

Plant-Distribution from the Standpoint of an Idealist.

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THE most interesting and at the same time the most mysterious features of plant-distribution centre around the rise of the great families. These ancient plant-groups belong so much to an era of other things, other ways, and other conditions, that the employment of such terms as "genera" and "species" in connection with their origin seems to be almost meaningless. All the influences that we see normally at work around us now could only relate to the differentiation of the family-types into genera and species; and any theory that on such grounds endeavours to apply the present to the past in deciphering their origin would apparently be attempting an impossible task. One ventures to think that only the hypothesis that finds its guide to the past in the abnormalities of the present could be of service here. This would seem to place the pre-differentiation era, the age that witnessed the rise of the great families, outside the field of the Natural Selection theory, and in default of its aid to cause us to look to the Mutation hypothesis for guidance. Yet, although Darwin came to reject the "sport," the original scope of his theory was large enough to admit it; and it may be, as the writer holds, that the antithesis between the two theories is more apparent than real. Yet the Mutation hypothesis was conceived in the spirit of Darwinism, was framed on Darwinian lines, and was formulated in Darwinian language; and it is not easy to understand how the two theories were allowed to acquire the appearance of being mutually exclusive. There is room for both within the boundaries of the theory of Natural Selection as Darwin first conceived it; and there is work for both schools in its extension, its improvement, and its emendation. Whilst the Mutationist would find a fruitful field for his labours in the era of the rise of the great family-types, the Darwinian evolutionist would be occupied with their subsequent differentiation into tribes, genera, and species.

The rise of the great families and the lesson of the Compositæ and the Gentians.—Two papers of great importance from this standpoint to the student of plant-distribution were published in the 'Journal of the Linnean Society' in 1873 and 1888, the first by Bentham on the Compositæ, the second by Huxley on the Gentians. They are important because, in dealing with the beginnings of the distribution of these two families, they ask the same questions and raise the same issues; and it is needless to add that, although in one case the methods employed were those of a great botanist and in the other those of a great zoologist, they bear in each case the impress of a master hand. Those interested in the subject will remember

that two years before the publication of his paper Huxley had outlined his views in two letters to Hooker, letters which are given in the 2nd edition of his 'Life and Letters,' by his son (ii. 465-6, 1903).

It is proposed to commence this paper with a comparison of the views held by these investigators respecting the early history of the distribution of the two families concerned. Both are agreed as to the original wide distribution of the primitive forms over the world, and both credit them with ignoring the great physical features of the globe, as at present displayed. Broad oceans, great deserts, and lofty mountain-ranges are all out of the reckoning in the respective discussions relating to the spread of these two families over the earth. Bentham holds to a very wide dispersion of the original stock of the Compositæ over the world when the physical configuration was very different from what it is in our day. Huxley speaks of a "primitively continuous area of distribution," and leaves the matter there. With reference to the state of differentiation of the original stock when it conquered the earth, Bentham holds that the Old and the New Worlds possessed the family at the earliest recognizable stage. Huxley hypothecated a widely spread primitive type that subsequently differentiated over the globe. Both, in imputing a high antiquity to the respective stocks, knowingly disregarded the lack of geological evidence, the one considering that the Compositæ dated back to an early geological period, the other holding that even the more specialized and consequently the more recent of the Gentians might have lived in the Cretaceous epoch. But Huxley went even beyond this when he assumed that the "Ur-Gentian" might be carried back "almost as much farther as probabilities permit us to carry the existence of flowering plants."

For neither Bentham nor Huxley were the main features of the distribution of these two families concerned with means of dispersal. Huxley makes but little appeal to them and Bentham discredits their efficacy. Bentham begins with a family already universally distributed, although he implies an original centre of dispersion. Huxley would have nothing to do with any such centres, and his plain words on this subject ought never to be forgotten by the student of distribution. All such notions were excluded for him in a type that followed the principle of *the simpler and older the type the greater its range*.—"The facts of distribution of the Gentianæ are (he writes) not to be accounted for by migration from any centre of diffusion to which locality can be assigned in the present condition of the world." The problem was for him essentially a matter of the local modification of plants at different points of a "primitively continuous" area. Both Bentham and Huxley are at one in their conclusion that the main features of the distribution of these two families were determined in ages geologically remote; and neither's view of the early stages in the history of their distribution leaves any room for an appeal to centres of

dispersion. If behind the facts of distribution lies the cardinal principle that the farther we trace a type back the more generalized are its characters and the wider its range, the question of its original home is obviously not raised.

What, we may ask, was the bearing of these views on general taxonomic principles? Bentham was dealing with a world-ranging family holding about a tenth of the total known number of Angiosperms and displaying relatively few of the difficulties presented by small families with restricted distribution. He followed orthodox lines and the results were not disquieting to the systematist, although, if he had pushed his conclusions home, a clash with prevailing practice would have happened. With Huxley it was very different. He was concerned with a much smaller family, one less widely distributed and displaying a preference for mountainous regions. To it he applied the same method of postulating a wide-ranging but little differentiated primitive type, and in so doing he raised many of the difficulties presented by the smaller families. But his method, as he perceived, considerably upset the accepted grouping of the Gentians, and in his enthusiasm in its advocacy he contended that "a revision of Taxonomy and Distribution from the point of view of the Evolution doctrine will hardly fail to revolutionise both." But the curious point is that as far as the early stages in the history of the Gentians are concerned the method advocated by Huxley was not Darwinism, as then conceived. It was pure Differentiation. With Bentham also, although clinging to the idea of a centre of dispersion, or of a home, for the Compositæ, he began with a world-ranging but slightly differentiated primitive type, and like Huxley with the Gentians he allowed it to work out its own lines of differentiation in the various regions of the globe. This is Evolution on a plane; and the implication is that since the rise of the great families in the Mesozoic ages little else has been effected.

The Differentiation hypothesis.—Although this hypothesis has rarely been formulated, there are various ways of stating it. It appears in a variety of guises in many a monograph of the families. The writer's mode of presenting it is to associate it with another theory relating to the differentiation of conditions, the modification of form being regarded as the response to the progressive differentiation of conditions. But it would be possible to deal independently with the differentiation through the ages of the family into tribes, of the tribe into genera, and of the genus into species. Yet the two are commonly implied, and it is hard to dissociate the idea of differentiation of type from that of diversification of condition. There may, however, be different ways of stating the relation. The following is the writer's method of doing so.

He has come to close quarters with the central problem in successive stages. In the first stage the world, as far as plants are concerned, was mainly a differentiating world in which wide-ranging generalized types had

differentiated in response to the progressive diversification of conditions originally uniform, a world in which the family differentiated into tribes, the tribes into genera, and the genera into species. But on perceiving that such a theory could only explain distribution where a continuous land-mass, not affected by unstable climatic conditions, was concerned, he came to recognize that the operations of the differentiating agencies had been largely controlled and directed by the divergence of the two great land-masses from the north, a control in its turn influenced by the secular fluctuations of climate and by the barriers that lay across the lines of migration. It may be stated that the progressive differentiation of floras in response to diversification of conditions has long been recognized. The era of world-wide floras, as Mr. C. Reid well puts it (*Encyclopædia Britannica*, edit. 10, vol. xxxi. p. 432), began to pass away after the Cretaceous age, and from that period onward plants have responded more and more to the differentiation of conditions and have arranged themselves more and more according to geographical boundaries and climatic zones. The general trend of events in later ages is sufficiently indicated by the frequent application to these early types by various writers of such epithets as "comprehensive," "generalized," "mixed," "synthetic," etc.

The views long advocated by Thiselton-Dyer brought about the first modification in the original interpretation of the theory, and the writer came in this way to lay stress on the point that the mingling of the floras of the eastern and western worlds might be regarded as the result of the successive migrations to and from the north polar region under the stress of climatic changes. The third stage was reached when he realized as a result of the statistical treatment of the subject, which is dealt with in later pages, that there was much in the distribution of the larger groups which the mixing of the eastern and western floras in the north polar regions would not explain. Though true of the smaller groups, as with species, the principle that the community between the Old and the New World is an affair of the north did not materialise with respect to families. On the contrary, it appeared, with regard to families of the first rank and the groups behind them, that the main features of distribution would have been much the same as they now are if the land of the globe had been gathered into a single mass. Thus the author came to distinguish between the larger and smaller groups in the response made to the great bi-cleavage of the land-surface of the globe, and to restrict the influences of the existing relations of land and sea to the smaller groups, as in the case of genera and species. This led him to perceive that if the differentiation hypothesis was valid the families and the larger groups behind them had not only ignored the bi-cleavage of the land-mass of the globe, but had been developed under conditions very different from those in which their genera and species had been produced.

