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CAWTHRON LECTURE
1936

"Links in the New Zealand Flora with the Remote Past."

BY

Rev. J. E. HOLLOWAY, D.Sc., F.R.S.N.Z.
Otago University, Dunedin.

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A SUMMARY OF THE PAST HISTORY OF THE PTERIDOPHYTA.

ERA.	PERIOD,		PTERIDOPHYTA PRESENT
Recent ...			Modern Ferns and relics of earlier Ferns and other Pteridophyta.
Tertiary (Cainozoic) ...			
Secondary (Mesozoic)	Cretaceous		
	Jurassic		Early Ferns: Lycopods and Horsetails much diminished.
	Triassic		
Primary (Palæozoic)	Permian		Era of maximum development of Pteridophyta as represented by Lycopods and Horsetails.
	Carboniferous		
	Devonian	Upper	
		Lower	The earliest known Flora of the Land, consisting of small Pteridophyta of simple organization.
	Silurian		
	Ordovician		Marine Algae (sea-weeds); the only plants known from these times.
	Cambrian		
Pre-Cambrian ...			No known plant life.

LIST OF PTERIDOPHYTA MENTIONED IN THIS LECTURE.

1. ANCIENT FOSSIL PTERIDOPHYTA.

a. Rhynia. Hornea. (Lower Devonian).

b. Lepidodendron. Sigillaria. (Carboniferous Lycopods).

c. Calamites. (Carboniferous Horsetails).

2. PRESENT-DAY PTERIDOPHYTA.

a. Osmunda (Royal Ferns). Gleichenia (Umbrella Ferns). Marattia (Horseshoe Ferns). Schizaea. All these families date from early Mesozoic.

b. Lycopodium (Clubmosses). Selaginella. Phylloglossum. Isoetes (Quillworts). These all are Lycopods.

c. Equisetum (Horsetails).

d. Ophioglossum (Adder's Tongue Ferns). Botrychium (Parsley Ferns).

e. Tmesipteris. Psilotum.

LINKS IN THE NEW ZEALAND FLORA WITH THE REMOTE PAST.

BY

The Rev. J. E. Holloway, D.Sc., F.R.S.N.Z.

INTRODUCTION.

The Plant Kingdom, considered broadly, consists of four main subdivisions, viz., the Thallophyta (Algæ and Fungi), Bryophyta (Liverworts and Mosses), Pteridophyta (Ferns and Fern Allies), and the Spermatophyta or Seed Plants (Gymnosperms and Flowering Plants). The subject of this lecture is the Pteridophyta, and more especially the Fern Allies. To-day the Pteridophyta, in actual numbers, is by far the smallest of these four groups, but it has not always been so. The fossil record shows that during a long period of time, in remote geological ages, this group constituted the main, or even, according to some botanists, the only vegetation of the land, and became a more extensive and noteworthy group than it is to-day.

Another name for this group is the Spore Plants or rather, the Higher Spore Plants, since the Bryophyta (the Lower Spore Plants) also reproduce by means of spores. In the Pteridophyta the spores are borne in large numbers in special spore capsules or sporangia which are distributed over the stems or leaves in a variety of ways. The Bryophyta also have spore organs termed sporogonia, these being larger and of a different build from those of Pteridophyta.

It will be useful at this stage briefly to refer to the life history of a typical Pteridophyte. It consists of two distinct stages or generations which have an independent existence. The spore gives rise to a small body on the surface of, or underneath the soil, and this bears the male and female sex organs with their sperms and eggs. This small body is designated the "gametophyte" stage of the life cycle since it bears the sex cells or gametes. The fertilised egg proceeds to develop into an embryo and thence into a young "sporeling" plant. The embryo absorbs nourishment from its parent gametophyte by means of a haustorial foot, but as soon as the sporeling has formed its own first root and leaf it attains independence of the gametophyte which sooner or later dies. The sporeling continues its growth and constitutes the "sporophyte" generation of the life cycle, so called because it is destined to produce the sporangia and spores. The latter when shed germinate to form gametophytes.

It is important to note that the alternation of gametophyte and sporophyte in the life cycle of the Pteridophyta is a regular one, and also that the two generations are morphologically distinct from one another and independent. Together they constitute the "plant," although in popular usage this term is usually given to the sporophyte alone, the gametophyte being overlooked on account of its relatively small size and shorter life.

The Bryophyta possess in principle the same kind of alternation in their life cycle. Here, however, the gametophyte is the more obvious of the two generations, although of a simple organisation, and is popularly regarded as the "plant." The sporophyte is of still smaller size, and never attains independence of the gametophyte. It develops no such specialised organs as root, stem or leaf. The gametophyte is large enough, and long-lived enough, to produce a succession of sporophytes, but each sporophyte, as its main effort, gives rise to but one spore capsule or sporogonium which occupies the greater part of its bulk, and then the sporophyte dies away.

The Algæ, of which the marine algæ or seaweeds are the largest and most widely known, also are of simple organisation without differentiation into stem, root and leaf. (Fig. 1). They have sex reproduction, and many of them have special sex organs, but these are scarcely comparable with the sex organs of Bryophyta and Pteridophyta. On the other hand the close similarity between the two latter groups with respect to the structure of the sex organs, and more especially of the female organ (archegonium) is significant. Most Algæ reproduce also by spores, but these are commonly swimming spores. The sporangia in which they are borne are hardly comparable with those of the Spore Plants. The outstanding difference between the Algæ and the Spore Plants is with respect to the phenomenon of an alternation of generations in the life cycle. In the Spore Plants it is regular and well marked. Many Algæ do not possess such an alternation at all. Others do, although it differs considerably in its nature in different Algal groups. It must suffice here to say that it is not at all clear whether or not any one of the types of alternation met with amongst Algæ is strictly comparable with that typical of the Lower and Higher Spore Plants. Some would answer in the affirmative, while others are very doubtful.

This then will serve to introduce the subject of the nature of a Pteridophyte and its similarities with and differences from a Bryophyte and an Alga. The fossil record proves that Pteridophyta, as a group, have had a long geological history, going back to the very early days of a Land Vegetation. As to their actual origin some hold that they arose from primeval marine Algæ which underwent a slow migration on to the dry land, developing features suitable to a subaerial life such as a definite and regular type of alternation, dry air spores formed in special sporangia, and an organisation of the sporophyte generation into stem, root and leaf systems with conducting, protective, and aerating tissues. Others hold that the first Land Plants to evolve from the Algæ were Bryophyta. They believe that it was certain of the latter which gave rise to the first Pteridophyta, both their gametophyte and their sporophyte generations undergoing progressive modification in the process, the one in the direction of simplification, and the other of elaboration into the perennial and self-supporting sporophyte. The comparative study of the existing members of these three groups raises the question as to the origin of the first Land Plants, but it is to the fossil record that botanists must look for final evidence.

