



Birbal Sahni
centenary, 1991

Revolutions in the plant world

Presidential address delivered by Birbal Sahni at the annual meeting of the National Academy of Sciences, 5 March 1938.

As the subject of my address today I have chosen a small theme embraced by that ocean of ideas that we call evolution. The particular aspect that I propose to deal with is revolutions in the plant world.

As in the history of nations, so also in that of plants and animals, we find that after a period of gradual change, which we generally call evolution, there comes inevitably a revolution—a period of rapid transition, when the balance of relations becomes upset and things begin to move faster and on a different plane. It would almost seem as if the very conditions that at first retard progress serve, in time, to bring about an acceleration, like the sediments that dam up the course of a river which some day must burst its banks to find a freer outlet for its pent up waters.

These revolutions in the organic world are the landmarks of geological history. Each of them marks a large-scale extinction of plant and animal life as well as a more or less sudden appearance of forms of life previously unknown. So striking is this fact of the sudden appearance of new species, genera and families that it is in sharp conflict with the Darwinian doctrine of natural selection as the only or even the chief explanation for the origin of new forms of life. Evolution in the sense of a gradual, orderly process of change is an undisputed fact. But evolution in this gradual sense is not the whole of organic evolution as revealed by the geological record. Periodic revolutions are an integral and essential part of evolution, and it may well be that they form the more important part, so far as the creation of new forms is concerned. At all events the orthodox idea of natural selection through the gradual accumulation of continuous variations utterly fails to explain some of the glaring facts of palaeontology.

The major revolutions in the plant world

I am not referring here to mutations in individual

species, but to transformations on a large scale, affecting a whole flora or fauna, such as we find when we trace the history of plant and animal life through geological time. The facts have been reviewed more than once by such eminent palaeobotanists as the late Dr D. H. Scott and Professor Sir Albert Seward. Speaking in broad terms, there were four or five such major revolutions, which Seward has aptly called 'nodal points in the history of evolution'¹.

(i) The first appearance of vascular plants must have marked a tremendous advance in the history of plant life. The date of this important event is still unknown but some early members of this land flora have been traced back to the Silurian period. An essentially similar type of vegetation seems to have continued through the Lower and Middle Devonian. (ii) But then a widespread change ushered in the flora which is familiar to us in the coal measures of Europe and America. This flourished during the Later Devonian, Carboniferous and Permian times. Till after the end of the Middle Carboniferous this Palaeozoic vegetation was fairly uniform in the northern and southern hemispheres. (iii) But in the Late Carboniferous and Permian floras we find a sharp contrast between the north and the south. The original southern flora was mostly killed out by a climatic revolution and there emerged a unique type of vegetation, the so-called *Glossopteris* flora, of which the origin has always been a great puzzle. We cannot call this change, great as it was, a worldwide transformation, but it was certainly one of the major events in the evolution of the plant world. We may conveniently speak of it as the Gondwana revolution, after the southern Gondwana continent on which the new flora mysteriously made its appearance. (iv) With the end of the Permian or early Trias the sharp contrasts between the northern and southern provinces disappeared. We find the essentially Palaeozoic flora, with its dominant seed ferns, Cordaitae, giant lycopods and calamites now giving place to

a more modern type of vegetation. Conifers and cycads are now much more prominent, while among the ferns several modern families can be recognized. The change is so abrupt that it threatens to shake one's faith in the doctrine of continuity in evolution. (v) The last great transformation came—or, to be more correct, became evident—in the early Cretaceous. As is the case with all revolutions, its beginnings must have been much earlier than its outward manifestation. We are now introduced to a new flora, essentially similar to that which we see today, with flowering plants as the dominant race. The Early Cretaceous angiosperms are quite modern in their structure, and distinct from any known in the older rocks. In spite of much recent work tending to trace the origin of the angiosperms to the earlier strata the gap remains essentially unbridged: of real links with the Jurassic we know very few.

These are, briefly, the main landmarks in the history of plant life; and similar 'nodal points' are seen in the fossil history of animals.

Breaks in the life-lines: Are they real or apparent?

