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## THE EFFECT OF THE HIMALAYAN UPLIFT ON THE GENETIC COMPOSITION OF THE FLORA OF ASIA\*

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FIRST of all I wish to thank the Fellows of the Indian Botanical Society for the privilege given to me to address the Society as its President. I am deeply conscious of this honour.

The subject I have chosen to speak to you today is "The Effect of the Himalayan Uplift on the Genetic Composition of the Flora of Asia".

The explanation of the present distribution of plants in any region of the world is based on the history of their past habitats, which include the geological history of the earth's surface—the history of its land and seas and mountain ranges—former land connections, the movement of glaciers and the existence of ice-sheets not to mention the climatic changes brought about as a result of all these. The choice of my subject presupposes that I have a knowledge of all these, as well as of the past and present flora of Asia. I must admit that my knowledge is very limited. I hope you will, therefore, forgive me if I am able to only touch the outer fringes of this vast topic. A great deal of data remains yet to be gathered before we can have a clear picture of the effect on plant life of the tremendous revolution which created the highest chain of mountains across Asia.

We now know that this earth of ours is a very old body. It is nearly 3,500 million years old according to the latest calculations from the rate of decay of radioactive minerals and the study of isotopes of elements found in Archean rocks. Periods of mountain building followed by Ice Ages have been the fate of our earth from very early times. This was followed by the regression of ice, erosion, resulting finally, in aridity and desert conditions. Evidence of this recurring cycle can be clearly seen in the rocks of every geological age (Wadia, 1955).

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Ice Ages are great testing times for organisms and since the dawn of life, our Earth has emerged from every Ice Age with something new and startling. The last Ice Age, which occurred only a million years ago, saw the advent of Man, while the great Ice Age of the Permian-Carboniferous probably laid the foundation for the origin of seed plants, which made possible at a later age for the rise of warm-blooded mammals and finally Man himself.

We know that for millions of years the great Paleozoic Sea known as the Tethys separated the southern continent Gondwana, from the northern, Laurasia and received the sediments brought by the rivers of both these land masses. We also know that in Paleozoic times, two distinct floras were developed on these two land areas. The present distribution of fossils of this period gives us a clue of the extent of these two continents. The *Glossopteris* flora associated with Gondwanaland is today found in such widely separated regions as Australia, South America, Africa and Peninsular India, that this fact alone may be considered as a proof for either the subsidence or movement of continental blocks which once formed part of Gondwana. To Birbal Sahni and his School of Paleobotanists, the world in general and India in particular is indebted for the elucidation of the history of plant life of the Gondwana period (see B. Sahni, 1936).

Flowering plants appeared on the earth about 160 million years ago. When first seen as fossils in the Cretaceous they were found to be as developed as they are today, so that, their origin is still shrouded in mystery. Considering the world as a whole, the Cretaceous was probably the age of the greatest submergence of the earth's land surface. With this great spread of seas, the climate of our earth was mild and equable. Upper Cretaceous rocks preserve even in high latitudes abundant remains of land plants belonging to genera now restricted to warm temperate or subtropical regions. Amongst these are figs, cinnamons, laurals and magnolias. The Tethys was a great highway for the transporting of the warmth of the tropics to the arctic zone and along the estuaries of its rivers grew the palm *Nipa* now found in the tidal swamps of India, Burma and the Andamans and the water chest nut *Trapa*, flourished in the basin of the Thames.

The transformation of the sediment of the Tethys into the mighty Himalayan range was ushered in by a period of great earth movements in the Mesozoic, which were responsible also for the breaking up of the southern continent of Gondwana into its fragments which now form Africa, South America, Peninsular India and Australia. Thus we may rightly exclaim with due apologies to the poet:

“There grows the tree where rolled the deep.  
O earth what changes has thou seen  
There, where the snow caps rise has been  
The stillness of the Central sea.”

The rise of the Himalayas has been described as “a great buckle in the earth's crust which raised the Central Asian plateau in late Tertiary

times, folding over in the Baikal region in the north against the solid mass of Siberia and curling as a great wave on the south against the firmly resisting mass of the Indian Peninsular”.

