The Transformations of the Plant World in Geological Time.¹

By Dr. D. H. SCOTT, F.R.S.

THE record of plant life in geological time is especially interesting from the fact that it shows a definite succession of phases of vegetation, each with a distinctive character of its own. So distinct are these successive floras that a high authority has even doubted whether the evolution of land plants was necessarily continuous. While the theory of descent remains undisputed among biologists, it has been suggested that there may have been, at certain periods, recurrent invasions of the land from the sea, thus giving the terrestrial flora a fresh start. Whatever we may think of this bold hypothesis, it at least serves to show that the diversity of the successive phases of plant life is more marked than their continuity. At present, however, we are concerned with the story, rather than the theory, of the succession of floras through the ages.

The word "transformation" is used for the change from one type of flora to the next. Four such great transformations are known.

1. From marine to land flora. The time of this profound change is unknown: it may have occurred about the Upper Silurian period, but some botanists would put it much earlier.

2. From the early land flora to the typical Palæozoic vegetation. Time, about the Middle Devonian.

3. From the Palæozoic to the Mesozoic type of flora. Time, Permian to Trias. This was the transformation which suggested to Prof. Seward his idea of discontinuity, referred to above.

4. From the typical Mesozoic to the modern type of flora. Time, Cretaceous. This transformation was the most important from our own point of view, as it ushered in the reign of the true flowering plants.

All these transformations, as we observe them, are apparent, not real; they mark the obvious changes in the flora, when the new groups became dominant. The actual origin of the new types must always have lain much further back than the date of the conspicuous transformation.

Of the hypothetical "Plankton" stage, when the ocean swarmed with unicellular creatures, as yet neither plants nor animals, we can have no geological evidence. The succeeding "Benthic" phase (to use Dr. Church's term), the age of the rooted *Algæ*, is well represented from the Cambrian onwards. Calcareous seaweeds naturally lend themselves best to preservation. Highly organised seaweeds, allied to our living Corallines, are present in the Cambrian. Calcareous *Algæ* of another class (*Siphonæ*) are found at least so far back as the Ordovician. The history of their evolution, all through the succession of strata, has been traced by Dr. Julius von Pia of Vienna, while the importance of calcareous seaweeds as rock-building organisms has been demonstrated by Prof. Garwood. A huge *Alga* (non-calcareous) known as *Nematophycus*, goes back to the Silurian. In the Lower Devonian of Canada, specimens three feet thick were described by Sir William Dawson. There is reason to believe that *Nematophycus* could live on land, but its structure is that

of a complex *Alga*. The Cambrian and Ordovician records are sufficient to show that in the ages previous to the first transformation (the invasion of the land) plant life in the sea had already attained a high grade of development.

THE FIRST TRANSFORMATION.—We have no satisfactory evidence of a land flora before the Upper Silurian,² and even then the records are scanty and scarcely free from doubt. *Psilophyton*, characterised by its leafless, spinous, forked stems and long, terminal spore-sacs, has been doubtfully recorded from the Wenlock beds of the Silurian, and is well known from the Lower Devonian. Among other Lower Devonian plants we have *Arthrostigma* (like a magnified *Psilophyton*), the moss-like capsule called *Sporogonites*, and naked forked stems or fronds (*Hostimella*). All are very simple, practically leafless plants, but there is little to show how the transition from marine life was effected.

Our best knowledge of the early land flora is derived from the Middle Devonian, but we must be on our guard here, for recent work in Germany has shown that vegetation was already far advanced at that period. In fact the Middle Devonian flora presents a mixture of apparently primitive forms and quite complex types of plants. Among the famous plants of Rhynie, Rhynia and Hornea are no more elaborate in external form than quite ordinary seaweeds, though fully equipped with a vascular system and stomata for life on land. Kidston and Lang's new genus, *Hicklingia*, may perhaps be somewhat nearer the *Algæ* than Rhynia. The more advanced *Asteroxylon*, with a leafy stem, is of the same age. Dr. Kräusel finds that, in a German species, no less than three form-genera, *Hostimella*, *Psilophyton*, and *Thursophyton*, occur as parts of the *Asteroxylon* plant. This quite agrees with the conclusions of Kidston and Lang.

