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1907.

ORDINARY GENERAL MEETING.*

COLONEL T. H. HENDLEY, C.I.E., IN THE CHAIR.

The Minutes of the previous Meeting were read and confirmed.

The Rev. William McKibbin, D.D., LL.D., was elected a member, and the following paper was read by the Secretary in the absence of the Author:—

PLANT-DISTRIBUTION FROM AN OLD STANDPOINT. By H. B. GUPPY, M.B., F.R.S.E. (Honorary Corresponding Member.)

IN this paper I have elaborated a theory of plant-differentiation which is briefly outlined in the preface and final chapter of my recent book on Plant-Dispersal. It is based on the view that observation can only discover the differentiation of types, the agencies concerned with type-creation being not evident to us.

Many of the most serious difficulties connected with the study of plant-distribution have their origin in the endeavours to discover the centres of dispersion or the homes of genera, tribes, and families, difficulties that are often intensified when we call in the aid of the geological record. Botanists appear to have been more persistent in this direction than zoologists; and we have something to learn from the circumstance that those who have taken the broadest views of distribution have often troubled themselves least with such speculations. If the standpoint adopted in this paper is correct, all such endeavours are misdirected and vain, since the difficulties would arise from an initial misconception of the problem.

The difficulties in distribution created by a misconception of the problem. Let us glance at a few of the difficulties that take their origin from the hypothesis that a genus can only have a

* Monday, April 8th, 1907.

single birthplace. Ravenala, a genus of the Musaceæ, offers us very singular instance of disconnected distribution. It contains only two known species, of which one (*R. madagascariensis*) is the Traveller's-tree confined to Madagascar, whilst the other (*R. guianensis*) is restricted to tropical South America. Then there is the genus Adansonia, to which the familiar Baobab-tree belongs. Of its four species, two are African, one belongs to Madagascar, and the fourth is Australian. Then we have the genus Mesembryanthemum, which, though mainly African, possesses a few Australian and South American species. Again, the breadth of an ocean lies in each case between the South American, Australian, and African species of Podocarpus. These examples have been selected because they raise the same questions that are suggested by the disconnected distribution of animals like the marsupials and the tapirs. Evidently we are not here concerned with capacities for dispersal.

The testimony of the rocks only adds to our difficulties in the search of the home of a genus. What are we to say, for instance, when many living genera of trees, both tropical and temperate, such as Eucalyptus, Ficus, Liriodendron, Myrsine, Quercus, etc., present themselves in association and without warning in the Cretaceous deposits of North America? How is it possible, again, to speculate on the home of Eucalyptus, when we know that it existed in Mesozoic times both in Europe and in North America? As far as concerns their former wide dispersal, the marsupials and the gum-trees behave in a similar fashion. Where, it may be asked, ought we to look for the home of Liriodendron? Found fossil in the Cretaceous and early Tertiary deposits of North America, Greenland, and Europe, its once numerous species are now only represented by a solitary species growing in North America and China. It would seem, indeed, with this evidence before us, that it is not legitimate to raise the question of a home at all.

But the difficulties are not restricted to the disconnected distribution of genera. The distribution of families presents almost insuperable difficulties when viewed from the standpoint of dispersion from a centre. It would indeed appear that the farther we trace them back in geological time, the wider is their range. Where, for instance, should we look for the home of the palms at present flourishing throughout the tropics but extending far north into temperate latitudes during Eocene times?

With some of the families that are well represented in the geological record we cannot even detect the commencement of the differentiation of their tribes. With the Taxaceæ, for example, most of the tribes established by the systematist for living forms are to be found in the Mesozoic deposits (see Pilger's "Taxaceæ," *Das Pflanzenreich,* iv, 5). With a family like the Aceraceæ, which practically consists of a single genus (Acer), the sections or subgenera based on the characters of existing species include all the Tertiary forms; and, stranger still, most of the sections of the genus that were confined to one or other side of the Atlantic in Tertiary times possess the same distribution now (see "Aceraceæ" by F. Pax, *Das Pflanzenreich*, iv, 163). We seem indeed to be rarely able to get at the beginning of things in the distribution of the flowering plants, whether it be a family, a tribe, or a genus.

THE FIRST POSTULATE OF THE THEORY OF DIFFERENTIATION.

In those families where we get a glimpse of the differentiation of the tribes we are apparently brought face to face with the differentiation of a world-ranging primitive stock. This is a point of the greatest significance in connection with the standpoint adopted in this paper. If behind the facts of distribution lies the cardinal principle that the farther we trace a type back the more generalised are its characters and the wider is its range, then we should be justified when working out the history of a family in postulating a world-ranging primitive parent type with the subsequent development of centres of differentiation over its area. The means of dispersal would then take a very secondary place as determining distribution except in the case of insular floras. This is the position which I will first endeavour to establish in the elaboration of the theory of differentiation. It will involve the possibility of the development of tribes and even of genera in more than one locality in the area of the family.

THE VIEWS OF MR. BENTHAM AND PROFESSOR HUXLEY.

I will first refer to some of the indications supplied by the great group of the Compositæ. Notwithstanding that it makes a poor show in the fossiliferous deposits, Mr. Bentham, the monographer of the family (see *Journ. Linn. Soc. Bot.* xiii, 1873), arrived at the conclusion not only that it is a very ancient plant-group, but that its primitive stock was already widely dispersed at an early period of its history. Both the Old and the New World possessed the family at the earliest recognisable stage, America, South Africa, the Mediterranean region, and Australia serving subsequently as "centres of differentiation" and becoming the homes of the tribes. The possibility of the differentiating process following the same lines at its early stages in distant parts of the world is clearly indicated in these conclusions, though it should be noted that this is not Mr. Bentham's interpretation. Although admitting the very ancient distribution over the world of the primitive stock, this botanist looked for the still earlier centre of dispersion, or, in other words, for the home of the family.

Now, it is noteworthy that Professor Huxley, Mr. Darwin's great lieutenant, in his remarkable paper on the Gentians (*Jour. Linn. Soc. Bot.* xxiv, 1888), which as a display of method may be regarded as a prophetic leap through two decades, would have nothing to do with centres of dispersion, or with movements of migration in explaining the distribution of this family. In two letters, giving some of his preliminary results, which were written to Sir Joseph Hooker in September, 1886, he says. . . . "It is clear that migration helps nothing as between the Old World and South American Floræ. It is the case of the tapirs (Andean and Sino-Malayan) over again" (*Life and Letters of T. H. Huxley*, second edition, 1903, ii, 464–5). His more matured opinions are given in his paper where he says . . . "The facts of distribution of the *Gentianeæ* . . . are not to be accounted for by migration from any 'centre of diffusion,' to which a locality can be assigned in the present condition of the world," and he recurs again to the parallel case of the tapirs, pointing out that with those animals "there have been no migrations, but simply local modifications of the genus at opposite ends of the primitive area, with extirpation in the intermediate space." The species of the world-ranging family of the Gentians fall, he says, into four groups, one primary and "least differentiated," to which the South American, the Antarctic, and the Arctic forms mostly belong, and the other three groups "specialised" and comprising the species of the rest of the northern hemisphere. There is, he remarks, "a strange general parallelism with the crayfishes" which, though widely distributed, "become most differentiated" in the northern hemisphere.

Like Mr. Bentham with the Compositæ, Professor Huxley regarded the Gentians as distributed over the world ages since, and this is a most important point for our theory of differentiation. The study of their means of dispersal would have been, no doubt, characterised by him as interesting, but unimportant. The existing Gentians he regarded as the relics of a widely spread Tertiary flora ranging over the two Americas and Eurasia. Like Mr. Bentham again, he is able to dispense largely with geological evidence, and, on *a priori* grounds, finds no reason to suppose that the distribution of the Gentianeæ in Miocene times was substantially different from what it is now. As concerning the possibility of putting a limit to this retrogression, he "does not think that any good grounds could be given for denying the existence of even the more specialised Gentianeæ in the Cretaceous epoch, whilst the *Ur-Gentian* (the hypothetical anemophilous parent type) may be dated back almost as much further as probabilities permit us to carry the existence of flowering plants." Professor Huxley's temerity was Homeric, since not only did his method of dealing with the genera on purely genetic lines involve the fate of the accepted arrangement of the family, but he extended his conclusions at a bound to the plant-world in general, and terminated his paper with the warning that a revision of taxonomy and distribution from the point of view of the evolution doctrine would hardly fail to revolutionise both.

