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WITH SIX PLATES AND 53 FIGURES IN THE TEXT.

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## ERRATA.

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- P. 79, line 14, *for north read south.*  
„ 80, line 8, *for 5 cm. read 5 mm.*  
„ 85, line 5, *for seedless read juvenile.*  
„ 116 and throughout the article *for Fig. 1 read Fig. 25.*  
„ 117 „ „ „ *for Fig. 2 read Fig. 26.*

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SKETCHES OF VEGETATION AT HOME  
AND ABROAD.

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[The aim of the series of papers of which this is the first is to record from time to time personal impressions and observations of characteristic floras in various parts of the world.

These articles will not necessarily contain new facts or conclusions; their primary object will be to portray, as vividly as possible, the striking features of interesting floras by those who have had opportunities of seeing them for themselves. The papers will be illustrated as much as possible by diagrams illustrating features of distribution, and by sketches of characteristic plants.

It is hoped that the series may help in some degree to promote still further that awakening interest in vegetation, as distinct from individual plants, of which there are many signs about us to-day.]

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I.—THE FLORA OF THE CEYLON LITTORAL.<sup>1</sup>

BY A. G. TANSLEY

AND

F. E. FRITSCH.

---

THE flora of the hundreds of thousands of miles of coast bordering the tropical seas of the world is marked by a very striking uniformity of character and composition. Not only is the facies of the vegetation, except in the driest regions, practically everywhere the same, but the actual species composing it have a very extended and sometimes a world-wide range. The botanist suddenly transported from the coast of Ceylon, for instance, to the shores of some island in the Malay Archipelago, two thousand miles away, could not tell that he had been carried further than round the next headland,—he would meet with exactly the same species growing in exactly the same way; while if he were taken much further still, to the West Indies, for instance, on the other side of the world, he would still be at fault for a few minutes at

<sup>1</sup> Our observations were practically confined to the S.W. and S. shores of Ceylon (Negombo to Hambantota); see map, Fig. 1.

least. Exactly the same type of flora would surround him, some of the same species dominant in the East would still form a leading feature of the vegetation, and only a closer examination would reveal the presence of New World species, and convince the traveller that he had been transported some twelve thousand miles across two great oceans and a great continent.

The causes of this striking uniformity are mainly two; first the great similarity of the conditions of life obtaining on tropical coasts, and secondly the fact that the great majority of the characteristic species composing the flora are adapted for distribution by ocean-currents, the fruits or seeds being specially fitted for floating and for resisting the effect of salt water. There can be no doubt that these plants are actually distributed by the great oceanic currents, and that this is not only one great cause of the wide distribution of the specialized tropical coast flora, but is also the means by which new tropical islands, *e.g.* coral atolls and volcanic islands, are colonised as they appear.

The late Professor Schimper made a detailed study of the Eastern tropical coast vegetation and it is to his results, fully set out in that most attractive book "*Die Indo-Malayische Strandflora*" (1889), that we owe most of our knowledge.

The flora of the Ceylon coast is a good example of the Indo-Malayan type, and as we have each had an opportunity, at different times, of examining parts of this vegetation for ourselves, we have thought an account of some of its aspects might not be without interest. Though we have nothing of special importance to add to Schimper's work, there are several smaller points of interest that we can bring out, and a first-hand sketch, even though a partial one, of the Ceylon littoral flora, of which no general account seems to have been published, may be of some value.<sup>1</sup>

From Negombo on the west coast of Ceylon to Hambantota on the south-east coast is a distance of about 160 miles. We have visited a considerable number of separate localities along this stretch, which comprises the whole of the south-western and southern shores of the island, and are able to give a very fair idea of its flora. In addition to this one of us has had an opportunity of examining the littoral flora at Trincomalie on the East coast, and a few observations made at this locality will be recorded in the following pages.

<sup>1</sup> The late Dr. Trimen's well-known "*Handbook of the Flora of Ceylon*" has been of great use in identifying plants, checking distributions, &c.

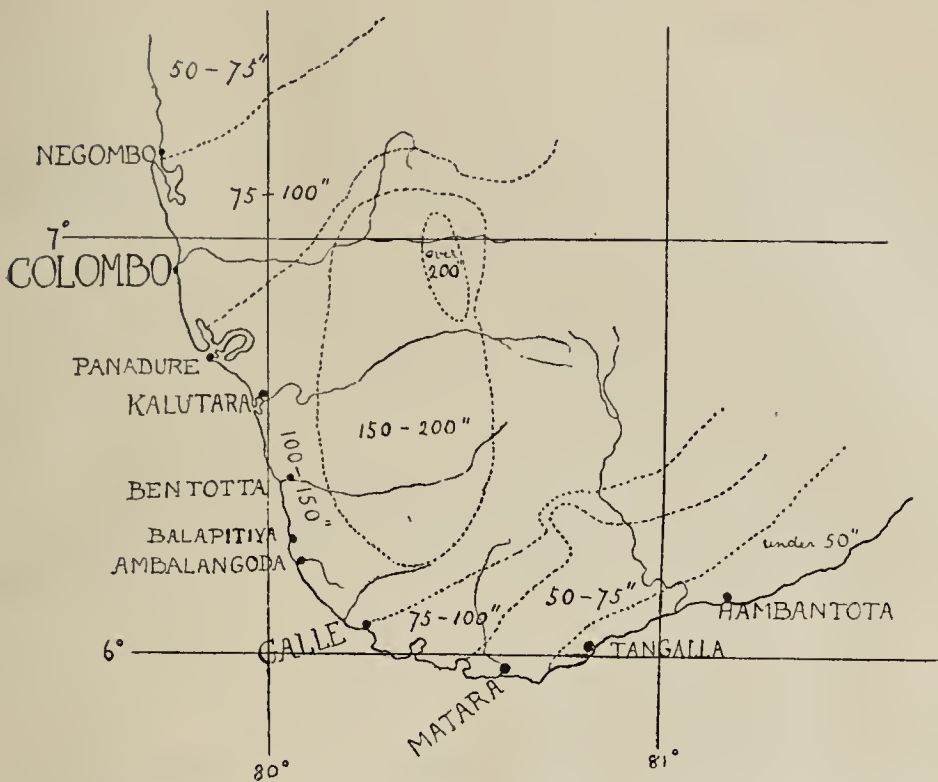


Fig. 1. Map of S.W. Ceylon with the coast-towns and villages mentioned in the text, and the rainfall regions from the Rainfall map in Trimen's "Handbook." Scale about 45 miles to an inch.

We may start with the recognition of the four formations into which, according to Schimper, the coastal plant-associations of the Eastern Tropics naturally group themselves:—

- |                                       |  |
|---------------------------------------|--|
| 1. The <i>Pes-caprae</i> -formation   | } on sand (or sometimes other soil), above tide marks. |
| 2. The <i>Barringtonia</i> -formation |  |
| 3. The Mangrove-formation             | } on tidal mud.  |
| 4. The <i>Nipa</i> -formation         |  |

This division no doubt forms the basis of a natural classification of the coast-vegetation, though it would be of great interest to endeavour to delimit the last three formations more exactly than has been possible hitherto.

The mangrove formation for instance, as Schimper truly says (p. 67), passes on the one hand into the *Barringtonia*-formation and on the other into the *Nipa*-formation. No better example of the intermingling of these three formations could be given than the vegetation on the river banks at Kalutara, described below (Part II.). An additional formation, to cover the *herbaceous* mud-vegetation is also required. Nevertheless we are not able to propose a new classification, since our experience is not sufficiently extended to warrant an attempt to modify Schimper's arrangement, which was founded on a much wider knowledge than we possess.

## PART I.—THE SAND FORMATIONS.

As the coast of Ceylon is approached from the sea a line of dark trees is seen fringing the low flat shore. The naive traveller, having read of mangrove swamps on tropical coasts, might, from a distance, take these trees for mangroves. As a matter of fact they are nothing but endless plantations of coconuts which fringe the sandy Ceylon coast for miles at a stretch. The mangroves flourish only on a muddy soil and in comparatively quiet water, and in Ceylon are not found on the actual seashore at all, but are confined to the muddy shores of the estuaries (often extending for several miles inland along the river banks), and big salt lagoons connected with the sea by comparatively narrow mouths. In this respect the Ceylon coast forms a striking contrast to the west coast of the Malay Peninsula, where high woods of magnificent mangroves (*Rhizophora* and *Bruguiera*) line the muddy shores of the protected narrow seas (Straits of Malacca) for miles.

Very nearly the whole of the coast-line of Ceylon under consideration is flat and sandy, and much of it is protected from the main force of the waves by a fringing coral reef. The rise of the tide is very little, probably never amounting to more than six feet, and often less, so that although the slope of the beach is usually slight, the distance between tide-marks is never great. As on all sandy coasts the zone between tide-marks is bare. Close above high tide-mark begins the *Pes-caprae*-formation, the typical herbaceous formation of sandy tropical coasts. Behind this comes the tree-belt. If the shore slopes up very sharply from high-tide mark, the tree-vegetation sometimes occurs immediately on the top of the bank, excluding the *Pes-caprae* zone altogether or leaving only a very narrow belt of it, as at Ambalangodda. Schimper writes<sup>1</sup> as if this were the normal case and the *Pes-caprae* vegetation were found mainly on sand-dunes; but on the Ceylon coast dunes are not well-developed and the *Pes-caprae* zone, varying from a few feet to perhaps fifty yards in breadth and occupying a very gently sloping sandy shore, is practically constant. The natural tree-zone (*Barringtonia*-formation or Beach-jungle) is poorly represented, for the simple reason that along the densely populated Ceylon coast most of it has been cut down and coco-nuts planted in its place. A few trees and shrubs of the *Barringtonia*-formation remain fringing the coco-nut-plantations. The coco-nut is of course itself a typical beach jungle tree, long ago planted all over the

<sup>1</sup> l.c., p. 77, and Pflanzengeographic, p. 416.

tropics, very largely inland, but particularly on the sea-coast where it flourishes specially well.

1. *Pes-caprae-Formation*. This, as we have said, extends to within a few feet of high tide-mark. The dominant plant along great stretches of coast is *Ipomœa biloba* (*Pes-caprae*), the great characteristic cosmopolitan plant of tropical sandy shores. It is a plant of creeping habit with richly branched stems lying on or just buried in the sand, rooting freely and strongly at the nodes, but seldom till lateral branches have developed, and with isolated petioled leaves, dark-green and glossy, which stand up two or three inches above the creeping stems (Fig. 2A), and when the plant is growing thickly form a thick verdure covering the sand. The leaves are typically deeply two-cleft like a goat's hoof—whence the

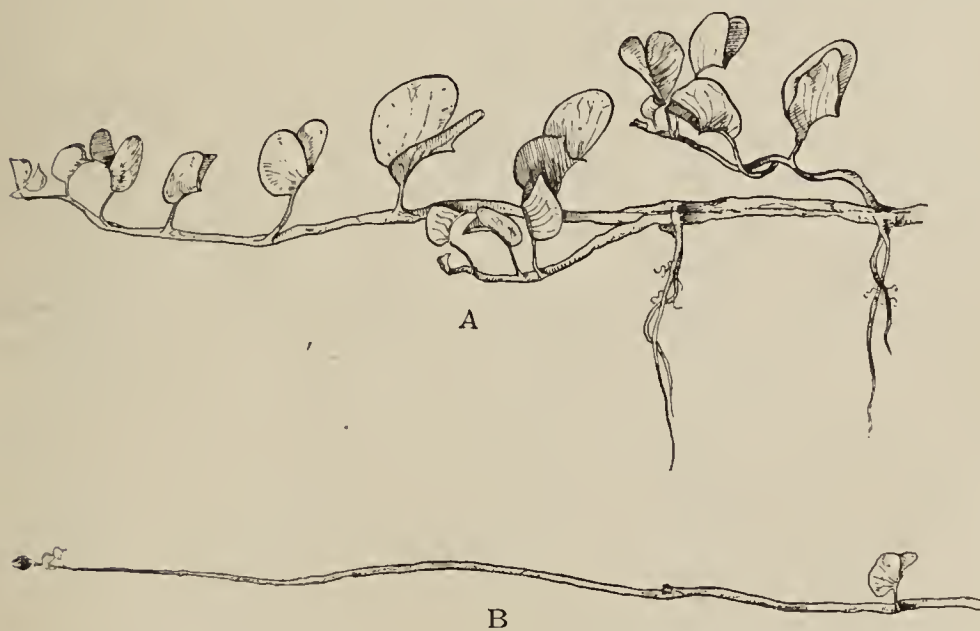


Fig. 2. *Ipomœa biloba* (*Pes-caprae*). A. Normal shoot, the main axis and laterals lying flat on the sand,  $\frac{1}{3}$  nat. size. B. Vorläuferspitz,  $\frac{1}{3}$  nat. size.

name. The two lobes diverge at an angle and stand obliquely up like the half-closed wings of a butterfly. This constant oblique position is no doubt an adaptation to the very strong light to which the plant is exposed. Like most pioneer sand-plants, *Ipomœa biloba* by means of its creeping and freely rooting habit binds the loose sand. Its apical growth is very rapid, the young stems often running out over the bare sand towards high tide-mark in long "Vorläuferspitze," *i.e.* quickly growing young shoots with very long internodes and rudimentary leaves (Fig. 2B). The covering of the sand with a network of unrooted shoots alone tends to check its movement by the wind, and very soon the new shoots firmly establish themselves

by throwing down bunches of strong roots from the nodes at which branches have arisen. If it should be overwhelmed by blown sand, as often happens, its great branched system of wide-stretching, firmly rooted shoots enables the plant to survive, and its quick growth soon brings young shoots to the surface to begin again their work of covering the sand with vegetation. In this respect it resembles its congener *Psamma arenaria*, which does identical work on our northern sandy coasts. Like *Psamma*, its power of growing to the surface of and binding the heaps of freshly blown sand enables it to form dunes if the supply of blown sand is considerable, but on the part of the Ceylon coast with which we are dealing dunes are not common,<sup>1</sup> probably because the fresh sand thrown up by the waves is not very abundant.

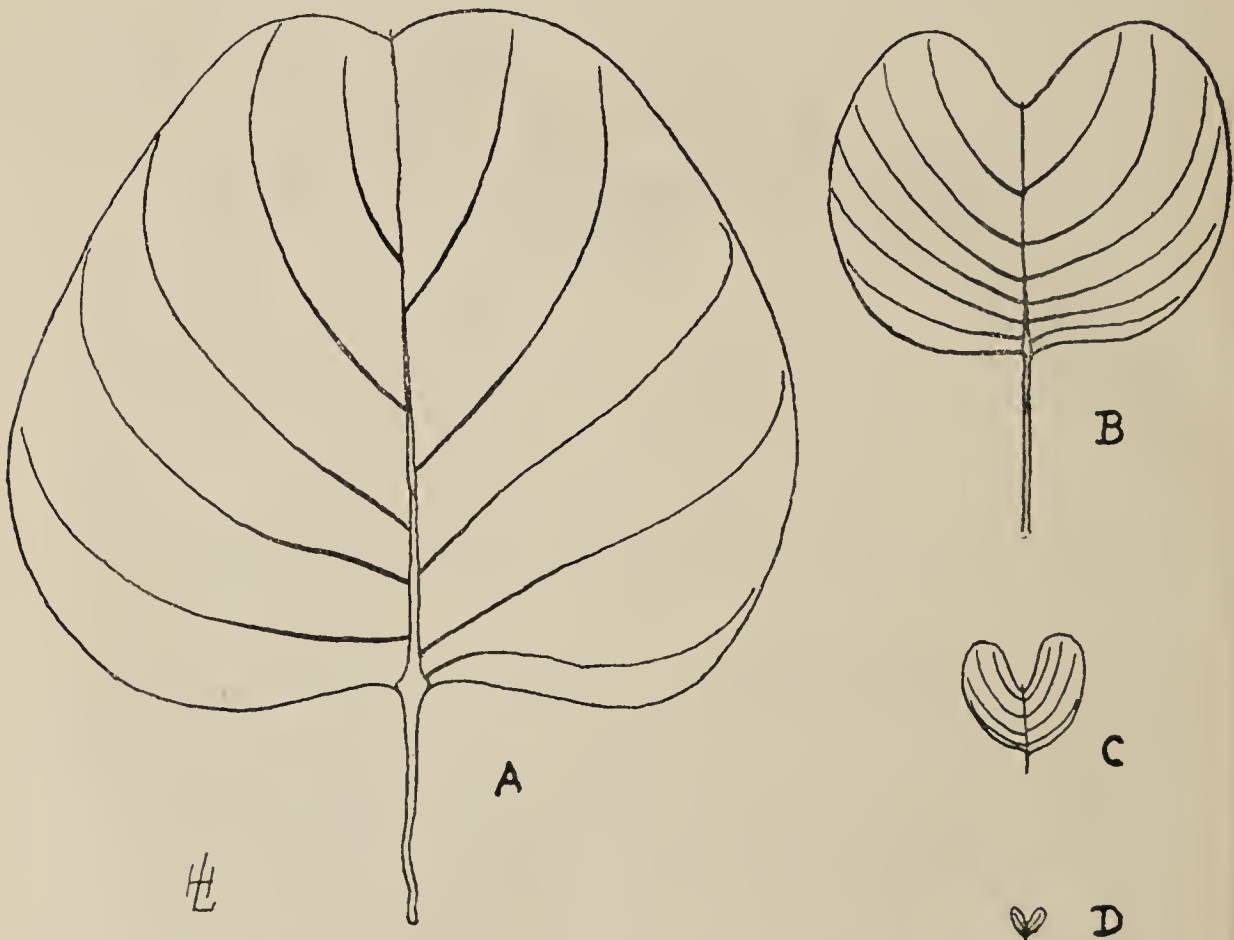


Fig. 3. *Ipomoea biloba*. Leaves to shew variation in size and shape according to habitat. A and B, Luxuriant forms from mud at Malacca. C, Normal leaf. D, Stunted form from very arid sand.  $\frac{1}{2}$  nat. size.

*Ipomoea biloba* is a very variable plant according to its situation. Its seeds can germinate in the most arid sand, but the growth of

<sup>1</sup> They exist in the neighbourhood of Hambantota, but *Ipomoea* does not occur there.

the seedling in such a position is very slow, the internodes are very short and the leaves very small (not more than a third of an inch long), deeply cleft and very succulent (Fig. 3D). On the other hand the plant is sometimes to be met with (*e.g.* at Malacca) growing most luxuriantly on mud, with enormous leaves six inches across, thin and practically entire, *i.e.* orbicular-cordate with the apices only slightly retuse (Fig. 3A and B).<sup>1</sup>

*Spinifex squarrosus* is another pioneer plant, but stands rather apart from the rest in some respects, although it possesses the same general habit. It is a bulky, very rigid, tough glaucous grass, which tends to form "pure" formations excluding other species. It is well described by Schimper (Indo-Malayische Strandflora, p. 80), and its method of seed-distribution by the detachment of the ripe heads, which are driven by the wind for long distances over the sand, is well known. When in flower the enormous spherical heads of spikelets with stiff pointed radiating "spindles" are very conspicuous.

We found this plant particularly common in the drier regions to the north and to the east of the wet zone which forms the centre of the stretch of coast under consideration, *e.g.* especially abundant at Negombo (61 inches of rain), Hambantota (36 inches) and Trincomalie (63 inches), though it undoubtedly also occurs at various spots in the wetter region (*e.g.* to the south of Bentotta—over 100 inches). *Ipomæa biloba* seems to diminish as *Spinifex* increases, in passing from the wetter to the drier region; thus at Tangalla (40 inches), about midway between Matara (69 inches) and Hambantota (36 inches) *Ipomæa* was developed in far less abundance than at Matara, although no *Spinifex* was found here; at Hambantota *Spinifex* is present alone and no *Ipomæa* was seen. On the other hand in some of the drier localities, *e.g.* Negombo and Trincomalie, both *Ipomæa* and *Spinifex* occur side by side; at the latter locality *Ipomæa* forms a fringe just above high tide-mark, holding the ground almost alone, whilst the *Spinifex* occupies the inner zone. It is possible that the growth of *Spinifex* is favoured by a dry locality, and the abundant development of this hardy plant might readily exclude a growth of the *Ipomæa*. Whether this relation really holds good can only be determined by more thorough observation.

A number of plants of similar habit accompany *Ipomæa* on the Ceylon coast, and sometimes replace it to a certain extent. Of these one of the commonest and most successful, growing along

<sup>1</sup> We are indebted to Dr. Stapf, of Kew, for confirming our determination of these extraordinarily diverse forms as all belonging to *I. biloba*.

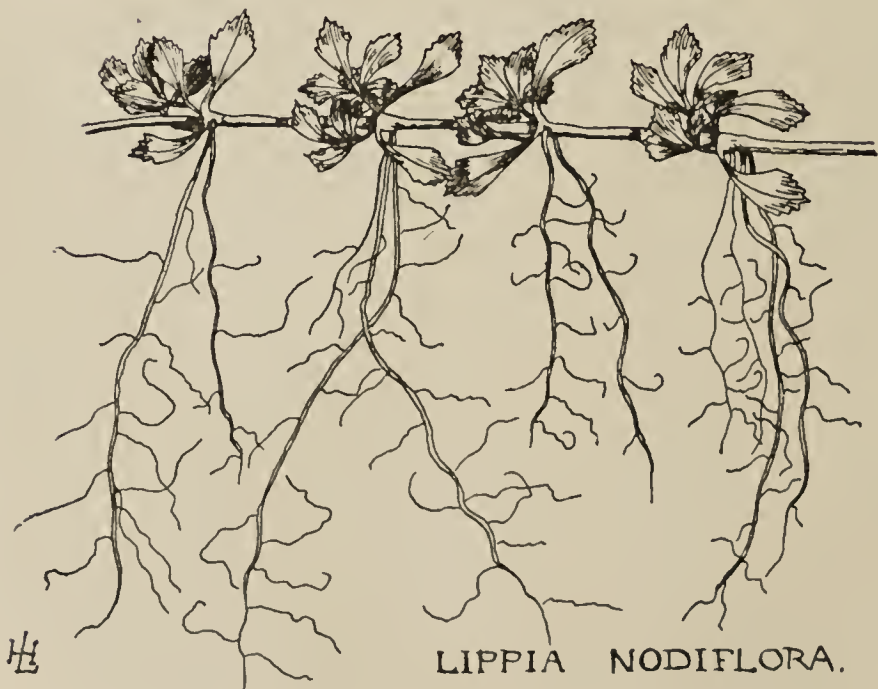
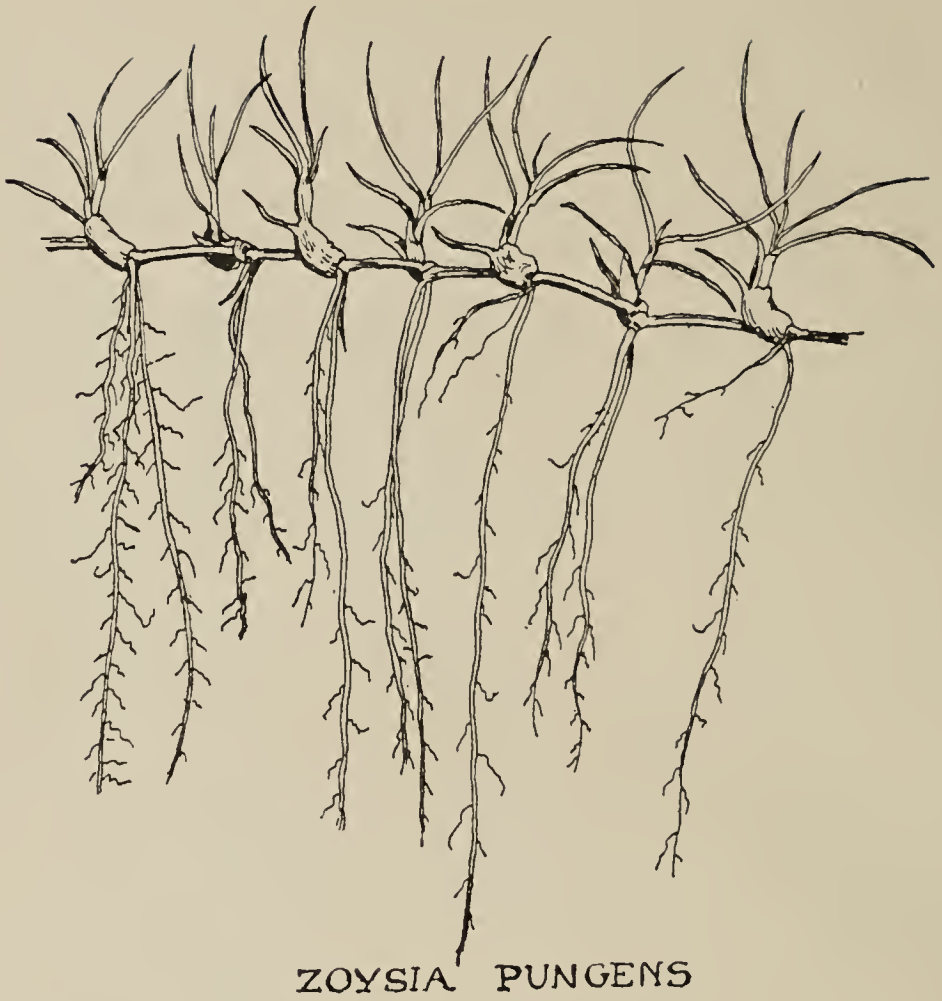


Fig. 4. Two characteristic creeping plants of the *Pes-caprae* formation.

with *Ipomœa* in the bare sand, is *Zoysia pungens* (Gramineae) (Fig. 3). This plant has a long rhizome, bearing erect axillary shoots with narrow leaves at frequent intervals, and fixed by numerous roots, very long compared with the height of the aerial portion (Fig. 4). The rhizome itself, like that of *Ipomœa*, may either lie upon the surface of the sand, or be buried in it. In the latter case its course is marked on the surface only by the star-like leaf-rosettes arranged in long lines. The sand in which it grows is often so loose that one can pull up several feet of rhizome by raising the end and gently lifting it out of the sand, and this in spite of the fact that the roots are very numerous and quite long.

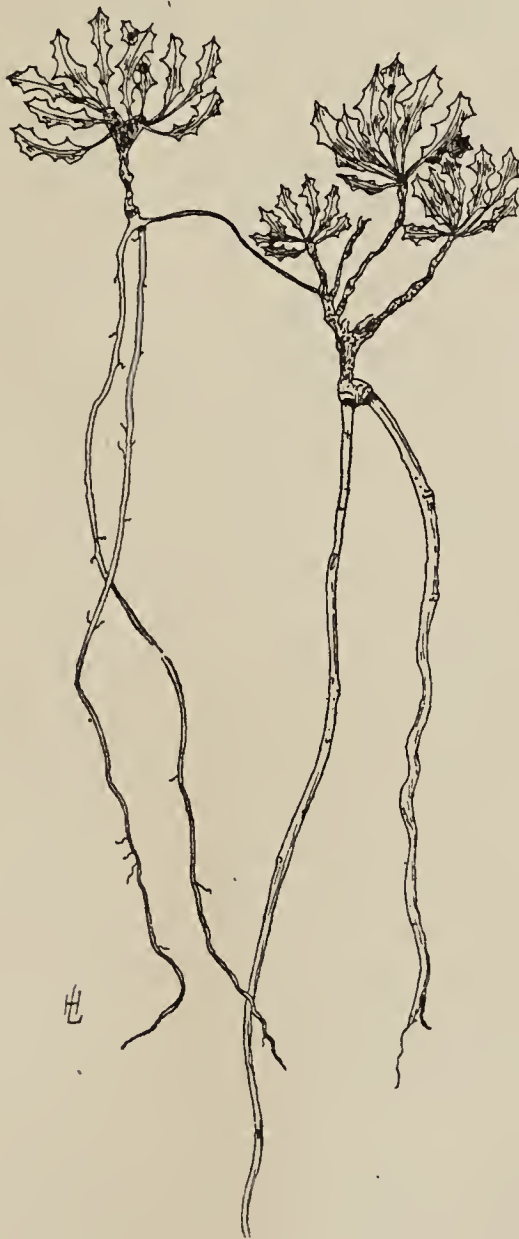


Fig. 5. An undetermined plant of the *Pes-caprae* formation shewing stoloniferous habit and very long tap-roots.

Another very common plant in the same situation is *Remirea maritima* (Cyperaceae). This has the same general habit as *Zoysia*, but the aerial shoots are more distant and bulkier, with numerous distichous linear leaves.

Three other plants of the same habit, *i.e.* with long creeping stems, throwing down numerous roots and sending up short shoots bearing rosettes of leaves with flowers, are *Hydrophylax maritima* (Rubiaceae), *Lippia nodiflora*, Fig. 4 (Verbenaceae), and *Launaea pinnatifida* (Compositae), common well-distributed plants, though not so abundant as the first three. *Sesuvium portulacastrum* (Ficoideae) is another procumbent form, also rooting at the nodes though rather more sparingly, and with ascending branches bearing cylindrical fleshy leaves. This plant is also common on tidal mud.

Two zones of the Pes-caprae formation can generally be distinguished; an *outer zone* in which the sand is not covered by a carpet of vegetation, but the creeping plants described above, particularly *Ipomœa*, *Zoysia* and *Remirea*, leave more or less wide spaces between. In the *inner zone*, the creeping plants almost cover the ground with a continuous carpet, and between them a number of other plants have settled down, plants that could not possibly colonise the bare sand, but which can live on the moister places protected by the creepers, and with a certain amount of humus, very likely often provided by the *Nostoc* mentioned below (cf. our northern "grey" or "fixed" dune flora.) Of these inner zone plants a few are confined to the seaside, while many others are inland weeds which find this a suitable habitat. Of the former, two remarkable bulbous plants, *Crinum asiaticum* and *Pancratium zeylanicum* must be mentioned first. They are closely allied members of the Amaryllidaceae, and are of strikingly different habit to any of the forms hitherto described. The bright green lanceolate leaves of *Crinum* are 2—5 feet long and stand obliquely erect. The inflorescence is a conspicuous umbel of very numerous white flowers. *Pancratium* is a much smaller plant of similar habit, bearing however only a single large terminal flower. The former is very common, especially in the damp region, scattered over the whole beach even in the outer zone close to high tide mark; and often forming a kind of thicket at the back of the formation at the foot of the beach jungle. *Crinum* is characteristically maritime; *Pancratium* also grows inland. Among the inner zone plants, certain habits are conspicuous. Many are more or less procumbent and some root at the nodes, though this habit is not so universal as in the pioneer

sand-plants. *Cyperus arenarius*, which is a characteristic sea-shore plant, *Ischæmum muticum* (Gramineae), both maritime and inland, *Cyanotis axillaris* (Commelinaceae) and *Portulaca quadrifida*, neither specially maritime, are examples. Many of the Cyperaceae common in the inner zone have a tufted habit, e.g. *Fimbristylis spathacea*, *F. tristachya* and the annuals *Bulbostylis barbata* and var. *pulchella*, *B. puberula* and *Cyperus pygmæus*. Of these the first is exclusively maritime, the next two are largely littoral, while the last two are not specially characteristic of the coast flora.

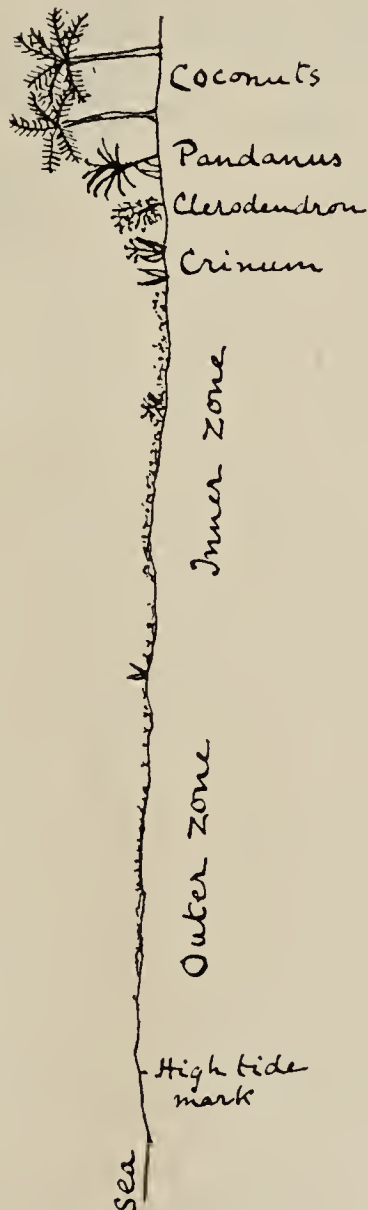


Fig. 6. Diagrammatic section perpendicular to the coast-line shewing the *Pes-caprae* formation and remains of Beech-jungle fringing the coco-nuts.

A certain number of Dicotyledons have a somewhat similar tufted habit, a number of stems arising from the top of a single

strong tap-root, as in many seaside and xerophilous plants all over the world. Of these *Evolvulus alsinoides*, *Polygala glaucoides*, *Tribulus terrestris* and the rather rare *Crotalaria nana* (Fig. 7) may be mentioned. None are exclusively maritime plants. Species of *Phyllanthus* commonly constitute a part of the sand-flora and resemble the plants just mentioned in habit, having a very long tap-root.



Fig. 7. *Crotalaria nana* (Papilionaceæ) shewing a typical habit of the inner zone plants.

Several leguminous plants, some shrubby, are common, e.g. *Canavalia obtusifolia*, with thick trifoliolate leaves and bright pink flowers, a conspicuous feature in some places, even replacing *Ipomœa biloba*, and confined to the seashore, *Crotalaria retusa* var. *maritima*, and *Tephrosia purpurea*, *Vigna luteola* and species of *Cassia*, *C. Tora*, *occidentalis* and *auriculata*. All of these, except the first two and

the last, which appears to occur more abundantly in dry localities, are common weeds throughout the tropics.

Of climbers we may mention *Passiflora foetida* (naturalised), *Tylophora asthmatica*, neither characteristic of the coast, and the striking Dioscoreaceous plant *Gloriosa superba*, with its scrambling stems arising from an underground tuber, and beautiful flowers. These all scramble over the shrubs or trail on the ground at the back of the formation.

The well known cosmopolitan tropical *Cuscuta*-like *Cassytha filiformis* (Lauraceae) is often found on various woody members of the strand flora. Of the remaining plants we have found in such a habitat, but few are characteristically maritime. *Stachytarpheta indica*, var. *jamaicensis*, introduced from tropical America, is apparently confined to the coasts, the type being a common inland roadside weed. *Leucas zeylanica*, a common lowland plant, is often met with on the sea-shore, where it assumes a dwarfed habit and becomes more or less succulent.

The differences between our observations, made at different times of the year, suggest that there is a certain periodicity in the development of the Ceylon coast-flora, though our data are not sufficient to enable us to go into details. Very little is known of such phenomena in these tropical climates, where the seasonal variations, though perfectly definite, are not nearly so extreme as in many other parts of the world. A year's careful study of the fluctuations in such a flora as that of the Ceylon coast would probably reveal many interesting facts in regard to the periodic development of many of the species.

At several points on the shore of Ceylon (*e.g.* Negombo, Bentotta) fresh-water pools occur in the sand not many yards from high tide level. These pools appear to owe their origin to fresh-water springs occurring in these localities, and at Negombo the natives can be seen digging down into the sand to get at this water, which they drink. At other localities these springs evidently rise to the surface and are the cause of the fresh-water pools which are found there. The floor of most of these pools, which often contain but little water, is covered by a very luxuriant algal flora, made up of comparatively few species of gelatinous Cyanophyceae. The commonest genera are *Nostoc* and *Lyngbya*, the former constituting little gelatinous yellow or greenish clumps amongst the sand at the bottom of the pools, whilst the latter gives rise to a yellowish web, covering the bottom or partly floating at the surface of the deeper

pools. A considerable number of unicellular blue-green species are found amongst the filaments of the larger forms. In a few cases green Algæ (*Oedogonium*, etc.) were found, occupying one or other of the pools, but the blue-green species are by far the most prominent and of these the *Nostoc* occurs in prodigious amount. It is a species (belonging to Section *Humifusa*, Thur. et Born. and possibly identical with *N. Passerinianum* Born. et Thur. var. *halophilum* Hansg.) with very short filaments, made up of small cells, each filament being as a rule surrounded by a yellow sheath, whilst the whole colony is contained in a hard, greenish or yellowish investment, which forms foliar expansions. It is not confined to the pools however, but also occurs in large quantity on the sand round about, almost to within the limit of high-tide mark. It lies loosely on the sand presenting a dry and withered appearance and is then of dark colour, so that at a first glance it is readily mistaken for the withered leaves of the *Ipomæa*, amongst the runners of which it is to be found in large quantity. It must serve as a rich manure for this latter plant and also for the coco-nut trees at the back of the *Ipomæa*-vegetation, where it occurs abundantly on the sandy soil. The same form was also met with on the sandy spit at Kalutara, where however none of the above-described fresh-water-pools were observed, and the same applies to its occurrence at Matara. This alga is so characteristic of the *Ipomæa*-vegetation at various points on the Ceylon coast, that our sketch of the latter would be incomplete without its mention; it would be interesting to determine whether the same or a similar form is found on other tropical coasts. In Ceylon the same alga was followed up for some way inland on the sandy soil of the coco-nut plantations and it was also observed near the Bentotta river about two miles inland; here also it occurred on a sandy substratum.

2. The *Barringtonia*-Formation (Beach Jungle). It is difficult to find a well developed example of this formation on the coast of Ceylon, at any rate in the region of high rainfall, and this for a reason that has been already mentioned,—it has been all cut down to make room for coco-nut compounds. All that remains of the Beach Jungle on the typical flat sandy coast such as we have described, are a few of the smaller trees or bushes, which fringe the edge of the compounds or are dotted over the inner zone of the *Pes-caprae*-formation. Of these the three most conspicuous and widely distributed are *Clerodendron inerme* (Verbenaceæ), *Scævola Königii* and *Pandanus odoratissimus*. These three are all ubiquitous

in the Eastern Tropics and form a conspicuous feature of all the sandy coasts.

*Clerodendron inerme* is an extremely common and characteristic feature of the coast-flora, though it is by no means confined to sand, but occurs freely among rocks, on steep banks and on mud. It is a low bush with small ovate leaves, and white flowers with long tubes and very long exserted stamens and style.

*Scævola Königii*, like several of the typical coast plants of the East, is a member of a mainly Australian family, the Goodenoviaceæ. The flower is remarkable for the corolla, which, at first tubular, splits down the posterior side to the base soon after the bud opens.

*Pandanus odoratissimus* (*fascicularis*) is also one of the regular and most conspicuous constituents of the Beach jungle-flora all over the East. The characters of the "Screw-Pine" with its striking prop-roots are too well known to need description. The common species is a small tree, ten or twenty feet high. It often forms a regular belt at the back of the *Pes-capræ*-formation, or on steeper coasts immediately above high-water mark.

*Cerbera Odollam* (Eve's Apple) is a conspicuous shrub or small tree (sometimes 20 feet in height) with large obovate acuminate bright green leaves, gradually tapering to the base and with the pinnate veins perpendicular to the mid-rib—so characteristic a feature of tropical Apocynaceæ. The flowers are white, abundant and sweet-scented. It is common as a hedgerow bush or tree all through the low country of Ceylon, usually close to water, and is particularly abundant on the coast in the neighbourhood of the estuaries, forming a beautiful feature of the vegetation. It flowers all the year round and so abundantly that flowers and fruits in different stages are always to be found upon it. The fruits are nearly spherical, with a bright green glossy skin and grow to a large size (3 to 3½ in. diam.) by the time they are ripe. Below the skin is a very thick fibrous layer containing numerous air spaces which make the whole fruit very light and enable it to float half out of the water. The one or two seeds are large and are contained in a hard endocarp in the centre of the fruit. The fruits are very common objects floating in the estuaries and lagoons of the coast. They can resist the salt water for a long time, and furnish an excellent example of adaptation to water dispersal, which is such a feature of many of the plants of the tropical coast flora. In germination the cotyledons remains enclosed in the seed, while the plumule forces itself between the two carpels and often grows

to a height of some inches and bears several leaves before any roots appear. Seedlings in all stages of development are very commonly met with in suitable spots on the coast, particularly on the banks of estuaries, but also in any spot which the fruit can reach and which is sufficiently damp.

There can be no doubt that these adaptations help to account for the great success and abundance of *Cerbera*. It flourishes equally well on muddy soil.

*Calotropis gigantea* (Asclepiadaceæ) is a large bush with large fleshy leaves and pale mauve flowers. It is a common wayside lowland bush, and is very often dotted about at the back of the beach. It appears to increase in the dry region, being distinctly more abundant at Tangalla (40") than in the wet region, while at Hambantota (36"), one of the driest places in the island, it forms a conspicuous feature of the background.

In passing from the wet to the dry region of the South coast very striking changes in the coast vegetation are met with. Certain plants increase and become dominant, while others fall into the background and disappear. At Tangalla, the ground west of the village slopes steeply up from the shore, and is partly covered with dense thickets of *Clerodendron inerme*, *Jatropha gossypifolia* (Euphorbiaceæ), a semi-shrub of the dry region found specially on the coast and the introduced *Euphobia Tirucalli*, a shrub with leafless cylindrical branches without thorns. This last plant is commonly used for hedges in the dry part of the low country. In the wet region an occasional specimen only is found, and these are quite small in stature, but as the country becomes drier it increases in size, till at Tangalla it becomes quite a tree; there are also regular thickets of *Pandanus odoratissimus*, and a considerable amount of *Calotropis gigantea*.

At Hambantota (36") very little of the Beach-jungle is to be met with, except that as already mentioned *Calotropis gigantea* forms a very prominent feature of the background; occasional bushes of *Scaevola Königii* are also found. Behind the *Spinifex*, on the flat sea-shore of the bay to the north of the town a sandy bank arises, whose more or less steep seaward side is almost devoid of vegetation, whilst beyond the summit the ground slopes slowly down to the sandy plain beyond and is covered by the low shrubby, xerophilous vegetation, which is characteristic of this, one of the driest regions in the island. The plants, found at the summit of this ridge, and thus forming a kind of background to the strand-

vegetation, present much the same character as the whole inland vegetation of this region. The commonest forms are a spiny species of *Capparis*, various species of *Acacia*, an unfortunately undetermined species of *Clerodendron*, and *Euphorbia Tirucalli*, which already forms a prominent feature of the vegetation at Tangalla: amongst these, species of *Vernonia* and *Blumea* are commonly found, whilst *Cassia auriculata* with its prominent flowers, is also often met with.

The other members of the Beach-jungle flora are found only as isolated trees, here and there on the edge of or among the coco-nuts, or about the coast villages, or forming part of woods on the shores of the estuaries where the soil is firmer than it is in the typical mangrove swamp. The commonest and most characteristic of these trees are *Terminalia Catappa* (Combretaceæ), *Calophyllum Inophyllum* (Guttiferæ), *Barringtonia speciosa* (Myrtaceæ), *Heritiera littoralis* (Sterculiaceæ), *Pongamia glabra* (Leguminosæ) *Hernandia peltata* (Lauraceæ), *Hibiscus tiliaceus* and *Thespesia populnea* (Malvaceæ). *Terminalia Catappa* (The Indian Almond) is not a native of Ceylon or India, but is extensively planted in the low country. In the Malay region it forms, according to Schimper, a feature of the Beach-jungle, and is called by him an "Etagenbaum." the branches spreading out in horizontal plates or "stories" with spaces between. This character is often but by no means always to be observed in the Ceylon trees of this species.

One of the chief common characters of these Beach-jungle trees, as of many other members of the strand-flora, is the adaptation of the fruits or seeds to distribution by ocean-currents. This subject is very fully treated by Schimper.<sup>1</sup> The fruits and seeds of all the above-mentioned trees are very common objects in the drift on the Ceylon coast.

Among somewhat less conspicuous but characteristic coast trees, may be mentioned *Dolichandrone Rheedii* (Bignoniaceæ), which occurs inland as well, and *Excæcaria Agallocha* (Euphorbiaceæ) both of which are also found in and about mangrove swamps. As we have already said, the line between Beach-jungle and mangrove-forest cannot be sharply drawn, though the typical forms of the two formations are of course totally different. Careful distributional and physiological work is wanted before we can obtain a more exact knowledge of the proper relations of these two formations.

<sup>1</sup> loc. cit. pp. 166-183.

INFECTION OF PLANTS BY RUST-FUNGI.

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**D**URING some work on the Uredineæ it was noticed that the germ-tubes produced by spores on the surface of infected leaves would radiate from it in a velvety pile, if the surrounding atmosphere was kept saturated with water vapour. This suggested that water vapour might be the body in search of which the fungus entered the stoma. For many years it had been known that germ-tubes will enter the stomata of leaves which they are quite incapable of infecting. The earliest reference to this fact which I have been able to find is in 1853.

While the experiments described below were being tried, a paper by Miss Gibson<sup>1</sup> appeared in the *NEW PHYTOLOGIST* recording a detailed investigation of these "futile infections," and concluding that the first entrance of the germ-tube was due to some body, to which the hyphae were positively chemotropic, common to all plants and possibly gaseous.

The identity of this common substance was already indicated in my own experiments by the behaviour of the germ-tubes in saturated air, and was tested directly by using a membrane of thin indiarubber, perforated with holes comparable in size with stomata. This membrane was arranged with one side exposed to air saturated (at 23°C) with water vapour, the other to the air of the laboratory. On the latter side were sown spores of *Puccinia glumarum*, var. *hordei* Eriks.

After two days the membranes were fixed, and microscopically examined, when germ-tubes were found entering the majority of these artificial stomata. That this entrance was not due to chance was shown by the many tubes which, when once inside, passed straight over other holes, in no case manifesting any tendency to return to the dry outer air.

The only apparent difference between these and natural infections was the absence of any marked vesicle at the end, which in nature is probably caused by chemical stimuli from the mesophyll cells.

Other substances may possibly share in attracting the germ-tube to the interior of the plant, but this conception of the germ-tube as growing from an area having a low partial pressure of water vapour to one with a higher pressure, accounts for all the facts known about the *first* entrance of the germ-tube.

<sup>1</sup> C. M. Gibson. Notes on Infection-Experiments with various Uredineæ, *NEW PHYTOLOGIST*, 3, p. 184, Oct. 1904.

Once inside the moist stomatal chamber the Uredine is in similar case to other fungi which penetrate directly into an epidermal cell from the outside, for it has now to penetrate into the mesophyll cells (by its haustoria.) It is however much better off than such other fungi, being in no danger of dessication and having moreover little or no cutin to penetrate; this may be one cause which has contributed to the present pre-eminence of the Uredineæ among the parasitic fungi.

W. L. BALLS.

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### THE ANATOMY OF PALM-ROOTS.<sup>1</sup>

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CONSIDERING the uniformity shown by roots in the general type of their vascular structure, all exceptional cases have a special interest. Von Mohl discovered deviations from typical structure in the roots of palms, and certain examples have been examined in detail by Cormack, and others. We now have in Dr. Drabble's work a comprehensive treatise on the root-structure in this natural order.

The paper deals with more than sixty species of Palms, and is divided into two parts. The second of these is devoted to separate descriptions of root structure for each species, while the first part contains a more general description arranged under different headings and followed by the theoretical conclusions.

All the component tissues of these roots were examined in detail, and thus a large number of valuable data have been accumulated. The chief interest of the subject naturally belongs to the different types of vascular structure present, but a few other matters should also be mentioned here.

The author (p. 441) confirms "Buscalioni's account of the centrifugal appearance of the xylem-elements of the bundle in the roots of Monocotyledons, followed by centripetal lignification." This is probably not a very restricted phenomenon, nor of any special importance. It may be seen in the roots of some ferns, and presumably in many other cases where the tracheides of the metaxylem are very large.

An interesting fact observed in the case of the adventitious

<sup>1</sup> On the Anatomy of the Roots of Palms, by E. Drabble, D.Sc.  
Trans. Linn. Soc., II. Series, vol. VI., p. 427, 1904.

root making its way through the cortex of the stem was that some of the cortical cells of the latter, in front of the root, resembled secretory cells in the nature of their protoplasm and nuclei. This character and the appearance of the adjacent cells suggested partial auto-digestion of the cortex preceding solution and absorption by the "poche digestive."

In the description of the root-apex, the author quotes Treub as having found in palm-roots a well-defined pleromic group, covered by an initial layer common to calyptrogen, dermatogen and periblem. His own observations referring to the apices of large roots of *Areca* sp. and *Kentia* sp. apparently revealed the presence of "a common initial group similar to that described by De Bary for *Vanda*.....". Considering the statements of Treub and others (as to the presence of more than one group of initials) and the difficulty of determining the median section when the apical meristem is bulky, it is to be regretted that the author did not examine smaller apices (including those of rootlets) for comparison with the large ones, which he chose for investigation.

As regards the vascular system, the special peculiarity of the adventitious roots of palms, stated in general terms, is that in their basal region they show several partial vascular cylinders instead of the single one, which is found nearer their apices. Numerous separate bundles form the attachment of the root-cylinder to the bundles of the stem; the bundles of attachment, if traced outwards, may be said to fuse together to form arcs or cylinders of vascular tissue, and these in turn fuse in various ways so as to produce ultimately the closed ring of the normal root. These fusions are generally accomplished in the basal region of the root, which is immersed in the cortex of the stem, but in certain cases the fusion is delayed, so that separate strands forming an incomplete cylinder are found in the free part of the root for a considerable distance. The root, external to the cortex of the stem, often contains a pith, in which there may be one or more free vascular strands. These are continuous proximally with vascular arcs or bundles of connection.

The author (p. 429) appears to attach importance to the fact that separate procambial strands in the apex are the precursors of the separate vascular strands of the root-base, and that the successive changes from vascular strands to a lobed cylinder, and finally to the normal cylinder of the root, are due to progressive changes in the procambial tissue of the meristematic apex. As far

as experience goes, however, the distribution of procambial tissue (which is simply young vascular tissue) does not yield any evidence, which is better than or essentially different from that derived from the mature structure.

Dr. Drabble (p. 452) concludes from his examination of the roots of Palms that "the central cylinder in these organs is not the simple structure, which Van Tieghem considered the root-cylinder to be, and upon which he based his conception of monostely." This conclusion is arrived at because the author traces the structure acropetally and expresses the normal root-cylinder in terms of the structure found in the basal region (describing it as formed by the *fusion* of separate strands) without stopping to consider which region is likely to be the more specialized one.

Now it is probable that the exact reverse of Dr. Drabble's method would lead one nearer to the truth of the morphology. The structure of the more distal part of the root conforms in general features to the type found in other Monocotyledons, while the basal region of the root in palms appears to possess a specialized structure in relation to the attachment of the large root-cylinder to numerous stem-bundles. Possibly the basal part of the root might be held to be an intercalated region, but it is more natural to regard its structure as having been attained by progressive modification of the normal structure (in the basal region) following the increase in the number of the bundles of attachment, which must have accompanied increase in size of the stele of the root. In any case the normal structure of the root cannot be regarded as derived from a structure similar to that of the basal region, which must be treated separately or as a modification of normal structure. Dr. Drabble bases his morphological views chiefly on two kinds of evidence, the behaviour of the procambial strands and the acropetal sequence of tissues. As the first of these probably has no value and the second appears to be entirely misleading, the further theoretical conclusions based on similar data need not be specially referred to.

The structure of the basal part of the root may, for descriptive purposes, be regarded as due to the breaking up of the root-stele into separate vascular arcs or cylinders. If one attempts a morphological explanation, one may hold that the morphology of the different tissues in this region is incapable of determination, the counterpart of this being found in the case of much specialised external members, or the structure may be partially and provi-

sionally explained in terms of the normal root-structure. On this view it may be suggested that the vascular arcs, etc. should be called "meristeles" and that a certain part (with indeterminate limits) of the ground-tissue may represent the pith of the distal part of the root, although continuous with the rest of the ground-tissue. It is now generally held that in some cases the endodermis may be differentiated from various tissues, *e.g.* in Strasburger's examples in the genus *Equisetum*, where it appears that in "astelic" forms the single ring of endodermis (shown in the monostelic species) has become interrupted between the vascular bundles, and new arcs of endodermis have been differentiated from the tissue adjacent to the inner and lateral surfaces of each bundle so as to unite with the external tangential strips of endodermis, thus forming complete sheaths. Hence the endodermis does not form a dependable morphological limit, but its local *absence* may have some significance. It is usually absent on the inner faces of the vascular arcs in the base of the root, and this would agree well with the theory of the breaking up of a normal root-cylinder, for where it is now absent would be just where the vascular tissue originally adjoined the pith.

Whatever view one takes as to the morphology of the tissues in the bases of these roots, it has no particular bearing on the structure of roots in general.

There is little doubt that in questions of the morphology of tissues, the comparative method is the most valuable. The careful comparison of the mature structure of corresponding parts in a series of related species, where the differences are slight, will often enable one to follow the steps in the modification of a tissue, that is, in the extent of this tissue and in the nature of its elements. It is probable that one will have to appeal to data of this kind for the confirmation of wider generalisations belonging to the same subject. Hence it must be regretted that greater prominence was not given to this method in Dr. Drabble's paper. From this point of view *Corypha umbraculifera*, which bears two kinds of roots, should certainly have been treated more fully.

In the roots of palms the author includes the sclerenchyma, accompanying the vascular tissue, with the latter, and only speaks of "pith"<sup>1</sup> when there is a central mass of *parenchyma*. By

<sup>1</sup> Dr. Drabble discards pith as a "separate morphological entity." This phrase certainly appears inappropriate, but it is quite justifiable to use the word pith for that part of the parenchyma or sclerenchyma of the stele, which lies in a definite position, *viz.* internal to the vascular tissue.

comparing these roots with those of certain other Monocotyledons one would probably come to the conclusion that the central parenchyma together with some of the sclerotic tissue (*e.g.* in Fig. 74) corresponded to the parenchymatous pith of a root of the type of *Acorus Calamus*. In any case it is more convenient to include all tissue internal to the innermost vascular elements as pith, whether it be sclerotic or parenchymatous or formed of both tissues. It should also be pointed out that the sclerenchyma, which unites the primary xylem and phloem, is described as part of the vascular cylinder, though if it happened to remain parenchymatous, as the corresponding tissue does in many roots, it would then probably be excluded as ground-tissue in Dr. Drabble's terminology. It would seem that an example of this kind is shown by the two types of roots produced by *Corypha umbraculifera*, but the description (p. 460) is insufficient to make this clear.

An interesting and exceptional type of root-structure is found in *Lalania Commersonii*, where the phloem groups are not restricted to the periphery of the stele but are scattered throughout the xylem.

Though Dr. Drabble's theoretical conclusions appear to lack due consideration of the special nature of the case he is dealing with, the paper contains many interesting observations and Plate 50 should be specially referred to as an example of a clear and useful method of illustrating the general characters of the vascular structure.

L. A. B.

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FORMATION OF A COMMITTEE FOR THE SURVEY  
AND STUDY OF BRITISH VEGETATION.

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A MEETING of British botanists engaged in work on the survey of the vegetation of different areas of the British Isles was held at Leeds on December 3rd, 1904. The object of the meeting was to discuss the present position of the vegetation-survey begun about ten years ago by the late Robert Smith in Scotland, and since continued by others.

The meeting was only a preliminary one, yet it was thoroughly representative. Mr. C. E. Moss (Manchester), Dr. W. G. Smith (Leeds), Mr. A. G. Tansley (London) and Mr. T. W. Woodhead (Huddersfield) were present, while Mr. M. Hardy (Dundee), Mr. F. J. Lewis (Liverpool), Mr. R. Lloyd Praeger and Dr. G. H. Pethybridge (Dublin) and Mr. W. M. Rankin (Portsmouth) communicated, expressing sympathy with the general objects of the meeting, and regretting their inability to be present. The unanimous response from almost all those actively engaged in vegetation-survey in the British Isles indicated the need of some closer co-operation than has hitherto existed.

It was therefore resolved to form a Committee of those present, together with the other gentlemen mentioned above (with power to add to their number), in order to co-ordinate the work which is being done, to secure uniformity of method so far as it may seem desirable, to have a ready means of discussing various topics that arise in connexion with methods and results, and generally to advance the interests of the survey. It is proposed to call the Committee "The Central Committee for the Survey and Study of British Vegetation."

The following provisional resolutions which were adopted among others may be of interest to botanists interested in the work.

*Scale of Maps.* The survey of the British Isles should be proceeded with. In those areas where the plant-associations are largely untouched by human agency and extend uniformly over considerable tracts, the scales of one inch to the mile or half an inch to the mile, which have been found suitable in the maps hitherto published should be adopted; the field work may be carried out on the one inch or six inch ordnance maps. In regions which are largely agricultural, general topographical maps on a scale of a quarter-inch to the mile are recommended, with the local features of botanical interest marked in some distinctive manner. Maps illustrating these local features, *e.g.* marshes, commons, natural woods, etc., on a scale of six inches or of twenty-five inches to the mile, or if thought desirable on an even larger scale, should be prepared as opportunity offers. In this way it is hoped to complete a first botanical survey within a reasonable time.

*Colours to be used.* Steps should be taken after consulting with cartographic experts to obtain uniformity in the printing of colours, a point on which some difficulty has been experienced in the past. The question of deciding upon a uniform comprehensive

scheme of colours for representing the British plant-associations should be deferred for the present, pending further experience and consultation.

*Photographs.* A collection of photographic prints of vegetation should be made, each print to illustrate a definite association or feature of an association, or a definite plant form characteristic of an association. The quality of the negative from which prints are accepted should reach a high standard. There should be no limit of size up to whole plate. Prints should be sent in unmounted and accompanied by a detailed explanation. The collection will be mounted on cards, properly arranged and indexed, will be kept in a definite place to be decided on later and will be available for reference.

At the next meeting of the Committee, which will probably be held in March, 1905, the provisional resolutions and constitution of the Committee will come up for confirmation. It is also proposed to consider at that meeting a scheme of terminology of the units of vegetation, which can be communicated to the International Botanical Congress to be held at Vienna in June, 1905.

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It may be of interest to make a short statement of the progress which has actually been made up to the present time with the work of survey and mapping.

*Areas mapped and published, or about to be published.*

ENGLAND AND SCOTLAND.

1. W. G. SMITH & MOSS. } Yorkshire (West Riding). The  
Pennines and eastward to the Vale  
of York. About 1700 square miles.
2. W. G. SMITH & RANKIN. } Scale  $\frac{1}{2}$ " (Geog. Journ., 1903).
3. LEWIS. The Pennines and Upper Valleys of the Eden and  
Tees. About 560 square miles. Scale 1"  
(Geog. Journ., 1904).
- \*4. MOSS. East Somerset. About 1000 square miles. Scale  $\frac{1}{2}$ "
5. ROBERT SMITH. Northern Perthshire. About 900 square miles.  
Scale  $\frac{1}{2}$ " (Scot. Geog. Mag., 1900).
6. ROBERT SMITH. Edinburgh District. About 700 square miles.  
Scale  $\frac{1}{2}$ " (Scot. Geog. Mag., 1900).
- \*7. W. G. SMITH and (the late) R. SMITH. Forfar and Fife.  
About 1500 square miles. Scale  $\frac{1}{2}$ " (Scot. Geog.  
Mag., 1904-5).

\* In the Press.

*Areas under Survey.* Messrs. Lloyd Praeger and Pethybridge, Co. Dublin (Ireland); Mr. Hardy (Scotland), west of Forfar, Fife and Perthshire, and northwards; Mr. Rankin, Lancashire west of the Pennines, and Hampshire; Mr. Lewis, extension of Westmoreland area, westwards and northwards; Mr. Moss, Cheshire and Derbyshire; Dr. W. G. Smith, Yorkshire Cleveland, Wensleydale and Swaledale; in addition some work is being done in North and South Wales, and in Aberdeenshire. It will be seen that considerable progress has been and is being made in this effort to obtain a systematic acquaintance with British vegetation, and to reduce it to a form in which comparisons can be made between regions widely apart. Gaps are still numerous, however, even in the mountain and moorland country, while considerable areas of ecological interest are untouched, and will probably remain so unless undertaken by fresh workers.

*Ecological Study of Vegetation.* The above mentioned surveys of wide areas carried out on a comparatively small scale and affording only a primary analysis of the vegetation, ought to be supplemented by work of a more detailed character. This is also being undertaken. Mr. T. W. Woodhead recently communicated some of his results to the Linnean Society (December 15th, 1904). Mr. Woodhead has devoted himself principally to the survey and study of woodland areas in South-West Yorkshire. The mapping is done on the ordnance survey maps of six inches and twenty-five inches to the mile, and all kinds of data bearing on the vegetation has been collected. The biological laboratory at the Technical College, Huddersfield, is available and suitably equipped for ecological research and is within easy reach of the woodlands. In the woods themselves convenient huts have been placed at the disposal of workers for the purpose of research, and every facility has been granted by the owners and by a neighbouring resident to those desirous of making experiments and observations on the spot. Mr. Woodhead is thus doing pioneer work in this department so far as this country is concerned. Mr. Tansley has also begun mapping work on a similar scale in Kent. The Committee is desirous of promoting this more detailed survey and study side by side with the mapping of large and more uniform areas, and will be glad to give further information.

Communications may be addressed to the Secretary of the Committee, Dr. W. G. Smith, The University, Leeds.

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SKETCHES OF VEGETATION AT HOME  
AND ABROAD.

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I.—THE FLORA OF THE CEYLON LITTORAL.

BY A. G. TANSLEY

AND

F. E. FRITSCH.

*(Continued from p. 17).*

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[PLATE I. AND TEXT FIGS. 8—16]

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PART II.—THE TIDAL MUD FORMATIONS.

THE formations that fall under this heading inhabit the tracts of mud, covered by water at high tide and left bare at the ebb, which are found on all flat coasts where great quantities of fine-grained alluvium are deposited. The coherent mud offers a very different substratum for vegetation from that afforded by loose sand, and enables plants to obtain a footing and form a permanent vegetation between tide-marks, a feat impossible to them in the case of sand, which is constantly being moved about by the water. The great enemy of tidal mud-vegetation is wave-erosion. Where this is constant plants cannot of course maintain themselves, being continuously liable to have their soil and themselves carried bodily away. On coasts and in estuaries exposed to vigorous tidal action, the processes of erosion and deposition of mud, of uprooting and re-colonisation by the plants can be studied in all its phases; and every case is to be met with from situations where plants can never establish themselves owing to a continuous tidal scour, through others in which alternate erosion and deposition allow of a transient vegetation only, to the more protected areas where the force of the tide is reduced to a minimum, and the mud

is permanently covered with vegetation. The vegetation of tidal mud is of course typically halophilous, since it is periodically bathed with salt water. The physiological relations of the plants are all profoundly affected by, and are certainly adapted to, the presence of large quantities of common salt. This leads, as is well known, to various structural features which have much in common with those found in xerophilous vegetation. The plant-associations inhabiting tidal-mud in temperate regions are exclusively herbaceous—in our own country the *Salicornia-Glyceria Suaeda* formation; in the tropics, on the other hand, a vegetation of arboreal habit, the well-known mangrove forest, has been developed.

### 3.—THE MANGROVE-FORMATION (TIDAL FOREST).

The existence and the chief physiognomical characters of this striking vegetation have been known to European botanists



FIG. 8. *Bruguiera gymnorhiza* and *Rhizophora conjugata* on the banks of the Bentotta river.

A group of the former in the foreground shows the short stilt-roots fused with the base of the trunk. Knee-roots are seen emerging from the mud on the right. Behind is a tree of *R. conjugata* sending very long branches supported by stilt-roots over the edge of the water.

(After a sketch by Dr. W. H. Lang).

ever since the first travellers returned from the East. Theophrastus, in his "Histories of Plants," describes mangroves from the Persian Gulf, apparently from the reports of the officers of Alexander the Great. The principal species and their characters are noted so exactly that they are easily recognised, and *Rhizophora* is rightly considered the pioneer.<sup>1</sup> The odd thing is that mangroves have never since been recorded from this region.

The genera *Rhizophora* and *Bruguiera* (Rhizophoraceæ) form the great bulk of the typical mangrove forest, and it is naturally from them that the popular notions of mangrove vegetation are derived. The species of these genera form moderate-sized trees, 30 to 50 feet in height when well developed, with dark-green leathery foliage. The leaves are decussate, petioled, oval, about 5 inches long, acute or mucronate at the tip, and are typically carried so that they diverge obliquely from the stem.

One of the most striking characters of *Rhizophora*—the mangrove tree *par excellence*—a character which naturally figures prominently in the descriptions of travellers—is the abundance of branching stilt-roots or "flying buttress" roots which spring in great numbers from the main stem and lower branches, and form an excellent support for the tree against the shocks of wind and tide (Fig. 8). These roots not only serve as a support, but are important as a means of supplying air to the parts buried in the mud. The aerial portion is covered with lenticels which communicate with the intercellular spaces of the richly lacunar cortex. Below the level of the mud the cortex increases in thickness and has a very spongy texture, so that it acts as a reservoir for the air taken in above.<sup>2</sup>

The other striking feature of the typical mangroves is of course their so-called "vivipary," *i.e.* the fact that the seed germinates while on the tree. The hypocotyl increases greatly in length and emerges from the fruit, carrying the radicle with it and eventually attaining a length of several inches, in *Rhizophora mucronata* sometimes as much as three feet. These long slender embryos hang from the branches of the tree "like candles in a grocer's shop," as Massart has it. When ripe they are easily detached and fall straight down like darts, striking deeply into the soft mud, if the tide is low, or falling into the water at high tide and often floating away on the ebb. In some species, *e.g.*, *R. conjugata*, the embryo is distinctly club-shaped, so that the lower

<sup>1</sup> Hugo Bretzl, Botanische Forschungen des Alexanderzuges, Leipzig, 1903.

<sup>2</sup> See below under *Sonneratia*.

end is weighted, helping a direct fall. According to Karsten<sup>1</sup> the seedling *Rhizophora* first float horizontally, but subsequently gradually take up a vertical position as the club-shaped lower portion becomes saturated with water. In this way the social habit of the tree is established; while at the same time the embryos which are carried away are able to resist the salt water for a great length of time, and if eventually deposited in a suitable spot continue their growth and thus secure the wide distribution of the species. Of course many embryos and seedlings perish through being left by the water in localities where germination, or at least growth into a tree, is impossible. Crossland<sup>2</sup> described a case on the coast of Zanzibar, where *Rhizophora*-embryos (evidently from his figure *R. conjugata*), floating in the vertical position, are planted by the falling tide in suitable crevices of the flat limestone rock which forms the shore. Here the trees appear to flourish perfectly well though there is but a thin coating of mud on the solid limestone. This corresponds with Schmidt's<sup>3</sup> remark (p. 14), that *R. conjugata* can grow on mud, sand, or even rock, thrusting its roots into the crevices.

The allied genus *Bruguiera* resembles *Rhizophora* very closely in habit and general appearance and is constantly associated with it, but lacks the characteristic stilt-roots—except very short



FIG. 9. Young knee root of *Bruguiera gymnorhiza*. The part bearing laterals is embedded in the mud, the upper part shows the sealing periderm exposed to the air. The thick spongy cortex is indicated on one of the cut ends. Half natural size.

<sup>1</sup> Ber. Deutsch. Bot. Ges., 1900, p. (53).

<sup>2</sup> Annals of Botany 17, 1903, p. 267.

<sup>3</sup> Bot. Tidsskrift, 1904, vol. 26.

ones at the base, which thicken with and often become fused with the trunk (Fig. 8)—and is therefore unable to grow in localities so exposed to the wind and tide. Its roots, however, are provided with another adaptation which serves the same purpose as the stilt-roots from the point of view of aeration, though destitute of mechanical function. The roots of *Bruguiera* grow horizontally close below the surface of the mud, and in places bend sharply up and then down again so as to project above the surface in the form of a knee (Figs. 8 and 9). Here again the whole of the root has a thick spongy cortex into which the air can penetrate through the part of its surface above the mud. The cortex of this aerial portion of the root always splits extensively, placing the lacunar system in open communication with the air. According to Karsten (loc. cit. p. 55), the exposed portion of the cortex bears numerous closely-crowded lenticels. The buried portions of the root are richly provided with laterals, a number of which penetrate downwards into the soil and help to fix the tree. The viviparous embryos of *Bruguiera* resemble those of *Rhizophora*, but are cigar-shaped, and never more than a few inches in length (Fig. 10).

The commonest species of these two genera, viz.: *R. conjugata*, *R. mucronata* and *B. gymnorhiza*, form, as has been said, the great bulk of the mangrove vegetation of the Ceylon coast, at least of the part examined by us; though they are never found, so far as we have seen, on the actual sea-coast line, but are confined to the edges of the estuaries and lagoons connected with the sea by narrow openings. In the lagoons especially, as at Negombo and Balapitiya, the mangroves are extremely well developed, extending close up to the mouth (in the latter locality, within about 50-feet of the sea). In the estuaries of the rivers, however, as at Bentotta, and Kalutara, part of the estuarine shores next the sea, where there are villages, have been frequently cleared of the mangrove vegetation, and artificial banks made in order that coco-nuts and other trees might be planted; and in such cases one frequently has to go some distance up the river before the untouched mangrove vegetation is met with.

Schmidt (loc. cit. p. 14) points out that *Rhizophora conjugata* is very indifferent to the quantity of salt in the water; we also have observed *Rhizophora* (and *Bruguiera*) in localities in Ceylon where the water was practically fresh (e.g. in the further portions of the lagoon at Negombo and in the lake at Balapitiya). The character of the plankton collected in the localities named bears quite a freshwater stamp.



FIG. 10. Seedling of *Bruguiera gymnorhiza*. The cigar-shaped hypocotyl has a cluster of roots, with fine fibrous branches, springing from its base. Above, the epicotyl with several leaves and terminal bud. One-third natural size.

Where *Rhizophora* or *Bruguiera*, especially the former, get a good start, they apparently exclude all other vegetation, notably at Balapitiya, where the short river leading into the lagoon is occupied by *Rhizophora* and *Bruguiera* only, to the practical exclusion of all other members of the mangrove vegetation. This is partly due no doubt to their very free fruiting, combined with the dropping of the embryos straight into the mud and the rapid development of the young trees, which initiates the closely packed

pure associations of these plants. But it is also largely due to the increase of a *Rhizophora*-formation by the sprouting of new branches just above the points of insertion of stilt-roots and the sending down of fresh stilt-roots from these new branches. In this way the edges of a clump of these mangroves continually grows, encroaching on the surrounding mud, and the whole becomes a perfect network of branches and stilt-roots, in which the separate trees can no longer be distinguished, and among which no other vegetation has a chance.