If the first chapter in the story of the Pteridophyta is still obscure, the subsequent chapters are to a very considerable extent well known for their abundant and often wonderfully complete fossil remains. Moreover, the latest chapter of all is not the least interesting one of the story. The Pteridophyta of to-day are well represented in the flora of New Zealand, and on this account may be regarded as proving a suitable topic for a Cawthron Lecture. I must add that a further reason which prompted me to select this subject was the fact that my own research work has consisted in endeavouring to follow out the life histories of certain of these New Zealand Pteridophyta.

THE PAST HISTORY OF THE PTERIDOPHYTA.

A knowledge of the past history of the Pteridophyta is necessary for the proper understanding of the existing members. Some of the latter, more especially of the Fern Allies, are closely comparable with Carboniferous Pteridophyta, and even, although less closely and certainly, with those of still more remote ages. On this account certain details must now be given concerning these ancient fossil members of the group.

(a) The Primitive Pteridophyta.

The earliest recognisable remains of fossil plants are of marine Algæ. These are found in Cambrian and Ordovician rocks (see Table p. 2). They are abundant, of various kinds, and some of very large size. The earliest known land plants are all Pteridophyta, dating from the

Silurian and Lower Devonian periods. These include a number of different types, but compared with those of succeeding geological times they are all of simple organisation and for the most part small size. The remains of Bryophyta, so far as is yet known, do not appear until the Carboniferous, but it must be noted that Liverworts and Mosses do not lend themselves well to fossilisation owing to their very small size and to the delicate nature of their tissues.

Information concerning the primitive Pteridophyta has been steadily accumulating during the past twenty years, with the result that the focus of botanical interest in these plants is shifting from the Lower Devonian to the Silurian period. It is of course always possible that future discoveries may locate them in still earlier Silurian rocks. These earliest known members of the group are not numerous, but are in many cases very well preserved. Plant fossils, as is well known, take the form of impressions in fine-grained rocks, and of casts, and, more important still, of petrifications in which the actual tissues of the plant have been impregnated with siliceous or calcareous solutions, with the result that these tissues can be studied microscopically in thin sections precisely as in the case of plants living to-day. Fortunately ample material of several of these early plants has been discovered remarkably well petrified. Even the impression type of fossil can be made to yield a certain amount of information concerning tissue structure, in addition to showing external form and appearance.

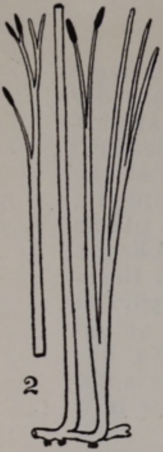
These fossil remains are always of the sporophyte generation. The gametophyte is not known, and, considering its small and delicate nature, it is very unlikely that it will ever be found fossilised. This is not of great moment, however, since in Pteridophyta the sporophyte plays by far the greater part in the life cycle.

From the evolutionary point of view, the problem of the actual origin of the organised sporophyte of the typical Pteridophyte is of outstanding interest. How did such features as stem, root and leaf, vascular tissues, and the sporangium originate? Such characters as these belong to plants possessing a thorough-going subaerial habit of life. In these respects Pteridophyta are widely different from either Algæ or Bryophyta. Types of plants intermediate to the former and either of these two latter groups might be difficult to classify. However it is known for certain that true Pteridophyta existed as early as late Silurian times, so that the actual origin will have to be sought still earlier. These earliest known Pteridophyta are certainly of extraordinary interest on account of their relatively simple organisation, and structure. They undoubtedly represent a stage in evolution intermediate to the Carboniferous Pteridophyta and some other pre-existing ancestral group. Even if botanists had not previously faced the problem of the evolutionary origin of the Pteridophyta, the discovery of these early Devonian and Silurian plants would force them to such a consideration. In certain respects some of them suggest a comparison with Bryophyta, while in others they seem to be more comparable with large Algæ, so that the question as to the actual origin of Pteridophyta remains unanswered. As has been well said, the scientific interest of these fossils is not that they solve a problem, but that they raise one in a very insistent way.

We will now turn to certain details of their organisation. Amongst the Algæ branching takes place by a simple forking of the apex (Fig. 1). Commonly the two arms of such a forking grow equally strongly, a repetition of the process results in the plant remaining of comparatively small size. In other cases one of the arms may grow more strongly than the other so that it becomes a continuation of the main axis, the smaller arm being left behind in a lateral position. Branching by apical forking is characteristic also of Bryophyta. In all Seed Plants, on the other hand, and also in a few Pteridophyta, there is a much more highly organised type of branching, in which the branch always originates as a bud arising laterally on the main axis. The apex of the latter remains intact and continues to elongate indefinitely, and a strongly growing main axis results. The earliest known Pteridophyta practically all seem to be small plants with the forking type of branching, and in some at least the two arms of each fork are always more or less equally developed (Fig. 2).

Some of these primitive Pteridophyta, as for example *Rhynia* (Fig. 2), are quite leafless. Others again have the upper parts of the stems covered with numerous small simple leaves similar to those of the Lycopods of later geological ages (cf. Fig. 3). In still others the ultimate forkings of the stems give rise to tufts of delicate leafless branchlets.

Some at least of these plants are known to be quite rootless (Fig. 2). One of them gives a clue as to how roots possibly originated in the first land plants, certain of the branches of its underground creeping axes becoming progressively finer at each forking, the more delicate branchlets undoubtedly acting as absorbing organs. Pteridophyta of later times possess true roots, but in many of them, even



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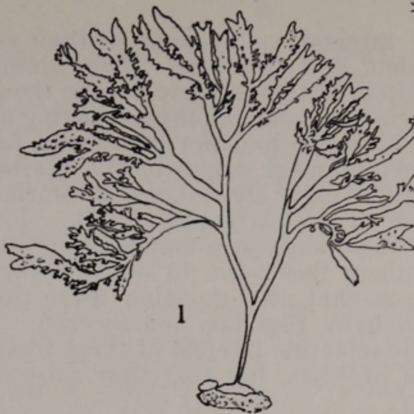

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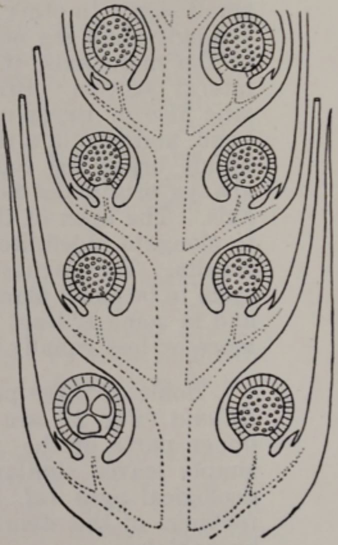

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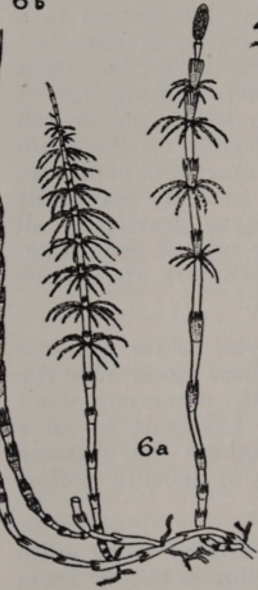

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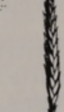

5a

Fig. 1. A typical seaweed (**Gigartina**), reduced size.
Fig. 2. **Rhynia** (restoration) reduced size.
Fig. 3 **Lycopodium Selago** x ½.
Fig. 4. **Lepidodendron elegans** (restoration), a large tree.
Fig. 5a. **Selaginella,** branch with cone x 2.
Fig. 5b. basal part of same cone in sectional view, magnified, showing sporangia.
Fig. 6a. **Equisetum pratense** x ½.
Fig. 6b. cone of same x 1½.

amongst those existing to-day, the roots branch by forking and do not show the more specialised method of a lateral endogenous origin of the rootlets characteristic of the Higher Plants.