The independent behaviour of the great families with respect to existing

geographical conditions opened to him a prospect of removing a serious difficulty that might have been fatal to the general theory ; and that was the difficulty of conceiving the early stages in the differentiation of a type in response to the first stages of the diversification of uniform conditions. Since characters become more constant and adaptivity to present conditions becomes less marked as one proceeds up the scale from the species to the family, it was obvious that if the hypothesis was to stand a different order of things had to be postulated for the development of the larger groups; an order of things in which instability of characters was associated with uniformity of conditions. The responses of our great family types to the changes in environment are negligible. Yet the distant age of the Cretaceous that witnessed the deployment of the Angiosperms, much as we know them now, must have been preceded by an era of great instability of floral characters—characters on which the taxonomist has based his families and his groups of families, and characters that have been more or less fixed during the ages that have since elapsed.

Obviously one was here face to face with a different order of things, but some time elapsed before further progress could be made in the elaboration of the theory. Having abandoned the position that uniformity of conditions and immutability of type went together, a position that was the logical sequence of the differentiation hypothesis as at first conceived, one had either to adopt the opposite view or throw over the theory. It was not a dilemma peculiar to the differentiation theory, since the mutationist and the Darwinian evolutionist experience a similar difficulty when they deal with the genesis of the larger groups, the development of the family requiring the instability of characters which are mainly constant under present conditions. The way out of the difficulty was suggested on reading the account by Dr. Willis of the extreme uniformity of conditions in which the Podostemaceæ and Tristichaceæ live in mountain-torrents and rushing streams around the tropics, a description of a state of things approaching the primeval state as far as uniformity is concerned. He describes the great morphological changes of the floral and vegetative organs under such conditions, modifications characterized as without any adaptive significance and as the result of free mutation in every direction (Proc. Roy. Soc. vol. lxxxvii. pp. 546, 548 ; 1914). He speaks of "the most astonishing variety of morphological structure" under conditions of life "absolutely uniform" (*Ibid.* p. 533). On the results of the investigation of these families for many years he builds a powerful argument for the Mutation theory, and one can scarcely doubt that in time he will adopt a standpoint not essentially different from that of the Differentiation hypothesis. But what one is concerned with here is the association of extreme uniformity of conditions with extreme instability of type. It is a picture of the abnormal side of plant-life.

In explanation of the remarkable mutations of the floral organs displayed

by the Podostemaceæ, Dr. Willis connects the dorsiventrality of these organs with that of the vegetative organs, thus introducing a factor apparently subversive of all taxonomic principles. There is in his warning of the insecurity of the taxonomist's position an echo of Huxley's defiant note respecting the revolutionizing effect of the evolutionary doctrine on the principles of taxonomy and distribution. Dr. Willis wields the Podostemaceæ, as Huxley wielded the Gentians, in his attack on prevailing principles. In the case of Huxley it was concerned with the differentiation of a wide-ranging primitive family type, and one can scarcely doubt that he struck a true note in his declaration. But it applied only to the second era, the era of differentiation, the age of influences still in operation, the age of normality, if we may so term it; and it ought to have a profound effect on the methods of the taxonomist and on the principles of distribution. In the case of Dr. Willis it is concerned with the abnormal side of plant-life and does not really affect the validity of prevailing taxonomic principles. The difference is very significant, since, in view of the position taken at the commencement of this paper, we can in our day only look in that direction for a clue to the influence at work during the first era in the history of the Angiosperms, the age that witnessed the rise of the great families, the age of abnormalities, as it may be called. It is in this first era that the Mutation theory will find its appropriate field of investigation, and it is here that the principles disclosed by Dr. Willis in his prolonged investigations on the Podostemaceæ will apply.

Before proceeding to deal in the two following paragraphs with my interpretation of the lessons to be learned from the behaviour of the Podostemaceæ and with their application to the first era, I may say that Dr. Willis left room for an interpretation of the same kind, but was prevented, as he tells me, from entering a domain of pure surmise.

Postulating for terrestrial plants an era when uniformity in environment was the rule—an era, one might imagine, of great atmospheric humidity, when persistent cloud-coverings blanketed the globe and when the same equable temperature everywhere prevailed,—the writer pictured a plant-organism under such conditions as behaving very much like a ship in a calm, drifting in a morphological sense in all directions and displaying unchecked and irresponsive variations of the floral organs of a kind very disquieting to the taxonomist and all non-adaptive in their nature. He came to see that such modifications would become more and more fixed as the differentiation of conditions proceeded, the degree of mutability varying inversely with the diversification of environment.

Stated in the language of the mutationist, this would imply that the mutations of the floral organs of our own day represent all that remains of the capacity for great morphological changes in the early ages of the history of the Angiosperms. A mutation as at present recognized is non-adaptive.

Yet it may be adaptive in another sense—namely, in its response to the remnant of the conditions of an age long passed away. One might regard it as the last kick of the organism in response to what remains of the primeval uniformity of conditions, its last effort to break through the ever-contracting ring of the differentiating agencies. The farther we go back the greater is the capacity for mutations and the greater will be the mutations; and it is argued that they ought to be more frequent and more extensive in plant-groups of large than of small range. A large mutation would usually be impossible nowadays except under conditions approaching those of the early ages in their uniformity. One would look for some approach to those times in the dense forests of tropical lowlands and in the forests of the cloud-belt or rain-zone on tropical mountains.

The ascription of periodicity to mutability by De Vries is well known, and appeals to this principle in elucidation of the rapid rise of the Angiosperms in the Cretaceous period have been made; but the question, why basic characters so mutable then are stable now, always remains. The position is well put by Harshberger in his great work, 'The Phytogeographic Survey of North America,' p. 173, 1911. "If this periodicity of mutation (so he writes) is recognized as an evolutionary principle, we have a reasonable explanation for the sudden appearance of so many new forms during the Cretaceous period, for during this stage of the development of the vegetable kingdom, through causes yet unknown, the progenitors of the existing phanerogams were in a high state of mutability."

A few remarks may here be made on the relation of the views of distribution here advocated to the Age and Area theory of Dr. Willis. If one for the moment ignores his adoption of the prevailing practice of building up a family from the species, there is but little that is essentially inconsistent with the differentiation hypothesis. Had he formally associated with his Age and Area principle the twin principle of Rank and Range, and all that it implies, he could not have avoided coming into line in this matter. Since he extends his views to the larger groups, his Age and Area theory is of general application, and his conception of the distribution of families, apart from his standpoint of their genesis, might very well have been acquired in a line of argument favouring the views supported in this paper. His discussions of the Dilleniaceæ, Menispermaceæ, and Podostemaceæ are cases in point. (See Ann. Roy. Bot. Gard. Peradeniya, 1902, 1907; Phil. Trans. Roy. Soc. Lond. 1915; Proc. Roy. Soc. 1914; Ann. Bot. 1915, etc.) Thus he connects the origin of these three pantropical families with the most primitive and most widely distributed genera—genera that almost possess the range of the families. This is differentiation pure and simple. Then again, though he departs from the principle of differentiation when he endeavours to find the original centre of dispersion or home of the Dilleniaceæ, he comes very near it in the case of the Menispermaceæ in his

inference that the primitive genera "must have commenced when there was still a possibility of reaching both the great land masses" (Phil. Trans. *ibid.* p. 338). This recalls Bentham's opinion respecting the Compositæ, that the two hemispheres, the east and the west, must have possessed the family at its earliest recognizable stage.

So, again, when he observes in connection with the Podostemaceæ and Tristichaceæ that "the only widespread genera are the non-specialised ones, whilst the more specialised the genus, on the whole, the less is its area of distribution" (Proc. Roy. Soc. 1914, p. 545), and when he remarks that "the larger the group and the fewer the characters on which it is based, the greater the likelihood of its being polyphyletic"—that is to say, of arising independently in localities remote from each other (Ann. Roy. Bot. Gard. Perad. p. 447, 1902),—he is expressing the differentiation standpoint. But the writer cannot conceive how the principle, often implied in the foregoing remarks, that the simpler the form the wider its range, could apply to groups that have been built up, as Dr. Willis infers, by the species taking the generic step, the genus the tribal step, and the tribe the family step (*ibid.*).

But, apart from this, there is a great deal that links together the two views of distribution; yet one may add that whatever view we take of distribution, whether that of the Darwinian evolutionist, or that of the Mutationist, or that of the advocate of pure differentiation, we all get into the same dilemma when we handle the larger groups. If we require for their development the mutability or instability of the characters on which the taxonomist bases his larger groups, characters that in our own age are relatively immutable, we cannot look to existing prevailing conditions for guidance in the matter. However, Dr. Willis in his account of the astounding modifications experienced by the Podostemaceæ, under conditions described by him as "unique" among plants, offers, as the writer has already explained, a way out of the difficulty.

