CUTICULAR STUDIES OF MAGNOLIALES

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Introduction

At a discussion on the origin of angiosperms held at Amsterdam in September 1935 it was casually suggested that the cuticles of Magnoliales may be worthy of investigation as they may resemble those of the Bennettitales. It therefore occurred to Professor Sahni that the question might be taken up by someone in the East as the material would be more easily accessible there. So it was at the suggestion of Professor Sahni that I took up the present work at Lucknow.

The question of the origin of the angiosperms is still by no means finally settled. A large number of investigators have tackled the problem from diverse angles. The Bennettitalean ancestry seems rather to have been set aside; more and more workers seem to be fascinated by the discovery of the Caytoniales by H. H. Thomas (1925 and 1931). While some of the Bennettitalean remains are almost complete as regards the various organs of the plants, the Caytoniales have so far definitely provided only the reproductive organs. Sagenopteris has been suspected to belong to Caytoniales, and there are strong reasons for this correlation though as yet it has not been demonstrated to be an absolute fact. The cuticle of Sagenopteris is said to resemble that of a mesophytic angiosperm and the stomata to be of the angiospermous
type (H. H. Thomas, 1931, p. 651). The stems of Caytoniales have still to be discovered. Thus we have still to await further discoveries of the other organs of the plant body. Further, Harris (1933) has given reasons to say that the Caytoniales cannot be considered to be angiosperms in the literal sense as Hamshaw Thomas was inclined to call them in his first paper (H. H. Thomas, 1925). Harris has given reasons for the belief that the stigma of Caytoniales gave direct access to pollen grains (see also Johri, 1935; Sahni, 1936).

In the meantime comparative studies of the Bennettiatales and Magnoliales need not be closed. Apart from the resemblances in the floral structure which seemed striking to the early workers, the wood anatomy of the two groups has been lately discussed (Gupta, 1934). It may not be just a chance that the only homoxylous angiosperms are found among the Magnoliales, and resembling the Bennettiatalean structure. Professor Sahni (1932) has already revived the view of the Bennettiatalean ancestry of angiosperms in these words: "The theory according to which the angiosperms have been derived from some gymnospermous group like the Bennettiatales through the Magnoliaceae or some related extinct family would thereby gain distinct support."

The external resemblances of the leaves of Bennettiatales with those of cycads led early workers to call the former fossil cycads. But Florin (1931) has found a means of distinguishing the Bennettiatales from the true fossil cycads by their epidermal studies.*

Florin has found that the Bennettiatales possess a more highly evolved type of cuticular structure, i.e., the "syndetocheile" (Florin, 1933) or compound-lipped type. That only the Bennettiatales and some members of the Gnetales among all the living and fossil gymnosperms show the advanced type of cuticular structure found also in the angiosperms may not be a mere chance. As we do not know much about the fossil history of the Gnetales, attention may again be focussed on the Bennettiatales.

The present work was undertaken to compare the cuticular features of the Magnoliales with those of the Bennettiatales on the one hand and the "haplocheile" gymnosperms on the other. While from this point of view almost the whole lot of angiosperms have been untouched, a beginning has been made in this study of one of the primitive families of angiosperms, the Magnoliales.

**Material and Methods**

The material available to me represents almost all the genera of the cohort Magnoliales of Hutchinson (1926, p. 81).

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* Thomas and Bancroft (1913) had also made this distinction though they did not have so comprehensive an idea of the Bennettiatalean cuticular structure as Florin.
Most of the material was obtained from the Sibpur Herbarium, Royal Botanic Garden, Calcutta. My material was taken mostly from old collections, some over fifty years old. It consisted of bits of leaves from the authenticated duplicate sheets of the herbarium. I have relied on the final identifications that were noted on the herbarium sheets. I am thankful to Messrs. Biswas and Calder for kindly allowing me to take the bits of leaves from the authenticated duplicates.

