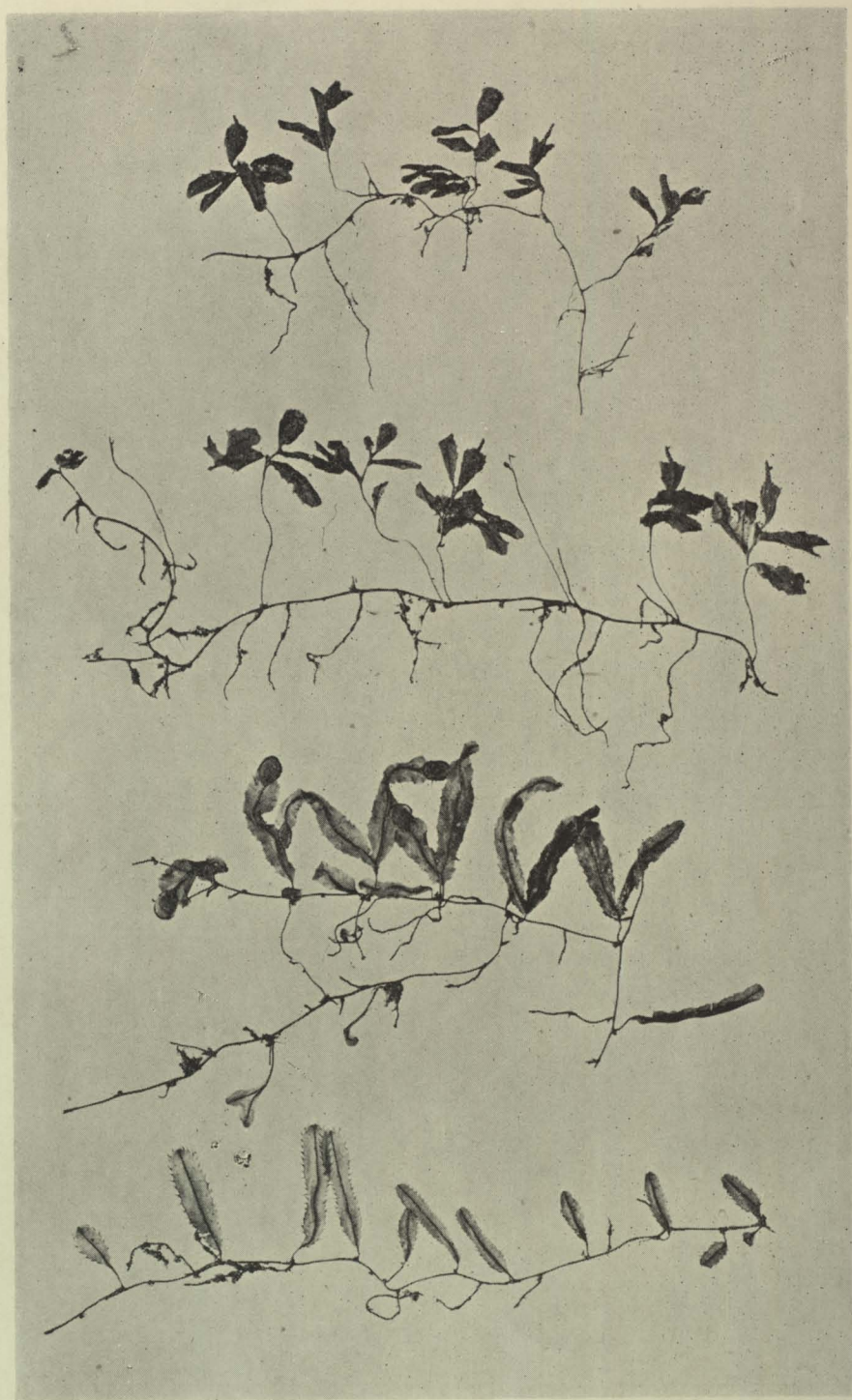
H. dilatatum Swartz. × $\frac{5}{8}$.

H. demissum Swartz. × $\frac{7}{8}$.

H. scabrum A. Rich. × ⅔.

H. flabellatum Lab. Mesophytic and stunted forms. × $\frac{7}{8}$.
H. rufescens T. Kirk (below). × $\frac{7}{8}$.

H. Malingii Metten (left). Nat. size.
H. ferrugineum Colla (right). Nat. size.



H. minimum A. Rich. (above). × 2.
H. Armstrongii Bak. (below). × 2.

H. Tunbridgense Smith. Four varieties. Nat. size.
H. peltatum Bearne (below). Nat. size.

on fallen logs, mossy boulders, &c. It occurs also at the bases of the mountains, and more especially in the valleys and creek-beds up to an altitude of about 1,300–1,400 ft., although it is here more locally and scantily distributed. *H. peltatum*, which is also a rupestral and low epiphytic species, is confined in Westland to ravines and creek-beds in the mountain-forests at altitudes above those to which *H. Tunbridgense* ascends. It is less common in Westland than on the eastern side of the South Island. In the Eastern Botanical District *H. Tunbridgense* is the rarer species, being apparently absent from the southern-beech forest. I have never observed the two species overlapping in their distribution on the Westland mountains, although, naturally, in accordance with the difference in the climate between a ravine and the neighbouring mountain-flank, the altitude at which the one species gives place to the other varies slightly from place to place. I have found intermediate forms at intermediate altitudes, which will be referred to below.

H. Tunbridgense is extremely variable in its frond-form, but from the fact that the different forms are not found intermixed, and that they are characteristic of slightly different stations, it would seem that they are the expression of small differences in the environment. Four such forms commonly to be seen in Westland are represented on Plate 68. That marked D shows the species in its normal state. A is a much larger-fronded form, with large sori, occasionally to be met with on the under-side of fallen logs. B is an attenuated form which I have met with both on bare overhanging tree-trunks, where the fronds are freely pendulous, and also more especially in thick moss on the wet rocky walls of narrow ravines. In the latter station fronds were found up to 6 in. in length in which the lateral pinnae throughout the frond remained so completely undeveloped as practically to function only as short peduncles to the sori. It was shown above that *H. ferrugineum* also adopts the attenuated form when growing in moss on the dripping vertical rocky walls of narrow ravines. The smallest form, C, is that adopted by *H. Tunbridgense* very commonly when growing at a rather greater height above the ground than usual. It no doubt represents an adaptation to a more variable atmospheric humidity. At Waimate in Canterbury, and in several localities in the neighbourhood of Nelson, I have found that this species assumes a form in which the segments of the frond are broader, the primary pinnae more developed, and the frond as a whole much larger and heavier than in any of the Westland varieties noted above. The sorus is also here especially large. This variety is not illustrated at Plate 68. Of all these varieties the latter alone can possibly be taken as indicating that in this species there may be fixed geographical races, but the extraordinary variability of *H. Tunbridgense* suggests that it represents a stock from which other species have diverged.

H. peltatum occurs in two main forms according as the situation is secluded or exposed. In narrow forest-sheltered gullies among the mountains this species may be found in thick wet moss on the horizontal boughs of the *Fuchsia* and *Olearia* shrubs which so commonly occur in these water-courses. Here it grows most luxuriantly, the fronds commonly showing when pendulous two or even more fertile zones (see Plate 68). It also occurs at the same altitudes in larger open creek-beds in close mats on the boulders, the fronds here being stunted and curled with imbricating pinnae. This species is never found in Westland on the actual flanks of the mountains, but is restricted to the more humid and sheltered gullies.

The chief characters separating *H. Tunbridgense* from *H. peltatum* relate to the branching of the pinna, the disposition of the sori, and the nature

of the indusium. In the latter species the pinnae are pinnatifid on the upper side only, whence the name "*unilaterale*," by which formerly it was known. Closely related to this character is the disposition of the sori on the upper side of the pinna in a row of from two to four, whereas in *H. Tunbridgense* they normally occur singly at the base of the pinna. Perhaps the most important distinction between the two species lies in the fact that the margins of the valves of the indusium in *H. Tunbridgense* are spinulose-dentate, but in *H. peltatum* are quite entire. For the most part these distinguishing features are very constantly present, so that the two plants can readily be identified. Occasionally, however, with respect to each of the characters just noted, I have found intermediate forms, and these have always occurred at altitudes at which the one species gives place to the other. Undoubted plants of *H. Tunbridgense* have been found showing the pinnae divided unilaterally, and in one instance with the sori in rows. Again, the margin of the indusium in this species is sometimes only slightly crenulate. On the other hand, the indusial margin in *H. peltatum* is occasionally distinctly crenulate instead of being quite entire. Referring to *H. peltatum*, J. D. Hooker (15, p. 12) says, "This differs from *H. Tunbridgense* β *cupressiforme* only in the entire lips of the involucre, otherwise these plants appear identical. I find the amount of toothing in the valves of *H. Tunbridgense* to vary extremely, sometimes amounting to a mere erosion, and at others the lips being even laciniated and spinulose, so that I can hardly doubt these two proving eventually the same species."

In the same connection I may note that the specimens of *H. minimum* sent to me by Mr. G. Anderson from Oxford, referred to above, showed in most cases the presence, but in others the complete absence, of the most important and usually invariable character which separates this species from small forms of *H. Tunbridgense*—namely, the occurrence of spine-like teeth on the backs of the valves of the indusium as well as on their margins. As mentioned above, the sori in this tiny species are usually borne singly on each frond, terminating the main rhachis, but occasionally fronds bear two sori. The sorus as a whole is unusually large, and the receptacle somewhat exserted, approximating in form to that of *H. multifidum*, so that *H. minimum* might conceivably be a much-reduced form of this species. J. D. Hooker (14, p. 104) suggests that *H. minimum* is akin to *H. multifidum*, but adds that both the small size of the former and the spinulose valves of its involucre afford excellent specific characters. He proceeds: ". . . between this plant [*i.e.*, *H. minimum*] and *H. caespitosum* of the Falkland Islands and Cape Horn much analogy exists, especially in size, locality, and habit. In each the fronds are generally once divided . . . both have the indusia free or nearly so, spinulose at the back of the valves, and, though often lateral in the latter plant, the fructifications are, especially on small specimens, very generally terminal, and may prove to be truly lateral in *H. minimum* should that plant be found in a more luxuriant state."

(f.) *H. demissum* and *H. bivalve*. (Plates 63, 70.)

Of the New Zealand species of the genus *Hymenophyllum* these two are the most characteristically terrestrial species. *H. demissum* occurs throughout Westland from the sea-coast to the stunted upper forest on the ranges. *H. bivalve*, in the mixed southern-beech and taxad hilly forests of the Nelson Province, and, more especially in its drier and lighter pure southern-beech forests, is an exceedingly abundant terrestrial plant along with *H. demissum*.

In Westland, however, *H. bivalve* is much more restricted in its distribution. It is not uncommon on the flanks of the ranges in north Westland, and even descends to the lowland hills, but I have not found it at lower altitudes, nor south of the Hokitika River. Throughout New Zealand it keeps to hilly forests in preference to those of the lowlands, and is undoubtedly an upland plant. These two species are alike in possessing a strong creeping rhizome with erect or somewhat decurved rigid deltoid fronds. *H. demissum* in Westland prefers a sloping well-drained forest-floor, and for this reason probably is not so abundant on the flatter wet floor of the lowlands as on the lower slopes of the hills and ranges, in which latter localities it occurs abundantly in extensive open colonies. In places where the forest-covering is especially close *H. demissum* may ascend the trunks of large trees and tree-fern stems to a height of 6–8 ft., but in Westland this is an unusual habit with this species. *H. bivalve*, on the other hand, shows a more marked tendency to become a low epiphyte, and this habit it preserves in other parts of New Zealand.

The frond-form in these two species scarcely varies, and even when epiphytic they possess the erect habit and deltoid form of frond-growth.

(g.) *The Remaining Species.*

It will be convenient to refer to the remaining species individually.