These revolutions in the organic world are one of the most striking revelations of palaeontology, as they still remain one of its greatest riddles. The question is: Will these gaps in the record be ever filled up by further research, or are they real breaks in the life-lines of the plant kingdom? Is the earth's crust a book of which pages here and there have been torn out and lost, or is it that these pages never existed, and we have to seek elsewhere for an explanation of the gaps in the story?

To some extent, no doubt, the suddenness of the change observed in a palaeontological break is unreal. We can never hope to know in the fossil state all the forms of life that have existed. Many of them were either not preserved or their remains were denuded away with the strata in which they were contained. Although many gaps in the rock-record in one area are supplied by fossiliferous deposits elsewhere, there must be many forms of life of which no trace was left at all.

The imperfection of the geological record is a fact of which the true value will probably never be estimated. But even after making the most liberal allowance for it the suspicion remains that it cannot account for everything. Even if we examine the known fossil record as a whole we find serious gaps in the evolutionary sequence which defy explanation, for they occur even where the strata lie in a conformable series. On a small scale these gaps are familiar to the palaeontologist because on them depends the zonal classification of rock systems. But sometimes we find even big changes in the fossil contents of an apparently conformable series. In the Narrabeen stage of the Hawkesbury series in New South Wales the lower part contains a typical

Glossopteris flora while only a few feet higher up, apparently without any serious break in the sedimentary sequence, there occurs a flora with *Thinnfeldia* (*Dicroidium*) and other forms, showing hardly any resemblance with the earlier flora. Even if a few plants occur in common between the two floras the general facies of the flora has completely altered.

Now, it is easy enough to imagine the extermination of a group, or even the greater part of a flora, as the result of a climatic revolution or through the introduction of new biotic factors. But what is difficult to picture is the sudden creation, apparently without intermediate forms, of a new group of plants or a new flora. It is with these sudden appearances that I shall mainly concern myself today.

Speaking of the great palaeontological break between the Palaeozoic and Mesozoic eras Seward made the following remarkable observation about fifteen years ago^{2,3}. He said:

'The threads of life seem to have almost snapped, and one wonders whence came the new arrivals which, to our restricted vision, appear as aliens rather than the direct descendants of Palaeozoic types.... We may be led astray by a too rigid faith in the doctrine of continuity.'

And again, referring to the periodic upheavals of the earth's crust and the birth of mountain ranges, he added that

'revolutions in the inorganic world... had their counterpart in the living world. Some chains of life were destroyed; a few persisted in an attenuated form, still producing an occasional new link, while from time to time fresh chains were forged.'

Seward was so impressed by the evident discontinuity between the life-lines of the Palaeozoic and those of the Mesozoic that he suggested that some of these fresh chains might even be without connection with those along which life had evolved in an earlier age.

Coming from a confirmed evolutionist, brought up in the old Darwinian school, and with an unrivalled experience of the botanical record of rocks, these remarks would not fail to create something of a sensation. But there can be no doubt that this picture of apparently unconnected chains of evolution, both in the organic and in the inorganic world, is strictly true to the observed facts of geology. In the absence of a satisfactory explanation a tentative hypothesis, however speculative, is better than a blank confession of ignorance, or a disheartening appeal to the imperfection of the geological record. And in this sense Seward's idea of *actual* disjunctions in plant life through the ages was a definite step forward.

But nevertheless, to most modern biologists any hypothesis of the origin of entirely new and unconnected lines of evolution must seem bold. And I confess that to

me the sudden emergence of the *Glossopteris* flora from the Gondwana Ice Age remains as much of a mystery as my first experience of a Jack-in-the-box!

Among others who have discussed this question are the great French palaeobotanists Grand'Eury and Zeiller, Guppy, the late D. H. Scott and Paul Bertrand.