It will thus be seen that on its biological side there is nothing original in the theory advocated by me in this paper. Though Huxleyan, it is not Darwinian, as will immediately appear.

The possibility of the development of the same form in different localities.—It has already been explained why Professor Huxley made no effort to determine the home of the Gentians. According to his views, this ancient family had differentiated from a primitive type in such a manner that he considered it probable that not only the larger tribal groups, but also the genera could have originated independently in different localities. In this connection, it should be noted, Professor Huxley came into line with Dr. Engler, whose work on the history of the development of the plant-world,* he had been recently reading. If we postulate, as was done by Professor Huxley, a primitive generalised type of a family, we are compelled to admit that in its earlier stages the differentiating process might follow similar directions in different localities. A tribe, and at times even a genus, might thus arise in more than one region; and if the primitive type were universally distributed, we might have the same tribes and genera originating on opposite sides of the globe. But we should be straining the argument if we endeavoured to urge that this was the general rule. Naturally, the chances in favour of such an occurrence would decrease with the progressive differentiation of the primitive type. It would be probable with the tribe, possible with the genus, and almost impossible with the species.

* *Versuch einer Entwicklungsgeschichte der Pflanzenwelt*, 1879–82.

Table showing the distribution of the species, genera and tribes
both the Old and

The figures for the Compositæ are those given by Mr. Bentham in his
have been prepared by myself from the materials supplied in the mono-

Families. (S = sub-family.)	Species.			
	Old World.	New World.	Common to both.	Total.
Cistaceæ	118	35	—	153
Aceraceæ	80	14	1	95
Halorrhagaceæ	116	31	5	152
Lythraceæ	143	302	6	451
Compositæ	4,858	4,463	63	9,384
Primulaceæ	446	71	15	532
Myrsinaceæ	613	319	—	932
Symplocaceæ	172	109	—	281
Monimiaceæ	84	166	—	250
Betulaceæ	58	18	6	82
Taxaceæ	78	18	1	97
Marantaceæ	79	205	1	285
Zingiberaceæ	761	89	—	850
Musaceæ	49	30	—	79
S. Orchidaceæ (Pleonandræ) ...	76	24	2	102
Alismaceæ	20	48	2	70
Scheuchzeriaceæ	11	2	4	17
Naiadaceæ	22	8	2	32
Typhaceæ	6	1	2	9
Sparganiaceæ	8	3	4	15
S. Araceæ (Pothoideæ)	76	495	—	571
Juncaceæ	136	111	34	281
Eriocaulaceæ	152	396	2	550
Total	8,162	6,958	150	15,270
Percentage	*53* p.c.	*46* p.c.	*1* p.c.	—
Percentage for *Compositæ* alone	52 p.c.	47 p.c.	1 p.c. (0·7)	—
Percentage for all the families except *Compositæ*.	56 p.c.	43 p.c.	1 p.c. (1·5)	—

Explanation of abbreviations in the last column.—C = cosmopolitan ;
hemisphere, chiefly in temperate latitudes ; S = southern hemisphere,
regions.

(*when established*), *of twenty-three families that are found in the New World.*

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monograph of the family (*Journ. Linn. Soc.*, 1873). The other results graphs of Dr. Engler's *Das Pflanzenreich.*

Genera.				Tribes.				
Old World.	New World.	Common to both.	Total.	Old World.	New World.	Common to both.	Total.	
4	2	1	7	—	—	—	—	N.
—	—	1	1	—	—	—	—	N.
4	1	2	7	—	—	3	3	S.
6	11	5	22	—	—	2	2	Tr.
309	343	78	730	1	—	12	13	C.
10	2	10	22	2	—	3	5	N.
21	8	3	32	1	—	2	3	Tr.
—	—	1	1	—	—	—	—	Tr.
20	6	1	27	—	—	5	5	Tr.
1	—	5	6	—	—	2	2	N.
6	1	3	10	3	—	2	5	C.
15	10	1	26	—	1	1	2	Tr.
34	2	2	38	2	—	2	4	Tr.
4	1	1	6	2	1	1	4	Tr.
4	2	1	7	1	—	1	2	C.
7	—	5	12	—	—	—	—	C.
1	2	2	5	—	—	—	—	CTe.
—	—	1	1	—	—	—	—	C.
—	—	1	1	—	—	—	—	C.
—	—	1	1	—	—	—	—	N.
8	2	—	10	4	2	—	6	Tr.
1	3	4	8	—	—	—	—	CTe.
1	6	2	9	—	—	2	2	Tr.
456	402	131	989	16	4	38	58	
46 p.c.	*41* p.c.	*13* p.c.	—	*27* p.c.	*7* p.c.	*66* p.c.	—	
42 p.c.	47 p.c.	11 p.c.	—	8 p.c.	0 p.c.	92 p.c.	—	
57 p.c.	23 p.c.	20 p.c.	—	33 p.c.	9 p.c.	58 p.c.	—	

CTe = chiefly in the north and south temperate zones ; N = northern chiefly in temperate latitudes ; Tr = chiefly in tropical and subtropical

Such a scale of chances is directly indicated in the foregoing table. Here we perceive that in a sample number of the families that are distributed in both the eastern and the western hemispheres, about two-thirds of the tribes, 12 or 13 per cent. of the genera, and one per cent. of the species, are common to the Old and New World. I have added this table, since it gives the data on which this important inference is based. The mere outlining of the numerous principles involved in its columns would afford material for a paper of some length, so that I will make no further reference to it here.

It is strange that the old doctrine of multiple centres was supported by a great Darwinian evolutionist. It was held by Sir William Dawson, a leader of the opposing school, who in one of his last works (*Some Salient Points in the Science of the Earth,* 1894), observed that the upholders of the theory of Natural Selection would "get rid of many difficulties of time and space," if they would admit the possibility of more than one centre. Like Professor Huxley, Sir William Dawson believed in the differentiation of "generalised or synthetic primitive types"; and since they both held the doctrine of multiple centres, they were fighting for the same cause, though oddly leading contending factions.

In this connection it is important to notice that in some families where the monographer has worked on genetic lines, similar to those adopted by Professor Huxley in the case of the Gentians, the same possibility of the independent development of plant-forms over the area of the primitive type presents itself. For instance, with the Eriocaulaceæ, the type-genus (Eriocaulon) from which Ruhland traces the descent of all the other genera of the family, is the only genus that is universally distributed.* So also with the Juncaceæ, the sub-genus which is regarded by Buchenau as nearest to the parent-type is widely spread over the world.† Now, it cannot be pretended for a moment that these forms, which come nearest to the original type of the family, are indebted for their wide distribution over the area of the said family to their exceptional capacities for dispersal. Rather ought we to assume that they have been developed *in situ* over the area originally held by the primitive type of the family, that they represent the earliest stage of the differentiating process, and that they have in their turn given rise to various centres of differentiation from which the other more

* "Eriocaulaceæ," by W. Ruhland, *Das Pflanzenreich*, iv, 30; 1903.
† "Juncaceæ," by Fr. Buchenau, *Das Pflanzenreich*, iv, 36; 1906.

localised groups (generic or otherwise) have been developed. The same process may be seen in operation within the limits of a genus. Many tropical genera, as I have shown in my book on *Plant-Dispersal,* possess in addition to the more localised species, a highly variable species that occupies the range of the genus, and establishes centres of differentiation all over the area.

It can scarcely be doubted that if we begin by postulating a world-ranging, generalised type, which in the course of ages differentiates *in situ* into tribes, genera, and species, we should be spared a sea of trouble in the investigation of plant-distribution. All the difficulties of disconnected distribution would disappear. Many botanists must have at times felt the need of an hypothesis of this kind, though few would be prepared to abandon the old position. Amongst those who in recent years have revolted against the habit (to use the words of Sir William Dawson) of laboriously devising expedients for the migration of plants and animals is Dr. Karl Mueller.* With the case of Liriodendron in his mind, he observers that "all explanations of origin by migrations and bridges cease, and we are forced back on the idea of autochthonous causes." So, again, the occurrence of a species of Baobab (Adansonia) in Australia and South Africa causes him to remark that "the enigma cannot be explained by migration; the same conditions of creation produced in different places the same type, only in different species."

