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## SECONDARY XYLEM IN PERENNIAL PLANTS\*

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### I. INTRODUCTION

EARLY literature of a few centuries before Christ shows that the Greeks and the Indians had some general knowledge of the different tissues in the stem of a plant, but during the next two thousand years little attempt was made to study these parts in any detail. The nineteenth century saw a great activity in the sphere of plant anatomy and the secondary xylem received attention for only the last one hundred years. Nägeli appears to be the first person to define the terms, 'xylem', 'phlœm' and 'cambium' as they are understood to-day, although sometime earlier Du Humel introduced the term 'cambium' (Eames and MacDaniels, 1925). In addition to these workers, Von Mohl, T. Hartig, Sanio and others made substantial contribution to our knowledge of anatomy and thereby laid its foundation well.

During the last hundred years, two important philosophical events affected the thought and the activities of botanical workers. The first was the publication of the *Origin of Species* by Darwin in 1859. The second was the *Mendel's Law of Inheritance*, first published in 1865 and twice forgotten, which ultimately led to the birth of the science of genetics during the first quarter of the present century. The impact of Darwin's theory of evolution came at a time when the anatomists had just started collecting data on the secondary xylem. Their field of investigation was vast but the actual achievement was very limited, and yet this did not prevent some workers from following the fashion of the day. Numerous theories on evolution were put forward, many of which later on turned out to be mere speculations. This brought about such a confusion that even to-day some botanists doubt the utility of studying the secondary xylem. On the other hand, the advancement in genetics during the last fifty years or so seems to have made little impression on the mind of the anatomists who specialize on secondary xylem. Except for some comparative studies of parents and offsprings (Chowdhury, 1931), nothing more seems to have been

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done. The anatomists, however, have not been idle. In fact, considerable progress has been made during the last forty years on different aspects of secondary xylem. In this paper I have planned to indicate in broad outlines some of the important achievements that have been made. These achievements can be placed under three heads, namely, study of variation, study of ancient plants and study of phylogeny. Finally, it is also my intention to suggest some lines of future investigation.

Here I wish to point out that sometimes conclusions drawn on the study of herbaceous plants have been applied to perennial plants. There is hardly any justification for this. Herbs live for a few months and complete the life-cycles within a year or so, while trees live for a hundred years or more. The primary objective in the herbs during their short life is the production of seeds to carry on the race, whereas the perennial trees, in many cases, do not produce seeds for the first fifteen to twenty-five years of their life. Furthermore, some perennial plants which are in the habit of bearing large quantity of seeds only every third or fourth year, have shown some relation between the production of secondary xylem and the seed-bearing habit. For example, *Shorea robusta* Gært. f. often produces very little secondary xylem a year before the seeding year. These facts provide sufficient justification for treating the perennial plants as a group and trying to understand different aspects of their life. Since production of secondary xylem is one of the main functions of the perennial plants, they provide an excellent material for the study of this organ.

A word of warning may not be out of place here. In the past, study of the secondary xylem present in the herbarium specimens has led to some confusion. Experience has shown that the anatomy of juvenile secondary xylem is often different from that produced later in life. There is, therefore, some risk in drawing conclusions based on the study of herbarium materials of perennial plants.

## 2. STUDY OF VARIATION

The first step towards an understanding of biological objects is the study of their variation. This, however, is not always recognised and as a result there is much confusion in the literature on plant anatomy. The study of variability in the secondary xylem has thrown considerable light on the way this tissue is organized and some of the findings are recorded below. In the perennial dicotyledons, three types of xylem have been recognised, namely, diffuse-porous, ring-porous and semi-diffuse porous or semi-ring-porous. Some overlapping in these three types has also been observed for some years now. But a recent study of these plants has brought to light some very interesting facts. There appears to be three sub-groups in the diffuse-porous type. The first contains those which always remain diffuse-porous showing little effect of the environment in which they grow. For example, *Acer* (*Sapindaceae*), *Cornus* (*Cornaceae*) and *Michelia* (*Magnoliaceae*). The second sub-group contains those which show usually diffuse-porous but occasionally semi-ring-porous structure. The anatomical variation exhibited by these does not seem to have any relation with their

environments. The typical examples are *Diospyros* (*Ebenaceæ*), *Juglans* (*Juglandaceæ*), *Swietenia* (*Meliaceæ*) and *Terminalia* (*Combretaceæ*). Finally, there are those which are diffuse-porous in favourable climate but turn semi-ring-porous to true ring-porous under extremely unfavourable conditions of growth, for example, *Betula* (*Betulaceæ*), *Grewia* (*Tiliaceæ*) and *Salix* (*Salicaceæ*).