H. australe (Plate 60) is not found in natural association with any other member of the family. It is fairly abundant in the heavy forest of the lowlands of Westland and up to an altitude of 500 ft. or 600 ft., but does not ascend much above 1,000 ft., and at the latter altitudes is only to be found in especially humid localities. It occasionally occurs on mossy rocks, but in Westland is typically a low epiphyte on the bases of large trees, up which, in very favourable localities, it may ascend to an extreme height of 10–12 ft. Like the last two species described, it has a strong creeping rhizome with an erect deltoid habit of frond, but it may occasionally be found growing most luxuriantly with pendulous fronds as much as 15 in. in length. Thus, judging from their habit of growth in Westland, the three species *H. demissum*, *H. bivalve*, and *H. australe*, taken in this order, present a gradual progression in the change from the terrestrial to the epiphytic station. A conspicuous character of the frond in *H. australe* is the very broad crisped wing, which extends almost to the base of the stipe. Altogether, in both its vertical and its regional distribution, this species must be considered more hygrophilous even than such large-fronded species as *H. dilatatum* and *H. scabrum*, which also possess an extended lamina. It is of interest to note that *H. sanguinoletum* may occasionally be found with the same crisped and broad wing-development as is so characteristic of *H. australe*, the two species being then somewhat similar in appearance.

As previously stated, I have not found *H. atrovirens* (Plate 60) in Westland, but since this species is evidently closely allied to *H. australe* a short comparison of the two may appropriately be made here. *H. atrovirens* has not been reported frequently in New Zealand, but it always appears to be a rupestral or low epiphytic plant, and occurs at rather higher altitudes than the other species, or " on stones in gorgy streams," as Mr. Cheeseman informs me. Thus the two species seem to be complementary in their distribution. As has already been shown, there are several such pairs of species in the New Zealand family. With regard to *H. australe*, there is no doubt that the frond becomes more luxuriant when pendulous than it is when erect-growing. I have received specimens of *H. atrovirens* collected from mossy gully-walls near Dunedin whose pendulous fronds were stated

by Mr. Cheeseman, to whom I submitted them, to be "a large slender state" of this species. Although for the most part each species has a very characteristic frond-form, yet it is evident that they are in a more plastic condition than such species as *H. demissum* or *H. bivalve*, and it seems likely that one species is a derived form of the other. Since *H. atro-virens* is endemic to New Zealand, it seems reasonable to regard it as the more specialized form of the two.

H. pulcherrimum (Plate 61) is the only New Zealand species of *Hymeno-phyllum* which is tufted in its growth-form. The rhizome is rarely more than 1 in. in length, generally less, being in some cases truly erect and in others inclined. In Westland it ranges from the middle lowlands to an altitude of 2,000 ft. It is most characteristic of the deep, closely sheltered creek-beds and ravines on the lower flanks of the mountain-ranges and outliers, where it is to be found as an abundant epiphyte in thick moss up to a height of 20 ft. above the ground. It does not seem to occur in the flat coastal forest, and hence may be regarded as an upland plant. The pendulous fronds of this species probably attain a larger size than do those of any other of the New Zealand family, in favourable localities frequently reaching a length of 2 ft. to 3 ft. It differs widely in form from any other New Zealand species.

H. Malingii (Plates 66, 76) is certainly the most peculiar species of the New Zealand family both in its frond-structure and in its distribution. The extremely xerophytic frond has been described and figured by Giesen-hagen (12), and L. Cockayne (9) has drawn attention to the fact that this plant is practically restricted to the dead trunks of *Libocedrus Bidwillii* (kawhaka), and has given photographic illustrations both of the frond and of the colony.

In Westland, *Libocedrus* is a common member of the subalpine forest association, but it also descends in places into the lowlands. The restriction of *H. Malingii* to the trunks of this tree in Westland I have found to be practically invariable. The similarity in the outer surface of the trunks of the kawhaka, rata, and mountain-totara, which together make up the subalpine forest association, led me to give particular endeavour to discover whether or not *H. Malingii* occurs on either of the two latter as well as on the former, but out of some thousands of trees examined from time to time I must say that I only once found this species growing on an old rata-stump, and then but scantily. On the kawhaka, however, it grows most abundantly, and must be reckoned an abundant species throughout West-land. As has been indicated, it prefers the lower parts of dead standing trees and old stumps, and it may also be found on fallen moss-covered logs which have almost mouldered away through age. It forms fairly close colonies, with the fronds pendulous and overlapping, and it has a characteristic habit of running vertically up a standing trunk in a narrow streak to a height of 18–20 ft., following a crack or groove in the stem-surface. Its slender rhizomes ramify in the still-firm outer wood to a depth of 2–3 in. by means of the innumerable cracks and fissures. It may be that these cracks not only serve to give the *Hymenophyllum* a firm holding-place, but also act as reservoirs of water. However, I have never seen any other member of the family epiphytic on the dead kawhaka.

H. Malingii is found also in Tasmania, and Rodway (25, p. 290) states that it there occurs "on the bark of *Athrotaxis selaginoides* Don in damp shaded places." L. Cockayne (9, p. 55) notes that it has been reported in the Waimarino district, in the North Island of New Zealand, on *Dacrydium intermedium*. Field (11, p. 67) states, without mentioning the locality, that

it occurs at high levels on the decaying trunks of *Phyllocladus alpinus*. Potts (24, p. 359) records it as occurring on the hills of Banks Peninsula, Canterbury, on *Podocarpus totara* as well as on *Libocedrus Doniana*. Cheeseman (7, note to plate 235) remarks on its abundance on dead trunks of *Libocedrus Bidwillii* in the forests to the west of Mount Ruapehu, North Island, but states also that it has been found in the South Island on *Podocarpus Hallii*. Its partiality for the stems of conifers may be determined by some chemical property in their tissues. I have found it, however, growing terrestrially and most luxuriantly in thick moss in sheltered places between large granite boulders on Mount Hope, in the Nelson District, and also on the vertical faces of some of the smaller of these boulders, a station which in this particular locality was commonly adopted also by several other species of *Hymenophyllum*. Although the *Libocedrus* was not here in the immediate vicinity, it was abundant at somewhat lower altitudes. Mr. F. G. Gibbs, of Nelson, informs me that he has found it in a very similar station on rocks on the forest-covered summit of Mount Parapara (Nelson District), *Libocedrus* being present near by with *H. Malingii* upon it. The distribution of this species remains, therefore, rather a puzzle. In districts where *Libocedrus Bidwillii* is not abundant it may be found on certain other conifers, but when the *Libocedrus* is abundant, as in Westland, it is apparently confined to that tree, although the others are present alongside.

Other species of *Hymenophyllum* are higher epiphytes than *H. Malingii*, and occupy more exposed positions, but none of these, except possibly *H. dilatatum*, *H. scabrum*, and *T. reniforme*, shows any anatomical modification of the frond in accordance with its station. On the other hand, the frond of *H. Malingii* is modified to an extreme extent, so that in this respect it is probably the most remarkable member of the family. It will be sufficient to state briefly that the frond has no assimilating lamina comparable to that of other species. The vascular bundle in all parts of the frond is encircled by thick-walled tissue showing pores in the cell-walls, the outermost limiting layer being thin-walled and protruding as long cylindrical papillae. These latter contain chlorophyll, and function as the assimilatory tissue. The papillae are separated from one another by narrow air-spaces, into which water can be drawn in times of rainfall and held during periods of drought. As a protection against transpiration and evaporation of this water-film, the entire outer surface is covered by closely interlocking stellate hairs whose bases extend down between the papillae, the stellate portions resting closely against their tips. So entirely is the surface of the cylindrical segments of the frond covered by these hairs that the latter impart to it a characteristic grey or rusty-brown colour, and it is only when the frond is completely sodden with water, so that even the cavities of the hairs are filled—a phenomenon but rarely to be observed—that the underlying green colour of the chlorophyll tissue can be seen.

Trichomanes strictum (Plate 74) is one of the two tufted New Zealand species of *Trichomanes*, the other being *T. elongatum* (Plate 75). The former is a fairly abundant plant throughout the forests of Westland, ranging from sea-level to an altitude of at least 1,500 ft. The latter is apparently absent from Westland, but it has been reported by Townson (27) from the Westport district. It is abundant in the northern part of the North Island, but is distributed more rarely and locally southwards. Both species are terrestrial in habit, and seek out the most shaded and secluded places in the forest. *T. elongatum* prefers the actual banks of small watercourses, although not confined to them. Other writers have drawn attention to the shade-loving habit of this species. In this respect,

and in the dark and at times almost black colour of its fronds, it may be compared with such other extreme shade- and damp-loving ferns as *Blechnum nigrum* and *Leptopteris superba*. Its fronds are frequently covered with small epiphyllous mosses and hepatics. Although *T. strictum* is more wide-ranging than the other species, I have observed that in Westland it is for the most part confined to the interior of the hollow fern-covered stumps of large decayed trees or to tree-base crevices or the under-side of overhanging banks. In such situations it has to be searched for before it can be seen.

In their favourite localities these two species occur mostly in colonies, and prothalli and young sporelings can commonly be found in abundance. Whether it is that in these sheltered places these species are avoiding the light, or seeking extremely humid conditions, or rather that they here find a more suitable substratum for a nursery-bed than on the leaf-covered, more open forest-floor, is not altogether clear. Being tufted in their growth-form, they are altogether dependent upon spore-germination for their continuance and spread. Probably the last-mentioned of these governing influences may be the most important, and in this connection H. Carse's observation (5, p. 76) is significant—namely, that at Kaitaia, in North Auckland, *T. strictum* occurs on the open moorlands on the margins of the man-made kauri-gum potholes — localities which I have myself found to shelter frequently young sporeling plants of *Lycopodium laterale*.

These two species are considered to be allied to the more widely spread *T. rigidum* Swartz, but they are quite distinct from one another as regards both the form of the frond and also the cellular structure of the lamina, although alike in general habit. Moreover, in *T. strictum* the pinnules are deeply dissected into long narrow segments, but in *T. elongatum* there is a much more continuous expanse of lamina, and the pinnules are rather toothed than segmented. This distinction between the two species is further emphasized by the fact that whereas the adult prothallus of *T. strictum* takes the form of a tuft of filaments, as in so many species of this genus, that of *T. elongatum* has but a brief initial filamentous stage, and develops into a large strap-shaped tissue-body whose meristem is situated at the base of a sinus at its forward end, the archegonia being borne on a series of cushion-like thickenings behind the meristem.

Trichomanes Colensoi (Plate 73) is a small mat-forming species which is abundant on the lower flanks of the ranges throughout Westland. It grows on the under-side of damp boulders and rocks both in the mountain stream-beds and on the sides of the mountain-valleys. It apparently does not occur in the lowlands. I have never found it on other than boulders or rocks, the small fronds being always pendulous from their under-side, although rigid enough to stand erect. Cheeseman states (6) that it is also epiphytic on trees—presumably at their base. In very sheltered localities the fronds grow luxuriantly, the pinnae bearing three or four sori, instead of, as is usual, only one or two. With this species may be compared *T. humile* (Plate 73), another small and delicate creeper. This plant, like *T. elongatum*, does not seem to occur in Westland, but is more characteristic of the northern districts of the North Island. It also, however, has been reported by Townson (27) from the Westport district, and it is, of course, possible that both species may yet be found to occur, though scantily, in special localities in Westland. *T. humile* is generally a terrestrial plant, growing in mats, in much the same way as *T. Colensoi*, on overhanging banks of streams and damp rock-faces and boulders, from the under-side

of which it is pendulous. Less frequently it may be found pendulous from the under-side of leaning stems or on the bases of tree-ferns along the watercourses. In the rather light forests of North Auckland *T. elongatum* and *T. humile* are almost invariably in close association on the banks of watercourses.

Four out of the seven New Zealand species of *Trichomanes*—viz., *T. Lyallii*, *T. venosum*, *T. Colensoi*, and *T. humile*—are exceedingly delicate and slender plants, which are unable to modify the frond-form by stunting or imbrication, and probably on this account are confined to such low epiphytic or rupestral stations as allow them to adopt the mat growth-form. All the New Zealand species of *Trichomanes* with the exception of *T. reniforme* occupy a restricted station.

B. *Description of Two Selected Localities.*

The above account of the species and of the associations in which they occur is based upon detailed field-notes taken in a large number of localities throughout Westland. In order to gather together these facts I now propose, before leaving this part of my subject, to give a description of the Hymenophyllaceae of two selected localities—viz., Mount Greenland, Ross, and the Otira Gorge (see map 2, on page 579).