Botanists are familiar with the fact that amongst Pteridophyta, fossil and recent, there are two types of leaves, viz., the small (microphyllous) and the large (megaphyllous) types. The entire Fern stock possesses the latter, here termed the frond, whereas all other Pteridophyta so far as is known have the former. It is widely held that these two leaf types represent two quite distinct modes of origin in geological time, the small leaves representing modified branches. The earliest known Pteridophyta provide material for the discussion of the origin of both these leaf types, and some of them, in their total lack of leaves of any kind, suggest a more primitive condition still.

It will be remembered that some modern Seed plants lack leaves or roots or both, but in all these cases it is beyond doubt that the plants have lost them through becoming specialised to some new and abnormal mode of life, so that there is no suggestion that they and their ancestors have actually retained throughout their long history a primitive condition. In their embryo and seedling stages it can readily be seen that the leaf and root system is represented, and that it is only in the later stages of development that the plant passes out of this normal condition and forms no more leaves and roots. Moreover, close examination will always show minute rudiments of leaves on the stems.

Is it possible that the leafless and rootless early Devonian plants had really lost these organs and were thus not in a truly primitive condition? Between this age, and let us say, the early Silurian, a long period of geological time intervened, and much could have happened to land plant life during this time. If it can be shown that these early Devonian plants had descended from a stock which had already attained to leaves and roots, it would simply indicate that really primitive Pteridophyta have not as yet been found. The test of the embyro and juvenile stages of development cannot be applied here since these are not known. But there is fairly convincing evidence to show that these plants are actually in a primitive condition. They show other features in addition to rootlessness and leaflessness which bear the imprint of primitiveness, more especially in the sporangium as referred to below. There are several different kinds, one of which *(Psilophyton)* reaches back at least to the later Silurian. They have been found in several widely separated parts of the world.

If their primitiveness be granted, it becomes clear that it is possible for some races of Pteridophyta to retain one or more primitive characters through long periods of time, viz., early Silurian to early Devonian, while other races are marching on to a higher grade of organisation. And if for a period of this duration, it is further possible that such characters may have been retained in some or other evolutionary line for longer still, even down to the present day.

As has been stated previously, the typical Pteridophyte sporangium has a different build from that of Bryophyta, and also occurs not singly but in considerable numbers on the sporophyte. There is also nothing closely comparable to it amongst the Algæ. Disregarding the great Fern group, which for the most part must remain outside the scope of this lecture, the sporangia in the Fern Allies usually occur singly in the axils (angles) of leaves, either scattered up and down the stems in patches (Fig. 3), or aggregated together into compact terminal cones or "strobili." (Figs. 4-6.) The cone arrangement is certainly, on the face of it, a more highly organised one than the scattered arrangement, and it has long been considered that the latter is actually more primitive. Cones are characteristic of most existing Fern Allies, and also of those of the Carboniferous, the classic age of the Pteridophyta, but they have not yet been recorded in any Lower Devonian or Silurian plant. On the other hand, one of the earliest known Silurian plants *(Baragwanathia)* from Victoria, and several from the Lower Devonian, are known to have had the scattered arrangement, the indication being that this then is a more or less primitive feature.

A still more simple arrangement of the sporangia on the axis, and at the same time a larger and more simple build of sporangium, is known in several of the Lower Devonian plants. Here the sporangia stand singly at the end of the branches (Fig. 2) and are not organs *sui generis,* as they seem to be in all other known Pteridophyta, but represent merely the dilated ends of the branches filled with spores. The plants which possess this type of sporangium, are those, such as *Rhynia* and *Psilophyton* and others of the same group (the Psilophytales), which also are so simply organised in apparently all other respects. It is even possible here to institute a comparison with the sporogonium of certain Bryophyta or with the fertile spore-bearing branches of certain seaweeds. To botanists this feature in the organisation of these particular early Pteridophyta is even more significant than the others which have been mentioned.

It is thus apparent that with respect to a number of important features the earliest known Pteridophyta may be regarded as more or less primitive.

(b) THE PTERIDOPHYTA OF THE UPPER DEVONIAN AND CARBONIFEROUS PERIODS.

We come now to the times of the succeeding geological periods. Here we find ourselves confronted wtih much more highly organised and diversified Pteridophyta, many of which are of tree dimensions. This is the great age of the Fern Allies, more particularly of the Lycopods and Horsetails. They formed forests on the swampy lowlands, giving rise to numerous coal seams, and they must have been spread over a large part of the earth, for their fossil remains have been found in many countries. Along with the Pteridophyta there existed a number of different kinds of early Gymnosperms, one group of which (the Pteridosperms) combined pteridophytic and gymnospermous characters in a way most significant from the evolutionary point of view.

With such an array of highly organised plant-types present, it is clear either that a very long period of time must have elapsed between the early Devonian and the Carboniferous periods, or else that the immediate forerunners of these types must have been already present in the former, although their fossils have not as yet been found in these rocks. On the other hand it is quite possible that some or other of the earlier primitive Pteridophyta persisted in suitable places into the Upper Devonian and Carboniferous times, although the fossil record has not as yet shown this to be the case.

Some of the Carboniferous Pteridophyta, except for their commonly greater size, are strikingly similar to some of those of to-day. Such are the *Lepidodendrons* (Fig. 4), *Sigillarias* and *Calamites,* household names to the botanist and the geologist. These plants are very thoroughly known in spite of their great antiquity. Innumerable fossils have been found, and a never-ending supply is still available, from the coal measures of many northern hemisphere countries, petrified plant remains being fortunately quite common.

The ferns also must be mentioned, since, although up to the close of the Carboniferous period they were few in number and formed a comparatively small part of the world's vegetation, they rose to a dominant position among Pteridophyta during the Mesozoic period, and retain that position to-day.

