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SUPPLEMENTARY SECTION

ON THE BEARING OF DEVONIAN BOTANY ON QUESTIONS AS TO THE ORIGIN AND EXTINCTION OF SPECIES.

[The theoretical views contained in this section, though necessary to give completeness to the subject, are not suitable for an official report, and are, therefore, printed separately by the author, for circulation to those who may be interested in them as matters of science.]

Fossil plants are almost proverbially uncertain with reference to their accurate determination, and have been regarded as of comparatively little utility in the decision of general questions of palæontology. This results principally from the fragmentary condition in which they have been studied, and from the fact that fragments of animal structures are more definite and instructive than corresponding portions of plants.

It is to be observed, however, that our knowledge of fossil plants becomes accurate in proportion to the extent to which we can carry the study of specimens in the beds in which they are preserved, so as to examine more perfect examples than those usually to be found in museums. When structures are taken into the account, as well as external forms, we can also depend more confidently on our results. Farther, the abundance of specimens to be obtained in particular beds often goes far to make up for their individual imperfection. The writer of these pages has been enabled to avail himself very fully of these advantages; and on this account, if on no other, feels entitled to speak with some authority on theoretical questions.

It is an additional encouragement to pursue the subject that, when we can obtain definite information as to the successive floras of any region, we thereby learn much as to climate, and vicissitudes in regard to the extent of land and water; and that, with reference to such points, the evidence of fossil plants, when properly studied, is, from the close relation of plants to those stations and climates, even more valuable than that of animal fossils.

It is necessary, however, that in pursuing such enquiries we should have some definite views as to the nature and permanence of specific forms, whether with reference to a single geological period, or to successive periods; and I may be excused for stating here some general principles, which I think important for our guidance, with special reference to the palæozoic floras which form the subject of this memoir.

- (1.) Botanists proceed on the assumption, vindicated by experience, that, within the period of human observation, species have not materially varied or passed into each other. We may make, for practical purposes, the same assumption with regard to any given geological period, and may hold that for each such period there are specific types, which, for the time at least, are invariable.
- (2.) When we inquire what constitutes a good species for any given period, we have reason to believe that many names in our lists represent merely varietal forms or erroneous determinations. This is the case even in the modern flora; and in fossil floras, through the poverty of specimens, their fragmentary condition and various states of preservation, it is still more likely to occur. Every revision of any group of fossils detects numerous synonyms, and of these many are incapable of detection without the comparison of large suites of specimens.
- (3.) We may select from the flora of any geological period certam forms, which I shall call specific types, which may for such period be regarded as unchanging. Having settled such types, we may compare them with similar forms in other periods, and such comparisons will not be vitiated by the uncertainty which arises from the comparison of so-called species which may, in many cases, be mere varietal forms, as distinguished from specific types. Our types may be founded on mere fragments, provided that these are of such a nature as to prove that they belong to distinct forms which cannot pass into each other, at least within the limits of one geological period.
- (4.) When we compare the specific types of one period with those of another immediately precedent or subsequent, we shall find that some continue unchanged through long intervals of geological time, that others are represented by allied forms regarded either as varietal or specific, and as derived or otherwise, according to the view which we may entertain as to the permanence of species. On the other hand, we also find new types not rationally deducible on any theory of derivation from those known in other periods. Farther, in comparing the types of a poor period with those of one rich in species we may account for the appearance of new types in the latter by the deficiency of information as to the former; where many

new types appear in the poorer period this conclusion seems less probable. For example, new types appearing in poor formations, like the Lower Erian and Lower Carboniferous, have greater significance than if they appeared in the Middle Erian or in the Coal Measures.

- (5.) When specific types disappear without any known successors, under circumstances in which it seems unlikely that we should have failed to discover their continuance, we may fairly assume that they have become extinct, at least locally; and where the field of observation is very extensive, as in the great coal fields of Europe and America, we may esteem such extinction as practically general, at least for the northern hemisphere. When many specific types become extinct together, or in close succession, we may suppose that such extinction resulted from physical changes; but where single types disappear, under circumstances in which others of similar habit continue, we may not unreasonably conjecture that, as Pictet has argued in the case of animals, such types may have been in their own nature limited in duration, and may have died out without any external cause.
- (6.) With regard to the introduction of specific types we have not as yet a sufficient amount of information. Even if we freely admit that ordinary specific forms, as well as more varieties, may result from derivation, this by no means excludes the idea of primitive specific types originating in some other way. Just as the chemist, after analyzing all compounds and ascertaining all allotropic forms, arrives at length at certain elements not mutually transmutable or derivable, so the botanist and zoologist must expect sooner or later to arrive at elementary specific types, which, if to be accounted for at all, must be explained on some principle distinct from that of derivation. The position of many modern biologists, in presence of this question, may be logically the same with that of the ancient alchemists with reference to the chemical elements, though the fallacy in the case of fossils may be of more difficult detection. Our business at present, in the prosecution of palæobotany, is to discover, if possible, what are elementary or original types, and, having found these, to enquire as to the law of their creation.
- (7.) In prosecuting such questions geographical relations must be carefully considered. When the floras of two successive periods have existed in the same region, and under circumstances that render it probable that plants have continued to grow on the same or adjoining areas throughout these periods, the comparison becomes direct, and this is the case with the Erian and Carboniferous floras in North-Eastern America. But when the areas of the two formations are widely separated in space, as well as in

time, any resemblances of facies that we may observe may have no connection whatever with an unbroken continuity of specific types.