Mount Greenland may be considered as the well-defined, heavily forested block of high land, outlying from the main ranges, rising immediately at the back of Ross, and thus not far from the coast-line, and encircled by the Mikonui and Totara Rivers. Its base is no more than 100 ft. above sea-level, and its long flat summit, 2,970 ft. in height, rises a little above the forest-line, so that it presents a favourable opportunity for the observation of the effect of increasing altitude upon the distribution of the Hymenophyllaceae, and of the difference in the humidity of the gullies and of the spurs and ridges.

The lower flanks and the larger valleys show only the characteristic lowland associations—viz., *H. dilatatum*, *H. scabrum*, and *T. reniforme* on horizontal boughs and tree-trunks; *H. ferrugineum* and *T. venosum* on tree-fern stems; *H. australe* and *H. Tunbridgense* on tree-bases, and the latter also on mossy stones and fallen logs; luxuriantly growing *H. sanguinolentum* and *H. multifidum* as mid-epiphytes; *H. demissum* on the floor; *T. strictum* in sheltered terrestrial nooks; *H. flabellatum* and *H. rarum* pendulous from the inclined trunks and boughs of the larger trees; and *H. Armstrongii* abundant on the stems of *Quintinia*, and occasionally also on tree-ferns. Such of the species as can occupy a high epiphytic station—viz., *H. sanguinolentum*, *H. multifidum*, *H. Armstrongii*, *H. rarum*, and *H. flabellatum*—ascend in the gullies into the tops of the tallest trees. The above species are present in abundance up to an altitude of 1,000–1,200 ft., and my notebook shows that the only other species observed below this altitude was *T. Colensoi*, in a very occasional colony, although no doubt *H. villosum* would also be present in the tree-tops at the upper limits of this zone, and possibly *T. Lyallii* also on tree-bases here and there. *H. bivalve* is apparently absent from Mount Greenland.

The track to the summit traverses the southern flank of the mountain at an altitude of about 2,000 ft. The humidity of the forest on shaded flanks at these altitudes is undoubtedly higher than on north-facing hillsides, or even than on the hillsides at lower altitudes, on account of the frequent presence of the mountain-mists. Hence these shaded upland flanks will be favourable localities for such Hymenophyllaceae as occur

at these altitudes. Here the rata is the dominant tree, and its irregularly-growing trunk and large horizontal boughs are thickly covered with sheets of *H. multifidum* and *H. villosum*. *H. flabellatum*, *H. rufescens*, and *T. Lyallii* are most abundant in colonies on the bases of the old rata and totara trees. The kawhaka is also present with *H. Malingii* upon its trunk, and *H. Armstrongii* is abundant on the stems of *Quintinia*. None of the typically lowland species occurs at these altitudes. These upland species are all present to the highest altitudes at which large trees are to be found, but it is noticeable that at about 2,200 ft. (this altitude varying according to whether the particular locality is a ridge or a flank) *H. multifidum* exchanges the epiphytic for the terrestrial station, and at the same time adopts its mountain form. *H. villosum*, *H. Malingii*, and *H. Armstrongii* at these altitudes are the only true epiphytes, the other species mentioned keeping to sheltered places at the very bases of the trees. Above 2,600 ft. the forest is only shrubby, and *H. multifidum*, *H. villosum*, and *H. Armstrongii* are alone present in their characteristic stations. The summit is clothed with scattered silver-pine, *Leptospermum*, and subalpine shrubs. Here, in a very stunted form, *H. multifidum* occurs in the heart of the larger grass-tussocks, and in moss under the shrubbery. On other outlying mountains lying nearer the main ranges *H. villosum* ascends with *H. multifidum* above the forest zone, the latter keeping to sheltered places in moss under rocks, but the former occurring commonly as an epiphyte on the lower moss-covered boughs of the shrubs.

A very deep sheltered ravine (Cedar Creek) descends from the shoulder of Mount Greenland into the upper Totara River, and the comparison of the species to be found here from bottom to top with those on the adjacent spurs indicates well the difference in the distribution which always goes along with the difference between the constantly high humidity of ravines and the more variable humidity of the less-sheltered spurs and ridges. Up to about 1,200 ft. the lowland species are commonly present in all parts, though along the creek-bed *H. dilatatum*, *H. scabrum*, and *T. reniforme* climb in sheets over inclined large trees to a height of 30 ft., whereas on the spur they are confined to the lower boughs of shrubby trees. These same species, and also *T. venosum* and *H. Tunbridgense*, attain their highest altitude on the sides of the valley at 1,500 ft., but in the bed of the ravine occur quite luxuriantly, although infrequently, still higher. These limits for *T. venosum* correspond with those for the tree-ferns. I must add that this particular ravine was especially secluded, and that in the gullies on other mountains situated nearer the main ranges, and on the ranges themselves, the above-mentioned species have a somewhat less altitudinal range. Above 1,500 ft. the forest-covering of the spur becomes more open and the floor drier; the rimu, black and white pine, and the miro are absent, as also are the climbing *Rubus*, *Rhipogonum*, and *Freycinetia*. Only the upland and wide-ranging Hymenophyllaceae are here present—*H. demissum* on the floor; *H. rufescens*, *H. flabellatum*, and *T. Lyallii* on the bases of the larger ratas, *H. multifidum* and *H. villosum* on low boughs; and *H. Armstrongii* on the *Quintinia*, as well as on mossy stones. It was noticed that *H. rarum*, which so generally accompanies *H. flabellatum* and is a still less hygrophilous plant, was, outside the gullies, for some reason by no means frequent. *Lycopodium varium* is also present in large spreading clumps on the floor of the spur. In the bed of the ravine, however, there is a well-closed high canopy up to at least 2,000 ft. altitude, and the other forest-stories are also dense. The tall rata and kamahi trees are here clothed to their tops with *H. villosum* and *H. multifidum*, and with *H. rarum* and *H. flabellatum* in sheets over the lower third of their trunks.

Above 1,800 ft. the actual creek-bed is covered with a dense shrubbery of *Fuchsia*, *Olearia*, and *Gaya Lyallii*, as is generally the case in mountain-gullies, and the stems and limbs of these shrubs are thickly clothed with a long wet moss in which *H. multifidum*, *H. peltatum*, and *H. pulcherrimum* occur in the greatest profusion and luxuriance. *H. villosum* is abundant also in the upper branches, and *H. Armstrongii* wherever the heavy moss is lacking. On the sides of the ravine at this altitude none of the low-land species is to be found, but all of those just enumerated, along with *T. Colensoi*, *H. demissum*, and the upland species generally, occur abundantly on the ground and on fallen logs or as low epiphytes. The hygrophilous *Leptopteris superba* and *Blechnum nigrum* are also commonly present. These are the localities *par excellence* for the Hymenophyllaceae. The upper reaches of the Hohonu River, on the north side of the Taramakau River, where it descends from the range of the same name, and also the deep secluded gorges along the base of the main ranges, show the same profusion of filmy-fern growth, more especially at the altitudes at which the lowland and the upland species meet. In those parts of Cedar Creek just described the wetness of the ground and the profusion of hepatics and ferns is in marked contrast with the dryness and openness of the spur-floor at corresponding altitudes. From 2,200 ft. upwards in the creek-bed the small mountain form of *H. multifidum* becomes very abundant in the heavy moss on the creek-sides. At this level the gully begins to open out as it approaches the shoulder of the mountain, and the *Fuchsia* shrubbery gives place to low-growing silver and mountain pine. Higher still the plant-covering and the filmy-fern flora is as already described for these altitudes.

The other locality to be described is the Otira Gorge, which lies on the Westland side of the dividing range, its lower end at the Otira Railway-station, at an altitude of 1,255 ft., ascending to 3,038 ft. at the summit of Arthur's Pass. Here the rainfall is extremely heavy, although the number of rainy days is rather less than at the coast-line. Wind is frequent and strong, that from the east being dry and cold, and persisting some-times for days at a time. Here, then, the restricting effect of the altitude upon the distribution of the Hymenophyllaceae will be re-enforced by the considerable fluctuations in the humidity due to the winds.

At the lower altitudes such characteristic lowland species as *H. dilatatum*, *H. scabrum*, *T. reniforme*, and *H. sanguinolentum* are only rarely present, being confined to the lower closely-forested portions of the lateral creek-valleys. Apparently none of the species which in the lowlands climb into the tree-tops can do so here. *T. venosum* occurs sparsely on the scattered tree-ferns, but *H. ferrugineum* is apparently absent. *H. Tunbridgense* also was not seen. *H. pulcherrimum* is not uncommon even in the more open creek-beds, where it may be found growing strongly as a low epiphyte in moss and humus with colonies of its prothalli and sporeling plants. It is evident that this species does not demand an especially humid atmosphere, and at the same time that it depends mainly upon root absorption for its water-supply. The presence of its prothalli in the humus in these localities is strong proof that this water-supply is always present. *H. bivalve* occurs as a low epiphyte more especially in the sheltered gullies, and *H. demissum* is abundant everywhere on the floor, ascending in shaded localities high up in the subalpine forest. The flanks of the mountains are covered with the rata-totara-kawhaka forest association, and on the bases of the trees *H. rufescens* and *H. flabellatum* are abundant. *H. rarum* is also to be found in this station, but on the shady sides of gullies rather than on the open flanks. As on Mount Greenland, this species seems to be more

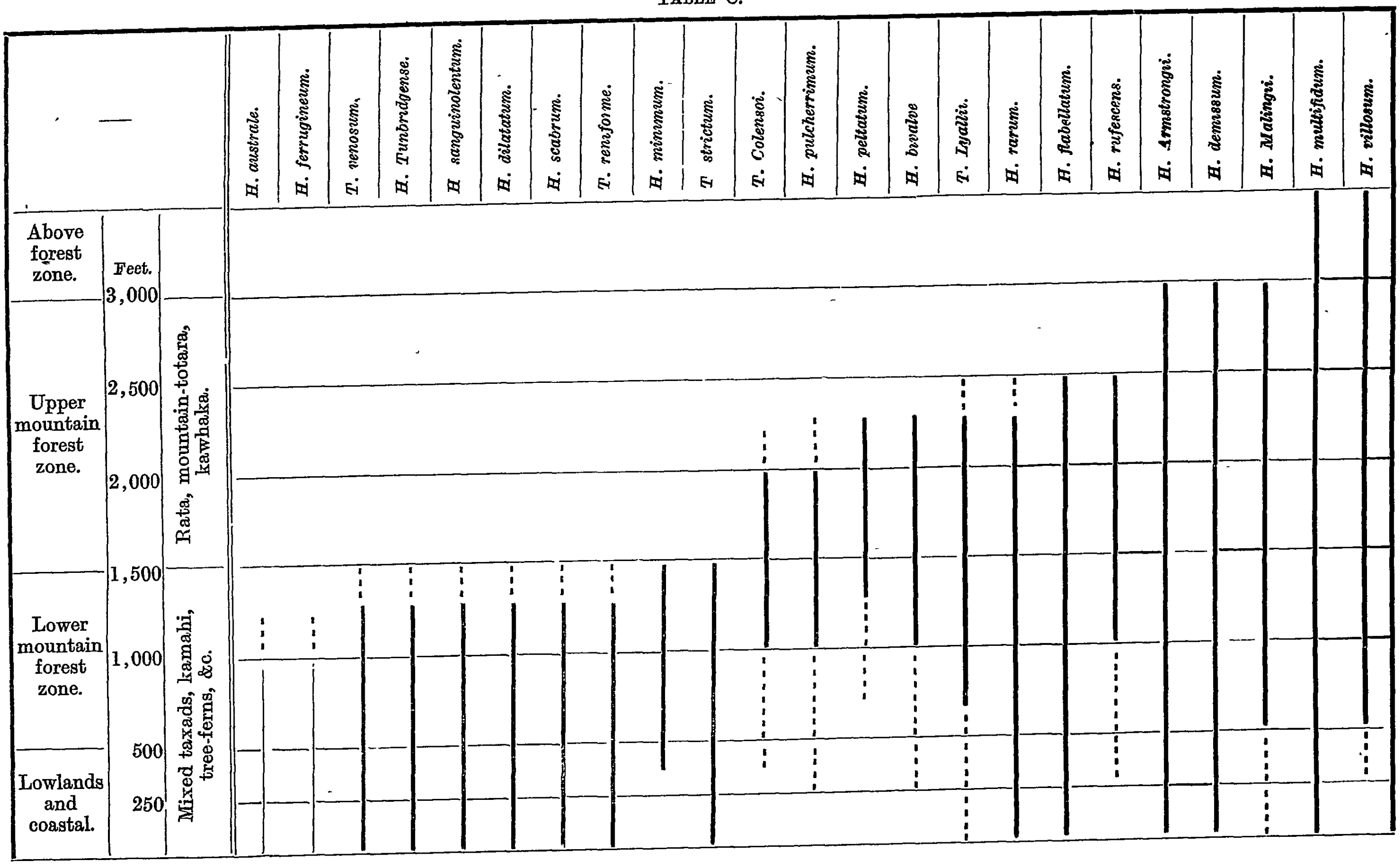
restricted in its distribution than *H. flabellatum*, although, as has been described above, it has a somewhat higher vertical distribution. *T. Lyallii* was not observed. *H. Malingii* occurs frequently on the kawhaka.

