TWENTYFIFTH
SIR ALBERT CHARLES SEWARD MEMORIAL LECTURE

PLANT ANATOMY AND EVOLUTION

BY

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INTRODUCTION

THE title of this lecture may seem to some of you too ambitious, especially to those who know that the subject of my specialization in botany has been mainly confined to plant anatomy. There is no doubt that this discipline has long been neglected not only in the universities of India but also those of outside India. This is a fact that the subject has never been a fashionable one, and only a few have been attracted to it. In spite of this drawback, plant anatomy has made commendable progress and brought forth fundamental knowledge which throws some light on the all pervading preoccupation of botanists namely, the evolution of Plant Kingdom. If you have the patience to keep my company in this sojourn in which I dwell upon what has been discovered by anatomists, you may ultimately find that there is some justification for the title of this talk.

Literature on evolution is vast. These have emanated from workers in Life Sciences as well as Physical Sciences. It is an impossible task for any body to cover all these within the time allotted to me. I, therefore, offer my apologies to the authors of many outstanding work, whose name has not been included in this talk.

To provide a background of this talk I plan to give you here a chronological history to the study of wood anatomy in which I have spent many years of my life.

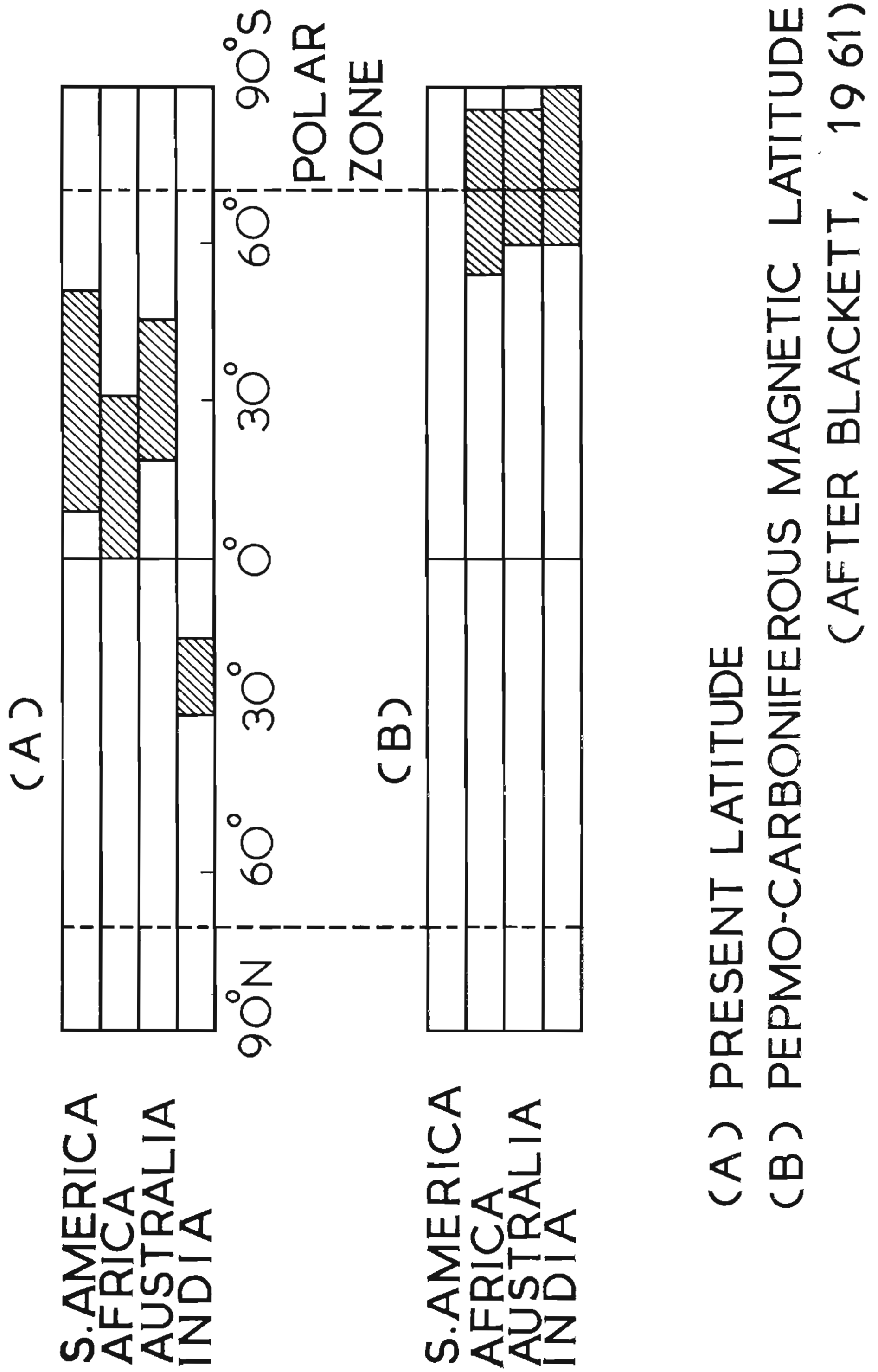
PRIOR TO 1918

If you pick up a text-book of botany published prior to 1918, you will find that it contains very little information on the secondary xylem, commonly known as wood. All that is said in the book is that after germination of the seed, the stem part of the plant shows the primary growth followed by the secondary growth. The plants dealt with are usually herbs and rarely perennials. This is all that was known to botanist in general about the secondary xylem, when the first World War started in 1914. The curse of a war is that you use the natural resources of your country many times faster than you do in peace time. Another problem that you face is that in peace time you are free to import woods from foreign countries which have been traditionally used for many years, and you do not bother to find out whether you have in your own country woods that can be used as substitutes for imported timbers. A situation arises when a nation has to be self-sufficient in raw materials that are rapidly destroyed in the war fields. Experience of the last two World Wars has brought out the fact that to keep the front line soldiers efficient and fit, you need more than six hundred articles — big and small — made of wood. Now the question arises what timber or timbers is best suited for a specific item of wooden article. During the first World War, the past experience was the only guide for this selection The next question was how to obtain those timbers from among the large number that are sold in the market. Recognition of woods before they are used, was therefore most essential. In fact, this was the problem for engineers of public works and ordinance factories.