The idea of mutation applied to fossil forms: A French theory of metamorphosis

Grand'Eury, with his long experience as a field geologist in the Coal Measures of France, tried to apply De Vries's idea of mutation to the succession of species in the strata. He was impressed by the sudden way in which one species of a genus gave place, in a succeeding bed, to another resembling it but yet quite distinct, and without any evidence of intermediate forms⁴. This he observed not in isolated species, but in groups of them. Thus the species *Pecopteris dentata* Br., *P. arborescens* Br. and *Sphenophyllum filiculme* Lesq. were succeeded respectively by *Pecopteris biotii* Br., *P. schlotheimii* Goepf. and *Sphenophyllum oblongifolium* Ger. Similarly *Odontopteris reichiana* Gut. he regarded as ancestral to *O. minor* Br. Such instances are, in fact, common enough, both in the plant and in the animal kingdoms: they supply the very basis for the zonal subdivisions of a rock-system.

One may, of course, say that these breaks are only apparent, not real. Scott did suggest that 'the succession of species in a continuous series of beds does not necessarily represent the course of evolution. What we actually find may rather be the result of migration, and the origin of the new species may have taken place elsewhere⁵'. And yet, with all the intensive work that has now gone on for decades, the missing links still elude us. Did they ever exist at all?, we ask. Grand'Eury, following De Vries, answers No. So all our search was for nothing. For aught he can say, there might have been a *metamorphosis of one species into another*, brought about through an internal directive force like that in the life of a frog or of an insect.

So much for Grand'Eury's theory of the transformation of species in geological time: essentially, as we have seen, a De Vriesian idea. But these transformations would hardly make a revolution in a flora unless the change overtook the majority of species at the same time. Zeiller⁶ took the idea a step further and suggested that mutations may have occurred not only in species but even in groups of higher rank, entire families arising at a bound from others pre-existing. Evidently he also thought that too much had been made of the imperfection of the record.

It would seem that certain facts of palaeobotany do lend some support to Zeiller's idea. Let us consider the geological history of two ancient families of ferns, the Zygopterideae and the Osmundaceae. Most botanists

agree that there is a phylogenetic relation between them. If we compare the extreme members of these two groups we can find hardly anything in common between them. And yet there is a genus like *Grammatopteris* which links them so closely together that it is difficult to decide whether it is a member of the one family or the other^{7,8}. The zygopterids, after making a number of vain efforts at survival, witnessed in the bizarre forms of their leaf traces, became extinct in the Permian and at the same time, as though from their ashes, arose the Osmundaceae, which survive to this day. The flowering plants seem to arise suddenly in the Lower Cretaceous, but just about this time a vast group, the Bennettiales, had become extinct, which for many years have been regarded among the nearest known relatives of the primitive angiosperms.

An idea somewhat similar to that of Zeiller was suggested in 1919 by H. B. Guppy⁹. According to him the evolution of flowering plants took place in two successive stages. In the first stage the great families of angiosperms were created. 'It was an age of mutations, free and unchecked, and an age of uniformity of conditions.' The second stage marked an era of differentiation in response to climatic and other changes. This is the era of the modern angiosperms, which may be said to have begun with the Cretaceous period. Although Guppy confines his remarks to the history of the angiosperms, it may be assumed that he would agree to apply the same general theory to other groups. Scott has shown, however, that the theory cannot stand a close analysis. For one thing, we know nothing of the time or the manner in which the first angiosperm families arose. Secondly, there is no evidence that conditions were uniform during the era of creation of the angiosperms, because this must have coincided with the era of differentiation of earlier groups such as the cycads, conifers and ferns which according to Guppy's hypothesis must have demanded varied conditions of climate.

Another ingenious theory we owe to the distinguished French palaeobotanist Paul Bertrand. He explains in quite an original way the sudden appearance of the different groups of vascular plants in the geological scale. Like other modern biologists he has grown sceptic about the genealogical trees that were once so much in vogue. Many of us now agree that most of the great groups of the plant kingdom probably originated much further back than we were accustomed to believe. But Bertrand takes the idea to the extreme point. According to him not only did all the great phyla of vascular plants arise quite independently of each other¹⁰ but they originated simultaneously and as far back as the Archaean period. The fact that in the geological record the different groups come into evidence at different periods, often suddenly and without any precursors, he explains by reference to the

well-known antithetic theory of the alternation of generations. The origin of the sporophyte from the gametophyte he regards as a sort of *metamorphosis* comparable with that seen among the insects and the amphibia. Bertrand writes: 'The gametophyte or prothallus is in fact a *larval stage* which may persist as such through millions of years till conditions favourable for a completion of the metamorphosis are realized¹¹.

