FERNS AND PALMS AS INDICATORS OF CLIMATE AND PALAEO-CLIMATE*

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THE living plant is a complex organization reacting to its environment in a variety of ways depending upon the nature of the latter. The environment of plants comprises a group of factors which operate individually as well as collectively and evoke a certain amount of response which expresses itself in some form of change. This change manifests itself in two ways: (1) change in the physiological processes of plants; and (2) change in the genetic constitution of the plant. The ever-fluctuating environment and the dynamic processes of life together make the life of a plant what it is. Individually, these changes take the form of adaptations to environment and collectively they express themselves in the sum total of plant life in a given area what we call vegetation.

The idea of vegetation, however, is always linked up with some sort of topography and locality and these are governed by the operation of some rhythmic changes of factors such as diurnal and seasonal variations, which also operate on the plant life. When they operate over a wide range of time, the reaction of the plant life expresses itself in a form that is termed as 'flora'

The idea of a flora is thus always associated with a definite environment in which mainly the climate and then the edaphic factors work together. In determining the flora of a place, therefore, the geologic past and climatic changes largely decide the types of vegetation which go to constitute a succession of vegetational forms spread over a long range of geological period. To put in other words, the flora of a place is primarily governed and determined by the climatic factors, because in any place, they, more than soil or topography, affect the nature of the flora. The climatic factors, sometimes referred to as atmospherics, are so powerful that they are chiefly responsible for controlling the distribution of plants. In recent years a large number of workers have expressed these ideas with reference to studies on the distribution of plants in many areas.

The intimate relation between the vegetation, flora, and the climate of a place is quite apparent in the case of living plants. But in the case of fossil plants it is not easy to know it, as one is dealing with quanta of time which are so large that it becomes impossible to speak of anything like vegetation of a particular locality. The difference arises out of three reasons: (1) that the places where the plants are fossilized are not necessarily the places where they were growing in situ: they only suggest that in these places the conditions for fossilization were rather favourable: (2) the extent to which these plants could be preserved depends on the woody or herbaceous nature of the plant; and (3) the nature of the plant undergoing preservation itself; whether it is capable of preservation as a whole or in parts only, or not at all.

A palaeobotanist, therefore, in interpreting the conditions under which fossil plants existed can at best only infer from the imperfect records at his disposal. Naturally, there are too many gaps in his understanding of the factors or forces which operated in the distant past. He, therefore, takes recourse to understanding the processes of living plants for the interpretation of those in fossil plants. In the determination of palaeo-climate, palaeobotanists have certainly no array of morphological, physiological and genetic data at their hands as in the case of the living plants. They are entirely guided by considerations of the first only. Very often they are completely ignorant of the life processes or genetic changes which might have taken place in the fossil plants they are handling. Their conclusions on the nature of palaeo-climate, therefore, are necessarily of the nature of inference based on analogy with living plants.

It is true that the living plants in response to changes in environment adapt themselves,

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and these changes are expressed, among other things, in their morphology and internal structure. If operative over a long time, they do indicate the nature of the environment under which the plants grew. For example, if a feature like aerenchyma or the thin cuticle is seen in dissimilar plants, it is generally indicative of marshy or aquatic habitat under which these plants were growing in a patch of vegetation. When the same factor controls the vegetation for a long time, it sets up a particular pattern in vegetational forms. Thus, the great forests of conifers in the northern zone of America, Europe and Asia, the desert belts found all over the world, tropical rain forests on both sides of the equator generally have plants which have many features in common. Similarity shown by some of them is so great that one is struck by it. For example, the maritime flora of the coastline of tropical countries and oceanic islands have a preponderance of palms which lends a colour and character to the scenery of the place. The huge climbers and epiphytic vegetation in the rain forests of many countries also present similar features. Once this intimate relation between the climate and vegetation of a place and its components is realized, it is easy to understand why certain plants in a locality are indicative of the nature of the climate of the place, e.g. the alpine plants and cold climate, mangroves and maritime conditions, cacti and euphorbias and arid conditions, etc. Such inferences, however, when they are to be drawn in the case of fossil plants, have to be very much safeguarded, as in the case of the fossil plants one is arguing from the converse; and yet the number of fossil plants in the flora of any age of any country is not wanting in such examples as bring a strong conviction regarding the palaeo-climates. It is within certain limitations that the fossil plants can be used as indicators of palaeoclimate. Unlike animals they are not able to easily migrate and hence, their testimony regarding palaeo-climate is more reliable than that of animals. It was a patent idea of various workers of the last century like Ettingshausen, Brongniart and Heer and others to use fossil plants as indicators of climate. But it was Seward who rightly cautioned against many wild generalizations in this matter. The terrestrial plants. generally speaking, can be relied upon, to a certain extent, because of their distribution