FIG. 11. Diagrammatic sketch of *Rhizophora conjugata* growing in a sheltered situation, shewing a well-developed pyramidal crown, and a bushy outgrowth on the free (left-hand) side from the lower branches above the stilt-roots. On the right-hand side, where the mud bank is indicated, there is supposed to be a continuous *Rhizophora*-wood.

The crowns of *Rhizophora* and *Bruguiera* appear to be usually rounded (Fig. 15), or, where the trees are growing in exposed

situations, irregular; but in some cases at any rate it has a markedly pyramidal form with an enlarged bushy base, as a result of the sprouting of new branches from above the stilt-roots as described above (Fig. 11, cf. also Karsten, *Bibl. Bot.*, Heft. 22, Tab. I.)

An interesting feature of the various members of the mangrove formation is the presence of protective structures enveloping the bud; in the *Rhizophoraceae* these are constituted by the stipules, and as Karsten points out (*loc. cit.*, p. 54) large amounts of mucilage are excreted from glands borne at their base, and this mucilage envelopes the whole bud. Similar glands, according to the same author, are found in *Sonneratia*, *Avicennia* and *Aegiceras*.

We may perhaps be allowed to call attention to some popular misconceptions of mangrove forests. References to "gloomy, fever-haunted mangrove swamps," with their "foul, treacherous mud," are often met with. The gloom of a mangrove wood is certainly not remarkable, and so far from the light being actually dim, Schmidt<sup>1</sup> has recently shewn that it is but little less bright than on the open sea, and far brighter than in the shade of an inland jungle. The mud is certainly not always stinking, and is frequently quite firm enough to bear one's weight. We have not met with the abundance of land-crabs described by some observers, but the amphibious fish (*Periophthalmus*), which spend half their time hopping about on land, are numerous and amusing. *Rhizophora* and *Bruguiera*, when well grown, are undoubtedly both handsome trees, and a fringe of mangroves with their thick dark green glossy foliage is certainly an embellishment of the shores of tropical estuaries.

Next in importance to *Rhizophora* and *Bruguiera*, among the Ceylon mangroves, comes *Sonneratia acida*. This species is very abundant and widely spread in the mangrove formation of the Ceylon coast, sometimes occupying a front situation on the shores of the estuaries and lagoons, and very often figuring largely in the tree vegetation of the stretches of muddy soil more or less affected by the tide behind the fringe of mangroves on the actual water's edge. In the last situation *Sonneratia* really belongs more to the "semi-mangrove" vegetation (see below) than to the true mangrove-formation. *Sonneratia acida* varies in stature from a

<sup>1</sup> Schmidt. *loc. cit.*, p. 12. The sensitive paper of the actinometer took on the standard tint after the following exposures; open sea,  $\frac{1}{4}$  to  $\frac{1}{2}$  sec.; under the shade of a *Rhizophora conjugata*, 2 secs.; in an inland jungle, 90 secs.

shrub a few feet high to a tree which may attain as much as 50 feet. Its leaves are obovate, of a light, rather dull green, forming a striking contrast to the dark glossy green of the *Rhizophora-Bruguiera* vegetation. The foliage is rather loose, and is disposed about the trunk and branches with something of the elegance, though not all the lightness, of the silver birch.

Like all the true mangroves, *Sonneratia* has aerial roots for the purpose of allowing air access to the tissues of the part of the root-system which is buried in mud. Long horizontal roots run close below the surface of the ground, sending down much-branched rootlets deep into the mud, and sending upwards straight unbranched roots which rise a foot or more above the surface. These upright aerial pneumatophores often form a perfect forest where the horizontal underground roots are numerous. Like the aerial parts of the stilt-roots of *Rhizophora*, and the knee-roots of *Bruguiera*, these aerial roots of *Sonneratia* possess a thick and richly lacunar cortex, the intercellular spaces of which are open to the air through the peeling of thin investments of cork (aerenchym). Trimen mentions that the aerial roots of *Sonneratia* are cut into slices and used by entomologists in their collecting boxes as a substitute for cork, owing to their spongy but firm and even texture. *S. alba* and *S. apetala*, which have similar pneumatophores, are also found in Ceylon, but they are very rare, and we have not met with them.

Westermaier has recently investigated the respiratory mechanism of these roots of *Sonneratia*, with interesting results. The cortex of the submerged and subterranean portions of the pneumatophores, as well as of the horizontal roots from which they arise, is highly lacunar; it lacks the characteristic supporting elements (trichoblasts) which occur in the rather less strongly developed cortex of the aerial part of the pneumatophore. In their place, however, it contains peculiar arc- or S-shaped cells ("Federzellen") which are capable of compression and expansion like springs, and lead to alternate collapse and distension of the cortex in this region, as the water rises and falls with the change of tides, or when the water is disturbed. Each compression of the cortex of these submerged parts forces a certain amount of the contained air out through the aerenchym of the aerial part of the pneumatophore, whilst in the subsequent expansion a supply of fresh air is sucked in from outside. We thus have a respiratory process, which is quite analogous to our own, although in

*Sonneratia* it depends on external periodic mechanical factors. Westermaier points out that in Schimper's description of the anatomy of the stilt-roots of *Rhizophora* there are indications that a similar respiratory mechanism occurs—a point which is well worth investigation, since it would be a very striking case of convergent development in two plants of different orders.

*Avicennia officinalis* (Verbenaceae) is another characteristic mangrove, forming a bush or small tree with oval pointed leaves covered underneath with a white down which gives the foliage a greyish tint. It has aerial roots or pneumatophores of exactly the same type as *Sonneratia*, though it belongs to a totally different family, but their cortex communicates with the air by means of lenticels. This plant is also viviparous, but the development of the embryo does not proceed nearly so far as in the Rhizophoraceæ. The whole fruit falls off the tree, the hypocotyl elongates a little, and lateral roots sprout from its swollen lower end, very quickly fixing the seedling in the mud. The cotyledons are fleshy and folded, and lie on the mud or are raised a little above it. It is a very widely distributed and common species in the East, and in protected places often forms pure formations on the water's edge. It is common in Ceylon, according to Trimen, but we saw very little of it (except at Negombo, where it forms a marked feature), though a stunted bush of this species was the only individual mangrove that we met with on the actual sea-shore. This was at Tangalla, where the bush in question was growing quite isolated, and certainly far from the nearest individuals of the species. It was evidently having a hard time, in a little shallow mud and sand which had collected in the hollow of a rocky promontory. The little patch of mud was nevertheless full of the characteristic upright roots.

*Acanthus ilicifolius* is the only member of the true mangrove-flora which is herbaceous. It forms low bushes only two or three feet high, with leaves exactly like those of the holly, and beautiful lilac-purple flowers of the ordinary *Acanthus*-type. This plant never grows where it is exposed to much tidal action, but is extremely common lining the front of the mangrove formation on the edges of the estuaries and lagoons. It is in fact the most characteristic waterside mangrove after *Rhizophora* itself, forming a dense belt round many of the little islands in the estuaries, with *Sonneratia*, *Bruguiera*, etc., behind (Fig. 12). Where the mangrove formation is well developed, *Acanthus* generally forms an abundant



FIG. 12. An island in the Bentotta river entirely occupied by Mangrove vegetation. A belt of *Acanthus* two or three feet high occupies the water's edge; behind in the centre is a tree of *Sonneratia acida*; on each side bushes, of *Bruguiera* and some *Chrysodium*.

(From a sketch).

constituent of the vegetation, and Schimper has already sufficiently described the important part it plays at Negombo, some of the smaller islands in the lagoon consisting practically of this plant only. On the other hand this is not invariably the case, for at Balapitiya *Acanthus* is only very slightly represented, whilst the rest of the mangrove vegetation is very well developed. This plant was also not met with at Ambalangodda. In other places, again, *Acanthus* is almost the sole representative of the typical mangrove-vegetation for considerable stretches along the estuaries (e.g. Kalutara, Bentotta). These very definite features in the distribution of this plant indicate that there are certain external factors, which will probably not be difficult to ascertain, determining its presence or absence at any locality. It is interesting to notice that it has stilt-roots somewhat like those of *Rhizophora*, though of course on a much smaller scale (Fig. 13). Sometimes it forms a thick undergrowth in a mangrove wood on soil not covered by the tide at high water.

*Ceriops Candolleana* is a member of the Rhizophoraceæ and resembles *Rhizophora* in its viviparous embryos, which reach a length of several inches before dropping from the tree. They are, however, both shorter and slenderer than those of *Rhizophora*. Some uncertainty seems to exist as to the root-system of *Ceriops*; Schimper enumerates it amongst the plants with pneumatophores, whilst Trimen describes stilt-roots as occurring in *Ceriops*, and this receives some confirmation from a figure (Fig. 19) in Schmidt's paper. Karsten,<sup>1</sup> however, does not refer to either type.

<sup>1</sup> Bibl Bot. Heft. 22, 1891, p. 49.

*Aegicerus majus* (Myrsinaccæ) also has viviparous embryos, which are, however, much smaller than those of the Rhizophoraceæ. They are strongly curved, so that the lower very sharply pointed end points outwards or upwards when hanging on the tree. This species is not very common in Ceylon. It furnishes another excellent instance of the same adaption being evolved in two totally distinct families, owing to similarity of environment.



FIG. 13. Shoot of *Acanthus ilicifolius* shewing mode of advance on the mud by means of stilt-roots. Half natural size.

*Lumnitzera racemosa* (Combretaccæ) is another not uncommon tree of the mangrove-swamps of Ceylon. *L. coccinea* is very rare, having been reported only from the Bentotta river. According to Sehimper it has knee-roots like *Bruguiera*. *Scyphiphora hydrophyllacea* (Rubiaceæ), much like *Lumnitzera* in appearance, is also rare—reported from Jaffna only. These three trees form a sort of transition to the “semi-mangroves.” Their adaptations have been little investigated.

At the conclusion of our description of the mangrove-vegetation we cannot omit to mention the characteristic covering of Algae, which is borne by the submerged parts of the roots of *Rhizophora*

and *Acanthus* and of the pneumatophores of *Sonneratia*. We have observed these Algae in almost every locality in Ceylon, where the above-mentioned genera are to be found, although where the mangroves are rare, the Algae are still rarer; thus at Kalutara the typical algal forms were only found after a lengthly search, whilst at Matara they were not discovered at all. Their absence is in part undoubtedly connected with the weak development of the actual mangrove element, but in part it would certainly seem to be due to the muddy character of the water; the rivers at Kalutara and Matara are both very turbid—at least at the time of the year at which we saw them—whilst the river at Bentotta is rather clearer and here mangrove-Algae were observed in considerable amount. In the lake at Ambalangodda, in which the mangrove-element is quite wanting, none of the typical algal forms were observed, whilst in the lake at Panadure the latter were found on the roots of the *Rhizophora* and *Acanthus* occurring there. These few remarks will suffice to show that wherever the mangrove-formation is at all well developed we meet with these Algae in connection with it, so that they must be regarded as an essential feature of this formation.

The species of Algae concerned belong in the main to the red and green groups, although a considerable part is also played by the blue-green element. The red forms belong to at least three distinct species (apparently *Delesseria Caloglossa Leprieurii* and two further species, which may be provisionally referred to the genera *Nemalion* and *Polysiphonia*; we are not in a position at present to publish the specific determinations) and one of these at any rate (*viz. Delesseria, Leprieurii*) was found in every locality where these Algae were typically developed. In clear water these forms are to be found covering the submerged parts of the stilt roots of *Rhizophora* to a depth of a foot or more below the surface, but in turbid water they are generally confined to within a few inches of the water-level, or they may be wanting altogether on most of the *Rhizophora*-roots. In these cases one generally finds an algal covering of another kind, consisting of green and blue-green forms, either below the belt of red forms or occupying the whole submerged surface of the root; the root then appears thickly coated with a dull green or brown fluffy covering, owing to the considerable percentage of muddy particles intermingled with the Algae. The most important green forms are a broad-celled species of *Conferva*, and a *Spirogyra* (the latter at Kalutara), with which a

varying and often predominating amount of filamentous blue-green forms are associated (*Lyngbya*). In some localities (*e.g.* Bentotta) the pneumatophores of *Sonneratia* are covered with a fairly dense growth of (apparently) the same red forms as occur on the *Rhizophora*-roots, whilst in other localities (*e.g.* Kalutara) a careful examination revealed no traces of Algae on the *Sonneratia*. It should be pointed out that the red forms are practically confined to the root-structures of these two plants. Small quantities of them were found in other situations (*e.g.* stone-work of landing-stage at Negombo, rocks near railway-bridge in river at Bentotta), but these were merely isolated occurrences. It seems probable that these forms are adapted to live on the peculiar spongy substratum afforded by the bark of the roots of *Rhizophora* and *Sonneratia*. As far as our observations go they become rarer as one moves away from the sea. It should be added that similar red Algae have been described by Schimper<sup>1</sup> and Goebel<sup>2</sup> for the American mangroves and by the former also for the Indian mangroves, but a careful investigation is much needed.

The roots of *Acanthus ilicifolius* and also some of its horizontal branches which dip into the water, afford a rather different substratum; this is evidently quite unsuitable for the above-mentioned Rhodophyceae, which are never to be found on them, although *Acanthus* often grows in the immediate vicinity of *Rhizophora* or *Sonneratia* bearing the red forms. The submerged portions of the *Acanthus* however almost invariably have a thin algal covering of another kind, composed of filamentous Cyanophyceae of the *Rivularia*-group.<sup>3</sup>

#### 4.—SEMI-MANGROVE OR SEMI-HALOPHYTE VEGETATION (INCLUDING *Nipa*-FORMATION OF SCHIMPER).<sup>4</sup>

All the species hitherto mentioned may be said to belong to the mangrove-formation proper, since they all shew definite adaptations, in their root-systems, and often also in their habit of

<sup>1</sup> Schimper, Indo-Malay. Strandflora. 1891. p. 65 ; Pflanzen-geographic. 1898. p. 827.

<sup>2</sup> Goebel, Ueb. einige Süßwasserfloridae aus Britisch-Guyana. Flora. Vol. 83. 1897. p. 436.

<sup>3</sup> The Algae of the mangrove-formation will subsequently be described in much greater detail by one of us.

<sup>4</sup> In the course of a further examination of the evidence before us we have decided to depart from Schimper's classification given on p. 3. Cf. below and especially our table on pp. 50, 51, where the relation between the semi-mangroves and the true mangroves is shown.

precocious germination and the form of their embryos, to the very special conditions of life obtaining in their characteristic habitats.

There are, however, a number of other trees which occur associated with the true mangroves, but in situations where the extreme conditions to which the mangroves are specially adapted do not obtain. These may grow, for instance, on muddy soil on the banks of estuaries, just above the uppermost level to which the brackish tidal water reaches, either immediately behind the true mangroves or even alongside of them on the banks, if the soil of the latter is well raised above the water. The shores of many of the Ceylon estuaries close to the coast-villages have been roughly embanked by the natives by means of rows of piles driven into the mud, behind which a soil of firm compacted mud has been made. The rough quay thus formed serves as a landing stage for boats, and the mud behind is suitable for the growth of coconuts, while the mangroves, which in all probability originally occupied the shores have been cleared away. In such situations the semi-mangroves referred to are commonly found, often mixed with the planted coconuts. On other parts of the estuarine shores, which are not embanked, but in which the water does not, at least normally, overflow the actual banks, these semi-mangroves are also found, often forming a natural rather open wood. As one passes away from the shores of the estuaries, and away from the sea, one sometimes reaches great stretches of muddy, soil in which these semi-mangroves form a conspicuous feature either as isolated trees or as clumps of trees, or forming more or less continuous woods.<sup>1</sup> In this sort of situation the true mangroves are relatively uncommon, though they are sometimes met with, especially on the banks of drainage channels, where these are present. Sometimes brackish water from the nearest river flows up these channels at high tide, and this must help to keep the soil of such mud flats relatively salt. It is probable that it is the decrease of salt in the soil, combined with the absence of true tidal conditions, which enables the semi-mangrove to get a footing and compete successfully with the more highly adapted tidal forms. On the other hand it is clear that the true mangroves can flourish

<sup>1</sup> These mud flats are not very well developed on the part of the Ceylon coast we have visited, probably because such land can be easily drained and used for cultivation, but in many places there are small areas of it. In other regions, however, e.g., in the neighbourhood of Malacca, they are very extensive and characteristic.

even on ordinary soil,<sup>1</sup> so it is not surprising that they should also be found in the intermediate situations mentioned. Schimper has already referred to the "Misch - und Uebergangs-formation" in the sort of situations we have just described, and calls it the "*Nipa*-formation." The remarkable palm *Nipa fruticans* certainly occurs typically in this kind of habitat, but the vegetation in question is far too mixed and varied to call by the name of a single species, which is very often absent altogether. It is possible that proper investigations would enable us to distinguish several different "formations" among this intermediate vegetation. For present purposes we shall refer to it as "semi-mangrove" or "semi-halophyte" vegetation, for want of a better name.

With regard to the actual specific composition of this vegetation, in the first place practically all the trees mentioned on p. 17 as belonging to Schimper's *Barringtonia*-formation (Beach-jungle) may be found in this sort of locality. They are probably all adapted to resist the effect of salty water, though to a less extent than the true mangroves. Information as to the range of soils they inhabit is very scanty, but they are certainly capable of growing in very muddy situations, as well as on the sand of the coast. We should put *Excæcaria Agallocha* and *Dolichandrone Rheedii* next to the true mangroves.<sup>2</sup> *Cerbera Odollam* is also often abundant in the same localities, especially in the more open spots.

We must next consider two characteristic and widely distributed plants of this vegetation, the palm *Nipa fruticans* and the fern *Chrysodium aurcum*.

*Nipa fruticans* has an underground rhizome, which sends up rosettes of gigantic pinnate leaves many feet long. One can climb about on the leaf bases, where the rachis is as thick as one's wrist and quite rigid. From the midst of these rosettes the inflorescences rise to a height of four feet or so. A female spike terminates the inflorescence and is surrounded by male spikes. Strong laterals may also terminate in a female spike. Each spike is covered by a single great bract of a beautiful orange-fawn colour. The male spikes burst through the substance of this bract and also through the single bracteole belonging to each. The fruits, with

<sup>1</sup> Cf. Schimper (Indo-Malayische Strandflora p. 198), who points out that *Bruguiera*, *Sonneratia*, etc., flourish in the Botanic Gardens at Buitenzorg. There is even a plant of the American *Rhizophora Mangle* in the *Victoria regia* house at Kew.

<sup>2</sup> Cf. Schimper, Strandflora, p. 61.

the remains of the withered male spikes attached to the stalks below, consist of a number of one-seeded obovate nuts, polygonal by mutual pressure, aggregated in a spherical mass as big as one's head. The nuts are of a rich dark chestnut brown and are perfectly adapted to floating. *Nipa* never grows where it is exposed to wave action, but rather on the muddy shores of quiet backwaters and lagoons close to the sea (e.g. Matara and Ambalangodda) or on river banks at some distance from the sea. In these situations, however, the base of the plant may be completely covered at high water. It also occurs on the mud flats above described, sometimes forming a pure thick jungle of great extent, as in Sumatra (Schimper). We did not find it in any such situations in Ceylon, however, where the plant is not very common, reaching the western limit of its distribution. We found it in the river at Kalutara, Bentotta (high up), and Matara and in Lake Madampe at Ambalangodda (abundant).

*Chrysodium (Acrostichum) aureum* (Fig. 14) is a very handsome striking fern, with an underground rhizome sending up simply



FIG. 14. *Chrysodium (Acrostichum) aureum*. Fronds about 4 feet high.  
(After a photograph).

pinnate aerial fronds to a height of several feet. It owes its generic name to the brilliant golden colour of the young pinnae.

The fertile pinnæ have the whole of their under surfaces covered with sporangia, giving the pinna a dark brown colour.

*Chrysodium* is an extremely abundant plant in the brackish marshes, and on the banks of the tidal rivers and often gives a character of its own to the vegetation. On the whole it distinctly increases in amount as one gets further from the sea, and in this respect may be placed, as Schimper places it, beside *Nipa*, but in Ceylon it is much commoner than the latter, and is found high up the rivers where the water is scarcely salt, in association with tall freshwater riverside herbaceous plants, such as *Susum anthelminticum*, *Phragmites Karka (Roxburghii)*, several species of *Cyperus*, e.g. *C. dilutus*, and *Colocasia Antiquorum*. *Chrysodium* is



FIG. 15. View of a brackish lagoon south of Matara with narrow belt of mangroves (*Rhizophora*, etc.) fringing the shore from which the low hills rise steeply. (After a sketch by Dr. W. H. Lang).

one of the cosmopolitan tropical "semi-halophytes." It is extremely abundant in the Malay region, covering immense tracts by the sides of the tidal rivers further from the sea than most of the true mangroves go, but often associated with *Nipa* and *Sonneratia*, and it is apparently equally common in America.

We had no opportunity of making a study of the junction of either mangrove or semi-mangrove vegetation with typical land-vegetation, but it may help the reader to form a more definite picture if we describe the succession of forms seen in passing up some typical tidal rivers on the Ceylon coast. The vegetation of the estuarine mouths of all these rivers tends to be spoiled by clearing, embanking, and planting of coconuts.

To take first the Bentotta river. Close to the mouth, coming down to the shore among the coconuts, were *Hibiscus tiliaceus* (plentiful) *Thespesia populnea* *Calophyllum Inophyllum*, *Terminalia Catappa*, *Excæcaria Agallocha*, and *Acanthus* in places lining the water's edge. Two or three hundred yards up was well developed *Rhizophora conjugata*, and in a small bay a varied collection of mangroves and semi-mangroves:—*Rhizophora*, *Bruguiera*, *Sonneratia*, *Hernandia*, *Dolichandrone*, *Hemitelia*, *Pongamia* with a small Leguminous liane. On the opposite bank, where a canal leads off to a lake about a mile away, good mangroves (*Rhizophora* with excellent stilt-roots, *Bruguiera*, *Sonneratia* and *Acanthus*) were developed for a short stretch, but very soon disappeared as one passed up the canal. A small island completely covered with vegetation had a continuous belt of *Acanthus* touching the water round its edge, while the centre was filled with bushes of *Bruguiera gymnorhiza* plants of *Chrysodium*, and one small tree of *Rhizophora*. Fig. 13 represents a similar island in the Bentotta river, but without *Rhizophora*. Further on up the river bank a liane of the Leguminous genus *Mucuna*, probably *M. pruriens*, with flowers and fruit, *Barringtonia speciosa*, and species of *Ipomoea* climbing over the trees. Many *Bruguiera*-embryos were noticed here floating vertically in the water with the calyx uppermost. Higher up again we met with tall riverside herbaceous forms, *Cyperus dilatatus* and *Phragmites Karaka*, at intervals, accompanied by *Chrysodium aureum* lining the banks; but for long stretches on both banks the true mangroves, *Acanthus*, *Rhizophora*, *Bruguiera* and *Sonneratia* were perfectly continuous to the exclusion of everything else, except an occasional *Excæcaria*. Further on still *Rhizophora* with its close characteristically gregarious habit excluded even the other mangroves. Sometimes, however, *Phragmites* and *Acrostichum* occurred in front of it. The whole of the riverside vegetation here was under water, solid banks being quite absent. Right behind the *Rhizophora* belt, *Nipa* occurred here and there, and in one place quite young plants of it were seen.

*Rhizophora* and *Bruguiera* here (3 miles from the sea) were seldom more than 30-feet high, while *Sonneratia* often attained 50-feet, shewing that it is able to flourish very vigorously far from the sea, though an occasional tree of it only was seen, up a side creek. The river in this region broadens out into a wide lake-like expanse with many backwaters. The whole of the banks here appear to be occupied by *Rhizophora* and *Bruguiera*, with an

occasional tree of *Cerbera* or *Barringtonia*, where the mangrove growth is less dense. We did not go any higher up the river, but we understand that mangroves extend many miles further, though we have no information as to where they definitely become subordinate to and finally disappear before the inland jungles. On the other bank the same phenomena are met with. *Rhizophora conjugata*, with fine pyramidal crowns and bushy lower foliage over the outermost stilt-roots (Fig. 11), reaching a height of 50 feet and forming, in some places, a regular forest. In one spot solid ground came down to the river bank, and here there was a gap in the mangroves, *Mesua ferrea* with its beautiful crimson young foliage, and *Vateria*, appeared behind, with *Terminalia Catappa* and *Cerbera* in front. Lower down again the bank was solid at intervals, and coconut compounds appeared close to the river, with mangroves (especially *Acanthus*), and semi-mangroves (e.g. *Terminalia*, *Sonneratia*, *Cerbera*), at intervals. Amongst the *Acrostichum*, which occurred here, an occasional *Pandanus* was met with. The impression left on one's mind was that at one time the mangroves, mainly *Rhizophora*, had fringed the entire estuary for several miles from the sea. The banks of the lower mile or two have been largely cleared at intervals and partially embanked for coconut planting, and on the solid mud above the water level thus provided the *Barringtonia-Terminalia* flora gets a footing, with an occasional patch of true mangroves, the embryos of which are brought down from higher up the river and germinate very freely wherever they can find a flat or sloping muddy bank exposed.

#### MATARA RIVER.

The river at Matara presents a distinctly different vegetation, though, as we shall see presently, largely owing to artificial causes.

The vegetation of the backwater not far from the mouth may be first described. The dominant waterside forms were *Sonneratia*, *Chrysodium aureum*, *Cerbera* and *Nipa* (plentiful and well-developed) with an occasional tree of *Heritiera littoralis* and *Terminalia Catappa* just behind the fringe. At the upper end of this backwater we found the freshwater *Jussiaea repens* with its brilliant white aerenchym-covered roots standing up in clusters.

A little island in the estuary below the backwater showed a perfect and complete zonation of *Acanthus*, *Sonneratia* and Coconuts in that order from the water's edge, with a little *Cerbera* and *Chrysodium* among the coconuts. The curious aquatic *Trapa*

*bispinosa* with its rosette of floating leaves forming a perfect mozaic on the surface of the water, a bladder on each petiole below the water serving to float the leaf, and much divided submerged leaves, was abundant here. Above the bridge the right bank of the river showed a constant succession of *Sonneratia* (bearing a *Loranthus* in places *Acanthus* and *Chrysodium*, all with their bases covered by the water. *Bruguiera* occurred as a very occasional and only representative of the Rhizophoraceae. Behind were *Phragmites* and *Cyperus*, and further back the land was occupied by a *padi* (rice) field quite submerged at high water. Behind this again came the first solid ground with a belt of *Calophyllum Inophyllum* and then coconuts. Half a mile above the bridge the long-petioled ovate-cordate leaved Aroid *Colocasia antiquorum*, a typical river-side plant, which has long been cultivated everywhere for its edible starchy rhizome appeared, together with the narrow-leaved *Susum antheleminthcum*. *Sonneratia* and *Acanthus* became less and less common, while *Cyperus* increased. Thus the tree vegetation becomes entirely re-placed by the typical tall river-side herbs (reed-marsh) vegetation, mainly *Cyperus*, *Colocasia*, *Phragmites*, *Acrostichum*, fringing the low artificial banks or *bunds* separating the stream from the *padi*-fields which here line each side of the river. Here and there on the bund is an occasional tree of *Sonneratia* or *Dolichandrone*. This vegetation is quite parallel with the *Phragmites-Typha-Scirpus* formation fringing a river-side at home, with an occasional alder or willow. Where solid ground came down to the river-bank *Heritiera*, *Barringtonia*, *Pandanus*, etc., were noticed.

Thus the lower part of the river at Matara differs strikingly from that of Bentotta, at any rate at present. The essential difference is the practical absence of the Rhizophoraceae, and not far up the replacement of the tree-flora by a reed-marsh-flora separating the river from *padi*-fields. The first point is difficult to explain, but there seems no reason to suppose that the area occupied by *padi* would not naturally support mangrove-vegetation, and it appears reasonable to conclude that the tree-vegetation has been cleared to make room for *padi*, the bunds or low banks thrown up to protect the *padi* being afterwards colonised by the river-side herbs.

#### KALU GANGA.

The river at Kalutara, the Kalu Ganga, may be described as a third example of estuarine vegetation; it is very characteristic of

the intermingling of Schimper's Mangrove, *Nipa*-, and *Barringtonia*-formations and of inland forms. It recalls the river at Matara in the scanty development of Rhizophoraceae, but the banks of the Kalu Ganga are thickly wooded and the scarcity of the mangroves seems more the result of natural causes here than at Matara. At many points the banks slope more rapidly out of the water than in the two preceding cases and this may be the cause of the great scarcity of the typical genera. Near the mouth of the river a short stretch of fairly characteristic mangrove (*Rhizophora*, *Bruguiera*, *Acanthus*, *Sonneratia*, *Cerbera Odollam*) is to be found on the north bank on either side of the railway bridge with occasional specimens of *Nipa fruticans*; *Dolichandrone Rheedii* is also very characteristic of this region, but becomes more abundant as we pass away from the mouth. *Heritiera littoralis*, and *Clerodendron inerme* were also occasionally observed on this part of the banks. On the other hand the island in mid-stream, which is joined to either bank by the railway bridge, bears no Rhizophoraceous species at all, *Sonneratia acida* and *Cerbera Odollam* forming the main part of the woody vegetation. *Barringtonia* occurs at a few points on this island. As one moves up stream away from the railway bridge a number of new plants slowly make their appearance (*Cynometra ramiflora*, *Ardisia humilis*, *Eugenia caryophyllea*, *Ixora coccinea*, *Hippocratea obtusifolia*), whilst the mangrove-element disappears more and more, giving way to *Nipa fruticans*, *Barringtonia*, etc., and occasional patches of *Pandanus*. Climbing plants also become commoner as we recede from the sea; a species of *Coumarus* is noticeable first, whilst subsequently *Flagellaria indica* and *Caesalpinia Nuga* become prominent features of the vegetation. In front of the shrubby and woody vegetation on the actual banks, one finds, as in all the Ceylon estuaries we visited, a very characteristic growth of marsh plants, rising up out of the water. On the island mentioned above this foreground is constituted by *Susum anthelminticum* and a species of *Cyperus*, the one generally replacing the other. The same two plants also form a fringe on the banks of the river together with other species of *Cyperus*, and as we go up stream *Phragmites Karka* partly replaces them and with its long runners forms a conspicuous feature of the vegetation. Still further inland *Chrysodium aureum* is very common down by the water's edge and together with *Nipa* and *Susum* presents a very characteristic appearance. In front of these a submerged species of *Aponogeton*, *A. crispum*, and diverse floating plants (*Nymphaea*,

*Limnanthemum*, etc.) form a gradual transition from the thick vegetation of the banks to the open water of the river.

The river at Kalutara thus shows a more pronounced conglomeration of different types of vegetation than either of the preceding rivers; not only do the different littoral formations intermingle freely, but typical inland low country plants play an important part on the banks at no great distance from the mouth. Probably, if we could have gone further up stream, it would have been found that in the Kalu Ganga the inland jungle dominates the river-banks to the exclusion of the littoral formations much sooner than in either of the preceding rivers.

#### BALAPITIYA.

As a last example of the types of vegetation under discussion a brief description of the lagoon at Balapitiya, which is situated about four miles to the north of Anbalangodda, may be given. The lagoon does not open directly into the sea like that at Negombo, but is connected with it by a narrow river about half a mile in length.

The banks of this river are clothed by a dense growth of *Rhizophora conjugata* and *Bruguiera gymnorhiza*, with splendidly developed root-systems; in between are isolated specimens of *Sonneratia* and *Calophyllum*, and a single tree of *Heritiera* was also seen here. *Acanthus ilicifolius* is however practically wanting, except for a small patch of it near the mouth. There were no floating plants in the river when we visited it, and its vegetation is altogether of a remarkably uniform character. It is the best example we have seen in Ceylon of a pure mangrove-vegetation fringing the banks of a river within a short distance of the sea—indeed the mangroves are much nearer the latter here than even at Negombo. The lake is a very extensive piece of water, projecting inland in several directions and containing several small islands, some of the more rocky of which are covered with a growth of *Gleichenia dichotoma*. At numerous points round about the lake *Rhizophora* and even more commonly *Bruguiera* are well developed and their abundant presence quite recalls the lagoon at Negombo, which has become classical through Schimper's description. In the lake at Balapitiya, *Sonneratia* is also very commonly represented, but the vegetation is by no means a pure mangrove-formation,—in fact far less so than at Negombo—for here and there we get *Pandanus* and *Susum* occurring, and *Chrysodium*

*aureum* is especially commonly present round the edge, fringing the more open country. Other common forms are *Cerbera Odollam*, *Clerodendron* sp. (*C. inerme*?) and the rather scarcer *Thespesia Lamphas*, whilst a number of climbers occur. Of typical lowland plants *Eugenia caryophyller* is very common in between the mangroves. *Limnanthemum* and *Nymphaea* cover the surface of the water in places.

The vegetation of the lake at Balapityia is thus, although to a considerable extent dominated by the mangrove formation, fairly representative of that intermingling of the littoral types of vegetation, which is clearly a common feature of the Ceylon estuarine waters. Our visit was too short a one however to enable us to collect data as to the cause of this intermingling in the lake under discussion, but it seems probable that both the above mentioned factors come into play here, viz: influence of man and steepness of banks.

We append a list of the mangroves and semi-mangroves of the Ceylon coast; the forms placed first are the most highly adapted mangrove forms with specialized embryos or roots. The species we found dominant are printed in heavy type, those we have not observed, but which are recorded from the Ceylon coast, are given within parentheses.

<i>Rhizophora mucronata.</i>	} TRUE MANGROVES.
<b>Rhizophora conjugata.</b>	
<i>Ceriops Candolleana.</i>	
( <i>Ceriops Roxburghiana</i> ).	
<b>Bruguiera gymnorhiza.</b>	
( <i>Bruguiera caryophylloides</i> ).	
<b>Sonneratia acida.</b>	
<i>Sonneratia alba.</i>	
<i>Sonneratia apetala.</i>	
<i>Avicennia officinalis.</i>	
<b>Acanthus ilicifolius.</b>	
<i>Aegiceras majus.</i>	
( <i>Carapa moluccensis</i> ).	
( <i>Lumnitzera coccinea</i> ).	
<i>Lumnitzera racemosa.</i>	} SEMI-MANGROVES.
( <i>Scyphiphora hydrophyllacea</i> ).	
<i>Excacaria Agallocha.</i>	
<i>Dolichandrone Rheedii.</i>	

Swamp species, often by the river-side with submerged bases.	Species preferring solid ground (Barringtonia-formation of Schimper) but often on mud close to mangroves.	SEMI-MANGROVES.
<i>Nipa fruticans</i> (sometimes on solid mud).	<i>Barringtonia speciosa</i> .	
<b>Chrysodium aureum</b>	<i>Cerbera Odollam</i> .	
passing to typical river-side (reed-marsh) forms.	<i>Heritiera litoralis</i> .	
	<i>Hernandia peltata</i> .	
	<i>Hibiscus tiliaceus</i> .	
	<i>Thespesia populnea</i> .	
	<i>Pongamia glabra</i> .	
	<i>Terminalia Catappa</i> .	
	<i>Calophyllum Inophyllum</i> .	
	<i>Pandanus odoratissimus</i> .	

THE GERMINATION OF SEEDS FROM DRIFT.

Sea-drift is of course found all over the world on flat or sloping coasts, and consists of miscellaneous debris thrown up by the tide. Its nature is naturally very various, according to the locality. On our own coast it is very largely composed of seaweeds which have been torn from their homes by the waves, but in the tropics parts of various flowering plants are much more largely represented. This is no doubt due to the fact that tropical coasts and river banks are more often clothed with a luxuriant woody vegetation, so that much more material derived from such plants drops into the water than is the case on the more sparsely clothed watersides of temperate regions. Among the miscellaneous mass of half decayed vegetable debris, leaves, small branches, pieces of wood, etc., there are usually many fruits and seeds, some strikingly well preserved others in all stages of disintegration. These belong mainly, though by no means exclusively, to the typical coast trees with which we have been dealing in the present paper.

Schimper's account<sup>1</sup> of the Drift-seeds and fruits of the coast-plants of the Eastern Tropics has already been alluded to (p. 17) He shews that the fruits and seeds of all the characteristic species possess features which enable them to float for long periods, and thus extends and consolidates the earlier and striking observations of Guppy, who found that certain species were able to germinate after floating in seawater for very long periods. Schimper also points out that the existence of the capacity for floating (in many

<sup>1</sup>Indo-malayische Strandflora, pp. 158-196.

cases the possession of a peripheral floating tissue) is not in the first instance to be regarded as a direct adaptation to sea-transport, since allied species of the same genus which live inland usually possess the same character developed to a less extent. The coast-species therefore presumably owe their wide distribution to the fact that the fruits or seeds of their ancestors were able to float for a considerable period because they possessed a character which had some quite distinct origin and significance.

This character helped them to colonise localities inaccessible to their accidentally less favoured congeners, and, under the stress of natural selection, has been increased and specialised in relation to the peculiar habitat thus adopted. Schimper gives an interesting account of his direct observations on the drift at Tjilatjap in Java, and we propose to add here some observations on the drift seen at one or two spots of the Ceylon coast.

By far the best example of drift on the actual sea front was seen at Kalutara (Oct. 28, 1900.) The river here, the vegetation of whose banks has been fully described above, flows into the sea very obliquely, a long sandy spit separating the estuary from the open sea. This spit is less than a hundred yards broad, and its centre is occupied by the regular *Pes-caprae* formation.



Fig. 16. Fruit of *Heritiera littoralis*. natural size.

On each side of this vegetation, between it and the water, the sand was largely covered with drift. Starting from the sea, the sand sloped pretty steeply up to a ridge which evidently corresponded to the high-water mark of normal tides. Along this ridge, or more often, along a second ridge, probably reached only by the highest tides, there was a thick line of drift, forming in places a dark blackish brown humus of disintegrated vegetable debris, several inches deep, among which were numerous fruits and seeds. The drift was composed of parts of plants, mainly twigs, leaves, and bits

of wood, apparently from riverside trees, bits of bamboo stem, fragments of coconut husks and leaves. Among the fruits and seeds were *Calophyllum Inophyllum* (very abundant), *Heritiera littoralis* (Fig. 15), *Pandanus*-nuts, *Dipterocarpus* and *Vateria* fruits, mangrove embryos, and many other undetermined forms. The sand around was blackened over considerable areas, apparently by the water spreading fine particles of humus thinly over it.

The thickest masses of drift were very moist and quite warm to the hand, and in this natural forcing bed many different plants had germinated. The thick line of brown-black humus with the fresh green leaves of the seedlings arising from it at intervals was a most striking sight. Of these the most conspicuous were *Cerbera Odollam*, *Calophyllum Inophyllum*, *Bruguiera gymnorhiza*, *Crinum asiaticum* and *Colocasia antiquorum* (from bits of old rhizome). The first two had perhaps little chance of establishing themselves on this spit of almost pure sand, even apart from the goats which constantly eat off the tops of the young plants; though the seedlings had often grown a foot or more high. Certainly for the mangrove the situation was impossible. But the last two species looked like really establishing themselves. They had already produced large healthy plants and many other individuals of the same species were growing on the spit. At the back of the spit, on the shore of the estuary, was more drift, and here also some seeds had germinated. On another part of the shore at Kalutara, seeds of *Ipomœa biloba*, evidently thrown up by the sea, were germinating in pure sand close to high-tide mark. The growth of the seedlings was extremely slow, the internodes being very short and the leaves thick and minute (Fig. 2, D), while there was a tap-root of great length. Only after some time were the typical creeping stems thrown out. *Canavalia obtusifolia* was found germinating in a similar spot, but this species is favoured by its large and very fleshy cotyledons.

We did not observe so abundant a drift, nor such obviously good conditions for germination, on the sea front at any other locality, though we found, at one time or another, the fruits or seeds of all the common coast trees thrown up by the water on to the sand.<sup>1</sup> But on the shores of the estuaries at the back of the spit which is so common a feature at the mouths of the rivers on this part of the coast we found in all cases drift-borne plants germinating and often establishing themselves.

<sup>1</sup> The occurrence, nature and abundance of drift is also clearly a variable, probably partly a periodic phenomenon, the study of which would be of interest.

The best example was at Matara. On the inside of the spit where the current impinges on the shore, there was quite a rich vegetation, probably all derived from drift. On the water's edge was a small tree of *Sonneratia* surrounded by quite a little thicket of *Acanthus*, *Cerbera* in all stages of growth, the larger bushes covered with flower and fruit in all stages, *Hernandia peltata* (good-sized plants), *Crinum asiaticum*, *Calotropis gigantea*, *Scævola Königii*, *Pithecolobium* (two small trees), *Cassia Tora* and *C. occidentalis*, the former abundant and covering many square yards. At the water's edge were thick masses of drift, including fruits or seeds of most of the species mentioned, many germinating freely, with *Cerbera* very conspicuous.

At a corresponding spot on the spit at Bentotta, there was a similar drift, in which mangrove embryos, both *Rhizophora* and *Bruguiera*, were particularly conspicuous; many had rooted and produced several leaves, though they apparently had no chance of succeeding. The abundance of these embryos here, and their absence at Matara, corresponds of course with the distribution of these plants in the two estuaries.

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#### SUMMARY.

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Our observations on the vegetation of the Ceylon coast and tidal estuaries may be summarised as follows. Practically the whole of the actual coast in the region dealt with is flat and sandy, and is destitute of mangrove vegetation. Where the rise from high tide level is very slight, the sandy strand is bare of trees and is occupied by the *Pes-caprae* formation. In this we can distinguish an *outer zone*, in which the sand is partially covered by the shoots of the typical creeping plants of this formation. Behind is an *inner zone* in which the sand is completely covered by the typical vegetation, mixed with many inland weeds.

Behind the inner zone again come the coconut plantations, often fringed with the remains of beach-jungle, some of the shrubs belonging to which frequently stand isolated in the midst of the *Pes-caprae* vegetation.

Where the shore slopes steeply this zonation is "telescoped," the outer zone of *Pes-caprae* disappearing and the inner zone being reduced to a narrow belt or itself being excluded.



Fig. 1.



Fig. 2.

Fig. 1. The Pes-caprae formation (outer zone). Ipomœa biloba (Pes-caprae) in foreground and middle distance; Zoysia pungens just behind the front plants of Ipomœa; young plant of Crinum asiaticum in middle distance.

The view is looking obliquely across the shore to the sea, with a wooded headland beyond.

Fig. 2. The Pes-caprae (inner zone) and Beach jungle formations. The thick carpet of vegetation in the foreground mainly composed of I. biloba. Behind, Crinum asiaticum (in flower), Pandanus odoratissimus (to right), and young Coconuts.

Both figures from photographs at Bentotta (Ceylon) by Mr. A. K. Coomaraswamy, by whose kind permission they are reproduced.



The mangrove formation is confined to the muddy edges of the tidal estuaries, which were probably at one time completely covered with this vegetation, (where the shores are flat and hence covered at high water) for some miles from the sea. *Rhizophora* and *Bruguiera* form the largest pure associations, but *Sonneratia* is practically ubiquitous and goes far up the rivers and on to the mud flats and swamps. *Acanthus* forms a well-marked zone on the water's edge in very many places. *Chrysodium aurcum* is a very abundant and characteristic riverside feature, usually beginning some little distance from the mouth and mingling with the fresh water reed-marsh formation. It is also extremely common on brackish swamps, often in company with *Sonneratia*. *Nipa* (rather rare in Ceylon) has a very similar habitat.

A series of transitional species lead from the typical highly adapted mangroves to the Beach-jungle trees, nearly all of which are found where the estuaries have definite banks above water level, and on the edges of the mangrove swamps. Where the banks slope steeply from the water's edge inland forms occur, while the mangroves and semi-mangroves are scanty or absent.

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*ERRATUM* :—By an oversight *Gloriosa superba* was described as "Dioscoreaceous" on p. 13 in the first part of this paper; *Gloriosa* is a member of the Liliaceae.

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"FASCIATION:" ITS MEANING AND ORIGIN.

By W. C. WORSDELL.

[TEXT-FIGS. 17—24.]

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I am profoundly impressed with the fact that all so-called "monstrosities," "sports," or "freaks," whether animal or vegetable, have no value or importance in themselves *as such*; on the other hand, that they are often of immense utility as

indications of the true nature of organs whose morphological character is doubtful; and, in almost every case, there is something useful to be gleaned from their study.

In the phenomenon of "fasciation,"<sup>1</sup> which literally means a "banding" or a "bundling," there would seem, at first sight, comparatively little that requires attention. Yet, as I hope to shew below, there are involved in a close consideration of this strange phenomenon, some by no means easy problems which demand solution.

I should like, first of all, to dwell for a while, upon two sets of phenomena, without a due consideration of which the facts of "fasciation" cannot in my opinion be understood. These two sets of phenomena are: (1) the *fusion* of organs or tissues which were once distinct; and (2) the *branching* of an organ or tissue which is primarily a unity.

#### I.—NEGATIVE DÉDOUBLEMENT OR COHESION.

Now in the first place I must necessarily define exactly what is meant by the expressions "fusion" or "cohesion," and "once distinct," ere we proceed to discuss the first set of phenomena. Let me here state at once my appreciation of the profound importance attaching to the recognition of the fact that there are two kinds of "fusion," "cohesion," "adhesion," or whatever term is preferred, as also to a clear distinction being drawn between the two. The two sorts of "fusion" may be called respectively (1) "*postgenital*" and (2) "*congenital*," in other words (1) "*real* or *mechanical*" and (2) "*ideal*." Now, the old school of botanists represented, *e.g.* by such writers as Schleiden, Duchartre, Moquin-Tandon, &c., were unable to make this distinction; they could only recognise one kind of fusion, as existing between organs, *viz.*, that which takes place subsequent to birth or development; a fusion which could be actually *observed* under the microscope, and of the existence of which there could, therefore, be no dispute. Where was the possibility of the existence of any other sort of fusion, than this? they asked. This is the *only real* fusion of organs that can be conceived of! But it is the old story once again! These older botanists, like some few, alas! to-day, fell into error owing to the fact that they relied, in the interpretation of the phenomena observed, entirely and solely on ontogeny or the *individual* development instead of on phylogeny or the history of the *race*. Above all, the *comparative* method was neglected and despised

<sup>1</sup>Latin "*fascia*" a banding.

which, along with the consideration of phylogeny, would have otherwise solved their problems. For instance (and here I at once begin to treat of certain cases of what I regard as *normal* cohesion), the andrœcium of *Cyclanthera*, one of the Cucurbitaceæ, consists of a single large organ arising as a central column in the flower; the older botanist, wholly ignorant of the proper method of procedure for solving such a structure as this, naïvely described it as an *axial* organ! But comparison with other members of the same order<sup>1</sup> is sufficient to shew that it almost certainly consists of a *fusion of several* (probably 5) *stamens* which are, of course, foliar organs. As no sign of such fusion is seen during the development of the organ, it must take place *congenitally*. What do we mean by this expression? We mean that the ancestors of the plant must have possessed five free, distinct stamens which in the course of time became fused into a single structure shewing no trace of its real composite character, so that to-day the organ arises at birth as a single, undivided structure. Yet we may imagine fusion occurring *within the parent-tissues* in this way: that at each of five centres cell-divisions took place which, before they culminated in the production of organs above the surface, spread on either side and towards the centre, so as to form a single large mass of dividing tissue which eventually became the seat of formation of the columnar andrœcium, but even this mass of tissue may have been formed simultaneously, so as to leave absolutely no trace in the ontogeny of the five original stamens. Another quite similar case is that of the ovary of the Primulaceæ, arising as a homogeneous ring-wall with no trace of distinct primordia; and yet, from the comparative method of research, we know perfectly well that it is composed of five carpels.

In most such cases, however, distinct rudiments first make their appearance, as in the gamopetalous corolla of Ericaceæ, indicating the presence of five petals; but congenital fusion of these petals early sets in, and the lower part of the corolla develops as a tube or cup; yet the polypetalous condition must be regarded as *primitive*.

It is well-known that the ovule and seed are amongst those organs where very considerable adaptations in structure have taken place in the course of time; amongst these, as especially well seen in Gymnosperms, are fusions between the envelopes, and between these and the nucellus enclosed by them. To cite an example: it

<sup>1</sup> There are other genera which exhibit a *partial fusion* of the stamens.

is my opinion that in the case of *Cycads* and *Cephalotaxus* the well-characterised and contrasted parts of the seed-envelope represent a congenital fusion between the two integuments which, in the remote ancestors of the plants, were quite free. In the same way, congenital fusion between nucellus and integuments along the greater part of the ovular axis, exists in all Gymnosperms.

In the ovule of the ancient ancestors of these plants, as seen in the case of *Stephanospermum*, the nucellus existed free and independent of the integument. Oliver regards the modern structure, *e.g.*, that of *Cycads* and *Torreya*, as having been derived from the older one by means of a "new intercalation" of tissue at the base of the ovule, which elevated the "real ovule," as he terms it, so that in the modern ovule nucellus and integument are free only at the apex of the organ. This view, while highly ingenious, is, to my mind, a mistaken and artificial one. In the first place, there is no evidence for supposing that any *elongation* of the ovule has ever taken place. The seed of *Stephanospermum* is approximately of the same length as that of most species of modern *Cycads*. Oliver admits that the "newly intercalated" tissue consists of integument and nucellus; if this be so, then he is surely illogical in the position assumed; for these two organs must, in that case, be *congenitally fused together*, since he starts out with the very proposition that the primitive condition from which the ovule is derived is that in which nucellus and integument are free; it therefore follows that these organs in the region of the "new intercalation" must also have formerly been free, for it is to my mind an absolute impossibility for a new tissue thus to suddenly drop upon the scene from nowhere, having arisen, that is to say, out of no pre-existing organ or organs. Again, if the "intercalated" region consists of a congenital fusion of nucellus and integument, as our author admits, why could not that region have been formed by simple congenital fusion of those two organs, for the greater part of their length in the ancestral ovule itself, which is the view I hold? The case before us is perfectly analogous to that of the formation of a gamopetalous corolla, which I regard as having originated from the congenital fusion of primitively free petals, as the facts of dialysis prove; it is not only the ontogenetically free tips which represent the *real* corolla, but the tubular portion as well, and there is here no "new intercalation"! In the case of *Torreya* it would indeed be "an evolutionary freak" for the chalaza to become elevated into the position to which our author assigns

it! If the chalaza be indeed situated here, what part of the ovule, I would ask, is represented by the tissue below it. This strange history is beyond my comprehension! The nature of the vascular system, I am convinced, cannot be a guide to the morphological history of the parts which it supplies, for it is a plastic tissue, being laid down just wherever it is needed. In my opinion "Archisperm" and "Hyposperm," except from a purely descriptive point of view, are myths. The *entire* ovule is as much the "real ovule" as is the entire theoretical ovule shewn in Fig 1, and the so-called "intercalated" tissue is only ontogenetically—not phylogenetically—*younger* than the upper region where the parts are free.

The phenomenon termed by Celakovsky "negative *dédoulement*" which occurs in flowers and elsewhere consists in a congenital or *ideal* fusion of two or more petals, stamens, &c., where in allied living forms or in the ancestors of the plants concerned, the two or more organs exist, separate and distinct from each other, as in the genus *Veronica* where the large posterior petal results from the phylogenetic fusion of the two posterior *lateral* petals of other members of the order.

An interesting example of *normal* fusion occurring between two organs of differing morphological value is afforded by the "winged" peduncle of the inflorescence of the Lime (*Tilia*); here the bract is congenitally conerescent with the stalk of its axillary flowering-branch. We may safely assume that this is a secondary modification, and that in the ancestors of the Lime bract and inflorescence were free and independent.

In the formation of an *inferior* ovary, as in the Apple and the Daffodil, the peduncle grows up around the superior ovary, congenitally fusing with it, and raising all the other parts of the flower into a position overtopping it. An interesting analagous illustration of the principle of congenital union occurring between two objects which were once distinct, we may obtain from the animal kingdom in the case of the Peacock; the central blue disc in the ocellus of the tail-covert which lies across the shaft of the feather, has a proximal *indentation*; this latter is an index to the probable fact that in the ancestral form there were two ocelli; one on either side of the shaft, which have become *incompletely fused* together. As a matter of fact, in the allied gallinaceous bird the Peacock-pheasant (*Polyplectron*), these two ocelli occur as a normal feature in this very position.

If we turn now to certain *abnormal* cases of this "ideal" fusion;

there are numerous instances recorded in flowers, of which I need cite but one. Velenovsky describes a flower of *Forsythia viridissima* Lindl. in which the four diagonally placed petals of the normal flower are represented by 2 large *lateral* petals which resulted from congenital fusion of each pair of normal petals, producing a character which, in the case of *Fraxinus dipetala*, belonging to the same order, is the normal one.

Very interesting are the instances of "double apples" recorded from time to time; all these cases I am rather inclined myself to regard as instances of partial reversion to the corymbose character of the fructification of the wild crab and other genera of Rosaceae, to which in fact a garden apple-tree sometimes actually reverts at its *second* flowering, where, instead of the terminal flower only, both this and the other flowers also of the corymb, produce fruit. In the cases figured by me there are obviously two flowers which have set fruit; in the first case (Fig. 17) the two



FIG. 17. Longitudinal sections of "double apples," shewing three stages in the degree of "coalescence." A Apples quite separate, and of unequal size, borne at the apex of a common pedicel; B Apples of equal development and partially united; C Apples of unequal development and much more intimately "coalescent."

pomes are perfectly free, in another case they are congenitally fused, yet only partially so, in the third case this fusion has proceeded much further, so that the ovary of the smaller pome has been partially absorbed into the tissues of the larger one. I regard the fusion as due to the fact that reversion to the primitive corymbose fructification being only partly successful, and two fruits only having been produced, these, owing to either one or both of them approximating in size and vigour to the condition of the ordinary cultivated apple, have necessarily become congenitally united owing to the lack of space for the complete individualisation of each pome. The double pome represented in Fig. 1 came from a tree which never bore any other form of fruit.

Post genital, mechanical or "real" fusion of parts is of comparative infrequent occurrence and is of little importance for my purpose; for examples I may cite the syngenesious anthers of the Compositæ, and shoots of Ivy, Elder, Beech, &c.

## II.—POSITIVE DÉDOUBLEMENT OR BRANCHING.

This phenomenon consists in a *congenital* increase or multiplication of parts or organs, and is especially well seen in many facts of floral morphology. The older writers were inclined to regard this as the main factor concerned in the evolution of the flower. But Celakovsky points out that it really only accounts for a comparatively small number of phenomena, the chief tendency being towards *reduction* in the number of parts. It is, perhaps, seen best in the ordinary "doubling" of garden flowers; as in the Rose and Daffodil. (I may here consider both normal and abnormal cases together.) Positive *dédoublément* is almost always *abnormal*. Leaving out of consideration the acyclic types of the Ranales, I may, perhaps, regard those cases, as in *Lythrum* and *Paris*, where the members of each perianth-whorl are greater in number than the 5 and the 3 which are the respective typical numbers for Dicotyledons and Monocotyledons, as examples of *normal* positive doubling. A similar case which at once suggests itself is that of the formation of the *pappus* in Compositæ (consisting as it does of great numbers of hair-like segments) from the primitive five-leaved calyx of the ancestors of that order. In abnormal flowers of various Monocotyledons, such as *Crocus*, *Iris*, *Tulip*, *Snowdrop*, &c., it commonly occurs that, either in alternate whorls or throughout the flower, four members are produced in the whorl instead of three; and this as the observation of intermediate

forms shews, results from the complete branching into two, of one of the members of the whorl. In the Wallflower it is not infrequent for the ovary to become quadri-instead of bi-carpellary, which is probably a reversion to the primitive condition in which the carpels were equal in number to the petals, sepals and inner stamens. Many Dicotyledonous flowers whose parts are in fours, are apt to become pentamerous, and in many pentamerous flowers I occasionally see an extra member or two added to each whorl.

In all flowers we may regard negative *dédoublément* or reduction of parts as a *progressive*, and positive doubling or an increase of parts as a *retrogressive* or *reversional* phenomenon.

To cite one case in which positive *dédoublément* takes place in foliage leaves, *Lonicera Periclymenum* normally produces two leaves in each whorl; occasionally, however, shoots occur bearing whorls of four leaves; the normal habit is probably the primitive one; similar cases occur in many other plants.

Twins, whether vegetable or animal, doubtless belong to this category. The fertilized egg-cell, instead of initiating its development into an embryo by means of a transverse division of its contents, which is the normal case, might divide by a *vertical* wall. Each sister-cell thus formed might then develop into an independent embryo. This would be congenital positive *dédoublément*, for the production of a single embryo is the normal and primitive character. In *Loranthus sphaerocarpus*, described by Treub, the fertilized ovum, divides by a vertical wall but the sister-cells develop together into a single pro-embryo, consisting of a double row of cells. Twin-flowers, if we regard the individual flowers themselves and not the shoot as a whole which bears them, afford another case in point.

### III.—NEUTRAL CONDITION.

All the phenomena cited under this head may be described as cases of *postgenital* positive doubling; this refers, of course, merely to their ontogenetic history. From the point of view of their phylogeny, however, much more is involved, and hence I place them under a distinct heading for separate discussion. The character, described in its simplest terms, which is common to all these cases, is this: that the organ or tissue at its first origin an integrity, becomes later branched or sub-divided *in its upper or younger region*. But I will postpone the consideration of the

meaning of this interesting phenomenon until after some instances of it have been cited.

I gathered a peduncle of *Plantago lanceolata* which bore twin flower-spikes at the summit; the peduncle itself was furrowed throughout its length and nearly twice the thickness of normal peduncles.

I found much thickened and furrowed peduncles of *Eryngium amethystinum* bearing inflorescences which were in some cases two-lobed others four-lobed at the apex.

Partial fusions (using this term in a purely descriptive sense) between the pedicels of the secondary umbels are very common in *Ceanothe crocata*; at the base of the free portion it is not uncommon for bracts to occur, and this might suggest to the worshipper of developmental data that the apparent fusion was due to mere intercalary growth of the main axis below the umbel and formed no real part of the secondary umbellular axis; but I cannot myself accept such a view. These "fusions" in *Ceanothe* appear to be one result of an upset of the equilibrium of the inflorescence; another is the occurrence of single, stalked flowers in the position of the umbellules, which is probably a reversion to the primitive character of simple umbels. A thickened, furrowed peduncle of a Dandelion bore twin capitula at the apex, which were perfectly distinct.

In *Primula Thomassonii* the thickened peduncle with its median furrow had forked a short distance below the insertion of the flowers, hence two umbels were present, one at the summit of each fork, the stalk of each of these being thickened and furrowed in its turn.

In *Campanula media*, of the four flowers born at the apex of an abnormal stem, two were quite free (though "fused" by their pedicels), while the other two were congenitally "united" to form a single flower; in another instance all four flowers were "coalescent" to constitute a single, horizontally-elongated flower containing about twenty carpels; in some cases the union between any two ovaries is not so complete as in others, a fairly thick wall separating the two, the styles being distinct; in others more intimate union occurs and the styles are united to form a thick, broad column. (Fig. 18.)

There was a remarkable case of *Narcissus poeticus* in which seven flowers were "united" in this way in one plane. The flower at one end of the row was almost free, this, its neighbour, and the

flower at the other end of the row contained tri-locular, while the others, which are much laterally compressed, contained two-locular ovaries; there was also a slight reduction in the number of perianth-lobes, stamens and styles, many of the latter being fused.

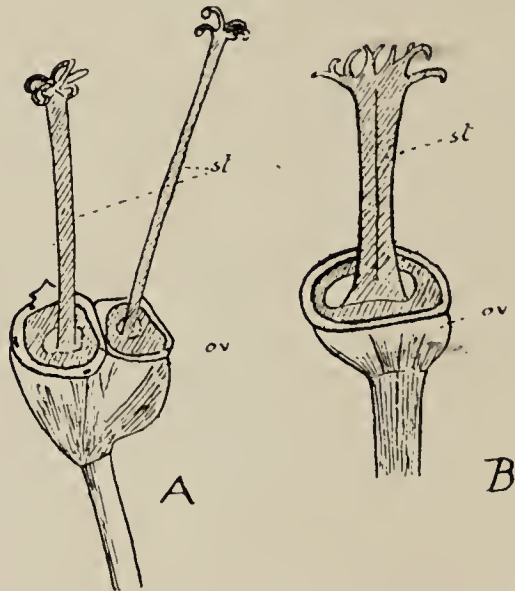


FIG. 18. Pistils of *Campanula media* shewing two stages of "concrecence." In A ovaries united, but styles free.

A Crocus, which I observed last spring, produced a flower of exceptional size and interest; it was the result of "fusion"<sup>1</sup> of two normal flowers; but instead of twelve, there were only ten perianth-leaves present, this being due to the fact that two of the members of the *outer* whorl of each flower had fused respectively with a member of the *inner* whorl of the other flower; hence these two leaves (the products of fusion) are situated obliquely, *i.e.* partly in the inner, partly in the outer whorl. There are six stamens alternating as best they can with the perianth leaves. There are two distinct styles and sets of stigma-lobes. The ovary is double the ordinary size, irregular and asymmetrical in contour, and composed of six carpels; it shows no obvious signs of being a result of fusion except in the increased number of its parts.<sup>2</sup> (Fig. 19.)

Allied to this case are the striking phenomena presented by many peloric terminal flowers, as in *Linaria vulgaris*, *Streptocarpus*, *Digitalis purpurea*; an instance of the latter came

<sup>1</sup> I beg the reader not to interpret this term in the *kinetic*, but in the purely descriptive and metaphorical sense, wherever in the description of the facts pure and simple I use such terms as "fusion," "fasciation," "cohesion," "coalescence," "union," they must be understood in this way.

<sup>2</sup> Dr. Church points out to me that in these cases of flowers we obtain the *pure* type of fasciation, devoid of spiral torsion, owing to the absence of secondary internodal elongation.

under my notice last summer, and as a result of its examination I draw the following conclusion as to the origin of many of such peloric blooms. Owing to precocious development (the outcome probably of luxuriant nutrition) of two or more uppermost lateral flowers of the raceme, the vegetative apex of the latter possesses no chance of further growth, while the said flowers not only entirely use up the apex, but owing to their close mutual proximity, inevitably become congenitally united<sup>1</sup> to form a quasi-single and perfectly terminal flower, differing from the normal flowers in its much larger size and in possessing radial, instead of dorsiventral, symmetry.

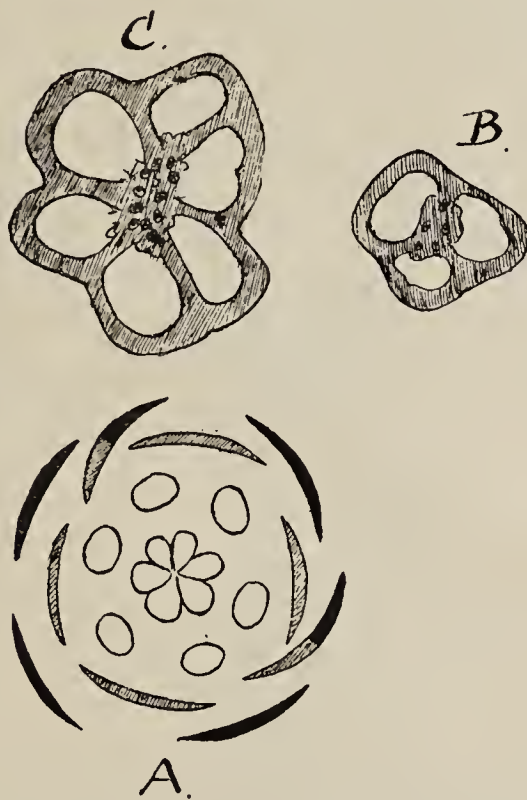


FIG. 19. *A* Floral diagram of "fasciated" flower of *Crocus*; *B* transverse section of ovary of normal flower; *C* ditto of "fasciated flower."

I saw last autumn on a shoot of *Marrubium vulgare* a cucullate foliage-leaf which was perfectly *terminal* to the shoot and of radial symmetry; this is an instance of a leaf, normally dorsiventral, which is becoming peloric.

All such cases as these represent a kind of "fasciation;"<sup>2</sup> for here no subsequent branching succeeds the primary fusion. Yet they cannot be regarded as equivalent to the cases of congenital negative *dédoublement*, for in this latter the ultimate product of fusion, except where the latter has been of comparatively recent occurrence,

<sup>1</sup> The term is here employed in its actual kinetic sense.

<sup>2</sup> See *infra*.

as in the case of the posterior petal of *Veronica* (the posterior *sepal* being here frequently present), is no larger in size than either of the original unfused organs, whilst the peloric flower is very much larger.

Celakovsky has admirably described the variations occurring in *Lonicera Periclymenum* as to the number of members present in each leaf-whorl of the stem. He regards the 2 membered whorl as primitive, the 3- & 4-membered as derivative therefrom. But numerous *intermediate* or *transitional* whorls occur in which, instead of two or four distinct and separate normal leaves respectively being found, one or more members of the whorl are more or less deeply or regularly forked or notched. (Fig. 20.) Similar divided

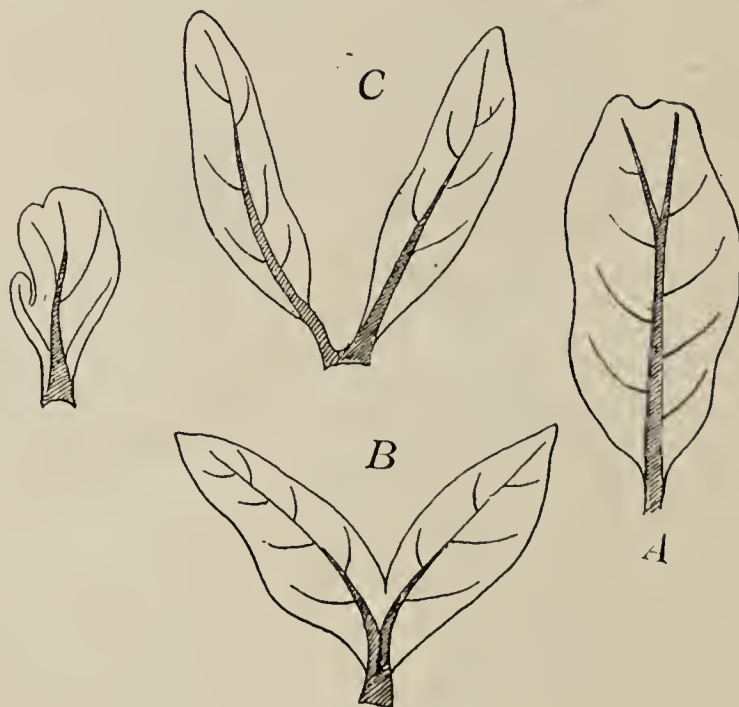


FIG. 20. Double foliage leaves of *Lonicera Periclymenum*; A slightly notched apex; B deeply forked; C development of two leaves instead of one, but both still attached to same base.

leaves occur in a great number of plants, as in *Euonymus japonicus*, *Scolopendrium vulgare*, &c., &c. I myself noticed in *Oxalis asinina* that some of the leaves were undivided, others had a very minute notch at the apex, others, again, were deeply forked; these last had thicker petioles than the undivided ones. The same phenomenon may be frequently seen in the cotyledons of the *Syeamore*.

I will now pass on to consider those weird, strange phenomena to which the term (an inappropriate one, as I shall shew) "*fasciation*" is usually applied. I hold that they are essentially identical in nature with those just enumerated.

They are well known and exceedingly common, and concern *axial* organs. The stem presents, instead of the usual cylindrical, a more or less band-or strap-shaped structure; this may either produce normal branches in a lateral position or may be entirely devoid of such. This strap-shaped shoot always branches or subdivides at the apex more or less deeply into a number (two or more), shoots of *equal value*, although not always of equal length; the fact that the internodes of some of the shoots are shorter than those of others and do not grow so rapidly in length, which is almost always the case, gives rise to the characteristic torsion of nearly all "fasciated" stems.

I observed a case, *Ranunculus acer*, in which the main axis of the inflorescence was thus "fasciated;" at the apex it bore a number of separate yet closely-approximated flowers, arranged in one plane, *i.e.* along a line. Laterally this axis bore a number of normally-constructed branches, and it was traversed longitudinally by numerous grooves and furrows. (Fig. 21.)



FIG. 21. "Fasciated" inflorescence of *Ranunculus acer* with *distinct* gynœcial cones at summit, and copious formation of normal branches on the main axis.

A similar "banded" shoot of *Campanula media* bore at its apex the flowers already described above. (Fig. 22.)