The statistical treatment of Distribution.—If the Differentiation hypothesis is valid, we may now ask what we should be justified in expecting from a statistical treatment of the main features of plant-distribution. If we listen to the story of the early stages in the distribution of the Compositæ and Gentianaceæ, as interpreted by Bentham and Huxley, we should expect that the larger plant-groups would to a great extent ignore the cleavage of the land of the globe into two large masses diverging from the north, and that the response made to the existing arrangement of land and sea would increase as we go down the differentiating scale, being least for the family and greatest for the species. On the other hand, we should expect a marked response of the larger plant-groups to the climatic differentiation of the latitudinal zones.

If in our investigations with the family as our starting-point we disclose a method and a system that could not be brought about by a procedure so haphazard as that involved in commencing the genetic sequence with the

species and ending with the family, then we shall make an important step towards the proper appreciation of the main problems concerned in distribution. That two such opposite methods should seem possible, as beginning in one case with the species and the other with the family, and that we should be indifferent to the result, whether it be chaos or order, are indications of failure to appreciate what really matters in plant-distribution.

It is by no means urgent to go back to the beginning of things, to account for the origin of families or even of species, to seek for centres of dispersion or the homes of plant-groups, to upset the world's geography, or to account for progressive evolution. What is urgent is to be able to state the main problem, and that cannot be done without some agreement about essentials. One cannot help thinking that if a hundred students of distribution were asked to do this, they would view the subject from such a variety of standpoints that the task of finding a common basis of agreement would be exceedingly difficult. The claim of the family for priority of treatment, which is supported in this paper, is founded on what Bentham terms in the case of the *Compositæ* the permanence of its characters. The very persistence of the family lies in the fact that these characters make little or no response to the extreme variations of existing conditions; and it is with the object of emphasizing its suitability for serving as a common ground of agreement that these pages have been written.

The response of the families to the bi-cleavage of the land-mass of the globe.—It is a remarkable fact that whilst the families of the Angiosperms respond in a marked degree to the differentiation of the climatic zones, they largely ignore the cleavage of the land into two great masses diverging from the north. Of the 272 families recognized in Engler's system 192, or 70·5 per cent., occur in both the eastern and western hemispheres (Tables I., II., III.). It would almost appear, as far as their occurrence in both hemispheres is concerned, that the general distribution of the families over the globe would not have been very different if all the land had been one continuous little-divided mass.

It may, however, be objected that this community of families between the Old and the New World may be mainly restricted to those most at home in the colder latitudes of the north where the American and Eurasian land-masses approach each other. If this were so, there would be but little force in the above contention that the family largely ignores the bi-cleavage of the land. But a glance at the columns of Table III. will convince one that this behaviour of the family is just as characteristic of the warm equatorial regions as it is of the colder northern regions. There are 120 families restricted to tropical and sub-tropical latitudes. Of these 73, or 61 per cent., are found in both the eastern and western worlds. There are 52 families that are only at home in extra-tropical regions. After removing those confined to the southern hemisphere, there remain 36, of which 23, or 64 per

cent., occur in both the Old and New Worlds. We obtain similar indications by also introducing the element of those families that are mainly, though not exclusively, either tropical or temperate. Thus, by extending the method employed in Tables IV. and V., we arrive at the conclusion that whilst 69 per cent. of the families that are mainly or exclusively tropical (158 in all) occur in both the Old and New Worlds, the proportion for families exclusively or mainly extra-tropical in the northern hemisphere (62 in all) is 77 per cent. (consult note at end of the paper). Under the circumstances the difference is small, and there is little to support the objection that the families common to the east and the west gather in high northern latitudes. But it would have been enough to point out that there is little room for such an objection in view of the fact that the proportion of tropical families that are common to the eastern and western worlds (69 per cent.) is very close to the proportion obtained for the families of the Angiosperms in the mass (70 per cent.).

The question whether the connection by families between the Old and the New World is chiefly a problem of the cold regions of the north, where the great American and Eurasian land-masses converge, is sufficiently answered by the behaviour of the seven terrestrial sub-families of the Araceæ. All of them occur in both the eastern and the western worlds, yet four of them are exclusively tropical, two are distributed in both the tropical and the temperate zones, and only one (Calloideæ) is restricted to cold northern latitudes. This last seems to be the only one of the seven sub-families that holds species common to the east and the west.

We have now raised a very interesting point. Although the families common to the two worlds do not gather in the north, the species behave in a very different fashion. It is there that the species common to the east and the west mostly congregate. Thus Harshberger states that of the 364 species of phanerogamic plants found in arctic western America, 320, or about 87 per cent., occur in temperate and arctic Asia; while of the 379 species in arctic east America, 239, or 63 per cent., are also found in the arctic regions of Europe ('Phytogeographic Survey of North America,' pp. 311, 312; 1911). The community of species rapidly diminishes as we leave the north behind until we reach the tropics, where with the exception of a few littoral, aquatic, and marsh plants, it disappears altogether, or is only represented by a few plants, some of them not free from suspicion as regards man's agency.

When we have two complementary families like the Myrsinaceæ and the Primulaceæ, the first tropical and the second temperate, it is the temperate family that alone displays a community of species between the two hemispheres.

The manner in which the proportion of species held in common dwindles as we go south is well illustrated by *Carex*. In the author's recent book on

the West Indies he has shown that the proportion of species which North America holds in common with Eurasia is 93 per cent. in the arctic regions, 40 per cent. in the sub-arctic regions, 24 per cent. in temperate latitudes, and 11 per cent. in the southern portion of the continent. If we take the total *Carex* floras of the eastern and western worlds in the northern hemisphere, we find that 80 per cent. of the species held in common are arctic, 29 per cent. sub-arctic, and 11 per cent. temperate. There are about 150 species common to North America and Eurasia, and of these two-thirds are arctic and sub-arctic species.

I am not able here to deal fully with the distribution of genera from this standpoint, but it cannot be doubted that the behaviour of genera common to both the eastern and western worlds will be intermediate between that of the species and families similarly distributed. This is established below in an analysis I have made of the list of the chief genera of the Angiosperms (about 3150) that is given by Dr. Willis in his 'Flowering Plants and Ferns,' 1908.

It has already been shown that whilst 69 per cent. of the families that are exclusively or mainly tropical (the subtropical regions being here included) occur in both the Old and the New Worlds, the proportion for families that are exclusively or mainly extratropical in the northern hemisphere is 77 per cent. On the other hand, with the genera that are mainly or exclusively tropical the proportion found in both worlds is only 23 per cent. (408 out of 1781), whilst with those mainly or exclusively restricted to regions beyond the tropics in the northern hemisphere the proportion is 42 per cent. (437 out of 1045). The genera, therefore, are in their behaviour intermediate between the families and the species. Whilst with the species nearly all (80-90 per cent.) of those common to the eastern and western worlds gather in the high latitudes of the north, with the families there is but a small tendency in this direction, and reasons have been before given for the belief that this tendency is even smaller than is above indicated. With the genera the proportions common to both worlds would be, as before noted, 23 per cent. for the tropics and 42 per cent. for the cooler latitudes of the north, and my figures suggest that north of the warm temperate region it would be at least 50 per cent.

Rightly interpreted, there should be a great significance in the principle that the tendency to congregate in the north on the part of plants represented in the eastern and western hemispheres is greatest and well marked with the species and least or non-existent with the family. The connections in the north belong to the later stages of the differentiating process, whilst the disconnections of the south date back to remote antiquity. One would have imagined that during the long ages that have passed the ocean-parted eastern and western worlds would have possessed scarcely a family in common, except in the north. Yet, as already shown, 69 or 70 per cent.

of the exclusively and mainly tropical families are common property of the Old and the New Worlds. All the influences that have been in operation in a differentiating world during an incalculable period of time have in a general sense not materially defaced the primitive family type, and the wonder is not that the differentiating agencies have done so much but that in this respect they have effected so little.

Yet, as we have seen, about 30 per cent. of the families do respond to the bi-cleavage of the land represented in the American and Eurasian hemispheres. (This applies, of course, only to the families in the mass, the proportion, as shown in a note to Table III., being much smaller, if we regard only the principal families.) But the differentiation, or the break-up, of the original family-type has proceeded far more rapidly in the New than in the Old World. In its development of new families the western hemisphere displays for its size nearly twice the capacity that is exhibited by the eastern hemisphere. Of the eighty residual families that are restricted either to one hemisphere or to the other (see Tables I., II.), one would have expected the Old World to possess by far the greater number, since the land-areas of the two hemispheres stand to each other in proportions exceeding two to one (O.W. 35; N.W. 15; based on data given in Whitaker's Almanack, 1917, p. 101, the polar regions being excluded, Australia being included in the Old World). But, to one's surprise, the difference in the number of families peculiar to each is relatively small, 45 being appropriated by the eastern and 35 by the western hemisphere. There will subsequently be occasion to mention this point again in association with another remarkable contrast presented by the New World with regard to the Old World.