Asteroxylon has some primitive features, and is, of course, to be reckoned as a member of the Early Devonian flora. It is the more remarkable, that on the same slab with *Asteroxylon* Dr. Kräusel found a specimen of *Cladoxylon*, a plant of singularly complex structure, hitherto only known from the Lower Carboniferous or possibly the highest beds of the Upper Devonian. Other highly organised plants were obtained from the Middle Devonian, and it is evident that in this formation earlier and later floras overlapped.

One of Kräusel and Weyland's Middle Devonian plants, *Aneurophyton*, resembles the contemporary American plant *Eospermatopteris*, the chief constituent of the fossil forest of Gilboa in the State of New York. Both appear to have had the stature and habit of Tree-ferns, but *Eospermatopteris* is described as bearing seeds, and is thus regarded as the earliest of the "Seed-ferns," which played so important a part in the Carboniferous flora.

In anatomical structure *Aneurophyton* recalls the famous "cone-bearing tree" of Hugh Miller, described by him some eighty years ago, from the Middle Old

¹ Substance of a lecture delivered before Section K (Botany) of the British Association at the Southampton meeting, 1925.

² I leave out of account the problematic *Archæoxylon Krasseri*, said to be a vascular plant from the pre-Cambrian of Bohemia. In spite of Dr. Kräusel's careful investigation, there is room for much scepticism as to this sensational record.

Red Sandstone of Cromarty. In this case only the wood is known, but Miller's fossil afforded the first evidence of highly organised plants in the Middle Devonian.

THE SECOND TRANSFORMATION.—It has become a little difficult to know where to place this. We have been accustomed to draw a sharp distinction between Early (Lower *plus* Middle) and Late (Upper) Devonian floras. Now we know that some very high types had appeared before the Middle Devonian period was over. The general *facies*, however, of the Upper Devonian vegetation was so distinctive that we may still regard it as marking the first appearance of a typical Palæozoic flora.

Here we meet with many plants with the habit of ferns, as, for example, the noble *Archæopteris hibernica* of Kiltorkan. Among such fern-like specimens there is little doubt that both true ferns and the so-called "Seed-ferns" were represented. Great club-mosses, comparable to those of the succeeding Carboniferous period, were already well developed. Plants with whorled leaves, of families more or less akin to the later calamites and horse-tails, were present. Stems, as highly organised anatomically as those of any modern conifer, indicate that gymnosperms were already flourishing. Leaves recalling those of the maidenhair tree may have belonged to some unknown type of seed-bearing plant.

Then we come, without any marked break, to the rich vegetation of Carboniferous times. The Lower Carboniferous shows the Palæozoic flora in its purest form. Seed-ferns were abundant and varied. Higher gymnosperms were finely represented by the great *Pitys* trees with leaves something like stout pine-needles. True ferns, usually of types strange to us, were common everywhere. Club-mosses attained a gigantic stature, and some of them had developed a kind of seed, an organ not known in this group after Carboniferous times. The calamite trees appeared, and in a distantly related family the cone of *Cheirostrobilus* was the most elaborate cryptogamic fructification known, either fossil or recent.

The still richer Upper Carboniferous vegetation is so well known as to need little description. New groups, both of true ferns and of the seed-ferns, appeared. The investigation of the vast Chinese flora of the period by Dr. Halle is now yielding fresh examples of the latter class.

The *Pitys* trees were replaced by the well-known Cordaitan family, of lofty stature, with long leaves like a dragon-tree, and little catkins, complex in structure. The club-mosses, calamites, and sphenophylls (a group remotely allied to the horse-tail stock) reached their zenith.