These prothallia or larval stages of plants are of various kinds. They are familiar to us in the Hepaticae, the Lycopodiales, the Psilotales and other groups. Often they are capable of perennating from year to year, and even of propagating themselves by buds and bulbils without the help of the sex organs.

Under certain conditions the dormant sex function becomes active and an embryo or sporophyte is formed as a sort of intercalation in the life-cycle. Like the prothallia, these sporophytes are subject to variation and differentiation in response to varied conditions of life, with the result that they evolve into so many species of vascular plants which we can now group into genera, families and orders.

If the course of events has been as here visualized, it becomes easy to understand Bertrand when he says that we shall never find any angiosperms 'as such in the pre-Cretaceous rocks, for the simple reason that these plants were then still in their prothallial or larval condition. With the dawn of the Cretaceous period the long-expected metamorphosis came and we see the angiosperms suddenly appearing in the form in which we know them today.

You will agree that Bertrand's hypothesis is nothing if it is not ingenious. Its chief merit is that it appears to solve one of the greatest puzzles of palaeontology without an appeal to the imperfection of the geological record. One feels tempted to follow it up in all its implications, particularly in connection with the theory of recapitulation, but this will lead us rather into a side track.

These courageous attempts to explain the transformations in the organic world at least indicate that we have advanced well beyond the Darwinian era. We no longer seek to explain everything by pleading the imperfection of the geological record.

Bertrand's bold hypothesis cannot be proved, but there seems nothing inherently opposed to the idea. We all know the classical example of that Mexican newt, the axolotl, which, for all we can say, reached its full development for the first time when it metamorphosed in captivity in the Jardin des Plantes at Paris. In the plant world too we know instances of species permanently arrested in the embryonic or seedling stage.

Thus, to all appearance *Welwitschia* is an 'adult seedling'. The vegetative organs are arrested at the seedling stage, the reproductive organs are mature. As

suggested several years ago¹², it would be an experiment worth performing to try and cultivate this plant in an environment where it could develop its vegetative organs also into the adult stage. The peculiar cytological behaviour of the gametophytes may be in some way connected with the hard life the plant has to lead. The restricted distribution of this aberrant monotypic genus on the edge of the S. W. African desert suggests that it is a species fallen on evil days, fighting against the forces of extinction by husbanding its vegetative resources for the more urgent demand of reproduction, like the precociously mature children in a starved population. The case seems parallel to that of the ephemeral flora of high altitudes and high latitudes where the season is too short to allow of a full vegetative development before flowering sets in and the seed must be formed against the approaching frost. I am reminded of a yellow carpet of flowering seedlings of a composite which I saw during a trek in Ladakh in the summer of 1920. They were eking out a precarious existence under the shelter of overhanging rocks at a height of 15,000 ft above sea level on the Rupshu plain.

The case of *Phylloglossum* is known to all students of botany. It affords another instance of arrested development, the spore-producing stage supervening soon after the embryo is able to support itself. Perhaps one day we shall have experimental vindication of Treub's theory of the protocorm. For it is by no means inconceivable that in these days of hormones the protocorm of *Phylloglossum* may be induced (like the axolotl) to mature into a fully developed *Lycopodium*-like vegetative body before it begins to produce sporangia.

From the work of Gudernatsch¹³ we know that tadpoles fed upon thyroid extract metamorphose prematurely into pigmy frogs, while the same larvae, if given thymus extract, grow into giant tadpoles and postpone their metamorphosis. It is possible that Klebs's classical experiments on the artificial control of thallophytic life histories will be extended to the lycopods and even to higher plants.

I may seem rather to have digressed from the main track of my theme, but what I have attempted to bring to the fore is the great importance of the environment not only in the life history of the individual but also in phylogeny.

Genetic consequences of the impact of environment

But perhaps the most significant advance in this connection has been recorded within the last two decades in the field of cytogenetics¹⁴⁻¹⁷. From palaeontology to cytology seems such a far cry that very few students of fossils have yet concerned themselves about these recent developments.