but not the water plants. These are indeed treacherous guides to palaeo-climate, although quite reliable as indicative of their habitat. In the terrestrial plants also when they are far too isolated by geographical or other barriers, they tend to mutate or become endemic; and it is not possible to know what was happening to fossil plants in their environment regarding both these phenomena, viz. isolation and mutation. A fossil plant, therefore, may be indicative: (1) of the extreme limits of the climate under which a particular set of plants prospered, especially within the limits of temperature or humidity; or (2) it may be a representative of an average plant of a community of plants growing in a locality in the past; or (3) it may represent a species of plants undergoing mutation; or (4) it may be one of the plants, like modern endemics, unable to spread due to limited range of adaptation to varied climatic conditions; or (5) it may be one of those plants which are completely inadaptable to environmental changes and are on way to extinction.

In the flora of any place one would expect to have plants showing all these possibilities and much will depend on what one would consider really is a species indicative of. It would be seen from the above that not all species would be serving as right indices of palaeo-climate prevalent at the time of deposition. If they are indicative of the extreme limits of the factors which really control distribution, then their testimony could be relied upon; but if they represent the conservative endemics or ever-changing mutants, their testimony cannot be relied upon and as such they will not be able to serve as guides to palaeo-climate.

After this brief theoretical prelude, it is time for us to consider some modern groups of plants with a view to illustrating some of the above points and finding out their reliability as indicators of palaeo-climate. I have chosen ferns and palms as they are generally believed to be very reliable for this purpose; and I lay a modest claim to the study of these two groups during the last 20 years.

The ferns, as a group, take their origin from a very distant past, from the Devonian period onwards and they have continued to be in their own even now. Many of the fossil ferns of the ancient times such as the Botryopterideae and Zygopterideae are extinct, but members of the Osmundaceae,

Hymenophyllaceae, Polypo-Schizeaceae, diaceae and Hydropterideae have survived through long ages. Thus, in the Tertiaries of North America and many other lands, not less than a dozen species of Osmundites are known. Several species of Aneimia have been recorded from Palaeo-eocene to Oligocene of Colorado, Texas, Wilcox and Wyoming in America. Representatives of genera like Adiantum, Cheilanthes, Dennstaedtia, Pteridium, Saccoloma, Gleichenia, Davallia, Cyathea, Athyrium, Matonidium. Onoclea, Blechnum, Lygodium, Asplenium, Dipteris and Polypodium are known in the Tertiary horizons of many lands, especially South and Central America, Australia and India. Some of these genera are known in fossils from lands where they do not exist today; or, if known, exist in very restricted localities under highly specialized conditions, e.g. some species of Gleichenia, Dipteris, Osmunda, Acrostichum, Matonia, etc. Among the Eusporangiate ferns, which bear close resemblance to the spore-producing parts of the Coenopteridineae, Ophioglossaceae is practically unknown in fossils, but species of Danaeopsis or Marattiopsis are not uncommon from the Jurassic period onwards. The Hydropteridineae as a group comes into existence from the late Cretaceous onwards, especially in the Tertiary period. Several species of Salvinia and Azolla are known from Korea, India, Japan, Australia, Southern Europe, British Columbia, Wyoming, Tenessee and England. But the family Marsileaceae is represented by a single species of Regnellidium known as Rodeites from the Eocene beds of Central India. The very fact that some of the common genera such as Polypodium, Adiantum or Pteris, whether living or fossil, have many representatives, is indicative of the fact that the species of these genera, probably due to mutation, were formed in adaptation to different climatic conditions. In this connection the work of Dr. I. Manton on Polypodium, and Dr. P. N. Mehra's on Adiantum and on Lygodium by the author and his collaborators is pertinent. In these genera polyploidy and apogamy have played an important part in the distribution of the species today, and so must they have done in the past also. Apparently in ferns like these, it is not the genus that is indicative of climate but only a species which will at best indicate a particular habitat. In the case of water ferns the reliability as indicators of climate is nil,