It has also been found that the true ring-porous are not confined to only temperate climate. They occur both in temperate and tropical climate; there may be more ring-porous trees in temperate countries than in tropical countries. The well-known genera of ring-porous trees in temperate climate are *Fraxinus* (*Oleaceæ*), *Quercus* (*Fagaceæ*) and *Ulmus* (*Ulmaceæ*) while in tropical climate there are *Tectonia* (*Verbenaceæ*) and *Lagerstræmia* (*Lythraceæ*).

The last group contains those which show all possible variations from the true diffuse-porous to true ring-porous structure in the one and the same tree. These variations have been found to be independent of the environmental conditions in which the trees grow. *Gmelina* (*Verbenaceæ*) is the only genus in which I have come across this phenomenon.

Some progress has also been made in the understanding of the variability that occurs in the cell elements which form the secondary xylem. Amongst the fibres, septate fibres have been studied in some detail at Dehra Dun (Purkayastha). These usually live longer than fibre-tracheids and produce septa which appear to lack secondary thickenings. In some genera, e.g., *Protium* (*Burseraceæ*) there is little effect of environment on the formation of septate fibres, while in others, e.g., *Lagerstæmia* (*Lythraceæ*), the percentage of septate-fibres varies from locality to locality depending on the environments (Plate I). Furthermore, the septate fibres and the crystalliferous are interrelated. Some septate fibres develop crystals in the later stage of their life and form what are known as crystalliferous fibres.

The variability of structure produced by the parenchyma cells is very complicated and at present far from clearly understood. A few years ago, an attempt was made to roughly classify the apotracheal parenchyma (Chowdhury and Ghosh, 1946). Further investigation shows that some genera exhibit considerable variation in the thickness of their apotracheal bands, while others vary only slightly or not at all. In the genus *Ficus* (*Moraceæ*), the thickness of the apotracheal band varies from 6 to 13 cells and is somewhat related to the rate of growth (Plate III), while in *Kydia* (*Malvaceæ*), the band is made up of mostly 2 cells and shows little effect of the width of the growth ring (Plate II). A clear picture is now also available of the rôle that the initial parenchyma cells play in the transformation of diffuse-porous woods into ring-porous woods (Chowdhury, 1953 a).

As regards rays, the horizontal tissues, attempts to classify them by different workers have not yet led to any general agreement. The basis of this disagreement may partly be due to the fact that many workers have tried to classify the rays by studying them at random on the tangential surface. It is quite possible that a study of their

cellular structure from the inception to maturity will remove some of the present confusions. At present two points require immediate attention: whether there is any basis for classification into homogeneous and heterogeneous rays and whether the homogeneous and heterogeneous arrangements of rays are plastic or not?

The study of variation in the secondary xylem and its cell-elements, has brought out three important points. Firstly, in some genera variation is caused by a change in the environmental conditions, while in others no such effect occurs. Secondly, all the cell-elements of any secondary xylem are not equally affected by environment. In this respect, each element appears to be controlled by its inherent characteristics. Thirdly, there are some risks in classifying mature tissues and elements without a knowledge of the different stages of their development from inception to maturity.

Confirmation of these findings would now appear to be necessary by experiments both in the field and in the laboratory. The anatomical variation at generic levels may be established by studying the secondary xylem obtained from various localities throughout its natural distribution. This will also indicate the effect of environment to some extent. By field experiment further effect of environment may then be eliminated. At this stage I was able to get over the time factor involved in the field experiments of perennial plants by studying materials from trees planted in botanical gardens. Where thought necessary, laboratory experiments may also be carried out by using the recent technique developed for studying cambium and its derivatives (Jacquot, 1953). Results of these investigations are sure to throw more light on the problem of variation in the secondary xylem.