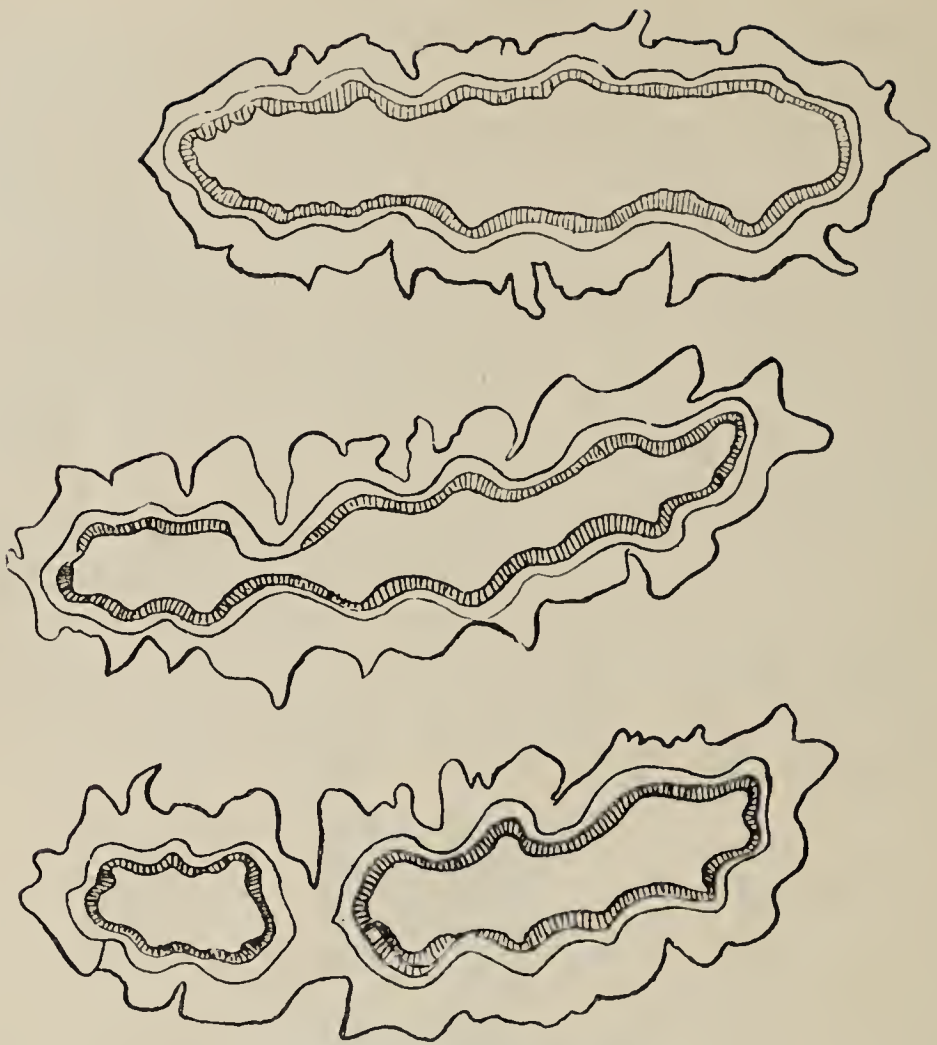


FIG. 22. Transverse sections of "fasciated" shoot of *Campanula media*, shewing various stages of "fusion" at different levels.

This "fasciation" is an extremely common phenomenon in *Cotoneaster microphylla*; the shoot in this case is in its lower part perfectly cylindrical and, perhaps, somewhat greater in diameter than the normal ones around it, (yet it is doubtful whether this is always the case); above, however, it broadens out and becomes strap-shaped, a number of distinct buds appearing at the tip. In a Syeamore-twigg there was a "fasciation" of four shoots of which one was immensely longer than the remaining three which were approximately equal in length.

*Rheum Moorcroftianum* sends up a number of "fasciated" flowering-shoots every year at Kew, so that it is almost a normal character for the plants under cultivation there; these shoots branch unequally at the apex and, when stripped of the flowers, somewhat resemble an irregularly formed fowl's foot. (Fig. 23.)

Perhaps the best known of all cases of "fasciation," and the more interesting inasmuch as it has become a fixed and inherited character under cultivation, is that of the Cockscomb: *Celosia*

*argentea* var. *cristata*; here the axis of the inflorescence assumes an expanded, fan-shaped contour, the flowers being aggregated in dense masses along the top of the arched and sinuous ridge or edge of the fan. Knight states that he maintained this "sport" in



FIG. 23. "Fasciated" fruiting-shoot of *Rheum Moorcroftianum*, entirely stripped of the fruits.

*statu quo* by growing the plants in pots provided with a constant supply of rich manure.

Alex. Braun describes fan-shaped, many times dichotomising, aerial fasciated roots in a Cactus: *Epiphyllum Hookeri*. In the "Gardeners' Chronicle" of the 30th May, 1874, an illustrated account was given of fasciated aerial roots in the Orchid *Aërides*

*crispum* (Fig. 24). I have not observed such abnormal roots myself. But I believe that in the aërial apogeotropic, dichotomising, respiratory roots of Cycads, with their curious coralloid appearance, we behold an exact instance of "fasciation" occurring as a *normal* feature of the plant; it is only necessary to compare such a root with that of the Orchid above-cited to see that this is true, the only difference between the two being that the Orchid-root grows downwards and the Cycad-root upwards!



FIG. 24. "Fasciated" aërial root of *Aërides crispum*.

One of the most remarkable examples of *normal* fasciation is to be seen in the development of the staminal "groups" in the flower of such orders as Hypericaceæ, Tiliaceæ, and Malvaceæ. A single primordium or rudiment arises in the first place, representing as Celakovsky points out, the *later* tendency towards fusion and integrity; but very soon this rudiment begins to branch, giving rise eventually to the group of stamens characteristic of the mature flower; this latter process represents the *older* tendency towards separation and plurality of parts.

As I have no desire to descend to the level of the encyclopædist, nor to unduly extend this article, I will now proceed to discuss the meaning of the phenomena which I have grouped under this third heading. For I hold that they are each and all due to one and the same cause and governed by one great underlying principle.

This latter may be expressed thus: that the structure before us represents the result, final product, or compromise of the strife waged between two opposing forces or tendencies, viz.; that which on the one hand, makes for fusion or integrity, called "negative *dédoublement*," which is the younger, and that which, on the other hand, makes for separation or

plurality of parts, or "positive *dédoublment*," which is the older of the two. None of the structures coming under this head can be the result of either of those two tendencies acting alone, for they are clearly *intermediate* in character between the two sets of structures, which I have described under I. and II. If the principle be clearly understood it is seen to shed a bright light upon these otherwise weird, inexplicable phenomena of "fasciation" or "banding"; it may be termed (1) the *ideal* or *morphological* explanation thereof, and is, to my mind, by far the most important of the three sets of causes to be mentioned. The structure at birth exhibits the influence of tendency I., viz.: that of "negative *dédoublment*"; later in life the influence of tendency II., viz.: that of "positive *dédoublment*," appears upon the scene; hence giving to the structure two distinctive characters whereby it exhibits in its lower and older region *fusion*, in its upper and younger region *branching* or separation. Hence in the development of an ordinary "fasciated" shoot we have precisely the same phenomenon presented to us as in that of a staminal group in a flower, *e.g.* of *Hypericum*!

Let us now consider (2) the *mechanical* or *real* cause of the phenomenon. It was my own opinion that the fasciated organ represents in itself from birth onwards the *equivalent* of two or more organs of which at the earliest stage there was absolutely no sign, and that, owing to the inherent tendency for these *latent* organs (if I may so term them) to assert themselves, the subsequent branching *gradually* (as shewn in the case of shoots by the appearance of furrows and ridges and a strap-shaped expansion of the organ) ensued. I am indebted to Dr. A. H. Church, of Oxford, for the more concrete and definite concept of "growth-centres." He says that in the normal shoot "growth is distributed at the apex of a shoot in such a manner that its *transverse-component* may be expressed by a plane circular construction around a central point (the *growth-centre*)," and "that the circular section of the vast majority of plant-axes is evidently the outcome of such a regular and symmetrical distribution from the 'growing-point'." The three exceptional cases he cites are (1) the *eladode*, (2) the *fasciated stem*, and (3) the *dorsiventral shoot*. I am here only concerned with (2), which Church explains as follows: "In the 'fasciated' system, the centric distribution around a point (the single growth-centre) is changed for an attempt at similar distribution around a number of such centres (cf. monstrous flowers of the Buttercup with two or three gynœcial cones, and double Daffodils) or around

a longer or shorter series of such points constituting a line, with the result that great disturbances ensue, owing to the impossibility of normal uniform growth expansion in such a system." Again he says: "A growing system might evidently have one such centre or more than one. One is the simplest case, and as a matter of observation is the general rule; on the other hand, the case of multiple growth-centres is included under the botanical title of *fasciation phenomena*."

There is a phenomenon known to students of psychology as "multiple personality"<sup>1</sup> in which, the normal and single controlling and directing conscious-centre in the brain becoming deranged, and the organism as a whole thus thrown, as it were, off its balance, a number of other subsidiary centres of consciousness assert themselves alternately, usurping control of the body; this gives rise to a species of madness. This appears to me an illustrative analogy for the case of the "fasciated" stem under discussion.<sup>2</sup>

In many cases there appears to be an immense number, even an infinity, of growth-centres involved or latent within the organ, which continuously and successively assert themselves as the organ increases in age, so that, as in the case of a fasciated Wallflower-shoot lying before me, the ultimate branches produced are very numerous and finely subdivided, eventually becoming resolved into foliage leaves pure and simple!<sup>3</sup>

Further, owing to the fact that in almost all "fasciations" some "growth-centres" are weaker than others, giving rise to branches which, while equal in grade or value to the others, are smaller in diameter, and less rapidly elongating, the curious twisting and torsion of the whole shoot is produced which is the almost invariable concomitant of a "fasciation."

But if now we suppose the normal single "growth centre" to be replaced by (i.e. to become segmented into) *two* only, and these two to be equally balanced as regards strength and development, the branching to which they give rise would be a case of pure *dichotomy*. This is the simplest form of "fasciation." Examples of it are to be seen in the leaves of *Lonicera*, &c., the *Crocus*-flower, the double spike of *Plantago*, the twin-headed *Dandelion*, which are described above. Church describes most interesting cases in the Sunflower (*Helianthus annuus*), of "strict dichotomy, which in

<sup>1</sup> I regard these examples, taken from other departments of Nature, as valuable aids in helping us to understand the origin of such structures as that under consideration.

<sup>2</sup> I am indebted to Dr. Church for reminding me of the analogy existing between these two sets of phenomena.

<sup>3</sup> Cf. the "phyton"-theory.

garden specimens may affect the whole of the lateral branch-system of the plant. Similar phenomena, but in a less perfect manner, may be noticed in such allied forms as *H. rigidus* and *H. strumosus*, in their garden varieties. In such cases the dichotomy may occur (I.) in the foliage region, giving long-stalked pairs of capitula; (II.) close behind the involucre region, giving twin-heads; (III.) within the involucre, resulting in the phenomenon of 'two-eyed' capitula, with a more or less perfect ray series between the two disks." I have myself observed this dichotomy of the third type in *Helianthus*.

When the equilibrium of the organism is upset from whatever cause there is often a natural tendency for it to *revert* in some of its characters to an ancestral condition. I myself am inclined to regard these cases of pleotomy and dichotomy, giving rise to the "fasciated" condition, as reversions to an ancient type of branching, a type which probably represents the line of least resistance for an organism when impelled, under powerful stimulus, to reproduce itself by the most rapid method possible. Just as in the cases of multiple personality, the "obsessing memories," latent in the sub-conscious mind under ordinary conditions, may, under the influence of certain stimuli, cause the organism as a whole to live in and focus its attention upon some past and long-forgotten condition; in the same way our higher flowering-plants very often lose their balance and live in the long-past branching conditions of Lycopods, Ferns and Algæ. In these latter cases, the branching is probably always primarily *in one plane*;<sup>1</sup> and is precisely the same phenomenon as the linear series of buds or branches at the apex of all fasciated shoots; and if we can imagine the successive dichotomies in their shoots to take place with extreme irregularity, inequality and lack of symmetry, we should probably obtain an ordinary "fasciation" such as occurs so often as an abnormality in the shoots of our Angiosperms. The leaves of the Ginkgoaceae are interesting for comparison in this connection. In *Ginkgo biloba* the dichotomy of the leaf has proceeded but a short way in the ordinary form; but other varieties reveal a much deeper primary, and the occurrence of secondary dichotomies. In the fossil form *Baiera gracilis*, the entire leaf is deeply divided up into narrow linear segments, like the leaf in the ferns *Actinopteris radiata*, and *Schizæa dichotoma*. The whole of such cases whether they occur in shoots or leaves, represent the phenomenon of *normal, stereotyped and symmetrical* "fasciation."

As to the third or physiological sub-division of the etiology

<sup>1</sup> Cf. Dictyotaceae.

of "fasciation": it is probably a pathological condition. In the majority of cases it is doubtless induced by superabundant nutrition which produces a subtle diseased condition, thus giving rise to a hypertrophied growth which destroys the balance of the organism. The crested form of *Celosia argentea* cannot, apparently, be maintained without abundantly manuring the potted plant.

Yet who shall say that we can trace the real innate physiological agency concerned in the production of this "monstrosity"? It seems fairly clear that the *environmental* factor is not the only one involved; for "fasciated" axes and leaves appear as isolated cases amongst others which are perfectly normal and where both are growing *apparently* under precisely similar conditions. It would appear, therefore, that the *individual idiosyncrasy* of the organ or plant itself is another, and very important, factor, which must not be left out of consideration.

The main object of this article has been to direct attention to the *morphogenetic* principles, which I believe underly the phenomenon of "fasciation." Along these lines I hold that it is explained as being the resultant of the more less equal conflict waged between two opposed tendencies or forces, viz.: that which, on the one hand, induces *integrity*, and that which, on the other induces *plurality* of parts.

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## CURRENT INVESTIGATIONS IN ECONOMIC BOTANY.

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A COURSE OF LECTURES DELIVERED AT THE UNIVERSITY OF LONDON  
DURING THE MICHAELMAS TERM, 1904,

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## I.—INTRODUCTORY.

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**I**N the course of a few lectures it is naturally impossible to deal with all, or even with the majority of most important of the problems engaging the attention of workers in the field of economic botany. Accordingly, selection has been made of those with which my duties in various parts of the world have brought me into contact, and are of interest as examples of current methods of economic botanical research. For these reasons attention is principally devoted in these lectures to four plants, the sugar-cane, the sugar-beet, cotton and maize.

In this, the first lecture of a course on what is practically a new subject in the botanical curriculum of London University, it is desirable to consider what we understand by the term "economic botany." Economic botany comprises the study of the plants and plant products, which directly or indirectly are of service to man, including their source, distribution, improvement, collection and preparation, their properties and uses.

Economic botany is one of the oldest, if not the oldest, study of mankind. Go where we will in the world, even amongst the lowest races of mankind, we find considerable knowledge of the wild plants of the country, and their properties and uses. On plants, primitive, in common with highly-civilized races, are ultimately dependent, to a greater or less extent, for their food, medicine and clothing. As an advance on the mere possession of knowledge of the properties and uses of indigenous plants, one often finds amongst savage races, successful cultivation of certain plants. This, in its turn, leads to practical efforts to improve plants by means of vegetative or seminal selection, which in the remote past have resulted in far-reaching results, dealt with in detail later. It should not be assumed that in the successful practice of the past the reason for each step was necessarily understood. The knowledge accumulated was purely empirical, yet it was attained by exactly the same method as much knowledge

is attained to-day, namely, by experiment, observation and inference. That the so-called savage does deliberately apply this method, was brought to my notice in a striking manner, only a few months ago, in an uncivilized portion of West Africa, where I found that localities for native "farms" were selected by the experimental planting of a few yams or a small patch of Indian corn, and I frequently saw in the "bush" little cultivated patches, often only a few yards square, which were evidently native experiment plots.

The study of systematic botany can be traced back to the search after plants for their economic uses. Sachs points out in the opening lines of his *History of Botany*, how "the authors of the oldest herbals of the 16th century regarded plants mainly as the vehicles of medicinal virtues: to them plants were the ingredients of compound medicines, and were therefore by preference named *simplicia*." He describes how the labours of the first German composers of herbals who went straight to nature, described the wild plants growing around them, and had figures of them carefully executed in wood resulted in the first beginning of a really scientific examination of plants. "In the effort to promote the knowledge of plants for practical purposes the impression forced itself on the mind of the observer that there are various natural groups of plants which have a distinct resemblance to one another, in form and other general characteristics."

Practice was in advance of exact knowledge in the appreciation of the beneficial action of leguminous plants. Again, the vexed question of the use of shade trees in tropical agriculture has had considerable light thrown upon it by the recent generalization that the time-honoured shade trees, with few exceptions, are members of the *Leguminosae*. In some cases the shade was no doubt directly beneficial, in other cases harmful, but in the latter the net result might still be beneficial owing to the counterbalancing action of the trees in increasing the fertility of the soil. The important results obtained in the remote past, have already been alluded to. For a comprehensive account, the classical work of De Candolle *On the Origin of Cultivated Plants* should be consulted. In the following table an attempt has been made to indicate, at a glance, the duration of time through which some of the more economic plants have been cultivated:—

Cultivated for more than 2000 years.

CEREALS.

Wheat.	Barley.
Oats.	Millet.
Sorghum.	Rice. Maize.

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Cultivated for more than 2000 years.

Cultivated for less than 2000 years.

STARCH PLANTS.

Potato.  
 Sweet Potato (*Ipomœa Batatas*)  
 Yams (*Dioscorea* spp.).  
 Cassava (*Manihot utilissima*).  
*Colocasia antiquorum*.  
 Bread Fruit (*Artocarpus (incisa)*).

LEGUMES.

Garden Pea ( <i>Pisum sativum</i> ).	Field Pea ( <i>Pisum arvense</i> ).
Bean.                      Lentil.	Pigeon Pea ( <i>Cajanus indicus</i> ).
Ground Nut ( <i>Arachis hypogea</i> ).	

FRUITS.

Banana.	Date.	Orange.	Raspberry.
Fig.	Vine.	Strawberry.	Melon.
Apple.	Plum.	Gooseberry.	Currants.

SUGAR PLANTS.

Sugar cane.	Sugar-beet.
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DYE PLANTS.

Indigo.	Madder.
Henna ( <i>Lawsonia alba</i> )	
Saffron.	

MEDICINAL PLANTS, ETC.

Hemp.	Tobacco.	Coffee.
Coca.	Tea.	Cinchona.

RUBBER PLANTS, ETC.

Ceara Rubber (*Manihot Glaziovii*).  
 Para Rubber (*Hevea braziliensis*).  
 Central American Rubber (*Castilloa elastica*).  
 Lagos Silk Rubber (*Funtumia elastica*).  
 Asam Rubber (*Ficus elastica*),  
 Gutta Pereha Tree (*Dichopsis Gutta*).

FODDER PLANTS.

The Hay Grasses of temperate climates and species of Trifolium and Medicago  
 Guinea Grass (*Panicum maximum*).  
 Sour Grass, West Indies, (*Andropogon pertusus*), etc.

FIBRE PLANTS.

Flax ( <i>Linum usitatissimum</i> ).	Sisal Hemp ( <i>Agave rigida</i> var. <i>sisalana</i> ).
Hemp ( <i>Cannabis sativa</i> ).	New Zealand Hemp
Cotton ( <i>Gossypium</i> spp.).	( <i>Phormium Tenax</i> ).

This table might be considerably extended, but as it stands it suffices to demonstrate that all the principal cultivated food plants

—the cereals, farinaceous plants, legumes and fruits—and also several of the more important plants yielding fibres, dyes, and narcotics are plants of ancient cultivation. Amongst the plants of recent cultivation only, we find some pleasant fruits of minor dietetic value, some medicinal plants, but practically all the fodder and rubber-yielding plants, and others whose products have come into demand owing to changes in the conditions of life of the human races, and progress in the arts and sciences.

As De Candolle well says, “Men have not discovered and cultivated within the last two thousand years a single species which can rival maize, rice, the sweet potato, the potato, the bread fruit, the date, cereals, millets, sorghum, the banana, soy. These date from three, four, or five thousand years, perhaps even in some cases six thousand years. The species first cultivated during the Græco-Roman civilization and later nearly all answer to these varied or more refined needs.....We must come to the middle of the present [Nineteenth] Century to find new cultivations of any value from the utilitarian point of view, such as *Eucalyptus globulus* of Australia and the *Cinchonas* of South America.” Reviewing the subject in the Twentieth Century, we can add the rubber plants as noteworthy examples of new, cultivated plants. It would appear that at a very early stage in the history of agriculture in different parts of the world, the plants of the greatest value to man (for instance for food), were recognised and cultivated, and no plants of equal primary value having since been found, the early selected plants have been improved by cultivation and distributed from land to land to the exclusion of others. Within recent years a similar sequence of events has resulted in certain plants, for instance a few species of *Cinchona* and certain rubber-yielding plants being cultivated to the exclusion of others of less importance. Owing to reckless extermination by man one such plant, at any rate, *Dichopsis Gutta*, has already passed practically into the group of economic plants only known in cultivation.

The history of other economic plants may have been similar, and it is possible that plants now only known in cultivation were once wild species, and have been exterminated owing to various causes. On the other hand some, no doubt, have been so changed by selection through long ages that they have attained separate specific rank, and are not known out of cultivation, whilst their ancestral types may still survive and be regarded closely related wild species.

(*To be continued.*)

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ON THE SIGNIFICANCE OF SPINES IN *DISCARIA*  
*TOUMATOU*, RAOUL. (RHAMNACEAE).

By L. COCKAYNE, PH.D.

(WITH PLATE II.).

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**D***ISCARIA TOUMATOU*, the 'Wild Irishman' of the Colonists, is a common New Zealand xerophytic shrub, or occasionally a small tree, chiefly remarkable for being abundantly furnished with rather long and very pungent spines, which are in fact shoots of limited growth capable of assimilating carbon dioxide. The characteristic stations of this plant are:—stable sand-dunes; stony plains, riverbeds and terraces; dry, frequently clayey hill-sides, and slopes of stony debris, or even rock-faces. In some places, the plants are isolated; in others, they form dense thickets, unpleasant to penetrate. The species under consideration, although closely allied to the Australian *Discaria australis*, Hook.<sup>1</sup> is endemic in the New Zealand biological region, being found in both the South and North Islands, but not extending northwards in the latter beyond about 37° north lat. A few plants are to be met with in Chatham Island, but it has not been recorded from the other outlying islands or from Stewart Island.

In stature, *Discaria Toumatou* varies much according to climate, being occasionally a small tree<sup>2</sup> reaching a maximum height of 6m. or so on river-flats in certain parts of the wet mountainous region of the South Island. More commonly it is a shrub, at times low growing (see Fig. 2, Plate II.) or even prostrate in the dryer districts or in extreme xerophytic stations. The exterior branches are very

<sup>1</sup> By J. D. Hooker in the *Flora Novae-Zelandiae* the New Zealand plant was named *D. australis* var. *apetala*.

<sup>2</sup> Kirk states it was formerly used for building purposes where large timbers could not be obtained. *Forest Flora of New Zealand*, 1889, p. 283.

numerous and form a rather dense, springy, interlacing mass. The terete spines are arranged decussately at distances of about 2cm. and measure 2cm. to 3cm. in length and 1mm. to 1.5mm. in diameter. Except at the actual pungent apices, they are bright green when young, as are also the flexible axes of the ultimate shoots, but finally they dry up, becoming brown and very hard, thus furnishing a most formidable protection against intruders. The small leaves,  $\pm 1.1$  cm  $\times$   $\pm 5$ cm. from the axils of which the spines are given off, are not very numerous at any time, and in the winter are quite wanting. In the spring the leaves are at a maximum<sup>1</sup> and occur for the most part on much reduced flowering shoots, given off just below the spines. Here too, ordinary long shoots arise; at first, owing to their spines not being nearly fully developed, they much resemble juvenile shoots, and these add to the leaf-area. But it is only during the above season that the leaves play any part worth considering in photosynthesis; at other times, it is only the spines and shoot-axes that are of moment in this regard.

The early seedling form is quite without spines, being an erect leafy plant. After attaining a height of several centimetres, varying probably considerably according to environment, spines commence to be developed from the axils of the leaves as in the adult, and the plant thenceforth becomes by degrees comparatively leafless and very spinous. The juvenile leaves are very similar to those of the adult, but are thinner and the earliest leaves are toothed.<sup>2</sup>

Two such seedlings artificially raised from seed in a greenhouse, after developing one or two spines, were placed by me more than three years ago in a glass case, so constructed as to keep the inside atmosphere constantly saturated with moisture, in order to see if the plants would continue to produce spines; *i.e.* if this artificial environment would inhibit the formation of spines. The conditions provided would not only expose the plants to moist air, but the light would be considerably more feeble than that of the normal stations of the *Discaria*. Such conditions indeed would be those of a rain-forest interior rather than of a plain or hillside in the open, however wet the climate.

After the plants had been in the moist chamber for one year, I took the photograph here reproduced, (Plate II., Fig. 1) fixing for

<sup>1</sup> The figure in Kirk's Forest Flora, loc. cit. shows this state of the plant.

<sup>2</sup> L. Cockayne. An inquiry into the Seedling Forms of New Zealand Phanerogams and their Development. Trans. N.Z. Inst., Vol. XXXII., 1900, pp. 92-94.

comparison in the soil of the pot a spiny adult shoot taken from a plant on a sand-hill near by. As no changes of any moment have taken place in the plants since the photograph was taken beyond increase in size and number of shoots, it suffices to show clearly the striking difference that exists in appearance between juveniles and adults, so that no detailed description of the two forms is necessary.<sup>1</sup> Here it need only be pointed out that the moist-air leaves are smaller and considerably thinner than those of the adult, and that, like those of the normal plant, they were cast off each year in the autumn. The twigs have a drooping habit, but sometimes arch upwards at their extremities, a light-reaction due to unequal illumination, as is also the more or less distichous arrangement of the leaves.

After being placed in the moist chamber, the plants developed no more spines and are now seedling plants in all respects except for the few spines, which were developed prior to the culture in moist air. Moreover it seems evident that such plants would remain in the seedling form so long as they were kept in an atmosphere constantly moist and exposed to a feeble light. Even an adult shoot on a full grown plant in the open and freely producing spines, may have any further production of such suppressed at once, if the shoot should continue its growth under slightly more hygrophytic conditions. Thus quite recently, I observed on the clay hills near Wellington, a shoot creeping near the ground whose apical portion was covered by grass. This shoot where fully exposed to the light was spinous as usual, but where shaded and in a slightly moister atmosphere was quite without spines.

From the above it follows that the production of spines in *Discaria Toumatou* can be controlled at will by specifically changing its environment—a plant exposed to a dry atmosphere and normal light producing spines, whilst one exposed to a moist atmosphere and a feeble light produces no spines, but in their place leafy shoots of unlimited growth.

That spines on xerophytic plants are an adaptation against the attacks of grazing animals is a matter of such general belief as to be admitted into certain botanical text books as a proved fact.<sup>2</sup>

<sup>1</sup> The result of this experiment is briefly mentioned in a paper read by me at the Dunedin meeting of Austral. Assoc. for Adv. of Sc. and published in Journ. Agric. and Past. Assoc. Canty., Jan. 1904.

<sup>2</sup> e.g. Strasburger's Text Book of Botany, 1903., p. 27. (Eng. Trans).

Also, so high an authority as Goebel does not consider Lothelier's<sup>1</sup> experiments with regard to the suppression of thorns and prickles by moist air culture as conclusive, since he writes<sup>2</sup> :—" I do not think that up till now any more has been proved than that in moist air the formation of prickles and thorns is retarded, there is no proof that it can be suppressed." I do not know, since botanical literature is not abundant in this distant land, whether fresh facts throwing light on this subject have been published since Goebel wrote the above. It however seems to me, that my experiment detailed above is a fairly crucial case, and that in *Discaria Toumatou*, at any rate, the spines are a direct response<sup>3</sup> to conditions of dryness, and function as a special " contrivance " for checking transpiration. If so, then they have nothing to do primarily with attacks of grazing animals, especially when it is borne in mind that New Zealand never contained such, excepting the various species of *Moa*. With regard to the effect of these giant birds on New Zealand Plants, it may be pointed out that, as they probably fed upon certain shrubs, protective adaptations might be expected in such. On this head, some observations of G. M. Thomson are of interest. In a paper dealing with the origin of the New Zealand flora,<sup>4</sup> he pointed out that plants with spines or prickles are extremely rare in New Zealand, while such, when they occur, are not usually endemic but rather species identical with or closely allied to those of lands where grazing animals are frequent. Certain species of *Aciphylla*, a palaeoceanic genus, form a striking exception to the above, as Thomson also remarks. Wallace is of opinion<sup>5</sup> that these " may have gained their spines to preserve them from being trodden down or eaten by the Moas." But in this case, there is distinct evidence to the contrary, for, as I specially noted when studying the plant-formations of the Waimakariri tableland, that most bayonet-like of plants, *Aciphylla Colensoi*, had its inflor-

<sup>1</sup> Recherches sur les plantes à piquants. Rev. gen. de bot. T.V., 1893.

<sup>2</sup> Organography. (Eng. Trans.) Pt. I., 1900., pp. 263, 264.

<sup>3</sup> I do not mean by this that dry air is the sole cause of spines being developed, but that it acts as a stimulus in calling forth a certain innate tendency in the plant, which at the same time has an equally great tendency to produce leafy shoots, and will do so on being subjected to the appropriate stimulus. How powerful this latter tendency is, is shown by the fact that the *Discaria* in spring frequently produces true reversion-shoots.

<sup>4</sup> Trans. N.Z. Inst. Vol. XIV, 1882, pp. 496-7.

<sup>5</sup> " Darwinism." p. 433.

escence frequently eaten<sup>1</sup> by sheep, although protected by very spinous bracts. It seems much more correct to consider the spines of *Discaria* and the pungent yucca-like leaves of the *Aciphylla* in question as xerophytic rather than protective "adaptations," especially when their minute structure,<sup>2</sup> which need not here be detailed, is considered.

Certain other peculiarities in the New Zealand flora support this view. Take for instance the case of the "whipcord Veronics." These are curious shrubs which in their form "mimic" certain species of *Cupressus*, one indeed being named by Hooker, *Veronica cupressoides*. All have scale-like, much reduced leaves, which are pressed very closely against the shoot-axis. They grow in those stations of the montane, subalpine and alpine regions, where transpiration is frequently excessive and changes of weather abrupt; some being found on those most extensive screes, termed in New Zealand "shingle-slips," which, as Schimper has stated,<sup>3</sup> are true alpine deserts. Others occur on dry rock-faces, river-terraces, stony slopes and the like. All these Veronics, so far as they have been investigated, are in their early seedling form typical hygrophytes, having numerous fully developed leaves.<sup>4</sup> Also as Goebel showed some time ago,<sup>5</sup> the adult speedily reverts to the juvenile form on cultivation in moist air. Subsequently I placed certain seedling whipcord Veronics in a moist chamber and thus cultivated them for a number of years. Plants of *Veronica Armstrongii*, T. Kirk<sup>6</sup> grown in this manner for six years, and *Veronica tetrasticha*, Hook f. for more than four years, did not assume the cupressoid habit, although both reached a considerable size, the latter plant indeed almost attaining its full adult height. *Pittosporum rigidum*, Hook. f., when growing normally in the open, is a shrub of most dense habit, well deserving its name; but a plant

<sup>1</sup> In winter hares feed upon the thick root, and for this reason amongst others, the thickets of this remarkable plant are less abundant than formerly.

<sup>2</sup> For Anatomy of leaf, stem and spine of *Discaria* see A.C. Finlayson on "Stem-structure of some Leafless Plants of New Zealand." Trans. N. Z. Inst. Vol XXXV., 1903. pp. 361-62; and for leaf-anatomy of *Aciphylla Colensoi*, see L. Diels, "Vegetations-Biologie von Neuseeland." Engler's Bot. Jahrb. Vol. XXII., 1896., p. 267. and Fig. 5A., p. 268.

<sup>3</sup> Pflanzengeographic, p. 797.

<sup>4</sup> Coekayne. Trans. N.Z. Inst., Vol. XXXI., p. 378, and Vol. XXXIII, p. 289.

<sup>5</sup> Pflanzenbiologische Schilderungen, Teil I., p. 19.

<sup>6</sup> See Fig. of juvenile plant and adult shoot. Trans. N Z. Inst., Vol. XXXI., plates 28, 29.

## 84 *Significance of Spines in Discaria Toumatou.*

which I observed in the shade of a subalpine *Nothofagus* forest, was quite twiggy and erect, still in fact, although fully grown and of considerable age, in the juvenile form.<sup>1</sup> The same may be observed in the equally xerophytic shrub *Corokia Cotoneaster*, Raoul, frequently a companion plant of the above *Pittosporum*.

At 1200m. on Mt. Torlesse, a mountain in the dry eastern climatic region of the South Island, I have seen that comparatively leafless, and most rigid, low-growing shrub, *Hymenanthera dentata*, R.Br. var *alpina*, T. Kirk, whose branches "usually terminate in a stout spine,"<sup>2</sup> where sheltered from the sun and wind against a rock, put forth semi-hygrophytic reversion shoots. Finally, leaving out of the question other striking cases, *Aristotelia fruticosa*, Hook. f., when growing in extreme xerophytic stations, has no leaves on its external branches, which at their exposed extremities become spine-like and almost pungent.<sup>3</sup>

From the above, there seems to be sufficient evidence to show how an organ so specialized as a spine may be directly caused by exposure to xerophytic conditions.

When discussing elsewhere<sup>4</sup> the history of the floras of the small outlying New Zealand islands, I have gone, though at no great length, into the bearing which this question of differences between hygrophytic juvenile and xerophytic adult forms of certain New Zealand plants has on the matter of former land extension of New Zealand. Suffice it to say here, that from the teaching of geology,<sup>5</sup> it has been concluded by Dicks<sup>6</sup> that in the east of "Greater New Zealand" there was in all probability a steppe or semi-desert climate, which would insist on xerophytic adaptations being acquired by such plants as were to successfully cope with their new surroundings,—just the climate, in fact, with which *Discaria Toumatou*, *Aciphylla Colensoi* and many other New Zealand xerophytes would be more in harmony, than with the one to which they are at present exposed. According to this view, hygrophytic juvenile forms, such as the *Discaria* here figured, and the species of *Veronica* referred to above, may without

<sup>1</sup> Trans. N.Z. Inst., Vol. XXXIII., p. 266.

<sup>2</sup> T. Kirk. The Students' Flora of New Zealand and the Outlying Islands., 1899, p. 44.

<sup>3</sup> See plate 18. Trans. N.Z. Inst., Vol. XXXVI., 1904.

<sup>4</sup> Trans. N.Z. Inst., Vol. XXXIII., pp. 277-282, and Vol. XXXVI., p. 317.

<sup>5</sup> F. W. Hutton. The Geological History of New Zealand, Trans. N.Z. Inst., Vol XXXII, pp. 173-178, and p. 182.

<sup>6</sup> loc. cit., pp. 296-8.

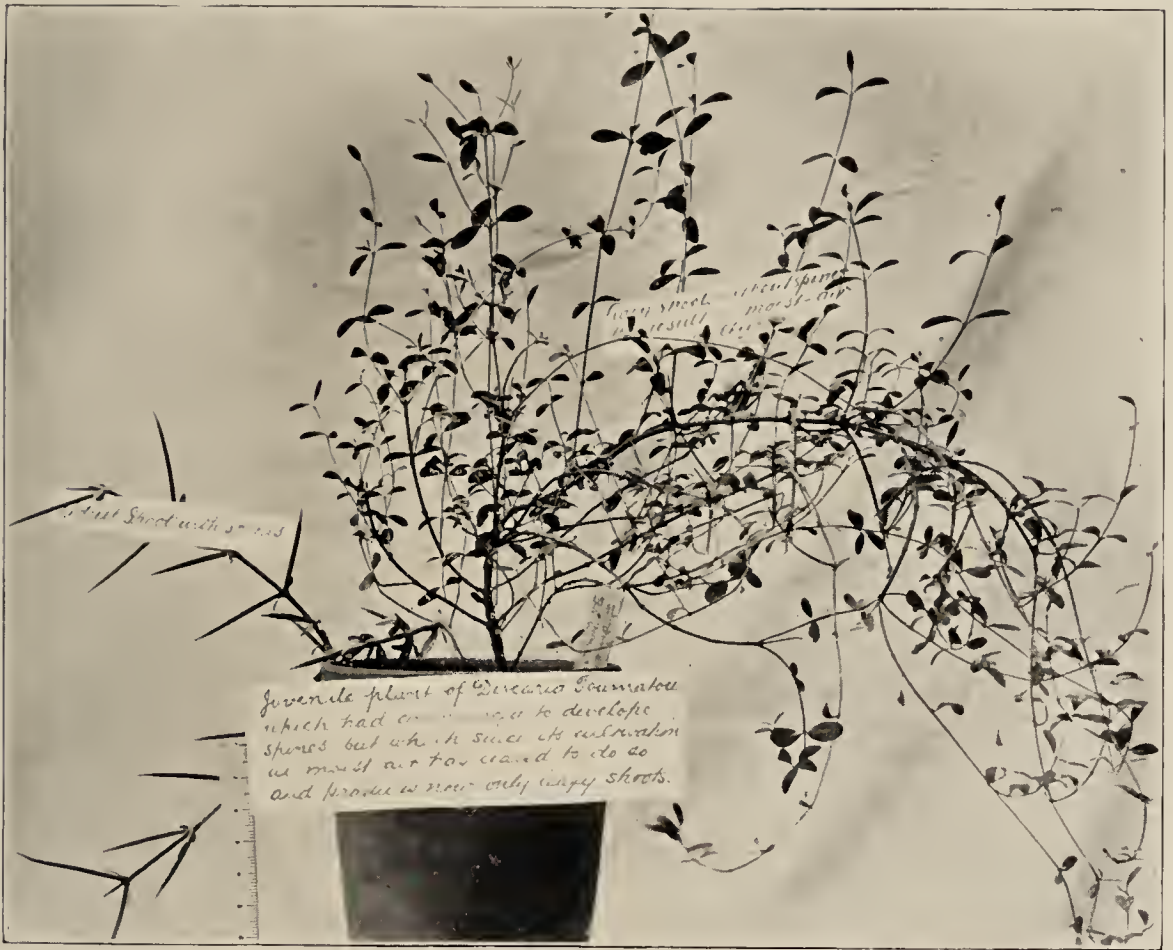


Fig. 1.



Fig. 2.



much stretch of imagination be considered reconstructed stem-forms, which inhabited Greater New Zealand or elsewhere during the earlier Pliocene or earlier still. As to whether, the normal spiny form of the *Discaria* and the artificial spineless form, *i.e.* the prolonged seedless-form, are really two distinct species, or merely the two extremes of one variable species, opens up far too wide a question for consideration here. It is obvious however, that the presence of either or both in a region would be entirely a matter of climate, station and competition with other plants and animals.

In conclusion, I must express my thanks to Professor Charles Chilton, D.Sc. for his kindness in allowing me to use the moist chamber of the Biological School, Canterbury College, Christchurch, New Zealand, for the completion of the above mentioned experiment.

Wellington, New Zealand,  
Jan. 23rd, 1905.

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DESCRIPTION OF THE FIGURES ON PLATE II. ILLUSTRATING  
DR. L. COCKAYNE'S PAPER ON THE SIGNIFICANCE OF SPINES  
IN *DISCARIA TOMATOU*.

Fig. 1.—Photograph of seedling plant of *Discaria* after twelve months' culture in moist chamber. On left is adult shoot placed on pot for purposes of comparison with seedling.

Fig. 2.—Photograph of *Discaria* in characteristic habitat. Fan of Creek from Mr. Torlesse, Eastern climatic region of Canterbury, S. Island of N.Z. Altitude about 700m. (Both photographs by the Author).

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THE CLASSIFICATION OF THE ALGAE.

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A REVIEW OF PROFESSOR OLTMANN'S RECENT BOOK.<sup>1</sup>

**A**FTER the large amount of work of all kinds that has been published on the Algae, more particularly on the green forms and on the plant-like Flagellata, during the last fifteen years, a putting together of the results in one or more general works has become urgently necessary to enable the student to appreciate the

<sup>1</sup> Morphologie und Biologie der Algen, von Dr. Friedrich Oltmanns. Erster Band, Spezieller Theil. Gustav. Fischer, Jena, 1904. Pp. VI. and 733, with 476 figures in the text.

advances that have been made and to obtain a general view of the whole body of our present knowledge.

Professor Oltmanns' bulky volume is the first (special) part only of his projected "Handbuch," of which he hopes to publish the second (general) part in the course of this spring. The present part of this extensive work will in itself, however, be of very great use to Algologists. Its full and clear treatment, with excellent and abundant illustration, of the very large amount of data now available, render it by far the most notable general work of reference on this fascinating group. At the same time it is full of interesting and suggestive discussions. As the author remarks in his preface, no general work has appeared since Falkenberg's *Algae* was published in Schenck's "Handbuch der Botanik" (1882), and though the parts of Engler and Prantl's "Natürliche Pflanzenfamilien" dealing with the *Algae* by various writers, have helped to bridge this long interval, yet the form of treatment necessarily imposed upon contributors to that invaluable undertaking has prevented the work of Wille, Kjellman and Hauptfleisch on the green, brown and red *algae* respectively, from quite filling the place of a detailed handbook or treatise in which the author is free to devote any amount of space he may think desirable to general descriptions, comparisons and discussions. Furthermore our knowledge of the *Algae* has increased so enormously, even since the publication of the parts of the "Pflanzenfamilien" dealing with them, necessitating in some cases a revision of our fundamental conceptions of their morphology, that a fresh treatment is urgently required.

A significant feature of the change which has occurred in the relative importance to be attached to the various groups in considering the morphology of the whole is the large amount of space devoted at the outset to the plant-like *Flagellata*, and to the unicellular forms generally. "The *Algae*," says Professor Oltmanns in his opening sentence, "go back phylogenetically to the *Flagellata*. That is a conviction which is continually making more headway . . ." And he goes on to point out that a recognition of this truth enables one to give a fixed position to many forms which have for decades been tossed backwards and forwards between Zoologists and Botanists. The work of Bütschli, and particularly of Klebs, established this fundamental starting-point for a consideration of the morphology of the *Algae* beyond all doubt. Wille took up the main phylogenetic thread at the point where the algal characters become definitely predominant, and developed its ramifications with considerable

success. Later, the Swedish algologists, Luther and Bohlin, have given good reason for supposing that the Flagellata gave rise to true algal descendants, not along one line only, but along several and finally Senn's treatment of the Flagellata in the "Pflanzenfamilien," though he does not accept Bohlin's conclusions, has further served to emphasise the importance of this group as precursors of the Algae.

Professor Oltmanns' treatment of the Flagellata is based on that of Klebs and Senn. That curious "algal Flagellate" *Hydrurus*, he includes in the Chrysomonadineæ (the yellow-brown division of the Flagellata) and such forms as *Phæocystis*, *Phæococcus* and even *Phæothamnion* (which in certain respects is quite a highly developed Alga and was actually placed by Wille among the pure green filamentous forms in the Chroolepidæ) are treated as an appendix to the yellow-brown Flagellates. This is indeed the least objectionable position for these lowly-organized fixed brown forms at present, since their cell-structure is in most cases typically flagellate. There is much to be said for considering them as efforts in the direction of algal evolution from a stock of Flagellates which ultimately gave rise to the Phæophyceæ proper, (Brown seaweeds), especially as the motile cell in these simple forms often shows the typical one-sided (monosymmetrical) structure characteristic of the zoospores and gametes of the Phæophyceæ; and this view is strengthened by the great importance which we must now attach, as a result mainly of the studies of the Swedish algologists to the characters of the algal motile cell. For the time being we are inclined to agree with Professor Oltmanns' view (p. 13) that it is too early to place these simple forms actually with the Phæophyceæ, and they are too miscellaneous a collection to be given a family of their own.

The series of Heterokontæ (spelt by our author with a c) of Bohlin is, we are glad to see, completely accepted by Professor Oltmanns. We regard the building up of this series out of many well-known and some newly discovered forms, a building up which was the cumulative work of Borzi, Lagerheim, Luther and finally Bohlin, as quite the most brilliant and notable advance in the morphology and classification of the Green Algae that has been made for many years. The striking cytological characters in which the forms assigned to this series agree:—their yellow-green pigment, contained usually in several discoid chromatophores without pyrenoids, the formation of oil instead of starch as an assimilative product, and

finally the characteristic motile form with two unequal flagella—serve at once to convince us of the natural character of the series and to extend the generalisation that constancy in cytological character is one of the most important of morphological features and therefore one of the most important marks of affinity in the Algae, and should entirely overrule similarity of conformation and habit of the thallus, and even resemblance in the form of reproduction. This generalisation was already well established in regard to the pure green, unicellular and colonial forms, while among the Heterokontæ we have a series of organisms ranging from *Chloramæba*, a naked, flagellate, amœboid form, through unicellular types which shew an increasing preponderance of algal features, to cœnocytic forms like *Botrydium*, and multicellular filamentous forms like *Conferva*, (recently found to possess motile anisogametes). A striking peculiarity of the Heterokontæ, as opposed to the pure green series, is the apparent rarity of gamogenesis, which has not reached anything like so high a stage of evolution as in the latter. Professor Oltmanns does not follow Bohlin in transferring the Vaucheriacæ to the Heterokontan series, and his decision is perhaps scarcely to be wondered at. Nevertheless the traditional position of *Vaucheria* among the Siphonales is certainly not satisfactory. With the exception of the formal resemblance given by the fact of its thallus consisting of a branched cœnocytic tube, a resemblance on which we can lay scarcely any emphasis in the absence of other evidence *Vaucheria* scarcely presents a single character in common with the other Siphonales. Pyrenoids and starch are absent, and the method of reproduction, both in the highly differentiated sexual process, and the curious and unique synzoospores, has no parallel whatever in the other families. Ernst's recently described *Dichotomosiphon*, which forms starch and has traces of internal ring-walls at the bases of the branches, but which in respect of its reproduction is undoubtedly a *Vaucheria*, does certainly take us some little way towards bridging the gulf, a gulf that nevertheless remains sufficiently wide. On the other hand we have a resemblance to the Heterokontæ in the absence of starch and presence of an oil in *Vaucheria* itself, while the antherozoids of the latter, with their often unequal, and laterally inserted flagella, seem to work in very well with the Heterokontan type, though the cilia of the Vaucherian synzoospore apparently fail to concur. On the whole we incline to a belief in the Heterokontan alliance, though *Dichotomosiphon* slightly weakens the case for such an affinity. Our

author's account of the many existing observations on the structure and behaviour of this curious group is excellent and interesting, though we note that Davis (Bot. Gaz. Vol. xxxviii., No. 2, 1904) has contradicted his account of oogenesis, affirming that of the numerous nuclei present in the young oogonium all but one are destroyed instead of wandering back into the parent tube. Davis' version certainly seems *a priori* more likely to be correct, but we ought to wait for confirmation of one or other of the accounts before we can regard the matter as settled.

Perhaps the most important consequence flowing from the establishment of the series of Heterokontæ is the weight which it compels us to attribute to the characters of the motile cell as a stable morphological feature. Wille had already separated the Conjugatæ from the rest of the Green Algae on very good grounds, and with the further break-up of the remaining families according to their zoospore-characters, we find the whole of the green forms (excluding the Characeæ) falling into three great series, separated by numerous distinctions of which the most striking is the locomotor apparatus of the reproductive cells. The only outstanding exceptions are the closely allied genera *Ædogonium* and *Bulbochæta*, (with which must be associated Stahl's striking form *Ædocladium*, described in 1891 but apparently never seen since), and *Derbesia*, a siphonous form usually placed close to *Bryopsis* on account of the strong resemblance of its vegetative structure to that of the latter genus. The zoospores of *Derbesia*, however, which were described by Solier in 1847 and of which no more recent account is available, are said to resemble those of the *Ædogoniaceæ* in possessing a crown of very numerous cilia attached round the anterior end, and therefore differ very strikingly indeed from the bi-flagellate type, which (with quadri-flagellate variations) is universal among the zoospores of the remaining green forms. This fact led Bohlin to separate the *Ædogoniaceæ* as a special series the Stephanokontæ and to be logical, *Derbesia* should go with them. Thus we have four great series of Green Algae, Isokontæ with two equal flagella, including the great majority of the genera, Heterokontæ with two unequal flagella, Stephanokontæ with a crown of cilia, and Akontæ with non-ciliated reproductive cells. The hypothesis is that each of these series or phyla—at any rate the first three—is separately derived from the Flagellata, the ancestors of each having the characteristic ciliation. In the case of the first two we have actual evidence of such derivation.

The strength of the case for this view, which has already been

briefly referred to, is increased by the fact (alluded to by Bohlin) that there is apparently no evidence of zoospores having increased the number of their cilia in the course of descent. There are in fact actually no transitional forms between the types of ciliation described, unless a certain amount of variation in length of the shorter flagellum of the Heterokontan type (in which the two flagella are sometimes of almost equal length) and the frequent occurrence of four flagella in the Isokontæ can be so considered.

It is further increased by the parallel—though less strong—evidence of a similar independent derivation from the Flagellata of the Brown and the Red Algæ. The possible connexion of the former with the Chrysomonadineæ through forms like *Phæothamnion* and *Phæocystis* has already been alluded to, and the similarity of their motile cells pointed out. There is absolutely no evidence of any connexion of the primitive members of the Phæophyceæ proper, e.g. the Ectocarpaceæ, with green filamentous forms.

In the case of the red forms the evidence of the connexion of the Rhodophyceæ with the Flagellates is at present very slight, but probably a better case could be made out for such a connexion than has yet been done, and we should certainly not be surprised at the discovery of further evidence pointing in this direction.

The net result of all these considerations is the conviction that the cytological characters of the primitive motile cell (its chromatophore, pigment and product of assimilation—handed on of course to the immotile cells of the thallus which have taken over the vegetative functions in the higher forms) and its locomotor apparatus, are of the first importance as constant morphological features and therefore as characters to which the greatest taxonomic weight must be attributed. We had hoped that Professor Oltmanns would have laid more stress than he has done on these points in so important a work as the one before us and we trust that he will give us a full discussion of the general bearings of these topics in his "Allgemeiner Theil."

After a useful summary of those groups of plant-like Flagellates, which are not clearly associated with algal forms—the Cryptomonadineæ, the Euglenaceæ, and the Dinoflagellata (with rather a full notice of Schütt's work on the cell-wall, etc. of the last named) Professor Oltmanns proceeds to treat the Conjugatæ and the Diatoms together under the name Acontæ, a term introduced in the "Revision of the Classification of the Green Algæ" published in this journal in 1902, and reprinted separately in 1903. This is an unfortunate proceeding. The term Akontæ was intended to

emphasise the phylogenetic importance of the motile cell and its consequences in accordance with Bohlin's principles to which we have just called attention afresh. In the view of the authors of the "Revision," the Conjugatæ are an isolated group of pure green forms whose origin is very doubtful and which are fundamentally distinguished from the other "pure green" phyla by the fact that their reproductive cells have no ciliation. The possibility of their union with the Diatoms appears to the authors of the "Revision" to be excluded by the difference of pigment (apart from other characters) since all the evidence appears to point to pigment as of absolutely the first importance as a taxonomic character. Since Professor Oltmanns does not adhere to this view it would have been better if he had avoided the term Akontæ altogether and called his composite Conjugatæ-Bacillariales group simply Zygoephyceæ (a name he has given as an alternative). The use of Akontæ in this sense introduces a further confusion in nomenclature which it was the object of the authors of the "Revision" to simplify on the promising lines established by the Swedish Algologists.

In his classification of the difficult group of the Conjugatæ, Professor Oltmanns deviates somewhat from previous arrangements. He includes *Genicularia* and *Gonatozygon*, usually placed with the Desmids, in the filamentous group (Zygnemaceæ). This is a change in the same direction as that made in the "Revision" where these genera are placed in a separate family Archidesmidiaceæ, intended to connect the filamentous forms with the more specialised Desmids. Professor Oltmanns goes further, and himself makes a separate group—the Mesotaeniaceæ—in which he places the genera *Mesotaenium*, *Spirotaenia* and *Cylindrocystis*, characterised by simple membranes and the production of four embryos from each zygote. These three genera, though nearer the Desmids proper than *Genicularia* and *Gonatozygon*, are certainly the least specialised forms of the latter. They exhibit the three types of chromatophore found in the filamentous forms, while most of the other Desmids shew some combination of plates and ridges. Professor Oltmanns considers that his Mesotaeniaceæ are the simplest and most primitive Conjugates (p. 53) and (if *Genicularia* and *Gonatozygon* are placed with the filamentous forms) they certainly seem to connect the Desmids and Zygnemales. He lays more stress on the mode of conjugation than on the form of the chromatophore, deriving the method of gamete union found in *Closterium* from that described by Archer in *Spirotaenia* and the Zygnemaceous type from that found in *Cylindrocystis*. He points out that a common character of

the Desmids proper is the production of *two* embryos from the zygote, while the Mesotaeniaceæ have four and the Zygnemaceæ one.

In the filamentous forms Professor Oltmanns makes *Debarya* the most primitive type on account of its mode of conjugation, and from this derives *Zygnema*, *Spirogyra* and *Sirogonium* on the one side and on the other *Zygogonium* and *Mongeotia*. He deliberately neglects the form of the chromatophore (which Palla made the basis of a classification of the filamentous Conjugatæ adopted in the "Revision") and quite frankly refuses to discuss the subject. This is, we think to be regretted, since the relative importance of such characters among the various groups of Algæ appears to be a most interesting and important topic. We cannot enter into it in detail here, but may say that while Professor Oltmanns' derivation of the various modes of conjugation is both interesting and ingenious, on his own shewing these processes sometimes vary to such an extent within the limits of a single genus or even of a single species that the propriety of using them to the exclusion of characters which are singularly constant within the genera must be seriously called in question; while the absence of any attempt to shew how one well-marked type of chromatophore can arise from another, how for instance the *Spirogyra*-type can be derived from the *Debarya*-type, is a serious defect when probable lines of evolution are being sketched out. We cannot resist the conviction that it is the cell-characters which have been constant for the longest time while the details of the conjugation of gametes, even the details of the behaviour of protoplasm upon which Professor Oltmanns lays stress, are much more likely to be easily modified. We should all admit, of course, that the incipient differentiation of sex seen in *Spirogyra* is an advance on the perfectly isogamous conjugation of *Debarya* or *Mongeotia*. The point is that more taxonomic weight should be attached to differences of cell-structure, because these appear to be more constant characters.

Having devoted so much space to a consideration of some of the more fundamental topics connected particularly with the more primitive green forms, there is but little left in which to do justice to the rest of Professor Oltmanns' work.

We should much like, for instance, to discuss in detail his classification of the unicellular "Isokontæ." This certainly shews a great advance on any previous classification put forward in a general work, though we are not in agreement with some of the details. However, as our author truly remarks, the making of a

new system of these forms has become a kind of sport to the Algalogist, and while probably the great majority of existing generic forms have now been described, we are in need of a good deal more detailed information as to their minute structure and life-history before we shall reach any sort of finality in their classification. They are certainly a most difficult group to deal with, since the genera are so numerous, their external form so various, and their cell-structure often difficult to observe with sufficient accuracy, unless good cytological methods, difficult to apply in many cases, are employed. Professor Oltmanns, it is interesting to note, separates Volvocales (the motile) from Protococcales (the motionless forms) and includes Tetrastromatales (in a somewhat narrow sense) in the former. While there can be no doubt that some of the mucilaginous immotile types are extremely closely related to the Chlamydomonadines, it seems unnatural to separate them altogether from numerous other unicellular immotile forms which our author puts in Protococcales. Surely it is most natural to draw the line at the point where the immotile phase of the life-history becomes dominant. Professor Oltmanns artificially simplifies his problem to some extent by omitting all reference to a certain number of genera. The "Scenedesmacceæ" practically correspond with the Selcnastromatales plus the Phyteliaceæ of the "Revision," and are no doubt a natural group. Of the remaining families there is not very much that need be said.

A group Ulotrichales is adopted by Professor Oltmanns to include the branched and unbranched filamentous types (the Ulotrichales of the "Revision" together with the Ulvaceæ and the CEdogoniaceæ). Neither the parenchymatous structure of the former, nor the characteristic motile cells and other peculiarities of the latter, seem to Professor Oltmanns to constitute sufficient reason for placing them in separate groups.

The genera included in the Chætophoraceæ, whose limits differ widely from those given by Wille, mainly follow the arrangement adopted in the "Revision," in which, largely on the ground of Huber's excellent researches, the epiphytic and endophytic forms were regarded as progressive reduction-series from the primitive *Stigeoclonium*-type. In the present work however *Aphanochæte* is given a separate family on the ground of its sexual reproduction. It is interesting to note also that he is inclined to accept Chodat's report of the existence of aplanospores, zoospores and gametes in *Pleurococcus* and to follow this author in considering the genus a reduced Chætophoraceous type. Certainly the cell-division and

thread-formation and branching which occur in *Pleurococcus* establish some case for taking it out of the Protoeoccales, but we can scarcely agree with a similar view of *Glococystis*. The Colcochætaceæ are rightly considered the highest segment of the Chætophoraceous series. The name Chroolepidaceæ is confined to the very natural little group of aerial forms—*Trentepohlia*, *Phycopeltis* and *Cephaleuros* (the Chroolepidæ of the “Revision.”)

Professor Oltmanns divides the filamentous cœnocyte pure green genera into two great groups: (1) Siphonocladiales including Cladophoraceæ, (with *Anadyomene*, *Microdictyon* and *Dictyosphaeria*), Siphonocladiaeeæ (*Siphonocladus*, *Chamædoris* and *Struvea*), Valoniaceæ (*Valonia* alone) and Dasycladaeeæ (with the usual genera), and (2) Siphonales. Though we entirely agree that the genera contained in the first three of these families should all be closely associated, the actual arrangement is unusual and seems insufficiently justified in the text. The Dasycladaeeæ, though often technically “siphonocladous” certainly stand apart from the other group in virtue of their many peculiar characters. It is more probable that they are derived from some strictly siphonous verticillate form in the neighbourhood of *Bryopsis* than from any of the true Siphonocladææ.

The treatment of Siphonales calls for no special remark.

We must pass very lightly over the great groups of the Brown and Red Seaweeds, though they actually occupy a little more than half the work. The Phæophyceæ are divided into three primary divisions—the Phæosporaceæ, Akinetosporeæ and Cyclosporeæ. The Phæosporææ are again divided into four great families—the Eetocarpaceæ, Cutleriaceæ, Sphaecelariaceæ and Laminariaceæ, and then again into sub-families. This arrangement permits a much readier general view of this difficult group than is the case when the non-eyelosporeous Phæophyceæ are arranged in a great number of coordinated families. The Akinetosporeæ are perhaps a somewhat provisional group, established to include the Tilopteridaceæ and Choristocarpaceæ with motionless spores. In the Cyclosporeæ we have, of course, the two families, Dictyotaceæ and Fuaceæ. The discoveries of Lloyd Williams have certainly brought these two families so much nearer together that it is no longer advisable to place them in separate cohorts as Engler does. Williams’ most recent papers, however, with his striking discovery of a true alternation of generations in the Dictyotaceæ, were, we suppose published too late to find a place in the present account. The description of the Fuaceæ is excellent, but we could have wished

that the cytological details of reduction, etc., in oogenesis, could have been included. It is, we think, a mistake to divorce such important details from the special descriptions of the groups they refer to, however necessary it may be to consider them again in the course of general discussions.

The Bangiales are treated as a separate group distinct from the Rhodophycæ, which name is taken as synonymous with Floridæ. The great feature of the treatment of the Red Seaweeds is a section of no less than 110 pages devoted to a description of their vegetative structure under two great heads—the “Springbrunnen-typus” and the “Zentralfaden-typus.” This detailed and yet generalised treatment enables one to obtain an “Uebersicht” of the structure of these forms in a way that has never been possible heretofore.

The reproductive processes of the Red Seaweeds, finally, occupy the concluding section of the work. Here Professor Oltmanns is dealing with a subject, to which his own work has contributed by far the most important advance of the last fifteen years. We need only note that in his arrangement of the families based on the structure of the sporophyte he follows Schmitz and Hauptfleisch in the main, departing from Schmitz's grouping only in comparatively minor points.

One of the principal risks to which an author is exposed in undertaking a full treatment of a group containing a very great number of varied forms is the danger of becoming lost in details. We do not for a moment suggest that Professor Oltmanns has actually fallen into this danger, but we do rather miss, particularly in some parts of his book, that broad evolutionary treatment, which we think might have illuminated and given more unity to this solid and well-informed work. The principles governing the evolution of plants are not always easy to disentangle, but in the case of the Algae, particularly the lower green forms, which are not, like the higher plants, burdened with a legacy of complex structure, there is rather an exceptional opportunity of obtaining a clear view of at least the proximate factors of evolution. It may be urged that this is scarcely a fair criticism to make on the “special part” of a work of which the “general part” is still unpublished, but the broad treatment referred to is wanted in actual connexion with the details to give them life and unity. It is perhaps hypercritical, however, to receive so solid, useful and attractive a work in such a spirit. We look forward to the author's “Allgemeiner Theil” with great interest.

A.G.T.

## REFORMS IN CELL-NOMENCLATURE.

SIR,

Is it possible that other Students have felt the need for a new term in Botanical Nomenclature to express the distinction between a cell with the reduced number of chromosomes in its nucleus, and a cell with the unreduced number? The Zoologist is not in the same case here as the Botanist, for in animals there is not the intercalation of repeated divisions between the reducing division and the formation of the gamete. To the Zoologist the term "somatic cell" has a well-determined signification, and though not so obviously applicable in the Vegetable Kingdom owing, among other reasons, to the gametophyte sometimes producing what has the appearance of a "soma," there is no absolute necessity to discard it in vegetable cytology. Granted then that the Botanist adopts the expression "somatic cell" for a cell with an unreduced number of chromosomes, we require a term for such cells as contain a nucleus with the reduced number of chromosomes. We have further the unfortunate habit of calling the first initiators of the gametophyte tissue "asexual spores," a term which tends to obscure their nature and prevent the full meaning of such work as that of Farmer on Apogamy in Ferns, and of V. H. Blackman on the Passage of Nuclei in Uredineae from being as obvious as it should be. I would suggest that all cells, containing nuclei with the reduced number of chromosomes, be called *haplocytes*, while the somatic cells with the full number might be called *diplocytes*. Thus "asexual spores," all cells of the gametophyte, including the gametes, come under the heading of haplocytes and this becomes a simple common denomination for such cells. We might call the spores "haplospores," or simply refer to them as haplocytic spores. Dr. Lotsy<sup>1</sup> has suggested the term "gones" as a common denomination of both "asexual spores" and gametes. The adoption of some common term seems requisite but, as pointed out above, it seems better to bring the non-specialized gametophyte cells into the same category and for this the term "gone" does not seem suitable. I suggest, therefore, the terms "haplocyte" and "diplocyte" as general descriptive terms.

There is another anomaly in Botanical Nomenclature, to which perhaps you will allow me to refer, as we find it almost universally in the best of text-books. I refer to the use of the expression "spermatozoid-mother-cell" for the cell which, by differentiation (not division), gives rise to the sperm. The expression sperm-cell, which is rarely used, seems preferable, as the former involves the use of the term mother-cell in two senses. In the majority of cases it is used for the cell which by division gives rise to two or four daughter-cells, but there is no division involved in the so-called spermatozoid-mother-cell.

Or is the latter an anachronism of the same character as "special mother-cell" for the remains of the pollen-mother-cell wall, which surrounded the young pollen grains? This latter anachronism has happily for some time gone out of use, and it would seem desirable that the expression sperm-mother-cell should also be discontinued.

M. BENSON.

Royal Holloway College,  
February, 1905.

<sup>1</sup> J. P. Lotsy, Die Wendung der Dyaden, etc. Flora, 1904. Footnote, p. 69.

SUGGESTIONS FOR BEGINNING SURVEY WORK  
ON VEGETATION.

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VEGETATION-SURVEY, *i.e.* a systematic record of vegetation on ecological lines, differs from the records collected in local and general "floras" (floristic records) as associated in Great Britain largely with the names of Bentham, Babington, and Hooker, in that its scope is broader and its method of attack quite different. The experience gained during a "laboratory phase" of botany is brought to bear on our native plants in their natural surroundings, while data derived from meteorology, geology, agriculture, and forestry are called in to aid. The movement is not confined to Britain, but is general throughout Europe and America. The English translation of Schimper's "Plant-Geography," and other works are available for reference regarding general principles, while a recent statement on the "Problems of Ecology" in this journal (October, 1904) reviewed some of the various aspects of the subject. The present "suggestions" are a response to inquiries regarding methods of work. The aim is merely to give hints, for organized instruction is impossible in a branch of science which is still in rather a tentative stage, and of which a working knowledge can only be acquired by careful and prolonged observation. A somewhat similar instruction is issued by the Zurich school (Professor C. Schroeter) with a title ("Fragenschema für Beobachtungen über pflanzengeographische u. wirtschaftliche Verhältnisse,") which indicates that the asking of questions and the noting of observations are important items in the work. The recently organized Committee for the Survey and Study of British Vegetation<sup>1</sup> have come to some conclusions regarding methods of survey, and these are given here for the general benefit.

The central idea of the work is that groups of individual plants, belonging to one or to several species, growing under common conditions of life, must be studied as units, in relation to those conditions, in order to obtain a complete knowledge of plant-life in its natural surroundings. This is the meaning of the study of *vegetation* as opposed to *floristic* study which aims merely at recording the occurrence of species in various localities. The simplest vegetation-unit we call a *plant-association*. Larger units, including groups of associations, we call *plant-formations* (see below). As the study of associations proceeds it becomes more evident how many plants of our flora are bound up into definite communities, although all do not thus fall into distinct groups.

Within recent years a series of botanical surveys, illustrated by maps, have been issued. These afford a primary analysis of vegetation only, include areas many miles in extent, and deal mainly with *formations*. There are also studies which have been limited to a single wood or pasture (see *New Phytologist*, January, 1905). The narrow "study" of an association or small group of associations, or the wider "survey" of formations grade imperceptibly into each other, for the study of a single wood or heath leads to comparison with other woods and heaths; while the general survey requires attention to the vegetation of single woods and other

<sup>1</sup> *New Phytologist*, Jan. 1905, p. 23.

limited units. Simplicity will be attained if the attention is at first restricted to some one common type of vegetation; the oak-wood so general throughout Britain will serve as an example.

*Formations.* A natural wood consisting entirely of oak trees has one dominant form—the oak—whose presence is determined by the prevalent climatic, soil, and other conditions, while its size and gregarious nature give it dominance; in this wood there may be other sub-dominant trees or shrubs (*e.g.*, birch or hazel), more or less isolated, but which, given the opportunity by removal of the oak, will become dominant forms; the motley carpet of the oak-wood is made up of many species dependent on the larger forms for shelter and shade, or living as epiphytes, parasites, and humus saprophytes, and including not only flowering plants, but ferns, mosses, lichens, and fungi. The vegetation of the oak-wood is thus a mixed community with complex relationships, its members struggling for existence and dominance, but it is a coherent whole and may be studied as a unit or *Formation*. The oak-woods of the present day are small and detached, but they are certainly the remains of an extensive oak forest which extended far and wide before it was cleared to make way for farm-land.

Other well-marked standard formations<sup>1</sup> are:—

Group I. Deciduous woods, *e.g.* Beech wood (native only in the South of England).

Group II. Coniferous woods, *e.g.* Scots Pine.

Group III. Xerophilous herbaeous and undershrub vegetation (including moorland): (*a*) Heather moor, where Ling (*Calluna*) is strongly represented. (*b*) Cotton-Grass Moor or Moss (*Eriophorum vaginatum*, etc.). (*c*) Grass-land, where grasses prevail, *e.g.* on the Chalk Downs and Mountain Limestone. (*d*) Grass-heath, where dominant grasses (*e.g.* *Nardus stricta*) are mingled with sub-dominant heath plants (*e.g.* *Calluna*, *Erica* spp., *Vaccinium* spp., etc.).

Group IV. Maritime: (*a*) Sand-Dunes. (*b*) Salt Marshes. (*c*) Shingle Beaches. (*d*) Sea Cliffs.

Each of these formations has a distinct appearance, due to one or more plants which dominate it. The presence of the dominant plant is determined by combined climatic and edaphic (soil) conditions, and in most countries man as tiller of the soil, as grazier, or as game-preserver has left his mark on the natural formations, or has displaced them by "substituted formations."

*Associations.* Within the limits of a formation, there exist smaller societies, each one with dominant, sub-dominant and dependent species of its own. Thus the undergrowth of an oak-wood may consist of a *Pteris-Scilla-Holcus* association, in which Bracken, Bluebell and Yorkshire Fog together cover a large area; again it may be a *Calluna-Vaccinium* association, or one of several others. Each association is determined by a set of factors, as a rule edaphic factors.

Work on vegetation may be concerned with the distribution of formations, or it may be a record of the associations of a smaller area. It may be a study of the conditions which determine the existence of a single formation or of an association. It is not easy to say with which of these it is best to begin; everything depends on the

<sup>1</sup> This list is by no means exhaustive of British plant-formations.

character of the country and on the tastes and aptitudes of the individual worker. Ultimately, however, the work will resolve itself into an examination of one or more formations or associations occurring within some selected area, and it is suggested that these should be mapped to give definiteness and coherence to the work. An area which can be frequently visited ought to be selected, and it is well to set out with at least one problem on which to focus attention. For example, in a wood it may be the investigation of why an association occurs in certain places, but is absent in others; or it may be a comparison of the vegetation on one kind of soil (*e.g.*, sandstone) with that on another soil (*e.g.*, limestone or chalk). An essential item of field-equipment is one or more note-books, preferably ruled in squares, and of a size as large as can conveniently be carried. Observations made are recorded *on the spot*, and in such a way that the notes will serve as an accurate diary for future reference. Mapping on any scale up to  $\frac{1}{25000}$  (twenty-five inches to the mile) can be done on the corresponding maps of the Ordnance survey; they show roads and land-marks which are easily located, and a system of symbols which aid in vegetation work. The "Description of Scales and Characteristics" sold by the Ordnance Survey Department (*6d.*) is useful, and it gives examples of all the available Ordnance maps. The 6-inch maps ( $\frac{1}{100000}$ ) are perhaps the most generally useful for indicating formations. For very detailed large-scale work ( $\frac{1}{5000}$ — $\frac{1}{6000}$ ), see Oliver and Tansley, *New Phytologist*, December, 1904.

The main points to be attended to in recording a formation or association are as follows:—

*A.* General description of the vegetation: (a) Forest or wood of timber-trees (close canopy); (b) Coppice, *e.g.*, Oak, Chestnut, etc., with and without "standard" trees; (c) Scrub or thicket of alder, willow, hazel, etc., or naturally shrubby trees; (d) Dwarf woody shrubs, *e.g.*, Ling, Bilberry, Gorse, etc.; (e) Grass-land, etc. It is convenient to name this by the dominant plants, *e.g.*, Hazel-bramble thicket, ling-bilberry moor, *Festuca ovina* grass-land. In the case of an association being recorded, the formation to which it belongs should be given. It is also necessary to note whether the association or formation is closed or open in character, *e.g.*, the undergrowth beneath Beech is frequently open, whereas in an Oak coppice it will probably be close; the vegetation on cliffs and scres is generally open, that on grass-land forms a close sward.