The main folding took place in Tertiary. The great outflow of the Deccan trap was followed by a depression to the north and west, and the sea in Eocene times spread over Rajputana and the Indus valleys as well as invading the area now known as Assam. Then followed a rise of land and subsequent retreat of the sea. Freshwater deposits which covered the marine strata were involved in this movement as fast as they were formed till the sub-Himalayan zone deposits, not older than Pliocene were tilted up and overtured in the great folding. The final rise of the Himalayas in late Tertiary was accompanied by movements which gave rise to the Naga Hills and Arakan Yoma in the East and the hills of Baluchistan and Afghanistan in the West.

This briefly is the sequence of events during the formation of the mighty Himalayan range. A downward thrust from the north, and a southern resistance to this thrust, resulted in the bending of the Himalayas in the Assam corner and less markedly in the north-west region. The direct effect of this great upheaval was the annexation of Arabia, which is a bit of Africa and of Peninsular India to the mainland of Asia, in other words the expansion of Asia geographically and floristically. Nearly all the important families of flowering plants were differentiated before the Himalayan uplift and a study of the development of the post-Himalayan flora of Asia may be established on the basis of the different modes of investigation which the present state of our knowledge places at our disposal.

Said Darwin in 1857 “no one ought to feel surprise at the much, remaining as yet unexplained on the origin of species if we make due allowance of our profound ignorance on the mutual relations of the inhabitants of the world at the present time, and still more so during past ages”. Even as he wrote this, in a quiet monastery in Austria a monk was experimenting on two varieties of garden peas, one tall and the other a dwarf, to study the mutual relationship between them. From these experiments Mendel discovered the random segregation of what he called “elements”, now known as “genes” whose variation controlled characters like colour and height and are responsible not only for the similarity existing between organisms but also for their differences. Mendel’s discoveries were contrary to the prevailing thought of the day and probably for this very reason, his great experiments remained hidden in the proceedings of an obscure journal until they were rediscovered in 1900.

What the effect on the scientific thought and attainment of the 19th century would have been if Darwin and Mendel had met, as Darwin and Hooker and Lyall had met and discussed the causes of variation in plants and animals is hard to imagine.

For over 50 years men of science wrangled about the “Evolutionary theory” of Darwin without finding the true answer to the causes of

variation which Darwin wrote about and which Mendel explained. The immense amount of experimental studies on inheritance of characters based on the work of Mendel and the discovery that chromosomes constitute the mechanism of this inheritance has been the outstanding contribution of the first quarter of the present century. Looking back on the last 30 years, further discoveries relating to the structure and behaviour of chromosomes, their constancy and variation in different plants, species and genera and the relationship between chromosome variation and external morphological character, has brought to light the evolutionary sequence of families of both the plant and animal kingdoms as well as the relation between wild and cultivated plants. It has explained the origin of many of our crop plants from more simple ancestral forms by hybridization or chromosome doubling or by a combination of both these processes. The method of chromosome analysis can be employed in tracing the race history of a genus in time and space or in tracing the evolution of a flora. The study of a few genera in a particular land surface can give us the trend of development of the entire flora and I propose to use this method to present briefly the genetical changes seen in a number of genera of Asian plants which came into contact with the Himalayan uplift.

There are indications that the Himalayas are probably still rising and the effect of recent elevation is reflected not only in the change of plant communities as was shown by the study of Pleistocene fossil flora in the Karwas of Kashmir by Puri (1946) but also in the change in the chromosome complex of certain genera which constituted the flora of Asia before the Himalayas attained their present height.