### 3. STUDY OF ANCIENT PLANTS

The ancient plants are known to provide the most reliable information on the evolution of the present vegetation. Those which are not so old, say about 5,000 years, are usually found during the archaeological excavations and the uncovering of silted beds. Pieces of wood and charcoal obtained by these methods show little difference between the secondary xylem of then and now. It may not be always possible to trace the old materials to living species but there is no doubt about their similarity with the living genera. The very old secondary xylem, believed to be remains of the ancestors of modern perennial plants, is normally recovered in fossilized state. Some petrified woods of Early Cretaceous age have shown complete similarity in all details of anatomical structure with those produced by the modern trees. Moreover, all the variations that are found in the modern secondary xylem, are also exhibited by these ancient woods. This leads one to conclude that in the secondary xylem of some perennial plants very little change has taken place during the last one hundred million years. At the same time there are fossil woods which show similarity with the modern woods only in gross but not in minute anatomy. This group raises two important issues. Do they show the different stages of evolution through which they had passed before they reached the present state

or do these fossil woods belong to some perennial plants which are no longer in existence? Till further information is collected on both these points, no conclusion can be drawn. This only means more work on fossil woods.

#### 4. STUDY OF PHYLOGENY

During the early post-Darwinian period two ideas dominated the activities of biological workers. It was believed that almost all parts of a plant could be interpreted with the help of the theory of functional adaptation. It was also believed that all members of a group of plants could be traced to a common ancestor. These common ancestors could again be traced back to a remote ancestor. In this way, the line of evolution could be traced back to a single organism. It was therefore a belief in the monophyletic origin of the Vegetable Kingdom. This view lasted unchallenged for about 3-4 decades and then some workers indicated the possibility of polyphyletic origin of plants. Since then both views have their supporters. Owing to innumerable gaps in our knowledge of the ancient plants, it is not known when, if ever, we shall be able to come to any definite conclusion on either of these two views.

For the last forty years or so, systematic anatomy of secondary xylem belonging to many families, has been studied in much detail in universities and laboratories. The results of these investigations have not only widened our knowledge of the anatomical structure of different families, genera and species, but also have given us an insight into the different rates of evolution that have taken place in the external morphology and the anatomical characters of xylem. Bailey (1951) has made some important remarks in this connection. In his opinion, all parts or tissues of an organism do not show a synchronised evolution. This fact is often lost sight of causing considerable confusion in our understanding of the classification and phylogeny of the dicotyledons. I should like to go a little further and say that Bailey's generalization applies not only to the tissues or parts of a plant but also to the elements which make up the tissues. In any case, synchronized evolution in different elements of a tissue does not appear to be a common occurrence. Furthermore, years' study of the secondary xylem has brought to my notice many cases of parallel or convergent evolution in the elements of this tissue, but I have not so far observed any case in which two woods belonging to different families have shown identical structure in all macroscopic and microscopic details (Plate IV).

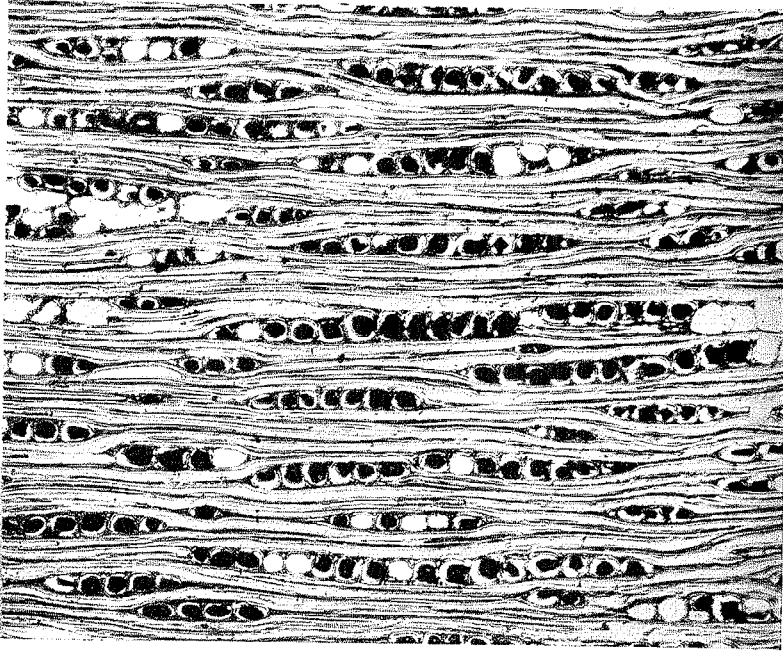
The origin of the dicotyledons being still obscure, there is no direct proof as to the type of xylem the primitive dicotyledons had. The comparative study of the fossil and modern secondary xylem has led to the belief that originally all dicotyledons had diffuse-porous woods and that the ring-porous structure developed later on as a result of changes in the climatic conditions. It has also been suggested that cold winters or alternating very dry and wet seasons have been responsible for the production of ring-porousness. After the discovery