These engineers at first relied on timber merchants to get the specific timbers that they wanted, but very soon these technologists realized that often they paid high price for buying so-called well-known timbers but landed with those which were more or less useless, and this ultimately cost lives of many soldiers in the war field. In the meantime engineer approached lumber-men and carpenters, who claimed that they could recognize timbers by their look because they were involved in the felling operation of trees and using them finally in the making of wooden articles. Help from these quarters was, however, disappointing. Finally, the supply department — a new department created during the war — approached some universities where botany was taught. Here the botanists confessed that they knew very little about wood but would be prepared to try and see what could be done. After some teething troubles some sort of working basis was established by the university workers and the reliability of wood anatomy as the best guide for recognizing isolated woods was established.

PERIOD BETWEEN THE FIRST AND SECOND WORLD WAR

The results obtained by botanists by the end of the First World War gave a stimulus for further research. Forest departments of many countries realized the value of the natural resources under their control and were willing to establish centres for research on wood anatomy with a view to utilizing their timber resources efficiently. The first centre was established at Madison, Wisconsin, U.S.A. and the second at Dehra Dun, India and the third at Princess Risborough, United Kingdom. On a small scale many other countries followed the suit. Within about ten years wood anatomists, though small in number, felt the necessity for establishing an international organization in order to keep in contact with each other and keep abreast of the progress made by different workers. In 1931, the International Association of Wood Anatomists was established, and S. J. Record of the Yale University, U.S.A was its first Secretary The main task before the Association was to make a general survey of anatomy in timber species belonging to various families. It may be pointed out here that it was natural for anatomists to accept the taxonomist classification which was initiated by Linneus many years ago and later improved upon by many workers. The work of anatomists was a laborious business and took many years, and I may say it is still going on. Results of this work, which were based on the anatomical structure visible on the cross, tangential and radial surfaces, with the help of low and high power light microscopes. The results were published countrywise in the form of books, bulletins and records. Within two decades there was a fair amount of data available to make the first survey (Chowdhury, 1948) and summarize the results. Much of this summary still holds good with minor modifications here and there. Some portion of this summary is given below: " It can now be said that the taxonomic classification of woody plants is in general agreement with the anatomical structure of their woods. There is a great deal of similarity in anatomical details of the timbers that belong to a family In fact, woods of some families show so much anatomical likeness that they can be recognized without the help of a compound microscope, for instance, Anonaceae, Dipterocarpaceae, Rutaceae, Sapotaceae, Ebenaceae and Lauraceae. Again, in Apocynaceae and Leguminosae, a great majority of the woods show similarity to such an extent that it is not so difficult to recognize most of the timbers belonging to these families. Lastly, there are other families which show a great variation in their gross