I desire, however, under this head, to affirm my conviction that, with reference to the Erian and Carboniferous floras of North America and of Europe, the doctrine of "homotaxis," as distinct from actual contemporaneity, has no place. The succession of formations in the Palæozoic period evidences a similar series of physical phenomena on the grandest scale throughout the northern hemisphere. The succession of marine animals implies the continuity of the sea-bottoms on which they lived. The head-quarters of the Erian flora in America and Europe must have been in connected or adjoining areas in the North Atlantic. The similarity of the Carboniferous flora on the two sides of the Atlantic, and the great number of identical species, proves a still closer connection in that period. These coincidences are too extensive and too frequently repeated to be the result of any accident of similar sequence at different times, and this more especially as they extend to the more minute differences in the features of each period, as, for instance, the floras of the Lower and Upper Devonian, and of the Lower, Middle, and Upper Carboniferous.

Another geographical question is that which relates to centres of dispersion. In times of slow subsidence of extensive areas, the plants inhabiting such areas must be narrowed in their range and often separated from each other in detached spots, while, at the same time, important climatal changes must also occur. On the re-emergence of the land such of these species as remained would again extend themselves over their former areas of distribution, in so far as the new climatal and other conditions would permit. We would naturally suppose that the first of the above processes would tend to the elimination of varieties, the second, to their increase; but, on the other hand, the breaking up of a continental flora into that of distinct islets, and the crowding together of many forms, might be a process fertile in the production of some varieties if fatal to others.

Farther, it is possible that these changes of subsidence may have some connection with the introduction, as well as with the extinction, even of specific types. It is certain, at least, in the case of land plants, that such types come in most abundantly immediately after elevation, though they are most abundantly preserved in periods of slow subsidence. I do not mean, however, that this connection is one of cause and effect; there are, indeed, indications that it is not so. One of these is, that in some cases the enlargement of the area of the land seems to be as injurious to terrestrial species as its diminution.

Applying the above considerations to the Erian and Carboniferous

floras of North America, we obtain some data which may guide us in arriving at general conclusions. The Erian flora is comparatively poor, and its types are in the main similar to those of the Carboniferous. Of these types a few only re-appear in the Middle Coal formation under identical forms: a great number appear under allied forms; some altogether disappear. The Erian flora of New Brunswick and Maine occurs side by side with the Carboniferous of the same region; so does the Erian of New York and Pennsylvania with the Carboniferous of those states. Thus we have data for the comparison of successive floras in the same region. In the Canadian region we have, indeed, in direct sequence, the floras of the Upper Silurian, the Lower, Middle, and Upper Erian, and the Lower, Middle, and Upper Carboniferous, all more or less distinct from each other, and affording an admirable series for comparison in a region whose geographical features are very broadly marked. All these floras are composed in great part of similar types, and probably do not indicate very dissimilar general physical conditions, but they are separated from each other by the great subsidences of the Corniferous limestone and the Lower Carboniferous limestone, and by the local but intense subterranean action which has altered and disturbed the Erian beds towards the close of that period. Still, none of these changes was universal. The Corniferous limestone is absent in Gaspé, and probably in New Brunswick, where, consequently, the Erian flora could continue undisturbed during that long period. The Carboniferous limestone is absent from the slopes of the Appalachians in Pennsylvania, where a retreat may have been afforded to the Upper Erian. and Lower Carboniferous floras. The disturbances at the close of the Erian were limited to those eastern regions where the great limestoneproducing subsidences were unfelt, and, on the other hand, are absent in Ohio, where the subsidences and marine conditions were almost at a maximum.

Bearing in mind these peculiarities of the area in question, we may now group in a tabular form the distinct specific types recognized in the Erian system, indicating, at the same time, those which are represented by identical species in the Carboniferous, those represented by similar species of the same general type, and those not represented at all. For example, Calamites cannæformis extends as a species into the Carboniferous; Asterophyllites latifolia does not so extend, but is represented by closely allied species of the same type; Prototaxites disappears altogether before we reach the Carboniferous,

TABLE OF ERIAN AND CARBONIFEROUS SPECIFIC TYPES.