In the Lycopods and Horsetails the sporangia are aggregated into very characteristic terminal cones (Fig. 4), although some of the smaller Lycopods are known to have had the scattered arrangement. A further degree of complexity in organisation is seen in the fact that in the *Lepidodendrons and Sigillarias* the sporangia and their spores were of two different kinds, male and female, the latter with large spores being placed at the base of the cone, and the former with more numerous minute spores occupying the upper portion. This condition, which is found, too, in some of the modern Lycopods (Fig. 5), is suspected by botanists to have arisen in other early groups of Pteridophyta also, and it is considered that from this came the distinction into pollen and seeds which is the characteristic feature of the Seed Plants.

(c) THE PTERIDOPHYTA OF THE MESOZOIC AND CAINOZOIC PERIODS.

The subsequent fossil history of the Pteridophyta can be more briefly told. In the early part of the Mesozoic the tree Lycopods and Horsetails apparently became extinct, being succeeded by smaller representatives of the same groups. These were widely distributed over the world, as shewn by their fossil remains, but played a comparatively small part in the general vegetation.

The Ferns are now the representative Pteridophyta. In the earlier part of the Mesozoic the chief fern families were, for example, the Umbrella ferns (Gleicheniaceæ), Royal ferns (Osmundaceæ), and Horseshoe ferns (Marattiaceæ), all of these families being still in existence at the present day, although in very much reduced numbers. Petrified stems of the Royal ferns have been found in Mesozoic rocks in various parts of the world, including several localities in New Zealand. At Curio Bay, near Invercargill, for example, there are the remains of an extensive Jurassic petrified forest, with the stumps of coniferous trees still standing, and trunks lying prone, and amongst them numerous petrified standing stems of one or more kinds of Royal ferns. On the beach at the same place the boulders contain the impressions of fern and conifer foliage. This is but one example of the great wealth of fossil plant material the world over, available for study.

Since the Mesozoic the Fern Allies have undergone still further diminution in size and importance. They are now but the much diminished representatives of ancestors which in the Carboniferous period ruled the earth. Some of these Fern Allies at the present time, judging from their distribution, seem to be heading towards extinction. The Ferns on the other hand remain as a very widespread and successful group, although the Early Mesozoic families have been more or less supplanted by those of more modern origin.

THE PTERIDOPHYTA OF TO-DAY.

The Pteridophyta of to-day belong mainly to the three groups Ferns (Filicales), Lycopods (Lycopodiales) and Horsetails (Equisetales). In addition there is the very small but botanically interesting *Psilotum* family whose ancestry is obscure.

As has been stated before, several existing Fern families date from the comparatively remote Early Mesozoic, or it may be even from the Carboniferous period. In addition to the Umbrella, Royal and Horseshoe ferns, there is the *Schizaea* family, and one or two others confined to the eastern tropics. These all, as their fossil remains show, formerly were much more abundant and widely distributed than they are now. A point of botanical importance about them is that their sporangia are of a more ancient type and much more comparable with those of the Fern Allies than are the very highly specialised small sporangia of the modern ferns.

A family which is commonly regarded as belonging to the great Fern stock, is that of the Adder's Tongue *(Ophioglossum)* and the Parsley fern *(Botrychium)*, together with a third, eastern tropical genus with but one species. The ancestry of this family is not known, but on various grounds it is considered probable that it dates back into the Carboniferous period. These plants have the large, frond-like type of leaf, but their sporangia are of an even more ancient type than are those of the Early Mesozoic ferns.

The Lycopods are represented to-day by four main types. Of these the *Lycopodiums* or Club Mosses and the *Selaginellas* are by far the most numerous. These are all of smaller size than even the Mesozoic Lycopods. They total about 600 species, of which the greater number belong to *Selaginella*. The latter are for the most part creeping plants, found mainly, although not exclusively, in warm and especially tropical countries. They are known to gardeners from being commonly grown in glass houses. Their cones have both male and female sporangia (Fig. 5). The *Lycopodiums* occur in most countries, in such places as open hillsides, or bogs, or hanging pendulous from trees in tropical forests. The popular name of Club Mosses arises from the long stiff cones which many have. They differ from the *Selaginellas* in several particulars, notably in the fact that their sporangia and spores are not differentiated into male and female.

These two genera have many features in common with some or other of the Carboniferous Lycopods. At the same time other of their characters bear the imprint of being of more modern origin. This presents a problem to the botanist since it is essential, if he is to appraise these plants aright, that he should be able to distinguish between what is really archaic and what is not. Sometimes the distinction is readily made, but in other cases this is not so, and then interpretations may differ.

The other two types of Lycopods consist of highly specialised little plants. The Quillworts *(Isoetes)* with about sixty species, distributed the world over, are amphibious in habit or totally submerged aquatics. They have an abnormally-shaped, cushion-like stem, surmounted by a tuft of stiff linear leaves, and with no definite cone. They have distinct male and female sporangia and spores. In spite of their curious habit of growth, they are considered on the sum total of their characters to be Lycopods, belonging to the same division of this group as *Selaginella*.

The remaining genus is *Phylloglossum* (see plate) which consists of only one species. This is a very small plant, no more than two inches high. It has a basal tuber to which it dies down, and by which it remains in a dormant condition over the dry months of summer and autumn. Plants which die down to their basal parts when the unfavourable season of the year sets in, are termed "geophytes.' They commonly show extreme modification of these basal parts in connection with the resting habit, after the well-known manner of bulbs and corms and stem tubers. *Phylloglossum* is found only along the south coast of Australia and the northern portion of New Zealand. In spite of its diminutive size and peculiar habits it has essentially the same kind of cone as *Lycopodium*. It is considered to be an offshoot from one particular section of that genus on the ground of its close agreement with the members of that section in several important particulars. It has been the subject of much attention from botanists.

The Horsetails are represented to-day by only one genus *(Equisetum)* with about twenty-five species. These belong mainly to the North Temperate Zone and to further north still, where they are common in cold wet soils as were their Carboniferous ancestors. They are not found in New Zealand, and will not be referred to again in this lecture, so that their great botanical interest must be

Phylloglossum (in situ). Auckland clay gum-lands.

Photo— T. L. Lancaster.

emphasised here. They have creeping underground stems, with erect, switchlike jointed branches from six inches to a few feet high, bearing stiff oval cones (Fig. 6). The leaves form small, toothed, scale-like sheaths at the joints of the stems. The Carboniferous Horsetails had precisely the same build and appearance, although they were for the most part of much larger size. The close similarity between the ancient and the modern Horsetails is very noteworthy, and holds also with respect to many details in the anatomy of the stems and cones. This is a most remarkable instance of the persistence of characters in an evolutionary line from a very remote period down to the present day. Such cases as this suggest that it is possible that characters have persisted in some Pteridophytes from still more remote times.

As has already been stated, the fossil history of the small *Psilotum* family is not known. It consists of two genera each with only one or two species. These are *Psilotum,* which is spread throughout many tropical and subtropical countries and Australasia, and *Tmesipteris* (see plate), which is confined to Australasia and its immediate neighbourhood. These two plants exhibit a simplicity in organisation, more particularly in their total lack of roots, which is considered by many botanists to warrant the drawing of a close comparison between them and some of the primitive early Devonian plants.