Speaking for myself, I confess that until a few months ago I had no idea of the bearing of these results upon our present problem. In an address recently delivered in Calcutta I was speculating on the sudden appearance, over a vast southern continent, of the *Glossopteris* flora immediately after the Gondwana glaciation. There can be little doubt that this flora was at least largely an indigenous product; it must have been evolved in Gondwana Land itself, from the hardier elements of the pre-glacial flora that survived the Ice Age, sheltered in ravines, on nunataks and in other local asylums. As the ice gradually melted away these few survivors must have found the conditions almost ideal for rapid multiplication, evolution and dispersal. And I tentatively suggested that 'It would almost seem that exposure to the rigours of the climate had quickened the pace of evolution, as if by inducing saltations on a large scale: a sort of natural vernalization, affecting not only the individual life-cycle, but the rate of evolution of species, possibly through aberrations in the nuclear cycle¹⁸'.

In vernalization a temporary chilling of the early stages of germination quickens the rate of development. The life history of the individual is telescoped into a shorter span of time. I am not aware that anyone has studied the cytology of vernalized plants. It would be interesting to know whether this telescoping effect is the outward manifestation of a detectable chromosomal change. Other things being equal, even this kind of an acceleration would hasten the rate of evolution of species by producing a larger number of generations in a given period of time. But I meant to carry the analogy much further by suggesting that *as a direct result of the glacial conditions there might have been produced chromosomal aberrations and gene mutations, leading to far-reaching genetic consequences*. At the time these ideas occurred to me I had no conception of the remarkable results already achieved in recent years by a number of workers in cytogenetics—results based not only upon observation but upon experiment under controlled conditions. The fact is that a large number of chromosome mutations have been produced artificially in a surprisingly wide range of plants.

Although this recent work is almost entirely the growth of the last two decades—indeed most of it is the product of only the past ten or twelve years—the literature is already too vast to be considered here in detail. Nor can I claim to be able to review it critically, though it is only fair to add that the importance of these results in the origin of new species and genera has been questioned, notably by Heribert Nilsson.

A brief statement of the recorded facts must suffice. Among the many agents that are now known to cause these aberrations are various chemicals, such as chloral hydrate and colchicine, narcotics and infections of various kinds such as may be due to fungal or insect

attacks, short-wave radiations such as X-rays and ultraviolet rays, centrifuging, grafting, hybridization and, what is of special interest from our immediate point of view, extremes of temperature, both high and low.

Confining our attention to the temperature effects alone, we are introduced to an impressive series of works by a number of authors whose ranks are steadily growing. I can only name a few of them: Avery, Belling, Bergner, Blakeslee, Borgenstam, Chizaki, De Mol, Dorsey, East, Elmanov, Farnham, Fernandes, Hagerup, Hollingshead, Koshuchow, Kostoff, Lundegårdh, Matsuda, Michaelis, Müntzing, Navashin, Peto, Radjably, Randolph, Rybin, Sakamura, Sax, Schloesser, Shimotomai, Takagi, Ternovsky and Tischler.

The range of genera on which these observations and experiments has been made includes, among many others, *Capsicum*, *Crepis*, *Cucumis*, *Datura*, *Epilobium*, *Hordeum*, *Nicotiana*, *Oenothera*, *Petunia*, *Pisum*, *Secale*, *Syringa* and *Zea*.

The cytological aberrations observed or induced affect both the vegetative and reproductive cells, and include, besides other irregularities, haploidy as well as various grades of polyploidy. In the roots of a plant the mitosis may be disorganized and a doubling of chromosomes may result (Lundegårdh). In *Datura* non-reduction in triploid and diploid forms may be greatly increased by temporary chilling (Belling and Blakeslee). In *Syringa* hyperchromosome gametes were produced as a result of low temperatures during the division of the pollen mother cells (Borgenstam). In *Nicotiana tabacum*, at a temperature of -0.5°C , a doubling of the chromosomes was observed in 20–25% of the pollen mother cells (Elmanov). By treating plants of winter rape to low temperatures during meiosis 8–13% of tetraploid plants were obtained (Schlosser). Heteroploid plants were produced in *Epilobium* and *Oenothera* by subjecting the plants to a sudden reduction of temperature during the period of flowering (Michaelis). Irregularities leading to the formation of dwarf as well as giant pollen grains were observed as a result of temperature effects during the division of the pollen mother cells (Shimotomai, Matsuda). In *Capsicum* Kostoff induced irregularities in the meiosis, resulting in polyploid gametes, by treating plants with alternating heat and cold. The case of rye is unique. The normal chromosome number is 14 ($n=7$), but we now know a haploid produced by cold treatment, a tetraploid obtained by heat treatment and a triploid formed by the twin seedling method (Müntzing). Other irregularities under the effect of high temperatures are reported by De Mol, Chizaki, Randolph, Sakamura and others.