DIFFICULTIES CONNECTED WITH FAMILIES.

But apart from questions connected with genera, many difficult problems concerning families appear much less formidable when we regard them from the standpoint of the differentiation theory. There is the matter of large and small families. Take, for instance, a great family like the Araceæ, distributed all round the globe, and possessing a multitude of genera. Then take a very small family like the Columelliaceæ, containing only one genus, limited to Ecuador and Peru. The family characters of the Araceæ are those of the undifferentiated primitive type. Where, we may ask, are the primitive family characters of the Columelliaceæ? They exist, but only as expressions of a simple family type, the genetic connections

* See *Trans. and Proc. New Zealand Institute*, xxv, 1892, for a translation by H. Suter of Dr. Mueller's paper in *Das Ausland*, July 20th, 1891.

with which have been disguised by later modifications. To raise a specialised genus to the dignity of a family is to reverse the natural order of things. It will be pointed out later on that nature seems to have reversed the regular process of differentiation in Oceanic islands, and in other localities where conditions of abnormal isolation prevail; but it will be shown that it is not nature that has reversed her processes, but the botanist that has changed his methods. If we accept the single-centre hypothesis, the birth of families presents itself as a very haphazard operation. One ranges the world, whilst another is confined to the tropics, a third to the north and south temperate regions, a fourth to only one of the temperate zones, a fifth to North America and Eurasia, a sixth to one continent only, and so on. By regarding these matters from the standpoint of the differentiation theory, we shall see that the difficulties have been largely created by ourselves, more especially through the loose employment of the term "family."*

We have first a world-ranging family, like the Compositæ, where the various tribes, differentiating *in situ*, collectively occupy the area of the primitive type. In other cases, however, differentiation has proceeded so far that the original tribes are ranked as families by the systematist; and we obtain a series of related families, each in its own region, but together holding much of the area of the world-ranging original type. Thus the closely related families of the Primulaceæ and the Myrsinaceæ, the first of the temperate regions, the second of the tropics, may represent the tribes that indicated the first step in the differentiation of a parent type that was once generally distributed over the earth when climatic conditions were more uniform than they are at present. Just as we may regard a widely distributed family like the Compositæ as representing in its tribes, genera, and species the history of the differentiation of flowering plants and of their conditions of existence on the globe, so we may see in the closely related Myrsinaceæ and Primulaceæ and in their respective genera and species the result of the differentiation of plant-forms and plant-conditions since the era of flowering plants began.

The custom among systematists of linking families together in such a way as to suggest a genetic connection offers evidence in favour of the differentiation hypothesis, more especially in

* Families should be ranked in grades according to their relation to the parent type. So also as regards genera and species the same system should be used.

those cases where the families concerned, though each in its own region, hold much of the globe between them. A striking instance of this has just been given; and another is noted below in connection with the primitive group of the Scitamineæ.

A good test of the efficacy of the differentiation theory is afforded by those families that are widely spread over the warm regions of the earth, yet stand well apart from all other families. Such families occupy regions now separated by the breadths of the Pacific and Atlantic oceans. Let us, for instance, take the Palmaceæ. The palms are numerous in tropical Asia and in tropical America, and we know that they extended in mass much farther north during the Tertiary period. What encouragement, therefore, can the facts of distribution afford us in searching for the home of the family, when they indicate that the farther we go back the wider is the range? To attempt it would be at once to involve oneself in a labyrinth of assumptions both geographical and botanical. Far fewer difficulties would attach themselves to the explanation supplied by the differentiation hypothesis that there was originally a world-ranging palm prototype which has differentiated *in situ* in various regions, and that its present concentration in equatorial regions is connected with the differentiation of the climate of the globe.

The Palmaceæ offer a suitable and familiar illustration of the argument here followed; but it would be easy to mention other tropical families distributed around the globe, where the attempt to discover a centre of development would be equally futile.* This could only be in any degree successful in the case of those more localised tropical families which belong to a group of closely related families, and are really the tribes of a primitive family that has disappeared in the process of differentiation. A good example is afforded in the case of

* As another instance I will take the Monimiaceæ, a family confined to the tropical and subtropical regions of the Old and the New World, and described by its recent monographers (Perkins and Gilg in *Das Pflanzenreich*, iv, 101, 1901) as so well defined and so natural in its characters that all its species may be regarded as derived from a single Old World stock that probably had its birthplace in Indo-Malaya. Since, however, all the five tribes are common to the Old and the New World, whilst one-fourth of the genera and two-thirds of the species are purely American, such an explanation raises a host of difficulties. According to the differentiation hypothesis, we should merely begin with a primitive parent type originally diffused in both the Old and the New World and subsequently differentiating at unequal rates.

the four closely connected families, the Zingiberaceæ, the Cannaceæ, the Marantaceæ, and the Musaceæ, which behave as tribes of the great plant-group of the Scitamineæ, once distributed (as assumed by the theory) as a generalised type over the warm regions of the earth and now represented by its original tribes as separate "families" in the different parts of its area.*

As another illustration of the working of the differentiation theory, I will take a family like that of the Pandanaceæ, that is restricted to the warm regions of the Old World, and displays but slight relationship to other families, excepting, perhaps, to the Sparganiaceæ of temperate latitudes. Here we would suppose that the differentiation of the original world-ranging type has advanced so far that the type has been lost seemingly beyond recognition. Until we can discover the representatives of the Pandanaceæ in tropical America we can only frame guesses as to the original type. That they exist there we are compelled to assume, but the primitive characters have been obscured in the differentiating process.

It will be thus perceived that the differentiating process has been by no means uniform in its results, and we will now proceed to look a little more closely into its working.

On the Determining Causes of the Irregular Rate of the Differentiation of Primitive Plant-Types.

It is assumed that the differentiation of plant-forms is a response to the secular differentiation of the conditions of existence, beginning with a time when uniform conditions and undifferentiated types prevailed. This, however, will be discussed when we deal with the physical side of the theory. Here we are especially concerned with the unequal rate of the change.

It would not be possible to frame a scale connecting the degree of differentiation of a family with its relative antiquity, for the sufficient reason that there is no indication of any uniformity in the rate of the process. As far as the geological record can at present guide us, we seem to be justified in assuming an equally great antiquity for all primitive phanerogamous types. But how great is the contrast in the

* The Zingiberaceæ are mainly Old World, the Cannaceæ and Marantaceæ are mainly American, whilst the Musaceæ are fairly well shared between the two hemispheres.

results of the differentiating change! We can scarcely doubt that the primitive aquatic family type of Naias, during its differentiation into 32 species now spread over the world, has witnessed the development from the primitive type of the Compositæ of its 13 tribes, of its 730 genera, and of its 10,000* and odd species that now between them occupy the land-surface of the globe. Other primitive family types have, however, during this period disappeared in the differentiating process, being only recognisable now in the common characters of a group of closely related families that occupy between them the area of the original family. Amongst such buried primitive families we have mentioned the Scitamineæ. In other cases, again, even the connections between the secondary families have disappeared, and we get solitary families restricted to particular regions and standing aloof from nearly all their kind. Of such families, that of the Pandanaceæ has already been cited as an instance.

What, we may now ask, is the explanation of this unequal rate of the differentiating process in the plant-world? The determining causes are to be found primarily in the lack of uniformity in the differentiation of the life-conditions, and secondarily in the lack of uniformity in the operations of the dispersing agencies.