although they are indeed extremely good indicators of the habitat in which they and associated plants occur. The same is true of Osmunda in which many polyploid races and species growing in different habitats are known in the living: and this is probably also true of its fossil species. Ferns like Marattia, Matonia, Alsophila and Cyathea today grow in extremely humid conditions. But different species of the same genus grow in widely separated regions having quite distinct topography and climate as in the vallevs of the Himalayas on both sides, or in comparatively dry regions of Peninsular India and in the tropical rain forests of Ceylon, Java and Malaya. Here the same species is seldom capable of growing in different localities. Like the Marattiaceae, therefore, tree ferns do indicate moist climate, but much will depend upon altitude and topography, and not on latitude only.

It is well known that ferns like *Helmin*thostachys, Dipteris or Acrostichum are highly specialized in their habitat. So are perhaps the epiphytic ferns. The former are quite reliable as guides to the climate and habitat in which they grow, but the epiphytic ferns indicate very little, as most of the epiphytic ferns lead a very precarious existence and complete their life-history somehow under the conditions available to them. Very often these conditions vary from year to year and, therefore, their testimony is not reliable.

From amongst the water ferns, Regnellidium and Salvinia are interesting in this connection. Regnellidium is endemic both in its present and past distribution. The habitat and the climate under which it grew in the past, therefore, could not have been different from that under which it grows today. The same thing, however, cannot be said to be true of Salvinia in which conservative species like S. auriculata and its fossil relative S. intertrappea have restricted geographical distribution due to apogamy, whereas S. natans, which is a fertile species, has a wide geographical distribution: this species produces polyploid races ranging from the cold temperate to the equatorial plains. In this genus, therefore, different races adapt themselves to different climates.

It will be seen from the above account, that due to plasticity of the sporophyte in producing different polyploid races to suit different environmental conditions and the unreliability of the gametophytic generation, ferns as a group do not really indicate climate in all cases. Individual genera and species do indicate that in a few instances, e.g. *Matonia, Helminthostachys, Cyathea, Acrostichum*, etc., but the majority of the common polypodiaceae do not do so. If this is true of the living species, it should be even more so in the case of the fossil species. And for determining the climatic conditions under which they existed, we have to exercise great caution while drawing inferences.