The important phenomenon known as "saprophytism" must here be referred to. *Psilotum* and *Tmesipteris* grow in humus on trees or in rock crevices, and are semi-saprophytic in their method of nutrition. Saprophytism occurs also in a number of other plants, both Pteridophytes and Seed Plants. This term, which comes from the Greek word for decay, refers not so much to the fact that these plants grow in decaying matter, but that they can acquire elaborated organic food substances from it.

Normal green plants usually absorb from the soil only inorganic salts and water. In their leaves they synthesize their sugars and other organic substances. Fungi, on the other hand, lack the green pigment chlorophyll and so are unable to synthesize sugars for themselves. Instead they secrete enzymes into the surrounding medium, a thing which the higher plants are apparently not capable of doing, and these enzymes digest the insoluble organic matter occurring there, with the result that the fungal hyphæ can absorb the now diffusible carbohydrate and nitrogenous matter and utilise it as food. Such higher plants as are saprophytes are also able to absorb organic matter from the soil through harbouring a fungus in their roots or underground stems. The plant receives some of this digested food from the fungus, along with no doubt other solutes and water, and is thereby relieved to a greater or lesser extent of synthesizing its own food or even of absorbing directly from the soil. It is to be noted that, in the case of many saprophytes, as a direct result of this habit of life, their leaves and roots or both show a marked tendency not to develop. It is important for our present purpose to emphasize this. Moreover this effect upon such plants may make itself apparent not only in their later stages of development, but in some cases in the embryo stage.

This phenomenon of saprophytism comes to a greater or less extent into the story of a number of the Pteridophyta of to-day, such as the *Lycopodiums*, and the Adder's Tongue fern and *Psilotum* families, and will be referred to again later.

THE PTERIDOPHYTA OF NEW ZEALAND.

New Zealand is noted for its Pteridophyta, both Ferns and Fern Allies. It is not only that there are many different kinds, representative of most of the existing families and groups, but also that they play for the most part a conspicuous part in the general vegetation and do not give the impression of being diminishing relics of a past order of things. There are, however, two important kinds which are not represented, viz., the *Selaginellas* and the *Equisetums*, although our fossil record shows that ancestors of the latter were present in Mesozoic times.

The reason for this large display is partly due to the fact that the flora of this country has been added to in past ages by a very considerable influx of plants from the Malayan tropics. The original flora dates, according to the the fossil record, from early Mesozoic times, but where that flora came from, history, as yet, does not relate.

(a) The Ancient Ferns.

The more modern ferns, of which New Zealand possesses a very large number, will not be referred to here.

Every New Zealander knows the single and the double "Crape ferns" or Prince of Wales Feathers *(Leptopteris)*. These, on account of the delicate texture of their large fronds, are two of the most beautiful of our wet forest ferns. They belong to the Royal Ferns, which to-day embrace only three genera the world over, with a comparatively very few species. Another member of this family is *Todea barbara*, a very large, clump forming, harsh fronded plant, to be found in the far north of the Auckland province. The New Zealand Umbrella ferns *(Gleichenia)* number five, three of which are of general occurrence. There are four representatives of the *Schizaea* family, three being species of *Schizaea* and the fourth the famous climbing fern *(Lygodium articulatum)* of the Auckland forests, which can climb one hundred feet or more into the tops of tall trees by means of the enormous elongation of its very slender fronds. The Horseshoe fern family has one representative *(Marattia fraxinea)*, found throughout the Auckland province southwards to Taranaki. It is a very large fronded plant like most of its tropical relatives.

These then are links in the New Zealand flora with the ancient fern vegetation of the Early Mesozoic age. This element is certainly a considerable one.

Of the still more ancient fern types represented by the Adder's Tongue fern family, this country has two *Ophioglossums*, one of which is common in native turf on hillsides, and one *Botrychium* which belongs to scrub and light forests. These plants, as with all members of their family, show a more or less abnormal habit of life in that they are geophytes and also semi-saprophytes. Their embryo development is noteworthy, but whether this is to be interpreted in terms of their undoubted archaic nature or of their abnormal habits, is not clear. The sporangia are borne on a special fertile region of the frond, but so peculiar is this region that it is the subject of two quite different interpretations.

(b) THE LYCOPODS.

New Zealand is well supplied with Lycopods, with the exception of *Selaginella*, and I propose to refer to them in some detail..

The general appearance of a typical *Lycopodium* is, in many respects, much like that of the Carboniferous *Lepidodendrons*, although on a very much smaller scale. The main stem is usually creeping. The erect branches are closely covered with the small type of leaf, and bear the oval or club-shaped cones at the tips of the branchlets. The old forking method of branching is especially well shown in the fertile regions and in the roots.

Some of the eleven New Zealand species are reputed to be amongst the largest of living Lycopods. For example, the branches of *L. densum*, when growing amongst scrub, have a stiffly erect treelike habit of growth up to six or eight feet high. This species belongs to the Auckland province, and is abundant on the clay gumlands. *L. fastigiatum* also has the appearance of diminutive trees, although of course these are only branches of the underground stem. It is an abundant hill and mountain plant throughout the country, and when growing at lower altitudes and sheltered places, its branches may attain a height of three to five feet. The tropical *L. cernuum* reaches from the north as far as western Nelson. The New Zealand variety of this species is very strong-growing with trailing stems up to ten or fifteen feet long. A fourth species, the climbing *L. volubile,* is well known throughout New Zealand from being so commonly used for decorations. It also must be included among the large members of the genus, and is another tropical species.

The *Lycopodiums,* to a much greater extent than the *Equisetums,* exhibit an intermixture of what are probably comparatively recent and adaptive features with others which are undoubtedly archaic. For example, some of them which occur in heavy tropical forests, hang pendulous from a lodging place on the branches of trees, and their cones are correspondingly long, narrow and whiplike and much branched. One of this kind *(L. Billardieri)* is common in New Zealand forests. Such a form of cone as this is best regarded as a more or less modern adaptation, since it is so obviously correlated with the unusual pendulous habit of the plant. The climbing *L. volubile* also has long and flexible pendulous cones.

On the other hand, there are a number of species belonging to the *selago* section of the genus, which have a general form and build apparently archaic (Fig. 3). They grow on the ground and do not have the usual creeping stem of the terrestrial species, but are more or less wholly erect. They show very clearly the forking type of branching. More significantly still they have the scattered arrangement of the sporangia up and down the stems. This latter feature, which we have previously noticed as occurring in some at least of the most ancient Pteridophyta that have yet been found, is so characteristic of these particular *Lycopodiums,* that it is commonly known to botanists as the selago-condition. The world-wide distribution of *L. selago* is itself an indication of considerable age. It is a fairly common mountain species in New Zealand.