[One may take this opportunity to observe that the excess in families in proportion to its area held exclusively by the New World is apparently not exhibited to the same degree by the genera. Of the 3150 genera of the Angiosperms named by Willis in his 'Flowering Plants and Ferns' (1908), the Old World appropriates 47 per cent. and the New World 25 per cent., about 28 per cent. being held in common. Of 529 genera belonging to 42 families dealt with in the 'Pflanzenreich' series, 51 per cent. are peculiar to the Old World, 32 per cent. to the New World, and 17 per cent. are common to both. The difference between the two worlds with regard to their peculiar families and genera may be thus expressed. With the families the difference would be as 9 (O.W.) to 7 (N.W.), but with the genera as 9 (O.W.) to 5 (N.W.).]

We have already observed that as many as 70 per cent. of the families do not respond to the great bi-cleavage of the land-surface of the globe, distributed as they are in both the eastern and western hemispheres. The response becomes greater and greater as we proceed down the scale from the family to the species. Thus the proportions common to the two

hemispheres are about 56 per cent. for the tribes, less than 20 per cent. for the genera, and about 1 per cent. for the species. As indicated in the table of results (Table I.), this subject has only been sampled for the tribes, genera, and species; but reference should there be made to the accompanying explanatory remarks. Yet the consistency in the results leaves no doubt that the general behaviour of the tribe, the genus, and the species is correctly illustrated in the above percentages. Here we perceive that the connection between the Old and the New Worlds is greatest with the family, less with the tribe, smaller still with the genus, and least with the species. Such a result is in perfect accord with what we should expect from the successive differentiations of a world-ranging family-type into tribe, genus, and species, the range contracting as one goes down the scale. The effect of the opposite method of regarding the species as diverging into the genus, the genus into the tribe, and the tribe into the family would be chaos.

But although 70 per cent. of the families occur in both worlds they represent in very different degrees the community in families between the east and the west. For instance, the original distribution of the generalized family-type in both worlds would be best exemplified now by a family of which all the tribes belong to both hemispheres. At the other extreme the connection implied by the community in families between the Old and the New World would be near its breaking-point in a family where no tribes were the common property of both hemispheres, and where most of the tribes were gathered together in one of them. The possibility thus presents itself of constructing a scale representing the various stages of detachment from a both-world distribution. Taking an imaginary family holding thirteen tribes the writer has framed such a scale, the first grade claiming the families where all, or nearly all, the tribes are common to both worlds, the complete detachment being illustrated in the eighth or last grade, where all the tribes are restricted to one and the same hemisphere. Such a grading of families would raise many difficulties, some of which ought not to prove insurmountable for the differentiation hypothesis. It is not possible, however, to do much more than draw attention to this method here. It will be sufficient to mention that the Compositæ, the Araceæ, and the Betulaceæ representing, respectively, the cosmopolitan, the tropical, and the temperate families, would find their place in the first grade. But the anomalies of this sort that are displayed in framing such a scale are in themselves instructive; and it is to be doubted whether a much more effective plan could be devised to illustrate the unequal value of families and to emphasize the necessity of grouping all families under a few great alliances. For instance, the Scitamineæ are represented in this scale by four families, the Marantaceæ, the Zingiberaceæ, the Musaceæ, and the Cannaceæ, which are scattered up and down its grades. From the stand-

point of the differentiation theory its place would obviously be in the first grade, together with the Compositæ and the Araceæ.

Having shown that the response to the cleavage of the land into two main masses, diverging from the north polar regions, increases with the Angiosperms as we go down the differentiating scale from the family to the species, being small with the family and very pronounced with the species, we will for a moment direct our attention to the behaviour of the great groups, or the cohorts, that lie immediately behind the families. As might have been expected, the response is even less than with the families. With the families about 70 per cent. ignore the cleavage. With the cohorts, on the other hand, 91 per cent., or 41 out of 45, are represented in both the eastern and western worlds (Table I.). It is noteworthy that the four cohorts that are exceptions to the rule hold in each case only a single family, the Cyclanthaceæ, the Leitneriaceæ, the Casuarinaceæ, and the Balanopsidaceæ, all of them tropical, the first two belonging to the New World and the last two to the Old World. They are all small anomalous families which have puzzled the systematist in his endeavours to place them. Together they represent the flotsam and jetsam of an ever-differentiating plant-world.

The response of the families to the differentiation of the climatic zones.—Although the families of the Angiosperms make a relatively small response to the bi-cleavage of the land-surface of the globe, their behaviour under the stress of climatic differentiation has been very different. From the tables (IV. and V.) it will be seen that nearly 60 per cent. of them are exclusively or mainly tropical, about 30 per cent. exclusively or mainly temperate, and about 10 per cent. fairly divided between the tropical and the temperate zones, all the regions outside the sub-tropics being regarded as temperate. Since the differentiation theory postulates an early age in the history of the Angiosperms when primitive generalized types ranged the globe and uniform climatic conditions prevailed, the later ages being occupied with the differentiation of types in response to the diversification of climate, it follows that the results for families above given represent a particular stage in the detachment or individualization of temperate floras.

When we look to the future and ask ourselves what will be the ultimate result of this gradual detachment of the temperate from the tropical floras, we shall be obliged to confess that there is little more to expect now. We might have looked far ahead to an age when the tropical and temperate floras would be sharply differentiated, an age when the world would be held by complementary families representing the independent expression of tropical and temperate conditions on the same type. But the influence of climatic differentiation is largely played out. Nature in the development of new forms seems to have mainly exhausted her efforts during the Upper Cretaceous period. That which has happened since has been principally the effect of the differentiation of ancient types in response to the progressive

diversification of conditions, and all we have to look for is the assertion of man's predominance in his replacement of natural floras by his cultivated plants and his weeds. The time for revolutions in the plant-world was spent geological ages ago ; and Nature in her present operations can offer us but little aid in unravelling the revolutionary past.

The subject of the detachment of the temperate from the tropical floras during the ages through which the differentiating influences have reigned supreme, brings up the question of the complementary families, those which, although now ranked as distinct families in the tropical and temperate zones, are so closely linked together that they may be regarded as the result of the differentiation of the same world-ranging family-type. Thus we may view the Primulaceæ in the temperate regions and the Myrsinaceæ in the tropics as complementary to each other and as representing the first step in the differentiation of a common parent type. In the same way and with the same implications we may link the Umbelliferæ (temperate) with the Araliaceæ (tropical), and the Chenopodiaceæ (temperate) with the Amarantaceæ (tropical).

But the effect of the secular differentiation of climatic conditions and of the individualization of the temperate zones has not always been the development of a world-ranging type into separate tropical and temperate families. Some, like the Compositæ, have, as far as the retention of family characters is concerned, defied the differentiating agencies. In yielding to the exigencies of the differentiation of climates, though still holding the world, they have retained in this case the essential characters of the family, on the absolute permanence of which, in the case of the Compositæ, Bentham lays stress. Others like the Scitamineæ are still confined to their original home in the equatorial regions of the globe, having failed to adapt themselves to the newly differentiated temperate zones. They have given rise to separate sub-families, often ranked as families, in the different warm regions of the globe, but in no sense as the result of the secular diversification of climate.

We have remarked that the work of the differentiation of floras is largely spent, as far as climatic influences are concerned. Yet, great as this work has been, we are, as the writer thinks, not justified in regarding it from any other standpoint than that of adaptivity. It is not the work that was carried on in those remote Mesozoic ages when the larger plant-groups, now represented by the alliances of families and by the cosmopolitan and pan-tropical families, were first developed. The characters that distinguished them then distinguish them now, and as far as their essential characters are concerned they have made but little response to the great climatic differentiation of the ages. The rise of the Xerophytes presents one of the most important and far-reaching results in the story of distribution and differentiation. Yet they are of the later and not of the earlier age ; and it is

questionable whether any truly natural family comparable with the great families has been developed through the changes inducing the xerophytic organization. They might disguise them, as in the case of the Cactaceæ and of some of the Euphorbiaceæ ; but the essential floral characters were produced in pre-xerophytic times. A family in its truest sense is born and not made.