Another very important and conspicuous group in the floras of the Southern Hemisphere since the Tertiary period is the group of palms. It is well known that South India, South Africa, South America and Australia are the parts of the most ancient land masses persisting from the Gondwana period onwards, and as such are expected to throw some light on the important features in the distribution of plants, whether fossil or living. Quite a number of fossil palms have been reported from Central America, Antigua, the Paris Basin, Italy, India, South Africa, Egypt, Ceylon and Malaya. These are also the places where, except in Europe, a large assemblage of palms is seen today. It may be inferred that their distribution may throw some light on their adaptability to environment and we shall now try to verify this. Palms as a class are considered to be maritime trees. While quite a large number of them no doubt occur that way, large genera like Phoenix, Sabal, Calamus and *Cocos* have members which rise from the coastal plains to progressively higher altitudes. Some of them are restricted to the coastal plains and estuaries and some rise to low hills up to about 200 ft. A few of them rise to an elevation of 2,000-6,000 ft. and some are restricted to higher altitudes only. Quite a few are endemic. Thus, Phoenix zeylanicus, P. reclinata, Sabal palmetto, Calamus hookerianus, C. radiatus, C. nicobarianus, Chamaerops humilis are mostly restricted to coastal plains and foothills, whereas Washingtonia gracilis, Hyphaene indica, Nephrosperma van.Huttiana, Oncosperma horridum and Phytelephas microcarpa occur generally in riverine and estuarine beds. The common fan palm, Borassus flabellifer, Archontophoenix alexanderi, Pinanga paradoxa, Areca triandra, Jubaea secunda, are restricted to low hills and seldom rise above 2,000 ft. elevation. Phoenix sylvestris, on the other hand, and Arenga wightii, Wallichia caryotoides, and W. dis-

tichia climb up to an altitude of 6,000 ft. Some species of *Phoenix* such as *P. acaulis* and Livistona australis, L. jenkinsiana, Plectocomia khasyana, Carvota urens, C. mitis, Pinanga gracilis and Areca nagensis occur between the elevation of 2,000 and 6,000 ft. Several species of *Calamus* rise from the coastal plains to about 6,000 ft. elevation in dense forests. For example, Calamus radiatus is mostly a coastal species and so are C. arborescens, C. rotang and C. viminalis. But the latter three are mostly restricted to estuarine forests. Some of the species of Calamus such as C. kingianus and C. brandisii and Wallichia densiflora, Plectocomia khasyana, P. himalayana, P. macrostachya do not descend to the plains and are palms of high altitude. Some of them are unique in their habitats, e.g. Phoenix paludosa is a mangrove. Nipa fruticans is an estuarine dweller. Sabal adansoni grows in desert regions. Phoenix dactylifera, P. canariensis and Eleis guineensis grow in oases and desert regions. A few palms such as Pritchardia pacifica, Lodoicea seychellarum, Calamus digitatus, Bentinckia valpanna, Hyophorbe americaulis, Vershaffeltia spp. and Oncosperma fasciculatus are more or less endemic.

It will be seen from the above list that in the palms, some of the genera such as Phytelephas, Nipa, Thrinax and Livistona are highly characteristic of the habitat they live in. But in the rest of them different species of the same genus adapt themselves to different altitudinal and environmental factors. In a genus like Phoenix or Calamus there are species which are spread from sea level to an altitude of 6,000-7,000 ft. above the sea level and hence it would be difficult to rely on the genus as a whole for inferring the climate under which it grew. In palms, as in ferns, therefore, the individual species in most cases are indicators of climate but not in all. Perhaps more than individual species an assemblage of plants showing similar features would be more reliable. In deciphering the fossil palms these facts would be of great importance, as in one's eagerness to recognize a fossil palm, one is apt to forget that it may not be a coastal palm and, therefore, be not one growing under a maritime climate. But as compared to ferns, due to their more conservative nature, palms show less number of mutants. And hence, they are more reliable as guides to climate when their identity with a living genus or species is

established. It is necessary, however, to note that a definite determination either of a genus or a species in fossil *Palmoxyla* is a task beset with numerous difficulties and hence, although one does get an inkling as to the nature of the genus, inferences regarding its climate have to be drawn very carefully. The only exceptions to this rule are such palms as *Nipa*, *Phytelephas* and *Calamus* which are known to choose a very definite type of environment. In the end, I desire to acknowledge my deep sense of gratitude to the members of this Section and to my numerous friends for the honour they have done me in electing me as the President of this symposium and to my colleagues for their help. I am deeply sensible of the debt I owe to all of them.*

*The address was illustrated with a number of slides and photographs.