All this rich and varied flora lasted on with little change into the Permian period and then came to an end. This, at least, was the case with the northern flora. Towards the close of the Palæozoic age, botanical districts became differentiated; the vegetation of India and the southern hemisphere was then different from that which prevailed in the north. The southern type (which made some local incursions into more northern areas) is known as the *Glossopteris* flora, from its most characteristic genus. *Glossopteris* and *Gamopteris*, plants with simple, fern-like fronds, were probably seed-ferns. The gigantic club-mosses were

absent from the southern flora and the calamites were of different kinds. The general *facies* of the vegetation was distinct from that of the north. The age of the *Glossopteris* flora is now determined as Permo-Carboniferous, but some of the genera still survived in early Mesozoic times. Hence the transition appears to have been less abrupt in the south than in the north.

THE THIRD TRANSFORMATION.—So far as the northern flora is concerned, the change was complete. From the Trias onwards we find no certain examples either of seed-ferns or cordaitan trees. So far as we know, the two great Palæozoic races of seed-plants had disappeared, though perhaps a few relics may have survived. The club-mosses of the Mesozoic are few and modest. The horse-tails begin to approach those of our own day; the ferns are exceedingly numerous and varied, and belong to more or less modern families, for the most part quite distinct from those of Palæozoic age.

The seed-ferns were replaced by a vast array of so-called cycads. These plants were no doubt allied to the recent family, but the great majority of the Mesozoic forms were far more highly organised in their reproductive apparatus. In like manner the cordaitans were succeeded by the conifers, of families not unlike those still living, and by the maidenhair trees, an important race in Mesozoic times. Further, the vegetation of the world again became, in a broad sense, uniform; the botanical districts of the late Palæozoic were obliterated.

Now all this was a vast change, for which we are as yet unable to account. Yet there are some indications that the transformation was initiated at an earlier period. Foliage of a quite cycadean character is known from Permian and even Carboniferous rocks, though the evidence from fructifications is doubtful. Among conifers we have *Walchia*, a well-known genus with probable Araucarian affinities, in the Upper Carboniferous and Permian. Leaves like those of the maidenhair trees also occur in Palæozoic rocks, though they are not entirely convincing by themselves. On the whole it seems fairly clear that some of the most characteristic Mesozoic groups had already begun to appear in Palæozoic times.

The desert conditions which were prevalent in the Triassic period may, as has been suggested, help to explain the rapid change in the character of the vegetation. It is also possible that the source of many of the Mesozoic races is to be sought in the *Glossopteris* flora of the south, where, as already mentioned, the transition seems to have been less sudden. We are not really driven to any such violent assumption as a new invasion from the sea.

THE FOURTH TRANSFORMATION.—This great change, which became manifest during the Cretaceous period (late Mesozoic), introduced the modern type of vegetation. It has been well said that "we are still living in the Cretaceous epoch." For us, the great point of interest is the sudden advent of the true flowering plants, the angiosperms.

It is evident that the transformation was already far advanced in Lower Cretaceous times, for Dr. Marie Stopes has found a number of dicotyledonous stems of that age, with a structure as varied and as complex as that of present-day trees. There is nothing primitive about these early dicotyledons.

The Lower Cretaceous flowering plants were contemporary and associated with members of the old Mesozoic flora, cycads, and so on, which were still predominant. In the Gault and Upper Cretaceous the angiosperms have gained the upper hand, and the vegetation assumes quite a modern character. Both monocotyledons and dicotyledons are present, in about the same proportions as in the living flora. Among the former, palms, reeds, and lilies, among the latter, willows, walnuts, beeches, oaks, planes, maples, bread-fruits (found in Greenland), laurels, gum trees, ebonies, and dogbanes indicate some of the families represented. In fact the evidence shows that, from about the middle of the Cretaceous epoch, flowering plants were flourishing very much as they are now, so far, at least, as families or even genera are concerned.