(A)
(B)
S.AMERICA
AFRICA
AUSTRALIA
INDIA
90°N
60°
30°
0°
30°
60°
90°S
POLAR ZONE
(A) PRESENT LATITUDE
(B) PEPMO-CARBONIFEROUS MAGNETIC LATITUDE
(AFTER BLACKETT, 1961)

anatomical structure. Classification of woods of these families though apparently difficult is not actually so; for, often it is possible to classify them under different families by studying their minute anatomical structure.

Now coming to further grouping in a family, it may be said that generic characters are mostly well defined. As a rule, different species in a genus show more or less a homogeneous structure. This does not, however, mean that the characters used for separating different genera are the same in every family. Certain characters or combination of characters may be found useful for distinguishing the genera within one family but those very characters may not be useful in another family An analysis of all the characters is usually necessary before an attempt can be made to separate the genera. Here, it may be pointed out that some overlapping of generic characters is not unknown to the anatomists, such as can be found in *Dalbergia* and *Pterocarpus* of Leguminosae and *Terminalia* and *Anogeissus* of Combretaceae and in others. But this does not offer much difficulty for classification, provided the limit of overlapping is clearly understood.

We now come to the species. It must be said at the outset that our knowledge of the anatomy of taxonomist's species is very limited. Differentiation of the species is at present possible only in exceptional cases such as, when there are a few species in a genus, or when a species constantly shows a line of specialization not present in the other species of the same genus. In the genera with a large number of species, it is not possible to separate all of them. What can, however, be done sometime is to lump different species into 2-3 groups within a genus, for instance *Shorea*, *Morus*, *Quercus* and *Pinus*. It will be realized that the characters which can be used at this stage of classification are usually of minor nature. The size and frequency of these characters are the only bases that can be used profitably. Attempts to find out the significance of anatomical variation within a species have also been made. . . . ."

One might say that those were the days of hectic activities and voluminous data were gathered, but they remained scattered in various books and journals. At this stage the famous book " Anatomy of the Dicotyledons " by Metcalfe and Chalk (1950) came out in two volumes. In this, Metcalfe compiled mostly anatomical data on herbs, and Chalk on trees and shrubs. This was a stage in the history of plant anatomy which may be called an age of descriptive anatomy There was only a limited attempt to interpret the data collected and their significance enunciated. As a result an atmosphere was brought about in which doubt arose as to the possibility of woods belonging to different families having the same anatomical structure. The feeling was so strong among anatomists that a symposium was thought necessary to determine the actual position. This symposium was held in Paris in 1954 (Chowdhury) during the Eighth International Botanical Congress. For many hours, anatomists working on living and fossil woods discussed the problem. It was agreed that the possibility of woods of different families producing exactly the same type of timber, was rather remote. When timbers are examined under hand lens or low power microscope, one might get the impression that there were some signs of convergent wood structure but this impression disappears when those very timbers are critically studied under high power light microscope.