The comparison of the stem wood tissues of a modern *Lycopodium* with those of a *Lepidodendron* brings out a point of interest. In the *Lycopodium* stem the wood develops altogether in an inward direction, that is towards the centre of the stem. It is obvious that only a very limited amount of wood can thus be formed, since it very soon meets at the centre and there is room for no more. This is known to have been the method of wood formation also in the stems of those early Devonian plants whose tissues have been found petrified, and in a number of Carboniferous Pteridophyta. With such an inefficient stemwood system as this, a plant could not grow to any great size. A vascular cylinder of this type is termed a "protostele," a name which is intended to suggest its primitive nature. It is of interest to note here that the larger roots of some modern *Lycopodiums* (e.g., the New Zealand *L. volubile, L. fastigiatum,* and *L. scariosum*) have a vascular cylinder indistinguishable from that of a typical *Lycopodium* stem, a fact which may be taken to bear upon the theory that roots originated as modified branches of creeping stems.

The first *Lepidodendrons* also had a simple protostele. One or two of these did attain considerable dimensions, but this was made possible by the very thick bark which gave rigidity to the stem. The later *Lepidodendrons,* however, and the *Sigillarias,* arrived at a vascular organisation more advanced than this. Surrounding the inwardly developed core of wood they possessed a zone of outwardly formed secondary wood, which could go on growing indefinitely from a cambium, thus enabling those plants to assume the dimensions of trees. Secondary growth is characteristic of the great Seed Plant group also, but is found in very few Pteridophyta except those of the Carboniferous period. It would seem then, either that the modern *Lycopodiums* have lost the ability to form this secondary type of wood, or, as is more likely, that they have descended from small Carboniferous Lycopods, more or less closely related to *Lepidodendron,* which themselves had never advanced to this condition. The same must be concluded for the modern *Selaginellas,* which also lack secondary thickening of the stems.

Again, the comparison of the cone of *Lepidodendron* with those of modern Lycopods is instructive. As has already been mentioned, there were two kinds of sporangia in the *Lepidodendron* cone, a few female sporangia below, containing a limited number of large female spores, and many male sporangia above containing the numerous minute male spores. The cone of *Selaginella* is essentially similar to this (Fig. 5). In the *Lycopodium* cone, on the other hand, the sporangia and spores are of one kind only, and this certainly indicates that these two modern genera have not come from one and the same Carboniferous stock. As a matter of fact it is known from the fossils that there were small Lycopods in the Carboniferous period as well as tree species, some of which bore only one kind of sporangium while others had the two kinds.

We turn now to the two highly specialised modern Lycopods. The aquatic Quillworts *(Isoetes)* have two species in New Zealand. These occur commonly around the margins of mountain lakes in a few feet of water. *Isoetes* possesses the sporangia and spores and vascular tissues of a true land plant, so is clearly one which has gone back to an aquatic life at some period of its history. Like *Selaginella* it has two kinds of sporangia, but with many more female spores per sporangium than has *Selaginella*. In this latter respect it is more like *Lepidodendron*. On comparative grounds botanists regard a large number of female spores to each sporangium as representing a more primitive condition than that in which there are only a few. It must be added that *Isoetes* has a much larger number than even *Lepidodendron,* and hence is regarded as having preserved a primitive condition to an especial degree. Its roots have the forked type of branching. Its cushion-like stem, which does not elongate in the manner of a normal shoot, is probably best regarded as having undergone extreme reduction, perhaps in accordance with the underwater mode of life. Whether *Isoetes* is one of those Lycopods which have retained the scattered arrangement of the sporangia, or has suffered reduction of the cone with that of the stem, cannot be stated. It is another example of the intermixture of ancient with modern characters in the present day Pteridophyte.

Phylloglossum (see plate) is a still further example of the same thing. As previously stated this small Lycopod has its closest relations with one of the sections of the genus *Lycopodium*. It has a very typical *Lycopodium* cone, but at the same time shows some peculiar features, and is regarded as having undergone extreme specialisation. It is to be found fairly commonly on the Auckland clay gumlands, although its diminutive size causes it sometimes to escape observation. It is a geophyte. In the late autumn it grows up from its resting underground tuber, forms a tuft of a few simple Lycopod-like leaves at the ground level, and then in the spring the stem elongates to form the very small stalk, an inch or two high, which terminates in the one cone. After the spores have been shed, the aboveground part dies down, and the plant rests by means of a new tuber until the next autumn.. It is without doubt specialised to the regular alternation of a favourable season of the year with an unfavourable one in which the top stratum of soil in which it is rooted is liable to become dried out. Its embryogeny has been the subject of a special theory which will be explained later.

Tmesipteris growing on a treefern trunk.

Photo— T. L. Lancaster.

(c) THE PSILOTUM FAMILY.

The last New Zealand Pteridophyta to be mentioned are *Psilotum* and *Tmesipteris*. The former is found only in the Auckland Province, but *Tmesipteris* (see plate) is quite common in all wet forests throughout both Islands, usually growing on the trunks of tree-ferns. These plants are quite rootless, and *Tmesipteris*, at least, is known to be so even in the embryo stage. They both have much branched creeping stems or rhizomes from which come the above ground forking branches. The leaves also are forked, but are considered as being of the small leaf type as in all the Fern Allies. The sporangia are curiously fused together in two's and three's, and these have the scattered arrangement on the stem. They are both to a considerable extent saprophytes. We shall return later to the question as to whether their rootlessness is the result of their saprophytic habits or is actually a persisting very archaic feature.

(d) THE GAMETOPHYTE GENERATION.

As was explained at the beginning of this lecture, all Pteridophyta have an alternation of two distinct and independent stages in the life cycle, viz., gametophyte and sporophyte. In the case of those Pteridophyta which bear distinct male and female spores, the gametophytes also are of two kinds but are very minute and form *inside* the spores. In all Pteridophyta where there is but one kind of spore, there is also but one kind of gametophyte, and the separation of the sexes does not take place until the sex organs are formed on it. In some of the Fern Allies the gametophyte is of a highly specialised nature. It has become completely saprophytic, has lost its chlorophyll, and lives altogether underground. The gametophytes are always rather inconspicuous, and those which in addition live underground are by no means easy to find. For this reason the gametophytes of some of the Fern Allies, and so also the embryo development, long remained unknown to science. All of the *Lycopodiums*, and all the members of the Adder's Tongue fern and the *Psilotum* families, have saprophytic gametophytes. Some examples from New Zealand species will now be given.