We know that all polyploids must have ultimately arisen from diploids except in the rare cases of reversal by parthenogenesis. Hence the path of polyploidy can be considered as the path of evolution of new species. Amongst the many species of fossil Magnoliaceae which have been identified with living plants, Seward (1926) mentions *Magnolia thomsonianum* as closely agreeing with *M. globosa* of Tibet, while Reid and Chandler (1933) consider the fossil seeds of Magnolias found in the London clay as being very closely related with the present-day species *M. nitida* of Yunnan and *Magnolia parviflora* of China. When these so-called "Living fossils" were examined cytologically I found them all to be diploids ( $2n = 38$ ). They also belong to a group of Magnoliaceae with "introse" dehiscence of anthers which the systematic botanist considers as more "primitive". In the case of the more advanced deciduous type with "extrose" dehiscence those from North China and Japan and Korea with small flowers were found to be diploids while 8 species from Upper Burmah, Nepal, Sikkim, Yunnan and Szechuan the provinces adjoining to the Eastern Himalayas were found to be hexaploids ( $2n = 114$ ) (Janaki Ammal, 1952). These include the magnificent large flowered *Magnolia campbelli* of Sikkim and Nepal Himalayas and the even more magnificent *M. mollicornata* of Yunnan. Thus ployploidy in Asian Magnolias is restricted to the deciduous Sino-Japanese types which have migrated along the Himalayas into India. All the evergreen species of *Magnolia* and the related genera

*Michelia*, *Talauma* and *Mangleitia* have remained diploids in the more humid tropical regions of Assam and Malaya.

The phenomena of high polyploidy in regions close to the glaciers of the Eastern Himalayas have been noticed in several other genera of plants including the *Camellia*, *Honeysuckles*, *Buddleias*, *Viburnums* and *Rhododendrons*. In these genera high polyploids occur in the region where the Himalayas bend over the plateau of Assam. This may be considered as a region of active speciation today. That such a region of active speciation also exists in the North-Western corner of the Himalayas is becoming more and more evident from the study of some of the medicinal plants of this region in particular in species of *Artemisia* (Sobti, unpub.) in which tetraploids have been noted from this part only.

The difference in the climates of North-Western and North-Eastern Himalayas—one cold and dry and other cold and humid—probably accounts for the difference in the rate of speciation by polyploidy in these two areas. In the Assam corner due to bending of the Himalayas, there is also a meeting of the Chinese and Malayan floras which probably encouraged hybridization and thus has contributed to the richness of the flora of this region.

The production of unreduced gametes as a result of extreme cold is responsible for the occurrence of triploids in regions subject to cold spells. A certain number of natural triploid seedlings have been often reported when seeds collected from high mountain ranges are germinated. This has been the case in *Viburnums* and *Rhododendrons*.

In nature, triploids are the source of what may be called "chromosome contamination". This is due to the formation of gametes with more than the normal complement of chromosome in triploids. When crossed back with the original diploid species these triploids or their progenies give rise to races with higher chromosome numbers. These eventually can result in species with different basic numbers.

In *Viburnum* the living species most closely related to fossil types and thus considered primitive are those with paniculate inflorescence. These are distributed in North Asia, Japan and the Himalayas and also in the mountains of Peninsular India. They have a basic chromosome number  $x = 8$ . The more widely distributed species of *Viburnum* which are found throughout the Northern Hemisphere today have a basic  $x = 9$ . We may consider the former with the lower numbers  $x = 8$  as being endemic relics in the same manner as 8-chromosome *Primula* of Central China (Stern, 1949). Unlike *Primulas* the 8-chromosome form of *Viburnum* has many polyploids in South-East Asia. One such is *Viburnum erubescens*  $2n = 48$  which must have, during pluvial times, migrated from the Himalayas to the Hills of Southern India where it occurs in isolation today. Repeated hybridization between diploid and triploids have resulted in even higher basic chromosome number ( $x = 10$ ) in *Viburnum*. These are found in close association with  $x = 8$  type both in China and India (Janaki Ammal, 1953).

For the study of the effect of altitude on speciation in Himalayan plant, we turn to the genus *Rhododendron* which has a wide distribution chiefly along mountains in the Northern Hemisphere. There are about 1,000 species in this genus. In Asia the greatest concentration is in China with belts extending into Tibet, Bhutan, Sikkim, Nepal and Assam.