of the semi-diffuse-porous or semi-ring-porous structure, once again the environmental conditions were said to be the reasons for the structural variation. However, our recent study (Chowdhury, 1953 *b*) of the three main types of secondary xylem in both fossil and modern plants, has thrown considerable light on their evolution. It appears that some modern genera belonging not only to the main types but also to their sub-groups, were in existence in the Tertiary period and even earlier. They show little change in their xylem anatomy during the last one hundred million years or so. Furthermore, the ring-porous trees are not of so recent origin as they were thought to be at first. There is no doubt now that some of them were in existence in the Early Eocene period. There are, therefore, sufficient data now to draw "the conclusion that the differentiation of genera took place during the Early Cretaceous period, and that the trends of evolution inherent in some genera have undergone little or very restricted change. Since then the evolution of the various species in a genus has been going on in different directions at different rates, depending on many factors, of which the important ones are the genetic variability, the structure of population and the nature of adaptation to environment and the mutation" (Stebbins, 1950).

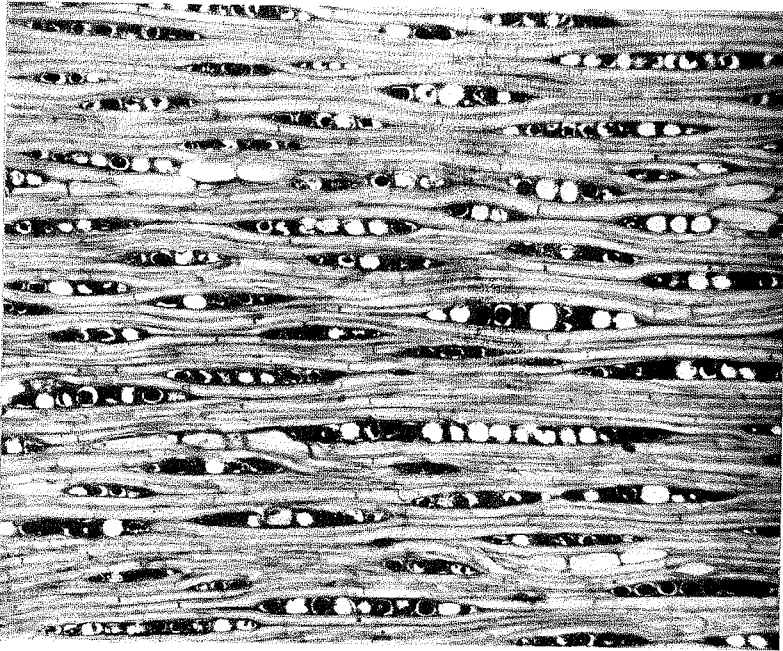
Attempts have also been made to determine the phylogenetic value of a single cell-element or a particular character of an element of secondary xylem. In his study of dicotyledonous woods, Chalk (1937) showed that fibres, parenchyma cells, vessel perforation plates and storied structure are of some value in this respect. He took the scalariform perforation plates as the least specialized and the storied structure as highly specialized. Those woods which do not show either of these, were considered as intermediates. He was of opinion that "whole forms a body of evidence that cannot be the result of chance". However, the most important contribution has been made by Bailey and his co-workers. For many years Bailey carried out an intensive study on tracheary elements and collected information on their length, end walls and perforations and intervascular pitting. By this means he built up stage by stage many phylogenetic series and ultimately the story of the evolution of the tracheary elements. According to him (Bailey, 1953) "The volumes of supporting data that have now accumulated, make the evolutionary story one of the most extensive, complete and convincing amongst either plants or animals."