*B.* Topography. Indicate the limits of the area as nearly as possible on the map, and note: (a) altitude from Ordnance Survey map, approximate slope and exposure towards points of the compass; (b) the geological name of the underlying rock (Geolog. Survey Drift maps), and its general character; (c) the soil, including texture and moistness, also whether derived from the rock, formed from peat or humus, or transported glacial or alluvial deposit; (d) soil-water, whether moving or stagnant, constant or variable, etc.

*C.* Flora, or a list of all the species occurring in the association. It goes without saying that a good field-knowledge of our native plants is most desirable if the notes are to be thorough; the assistance of a good field-botanist is most useful. The list, made at any time, will, of course, include plants not in flower, and here again most observers will have something to learn. If an unknown plant occur in the association, it may be collected, numbered and

preserved, till flowers are found or some one can name it. A mere list of plants is not sufficient, it should be classified as much as possible. The following method is simple, but others are in use:—

Larch wood with a few Spruces, trees about 70 feet high, and from 6 to 10 feet apart: two distinct associations found, *Calluna* and Bracken, the latter in hollows, the former occupying the larger, more level floor of the wood. (Soil—thin peaty humus, overlying Liassic Limestone, 650 feet alt., Clevelands, N. Yorks.)

*Calluna*-Association:

Social Species:

Dominant, <i>Calluna Erica</i> , 40—50 p.c.	} about 70 <sup>0</sup> / <sub>0</sub> <sup>1</sup>
„ <i>Erica cinerea</i> , 20—30 p.c.	
Sub-dominant, <i>Vaccinium Myrtillus</i> , 5—10 p.c.	
Sub-dominant, <i>Festuca ovina</i>	} about 30 <sup>0</sup> / <sub>0</sub> <sup>1</sup>
„ <i>Aira flexuosa</i>	
„ <i>Agrostis vulgaris</i>	
„ <i>Anthoxanthum odoratum</i>	

Isolated Species:

Characteristic:	1. <i>Potentilla sylvestris</i> .
„	2. <i>Galium saxatile</i> .
„	3. <i>Oxalis Acetosella</i> , etc., in decreasing abundance.

Sporadic: *Carduus arvensis* (from farm-land).

From this list one learns that certain plants of the undergrowth are social, occurring in patches; of these, two dominate and give the association its physiognomic and ecological character, while others, though social, are only sub-dominant here. The percentages show roughly that Ericaceæ occupy about twice as much ground as the grasses, and that ling forms about half the vegetation, Bell-Heath a quarter. These seven species are supplemented by others which occur isolated here and there; they are noted so that the more abundant are first, the rare last; amongst the rare forms one may find sporadic species, which have been introduced, but will probably not survive long, unless the conditions are changing.

D. Ecological study proper or observations on the relation of plants to their environment. It is simpler here to attempt one or two of the dominant species only, or it may be done with the association as unit. Here there is much scope for original observations, and the working out of problems, since the ecology of few British plants or associations has been attempted, and the methods to be adopted, which must necessarily vary greatly according to the particular problem investigated, have still, for the most part, to be elaborated. A given plant occurs here and not there; is it climate, slope, sun or shade; or is it soil, its moisture, its texture, its acidity, or lime-content, or what? Soil examination may include preparation of soil-sections or the use of boring-rods, while lime-content may be tested with acid, and soil-water may be estimated by the weighing of fresh, air-dry, and desiccated samples.<sup>2</sup> The morphology of plants, their mode of growth, hibernation, and

<sup>1</sup> These percentages can be estimated by eye according to the proportion of ground in a small sample area covered by the different forms of vegetation.

<sup>2</sup> “The Soil” by A. D. Hall (Macmillan, 1903) gives much useful information.

structure, as well as their special physiology, also of course, have an intimate relation to their place in vegetation.

Some of the results to be expected from such records as those suggested have already been indicated. One more line of research may be pointed out:—the succession of associations on a given area. The farm-land of to-day is a formation substituted by man in place of primeval forest, or other natural formations; the grazing of man's herds confined within a limited area also brings about changes. This displacement of one vegetation by another can be seen on a stretch of moorland where man's influence is extremely slight (*vide* F. J. Lewis in Westmoreland). Changes in climate or more local changes in drainage are followed by such a succession as Moor tarn, *Sphagnum*-bog, Heather-moor. The succession on sandy coasts is frequently:—loose dune ridge and dune hollow, semi-fixed dune, fixed dune, grass heath or even heather-moor (*vide* W. G. Smith in Forfar and Fife). The Fen country shows equally good successions, and this might be said of many parts of Britain.

Nothing has been said of Cryptogams, and so far as knowledge of them goes there is very little to say. Yet Lichens, Algae and Mosses play an important part in preparing the substratum for higher plants, hence their ecological study should be productive. Fungi as saprophytes and parasites are already recognised as being confined to many definite substrata of living or dead organic matter. Marine Algae have well-marked zones of coast distribution.

The following is an outline of work that may be done on Pond-Algae. Any area chosen for survey-work is likely to contain one or more pieces of water, and the study of the vegetation of these latter is necessary to give a complete record of the area studied. The plant-growth in such water generally consists of a limited number of Phanerogams and of a great mass of fresh-water Algae; little or nothing is known about the ecology of these latter. The main points to be noted in the survey of aquatic vegetation may be classified under approximately the same headings as were employed above for the land-vegetation.<sup>1</sup>

A. General Description of the Vegetation:—Note at least each month the dominant and sub-dominant Phanerogamic aquatics and the general character of the Algae (ponds with and without *Cladophora* or *Rhizoclonium*; presence or absence of *Vaucheria*; Diatom-Associations; Conjugate-Associations, etc.) Note the relative abundance of Phanerogams and Algae each month and whether the latter are attached or free-floating, or both.

B. Determination of Prevailing Conditions:—The following are the main points to notice, although other features will probably occur in the course of actual survey: minimum, mean, and maximum temperature of water (frequent readings!); average conditions of illumination (shading due to surrounding vegetation; shading of Algae by Phanerogamic aquatics; muddiness of water; average number of hours of daily sunlight); conditions of aeration (whether stagnant or with in- and outflow; whether exposed to prevailing winds; rainfall); changes of water-level (note frequency and extent); chemical composition of water (percentage of organic substance present; dissolved lime and other salts); nature of

<sup>1</sup> A preliminary paper dealing with the general character of the algal vegetation of ponds and with the general problems of this kind of work will be published shortly.

bottom (sandy, rocky, clayey, etc.); animal life present; general character of weather in week preceding the collection of each sample.

C. Flora or list of all the species occurring in each piece of water:—It is very important to collect carefully and make sure of getting a characteristic sample of the algal vegetation at least each month *during the course of a complete year*. A characteristic sample must contain all the different kinds of Algae present in about the same proportion as they actually occur in the pond; each collection should be supplemented by careful notes made on the spot. A little experience enables one to distinguish broadly the different genera of filamentous Algae by colour, texture, mode of attachment, etc. Hints on the collection of Algae will be found in West's "British Freshwater Algae" (Cambridge University Press, 1904, pp. 6-8); a long bamboo pole (or collapsible fishing rod) with a piece of bent copper wire attached to one end will be found very useful for collecting in larger ponds. Material not to be examined at once is best preserved in formalin (3% for samples with many conjugates; otherwise 4-5%). The Algae or other aquatics which play an important part in the vegetation of the pond in the course of a year may be classified as dominant and sub-dominant according to the duration of their dominance. Certain of the rarer species will be found to be characteristic of each pond.

D. Ecological Study of Aquatic Vegetation:—There is a large scope for research here, especially as regards the algal vegetation. We know very little as yet as to why an algal species or genus is found in one pond and not in another, and careful observation of the algal flora combined with the prevailing conditions must undoubtedly afford valuable data; these must be supplemented by experimental research. Other points of no less importance, which are connected with the survey of algal vegetation are:—the period of the year at which each algal form flourishes best (possibly different under different conditions); and the accumulation of external conditions, which lead to the various reproductive processes. These can only be settled by observations (monthly or better even fortnightly) extended over a number of years and made on a large number of different pieces of water. Such data will be most valuable if brought together at a single point; it is consequently suggested that anyone undertaking survey-work on an area, including pieces of water should forward monthly or fortnightly samples of the algal vegetation to Dr. Fritsch, Botanical Department, University College, London, W.C., who will endeavour to furnish a list of the Algae present in each sample in return. Further particulars as to the survey of aquatic vegetation can be obtained from the same source.

It is of course impossible to prescribe for all the possible lines of ecological study which may be undertaken on the varied vegetation of Britain. A communication to the Secretary of the Committee (W. G. Smith, University of Leeds) will however enable workers to obtain assistance from the member most likely to aid. The list of members (New Phytologist, Jan. 1905) includes workers in touch with many parts of Britain. A certain amount of literature is available, not much, but the list is too long to give here; the Committee will however be able to indicate useful papers.

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CURRENT INVESTIGATIONS IN ECONOMIC BOTANY

(Continued from p. 78).

BY WILLIAM G. FREEMAN.

SUGAR-PRODUCING PLANTS.

Sugars play an important part in the life-processes of plants, and the majority of the higher plants are, strictly speaking, sugar-producers. The sugar-producing plants of economic importance are those from which sucrose (saccharose or cane sugar) can be profitably obtained on a commercial scale.

Many plants contain sucrose, but for one reason or another they are not utilized as sources of sugar, *e.g.* carrot and parsnip roots, many fruits, etc. Other plants are used in various parts of the world to supply sugar for local requirements, *e.g.* the Palmyra palm (*Borassus flabelliformis*); the coconut palm (*Cocos nucifera*); the sugar palm (*Arenga saccharifera*); the date palm (*Phœnix dactylifera*); Indian corn (*Zea Mais*); *Sorghum* sp.; and the sugar maples (*Acer saccharinum*, and other species. Finally there remain the sugar cane (*Saccharum officinarum*) and the sugar beet (*Beta maritima*) which furnish practically the whole of the sugar supply of the world.

In the biennials such as the beet, carrot, and parsnip, the sugar forms the principal food-reserve of the plant and is accumulated in the roots during the first year's growth, at the end of which period it is, under conditions of cultivation, appropriated by man. In the sugar cane, maize and sorghum the sugar is again the food reserve, but is stored in the stem, and thus obtainable without causing the death of the whole plant as is entailed in the beet-root. In the palms mentioned above and the sugar maples, the sugar may be intercepted, by appropriate methods of tapping, *en route* to points of vegetative activity, and the same individuals may yield their contribution of sugar for many years without receiving great

injury. The visible annual sugar crop of the world, at the present time, is about 10,000,000 tons, of which the sugar cane yields about 4,000,000 tons and the beet the remainder. Speaking generally the sugar cane is a tropical or sub-tropical plant, whilst the sugar-beet is a plant of temperate regions. America and the West Indies produce the greater portion of the world's supply of cane sugar, whilst practically all the beet sugar is of European growth.

#### THE SUGAR CANE.

Before proceeding to the discussion of the methods of improving the yield of sugar from the sugar-cane, it will be well to refer briefly to a few features in the cultivation of the plant and the preparation of sugar.

*Saccharum officinarum*, in common with some other grasses, possesses the power of putting out adventitious roots from its stem. This constitutes a most important factor in the cultivation of a monocotyledon, and the sugar cane, from time immemorial, has been propagated by means of stem-cuttings, each internode of a sugar-cane stem having a lateral bud and a zone of adventitious roots ready to start into growth under suitable conditions. From cane cuttings, ripe plants are produced in twelve to fifteen months in the tropics, and this method of propagation is exclusively employed in cane cultivation. The fact that seedling canes have, of recent years, been raised in large numbers does not affect this generalization. The young seedling cane is a very delicate plant, and is of little value as a source of sugar in its first year. Accordingly canes, raised from seed, are grown until they are of sufficient size to yield a stock of cuttings from which a normal crop can be grown and tested, and if the variety prove a good one it is, like the older varieties, perpetuated by cuttings. It is important to bear in mind the fact that all crops of sugar canes are obtained from cuttings of previous crops in dealing with questions of heredity and transmission of disease.

The lateral buds of the cuttings give rise to shoots which finally reach eight, ten, twelve and even sixteen or more feet in height, and by the development of secondary buds a clump of ten or more canes often arise from each cutting. Such a clump is often termed a "stool" of canes. With the advent of the dry season in the tropics, or cold weather in extra-tropical countries, the sugar cane receives a check in its vegetative growth and commonly flowers. It is about this period that it usually contains its highest percentage of sucrose, and is ready for cutting. By

passing the canes through mills the juice is expressed, and the crushed cane left is known as "megass" or "bagasse"; and although apparently refuse material is of importance to the planter, being his principal fuel for evaporating the juice, and a cane extremely rich in sucrose, but yielding little megass, might not be so profitable to a planter as a cane poorer in sugar, but furnishing him with a more plentiful supply of fuel. The manufacture of the various grades of sugar from the raw juice presents chemical questions concerning purification and crystallization which are outside our province. It may, however, be mentioned that after the crystallizable sucrose has been obtained, there is left the uncrystallizable glucose in the form of molasses, which, by suitable fermentation, yields the second by-product of sugar, namely rum. Recently a third by-product has been prepared from the finest portions of the megass and molasses and under the name of "Molascuit" has become recognized as a valuable cattle food.

The minor problems in sugar cane cultivation naturally vary in different parts of the world, but everywhere the principal objects of the planter and scientific worker are to produce :

- (i). Canes of high sugar content, and of good working qualities.
- (ii). Canes resistant to disease, drought, etc.

It is not only desirable that the canes should have a high percentage of sucrose in their juice, but that they should be heavy croppers and so give a large return per acre. By the term good working qualities, it is understood that the canes are easily crushed, yield a fair proportion of megass, and present no special difficulties of cultivation.

The magnitude of the interests involved has caused an enormous amount of time and labour to be spent on the improvement of the sugar cane. The principal means adopted in attempting to attain this object are :—

- (i). Bud Variations or Sports.
- (ii). Chemical Selection.
- (iii). Seminal Selection.

There occur throughout the sugar-producing countries a very large number of different varieties of sugar-cane, differing in colour of stem, habit, yield of sugar, resistance to disease etc. These varieties are usually locally known by names, often descriptive, fanciful, or indicative of their place of origin, *e.g.* White Transparent, Purple Transparent, White Tanna, Bourbon, Queensland Creole,

Striped Singapore, etc. Canes have during past centuries been distributed so extensively from country to country, that several of these varieties are doubtless descendants of one original stock, but as their recognized distinctions are mainly differences in epidermal colouring and habit, exact correlation between the varieties of two countries is extremely difficult.

The origin of almost all of these old established varieties is unknown. Amongst them are many of the finest sugar producing canes, although unfortunately some are now very subject to disease in the localities where they were formerly grown with such success for instance the Bourbon in the West Indies, and the Cheribon in Java. It is possible that some of these canes have been obtained by slow selection through long periods, or they may have arisen as "Sports" or "Bud Variations," and been perpetuated.

#### SPORTS OR BUD VARIATIONS IN THE SUGAR CANE.

The name bud variation is usually restricted in the sugar cane to cases where canes are produced differing in colour from the parent stem. In one case on record<sup>1</sup> a cane, with a red and yellow striped stem, gave rise to branches, some of which were striped like the parent cane, whilst others were plain yellow without any stripes. Cuttings from these branches give rise to plants true to their respective colours, *i.e.* bearing canes with stems all striped or all plain yellow, and, as will be shown later differing in their yield of sugar.

The following instances serve to show that the phenomenon has been noticed and put to good account in many parts of the world. In Mauritius eight or nine such sports were in cultivation in 1890, and some were reported as being very fine canes and extensively planted, being hardy and yielding more sugar.

Single "joints" in some Queensland canes were either striped or unstriped and each joint treated as a cutting gave rise to canes of its own colour, and the unstriped canes were of higher sucrose content than the striped canes.

The most exact recent information available is from Barbados in the Annual Reports of sugar cane experiment work carried out by d'Albuquerque and Bovell. The striped cane, already noticed, gave rise to shoots, some striped and some yellow. Cuttings from the striped and yellow shoots were planted separately under identical

<sup>1</sup> The lecture form has been retained, but a bibliography of the principal papers, etc., referred to will be given at the conclusion.

conditions. They bred true to colour, and shewed on analysis the following differences :—

	Canes per acre tons.	Juice per acre galns.	Sucrose per gallon.	Quotient of Purity.	Sucrose per acre.
Striped Canes.	21·80	2·696	2·310	93·03	6,228
Yellow Canes (Sport).	27·27	3·555	2·270	91·64	8,070

The sport cane in this instance gave a yield of sugar at a rate nearly 25 per cent. above that of the parent cane, the result being due to the heavier yield of the sport cane rather than to its intrinsic superiority, its juice being, as a matter of fact, less rich in sucrose, and less pure than that of the parent. The result of one year's experiment is not sufficient to demonstrate conclusively that the sport will permanently be superior to the parent cane, and experiments are being continued to allow of further evidence being obtained. The example will serve, incidentally, to indicate some of the different factors which have to be taken into account in determining the value of a sugar cane as a commercial source of sugar.

Experience in Queensland, Mauritius and Barbados proves that in bud variation there is a possible means of obtaining new varieties of sugar cane which may be superior to the parent plants. The process cannot, however, be controlled exactly, and it is only by close observation and experimental rearing, and testing of sports as they arise that beneficial results are to be looked for. This method of improving the stock of canes lacks opportunities for working steadily and systematically to a definite end, such as is afforded by chemical selection and controlled hybridization.

#### CHEMICAL SELECTION OF SUGAR CANES.

We will now turn to the consideration of the methods employed and the results obtained in the second mode of improving the sugar cane, namely that which is usually known as "Chemical Selection." As has already been pointed out canes vary greatly in richness, or to be more precise in the percentage of cane-sugar or sucrose contained in their juice. On *a priori* grounds it would appear reasonable that if a large number of canes of a given variety were analysed it would be found that the percentage of sucrose in their juice varied, that a comparatively few would have a very low per-

centage, a comparatively few a very high percentage, but that the greater number would more or less approximate to the mean richness of sucrose for the particular variety. Supposing now that the plants richest in sucrose are selected to form the parents of the next generation it would appear probable that their sugar contents would be found to show similar differences, a few would be high, a few low, but the greater number would again approximate to the mean of this series, and the mean of this the second generation should, theoretically, be slightly higher than that of the first generation from which it has been raised by selection of the richest canes. Imagine this process repeated for many generations, resulting each time in slightly raising the mean sucrose contents, and we see that there appears to be at hand a method of increasing the yield of sugar from a given variety of cane. The method is a vegetative or asexual one exactly as bud variation, but whereas in the latter case all the experimenter can do is to put to the test any cane which shows unusual characters of colour, etc., which may or may not be correlated with variations in the richness of the cane in sucrose, in chemical selection he is enabled to proceed along well defined lines, and to work steadily towards a definite goal, the production of a race of canes of increased sugar content. Any success in bud variation depends on taking advantage of naturally occurring large differences, in chemical selection reliance is placed on increasing the sucrose yield by the integration of small differences, which are only recognizable by the chemical analysis of the juice of the individual canes.

The mode of conducting experiments, outlined above, appears easy, but in actual practice many difficulties are encountered and it is by no means a simple matter to carry on work in chemical selection of sugar canes so to obtain results which shall be absolutely reliable and above criticism. In the first place different portions of an individual cane yield juice varying greatly in composition; at any particular time the younger internodes are relatively rich in glucose and poor in sucrose, whilst the older or basal points are relatively poor in glucose and rich in sucrose. Again a sugar-cane plant comprises a number, say ten to twenty, of separate canes or stalks which may vary, as will be shown later, very considerably in the richness of their juice when examined simultaneously, and there is no reliable criterion to enable one or other cane to be selected as representative of the whole plant. Finally, to mention any one other difficulty, it is essential that the

canes raised from a series of selected cuttings shall be grown under exactly similar conditions, otherwise it is impossible to deduce any reliable conclusions from differences found in the second generation, which might be the result of the selection practised or due to differences in environment, mode of treatment, period of cutting or other factors the exact result of each of which it would be impossible to distinguish.

The earliest experiments in chemical selection of sugar canes appear to have been made by Thompson and Edson, at Calumet Plantation, Louisiana, in 1890 to 1892. They first ascertained by a series of tests that if a cane was cut transversely into four equal portions, the juice of the third portion, counting from the base, represented in its composition the average of the juice from the cane as a whole. A number of canes were taken, the juice from the portion indicated of each analysed. Two groups of canes were selected, (a) those richest in sucrose—the “high canes,” (b) those poorest in sucrose—the “low canes,” and ordinary cuttings from the upper parts of these canes were planted. The following year the canes grown from the cuttings were reaped and analysed, and the results may be tabulated as follows:—

		Planted 1890.			Reaped 1891.
		Average of Sucrose per cent.			Average of Sucrose per cent.
High Canes ..	..	14·7	...	...	11·2
Low ,, ...	...	11·9	...	...	10·9

Very similar experiments have been made by Bovell and Harrison, and Bovell and d’Albuquerque in Barbados, Borame in Mauritius and Watts in Antigua. The work of Watts affords the most recent results and accordingly it will be convenient to summarize this. Watts’ experiments have been continued over four years, and have consisted in selecting a series of “high” and “low” canes respectively. Each year the ten richest *individual canes* from the “high” plot have been taken and the ten poorest from the “low” plot and three cuttings from each planted out to furnish the crop of the succeeding season, and as the result of the growth of these cuttings, there have usually been about 100 to 150 canes suitable for examination in each annual series. Canes of less than ten internodes are rejected, and of each of the others the portion below the middle of the fifth internode from the base is cut off and the composition of the juice ascertained.

The results obtained by Watts in his experiments between 1900 and 1904 are summarized by himself as follows:—

	Planted 1900.	Reaped 1901.	Planted 1901.	Reaped 1902.	Planted 1902.	Reaped 1903.	Planted 1903.	Reaped 1904.
“High” Canes ...	2.296	1.925	2.113	2.011	2.290	2.128	2.304	2.136
“Low” Canes ...	1.699	1.905	1.587	1.793	1.305	2.035	1.841	1.937
Difference on Canes Planted	0.597	—	0.526	—	0.985	—	0.463	—
Difference on Canes Reaped	—	0.020	—	0.218	—	0.093	—	0.199

The figures given throughout this table indicate the pounds of sucrose per gallon of juice in the basal portions of the canes analysed. In the column “Planted” is given the average sucrose per gallon contained in the basal portions of the ten canes from which the thirty cuttings were taken, whilst in the succeeding column, “Reaped,” is recorded the average sucrose per gallon in the basal portion of the canes (those of less than ten joints excepted) grown from these cuttings.

The sucrose contents of any variety of sugar cane differ greatly in successive seasons, one of the most important factors being the rainfall; a wet season resulting in juice comparatively poor in sucrose, whilst a dry season has the opposite effect. For this reason conclusions based on the results obtained in different years cannot be drawn. If, however, the theoretical considerations, sketched earlier, have been realized we should find that the differences between the “high” and “low” canes increase with the duration of the experiment, that is to say that the mean sucrose content of the “high” canes rises whilst that for the “low” canes falls. Taking the first and last terms of the series such a result is seen to have been obtained. In 1901 the “high” canes reaped contained 0.020 of sucrose per gallon of juice more than the “low” canes, and after three years of selection the “high” canes contained 0.199 of sucrose more than the “low” canes per gallon of juice. In other words whilst in 1901 the “high” canes were only 1.05 per cent. richer in sucrose than the “low” canes, three years chemical selection increased this advantage to 10.27 per cent.

On the other hand it must be remembered that the progress has not been uniform, the differences, expressed in pounds of sucrose, during the years of the experiment being 0.020, 0.218, 0.093,

and 0.199. Further evidence is needed, and is being sought, before any definite conclusions can be drawn as to whether this method is a reliable and practicable one for improving the sugar contents of a cane to the extent of raising races of cane superior to the original stock.

In the experiments conducted by Thompson and Edson, Bovell, Borame and Watts the unit of selection has throughout been the individual cane or stalk of which several are borne by each cane plant. It is possible that the individual canes of one plant vary considerably in sucrose contents, and that whilst one is rich the others are poor in sugar. Richness in sucrose of an individual cane might on this view be only an accidental circumstance and not necessarily a characteristic of the plant as a whole. Accordingly it is possible that it might be advisable to select *plants* rich in sucrose, rather than individual canes. This, in short, is the view of Kobus of Java and the following summary will indicate the evidence on which it is based and the results obtained by him, working along these lines.

Kobus first endeavoured to ascertain whether the percentage of sugar was constant or not in the different stems, or canes, of one plant. To this end he analysed about 500 canes belonging to 134 plants of "Fiji Cane." He found that the percentage of sugar varied considerably, that in fact in only a few plants were the differences less than two per cent., variations of three to four per cent. being more usual, and as much as seven to eight per cent. not uncommon. The following instances will suffice to indicate the variation found, the figures on each line referring to the individual canes of one plant:—

Percentage of Sucrose in the Canes of Separate Plants.						Variation.
15.42	15.38	14.12	9.94	8.74	—	6.68 %
13.52	12.14	6.92	—	—	—	6.60 „
5.74	9.24	11.22	8.42	13.76	6.76	8.02 „
12.52	13.40	13.02	—	—	—	0.88 „
12.26	12.02	12.68	—	—	—	0.64 „
14.74	14.64	14.10	—	—	—	0.64 „

Other varieties were also analysed and differences corres-

ponding to these found to occur in all, but greater variation was found in varieties which had been for a long time in cultivation than in newer varieties comparatively recently raised as seedling canes.

From these and other considerations Kobus came to the general decision that it was advisable to take plants and not separate canes as the selection units, and to experiment with varieties of sugar-cane which exhibited comparative small variations in their sucrose contents.

A large number of plants of a variety were analysed and cuttings taken from:—

(a) "High" plants, containing 14 per cent. and over of sucrose.

(b) "Low" plants, containing 10 per cent. and less of sucrose.

In the following year the plants grown from the cuttings were reaped and analysed, and the results obtained may be tabulated thus:—

FIJI CANE.

Sucrose per cent.	"High" Plants.		"Low" Plants.	
	No. of Plants.	Per Centage.	No. of Plants.	Per Centage.
3-4	—	—	1	0.3
4-5	—	—	—	—
5-6	—	—	2	0.6
6-7	—	—	4	1.2
7-8	1	0.3	8	2.5
8-9	8	2.7	19	5.8
9-10	13	4.4	34	10.4
10-11	27	9.2	52	16.0
11-12	40	13.6	63	19.3
12-13	46	15.6	63	19.3
13-14	70	23.8	51	15.6
14-15	49	16.7	12	3.7
15-16	32	10.9	17	5.2
16-17	8	2.7	1	0.3

In this experiment it will at once be noted results were obtained which approximate very closely to our preliminary theoretical considerations. By choosing canes comparatively rich and poor in sucrose, progeny was raised comprising in each case poor canes and rich canes, but those of the rich parent plants grouped themselves about a mean distinctly higher than that of the descendants of the poor parent plants. The means of the two series are indicated in the table above by the figures in italics. The actual mean sucrose content for the high series was 13·2 per cent. and for the low series 11·7 per cent.

Similar experiments were conducted by Kobus with other varieties of canes, with, on the whole, confirmatory results.

The following table shows the percentage of sucrose in the "high" and "low" plants obtained with plot experiments of seven varieties of canes. Careful precautions were taken in these experiments to ensure reliable, comparative results, but as to the nature of these space will not allow of entering here:—

Variety of Cane.	"High" Plants, Sucrose per cent.	"Low" Plants, Sucrose per cent.	Increase in Sucrose, per cent.
White Manilla ..	13·50	12·68	19·7
Black Manilla ...	16·62	15·70	27·9
Puri ... ..	14·74	10·54	43·1
Z·Z·100... ..	17·79	17·54	8·1
Chunnee ...	13·61	10·49	21·5
Cheribon ...	15·63	13·36	44·0

The experimental work on chemical selection has great interest if only for the information it has afforded as to the normal variation in chemical composition of the juice in plants of one variety of sugar cane, and in the individual canes springing from one plant. From the more strictly economic point of view the method, as shown above appears to afford a means of increasing the sucrose contents of a given variety. At any rate the results obtained, in whatever parts of the world experiments have been made, show that the selected canes rich in sucrose have uniformly given rise to progeny of higher sucrose content than the progeny of poor canes. As, however, in most other cases of highly cultivated

plants it must not be expected that, as the result of one or two years' work, races of canes will be obtained permanently richer in sugar than the stock from which they were derived. The selection must be continuous, and the principal practical lesson gained so far is that every cultivator of sugar cane should take care to select as the source of his future crop the best canes to hand.

(To be continued.)

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THE SPORANGIA OF *STAUROPTERIS OLDHAMIA*,  
BINNEY.

(*Rachiopteris oldhamia*, WILL.)

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THIS fossil was originally described by Binney, in January, 1872,<sup>1</sup> under the first name given above; it is, however, better known to botanists by Williamson's name, *Rachiopteris oldhamia*. The generic name *Rachiopteris*, was, as is well known, adopted by Williamson as a common designation for Fern-like petioles and stems with structure preserved. The heterogeneous group thus constituted has proved of some temporary utility, but is clearly destined to be again broken up, as our knowledge of the various types embraced in it becomes more advanced. In the present instance, as we are now in a position to describe the fructification (or at least a fructification) of the plant, the time has evidently come to remove it from the *Rachiopteris* lumber-room, and re-instate the species in its own genus, so appropriately named by its discoverer.<sup>2</sup>

*Stauropteris oldhamia* is one of the commonest fossils in the calcareous nodules of the Lancashire and Yorkshire Coal-Measures. The main features in its structure were described by Williamson in 1874.<sup>3</sup> Although the word "stem" is employed in his description,

<sup>1</sup> Proceedings of the Manchester Literary and Philosophical Society, 1872.

<sup>2</sup> σταυρῶς, a cross.

<sup>3</sup> On the Organization of the Fossil Plants of the Coal-Measures, Part VI., Phil. Trans. R. Soc. Vol. 164, p. 685, Figs. 20--27. The fossil was subsequently described by Felix, Untersuchungen über den inneren Bau Westfälischer Carbonpflanzen, 1886. Abhandl. d. k. geolog. Landesanstalt Bd. 7, Heft. 3, Berlin, p. 13.

there is no reason to doubt that the whole structure as known to us at present, is nothing but the highly ramified petiole and rachis of a compound frond. The stem on which it was borne is still to be discovered.

The large petioles, 3 mm. or more in diameter, show, in transverse section, the well-known cruciate form of the xylem, described and figured by Williamson, the character on which Binney's generic name was based. The general form of the stele, as a whole, is approximately square, the phloem filling up the bays between the xylem-arms, and sometimes extending to the middle, so as to more or less completely break up the wood.

Though 4-armed the wood is not properly described as tetrarch, for there are often at least two groups of small elements, no doubt the protoxylem, at the periphery of each arm. The tracheides are scalariform; Williamson was unable to detect any true spirals, but they occur, though sparingly, at the protoxylem-angles.

The phloem contains large sieve-tubes, often well-preserved, and showing the sieve-plates on their lateral walls very plainly. They are of the usual Fern-type.

Leaving the pericycle and endodermis for consideration on another occasion, we may pass on to the cortex. This consists of long cells, often trumpet-shaped at the ends; the outer layers are, as a rule, narrower and more sclerotic than the inner. In well-preserved specimens the periphery of the rachis is occupied by a zone of delicate, lacunar tissue, the cells of which are often radially elongated, like a very lax palisade. This zone is bounded by the epidermis, in which scattered stomata are found. The whole no doubt constituted the assimilating tissue of the rachis, which, as we shall see, was very necessary in the absence of vegetative leaflets. The assimilating tissue extends onto branches of all orders, and may even be found on the fine ultimate ramifications which bear the sporangia (Fig. 2c). The rachis is abundantly and repeatedly branched, and as Williamson showed, the branches are given off in pairs, both branches of the pair springing from the same side of the parent-axis.<sup>1</sup> The branches are of various orders; those of intermediate dimensions commonly have a three-armed, instead of a four-armed xylem, and the two structures are often found in connection, as figured by Williamson.<sup>2</sup> The ultimate ramifications are excessively delicate, from  $150\mu$  to  $200\mu$  in diameter.<sup>3</sup>

<sup>1</sup> Williamson, loc. cit., p. 687, Figs. 25A and B, 26.

<sup>2</sup> Loc. cit., Fig. 26.

<sup>3</sup> Williamson, loc. cit., p. 686, Fig. 24.

These little branchlets, described by Williamson as "more like the ultimate fibre of a root than a stem," are present, in most of the sections, in countless numbers, occurring in dense, faggot-like groups. They are found in direct connection with the typical triareh branches from which they spring, so that the relation between the various orders of ramification, as parts of the same frond, is clear throughout.

The minute branchlets themselves undergo branching, but without much further diminution in size.

It is rare to find any sign of vegetative leaflets accompanying the rachis of *Stauropteris*, and where such structures are found there is so far no proof that they belong to our plant. Their absence was noticed by Williamson, who speaks of "not discovering any trace of a leaf [leaflet] or leaf-attachment" (p. 687). He adds: "If they bore leaves they must have been very small terminal ones, resembling in their position those of some of the *Adiantums*." For this hypothetical suggestion, however, there is still no evidence. All the appearances point to the frond, as it commonly occurs, having been merely a compound naked rachis, destitute of any laminar expansions. The conclusion is at once suggested that such a frond could only have been a fertile one.



Fig. 1. *Stauropteris oldhamia*, Binney. Empty sporangium borne terminally on an ultimate branchlet of the rachis, in which the vascular bundle is seen.  $\times 37$ . From a photograph by Mr. L. A. Boodle. London University Collection, 77. From Oldham, Lanes.

In a large majority of the sections of *Stauropteris oldhamia* sporangia are present, often in considerable numbers, and, so far as I have observed, all of the same type. These sporangia are often

fragmentary, but in many cases are exceedingly well preserved, still containing their spores. I have been acquainted with these sporangia for the last ten years, but have only recently obtained proof of their connection with *Stauropteris*. In several instances, four of which are figured in the present paper, the sporangia are found attached terminally to the finest branches of the rachis. This is clear in Fig. 1, from a photograph. The vascular bundle of the fertile branchlet is seen at two places, and the structure is in all respects that of the ordinary ultimate ramifications of the rachis. In this case the sporangium is empty.

In Fig. 2A, the connection of the branchlet with the sporangium is very well shown, the tissues of the one organ passing over quite continuously into those of the other. The sporangium itself is here in an excellent state of preservation and full of spores.

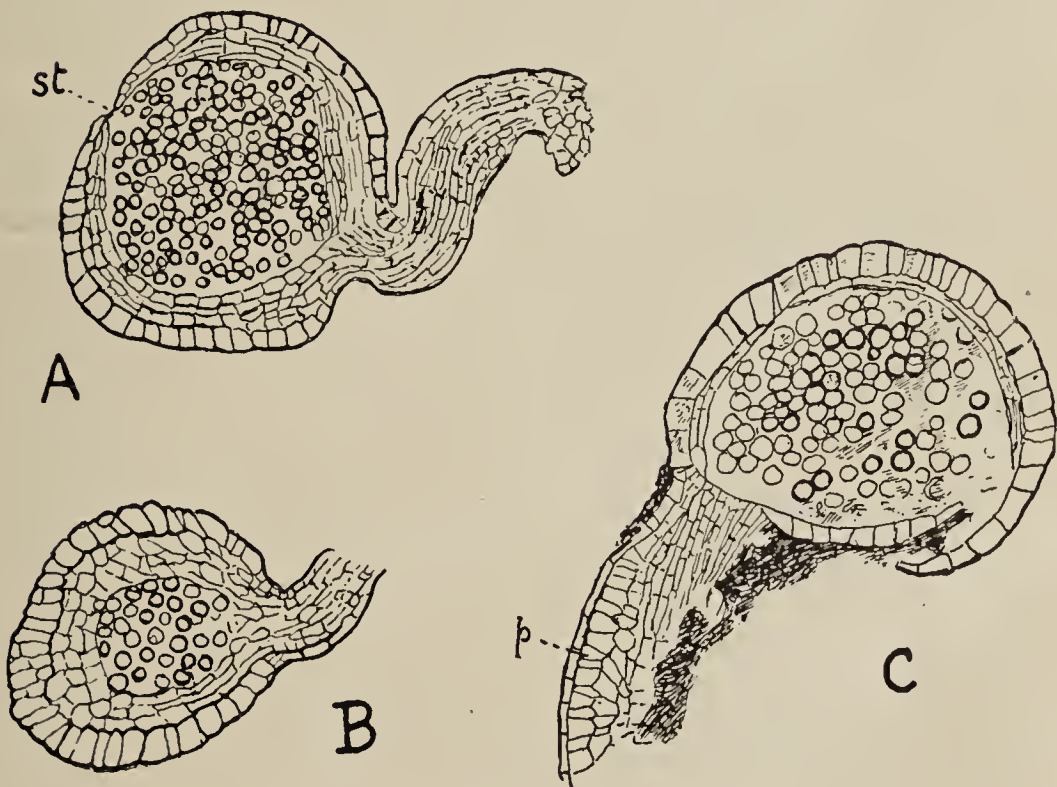


Fig. 2. *Stauropteris oldhamia*, Binney. A.—Sporangium in nearly median section, attached terminally to an ultimate branchlet of the rachis. *st.*, stomium, Scott Coll., 2213. B.—Sporangium in tangential section, attached to a short piece of a branchlet. Scott Coll., 2207. C.—Sporangium with wall burst, attached as before. *p.*, palisade tissue of branchlet. Scott Coll., 2219. All figures  $\times$  about 50. From sketches by Mrs. D. H. Scott. The specimens are from Shore Littleborough, Lancs.

Fig. 2c, again shows the connection between sporangium and rachis quite clearly. The branchlet bearing the sporangium is damaged on one side, but on the other the continuity of its epidermis with the sporangial wall is especially evident. This

section is of interest as showing the palisade-like hypodermal layers of the branchlet; the tissue is, however, denser in this position than on the larger branches of the rachis. Here, again, the sporangium is full of well-preserved spores.

In the specimen represented in Fig 2B, only a short piece of the rachis bearing the sporangium is preserved, but the continuity of the tissues is especially well shown. In this case the sporangium is cut tangentially, so that only a comparatively small part of the spore-containing cavity is exposed.

A few details as to the sporangia themselves may now be added.

In form the sporangium is nearly spherical; in six sporangia measured the average dimensions were  $740\mu \times 640\mu$ . The larger diameter is sometimes transverse, sometimes longitudinal, and we cannot suppose that the exact natural form is retained. The natural dimensions may have been slightly in excess of those given, as the sections would seldom be precisely median.

The outer layer of the sporangial wall is formed of square or columnar cells about  $50\mu$  in height, the width varying from  $24\mu$  to nearly  $50\mu$ . Nothing of the nature of an annulus has been observed in any of the numerous sections examined, but on the side opposite the attachment of the sporangium there is a well-marked stomium of small cells only about  $20\mu$  in height (Fig. 2A). In some cases the dehiscence of the sporangium through the stomium is clearly shown.<sup>1</sup> In all well-preserved specimens there is a fairly thick lining tissue within the outer wall; it consists of several layers of small thin-walled cells, and seems to have been interrupted only at the stomium. The lining tissue is continuous below with the parenchyma of the supporting rachis. Remains of this tissue are found even in old and empty sporangia (Fig. 1). The spores are approximately spherical in form, with a diameter of  $32-40\mu$ . The wall is smooth; in favourable cases the triradiate marking can be clearly recognized, indicating that the spores were of the tetrahedral type. No indications of a multicellular structure have been detected.

The results of the present preliminary investigation, which I hope before long to be able to pursue further, may be summed up as follows:—

*Stauropteris oldhamia*, Binney, in the form in which it

<sup>1</sup> In Fig. 2c, however, it is doubtful whether the bursting of the sporangium was natural.

commonly occurs, was a fertile frond, consisting of a highly compound rachis, without leaflets.

The sporangia were borne on the numerous fine ultimate ramifications of the rachis, each sporangium being seated terminally on a long branchlet.

The sporangia have a terminal stomium, but no annulus. The wall is several cells thick.

The numerous spores are spherical and of the tetrahedral or radial type.

Williamson, in 1874, discussed the question whether his *Rachiopteris oldhamia* was a Fern or a Lycopod, and rightly came to the conclusion that the balance of evidence pointed to its being a Fern, though, as already mentioned, he was puzzled by the absence of leaflets. The Lycopods no longer come into the question, but we may well hesitate whether to refer our fossil to the true Ferns or to the Pteridospermæ.

The general structure of the rachis is altogether Fern-like, but not more so than in a typical Pteridosperm such as *Lyginodendron*. The scalariform structure of the tracheides might be cited as a Filicinian character, but this is really of no weight; in the foliar bundles of *Medullosa anglica*, for example, scalariform tracheides completely replace the pitted elements which are so abundant in the steles of the stem.<sup>1</sup> From the characters of the rachis, in fact, no conclusion can be drawn. The sporangia bear a general resemblance to exannulate sporangia of Ferns, but present no features sufficiently characteristic to settle the question, especially while we are still so ignorant of the structure of the pollen-sacs of the Pteridosperms. The way in which the sporangia are borne, terminating long and slender branchlets of the rachis, cannot probably be paralleled among recent Ferns; among fossils the nearest known analogy is offered by the fructification of *Zygopteris*,<sup>2</sup> where the sporangia are likewise borne terminally, though on much shorter ultimate branches of the rachis than in our plant. *Zygopteris* and the other Botryopteridæ still rank among true Ferns, though their position is not, perhaps absolutely secure. On present evidence the systematic position of *Stauropteris* must remain an open question. That it shows affinity with the Ferns is certain, but it would not be surprising to find that, like so many

<sup>1</sup> Scott, Structure and Affinities of Fossil Plants from the Palaeozoic Rocks, III. On *Medullosa anglica*, Phil. Trans. R. S., B. vol. 191 (1899), p. 95.

<sup>2</sup> Renault, Cours de Bot. Fossile, Vol. 3, Pl. 16, Fig. 3, 1883.

other Fern-like plants of its period, it had crossed the Spermophytic frontier, so that its sporangia described above were in reality of the nature of pollen-sacs.

All the sections were prepared by Mr. Lomax, of Bolton.

I am indebted to Mr. L. A. Boodle, F.L.S. for the photograph reproduced in Fig. 1, and to my wife, Mrs. D. H. Scott, F.L.S., for the sketches in Fig. 2, A—C.

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### THE BIOLOGICAL LIMITATIONS OF THE METHOD OF PURE CULTURE.

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THE use of pure cultural methods in the study of the lower organisms has been a late development, but it has been adopted with an eagerness and practised with a faith that is not surprising when one reflects that all recent advance in certain sections of biology has been rendered possible by its means. When bacteria, for example, first became objects of special study, progress was slow and uncertain, and it became evident that some such method was absolutely essential. Previous to the use of plate-cultures with solid media by Robert Koch, a pure culture had rarely been obtained; afterwards the science of bacteriology progressed by leaps and bounds, for Koch's method furnished a means, simple as it was efficient, whereby single individuals in a mixture of bacteria could be separated and kept apart, while each grew and reproduced independently. Colonies were thus formed which consisted of one species alone and which were large enough to be successfully manipulated and propagated further in pure culture.

It is surprising that a similar method should not have been already practised more extensively in the study of other groups. In the case of the lower green algae, for example, great confusion has existed as to the proper identity and morphological relations of many forms. To attack such problems there was no need to wait for such an epoch-making discovery as that of Robert Koch, for the aim of the worker would have been merely to trace the life history of the species in question apart from other forms with which it might be confounded morphologically; in such cases a strictly pure culture is not necessary or desirable, and cultures sufficiently pure for the purpose can be obtained by comparatively simple means. In the case of bacteria, on the other hand, a class

containing vast groups of organisms morphologically indistinguishable from each other, and only to be separated by their behaviour, it is necessary to obtain the object of study absolutely alone. Of course the same necessity holds for all cases in which the nutrition of the organism is the subject of investigation. It is much to be desired that the chemical physiology of many of the lower organisms, about whose nutrition we have little or no exact knowledge, should be worked out in this way.

The study of bacteria, in so far as it has hitherto proved successful, has concerned itself almost entirely with the investigation of the group in strictly pure culture, and the enormous amount of valuable research, completed in so extraordinarily short a time, is largely due to the fact that this modern branch of science was attacked, in this respect, in so scientific a spirit.

At the same time it should be recognised that the pure culture of an organism does not always furnish a satisfactory condition for the complete elucidation of its physiological activity. The bacteria which have been studied with the greatest enthusiasm are certain specialised groups possessing pathogenic properties when living as parasites upon certain animals; and in many such cases the pure culture method seems very adequate. For when developing to such an extent as to cause disease in the highly specialised medium provided by the host, such organisms are existing in a culture that is practically pure; hence the study of these bacteria in pure culture is an approximation in this respect, to the conditions obtaining in nature, or at least in that part of their life-history of most importance to us.<sup>1</sup>

But there are many other classes of bacteria which do not exist in a condition approaching isolation in nature. Such are the vast groups of non-parasitic forms which carry on important processes in the soil, in the sea, in rivers, etc. For the study of such organisms it must be allowed that the method of pure cultures is strikingly artificial and that one must not therefore be disappointed if in using such a method one fails to elucidate their natural activity, or to reproduce in the laboratory the phenomena occurring in the field. Bacteria concerned with important processes in the soil, for example, have been found, when studied in pure culture, to yield most unexpected and apparently contradictory results, which may doubtless be traced to this artificial change

<sup>1</sup> Of course the life-history of pathogenic bacteria outside the host is also a subject of very great importance, and to this different conditions necessarily apply.

of environment, and it is certain that our knowledge of these organisms would be materially advanced if attempts were also made to study them when associated with the forms accompanying them in nature. Hitherto this has rarely been done, but the following examples may serve to illustrate the point.

In 1895, Winogradsky isolated from the soil *Clostridium pasteurianum*, an organism which possessed the specific property of fixing free nitrogen from the air. Before the isolation was completed, a stage was reached when the investigator was working with a mixture of three microbes only, two bacteria, and the *Clostridium* which proved to be the nitrogen-fixing agent. The culture was robust, fixed nitrogen with ease, and continued to do so throughout a series of generations. A separation of the mixture was then attempted and pure cultures of the two bacteria were easily obtained, but neither when together or alone, could either of them fix the nitrogen of the air, or develop in a culture fluid deprived of combined nitrogen. The *Clostridium*, on the other hand, was isolated with the greatest difficulty; satisfactory pure cultures were at last obtained, but only when cultivated under strictly anaerobic conditions, and these cultures could only be induced to grow and fix free nitrogen if air were excluded and nitrogen were caused to bubble continuously through the culture-fluid. This striking difference between the external conditions required by *Clostridium pasteurianum* when growing in nature, as contrasted with a pure culture, must find explanation in the result of some symbiosis with other organisms, and Winogradsky was able, as a consequence of work with mixed cultures, to offer the following solution. *Clostridium pasteurianum*, itself a strictly anaerobic organism can flourish and do its work under aerobic conditions if associated with an extremely aerobic species which absorbs the oxygen of the air with energy, thus creating an anaerobic environment for the *Clostridium*. Such associate or associates, moreover, themselves unable to assimilate free nitrogen, can in their turn feed upon the nitrogen fixed and elaborated by *Clostridium pasteurianum*.

The organisms concerned with nitrification in the soil may be taken as a second example. These bacteria are of two classes, the first attacks the ammonia and converts it to nitrites, while the second completes the oxidation to nitrates. Their study in pure culture presents great technical difficulties from the surprising fact that they are unable on account of the organic matter present, to grow upon the culture-media ordinarily employed in bacteriological

study, and they were first isolated by Winogradsky upon media composed of a silica-jelly impregnated with certain inorganic salts. The detailed further study of the pure cultures proved them to be highly susceptible even to traces of organic matter which might be in their neighbourhood, and this fact, surprising enough in the case of soil organisms, has been found also true of the organisms concerned with nitrification in sewage filters, where the amount of organic matter accumulated is comparatively large. An explanation for such an apparent anomaly may doubtless again be found in the artificial conditions obtaining when these organisms are separated from the others accompanying them in nature, and this view was in one case experimentally confirmed as follows. The organism in question, isolated from a sewage filter, was concerned with the oxidation of nitrite to nitrate, and when in pure culture was quite unable to grow in bouillon; inoculated culture tubes remained indefinitely without sign of growth, and on re-inoculation into a nitrite-containing medium no oxidation occurred, shewing that the organism had perished. This *Nitrobacter* was accompanied in nature by, and separated with difficulty from, an extremely small bacillus, which was not a nitrate-producer, and grew abundantly in bouillon and other nutrient media. The mixed culture of these two organisms proved very instructive. When inoculated into bouillon a copious growth occurred, and after six days the growth was sub-cultured into an inorganic nitrite-containing medium and also into fresh bouillon. After another six days the second bouillon culture was similarly treated and the operation repeated four times. It was found that even after four successive generations in bouillon, the inoculated nitrite medium showed production of nitrate, and one is forced to conclude that the *Nitrobacter* was able, under these conditions, not only to survive inoculation into bouillon, but even to multiply there. This behaviour of the *Nitrobacter* must clearly be attributed to the presence of the accompanying organism, which in some way protects it from substances present by which its growth would otherwise be inhibited. How this protection is compassed is at present quite unknown, but we cannot too strongly insist on the importance of attempting to study more closely such cases of symbiosis, which abound in nature.

The pure culture then, in such instances, is only a stage—though a necessary one—in the evolution of a perfectly scientific method of study. It is obvious that the next step should be to reproduce nature more exactly, by making and studying *mixtures* of

pure cultures. These would increase in numbers and complexity as the science develops, and we might then expect to be in a position to investigate bacterial processes, as they occur in nature, more fairly and with greater success.

HARRIETTE CHICK.

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## THE PRINCIPLES OF MORPHOLOGY.—I.

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### INTRODUCTION.

It is by a study of the evolution of the forms of life composing the vegetable kingdom that the science of morphology has been gradually built up. It is a study exceedingly important in itself, and quite distinct from that of physiology, which deals solely with the functions which those various structures perform.

The principles of morphology are the inherent and essential laws governing the production of form in the vegetable world, which we deduce by means of a study of the *phylogenetic* sequence<sup>1</sup> (or what we regard as such) of forms, through family after family of plants.

As regards the external conformation of the typical plant, I believe myself that an exceedingly limited number of fundamentally discrete and individually distinctive organs (*organs sui generis*) occur which have been laid down as such from nearly the commencement of the plant's evolution, viz. the *caulome*, *phyllome*, and *rhizome*,<sup>2</sup> for it seems quite possible to trace these under their innumerable and infinitely varying forms from the earliest and most primitive types onward to the very highest; and not only that, but also along all the distinct phyla into which the Vegetable Kingdom has become split. And hence, to take an illustration, we should expect *homologous* organs to occur, in each of the great phyla, Lycopods, Equisetaceæ, Ferns and Flowering Plants, at *every stage* in the individual life-history of the plant. The "morphology" of any doubtful organ would hence be often arrived at by means of a close *comparative* study of related organs (or what we regard as such) throughout the entire range of vascular plants. This comparison must necessarily be exceedingly fundamental and

<sup>1</sup> It is just here where, in the absence of perfect *objective continuity* of the forms concerned, the *subjective* interpretation of such facts as are available, plays so predominant a part.

<sup>2</sup> This word is here used in its literal, original sense, not in that of our text-books.

uninfluenced by prejudiced conceptions of the phylogeny of any particular group. I believe also that teratological phenomena are in this direction very helpful, for in these strictly-limited manifestations of morphological law, we find the organs assuming forms, the replicas of which will be found for the searching in other departments of vegetable life. The facts of *individual development* will also sometimes be of use, but very often also misleading, on account of the fact that many of the recapitulative stages derived from the race-history are missed out owing to the abbreviated course taken by the ontogeny.

It is, then, owing to the stereotyped fixity of the three categories of organs, whereby no obliteration of the distinctive boundaries of each, *i.e.* no fusion or confusion of any two categories, ever takes place, that a definite science of morphology becomes possible. Each type of organ, whether caulome, phyllome or rhizome, has evolved, through infinite variation, along its own line, diverging away from each of the other types, precisely in the same way as genera and species of plants have evolved into distinctive entities. In any particular case, where it is especially difficult or impossible to determine the morphological nature of an organ, this must be attributed solely to our own ignorance and inability to trace all the stages in modification which the particular organ in question has undergone during the period of its evolution.

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## THE ORIGIN OF THE VASCULAR PLANT.

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### I. THE ALTERNATION OF GENERATIONS.

**T**HE vegetable kingdom, doubtless, was at one time constituted solely of *unicellular* organisms which eventually gave rise by successive cell-divisions both to the *filamentous* and *lamelliform* types. Filamentous aggregations, forming so-called *individual plants*, were produced by branching of these filaments; yet multiplication of the thallus also eventually occurred by means of tissue-formation, either in the form of a true tissue, as in Liverworts and Mosses, or of a false tissue, such as that of Seaweeds and Fungi. The thallus of these early plant-types assumes various forms; it is either dorsiventral, as in Liverworts; cylindrical, as in the Mushroom-stalk and prothallus of some Lycopods; partly cylindrical and partly isobilateral, as in Brown Seaweeds, or filamentous, as in many Algæ, Fungi, Prothalli, and the Moss-protonema.

The most primitive unicellular plants were almost certainly *asexual*, the *sexual* character being a subsequent modification; for the undifferentiated must precede the differentiated along the main path of evolution; and the very earliest and most important form which differentiation assumes is the production of the two opposite yet complementary poles: the positive and negative, or male and female sex, by the blending of which the greatest amount of vitality and capacity for variation is infused into the product.

Now, the asexual unicellular forms most probably have given rise to *asexual filamentous* organisms, and these must have been the earliest progenitors of all filamentous Algæ<sup>1</sup> with which we are acquainted to-day. Sooner or later, however, sex also arose in these filamentous and other thalloid forms; it is a noticeable fact that in thallus-forming plants both sexes occur as a rule on the same plant.

There can be no doubt that the spermatozoid and oogonial cell of certain more advanced filamentous Algæ, e.g. *Vaucheria*, are the exact homologues of the free-swimming male and female gametes of other more primitive forms, such as *Ulothrix*. In any case, in the primitive forms the result of fertilisation was (at any rate frequently), the germination of the zygospore *directly* into a new filamentous plant which was *asexual*, inasmuch as it did not produce sexual organs but, on the contrary, neutral *zoospores*. Each of these latter, on germination, produced the sexual plant once again. Here we see a distinct *alternation of generations*; but it is an *homologous* alternation of generations, *viz.*, between a neutral or gonidial and a sexual or oogonial generation respectively; the two generations are homologous because both exhibit the same mode and habit of growth in every respect, they are precisely the same plants differing only in the character of their reproductive organs. Examples are afforded by *Ulothrix*, *Vaucheria*, *Dictyota*, &c. amongst the Algæ. A very interesting example of this method of alternation is found in the Moss, where the primitive asexual filamentous *protonema* gives rise (herein exhibiting a striking adaptation to its acquired land-habitat) by *vegetative budding*, and no longer by zoospores, to the leafy Moss-plant.<sup>2</sup> Yet another instance of this homologous alternation of generations is to be observed in the higher Fungi and Floridæ; in the former the ascus and basidium and in the latter the carpo-

<sup>1</sup> I use this term to include also all primitive Fungi.

<sup>2</sup> Here the two generations differ altogether in habit and mode of growth; nevertheless they are clearly equivalent to the two generations constituting the homologous alternation in the Algæ.

spore, are to be regarded as the equivalents of the archegonium and oogonium in Muscineæ and Algæ. In the two latter groups the investment or wall of the female organ is formed before fertilisation; in the former groups (Fungi and Florideæ) it is formed subsequent to that process, this being analogous to the varying periods of formation of the endosperm in Gymnosperms and Angiosperms. There exists no sufficient difference between the two generations here produced to render it other than a case of homologous alternation of generations in these plants.

This probably represented the cycle of life for many an age. The fact that, as in *Vaucheria*, the two generations blend at certain points, or that, as Klebs has shewn, either can be produced at will by modifying the immediate conditions of life, does not affect the reality of the presence of the above-described alternation of generations, for these *secondary* modifications are just what might be expected to occur in such plastic organisms as these primitive Algæ. In *Edogonium* the neutral generation, as an independent stage, has been cut out of the life-cycle, and the oospore divides directly into four zoospores, each of which reproduces the sexual plant. This zoospore-formation in the oospore represents the first faint fore-shadowing of an entirely new generation in the life-cycle, *viz.*, that which Celakovsky has termed the "antiphyte" or the "antithetic" generation. In *Coleochæte* this suggestion of the new generation is to hand in plainer terms, for the contents of the oospore divide up into a small parenchymatous tissue from each cell of which a zoospore is rounded off which, escaping, the empty cell-frame-work is left behind, thus differing from *Edogonium* in which each *entire* cell itself becomes a zoospore. Yet in *Coleochæte* the actuality of a new antithetic generation is not attained; the complete absence of a limiting wall of sterile cells debarring this structure from attaining to the rank of anything resembling a *unity* in itself. This distinction has been reserved for *Riccia*, the most primitive of the Bryophytes, in which we discover the first appearance, in its lowest terms of simplicity, of the antithetic sporophyte generation.<sup>1</sup> In the higher Liverworts and in the Mosses this sporangium became much more elaborated, and became, although remaining attached to the thallus, a distinct plant of an *entirely new type*. For, in the first place, the *mode of growth*, i.e. the method of tissue-formation and

<sup>1</sup> Hence the above-described structures in *Edogonium* and *Coleochæte* represent the actual and real *progenitors* of the antiphytic generation which is, therefore, very far from arising *ex nihilo* or from being a "morphological Melchisedec," as Scott so strangely imagines.

the entire habit, secondly, the function of spore-production or fructification, stamp this sporophyte generation as *antithetic* when compared with the so totally different and vegetative sexual generation. Nevertheless, the two generations are but two opposed and complementary phases, the two poles, the active and passive, vegetative and fruiting, of a single, individual life-cycle, which is a unity in itself. To one who clearly fathoms the real meaning of this antithetic alternation of generations the whole of the opposition offered to it by the supporters of the "homologous" view seems utterly wasted and beside the point; it is the same as saying that night and day are identical; fundamentally, the two generations are in no other sense antithetic to one another than are the two periods of night and day; for different functions correspondingly different structures and different qualities are required, and nothing could be more antithetic than the respective functions of the sexual and sporophyte generations.

The Fern-plant may sometimes arise from a vegetative cell of the prothallus instead of from the fertilised egg-cell; sporangia may arise on it, indicating the presence of a latent Fern-plant springing from vegetative tissue of the thallus; these facts cannot possibly disturb the *antithetic* relationships of Fern-plant and prothallus. It simply has nothing to do with the matter. Protonemal filaments may occasionally arise from *inner stalk-cells* of the Moss-sporogonium; this is due to the fact that these cells are *sterilised spores* which are merely reverting back to their primitive function; Pringsheim never succeeded in inducing sprouting of the superficial cells of the stalk, for these were the earliest to lose the reproductive function.<sup>1</sup> All these *abnormal* happenings, as well as those of apospory in Ferns, do not, to my mind, touch in any conceivable way, the question of alternation of antithetic generations. Those who believe that the facts of apogamy, for instance, prove the existence of an *homology* between the two generations, surely completely misunderstand what we really mean by *antithetic alternation*! These very interesting abnormal cases merely prove, to my mind, that the two generations are very intimately related (yet not homologously)

<sup>1</sup> It is merely the character of the individual cells or cell-groups, producing the apogamous or aposporous individuals, not that of the generations themselves, which is affected by these occurrences. These latter tend, on the contrary, to strengthen the view of antithetic alternation which could only be overthrown if it could be demonstrated that a prothallus ever developed from an archegonial cell, or that a sporogonium could ever arise from a spore or from a chopped-up sporogonial-stalk! This has never yet been accomplished.

and represent the two *opposed* facets of the dual whole, each with its distinctive character and function. At first the sporophyte generation is subsidiary in development to the sexual, as in the Bryophytes. Gradually, for purposes of economy, the pendulum swung to the other extreme as the sporophyte evolved apace, until, as in the Fern, nothing could be more striking than the contrast exhibited between the sexual "prothallus" and the strong-growing neutral Fern-plant. Are these homologous? Finally, the sexual generation, as in Phanerogams, entirely lost its footing as an independent plant, and became completely absorbed into the sporophyte; and there it is unto this day.

In the antiphytic generation there obtains an interesting *homologous* alternation of generations between the different kinds of shoots on one and the same plant, *viz.*, between the vegetative and the reproductive shoots; here, as in the homologous generations of the Algæ, the distinct generations agree as to their mode of development and habit, yet differ widely in their respective functions.

## II. ORIGIN OF THE SPOROPHYTIC SHOOT.

As all higher vascular plants must belong to the *antiphytic* generation we must now enquire how the primitive sporogonium gave rise to the leafy shoot. Bower's hypothesis is this: that sterilisation of the sporogonial head occurred, such that the sporogenous became transformed into vegetative tissue; further that this sporogonium became itself the *main axis* of the future stem, while lateral appendages, the future foliar members, were formed by means of *lateral projections* into space from the said sporogonium, to which the sporogenous tissue became relegated. Now this view seems to me quite untenable. For Bower clearly endows the modern foliar organ with the character of a "morphological Melchisedec." That such a highly-distinctive, morphologically-concrete and assertive organ as the "phyllome," should have had no parentage, *i.e.* should have developed, *unlike all other known organs*, out of no pre-existing organ which in any degree whatsoever resembled it in character—this appears highly unnatural; no analogy for it is anywhere to be found. It is surely quite an artificial conception of phylogenetic origins which we are asked to entertain. No! the primitive foliar organ could only have arisen by means of easy transformation out of an organ *not altogether dissimilar* from it which was already on the scene; and this organ was the sporogonial capsule. This process is very different from that of the *projection* from the

capsule of a number of *entirely new* organs, a manœuvre to which the capsule would have been up to that time a complete stranger! Bower also, I think, places the cart before the horse in taking as his model for the protrusion-theory the ontogenetic origin of lateral leaf-members on the axis of the higher plants. Surely ontogeny must take its clue from phylogeny, and not *vice-versâ*.

The facts of embryology yield us all the clue we need for discovering the truth. In Jungermanniaceæ the epibasal quadrants in the embryo give rise to the capsule or sporogonial head; in Monocotyledons the same two quadrants give rise to the *cotyledon*, which is therefore *terminal*. In *Ceratopteris*, a Fern, the epibasal quadrants also are used up in forming the terminal cotyledon. Hence it is clear that sporogonial capsule and the cotyledon of the Monocotyledons and *Ceratopteris* are each and all homologous structures. By dichotomous branching, the Dicotyledonous embryo produces a cotyledon from *each* of the epibasal quadrants or from the whole embryonic head<sup>1</sup>. This leads me to remark that it is certain that the Dicotyledons are not so far removed from the Monocotyledons as to make the embryological history of both is anything but similar. It can hardly be so different in the two classes as is usually supposed. We know now several Dicotyledons which have a single entire cotyledon or in which the single cotyledon is forked more or less deeply<sup>1</sup>; in some cases also it is in a direct line with the hypocotyl. In almost all cases, in both classes, the cotyledons arise long before the existence of any axis on which they could be borne as lateral appendages: this agrees with the phyton- or sporogonial theory, but not with the lateral appendage hypothesis; and this axis does not assert itself until quite a late period in the Monocotyledons. If the development of the Dicotyledonous embryo is to be regarded as resembling in any degree that of the Monocotyledonous embryo, the single cotyledon must, in the former group, have dichotomized to form the normal two members and the plumular shoot must be considered as arising in a position *lateral* to *both* cotyledons, and therefore, exactly between the two; yet it is the dichotomized cotyledon, and not the plumular shoot, which is to be regarded as primarily terminal to the hypocotyl. The *actual* ontogenetically terminal position of the plumule is a *secondary* adaptation; in some plants we see also how it becomes enclosed in the basal sheathing portion of a single, tubular cotyledon, which is terminal to the hypocotyl.

<sup>1</sup> This is exactly comparable to the forking of the sporogonial head observed in *Diphyscium foliosum*.

On this subject I am obliged to differ radically from the entire point of view assumed by Miss Sargent in her monograph of Monocotyledonous seedlings.

In most Pteridophytes and in the Moss a single quadrant is employed in forming the cotyledon and capsule respectively; here again therefore we see the homology between these two organs. The primitive type is obviously the perfectly terminal capsule. And we may take the Monocotyledonous embryo with its terminal cotyledon as representing the primitive type in Angiosperms, and the subsequent formation of the leafy stem from it will be an index to that of the leafy stem from the original sporogonium in the case of Cormophytes generally. From the hypocotyl of the Monocotyledonous embryo arises a second shoot-member ("Sprossglied") quite comparable to the first, consisting of terminal leaf and basal stem-segment ("Stengelglied"); from this a third arises, and so on, until finally an apical growing point arises on the axis, which asserts itself *precociously* time after time, *i.e.* before the morphologically-terminal leaf of each stage of the sympodium has had time to develop. The primitive sympodium with its perfectly terminal leaf at each successive stage thus becomes merged into the purely secondary monopodium in which a central main axis predominates, bearing the leaves in a lateral position. This monopodial construction, however, is a *pure illusion*, the phantasmagoria which has led away the majority of botanists on the most unwitting of wild-goose chases. The fact is we need to entirely amend our artificial conception of a leaf as a purely lateral appendage to an axis. We are misled all along the line into believing these *secondary* modifications to be the original types. Nothing, to my mind, is more natural and reasonable than the conception of our modern leafy stem having arisen out of the sympodial *repetition* of a number of sporogonial heads, each stem-segment being the homologue of a seta and each leaf that of a capsule.<sup>1</sup>

But I may here emphasize the belief that as in *Riccia*, the most primitive Liverwort, the *entire* embryo forms the capsule, it becomes highly probable that the next most primitive type is that of Jungermanniaceæ and *Ceratopteris*, in which the epibasal half of the embryo gives rise to the capsule, while phylogenetically later

<sup>1</sup> The antagonists of this view have a favourite way of maintaining that *no evidence* is available in support of it; this is a complete mistake: the evidence is not only present, but to my own mind, clear and convincing, *viz.* that of *embryological data*, which have been given above at sufficient length for my purpose.

stages are afforded by such types as the Fern and *Equisetum*, in which the cotyledons are relegated to a more and more restricted area of the epibasal region. It is possible that the primitive condition of *Ceratopteris* has been *retained* owing to its aquatic habit; in view of my belief that the Monocotyledons as a class are in many ways so much more primitive than Dicotyledons, *viz.*, in their vascular anatomy, mechanical strengthening apparatus of the stem, construction of flower, etc., I hold the idea of the cotyledon as being the result of fusion of two organs as untenable and highly unlikely. The facts of *comparative embryological* history are, in my opinion, as valuable evidence as any other for deciding the morphology of an organ; at this early stage modifications and later adaptations have often not had time to assert themselves and, more or less clearly, the phylogenetic history is recapitulated. This is an instance in which phylogeny must take its clue from ontogeny, being the converse of what I stated above.

This being the mode of development it follows that the primitive foliar organ was a *fertile sporophyll* and that the vegetative leaf is a purely secondary structure. Also that the primitive foliar organ possessed *radial* symmetry of construction and that the dorsiventral character is a secondary one. And this for the reason that the primitive leaf was a *terminal* organ. The former we see still retained in the sporophylls of *Ginkgo*, the female sporophylls of *Bennettites* and of Conifers and Gnetaceæ; in these last two the leaf has actually become reduced to a sporangium, thus strikingly resembling the far-back ancestor. It appears to be a *mathematical* necessity (as we have recently learned) for all lateral foliar appendages laid down on an axis to assume a dorsiventral, bifacial structure quite apart from any consideration of function in connection with light, &c.

Another conclusion follows from this doctrine, *viz.*, that *sporangia* are not organs *sui generis*, as Bower and others suppose, but are parts or segments of the primitive leaf; and, as we know in the case of pollen-sacs and ovules, may become transformed into ordinary vegetative tissue. Also we see the same two embryonal quadrants which, in the Bryophyte, produce the sporogonial capsule, in the vascular plant producing purely vegetative organs.

The primitive leaf and primitive sporangium, therefore, were one and the same thing, *viz.*, the original and simple (not the modern, complex structures, *e.g.* of *Polytrichum*) sporogonial capsule of the *primeval* Bryophyte. He who sees deeply and clearly enough

perceives how very much more natural and easier this theory of Celakovsky's is, than those either of Bower or of the adherents of the "homologous" view, for in the process of its application, it does not violate, as both the other theories appear to do, the basic first principles of morphology. These demand that, if any two organs or structures are to be regarded as *homologous*, it must be shewn that the two bore a common origin, and that there exists an easy gradation in the characters of form and structure between the two; in other words, that the one can arise by means of easy transformation of the other. I maintain that these conditions are afforded in the embryological data cited above, but that the theories of Bower and of the supporters of the "homologous" theory are without them. The latter have never brought forward a single instance in which the one generation graduates, either as regards structure, function, or genetic development, into the other; *i.e.*, no *real* homologous relationship between the two has ever yet been established. As regards Bower's brand-new contrivance for *creating* foliar organs; it has no basis in any similar performance that has ever happened previously. The same may also be said with regard to his scheme for endowing the apex of the sporogonial capsule with tissue-forming facilities! I ask: where are the originals and where is the primitive substratum for all this?

Hence we see that the leafy stem, considered as a monopodium, is a purely secondary structure, and that primarily and in essence it is a *sympodial* construction, consisting of a succession of phytons branching one out of another, which are nothing more nor less than vegetatively developed sporogonia. In this way only could the leafy stem have been built, for that a structure of *limited growth*, like the sporogonium, could give rise to the stem out of its own tissues in the way Bower supposes is a quite unreasonable supposition.

The three morphological categories of organs, *viz.*, the *leaf*, *stem*, and *root*, which have persisted and remained distinct each from the other ever since the antiphytic generation attained any development find their natural origin, therefore, in the *capsule*, *seta*, and *foot* or *sucker* respectively of the primitive Bryophytic sporogonium. They have become more and more distinct from each other ever since.