(1) *The lack of uniformity in the differentiation of the life-conditions.*—Since that ancient period when similar conditions of existence occurred over most of the earth and swamps prevailed, the primitive life-conditions have been broken up to a much greater extent for some kinds of plants than for others. Thus, whilst the aquatic habit comes nearest to the primeval condition, the terrestrial habit has differentiated in a thousand ways on account of the great diversification of modes of life and the resulting large number of possible combinations of all that goes to determine the conditions for plant-life on the land. Aquatic plants might therefore be expected to have changed much less rapidly than land plants; and the more complete the submergence, the slower would have been the change. Very few, if any, of the families containing only aquatic or subaquatic plants possess as many as 100 described species. In most cases the number falls far short of this, Naiadaceæ

* A generation (33 years) has passed away since the publication of Mr. Bentham's monograph on this family, when the described species were placed at about 9,400. The number must have been considerably increased since that date.

having 32 and Sparganiaceæ only 15; while Alismaceæ and Potameæ each possess about 70. On the other hand the species of many land genera amount to hundreds, and those of the families not infrequently mount to thousands. The vast family of the Rubiaceæ contains genera like Psychotria that comprise between 600 and 700 described species. Those of the Compositæ number about 10,000; whilst those of the Leguminosæ, Labiatæ, and Gramineæ run also into thousands. However, taking the small families with the large, we should be well within the mark if we assumed that for every aquatic species ten land species have been developed, or, in other words, that the differentiation has been ten times as rapid among land plants. From a rough computation I should imagine that the average number of species in a land family would not be less than 600 and in an aquatic family not more than 40, so that the assumption errs on the safe side.

Although the family type represented in the aquatic genus Naias must be very ancient, it can scarcely be said to have advanced beyond the first stage of differentiation.* The tardy differentiation of aquatic plants is primarily due to the slow response of their conditions of existence to the secular differentiation of the earth's climate; but this retarding influence has been intensified by their freedom of dispersal through the agency of waterfowl. This brings me to the second cause of the unequal rate of differentiation over the world.

(2) *The lack of uniformity in the operations of the dispersing agencies.*—Although this cause is the least important of the two, it is necessary to discuss it because the standpoint adopted may not be familiar to all. It is well known that isolation favours differentiation, and, since all means of dispersal tend to retard this process, it follows that the agents which, like the winds and currents, have been most uniform in their operation in space and time will, as a rule, have been most effective in retarding change, whilst those which have been irregular in their action, as in the case of birds, will have been less effective in checking the process. This difference, however, is one of degree and not of kind, since all nature has responded to the secular differentiation of climate and to the diversification of the surface conditions, the winds, the currents, and birds alike, but organized beings most of all.

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* "Naias forms a distinct and apparently primitive type of Monocotyledon" (Rendle in the monograph on the Naiadaceæ, *Das Pflanzenreich*, iv, 12, 1901).

As illustrating the results of the different agencies of dispersal in the same region, I will take the case of the Tahitian group in the mid-Pacific, making use of the data given in my book on *Plant-Dispersal.* The observations of Dr. Treub and of Prof. Penzig on the stocking of Krakatoa with its plants justify us in assuming that the agency of wind in mid-ocean would be almost entirely confined to the transport of the spores of cryptogams. On the other hand the observations of many observers have shown that the agency of birds is restricted mainly to the inland flowering plants and the agency of currents to the shore plants. The effect of these agencies on the differentiating process of the plants concerned is of course displayed in the degree of endemism, or in other words, in the proportion of peculiar species. It thus appears, as is clearly indicated in the case of the Tahitian Islands in the accompanying table, that the differentiating process has been much more retarded where either the winds or the currents have been the agents of dispersal than where the birds have been the agents. Among the shore-plants, which are mainly dispersed by the currents, only 1 or 2 per cent. of the species are peculiar, and amongst the wind-dispersed ferns and lycopods 8 per cent. are peculiar, whilst amongst the inland flowering plants as many as 43 per cent. are confined to the group. In the Hawaiian Islands, where the isolation has been markedly greater than with the Tahitian group, 80 per cent. of the flowering plants and 45 per cent. of the vascular cryptogams (ferns and lycopods) are peculiar, the true littoral flora being very scanty, owing to the position of the islands with regard to the currents.

Table illustrating the relation between the proportion of peculiar species in the Tahitian flora and the mode of dispersal.

Station and Character.	Prevailing mode of dispersal.	Total number of species.	Proportion of peculiar species.
Coast flowering plants	Currents ...	55–60	1 or 2 per cent.
Ferns and lycopods ...	Winds ...	154	8 per cent.
Inland flowering plants	Birds ...	260	43 per cent.

Now we have no reason to assume that the winds are less effective in carrying the spores of ferns and lycopods than they were in the earliest epoch of the floral history of the Pacific islands. On the other hand, with the flowering plants, which depend almost entirely on birds for their dispersal, the operations of the dispersing agencies over this ocean have been, as I have shown in my book, always irregular, and are now for the most part suspended, the results displaying themselves in the far greater number of peculiar species. In the case of Hawaii the contrast between the endemism of the flowering plants and of the vascular cryptogams is indeed much greater than is indicated by the proportions of peculiar species, since its flora contains nearly thirty peculiar genera of flowering plants against only one or two amongst the ferns and lycopods. However, these islands of the Pacific only illustrate operations of far greater antiquity in continental areas; but with the insular floras we are better able to compare the effectiveness of the dispersing agencies and to eliminate many of the disturbing factors of continental floras.

In continental regions the bird has been only one of several agents that keep the different areas in touch with each other by transporting seeds. But in the stocking of the isolated archipelagoes of the Pacific the influence of birds has been predominant. However, seed-dispersal over that ocean is now practically suspended, and the birds that once carried seeds from group to group, having long since ceased to wander, are now represented by distinct species in the several archipelagoes. The plants once dispersed by them have responded to the change and have differentiated in the various groups, so that strange inland plants and strange forest birds go together in the Pacific islands. The nature of the connection between freedom of dispersal and specific differentiation was well brought out in the collections made by Beccari in Borneo.* Thus he found that whilst 30 per cent. of the numerous species of Ficus were peculiar, as many as 85 per cent. of the palms had not been found elsewhere, the explanation lying in the "facile dissemination" of the species of Ficus by birds as compared with the palms.

Whilst plants as a whole have responded through the run of the ages to the differentiation of climate, in the case of those possessing edible fruits the bird has largely determined the rate of the change. With the secular drying of the globe the

* See the author's book on *Plant-Dispersal*, p. 504.

changes of climate, bird, and plant have often gone on together, the range of the bird being controlled by the climate and the distribution of the plant being largely dependent on the bird. The bird generalised in type that once ranged the globe is now represented over its original area by a hundred different groups of descendants, each confined to its own locality. Climate, once so uniform, now so diversified, has by restricting the range of the bird favoured the process of differentiation, whilst those plants that are dependent on the birds for their distribution have in their turn responded to the changes. It is not possible to deal farther with this subject here, but much will be found on these subjects in my book on *Plant-Dispersal*, sepecially in the last two chapters.

THE TRUE FUNCTION OF THE AGENCIES OF DISPERSAL.

Regarding the study of plant-distribution as being almost entirely concerned with continents, since islands cover a very small proportion of the area of the globe, I am strongly inclined to the view that the function of the dispersing agencies has been chiefly limited to irregularly impeding the process of differentiation that is itself primarily determined by the secular changes in the climatic and surface conditions of the earth. If the diversification of forms depended only on physical conditions the earth's floras would be full of monotony. Variety begins when the agencies of dispersal interfere. Though naturally efficacious in stocking islands with their plants, the dispersing agencies acquire quite a different significance in continental regions. We are there brought face to face with problems concerned with station in its most comprehensive sense, with past changes in the history of climate and in the arrangement of land and sea, and with those mysterious revolutions in plant-forms that have affected the whole world. We cannot appeal to the dispersing agencies for an explanation of the distribution of the great primitive families, such as the Amentiferæ, the Araceæ, the Coniferæ, the Palmaceæ, and the Scitamineæ, that now in different latitudes encircle the globe. Nor could they aid us in the case of a genus like Acer that goes back to the Secondary epoch and existed, as already shown, in early Tertiary times on both sides of the Atlantic.