Erian Types. Represented in Car	bonifer by iden-	ou by re-	Erian Types. Represented in Car	bonifer by iden-	ous lated forms.
1. Syringoxylon mirabile 2. Nematoxylon 3. Prototaxites 4. Aporoxylon 5. Ormoxylon 6. Dadoxylon 7. Sigillaria Vanuxemii 8. S. palpebra 9. Didymophyllum 10. Calamodendron 11. Calamites transitionis 12. C. cannæformis 13. Asterophyllites scutigera 14. A latifolia 15. Annularia laxa 16. Sphenophyllum antiquum 17. Cyclostigma 18. Arthrostigma 19. Lepidodendron Gaspianum 20. L. Veltheimianum 21. Lycopodites Matthewi 22. L. Richardsoni 23. L. Vanuxemii 24. Lepidophloios antiquus 25. Psilophyton princeps 26. P. robustius			27. Cordaites Robbii 28. C. augustifolia 29. Cyclopteris (Archæopteris). 30. C. (Aneimites). 31. C. Brownii 32. C. varia. 33. Neuropteris polymorpha. 34. N. Serrulata 35. N. Dawsonii 36. N. retorquata 37. N. resecta 38. Sphenopteris Hœninghausi. 39. S. Harttii. 40. Hymenophyllites curtilobus. 41. H. obtusilobus. 42. Alethopteris discrepans. 43. Pecopteris serrulata. 44. P. preciosa. 45. Trichomanites. 46. Callipteris. 47. Psaronius 48. Cardiocarpum 49. C. Crampii. 50. Antholithes. 51. Trigonocarpum	•	* * * * * * * * * * * * * * * * * * * *

Of the above forms, fifty-one in all, found in the Erian of Eastern America, all, except the four last, are certainly distinct specific types. Of these only four reappear in the Carboniferous under identical species, but no less than twenty-six reappear under representative or allied forms, some at least of which a derivationist might claim as modified descendants. On the other hand nearly one half of the Devonian types are unknown in the Carboniferous, while there remain a very large number of Carboniferous types not accounted for by anything known in the Devonian. Farther, a very poor flora, including only two or three types, is the predecessor of the Erian flora in the Upper Silurian, and the flora again becomes poor in the Upper Devonian and Lower Carboniferous. Every new species discovered must more or less modify the above statements, and the whole Erian flora of America, as well as the Carboniferous, requires a thorough comparison with that of Europe before general conclusions can be safely drawn. In the meantime I may indicate the direction in which the facts seem to point, by the following general statements:-

1. Some of the forms reckoned as specific in the Devonian and Carboniferous may be really derivative races. There are indications that such races may have originated in one or more of the following ways:—(1) By a natural tendency in synthetic types to become specialized in the direction

of one or other of their constituent elements. In this way such plants as Arthrostigma and Psilophyton may have assumed new varietal forms. (2) By embryonic retardation or acceleration,* whereby certain species may have had their maturity advanced or postponed, thus giving them various grades of perfection in reproduction and complexity of structure. The fact that so many Erian and Carboniferous plants seem to be on the confines of the groups of Acrogens and Gymnosperms may be supposed favourable to such exchanges. (3) The contraction and breaking up of floras, as occurred in the Middle Erian and Lower Carboniferous, may have been eminently favourable to the production of such varietal forms as would result from what has been called the "struggle for existence." (4) The elevation of a great expanse of new land at the close of the Middle Erian and the beginning of the Coal period, would, by permitting the extension of species over wide areas and fertile soils, and by removing the pressure previously existing, be eminently favourable to the production of new, and especially of improved, varieties.

2. Whatever importance we may attach to the above supposed causes of change, we still require to account for the origin of our specific types. This may forever elude our observation, but we may at least hope to ascertain the external conditions favourable to their production. In order to attain even to this it will be necessary to inquire critically, with reference to every acknowledged species, what its claims to distinctness are, so that we may be enabled to distinguish specific types from mere varieties. Having attained to some certainty in this, we may be prepared to inquire whether the conditions favourable to the appearance of new varieties were also those favourable to the creation of new types, or the reverse—whether these conditions were those of compression or expansion, or to what extent the appearance of new types may be independent of any external conditions, other than those absolutely necessary for their existence. I am not without hope that the further study of fossil plants may enable us thus to approach to a comprehension of the laws of the creation, as distinguished from those of the continued existence of species.

In the present state of our knowledge we have no good ground either to limit the number of specific types beyond what a fair study of our material may warrant, or to infer that such primitive types must necessarily have been of low grade, or that progress in varietal forms has always been upward. The occurrence of such an advanced and specialized type as that of Syringoxylon, in the Middle Devonian, should guard us against these errors. The creative process may have been applicable to the highest as well as to the lowest forms, and subsequent deviations must have included

^{*} In the manner illustrated by Hyatt and Cope.

degradation as well as elevation. I can conceive nothing more unreasonable than the statement sometimes made that it is illogical or even absurd to suppose that highly organized beings could have been produced except by derivation from previously existing organisms. This is begging the whole question at issue, depriving science of a noble department of inquiry on which it has as yet barely entered, and anticipating by unwarranted assertions conclusions which may perhaps suddenly dawn upon us through the inspiration of some great intellect, or may for generations to come baffle the united exertions of all the earnest promoters of natural science. Our present attitude should not be that of dogmatists, but that of patient workers content to labour for a harvest of grand generalizations which may not come till we have passed away, but which, if we are earnest and true to nature and its Creator, may reward even some of us.