STUDY OF VARIATION

While recording the detailed anatomical structure of any dicotyledonous wood from different sources, one cannot avoid noticing the variation each species shows, and this is linked up with their classification Each wood exhibits different tissues which make up the gross structure. Here one comes across tissues which vary a great deal but there are others which do not. Classification is done based on tissues which vary the least. The plasticity of the least variable tissues has also to be studied in depth in order to make a key for their identification. All this work means considerable labour but all the same the ultimate results lead one to identification without any doubt. In this context, the study of variation of paratracheal and apotracheal parenchyma cells may be mentioned (Chowdhury & Ghosh, 1946) and also the variation in ring-porous, semi-ring-porous and diffuse-porous woods (Chowdhury, 1953)

Following the general trend prevalent among biologists attempts were made by anatomists to determine the line of evolution in wood elements. Irving Bailey and his school at Harvard were the pioneers in this field. Bailey's first paper along with Tapper on " Size variation on tracheary cells " was published as early as 1918. The subsequent papers established without any doubt the way the tracheary elements evolved in the Plant Kingdom. This classical work will remain the standard for study of any cell element of wood in depth. However, later his school studied other elements and tissues of wood, taking it for granted that there has been a synchronized evolution of all cell elements in the manner it was established in the tracheary elements. This brought in a great deal of confusion (Chowdhury, 1948; Chalk, 1950) because the cell elements and tissues were not evolved at the same rate.

With experience, anatomists realized that some of their earlier hypotheses were no longer tenable. For instance, xylem in herbs and trees can no longer be lumped together for generalization. The former lives a year or so, and after producing seeds dies, while the latter does not produce seeds during the first 20-25 years of its life. This brings out the rate of evolution in the secondary xylem of herbs 20-25 times faster than that of trees. It is now for anatomist to make use of this important fact in the study of xylem.

Tomlinson's work (1961-62) on arborescent monocotyledon is of interest in this context. He finds certain groups as Palmae, Pandanaceae, Strelitziaceae and to lesser degree Agavaceae suitable for such a study. He concludes by saying " The phylogenetic relation between arborescent and herbaceous forms in monocotyledons is not clear."

Cheadle (1959) made an intensive study on the evolution of vessel members in monocotyledons. The conclusions he arrived at were more or less in agreement with those worked out by Bailey and his students. Cheadle's study brought out some other interesting facts. He pointed out that vessel may be entirely absent throughout in some aquatic monocotyledons, and that in some terrestrial forms vessels may be absent throughout the plant except for extremely primitive ones in the last formed metaxylem of the root. The most important information he revealed was that there was no evidence of reversibility in any of the changes that took place during evolution.

Then an assortment of evolutionary trends was also worked out in the bark of dicotyledons, such as sieve tube elements and others. All these facts are of considerable importance in our understanding of anatomy of seed plants.

I must say here a word on methodology. This is about the recent invention of electron microscope. This instrument has helped us to see much minute structure of plant which was not visible under high power light microscope. It still remains to be seen if it would reveal facts that would help us to have a better understanding of the evolution of plants.

STUDY OF PHYLOGENY

Having given a bird's eye view of what the plant anatomists have achieved during the last 50 years or so, I now plan to analyse these results with regard to the evolution of seed plants in general and angiosperms in particular.

As living organisms, the higher plants have many organs. Each organ is made up of different tissues. Each tissue has its cell elements. All these anatomical structures are visible when examined under microscope. Prior to the use of microscope, plants were classified for the first time by taxonomist who brought in some sort of order when there was nothing but confusion in the recognition of various plants. In their attempt to classify higher plants, they first took the habit of plant as the basis, and put them under three broad groups; herbs, shrubs and trees. Later the characteristic features of the flowers and then the fruits they produced, were used for further classification into sub-groups. This proved to be a very efficient and quick method for both amateurs and professionals. Later on when Darwin's theory was accepted by biologists, taxonomists of seed plants began to look for the line of evolution in their own discipline. This journey has been rather rough and there appears to be no sign yet for a consensus of opinion on this score.

After Darwinism another earth-shaking discovery was Mendelism. The latter produced cytogeneticists, who began to speak in an entirely different language. This resulted in the birth of two classifications; one by classical taxonomists and the other by cyto-taxonomists. Instead of simplifying the classification of living organisms, bifurcation produced an atmosphere of complication. At this time in the study of taxonomy, all biologists put their heads together and brought out a system called Neo-Darwinism. After some decades there was again an urge to collect and utilize additional source of data to solve the problems, the taxonomists were facing. A new system of classification was brought into use. Its name was chemo-taxonomy. All these innovations give one the impression that they are now after a synthetic classification which will cover data from all available sources, and the final decision will be made with the help of a computer. There is no doubt that it is a laudable idea for workers in the laboratories of affluent countries. But what about the taxonomists working in many countries which are not-so-well off ? Again, what about the hardy amateurs of affluent countries who have contributed so much to plant taxonomy. I hope this matter will receive serious consideration from taxonomist in general.