The distribution of so many families in both the Old and the New World, whether in tropical or in temperate latitudes, would of itself suggest to us that in investigating means of dispersal we only touch the fringe of a great problem. The view that such investigations go a very little way towards explaining the facts of general distribution is in accord with the view elaborated in my book that nature has made no especial provision for seed-dispersal. The instability in the past as well as in the present of the fruit as compared with the flower, and its relative unfitness for purposes of classification, are facts which point in the same direction. If we accept the principle of the differentiation *in situ* of universally distributed types in response to the secular differentiation of their life-conditions, we see at once the accidental character of the working of the dispersing agencies.

The Theory of Differentiation briefly stated.

The hypothesis is one that connects the differentiation of plant-types over the earth with the secular differentiation of the life-conditions. With the creation of these types we are not concerned, since we are only witnesses of the processes connected with their diversification. Although this view is advanced in the preface and final chapter of my book on *Plant-Dispersal*, a work dealing mainly with insular floras, I had not then sufficiently grasped the idea that whilst the study of means of dispersal explains much in the case of floras of oceanic islands, it goes a very little way towards solving the great problems connected with continental floras. Only the later phases in the history of plant-distribution are illustrated in the islands. Principles of great weight in the stocking of oceanic islands shrink considerably in their importance when we apply them to the plant-distribution of the globe.

Now what, we may ask, is the significance of a differentiating world? This process has been at work on our globe from the beginning, and its operations are to be observed alike in the infinitely great and in the infinitely small. In those first ages when dense envelopes of mist and cloud screened off the direct rays of the sun from the earth's surface, when the air was ever saturated with aqueous vapour, and when the life-conditions were uniform over the globe, the same generalised plant-types were distributed over the earth. Then ensued a process of desiccation which is still in operation, and it is with a world that has for ages been drying up that the significance of differentiation lies.

The origin of the tribes is to be connected with the earlier stages of the process, those, for instance, concerned with the emergence of the continents and the first development of climates. With the further differentiation of the life-conditions within the tribal area is to be associated the birth of the genus; and in response to the further specialisation within the generic area of the conditions of existence arose the species. In the plant-world the process of change has ever been from the general to the special, the family becomes specialised in its tribes, the tribe in its genera and the genera in its species. With each step in the differentiation scale, the geographical range would become more and more contracted, until whilst a family occupied a continent or ranged the world a species would be usually restricted to a very limited area. This is a theory somewhat idealised, but nature has ever been best symbolised by broad ideas. The dispersing agencies, for instance, would tend to blur the outlines, but the main features of distribution would remain unchanged. What explanation, I would ask, that assumes only a single centre of development could explain the behaviour of families distributed in both the Old and the New World? Here we find, as I have before remarked, that whilst most of the tribes occur in both hemispheres, most of the genera, and almost all of the species, are restricted either to one or the other.

The theory here advocated is concerned only with the normal differentiation of primitive types in response to the secular differentiation of the physical life conditions. It does not concern itself directly either with the abnormal plant-forms that have arisen under exceptional conditions of isolation as on oceanic islands, or with the floral modifications and monstrosities that have been developed in later ages through the establishment of a close biological relation with insects, birds and other creatures, but it holds that we ought in all cases to be able to penetrate the disguise. Such forms have not been produced on the lines of development which begin with the differentiation of a primitive family type and represent the response of the plant-world through the ages to the differentiation of the physical world. They are essentially distinct, and the generic value cannot possibly be the same for genera of such different histories.

General Application of the Theory of Differentiation.

I will conclude the first part of this paper with a few general reflections. In the first place I would say that if we are not too curious about beginnings the theory of differentiation should appeal to the idealist. Plants do not stand alone in its application. The same great process of change from the simple to the complex may be witnessed alike in the history of the cosmos, in the development of a world, in the diversification of its life conditions, and in the infinite variety of its organisms. We see its workings not only in the plant and in the animal, but even for man we can postulate a universally distributed generalised type from which the principal races have originated for the most part in the regions now serving as their homes. The early history of man is the history of a widely spread primitive human type differentiating *in situ*. I do not believe that if such a position were adopted for the apes it could be seriously objected to. No one, I imagine, would think it worth while to look for their home in any one locality, since like the palms they are distributed around the warm regions of the globe with the breadths of oceans dividing them. Like the palms also they had a wider distribution in Tertiary times, when they extended far into north temperate latitudes. One may say of the apes as Prof. Huxley remarked of the Gentians after vainly searching for their home . . . . "It is clear that migration helps us nothing as between the Old World and America. It is the case of the tapirs (Andean and Sino-Malayan) over again." We may indeed add that with man's distribution it is the case of the apes over again. How else can be explained the circumstance that in point of culture man has differentiated on the same lines during his earliest stages *all over the globe*, and that independent lines have been followed only in the later stages.

But the principle of differentiation affects us in a yet more extended sense. Our customs, our amusements, our sciences and even our creeds come under its sway. The differentiation of a creed follows the same law that determines the differentiation of a plant type. It is the birth of a creed that lies outside the law just as type-creation lies beyond our field of observation. All indeed who exercise the creative art, the discoverer of a new ideal, the inventor of a new machine, stand to that extent outside the law of differentiation. Difference in itself is not progress. Its end is extinction. Yet the simplest creative act can set the law at defiance. The progress of a nation, of a science, of a creed, lies not in differentiation or in specialisation, but in the genius of its great men. In the case of human effort we may call it what we like, genius, inspiration, or intuition. Yet man is only his Creator's instrument by which in the ages to come He will reshape the world.

PART II.

ON SOME OF THE EVIDENCE BEARING ON THE THEORY OF DIFFERENTIATION.

The second part of this paper is devoted to a further discussion of the testimony favouring the differentiation hypothesis. The principle of the concurrent differentiation of plants and their life-conditions is either tacitly assumed or directly implied in the writings of several botanists. Of many again it may be said that whilst "evolution" is always on their banner, "differentiation" is ever on their lips. Indeed it is not easy to take up a book dealing with the development or with the distribution of plants and animals without discovering some pregnant sentence connected with this theory. There are others who state the theory both on its physical and its biological side so aptly and concisely that one wonders how they did not see their limitations and accept it as a good working hypothesis. Their difficulty, however, lay in the fact that differentiation acts only within the type, and that if we wish to discover the progressive development of types we must look elsewhere for the causes. The position adopted in this paper is that these causes are hidden from us, and that the only operations evident to us in nature are those concerned with diversification of already existing types.

The theory here advocated is two-sided. On the one hand there are the differentiating life-conditions which mainly find expression in the diversification of climate, and on the other hand there are the differentiating organisms. The connection between the organism and its conditions is implied in the prevailing views of adaptation apart from any particular theory, and I need not labour that point. The subject then has its physical and its biological side, and although we are here immediately concerned with plants, it should not be forgotten that if the hypothesis is a workable one it will apply also to animals.

The Physical side of the Differentiation Theory.

Little can be said here of the earliest stage of the conditions of life on the earth, an age when uniformity of conditions prevailed, an era, indeed, of Cimmerian gloom, when the sun's rays were screened off by dense envelopes of cloud and mist, and when the air was ever heavy with aqueous vapour. It is the story of Genesis, and whilst seer and bard in all ages have made it their theme the man of science has not been able to disprove it. We may differ as to the details connected with the emergence and building up of the continents; but geologists seem generally agreed that in the process of time the land surface has become less insular and more continental (Sir A. Geikie, in *Encycl. Brit.*, xxviii, 635), that indeed the continents originated as islands, which have become united through successive movements of emergence, or, to put it briefly, that the continents have grown with the ages. We remember how Suess and other geologists emphasise the view that the great land-masses possess in each case a region which, since palæozoic times, has never been submerged and has served as the nucleus for the growth of each continent.

We get on somewhat firmer ground when we come to the differentiation of the life-conditions that finds its expression chiefly in the diversification of climate. With the cooling of the earth and the emergence of the land the uniformity of life-conditions began to pass away, and climates as such commenced to develop. There is, however, an important preliminary consideration to be borne in mind. Climatic changes during the secular cooling of the earth would assume a double character. There would be the general alterations affecting the whole globe, and there would be the more localised changes marking climatic differentiation. The first would be concerned with the general lowering of temperature, the decrease in humidity, the increased influence of the sun's rays, and the development of the seasons. The second would be concerned with the climatic characteristics of each region or locality. Whilst the earth's climate has, generally speaking, been getting cooler, drier and more sunny, it has also become infinitely more diversified.