There are several forms of gametophyte in the *Lycopodium* genus which probably represent modifications of a single original type. The simplest and probably least modified of these is that of *L. cernuum* and its near relatives (Figs. 7-8 and 14-15). It is very small and delicate, being 1-2 m.m. in height, somewhat of the dimensions of the head of a pin. It is placed erect in the soil with its crown

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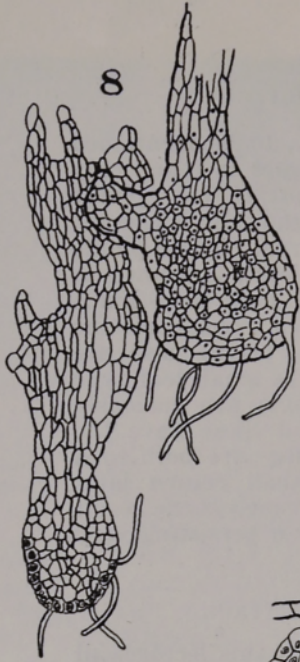

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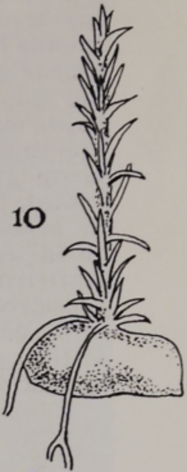

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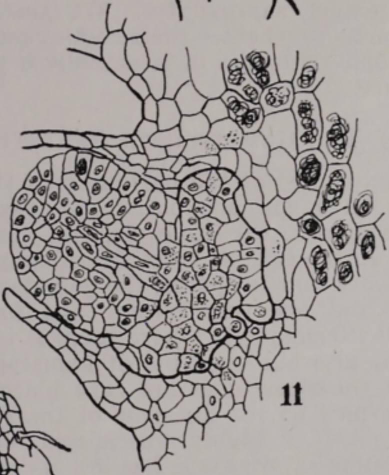

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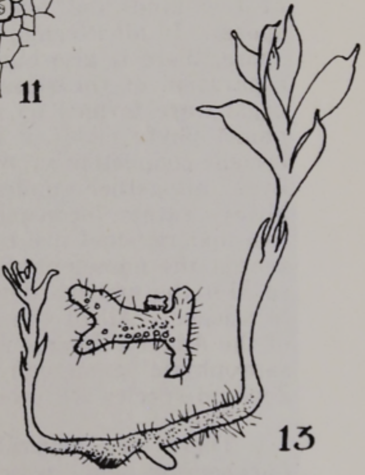

Fig. 7. **Lycopodium cernuum**; gametophyte bearing a young plantlet x 18.
Fig. 8. **L. laterale**; ditto, in sectional view x 42.
Fig. 9. **L. laterale**; young plantlet showing protocorm x 4.
Fig. 10. **L. laterale**; older plantlet x 6.
Fig. 11. **Tmesipteris**; embryo in sectional view x 75.
Fig. 12. **Tmesipteris**; portion of gametophyte bearing a young plantlet x 25.
Fig. 13. **Tmesipteris**; an older plantlet detached from its gametophyte x 12.

just at the surface. The crown is covered with green lobes, so that this gametophyte, possessing a little chlorophyll, is partly self-nourishing. Its basal part takes the form of a tubercle in which the fungus is lodged. The sex organs are situated beneath the lobes. There can be no doubt that a completely self-nourishing mode of life must be regarded as the normal and original one for both gametophyte and sporophyte in Pteridophyta, saprophytism being a highly specialised and abnormal phenomenon. Thus a gametophyte, like that of *L. cernuum,* which is only partly saprophytic, will represent better what the original type of the genus was than those which are completely saprophytic. Three of the New Zealand *Lycopodiums* have a gametophyte of the *cernuum type,* viz., *L. cernuum, L. laterale,* and *L. ramulosum,* and that of *Phylloglossum* closely corresponds.

In all other sections of the genus the gametophyte is subterranean and wholly saprophytic. It is heavily infected with the fungus, and the variety of forms which it takes seems to be determined largely by this. In some species, for example the New Zealand *L. volubile* (Fig. 18), *L. fastigiatum,* and *L. scariosum* (Fig. 19) the gametophyte is relatively large. There is an irregularly shaped crown on which the sex organs are situated, and a massive conical basal region in which the fungus is located in specialised tissues. Again, in those species which are epiphytic on trees, or which grow in humus on rocks, such as the New Zealand *L. Billardieri, L. Billardieri var. gracile,* and *L. varium,* the gametophyte is much branched and up to 8 m.m. long, looking like a tuft of small rootlets (Figs. 20-22). It begins as a small tubercle containing the fungus, but branches extensively, the fungus keeping pace in the tissues of the slender branches with their elongation.

It is of course impossible to state for certain how these modifications have come about, or how modern they are. A comparative study of them, however, suggests very strongly that they are due partly to the extent to which the tissues are infected with the fungus, and partly to the type of substratum to which the different species of *Lycopodium* have become adapted. It is significant that individual gametophytes of certain species are occasionally more or less intermediate between the various types. In the New Zealand *L. ramulosum,* for example, the gametophyte sometimes takes an abnormal form in the direction of branching or of a somewhat massive build (Figs. 16 and 17).

The gametophytes of *Psilotum* and *Tmesipteris* (Figs. 23 and 13) have also been discovered in New Zealand, as well as in Australia. They are both subterranean and completely saprophytic. They are closely similar to one another, that of *Psilotum* being somewhat the larger and up to 12-15 m.m. in length. The gametophyte is cylindrical in build, and usually shortly branched, and, unless intact at the forward end, might readily be mistaken for a piece of the brown rhizome of the sporophyte. Its tissues are occupied by the fungus throughout its length except in the apical growing regions, and the male and female sex organs occur intermixed over the entire surface.

It is well known to botanists that the gametophyte in existing Pteridophyta takes a variety of forms, and is more or less plastic in nature. Hence, however important it may be in the study of the life cycle of these modern plants, it cannot be relied upon to yield convincing information as to the form that it took in the Pteridophyta of fossil times.

(e) THE EMBRYO OF CERTAIN PTERIDOPHYTA.

The knowledge of Pteridophyte embryology of course goes hand in hand with the knowledge of the gametophyte generation. In a number of cases the embryo has provided important evidence with respect to the interrelationships of the existing members of this group, and even also as to their past history. At the same time it has to be remembered that drastic modifications in the habits and form of the gametophyte may also affect to some extent the form that the embryo takes, so that it becomes necessary to distinguish between those features in the embryogeny which are probably of an ancient character and those which are more recent and adaptive. Two examples will be given here from Pteridophyte embryology which are of especial interest to botanists, and in the consideration of which New Zealand material has played a part.

The embryo of those species of *Lycopodium* which belong to the *cernuum* section of the genus, passes through a developmental stage which has been given the name of the "protocorm." This name was intended to signify that this stage is of a very archaic nature. As the embryo develops it forms a green tuber-like organ—the protocorm—which possessing chlorophyll, and being attached to the soil by absorbing hairs, is no longer dependent upon the gametophyte for nourishment. The young sporophyte, then, at this stage consists practically altogether of the protocorm, the foot by which it is attached to the gametophyte being very small. It is not till later, sometimes much later, that the first leaves and the stem apex make a belated appearance on the upper surface of the protocorm (Figs. 7-8).

