Reflections

In this issue, honouring the great Indian palaeobotanist Birbal Sahni, we have chosen to print an abridged and slightly edited version of the Presidential Address delivered by him at the Annual Meeting of the National Academy of Sciences, India, on 5th March 1938, an address reproduced in full in the journal *Current Science*, Vol 61, 1991, pp.594-600. It is an interesting address to read with the benefit of a further 65 years of evolutionary research, for the topic Birbal Sahni chose to discuss then is still a live issue in evolutionary biology today. Basically, the issue is that of the repeated pattern of the sudden (in geological terms) appearance of new species in the fossil record, after a long period of stasis, without evidence of any intermediate forms that would be expected under the notion of evolution as a gradualistic process of transformation of one species into another. This issue came into prominence once again in 1972 when Niles Eldredge and Stephen Jay Gould put forward the theory of punctuated equilibrium to explain this pattern in the fossil record (see *Resonance* 2002 Vol 7, No.11, pp.2-5).

It is worthwhile, when reading this piece, to remind oneself of the year – 1938. The Neo-Darwinian synthesis was far from complete, population genetics theory was yet to be appreciated by the majority of evolutionists, and the clear distinction made today between mechanisms and rates of micro-evolution (adaptive evolutionary change within populations of a species) and macro-evolution (origin of new species, genera etc.) was far fuzzier. These were also the days when Darwinism was equated with gradualism, the notion that new species arose *only* by the slow, incremental transformation of pre-existing species. In fact, gradualism is not central to a Darwinian view of adaptive evolution as occurring largely through natural selection, and is no longer considered an important part of Darwinism today. Even in Darwin's time, his friend T H Huxley had tried to convince him to drop his emphasis on gradualism, calling it a 'mill-stone'.

What I found most interesting about this address by Birbal Sahni is the intimate look it gives us at the workings of a first-rate scientific mind. Faced with the empirical evidence of sudden appearance of new flora in fossil strata, Sahni discusses with clarity, and rejects, the possible explanation that the data could be explained as mere imperfections in the fossil record. He then goes on to critically discuss various speculative hypotheses that had been proposed to explain the observed patterns in the fossil strata. Finally, he goes beyond his own field of specialization to the relatively new field of experimental cytogenetics, and marshals evidence supporting his hypothesis that adverse climatic conditions may, in fact, lead to major changes in chromosome number, thus facilitating the rapid evolution of new species. This is a great example of a scientific mind at work: examining data critically, proposing hypotheses, and marshalling evidence from disparate fields of research in order to put the hypotheses to empirical test. The notion of environmental change somehow facilitating rapid evolution also resonates today in light of recent findings on the unmasking of genetic variation in stressful conditions, and the conversion of non-additive to additive genetic variance during population bottlenecks or environmental change. Stasis and rapid evolutionary change, as well as evolvability, and its evolution under different environmental scenarios, are today topics receiving much attention from evolutionary geneticists, and Sahni's early speculations about the role of cytogenetic changes in periods of rapid evolutionary change are a sobering reminder that we often keep re-discovering, under ever newer names, the same basic ideas and insights that have periodically occurred to our many predecessors in the quest for understanding that is science.

Amitabh Joshi

Revolutions in the Plant World

Birbal Sahni

Presidential address delivered 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 things begin to move faster and on a different plane. 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.

(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 southera 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, Cordaiteae, giant lycopods and calamiles 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.

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. 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? To some extent, 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. 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. 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.

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 forms. Grand Eury believed 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. But these transformations would hardly make a revolution in a flora unless the change overtook the majority of species at the same time. Zeiller 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. Certain facts of palaeobotany do lend some support to Zeiller's idea. Consider the geological history of two ancient families of ferns, the Zygopterideae and the Osmundaceae. 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. 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 Osmundaccae, which survive to this day.

An idea somewhat similar to that of Zeiller was suggested in 1919 by H. B. Guppy. 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. Scott has shown, however, that the theory cannot stand a close analysis.

Another ingenious theory we owe to the distinguished French palaeobotanist Paul Bertrand. According to him not only did all the great phyla of vascular plants arise quite independently of each other 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 realized.'

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.

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 cytogenetics. From palaeontology to cytology seems such a far cry that very few students of fossils have yet concerned themselves about these recent developments. Recently 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 must have evolved in Gondwana Land itself, from the hardier elements of the pre-glacial flora that survived the Ice Age. 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 cycle'.

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 cytogenctics – results based upon experiments under controlled conditions. A large number of chromosome mutations have been produced artificially in a surprisingly wide range of plants. Among the many agents that are now known to cause these aberrations are various chemicals, 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. 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 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. In *Datura* non-reduction in triploid and diploid forms may be greatly increased by temporary chilling. In *Syringa* hyperchromosome gametes were produced as a result of low temperatures during the division of the pollen mother cells. 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. By treating plants of winter rape to low temperatures during meiosis 8-13% of tetraploid plants were obtained. Heteroploid plants were produced in

Epilobium and *Oenothera* by subjecting the plants to a sudden reduction of temperature during the period of flowering. In *Capsicum* irregularities in the meiosis were introduced, 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.

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), × 2, × 3, etc. up to × 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. pallcscetis* (n=40).

Hagerup's observations on polyploid ecotypes in *Vaceinium* are equally interesting. *V. uligiiiosum* forma *microphylia* (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.

Müntzing (1930) for the first time succeeded in 'creating' a synthetic species *Galeopsis tetrahit* (n = 16) by crossing *G. pubeseens* (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. Comparing the morphological characters of natural 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 grains, 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. From 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 writes: '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.

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?

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.