Now in the response made by plants to the changes of climate, or to the conditions of existence determined by them, we ought to be able to distinguish two corresponding sets of effects, one characterising plants in general, and corresponding to the secular change of climate over all the earth, the other concerned with localised associations of plants, and connected with the diversification of climates in individual regions. Such effects would have nothing to do with the development of the great classes of plants. The moss, the fern, and the flowering plant would in each case display in its characters the double impress.

The response to the *general change in the earth's climatic conditions* would be denoted by some change that plants of all the great groups have undergone. Here, for instance, might be placed the genesis of the rest-period of the seed, which would then be regarded as an adaptation to seasonal variation, or in other words, as a result of the development of the seasons (see chapter xxxi of my book on *Plant-Dispersal*). Here also might belong the transition from the dehiscent to the indehiscent seed-vessel or spore-case, which, as observed by Professor F. W. Oliver (address Botan. Sect. Brit. Assoc., 1906), is to be found in every group of plants, whether of cryptogams or of phanerogams. Behind the interesting fact that the capsule is older than the berry may lie many chapters in the climatic history of our globe.

The response to the *diversification of climate*, or to the conditions determined by it, would be found in the successive differentiation of tribes, genera, and species, the tribes reflecting the first great changes influencing large portions of the globe, the genera corresponding to subsequent changes affecting considerable sections of the tribal areas, and the species to still later changes affecting limited localities within the generic areas. Every plant thus bears within it the double impress of the changes in climatic conditions, or in other words, two sets of characters, one very ancient, which it possesses in common with all other plants, the result of such general changes as the lowering of the earth's temperature, the decrease of humidity, the increase of light, and the development of the seasons, the other, more recent, which it shares with a relatively small number of plants belonging to its own association, the immediate result of locality. It may be that the floral organs have mainly responded to the secular changes of climate that affected the whole globe, whilst the vegetative organs chiefly reflect the influence of the localised or differentiating climatic changes.

It will be sufficient now to refer briefly to the general desiccation of the globe, one of the most conspicuous in the secular alterations of climate that have influenced plant-development, reserving the diversification of climate for consideration with the differentiation of floras with which it is so intimately connected.

The desiccation of the globe.—The conception of a desiccating world is by no means novel amongst men of science. We find it most recently alluded to in the pages of Suess,* where we learn that during the seventeenth and eighteenth centuries it was held by philosophers and naturalists, more particularly by

* *Das Antlitz der Erde* French edition, tome ii, chap. i.

De Maillet and Celsius. Some of the wildest guesses of De Maillet have been perilously approached by modern philosophers.* For him all organisms were originally marine, their further development proceeding as the land emerged through the lowering of the sea level by evaporation. Although such a view may appear antiquated and absurd, the doctrine implied need not be condemned because we disapprove of the explanation of the lowering of the sea. It will appear later on in this paper, that as regards the origin of the vegetation of the earliest land surface, the principle there involved is an accepted doctrine of to-day. In recent years "the theory of desiccation," as it is termed by Suess, figures conspicuously in the story of the end of the world by Flammarion, the distinguished French astronomer.† For that brilliant writer, this planet is essentially a desiccating world. As the primitive heat is lost in space, the waters penetrate farther and farther into the earth's mass, being locked up in various combinations (chemical and mechanical), and the world dries up.

Evidence of the progressive desiccation of the earth during and since Tertiary times is displayed in all the large continental areas. We find its later effects in the desert areas of Asia, Africa, the two Americas, and Australia. Prince Krapotkin has advocated the view that in recent geological times, and indeed down to our own day, the earth has been passing through an age of desiccation. He points to Asia‡ as a continent that has long been drying up. As indicated by the evidence of its sea borders, it is experiencing, he says, a rapid movement of emergence; whilst the great lake systems that once occupied its interior have mainly disappeared. One can learn much from the pages devoted by Suess to the origin of Lake Baikal, of the numberless fresh-water lakes that in Tertiary times covered a greater part of northern Asia, but have now dried up, and we can read there also of the more ancient seas whose place they occupied. A large part of the Tertiary deposits of the world are lacustrine. 'The Tertiary has even been called the

* In the pages devoted to De Maillet by Quatrefages in his book *Charles Darwin et ses précurseurs français* (chap. i, 1870), we find that he held, but in another shape, the view implied in the now familiar sentence, "the moss-grown fragments from the ruins of another world."

† *La Fin du Monde*, Paris, 1894.

‡ *Geographical Journal*, February and March, 1904; see also his articles on Russia, Siberia, Turkestan, Volga, etc., in *Encyclopædia Britannica.*

age of lakes."* Yet, as in Asia, these beds must have originally been laid down on the deposits of earlier seas.

Those who have read Professor Gregory's recent interesting book, *The Dead Heart of Australia*, will remember that, when alluding on pages 153-4 to Prince Krapotkin's view of a general desiccation, he does not commit himself to an opinion for or against it; but only observes that a period of universal desiccation is not needed to explain the shrinking of Lake Eyre. Anyone who cares to go farther into this matter will find an abundance of data to elaborate; but it may be at once remarked that it is nothing to the point to urge that there has been no marked alteration in climate during the last two or three thousand years in vegetated regions long familiar to us, such as in South Europe. What we have to learn is whether the desiccating centres, that is to say, the desert areas, have been increasing in historic times. If the answer depended on the data supplied by the Asiatic continent, it would be certainly affirmative.

On the tropical sea-borders of a continent such a progressive desiccation would be indicated by the retreat of the mangroves towards the equator. In fact, if the process is still general, there would be a continuous shrinking of the areas held by mangrove swamps in warm regions. In Chapter xxxii of my work on *Plant-Dispersal* I have given reasons for the belief that the mangroves of the west coast of South America are retreating towards the equator owing to the advance northward of the arid climatic conditions of the Peruvian sea-border.† There are also some grounds for thinking that within historic times the typical mangroves have withdrawn in Western Asia from the Persian Gulf to the mouth of the Indus.‡

The Biological Side of the Differentiation Theory.

That, with climate as with plants, the line of the development has been from the general to the special, is a doctrine, I imagine, which has been commonly accepted. The principle of the differentiation of floras in the course of geological periods has

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* *Geology*, by Chamberlin and Salisbury, iii, 193.

† According to Sir Martin Conway, as quoted by Prof. Gregory, the progressive desiccation of the southern part of South America is indicated by dwindling glaciers, disappearing lakes, and by the transformation of cultivated areas into regions of aridity.

‡ See a note in *Geographical Journal* for September, 1903, on a work by Dr. Bretzl dealing with the plants referred to in the account given by Theophrastus of Alexander the Great's expedition to India.

been received by most botanists, and by many its connection with physical causes has been either tacitly assumed or directly implied. The differentiation of the plant and of its conditions have ever gone on together. As indicating the general position, I will here quote from the address of Professor F. W. Oliver to the Botanical Section at the last meeting of the British Association. . . "It is generally conceded (he said) that the primitive vegetation arose in the waters, and that with the parting of the waters and the emerging of land and continents this primitive stock of plants was sufficiently plastic to take advantage of the new conditions, throwing up successive hordes which affected a footing on the land, and in time peopled the whole earth with forms adapted to the varying habitats and climates as they differentiated."

Nature would thus seem all attuned, but there is a rift within the lute and a jarring note strikes on our ears. The sudden appearance of the Angiosperms in the Lower Cretaceous period without a warning note interrupts the harmony of nature's processes. We can, it is true, detect the same principles at work both before and since the Chalk, yet the break remains. But little can be said here of the indications of Palæozoic times, though as far as my data go, they seem clear enough. It appears to be generally recognised that during the early part of the Carboniferous epoch uniformity of climate and of vegetation prevailed over the world.* With the Coal Measures, to employ the words of Dr. Scott, "a differentiation of floral regions began," and we find at the close of the Palæozoic eras, that the world's plants, though everywhere constituting, as Mr. Newell Arber observes, another great epoch in the history of the vegetable kingdom, had grouped themselves into two great floras, the Northern and the Southern.