Rhododendrons fall under three groups:—

The deciduous Azalias; "Lepidotes" with stellate scaly hairs and the simple-haired "non lepidotes" which Hutchinson considers as being the most "primitive" and related to the Dilleniaceae from which he considered *Rhododendron* to have been descended. All non-lepidotes are diploid ( $2n = 26$ ). Lepidotes are found in altitudes up to 18,000 in the Himalayas and are often the last vestiges of flowering plants in these regions. Polyploids are found only in the lepidote section in Asia and polyploidy is confined to those species distributed in the Eastern Himalayas (Janaki Ammal, 1950). It is interesting to note that one species *R. lapponicum* which is circumpolar has remained a diploid!

The most prevalent type of polyploidy found in *Rhododendron* was the tetraploid ( $2n = 56$ ). The beautiful *R. cinnabarium* of Sikkim and its related species *R. concateucens* of Assam are hexaploids ( $2n = 78$ ). The *Rhododendrons* of Sikkim and Bhutan, Assam and Northern Burma are in fact markedly devoid of tetraploids; hexaploids and diploids being found in association sometimes within the same species. This is especially common in the Lapponicum series which inhabit the high mountains of Tibet, Yunnan and Szechuan. *R. idoncum* of Yunnan and *R. flavidum* of Szechuan and Tibet are good examples. More polyploids than diploids were found in the 2 series—Lapponicum and Triflorum. This group of hardy mountain plants have adapted themselves to life on high altitude by polyploidy.

Unlike many other genera of plants *Rhododendrons* decrease in size as they increase in polyploidy. I quote Kingdom Ward who knew *Rhododendrons* intimately in the wild "the highest alpine do not flower before June by which time enough snow has been melted to expose them". In general I have noticed within each series that the earliest flowering species are diploids and the later ones tetraploids. Thus polyploidy has been one of the ways in which *Rhododendrons* have been able to combat the inclemency of altitude. They literally climb higher, by increasing their chromosome number and survive by the late flowering associated with polyploidy. The presence of diploid and hexaploids and the association of triploids in the same vicinity seem to point out that hexaploid are derived from diploids by the doubling of chromosome of a triploid. This phenomena is found not only in *Rhododendron* but in other plants of the Himalayas. You will recall that the deciduous magnolias of Japan and China are diploids while those of Sikkim and East China are hexaploid. Hexaploids are also

found in *Camellia* in close proximity of diploid species (Janaki Ammal, 1952).

One of the effects of the Himalayan uplift was to cut away the moisture bearing winds of the Indian Ocean from penetrating into the heart of Asia. While the glaciers of the Ice Age lasted, abundant water was available from the melting of ice in Summer. As the deep glaciers receded the mountain streams dried up or were lost on their way to the northern rivers so that what was once wooded forest became the bleak desert of Gobi and Lop-Nor. Tree trunks buried in the sand have been discovered by travellers. Amongst them are those of mulberries. The genus *Morus* to which mulberries belong may be considered as a typical East Asian genus. As fodder plant for the silkworm the diploid species *Morus alba* and *M. indica* ( $2n = 28$ ) have been widely disseminated in all countries of Asia from very early times. Only one species *M. rubra* is indigenous to America and this resembles the Siberian form of *M. alba* and has the same chromosome number  $2n = 28$ .

*Morus nigra* the black mulberry has the distinction of having the highest chromosome number in flowering plants ( $2n = 308 = 22x$ )—Persia is recorded as its original home. The origin of such a high polyploid surrounded by diploid species remained a genetical puzzle till the missing links in its chromosome history was found in *Morus cathyana* of Central China with  $2n = 56, 84, 112$  (Janaki Ammal, 1948). Today the distribution of *Morus nigra* and *M. cathyana* is broken by the deserts of Lop-Nor and Gobi and the tree trunks buried in the sands give evidence of past continuity. The ancient silk route across Asia through which the black mulberry was introduced from China to Persia also passes through this territory.

I have dealt with the race history of only a few genera of Asian plants associated with the Himalayas. A fuller picture of the effect of the Himalayan uplift on the genetic composition of the flora of Asia will be revealed when cytogeographical studies are extended to cover more genera of Himalayan plants.

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