Throughout the whole Otira neighbourhood the two species *H. villosum* and *H. multifidum* are dominant. On the lower forest-clad hillsides the latter species keeps its mesophytic form and epiphytic habit, but on the open mossy rock-walls of the ravines and larger gullies it occurs with *H. villosum* in its stunted mountain form, the two species forming abundant and extensive sheets. In such situations the villous nature of the rhizomes and fronds of *H. villosum* is strongly developed (see Plate 59), and also the young fronds of *H. multifidum* are densely clothed with hairs. The other characteristic mat-formers, *H. rarum*, *H. Armstrongii*, and *H. minimum*, are occasionally to be found also on the damp walls of these narrow ravines. *H. villosum* ascends the forest-clad mountain-flanks higher than any other species, and it is noticeable that it keeps the low epiphytic in preference to the terrestrial station right up into the zone of subalpine scrub. The mountain form of *H. multifidum* is restricted to damp rock-sides and other especially damp mossy terrestrial stations wherever these occur, for, contrary to what is the case on Mount Greenland, the floor of the Otira forest generally at the higher levels seems to be too liable to drying for this species to occur there. The main Otira Gorge river-bed provides on its rocky sides very favourable situations for *H. multifidum*, and it here ascends with *H. villosum* to the summit of the pass. *Lycopodium varium* is also extremely common on rocks throughout the gorge. Along the open summit *H. multifidum* is only to be found on occasional damp rock-faces, but *H. villosum* is abundant everywhere as a low epiphyte on the *Olearia* and *Gaya* shrubbery, and in moss on boulders in the most exposed situations.

It is evident that the lowland Hymenophyllaceae do not ascend at Otira to as high a level as they do on Mount Greenland. It is the hairy upland species, such as *H. villosum*, *H. flabellatum*, *H. rufescens*, and *H. Malingii*, along with the mountain form of *H. multifidum*, whose young fronds also are hair-covered, which are here most in evidence, whose characteristic zone on Mount Greenland lies at a rather higher level. As has been indicated above, the difference is probably due to the occurrence of drying easterly winds at Otira, these being more negligible at Mount Greenland. In the neighbourhood of Otira it is noticeable that after several days of this wind certain of the epiphytic filmy ferns are very much shrivelled, and even the large-leaved shrubs show signs of wilting, but the ground-growing and the hairy filmies are little affected. *H. villosum*, even in its epiphytic station, is rarely shrivelled, although the fronds become much inrolled, and it is no doubt this capacity of withstanding drying that enables it both to preserve the epiphytic station at high altitudes and to ascend higher than any other species.

In the following Table C is summarized in diagrammatic form the altitudinal distribution of the Hymenophyllaceae in Westland. Since, in the case of not a few of the species, the altitudinal range varies somewhat from place to place, this table is merely intended to give a general comparative survey of the family in its differentiation into lowland and upland species, and into those which are restricted in their range and those which are more wide-ranging. The dotted continuations of the lines indicate the observed spread, beyond their characteristic altitudes, both of the lowland species upwards in sheltered mountain-gullies and also of the mountain species down into the lowlands.

TABLE C.


Above forest zone.
Upper mountain forest zone.
Lower mountain forest zone.
Lowlands and coastal.
Feet.
3,000
2,500
2,000
1,500
1,000
500
250
Rata, mountain-totara, kawhaka.
Mixed taxads, kamahi, tree-ferns, &c.
H. australe.
H. ferrugineum.
T. venosum.
H. Tunbridgense.
H. sanguinolentum.
H. dilatatum.
H. scabrum.
T. reniforme.
H. minimum.
T. strictum.
T. Colensoi.
H. pulcherrimum.
H. peltatum.
H. bivalve
T. Lyallii.
H. rarum.
H. flabellatum.
H. rufescens.
H. Armstrongii.
H. demissum.
H. Malingii.
H. multifidum.
H. villosum.

C. *The Growth-forms and their Relation more especially to the Vertical Distribution.*

On account of the constantly high humidity in the lowland forests of Westland, the Hymenophyllaceae are there to be found at their optimum development. Throughout Westland the epiphytic station is, taking the family as a whole, the characteristic one, and a number of the species adopt a luxuriant pendulous habit with irregularly elongated fronds. This very luxuriance serves to throw into greater prominence two facts—viz., that certain thorough-going epiphytes are able to adopt a stunted and imbricated frond-form with a mat-like habit of growth, and in this state to flourish even in the forest-canopy and in other exposed stations, other epiphytic species being quite incapable of doing this; and, secondly, that certain terrestrial or low epiphytic species preserve the deltoid form of frond unmodified. The growth-form of each species and the extent to which it can be modified must thus be regarded as an important factor in the determination of its distribution. In the case of some of the species the growth-form will restrict the distribution, but with others the ability to modify it will act in the opposite direction.

(a.) *The Tufted Growth-form.*—This growth-form is known to be confined almost exclusively to certain species of the genus *Trichomanes*. The tufted species, *T. elongatum*, *T. strictum*, and *H. pulcherrimum*, do not occupy any considerable place in the physiognomy of their surroundings, since they cannot form sheets as do the creeping species. They occur generally singly, although a close search will often reveal the presence of a scattered colony which has originated from a single old plant. The two first-named species prefer secluded overhung situations where frequently no dripping water can reach the fronds. In the case of *T. elongatum*, whose frond-lamina is more extensive than that of *T. strictum*, the presence of epiphyllous mosses and hepatics, however, proves the constant wetness of the fronds, and shows that in its secluded station there must be considerable condensation of water-vapour upon the frond-surface. The root-system of both species is well developed and the stem-xylem is large, so that, when also the small number of fronds is considered, it must be concluded that these plants obtain most of their water, and certainly all their nutrient salts, by root absorption. In his laboratory experiments with Jamaican species Forrest Shreve (26, p. 194) found that in the case of *T. rigidum*, whose growth-form is identical with that of the two species here considered, the extremely low water-loss from surface-dry leaves in a very moist atmosphere could not be met by root absorption. At the same time, he states that no other Jamaican species, even the most hygrophilous, behaved in this way, and he is inclined to find the explanation of it in *T. rigidum* in the fact that the lateral walls of the cells of its frond-lamina are greatly thickened and that thereby the rapid passage of water outwards from the veins is hindered. These tufted terrestrially-growing species of *Trichomanes* show no marked modification in the frond-form in the way of increasing the frond absorption, beyond the facts, previously mentioned, that there is a very slight zone of multi-layered lamina in the frond of *T. elongatum* where the larger veins converge, and also that the frond-lamina of this species is more extensive than that of *T. strictum*, so that in this respect they may be regarded as representing more or less nearly the original frond-form of the family. At the same time, it is, of course, possible that in other ways they may have departed from the primitive character of the family in accordance with their specially hygrophilous habits. Their growth-form restricts

them to situations where they can root in the soil and where this is continuously damp.

H. pulcherrimum is a tufted species which in Westland occurs altogether as an epiphyte. Its fronds are large, with a much greater total extent of lamina than in the two last-named species. Moreover, the frond-form is not fixed, as in the two others, but is readily modified into a pendulous, much-elongated form. Pendulous fronds are frequently bathed in rain-water which has splashed from the leaves of the trees or has run down over the surface of the bark and through the mass of moss and humus in which the plant is growing, so that this species is not so dependent upon root absorption as the two above mentioned. Its root-system is, however, well developed, and it is confined to forks of trees and other epiphytic places where there is a considerable accumulation of humus. It has been indicated above in the paragraph dealing with Otira that this species probably, after all, demands a constant root supply of water rather than a constantly high atmospheric humidity, although, of course, it will attain its most marked luxuriance if the latter factor be also present. It would appear that *H. pulcherrimum* cannot occur on the flat floor of the forest as does *T. strictum*, for it has departed from the typically erect terrestrial habit; nor can it descend to the lowlands, for there the branches of the trees do not, as a rule, carry much moss and humus, and are liable to occasional drying.

(b.) *The Open-creeping Terrestrial Growth-form.*—The representatives of this class are *H. demissum* and *H. bivalve*. The fronds of these species are strongly erect or somewhat decurved, and are of an invariable deltoid form, and hence of limited size. The rhizome and root-system is well developed. Among the Hymenophyllaceae the typical epiphytic species show special frond-modifications in accordance with this station in the way of the extension of the lamina, and especially in the departure from the erect deltoid form of frond of limited size; but such modifications are altogether lacking in *H. demissum* and *H. bivalve*, even when they become low epiphytes, as the latter frequently does, and the former occasionally. It may well be that the inability to modify the frond-form in order to extend its function of absorption prevents these two species from becoming thorough-going epiphytes. Of the two, *H. demissum* possesses the greater extension of lamina, so that it is not obvious why this species should show the much less marked tendency to become epiphytic. The adoption of the creeping habit certainly makes it possible for a plant to take up an epiphytic station.

(c.) *The Open-creeping Epiphytic Growth-form.*— The small epiphytic species are considered by themselves below. In the species of this third class there is usually a modification of the frond in accordance with the epiphytic habit. *H. australe* is a good example of the transition from the terrestrial to the epiphytic station, occurring in Westland always at the bases of large trees and climbing upwards a few feet. It retains the erect deltoid form of frond, but shows a considerable extension of the lamina by means of the broad crisped wings. It occasionally is pendulous, and the fronds then show a marked increase in length. *H. atrovirens*, which is probably a form of this species, is erect with deltoid or lanceolate fronds when terrestrial, but pendulous and elongated when growing on vertical rock-faces in sheltered ravines. The rhizome and stipe of *T. reniforme* is comparatively stout, but, with the exception of *H. Malingii*, the frond shows the greatest degree of modification in the New Zealand family. The

study of the sporelings of this species shows that the completely webbed character of the mature frond, and possibly also the multi-layered condition of its lamina, are to be regarded as special modifications. Another stoutly-growing species with considerable frond-modification is *H. dilatatum.* Here the extent of lamina is certainly, taking into consideration the size of the frond, the greatest in any of the New Zealand species. *H. scabrum, H. sanguinolentum,* and *H. multifidum* also show a large frond-development in the pendulous state, the first-named attaining an extreme length of 2½ ft. to 3 ft. In the mid-epiphytic station in the lowland forests the lateral pinnae of the fronds of *H. sanguinolentum* and of *H. multifidum,* as well as the main rhachis, frequently tend to elongate into tails. *H. villosum,* although a characteristic epiphyte, shows a poor extent of frond-lamina, and the frond preserves more or less invariably the erect deltoid form. To this statement must be added the fact that it is a mountain and not a low-land plant, and that whereas the mid-epiphytic station in the lowland forests enables the species to make the most use of atmospheric water by frond absorption, the same station in the mountain-forests, especially at such elevations as *H. villosum* can ascend to, where the atmospheric humidity is more variable, is of value rather on account of the water-supply in the damp mossy clothing of the tree-branches. When, however, it occurs as a low epiphyte at the bases of the ranges, in which localities and station there is a more constantly high atmospheric humidity, its fronds frequently show a well-marked tendency to an elongation of the main rhachis, and they may also be pendulous.