It was not, however, until after the sudden appearance of the Angiosperms in the Lower Cretaceous period that the ages of world-wide floras began to pass away, and plants came to be "distributed more markedly according to geographical provinces and in climatic zones." Through the Tertiary period the process of differentiation of floras was continued; and accordingly we find that the farther we go back in that period from the

* See the article on Palæobotany in vol. 31, *Encycl. Brit.*, p. 421 (Dr. Scott) and p. 422 (Mr. Seward); also Mr. Seward's address (*Brit. Assoc.* 1903); also Prof. Hull's *Coalfields of Great Britain*, 5th edition, 1905; also Mr. Newell Arber's *Catalogue of the Fossil Plants of the Glossopteris Flora in the British Museum*, 1905

present time the greater is the similarity between the widely removed and now dissimilar floras of North America, Europe, and Australia. (I have here quoted Mr. Reid's article on Tertiary floras in volume 31 of the *Encyclopædia Britannica.*)

The extension of tropical plant-forms far north into the temperate latitudes during early Tertiary times is well known, and Saporta long since placed the northern limit of tropical vegetation in the Eocene age at 55° N. These plants retreated towards the equator as the development of climatic zones proceeded, and many of them yet exist in a generic sense within the tropics. Temperate genera like Acer, that flourished in early Tertiary times in Arctic latitudes, followed in the rear of the tropical genera in their withdrawal towards the south. The shifting area of this genus in geological time is clearly elucidated by Pax in his recent monograph on the Aceraceæ (*Das Pflanzenreich*, iv, 163). Speaking generally, during the earlier and middle Tertiary times this genus extended in the northern hemisphere from far within the Arctic Circle to the 40th parallel of latitude, and perhaps farther south. As the ages passed away it abandoned the Arctic latitudes and advanced to within the tropics, so that its average range at the present time is confined between the parallels of 20° and 60° N., although individual sections have indeed penetrated farther south into Malaya, reaching Sumatra and Java. Of the earlier history of Acer we apparently know but little; but the facts, scanty as they are, are very suggestive. Among the fruits found by Mr. Newberry* in the Amboy clays of New Jersey, the equivalent of the White Chalk of England, were those of a species of Acer "quite unmistakable" in character. They were associated in this locality, which is situated near the 40th parallel, not only with the remains of several genera, such as Populus and Quercus, that are now mostly confined to temperate latitudes, but with many others, such as Cinnamonum, Ficus and Myrsine, that are now mainly restricted to tropical regions. The pre-Tertiary history of Acer would thus seem to belong to an age when the distinction between tropical and temperate floras had not been established.

It is the occurrence of these "mixed" angiospermous floras during Cretaceous and Eocene times in extra-tropical regions

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* U.S. Geolog. Survey, *Flora of the Amboy Clays*, by J. S. Newberry, 1895.

that is especially discussed by Chamberlin and Salisbury in their recent great work on Geology. Whatever may be the opinions of these two American authors concerning the occurrence of a universal warm climate during the early geological periods, a notion that they reject altogether, they hold no uncertain views relating to the differentiation of climates and floras in later ages. The same mixed flora, in which plants now confined to separate tropical and temperate regions were associated, extended, as they remark, in Upper Cretaceous times in Europe and North America over thirty-five degrees of latitude, reaching as far north as Greenland. Such a flora, they suggest, would imply "climates of a less differentiated or less diversified nature." These mixed or undifferentiated floras also occurred in the Eocene, and the authors lay stress more than once on the association in the deposits of this age of palms and poplars. "Probably the true view," they write, "is that the mixed or undifferentiated flora of the Cretaceous and Eocene, when it came to be subjected later to severe climatic and other crucial conditions, became modified into adaptive groups, some of which came to be restricted to the tropical regions and are now known as tropical plants, others to the temperate, and still others to the boreal regions, acquiring corresponding designations." In another place they term this process "adaptive differentiation" (vol. iii, pp. 226–7).

The process of the dissociation of the mixed floras extended, as they observe, into the Miocene, when occurred "the gradual removal to the south of the forms now regarded as tropical or subtropical, and the concentration at the north of the forms that now characterise those latitudes." Here they are undecided as to whether this was the result of "natural differentiation and segregation of the previously mixed forms" or of "a progressive differentiation of climate" (vol. iii, p. 283). However, they leave us no longer in doubt in the matter when writing of the continued dissociation of the mixed floras in the succeeding Pliocene period. "The Pliocene (they observe) was characterised by a still further sorting out of the mixed flora of previous periods and by the southerly migration of what are now tropical and sub-tropical plants." The evidence, as they proceed to show, indicates not only "a general differentiation" of plants but also that "the climate was becoming differentiated, and on the whole cooler than it had been in earlier Tertiary periods" (vol. iii, pp. 320–1).

And now, in conclusion, I think I may claim to have shown that, as far as the cited opinions indicate, the differentiation theory presents us with a good working hypothesis, at least for the age of the Angiosperms which began in the Upper Cretaceous epoch. Beyond yawns a gap between the present and the ancient order of vegetation. It has not been bridged over, and seems unfathomable. "Whence came the Angiosperms?" is the question that students of past floras are ever putting to themselves. Did they come across the gap? To this at present there is no reply. "We are profoundly ignorant," says Mr. Seward, "of the means by which nature produced this new creation" (Brit. Assoc. Address, 1903).

Discussion.

The Secretary (Professor Hull, F.R.S.), in moving a vote of thanks to Dr. Guppy—who was unable to be present in consequence of being detained in Jamaica—considered the paper as one of unusual interest from the point of view of a naturalist. It gave us in a condensed form the results of observations carried out in various countries, and treated at large in the author's most recent work, *Observations of a Naturalist in the Pacific*, vol. ii,* dealing with the subject of "Plant-Dispersal." This is a highly complicated subject, involving as it does not only the agencies by which dispersal of the seeds and spores of plants is effected, but the changes in the distribution of land and sea, owing to which lands once connected have become separated and isolated, by which climates have been altered, and by which differentiation of genera and species has been advanced. I think it must be admitted that Dr. Guppy has made out a very strong case in favour of his theory that an original wide-spread parent-form of a plant has, owing to physical changes, become disunited into separated areas, in which differentiation has progressed, resulting in the production of fresh genera and species; nor is it improbable that this process may in some cases have resulted in the production of identical genera and species, rising from independent originals or tribes. How otherwise can it be explained that 13 per cent. of the genera and 41 per cent. of the species belonging to 24 families are common to the Old and New Worlds which have

* Macmillan and Co., 1906. The volume has been presented by the Secretary to the Library of the Institute.

been physically disconnected by the ocean for several geological ages, certainly since the Cretaceous period?*

Dr. Guppy closes his paper by asking the question, "Whence came the Angiosperms which appear with the Upper Cretaceous period with such startling suddenness?" Down throughout the Mesozoic ages, the flora of the world was (as far as our knowledge extends) restricted to Conifers, Cycads, Ferns, and Equisetums—a gloomy and flowerless vegetation. Hitherto no examples of dicotyledonous plants had appeared, but with the Upper Cretaceous period a change in the flora took place so remarkable that Prof. Oswald Herr characterises it as "a new fundamental conception" introduced into the Vegetable Kingdom. It reminds one of the change which took place over Western Europe in architecture when the light and graceful "Early English" style replaced the massive and heavy "Anglo-Norman." To this change we are indebted for our forest trees, the oak, the walnut, the willow, the poplar, the plane, the hornbean, the liriodendron, the fig, magnolia, the myrtle, and the eucalyptus. Later on in early Tertiary times, fruit trees and flowering plants established their range, supplying us with food and decorating our hills and valleys. As the period for man's abode on earth approached, nature, under a guiding Providence, furnished and decorated his dwelling place. To the question above stated, Dr. Guppy gives no reply. It is so far an unsolved problem, which the geologist would try to answer by stating that the gap in time between the Lower and Upper Cretaceous was so immense that by a process of evolution the change resulted; but a botanist of eminence, Mr. Seaward, in his address to the British Association, states, "We are profoundly ignorant of the means by which nature produced this new creation."† The reply which refers all such facts to "the imperfection of the geological record," has been characterised by an eminent man of science as "the inflated cushion on which you try to bolster up the defects of your hypothesis." Not a bad illustration!