Leaving aside the taxonomists' action to determine phylogeny, let us now find out what anatomists, the camp-followers of taxonomists, have to contribute to this theme. The data collected by physiological anatomists some decades back and the conclusions arrived at, need re-examination, because of the additional data brought to light during the intervening period. To start with, anatomy of a plant growing in some particular ecological niche does show some difference from that of normal habitat. This is important. But is it the all pervading consideration ? Repeated attempt to determine the reason for this difference has revealed that it is the genetical make up of the plant and not the ecological set up in which it grows is responsible for this. In the language of geneticists all these variations are brought about by genes. More about the genes is in the later part of this talk.

Now let us refer back to the earlier part of this talk on the achievement of wood anatomists. The most important point that comes out from its analysis is that all the tissues and their cell elements have been evolved in a non-synchronized manner.

THE WILD SPECIES OF GOSSYPIUM

THE GENOMES OF GOSSYPIUM*

Species	Genome	Species	Genome
Asiatic and African (n = 13)		American (n = 13)	
G. herbaceum	A1	*G. thurberi*	D1
G. arboreum	A2	*G. armourianum*	D2-1
		G. harknessii	D2-2
G. anomalum	B1	*G. klotzschianum*	D3-K
G. triphyllum	B2	var. *davidsonii*	D3-D
		G. aridum	D4
G. stocksii	E1	*G. raimondii*	D5
G. somalense	E2	*G. gossypioides*	D6
G. areysianum	E3	*G. lobatum*	D7
G. incanum	E4		
G. longicalyx	E5		
Australian (n = 13)		Polyhybrid species (n = 26)	
		New world (cultivated)	
G. sturtii	C1	*G. hirsutum*	(AD)1
G. robinsonii	C2	*G. barbadense*	(AD)2
G. australe	C3	Wild in Hawaiian islands	
		G. tomentosum	(AD)3

*After Saunders, 1961

The rate of their evolution is entirely different from one another. This is true not only for the reproductive parts of the plant and its woody parts but also for the researches that have been carried out by cytologists, embryologists, morphologists and others. This may lead one to think that the labour involved in tracing the line of evolution in the above mentioned disciplines has been a futile exercise. But this is certainly not the case. After all, we would have never known the complexity of evolution if we had not gone through these exercises. Whatever knowledge we now possess is a step forward in our understanding of the evolution of the dicotyledons.

This much is for living dicotyledons. Let us now see what the fossil dicotyledons can tell us about our problem. Wood remains of angiosperms have been recorded from the early Cretaceous to the Pleistocene. These woods have given us no clue which type was evolved first and which followed. In this context, I can do no better than quote here what Delevoryas (1966) has to say.

"The most important evolutionary event that occurred during the Mesozoic Era was the appearance of angiosperms. Exactly when they appeared first is still unknown, but the Cretaceous Period is the time of their rapid spread. Angiosperm-like plants in the form of impressions resembling palm leaves are known from the Triassic Period. Other pieces of evidence that are still not completely validated consist of pollen grains, pieces of wood and leaf impressions. Whatever their origin, the group or groups from which they arose are still unknown, it is certain that their spread was spectacularly rapid. Early in the Cretaceous, angiosperm fossils are few but they increase in number and in geographic range later in the Cretaceous, and by the end of the period they had attained an amazingly widespread distribution In fact, by the late Cretaceous the flowering plants have become the dominant group of vascular plants on the earth."