These are my views (derived chiefly from a study and appreciation of Celakovsky's luminous writings), as to some of the principles of morphology underlying the evolution of the higher plant.

W. C. WORSDELL,

## CYTOLOGY AND CLASSIFICATION.

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 A LECTURE

 BY AGNES ROBERTSON, D.Sc.
 

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IT seems at first sight as though the intimate way in which the structure of the living cell is bound up with the physiological functions it has to perform would prevent cytology throwing much light on classification. The cell may be compared to a busy modern town, with an energetic and progressive municipality, bent on having thoroughly up-to-date sanitation, water-supply, locomotion, etc., and consequently making a clean sweep of any antiquated or obstructive buildings. The inevitable result of this is of course the removal of many historic landmarks. But just as in the most modernised town the antiquary generally manages to find some corner which the besom of reform has failed to reach, so the morphologist may hope for some clues to the pedigrees of the plants with which he is concerned from a consideration of the less obvious points in their cytology.

In the lower comparatively unspecialised plant types, in which the whole body is made up of similar cells, (*e.g.* certain Algæ), almost the only place in which we can look for characters of taxonomic value is in the structure of the cells themselves. If we compare the cells of two such plants living under the same conditions, it seems safe to assume that the characters in which they differ are phyletic, for such differences cannot be accounted for as a modern response to external conditions, (compare for instance *Spirogyra* with its spiral, and *Zygnema* with its stellate chromatophores). The importance of cytological features in classification holds good throughout the Algæ. The unicellular genus *Chlamydomonas* contains nearly thirty species, discriminated by their remarkably constant cytological characters! We may imagine that the Algæ are still trying experiments as to the most efficient kind of cell and chromatophore, and have not yet reached a definite conclusion. The Siphonææ are testing the advantages of a coenocytic body, but have "only succeeded in producing the elaborate but puny mockery" of the higher plants which we find in *Caulerpa*. Another group, the Cladophoræææ, has adopted an incompletely septate body, and so on. When we turn from these smaller groups to the half-dozen or so large classes into which the Algæ are divided, we find that they are based almost exclusively on cytological characters. For instance, the class Heterokontææ,

which according to West<sup>1</sup> "seems a very natural one," is divided from the Chlorophyceæ by the possession of parietal discoidal chromatophores of yellowish green colour without pyrenoids, and a fatty reserve substance in lieu of starch.

The main character separating the Fungi from the Algæ is a cytological one,—the absence of chlorophyll. Also the cell-walls shew some difference, those of the Algæ consisting of cellulose, while in many Fungi<sup>2</sup> this is replaced by chitin. The Mosses<sup>2</sup> and Liverworts<sup>3</sup> only give cellulose reactions after prolonged treatment with potash, owing to the combination of the cellulose with aromatic antiseptic bodies such as sphagnol. Amongst the Ferns and Phanerogams there seems to be nothing sufficiently constant in the structure or composition of the cell walls to be of use in classification.

Chloroplasts are not the only cell contents which have some systematic value. Pyrenoids, for instance, are never found outside the Algæ except in *Anthoceros*. The form of starch grains seems to be a character that might be more made use of than it is; the Chenopodiaceæ have compound grains, while in Rye, Wheat, and Barley they are simple and lenticular, and so on.

The question of how far the chief organ of the cell, the nucleus, gives serviceable indications of affinities is at present very difficult to answer, since our knowledge of nuclear structure in the different groups is so very incomplete. We can trace a certain general advance in complexity as we pass from lower to higher forms, and though whenever a nucleus occurs with a simple structure and a simple method of division we are confronted with the question of whether it is primitive or reduced. The Myxophyceæ (or Cyanophyceæ), which are probably the most lowly of the Algæ, used to be regarded as possessing no specialised nucleus at all. There is however a central body of a curious radiating form without, it is true, either nuclear membrane or nucleolus, which seems to possess some of the attributes of a nucleus. In the other Algæ we meet with a more normal type of nucleus, and some cases of karyokinesis have been described. Unfortunately too little work has been done on the nuclear structure of the Algæ in general to allow us to draw any conclusions as to its value in determining their affinities; the same holds good for the Fungi. Amongst the

<sup>1</sup> G. S. West. "The British Freshwater Algæ." Cambridge, 1904.

<sup>2</sup> C. van. Wisselingh, "Mikrochemische Untersuchung über die Zellwände der Fungi." Reviewed Bot. Zeit. September 1, 1898.

<sup>3</sup> F. Czapek. "Zur Chemie der Zellmembranen bei den Laub- und Lebermoosen." Reviewed Bot. Zeit. December 16, 1899.

higher plants there is remarkable uniformity in the structure and method of division of the nucleus, and the number of chromosomes seems generally to be constant for any given species. It seems natural to expect that this number would be the same in closely related plants, and this turns out to be the case in a good many instances. Twelve seems to be the prevailing number in the gametophytes of the Coniferæ (excluding Taxæ), sixteen is the reduced number in six species of Orchidaceæ,<sup>1</sup> all belonging to different genera, which were examined by Strasburger and Guignard, while ten were counted by Strasburger and Frye in two species of *Asclepias*,<sup>1</sup> six by Coulter and Chamberlain, and Atkinson in *Trillium recurvatum*<sup>1</sup> and *T. grandiflorum*<sup>1</sup> and eight by Murrill and Land in two species of *Silphium*.<sup>1</sup> When there is a difference between the chromosome numbers in two closely allied plants it is worthy of notice that not infrequently they are related to one another in the proportion of one to two. For instance there are eight chromosomes in the sporophyte of *Pallavicinia*<sup>2</sup> and sixteen in *Pellia*,<sup>3</sup> twenty in one species of *Drosera*<sup>4</sup> and forty in another, eight in the gametophyte of *Pontederia*<sup>5</sup> and sixteen in *Eichhornia*.<sup>6</sup> There is also a possible case of this particular variation occurring within the limits of the same species, for it has been recorded that there are twelve chromosomes in certain filaments of *Spirogyra triformis*,<sup>4</sup> whilst in others, indistinguishable from these in every other respect, only six are to be found. It certainly seems more likely that this is *not* a case of true dimorphism, but that the threads with six chromosomes had gone through a process of reduction in preparation for conjugation. However van. Wisselingh, who described the occurrence of these two forms, left this point undetermined.

We have only referred at present to the structure of vegetative cells, but it is in the cytology of reproduction that clues to phylogeny are more readily to be found. Darwin in a classical passage quotes Owen who says, "The generative organs, being those which are most remotely related to the habits and food of an animal, I have always regarded as affording very clear indications

<sup>1</sup> Coulter and Chamberlain. "Morphology of Angiosperms," 1903, p. 81 and 82.

<sup>2</sup> J. B. Farmer. "On *Pallavicinia decipiens*." *Annals of Botany*. Vol. VIII. 1894, p. 35.

<sup>3</sup> J. B. Farmer. "On Spore-Formation and Nuclear Division in the Hepaticæ." *Annals of Botany*. Vol. IX. 1895, p. 469.

<sup>4</sup> Rosenberg quoted by R. P. Gregory. "Spore Formation in Leptosporangiate Ferns." *Annals of Botany*. Vol. XVIII. 1904, p. 445.

<sup>5</sup> Coulter and Chamberlain. "Morphology of Angiosperms." 1903, p. 81.

<sup>6</sup> C. van Wisselingh. "Ueber Kerntheilung bei *Spirogyra*." *Flora* 1900.

of its true affinities. We are least likely in the modifications of these organs to mistake a merely adaptive for an essential character." Darwin adds, "With plants how remarkable it is that the organs of vegetation, on which their nutrition and life depend, are of little signification; whereas the organs of reproduction, with their product the seed and embryo, are of paramount importance!"

Amongst the Algæ we meet with a really extraordinary variety in the structure and cytology of the sexual organs. To convince oneself of this it is only necessary to think of the differences between a few examples taken at random, such as the conjugation of *Spirogyra*, the oogonia and curious "dwarf males" of *Ædogonium*, the procarp, trichogyne, and spermatia of the red Algæ, the oogonia and antheridia of *Vaucheria*, the biciliate gametes of *Ulothrix*, and the free naked eggs of the Fucaceæ! Two small sub-groups of the Algæ, which are apparently by no means distantly related, may shew a degree of difference in their reproductive processes which among the higher plants would justify us in assigning them to altogether different divisions of the vegetable kingdom. As continually happens in thinking of any morphological subject we are again reminded of a passage in the Origin of Species. "That the mere physiological importance of an organ does not determine its classificatory value, is almost proved by the fact, that in allied groups, in which the same organ, as we have every reason to suppose, has nearly the same physiological value, its classificatory value is widely different. . . . As in most groups of animals, important organs, such as those for propelling the blood, or for ærating it, or those for propagating the race, are found nearly uniform, they are considered as highly serviceable in classification; but in some groups all these, the most important vital organs, are found to offer characters of quite subordinate value. Thus . . . in the same group of Crustaceans Cypridina is furnished with a heart, whilst in two closely allied genera, namely Cypris and Cytherea, there is no such organ; one species of Cypridina has well-developed branchiæ, whilst another species is destitute of them."

The sexual organs of the Fungi, in the cases where they occur and are functional, are distinguished from those of the Algæ by a cytological character, the non-motility of the sperm cells. As an instance of the treatment of a phylogenetic problem from a cytological stand point we may mention Mr. Blackman's recent suggestion as to the affinities of the Uredineæ which is based on

his discovery of the process of "fertilisation" preceding accidium formation.<sup>1</sup> He concludes that the Uredineæ cannot be considered as a mere sub-division of the Basidiomycetes as in the well-known classification of Brefeld, but must be looked upon as a distinct and far more primitive group. He would rather regard the Basidiomycetes as reduced apogamous forms of the Uredineæ.

Among the higher Cryptogams the most striking cytological feature which is useful in differentiating large groups is the character of the antherozoids (biciliate in the Bryophytes and Lycopods and multiciliate in the Ferns). Amongst the Phanerogams as a rule the male cells have lost their power of locomotion, and therefore when ciliated sperms were discovered in the Cycads and *Ginkgo* it became clear that this was one of the most important points to be taken into account in placing these plants in a natural system. *Ginkgo* which had been assigned to the Taxaceæ was removed into an alliance of its own, and the view that the Cycads were primitive Gymnosperms with a filicinian ancestry received confirmation. As regards fertilisation, the Conifers appear to have one common feature in which they differ from all other plants. The membrane of the egg nucleus is pushed in by the male nucleus, which finally comes to lie within it, both walls being intact. This was first described by Blackman<sup>2</sup> for *Pinus*. The large size and comparatively scanty chromatin of the egg nucleus seems also to be a characteristic feature of the group. There is another point in which I think one might expect to find constancy in related plants, but in which the Gymnosperms turn out to be highly variable, the behaviour, namely of the male cytoplasm. In *Taxodium*,<sup>3</sup> for instance, the whole male cell enters the egg; and the male cytoplasm forms a sheath round the fusion nucleus and takes part in the formation of the embryo, whereas in *Sequoia*<sup>4</sup> the male nucleus slips from its cytoplasm and enters the egg naked! Unless one imagines that these two plants have a radically different mechanism for the transmission of hereditary qualities, one is forced to conclude that it is the male *nucleus* alone that carries the

<sup>1</sup> V. H. Blackman. "On the Fertilisation, Alternation of Generations, and General Cytology of the Uredineæ." *Annals of Botany*. Vol. XVIII 1904, p. 323.

<sup>2</sup> V. H. Blackman. "On the Cytological Features of Fertilisation and Related Phenomena in *Pinus silvestris* L." *Phil. Trans. Roy. Soc.* Vol. 190B, 1898, p. 395.

<sup>3</sup> W. C. Coker. "On the Gametophytes and Embryo of *Taxodium*." *Bot. Gaz.*, July, 1903.

<sup>4</sup> A. A. Lawson. The Gametophytes, Archegonia, Fertilisation and Embryo of *Sequoia sempervirens*. *Annals of Botany*, Vol. XVIII., 1904.

paternal characters, and that the cytoplasm, in the cases where it takes part in embryo formation, has a merely nutritive function.

The Angiosperms are very sharply marked off from the Gymnosperms by the cytology of their reproductive organs. The endosperm and archegonia of a gymnospermous ovule can be homologised without difficulty with the female prothallus of a fern or Lycopod, but at present the structures in the angiospermous embryo-sac stand alone, unless, as has been suggested, the gulf is to some extent bridged by such a form as *Gnetum Gnemon*, in which the archegonia are reduced to egg cells, and most of the endosperm tissue is developed after fertilisation. It is a question, however, whether this actually represents a stage in the evolution of the angiospermous ovule, or is merely a blindly ending side branch of the Gymnosperms, which has happened to develop in rather the same direction as the Angiosperms. In sub-dividing the huge group of the Angiosperms cytological evidence is of little avail. The extraordinary constancy of embryo-sac structure throughout the group, and the occurrence of "double fertilisation," both in Dicotyledons and Monocotyledons, point to the ancientness of the whole stock, but give no help in determining inter-relationships. However, "where differences exist between the Archichlamydeæ and the Sympetalæ, Monocotyledons are connected in these particulars with the Archichlamydeæ<sup>1</sup>."

Pollen development furnishes one character of a certain slight taxonomic value, for it is found to be characteristic of Monocotyledons to produce four microspores in one plane, whereas in Dicotyledons they are arranged in a pyramid. Such a difference as this can hardly be explained except as an ancestral trait.

Enough has perhaps been said to justify the conclusion that cytology, though it is such a new science, has already given some help in questions of classification and phylogeny. The fertilised egg of any plant, though but a single cell, bears that within itself which determines within narrow limits the whole course of the life-history, and the eggs of any two species must possess (if only we could observe and define them!) perfectly definite characters correlated with the specific differences exhibited by the mature plants. If ever perfected methods of observation should enable us to detect these subtle distinctions, Cytology will become the very basis of Classification.

<sup>1</sup> E. N. Thomas. "A Consideration of the Bearing of Fertilisation Phenomena and Embryo-sac Structure on the Origin of Monocotyledons." Brit. Ass. Rep., Southport, 1903, p. 857.

## THE BRITISH FRESHWATER ALGÆ.

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A Treatise on the British Freshwater Algæ. By G. S. West, M.A., A.R.C.S., F.L.S., Professor of Natural History at the Royal Agricultural College, Cirencester; etc. Cambridge: at the University Press, 1904. Price 10/6.

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A NEW systematic account of the British Freshwater Algæ has been urgently needed for some time. Cooke's work, published in 1882-4, is not only unsatisfactory in many respects, but is quite out of date; and during the last fifteen years so much has been done, not only in the investigation of our British forms, but also in the advancement of our knowledge of the general morphology and life-histories of these fascinating plants, that a treatment on entirely fresh lines had become imperative.

Mr. G. S. West, together with his father, Mr. W. West, has been almost alone in this country during recent years in upholding the traditions so worthily established by Ralfs and Hassall. Their contributions to our systematic knowledge of the freshwater algæ have been numerous, and always distinguished by independent research and scholarly accuracy of treatment. It is quite safe to say that no one else in Britain possesses Mr. West's wide knowledge of the green freshwater forms, so that British algologists will naturally welcome the present work with special pleasure.

Mr. West devotes thirty-three pages to his Introduction, and to a brief treatment of general topics connected with the Algæ, such as the general features of their structure, polymorphism, the principles upon which their classification is based, and so on. The Introduction contains some very interesting remarks on the distribution of freshwater algæ in the British Isles, from which it appears that the mountainous districts of the north and west, consisting of Palæozoic and igneous rocks, contain a far greater number both of species and individuals than other parts of the country, and especially than the Fen districts of East Anglia, which certainly might have been expected to possess a more various algal flora, considering the great extent of water and the very numerous aquatic phanerogams they contain.

The pages devoted to the different methods of multiplication and reproduction obtaining among the Algæ, would, we think, have gained considerably if these topics had been treated from the evolutionary standpoint; the relation of vegetative cell-division among the primitive motile forms to zoospore-formation, and of this to the isogamous union of planogametes form the logical basis

of the consideration of the reproductive processes of Algæ. The treatment of gamogenesis and sex is not unexceptionable. On p. 15 it is clearly implied that all gamogenesis among Algæ is sexual *i.e.* depends on the union of a male and female cell. Surely this is most misleading to the student. In the most primitive types "sexual differences" cannot be truly said to be "scarcely appreciable"; they simply do not exist, and on this fact depends the whole modern theory of the evolution of gamogenesis. The word "sexual" is much better confined to types where there is a clear binary differentiation between the gametes, though unfortunately the term is constantly used as a synonym for "gamogenetic." But in this latter sense the phrase "sexual differences" has no meaning. We cannot see the advantage of describing the fertilization-process of Rhodophyceæ as "carpogamous heterogamy," with "no specially differentiated female cell." The fact that the carpogonial cell may be externally similar to the other cells of the carpogonial branch does not seem to warrant the implication that the process of fertilization differs in any essential respect from that obtaining in other algæ; nor does the "carpogamy" properly qualify the "heterogamy."

The treatment of alternation of generations is also, we think, too formal, and suffers from the absence of the evolutionary point of view. We may fairly say that no one would have spoken of an alternation of generations among the Algæ if it had not been for the phenomena of alternation seen in the Archegoniata. The phenomenon of the division of the zygote into a number of cells, each of which gives rise to a new plant, is not, in origin, an alternation of generations at all, but merely a phenomenon of polyembryony. The most that can fairly be said is that it foreshadows the development of a complex and semi-independent fruit-body such as we see in the higher Bryophytes, and, on the "antithetic" theory of Celakovsky and Bower, the true alternation of distinct individuals seen in the Pteridophytes. On the "homologous" theory the Algæ may foreshadow the Pteridophytic alternation in another way; for we may conceive that an Alga reproducing itself both by gametes and by zoospores might acquire a rhythm or periodicity of such a nature that each mode of reproduction became restricted to alternate generations, and thus gave rise to the state of things that we have in *Dictyota*. So long as we remain in ignorance of the nuclear reduction-phenomena in the green Algæ, all this must of course be purely speculative, and Mr. West may perhaps be of opinion that a discussion of such topics is out of place in the

introduction to a systematic work. Meanwhile it is important that students should not be given the impression that the phenomena of sex-differentiation and alternation of generations must be "read into" the life histories of primitive forms which are in fact innocent of such complications.

The section on "Polymorphism" contains a very moderate and just, though brief, treatment of this very controversial topic. Nevertheless the statement that "all those Algæ which exhibit an alternation of generations are polymorphic" again seems very misleading. Surely alternation of generations is quite a distinct phenomenon from polymorphism, as usually understood, which presumably refers to the production of different *alternative* vegetative forms by one species. The facultative production of different kinds of reproductive cell by the same plant, which Klebs and others have established in many algæ, and which may have given rise to homologous alternation in a form like *Dictyota*, might no doubt logically be referred to as "polymorphism of reproductive cells." But the succession of definite phases in a life-history cannot be included under the concept without a confusion of thought.

The section on Phylogeny and Classification follows in its main ideas, so far as the Green Algæ are concerned, the views put forward by Bohlin and by Blackman and made the basis of the "Revision of the Classification of the Green Algæ" published in this journal in 1902. Various alterations based on the author's own experience have been introduced.

Mr. West, like Professor Oltmanns, accepts Luther's Class Heterokontæ, regarding it as a "very natural" group. We may look upon this series as now well on its way towards general acceptance among algologists. Mr. West also agrees with Professor Oltmanns in refusing to admit the affinity of the "Vaucheriales" with the Heterokontan forms. The arguments for and against this position have been discussed in the recent review of Professor Oltmanns' book in this journal.

The rest of the green forms are still grouped under the old name Chlorophyceæ, since Mr. West refuses to accept the thorough going breaking-up of this heterogeneous class and the establishment of different series based on the characters of the motile cell, proposed by Bohlin and adopted and carried further in the "Revision." "This arrangement," says Mr. West, "is based upon the assumption that the CEdogoniales and the Conjugatæ are phylogenetically independent of 'Isokontæ' and that all three groups have arisen from the Flagellata. Be it remembered,

however, that there is no direct evidence in support of the view that the *Œdogoniales* and *Conjugatæ* are phylogenetically independent of the rest of the *Chlorophyceæ*." And he goes on to insist that his long intimate acquaintance with the *Conjugatæ* has tended to shew that they at least have not had a direct origin from Flagellate ancestors. There is something to be said for Mr. West's contention here. It is implied though not specifically stated in the Introduction to the "Revision" that the *Conjugatæ* had an independent Flagellate origin, but the authors of that work scarcely intended to emphasise the point. Their view is better expressed in the remark that "we have not at present sufficient evidence, in the complete absence of zoospores, to settle the phylogenetic origin of the group" (p. 2 of Reprint), though they elsewhere state that "it may possibly have been derived from a primitive motile form" and call attention to the analogy with *Chlamydomonas Braunii* in the peculiar mode of conjugation (p. 45). It nevertheless seemed to them desirable to separate the *Conjugatæ* from the other green algæ on account of the very striking and sharply marked characters presented by the group, both in cell-structure and in the mode of reproduction. There is certainly no good evidence that the *Conjugatæ* have arisen from any existing Isokontan filamentous forms. We will deal with Mr. West's "proof" that they arose from filamentous ancestors presently. It is perfectly true also that there is no direct evidence for the separate origin of *Œdogoniales* from Flagellata with an anterior crown of cilia. The case for their separation as "*Stephanokontæ*" is an *a priori* case, and rests on the great constancy of the zoospore-characters in the other series (including *Phæophyceæ*) and the absence of intermediate forms between the bi-flagellate or quadri-flagellate type of motile cell and the multi-flagellate type. Once the great importance of the motile cell as a taxonomic basis is admitted, this indirect evidence acquires, in our opinion, very considerable weight and appears to justify the application of the Luther-Bohlin conception throughout the Green Algæ. It must, however, be admitted that such an extension of the principle does not at present rest on the same solid ground as in the case of the *Heterokontæ* and *Phæophyceæ*.

We notice that in Mr. West's phylogenetic table (p. 30) the dotted line of origin of the *Œdogoniales* does not connect with any existing group, but arises freely and independently on the level of the *Protococcoideæ*. We should be inclined to carry the line down a little further, into the region of the Flagellata. That is all the difference.

The Chlorophyceæ of Mr. West are divided into a number of "orders," a taxonomic unit corresponding to the "Series" of Engler's Syllabus. The separateness of the CEdogoniaeæ is so far recognised that they are allowed a separate "order"—CEdogoniales. The Chætophorales almost correspond to the Ulotrichales of the "Revision." We prefer the latter name since it is taken from a more primitive type than the "hair-bearers." The Ulvaceæ are separated in a special "order," the Ulvales, as in the "Revision," and the Prasiolaceæ are given another—the Schizogoniales,—with the remarks that "the genus *Prasiola* has no relationship to the Ulotrichaceæ" and "Ulvales and Schizogoniales are parallel groups, each of which has had a separate origin from the Protoeocoeideæ." This is very likely. Bohlin is followed in assigning *Microspora* not only to a separate family, but to a separate order—Microsporales. The Cladophoraceæ, Pithophoraceæ and Sphæropleaceæ are placed together in the Cladophorales, which Mr. West refuses to unite with the Siphoneæ. But a comparison of the cytological characters of a cœnocytic segment of *Cladophora* with those of some of the Siphonocladæ, e.g. *Siphonocladus* itself, most strongly suggests that Schmitz was right in deriving the Cladophoraceæ from a Valoniaceous type in which there has been a preceocious segmentation of the cœnocytic thallus.

The Conjugatæ are primarily divided in the classical way—the filamentous forms (Zygnemaceæ) into Mesocarpæ and Zygnemæ (including *Spirogyra*). We have recently given reasons for preferring, with Palla, to classify these forms according to the nature of their chromatophores. Mr. West is a specialist on the Desmids, and, as he points out, it is very interesting to note that his conclusions as to their classification, founded on a careful comparative study of their external form and its variations, coincide very closely with Lütkemüller's conclusions drawn from the minute structure of their cell-walls. This fact gives his classification a very solid basis, and we must certainly accept it as most nearly representing the truth.

With regard to the question whether the Desmids or the filamentous Conjugates represent more closely the ancestors of the group, Mr. West holds very strong views. Not only in the present work, but elsewhere he repeatedly states that he has "proved" that the Desmids are descended from filamentous Conjugates. For instance (p. 27), "it has been clearly shown that the Desmidiaceæ is unquestionably a family of Conjugates derived by retrogression from filamentous ancestors, and therefore they cannot by any possible means have had a direct origin from unicellular motile

organisms." Now there is not the slightest justification for this strong language. Scarcely a single one of the facts or considerations that Mr. West has adduced in support of his contention that the Desmids are descended from filamentous forms, but could be used to support the view that the filamentous forms are descended from Desmids, or, at any rate, unicellular common ancestors of the two groups. It is the old story of a series which can be read either way. It is just as easy to suppose that the primitive Conjugates were simple unicellular forms (nearest the Saccodermæ) with isogamous conjugation, and that these gave rise on the one hand to filamentous types with incipient sexual differentiation, and on the other to unicellular types with complicated external forms and very occasional sexual differentiation, as to suppose that sex was gradually lost in the evolution of Desmids from Zygnemaceæ. The occasional "reversion" to sex in *Hyalotheca* may just as well be a progressive modification. The absence of zoospores (p. 148, footnote) is no evidence, because the hypothetical filamentous ancestors of the Zygnemaceæ are every bit as likely to have possessed zoospores as the unicellular ancestors of the Desmids on the other hypothesis, judging by the actual distribution of motile cells in the existing filamentous and unicellular algæ respectively. The only piece of evidence brought forward by Mr. West that seems at all cogent is the great resemblance between *Microspora Löfgrenii* and *Zygnema pachydermum*, and this may of course be accidental. The most likely view of the phylogeny of the Conjugates seems to be that indicated above, a common origin of both sections from unspecialised unicellular forms with isogamous conjugation, forms which may have lost their motility for a longer or shorter time. Mr. West's view is certainly a possible one, but to speak of "proof" is little short of ridiculous.

The Protococcoideæ, always a difficult group to classify, is divided into a number of families of which the first is the "Chætopeltideæ" containing genera, characterised by loose aggregates of seta-bearing cells, regarded in the "Revision" as reduced members of the higher Chætophorales (Ulotrichales). There seems no sufficient reason for separating these forms altogether from the typical setiferous types. Of the other families distinguished, the "Protococcaceæ (Autosporaceæ)" is undoubtedly natural, at least in the main. It includes many of the same forms as the Selenastraceæ of the "Revision," the bulk of the motionless freshwater-plankton types, often with a curved cell-form, reproducing themselves by *autospores*, often forming cœnobia. Mr. West's removal of

*Hormospora*, *Glæotila* and *Radiofilum* to Ulotrichaceæ, and his placing of many of these unicellular genera, we are quite prepared to accept. A full discussion of the author's arrangement of the Proto-coccales would occupy too much space, but we cannot help expressing the conviction that they are more naturally divided into three series according to the three main tendencies of evolution seen in the group, tendencies whose reality Mr. West fully accepts in his Introduction.

The Diatoms are given a class to themselves and the Myxophyceæ (Cyanophyceæ) another. Mr. West is surprised that the earlier name, Myxophyceæ, has never been adopted in text-books. The reason no doubt may be found in the fact that it is much more convenient to have a "pigment name" uniform with the others. The law of priority is troublesome enough to the average botanist when applied to genera and species, where we suppose it is really necessary,—witness the disappearance of *Conferva* before *Tribonema* in the present work,—but to expect us to bow to it in the case of larger groups is to strain our endurance too far. We must adopt the group names that are most convenient or most in accord with the present state of knowledge. Finality of group-nomenclature can only be obtained by a gradually reached consensus of expert opinion; it cannot be forced upon us by the operation of an arbitrary law.

We think it a mistake to include *Glaucocystis* in "Myxophyceæ"; the cytological type is so different that, its pigment notwithstanding, this genus should not be associated with the entirely isolated typical blue-green algæ. There is no evidence of phylogenetic connexion.

One curious feature of the present book which is rather in accord with the non-evolutionary treatment of some of the morphological topics considered in the Introduction, is the old-fashioned plan of arranging the systematic part so that we begin with the highest forms and end with the lowest. It is difficult to see what advantage is gained, while the disadvantage of departing from the evolutionary sequence is clear.

In spite of the apparent weakness in some points, there is no doubt that Mr. West has conferred a very considerable boon upon British algologists in producing this work. The careful description, the large amount of first-hand information, the abundant original illustration of British species from named localities, combine to render the systematic treatment a work of very high value.

A.G.T.

Physiologische Pflanzenanatomie, von Dr. G. Haberlandt. Dritte, neubearbeitete und vermehrte Auflage. Leipzig, Engelmann, 1904.

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WHEN the first edition of this book was issued in 1884 it came as an exposition of the results obtained during the course of the first decade after the publication of Schwendener's "Mechanische Princip im anatomischen Bau der Monokotylen." The work of Schwendener and his pupils was the first systematic attempt to consider the details of plant-structure in the light of adaptation to function. Many of the earliest pioneers of plant-anatomy had been rightly dominated by the desire to discover the uses of the structures they unravelled, but premature attempts to speculate on such questions, while physics and chemistry and the knowledge of the general economy of plant-life were yet in a very rudimentary condition, led to the promulgation of some very grotesque theories. Hugo von Mohl rendered a conspicuous service to anatomy by rigidly confining himself to descriptive work and, bringing back the subject to the region of objective reality, well and surely laid the foundation stones of the modern fabric of descriptive anatomy. Von Mohl was succeeded by a series of workers, among whom Nägeli, Sanio and Hanstein are the most conspicuous names, largely dominated by the idea that the history of development gives the true key to the interpretation of structure, and under this influence the formation of the different tissues of the higher plants was largely worked out.

Thus the ground was prepared for the work of the Schwendenerian school—a thorough knowledge of the facts of structure and development of tissues, together with the more advanced knowledge of plant-physiology, enabling their interpretation as a series of mechanisms for the performance of the various work of the plant-body to be undertaken with more prospect of success than was possible half a century earlier.

Since the publication of Haberlandt's first edition yet another direction has been impressed upon anatomical study. The consideration of the phylogenetic history of tissues, foreshadowed by Russow many years ago, and by no means neglected by Haberlandt himself, has become the basis of much of the best work of the last fifteen years, and as in other departments of biology, undoubtedly furnishes a valid basis for the comparative study of form. But even this historical method tends to become barren and rather formal without constant reference to function, and it is only in a combination of the two points of view, the historical and the physiological,

that we find a logically satisfactory method of attack. It should never be forgotten that though an organism is a machine, it is not a brand-new one constructed to fulfil its present functions, but has been built up and modified step by step according to the slowly changing needs of its ancestors.

Ever since the original publication of Haberlandt's work, to which his own research has in almost every part greatly contributed, his book has been the standard account of physiological anatomy. The logical division of the subject, the lucid style, and the clear distinction of well ascertained fact from speculative suggestion have combined to render it a model text-book. The second edition, published in 1896, was greatly enlarged and brought up to date, while the present (third) edition has undergone the same process, though, appearing after a shorter interval it has not been enlarged to the same extent. The book now consists of over 600 pages with 264 illustrations. The old division into sections dealing with the different physiological tissue-systems is retained, the principal change from the second edition being the addition of three new sections, on the apparatus of movement, on sense-organs, and on mechanisms for the conduction of stimuli, respectively.

The second of these sections begins by shewing that in the course of progressive division of physiological labour, special sensitiveness, at first diffused over the whole protoplasm of an organism, becomes gradually restricted to separate tissues, though these may be primarily adapted to some other function. As an example we may take the epidermis, which in many tendrils, for instance, is the tissue sensitive to contact-stimuli, while in leaves it is very probable that this layer, though primarily a protective and water-storing tissue, is also the light-perceiving organ.

In the highest grade of adaptation, the perceptive power is localised in a tissue whose sole function it is. In such cases, of course, the anatomical structure of the organ is clearly adapted to its function, and the term sense-organ is properly applied. As Noll pointed out, it is to the fixed *ectoplasm* of the cell in all cases that we must look for the reception of definite external stimuli, whether in non-specialised or in specialised sense-cells.

The sense-organs are treated under "Sense organs for mechanical stimuli"—tactile pits, papillæ, hairs and bristles, "sense organs for geotropic stimuli," and "sense organs for light-stimuli." There is an excellent account given of the "statolith" theory of the mechanism for the perception of geotropic stimuli, but there appears to be no reference to the "radial pressure" theory, and in the present

controverted state of this question this seems a serious omission. In dealing with sense-organs for light-stimuli, an interesting view is put forward that the epidermal cells of the upper sides of cuphometric leaves act as lenses, tending to concentrate the light rays on the central part of the inner cell-walls; a shifting of the direction of the incident rays will then shift the spot of light from the centre of the inner wall, and this might act as a stimulus leading to a movement which would bring back the light spot to its position of rest.

In the section devoted to "Mechanisms for the conduction of stimuli," intercellular protoplasmic connexions are reviewed from this point of view, and an account is given of the hydrostatic mechanism for the transmission of contact stimuli in *Mimosa pudica*, discovered by the author some years ago.

In the account of the rudimentary conducting strand in the stem of Polytrichaceæ it is stated that there is no sheath structure limiting the cylinder from the cortex. This is true of the aerial stem but not of the rhizome-like underground stem, where an extremely well-marked, though incomplete, endodermis is very obvious. No mention is made of the radially organised root-like structure of this underground stem.

We have no space to enter upon a review of any more of the many topics discussed by the author in this comprehensive work; but we can certainly assure him of the fulfilment of the hope expressed in the preface of this edition, that the book, now entering upon the third decade of its existence, may "jung genug geblieben sein, um auch fernerhin nicht nur lehrend und überliefernd, sondern vor allem auch anregend wirken zu können."

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THE UNIVERSITY OF LONDON ADVANCED  
LECTURES IN BOTANY.

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THE second year of the three years' scheme of these lectures, of which notices have already appeared in this journal has now been completed.

In the Lent term a course was delivered at University College by Mr. V. H. Blackman, of the Natural History Museum, on "The Ascomycetes with special reference to the Origin of the Ascus." Microscopic demonstrations were arranged to accompany the lectures. During the present term Dr. F. F. Blackman, of Cambridge, has given a course of eight lectures, also at University College, on "The CO<sub>2</sub>-economy of Plants," very largely based on

current work carried out in his laboratory. This course was divided into three sections, devoted respectively to the "Chemistry," the "Physiology," and the "Biology" of the subject. The opening lecture dealt with the modern theory of the chemical organisation of the living cell as "a colloidal honeycomb of catalytic agents." In the treatment of the "Physiology" of  $\text{CO}_2$ -economy the lecturer was largely concerned with the important demonstration that the so-called "optimum" is at least, in the case of many processes, an "illusion of experimentation" whose cause is to be sought in that limitation of the rate of the process by some other factor. This demonstration led to the conclusion that the distinct chemical reactions proceeding in the cell are falling into line, as regards their dependence on external conditions, *e.g.* temperature, with chemical processes *in vitro*. In the concluding section the spatial relations of  $\text{CO}_2$  to plants, and the possible secular changes in the composition of the atmosphere, as well as the relation of the gas to the ontogeny and the phylogeny of plants, were reviewed.

The programme for next session has been revised, and now includes a course in the autumn on "The Facts of Heredity" by Mr. Bateson, and another in the Lent term by Professor Oliver on "The Origin of the Gymnosperms," while in the third term Professor Farmer will deal with the "Bryophyta."

Courses for the following session are now being arranged by the Board of Studies.

It will be seen that the high standard of these courses is being fully maintained, and we have every reason to congratulate the organisation of the University of London on this result of its reconstitution. The maintenance of a continuous series of first-rate advanced courses by leading English botanists, embodying the methods and results of current research, and furnishing opportunities of the best kind to all advanced students with access to London, is an achievement of very high value.

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PROVISIONAL SCHEME OF THE NATURAL  
(PHYLOGENETIC) SYSTEM OF FLOWERING PLANTS.

BY HANS HALLIER, PH.D. (Hamburg).

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AS the son of a well known botanist and the grand-nephew of M. J. Schleiden, the centenary of whose birth was celebrated last year at Hamburg and Jena, I have by inheritance and education a passion for botany, and for nearly thirty years I have taken a zealous interest in taxonomy. Even at the age of seven to thirteen years I used to accompany my father, the late Ernst Hallier, formerly professor of botany at the University of Jena, on the botanical excursions which he undertook every Saturday or Sunday with his students, in order to introduce them to the principles of systematic botany. In these instructive excursions I soon gained a knowledge of the botanical names of plants and of our native flora, and learned the natural system by immediate intuition and comparison of the objects themselves, independent of the sometimes very dogmatic views of the standard-books, or, as we say in Germany, "mit einem noch nicht durch Fachkenntnis getrühten Blick." Later, at the University of Jena, I was introduced by the works of Darwin and the lectures and practical instructions of Ernst Haeckel, to the marvellous series of discoveries, to which the evolution-theory had been the impulse. In the Botanical Laboratory of Professor L. Radlkofer and Dr. H. Solereder at Munich, I recognized that not only the external characters of plants must be examined in determining their affinities, but that comparative anatomy is also indispensable to systematic botany.<sup>1</sup> During a four years' stay at the famous botanic garden of Buitenzorg and during an expedition into the

<sup>1</sup> See H. Solereder's *Systematische Anatomie der Dicotyledonen*. Stuttgart, 1899.

centre of Borneo<sup>1</sup> I had an excellent opportunity of examining representatives of nearly all the natural orders of Flowering Plants under natural conditions. The academical lectures of Professor Ernst Stahl, as well as the personal influence of this suggestive botanist and of Professor Jean Massart, my enthusiastic companion in many excursions in the vicinity of Buitenzorg<sup>2</sup>, induced me to apply to systematic botany, the results of plant-ecology and morphology. As a result of these various influences I reached the conviction that there can exist only one really natural system, namely that which is identical with the tree of descent; to reconstruct this, systematic botany should be founded on a much broader and more universal base than at present, comprehending not only the morphology of the reproductive organs, but also all the other branches of botany, such as comparative morphology of the vegetative organs; comparative anatomy, ontogeny and embryology; phytochemistry, physiology and ecology; structure of pollen and seed coat; relations to climate, seasons and to the surrounding organic world; plant geography; palaeo-phytology, etc.

Thus since the elaboration of my first botanical publication (in 1890-2) till now I have always paid special attention to these points in reference to natural affinity. The results of these comparative studies have been published in a series of papers, most of which refer not to the whole system of flowering plants, but to single orders or alliances. It was only on my second voyage to the tropics, that I felt impelled to publish, in April 1903, a provisional account of my system as a whole. At that time I had to take into account the possibility that the Tagal people might not let me out of the Phillipine Islands, or that a typhoon might throw me into a shark's mouth or into the depths of the South Sea, and I therefore thought it wise to publish my system at once, incomplete as it was. Moreover I hoped, that during my absence competent botanists would have time and leisure to digest my new system and to subject it to discussion, but in this latter point I am somewhat disappointed. Hitherto reviews on my system have been few in number and several of them very diffident or even unfavourable. The more favourable ones are the following.

<sup>1</sup> The results of the botanical explorations of this expedition have been described in the *Natuurkundig Tijdschrift voor Nederlandsch Indië* LIV. (1895) pp. 406-449 and in the *Naturwissenschaftliche Wochenschrift*, XI. (Berlin 1896).

<sup>2</sup> See his interesting descriptions of these trips in his paper, *Un botaniste en Malaisie*, published in the *Bulletin de la Société royale de botanique de Belgique*, XXXIV. (1895), part I.

In the preface to his German edition of Warming's Manual of Systematic Botany (1902), Moebius refers briefly to my opinion that the *Sympetalae* are of polyphyletic origin. On pp. 411 and 137 of the sixth, and on pp. 418 and 443 of the seventh edition of Strasburger, Noll, Schenek and Karsten's Text-Book of Botany (Jena, 1904 and 1905), Karsten recapitulates my opinions of the origin of Dicotyledons, Monocotyledons, *Choripetalae*, *Sympetalae* and *Amentiflorae*. In his paper entitled, Die Grundlagen des Hallierschen Angiospermensystems, eine phylogenetische Studie (*Beihefte z. Botan. Centralblatt*, XVII. (1904), pp. 129-156), Gustav Senn, lecturer on Systematic Botany at the University of Basel, undertakes a very careful and critical examination of the principles on which my new system is founded, and in Just's Annual Report on the botanical literature of 1903, Fedde reports at great length on my different publications of that year. Only partly favourable are Wettstein's reviews of my paper on morphogeny and phylogeny (Hamburg, 1903) in the *Oesterreichische Botan. Zeitschrift* LIII. (1903) and in the *Botanische Zeitung*, LXI. (1903), section II. pp. 311-314. Unfortunately, with few exceptions, this eminent botanist does not indicate precisely nor in detail which of my opinions he considers as unacceptable, and in his remarks on Gnetaceæ, I am convinced that his criticism is not well founded. In external characters, as in anatomical structure, the Gnetaceæ approach very closely to certain Loranthaceæ, and to *Myzodendrum*, and there is much evidence that they belong to this cycle of affinity, if only we presume that the so-called nucellus of *Gnetum* represents not a single ovule, but a placenta with several ovules, as Treub has indicated in some Loranthaceæ.

The most striking point in the reception of my system is the silence of Professor Engler. I am much disappointed that a scientific journal which is a recognized centre for systematic botany and plant-geography has been unable to discuss *in extenso* a new system, which is exceptional by the complexity of principles applied in it. But in the volumes of the *Jahrbücher* since 1902, there is no mention of my publications, and the same is the case in the monographs of the "*Pflanzenreich*." In Köhne's Monograph of Lythraceæ (Oct. 1903) and in Winkler's Monograph of Betalaceæ (June 1904) my publications treating the same topics are neglected. Only Buchenau in an appendix to his monograph of Alismataceæ refers to Miss E. Sargent's and my own suggestions on the mutual relations of Monocotyledons and Dicotyledons.

The general features of my system are the following: The Angiospermae are a natural (monophyletic) group, and not a polyphyletic one, as suggested by Engler in Engler and Prantl's *Natürlichen Pflanzenfamilien*, Nachtrag zu II.—IV. (1897), pp. 364—369. The *Amentaceae* are not to be considered as old types, remaining in a lower state of development, and allies or descendants of Gymnospermae, but, on the contrary, as the highest and most reduced types of one of the lines of Dicotyledons. They and all the other lines of Dicotyledons have been developed by reduction in flower and fruit from the *Polycarpicac*, the latter group being derived immediately from *Bennettitaccac* or other extinct Cycadales. In the same manner the *Liliiflorae* and all the other syncarpous Monocotyledons have been derived by union of the carpels, by reduction in the number of parts, by epigynous insertion of the perianth, and by other changes in the structure of flower and fruit from the polycarpous Monocotyledons (*Helobiac*), which latter group originated immediately from the polycarpous Dicotyledons (*Polycarpicac* and *Ranals*). In the Dicotyledons the *Apctalae* and *Sympetalae* are unnatural groups of polyphyletic origin.

Agreeing in some points with mine, and likewise phylogenetic, is the system which Professor C. E. Bessey, of the Nebraska University, published eight years ago in the *Botanical Gazette*, Vol. XXIV.

I do not claim for my system the position of an infallible gospel or of a "Nolimetangere," the latter very significant expression being used by Professor Karsten on p. 443 of the seventh edition of the Bonn Text-Book of Botany (1905). On the contrary, I freely confess that my system gives only an approximate idea of the lines of descent and of the mutual relations of the Flowering Plants; it is only one step in the further progress of phylogenetic botany. But I am sure that this step is not a wrong and useless one, and that it will lead to a broader knowledge of the natural affinities of Flowering Plants.

The following is a chronological enumeration of the publications in which I have worked out my system.

1. Versuch einer natürlichen Gliederung der Convolvulaceen auf anatomischer und morphologischer Grundlage. Engler's *Botanische Jahrbücher*, XVI., 4—5 (1893), p. 486.

2. Betrachtungen über die Verwandtschaftsbeziehungen der Ampelideen und anderer Pflanzenfamilien. *Natuurkundig Tijdschrift voor Nederlandsch Indië*, LVI., 3 (1893), p. 486.

3. Die indonesischen Clematideen des Herbariums zu Buitenzorg. *Annales du jardin botanique de Buitenzorg*, XIV, 2 (July, 1897), p. 249. Contains some general remarks on differentiation and reduction.

4. Ueber die Gattung *Erycibe* und die biologische Bedeutung der stammbürtigen Blüten und Früchte. *Bulletin de l'herbier Boissier*, V., 9 (September, 1897), p. 753. A few general remarks.

5. Ueber Kautschukliancn und andere Apocyneen, nebst Bemerkungen über *Hevea* und einem Versuch zur Lösung der Nomenklaturfrage. Jahrbuch der Hamburgischen wissenschaftlichen Anstalten XVII., z. Beiheft (November, 1900), pp. 200—202.

6. Ueber die Verwandtschaftsverhältnisse der Tubifloren und Ebenalen, den polyphyletischen Ursprung der Sympetalen und Apetalen und die Anordnung der Angiospermen überhaupt. Vorstudien zum Entwurf eines Stammbaums der Blütenpflanzen. Abhandlungen, herausgeg. vom Naturwissenschaftlichen Verein Hamburg, XII. (June 1901), 112 pp., with a complete index of the plant names.

7. Ueber die Morphogenie, Phylogenie und der Generationswechsl der Achsenpflanzen. Vorläufige Mittheilung.—Berichte der Deutschen Botanischen Gesellschaft, XX., (November 26th, 1902), pp. 476—478.

8. Ueber eine Zwischenform zwischen Apfel und Pflaume.—Verhandlungen des Naturwissenschaftlichen Vereins, Hamburg, 3 series, vol. X. (1902), pp. 8—19

9. Beiträge zur Morphogenie der Sporophylle und des Trophophylls in Beziehung zur Phylogenie der Kormophyten.—Jahrbuch der Hamburg, Wiss. Anst. XIX, 3, Beiheft (January, 1903), pp. 1—110, with 1 plate.

10. Ueber *Hornschuchia* Nees und *Moseuodendron* R. E. Fries, sowie über einige Verwandtschaftsbeziehungen der Anonaceen.—Beihefte zum Botanischen Centralblatt, XIII., 4 (February, 1903), pp. 361—367.

11. Ueber die Abgrenzung und Verwandtschaft der einzelnen Sippen bei der Scrophularineen.—Bull. herb. Boissier, ser. 2, vol. III., 3 (March, 1903), pp. 181—207.

12. Ueber die Verwandtschaftsverhältnisse bei Engler's Rosalen, Parietalen, Myrtifloren und in anderen Ordnungen der Dikotylen.—Abhandl. Naturw. Verein Hamburg, XVIII. (March 1903), 98 pp.

13. Ueber den Umfang, die Gliederung und die Verwandtschaft

der Familie der Hamamelidaceen.—Beihefte z. Botan. Centralbl., XIV. (1903), pp. 247—260.

14. Vorläufiger Entwurf des natürlichen (phylogenetischen) Systems der Blütenpflanzen.—Bull. herb. Boissier, series 2, vol. III, No. 4 (April, 1903), pp. 306—317.

15. Ueber die Gattung *Daphniphyllum*, ein Uebergangsglied von der Magnoliaceen und Hamamelidaceen zu der Kätzchenblüthlern.—Botanical Magazine, XVIII. (Tokio, June, 1904), 15 pp.

16. Ein zweiter Entwurf des natürlichen (phylogenetischen) Systems der Blütenpflanzen. Vorläufige Mitteilung.—Berichte der deutschen bot. Gesellsch., XXIII., 2 (March 29th, 1905) pp. 85—91.

17. Neue Schlaglichter auf das natürliche System der Dikotyledonen. Phylogenetische Betrachtungen. Gera-Untermhaus, W. Koehler, July, 1905.—12 pp.

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#### A.—SPOROPHYTES.

##### I. FILICALES.

##### II. LYCOPODIALES (near Equisetales and Cycadales, derived from Marattiales).

a. ISOPORAE. 1. Psilotaceae. 2. Lycopodiaceae.

b. HETEROSPORAE (Ligulatae).

3. Selaginellaceae. 4. Isoëtaceae. 5. Lepidodendraceae.  
6. Bothrodendraceae. 7. Sigillariaceae.

##### III. EUISETALES (near Lycopodiales and Cycadales, derived from Marattiales).

1. Sphenophyllaceae. 2. Protocalamariaceae. 3. Calamariaceae.  
4. Equisetaceae.

#### B.—SPERMATOPHYTES.

a. GYMNOSPERMS (excluding Gnetaceae).

1. Cycadaceae (derived from Marattiales). 2. Bennettitaceae (derived from 1). 3. Coniferae (including Salisburieae and Taxaceae (derived from Cycadaceae or near Cycadaceae, Equisetales and Lycopodiales, immediately from Marattiales).

b. ANGIOSPERMS.

#### ∞ DICOTYLEDONS.

##### I.—POLYCARPICAEE (containing oil-cells).

\* MAGNOLINEAE (hypogynous, Eupomatia and Trochodendrum excepted).

1. Magnoliaceae. a. Drimytomagnolieae (hypothetical group, derived from Bennettitaceae or near them from Cyca-

daceae, and uniting the primary characters of b, c and d). b. Illicieae (including *Trochodendrum?* and *Tetracentrum?* Descendants of a). c. Schizandraceae (descendants of a or b). d. Magnolieae (descendants of a).

2. Canellaceae (descendants of 1b).
3. Anonaceae (including *Hornschurchia*; derived from and (for instance, by *Anona squamosa*) connected with 1c).
4. Myristicaceae (descendants or only a tribe of 3).

\*\* LAURINEAE (perigynous or epigynous).

5. Calycanthaceae (descendants of 1c).
6. Monimiaceae (including *Gomortega*; near 3 and 5, derived from 1c).
7. Lauraceae (including *Hernandiaceae*; allied to 5 and 6).

II.—RANALES (no oil-cells):

8. Berberidaceae (including *Lardizabaleae*, *Podophylleae*, *Glaucidium* and *Hydrastis*; near 3, 6 and 7, descended from 1c).
9. Menispermaceae (descended from *Lardizabaleae*, or close to them from 1c).
10. Ranunculaceae (descendants of extinct *Podophylleae*).
11. Nymphaeaceae (origin near *Anemonopsis*, *Trollius*, *Caltha*, *Ficaria*, *Ranunculus*, *Batrachium* and extinct *Helleboraceae* with acyclic polymerous perianth; ancestors of *Helobiae* and of the whole division of *Monocotyledons*).
12. Ceratophyllaceae (including *Circaeaster?* Descendants of *Cabombeae*).

III.—RHOEADALES (excluding *Moringaceae*; no oil-cells).

13. Papaveraceae (including *Fumariaceae*; allied by *Romneya* to *Paeonia* and descended from *Paeonieae* or *Podophylleae*).
14. Capparidaceae (including *Tovaria!* Near 13 descended from 8).
15. Resedaceae (near *Tovaria*, *Pteropetalum*, *Ritchiea* and *Crataeva* descended from *Capparidaceae*).
16. Cruciferae (descendants of 14).

IV.—PIPERALES (excluding *Lacistemaceae!* Containing oil-cells; most of them with stipules; mostly with perianth).

17. Lactoridaceae (descendants of 1b?)
18. Piperaceae (including *Saurureae*; near 17, descended from 1b?)
19. Chloranthaceae (allied to 18).
20. Myrothamnaceae (allied to 17—19?)

V. MALVALES.<sup>1</sup>

21. Sterculiaceae (including *Dombegae*, *Triplochiton!* *Buctacrieae!* and *Goupia!* Near 3 originated from 1a).
- ! 22. Papayaceae (descendants of 21).
- ! 23. Euphorbiaceae (excluding *Buxaceae!* and *Daphniphyllum!* Near 22, 24, 28, 29, 117, etc., descended from 21).

<sup>1</sup> The arrangement and limitation of this and the following cohorts is only a provisional one and is very difficult, because most of them represent parallel lines, having the same point of departure in *Sterculiaceae*.

- 24. Bombacaceae (descendants of 21).
  - 25. Malvaceae (descendants of 24).
  - 26. Elaeocarpaceae (allied to 21, 24 and 27).
  - 27. Tiliaceae (including Ropalocarpus and Catostemma ; descendants of 21).
  - ! 28. Rhamnaceae (including Neopringlea? Allied to 21, 23, 27, 29, 62, etc.)
  - ! 29. Urticaceae (including Ulmaceae, Moraceae and Cannabineae ; allied to 23, 27 and 28).
  - ! 30. Dipterocarpaceae (allied to 21, 24, 26 and IV.)
- VI.—EBENALES (descendants of V.)
- 31. Sapotaceae (allied to 26, 30, 32—35).
  - ! 32. Convolvulaceae (including Cuscutae, excluding Nolaneae ; allied to 31).
  - 33. Ebenaceae (excluding Brachynema ; allied to 31 and 35).
  - 34. Symplocaceae (allied to 35).
  - 35. Styracaceae (allied to 30, 31, 33, 34, 54, 80, 101, 111, etc.)
- VII.—GERANIALES (near 62 – 64, descended from 21).
- 36. Zygophyllaceae (excluding Peganum ! Allied to 38 and 39 ?)
  - 37. Cneoraceae (allied to 36 ?)
  - 38. Oxalidaceae (allied to 39, 63 and Mimoseae).
  - 39. Geraniaceae (descendants of 27).
  - 40. Linaceae (including Erythroxyton and Humiriaceae ; allied to 38, 39 and 63).
- VIII.—MYRTIFLORAE (excluding Onagraceae, Trapa and Haloragidaceae ; descendants of V.)
- 41. Lecythidaceae.
  - ! 42. Caryocaraceae (allied to 41, 43 and 54).
  - 43. Rhizophoraceae (including Anisophylleae ; allied to 21, 24, 30, 31, 41—42 and 44).
  - 44. Lythraceae (including Rhynchochalyx, Alzatea, Sonneratiaceae ! and Punica ! Descendants of 41 ?)
  - 45. Myrtaceae (excluding Heteropytis ! Descendants of 41).
  - 46. Melastomaceae (descendants of 45).
  - 47. Combretaceae (descendants of 41 ?)
  - 48. Geissolomaceae.
  - 49. Penaeaceae.
  - 50. Olmiaceae.
  - 51. Thymelaeaceae (descendants of 47 ?)
  - 52. Elaeagnaceae (same origin ?)
- IX.—ROSALES (near VIII., originated from V.)<sup>1</sup>
- ? 53. Saxifragaceae (excluding Parnassia ! Brexia, Tserba, Roussea and Anopterus ? Ribes ? Bauera !)
  - 54. Rosaceae (excluding Stylobasium, including Plagiospermum ! Dichotomanthes ! and Corynocarpus ! Near 26, 34, 35, 41, etc., and originated from V.)
  - ! 55. Anacardiaceae (allied to Pomeae, Amygdalae and Chrysobalaneae).
  - ! 56. Sabiaceae (allied to 55).

<sup>1</sup> It is at present difficult to define this big cohort accurately ; it will probably be divided into several after a more exhaustive examination.

57. Burscraceae (allied to 55 and 56).
58. Simarubaceae (allied to 54—57).
59. Koeberliniaceae (allied to 58?)
60. Coriariaceae (allied to 58?)
61. Meliaceae (near 22—24, 62, 72, 117, etc., descended from 21).
62. Rutaceae (including Heteropytis! Near 23, 27, 28, 61, etc., descended from 21).
63. Connaraceae (near 38, 40, 64, etc., descended from 21).
64. Leguminosae (including Moringa! Near 54, 61—63. etc., descended from 21).
- ! 65. Proteaceae (allied to 64! and 68?)
66. Polygalaceae (allied to 54, 61, 64, 67—70, etc.)
67. Trigoniaceae (allied to 66, 68 and 69).
68. Vochysiaceae (allied to 65? 66, 67 and 69).
69. Dichapetalaceae (allied to 65?—68).
70. Salvadoraceae (allied to 54, 66—69?)
71. Melianthaceae (allied to 54, 58, 61, 63, 64, 66, 72, etc.)
72. Sapindaceae (including Hippocastaneae; allied to 54, 61, 64, 71, 73, etc.)
73. Aceraceae (allied to 72, 74 and 75?)
74. Staphyleaceae (allied to 73, 75? and 76).
75. Malpighiaceae (allied to 73? and 76?)
76. Celastraceae (allied to 74, 75? and 77).
77. Hippocrateaceae (allied to 76).
- ! 78. Aquifoliaceae (allies or descendants of 80).
79. Cyrillaceae (allied to 78?)
80. Ternstroemiaceae (excluding Bonnetiaceae; including Eucryphia! Medusagyne! Marcgraviaceae! Pentaphylax! Tetramerista? Brexia=Thomassettia, Ixerba, Roussea and Anopterus? Stachyurus? Near VI. and 54, descended from V.)
- ! 81. Pittosporaceae (allied to 80 and X.)
82. Chlaenaceae (allied to 80 and V.)
83. Ochnaceae (allied to 80, 81 and X.)
84. Guttiferae (including Bonnetiaceae; allied to 80, 83 and 87).
85. Quiinaceae.
86. Brunelliaceae.
87. Dilleniaceae (allied to V., 80, 83 and 84).

X.—ERICALES (including Primulales, excluding Plumbaginaceae; near 81 and 83, descended from 80).

88. Clethraceae.
89. Pirolaceae.
90. Lennoaceae,
91. Ericaceae (including Vacciniaceae).
- ! 92. Empetraceae (descendants, or only a tribe of 91).
- ! 93. Tremandraceae (including Bauera! Descendants, or only a tribe of 91).
94. Epacridaceae.
95. Diapensiaceae.
96. Theophrastaceae.
97. Myrsinaceae.
98. Primulaceae (connected by Cyclamineae with 97).

## XI.—SARRACENIALES (descendants of X!)

- 99. Sarraceniaceae (allied to 89, 95, etc.) a. Sarraceniaceae.  
b. Nepentheae.
- 100. Droseraceae (including Roriduleae! excluding Parnassia!  
Allied to 89, 93—95, 99, etc.)

## XII.—SANTALALES.

- 101. Olacaceae (including Opilicæ! Champereia! Icaeiaceae!  
Brazzeia! Erythropxyis? Rhaptopetalum! Egassea  
Pierre! Scytopetalum! Alangium! Marlea! Braehy-  
nema! Aneistroeladus! and Sibangea? Near 22, 23, 26,  
27, 30, 33, 35, etc., descended from 21).
- ! 102. Ampelidaceae (allied to 101, etc.)
- 103. Grubbiaceae.
- 104. Santalaceae.
- 105. Myzodendraceae.
- ! 106. Gnetaeae (allied to 104, 105 and 107).
- 107. Loranthaceae (allied to 101—106).

## XIII.—UMBELLIFLORAE.

- 108. Cornaceae (excluding Alangicæ! descendants of 101?)
- 109. Araliaceae (including Umbelliferae; descendants of 108?)
- 110. Adoraeeae (allied to 109?)

## XIV.—AMENTIFLORAE.

- ! 111. Hamamelidaceae (including Daphniphyllum and Balanops!  
Cereidiphyllum, Euptelea and Eucommia! Platanus!  
Leitneria! Buxae and Stylocereae! Near 26—30, 35,  
101, 108, etc. descended from V.)
- 112. Myriaceae (near Leitneria, descended from 111).
- 113. Salicaceae (near Leitneria, 112 and Daphniphyllum,  
descended from 111).
- 114. Juglandaceae (allied to Daphniphyllum, 115a and 116).  
a. Julianieae. b. Juglandeae.
- 115. Betulaceae (near Corylopsis, Hamamelis, Parrotia, etc.,  
descended from Hamamelidoideae). a. Coryleae.  
b. Betuleae. c. Casuarineae.
- 116. Fagaceae (allied to 114 and 115a).

## XV. PASSIFLORALES (including Campanulatae).

- 117. Flacourtiaceae (including Laeistema? near 22—29,  
descended from 21).
- 118. Violaeeae (allied to 117, 119—121, 125, 131, 132, 138, etc.)
- 119. Cistaceae (allied to 118).
- 120. Coehlospermaceae.
- 121. Bixaeae.
- 122. Passifloraceae (near 22 and 23, derived from 21).
- 123. Achariaceae (descendants of 122).
- 124. Malesherbiaceae (same origin).
- 125. Turneraeeae (same origin).
- ! 126. Onagraeeae (including Trapa!, near 125, descended  
from 122).
- 127. Grossulariaceae (allied to 126?).
- 128. Elatinaceae (allied to 126?).
- 129. Datisceaeae (excluding Tetrameleae?, allied to 126 and  
130?).

- ! 130. Halorrhagidaceae (including Hippuris! and Callitriche; descendants of 126?).
- ! 131. Balsaminaceae (near 123, 126, 132, etc., descended from 122). a. Parnassieae; b. Limnantheae (including Macgregoria?); c. Tropaeoleae; d. Balsamineae.
- ! 132. Gentianaceae (near 136, 131, 138, etc., derived from 122).
- ! 133. Aristolochiaceae (near 137, derived from 122).
- ! 134. Rafflesiaceae (reduced parasitic Aristolochiaceae).
- 135. Loasaceae (allied to 126, 136, 137 and 138).
- 136. Begoniaceae (allied to 135 and 137).
- 137. Cucurbitaceae (near 133, 135 and 136, originated from 122).
- 138. Campanulaceae (including Stackhousia? and Peganum! Near 123—126, 131, 132, 135—137, descended from 122).
- 139. Goodeniaceae (allied to 138).
- 140. Candolleaceae (allied to 138—139).
- 141. Calycraceae (allied to 138—140 and 142).
- 142. Compositae (descendants of 138).

XVI.—CENTROSPERMAE.

- 143. Crassulaceae (including Cephalotus; near 132, descended from 122?).
- ! 144. Cactaceae (descendants of 122).
- ! 145. Hydnoraceae (reduced parasitic Cactaceae).
- ! 146. Balanophoraceae (including Cynomorium; still more reduced Cactaceae).
- 147. Aizoaceae (allied to 144).
- 148. Thelygonaceae (allied to 147).
- 149. Portulacaceae (allied to 144, 147—148).
- 150. Basellaceae (allied to 149).
- 151. Phytolaccaceae (allied to 144, 147—150).
- ! 152. Tamaricaceae (including Fouquiera! and Frankeniaceae! allied to 144).
- 153. Caryophyllaceae (allied to 143, 147—152, etc.).
- 154. Polygonaceae.
- ! 155. Plumbaginaceae (allied to 152—154 and 156).
- 156. Nyctaginaceae (allied to 155).
- 157. Amarantaceae.
- 158. Chenopodiaceae.
- 159. Batidaceae.

XVII. CAPRIFOLIALES.

- 160. Caprifoliaceae (including Sambucus, Silvanthus and Carlemannia; descendants of 126?).
- 161. Valerianaceae (descendants of 160).
- 162. Dipsacaceae (descendants of 161).

XVIII. TUBIFLORAE (in a wider sense; descendants of 21).

- a. CONTORTAE (excluding Olcaceae, Salvadoraceae and Gentianaceae).
- 163. Apocynaceae (including Asclepiadaceae; descended from and by Tabernaemontana, etc. connected with 21).
- 164. Loganiaceae (including Gelsemium, excluding Buddleioidae! Plocosperma? and Desfontainea! Allied to 163, 165, 166 and 173).

- ! 165. Rubiaceac (excluding *Silvianthus* ! and *Carlemannia* !  
Near 163 and 164, descended from 21 ?).
- b. TUBIFLORAE (in the proper sense; excluding *Convolvulaceae* !).
- 166. Bignoniaceac (including *Paulownia* ! and *Wightia*.  
Near *Hippocastanaceae*, 163 ! and 165 ? descended from 21).
- ! 167. Oleaceac (reduced Bignoniaceac).
- 168. Myoporaceae (excluding *Zombiana* ? and *Oftia* ! Reduced  
*Crescenticac* ?).
- 169. Pedaliaceae (including *Martyniaceae* ; descendants of  
166).
- 170. Acanthaceae (including *Zenkerina* ! Same origin).
- 171. Verbenaceae (including *Phryma* ? and *Buddleioideae* !  
Same origin).
- 172. Labiatae (descendants of 171).
- 173. Scrophulariaceae (including *Plocosperma* ? *Desfontainea* !  
*Columellia* ! *Oftia* ? *Tetrachondra* ! *Globulariaceae* !  
*Plantagineae* ! *Lentibulariaceae* ! *Orobanchaceae* ! ;  
excluding *Paulownia* ! *Wightia* ! *Brookca* ! *Uroskinnera*,  
*Dermatobotrys* ! *Ourisia* (partly) ! *Rehmannia* ! and  
*Zenkerina*, Descendants of 166).
- 174. Gesneraceae (including *Brookca* ! *Uroskinnera*, *Dermatobotrys* !  
*Ourisia* (partly) ! and *Rehmannia* ! Close to  
173, descended from 166).
- 175. Solanaceae (excluding *Retzia* ! including *Nolaneae* !  
allied to 173),
- 176. Polemoniaceae (allied 175 and 166).
- 177. Boraginaceae (excluding *Tetrachondra* ! ; close to 171,  
descended from 166).
- 178. Hydrophyllaceae (descendants of 177 ?).

β.—MONOCOTYLEDONS (descendants of 11)<sup>1</sup>.

XIX.—HELOBIAE.

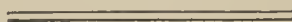
- 179. Butomaceae (derived from extinct *Nymphaeaceae*).
- 180. Alismaceae (allied to 11 and 179).
- 181. Hydrocharitaceae (descendants of 180).
- 182. Potamogetonaceae (allied to 180).
- 183. Aponogetonaceae (allied to 180 and 182).
- 184. Juncaginaceae.
- 185. Triuridaceae.

Etc., Etc.

<sup>1</sup> This division to be worked out later.

Hamburg, Government Botanical Museum.

*May 1st, 1905.*



## THE PRINCIPLES OF MORPHOLOGY.—II.

## THE EVOLUTION OF THE SPORANGIUM.

IN continuation of the line of thought adopted in the last article, I would point out that the primitive origin and point of departure for *everything* that we find in the sporophyte generation, from which every subsequent tissue, organ and individual plant has evolved, is the undifferentiated sporogonium like that of *Riccia*, in which the three morphological categories of "stem," "leaf" and "root" find their point of fusion in one well-nigh homogeneous spore-producing body, which is one of the simplest of thallus-structures. At this point the entire plant may be said to consist of sporogenous tissue, enclosed within a limiting sterile layer of cells. The next step in differentiation was that in which, during vertical elongation of the organ, a *foot* or sucker, the homologue of the future root of the higher plants, became sterilised out of the fertile tissue. Such a stage is represented for us in the Liverwort *Sphaerocarpus*. From this point more than one diverging line of evolution must have proceeded; one of these gave rise to the modern Bryophytes in which the capsule, while remaining, as a rule, unbranched, became highly specialised and complex in structure, this complexity being a wholly secondary character. Another line, however, must have proceeded by way of branching, or, rather, duplication, of the sporogonium in the manner I described last time, producing thereby the earliest and most primitive vascular Cryptogams. The sporogonial capsule and every subsequent exact duplication thereof is at once the *primary sporangium*, and the primary "leaf," possessing radial symmetry of construction; their fused setæ constitute the axial substratum on which these primitive organs are borne, and is unequivocally a *compound* structure. The mode of branching of the whole would be eventually repeated in each lateral sporogonium, and, at the same time, sterilisation of the sporogenous tissue, combined with the assumption of a bilateral character of the primitively radial organ would take place.

Hence it is certain that foliage-leaves are a purely secondary adaptation, for they must have originated by complete sterilisation of the primary sporangia. It is obvious that, out of these latter, any degree of subsequent differentiation can be postulated.

It seems not unnatural to suppose that one of the earliest types of sporophyll, in which a certain amount of sterilisation had taken place, was that which possessed radial symmetry and a single

large, *terminal* sporangium. We may imagine, further, a subdivision of this latter into three parts, as in the male sporophyll of *Welwitschia* and if, of these three, we postulate two inferior and one superior sporangium, of which the former, during the continued process of sterilisation, became modified into two vegetative lobes, while the latter became further sub-divided into two, three, four or, even more parts, we should obtain the type of sporophyll of the *Psilotaceæ*. The primitive type in these plants may have been retained owing to their early adoption of a saprophytic habit; this seems more probable than the view that they represent a case of reduction. A similar stage to that of *Psilotum* and *Tmesipteris* is seen in *Sphenophyllum majus*, with 4-or 5-partite synangium and in *S. trichomatosum* in which a single sporangium occurs in or near the axil of the sporophyll. The next stage in differentiation was that in which the sporophyll became still further forked, and the synangia correspondingly increased in number, as in some forms of *Tmesipteris* and in *Cheirostrobis*. Again, the synangium became raised up on a stalk from the top of which the one or two sporangia were pendulous, as in other forms of *Tmesipteris* and *Sphenophyllum*. In *S. Dawsoni* there are two such sporangiophores to each "bract." This latter really represents the sterilised inferior sporangium or synangium and is here simple and unforked. The term "bract" is of merely descriptive value. In *S. Römeri* there are three whorls of sporangiophores; each is more or less peltate, bearing two pendulous sporangia, and is fairly massive. A much greater elaboration of the structure of the sporangiophore is found in *Cheirostrobis*, which plant, although doubtless a very primitive type as a whole, has yet, as regards its sporophylls, become very highly differentiated and specialised; the same remark applies, although in less degree, to *Sphenophyllum*. In *Cheirostrobis* each sporangiophore belonging to each lobe of the palmately-divided sporophyll is a perfectly peltate structure bearing 4 elongated sporangia.

Before proceeding to mention the peculiarities of further types, I will pause here to consider the exact morphology of these various "sporangiophores." In some forms of *Tmesipteris* this structure is replaced by a *leaflet* perfectly resembling the normal leaflets or lobes of the sporophyll. Here we see an excellent and rare case of a *ventrally*-placed leaflet. It shews clearly, to my mind, that the sporangiophore of *Tmesipteris* is exactly homologous with such. But if so, then are the sporangiophores of

*Sphenophyllum Dawsoni* also homologous with a leaflet or segment of the sporophyll, for they are structures clearly similar in character to the sporangiophores of *Tmesipteris*; and inasmuch as these organs in *S. Römeri* connect those of *S. Dawsoni* and *Cheirostrobis* together, it follows that even the complex sporangiophore of this last-named plant is the homologue of a leaflet. And I maintain also that the case of *Tmesipteris* shews that the synangium or compound sporangium, occurring in the best-known forms of *Tmesipteris*, in *Psilotum*, and in *S. majus* and *S. trichomatosum*, is also the homologue of a leaflet. And we may remind ourselves again that this ventrally-placed synangium or leaflet is merely the superior of the 2 or 3 original, *terminal* sporangia into which the still more primitive single terminal sporangium became divided.