The question arises regarding the open-creeping, strong-stemmed epiphytes such as *H. dilatatum, H. scabrum,* and *T. reniforme,* which in creek-beds at the base of the ranges can occur rupestrally and adopt a more erect habit of growth, as they do also very generally in the more light forests of other parts of New Zealand—why do they not also occur on the floor or on fallen logs in the lowland forests of Westland ? It may be that with such species the need for light in the heavy dense forests causes them to keep to the epiphytic station, and it is to be noted that where in Westland they do occur terrestrially at higher altitudes it is in such less-shaded localities as creek-beds.

As has been mentioned, the fronds of the pendulous epiphytes will frequently be bathed in water which has soaked down from the branch or trunk on which they are growing. No doubt the fronds also absorb nutrient salts in this way. In his experiments already quoted, Forrest Shreve (26) showed that the ground-growing, more hygrophilous Jamaican species do not absorb uncondensed atmospheric moisture by the fronds, but that the high epiphytes do, although the actual amount so obtained is small. The rhizomes and roots of the large-growing mid-epiphytic New Zealand species are not usually embedded in moss, but simply cling closely to the tree-surface, so that there is no considerable root water-supply available for them. *T. reniforme,* whose fronds are generally rigidly erect, prefers the larger surfaces of tree-trunks, but the other species of this class, with the exception of *H. australe* and *H. villosum,* prefer the under-side of horizontal boughs from which they can hang free.

(d.) *The Thin-stemmed Close-creeping Epiphytic Growth-form.*—There are a few species which show in the filiform nature of their rhizomes and stipes, and, in the case of certain species, in their hairy character, a still further modification in accord with the epiphytic habit. *H. flabellatum, H. rarum,* and *H. Malingii* are typical members of this class, and also certain of the smaller-growing species. They are always pendulous, the first two being

characteristically confined to the under-side of inclined trunks and large boughs, and they grow generally in close colonies. It is obvious that the thread-like stems of these species could not carry an adequate water-supply from the substratum even if this were available. On the other hand, there is a very large extent of lamina in proportion to the size of the frond, this being especially the case in *H. rarum;* while in *H. Malingii,* as has been noted, there is a very remarkable and effective frond-modification for the purpose of frond absorption. *H. ferrugineum* is also invariably pendulous with overlapping fronds in its station on tree-fern stems, and the rhizome and stipe is slender, though not so much so as in the three above-mentioned species.

It is significant that these four species, which are thus so dependent upon frond absorption, show withering in times of drought to a markedly less degree than do other epiphytic species. In the case of *H. Malingii* the nature of the frond-tissues readily explains this. It has been suggested that the peculiar colour of the fronds of *H. rarum* and *H. flabellatum* may possibly serve to mask the cell-protoplasm from excessive transpiration. *H. ferrugineum* is one of the hairy species. Its fronds are almost rusty-brown in colour owing to the dense clothing of stellate hairs on the margins of the segments and on the costae on both surfaces of the frond (see Plate 76). So closely do the hairs interlock that they cannot help but shield the lamina from air-movements. However, it must be remembered that this species is more restricted in its distribution than the other three, and is distinctly hygrophilous. *H. ciliatum,* which very doubtfully occurs in New Zealand, seems to be of much the same slender pendulous growth-form as *H. ferrugineum.* In this species also the margins of the segments, and to a less extent the costae, are clothed with stalked stellate hairs. Forrest Shreve notes (26, p. 193) that the three Jamaican hairy species of *Hymenophyllum* are the most resistant to drying and insolation of any. From experiments he concludes that the cavities of the frond-hairs have no great importance as reservoirs of water. He observes also that under natural conditions these hairy fronds do not often become saturated with rain-water, a fact which I may state is true also of the New Zealand hairy species. However, it may well be that the hairs hinder transpiration, and this will certainly be so in the case of the densely-clothed young fronds. I may add that thick-walled colourless unicellular bristles are borne in large numbers on the margins of the prothalli of the terrestrial *T. elongatum,* and are especially in evidence overlapping their growing-points. Each arises from a single otherwise unaltered marginal cell. Whether the hairs in this case serve as a mechanical strengthening or for holding a film of water cannot here be stated. *H. flabellatum* is characterized by a dense woolly tomentum on the rhizome and stipe of the mature frond, and this on the young frond shields the lamina also. This will act as a protection for the growing parts of the plant, and hence may be considered of special importance with respect to the epiphytic station. In this connection it is to be noted that on the mountain-flanks this species may frequently be found showing the tomentum as a persistent although more or less scanty clothing on the rhachis and costae of the mature as well as of the younger fronds.

(e.) *The Mat Growth-form of the Small Species.*—The nine smallest species —viz., *T. Colensoi, T. humile, T. Lyallii, T. venosum, H. rufescens, H. Tunbridgense, H. peltatum, H. minimum,* and *H. Armstrongii*—are all creeping mat-formers, a growth-form which is, of course, very effective both in hindering transpiration through the overlapping of the fronds and also in holding water and humus against the roots. The stipe of *T. humile* and

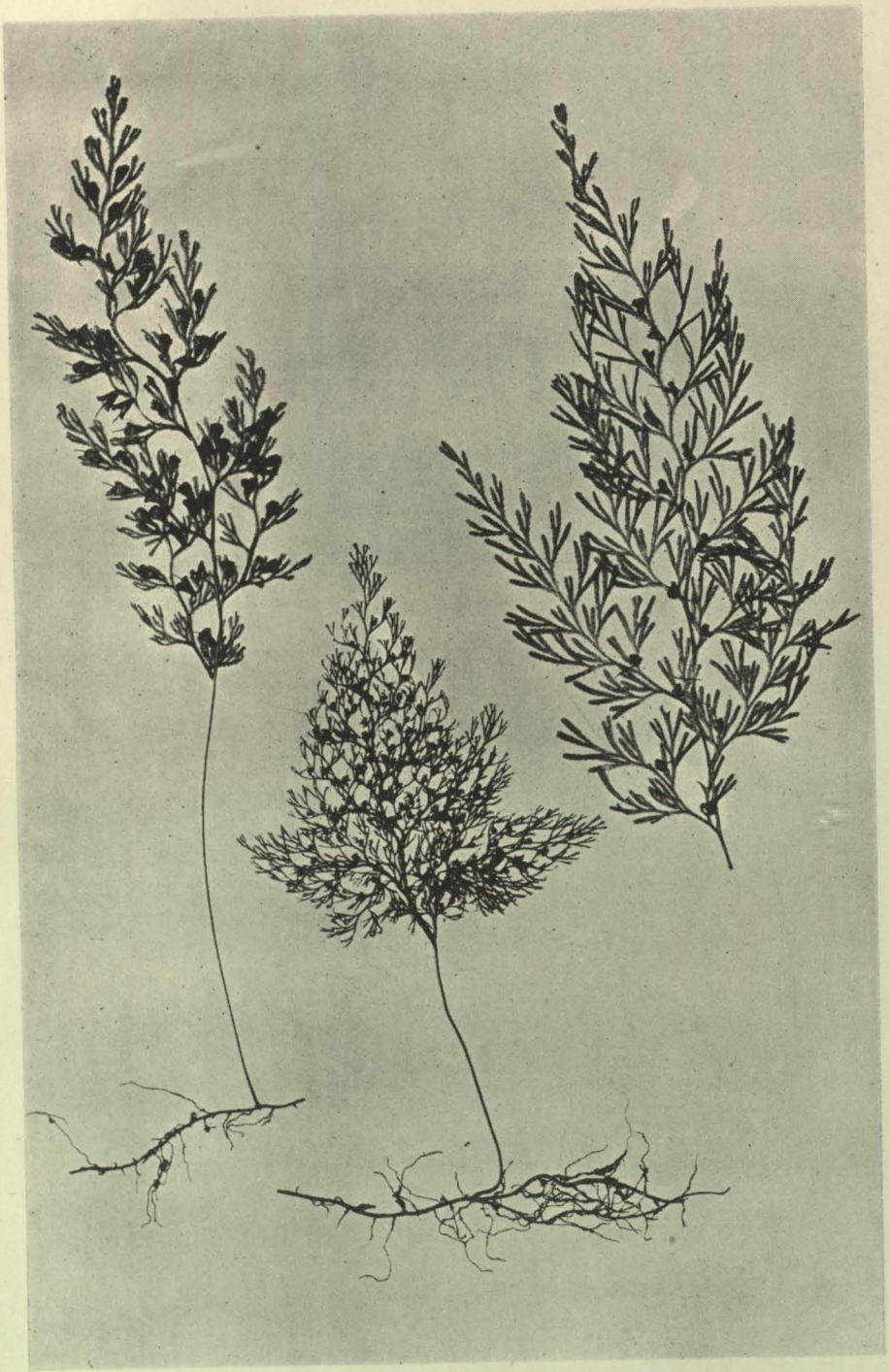
T. venosum is flexible as well as slender, so that their fronds are pendulous and irregularly elongated. In this respect these two species are more modified than the others of this class. Occasionally, however, erect fronds of *T. venosum* may be found which are less modified from the deltoid form (see Plate 72). In especially humid localities the fronds of *H. peltatum* and *H. Tunbridgense* also may become pendulous and elongated. The tiny fronds of the other small species preserve a more or less rigid habit of growth, even when, as in *T. Colensoi*, *T. Lyallii*, and *H. rufescens*, they keep to overhung stations, and the fronds remain rigid and practically unmodified in form. Most of these small species are probably best interpreted as reduction forms. The frond of *H. rufescens* is typically deltoid, and it is to be noted that *H. flabellatum*, to which the other species is undoubtedly closely allied, also frequently adopts a very similar form in mountain stations.

The hairy covering of the fronds of *H. rufescens* and *T. Lyallii* probably acts as a protection against drying in the same way as has been suggested for *H. ferrugineum*, and thus plays a part in enabling these species to endure a somewhat more exposed position than such other mountain species as *T. Colensoi*. No doubt the base of large trees at the misty altitudes at which these two species abound is for the most part a sheltered and humid station; but the reason why they prefer high to low altitudes is best sought in the supposition that they are mountain forms of lowland plants.

In the case of all these small delicate species the mat is the natural growth-form when growing on surfaces of any extent, although *H. Armstrongii* and *H. minimum* are small enough to be able to bury their fronds in moss, and thus to spread as more open creepers on to the smaller surfaces of tree-branches. *H. peltatum* alone of these small species can become stunted with imbricating pinnae, and it is in this form that it occurs in exposed positions. It is certain of these small species which show, especially in their more exposed stations, the mat-form in the most pronounced state in which it is to be found in the family. Possibly the inability to shield the lamina by imbrication and inrolling of the pinnae is an important reason why such small species as *H. Tunbridgense* and the other typically low epiphytes of this class are so restricted in their vertical distribution.

(f.) *The High Epiphytic Stunted and Imbricated Mat Growth-form.*—The last growth-form to be considered is that illustrated by certain normally large-fronded species, which, on account of their ability to adopt the mat habit together with an extremely stunted and imbricated form of frond, accompanied in certain of the species by inrolling of the frond-segments, are able in the lowlands to endure high epiphytic conditions, and, in the case of two of the species, to exist in exposed subalpine stations. These are *H. sanguinolentum*, *H. multifidum*, *H. villosum*, *H. rarum*, and *H. flabellatum*. These species all occur commonly along with the small *H. Armstrongii* in the tops of the forest-trees in the lowlands, both in the heavy forest of the coastal flats and of the terraces, and also in the black-pine and white-pine stands of the river-flats, the latter of these localities being more exposed to the mountain winds. As has been noted, *H. villosum* does not occur below the middle lowlands.