In summing up it may be said that the secondary xylem is a suitable material for studying the origin of the modern perennial plants. The first step will be to have a clear understanding of the variation in the anatomical structure. The part played by the environment may not be so important as has hitherto been believed. In the light of the modern research on the degree of plasticity of genotype, there is much that still remains to be done. Time factor no doubt plays a great part in the field experiments on the perennials but this can be partly got over, as has been mentioned elsewhere in this paper. In any case, considerable information can be gathered from the material obtained from various localities throughout the natural distribution of the genus. Analysis of these data will indicate what further field experiment is

Septate Fibres in *Terminalia tomentosa*

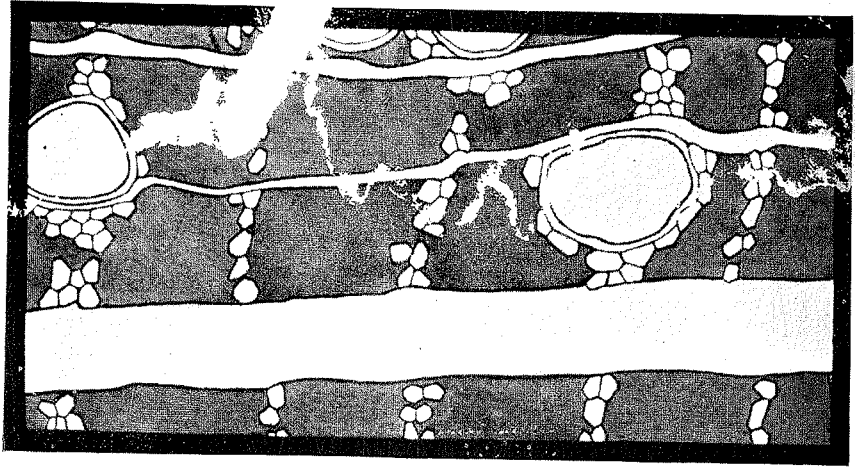


Scanty septa

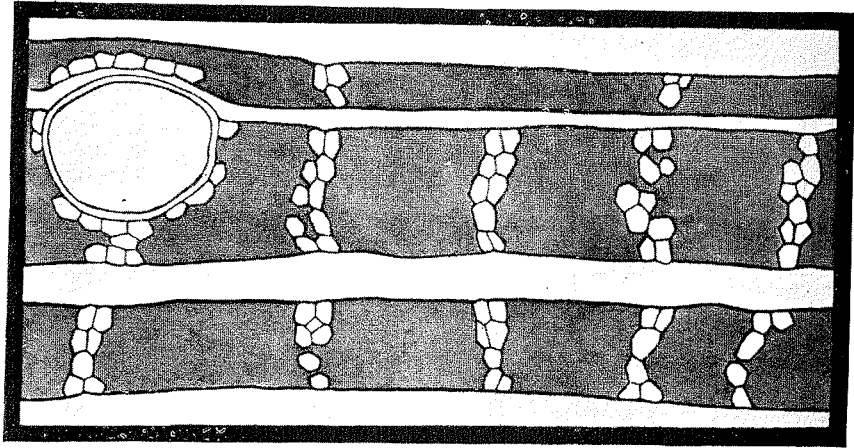


Numerous septa

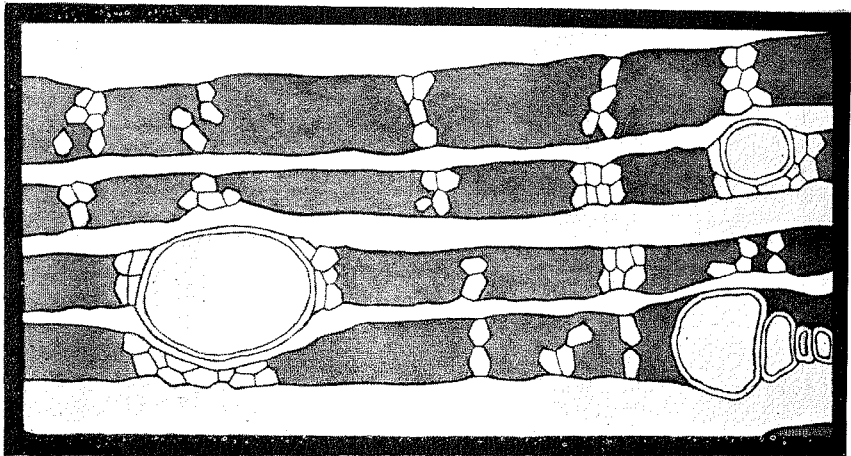
Apotracheal Parenchyma in *Kydia* spp.



10 rings per inch



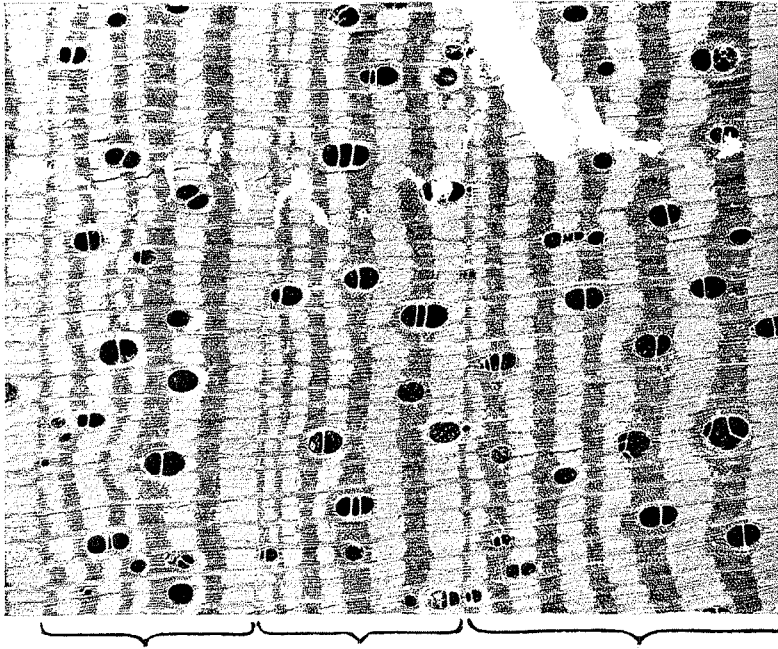
8 rings per inch



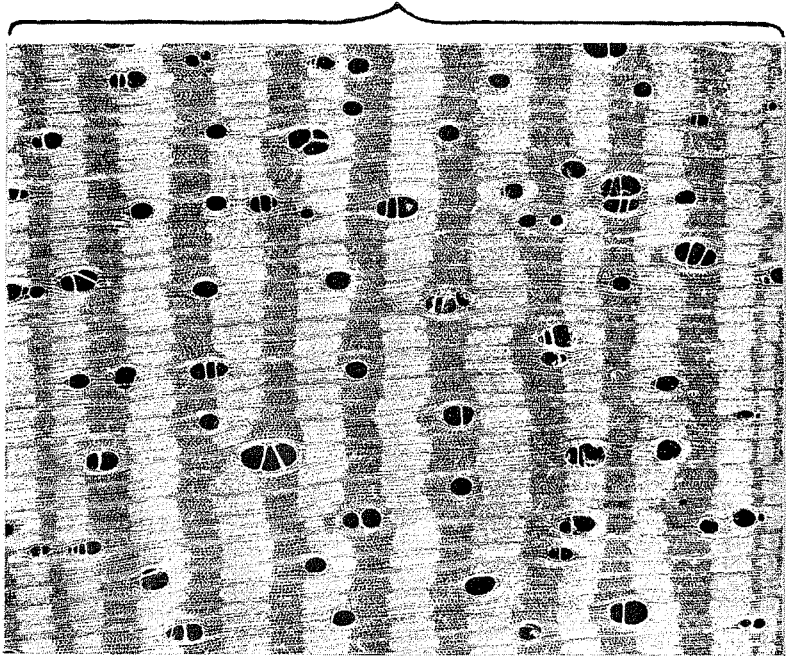
2 rings per inch



Apotracheal Parenchyma in *Ficus* spp.