Dr. R. P. Colles.—In reply to your very courteous request

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* In the Animal Kingdom the development of the horse both in America and Europasia gives us an example of the process of nature above referred to.

† *Brit. Assoc. Report*, 1903, p. 847.

that I should send you, in writing, the remarks I made after the reading of Mr. Guppy's paper on Plant-Distribution, I can only repeat my answer that they are not worth it, except, perhaps, as relating to the Chairman's opinion that the author had not given sufficient importance to human agency as one of the means employed in the distribution of plants.

Many years ago I was for some time at Landawur, in the Himalayas, where there is a military sanatorium about 7,000 feet above sea-level. The steep sides of the mountain were wooded, principally with evergreen oak, the branches of which were thickly fringed with ferns; there were also rhododendrons growing as high as elms, with dark red flowers. Here and there, on the lower slopes, were small pine woods of wonderful beauty, and, I may also add, full of leeches, with which one's feet became covered when climbing up or down the steep khud (precipice) on which they grew. There were single dahlias growing wild on the mountain side in the places where there were no trees, forming patches of brilliant colour—scarlet, sulphur, and white. It was supposed that they were indigenous to the soil, and people wondered at this, as the extremes of climate in the Himalayas and the want of moisture for many months would be against the growth of such a plant. But our innocent speculations were one day ruthlessly overturned by someone saying, that in a little graveyard on the side of the hill above us, one of the graves had, some time ago, been planted with dahlias and that they had spread freely, partly from seed and partly from the clearing out of rubbish and superfluous clay, probably containing fragments of dahlia roots which were thrown down the hillside from the graveyard. In this case human agency would account for the appearance of this flower, but it would be interesting to learn if it still exists in the same latitude, or if it has gradually died out, as it might well have done after the lapse of years since I saw it there in 1872.

Colonel T. H. HENDLEY, C.I.E. (CHAIRMAN).—Is enough stress laid upon the importance of human agency in the distribution of plants or in the changes in climate which affect it? For example is not the dessication of large tracts of country due, in some cases, to neglect to maintain canals and other irrigation work, as has been the case in Mesopotamia; or to somewhat similar causes, as in the Western parts of the Punjab and Rajputana; or in others to diminution of the population from war or famine which has thrown land out of cultivation, as in Palestine.

Was not the decay of prosperous regions, owing to a change of climate, caused by wasteful destruction of forest, as well as those already cited, and has not land planted with vegetation, especially trees, led to increased rainfall and the introduction of new plants? Is not this the case in Egypt?

As to the dispersal, how are we to account for such cases as the appearance in India of large specimens of the Adansaria digitata, which is an important member of a genus confined to Africa and Australia (as Mr. Guppy says)? I have seen this magnificent tree, at one time thought to be the oldest tree in the world, in the ruins of Mandra, the famous capital on the Narbuda of the Sultans of Malwa, and it is found in other parts of India. Some believe it was introduced by the Portuguese only 300 years ago; others put back its introduction to a much earlier date.

In any case, is not too much importance attributed to time in these questions? If the Portuguese theory regarding the introduction of the Baobab into Western India is accepted, only 300 years are required for a wide dispersal. Of other cases we have more accurate knowledge. Most of the European garden vegetables now in use in India, we learn on the authority of the Physician Bernier, were first introduced into the country a few centuries ago.

The Emperor Baber has told us that before his time there was little fruit in the country, and it is certain that tobacco was unknown before the Moghul period, because the Emperor Jehangir, like so many other great Sovereigns of the time, threatened its use with death.

Instances such as these might be multiplied indefinitely, I think, in proof of the view that human agency is of immense importance in plant distribution.

Mr. MARTIN L. ROUSE.—The theory of the author of this learned paper is that every order or tribe was at the first created over a large proportion of the Earth's surface, and that, by the accidents of climate, exposure to wind or sun, elevation and character of soil, each split up into manifold genera and species more and more remote from one another over the vast region once covered by the original order or tribe. This agrees with the view of Linnæus, himself—whose reverent spirit none can impugn—for he thought that "Omnipotence created the orders, climate shaped these into genera, while the accidents" aforesaid "discriminated the genera into species." Doctor Guppy establishes his theory by the following arguments:—

1st. That the genus or sub-genus which contains more than any other the characters of an order, and appears thus to be the parent of its other genera, is the very one which is most widely distributed (of which phenomenon he, however, only actually cites two examples).

2nd. That among 23 orders and sub-orders that have been examined we get a result in a descending scale such as the theory would lead us to expect—namely that 92 per cent. of the tribes, 11 per cent. of the genera, and only 1 per cent. of the species are common to the Old World and the New.

3rd. That since the conditions under which land plants live differ far more amongst themselves than those under which fresh-water plants exist, we should expect to find far more species of land orders than of fresh-water ones; and, as a fact, we find ten times as many of the former as of the latter.

4th. That where the agencies of dispersal (currents, winds, and birds) have their fullest play in maintaining original species, there the number of strange species found is smallest.

The case is very strong against the common theory of dispersal of genera from single centres, which other arguments of the author show to be untenable; but he does not overthrow the view that every genus, and perhaps every species, was originated in one or more of its present abodes. If the species and genera of each order are the result of differentiation, we should expect to see them forming hybrids between themselves; whereas even the species will not do this naturally—and to bring it about artificially is no easy task—all the proper stamens of the fruiting flower having first to be cut away, for if any of its own pollen be at hand its stigma will receive and assimilate this by preference and yield a flower lik itself.* In an article written a year ago from Palestine to the *Gardeners' Chronicle*† by our fellow-member Mr. Arthur Sutton, he described the abundance and beauty of two plants that grow side by side in many parts of Palestine—the *Anemone coronaria* and the *Ranunculus Asiaticus*. The form of the flowers is, he says, the same,

* Chambers's Encyclopædia, *Hybrids.*

† For April 28th, 1906.

and the prevailing colour of both is a deep red or scarlet; but the *Anemone*, like all its genus, is without a calyx, while the *Ranunculus*, of course, possesses one; and whereas the lovely shades of colour in the *Anemone*, varying from a pure white to deep mauve, found in comparatively few districts, are never seen in the *Ranunculus*, the rare tints of bronzy yellow, sometimes seen in the *Ranunculus* are never displayed in the *Anemone*—the plant that has no calyx never exchanging tints with the plant that has one. Again, the plant without a calyx always begins to bloom two or three weeks before the other. So there is no hybrid between *Anemone* and *Ranunculus*. And yet they have bloomed in company for ages and in all positions and climates of Palestine—on the low plain of Sharon near the sea, by the Lake of Galilee, 700 feet below sea-level (where tropical plants thrive), and on the slopes of Mount Carmel, 1,500 feet above sea-level (where hail and snow are frequent); which fact, as Mr. Sutton points out, ought, on the theory of evolution, to have wrought some lasting change of form in both plants: but there has been neither hybridizing nor differentiating whatever. Similarly, the few plants that have been found in Egyptian mummy coffins are identical with their present-day representatives; and in the parallel case of animals Mr. Sutton cites a work published by Messrs. Lortet and Gaillard, of Lyons, entitled *La Faune Momifiée de l'Ancienne Egypte*, which "shows clearly that the species embalmed 20, 30, or even 70 centuries ago have not changed in the least."

Two instances alone are insufficient to support the author's first argument; one would like to know how many more he has in reserve.* And as regards his third argument, since the surface of actual land is far greater than that of lakes, rivers, and streams, and has been so ever since the creation of man, and since fresh-water plants can grow only along their borders or in their slower currents, we should expect to find a smaller variety of fresh-water plants than of land-plants in the world; and, as a fact, we have a smaller number of families and genera as well as of species of the former.

A cordial vote of thanks to the Author was then put from the Chair, and carried unanimously; the meeting then adjourned.

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* Perhaps these may be found in his volume referred to by the Secretary.