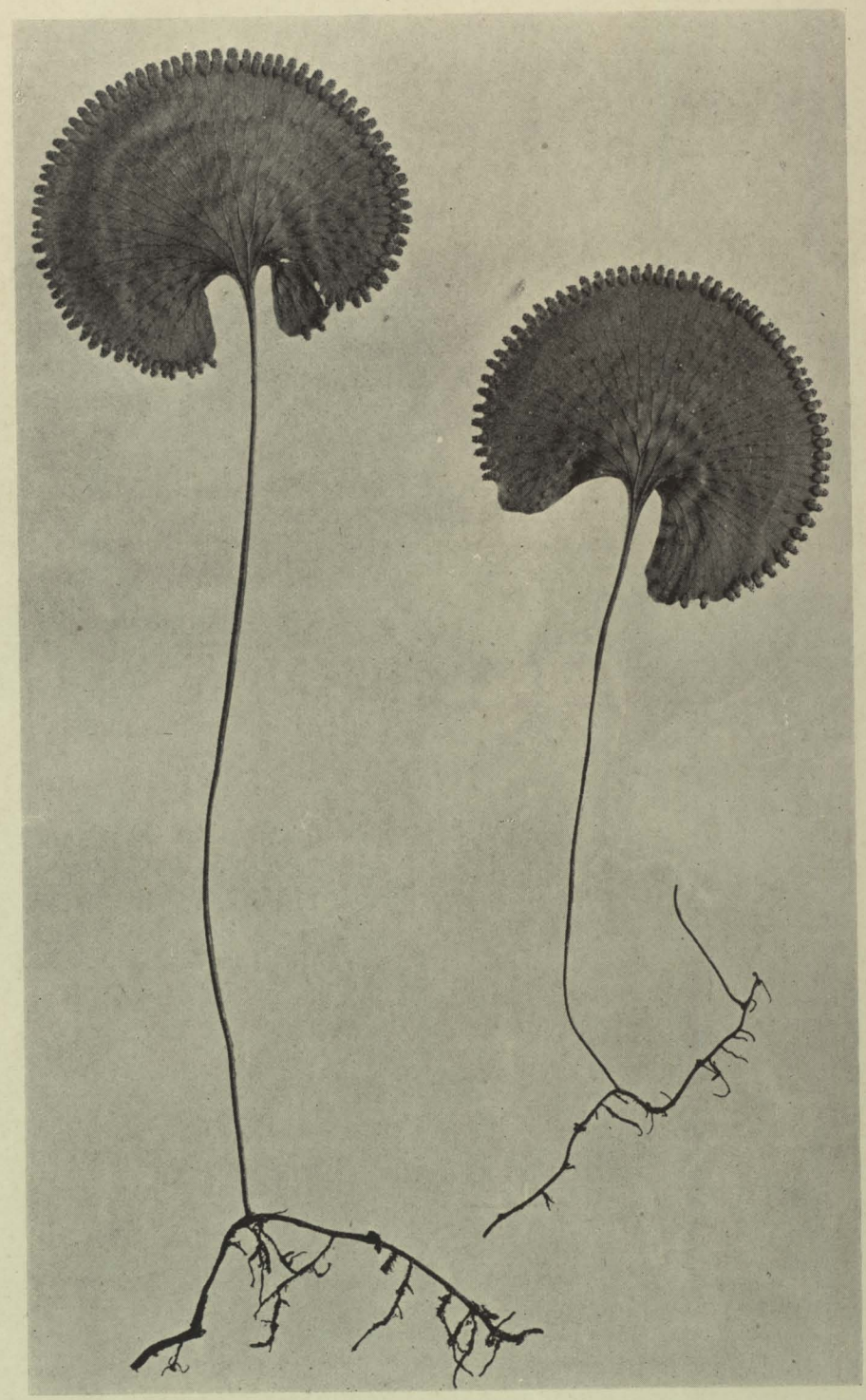
H. villosum and *H. multifidum* are able to endure greater degrees of desiccation than the other species, as is shown by the fact that they alone flourish in exposed positions above the forest-line. As high epiphytes in the lowlands these two species and *H. sanguinolentum* show the stunting of the frond and imbrication of the pinnae with inrolling of the segments,



H. multifidum Swartz. Showing tree-top form (left), upper third of frond of mesophytic form (right), and mountain form (below). All nat. size.

Face p. 608.]

H. bivalve Swartz. × $\frac{2}{3}$.



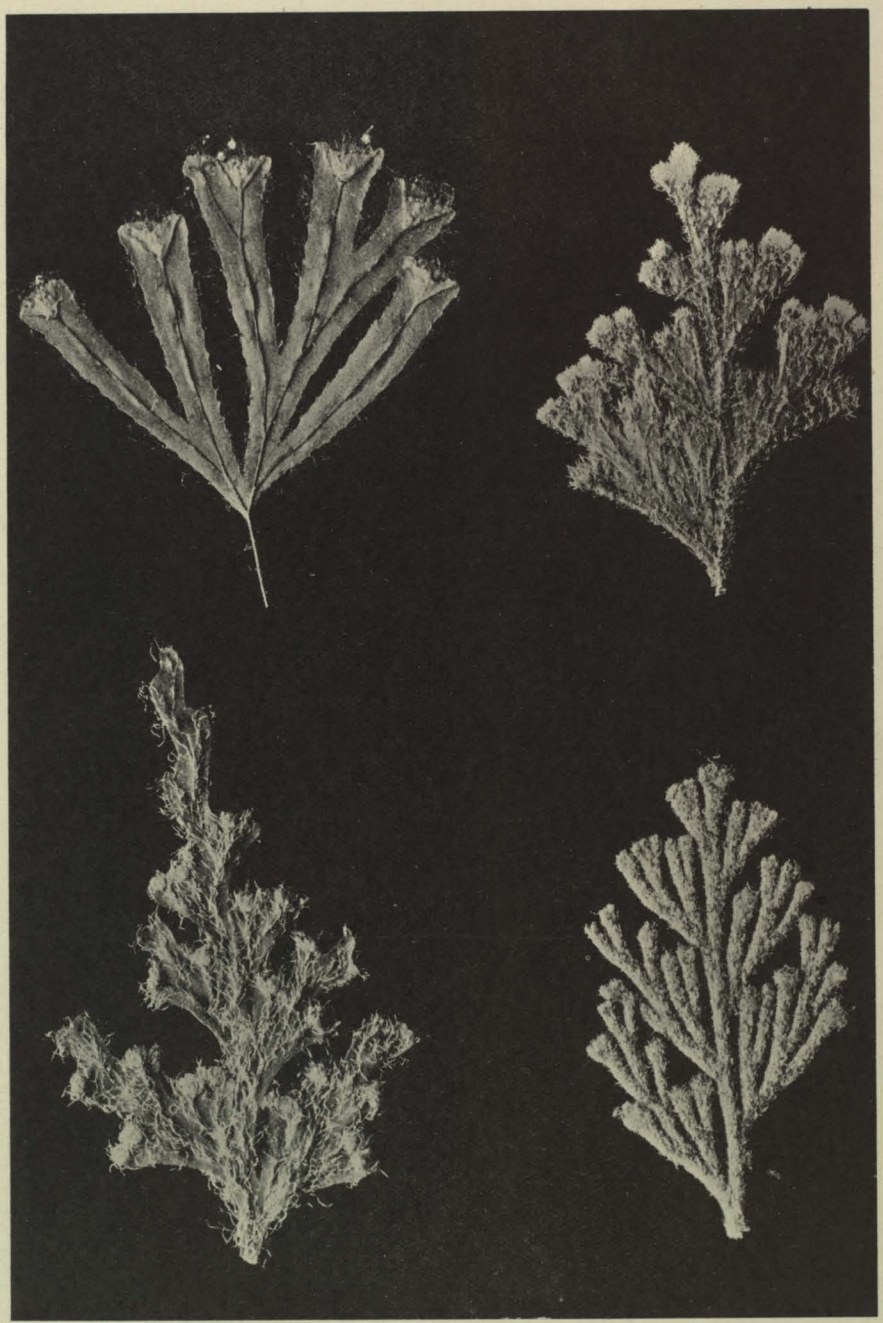
T. reniforme Forst. × $\frac{7}{9}$.

T. venosum R. Br. Showing three forms. Nat. size.
T. Lyallii Hook. & Bak. (below). Nat. size.

T. Colensoi Hook. f. Showing two forms (above). Nat. size.
T. humile Forst. (below). Nat. size.

T. strictum Menz. × $\frac{7}{8}$.

T. elongatum A. Cunn. × ½.



T. Lyallii Hook. & Bak. (left, above); *H. ferrugineum* Colla (right, above); *H. rufescens* T. Kirk (left, below); *H. Malingii* Metten (right, below). Portions of fronds showing hairs. All × 4

but they do not here adopt so characteristically the mat growth-form. On the other hand, the frond-segments of *H. rarum* and of *H. flabellatum* are apparently unable to inroll, but these two species keep their high epiphytic station by the imbrication of the pinnae along with the adoption of the close mat growth-form. For this reason they keep to the larger surfaces of the main trunk and of the larger limbs in the tree-tops in the lowlands, whereas the other three species creep out also on to the small branches. It must be noted also that as a high epiphyte *H. multifidum*, although much stunted, does not adopt the peculiar "mountain form," this being only found in its terrestrial station.

Above the forest-line, and in exposed subalpine localities generally, *H. villosum* and *H. multifidum* adopt the close mat growth-form. Of these two species the former can certainly exist in the more exposed positions, *H. multifidum* seeming to need always a damper, more shaded situation. Moreover, whereas the latter is here always rupestral, the former is frequently a low epiphyte, being then an open creeper in the moss. Possibly it is the possession of the villous clothing of the fronds and rhizomes which gives *H. villosum* the extra advantage, although it must be said that at these altitudes *H. multifidum* also shows this character, but to a much less extent. As a mountain plant the fronds of the last-named species are typically deltoid in form, and in the most exposed situations are strongly decurved so as almost to bury themselves in the mossy substratum.

As indicated previously, the significance of the imbrication of the pinnae, the inrolling of the frond-segments, and the stunting and overlapping of the fronds of these mat-formers lies in the fact that transpiration is thereby hindered, and probably also water is held against the frond-surface. Moreover, the underlying stratum of interwoven rhizomes and roots, and the accumulated humus of the dead fronds and of the moss, is able to hold water over considerable periods of drought.

D. *The Bearing of the Distribution of the Species upon the Subject of the Phylogeny of the Family.*

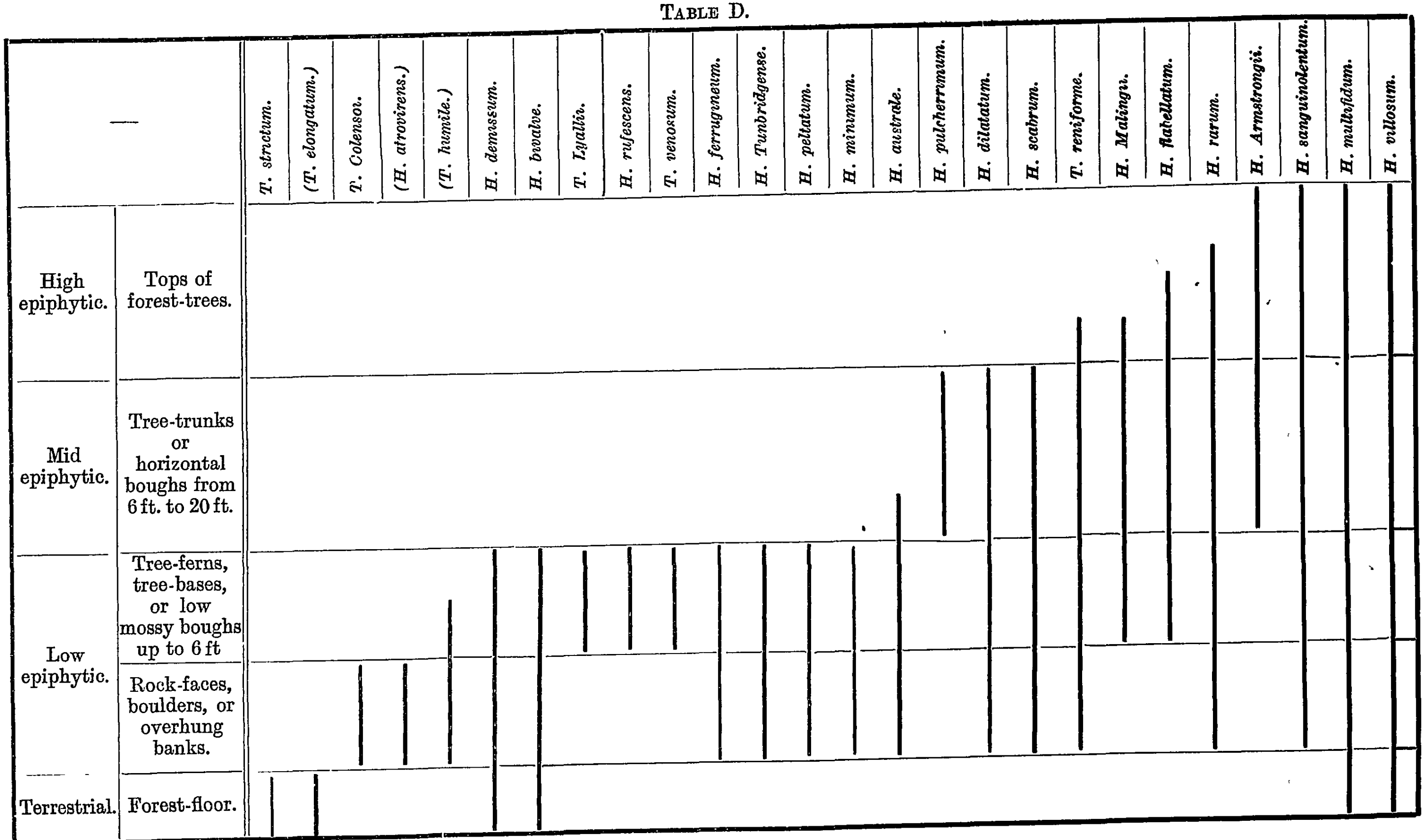
In the foregoing pages both the vertical and the altitudinal distribution of the various species has been considered. These facts will now be collected and their general bearing upon the subject of the phylogeny of the family discussed. The altitudinal distribution of the family has been summarized in Table C, on page 603.