The protocorm is certainly neither a stem nor a root. It occurs in a genus *(Lycopodium)* which has an ancient lineage. It occurs throughout a particular section of this genus whose gametophyte has a special claim to be considered ancient on account of its partly self-nourishing nature. Moreover, it occurs also in the embryogeny of *Phylloglossum* which at one time was regarded as a sort of persisting archaic Lycopod. It was concluded, therefore, by some botanists that the protocorm represents a very primitive organ, which, it was suggested, actually played a part in the original establishment of the sporophyte as an independent generation in the Pteridophyte life cycle. It became known that in the New Zealand species belonging to the *cernuum* section the protocorm may grow to a considerable size and even branch, and constitutes the main body of the young sporophyte for a lengthy time .(Figs. 9-10).

This theory has now been discredited and the term "protocorm" is being given up. The plants which possess this feature belong to habitats in which the top stratum of soil in which the young sporophytes are located is liable to dry out during the summer. It is now considered probable that this organ is a more or less recent modification, which has arisen in connection with the need for the embryo to tide over such an unfavourable season. The type of gametophyte which invariably goes with the "protocorm" is one which, although more or less self-nourishing, is certainly abnormal in its small size and delicate nature and is quite unfitted to carry a young sporeling over even a short dry period. Whether or not its minute size is itself a recent feature, and has directly led to the formation of such an organ as the "protocorm," can only be surmised.

The second example to be mentioned is the completely rootless nature of the embryo of *Tmesipteris*. The embryogeny of *Psilotum* is not known. The *Tmesipteris* embryo consists of two organs only, the shoot and the foot by which the shoot is attached to the gametophyte (Fig. 11). There is no other Pteridophyte whose embryo is of so simple a nature as this. The shoot early begins to branch (Fig. 12) and soon becomes detached from the gametophyte leaving the foot embedded in the tissues of the latter. For a considerable time the young sporophyte consists solely of the shoot or stem, living under the soil, and dependent entirely for its nutrition upon the fungus in its tissues. Later on, any one or more of its branches may turn up out of the soil, and begin to form leaves, but no roots are ever developed (Fig. (13).

Thus *Tmesipteris* does not exhibit the organisation usual in Pteridophyta, in which stem, root and leaf organs are all present, being differentiated more or less early in the embryo. One possible interpretation, which is strongly held by some botanists, is that it belongs to a group of plants whose ancestry reaches back through the ages to the earliest days of Pteridophyta, and which has retained throughout that enormous period of time some at least of the features of an originally simple organisation. The other interpretation is that *Tmesipteris* has undergone great modification as the direct result of its strongly saprophytic habits, involving the total reduction if its root system.

Those botanists who incline to the latter view point to the fact that modification of some sort, and not infrequently root reduction as well, accompanying the saprophytic habit, is known in a number of other plants besides *Tmesipteris.* However, in these cases the embryo possesses a root or a rudiment of a root, even though this may be functionless, this being a convincing proof that such plants belong to a stock which once possessed a root system. The fact that the embryo of *Tmesipteris* lacks all trace of a root is an argument in favour of the view that this plant is actually in a primitive condition. The fossil record, moreover, shows that rootlessness was apparently a prevalent condition of the Pteridophyta of the early Devonian period, and it also shows that several groups of Pteridophyta have retained ancestral characteristics, in some cases quite unaltered, for exceedingly long periods of time.

Each point of view is thus possible. For the present it is simply a question of their relative probability. There the problem must stand until further information is forthcoming.

Fig. 14. **Lycopodium ramulosum:** young gametophyte x 25.
Fig. 15. **L. cernuum:** mature gametophyte in sectional view x 25.
Fig. 16. **L. ramulosum:** branched gametophyte x 12.
Fig. 17 **L. ramulosum:** massive gametophyte with plantlet (spor.) x 12.
Fig. 18. **L. volubile:** gametophyte with plantlet (spor.) x 6.
Fig. 18a. **L. volubile:** gametophyte in sectional view x 20.
Fig. 19. **L. scariosum:** medium aged gametophyte x 6.
Fig. 19a. **L. scariosum:** in sectional view x 20.
Fig. 20. **L. Billardieri var. gracile:** complete gametophyte x 6.
Fig. 20a. **L. Billardieri:** var. gracile basal region in sectional view x 85.
Fig. 21. **L. varium:** gametophyte with young plantlet (spor.) x 6.
Fig. 22. **L. Billardieri:** gametophyte, basal region lacking x 6.
Fig. 28. **Tmesipteris:** complete gametophyte with young plantlet (spor.) x 6.


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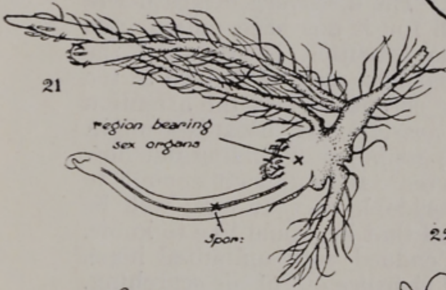
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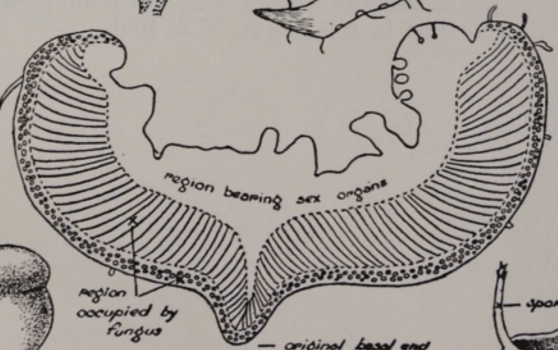
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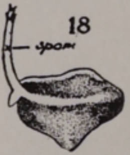
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CONCLUSION.

Existing Pteridophyta, including those of New Zealand, still hold no doubt some as yet unrevealed facts of importance relative to the history of the group, but in general it may be said that the stage of botanical research has now been reached at which these plants are fairly well known. On the other hand information continues to increase with respect to those of remote times, and most interesting of all, those of the Silurian period. There is no doubt that the rocks of these early ages hold a large supply of plant remains waiting to be found.

It has been well said that "Science is the work of the human mind, whose fate is rather to study than to know, to search for truth than to find it." In other words, the duty of pure science is to concentrate upon the searching rather than upon the finding. The discovery of truth wil only come about if the search for it has been patient an with the open mind. If the attention is set upon th finding it is possible that conclusions may be arrived at to hastily, conclusions which are erroneous. If the attentio is set upon the finding it is possible that botanists migh become pessimistic as to the possibility of finding out ho a Land Flora actually originated. It is difficult enough t understand some modern Pteridophytes. It may well b that Man will never find out all that he would like to know It is providential that he is endued with unlimited hop and that he can get much real pleasure out of his searchin

The photos. of *Tmesipteris* and *Phylloglossum* a from negatives kindly lent by T. L. Lancaster, Esq., M.Sc F.L.S., Lecturer in charge, Botany Dept., Aucklan University College. Figs. 1-6 have been taken fro various sources. Figs. 7-23 are from papers by the writ published in the Trans. N.Z. Inst.

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