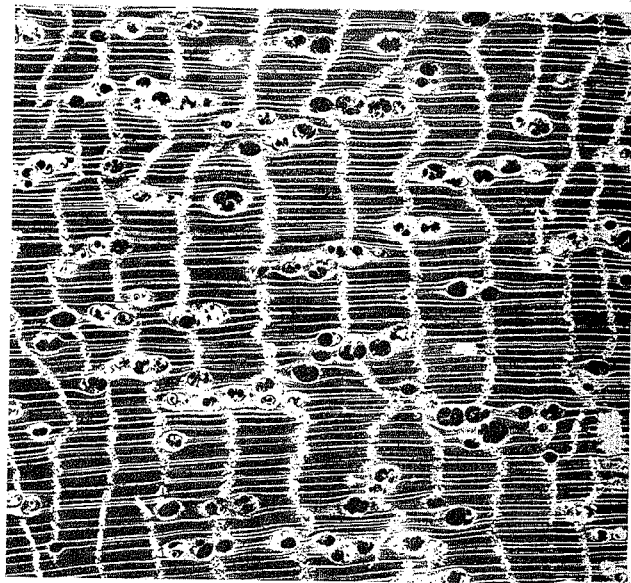


8 Growth rings

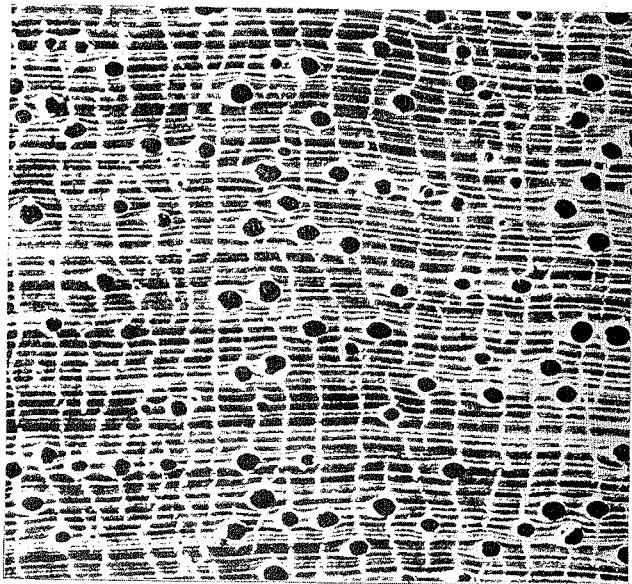


1 Growth ring

Family Affinity of *Parastemon* and *Mesua ferrea*



*Mesua ferrea*



*Parastemon*

necessary. When complete information is available, the laboratory experiments in culture media may be taken up. Here caution is necessary to create as far as possible the conditions that are normally met with in the perennial plants. The continuity of vital activity for many years has to be carefully looked into. In course of these investigations, information on the inception, development and maturity of different cell-elements may be found out. It will also be necessary to know how one type reduces in number and another type increases proportionately. Thus we shall have a clear understanding of the secondary xylem and its limitations. Along with this study, we must not neglect to check up our observations with the records of the past. Study of the fossil secondary xylem must be continued so that we shall some day in future be in a position to build up a history of evolution of the xylem of the modern perennial plants.

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## EXPLANATION OF PLATES

- PLATE I. Tangential section of *Terminalia tomentosa* showing variation in the occurrence of septate fibres. ( $\times 110$ )
- PLATE II. Apotracheal parenchyma in *Kydia calycina* showing no effect of rate of growth on the number of cells in the band. ( $\times 110$ )
- PLATE III. Apotracheal parenchyma in *Ficus* spp. showing effect of rate of growth on the number of cells in the band. ( $\times 15$ )
- PLATE IV. End view of *Parastemon* (*Rosaceae*) and *Mesua ferrea* (*Guttiferae*). Note apparent family affinity in gross structure but there is considerable difference in minute anatomy. ( $\times 12$ )