It is now clear that both living and fossil angiosperms studied so far do not allow us to pronounce definitely when the angiosperms first appeared on this earth

Some new information which have recently come to our knowledge through the work of geophysicists and cytogeneticists is worth mentioning here. In his search for the origin of cultivated cotton, Saunders (1961) lists the genomes of wild *Gossypium* in the present geographical set up of the continents. He finds in the wild cotton of Asia and Africa, the genomes A, B and E; in Australia, the genome C, and in South America, the genome D. Although these continents are now far apart yet in the past history of the earth all the four formed one single mass. And that was during the Permo-carboniferous Era (Blackett, 1961) From these data one can visualize the existence of a primitive germplasm of *Gossypium* having the potentiality of producing the five distinct genomes with which they are now endowed. These evidences would lead one to think of the possibility of existence of dicotyledonous plants as early as 300-250 m.y back. Such a conclusion should not come as a surprise to palaeobotanists as a group, because the presence of evidence of angiosperm-like remains have been known to occur during the Triassic period of geological history (Delevoryas, 1962).

Now we may consider some evidence from the recent plants. For the last half a century cytogeneticists and archaeologists have taken concerted action to unveil the origin of cultivated food plants. Their attention has been naturally confined to some of the grasses which now form our staple food. The genus *Triticum* has received the greatest attention *Triticum* (*T boeoticum*) is a wild grass belonging to the diploid group, growing in an area spreading from western Iran to south-eastern Turkey When it came in contact with another wild grass of the genus *Aegilops* (*A. speltoides*) it turned into a tetraploid *Triticum*. After some years, one of these tetraploids came in contact with another species of *Aegilops* (*A squarrosa*) and produced hexaploid *Triticum* which now form the wheats we eat every day. All this happened within the last 10,000 years (Mellart, 1967). I have been working on this problem for almost a decade now. The lesson I have learnt about the evolution of this plant I put before you for what it is worth. It seems to me that two important factors have been responsible for its fast evolution. In the order of importance it was the nature of the germplasm of these two genera. In both, the germoplasm was capable of receiving and combining with that of the other one in their attempt to improve the survival value. The environment no doubt allowed such a union, but the part it played was a minor one. What we see is probably one of various courses that many plants went through to survive. Furthermore, it is now believed that "Evolution is incredibly complex but at the same time an integrated and unitary process (Simpson, 1955). What has been seen in the genus *Triticum* is one of them — and not the standard for all.

What I have already stated may give one the impression that botanists have very little to contribute on the evolution of Plant Kingdom. But actually it is not the case. We have an enormous quantity of data on evolution. In the past these data have been used, in my opinion, rather injudiciously resulting many theories, some of which are controversial, and even contradictory. This can be put right if we only do a little re-thinking and in common language, mend our fences. Let us talk about only the undisputable land-marks in the evolution of Plant Kingdom and not speak of the lines of evolution in various parts of a plant.

It is generally accepted that the earliest plant life was in existence in the form of simplest filaments living in aquatic environment Then came an age of terrestrial life but still in simple form with green, pigments. Land plant of this age had to survive by producing a root-system. The next improvement was the development of conducting tissues, which have given them the name vascular plants. Here the evolution of stele took place, which ultimately led to the formation of xylem, cambium and phloem. This is the way, I feel, anatomists should trace the evolution of wood and for that matter the evolution of angiosperms. If we confine ourselves to these major features, our corporate partner, the Palaeontologists, in this venture to unveil "the procession of life", will appreciate our contribution much better than they do now.

This almost completes my talk. But in view of the mention of genetics and its ramification in life sciences, I believe it will be appropriate for me, as a biologist, to end this talk by saying just a few words on the present controversy that is going on about "Genetic Engineering". The outstanding workers on genetics and biochemistry are discussing among themselves on the advisability of undertaking such a step. Much has been said in its favour and against. I gather from their opinion that there is a great risk in undertaking this experiment due to the fact that our knowledge on DNA is still rather limited. Because of the risk involved to the extent of annihilation of the entire *Homo Sapiens* from the face of this earth, will it not be judicious for us to wait for a few more years, while carry out further research on DNA, and then decide the steps we should take. There is no doubt that in all progressive steps in science involve some risks but in this case the risk appears to be an extremely serious one. In this context, we should pay heed to what one of the greatest living biologist, Albert Szent-Gyorgi has said, and I quote it below:

"This is an age of much knowledge and little wisdom".

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