Among the most significant observations in nature are those recorded by Hagerup, Müntzing, Navashin and Tischler. An adequate idea of these remarkable works can only be gained by a reference to the original

sources. But I shall attempt briefly to review these results as they strike a palaeobotanist enquiring into the plant revolutions of the geological past.

Hagerup's interest in this field led him to study cytologically the floras of extreme climates, for example, those of Greenland, Iceland and the Faroe Islands on the one side and, on the other, the flora of the hot and arid African Sahara near Timbuctoo: regions where the struggle for existence is keenest and 'natural selection' of the hardiest forms takes place. *Empetrum hermaphroditum*, a new tetraploid bisexual species described by him in 1927, is a genetically constant type, presumably derived from the unisexual diploid form *E. nigrum*. It lives in higher latitudes than its diploid progenitor, as if tetraploidy had given it greater hardiness and vitality. In the genus *Bicornes*, which has a graded series of species ($n=6$), $\times 2$, $\times 3$, etc. up to $\times 8$, Hagerup finds that it is always the highest polyploids of the series that grow furthest north. In the Sahara, too, he found that the polyploids differed from the diploids morphologically, ecologically, geographically and genetically. They were usually the largest individuals ('gigas' forms) and were more hardy against the heat and drought. Of three species of *Eragrostis* at Timbuctoo *E. cambessediana*, with $n=10$, is an annual which dies down in the hot weather; *E. albida*, with $n=20$, lives in drier situations on the dunes and is a perennial; the hardiest form is the giant *E. pallescens* ($n=40$).

Hagerup's observations on polyploid ecotypes in *Vaccinium* are equally interesting. *V. uliginosum* forma *microphylla* ($n=12$) is a dwarf diploid with a circum-polar distribution, while the tetraploid form *genuina* ($n=24$) extends far and wide into Central Asia, Japan and North America. Thus it is not always the form with the greatest number of chromosomes that is the hardiest. In *Orchis* Hagerup finds that 'the tetraploid individuals have by far the greatest ecological and geographical range', extending furthest north in the Faroe Islands and N. Iceland. They also have a later and longer flowering period than the diploid forms.

Among the few records from this country relating to this question is Bhaduri's¹⁹ statement that the common weed *Solanum nigrum* is represented in India by diploid, tetraploid and hexaploid races. Since in Europe and North America only hexaploids have been found, a southern origin for the species seems suggested. It would be interesting to know whether the diploid, tetraploid and hexaploid forms show a progressive geographical range even within India.

Müntzing²⁰ has given an admirable analytical summary of the literature on polyploidy. While some authors, like F. von Wettstein, are sceptic about the significance of polyploidy in the origin of new species, Müntzing belongs to the larger group of geneticists, including Hagerup, Tischler, Blakeslee, Avery, Jørgensen, Darlington, Babcock, Sax, Fernandes, Lilienfeld and

others, who attach fundamental evolutionary importance to it.

Müntzing (1930) for the first time succeeded in 'creating' a synthetic species *Galeopsis tetrahit* ($n=16$) by crossing *G. pubescens* ($n=8$) with *G. speciosa* ($n=8$); similarly Heribert Nilsson (1931) combined *Salix viminalis* ($n=19$) and *S. caprea* ($n=19$) into *S. cinerea* ($n=38$). Both the synthetic forms were already known to occur in nature, and presumably arose by hybridization. These facts are a striking vindication of Winge's theory of the origin of polyploids and of Lotsy's (1925) idea of the origin of new species by hybridization. More recently (1935) the Japanese botanist U obtained *Brassica napus* ($n=19$) from *B. campestris* ($n=10$) and *B. oleracea* ($n=9$).