Table D, on page 610, sets forth in diagram form the vertical distribution of the members of the New Zealand family as it is to be seen in Westland, the three species which do not occur there being also included for reference, their names being placed in parentheses. As the station in the forest adopted by a species varies very often with the particular locality, and is especially affected by the altitude, this table must be regarded as indicating the full vertical range of which each species is capable in Westland.

From this table the following generalizations can be made:—

1. The species whose fronds apparently cannot vary from the erect deltoid regular form of growth—viz., *T. strictum*, *T. elongatum*, *H. demissum*, and *H. bivalve*—are either altogether restricted to the forest-floor or have only to a very restricted extent acquired the epiphytic habit. *H. australe* and the allied *H. atrovirens* illustrate the beginning of the modification of the typical terrestrial form of frond along with the adoption of the epiphytic habit.

TABLE D.


T. strictum.
(T. elongatum.)
T. Colensoi.
(H. atrovirens.)
(T. humile.)
H. demissum.
H. bivalve.
T. Lyallii.
H. rufescens.
T. venosum.
H. ferrugineum.
H. Tunbridgense.
H. peltatum.
H. minimum.
H. australe.
H. pulcherrimum.
H. dilatatum.
H. scabrum.
T. reniforme.
H. Malingii.
H. flabellatum.
H. rarum.
H. Armstrongii.
H. sanguinolentum.
H. multifidum.
H. villosum.
High epiphytic.
Tops of forest-trees.
Mid epiphytic.
Tree-trunks or horizontal boughs from 6 ft. to 20 ft.
Low epiphytic.
Tree-ferns, tree-bases, or low mossy boughs up to 6 ft
Rock-faces, boulders, or overhung banks.
Terrestrial.
Forest-floor.

2. The smallest species of all—viz., *T. Colensoi, T. humile, T. venosum, T. Lyallii, H. rufescens, H. Tunbridgense, H. peltatum,* and *H. minimum*—in which frond-modification has taken place probably more especially in the direction of reduction, are restricted to special low epiphytic or rupestral stations. The tiny *H. Armstrongii* is an exception, in that it ascends into the tree-tops.

3. The species of *Trichomanes* have markedly a more restricted vertical range than those of *Hymenophyllum,* and occupy more specialized stations. The only exception to this is the large creeping *T. reniforme,* which, in the multi-layered condition of its frond-lamina, and in its ability to inroll the frond closely, possesses special powers of resisting desiccation.

4. The species which show most characteristically the epiphytic habit are those which have acquired, by elongation of the main rhachis and sometimes of the primary pinnae of the frond, or by extension of the lamina into wings, the greatest extent of frond-surface for the purpose of frond absorption. These are *H. dilatatum, H. scabrum, T. reniforme, H. flabellatum, H. rarum, H. sanguinolentum, H. multifidum, H. pulcherrimum,* and the peculiar *H. Malingii.* Two exceptions to this statement are the mountain species *H. villosum,* whose epiphytic station under the variable atmospheric humidity conditions of high altitudes is of value, probably, mainly on account of the damp mossy clothing of the tree-branches, and *H. Armstrongii,* whose tiny fronds are buried in and wetted by even the thinnest moss substratum.

5. The species which possess the greatest vertical range are those normally large-fronded epiphytes which are able to modify the entire growth-form by stunting of the frond, imbrication, and inrolling of the frond-segments, and by growing in close mats, and which are enabled through the possession of one or more of these modifications to flourish in the tree-tops. These are *H. multifidum, H. sanguinolentum, H. villosum, H. rarum,* and *H. flabellatum. H. Armstrongii* has the same wide range, and, as has been indicated, is the only one of the small-growing species able to ascend higher than a low epiphytic station. None of the hairy-fronded species are high epiphytes, for *H. villosum* is only really villous at high altitudes, outside of the forest, and *H. Malingii* keeps to the low or mid epiphytic station. The frond of *H. flabellatum* also only becomes villous at high altitudes.

6. Comparison of Table D (page 610) with Table C (page 603) shows that the species which have the greatest vertical range in the forest are also those which have the greatest altitudinal range in the district. There is, however, one exception to this—viz., *H. sanguinolentum,* which does not ascend above 1,500 ft.; and there are strong reasons for regarding *H. villosum* as the mountain form of this species. The species which occupy in the lowlands and in the lower mountain-ravines a high epiphytic station become on the flanks of the mountains low epiphytes or even terrestrial plants.

These conclusions have a certain bearing upon the larger question of the phylogeny of the family. With regard to this it will be necessary first briefly to consider other sources of evidence.

From the comparative study of the spore-output of the different members of the family, Bower (4) concludes that the sporangia are larger and the contained number of spores higher in *Hymenophyllum* than in *Trichomanes,* a fact which points to the former genus being nearer the Simplices than the latter. The smaller number of spores per sporangium in *Trichomanes* is compensated for in that genus by the extraordinary growth of the receptacle

with continued formation of sporangia, a character which is certainly a specialized one. It is noteworthy that this character is strongly developed in *H. multifidum*, and not infrequently also in *H. minimum*, but to a small degree in *T. reniforme*. It is completely absent in *T. Lyallii*, a species which is regarded as intermediate between *Hymenophyllum* and *Trichomanes*, and whose prothallus, it may be added, is of the strap-shaped form characteristic of the former genus.

The prothalli of *Trichomanes* are known to be of a filamentous nature, though in some species I have found—as, for example, in *T. reniforme*, *T. Lyallii*, and *T. elongatum*—that the filamentous stage is short, and is early replaced by a flat multicellular expansion. It was at one time considered that this filamentous character is primitive, but the consensus of opinion is certainly now in favour of regarding it as secondary.

In his comparative study of the stem-anatomy of the Hymenophyllaceae, Boodle (2) concludes that with regard to this character *H. dilatatum*, *H. scabrum*, and *T. reniforme* are the most primitive in the existing family, and that the species of *Trichomanes*, on the whole, show greater modification of this type of stelar anatomy by reduction, or in some cases by amplification, than do the species of *Hymenophyllum*.

Other evidence has been adduced in favour of regarding these same three species as representing the least-specialized part of the family. They are known to have a frond-lamina which is several cells in thickness, whereas in the family as a whole it is only one cell in thickness, which latter character is regarded as a modification adopted in accordance with the hygrophytic habit. Not only do these three species in this respect stand apart from the rest of the family, but Bower has shown (3) that in the basal parts of the adult fronds of *T. reniforme* and *H. dilatatum* the segmentation at the edge of the lamina is by alternating oblique walls, as in ordinary leptosporangiate ferns, and not by repeatedly transverse walls, as is usual in the Hymenophyllaceae.

It is found that the filmy habit in the family as a whole is accompanied by structural reduction in other organs, pseudo-veins, representing reduced veins, being present in the fronds of some small species of *Trichomanes*, and roots being very rudimentary, or in some cases altogether absent in others. As has been mentioned, Boodle found a very simple stem vascular structure more especially in the small species of *Trichomanes*, which he regarded as occupying the last place in a reduction series.

Generally speaking, then, the whole family is to be considered as much simplified in accordance with its hygrophily, and this simplification has proceeded, hand in hand with certain other features in specialization, further in *Trichomanes* than in *Hymenophyllum*.

It remains to be seen whether or not the facts concerning the New Zealand species brought forward in this paper throw any further light upon this subject.

It has been shown that the multi-layered condition of the frond-lamina in *H. dilatatum*, *H. scabrum*, and *T. reniforme* is developed secondarily in the ontogeny, being found in the fronds of the sporeling plants only immediately alongside the veins, and not being referable to the activity of the marginal meristem. This seems to suggest that the possession of this character must not necessarily be adduced in favour of regarding these species as the most primitive in the family. However, Bower (4, note at bottom of p. 65) has pointed out that *T. reniforme* is the one species of *Trichomanes* which has a large output of spores per sporangium.

Although these three species obviously show specialization in frond-form in the way of extension of the lamina and departure from the strictly deltoid form in accordance with the epiphytic habit, they have not become so thoroughly modified as have the thin-stemmed and invariably pendulous species of *Hymenophyllum*, or as have, on the other hand, the small reduced species of *Trichomanes*. Moreover, the extent of specialization in these three species has not apparently resulted in any great modification of the stem vascular system. Nevertheless we might expect to find species in the family representing more nearly still the primitive stock.

Emphasis has been laid upon the fact that the terrestrially-growing *H. demissum* and *H. bivalve* possess the deltoid frond-form which certainly seems to be the least modified in the existing family. Boodle also has shown (2) that the stem vascular anatomy of *H. demissum* corresponds very closely with that of the above-named three species. I would suggest that *H. demissum* and *H. bivalve* give a better idea as to the primitive stock of the family than does the *H. dilatatum* group. If this is so, then we may perhaps regard this primitive stock as possessing a much-dissected form of frond with little extension of lamina.

Boodle (2) found that the stem-structure of several erect tufted species of *Trichomanes* differed from that of the *H. dilatatum* group only in so far as it showed a solid circular core of metaxylem intermixed with parenchyma, instead of a more or less broken xylem cylinder enclosing the centrally placed protoxylem and parenchyma. He concluded that with regard to the stem-anatomy the upright tufted species are not far removed from the *H. dilatatum* group, and he states that it is doubtful whether they are to be regarded as more primitive than the latter or as more specialized. The suggestion that these tufted terrestrial species represent the original stock most nearly of all, not only in their stem-anatomy but also in their growth-form, is one which should be seriously considered. The family as a whole is much modified in accordance with the function of frond absorption or in the way of reduction, and such tufted species as *T. elongatum* and *T. strictum* show such modification to the least extent with respect to their general growth-form and frond-form. It seems natural, therefore, to conclude that their stelar structure will also be little modified, while, on the other hand, we might well expect that the creeping *H. demissum* with its larger number of fronds and consequent less dependence upon the root and stem vascular system, and still more the species of the epiphytic *H. dilatatum* group with their much greater powers of frond absorption, would show an appreciable reduction in the amount of stem-metaxylem.

The generalization that, on the whole, the species of *Hymenophyllum* seem to have diverged from the primitive stock in one direction and the species of *Trichomanes* in another, and that this primitive stock can still be traced in the modern family, is in accordance with what has been set forth in this paper with regard to the general biology of the New Zealand species. The species of *Trichomanes* keep nearer the floor and, with the exception of *T. reniforme*, are either much reduced or remain for the most part unmodified, whereas the species of *Hymenophyllum* nearly all show, though in different degrees, a particular type of modification which has resulted from the epiphytic pendulous habit.