We still have no clue to what Darwin called the "abominable mystery" of the sudden appearance of the higher plants. We have seen that they already existed, fully developed, in Lower Cretaceous times. It is interesting to inquire whether we have any earlier records. They are very scanty. Prof. Seward has described, from the Stonesfield Slate of Middle Jurassic age, simple, ovate leaves, like those of a dicotyledon. We cannot be certain; for there are ferns such as *Drymoglossum* with fronds somewhat similar, but dicotyledonous affinities are strongly suggested.

Much more important are Mr. Hamshaw Thomas's

discoveries in the Lower Oolite of Yorkshire, a little older than the Stonesfield Slate. He has found fruits, ranged in two rows on a stalk, each fruit enclosing a number of seeds. Thus the structure was undoubtedly angiospermous in the literal sense, for the fruit was closed. Associated with these organs Mr. Thomas finds branched stamens, with four-lobed anthers like those of an angiosperm, and also compound palmate leaves. He gives good reasons for thinking that all these remains belonged together. It is evident that Mr. Thomas's fossils throw a new light on the early history of the angiosperms, though their relation to the main line of descent is still an open question.

The series of transformations we have briefly sketched is sufficiently striking. What has been called the succession of dynasties is, no doubt, the great feature in the past history of the kingdom of plants. We have, as yet, little to show by what means one dynasty succeeded another, or how the successive dominant races were related. That each new type arose much earlier than its full manifestation is obvious, and, as we have seen, there is often direct evidence of precursors in an age previous to the transformation of the flora. To unravel the course of descent in the transition, apparently so abrupt, from each flora to the next in succession, is at present a task beyond our powers; we have attempted nothing more than to state the problem.

Photochemical Problems.

THE subject of photochemistry is one to which increasing attention is being given at the present time, as is exemplified by the large attendance and spirited controversies in the meeting, very international in character, held by the Faraday Society at Oxford on October 1 and 2. Whilst as a specialised field for the study of the action of light on chemical substances it is not without interest, in a broader sense it is the most important of all the sciences, for not only does it provide a common meeting-place for physicists, astronomers, and chemists, but, as the botanists have long observed and the medical profession is now realising, life is in great measure dependent on photochemical action.

In all photochemical reactions it is necessary to distinguish between what are termed primary and secondary processes. The first action of the light in producing chemical change is to undergo absorption by a molecule, thus converting it into an "activated" or "excited" molecule. According to the quantum theory all molecules excited or activated in this way become a distinct species characterised by a definite energy constant, which, in certain cases, is directly related to the frequency of the radiation absorbed by the relationship due to Stark and Einstein, $E = h\nu$.

It is these activated molecules which are the reacting species in photochemical processes and, according to some investigators, notably Perrin, in thermochemical change also. If all reactions were simple, it is clear that for every quantum of light absorbed one molecule should enter into chemical reaction and we should obtain a very simple relationship between the amount of chemical action obtained and the number of light quanta absorbed. Closer consideration, however, indicates that this simple law may be but rarely fulfilled,

for such an excited molecule may perform one of three possible operations. It may fluoresce and thus lose its newly acquired energy by the emission of radiation. Again, it may collide with another molecule, when one of two possibilities are open to it: on collision the internal energy may be liberated in the kinetic form, resulting in what is termed a supra elastic collision, or the internal energy may be handed on to the molecule it comes in contact with, this molecule then departing as an active molecule, a process termed photosensitisation. Finally, the possibility of chemical reaction on collision is presented. It is little wonder that in many reactions the photochemical efficiency is low.

In addition to such reactions there exists an ever-increasing group in which the photochemical yield is much greater than is to be anticipated from consideration of the amount of light absorbed, or, one quantum apparently can cause several, in some cases tens of thousands of molecules to undergo reaction. Such reactions are now designated as "chain" reactions, and the various hypotheses as to their mode of action are at present a matter of heated controversy. One of the simplest explanations is that of the "atom" chain, which may be represented in operation in its simplest form by the following sequence of operations:

in which the primary photochemical process of activation (1) is followed by a series of steps 2, 3, 4. It is clear that 3, 4 represent two links in a chain which can only terminate when an atom is arrested in some manner.