Passing on to the Calamariaceae, let us imagine an axillary sporangium like that of *Sphenophyllum trichomatosum* becoming elaborated into a peltate sporangiophore (it has been seen how just such an elaboration has taken place in the Sphenophyllales); we should then obtain the case of *Palæostachya*. But how are we to elucidate the relationship of the sporangiophores of *Calamostachys*? It seems highly probable that those of *Cheirostrobis*, *Palæostachya* and *Calamostachys* are each and all identical structures and that all must, therefore, be regarded as partaking of the nature of subdivisions of sporophylls, and not as independent organs. Bower well points out how the members of each succeeding whorl of sporangiophores are superposed to each other, and how the alternate succession of the sterile leaves is not disturbed by the intervening fertile whorls; also that the number of sporangiophores in a whorl is only about half that of the sterile leaves. These facts tend to prove that the sporangiophores are not independent foliar organs. Scott, finding a difficulty in regarding those of *Calamostachys* as of the nature of ventral lobes of the sporophyll, cuts the Gordian knot by the facile ascription to them of *sui generis* rank. This is also Bower's view of the matter.

Yet I cannot agree with Scott that the view which regards the sporangiophores of *Calamostachys* as homologous with those of *Cheirostrobis* is a forced one; for it seems to me that there are clear grounds for holding such an idea and a relatively easy method of explaining the apparently independent position on the axis of the sporangiophores of *Calamostachys*. Holding the view, as I do, that each foliar organ possesses not only a "foliar base," confluent with the axis below, but also a corresponding upward extension on the

axis, giving thus to each leaf a sort of sole-like expansion to its axial insertion, the sporangiophores of *Calamostachys* may, therefore, be regarded as *still inserted upon the sporophyll*, viz: upon the upward extension of its basal portion, although they *appear* to be so entirely separated therefrom. It is thus probable that a *gradual shifting* of the sporangiophore from the upper surface of the sporophyll (*Cheirostrobis*), first to its axil (*Palaeostachya*), and finally entirely on to its upper axial foliar base (*Calamostachys*), has taken place.

In the case of *Equisetum* and *Archæocalamites*, where *sporangiophores only* occur on the axis, it seems not at all unreasonable to suppose that the sporophylls themselves have become completely eliminated (the antiquity of *Archæocalamites* need not interfere with this view), and thereafter the sporangiophores themselves became *rearranged* owing to the requirements of space-economy. Such elimination of members, succeeded by a rearrangement of those remaining, is seen, I would submit, in the androecium of certain flowers, e.g. *Tropæolum*, where two whorls of five are now represented by a single whorl of eight. Hence, in the two above-named genera the sporangiophores may be regarded as complete sporophylls in themselves.

In the Lycopod-phyllum, which probably also branched off from the Sphenophyllales, no great development of the sporangiophore, apparently, ever took place. In *Spencerites* the entire sporophyll curiously simulates in shape the sporangiophore of a Calamite, inasmuch as it is peltate, yet betrays its distinct origin by bearing a single sporangium on the *upper* lobe only of the leaf. *Sigillariostrobus Crepini* would appear also to belong to this type.

In *Lepidodendron*, *Sigillaria*, *Isoëtes*, *Lycopodium*, *Selaginella* and *Phylloglossum* the sporangium is situated on the upper surface of the sporophyll. In some of these cases, as in *Lycopodium*, a distinct sporangiophore or sporangial pedicel is present, although of small development.

Now it is extremely interesting to note that in this phylum of plants we find a perfectly parallel case to that existing in the Equisetales, as regards the *varying position* on the sporophyll of the sporangium (or sporangiophore). In the fossil genera and *Isoëtes* nothing could be more conspicuous than the clearly-defined foliar origin and position of these structures. In some species of *Lycopodium*, however, the sporangiophore is in a perfectly *axillary* position, thus exactly corresponding to the case of *Palaeostachya* in the parallel phylum. Now mark the case of *Selaginella*: here the

sporangium always arises ontogenetically in the apparently axial position, some distance above the insertion of the sporophyll, so that it has actually been described as arising on the axis itself. But, during subsequent development, the sporangium becomes carried downwards on to the actual free base of the sporophyll, which seems to shew that it was from birth already situated on an upward basal extension of the sporophyll which is embedded in the axis. Now, suppose the ontogenetically primary position of the sporangium of *Selaginella* to become fixed and the subsequent transposition on to the free portion of the leaf to become completely eliminated (a state of things which might easily have come about), we should have a precisely parallel case to that of *Calamostachys*.

For the existence of such an upward basal extension of the sporophyll as I have assumed above, there is further corroboration in the fact that it clearly obtains in the higher plants, e.g. in Primulaceæ, where the ovules are situated in the same pseudo-axial position as the sporangiophores and sporangia of *Calamostachys* and *Selaginella*.

Turning now to the Ophioglossaceæ, I must almost entirely agree with the conclusions of Celakovsky and of Bower in the view that, in order to explain the peculiar position of the "fertile spike" on the upper surface (in most forms) of the sporophyll, the theory of a gradual and, eventually, highly complex elaboration by means of progressive sterilisation, must be adopted. This complex structure must have been derived from the simple sporangium or sporangiophore of a Lycopod. We see an incipient stage of sterilization and differentiation in the case of *Isoëtes*. Imagine this proceeding further and in a different direction, and we might obtain at length the "spike" of *Ophioglossum* and, finally the very highly-differentiated "spikes" of *Botrychium* and *Helminthostachys*. The interesting parallelism in elaboration between the sterile and fertile portions of the sporophyll is a point to be noted.

An important parallelism may also be observed if we compare together the cases of the simple *Lycopodium*-type and the complex type of the Ophioglossaceæ on the one hand, and, on the other, the type of the simpler *Sphenophyllums*, e.g. *S. trichomatosum* and Psilotaceæ, and the complex type of *Cheirostrobos* or of *S. Römeri*. In *Cheirostrobos* we also see, as in Ophioglossaceæ, a highly-differentiated sporangiophore with a correspondingly-developed sterile portion of the sporophyll.

In certain forms of *Ophioglossum*, e.g. *O. palmatum*<sup>1</sup>, there are a number of sporangiophores which are borne, no longer in the medianly ventral position on the sporophyll, but either on its actual margins or on the surface, a short distance away from the margin; this latter position is precisely equivalent to the position of the ovules on the carpels in the case of very many higher plants. The marginal position of the highly elaborate sporangiophores at once invites comparison with the pair of basal elaborately-subdivided fertile pinnæ of the Schizæaceous genus *Aneimia*. There is no doubt in my mind that these latter are structures homologous in every way with the "fertile spikes" of *Ophioglossum palmatum* and therefore with those of *O. vulgatum*: and, a necessary consequence also, with the sporangia of the Lycopods. All these structures represent *morphologically* a leaflet or segment, whether ventral or marginal in position, of the sporophyll.

I am inclined to find the primitive type in the single undivided sporangium of the Lycopods, which, in the case of four genera, has persisted down to the present day; this single sporangium by means of elaboration, gave rise to the type of our British *Ophioglossum*, *Botrychium* and *Helminthostachys*. But the sporangium, as in *Psilotum* and *Tmesipteris*, became divided into two or more parts; and, by means of elaboration of each of these, the type of *O. palmatum* and of *Aneimia* arose. The orientation of the fertile pinnæ of this latter plant—connivent across the ventral face of the leaf—suggests their real origin.

On these grounds I am inclined to assign an intimate relationship in origins to the Ophioglossaceæ and Schizæaceæ. The saprophytic habit of the former class, as is also the case in Psilotaceæ, has probably been a prime factor in causing them to retain several primitive characters, and this, to my mind, seems a very much more reasonable hypothesis than that which implies a reduction on that account.

That the Ophioglossaceæ exhibit certain Filicinean features in their organisation, while at the same time showing clear signs of an alliance with the Lycopods, must be ascribed to the fact that they stand much nearer the primary common point of departure of the Filicineæ and Sphenophyllales than do any of the members belonging to the Lycopodiales. They are, in other words, a much more *generalised*

<sup>1</sup> Here also we see *dichotomy* of the sporophyll, as in that of Psilotaceæ, *Cheirostrobis* and the vegetative leaves of some species of *Sphenophyllum*.

group<sup>1</sup>. It would almost seem preferable, therefore, to place them in a distinct phylum of their own; yet in view of their evident close resemblance to certain of the Schizæaceæ, e.g. *Aneimia*, I am rather disposed myself to regard them as Ferns of a very primitive and elementary type. It must always be remembered that this latter is a very vague term indeed; that there are Ferns *and* Ferns; and that it does not necessarily follow that, for instance, the Polypodiaceæ are anything but very remotely allied to such a group as the Schizæaceæ, this latter standing nearer to the ancient generalised type as shewn both by its sporangial tissues and stem-anatomy, yet at present it appears to be following a very "Filicinean" course of evolution! So do the Ophioglossaceæ, at any rate as regards the evolution of their foliar organs.

The "primary sporangium," a lateral repetition of the primitive sporogonium, constitutes then the matrix out of which all subsequent sporophylls, sporangiophores and sporangia have evolved. The terminal sporangium became divided into superior and inferior (adaxial and abaxial) portions. Sterilisation and sub-division of the former gave rise to the type found in the Sphenophyllales, Equisetales, Lycopods, Ophioglossaceæ and Schizæaceæ (at any rate *Aneimia*). The same process taking place in the inferior or abaxial sporangium probably gave rise to the complex assimilating and sporangiferous sporophylls of the typical Ferns. The sporangia at first were *marginal* structures, i.e. *terminal* to lateral segments of the leaf, e.g. Osmundaceæ, Hymenophyllaceæ, Schizæaceæ, Lyginodendron; there subsequently arose a tendency for them to become displaced on to the *lower* surface of the sporophyll, as in Schizæaceæ, Polypodiaceæ, male sporophylls of Coniferae, Cycadaceæ.

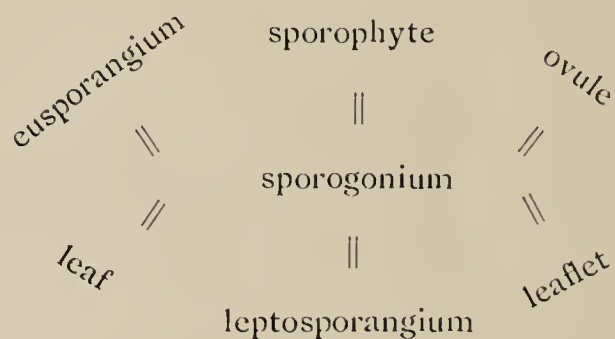
A curious equivalence, probably due to reduction of the sporophyll, is found between the "primary sporangia" or secondary sporogonia and the ovules of Gnctaceæ and Coniferac; in these latter the *entire leaf* is the sporangium just as it was in the far-back primitive condition.

<sup>1</sup> The idea must not be entertained that the Ophioglossaceæ have sprung from the Lycopodiales, or even from the Sphenophyllales. They have probably been derived more or less directly from that remote generalised group which combined the characters of Filicineæ and Sphenophyllales. This very simple view would amply suffice to explain the peculiar mixed characters of this group.

*Isoetes* is evidently closely allied to the Lycopodiales; but, probably owing to its aquatic habit, it has retained certain characters of the same generalised ancestor which its modern allies have lost, probably owing to the specialisations induced by their land-habitat.

It is obvious from all that has been said above, that the sporogonium of the primitive Bryophyte is at once the homologue: (1) of every type of *foliar organ*; (2) of every type of sporangiophore; (3) of every type of sporangium, whether eu- or lepto-sporangium, no matter in what group of plants it may occur; (4) of the entire sporophyte. This is the doctrine of *variously-graded* homologies. The deductions from this idea are *apparently*, but only apparently, absurd; thus: the sporogonium of a Bryophyte must for instance, be rigidly homologous both with an oak-tree and with every single *nucellus* contained by every ovule of that oak-tree.

The idea may be graphically represented thus:—



I do not intend to enter here into the homologies existing between the ovule and its various parts and corresponding organs occurring in the vascular cryptogams, as I have comparatively recently done so in a paper contributed to the "Annals of Botany."

In conclusion I should mention that for much of the contents of this paper I am greatly indebted to Professors Celakovsky and Bower.

W. C. WORSDELL.

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## THE VIENNA INTERNATIONAL CONGRESS.

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THE second Quinquennial International Botanical Congress was held this year at Vienna, and lasted from June 11th to June 18th.

Though not the most accessible place for Western European and American botanists, Vienna is a most important *locale* of botanical activity; it is also a magnificent centre for visiting the flora of Central Europe, and this fact was taken advantage of by the organisation of various excursions. One of these, through parts of Southern Austria and the Balkan States took place during the month preceding the meeting. About 600 people attended the

Congress. Of these there were twelve Americans and six British representatives. Professors Wiesner and von Wettstein were joint Presidents of the Organising Committee, and Dr. Zahlbruckner, the energetic Secretary.

The Congress was inaugurated by a supper in the Hall of the Kaufmännischer Verein, where Professor Wiesner welcomed the guests. The official opening at which the world-famed geologist, Professor Suess, greeted the members, was held on the Monday morning in the great "Festhalle" of the University.

The papers which formed part of the actual work of the meeting were arranged in groups under general heads. One of the most interesting of these was the Development of the European Flora since Tertiary times. The subject was introduced generally by Professor Engler of Berlin, whose work in this branch of historical plant-geography is well-known. Professor Engler is indefatigable in developing our knowledge of the distribution of plants, not only by his own work, but also by his inception of large schemes for bringing together the rapidly advancing knowledge of distribution, both in Europe and in the world at large. On this occasion he put in a timely plea for the preservation of specimens of typical European plant-formations, especially of those which throw light on the evolution of European Vegetation. Many of these are threatened with destruction in the immediate future by the activity of man in clearing, draining and building. A pressing instance was mentioned by Dr. Lauterborn in the primitive forests of Bosnia, which are apparently threatened with imminent destruction. This is a subject that should be urged on the attention of the Governments of the different countries, though as far as Great Britain is concerned it is probable that we shall have to look to private munificence if anything is to be done.

One of the most important features of the Congress was undoubtedly the conference on botanical nomenclature (under the able and genial presidency of Professor Flahault) which had to discuss the recommendations of the commission on nomenclature appointed by the Paris Congress of 1900. The work of the conference was only rendered possible by the labours of Dr. Briquet, who had collated the very numerous emendations and modifications of De Candolle's code submitted during the five years that have elapsed since the Paris Congress by various societies, institutions and individual botanists. These suggestions had been discussed and voted on by the commission, and the resulting recommendations of this body were drawn up by Dr. Briquet and submitted to the present conference, which was attended by about 150 members. The work of the Conference which sat every afternoon from 3 o'clock till a late hour was naturally very heavy, but a very earnest desire was evinced to arrive at some solution of the difficult questions involved, and several compromises were agreed to. The code of laws adopted, based on De Candolle's, will consist of "rules" and "recommendations," the former having the force of binding laws, while the latter merely put forward suggestions for the guidance of systematic botanists.

One of the most important results secured, and one that will certainly be welcome to the non-systematist, was the passing by an overwhelming majority of a list of generic names, established by

long usage, which are to be retained though contrary to the strict law of priority. The conference also held that a name once given, though inappropriate or even misleading, must stand.

Lectures by leading botanists were a feature of the meeting. Thus Professor Goebel dealt with "Regeneration" and Dr. D. H. Scott with "The Fern-like Seed-Plants of the Carboniferous Flora."

There was a very fine Botanical Exhibition in the Orangery of the Imperial Palace at Schönbrunn, just outside the city. This consisted of all kinds of objects connected with Botany, conspicuous among which were living cultures of Algæ from the Adriatic and elsewhere.

The social side of the meeting was extremely well organised. The Emperor had invited the principle botanists to a court-reception, but this unfortunately had to be cancelled owing to the death of the Archduke Joseph. Every evening there was an expedition or entertainment of some kind: one to the Kahlenberg, from which there is a splendid view of the whole town; an academical feast in the Hutteldorfer Brauerei, with songs by students; one in the Prater with fine choral singing and an excellent amateur comic entertainment, after which there was dancing.

Professor Suess gave a lunch-party at the Grand Hotel, and Frau von Gerold, the President of the Damencomité which looked after the interests of the lady-visitors, entertained some of the members at her country house. The Damencomité arranged a full programme of sight-seeing for the ladies, and entertained them all to a "Jause" (an Austrian form of tea party) in the Stadtpark.

On the last day there was an expedition to the Schneeberg, 6810 feet, where some good botanising was done, and the members dined together at the hotel near the summit. During the railway journey back the members walked from one carriage to another saying goodbye.

Altogether the arrangements of those responsible for the social side of the gathering were extremely successful, particularly in enabling the members to get to know one another personally.

In response to an invitation from the Belgian Government, conveyed by Professor Errera, Brussels was selected as the place of meeting for the next Congress, to be held in 1910.

We are indebted to Dr. A. B. Rendle and to Mrs. D. H. Scott for the information contained in this brief account of the Congress.

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## REVIEW.

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"PFLANZENPHYSIOLOGIE," Vol. II., Part 2; pp. 353-986,

By Dr. W. PFEFFER, Engelmann. Leipzig, 1904.

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WITH this part, the new edition of Professor Pfeffer's well-known Handbook is brought to a conclusion. As the author explains, the completion of the second volume, the first part of which

appeared in 1900, has unfortunately been delayed by illness. It is not necessary now a days to point out to botanists the value of the book; suffice it to say, that like the earlier parts, this one displays that philosophical method of treatment, fullness of discussion and wealth of reference to the literature which make the Handbook a really monumental work.

The first half of the second volume dealt chiefly with growth in general; the second part deals first with curvatures, under the headings of autonomous curvatures, movements of climbing plants, curvatures produced by mechanical and chemical stimuli, photonastic, thermonastic and hydronastic curvatures; and there is a special section on the movements in connexion with the opening of such organs as fruits, anthers, sporangia, and with the ejection of seeds and spores. A long chapter is devoted to tropistic curvatures (curvatures produced by a one-sided stimulus in contradistinction to such movements as photonastic, which are brought about by a general diffused stimulus) which are classified under ten heads. A section is devoted to the conditions of stimulation and the nature of the stimulation-process in the various tropisms. In relation to the much debated question as to the nature of the geotropic stimulus. Pfeffer's view is that neither the statolith theory in general nor the starch grain theory of Nemec and Haberlandt in particular, can yet be accepted. He still considers it possible that the effect may be brought about by difference of pressure in the cell, nor does he consider the existence of a high osmotic pressure in the cell as any objection to the view that slight difference of pressure may so act. There is in conclusion a chapter on locomotor movements of plants and on protoplasmic movement, one on the production of heat, light and electricity, and a final chapter with a general review of the intake and output of energy by the plant.

With this part there is also provided an index of authors and a subject index to the whole volume. The latter index is fortunately a full one, and will do something to make up for the differences of style and lack of co-ordination between the various parts of the work, which in spite of all its merits makes it by no means easy of reference. In this connexion it seems a pity that in the English edition the numerous cross-references, which also help to mitigate the effect of the lack of co-ordination, should, so far, have been largely omitted.

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## LABORATORY NOTE.

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### CONGO-RED AS A STAIN FOR UREDINEÆ.

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CONGO-RED in 1% watery solution has been found very useful in staining the hyphæ of the Uredineæ, as the cell-walls of the fungus are tinged a bright red, whilst the host-cells remain usually untouched or only take the stain very lightly. Sections (microtome sections were mostly used) are stained for a few (2-10) minutes, and the fluid is then washed off directly with alcohol if a strong stain is required, or with water first if only a slight stain

is necessary. It forms a particularly good contrast stain with iron-alum-haematoxylin for the nuclei. Material fixed in alcohol or acetic alcohol stains the most readily and effectively; it also works very well after fixing fluids containing chromic acid only, but then the stain takes somewhat longer and is not quite so bright. The rapidity of the stain and the density of the result are increased by the addition of a few drops of ammonia to the solution, a modification which is specially helpful in treating refractory chromic material. The stain fades very quickly in ordinary xylol-canadabalsam, probably owing to a slight acidity of the medium (neutral balsam was not tried), but it keeps very well in xylol-dammar and in gum-thus.

The effect of such a stain does not necessarily mean that the cell-wall in the Uredineæ consists largely of cellulose, for the value of Congo-red as a test for this substance has been called in question by the observations of Heinricher and Challon.

V. H. BLACKMAN.

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#### UNIVERSITY OF LONDON ADVANCED LECTURES.

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[Owing to an oversight all reference was omitted, in the note under the above title in the last number of this journal, to Dr. Rendle's Course on Tubiflorae given contemporaneously with Dr. Blackman's on CO<sub>2</sub>-Economy. Dr. Rendle's Course was delivered at the Chelsea Physic Gardens. The following is a brief notice of the scope of the Course].

The subject of the lectures was the Cohort Tubiflorae as recognised in Professor Engler's *syllabus*. The introductory lecture included a discussion of the position of the cohort as a member of the great group of Dicotyledons, the *Metachlamydeae*. It was pointed out that while there was considerable evidence in favour of a polyphyletic origin of the group, there was a very general opinion that, at any rate, Tubiflorae must remain as representing a number of nearly allied orders standing somewhere near the top of the Dicotyledonous tree. The orders were then taken *seriatim*, and their morphology, vegetative and floral, the principles of their sub-division into tribes and genera, and their geographic distribution were studied with the help of a large series of lantern slides, of living specimens grown in the Chelsea Gardens, and also of wild British examples. It was seen that, although there might be some difficulty in separating the constituent orders in distinct cohorts, it was possible to recognise several more or less well-marked sub-divisions. Starting with Convolvaceae and Polemoniaceae we pass from a radially symmetrical flower, in which moreover the bicarpellary character has not become so rigidly set, through Hydrophyllaceae, Boraginaceae and Solanaceae, where the tendency towards zygomorphy is increasingly marked, to the still more specialized members of the group represented by Scrophulariaceae and its (often very) closely allied orders, Acanthaceae and Labiatae. Constant reference was made throughout to cross affinities and the recurrence of closely similar types of floral conformation in different orders, doubtless associated with the adoption of similar methods of pollination.

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SOME POINTS IN THE ANATOMY OF *ACROSTICHUM*  
*AUREUM*.

By ETHEL N. THOMAS.

[WITH PLATES III. AND IV., AND TEXT-FIGS. 27—40.]

A CERTAIN interest attaches to *Acrostichum aureum* inasmuch as it is the only Vascular Cryptogam now known whose habitat is the salt-swamp.

In view of the probability that many of our fossil Vascular Cryptogams were swamp-plants the investigation of this Fern seemed very desirable. Professor Oliver therefore suggested that I should examine material sent to him from Ceylon by Mr. A. K. Coomáraswámy.

*Acrostichum aureum* (= *Chrysodium vulgare*), so-called from the colour of its young leaves, is a handsome plant of bush-like growth forming a marked feature of the Mangrove Flora of Ceylon<sup>1</sup>. It has an erect stem with long up-standing pinnate fronds, the upper pinnæ of which are slightly smaller and fertile. From among the bases of the fronds numerous stout roots descend almost vertically in a tangled weft.

ADAPTATION TO CONDITIONS.

It is the roots which show the most interesting modification in connection with the peculiar mode of life. Each root is clothed with a soft brittle tissue which drops away in patches, leaving the central strand exposed—like a wire imperfectly covered with wool. This appearance is found on sectioning to be due to a great development of the middle cortex, which is furnished with huge lacunae (Pl. III., fig. 3). The cells lining the lacunar chambers are very irregular in shape, and connect up with one another by numerous short arms. The membrane between the arm of one cell and that of another is sclerised, and perforated with numerous scalariform or rounded pits (Pl. III., fig. 1).

<sup>1</sup> Tansley and Fritsch. "The Flora of the Ceylon Littoral,"  
NEW PHYTOLOGIST, Vol. IV., Nos. 1, 2 and 3.

In transverse section these dividing septa appear as round or oval pitted areas upon the more or less oval cells (Pl. III., figs. 2 and 4).

In longitudinal section the cells are somewhat elongated, and frequently present the appearance of a flask with laterally directed neck (Pl. III., fig. 5). It is only when the arms are presented to the observer end on, that their septa are seen as perforated discs, and as the walls of the chambers are usually but one cell thick, it is clear that they are found only on the cells of the radial wall in a tangential section (Pl. III., fig. 6) and on the tangential cells as seen in a radial section. The tangential and radial cells in these sections respectively, shew the arms in profile (Pl. III., fig. 6).

The connecting arms frequently expand at the cross wall, recalling the similar expansions seen in sieve-tubes and "trumpet hyphae."

Karsten<sup>1</sup> has described similar tissue in several Mangroves, notably in the roots of *Bruguiera gymnorhiza*. He figures disc-like connecting walls, which look almost precisely like those just described, but he does not mention any perforations. On the other hand the cells of *Bruguiera* possess thickening bands not found in *Acrostichum aureum*. Experiments on mangroves and on water plants have shown that such tissues are for the purpose of aeration, and we cannot doubt that here too the same function is performed.

The "air tissue" is found most abundantly on the proximal portion of the large roots. At the distal end it is almost absent, and the lateral roots form short sharp spines similar to those found on the aërial roots of *Dioscorea prehensilis*.<sup>2</sup>

The very close similarity of response met with in the mangroves, whose members are drawn from very widely separated orders of flowering plants, has always been a point of considerable interest, but this parallelism of development is brought out with much greater force, when we find the same response in the one member of this œcological association derived from the Vascular Cryptogams.

Under normal conditions, roots are very constant in their general anatomical features, and this is doubtless correlated with the constancy of the medium in which they grow, and of the functions which they have to perform. When one or both of these conditions is unusual, as in the present case, a very definite modification is met with, and this modification can with greater certainty

<sup>1</sup> G. Karsten. Ueber die Mangrove-Vegetation in Malayischen Archipel. Bibliotheca Botanica, Heft 22, 1891.

<sup>2</sup> Hill and Freeman. The Root-structure of *Dioscorea prehensilis*. Annals of Botany, 1903.

be referred to the altered circumstances than in the case of shoot structures, which come under the influence of far more complicated factors.

This being so, it is not without interest in this connection, to consider the structure of the roots of fossil plants known to us.

The markedly lacunar character of the middle cortex of Calamite roots instantly occurs to one, and indeed the young root of *A. aureum* (Pl. IV., fig. 8) bears a surprising resemblance to the young Calamite root<sup>1</sup>. Still more striking is the immense development of middle cortex in Stigmarian roots, where the tissue was evidently of a very delicate nature, for it is rarely preserved except at the edges, where it joins the inner or outer cortex. It is highly probable that it was lacunar in character. A lacunar middle cortex has been described by Bower<sup>2</sup> in the axis of *Lepidostrobus Brownii*, and the prevalence of three distinct zones in most *Lepidodendra*, and to a less extent in living *Lycopsids*<sup>3</sup> is commented upon. The middle zone is always composed of delicate parenchymatous cells, arranged loosely, and frequently forming lacunae. The inner and outer cortical zones are generally each composed of a few layers of thick-walled or sclerenchymatous cells.

Turning now to the fossil Ferns and Gymnosperms we find here also plentiful instances of lacunar cortices. Among the Ferns proper the roots of *Psaronius* show a marked lacunar cortex which is also found in "Kaloxylon"—a root probably to be assigned to *Lyginodendron*, but at any rate belonging to a member of the *Pteridosperms*.

#### VASCULAR ANATOMY.

##### *Root.*

The roots, both large and small, are formed on a triarch plan, but the stouter roots have in addition three alternating protoxylem groups, quite different in character from the main groups. The xylem arms of the small triarch roots are very wide—almost as extended as the alternating phloem groups—and each blunt extremity is obviously composed of two protoxylems, reminding one of the structure of a *Sphenophyllum* stem. I can find nothing quite comparable in any described Fern.

<sup>1</sup> Williamson & Scott. "Further Observations, Etc." Part II., The Roots of Calamites, *Phil. Trans.*, Vol. 186, B. 1895.

<sup>2</sup> F. O. Bower. Structure of the axis of *Lepidostrobus Brownii*, *Annals of Botany*, 1893.

<sup>3</sup> The name "Lycopsida" is used throughout in the sense proposed by Professor Jeffrey to include all "Vascular Cryptogams other than Ferns."

The protoxylem groups of rootlets still enclosed in the parent tissues seem to be single (Pl. IV., fig. 8).

In the stout roots (Pl. III., fig. 3 and Pl. IV., fig. 7), as has been mentioned above, the three phloem groups are always bisected by a narrow, pointed, single protoxylem group, which alternates with the characteristic wide double protoxylem poles. As the phloem groups are shallow, this gives the large xylem body an almost circular appearance, although the triangular plan is quite discernible. The rounded contour of the xylem body, coupled with the comparative smallness of the phloem groups, and the presence of a great quantity of parenchyma in the xylem gives rise to a very stem-like appearance, recalling indeed the stem of *Gleichenia*.

The only Fern root I have seen figured in the readily available literature with which it can be even remotely compared, is that of *Angiopteris evecta*.<sup>1</sup> This has a polyarch structure and is altogether planned on generous lines. It approaches the root of *Acrostichum aureum* in the disposition of its abundant parenchyma. The stout roots of the latter plant, however, bear a far more striking resemblance to the petiole of *Lygodium japonicum*!<sup>2</sup>

We see then that in the character of the stele and of the cortex the roots of this Fern are exceptional and shew distinct resemblances to the stem-type. It will be remembered that Westermaier<sup>3</sup> has pointed out that the *pneumatophores* or air-storing roots of the mangroves proper have many stem characters. These organs are in fact intermediate in structure between true stems and roots. Thus the primary xylem is more or less centrifugal in development, and phloem may occur on the same radius. They are further provided with a pith and have no root-cap.

Many pneumatophores have a peculiar development of the periderm for purposes of aeration. The phellogen forms layers of loose parenchymatous cells—"aerenchyma"—alternating with true cork layers. The phellogen arises in the cells of the outer cortex, thus being superficial in origin—another shoot-like character.

I have frequently noticed a very regular disposition of the cells of the outer cortex of the root of *A. aureum*, and have occasionally observed a distinct tangential wall in some of the large rounded cells of a continuous layer. This appearance suggested the possi-

<sup>1</sup> R. Shove. Ann. of Bot., 1900.

<sup>2</sup> Boodle. Anatomy of the Schizaeaceae. Annals of Botany, 1901.

<sup>3</sup> Westermaier. Zur Kenntnis der Pneumatophoren. Botanische Untersuchungen im Anschluss an eine Tropenreise, Freiburg, 1900.

bility of secondary cortex arising, for the production of special air-absorbing tissue.

Turning now to fossil roots, we find that they had very frequently characters which we regard as appertaining more strictly to shoots. The large Calamite roots have always a good pith and extensive cortex (see above). The anatomy of Stigmarian axes is of so indeterminate a type, that some divergence of opinion has arisen as to their morphological nature. It is best perhaps frankly to own them intermediate in character, like the rhizophores of their living allies, the Selaginellas.

The prevalence of centripetal development of the xylem in the shoots of Vascular Cryptogams removes one of the most constant differentiating features between the root and shoot as known in the Higher Plants. Nevertheless it seems to be only in the Lycopsidea that other characters combine to render morphological limitations obscure.

The peculiar nature of the periderm of fossil plants is frequently remarked upon. In root and shoot alike it arises from the cells of the outer cortex; while “‘periderm’ and ‘bark’ . . . . were very different in nature and function from the recent tissues which answer to them morphologically.” It is doubtful whether any of the periderm cells became suberized, for the tissues exterior to it remained fresh, and it is conceivable that some of its delicate parenchymatous cells—such as those described for *Sigillaria spinosa*—may have had an aerating function.

#### *Stem.*

The chief conducting system of the stem forms a continuous cylinder, consisting of xylem elements in the centre, and clothed within and without with phloem, pericycle and endodermis in the manner characteristic of a solenostele. There are in addition a few slender accessory steles, lying in the ground tissue enclosed by the solenostele. The ground tissue immediately surrounding the solenostele, on the inside and on the outside, is differentiated into a broad band of sclerenchyma. There is a third sclerenchymatous sheath round the exterior of the stem. The solenostele is roughly triangular in transverse section, following the general contour of the stem (Text-fig. 27).

#### *Petiole.*

The petiole shows a far more complicated vascular system than we should expect from the comparatively simple arrangement in the stem.

<sup>1</sup> Scott. “Studies in Fossil Botany,” p. 227.

Instead of the horseshoe leaf-trace, so frequently correlated with the solenostele, we meet with a bewildering number of small bundles, at the first glance giving almost the impression of being arranged in three concentric series. The position of the protoxylem elements in these bundles at once attracts attention (Text-fig. 36).

The bundles forming a row along the flattened upper (adaxial), side<sup>1</sup> of the petiole, have their protoxylem groups uppermost in the normal manner (Text-fig. 36). The protoxylem groups of the semicircle of bundles arranged around the periphery of the convex under (abaxial) side are also directed towards the upper surface but within them is a smaller semicircle of bundles with inversely orientated protoxylem groups. This series, however, appears to be continuous at its ends with the outer series, and gives rise to the suspicion that they represent a lateral indentation of bundles arranged on the horseshoe plan.

The central internal system, and the upper row of bundles first alluded to, can similarly be explained as elaborations of the free ends of the horseshoe.

From an examination of the petiole alone, Mr. Gwynne-Vaughan, in a letter to Professor Oliver, has expressed his belief that the vascular system of the petiole of *Acrostichum aureum* can be "thus resolved." I fortunately had in the material at my disposal, a young plant from which a microtome-series of the base of one of its youngest fronds was obtained. It revealed the petiolar vascular system described above, but in its simplest terms (Text-fig. 34). The peripheral series of the lower side is composed of six bundles; within this is the inverted series consisting of only four bundles—two on each side and separated by a space. The central system is represented by one large bundle with several protoxylem groups. It is only slightly displaced from the middle of the row of bundles on the upper side.

#### *Node.*

A series of transverse sections was made through the stem, and they probably included the insertion of the petiole just described.

As the node is approached from below, the first sign of the departure of the leaf-trace, is the bulging of the solenostele at one of its angles to form a horseshoe-like loop (Text-fig. 27). Very soon, however, the continuous horseshoe is broken up into bundles. This

<sup>1</sup> In Text-figs. 34 to 37 the upper (adaxial) side of the petiole is turned downwards to correspond with the position of the leaf-trace in Text-figs. 27 to 33.

Fig. 27.

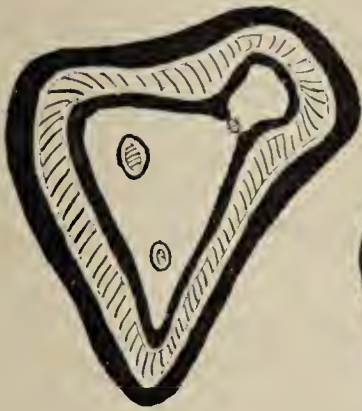


Fig. 28.



Fig. 29.

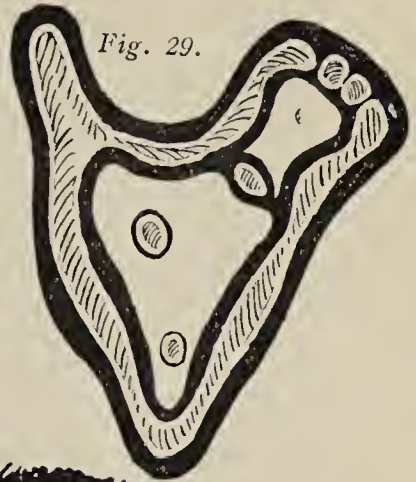


Fig. 30.



Fig. 31.



Fig. 32.



Fig. 33.



Black = sclerenchyma ; cross hatching = xylem ; white = ground tissue, except that immediately surrounding xylem, which represents phloem + pericycle + endodermis. [For explanation of Figs. see next page.]

- Fig. 27. Triangular solenostele of stem at beginning of departure of leaf-trace. Two accessory steles in ground tissue, and one across future leaf-gap.
- Fig. 28. Leaf trace becoming divided into bundles of *Series a*.
- Fig. 29. Ditto, further advanced. Root passing out on left.
- Figs. 30, 31. Further differentiation of bundles of *Series a*, and involution of the sides of trace to form *Series b*.
- Fig. 32. Fusion of penultimate portions of trace to form large bundle from which *Series c* will arise.
- Fig. 33. Commencement of differentiation of bundles of *Series c* from ends of trace.

is effected by sclerenchymatous elements, which, penetrating the vascular tissue from both sides, isolate portions of it, and thus give rise to the bundles of *Series a* (Text-figs. 28 and 29).

The sides of the original horseshoe now become infolded, and at the same time give off bundles forming the inverted *Series b* (Text figs. 30, 31, and 32).



Fig. 34.

- Fig. 34. Base of young petiole. *Series a* consists of six bundles; *Series b* of four. The large bundle is the only representative of *Series c*, while the bundles on each side of it belong to *Series d*. N.B. Px. groups indicated by black dots as also in Figs 35 and 36.

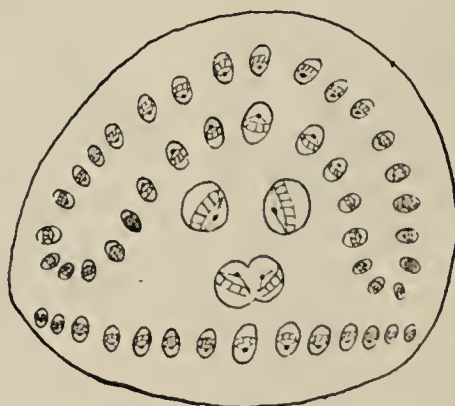


Fig. 35.

- Fig. 35. Older petiole, some distance from base. *Series a* composed of many bundles and forming a continuous curve with the inverted bundles of *Series b*. *Series c* composed of three bundles. *Series d* forms a row along the flattened upper surface. (See E of Fig. 37.)

The portions of the horseshoe just below the involuted sides

now fusc, forming a three-armed structure, the lateral arms of which give off bundles to form the *Series d* of the upper side; the middle arm forms the large bundle with many protoxylems, which will give rise to the central *Series c*. (Text-figs. 33 and 34).

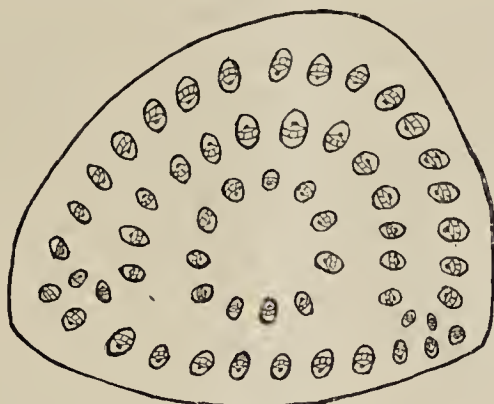


Fig. 36.

Fig. 36. Base of very old petiole. *Series a, b* and *c* much as in Fig. 35, but *Series c* composed of a ring of bundles. (See F of Fig. 37.)

The presumption therefore of the essential horseshoe character of the complicated leaf-trace seen in the mature petiole, is entirely justified by the detailed examination of its origin at the node. The method of the elaboration of the horseshoe into its final form can thus be very clearly made out (Text-fig. 37). It consists essentially of the involution of the sides of the horseshoe, and fusion of the lateral portions near the free ends, while at the same time the whole structure becomes divided up into bundles. The process may be divided roughly into four stages (i.) differentiation of the middle portion of the horseshoe into *Series a* (Fig 37, A & B); (ii.) infolding of the sides of the horseshoe and differentiation from them of *Series b* (Fig. 37, C & D); (iii.) fusion of opposite sides of the horseshoe just above the free ends, and differentiation from these ends of *Series d* (Fig. 37, E); (iv.) formation of *Series c* from fused portion (Fig. 37, F).

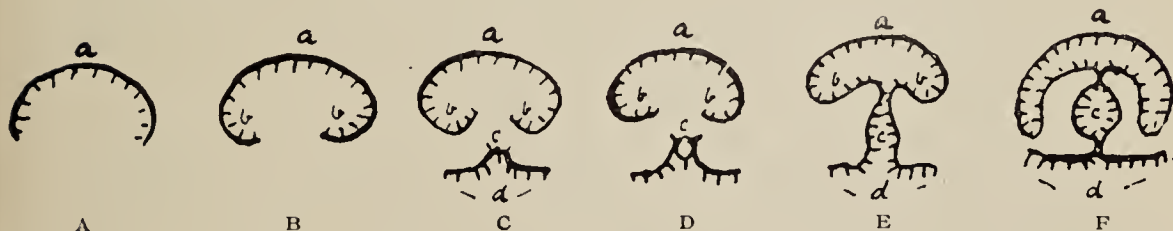


Fig. 37.

Fig. 37. Purely diagrammatic representation of stages in formation of complicated leaf trace. It is represented as a continuous curve, while the short projecting teeth indicate the position of the protoxylem groups. Notice that they are on the inside of the curve.

A & B. Curve of *Series a*. (Figs. 27-29.)

C & D. Involution of sides of curve to form *b*. (Figs. 30-33.)

E & F. Differentiation of *Series c* and *Series d* from ends of horseshoe shaped trace. (Figs. 34-36.)

The whole matter is somewhat obscured by the over-lapping of the above stages, which nevertheless are fairly well defined. The trace loses its connection with the stem-stele during stage (iii.)

*Accessory Steles.*

At each node one of the internal accessory steles mentioned above, approaches the gap formed by the out-going leaf-trace, and later closes this gap by fusion with the free ends of the solenostele. In longitudinal section they appear as short irregular strands which branch and fuse, but always end blindly (Text-fig. 38).



Fig. 38.

Fig. 38. Longitudinal section of stem. It shows the irregular form of the short blind internal accessory steles.

*Leaf Blade.*

The lamina of the leaf is more highly differentiated than is usual among Ferns, and shows many features obviously correlated with the exceptional habitat of this species (Pl. IV., Fig. 9).

It is markedly bifacial, the upper half being characterized by a large-celled hypoderm, and beneath this two layers of elongated closely-set palisade cells. The lower half, which occupies about two-thirds of the total thickness, consists chiefly of loosely-arranged spongy mesophyll cells with plentiful lacunae. The hypoderm on this side is frequently interrupted by the stomatal air chambers. The stomata themselves are flush with the surface, and not raised from it, as in some of the other species of *Acrostichum* examined.

Such xerophilous features obtain in all the plants of the Mangrove swamps<sup>1</sup>—and are no doubt connected with the percentage of salt in the water,—but the adaptation is certainly more impressive here, in the leaf of a Pteridophyte which usually has a far simpler organization. The other species examined show a uniform mesophyll and no hypoderm, while the stomates project from the surface, raised on a little dome of cells.

*Other Species of Acrostichum.*

For purposes of comparison several other species of *Acrostichum* have been examined. With the exception of *A. crinitum*, which is an erect-growing plant, these had all creeping rhizomes. All the species cut, however, without exception, showed a dictyostelic structure with a leaf-trace composed of two to five strands arranged in a simple loop (Text figs. 39 and 40).

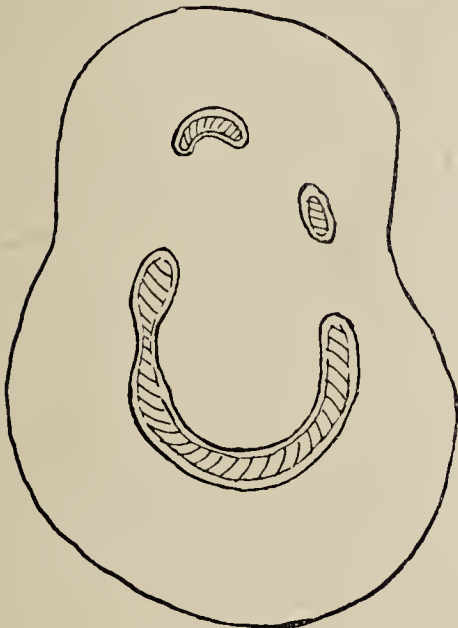


Fig. 39.

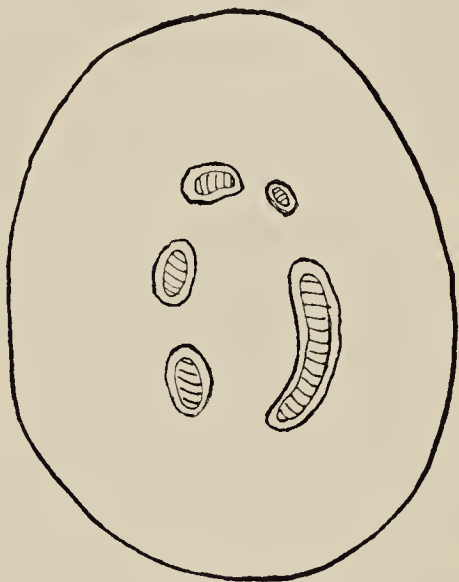


Fig. 40.

Figs. 39 & 40. Generalized diagrams of anatomy of stems of other species of *Acrostichum*. The three bundles of the leaf trace passing off.

*A. quercifolium* is the simplest. Its leaf receives two small strands which pass up the petiole unaltered.

*A. tomentosum*, *hybridum*, *conforme* and *crinitum* are very similar in behaviour. Usually about three strands pass off to the leaf, and these frequently soon divide to form five.

The dictyostely of these species is very obviously related to solenostely, and evidently results from the over-lapping of the leaf-gaps.

<sup>1</sup> Areschoug. Untersuchungen der Mangrove-Pflanzen. Bibl. Bot. Heft. 56, 1902.

*A. lomarioides* shows a somewhat different state of affairs. Its vascular system consists of an irregular circle of bundles, whose existence obviously bears no relation to the leaf gaps.

#### CONCLUSION.

We see then that in the facts brought forward here, there are two distinct centres of interest.

With regard to its vascular anatomy *Acrostichum aureum* presents us, perhaps, with the most complicated petiolar system, coupled with a solenostelic stem structure, which has yet been described. Nevertheless, the horseshoe curve upon which the continuous or broken leaf trace of the Polypodiaceæ is constructed can easily be distinguished.

This anatomical structure cannot be readily referred to the habit of the plant, for although the dictyostelic species first examined were all prostrate creeping forms, the erect growing species *A. crinitum*, which was obtained with some difficulty, proved to be dictyostelic also, and in all respects quite similar to the others. *A. aureum*, however, certainly differs from *A. crinitum*, in its infinitely more robust and bush-like growth, as in the possession of a solenostele, and massive, complicated leaf-trace.

The consideration of the structure of this plant in relation to its mode of life, has shown as we should have expected, that it is the roots which are most modified.

This modification is seen in the very abundant development of lacunar cortex and further in a somewhat stem-like vascular anatomy. Both these features are characteristic of the roots of the mangroves, and *A. aureum* therefore shows very strikingly how similar may be the response to common conditions, even in plants separated very widely from a systematic point of view. We have seen that the characteristics dwelt upon here, are, in addition features very common in fossil roots, particularly in those of Lycopside affinity. We have here then a vascular Cryptogam, which, growing at the present day under swamp conditions, shows special characters which are common also in the roots of fossil plants. As far as it goes, this is in support of the theory that many of our fossils were swamp plants. Dr. Scott remarks in his "Studies" that the lacunar character of Calamite roots points to life in water or wet mud. From the great development of vascular tissue, the latter seems more probable.

I cannot avoid the conclusion that very probably the upper portions of the roots of *Acrostichum aureum* are exposed, and may

function somewhat as the "prop"-roots of other mangroves. As a mere speculation, it seems to me even more probable that the Stigmarian axes of the ancient Lycopods were prop-roots, for they were known in many cases to "strike sharply down at an angle of 50° or 60° and only begin to take a horizontal course at some distance from the main trunk."<sup>1</sup> Their anatomy lends support to the view by analogy with that of the prop-roots of flowering plants.

When we consider the part that these members have to play, it is not surprising that the anatomical structure is intermediate between that of a root and a shoot, for the mechanical requirements of both must be met. On the girder system a medullated axis is recognized as most suitable to support a weight, while a central solid core best withstands the strains resulting from the forces to which a root is subjected.

Prop-roots in tidal swamps must be liable to stresses from the shifting nature of the surrounding medium, and in accordance, on the one hand, with the amount of weight which the structure is called upon to bear, and, on the other hand, with the amount of strain induced, a preponderance of shoot or root-characters may be expected.

In this connection it may perhaps be permitted to hazard an almost unsupported suggestion.

The root characters common to our fern, to the mangroves, and to fossil plants particularly of Lycopsidan affinity, have been sufficiently insisted upon; also the fact that these characters obtain largely in the living members of the latter phylum.

It seems then that an imperfect differentiation of root and shoot is characteristic of the Lycopside and may be correlated with the comparative insignificance of their leaves. Lycopside undoubtedly bulked largely in the coal measure vegetation, and evidence seems to be stronger as to the petrification of these plants *in situ* than in the case of members of other groups. We may perhaps take this as far as it goes as indicating suitability to swamp conditions.

The lacunar character of the plants, the imperfect differentiation of root and shoot, and the small leaves are all consistent with, and perhaps partly due to a swamp life, with its plentiful water supply and peculiar mechanical conditions. It may be that their descendants were never quite able to throw off the shackles of their ancestry, and to this day retain many of the characteristics of their forbears, together with a moisture-loving habit.

<sup>1</sup> Scott, "Studies in Fossil Botany," p. 220.

It is frequently contended that a moister climate obtained during the carboniferous epoch, and however this may be with regard to general atmospheric conditions,<sup>1</sup> it is clear that a damp heavy air would exist in the swamp itself.

If future knowledge should prove that such really were the conditions under which the greater number of the ancient Lycopods flourished, and evidence accumulate in favour of the view that such plants were essentially ill-adapted to the driest terrestrial conditions,<sup>2</sup> we should be furnished with a clue to the cause of the decadence of this group and the total extinction of its arborescent forms.

It has been pointed out to me that mountain ranges are the best means of wide distribution, and from such situations these plants would, on our hypothesis, necessarily tend to be excluded.

The lines of thought suggested by the examination of *Acrostichum aureum* have led me rather far into the realms of pure speculation, and for this I must beg to be excused.

My warmest thanks are due to Professor Oliver and to Mr. Tansley for their very kind and helpful interest in the progress of the work.

<sup>1</sup> Seward, "Fossil Plants as Tests of Climate."—Sedgwick Prize Essay, 1892.

<sup>2</sup> Monarch roots must be less effective as absorbent organs than those furnished with more than one protoxylem group.

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#### EXPLANATION OF PLATES.

##### PLATE III.—THE ROOT.

Fig. 1. Portion of middle lacunar cortex of root as seen in transverse section (Fig. 3) enlarged. The *vertical* arms of its irregular cells seen on end—most show a pitted area. ( $\times 100$ ).

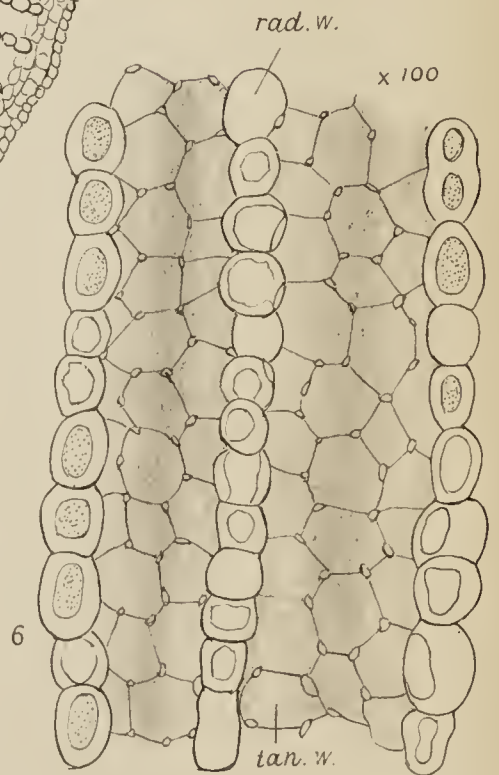
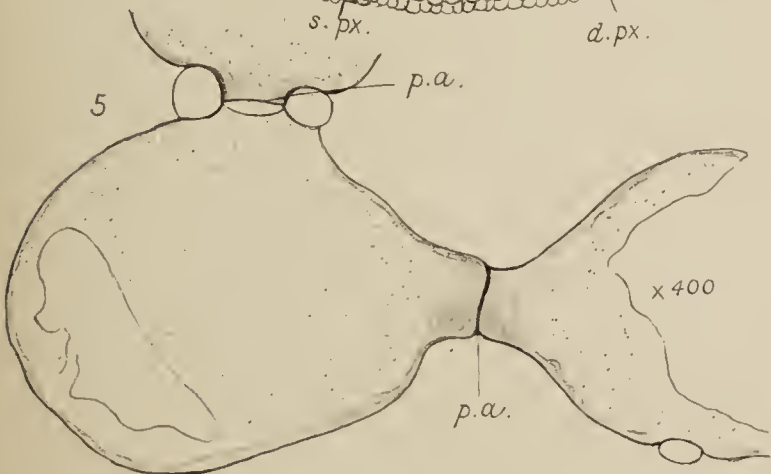
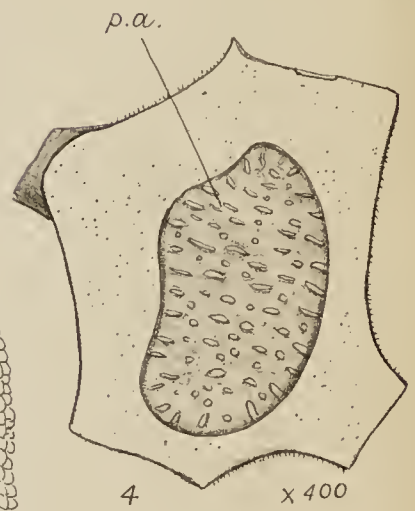
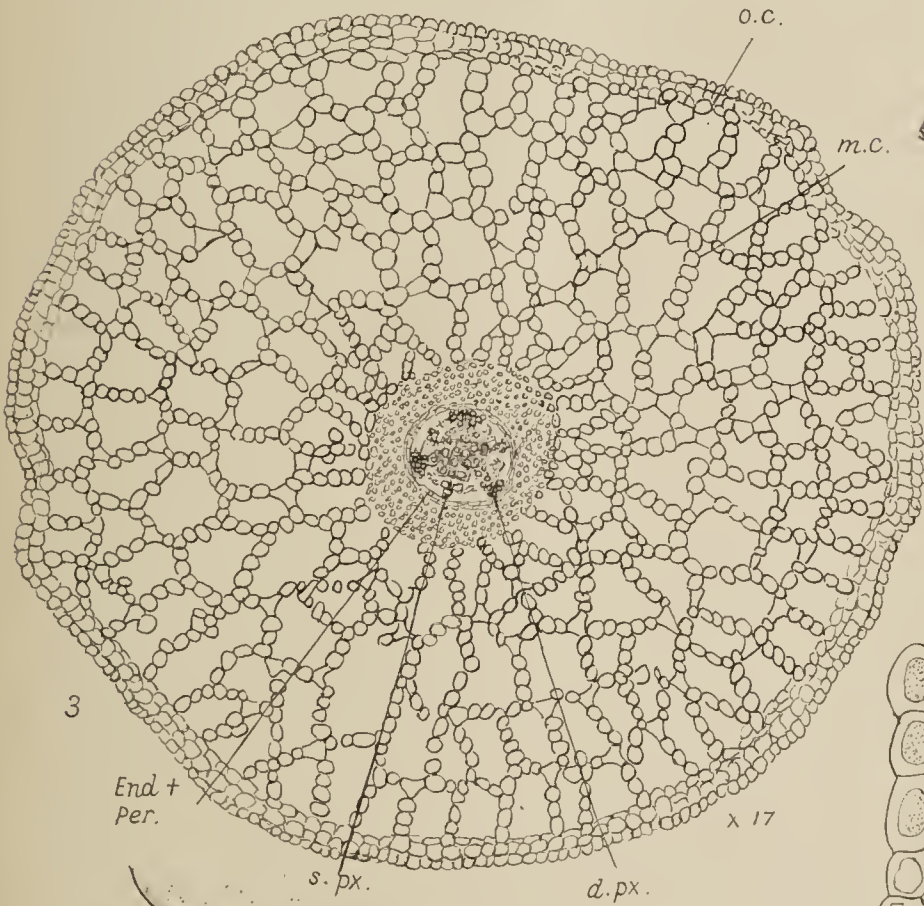
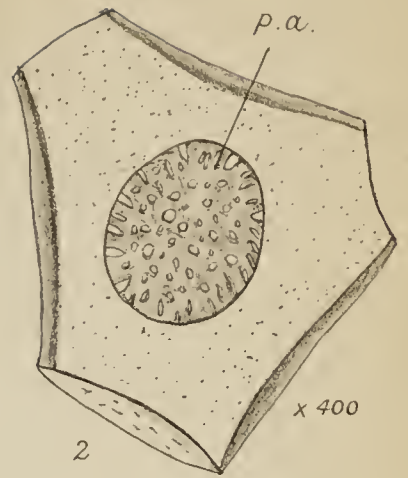
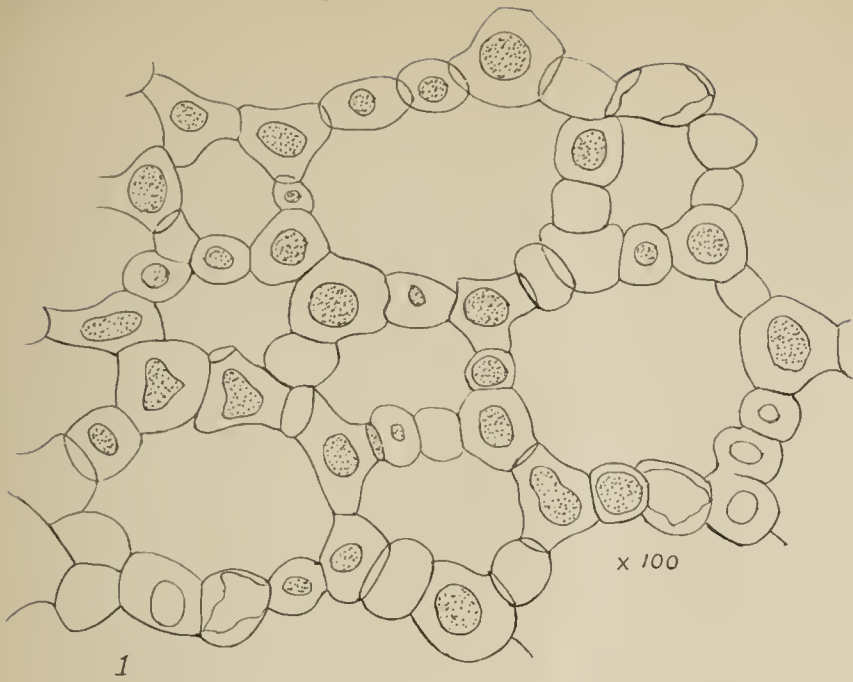
Fig. 2. Single cell of tissue shown in Fig. 1 under greater magnification, *p.a.*, pitted area. ( $\times 400$ ).

Fig. 3. Transverse section of stout root. *o.c.*, outer cortex; *m.c.*, middle lacunar cortex; *i.c.*, inner sclerenchymatous cortex; *end.* and *per.*, endodermis and pericycle; *d.px.*, double protoxylem group of stele; *s.px.* single protoxylem group. ( $\times 17$ ).

Fig. 4. Single cell of tissue shown in Fig. 1. *p.a.*, pitted area (cf. Fig. 2). ( $\times 400$ ).

Fig. 5. Portions of three cells of tangential wall of lacunar chamber of middle cortex as seen in tangential longitudinal section (cf. Fig. 6). *p.a.*, lateral view of pitted area between arms of neighbouring cells. ( $\times 400$ ).

Fig. 6. Portion of middle lacunar cortex of root as seen in tangential longitudinal section. *rad. w.*, cells of radial walls of lacunar chambers seen on end, many show pitted areas; *tan. w.*, cells of tangential wall viewed from the side. ( $\times 100$ ).





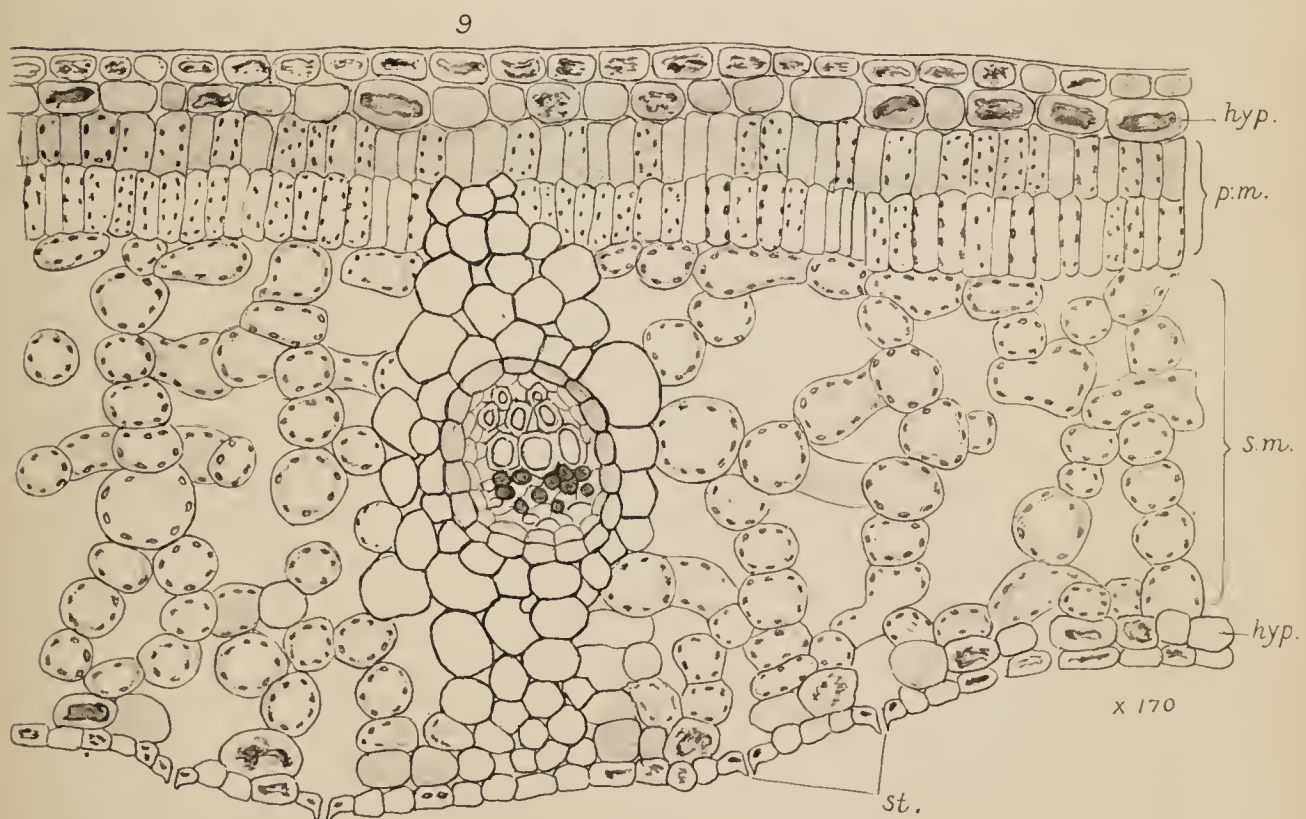
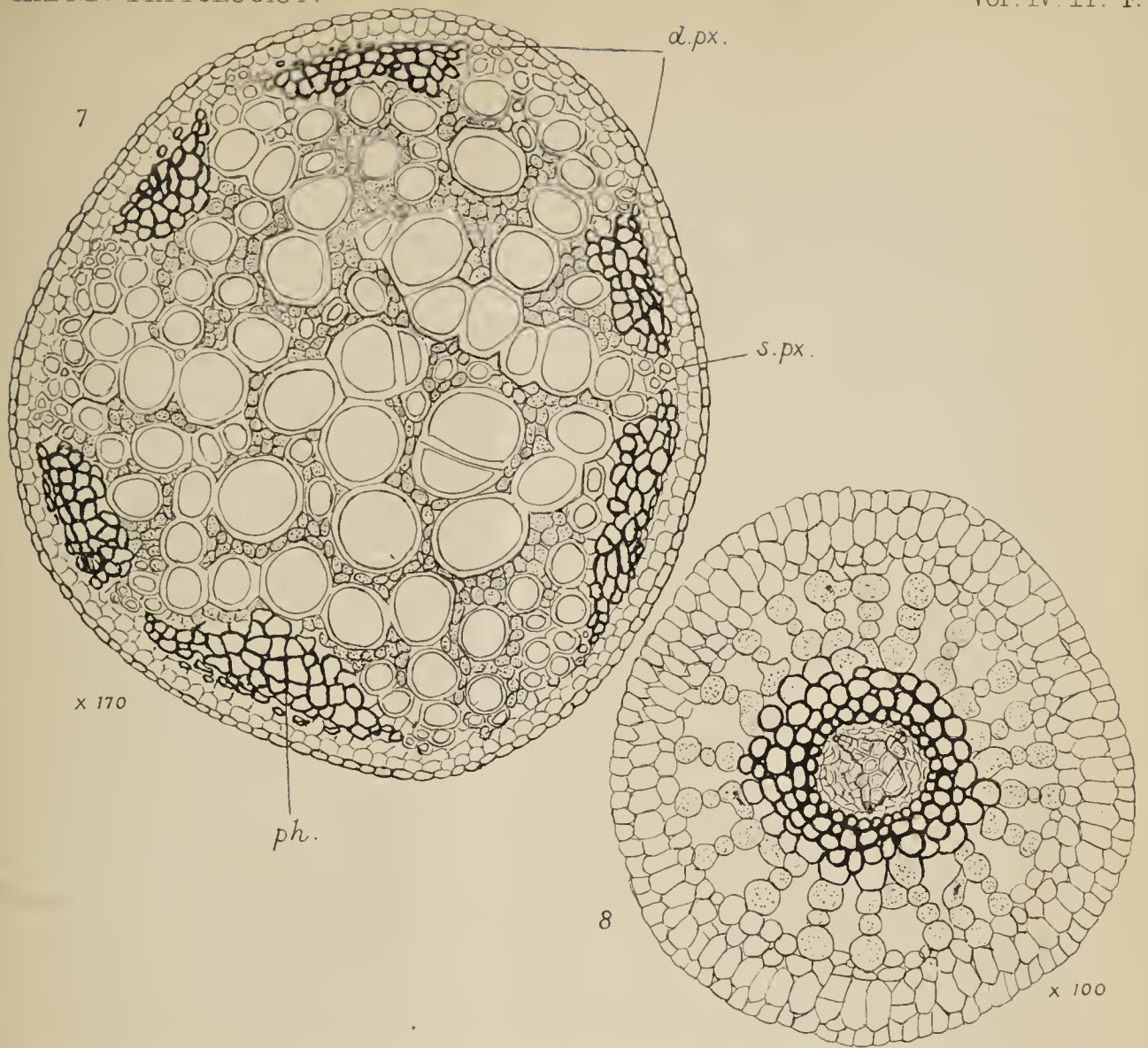




PLATE IV.—THE ROOT (Figs. 7 & 8). THE LEAF BLADE (Fig. 9).

Fig. 7. Transverse section of stele from root similar to that shown in Fig. 3. The drawing is bounded by endodermis and pericycle; *d.px.*, double protoxylem groups, of which there are three; *s.px.*, single protoxylem group, of which there are also three, alternating with the three double groups; *ph.*, phloem groups, composed almost entirely of sieve tubes. The centre is occupied by the large xylem body consisting of tracheides and very plentiful parenchyma. ( $\times 170$ ).

Fig. 8. Transverse section of rootlet as it passes through the cortex of the parent root; *o.c.*, outer cortex; *m.c.* middle cortex; *i.c.*, inner cortex. Compare the relations of the three cortical zones in much older root (Fig. 3). Note that the middle cortex here consists of cells with living contents. ( $\times 100$ ).

Fig. 9. Transverse section of the lamina of the leaf; *hyp.*, hypodermis; *p.m.*, palisade mesophyll; *s.m.*, spongy, mesophyll; *st.*, stoma. ( $\times 170$ ).

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## THE OSMOTIC STRENGTH OF CELL SAP IN PLANTS GROWING UNDER DIFFERENT CONDITIONS.

BY ERIC DRABBLE AND HILDA LAKE.

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COMPARATIVELY few observations on the osmotic strength of cell sap in plants growing under different physical conditions seem to have been made. The most familiar is probably Mr. Francis Darwin's determination for the Dandelion, given in his "Practical Physiology of Plants." The method employed by him consisted in cutting the inflorescence-stalk longitudinally and placing strips of the stalk in pure water. This resulted in curvature of the strips in an outward direction—*i.e.*, the cells occupying the inner face of the strip expanded more than those occupying the outer face, owing largely to the mechanical arrangement of the tissues in these regions. The curled strips were then placed in solutions of potassium nitrate of known strengths, and the solution in which the strip retained the same degree of curvature was taken as isotonic with the cell sap. This method gives very accurate determinations of the strength of the sap, but is only applicable in relatively few cases. A method involving observation of the plasmolysis of the cells can however be very generally applied. By this means a number of plants have been examined with regard to the strength of their cell sap. A series of solutions of sodium chloride was made of the following concentrations in gram molecules—.10, .11, .12, etc., up to .30. Portions of the plant the strength of whose cell sap was to be determined were placed in pure water. Strips of the epidermis of the leaf were placed in a drop of the solution on a slide, and gently covered with

a cover glass. Under a  $\frac{1}{8}$ -in. objective the effect on the cells was readily observable. The solution which *just failed* to plasmolyse was taken as isotonic with the cell sap. Thus, if  $\cdot 13$  plasmolysed the cells while  $\cdot 12$  did not, then  $\cdot 12$  was taken as the strength of the sap. The most convenient plants for these determinations proved to be those with a red colouring matter in the epidermis, since in these the first appearance of plasmolysis was readily seen. Experiment has shown that but little difference in the strength of sap obtains between the red and colourless cells from the epidermis of the same leaf.