With regard to the altitudinal distribution, I have noted that in the New Zealand family several pairs of species are found concerning which not only the complementary regional distribution of the two members of

each pair, but also the fact that at intermediate altitudes intergrading forms are to be found which link up the two members in every important particular, point to one member in each of these pairs being a specialized form of the other. Additional data bearing upon this point will be noted in my second paper. These pairs of species are—*H. sanguinolentum* and *H. villosum*; *H. flabellatum* and *H. rufescens*; *H. australe* and *H. atrovirens*; *H. Tunbridgense* and *H. peltatum*. It is to be further noted that *H. villosum*, *H. rufescens*, and *H. atrovirens* are endemic to New Zealand. I must add, however, that in the case of possibly all of these pairs both members are sometimes to be found side by side at intermediate altitudes, each presenting its distinctive characteristics. Here, then, it seems there is direct evidence of the evolution of the family taking place in accordance with variation in the climatic conditions. Whether or not such derived forms are truly "fixed" must be determined by properly-carried-out experimental cultivation, or perhaps better still by wide and detailed field-study. This, of course, touches upon the much wider question as to which of the mountain or other highly specialized species of a country, such as, for example, New Zealand, are true-breeding species, or whether, rather, they are not true species at all, but merely "forms" which preserve their distinctive character only so long as they remain under the control of certain environmental conditions. A family, such as the Hymenophyllaceae, or a particular species, which is in a highly plastic condition, can be expected to afford examples which should be of great interest and importance in the consideration of evolutionary problems. One other such example must be referred to. *H. multifidum* in Westland is to be found in two distinct forms, the one when epiphytic and the other when terrestrial at higher altitudes. In the lowlands this species, as has already been described, has a wide vertical range and shows itself capable of great corresponding variation in its form, but even when most stunted as a high epiphyte it never exhibits the form which it has as a terrestrial mountain-plant. This terrestrial variety is very distinct, and it may even be found occasionally in more lowland situations growing in moss on the ground in exposed places. It might therefore be concluded that the mountain form is either a "fixed" variety of the lowland or that it is the direct result of the terrestrial habit. However, at the base of the ranges one may sometimes find the lowland form growing more or less erect on mossy boulders in various stages of stunting, in at least one instance my notes recording the fact that both the lowland and the mountain form were existing side by side in such a station; and also, at higher altitudes, where the mountain form is most abundant on the floor and the other altogether absent, one may find on especially sheltered and overhanging banks fronds of this species showing every gradation between the two forms. Also, although the mountain form is almost invariably restricted to the terrestrial station, it may be found occasionally at high altitudes in especially damp localities climbing shrubby trees to the height of 6 ft. to 8 ft. L. Cockayne experimentally cultivated plants of this species (which showed the extreme decurved deltoid and strongly inrolled mountain form) which he had brought from the exposed summit of the subantarctic Auckland Island. He states (8, p. 267), "Plants . . . cultivated in the moist chamber of the Canterbury College Biological School have their new fronds not in the least degree curled up, and of a bright green, contrasting strongly with the almost black curled fronds. Such young fronds are at first erect, with their

pinnae plagiotropous, but finally the stipes bend so as to bring the whole surface of the frond into a horizontal position. . . . By March, 1904 [*i.e.*, nine months after the beginning of the experiment], the new fronds of the curly leaved form were identical with those of the type."

It can only be concluded from these apparently conflicting lines of evidence that not only are the epiphytic and the terrestrial stations able to produce very distinct effects upon the growth-form of this species, but also that it is in such a highly plastic condition that it responds quickly to smaller changes in the humidity and other growth-conditions than attract our observation.

In connection with the subject of the vertical distribution of the species brief reference must be made to the fact that the general epiphytic flora of the forest tree-tops in the Westland lowlands provides a very good indication of the nature of the climatic conditions which the six high epiphytic species of *Hymenophyllum* are able to endure. I have found that throughout the lowlands the high epiphytic flora, in addition to this group of filmy ferns, is made up almost exclusively of the orchids *Dendrobium Cunninghamii*, *Earina suaveolens*, *E. mucronata*, *Sarchochilus adversus*, and *Bulbophyllum pygmaeum*, certain species of *Polypodium* — viz., *P. diversifolium*, *P. Billardieri* (= *P. australe*), and *P. grammitidis*— *Cyclophorus serpens*, and *Asplenium flaccidum*. Other plants as well occur in the tree-tops, such as *Lycopodium Billardieri* and species of *Astelia*, although these are by no means so frequent as those above mentioned. These all show striking structural features in correspondence with the variable conditions of the tree-tops, but such modifications are completely lacking in the high epiphytic Hymenophyllaceae which withstand those conditions by the adoption of the mat growth-form and by the imbrication of the fronds alone. It must be added that the above-mentioned epiphytic orchids and ferns, &c., in spite of their xerophytic characters, tend to adopt the rupestral habit in the less wet districts of New Zealand, and are more or less absent from the dry southern-beech forests of the Eastern Botanical Districts, showing that the tree-top conditions in the Westland forests are by no means severe. Miss K. M. Curtis (10) has described the special xerophytic features in the anatomy of the New Zealand epiphytic orchids. The following extract is taken from the summary at the end of her paper: "The velamen consists of one row of cells in *Bulbophyllum pygmaeum* . . . and two or three rows in *Sarchochilus adversus*. The number in the two species of *Earina* and in *Dendrobium Cunninghamii* is more variable, ranging from three to five or more . . . A great number of spirally thickened water-storage cells are present in the cortex of the root of *Sarchochilus adversus;* they are also to be seen, though less frequently, in the two species of *Earina* . . . The leaves of *Bulbophyllum* are succulent . . . pseudo-bulbs are present (consisting of large spirally-marked water-storage cells and small assimilatory cells) . . . The leaf of *Sarchochilus* is very succulent." The high epiphytic polypodies and *Asplenium flaccidum* are also structurally adapted for this station both in the thick fleshy nature of their stems and in the succulent or coriaceous character of their fronds. The fronds of *Cyclophorus serpens* are an extreme example of this. They are very thick and fleshy, the palisade water-tissue being up to eight or nine cells in thickness, and the under surface, as also, though to a somewhat less extent, the upper surface, being densely clothed with a tomentum of closely interlocking stellate hairs. The epiphytic

Lycopodium and the Astelias are also well adapted for their station. The delicate nature of the frond-lamina of the high epiphytic Hymenophyllaceae, and the complete absence of any water-storing tissue, frond-tomentum, or cuticle, is in striking contrast to the structural modifications in the other high epiphytes.

As a result of his investigations into the physiology of the Jamaican Hymenophyllaceae, Forrest Shreve concludes (26, p. 208) that the xerophily of the epiphytic species "resides not at all in their structure, but in the capacity of the protoplasmic utricle to withstand the removal of the sap which is its source of water and nutrient salts." The facts with regard to the New Zealand epiphytic species go to show that this statement must be somewhat modified and amplified before it can be applied to the family as a whole. The frond of *H. Malingii* shows a truly remarkable structural modification, even although this species occupies only a mid-epiphytic station. It is possible that the multi-layered condition of the fronds of *H. dilatatum*, *H. scabrum*, and *T. reniforme* is to be regarded as a recent modification rather than as a primitive feature. But a most important and effective modification in accordance with the epiphytic station is that which takes place in the growth-form, and it is probable that further study of the family will show that elsewhere also this is partly responsible for the wide vertical and altitudinal range of this hygrophilous family.

General Conclusions.

1. The distribution of the New Zealand Hymenophyllaceae is best studied in Westland, for the following reasons: (*a*) Nearly all the species are there present in abundance; (*b*) the constantly high humidity of the forest-interior enables them for the most part to adopt the epiphytic station; (*c*) the presence of only one type of forest reduces the question of their regional distribution to the simple one of the effect upon the family of altitude alone; (*d*) the effect of altitude upon the plant-covering generally is known to be more marked in the latitude of Westland than farther north.

2. In Westland a certain proportion of the species belong altogether to the lower altitudes, others, on the other hand, to the mountains, while a few range from sea-level to the subalpine forest, and two—viz., *H. villosum* and *H. multifidum*—extend into subalpine altitudes above the forest zone. The details of their altitudinal distribution are set forth in Table C, on page 603. This differentiation among the members of the family may be seen also in other parts of New Zealand, although farther northward it is modified by the increasing altitude attained by the lowland species and by the forest-covering generally.

3. The conclusions reached as to the vertical distribution of the species in Westland are set forth in Table D, on page 610. As will be shown in a subsequent paper, these conclusions are borne out by the behaviour of the species in other parts of New Zealand, except that in the drier districts, and also in the pure southern-beech forest where this occurs both under light and under heavy annual rainfall conditions, the epiphytic habit of the family generally is restricted in accordance with the more variable atmospheric humidity there experienced.

4. Those species which have the widest vertical range in the lowlands of Westland are, with the exception of *H. sanguinolentum*, those also which have, both in Westland and in other parts of New Zealand, the widest altitudinal range.

5. In Westland a large proportion of the species invariably form groups according to their habits. These groups can be recognized also in other parts of New Zealand, but differences between the members of the several groups are brought to light by their behaviour in lighter types of forest and under more variable climatic conditions, which differences are in some cases discernible also in their behaviour in the Westland forests.

6. A progression can be traced in the New Zealand family from species which are invariably terrestrially-growing to those which are invariably epiphytic, and this goes hand in hand with a progressive modification in the frond-form, in the relative extent of frond-lamina, and in the thickness of the rhizome and stipe, indicating a change from root to frond absorption. The species which occupy the most exposed positions both in high vertical and in high altudinal situations, or on exposed rock-faces, do so by means of their ability to adopt a stunted imbricated frond-form combined with a mat growth-form.

7. Certain mid-epiphytic species have progressed to a modification of the structure of the frond-tissues which undoubtedly aids them in retaining this station. Of these *H. Malingii* is the most notable example. It is suggested—and reasons are given—that the multi-layered condition of the frond-lamina in *H. dilatatum*, *H. scabrum*, and *T. reniforme* is an acquired and not a primitive character.

8. The species of *Trichomanes* are far more restricted in their distribution and in the ability to modify the frond-form than are those of *Hymenophyllum*, the only exception to this being *T. reniforme*, which in Westland is a characteristic mid-epiphyte, and which possesses a peculiar but fixed form of frond, and along with it the ability to inroll the frond closely.

9. The smaller species, both of *Trichomanes* and of *Hymenophyllum*, commonly adopt the mat growth-form even in their low epiphytic stations, this being especially marked in those of the former genus.

10. Four pairs of closely related species may be distinguished in the New Zealand family—viz., *H. sanguinolentum* and *H. villosum*; *H. australe* and *H. atrovirens*; *H. flabellatum* and *H. rufescens*; *H. Tunbridgense* and *H. peltatum*. From the fact that in the case of each of these pairs the two members are more or less complementary in their altitudinal distribution, and also that intermediate forms are to be found at intermediate altitudes, it would seem that one member in each pair is a derived and possibly a mountain form of the other. The occasional existence of the two members side by side in the case of at least three of these four pairs, under apparently identical environmental conditions, makes more difficult the understanding of the exact relation of the two members to each other.

11. The suggestion has been put forward that in view of the fact that the greatest modification of the existing family so far as the New Zealand species are concerned, apart from the probable reduction in size of many species, has been in the direction of the adoption of the epiphytic habit with the tendency towards dependence upon frond absorption rather than upon root absorption, that therefore the more primitive growth-form and frond-form and stem-anatomy is to be looked for in the typically terrestrial members of the family, and possibly in the tufted species, rather than in any of the other members.

12. It is suggested that the inability of the larger epiphytic species to adopt to any noticeable extent in the lowland forests of Westland the terrestrial or low epiphytic station may be due to the need in the dark forest-interior of seeking the maximum illumination possible. Possibly this explains the fact that in Westland *T. venosum* and *H. ferrugineum*

are the only species which occur on tree-fern stems, although in lighter forests in other parts of New Zealand *H. rarum* and *H. flabellatum* quite commonly adopt this station, and other epiphytic species also occasionally.

13. The fronds of many of the New Zealand species can recover after a considerable degree of drying and shrivelling. The observations of the present writer with regard to this phenomenon relate only to the larger epiphytic species of *Hymenophyllum* and to *T. reniforme*. The typically terrestrial species and the low epiphytes, and also the small species generally, rarely are found shrivelled. Certain larger epiphytic species possessing filiform stems—viz., *H. rarum*, *H. flabellatum*, *H. Malingii*—are probably the most rarely shrivelled of the epiphytes, all apparently possessing special modifications for resisting desiccation. *H. villosum* can both withstand drying, and also recover from it when affected, to the greatest extent of all the New Zealand species.

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