It may here be added that the process of detachment of temperate families from the tropics has not been uniform in the two hemispheres, the east and the west, the tendency to the differentiation or detachment of temperate families in the Old World being far more marked than in the case of the New World. Thus, with the exclusively Old World families 44 per cent., or 20 out of 45, are restricted to the tropics, using that term as including the sub-tropics ; whilst with the exclusively New World families the proportion is as high as 77 per cent., or 27 out of 35 (Table III.). Thus it also appears that the tropics of the American continents actually possess a greater number of peculiar families than those of the Old World. This feature of American plant-distribution is to be associated with another feature, already alluded to and illustrated in the same table, the New World in its entirety owning nearly as many peculiar or endemic families as the Old World, 35 against 45, though barely half its size. In the New World, therefore, there has been not merely a greater development of families, but a greater segregation of such families within the tropics. In other words, although the process of detachment of temperate families from the tropics has been far less effective in the New World than in the Old World, the differentiation of new families in the American tropics has been far greater. This is one of the lessons supplied by the western hemisphere when treated statistically from the standpoint of the differentiation hypothesis. [Reference has before been made to the contrast in behaviour of the genera in one of these respects.]

Before quitting the subject of the influence of the differentiation of the climatic zones on the development of the families, a few remarks may be devoted to the numerical distribution of the families of the Angiosperms in the north and south hemispheres, which is illustrated in Tables VIII., IX., X. The matter cannot be discussed at any length here ; but it may be observed that the numerical apportionment is much as though the land-areas in the two hemispheres were approximately the same in extent. Yet within the limits of vegetation there must be at least $2\frac{1}{2}$ times as much land in the northern as there is in the southern hemisphere. The differentiation of families has thus been far more active in the south than in the north, a result that might be attributed to the much greater isolation of the southern land-masses.

The larger plant-groups behind the families.—We have already dealt with the cohorts in connection with the families, and it has been shown that as

far as the principle of differentiation is concerned they behave conformably with their position in the differentiating scale just above the families. Before one proceeds to deal statistically with the large groups of the Angiosperms that lie behind the cohorts, a word may be said regarding the needs of the differentiation hypothesis in this respect. Between the 45 cohorts and the two classes of the Monocotyledons and Dicotyledons, there is a considerable break or gap in the differentiating scale, which cannot be very satisfactorily bridged over by dividing up the Dicotyledons in a few groups as is done below. The advocate of the differentiation theory, and the writer ventures to think that his need is also that of the systematist, requires an intermediate group holding about a score or two dozen great alliances, each of them cosmopolitan or pantropical, and all families of restricted range will have to be reduced to terms of an alliance. Here geographical considerations would be foremost, and the complemental families as above described would take a prominent part in building up an alliance which would either possess the tropics or hold the world, the pantropical and cosmopolitan alliances being regarded as of equal value, notwithstanding the failure of the first-named to respond to the differentiation of the temperate zone. The object would be to restore the original world-ranging generalized types; and if the number of such great alliances should exceed the limits above named, they would serve to displace the cohorts which could then be very well dispensed with. One would commend the use of familiar designations for all the alliances, such as Compositæ, Rubiaceæ, Ericales, Leguminosæ, Scitamineæ, Aroideæ, Palmæ, etc. But in restoring the original type in the shape of an alliance we should give it the name of the tropical parent form where a cosmopolitan alliance is concerned. Any names like Geraniales and Primulales that would seem to credit the alliance with an origin in the temperate zones should give place to the name of the older tropical forms.

The Monocotyledons and Dicotyledons.—Notwithstanding the great disparity in the number of families they hold (Monocotyledons 43, Dicotyledons 229), some interesting comparisons can be made. In the first place, it will be worth while ascertaining how they stand to each other with reference to the proportion of families occurring in both hemispheres, the east and the west. They differ but little in this respect, since the proportion is 76·8 per cent. for the Monocotyledons and 69·4 per cent. for the Dicotyledons (Table II.). This approximation exists in spite of the circumstance that 30 per cent. of the Monocotyledonous families are aquatic or sub-aquatic (Table V.). Of the 272 families of the Angiosperms 26 are aquatic or sub-aquatic, and of these half (13) are Monocotyledons. It would therefore appear that as regards the occurrence of a family in both the Old and the New Worlds it behaves the same, whether monocotyledonous or dicotyledonous, or whether aquatic or terrestrial in habit. This independence of the proportion of aquatic plants is also displayed, as will subsequently be shown, by the

subdivisions of the Dicotyledons with respect to this feature in distribution. Sympetalæ and Monocotyledons are distributed in the same proportions in both worlds, as respects their families, although the first holds only 2 per cent. of aquatic families and the second as much as 30 per cent. Yet it is true that the large proportion of aquatic families exercises an influence in determining the distribution of Monocotyledons ; but, as is established below, that influence is mainly concerned in curtailing their latitudinal extension and affects but slightly, as already shown, their response to the bi-cleavage of the land, as indicated by the proportion of families existing in both hemispheres.

Although the Monocotyledons and the Dicotyledons are at one in the similar responses of their families to the great cleavage of the land, they differ much in the responses made by their families to the differentiation of the latitudinal climatic zones. Whilst, as shown in Tables IV. and V., both classes hold about the same proportion of exclusively or mainly tropical families, 58 and 59 per cent. respectively, yet in the case of the Dicotyledons nearly all of the residue are either mainly or exclusively temperate, while with the Monocotyledons two-thirds of the remainder are fairly well shared between the tropical and temperate zones. It is thus evident that as regards the differentiation or separation of temperate floras from the original tropical floras, the Dicotyledons are in a much more advanced stage than the Monocotyledons. The equal sharing between the tropical and temperate zones of a family originally tropical represents the first stage in the detachment of a temperate family. The appropriation of a family by the temperate zones represents the last stage in the detachment of a family from its original abode in the tropics. This last stage has been attained by 21 per cent. of the families of the Dicotyledons and by only 7 per cent. of those of the Monocotyledons (Tables IV., V.), the last-named having lagged behind the Dicotyledons to a marked degree as regards the differentiation or detachment of temperate floras. The contrast may be stated in another way. Thus, whilst 34 per cent. of the families of the Dicotyledons are either temperate or mainly temperate, the proportion for the Monocotyledons is only 14 per cent. This may be due to the greater prevalence of aquatic families among the Monocotyledons. Here the proportion is as much as 30 per cent., that for the Dicotyledons being under 6 per cent. (Table V.). The explanation would be that aquatic conditions present a much smaller contrast between the temperate and tropical zones than is offered by those of land plants.

The conclusions to be drawn from the behaviour of the great plant-groups of the Angiosperms.—Although the present arrangement of the main land-masses and of the oceans is largely ignored by the great plant-groups, the response becomes more and more evident as we go down the differentiating scale. It goes without saying that in whatever way we split up the Dicotyledons, whether in two or three or four groups, all the primary groups of

the Angiosperms, commencing with the Monocotyledons and ending with the Sympetalæ, take no heed of the present distribution of land and water. But there is a slight response for the cohorts, 9 per cent. of them being restricted to either the New or the Old World. Of the families 30 per cent., of the tribes about 44 per cent., of the genera at least 80 per cent., and of the species about 99 per cent. respond to the cleavage of the land into two main masses diverging from the north polar regions (Table I.).

This contrast in the behaviour of the larger and lesser plant-groups implies a very great contrast in geographical and climatic conditions. There would seem to have been a pre-differentiation era that corresponded with geographical and climatic conditions very different from those that now prevail. At that time generalized types ranged the globe and the conditions were far more uniform than at present. It was an age, we imagine, when floral mutations were relatively unchecked. After that era the age of differentiating conditions began, the effect of the progressive differentiation of conditions being to restrict more and more the play of mutation in the case of the floral organs, so that in our age the capacity is rarely exercised. In the pre-differentiation era the generalized type had the whole earth for its range and uniformity of conditions for its "mise-en-scène," a setting that was destroyed when climate began to individualize. During such an era reigned other things, other ways, and other conditions.

If we were to draw a line dividing this distant era from the succeeding ages of differentiation, we should draw it just below the great family groups as illustrated by the Compositæ and the Araceæ; and if we were to contrast the geographical conditions, we should point to the fact that whilst the family and the groups behind it or above it mainly or entirely ignore the existing arrangement of land and sea, the genus and the species are in a sense the offspring of it. Distribution in the distant past was chiefly a story of generalized family types. In the later ages it has been principally a story of the genus and the species and of adaptive response to the progressive differentiation of conditions. The failure of the larger plant-groups to respond to the great bi-cleavage of the land-mass and their subsequent ready response to climatic differentiation mark out the two great eras—the pre-differentiation age and the age of differentiation that followed.