Some of the results are given below:—

Plant.	Locality and Conditions.	Strength of Sap in Gram Mols. of N. & Cl.
<i>Taraxacum Dens-leonis</i>	Damp grass at side by ditch, near Thames, at Kew	$\cdot 11$
<i>Elodea canadensis</i> ...	College fresh-water tank ...	$\cdot 12$
<i>Saxifraga sarmentosa</i>	Cool House, Chelsea Physic Gardens	$\cdot 13$
<i>Spiraea</i> sp. ...	Shrubbery in Sir Joseph Hooker's garden, at Sunningdale	$\cdot 13$
<i>Mahonia</i> sp. ...	Ditto ditto	$\cdot 13$
<i>Geranium Robertianum</i>	Northfleet, near, but not in, salt marsh	$\cdot 17$
Ditto ...	On rocks above Cwm Idwal, near Twll Du	$\cdot 23$
<i>Hieracium</i> sp. ...	Ditto ditto	$\cdot 28$
<i>Vaccinium myrtillus</i>	Ditto ditto	$\cdot 28$

From this series it is evident that a greater concentration of cell sap occurred in those plants which had been most strongly subjected to factors tending to promote loss of water by transpiration. *Taraxacum* growing in long grass by a fresh-water ditch. *Elodea* completely submerged in fresh-water, *Spiraea*, and *Mahonia* in a shrubbery, showed comparatively low osmotic equivalents. In

all these cases the danger of excessive loss of water was small. *Geranium Robertianum* growing near a salt marsh was, however, in a different physical environment, and the presence of salt is usually associated with a marked xerophytic tendency. Here the cell sap was found to be of considerably greater strength than in the other plants mentioned above. The conditions on the rocks above Cwm Idwal again are such that plants growing there are subjected to strong insolation and high winds. Here again a high strength of cell sap was found in the three plants investigated—.23 and .28 gram molecules.

At first sight it would appear that in the greater strength of the cell sap might be found a valuable xerophytic character, the presence of salts in solution being known to retard evaporation. But the concentration of the cell sap is so slight that but little importance can be attached to this as a means of checking loss of water. If, however, the effect on the *absorption* of water be considered, it at once becomes evident that a very important physiological benefit may accrue to plants with increased strength of cell sap. Many plants growing in high latitudes and exposed to wind and insolation are well provided with a hairy coating to the epidermis. This is usually regarded as a means of checking transpiration, and doubtless it does play an important part in this respect. At the same time it must be remembered that many plants with hairy epidermis are capable of absorbing water through the general leaf surface. Plants growing in mountain regions and in other situations conducive to a xerophytic habit are frequently exposed to periods of drought, during which only slight and transient showers fall—quite insufficient to penetrate the earth and reach the roots. The leaves, however, are wetted, and in those plants which have a relatively high concentration of the cell sap the water will be rapidly absorbed. It is conceivable that in this way a high osmotic strength of sap may prove to be a valuable physiological character in connection with water-absorption. The strength of sap as determined by the sodium chloride solution is being worked out in atmospheres, allowance being made for ionization of the salt. Further experiments on plants from various localities are being conducted, and the relation of the strength of sap in the guard cells to that of the rest of the epidermis is also being investigated.

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ECOLOGICAL EXPEDITION TO THE BOUCHE D'ERQUY,  
1905.

SOME account was given a year ago in this journal ("A Second Experiment in Ecological Surveying"—NEW PHYTOLOGIST, Vol. III., p. 200), of an expedition organised by the Botanical Department of University College, London, for the study of salt-marsh vegetation as developed in a small estuary known as the Bouche d'Erquy, on the North Coast of Brittany. Last year the work was practically confined to mapping the vegetation of the area on a scale of 1:240, and of a typical sample on a scale of 1:60. The smaller area was also levelled, so that a detailed contour map could be constructed.

In the present year (Sept. 2-16), a similar expedition was organised, consisting of about 20 persons; the general map was completed and levelled, and at the same time an attempt was made to study in greater detail the vegetation of a number of small typical areas in which the vegetation is sensibly homogeneous. This was done by selecting a number of "stations," located in such homogeneous areas, and investigating the vegetation of each by means of the excellent "chart-quadrat" and allied methods recently devised by Dr. Clements,<sup>1</sup> while simultaneously studying the physical conditions to which the vegetation of each station is exposed. In the case of the Bouche d'Erquy it is impossible to resist the conviction that the striking local variations of the vegetation are primarily due to differences in the salinity and water-content of the soil, so that the study of conditions was mainly restricted to a series of determinations of these factors during the period between two successive cycles of spring-tides.

The organisation of the work of the party was determined by these considerations as follows.

The whole party was divided into three sections, each under the direction of a member of the staff.

Section I. occupied itself with the charting of "quadrats" located in the vegetation of the different "stations." A quadrat was always charted on a square decimeter of sectional paper, the scale and therefore the area of vegetation varying with the requirements of the particular station. So minute and crowded are the individual plants in most cases that Clements' standard

<sup>1</sup> F. E. Clements. Research Methods in Ecology, Lincoln, Neb., U.S.A., 1905.

scale of 1:10 is rarely possible. A scale of 1:5 was usually adopted and sometimes a scale of 1:2.5, while a specimen square decimeter was usually also taken and charted on a scale of 1:1. A "belt-transect"<sup>1</sup> of 1-dm. width and 12-m. length was taken across one of the most characteristic examples of zonation and charted on a scale 1:5; while a "layer-transect"<sup>1</sup> along one of its boundaries was charted (to true vertical scale) on a scale of 1:10. Though time did not, unfortunately, permit of completing the series of charts, yet a collection of over 50 was made, which with photographs of the quadrats and stations, and habit-drawings in water colour of typical plants, forms an exceedingly useful detailed record of the vegetation of the area. The quadrats were permanently marked by means of stakes driven into the ground, and it is expected that a comparison of the charts with a similar series made next year will throw great light on the stability or otherwise of the vegetation.

The work of Section I., as will be seen, was based almost entirely on Dr. Clements' methods, which promise to become an indispensable means of investigating the phenomena of vegetation in adequate detail.

Section II. occupied itself mainly with determinations of the amount and salinity of the water in earth-samples from the different stations. Broadly speaking it was found that after a tide had covered the area the salinity of the water from one station did not differ very markedly from that of another or from that of sea water. It was hoped to be able to trace the course of increasing salinity during the period between two spring-tide cycles, but heavy rain prevented any such effect, which might perhaps be discoverable in dry weather. The washing-out effect of the rain was, however, considerable, and to some extent differential. Striking local variations in salt content, both horizontal and vertical, were met with, but were not easy to explain nor to correlate with the variations of vegetation. The general result was that the recognition that the problem of salinity distribution and its effect on vegetation is a complex one, and that a good deal more work is necessary before the roads to its solution can be attained. It is thought that there is a better prospect of successfully correlating water-content and salinity with the vegetation phenomena early in the growing season, at the time of, and shortly after, the germination of seedlings.

The work of Section II. was made possible by securing an

<sup>1</sup> Clements, *op. cit.*

empty cottage with a big room, on the end of the marsh. This was turned into a temporary laboratory, where the necessary weighings, titrations, and dryings were carried on. Most of the apparatus employed has been left at this cottage, which will be available for future work.

Section III. completed and extended the general map made last year, and levelled the whole area.

Of minor pieces of work, outside the sectional organisation the following may be mentioned. Countings of the numbers of seedlings on given selected areas at different periods between April and September were made, so as to trace the course of competition etc., on the annuals during the growing season. Last year's "grid-system" was re-surveyed and the changes noted. A good zonation in the *Fucus*-association was discovered and mapped.

The organisation of the expedition worked exceedingly well and smoothly. As a part of the training of advanced students it is felt that these expeditions are of very high value. As a scientific investigation the particular piece of work grows in magnitude and complexity as attempts are made to face the various fundamental problems involved; while it certainly does not diminish in interest and attractiveness.

A. G. T.

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#### A NOTE ON VASCULAR TISSUE.

BY E. DRABBLE.

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SO many leading anatomists have endeavoured to exalt the central cylinder of vascular plants into a tissue system of a nature quite distinct from the ground-tissue (or according to most authors the cortex) that it might almost be concluded that this view had been established. Nevertheless there is a point of view from which the structures in question assume a totally different aspect. As indicating certain difficulties in accepting some of the views that now to a large extent hold the field, rather than as an attempt to advocate any alternative scheme, the following notes have been put together.

Only two theories will be considered at any length. In the first place we have the conclusions drawn by Mr. L. A. Boodle as the result of his extensive work on the anatomy of various groups of ferns (1, 2, 3), and according to him the most primitive existing form of cylinder is the so-called *protostele*—a central strand of xylem surrounded by phloem with a ring of endodermis enclosing the whole. By the non-development of tracheidal tissue in the centre of the

strand a parenchymatous pith arises. On the inner face of the tracheidal tube phloem may appear and an internal endodermis then cuts this off from the central parenchyma; this parenchyma is still regarded as part of the central cylinder. By the development of a cylinder of vascular tissue, incomplete in certain places, the dictyostelic condition supervenes, the external and internal endodermis being continuous through the gaps. By the overlapping of these gaps a very complicated open network—such as is found in *Aspidium*—results. In the ferns, then, gaps are intimately associated with the development of leaf-traces. Through the gaps the internal—according to this view “stelar”—and the external—“extrastelar” parenchyma becomes continuous. Yet, although the parenchyma of external and internal origin may be precisely similar and absolutely continuous, it is held that a very essential difference exists between them, although the boundary cannot be determined. Hence a purely abstract consideration is introduced. The importance of the endodermis as a morphological boundary between intra- and extra-stelar tissues is abandoned, since, if it were maintained, the only possible conclusion would be that in the dictyostelic form the intra-cylindrical and extra-cylindrical parenchyma are of the same nature—*i.e.*, both “extra-stelar,” the xylem and phloem alone representing the original protostele. It is indeed quite necessary to this theory that the endodermis as a morphological layer be abandoned. Hence it is rather curious to find Mr. Boodle distinctly stating (4) that “although the presence of an endodermis is probably no guide, its local absence may have some morphological significance.” This statement refers to a condition in certain palm-roots where the endodermis is locally absent between xylem and parenchyma. It certainly seems to follow from this statement that Mr. Boodle holds the absence of an endodermis may prove that morphological continuity exists even between vascular tissue and parenchyma. It may justly be urged that much more would it tend to indicate such a morphological continuity in a continuously developed tissue wherein no difference of any sort can be seen. Still Mr. Boodle refuses to accept this view, at the same advocating the other.

Apparently Mr. Boodle holds that development gives no clue to morphological relationships of tissues—at all events that *apical* development is valueless. Now it would seem that many plants, perhaps all,—which in the mature state possess a dictyostelic arrangement, commence life with a protostele. The successive stages of development culminating in the dictyostele can be readily followed. Here, we should have thought, is a very valuable piece of evidence to the

upholders of the theory now under discussion, if they can abandon the endodermis at all stages as a morphological guide. And it must be emphatically stated that only by change in the mode of apical development are the successive steps from the protostele to the diatystele brought about. Indeed, "Von Baer's law," if applicable to the stems of plants at all—as it would very strongly appear to be—is carried through by progressive changes in the meristem and procambial tissues at the apex—apical development being the mode of ontogeny met with in the stems of vascular plants. Mr. Boodle says that apical development is of no value, because it shows no more than can be seen in the various regions of the mature stem. It at all events shows just as much, and hence, if apical development be of no value, neither is a comparison of the successive mature regions. The great faith of this school seems to rest on "a comparison of closely related forms;" undoubtedly this is an extremely valuable method, but the conclusions drawn therefrom do not necessarily bear out Mr. Boodle's views. They just as strongly support the views of Dr. Jeffrey (8, 9, 10, 11), or Professor Farmer (7), or the present writer (6). If comparative work shows one thing more strongly than another, it is that the only distinction to be drawn is that between vascular and non-vascular tissues (cf. Dr. Chandler's paper on "The 'Seedlings' of Ferns" (5). Each plant solves its own difficulties in its own way, though doubtless closely related plants generally adopt similar methods, as we should naturally expect if the difficulties surmounted were encountered before the segregation of the species in question. It would be very interesting to see how the supporters of this view would deal with the case recently described by Van Tieghem, of two members of the same genus in the *Calycanthaceae*, in one of which the inverted bundles lying outside the central cylinder are said to be of "stellar," in the other of "extra-stellar" origin.

According to this theory, then, the conception of the central cylinder seemed to be that of an originally parenchymatous strand occupying the centre of the stem in which a more or less continuous development of conducting tissue is differentiated. How the cylinder is to be delimited before the development of vascular tissue is not very clear, since the initial stratification described by Hanstein admittedly fails to serve in the light of Dr. Schoute's (12) results for the phanerogams and Mr. Boodle's for the ferns. If the mere development of vascular tissue is all that is required to constitute a central cylinder, then the not infrequent development of vascular strands in the cortex associated with the paren-

chyma must surely militate against the exaltation of the central cylinder to a rank of eminently different order from the external tissues. It is rather difficult also to understand the attitude adopted with regard to that portion of the leaf traces which traverse the cortex. Are they of cylindrical or extra-cylindrical nature?

In Dr. Jeffrey's (9, 10, 11) opinion, a very different view must be taken of the internal parenchyma in angiosperms and the more highly developed ferns. As the outcome of a long series of investigations on the development of seedlings in both classes, Dr. Jeffrey agrees with most other investigators in regarding as the primitive form of cylinder the solid rod of xylem surrounded by phloem and cut off from the cortex by an endodermis. Phloem is then said to appear within the rod of xylem, and after the appearance of a few leaf traces an internal endodermis arises, cutting off the internal phloem from a central parenchyma now appearing. This central parenchyma is continuous with the cortex through the leaf-gaps and is regarded as "intruded cortex"—a view diametrically opposed to that discussed above. The late formation of a dictyostele is simply owing to the overlapping of large leaf-gaps through which external and internal "cortex" are continuous. In the plant which has passed the seedling stage—particularly in the Phanerogams—the internal endodermis can no longer be detected. Nevertheless, Dr. Jeffreys regarded the internal parenchyma as being of the same nature as the external cortex.

If the perhaps rather misleading term "intruded cortex" be replaced by the term "ground parenchyma" or "ground tissue" (to allow for the frequent development of sclerenchyma) we arrive at the conception of a ground-tissue system through which run the vascular strands. In the most primitive case the vascular system is a solid strand, in others a hollow cylinder, enclosing ground tissue; in others again it is a network of conducting strands (6). This offers a very simple and natural method of regarding the vascular system of plants, and entirely obviates the necessity for any abstract distinction between vascular tissue, potential-vascular tissue, and non-vascular tissue which likewise may develop vascular tissue, but which does not belong to the vascular system.

If Dr. Jeffrey's results be regarded from a physiological point of view the distribution of the endodermis as described by him assumes a perfectly natural aspect. It cuts off vascular from non-vascular tissue, and no abstract consideration necessitates the postulation of a theoretical boundary between the extra-cylindrical and intra-cylindrical ground tissue such as is demanded by the other

view. The disappearance of a differentiated endodermis in the older parts of a phanerogamic seedling with secondary thickening is perhaps to be expected, if, as may be the case, it functions as a means of cutting off the actively conducting tissues from the parenchyma. In the older regions, in which secondary thickening has set in, the directly functional conducting tissues may be cut off from the parenchyma by the now non-functional tissues of earlier development.

A striking fact, which has perhaps some bearing on the question, is the general association of the endodermis with the phloem. In ferns it is present around the phloem of the protosteles. Then phloem appears in the centre of the xylem strand, and concurrently with the appearance of parenchyma within this an endodermis cuts it off from the internal phloem.

In the seedlings of *Livistona Mauritana* and *Phoenix dactylifera* the bundles in the cotyledon-sheath are in certain regions associated with a euticularized sheath of endodermis-like appearance. In many cases this is best developed in, and may be limited to the phloem portion of the bundle, being wanting on the internal face of the xylem.

Without in any way admitting an adherence to the statolith theory, it is interesting to note that the endodermis is the region of statoliths in many plants, and that it is only with the younger regions that the tropistic power is usually associated. The fact that starch grains are often present in the endodermis after complete depletion of other regions may possibly be associated with the peculiarity of the cell walls.

- 1 Boodle. I. Comparative Anat. of the *Hymenophyllaceae*, *Schizaeaceae*, and *Gleicheniaceae*. II. The *Schizaeaceae*. Ann. Bot. XV.
- 2 Boodle, Ibid. III. The *Gleicheniaceae*. Ann. Bot. XV.
- 3 Boodle. Further observations on *Schizaeaceae*. Ann. Bot. XVII.
- 4 Boodle. "The Anatomy of the Roots of Palms." NEW PHYTOLOGIST, 1905.
- 5 Chandler. On the Arrangement of the Vascular Strands in the "Seedlings" of certain Leptosporangiate Ferns. Ann. Bot. XIX.
- 6 Drabble. The Anatomy of the Roots of Palms. Trans. Linn. Soc. 1904-05.
- 7 Farmer and Hill. On the Arrangement of Vascular Strands in *Angiopteris evecta*. Ann. Bot. XVI.
- 8 Faull. The Anatomy of the Osmundaceae. Bot. Gazette, XXXII.
- 9 Jeffrey. Trans. Brit. Assoc., 1897.
- 10 Jeffrey. Morphology of the Central Cylinder of Angiosperms. Trans. Canadian Institute, 1900.
- 11 Jeffrey. Structure and Development of the Stem in the Pteridophytes and Gymnosperms. Phil. Trans., Ser. B., Vol. CXC.V., 1902.
- 12 Schoute. Die Stelär-Theorie. Gröningen, 1902.

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ECOLOGY IN ITS PHYSIOLOGICAL AND PHYTO-  
TOPOGRAPHICAL ASPECTS.<sup>1</sup>

BY F. F. BLACKMAN AND A. G. TANSLEY.

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DR CLEMENTS' book is at once the most ambitious and most important general work on Ecology that has been published during the last seven years. Warming's "Plantensamfund"—better known in its German dress as "Öcologische Pflanzengeographie"—performed the indispensable service of gathering up the scattered ecological work of several decades and presenting it under a single clear and comprehensive point of view. How excellently the Danish Professor performed that service is well known to all who have read his model text-book. A few years later Schimper presented the results of many years of travel and enquiry in a magnificent volume—the "Pflanzengeographie auf physiologischer Grundlage." The wide knowledge of the author, extending over the vegetation of many lands, his many-sided treatment of the subject-matter, the industry and ingenuity with which he used every available source of information to throw light on the infinitely varied conditions of plant-life, and finally the wealth of pictorial illustration by means of which he brought home to his less travelled readers the aspects of vegetation all over the world, combined to render his work at once important as a contribution to science, encyclopædic as a record of what was known, and fascinating as an unrivalled picture-book of vegetation.

The immediate result of the publication of these two pioneer works was to stimulate interest in this branch of botany all over the world. Everywhere young botanists turned to the vegetation around them and began to observe and record. In so far as it took workers out of doors and turned fresh attention to the phenomena of plant-life under the conditions of nature, this effect was all to the good. But

<sup>1</sup> "Research Methods in Ecology." By F. E. Clements, Ph.D., Associate Professor of Plant Physiology in the University of Nebraska. Pp. XVII. and 334. 85 Figures in the text. \$3. Lincoln, Nebraska, U.S.A.

the quickened activity brought its own dangers. The variations of plant combinations are almost infinite, and while it is comparatively an easy task to describe and photograph some of these combinations, adding a few notes on the more obvious physical conditions, it is a task of great, perhaps unexampled, difficulty to investigate the real causal relations of the one to the other. While the former pursuit, whose facility has proved fatally attractive to some, leads only to the piling up of endless, more or less unrelated, observations, the latter, when carried out successfully even over a narrow field, leads to genuine additions to scientific knowledge, and, like all real advance, immediately gives vantage points from which clearer views of obscure phenomena can be obtained.

From this point of view Dr. Clements' book is timely. The protests of the author against the prevalent dilettantism are vigorous and trenchant. "The bane of the recent development popularly known as ecology," he says, "has been a widespread feeling that anyone can do ecological work, regardless of preparation. There is nothing in modern botany more erroneous than this feeling. . . . The comprehensive and fundamental character of the subject makes a broad special training even more requisite than in more restricted lines of botanical inquiry." "The organic connection between ecology and floristic has produced an erroneous impression as to the relative value of the two. Floristic has required little knowledge, and less preparation; it lends itself with insidious ease to chance journeys or to vacation trips, the fruits of which are found in vague descriptive articles, and in the multiplication of fictitious formations. . . . The great readiness with which floristic lists and descriptions can be made has led many a botanist, working in a small area, or passing hurriedly through an extended region, to try his hand at formation making. From this practice have resulted scores of so-called formations, which are mere patches, consocieties, or stages in development, or which have, indeed, no existence other than in the minds of their discoverers. The misleading definiteness which a photograph seems to give a bit of vegetation has been responsible for a surplus of photographic formations, which have no counterparts in nature."

The criticisms contained in these extracts are sane and salutary, and the points are emphasised by reference to adequate methods of investigation. Dr. Clements is in favour of laying out a plan of work lasting several years and extending over a wide region. One or more seasons are devoted to "reconnaissance," which consists in

exploration and in becoming thoroughly acquainted with the "floristic" of the region chosen. Small typical areas are then selected and are studied by exact and exhaustive methods till a thorough knowledge of the vegetation is obtained. These results are then applied to the whole area originally traversed. This method has been applied by Dr. Clements to the Colorado mountain vegetation, and it is not too much to say that ecologists all over the world are looking forward with the greatest eagerness to the publication of his work—the only ecological investigation which, so far as we know, has hitherto been undertaken in so earnest and serious a spirit. Meanwhile Dr. Clements has published "The Development and Structure of Vegetation" and "Research Methods in Ecology" in order to make clear his general view of vegetation as an "organism" with specific development, structure and functions, and to expound his systematised methods of research.

Before proceeding to consider the present work in detail it is important to note that Dr. Clements claims ecology, at the outset, as "the central and vital part of botany," and in this we believe he is perfectly right. His views on the relation of ecology and physiology are of such interest that we are constrained to quote a considerable passage.

"There can be little question in regard to the essential identity of physiology and ecology. This is evident when it is clearly seen that the present difference between the two fields is superficial. Ecology has been largely the descriptive study of vegetation; physiology has concerned itself with function; but when carefully analyzed, both are seen to rest upon the same foundation. In each, the development is incomplete: ecology has so far been merely superficial, physiology too highly specialized. The one is chaotic and unsystematized, the other too often a minute study of function under abnormal circumstances. The greatest need of the former is the introduction of method and system, of the latter a broadening of scope and new objectives. The growing recognition of the identity of the two makes it desirable to anticipate their final merging, and to formulate a system that will combine the good in each, and at the same time eliminate superficial and extreme tendencies. In this connection, it becomes necessary to point out to ecologist and physiologist alike that, while they have been working on the confines of the same great field, each must familiarize himself with the work and methods of the other, before his preparation is complete. Both must broaden their horizons, and rearrange

their views. The ecologist is sadly in need of the more intimate and exact methods of the physiologist: the latter must take his experiments into the field, and must recognize more fully that function is but the middleman between habitat and plant. It seems probable that the final name for the whole field will be physiology, although the term ecology has distinct advantages of brevity and of meaning."

With the general sense of the foregoing passage we are in cordial agreement. No one can doubt that ecological problems are at bottom physiological problems; and while the present superficiality of ecology must be admitted, it is, we think, equally true that the outlook of the typical modern physiologist requires widening, in the direction of realising much more vividly the necessity of studying a plant's functions under its natural conditions of life. In fact the serious application of the methods and concepts of modern physiology to ecological problems is now certainly an urgent desideratum.

At the same time it should, we think, be clearly recognised that there is a sense in which physiology is distinct from ecology, and that the proper function of the physiologist in the narrower sense is essentially "intensive and analytical," since it is, or should be, his special business to analyse the vital processes into their constituent factors, which in nature normally work together, and to show how these factors may be brought into line with chemical and physical laws. The "extreme specialistic tendencies" deplored by Dr. Clements must in our opinion be allowed full play, and the "analytic methods," which, as he says, "have dominated research to the exclusion of synthetic ones," should be understood as fundamental and logically prior to the synthesis which he rightly desires. Modern physiology suffers not from real analytic methods, but from crude and misleading analysis, which fails to get to the root of the matter. Till we have a rational physiology, soundly based on the laws of chemistry and physics on the one hand, and frankly recognising the "biological point of view," *i.e.* the peculiar conditions obtaining in all living organisms, on the other, we can scarcely expect to gain a great deal by the extension of the arena of the physiologist to ecological problems. Crude concepts carried into a wider field cannot give anything but unsatisfactory and inconclusive results, and the place to clear up the confusion and arrive at clearer and more rational ideas is primarily the laboratory, for it is only there that the conditions for the necessary exactness of experiment

can be realised. In other words our author appears to be rather premature in his effort to "anticipate the final merging" of the two subjects, though as an ideal to be borne constantly in mind this merging is a perfectly sound conception. We shall presently have to advert to some instances in the present work in which the physiological methods and concepts applied seem hardly adequate to the solution of the problems attacked.

The work before us is essentially a handbook of methods, dealing incidentally with the actual problems which vegetation presents. Its first great merit is its comprehensiveness. It will be clear from what has been already said that the subject matter of ecology is conceived in no narrow spirit, and as a matter of fact no conceivable factor which can affect vegetation appears to be neglected, while quantitative methods which aim at the greatest possible accuracy are applied to each.

The book is divided into four parts or "chapters." The first, under the heading "The Foundations of Ecology," discusses "The Need of a System," and contains the ideas upon which we have already commented. We think Dr. Clements easily establishes his case for a "system," and his view of "The Essentials of a System," based on the absolutely fundamental importance of the habitat, its effect on the plant and the reaction of the plant upon it, may be said to be almost self-evident, though we do not imply that it does not require plain statement.

*(to be continued).*

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## THE BRITISH ASSOCIATION IN SOUTH AFRICA.

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TO those who attended the South African Meeting of the British Association, the occasion must ever remain a memorable one. Though, owing no doubt to the prolonged absence from England entailed by the journey, many familiar faces were absent, yet the meeting had its compensations in the old friendships renewed, and the new ones formed, as well as in the varied botanical and other interests afforded by the extended tour undertaken by the party.

A very unusual feature was the holding of the meetings themselves at two distinct centres, *i.e.*, Capetown (August 15th–18th

and Johannesburg (August 28th—September 1st). In addition, evening lectures were delivered at a number of the chief towns visited *en route*.

The meetings of Section K were well attended, and though the proceedings were not characterised by any startling developments, the interest was well sustained throughout. In addition to a fair contingent of members from England, local botany was strongly represented, and there were also two distinguished foreign botanists present at the meeting, Professor Engler of Berlin, and Professor Douglas Campbell of California.

As was to be expected, the papers communicated to the section were considerably fewer than last year, and this enabled afternoon sittings to be dispensed with, except in one case to be mentioned later. As was fitting upon an occasion of this kind, a considerable number of the papers dealt with South African Botany. Another feature, which it is to be hoped may become an annual one, was the presentation of several general accounts of recent work. Discussion of the papers read was too often conspicuous by its absence; this being largely due to the somewhat prevalent habit on the part of authors of exceeding the time limit which it is found necessary to impose.

#### CAPE TOWN.

At Cape Town the sectional meetings were held in the Botanical Department of the South African College. The rooms, which have been recently constructed under the direction of Professor H. H. W. Pearson, were admirably adapted for the purpose, and Professor Pearson is to be congratulated on the thoroughly up-to-date and convenient building in which his department is housed.

A word of thanks is due to Dr. Marloth and to Professor Pearson, who acted as local secretaries. The arrangements they had made were admirable, and contributed in no small measure to the success of the meeting.

In the Committee Room, Dr. Marloth, with the help of Miss Kensis, had arranged a most interesting display of living South African plants, particularly desert forms from the Karroo and a characteristic collection of heaths and other flowers from the South-West District of Cape Colony. A number of ecological photographs, largely taken by Dr. Marloth himself in different parts of the Colony, were also exhibited.

Wednesday, August 16th. As it had been arranged for the President, Mr. Harold Wager, to deliver his address in Johannesburg, he opened the proceedings in Cape Town with a few suitable introductory remarks, and then introduced Professor R. W. Phillips, who delivered a semi-popular lecture on "The More Recent Advances in our Knowledge of Seaweeds." Dealing first with the attached shore vegetation, the lecturer pointed out that much yet remains to be done, particularly in regard to the reproductive processes of groups such as the Siphonaceae and Laminariaceae.

But a considerable advance has been made in recent years. Oltmanns has completely changed the older views regarding the act of fertilisation in the Red Seaweeds. Amongst the Brown Algæ, Lloyd Williams has discovered motile antherozoids in the Dictyotaceae; while Mottier, and later Williams, have shown that a true reduction division occurs in *Dictyota*, in the mother cells of the tetraspores. This points to the existence in this plant of a definite alternation of generations, the two generations being externally indistinguishable unless reproductive organs are present, though they essentially differ in the number of chromosomes present in their dividing nuclei. Professor Phillips also dealt with the distribution and composition of the floating oceanic plankton.

Professor Douglas Campbell read a short note on the prothallium of *Gleichenia pectinata*, and Professor Potter discussed the healing of parenchymatous tissues in plants.

The rest of the morning was occupied by a discussion, opened by the President, on "Educational Methods in the Teaching of Botany."

Mr. Wager animadverted upon the methods usually employed in teaching botany, in both universities and schools, and said that they neither afforded an adequate training in scientific method, nor developed a real interest in the subject. The really important part of a botanical course was the practical work, which should be both observational and experimental. Lectures ought to be entirely subsidiary to practical work, and should not be so much the means of imparting information, as discussions on the facts learned by the students during such work. At present examinations occupy far too important a position, and become, instead of mere tests of the work done, an end in themselves. Examination syllabuses are usually far too full, and leave little room for originality on the part of the teacher. Professor Campbell gave a description of the

methods employed in the Stanford University of California, and emphasized the need of having, in a university, a staff sufficiently large to deal effectively with the various branches of a subject such as botany. Both he and Mr. Seward, while agreeing with the main contentions of the President, were inclined to lay more stress than the latter on the importance of lectures, especially in the case of advanced classes. Miss Lilian Clarke gave a most interesting account, illustrated by lantern slides, of the teaching of botany in the James Allen School for Girls at Dulwich. A specially designed laboratory, thoroughly well lighted, has been fitted up with tanks, etc., so that living plants of various kinds can be kept and studied at all seasons of the year. There is also a garden, in which beds are set apart for halophytes, desert plants, climbers, etc., each girl having charge of one of these plots. No definite lectures are given, but the girls make observations and conduct experiments themselves, both in the garden and in the laboratory.

Thursday morning was devoted to papers by Professor Engler and Dr. Marloth on the Vegetation of Tropical Africa and South Africa respectively.

Professor Engler first called attention to the similarity which exists between the plant formations of every large continental tropical country. He dealt successively with the following formations, and their subdivisions, which can be distinguished in the vegetation of tropical Africa. The halophilous littoral formations; the hydrophilous and hygrophilous formations, found particularly in equatorial West Africa, and eastwards to the Bahr el Ghazal; the sub-xerophilous formations which occur in the plains as well as the mountains, and the true xerophilous formations of the dry East African steppes, the Sahara, etc. He then discussed the affinities of the flora as a whole, concluding that while the dominant floral element is a native tropical African one, there can be distinguished in addition elements derived from such floras as the Madagasean, Indian, South African, boreal, Mediterranean and even the tropical American. These foreign elements, however, are not distributed equally among the various formations.

Dr. Marloth discussed the phyto-geographical sub-divisions of South Africa, dealing with his subject both from the ecological and systematic points of view. The botanical regions suggested by the author differ in some respects from those proposed by Dr. Bolus and other authorities. Both Dr. Marloth's paper and that of Professor Engler were illustrated by a number of beautiful lantern slides.

On Friday Professor Pearson gave an account of his researches on the development and germination of the spores of *Welwitschia*. The material used had been collected in Damaraland in 1904, but unfortunately, owing to the unsettled state of the country, Professor Pearson found it impossible to stay long enough to obtain a complete series of stages. However, the work accomplished has been sufficient to render it necessary to modify some of the recent views put forward as to the relationships of this genus.

Mr. F. B. Parkinson read an interesting paper on irrigation farming on the Orange River. He dwelt on the impossibility of successfully carrying on agriculture in a climate such as that of Central South Africa, without recourse to irrigation, and then described how the various difficulties which presented themselves at the farm of Baviaankrantz on the Orange River, had been overcome. The author showed that it was quite possible, by means of irrigation, to cultivate crops profitably, provided that the land cultivated was not too far from the source of water supply.

In addition to the work of the sectional meetings, the oversea botanists took the opportunity, while at the Cape, of seeing something of the vegetation of the country. The season was early spring, but though the local members often told us how much better the country would look in six weeks time, yet, where everything was new, even the spring flora afforded enough and to spare of interest. Some members, who arrived a week or two before the meeting, visited the Karroo and other localities, while during the meeting (Thursday afternoon) Dr. Marloth arranged a botanical excursion to the Lion's Head, afterwards descending to Camp's Bay. On this occasion magnificent groves of the silver-tree (*Leucadendron argenteum*) were passed through, and many other interesting plants observed. Occasionally one's preconceived ideas received a rude shock, as, for instance, when a small woolly umbellifer, with the habit of a *Gnaphalium*, was pronounced by Dr. Marloth to be a species of *Hydrocotyle*.

Then on Saturday, before sailing for Durban, Table Mountain was ascended. This proved one of the red-letter days of the whole tour. The day was perfect, and the views obtained magnificent, while the whole climb was one long succession of botanical interests. To those who had never before seen Proteaceae and Restiaceae in their native haunts, the day was a fascinating one, while some beautiful forms of heath, and numbers of other new and strange plants were in flower.

## JOHANNESBURG.

The sectional meetings were held in the C.S.A. Railway Offices. Tuesday, August 29th. The President of the section, Mr. Harold Wager, F.R.S., gave his address "On Some Problems of Cell Structure and Physiology." He first briefly traced the history of the study of cytology, from the 17th Century to the present time, showing how the earlier ideas regarding the cell and the relative importance of its parts have gradually changed. "It is, however," to quote from the address, "mainly to the researches of the last thirty years that we owe our knowledge of the many complex cell-activities at work in living organisms, and we are still only just on the fringe of the great problems which cytology has to solve." Taking the cell of the higher plants, the President discussed the nature of the various structures which together constitute the protoplast of the living cell; dealing in turn with the cytoplasm, nucleus, nucleolus, chloroplast, centrosome and other cell organs.

One very interesting feature of the address was the description of a number of experiments (most of them Mr. Wager's own) which show that many of the characteristic appearances and activities of the cell, can be imitated artificially. Thus, if a mixture of olive oil, alcohol and water be poured into a petrie dish, its granular appearance is at first comparable to that of a resting nucleus. As the alcohol evaporates, however, currents are set up which result in the rearrangement of the oil globules in such a way as to closely imitate the prophases of nuclear division. Similarly, artificial asters can be produced by dropping alcohol or turpentine on to smoked glass, while the oil-foam experiments of Butschli are too well known to need more than a passing reference. But, in spite of the suggestiveness of these experiments, Mr. Wager remarks that "without admitting the necessity of anything akin to a special vital force, we are compelled to admit that vital phenomena do not at present admit of a merely mechanical explanation."

Referring to the difficulties of interpretation when dealing with dead fixed cells, Mr. Wager pointed out that so far comparatively little progress has been made in the elucidation of the structure of the living cell. He mentioned in this connection the suggestion that has been made to utilize the ultra-violet rays, to which chromatin and certain other substances are opaque, in researches of this kind.

Finally the address dealt with the nuclei of the lower plants, and with the problem of the evolution of the nucleus. The suggestion was put forward that there were originally "two distinct

lines of nuclear evolution, leading respectively to the central body of the Cyanophyceae, and the nuclear apparatus of the yeast plant." But between these groups on the one hand, and the Algæ and true Fungi on the other, so far as the nucleus is concerned, "there are gaps which we cannot bridge at present."

It is impossible, in a short sketch, to deal in any way adequately with the many points of interest raised by Mr. Wager in the course of his admirable address: but this is the less necessary as the address itself has already been printed in *Nature* (September 21st).

Mr. A. C. Seward gave an interesting account of the Fossil Floras of South Africa. He drew attention to the fact that our knowledge of these floras is still incomplete, and pointed out that collectors may do much to remedy this defect.

Mr. T. R. Sim also read a paper on the distribution of South African Ferns.

Wednesday was a full day, as it had been decided to take the papers originally arranged for Friday morning on that day, in order to leave Friday free for a special excursion to the Magaliesberg.

In the morning, Professor F. E. Weiss, in presenting the report of the Committee for the Registration of Photographs of Botanical Interest, contributed a paper on the value of Botanical Photographs. The paper was illustrated by a fine series of lantern slides, which strikingly exemplified the value of such photographs for teaching and other purposes. Professor Weiss pointed out that photography can be usefully employed in such studies as geographical distribution, morphological and pathological botany, and even for cryptogamic work.

The Committee referred to above has already established a fair collection of photographs, but is anxious to receive further help from scientific photographers in all parts of the world. In addition to this collection, the recently formed Committee for the survey and study of British Vegetation, has decided to collect a series of ecological photographs illustrating British plant-associations.

Mr. J. Burtt-Davy discussed the climate and life-zones of the Transvaal. According to altitude and climate three more or less well-defined zones can be distinguished: (i.) The Low Veld, 600-ft.-1500-ft., a dry, tropical, well-wooded region: (ii.) The High Veld, 4000-ft.-6000-ft., a treeless, grassy plateau: (iii.) The Middle Veld, 1500-ft.-4000-ft., intermediate between the other two. It is covered for the most part with *Acacia* "bush" and low trees, with intervening open grassy places. Each of these zones is charac-

terised by differences of climate, native vegetation, and the crops it is capable of producing.

Professor Potter gave an account of some experiments which prove that a certain soil bacterium has the power of slowly decomposing amorphous carbon, with the evolution of  $\text{CO}_2$ . He suggested the possibility of the carbon at present locked up in our coal fields being rendered available for plant-life without the intervention of direct combustion.

Dr. Horace Brown read a paper on "The Dissipation of Absorbed Solar Radiation by Xerophilous Plants." The author discussed first the case of ordinary foliage leaves, and pointed out that such leaves may be subjected to intense solar radiation without acquiring a dangerously high temperature, because a large proportion of the heat absorbed is utilized in the vaporization of the water of transpiration. But in the case of xerophilous plants, transpiration is at a minimum, and some other safety valve is therefore necessary. Dr. Brown maintains that this is to be found in the loss of heat due to thermal emission. Experiments were conducted (in collaboration with Dr. Wilson) which resulted in the obtaining of a numerical expression for the thermal emissivity of the leaves of several species of plants. The results show that in this emission of heat from the surface of leaves, a sufficiently powerful cooling effect is produced, to prevent the undue heating of plants, even when exposed to strong solar radiation under arid conditions.

Mr. R. P. Gregory gave an interesting paper on "Some of the Problems of Heredity." Having discussed the general principles of Mendelian Inheritance, Mr. Gregory described some experiments conducted by Mr. Bateson and himself on the genus *Primula*, in which the character of heterostyly was found on the whole to conform to Mendel's Law—the short style being dominant, the long recessive.

In the afternoon Mr. I. B. P. Evans read a paper on "Infection Phenomena in the Uredineae," and Dr. Schönland one on "South African Succulents." Papers were also contributed by Dr. G. Potts and Mr. J. Medley Wood.

Thursday was devoted to excursions, chiefly to Pretoria and the neighbourhood. A number of botanists visited, during the day, the Government Experimental Grounds near the town. Mr. Burtt-Davy is here carrying on an extensive series of tests with introduced seeds, etc., chiefly of grasses and other fodder plants. An

interesting exhibition had also been arranged by the Agricultural Department in Pretoria, of the various kinds of crops produced in the Transvaal—fruits, cereals, cotton, tobacco, etc., etc.

On Friday Mr. Burt-Davy organized a most successful botanical excursion to the Magaliesberg Mountains. Though, in consequence of the long winter drought, most of the vegetation was brown and dry, many plants were in fruit, and some in flower. The most striking feature, however, and the primary object of the expedition was the famous "Wonderboom," a remarkable specimen of *Ficus cordata*. Originally a single tree, the plant has gradually travelled outwards by the rooting of decumbent branches, until it has become quite an extensive grove of separate trees. After an *al fresco* lunch, which the local Committee had kindly provided for us, the President and Mr. Burt-Davy energetically spent the afternoon in surveying and mapping the entire grove formed by the "Wonderboom."

In addition to the set excursions, the members of Section K had many other opportunities of seeing something of the various types of vegetation characterising the different districts which were passed through during the tour.

Of the kindness and hospitality with which we were everywhere received, and which made the tour almost resemble a royal progress through South Africa, much has been written elsewhere. For the rest, though it has been suggested that the trip partook somewhat of the nature of a huge excursion, yet I think that the botanical members at least, of those who visited South Africa, are agreed that, for once in a way, it was well for the British Association to go further afield, and to explore "fresh woods and pastures new."

R.H.Y.

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ON THE POSSIBLE EXISTENCE OF A FERN STEM  
HAVING THE FORM OF A LATTICE-WORK TUBE.

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BY D. T. GWYNNE-VAUGHAN.

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IN most *Polypodiaceae* the vascular system of the stem has the form of a tubular lattice-work imbedded in a matrix of ground-tissue, and lying about half way between the axis of the stem and the periphery. In the light of recent researches it may be safely

stated that this arrangement has been derived in the course of evolution from a single solid central cylinder with a central mass of xylem. It follows, therefore, that certain regions in the stem primitively occupied by vascular tissue are now occupied by ground-tissue. The exact manner in which this change took place is as yet undecided and is still under discussion. Nevertheless, as regards the *Polypodiaceae* at least, whatever the process itself may have been, there is a strong probability that it first of all came into action at certain points at the periphery of the protostele situated immediately above the departing leaf-traces. According to one view, at these points the vascular elements of the protostele have been directly transformed into ground tissue; according to another they were not formed at all, but their place has become occupied by the elements of the cortical ground-tissue lying immediately without them. In either case the recognizable outline of the central vascular cylinder would become changed at the points in question and the cortical tissue would appear to, or actually would, project inwards into the stele so as to form so many deep bays or pockets. These "endodermal pockets," as they have been called, at first end blindly below, later on, however, the pocket belonging to one leaf reaches down to meet that of the leaf next below, and thus the solid protostele becomes converted into a tube with perforated walls. A further increase in the relative size of the perforations will produce a structure that may be conveniently pictured as a tubular lattice-work.

In this last condition of the vascular system the question as to what has become of the "stele" as a morphological unit leads naturally to the expression of two diverse opinions. In the first place it is obvious that the separate strands of the lattice-work (meristeles) correspond to parts only of the original protostele. Now according to what may be called the theory of transformation the ground-tissue lying within and between the meristeles also corresponds to a part of the original protostele, and, therefore, the stele as a whole is still to be regarded as theoretically circular in outline. On the other hand, according to what may be referred to as the theory of substitution, the central ground tissue is cortical in origin, the protostele is broken up into several separate parts, and the "stele" as a whole cannot be said to exist at all.

While admitting freely the great theoretical interest attached to this question, it seems to me that, whichever view of the point be taken, the real essential worth of the conception of the stele will

still remain undisturbed. For this, in my opinion, lies chiefly in the phylogenetic significance attached to the idea that has led to the derivation of the various types of vascular system from a primitive protostele, and renders it necessary that an attempt should be made in each particular case to reconstruct in detail the series of phylogenetic modifications that have produced the type in question. With this object in view the nature and origin of all internal endodermes, ground tissues, etc., becomes a matter of considerable importance, and they therefore deserve the most careful investigation. It also becomes necessary to draw a clear distinction between such of these internal tissues as have been from their first appearance always in direct continuity with the corresponding tissues on the outside of the protostele, and those which were altogether central in origin, and have either remained entirely distinct from the corresponding external tissues, or only became continuous with them at a later period in their history.

It is evident that the aforesaid changes in the structure of the vascular system described above are due chiefly, if not entirely, to the influence of the leaf-traces, and that they advance in measure as the importance and size of the leaf-trace increases relative to that of the stem. It follows naturally that a change in the relative importance of the vascular supply of the leaf and that of the stem should correspond to a similar change in the relative importance and predominance of the leaf and stem as a whole. It is also reasonable to suppose that the increasing importance of the leaf as a whole, if carried beyond a certain degree, might express itself upon the structure of the solid axis of the stem in a manner similar to that in which the increasing importance of the *leaf-trace* expressed itself upon the originally solid *vascular cylinder* of the stem. These considerations appear to me to throw an interesting light upon the somewhat peculiar type of stem structure possessed by a few ferns of which *Onoclea germanica* W. may be taken as a good example.

If a series of transverse sections passing through several consecutive nodes and internodes in a well-grown erect stock of *Onoclea germanica* be made, attention will at once be drawn to the fact that the continuity of the plates of tissue that form the sections is interrupted by a number of holes or lacunae (figs. 41 and 42). These lacunae are lined by the epidermis of the stem, and if followed upwards through the series of sections they will be found to communicate with the exterior just above the point of insertion of the

petioles. In fact the epidermis of the stem at the axil of each leaf has sunk deeply inwards so as to form a pit or pocket projecting into the ground tissue of the stem. These epidermal pockets, as they may be called, run downwards for about three or four millimetres, and at the same time penetrate so far inwards that they reach right into the central ground tissue within the lattice-work tube of vascular strands; there they end blindly. The leaves are inserted so closely together that from three to six of these pockets may be cut across in one transverse section. Their size and form will vary from one section to another according to the distance of the section below the insertion of the leaves to which they respectively belong. In



Fig. 41.



Fig. 42.

Figs. 41 and 42. *Onoclea germanica*. Transverse section of the erect stock. In all the figures the epidermal pockets are left blank, the ground-tissue of the stem is dotted, the meristele of the stem are shaded black and the leaf-traces are shaded with parallel lines.

many sections a definite stem hardly appears to exist at all, but the axis of the plant is apparently made up of a number of petiolar bases inserted one upon another (fig. 41). All the vascular strands in the axis appear to lie in these leaf bases, but by tracing their course upwards through a series of sections it is seen that the larger of them (after giving off the small leaf-traces) pass inwards before the petiole is free from the stem, and then move over so as to take up the same position as before in a ridge that continues the base of a higher petiole. These strands (shaded black in the figures) are therefore strictly cauline and constitute the vascular lattice-work proper to the stem.

The stolon of *Onoclea germanica* is much narrower than the erect stem. Its leaves are separated by long internodes and there

are no epidermal pockets. However, where the stolon thickens out to form the erect stock the epidermal pockets begin to appear; at first one only in each transverse section (fig. 43) then rapidly increasing in number as the leaves become crowded together.

*Onoclea sensibilis* L. also possesses epidermal pockets but they are much less conspicuous than in *O. germanica*, and they barely reach so far as the central ground-tissue. They appear in the sections as narrow concentric slits and the leaves are inserted so far apart that only one pocket is present at a time.



Fig. 43.



Fig. 44.

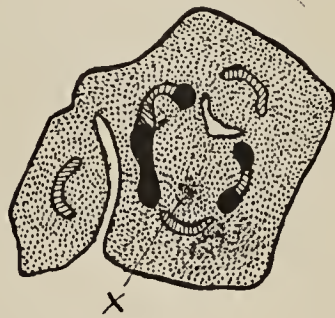


Fig. 45.

Fig. 43. *Onoclea germanica*. Transverse section of a stolon where it enlarges to form an erect stock.

Fig. 44. *Cystopteris fragilis*. Transverse section of the stem.

Fig. 45. *Aneimia Phyllitidis*. Transverse section of the stem. One epidermal pocket is just about to appear at X.

The stem of *Cystopteris fragilis* Bernh. furnishes almost as good an example of the development of epidermal pockets as *Onoclea germanica* itself, although the whole structure is on a smaller scale. Not more than three pockets were found in any one transverse section (fig. 44), but they are relatively large and run downwards for about 4 *m.m.* reaching clearly into the internal ground-tissue. The suggestion that the axis of the plant is merely a series of leaf bases inserted one upon the other is even more striking than in *Onoclea germanica* for the vascular lattice-work of the stem is a very loose one with relatively large gaps.

Typical epidermal pockets are also to be found in *Aneimia phyllitidis* Sw. and *A. hirta* Sw. Not more than three of them occur in any one section, and they are more or less crescentic in form (fig. 45). Although less conspicuous than those in *Onoclea germanica* they reach well into the central ground-tissue within the vascular ring; indeed, in some cases they were still visible on the inner side of the leaf trace even after the latter had joined on to the meristemes of the stem. In one specimen of *Aneimia phyllitidis* that I examined the slender first-formed region at the base of the

## 216 *Possible Existence of a Lattice-Work Fern Stem.*

stem was still preserved in excellent condition; and here it was easily ascertained that the very early leaves of the young plant had no epidermal pockets in their axils. Again when at length these do appear they are at first comparatively shallow, and end blindly in the cortex without reaching so far in as the vascular ring.

The similarity between the development of these remarkable fern stems, and the manner in which their particular type of vascular system is assumed to have arisen, is very striking; so much so that the temptation to carry the analogy a step farther, and to speculate upon the possible existence of a stem possessing a structure corresponding to the tubular condition of the stele, is almost irresistible. It is only wanted that the epidermal pocket from each leaf should become continuous with those from the leaves inserted lower down, and the stem itself would become a lattice-work tube. In *Onoclea germanica* they sometimes very nearly do so, but actual continuity was never seen to occur. Moreover, it is very difficult to imagine how such a stem could possibly arise from an apical meristem with a single initial cell; except, perhaps, by some such clumsy expedient as the supposition of a one-sided growth that would shift the initial cell all round the termination of the tube. But I know of no precedent elsewhere for such a mode of growth. These fern stems present, of course, no difficulties to those who regard the sporophyte stem as a system of concrescent "phytons," or "shoot-segments," which arise successively one upon another. According to this theory the free terminal part of the "shoot-segment" becomes the leaf, while the basal part fuses with the bases of other "shoot-segments" to form the aggregate stem. If, with Celakovsky, each "shoot-segment" be regarded as an individual, and equivalent to a Bryophyte sporogonium, the whole plant now becomes a composite organism consisting of repetitions of a sporophyte by some form of budding, each individual with its own independent growth. It appears to me, however, that the theory of "phytons" receives no real support whatever from the plants in question, for their type of stem structure cannot in any sense be regarded as primitive. It is, on the contrary, in each particular case, the latest expression of a long series of advances from the primitive solid stem, with its single solid central protostele.

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ON THE STAGES OF DEVELOPMENT REACHED BY  
CERTAIN BIOLOGIC FORMS OF *ERYSIPHE* IN CASES  
OF NON-INFECTION.<sup>1</sup>

[PLATE V.]

BY ERNEST S. SALMON.

THE morphological species *Erysiphe Graminis* DC. has been proved to consist of a number of "biologic forms," each of which is sharply restricted either to a single host-species, or to a few closely-allied species.<sup>2</sup> Thus the biologic form on wheat cannot infect barley, rye, oat, &c.; that on barley cannot infect wheat, rye, oat, &c.; and so forth. In some cases this specialization of parasitism has proceeded to such an extent that we find distinct and sharply-marked biologic forms on very closely related host-plants; thus, the two biologic forms on *Bromus commutatus* and *B. racemosus* are unable to cause the reciprocal infection of their host-plants, notwithstanding the fact that the two plants are so close morphologically that the majority of systematists consider that *B. racemosus* is nothing more than a variety of *B. commutatus*.

Now in these cases when the conidia of a certain biologic form are sown on the host-plant of another biologic form of the same morphological species, although no true infection, involving the production of a mycelium and conidiophores, results, yet the conidia germinate and reach certain further stages of development. The object of the experiments described below was to investigate these stages of development, and to ascertain at what stage and in what manner the action of the "wrong" host-plant stopped the further growth of the germinating conidium. The inoculations made were as follows:—(1) Conidia from wheat were sown on barley; (2) Conidia from *Bromus mollis* and *B. racemosus* were sown on *B. commutatus*; (3) Conidia from oat were sown on wheat. These cases were selected because it has been proved by a very large number of experiments that no true infection resulted when these inoculations were made [see (1), (2), (3) and (4)]. We will consider separately the results obtained in each case.

(1) Conidia were taken from wheat and sown at a marked place

<sup>1</sup> From the Jodrell Laboratory, Royal Botanic Garden, Kew.

<sup>2</sup> A general account of the phenomena met with in the specialization of parasitism in the *Erysiphaceae*, and a definition of "biologic forms" have been given by the writer in this journal (Vol. III., p. 55.)

on six leaves of barley and on one leaf of wheat.<sup>1</sup> After 24 hours one barley leaf was examined microscopically.<sup>2</sup> A germ-tube, provided with an appressorium, had been produced by nearly all the conidia. In the greater number of cases a tube penetrating the epidermis had been emitted by the appressorium, and had formed an incipient haustorium in the host-cell. (Pl. V., figs. 3 and 7 *i.h.*) The incipient haustorium, which was often of a smaller size than those represented, consisted of a roundish refractive body. The actual point of penetration could be seen very clearly; viewed from above it appeared as a minute circular hole at the focus just below the lower wall of the appressorium of the germ-tube, where it was closely applied to the epidermis. At this stage of development, marked by the penetration of the host-cell and the production within it of a small refractive body, the incipient haustorium, the growth of the germinating conidium generally ceases. Several conidia, however, were observed which had developed a larger, apparently normal, young haustorium in the epidermal cells (Fig. 4).

At the end of 48 hours another barley leaf was examined. Here the same formation of the small refractive bodies—the incipient haustoria—was observable. It was clear, too, that in the majority of cases these bodies had ceased growth, and in some cases, even by this date, they were beginning to become disorganized. As in the first leaf, a few instances were observed here and there in which a conidium had produced in an epidermal cell (sometimes the subsidiary cell of a stoma) a normal, apparently vigorous haustorium, which had now developed at its ends the lobed processes characteristic of the present species (Fig. 2).

On the 3rd day, in the barley leaf examined, the gradual disorganization of the incipient or arrested haustorium (still visible as a small highly refractive body) was general and could be clearly seen in the majority of cases (Fig 7 *d.h.*) In this leaf again a few of the germinating conidia had formed a full-sized, apparently normal, lobed haustorium; in these cases no further growth, as a rule, had resulted; in one or two cases, however, a few short, weak hyphae had grown out from the appressorium (as *e.g.* is shown in Fig. 5).

On the 5th day the two barley leaves examined showed the complete arrest of nearly all the incipient haustoria, which were

<sup>1</sup> The barley and wheat leaves were cut off from seedling plants and, after inoculation, were kept on damp blotting paper in a Petri dish.

<sup>2</sup> A useful and quick method of rendering such leaves sufficiently transparent to show the germinating conidia *in situ*, is to immerse them for a few hours in a mixture consisting of two parts of alcohol and one part of acetic acid.

now mostly disorganized; here and there, however, a conidium could be seen which had formed a full-sized lobed haustorium, and in a few cases, a short weak hypha proceeded from the appressorium.

On the 6th day the control wheat leaf (inoculated from the same source) was examined, and was found to be virulently infected, the inoculated area being now covered over with a continuous powdery *Oidium*-patch, and the epidermal cells of the leaf containing many hundreds of large lobed haustoria. In the barley leaf only numberless refractive bodies, the incipient or arrested haustoria, for the most part disorganized, could be seen; in many cases they were still attached to the withered germ-tube of the conidium, but were often without any such attachment and quite solitary.

(2) Several leaves, cut off from seedling plants of *Bromus commutatus*, were inoculated with conidia either from *B. mollis* or from *B. racemosus*. Conidia from such a source had been previously found to be unable to cause any visible infection of *B. commutatus* (see 3). In the present experiments, also, no visible signs of infection appeared on the leaves. Microscopic investigation, however, showed that the conidia had germinated and produced in many cases fair-sized haustoria, which had frequently developed the finger-like processes (Figs. 5 and 6). In a few of these cases, a short hypha was produced from the appressorium (Figs. 5 and 6). Nevertheless, no further growth beyond this stage of development was reached, and no true infection resulted.

(3) Conidia were taken from oats, and sown on five wheat leaves (attached to vigorous young seedling plants); at the same time one leaf of one of these seedling wheat plants was inoculated with conidia taken from wheat. By the 5th day the leaf last referred to had become virulently infected, the epidermis at the inoculated place being nearly covered over with patches of mycelium, bearing hundreds of young conidiophores; and nearly every epidermal cell contained one or more large lobed haustoria. No trace of external infection appeared on the five other wheat leaves, but on microscopic examination it was seen that many of the conidia had germinated and produced in the cells small refractive bodies—incipient or arrested haustoria—quite similar to those shown in Fig. 3.

The results of the above experiments afford proof that the immunity to the attacks of the conidia of other "biologic forms" possessed by certain host-species is not due to the failure of the

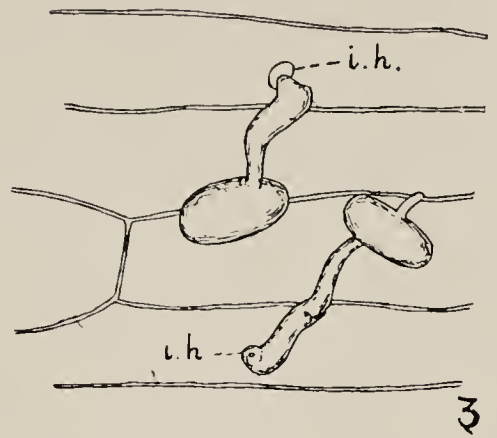
germ-tube of the conidium to penetrate the leaf-cells of the plant, but is due to the inability of the fungus to develop further the incipient haustorium which is formed, or to the incapacity of the fully-formed haustorium to adapt itself to the intra-cellular conditions. The incipient haustorium becomes arrested and gradually disorganized under the influences at work in the cell of the "wrong" host-plant, or if the haustorium attains to its full size it is hindered by these influences from carrying on its normal functions, and thus supplying to the fungus the food necessary for the production of mycelium, &c.

We are justified in assuming that susceptibility or immunity, at all events in the case of these host-plants and their "biologic forms," by no means depends on the absence or presence of a chemotactic substance in the cells of the host-plant, as Masee (8) supposes, but *on the capacity or incapacity for maintaining certain working-relations between the haustorium and the host-cell*. Immunity in these cases depends on the power possessed by the host-plant of preventing by means of certain physiological processes the attainment of that balance whereby these working-relations are brought about and maintained. True infection does not merely depend on the attacking of the cell by the penetration-tube,—a process with which chemotaxis may be concerned—nor even on the successful production of the haustorium, but is determined by far more complicated factors, concerned it may well be with the production of special substances by the protoplasm of both the haustorium and that of the host-cell. We may confidently expect that with the discovery of the precise nature of the physiological inter-relations between the haustorium and the host-cell the causes of the immunity and susceptibility of the host-species of "biologic forms" will be explained. With regard, too, to the question of the raising of "immune" races of plants of economic importance, it will probably be found that the place of the decisive conflict between host and parasite (the result of which gives immunity or susceptibility to the plant) will be intracellular rather than extracellular.

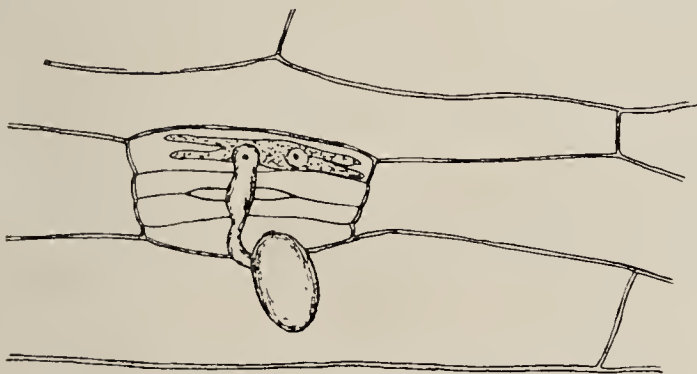
The results obtained in the present experiments support the view advanced by Marshall Ward fifteen years ago, that in cases of true infection through the formation of haustoria, "the mycelium enters into a peculiar symbiotic connection with the cells, and for some time merely taxes them, as it were, rather than injures them directly" (6), (7). Using "symbiosis" in this sense, we may say



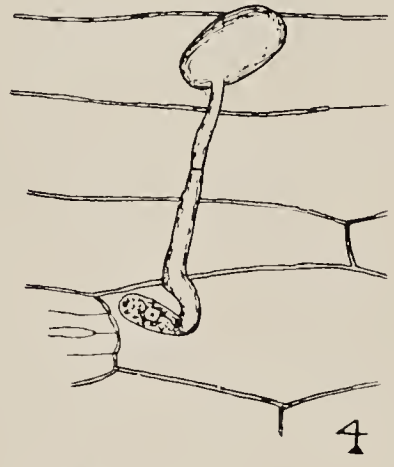
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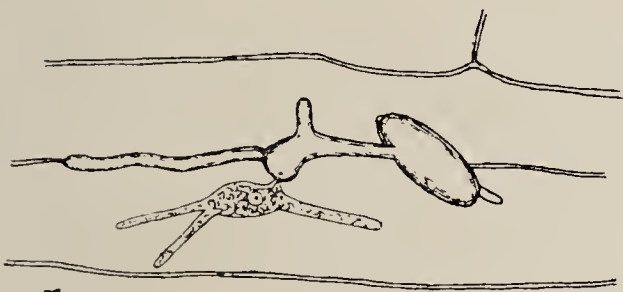
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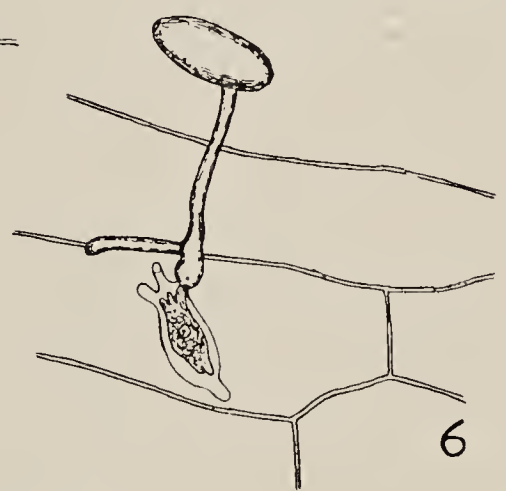
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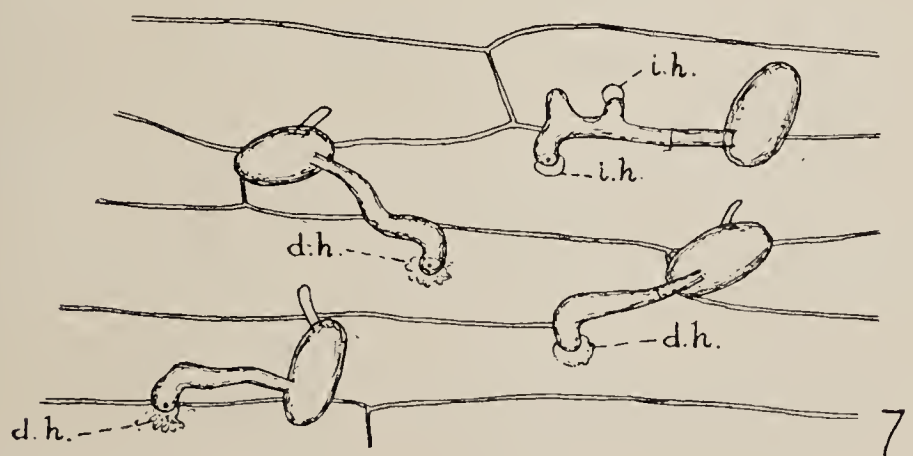
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that the cases of non-infection described above are due to the inability of the haustorium to carry on its normal functions under the conditions obtaining in the cell, *i.e.*, they are evidences of defective symbiotic arrangements between the parasite and host.

An interesting variation in the behaviour of the germinating conidium of *E. Graminis* was observed. As a rule, when the conidium germinates, the germ-tube at once pierces the epidermis, and forms a haustorium in the epidermal cell. The germ-tube can often be seen passing over an open stoma, as in Fig. 2, where the haustorium has been sent into the subsidiary cell. No case has hitherto been recorded of the entry of the germ tube of the conidium through a stoma, all authors having described only the process of direct penetration of the cuticle. In the present experiments, a very few cases<sup>1</sup> were observed in which the germ-tube of the conidium, instead of passing over the open stoma, entered it, and growing inwards through the respiratory cavity, had come into contact with the mesophyll-cells (Fig. 1). At this stage the experiment had been concluded by the fixing of the material, so the further growth, if any, of the germ-tube could not be observed. Whether there is any infection in such cases,<sup>2</sup> and whether conidia of *E. Graminis* show similar behaviour when sown on their "right" host-plant, are points which must remain doubtful for the present. This entry, in exceptional cases, of the germ-tube through the stoma is of interest in connection with the fact, which I have lately recorded (5), that under cultural conditions, *E. graminis* possesses the power of growing as an endophytic parasite.

<sup>1</sup> Six cases, in all, were observed among the many hundreds of germinating conidia seen.

<sup>2</sup> In the case of urcdospores, Miss Gibson has shown, in a recent paper in this journal (Vol. III., p. 184), that entrance of the stoma by any germ-tube is no index of the capacity of that germ-tube to infect the leaf.

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[For Description of Plate V. see over.

## EXPLANATION OF PLATE V.,

ILLUSTRATING MR. E. S. SALMON'S PAPER ON "CERTAIN BIOLOGIC FORMS OF *Erysiphe* IN CASES OF NON-INFECTION."

Figs. 1, 2, 3, 4, 7. Conidia of the "biologic form" of *Erysiphe Graminis* on wheat germinating on the epidermis of barley leaves; *i.h.*, incipient haustoria; *d.h.*, haustoria in process of disorganization. In Fig. 1 the germ-tube has entered a stoma; in Fig. 2 the germ-tube has passed over the open stoma, formed an appressorium, and developed a haustorium in the subsidiary cell.

Figs. 5, 6. Final stage of development reached by two conidia of the "biologic form" of *E. Graminis* on *Bromus racemosus* germinating on the epidermis of a leaf of *B. commutatus*.

(All the Figures  $\times 400$ .)

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 THE CYTOLOGY OF COTTON.

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 PRELIMINARY NOTE.
 

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**A**N examination of the cotton flower at various stages of its development has provided the following information:—

The development of the sex-cells from a sub-epidermal arche-sporium is normal, reduction of the mother-cell taking place in the usual way, although very rapidly, and producing gametes with ten chromosomes, the zygote nuclei apparently containing twenty. The tetrad cell nearest the micropyle becomes the megaspore. Fertilisation occurs within twenty-four hours of pollination, the two polar nuclei fusing just before the union of the second male nucleus with one of them. The tube nucleus also passes into the embryo sac, but degenerates. After three days the egg cell divides into two, the endosperm nucleus having now produced over one hundred daughter nuclei, whose divisions are very irregular. No suspensor is differentiated by the embryo.

The initial stages of development of the cotton fibre are quite at variance with the accepted accounts, the cotton itself being a simple epidermal hair.

The nucleoli, which are seen in many cases to be continuous with the reticulum, retain their individuality in the first few divisions both of the egg and of the triple nucleus. The linin thread also appears to persist in the reduction of the male mother-cell, until after the chromosomes have attained their usual contracted form, and the multipolar spindle is appearing, but owing to their small size detailed investigation of the reducing cells is difficult.

The full account will be published later.

W. L. BALLS.

Cairo, Oct., 1905.

THE  
NEW PHYTOLOGIST.

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SKETCHES OF VEGETATION AT HOME  
AND ABROAD.

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II.—SOME ASPECTS OF THE VEGETATION OF SOUTH AFRICA.

BY F. E. WEISS, D.Sc.

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PART I.—THE FLORA OF THE CAPE PENINSULA.

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It has been suggested to me by the Editor that an account of the more striking features of the vegetation of South Africa, as they presented themselves to members of the British Association during their recent visit to the South African Colonies might be of interest to the readers of the NEW PHYTOLOGIST. I propose therefore in the present article to deal with some aspects of the flora of the Cape Peninsula, which may in some degree be taken as typical of the South Western Coast, a botanical region very clearly differentiated from the Eastern Coast region. A description of the vegetation of the latter and of the central high plateau of South Africa will follow in a subsequent issue.

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THE Cape Peninsula is the most thoroughly explored and at the same time botanically the richest portion of the South Western Coast region. Comprising an area of 197 square miles or about a quarter larger than the Isle of Wight, it contains 2100 species of native flowering plants or considerably more than the whole of the British Isles. This richness is no doubt in part due to the great range in climatic conditions offered by the mountainous headland and the low-lying Flats. The temperature, it is true, owing to the proximity of the sea, shows few extremes and these are of short duration. It fluctuates mainly from a winter average of 54°F (12° 5 C) to 68°F (20°C) for the six summer months. But the great differences of altitude naturally induce considerable variations in the amount of precipitation and the annual rainfall on the frequently cloud-capped Table Mountain is about 62 inches (1500 mm.), while at Wynberg on the lower slopes (250 ft. above the sea) it averages only 42 inches (1000 mm.), and in Capetown itself only 23.8 inches (600 mm.), the bulk in all three cases falling during the six winter months.