This brings us to the fascinating subject of intraspecific chromosome races, of which Müntzing has made a comprehensive study. The great majority of these are intraspecific polyploids, but sometimes it is difficult to decide whether we are not dealing with two or more closely related but distinct species. Comparing the morphological characters of such polyploid races with those of experimental polyploids the conclusion is that an increase in the number of chromosomes very often goes hand in hand with a general quantitative increase in the body of the individual, expressed in the term gigantism. Thus, compared with the diploid the tetraploid may be more robust, have a thicker and taller stem, larger leaves, larger flowers and larger seeds and pollen grains²¹, even a larger cell size. But 'there is an optimum for chromosome increase beyond which the individuals become less vigorous if they are viable at all'.

Similarly, chromosome increase is frequently expressed in a change in ecological behaviour and geographical distribution. We have seen that polyploids, being on the average more hardy, often have a more northern and alpine distribution; or they may be better able to withstand extremes of heat and drought. It would almost seem as if any adverse conditions of climate may bestow hardiness upon a species.

Again, through a chromosome increase a race of annuals may become a race of perennials* and Müntzing²⁰ actually finds that within a given genus the perennial species on the whole have higher chromosome numbers than the annuals. Fagerlind is even reported to have found that the summer form of one and the same species (e.g. *Galium palustre*) may be a diploid while its autumn form is octoploid.

These facts have an obvious importance in the invasion of new areas by hyperchromosome forms, which then are able to hybridize with forms previously

*It may be useful to compare the chromosome numbers of the trees, shrubs and herbs in the families of angiosperms. This may give a clue as to whether the tree habit is primitive, or derived from the herb and shrub habit through a chromosome increase.

inaccessible to them. Similar ideas have been expressed by Navashin, whose work on chromosome races in the genus *Crepis* is well known²².

Tischler²³ of Kiel has made statistical studies on chromosome numbers in relation to climate, ecology, geographical distribution and taxonomy, considering for the first time the flora of a province as a whole.

After a cytological analysis of the flora of the Halligen^{24,25}, a group of small islands in the North Sea liable to frequent flooding by sea water, Tischler finds that, among the weeds introduced by man, those that have become permanently settled to these difficult conditions are 100% polyploids while others, which are occasional visitors not yet completely acclimatized, have only 30% polyploids. The indigenous flora has 50%, that is, about the same percentage as Schleswig-Holstein, the northernmost province of Germany. In Schleswig-Holstein, we know the chromosome numbers of as many as 73% of the species, and of these, according to Tischler, about half are polyploids. About the same percentage of polyploids occurs in East Prussia. Iceland, so far as available records show, has 55% while Sicily has only 30% polyploids. From such comparative data on the chromosome numbers of northern and southern floras in Europe, Tischler draws a conclusion of special interest in our present enquiry. He writes²⁵: 'It seems reasonable to conclude that the influence of the glacial periods [of the Pleistocene age] has enhanced the number of polyploids and decreased that of diploids, for the latter could not survive in the competition.'

The great frequency of polyploids among angiosperms (it has been conjectured that about half the angiosperms are polyploids) and the existence of so many series of chromosome multiples, indicate that polyploidy plays an important part in the origin of new species. As Fernandes (1931) says, it is reasonable to agree that it may have influence on the evolution of genera.

Enough has been said to show how intimately this recent work has brought our problems of cytology into relation with the problems of plant-geography, adaptation and evolution. One might well ask, if only Darwin and Wallace had had an inkling of these remarkable results in their day, what use would they not have made of them in the theoretical structure of their great work?

But what of that problem of *revolutions* in the plant world, which is here our main concern? That question still defies solution, but after what we know of the direct effect of climatic factors on the genetic constitution of plants is it unreasonable to relate at least some of the great transformations in the plant kingdom with climatic revolutions in geological time? Cannot the Gondwana glaciation, for example, have been directly responsible for initiating changes which resulted in the rapid evolution of a flora that was essentially new? For, if it has been possible for us to

produce such startling results as those briefly described above within the brief space of two or three decades, is it impossible that climatic oscillations on that vast continent, acting on a flora through thousands of years, may in the course of generations have induced changes of a revolutionary nature?