What is earliest in distribution belongs to the family and the large groups behind it. What is recent belongs to the genus and the species. To employ the terms "genus" and "species" when speaking of an age different in almost every respect from the present one is to muddy the waters, or, rather, to confuse the issues. Such a habit assumes that the present is like the past, that we can picture what has been from what is. Yet to think only in terms of genera and species is to ignore the better half of the story of the development of the plant-world. The age that witnessed the rise of

the great families and the age that witnessed their subsequent differentiation are things apart, and cannot be dealt with by the same method.

If one were asked how such a view of distribution could be reconciled with that of the animal world, one might reply that since plants and animals have been developed on quite different plans, the plant requires an application of the Darwinian theory of evolution, in which this distinction is recognized. In the one case development has centred around provisions for securing the continuance of the like. In the other it has been concentrated on the production of a higher order of beings culminating in Man. The first secured, the second became possible.

Note on the sub-divisions of the Dicotyledons.

In order to make a further statistical comparison of the Dicotyledons with the Monocotyledons, the number of families in the first being according to Engler's system more than five times those of the second, the Archichlamydeæ have been broken up into four groups, making with the Sympetalæ five groups for the class. For this purpose the system of Engler was preferred, since a scale of development is implied in the arrangement adopted; whilst with that of Bentham and Hooker the placing of more than a fifth of the families there recognized in the Incompletæ makes a linear classification impracticable. Yet it was the Incompletæ that led the writer to pay attention to this matter, with the result that the group viewed from this standpoint appears to be very far from an anomalous group. On the contrary, when treated statistically it proves to be the most typical, as far as percentages are concerned, of all the groups of the Dicotyledons.

Assuming that the series—Monocotyledons, Archichlamydeæ, Sympetalæ—represents a scale of plant-development and that the same is indicated in the arrangement of the groups of families of the Archichlamydeæ, the writer broke up the last-named into four groups and obtained the following succession:—

Monocotyledons, holding 43 families.

Dicotyledons	{	Archichlamydeæ	Group A. Cohorts 1-14 with 37 families.				
			"	B.	"	15-18	" 41 "
			"	C.	"	19-21	" 42 "
			"	D.	"	22-26	" 58 "
		Sympetalæ, holding		51 families.			

Group A includes 25 of the 37 families in Monochlamydeæ or Incompletæ of Bentham and Hooker. Group B comprises the cohorts Ranales, Rhœadales, Sarraceniales, and Rosales; Group C, the cohorts Geraniales, Sapindales, and Rhamnales; and Group D, the cohorts Malvales, Parietales, Opuntiales, Myrtifloræ, and Umbellifloræ.

Together here we have six groups which we will term the Primaries, and

in order to give point to their statistical treatment we will assume the truth of the implication of Engler's system that they represent a genetic sequence commencing with the Monocotyledons and terminating with the Sympetalæ. It would have been possible to discuss this matter at considerable length; but as the treatment is purely tentative a few general remarks will be here sufficient, and the columns of the tables (II., IV.-VIII.) will be allowed largely to tell their own story.

It will be at once noticed that whilst the six primary groups of the Angiosperms behave with comparative uniformity in matters concerned with the bi-cleavage of the land-mass, as reflected in their distribution in the Old and New Worlds, they often present marked contrast in their responses to the differentiation of the climatic zones. Thus, to take their behaviour in the first case, the proportions of families occurring in both the east and west hemispheres vary only between 62 and 77 per cent. (Table II.); and if we limit the comparison to the families of world-wide distribution, termed cosmopolitan in the table, the percentages range only between 21 and 33 (Table VII.). We find a like agreement in the proportion of families confined either to the Old or to the New World. Thus, the percentage of families restricted to the eastern hemisphere varies only between 12 and 24 and of those peculiar to the western world only between 11 and 14 (Table II.). This conformity is remarkable when we reflect that in small groups of this kind we can only appreciate general approximations or marked deviations. The similarity in behaviour on the part of the six primary groups respecting the distribution of their families in the eastern and western hemispheres is quite independent of the proportion of aquatic and sub-aquatic families in each group, which is as high as 30 per cent. for the Monocotyledons and as low as 2 per cent. for the Sympetalæ (Table V.).

Yet this similarity in behaviour disappears when we regard the response made by these six primary groups to the differentiation of the climatic zones. As indicated in Table V., they display great variety in the appropriation of their families by the tropical and temperate zones. Thus Groups C and D of the Archichlamydeæ are the most tropical; and Group B and the Sympetalæ are the least tropical; whilst the Monocotyledons and Group A stand between. On the other hand, the Monocotyledons are by far the least temperate of all the groups, which is to be associated with the fact that a much larger proportion of the families are in a transition state—that is, are equally divided between the zones—than is the case with the other groups. Then again Group A is in these respects the most average of the six primary groups, approaching nearest in its behaviour to that of the Dicotyledons in the mass and nearer still to that of the Angiosperms. It comes closest to the Incompletæ of Bentham and Hooker, a result to be expected since the two equal-sized groups hold about two-thirds of their families in common; whilst the group of the Incompletæ in its response to

the differentiation of the climatic zone is the most typical of all, making a near approach to the Dicotyledons in their entirety and the nearest of all to the Angiosperms in the mass (Table V.).

Comparison may now be made between the Monocotyledons and the Sympetalæ as representing the extremes of the series constituted by the six primary groups. It has been shown in an earlier page that with regard to the detachment or differentiation of temperate floras from the original tropical flora the Dicotyledons are far in advance of the Monocotyledons. But, as indicated in the columns of Table V., the five groups of the Dicotyledons exhibit considerable divergencies in their behaviour in this respect; and it is not possible to construct a series with the Monocotyledons and the Sympetalæ at the extremes. Yet in view of the position of these two groups at the extremes of the series accepted by some systematists, a brief comparison may be profitable. The escape of the Sympetalæ from the tropics, as contrasted with the lagging behind of the Monocotyledons, is illustrated in different fashions in the columns of Tables IV., V., and VII. Nearly all the tropical families of the group last named, that is 23 out of 25, are exclusively tropical. With the Sympetalæ only 14 out of the 25 tropical families are exclusively tropical. Then, again, whilst 12 out of the 43 families of the Monocotyledons are fairly well shared between the tropical and temperate zones, with the Sympetalæ the number of families shared is 4 out of 51, or only about 8 per cent. The bulk of the non-tropical families of the Monocotyledons are in fact in the transition state. With the Sympetalæ the non-tropical families have in most cases reached a further stage and are more or less completely detached from the tropics. Whilst with the Monocotyledons the families exclusively tropical amount to 53 per cent. and those exclusively or mainly temperate to only 14 per cent., with the Sympetalæ only about 27 per cent. of the families are confined to tropical regions and as many as 43 or 44 per cent. are exclusively or mainly temperate. A possible explanation of the contrast in behaviour between these two groups is supplied in the great predominance of families of aquatic habit in the Monocotyledons (see Table V.); but this is a matter discussed in the following note.

Note on the influence of aquatic and sub-aquatic families on the distribution of the Angiosperms.

The apportionment of the families of aquatic habit between the larger groups of the Angiosperms and their distribution over the eastern and western hemispheres are illustrated in Tables V. and VI. Of the 26 aquatic families recognized by the writer, 13, or half, are appropriated by the Monocotyledons, 12 belong to the Archichlamydeæ, and only 1 to the Sympetalæ, namely the Lentibulariaceæ. It has been shown that it makes

but little difference in the distribution of the larger family-groups in the eastern and western hemispheres whether they hold many or few aquatic families. Thus the Monocotyledons holding 30 per cent. of these families and the Sympetalæ holding only 2 per cent. are distributed in the same proportion over the Old and New Worlds, in each case about 77 per cent. of their families being common to the two hemispheres (Table II.). The aquatic families are therefore quite neutral in their influence on the general response of the Angiosperms to the great bi-cleavage of the land-mass of the globe.

On the other hand, they sometimes seem to have a marked influence on the response made by families to the differentiation of the climatic zones. Thus, as shown in the previous note, the Monocotyledons lag behind the Sympetalæ to a marked degree in the detachment of temperate families from the tropics; and the implication is that since the former hold as many as 30 per cent. of aquatic families, and the latter as few as 2 per cent., the influence of the aquatic habit in checking the process of differentiation is displayed in the diminution of the climatic contrast between the tropical and temperate zones. Yet, although this may sufficiently explain the lagging of the Monocotyledons in the tropics as compared with the Sympetalæ, it will not explain why amongst the primary groups of the Archichlamydeæ those that are most tropical, like C and D, hold the smallest number of aquatic families (Table V.).

Note on the relative proportions of "both-world" families in the tropics and in the extra-tropical regions of the northern hemisphere.