Furthermore taking into consideration the physical differences of the soil, the dry sandy zone along Table Bay and False Bay, the marshy areas on the Cape Flats, the steep mountain slopes and precipitous cliffs of Table Mountain, and lastly its rain-drenched tableland, 3000 ft. above the sea, we have apparently all the conditions for a very varied vegetation. And yet we do not find such distinct zones of vegetation as we might be led to expect from the physical conformation of the Peninsula, nor such plant-formations as meadow, wood, and moorland into which our European vegetation would under similar conditions differentiate itself. The native vegetation of the Cape Peninsula and indeed of the South-Western region is really very uniform in character, consisting in the main of shrubby plants with small and often heath-like leaves of a bluish-green hue. This extensive "bush" formation is one of the most marked characteristics of the Cape flora. There are no natural forests or even woods, only here and there on the slopes of Table Mountain groves of Silver Trees (*Leucadendron argenteum*), while other tree-like plants are dwarfed in stature and confined to the steep ravines of the Eastern side of Table Mountain. Equally noticeable is the absence of natural meadowland, grasses where they occur do not form a continuous covering, but grow in detached clumps. The scarcity of tall trees and the general absence of luxuriant growth is probably attributable to the coincidence of the vegetative period with the winter season, and this is borne out by the striking contrast of the vegetation of the South-Western region with that of the East coast, in which the rain falls mainly during the summer months. Similarly we must correlate the smallness of the leaves of the shrubby vegetation and their frequently "ericoid" structure with the very dry nature of the summer months, which necessitates considerable protection against excessive transpiration. But though at first sight and at a distance this dominance of bush-formation gives an aspect of sameness to the vegetation of the Cape Peninsula, yet when examined in detail all such uniformity disappears owing to the wonderful richness in species which characterises the Cape flora. For not only do we find in the bush an exceedingly large number of species of *Erica* and of other plants which are commonly of shrubby growth in Europe, but such large natural orders as the Compositae and Polygalaceae, of which we in England only possess herbaceous representatives, are here found in bush form and in innumerable species. The active competition, too, of so great a variety of plants of shrubby habit and

with foliage adapted to the dry summer months, makes it more difficult for any one species to become dominant over a large patch of ground, and thus though there may be in the bush plants of a sociable habit which could form continuous growths like the ling, the cowberry, the bilberry and the bracken do on our moorlands and mountain sides, yet they are rarely able to establish themselves in such a dominant form. During a residence of twenty-seven years Dr. Bolus has only seen two species growing in such quantity and proximity as to give, when in flower, a colour to the mountain-side when viewed at a distance. These were *Erica hirtiflora* and *Podalyria calycitrapa*,<sup>1</sup> a papilionaceous shrub with large mauve-coloured flowers.

Of course the conditions of life along the shore differ considerably from those of the mountain slopes, and the plants found there are of quite a distinctive type. Along the coast-line of Table Bay, bounding the "flats," the vegetation resembles in aspect, though not in genera and species, that of our own shores. Sand-binding grasses occupy the extreme litoral zone forming and covering the lower sand-hills, while the somewhat higher dunes behind them are clothed with various plants with succulent leaves such as *Mesembryanthema* with large purple and yellow flowers. Occasionally one finds a clump of *Euphorbia Caput-Medusae* with its succulent water-storing stem. Behind the sand-hills the extensive Flats are covered with a bush-formation of more or less heath-like plants similar to that found on the mountain slopes, though in and around the numerous shallow pools or "Vleis" grow many marsh-plants including often the beautiful Arum Lily (*Richardia aethiopica*) which is still more common in damp meadows and hedgerows around the farms. The larger Vleis are often covered with the sweet-scented white inflorescences of the Cape Pond-Weed (*Aponogeton distachyon*) of which the starch-containing tubers, as well as the young inflorescences, are eaten as vegetables.

Of the "bush" which covers the drier portions of the Flats, the foot hills and the slopes of Table Mountain, it is impossible to give an adequate and at the same time a concise account, owing to the great variety of its constituent plants, but attention should perhaps be drawn to a few of the commoner or more remarkable forms. Among the shrubby composites one notices the Rhenoster bush (*Elytropappus*) (see Fig. 48) with small imbricating leaves,

<sup>1</sup> H. Bolus. Flowering Plants and Ferns of the Cape Peninsula. Trans. of the South African Phil. Soc., Vol. XIV., Part 3, 1903.

giving its branches a Cupressus-like appearance, while its greyish colour helps to give a lighter tint to the vegetation. Various forms of *Helichrysum*, of *Osteospermum*, with conspicuous yellow flowers and hard stony fruits, and numerous species of *Senecio* are among the more prominent of their family. Of the genus *Erica*, 90 species are found in the Cape Peninsula, growing as stated above, more or less singly among the other shrubs. In



Fig. 46.



Fig. 47.



Fig. 48.



Fig. 49.



Fig. 50.



Fig. 51.

Figs. 46—51. Types of reduced foliage from the "Bush."

Fig. 46.—*Brunia nodiflora*.

Fig. 47.—*Passerina filiformis*.

Fig. 48.—*Elytropappus rhinocerotis*.

Fig. 49.—*Murraltia*.

Fig. 50.—*Cliffortia*.

Fig. 51.—*Phyllica*.

August the beautiful *Erica cerinthoides* was in full bloom, while *Erica baecans* and *E. Plukenetii* were among the more showy forms. These narrow-leaved heaths and the hard-leaved *Brunia nodiflora* (Fig. 46) with its globular tufts of white flowers were to be seen on

all the drier slopes, while purple flowered *Muraltias* (Fig. 49) (Polygalaceae) and the singular diœcious shrub *Cliffortia* (Fig. 50) (Rosaceae) were often found in more sheltered situations, as for instance in the groves of Silver-trees.

Most noticeable, because growing somewhat taller and more tree-like are the Proteaceae. Of these only the Silver-tree grows to a considerable height, the others are but dwarf-trees, with a short stem and bearing leaves of hard leathery texture, which often assume a vertical position. The Silver-tree (*Leucadendron argenteum*) has a more delicate foliage, the leaves being protected with a covering of fine silken hairs, and this species is more limited in its distribution than are some of the other species of *Leucadendron*. It is also of more sociable habit, or possibly its more rapid growth enables it to outgrow the competition of the surrounding shrubs, and to form the definite groves which are found on the slopes of Lion's Head and of Table Mountain. The other species of *Leucadendron* and the numerous forms of *Protea* (the Sugar-bush) are slower growers and occur generally singly or in small groups among the other plants (Pl. 6, Fig. 2). It was most interesting to see the long-tailed Sugar-birds (*Promerops*) flitting about among these Sugar-bushes, from the large and often beautifully coloured inflorescences of which they suck the nectar. The sight of these birds reminded one of the fact that flowers which are pollinated by birds are a characteristic feature of the flora of South Africa. Not only are the Sugar-bushes visited by various sugar-birds and sun-birds belonging to the genera *Promerops* and *Nectarinia*, but several species of *Erica*, with long and curved corolla tubes, and many Aloes, are ornithophilous according to the observations of Scott-Elliott<sup>1</sup> and Marloth.<sup>2</sup>

Between the ericoid shrubs and Proteaceous dwarf-trees are found numerous Restionaceae, which so largely take the place of the grasses in South-West Africa, and which are readily recognisable by the large brown bracts by which their unisexual inflorescences are protected (Pl. 6, Fig. 1). Their vegetative organs as shewn by Pfitzer<sup>3</sup> are peculiarly well protected by sunk stomata, etc., against summer droughts. Like the Proteaceae the family of Restionaceae is largely restricted to the South-Western

<sup>1</sup> Scott-Elliott. Ornithophilous Flowers in South Africa. *Annals of Bot.*, Vol. IV., 1890.

<sup>2</sup> Marloth, R. Die Ornithophilie in der Flora Süd Africas. *Ber. d. deutsch bot. Ges.* 1901.

<sup>3</sup> Pfitzer. Pringsheim's Jahrbücher f. w. Bot., Vol. VII.

portion of South Africa, and both natural orders are also characteristic constituents of the Australian Flora.

In the shelter of the "bush" will be seen during the wet months of winter and spring many monocotyledonous plants with brightly coloured flowers, which form so considerable a proportion of the flora of the Cape Peninsula. Of these the Iridaceae and the Orchidaceae are the most numerous, the latter being represented only by terrestrial forms, of which some, like *Disa grandiflora* are of exquisite beauty. The underground storage organs of both these groups of plants make it possible for them to last out in a resting condition during a long dry summer, while they come up one after the other at the commencement of the winter rains. One member of the Iridaceae, however, *Bobartia spathacca*, which is very common on the mountain slopes, has long filiform leaves of excessive toughness, and is as admirably protected as the Restionaceae against the summer drought (Figs. 52 and 53.)

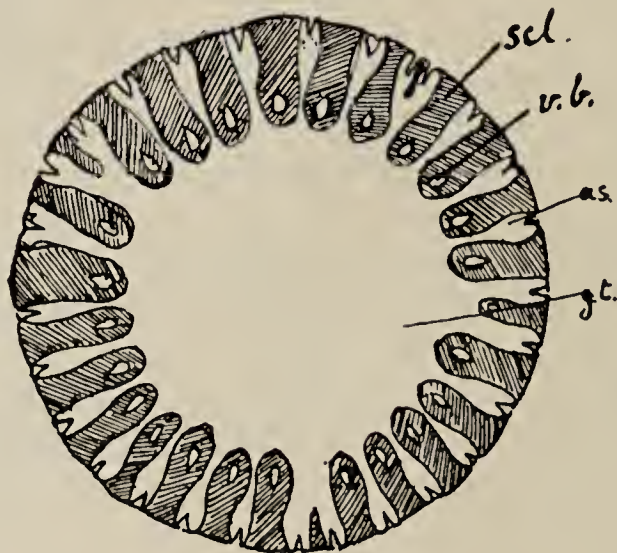


Fig. 52.

Fig. 52.—Transverse section of the filiform leaf of *Bobartia Spathacca*, shewing the assimilating tissue (*as.*) protected by deep flanges of sclerenchymatous tissue (*scl.*) in which run the vascular bundles (*vb.*) The centre of the leaf is occupied by wide-celled parenchymatous ground tissue (*gt.*)

The numerous species of *Oxalis*, which, with their bright yellow, white or purple flowers form so conspicuous a feature in the vegetation of the Cape Peninsula, exhibit no great adaptation of their foliage to the dry summer climate, but like the Iridaceae their subterranean tubers or corms enable them to remain dormant during a prolonged adverse season.

A point of some interest is the occurrence of small annuals,

which, though not so numerous as in European Countries, come up during the wet winter season between the perennial shrubs. It is true Scott-Elliott<sup>1</sup> has doubted the existence of any really indigenous annual in the Flora of the South West Region and Schimper<sup>2</sup> has accepted this view, but Dr. Bolus<sup>3</sup> has been able to compile a list of nearly 200 species of undoubted annuals for the Cape peninsula alone. Just as in the case of the tuberous and

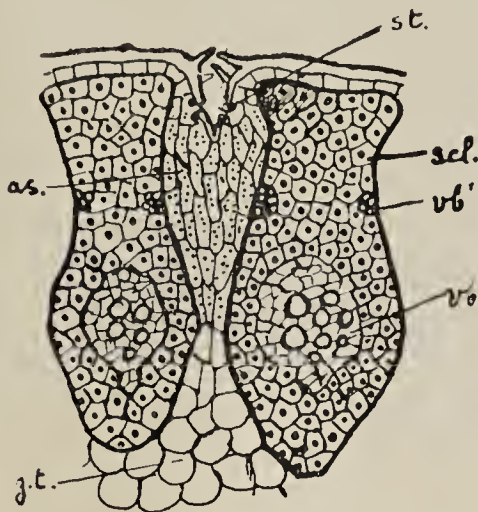


Fig. 53.

Fig. 53.—Enlarged view of one of the groups of assimilating cells (*as*) with which the deeply sunk stomata (*st.*) communicate. On either side of the assimilating tissue are groups of sclerenchyma (*scl.*) containing the vascular bundles (*vb.*) and supporting two small vascular branches (*vb'*) which are connected with the assimilating tissue.

bulbous plants so in the case of the annuals the vegetative organs show no special climatic adaptation, as the rainfall is plentiful during their period of development, and their only requirement is to mature their seeds before the dry season stops their growth. They are therefore generally small in stature but bear often comparatively large and brightly coloured flowers, which is necessary owing to the severe competition for the visits of insects, which must exist between the small annuals and the numerous flowering shrubs between which they grow. Various species of *Nemesia* (Scrophulariaceae) were particularly noticeable on the excursions we were privileged to make under the guidance of Professor Pearson and of Dr. Marloth. Other annuals belonging to the Cruciferae Compositae and Lobeliaceae were also to be found.

<sup>1</sup> Scott-Elliott, G. F. Notes on the Regional distribution of the Cape Flora (Trans. of the Bot. Soc. of Edinb. Vol. 18, 1891, p. 243).

<sup>2</sup> Schimper, A. W. F. Plant Geography on a Physiological Basis.

<sup>3</sup> Bolus, H. Science in South Africa, 1904.

Root parasites form a distinct feature of the Cape Flora, and besides several species of *Thesium* we were lucky enough to find a brilliant scarlet *Harveya* on the slopes of Table Mountain. As we approach the precipitous rocks which separate so sharply the mountain slopes from the flat top of Table Mountain we find near the water courses numerous plants of *Drosera cistiflora*, while near the rocks especially where there is dripping water the presence of *Fossombronia* and *Anthoceros* shews that we are approaching regions of greater rainfall and more permanent moisture. These signs were very noticeable on the excursion to the top of Table Mountain, where the boggy stretches abound in numerous Cyperaceae, while the banks of the streams feeding the large reservoirs were rich in ferns, including *Todea africana*, and the rocks around the water courses were covered in sheltered situations with filmy ferns, *Hymenophyllum tunbridgense* and *H. rarum* being the most conspicuous. This uppermost zone of vegetation is not so typical of the South Western Flora as the plants on the slopes of the mountain, where the rainfall is less heavy, but it adds greatly to the fascination which the Cape Peninsula has for every botanist interested in plant formations.

Comparing the flora of the Cape Peninsula with that of other portions of South Africa, one cannot fail to be impressed by the striking difference between the vegetations of the Eastern and the Western Coast regions. For while the East Coast possesses a more luxuriant vegetation and a greater number of trees, entire families of plants such as the Proteaceae, Restionaceae and Ericaceae which are dominant in the Western flora are practically absent from the Eastern region. On the other hand there are in the Cape flora no representatives of the Apocynaceae and Acanthaceae, of which considerable numbers are dispersed through the remainder of extra-tropical South Africa. These facts seem only explicable by the supposition that we have in the South Western region the remainder of an ancient flora formerly spread over a much wider area of South Africa and which has been driven Westward and Southward by an immigration of other forms from the North. A few Proteaceae such as *Faurea soligna* and some species of *Protea* remain in the central Plateau of South Africa as the hardy and scattered remnants of the more ancient flora persisting among the newer arrivals. The cause of this Westward migration of plants requires still to be elucidated and the former connection, if any, of this ancient Western Flora with that of Australia, with



Fig. 1.



Fig. 2.

Fig. 1. Tuft of *Elegia equisetacea* (Restionaceae) showing characteristic brown scales round the inflorescences. In the background one of the shrubby Compositae, probably *Helichrysum*.

Fig. 2. *Protea speciosa* in flower and seen standing out from the "bush" consisting of low "ericoid" shrubs.



which it has so many affinities remains as a fascinating subject for conjecture.<sup>1</sup>

A suggestive parallel to this migration of plants, but one of more recent occurrence, is offered by the immigration into South Africa of the vigorous Bantu races from the North. These, divided into many branches, have displaced and driven Southward the more ancient inhabitants of South Africa, the Bushmen and the Hottentots, who, physically weaker and with less capacity of organisation, are gradually becoming extinguished by the victorious immigrants. The still more recent advent of the European races to Cape Colony has brought a new peril to the ancient flora, as is clearly shown by very flourishing plantations of oaks and pines on the lower slopes of Table Mountain and along the edge of the Flats near Kenilworth. The pines particularly, mainly Stone Pines and Cluster Pines (*Pinus pinea* and *P. pinaster*), natives of the Mediterranean region, which possesses a climate very similar to that of the South West region, seem quite at home in the Cape Peninsula and seed freely there. As they have hardly any tree flora to compete against, their extension may have a very serious effect upon the bush vegetation, which they tend to displace. The introduction of Australian plants too, such as various species of *Eucalyptus*, *Grevillea* and *Hakea*, all well suited to the climatic conditions of Cape Colony, may cause many of the older connections of the Australian flora to be replaced by their newer and possibly more vigorous relatives. Nowhere indeed does the influence of man more seriously threaten to destroy the existing flora than in the comparatively treeless Peninsula of the Cape of Good Hope. It should be added that the prevalent custom of annually burning the vegetation on many of the mountain slopes is also helping to accelerate the extinction of many of the less hardy plants.

The above somewhat condensed account of the flora of the Cape Peninsula will be sufficient to show what an interesting field of study it presents to students of the Geographical distribution of plants, whether they incline to an ecological or a systematic study of the same. In addition to the literature mentioned in the notes, an interesting description of the vegetation of the Peninsula, given

<sup>1</sup> Sir Joseph Hooker in his classical essay "On the Flora of Australia" . . . . An Introductory Essay on the Flora of Tasmania, 1859, considers both floras to have had a common origin in a vast Antarctic Continent of which the greater part has been submerged. See also C. B. Clarke on the "Antarctic Origin of the Tribe Schoeneae." Proc. of the Roy. Soc. Vol. 70, 1902,

by Dr. Engler under the title of "Die Frühlingsflora des Tafelberges bei Kapstadt (Notizber. des Königl. botanischen Gartens zu Berlin, 1903).

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ECOLOGY IN ITS PHYSIOLOGICAL AND PHYTO-  
TOPOGRAPHICAL ASPECTS.—A REVIEW.<sup>1</sup>

BY F. F. BLACKMAN AND A. G. TANSLEY.

(Continued from page 203).

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FROM the foregoing examination of the scope and aims of Ecology we turn to consider its methods and procedure, more particularly those in the comprehensive scheme drawn up by Dr. Clements, by which the intentions of Ecology are to be realised.

The ecological investigator in the midst of vegetation finds himself in the presence of a state of equilibrium between the organized and the unorganized, between "The Habitat" of the one part and "The Formation" of the other part, the latter coterminous with and interpenetrating the former, and consisting of the congeries of ecads<sup>2</sup> and species characteristic of the given habitat. Such equilibrium may well stimulate analytical enquiry into its nature.

The Habitat can be analysed into physical factors such as water-content of soil, humidity of air, light, temperature, chemical composition of soil, wind, altitude, etc. The problem before the investigator here is to determine which are the essential factors affecting vegetation and to provide a satisfactory method for measuring each. Consideration of this branch of the enquiry occupies Chapter II. of Dr. Clements' book.

"The Formation" as an organic whole is dealt with in Chapter IV., while "The Plant" as the unit of the Formation occupies Chapter III. The Plant, like the Habitat, can also be analysed, and reveals innumerable structural details. Certain structural attributes of plants may be traced directly to the common attributes of protoplasm, others are cosmopolitan and not characteristic of any habitat, or due to inheritance, irrelevant to the habitat. A consi-

<sup>1</sup> "Research Methods in Ecology." By F. E. Clements, Ph.D., Associate Professor of Plant Physiology in the University of Nebraska. Pp. XVII. and 334. 85 Figures in the text. \$3. Lincoln, Nebraska, U.S.A.

<sup>2</sup> An "ecad is a habitat form due to origin by adaptation,"

derable group of structural characters, however, with limits not yet defined, has clearly a connection with the nature of the habitat, as has long been recognised from the comparison of hydrophytes, mesophytes and xerophytes.

The problems as regards the plant are, as with the habitat, selection and measurement, but the material is more intricate. When the right structural features have been determined upon (which in detail often presents difficulties), and rightly measured, the investigator is brought face to face with the fundamental problem of Ecology, namely, the nature and mechanism of the correlation between habitat and plant, between factors and structure.

#### CORRELATION OF FACTOR, FUNCTION AND STRUCTURE.

Dr. Clements regards this correlation as close, comparatively simple and of wide application, and it is this conviction which enables him with unwavering stoutness of heart to plan a complete scheme for measuring everything and correlating everything on lines which he hopes are final, though the essential nature of the correlation has yet to be expounded.

The connection between the factors of the habitat and the structure of the plant is, naturally, Function, and Dr. Clements takes the simplest view of the co-ordination of these three, and presents such a superficially complete scheme, that we are compelled to try and point out that this simplicity certainly does not correspond with the real complexity of the plant as a functional machine: the attainment of a complete exposition of these correlations will be practically the last word of philosophical botany.

Function, says Dr. Clements, is "but the middleman between habitat and plant," and in his anxiety to get everything systematically arranged and at once "anticipate the final merging of physiology and ecology," he is prepared to hypothecate a complete set of physiological relations of the simplest sort in order to pass, with as little resistance as possible, from the characters of the habitat to the structural characters of the plant. We may give an outline of his conceptions on this subject almost in his own words (pars 144—151).

1. "Whatever produces a change in the functions of a plant is a *stimulus*."

2. The immediate *response* to a stimulus is always functional (adjustment). The nature and intensity of the stimulus determine

whether this is followed by a corresponding change in structure (adaptation). Many responses are functional alone.

3. The amount of response is proportional to the stimulus for a given individual.

4. "Axiomatically there is ordinarily an essential correspondence between the amount of adaptation and that of adjustment."

Nothing could be simpler than this which is the conception for an individual plant. If different species are to be compared we find the following additional conception.

5. "Many species are extremely plastic and respond to slight stimuli, others are comparatively fixed and respond only to much greater stimuli. For different plants response is only equal when they are equally plastic. This correspondence between adjustment and adaptation is profoundly affected by the structural fixity of the plant."

We do not find ourselves in full sympathy with any of these fundamental principles. To Dr. Clements' conception of "*stimuli*" as implied in the first and third of them, we must take serious exception. *All* the factors of the habitat are throughout the book spoken of as stimuli, dry air stimulates transpiration, light stimulates the plastid in photosynthesis, and light-stimulus causes structural changes in the leaf (as in sun and shade leaves), etc.

All these changes in the plant are of the fundamental nature of work done, as evaporation of water or formation of carbohydrates or formation of structural parts. If this work is the direct outcome of energy flowing in from without, then we have a direct equation of energy and work as much as in the expansion of an iron bar by heat, and there is no justification for applying the special word stimulus to the inflowing energy. Thus it is in transpiration and in photosynthesis. When, as in growth-changes, the work done is the equivalent of potential energy of the reserves of the plant, the inflowing energy only sets the conversion going, and the special word stimulus should be reserved for this indirect causation.

Dr. Clements confounds analysis by grouping these two categories together as stimuli, and as all producing proportional responses. The first produce effects equal and *a fortiori* proportional to the causes, but are not stimuli; the second are really stimuli and produce effects which are not equivalent to the causes, but may happen to be proportional to them if the mechanism

through which the stimuli work to the response should be so constructed as to determine this. Whether this is so or not is a matter for precise investigation in any given case; even if proportionately hold in both, it is desirable to keep these two categories of causation apart.

We turn now to consider the second and fourth principles, which determine the relation of "adjustment" and "adaptation."

If external causes affecting function were truly stimuli, the term "adjustment" as suggesting something akin to adaptation would be suitable, but not otherwise.

We find no clear statement of the intended relation between adjustment and adaptation as parts of one chain of causation, and so we have tried to think out what our author understands by change of function being followed by a *corresponding* change of structure. Let us consider the effect of bringing a plant into increased dryness of air. Suppose the drier air increases the evaporation, *i.e.* transpiration, 10% per unit area, a change of structure *corresponding* to this would be such an enlarging of stomata or thinning of cuticle as would have effected a 10% increase in the previous conditions. If any adaptation followed, it would be an *antagonistic* change of structure to bring the total transpiration back to the original suitable amount, say by reducing the leaf area by 10% or by thickening the leaf, etc. So it is with roots in general as with the transpiring organs; an alteration of water-content of air or of soil produces antagonistic structural change, tending to neutralise the effect of the change. This tendency to keep to a definite amount of transpiration must in some cases be correlated to questions of quantity of growth, for the chief biological significance of transpiration is in providing mineral elements for further formation of new matter. The amount of growth a plant performs is partly an individual matter and partly a question of temperature, so that we traverse a complex nexus of causation, and we might well get the following state of things—that in regions of low temperature, keeping down the amount of growth, a plant would respond to drier air by structural change antagonistic to increased transpiration, while in a warmer region it might respond to drier air by greater development of root-system and so obtain more salts for the greater possibility of growth. Other such schemes of correlation could be suggested for future experiment. The *quantity* of growth characteristic of a given form is an important *qualitative* structural character, and one to which no attention seems to be paid in this work.

There is further another class of disturbing factors not taken account of in Dr. Clements' simple scheme of correlations, a class that may be called limiting factors. For instance the statement that photosynthesis in Nature is proportional to light intensity is only true up to a limit set by the amount of  $\text{CO}_2$  that can reach the plastids by diffusion. With greater intensities of light beyond that limit there can be no further increase of photosynthetic work and the light energy absorbed is deflected to some other work. It is of the first importance to note that the available  $\text{CO}_2$  becomes a limiting factor to assimilation within the middle range of normal illumination (at somewhere about  $\frac{1}{5}$  of full summer noon-tide illumination). This limitation is therefore daily at work and it results that the proportionality between "light stimulus" and "photosynthetic response" will be in practice sharply arrested at some arbitrary point depending on the structure of the leaf.

Then, again, as regards transpiration we have also a natural arbitrary limitation to the (inverse) proportionality which it fundamentally bears to the humidity of the air. As long as the stomatal openings remain of the same size there is a proportionality between dryness and stomatal transpiration. But at a certain dryness of surrounding air—individual to the plant—the stomata close and put an end to the proportionality of factor and response as an actual general working relation in the habitat.

Facility of conduction of water must too be sometimes a limiting factor in determining whether a drier habitat produces increased absorbing root system or decreased transpiring leaf system.

The fifth principle is a hypothesis to explain the fact that many bog plants are notoriously xerophytic in structure and that many sun plants transplanted to a much diminished light show no structural change. This conception of varying plasticity of species causes the reader some uneasiness in its present purely hypothetical form as it would be so easy to apply it in apparent explanation of all exceptions to the expected correspondence between factor and functional and structural response.

In fairness to Dr. Clements it must be stated that he does not regard all these principles as incontrovertible. He says at the end of them "the unimpeachable facts are relatively few in this domain and their present correlation slight. In the treatment which follows the *method of multiple working hypotheses* (our Italics) is uniformly employed. No apology is necessary since the whole endeavour is to indicate the proper point of attack."

This frankness cannot be allowed to disarm the critic because except in this paragraph the hypotheses are presented with very little qualification and because out of *multiple* hypotheses a clever botanist can hardly help creating a beautiful growth which looks like a plant but which experiment may prove to be a mirage.

Though Dr. Clements' simple hypothetical scheme of correlation between factor, function and structure will not stand analysis in its present form, yet a more adequate and complex form of it might perhaps be constructed by recognizing that some factors affecting functions are direct equations of energy while others are stimuli, by allowing for the abrupt discontinuance of a relation by limiting factors, and by recognizing that adaptation is often antagonistic to adjustment and almost to be regarded as an *alternative* to it.

On the broad issue we think the verdict must be that this department should be handed over to the laboratory physiologist for that intensive analytical study which Dr. Clements deplors before the synthetic treatment of these correlations which we all desire becomes possible.

#### FACTORS OF THE HABITAT.

From this consideration of the foundations of the correlation between habitat and plant we may pass to Dr. Clements' treatment of each of them separately.

Dr. Clements opens his chapter on "The Habitat" by defining it as the sum of *all* the factors in the environment. In the first class of importance he places three, to wit, water content of soil, humidity of the air, and light. These are the differentiating factors between habitats and on them the qualitative structural differences of ecads depend. As a factor, temperature is of great importance, naturally, but *differences* of temperature are regarded as only causing quantitative structural effect not qualitative differences and so are not further considered.

Dr. Clements' ideal is to obtain abundant measurements, or where possible, continuous records by automatic instruments as to all these and other factors, separately, so that the habitat may be definable in exact quantitative terms. It is expected that finally there will come out a correlation between the means or the sums of the intensities of these various factors (stimuli of Dr. Clements) during the vegetative period and the various functional activities and structural modifications of the plant.

We may briefly mention the methods proposed by Dr. Clements

for measuring separately, water content, humidity of air, and light and give some critical comments on each.

For measuring water-content no continuous recording method is satisfactory and the procedure is to take, at proper times, samples of soil with a borer and determine the water content directly. Dr. Clements lays great and proper emphasis on the fact that all the water in a soil is not available for the plant. Wilting and death by desiccation take place before all the water present is withdrawn by the roots from a drying soil. The whole water-content of a soil (holard) is divisible then into the physiological water (chresard) and the non-available residue (echarde). The chresard alone concerns the plant and as the echarde varies greatly in different types of soil from  $\frac{1}{2}\%$  in gravel to 12% in clay it follows that knowledge of the holard alone is insufficient. The echarde of a given habitat is experimentally ascertained by isolating a block of soil by impermeable plates, allowing it to dry slowly and determining its water-content at the time when the plants growing on it are wilting irrecoverably; a point of time which in practice it is, however, not easy to be certain about.

While the chresard of the soil affects the roots and absorption by them, the humidity of the air (Dr. Clements' second factor) directly affects transpiration. The more water-vapour there is in the air, the more of these molecules impinge upon the evaporating surfaces of the plant and are reabsorbed by them, so diminishing the net loss of water.

This factor is to be measured by direct observations with a "wet and dry bulb psychrometer," or by a recording hair-psyehrometer. Dr. Clements discredits the stationary instrument and recommends the use of the "sling" psychrometer or the "egg-psyehrometer," an ingenious portable instrument of his own invention, on the same principle, made out of two thermometers and an egg-whisk. In both these the thermometers are kept in rapid (it should also be standard) movement through the air. By this procedure a uniform rate of movement of air over the wet bulb is substituted for the variability of natural wind. Now the faster the wind, the quicker the water-vapour is swept away from the evaporating surface, and the fewer molecules pass back again, so that the water-loss is increased, even though the humidity of the distant air in general remains unchanged. In still air the evaporation is much diminished and the thermometer readings indicate a humidity number which is too high. From a meteorological point

of view the moving instrument is therefore more accurate, but it must be pointed out that the leaf itself is a *stationary* wet surface and evaporation from it varies with every change of wind velocity. If then one wishes for information about transpiration and not merely, as in meteorology, to know the actual relative humidity of the air away from the plant it would seem to be wiser to use the old fashioned stationary wet bulb thermometer. Errors due to variable wind would then be similar on both, instead of it being necessary to measure the rate of the wind and to attempt to allow for it

From this parallel between evaporation from a stationary surface and from a leaf, one is led to wonder whether direct measurements of the rate of evaporation from a wet surface (by an atmometer) would not be more luminous biologically. Even if Dr. Clements has considered this point and decided against it, we think it would have been helpful to have discussed it in his pages. There is, however, a regrettable scarcity of discussion on debatable points throughout many parts of the book.

The third important factor in modifying function and structure is light. In natural habitats this is a troublesome factor because in the form of solar radiation it is bound up with heat radiation (apart from air temperature) and generally with smaller relative humidity. The leaves in direct insolation may be heated up to even 10°C above the air temperature and this may well produce disturbing effects on leaf-function which have not yet been sufficiently allowed for.

The intensity of the light in the habitat is measured by a useful form of disc photometer containing "solio" silver paper. The intensity of darkening of this on exposure is compared with standard tints and thus the illumination (only taken about noon) is expressed in fractions, the cloudless noontide sunlight at the summer solstice, being taken as unity. Dr. Clements gives a way of calculating the position of the sun and so the intensity of sunlight at any hour of the year. In his table of intensities however he neglects to state whether the calculation is for the sun alone or for the "total light," *i.e.* the sun plus the diffuse light; and also whether it refers to the illumination of a surface always at right angles to the rays of the sun as it moves, or to a surface fixed approximately horizontal, as are most leaves. From inspection, the calculation seems to be intended for the former while the latter would appear the more directly biologically useful

We are surprised not to find during the consideration of light-intensity more definite recognition of the diffuse light of the sky as an entity, measured in intensity for each position of the sun when the sky is clear and much greater, though no longer calculable when the sky is hazy or filled with white cumuli. The total light from a sky full of white cumuli reflecting on to the earth may be several times as intense as that of the direct sun *alone*, as Weber has shown. So with the momentary combination of white clouds and the sun shining between, a total light of intensity exceeding Dr. Clements' unity may be easily arrived at, though he regards unity as the maximum possible.

Plants grow in habitats of various illumination from unity (at noon) to .002 in the deepest shade-habitats. Dr. Clements has tried to obtain an idea of the "effective difference" of light-intensity required to produce structural modification. He finds it to be very large, and that transferring a plant from a habitat of full insolation (unity) to habitat of 0.1 illumination may produce no modification. It is interesting to note in this connection that photosynthesis is not reduced by diminishing illumination till the limiting value due to the paucity of  $\text{CO}_2$  is reached. Dr. Clements correlates structural change of the leaf (to a shade-form) with intensity of photosynthesis and it may well be that if this is so,  $\text{CO}_2$  as a limiting factor is responsible for this apparent insensibility to change at high intensity of illumination: lower in the scale the leaf might be more sensitive. The Plant (Chapter III.) in its functional and structural aspects now claims our attention for a short discussion.

Even if the factors of the habitat cannot be quantitatively correlated with measured functional and structural response, which endeavour Dr. Clements holds to be the only justification for exactly determining them, it seems to us that considerable value attaches to such precise knowledge of habitat in relation to the general investigation of the correlated formation as a whole.

#### FUNCTION AND STRUCTURE OF THE PLANT.

The difficulties are here more subtle than with the habitat because the value of structure and the correct measurement of it depend upon a precise knowledge of its function, and as to details of this sort our knowledge is not well established. The leaf is the only organ which exhibits a wide range of obvious grades of structure in correlation with varying habitat. The extremes of this

series occur in bright dry habitats and in shady damp habitats respectively. In spite of much comparison of xerophyte sun leaves with hydrophyte shade leaves, it is not yet certain which structural features are a correlation with water-factors and which with light-factors.

Dr. Clements regards transpiration as a functional response to water-stimulus and variation in functional leaf-area as the chief structural adaptation to the same stimulus. The processes of adjustment and adaptation which are to be regarded as two aspects of the same response he styles "hydroharmose." Dr. Clements soundly recommends the study of transpiration in the actual habitat and by the best method, that of weighing plants potted in the natural soil, or in prepared soil with controlled amounts of water. When he comes to correlate transpiration with structure he would like to be able to measure the surface of all the mesophyll cells that abut on the air-spaces in the leaf as the real source of the vaporisation. Failing the possibility of this, he resigns himself to correlating the function to the area of the leaves, multiplied by a factor for the number of stomata. He hopes by introducing further factors for light, heat and humidity to get an exact mathematical expression for the amount of transpiration for any plant, and so make it possible "to compare species of different habitats on an exact basis."

In spite of the desire for great exactitude it seems to be overlooked that it is not purely the number of stomata which affects transpiration, but also the diameter of their pores, which is ignored. According to the measurements of Weiss there is a general tendency for crowded stomata to have small pores, and sparse ones to have large pores, and thus variations in number tend to be neutralised out. The closing of stomata in the drier grades of air, which has been already referred to, would appear in itself to be enough to throw out any calculation of transpiration based on external factors. The temperature of the transpiring leaf is the fundamental factor, since it provides the energy for the evaporation, and this also in ordinary field-work remains quite indeterminable, being, in direct insolation, much above the temperature of an adjacent thermometer.

As regards Adaptation to water stimulus, Dr. Clements admits that it is not yet possible "to connect each adaptation quantitatively with the corresponding adjustment," and so only sketches the well known varied ways of reducing transpiration.

Photoharmose, or the response of the plant, functionally and structurally, to "light-stimuli" is treated in the same way as Hydroharmose.

The light-factor has not the dual relation that holds for water, so one might expect that a closer treatment would be possible, but this is not so, for reasons that will emerge later. Sun leaves, in unit intensity, and shade leaves in intensity  $\cdot 002$ , show much difference in structure, but an undetermined part of this is correlated with transpiration.

As regards the "adjustment" of photosynthetic response to different light-intensity, Dr. Clements states that the "efficient difference" is very large with intense natural light: this we interpret as the operation of the  $\text{CO}_2$ -limiting factor. At very low intensities it is suggested, however, that the efficient difference again becomes large, a quite isolated conception.

Dr. Clements has some puzzling ideas as to the significance of leaf structure in photosynthesis. He says that "the fundamental response of the chloroplast to light-stimuli is the production of chlorophyll." All workers on the subject have held that light causes destruction of chlorophyll, which is replaced by metabolic change. Also, the absence of chloroplasts from the epidermis of sun leaves is attributed to the absence of  $\text{CO}_2$  in that tissue; but this could hardly apply to the lower epidermis near the stomata. Of the light energy absorbed by the chloroplast 2.5% is said to be used in photosynthesis: there can be no constant ratio like this, but all must depend upon the intensity of the light. The photosynthetic activity of a leaf, it is proposed to measure by the number of plastids in a column of constant width taken right through the leaf.

As an adaptation to light-stimuli, we find in sun leaves, thicker and smaller lamina, thicker cuticle, less air space and more developed palisade; but it is not proposed to measure these precisely. Nordhausen has recently shown that this leaf-structure is partly due to past history and so to be found already in the folded bud, and partly due to the effect of the conditions in which the leaf develops.

In conclusion of this section we may point out that the whole intensity of the light falling on a leaf is not available for photosynthesis, any more than the whole water-content of the soil is available for the roots. The maximum utilisable amount of light is

just that amount corresponding to the  $\text{CO}_2$  diffusing in from outside (which depends on the porosity of the leaf), plus the  $\text{CO}_2$  produced inside in respiration. These values can only be obtained by experiment and, till known, we cannot be said to know the light-factor of the habitat from the point of view of photosynthesis. If the intensity of the factor is not critically known how can structure (especially until its functional mechanism is fully understood) be correlated with it quantitatively? What seems to be next wanted is critical analytical experimental work combining laboratory methods with field conditions in order that the fundamental principles of these correlations in Nature may be worked out. Each plant of a given habitat may prove to be a different equation to the same final value, that of the habitat, and it may well be thought that the functional significance of the factors must be worked out before anything more can be got out of the formation from this point of view than will be revealed to acute observation without measurement.

#### METHODS OF VEGETATION ANALYSIS.

In his fourth chapter, "The Plant Formation," Dr. Clements passes to the methods of proximate analysis of the phenomena of vegetation, in other words to Phytotopography proper. At the outset he insists on the need of exact methods, and puts forward the "quadrat-chart" as the basis of investigation. A "quadrat" is simply a square area of convenient size marked off in a plant formation for the purpose of analysis, and the "quadrat-chart" is a record of the vegetation on the quadrat in the form of a map on which the position of each individual plant is recorded.

The quadrat-chart may be regarded as a fundamental instrument in the study of the formation, and, together with allied methods, furnishes the only means of obtaining detailed and accurate information of the minute structure of vegetation. Among the more immediate uses of such information are, the possibility it gives of exactly comparing the structure and composition of different parts of the same formation, and of similar formations in different localities, the means it furnishes of ascertaining exactly the amount of change in any given formation from year to year, and especially the possibility of accurately tracing the successive stages in the development of vegetation on new and denuded soils. Of its ultimate uses it need only be said that the quadrat-chart will form

an indispensable part of the data necessary for the correlation of vegetation with the physical factors of the environment when, and if, the mechanism of this correlation reaches a practicable stage.

It is obvious that a single quadrat presents a fair sample of a formation only when the formation is sensibly homogeneous. When this is not the case it is necessary to locate several quadrats in different typical samples.

The technique of quadrat charting cannot be entered into here,<sup>1</sup> but it should be mentioned that a photograph is also taken of each quadrat by placing the camera at a suitable distance on a line drawn at right angles from the middle point of the front boundary of the quadrat, and tilting it forward so as to get a perspective view of the quadrat of greater depth than could be obtained if the camera were horizontal. Such a photograph supplements in an important way the information obtainable from the chart, since it shews the height and habit of the individual plants. In certain cases where the vegetation is low and uniform a photograph of the quadrat taken from vertically above it, *i.e.*, a photographic chart, is valuable, but in most cases it is impracticable.

Just as the quadrat is used to record the structure of a homogeneous formation, so the "transect" records the succession in space of zonally arranged vegetation. The transect is simply a section of the vegetation drawn across the direction of zonation. It is charted by recording to scale on a straight line the individual plants touching a tape laid down in the desired direction (line transect), or by recording in the same way as on a quadrat chart, the plants occurring on a belt of uniform breadth, *i.e.*, between two parallel tapes (belt transect).

A further method is necessary to record the height of the different plants, of special importance in the case of layered formations. This is done by means of the layer-chart corresponding to the line-transect, but on which the height of each plant touching the tape is recorded by a proportional vertical line.

Any quadrat or transect on which it is desired to record changes in the vegetation can be made "permanent" by driving in labelled stakes at its corners and carefully locating the position so that it can be found again.

Quadrats and transects can be "denuded" by removing their

<sup>1</sup> It is proposed soon to publish in this journal a detailed account of the quadrat and allied methods of recording the structure of vegetation, on behalf of the Central Committee for the Survey and Study of British Vegetation.

vegetation, in order to study its regeneration. This method furnishes an important parallel to the study of the development of vegetation on new or naturally cleared soils, and the phases of migration and competition can be studied at will, and, if desired, under controlled conditions as well.

The "migration circle" is designed to record the migration of a species by dissemination or other propagation from an individual plant or group of plants as a centre. The centre is permanently fixed by driving a labelled stake, and the position of each plant is recorded on a chart corresponding with the circle, by means of radial tapes and corresponding lines on the chart. The denuded circle bears the same relation to the ordinary circle that the denuded quadrat does to the ordinary quadrat. The "denuded circle," it may be remarked, is necessary in studying migration in a formation in which closely crowded annuals predominate.

All the above methods are, in our opinion, of the greatest value in studying vegetation, and Dr. Clements is to be congratulated on working them out. It may be thought that they would naturally occur to anyone who had to face the problem of the minute structure and development of vegetation, but the fact remains that no one has hitherto worked them out, probably because no one but Dr. Clements has clearly and explicitly recognised the fact that vegetation has a specific structure and development which can be recorded and studied by exact methods. One of us has applied most of the methods in question to more than one type of formation since the publication of Dr. Clements' book, with the result of acquiring the conviction that the very close attention to the details of vegetation demanded leads to the recognition of features which would otherwise escape notice. The procedure may be compared to that of drawing a tissue-section under the microscope, which forces the attention to points of detail, often of great importance.

Dr. Clements' treatment of cartography (*i.e.*, the making of vegetation maps, a *map* being distinguished from a *chart*, in that the former records formations or regions of vegetation, while the latter records individual plants) is somewhat meagre, confessedly so, since as he says, "no attempt is made to describe the general cartographic methods used by other ecologists, notably Flahault." Our author is anxious that "cartographic methods should be clear and simple, and that they should be uniform, so that charts and maps of widely separated formations may be directly compared without difficulty." No doubt these are very desirable objects, but

Dr. Clements hardly seems to appreciate the great obstacles to their attainment, though he admits that "it is not to be expected that uniform methods will come into general use immediately."

In the matter of scale, for instance, Dr. Clements rightly insists on the desirability of a universal decimal scale, the different categories being employed according to the size of the area mapped. The advantage of such a system is obvious, but the practical difficulties are immense. In countries, such as our own, where decimal units of measurement are not employed in topographical map-making, it is practically out of the question to prepare vegetation maps on a decimal scale, simply because the existing topographical maps have to be used as a basis.

Then again, with regard to colour, Dr. Clements gives a universal colour scheme based on the colour standard of Saccardo's Chromotaxia, and apparently intended to include all possible formations and their varieties. Such a scheme might be successfully applied to small scale maps of the vegetation of considerable portions of the earth's surface, such as a country as a whole, or in some cases to smaller areas. But in many instances in which it is desirable to have coloured vegetation maps, *e.g.*, on scales between 1:10,000 and 1:1,000, the number of "associations" or "consocieties" (to use our author's term) which it may be desired to show would make it impossible to use easily distinguishable tints, keeping within the limits of the prescribed formation colour. Undesirable and bewildering as the present confusion of colours undoubtedly is, there seems no escape from it till more experience has taught us exactly the types of vegetation unit which we want to map in colours—at least that is the present conclusion of phytocartographers in this country. When that experience has been acquired it may be possible to arrive at a general agreement with regard to the colouring of maps within certain limits of scale, but it may fairly be doubted if enough easily distinguishable tints exist to make possible the application of a universal scheme to all coloured vegetation maps. If they do, so much the better.

It is to be hoped that enough data to furnish the basis of an agreement may be available by 1910, the date of the next International Botanical Congress. This is certainly a question only to be settled by international agreement, and it seems premature to put forward a scheme with any hope of general acceptance. Meanwhile systems of symbols which can be reproduced in black and white may be employed, especially for the larger scale maps of small

areas, so as to relieve the pressure on the colour tints. The whole subject has not yet passed beyond the experimental stage, and what we require is suggestion and trial in various fields rather than a universal scheme.

The description of the making of medium-scale formation maps by means of the plane table and camera, using a commanding elevation as a base of observation, is of great interest to workers in hilly districts; and the determination of the general outlines of regions, provinces and vegetational zones, by recording the range of typical dominant genera on provincial and continental maps, is also of importance, particularly to continental ecologists.

Several pages are given to the technique of photography from the stand-point of the ecologist, all the necessary operations being treated of consecutively. We have no space to criticise this treatment in detail, but it may be said that many useful hints are given, and while it is quite possible to obtain good vegetation photographs in other ways, the beginner will do very well to follow Dr. Clements' instructions till he has acquired enough experience to put him in a position to vary his practice with advantage should he so desire.

The section on Formation and Succession Herbaria is, we think, admirable. As "basal material for developing the subject of comparative phytogeography" their importance is fundamental, and for educational purposes they are of unique value. Comparative ecological phytogeography based on such herbaria is, in our opinion, of far more value as a mental discipline than taxonomy based on ordinary floristic herbaria.

#### DEVELOPMENT AND STRUCTURE OF THE FORMATION.

Having in the sections just reviewed dealt with the methods of investigation and record of the formation, Dr. Clements now passes on to consider the facts of its Development and Structure. His view of vegetation as an organism is as legitimate as the familiar idea of a human society from the same point of view. Both conceptions are useful and desirable so long as it is remembered that they are essentially analogical, that these quasi-organisms do not possess many of the essential features of real organisms. The incomplete correspondence of organisms and quasi-organisms is illustrated by the statement that "the functions of a formation are association, invasion and succession"; since none of these occur as functions or normal activities in a stable or adult vegetation, it would be truer to regard by them as processes or activities of the

development of the quasi-organism. Dr. Clements' discussion of this part of the subject is characterised by close and apparently exhaustive logical analysis, most of which is original and much of great value as laying down fundamental principles in a subject that has suffered in the past from lack of this kind of treatment.

It is impossible in the space at our disposal to criticise this closely knit exposition in detail. While, as we have said, much of it is of great excellence, it is not wholly free from doubtful statements, nor, in parts, from a tendency to over-elaboration. As an instance of the former we may take the following sentence (p. 208), "Accepting the easily demonstrable fact that an excess of salts in the soil water, as well as cold, tends greatly to diminish the available water of the soil, *i.e.*, the chresard, it is at once seen why saline and arctic plants are as truly xerophytic as those that grow on rocks or in desert sands." This statement assumes the validity of a simple explanation of a phenomenon which is by no means thoroughly understood. The hypotheses that have been put forward by Schimper and others have, so far as we know, not been experimentally tested, and it seems almost certain that the conditions involved are not susceptible of explanation by a simple conception such as that of Dr. Clements.

The concepts of *migration*, *ecesis* (the becoming established of migrants), *reaction* (of the habitat on the invaders) and *competition*, as successive processes in the phenomena of *invasion* and *succession*, which are fundamental in the development of vegetation, are valuable as furnishing an analysis of this important and rather neglected field, but the treatment in some cases appears to amount to little more than a somewhat lengthy enumeration of special cases.

The treatment of Barriers, of Endemism, and of Polyphyletic and Polygenetic is good and helpful. The distinction drawn between the two last is clear and logical, while the strong probability of the occurrence of both in nature is clearly shown. It is plain that if in polyphyletic the convergence is sufficiently great it is impossible to deny "naturalness" to the resulting aggregate, whether species or genus. This whole subject is however complicated by our ignorance of the origin and nature of hereditarily constant species, whether adaptive or not, for of some of the examples cited by Dr. Clements it might be asserted that, though commonly known as species, they are not really so, but only ceeds with marked structural differences. Convergence in such a case would not be real polyphyletic.

The general treatment of "Invasion" and the long section devoted to "Succession" are most excellent and interesting; the latter, with its descriptions of numerous examples, evidently gains greatly from the author's studies on the Colorado mountain vegetation, to which we have already alluded. The talus or "gravel slide" succession in which a final *Picea-Pseudotsuga* forest arises as the last term of a series of seven stages of development, is a particularly extensive and complete example of fully studied vegetation development.

Under "The Structure of the Formation" Dr. Clements first considers the principles of zonation and alternation, to which all the structures actually found are due. The concept of zonation is the oldest in phytogeography, vegetation-zones having been recognised by Tournefort in 1717, but apparently no general analysis has hitherto been attempted. "Zonation", says our author, "is the practically universal response of plants to the quantitative distribution of physical factors in nature." It would perhaps be more accurate to say that it is the response to regular spatial quantitative change of the physical factors, wherever such change occurs; and the extremely widespread and constantly recurrent existence of this type of distribution is the cause of the almost universal occurrence of zonation. The detailed treatment of this subject is again excellent.

The other general principle governing formational structure and distribution is that of "alternation", which was first stated by Dr. Clements in his "Development and Structure of Vegetation" (1904). It is "that phenomenon of vegetation in which a formation recurs at different places in a region, or a species at separate points in a formation." "Alternation is the response of vegetation to heterogeneity of the earth's surface." It is in such cases the expression of the breaking up of the earth's surface into different types of habitat and obtains everywhere within the major zones of the globe in areas of different rank down to the "patches" found in the smaller units of vegetation while heterogeneity of habitat is one great cause of alternation, there is another cause which Dr. Clements seems to neglect in his general discussion though he recognises it in his treatment of the sub-divisions of the formation (p. 295). That is the historical cause, the occurrence of a species or group of species in one part of a given uniform habitat, and not in another, through historical accident, simply because certain plants arrived at a certain spot first and other plants at another,

physically identical, adjacent spot. Though in this kind of phenomenon may often be an incident in the development of a succession, it certainly occurs within stable formations, and appears to be a primary cause of alternation which should we think be divided into two categories accordingly,

In dealing with competition, which has an important influence on alternation, Dr. Clements insists that plants do not actively compete, in the sense for instance of pushing one another out of any given area, but that "one individual can affect another only in as much as it changes the physical factors that influence the latter." That is of course perfectly true, but we do not recognise the existence of any "impression", at least among botanists, that competition can ever mean more than this. As a fact this is precisely the way competition works in civilised human societies. There is no physical struggle, but there is a using up of the means of subsistence that would otherwise be available for the weaker members. This appears to us to be the sense in which the word competition is ordinarily used.

Dr. Clements' treatment of "The Formation in Detail" is of great interest and importance. He rightly defines the formation as in strict relation with the habitat. "As effect and cause, it is inevitable that the unit of the vegetative covering, the formation, should correspond to the unit of the earth's surface, the habitat." But he seems to underrate the difficulty of applying "the final test" *i.e.* "an efficient difference in one or more of the direct factors," while he overrates the arbitrariness of the concept of species in taxonomy. If you get a gradual and continuous change of one or more factors in passing away from a given spot characterised by a definite assemblage of plant-forms you may pass through a region which shows a continuous change in vegetation structure and composition till you arrive at quite another definite assemblage. At what point is "the final test" to be applied? The difficulty here seems to be fairly comparable with the difficulty of delimiting species in taxonomy. Critical study will in very many cases enable us satisfactorily to delimit formations which at first present bewildering difficulties. The same is true of species. There may be cases in which the difficulties are so great that there is still room, after the best investigation we can give, for difference of opinion as to whether the assemblages in dispute shall be "split" or "lumped"; which means that the subjective element cannot at present be entirely eliminated. The same is true of species,

Meanwhile we are convinced that both species and formations have a real objective existence, though widespread doubt exists in both cases, especially among those who have not given attention to their actual study. The real differentiating factors in the two cases are probably of entirely different nature and in both cases we are far from having explored them to the bottom. Nevertheless we have full confidence that finality in these provinces will be reached in the course of future work. The work of Jordan, of De Vries, and of the Mendelians seems to furnish a beginning in the one province, while Dr. Clements' researches constitute an important advance in the other. Meanwhile it is difficult to resist the conviction that the differences to which the skilled systematist and the skilled phyto-geographer attach importance are the external expression of real breaks in the grouping of causal factors. That there is an enormous amount of careless and quite valueless species-making and formation-making is unfortunately true, but that we are on the paths of progress towards attainable goals seems to us certain.

If these conclusions be valid, it follows that both species and formations have an objective existence, while all higher classificatory units are of the nature of abstract groupings. The lower units into which the species and formation may be divided, on the other hand, are concrete, and have to be investigated.

The primary divisions of a formation, which are usually known as *associations*, Dr. Clements prefers to call *consocieties*. We doubt if his objection to the employment of the word "association" in this sense, based on an anticipated confusion between its abstract and concrete uses, is serious, and we prefer the older term. Dr. Clements attributes the development of "consocieties" to "alternation" and from his discussion of the latter, to which we have already referred, it would appear that "consocieties" in his view are due to differences of habitat. But from his discussion of the formation it would seem that difference of habitat gives rise to different formations and to zonation within the formation, but presumably not to "consocieties," which would have to be referred to we have called "historical accident." "There is an inherent tendency to the segregation of facies, arising out of physical or historical reasons, or from a combination of both. . . . The primary areas which thus arise have been called associations," *i.e.*, "consocieties." Does this mean that "consocieties" may or may not be due to efficient difference of habitat? This is a point of capital importance, and the analysis is by no means clear.

Of the lesser sub-divisions of a formation, we are not familiar, in nature, with the *society* and the *community* as distinct from the association (consocieties), but we refrain from expressing any opinion without further study in the field. The *family* is clearly a natural unit; it is the group composed of parent and obviously derived offspring.

The sections on investigation, classification and relationship of formations are extremely good, and so is the final one on "experimental vegetation."

On the whole the fourth chapter, which we have reviewed at considerable length, contains, in our opinion, by far the most important contribution to the science of vegetation that has been made for many years. Though the points to which exception is taken naturally bulk largely in a critical review, they are few indeed compared with the whole extent of the chapter. This thorough careful and logical exposition of a difficult and little understood subject is worthy of all praise and is so largely original as to lay all ecologists under a heavy debt of obligation to Dr. Clements.

#### NOMENCLATURE.

The question of nomenclature we have left till the last. In 1902 Dr. Clements published in Engler's *Jahrbucher* a "System of Nomenclature for Phytogeography," which consisted of a number of formal rules (including a law of priority) and a formidable series of formation-names derived from Greek with a uniform termination, etc. This system had the disadvantage of being published accompanied by a rather hostile note from Professor Engler, objecting to a law of priority, to the abolition of vernacular names, and deprecating too great "Schematismus" on the ground that it would frighten people away from the subject. In the present work Dr. Clements carries his scheme yet further and embodies it in a glossary at the end of the volume. It is impossible to give any account of the system within reasonable limits of space, but we cannot help feeling that it does carry "Schematism" to altogether impracticable lengths. We quite admit that the average human mind never gives a logical and consistent scheme of this kind a really fair consideration. It is altogether averse from having a new language suddenly created and thrust upon it, however suitable the language may be. For this very reason Dr. Clements' effort is hopeless, precisely because it runs directly counter to an almost universal and overwhelming prejudice. At the same time we cannot think that a scheme of the kind is so necessary to avoid confusion as he

imagines. Some correlation and uniformity is certainly needed, and we hope it may be attainable by the Committee which will report at Brussels, but the aim should be the minimum of necessary new terms, and we can see no good reason why vernacular formation-names should be abolished in favour of Greek, provided they are properly sub-ordinated in a logical classification.

Many of the terms employed in the earlier part of the present work are admirable and will no doubt come into general use. *Holard, chresard, echard, ecad* and some others may be taken as examples, but the advantages of substituting *xerad* for the perfectly established *xerophyte*, etc., in the interests of formal uniformity are not obvious.

Looking back on the subject of this somewhat lengthy review, we perceive clearly that it possesses the defects of its qualities. A comprehensive logical view of the proper ultimate objects of the worker in the enormous field with which it deals, reinforced by a resolute and dauntless determination to get to the bottom of its infinitude of complex problems is its outstanding and commanding merit. That this admirable resolution is likely to meet with success along the exact lines laid down by the author in his second and third chapters we have seen rather grave reason to doubt. Premature anxiety to correlate habitat and formation as quickly and simply as possible involves serious entanglement in crude and misleading conceptions of the relation of plant and environment. The first analysis of the complex forms and activities of vegetation itself is a much more practicable task and meets with striking and often brilliant success. It seems we must not be in too great a hurry with our attempt to formulate the plant universe, but in some places be content to walk slowly and warily. For the present the first analysis of vegetation must go on its own way to some extent divorced from the investigation of fundamental causes, though we should never neglect a real opportunity of bringing the one into relation with the other.

In the meantime we can be truly grateful to Dr. Clements, not only for his great and lasting positive contributions to our subject, but also for his bold and serious presentment of the ideal.

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THE CENTRAL COMMITTEE FOR THE SURVEY AND  
STUDY OF BRITISH VEGETATION.

A BRIEF account of the work of this organisation during 1905 may serve to mark the progress in this country of that side of Botany indicated in its title.

The second meeting was held at 3, Taviton Street, London, on March 17th; the third meeting at Liverpool on November 18th and 19th was held partly at the Exchange Hotel and partly in the Hartley Botanical Laboratories of the University. Every one of the ten members has attended one or both of these meetings, in spite of a distribution so wide as Portsmouth, Dublin and Dundee. The programme for each meeting was drawn up after consulting each member, hence the *Agenda* may be regarded as fairly representative of topics and difficulties frequently arising in the development of the subject, and therefore of some general interest to botanists. The reasons for the formation of this Committee have already been stated in these pages (Jan. 1905), and a year's experience has demonstrated the need of organising, so as to ensure that future work may be progressive and still correlated. The principle topics of discussion and decisions are grouped for convenience.

*Scale of Maps.* The relative merits of the different scales of ordnance survey maps have already been compared,<sup>1</sup> the "six-inch" maps being recommended in most cases for field-records. As regards published maps, it was resolved "that it is not desirable to limit maps in published papers to any definite scale, but that a scale should be used proportionate to the features which the map is intended to show." This resolution was necessary, because some of the maps have been published on the half-inch, while others appear on the one-inch scale. In the latter the vegetation has been analysed into smaller elements, and publication on the lesser scale would have insufficiently displayed the observations made. The Committee does not at present favour the fixing of any definite scale, since this would destroy the elasticity necessary in the present experimental phase of botanical survey.

*Nomenclature of Units.* A series of resolutions relating to the use of the terms Formation, Association, Zone, and Region are summarised in Pamphlet I. These, however, are provisional and subject to the conclusions of the International Committee appointed to standardise the nomenclature of plant geography. This body met during the International Congress of Botanists at Vienna this year. A member of the Committee (Mr. T. W. Woodhead) was present, and submitted a report to the Liverpool meeting. It appears that the needs of the nomenclature for systematic botany fully occupied the time available, and that no definite decisions were arrived at. The Committee for Plant Geography was re-appointed to continue its work till the next meeting of the International Congress in 1910. The name of the Secretary of this (the British) Committee was added to the International Committee, so

<sup>1</sup> "Suggestions for Beginning Survey Work on Vegetation." *NEW PHYTOLOGIST*, April, 1905; this (re-printed as Pamphlet I.) may be obtained from the Secretary (W. G. SMITH, University of Leeds) or from the Editor of the *NEW PHYTOLOGIST* post free 3d.

that the British Committee will be able, as a body, to participate in the solution of a difficult question.

*Colours and Symbols to be Used on Maps.* It was agreed that distinctive colours should be allotted to "formations"; in the case of smaller units no restriction was passed, since the representation of these must depend to a great extent on the scale of the maps and the object of the author. The use of black and white symbols, to be used instead of colours, is under consideration, with the object of preparing a scheme which will be distinctive, yet sufficiently plastic, to allow for future work. The whole question of standardising colours and symbols is, however, postponed till the primary botanical surveys have been extended over wider areas. The Committee propose to obtain advice from geographers and map-printers before finally fixing on any scheme. At Liverpool a movement was initiated, which it is hoped will secure more uniformity in the colouring of maps, and better results generally than have hitherto been obtainable.

*Recording of Frequency of Species.* The importance of making the field-records as accurate as possible is recommended. A resolution was passed at the London meeting which, without restricting any methods in use, recommended the percentage system given in Pamphlet I. At Liverpool, the "quadrat method" (see F. E. Clements' "Research Methods in Ecology," 1905) was also approved for shewing vegetation in greater detail by means of charts of small areas. Mr. Tansley was asked to prepare an account of this and allied methods for the *NEW PHYTOLOGIST*, and as a re-print for the Committee (Pamphlet II.)

*Photographs.* The formation of a collection of photographs, sketches, etc., illustrating features of ecological interest was resolved upon at the first meeting in Leeds. This originated a suggestion from the Botanical Photographs Committee of the British Association, which will increase the value of the collection. It is proposed that photographs of ecological value collected by both Committees be formed into one collection housed at University College, London, and arranged in a manner likely to ensure easy reference. A duplicate collection will also be formed, which may be lent out for short periods under certain conditions. It is in this way intended to facilitate comparison of the vegetation of areas widely apart in Britain. Many of the photographs may also be purchased from the owners in the form of prints or lantern slides.

The meetings have also been utilised for the suggestion of new lines of work. The recording of the succession of vegetation on small areas or over large districts, has been emphasised several times. It has also been proposed to utilise the existing detailed maps of vegetation in making synthetic or general maps comparable with those published by several foreign botanists. The importance of careful investigations on the influence of edaphic conditions on the distribution of plants is already being demonstrated by the work of Professor Oliver and Mr. Tansley on plants of the salt-marsh, and by Mr. Woodhead's woodland investigations. An important step towards the study and survey of pond-life, to include plants other than flowering plants, was proposed by Dr. Fritsch in Pamphlet I. (see also N. Walker, *Naturalist*, October, 1905).

The members present at Liverpool will probably long remember the excellent series of communications on recent work. During the vacations of the year, every member has been actively engaged in out-door observations, and there was a natural curiosity to hear the latest results and to compare notes. The short reviews of recent work given by members were followed with keen interest. Messrs. Lloyd Praeger and Pethybridge (Dublin) exhibited their new map and gave a summary of their work during the past few years in the district South of Dublin (Proc. Roy. Irish Academy XXV., Dec. 1905). The map had arrived from the printer just in time for this meeting, and was examined with great interest as the first detailed map dealing with Irish vegetation, as well as the first printed by the Ordnance Survey Department. The results have a further interest in that the authors frankly stated that they set out in a sceptical attitude as to the existence of plant associations. The new map has the additional value that the vegetation surveys, hitherto almost limited to the drier Eastern side of the British Isles, have now been carried into the moister Western regions. The new moorland types of vegetation designated *Scirpus*-moor and *Racomitrium*-moor respectively, are indications of the influence of conditions not found on the Eastern coasts; Mr. Lewis was able to confirm the wide occurrence of these in Western Scotland and the similarity between his photographs and the Irish ones was very striking. This is not the place to review this paper, but the discussion which followed the summary at Liverpool shewed clearly how heartily the members welcomed the latest work of observers whose names are already well known in connection with Irish botany. A forecast of the next district to be dealt with was contained in Dr. Pethybridge's description and field-maps of the maritime associations of the coast north of the Liffey estuary. This has many features in common with those observed by other members on the coasts of the English Channel and the Eastern coasts of Scotland and England.

Mr. F. J. Lewis (Liverpool) gave a summary, with illustrations, of his recent work on the Peat Mosses of South-west Scotland (Roy. Soc. Edinburgh, Sept. 1905). To this he added his more recent observations on the Peat of North-west Scotland. The main features, which are strikingly uniform over the South-west area, are the occurrence of a lower-bed of Birch remains, a middle stratum with arctic Willows, etc., and an upper forest bed of Scots' Pine or Birch. In North-west Scotland the lower Birch bed is frequently absent, and the upper forest beds are sometimes doubled. Between these layers of a drier forest or heath vegetation, there are thick strata of remains which indicate wet bog conditions. This system of continuous investigations on peat bogs has already greatly advanced our knowledge of the composition of peat, and of the succession of vegetation on moors, while the bearing of the work on glacial theories is evident.

Mr. C. E. Moss (Manchester) compared the vegetation of Somerset and Derby, two areas which he is now surveying. The Mountain Limestone of the Mendips and the Pennines presents a sequence of plant formations from the Ash woods of the valleys upwards through Hawthorn scrub and limestone grass pasture on the slopes, to a pasture with heath plants on the plateaux. The abundance of Ash with an almost complete absence of Oak on the

limestone has been confirmed after careful investigation. The existence of Heather on limestone referred to in the earlier survey of the Pennines, is further established in Mr. Moss's areas, considerable tracts occurring on the plateaux both in Derby and Somerset. Mr. Rankin (Portsmouth), in a communication, reported Heather on limestone on the borders of Yorkshire and Westmoreland, and submitted photographs showing *Calluna* and *Sesleria caerulea* growing together on a limestone heath.

Mr. A. G. Tansley, dealing with features of heath-associations of the Lower Greensand, introduced some methods of recording which have not yet been utilised in the moorland surveys. The reconstitution of a heath vegetation on places cleared by man was shown by an interesting series of quadrat charts. The intrusion of Gorse and Grasses into a *Calluna-Erica-Pteris* vegetation was also traced. A general discussion of the probable origin and relationships of the different types of Lower Greensand vegetation was also given.

Professor F. W. Oliver gave an example of his ecological studies on a salt-marsh in Brittany. The well-defined limits of certain plant associations has led to a careful periodic examination of the growth of annual species. It has been found that although seedlings come up almost uniformly amongst the open vegetation, a process of sorting-out ensues, seedlings dying off under certain conditions of soil-moisture and salinity, while they flourish under other conditions.

These communications will give some idea of the scope of the work of the Committee. It will, we believe, be admitted that they mark an advance towards the elucidation of problems of which even the simplest are not easy to solve. The effect of organisation is to stimulate and to suggest wider outlooks, while at the same time it prevents overlapping of effort and secures that no part of the field of ecology is neglected. The number of members on the Committee is small, but these represent several spheres of work, and are distributed over the whole of Britain. The limited size of this body of workers has many advantages since each one has a direct influence on the work in hand. It is at present a question for the Committee, how far it might be extended into a wider organisation without lessening efficiency.

W.G.S.

#### OCCASIONAL NOTES.

A VERY pleasant function took place in the Physiological Laboratory of the new Botany School at Cambridge on Saturday, October 28th, when a fine portrait of Mr. Francis Darwin, painted by Mr. Rothenstein, was presented to the Botanical Department of the University by Mr. Darwin's old pupils. At the same time a beautifully bound collection of the autographs of the donors was given to Mr. Darwin.

The occasion of the painting of the picture was Mr. Darwin's retirement from the Readership in Botany last year. It occurred to some of his old pupils that the event could not be allowed to pass without some expression of the admiration and affection universally felt for their old teacher. It was decided that the most appropriate form this feeling could take would be to ask Mr. Darwin to sit for a portrait-drawing to be presented to the University Laboratory. Mr. Rothenstein, who undertook the commission, preferred to paint an oil portrait and generously offered

to substitute it for the proposed drawing. The result was most satisfactory to all concerned, the oil being a beautiful picture and a dignified presentment of its subject.

There was a large gathering of Mr. Darwin's old pupils on the occasion of the presentation, about sixty people being present. Mr. F. F. Blackman explained the circumstances leading up to the gift. Mr. Seward presented the portrait and Professor Marshall Ward accepted it on behalf of the Department. Professor J. Reynolds Green, as Mr. Darwin's oldest pupil, then presented the book of autographs, and Mr. Darwin replied. Finally Professor Oliver thanked the Cambridge botanists and particularly Mr. Blackman, who had organised the proceedings.

The impossibility of adequately expressing, at any rate in the English language, what was in the minds and hearts of everyone present, was very keenly felt. Reference was made by nearly every speaker to Mr. Darwin's decision to return to Cambridge after his brief period of residence in London, a decision as much regretted by his London colleagues as it is welcomed by those of Cambridge.

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Some of the most useful catalogues of botanical literature published are those of Messrs. Wm. Wesley & Son, 28, Essex Street, Strand. The last of these is mainly devoted to Plant Geography. There are 1,244 titles under this head, which includes floras, and monographs of genera, etc., devoted to particular countries or regions. The titles are arranged under geographical headings—General, Great Britain and Ireland, Continental Europe, Asia, Africa, America, and Australia. We would suggest that in the case of a useful and comprehensive catalogue of this kind, an effort should be made at more completeness in the case of the most important works, *e.g.*, Drude's "Handbuch der Pflanzengeographie" and "Atlas" should appear under "General," and the papers of Robert and W. G. Smith, etc., under "Great Britain and Ireland"; also Engler and Drude's series of "Vegetation der Erde" should be included. The price of the catalogue is 6d.

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We have received a prospectus of a new Journal, the "Bio-Chemical Journal," the first number of which is to be issued in January. "Contributions are invited, dealing with all portions of the subject of Bio-Chemistry in its widest sense, both Botanical and Zoological." The Journal will be issued monthly, so far as material is available, and each volume will consist of about 480 pages. The subscription will be 15/- a volume. The Journal has been financially guaranteed for a number of years. The Editors are Messrs. B. Moore and E. Whitley, Bio-Chemical Department, University of Liverpool.

In view of the enormous increase of work dealing with this fundamental subject, the cheapness of the proposed Journal, and the excellent auspices under which it is issued, there should be a cordial and widespread response to the request for support. We may hope that some of the excellent work being carried on in this country on plant Bio-Chemistry, small though it is in amount compared with that done on the animal side, will be represented in the pages of the new Journal. A half-yearly article on the progress of Bio-Chemistry would probably add greatly to the attractiveness of the new Journal in the eyes of many prospective subscribers.