It must be confessed that even if the hypothesis here suggested is correct we shall still have to assume that many intermediate types must have perished without leaving a trace, or that their remains should be looked for in the very earliest plant-bearing Gondwanas, *even in the glacial beds themselves*. This will show at once how important it is to investigate these earliest of the Gondwana floras. For at present the differences between the pre-glacial and post-glacial floras are too large, both in the degree of the change and in the number of forms affected: in none of our experimental mutations have we yet been able to produce changes of such magnitude.

Thus the main problem of organic revolutions stands where it was, but the broad fact remains that some of the periods of the most active creation of new forms of life have coincided with the physical revolutions of the geological past.

1. Seward, A. C., *Q. J. Geol. Soc.*, 1923, **79**, lxxvi-civ.
2. Seward, A. C., *Q. J. Geol. Soc.*, 1924, **80**(2), lxi-xcvii.
3. Seward, A. C., *J. Linn. Soc. (Bot.)*, 1922, **46**, 219-240.
4. Grand'Eury, M., *C. R. Acad. Sci. (Paris)*, 1906, **142**, 25-28.
5. Scott, D. H., *Extinct Plants and Problems of Evolution*, 1924.
6. Zeiller, R., *Rev. Mois Paris*, 1907, **3**.
7. Sahni, B., *Ann. Bot.*, 1932, **46**, 863-877.
8. Corsin, P., *Contribution à l'étude des fougères anciennes du groupe des Inersicaténales*, Lille, 1937.
9. Guppy, H. B., *J. Linn. Soc. (Bot.)*, 1919, **44**, 439-472.
10. Bertrand, P. and Corsin, P., *C. R. Acad. Sci. Paris*, 1936, **203**, 465.
11. Bertrand, P., *C. R. Acad. Sci. Paris*, 1937, **205**, 1253.
12. Sahni, B., *J. Indian Bot. Soc.*, 1925, **4**, 202-216.
13. Gudernatsch, *Zentrabl. Physiol.*, 1912, **26**, 323.
14. Dobzhansky, T., *Genetics and the Origin of Species*, Columbia University Press, New York, 1937.
15. Sax, K., *J. Arnold Arbor.*, 1936, **17**, 153-159.
16. Timofeëff-Ressovsky, N. W., *Biol. Rev.*, 1934, **9**, 411 ff.
17. Macfarlane, H. J., Muller, O., Winge, H., Kihara, H. B., Frost, E. B., Babcock, A., Franklin Shull, C. B., Davenport and Calvin B. Bridges, *Curr. Sci.*, 1938, 1-39 (special number on genetics).
18. Sahni, B., 'Recent advances in Indian palaeobotany', Presidential address, Botany Section, 25th Indian Science Congress, Lucknow University Studies, Lucknow, 1938, no. 2, pp. 1-100.
19. Bhaduri, P. N., *J. Indian Bot. Soc.*, 1933, **12**, 56-64.
20. Müntzing, A., *Hereditas*, 1936, **21**, 263-378.
21. Müntzing, A., *Hereditas*, 1936a, **21**, 383-393.
22. Navashin, M., *Univ. Calif. Publ. Agric. Sci.*, 1929, **2**(14), 377-400.
23. Tischler, G., *Bot. Jahrb.*, 1935, **67**, 1-36.
24. Tischler, G., *Cytologia*, (*Fujii Jubiläumband*), 1937, 162-170.
25. Tischler, G., *J. Indian Bot. Soc.*, 1937a, **16**(3), 165-169.
26. Hagerup, O., *Hereditas*, 1932, **16**, 19-40; 1933, **18**, 122-128; 1938, **24**, 258-264.
27. Navashin, M., *Genetics*, 1925, **10**(6), 583-592.
28. Tischler, G., *Biol. Zentrabl.*, 1928, **48**, 321 ff; *Ber. Deutsch. Bot. Ges.*, 1929, **47**, (30)-(49).