The statement on page 447 that 61 per cent. of tropical families and 64 per cent. of northern extra-tropical families occur in both the Old and the New Worlds is based on data given in Table III. Here we are concerned with families purely tropical and purely northern extra-tropical. But for the statement that follows it the data are only partially supplied in the Tables, as in IV., V., etc. It is there asserted that 69 per cent. of exclusively or mainly tropical families and 77 per cent. of exclusively or mainly extra-tropical families in the northern hemisphere are found in both the Old and the New Worlds. But to obtain these results it was necessary to eliminate the southern extra-tropical elements; and to avoid the necessity of giving another complicated set of tables I have here given the data on which this assertion is based. They are as follows:—

The total of 153 exclusively or mainly tropical families is made up of 120 exclusively tropical and of 33 tropical and north temperate families but *mainly tropical*. (In these connections it should be stated that the tropics include the subtropics and the north temperate all the northern extra-tropical regions.) Of the exclusively tropical 73 and of the mainly tropical all occur

in both worlds. This gives a total of 106 both-world families out of a total of 153 mainly or exclusively tropical families, or 69 per cent.

The total of 62 families exclusively or mainly extra-tropical in the northern hemisphere is made up of 36 exclusively north temperate and 26 north temperate and tropical but *mainly north temperate*. Of the exclusively north temperate 23 and of the mainly north temperate families 25 exist in both the Old and the New Worlds. This gives a total of 48 both-world families out of a total of 62 northern extra-tropical families, or 77 per cent.

It is worth noting the manner in which, according to these results, the both-world families tend to congregate in the intermediate region between the tropics and the north temperate zone—that is, among the tropical and north temperate families that are mainly tropical and among the north temperate and tropical families that are mainly north temperate. Considerable importance attaches itself to the interpretation of this tendency.

TABLE I.

(See Explanatory remarks.)

A.—The distribution of the Angiosperms between the Old and New World.

	Primaries.		Cohorts.		Families.		Tribes.		Genera.		Species.	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Old World	2	4.5	45	16.5	39	24.5	579	46	9889	52
New World	2	4.5	35	13.0	31	19.5	512	41	8874	47
Both Worlds	100	41	91.0	192	70.5	89	56.0	168	13	197	1
	6	100	45	100	272	100	159	100	1259	100	18960	100

B.—Compositæ excluded.

	Tribes.		Genera.		Species.	
	No.	%	No.	%	No.	%
Old World	38	26	270	51	5031	52.6
New World	31	21	169	32	4411	46.0
Both Worlds	77	53	90	17	134	1.4
	146	100	529	100	9576	100

C.—Compositæ alone.

	Tribes.		Genera.		Species.	
	No.	%	No.	%	No.	%
Old World	1	..	309	42	4858	51·8
New World	343	47	4463	47·5
Both Worlds	12	..	78	11	63	0·7
	13	..	730	100	9384	100

D.—Genera.

	No.	%
Old World	1472	46·7
New World	800	25·4
Both Worlds	878	27·9
	3150	100

Explanatory remarks.—With reference to sub-table A it may be remarked that the materials are complete for the larger groups, the primaries, the cohorts, and the families. For the tribes the matter has been sampled. In this respect the data for 23 families and sub-families were tabulated in a paper by the writer published in the 'Transactions' of the Victoria Institute for 1907. Those for 19 others have since been added, making a total of 42; and on these the results for the tribes, genera, and species are based. The volumes of the 'Pflanzenreich' series have here been used, except with the Compositæ, where Bentham has been followed. In the early paper only the tribes designated as such were utilised. In this sub-table all intermediate groupings between the genera and the family are employed under this head where it is practicable.

In sub-table B all the materials in sub-table A are used with the exception of those for the Compositæ, which are treated separately in sub-table C.

In sub-table D are given the results of an analysis made by the writer of the list of chief genera (about 3150 for the Angiosperms) that is given by Dr. Willis in his 'Flowering Plants and Ferns' for 1908. The increase in the percentage of genera common to the eastern and western hemispheres is due to the fact that the list is only concerned with "chief" genera; and it is obvious that the number of genera with limited distribution that are here excluded is very large, and would have gone far to pull down the percentage of both-world genera. Probably in a complete list of genera the percentage found in both worlds would be nearer that for the Compositæ, where the proportion is 11 per cent.; and there is therefore much to support the estimate adopted in this paper of "less than 20 per cent."

TABLE III.

The Families of the Angiosperms distributed according to hemispheres (east and west) and to latitudinal zones.

(For the sake of comparison the results for the Cohorts are given in the last column.)

		No.	Percentage.	Cohorts.
Old and New Worlds or East and West Hemispheres.	Cosmopolitan	70	25.7	26 = 57.8 %
	Tropics	73	26.8	11 = 24.5
	Tropics and North Temperate ..	15	5.5	1 = 2.2
	Tropics and South Temperate ..	8	3.0	
	North and South Temperate	14	5.1	2 = 4.5
	North Temperate	9	3.3	
	South Temperate	3	1.1	1 = 2.2
		192	70.5	41 = 91.2 %
Old World or East Hemisphere.	General			
	Tropics	20	7.3	2 = 4.4 %
	Tropics and North Temperate	
	Tropics and South Temperate ..	5	1.8	
	North and South Temperate	2	0.7	
	North Temperate	8	3.0	
New World or West Hemisphere.	South Temperate	10	3.7	
		45	16.5	
	General			
	Tropics	27	10.0	2 = 4.4 %
	Tropics and North Temperate ..	1	0.4	
	Tropics and South Temperate ..	1	0.4	
	North and South Temperate	
	North Temperate	3	1.1	
	South Temperate	3	1.1	
		35	13.0	
		272	100	45 = 100

NOTE.—The Tropics include the Subtropics, and the Temperate zones include all extra-tropical regions. It is important to remember that the families are here treated in the mass, the small with the large. Practically all the great families would be represented in both the east and west hemispheres. The author has made a list of the principal families, those holding the largest number of genera and species. They number about 90, and at least 95 per cent. of them are found in both hemispheres. The distribution of families in the north and south hemispheres is also dealt with in different fashions in Tables VIII., IX., X.

TABLE IV.

Distribution of the Families and Cohorts of the Angiosperms according to climatic or latitudinal zones.

(This Table is supplementary to Table V.)

A. <i>Families.</i>						
	Exclusively tropical.	Tropical and temperate but mainly tropical.	Equally shared between tropical and temperate zones.	Temperate and tropical but mainly temperate.	Exclusively temperate	Total.
Archi- chlamydeæ. {	A 17	4	4	4	8	37
	B 15	5	4	7	10	41
	C 18	11	1	1	11	42
	D 33	7	3	5	10	58
Total	83 (46·6%)	27 (15·2%)	12 (6·7%)	17 (9·6%)	39 (21·9%)	178
Sympetalæ	14 (27·5%)	11 (21·6%)	4 (7·8%)	12 (23·5%)	10 (19·6%)	51
Dicotyledons ..	97 (42·3%)	38 (16·6%)	16 (7·0%)	29 (12·7%)	49 (21·4%)	229
Monocotyledons .	23 (53·5%)	2 (4·6%)	12 (27·9%)	3 (7·0%)	3 (7·0%)	43
Angiosperms ..	120 (44·1%)	40 (14·7%)	28 (10·3%)	32 (11·8%)	52 (19·1%)	272
B. <i>Cohorts.</i>						
Angiosperms ..	10 (22·2%)	12 (26·7%)	17 (37·8%)	4 (8·9%)	2 (4·4%)	45

Explanation.—Engler's system is followed. The temperate include all extra-tropical regions, and the subtropics are comprised in the tropics. Cohorts 1-14 are placed under A, 15-18 under B, 19-21 under C, and 22-26 under D. Table V. should be consulted in this connection,

TABLE V.
The Families of the Angiosperms distributed according to climatic zones.
(In Table IV. a different arrangement of the columns is adopted for the second series.)

	Mono- cotyledons.	Archichlamydeæ.				Sympetaleæ.	Incompleteæ.	Archichlamydeæ.	Dicotyledons.	Angiosperms.
		A.	B.	C.	D.					
Tropical	% 58 (25)	% 57 (21)	% 49 (20)	% 70 (29)	% 69 (40)	% 49 (25)	% 59 (23)	% 62 (110)	% 59 (135)	% 59 (160)
Temperate	14 (6)	32 (12)	41 (17)	28 (12)	26 (15)	43 (22)	33 (13)	31 (56)	34 (78)	31 (84)
Shared equally	28 (12)	11 (4)	10 (4)	2 (1)	5 (3)	8 (4)	8 (3)	7 (12)	7 (16)	10 (28)
	100 (43)	100 (37)	100 (41)	100 (42)	100 (58)	100 (51)	100 (39)	100 (178)	100 (229)	100 (272)
Exclusively tropical	% 53	% 46	% 37	% 43	% 57	% 27	% 44	% 46	% 42	% 44
Tropical and temperate } but mainly tropical ... }	5	11	12	26	12	22	15	15	17	15
Shared equally	28	11	10	2.5	5	8	8	7	7	10
Tropical and temperate } but mainly temperate. }	7	11	17	2.5	9	23	13	10	13	12
Exclusively temperate ...	7	21	24	26	17	20	20	22	21	19
	100	100	100	100	100	100	100	100	100	100
Aquatics	13=30%	1=2.7%	7=17%	2=5%	2=3.5%	1=2%	3=8%	12=7%	13=5.7%	26=9.5%

Explanation of Table V.

The system of Engler is adopted, the Incompletæ of Bentham and Hooker being added for the sake of comparison. The Archichlamydeæ have been divided by the writer into four groups:—A.=cohorts 1-14; B.=cohorts 15-18; C.=cohorts 19-21; D.=cohorts 22-26. The subtropics are included in the tropics and the extra-tropical zones are classed as temperate.

The general results are given in the first series and the details in the second series. Thus it is there shown that in the first series the tropical families include those that occur also in temperate regions, but are mainly tropical, and the same with the temperate families, which include those that are mainly as well as those that are exclusively temperate. The third series deals with the aquatic and subaquatic families, concerning which other particulars are given in Table VI.

In the first series the absolute numbers are enclosed in parentheses. In the second series they are omitted, but they are given in Table IV.

By following Engler's system in the cases of the Cytinaceæ, the Cupuliferæ, and the Piperaceæ of the Incompletæ the number of families has been increased from 36 to 39 for that group.

TABLE VI.

Distribution of Families of aquatic and subaquatic habit in the Old and New Worlds.

	Old and New Worlds.	Old World.	New World.	Total.
Monocotyledons	11	1	1	13
Archichlamydeæ A	1	1
" B	3	3	1	7
" C	1	..	1	2
" D	2	2
Sympetaleæ	1	1
	18	4	4	26

Other details are given in Table V. and the groups A, B, C, D, are there explained.

TABLE VII.
(Illustrating the proportion of Cosmopolitan families, and of families confined to the tropics of the Old World and the New World, either separately or conjointly.)

	Mono- cotyledons (43).	Archichlamydeæ.				Sympetalæ (51).	Archichlamydeæ (178).	Dicotyledons (229).	Angiosperms (272).
		A (37).	B (41).	C (42).	D (58).				
	%	%	%	%	%	%	%	%	%
Cosmopolitan	32.6	21.6	26.8	21.4	20.7	31.4	22.5	24.5	25.7
Restricted to tropics of the Old World	9.3	8.1	9.8	2.4	10.3	3.9	7.9	7.0	7.4
Restricted to tropics of the New World	11.6	8.1	7.3	9.5	13.8	7.8	10.1	9.6	10.0
Restricted to tropics of both Worlds	32.5	30.0	19.5	31.0	32.8	15.8	28.6	25.7	26.8
Total restricted to the tropics	53.4	46.2	36.6	42.9	56.9	27.5	46.6	42.3	44.2

Explanation.—The figures in parentheses represent the total number of families in each group. In the case of the Archichlamydeæ cohorts 1-14 are placed under A, 15-18 under B, 19-21 under C, and 22-26 under D. The Cosmopolitan families have been added for the sake of convenience only. The table is used in this way. The Monocotyledons, which comprise 43 families, possess 32.6 per cent. of cosmopolitan families, 9.3 per cent. of families restricted to the tropics of the Old World, 11.6 per cent. of families restricted to the tropics of the New World, and 32.5 per cent. to the tropics of both Worlds, the general total of families confined to the tropics (including subtropics) being, therefore, 53.4 per cent. Tables IV. and V. should be referred to in these connections.

TABLE VIII.

The distribution of the Families of the Angiosperms in the North and South Hemispheres.

(Engler's system is followed. In the subdivisions of the Archichlamydeæ, as adopted by the writer, group A. holds cohorts 1-14 ; B. 15-18 ; C. 19-21 ; and D. 22-26. The tropics include the subtropics, and the temperate zones signify all extra-tropical regions.)

	Mono-cotyledons.	Archichlamydeæ.					Sym-petalæ.	Dico-tyledons.	Angiosperms.
		A.	B.	C.	D.	All 4 groups.			
Cosmopolitan	14	8	11	9	12	40	16	56	70—25·7%
North and South Temperate .. }	3	2	3	3	..	8	5	13	16— 5·9
North Temperate	2	4	5	5	16	4	20	20— 7·4
Tropics and North Temperate .. }	..	4	2	3	2	11	5	16	16— 5·9
Tropics	23	17	15	18	33	83	14	97	120—44·1
Tropics and South Temperate .. }	3	..	3	1	1	5	6	11	14— 5·1
South Temperate	4	3	3	5	15	1	16	16— 5·9
	43	37	41	42	58	178	51	229	272—100

TABLE IX.

The distribution of the 272 Families of the Angiosperms in the North and South Hemispheres.

Cosmopolitan	70—25·7%
North and South Temperate	16— 5·9%
Exclusively or mainly North Temperate	26— 9·6%
Exclusively or mainly Tropical	139—51·1%
Exclusively or mainly South Temperate	21— 7·7%
	272—100·0%

NOTE.—The Angiosperms are here treated in the mass as in the last column of Table VIII., but with a little different arrangement. All extra-tropical regions are classed as temperate.

TABLE X.

The distribution of the 272 Families of the Angiosperms in the North and South Hemispheres.

(The data in Table III. have here been utilised. The tropics include the sub-tropics, and all other regions are classed as temperate.)

North Temperate in varying degree	122 or 45 %
Tropical " " 	220 or 81 %
South Temperate " " 	116 or 43 %

NOTE.—The total number of families represented to a greater or less extent in temperate regions, that is in regions outside the tropics or subtropics, is 152 or 56 per cent. The representation in the tropics is above shown to be 220 or 81 per cent.

SUMMARY.

From a consideration of the problems of plant-distribution, the writer is led to regard the history of the Angiosperms as resolving itself into two principal eras :—

(1) The era that witnessed the rise of the great families, a period of relatively uniform conditions.

(2) The era that witnessed the differentiation of these family types in response to the differentiation of the climatic and other conditions.

It is argued that conclusions drawn from the prevailing influences now in operation could only be applied to the differentiation of the ancient family types—that is to say, to the second era in plant-history. It is not possible, so it is held, to apply a theory based on the present to an age of other things, other ways, and other conditions. Only the hypothesis that finds its guide to the past in the abnormalities of the present can be of service to us in the interpretation of times so different.

The subject is introduced by a reference to two papers, contributed to the 'Journal of the Linnean Society,' which have an important bearing on the subject, the one by Bentham on the Compositæ, the other by Huxley on the Gentians. Then follows a statement of the differentiation hypothesis which involves the differentiation of primitive world-ranging types in response to the progressive differentiation of their originally uniform conditions. Allusion is then made to the dilemma into which all theorists fall when they come to handle the larger groups, the very persistence of which in our own age depends on the stability of their essential characters. If stable now, why so unstable then? We are thus forced to the conclusion that in the distant era

that witnessed the deployment of the Angiosperms instability prevailed. It was an age of mutations, free and unchecked, and an age of uniformity of conditions, the mutability decreasing and the modifications becoming more and more fixed with progressive differentiation of conditions, an explanation suggested by a perusal of the accounts by Dr. Willis of his prolonged investigation on the Podostemaceæ.

The distribution of families is then treated statistically ; and it is shown that whilst they largely ignore the cleavage of the land into two great masses diverging from the north, they respond in a marked degree to the differentiation of the climatic zones. Behind their disregard for the present arrangement of continents and oceans lies the story of the first era, and behind their ready response to climatic differentiation lies the story of the second era. In the circumstance that the response made to the bi-cleavage of the land-mass is absent or small with the larger groups and becomes greater and greater as we go down the differentiating scale until it attains its maximum in the species, is recognised the contrast of conditions between the pre-differentiation era and the era when differentiation reigned supreme. It is held that there is a method here disclosed that could only arise by the family differentiating into the tribes, the tribe into the genera, and the genus into the species, since the opposite method of commencing with the species would produce chaos.

The paper ends with the application of the statistical treatment to the larger groups behind the families, and it is shown that whilst the Dicotyledons display a much greater tendency to detachment from the tropics than the Monocotyledons, the Sympetalæ stand foremost in this respect amongst all the groups of the Dicotyledons. It may be added that there is a large amount of material in the ten tables which from considerations of space could not be discussed. These data have therefore to tell their own story.