Leaves of a few genera unrepresented in the Sibpur Herbarium were obtained by Prof. Sahni from Mr. Humphrey Gilbert-Carter, Director, University Botanical Garden, Cambridge, to whom also my thanks are due.

The following types have been examined:—


*Lactoris*, *Himantandra* and *Zygogynum* were unrepresented.

Cuticular preparations were made in the same way as with the fossils, so as to have a uniform method. The bits of leaves were first soaked in warm water so that the dried up cells might regain the original shape, and then immersed in Schultze's macerating fluid. They were then treated with a solution of potassium hydroxide. After this treatment only the cuticles were left unaffected. On washing in water and shaking vigorously in a tube the cuticles were separated from the oxidised tissues. They were then stained in Bimarck Brown and permanent slides were prepared.

Microtome sections were prepared in some cases, but it was difficult to obtain good sections as the cuticles were brittle and the leaves hard. But enough sections were got to correlate the surface and sectional views of stomata. Hand sections of fresh material of *Michelia champaca* were quite satisfactory. With the oil-immersion lens it was possible to study the hand-sections by focussing different levels with the fine adjustments of the microscope. Modelling with plastic wax was of use in elucidating the structures.

Cuticles of more than one leaf could not be examined in the majority of cases as the material consisted of small bits of single mature leaves.

*Previous References*

By far the most important work on the cuticles of living gymnosperms and the Bennetitales is by Rudolf Florin. In his memoir, "Untersuchungen zur Stammesgeschichte der Coniferales und Cordaitales" (1931), he has given a summary of all the essential features described in the previous works.
Among the earlier works Porsch's (1905) seems to be the most important as it is a comprehensive study of the epidermal structure with a view to establish phylogenetic relationships among plants. But he has argued too much for the influence of ecological factors on the epidermal structure of plants (see Thomas and Bancroft, 1913, p. 1; and Florin, 1931, pp. 180-94). Conclusions of recent workers seem to show that the cuticular studies cannot be utilised on a wide scale for the solution of phylogenetic problems, but can be well applied for generic and group demarcations within restricted limits (Florin, 1931: Introduction).

The cuticular structure of the angiosperms is practically uninvestigated from the phylogenetic point of view. Florin (1931, p. 523) remarks that a detailed and extensive investigation of the epidermal structure of the angiosperms has to be taken up before conclusions as to the phylogenetic and generic affinities can be drawn.

On the basis of the ontogenetical studies of the stomata in the Coniferales and Gnetales Florin (1931 and 1934) has distinguished two essentially different types of development. The primitive type met with in the Coniferales, Ginkgoales, Cycadales and Ephedra† is called by him "haplocheile" or simple-lipped (Florin, 1933') and that found in Welwitschia and Gnetum the "syndetocheile" or compound-lipped. Among the fossil forms he has found the latter type only in the Bennettitales.

In the haplocheile type the mother cell of the guard cells divides but once forming the two guard cells. The subsidiary cells are formed by the surrounding epidermal cells which were contemporaneous with the mother cells of the guard cells.

In the syndetocheile type (which is regarded as more advanced because there is greater differentiation in the epidermis) the mother cell first gives rise to two cells (see Figs. 59, 60). One of these cuts off a third middle cell. The latter is the mother cell of the guard cells. Thus both the guard cells and the lateral subsidiary cells are the result of divisions of a single original mother cell.

From an examination of the illustrations given at the end of the paper it will be clear that the Magnoliaceae (except in the case of the two plants to be mentioned below) possess the syndetocheile type of stomata.

Florin in his study of the Coniferales has taken into consideration the epidermal structure in the seedlings and in the cotyledons. From this study he comes to the conclusion that more variations are seen in the cotyledons

† Casuarina among the angiosperms is said to possess the gymnosperm type—Zimmermann (1926, p. 160) after Porsch.
than in the mature leaves, though within narrow limits. The epidermis of both the cotyledons and the foliage leaves is little influenced by the external factors (Florin, 1931, p. 221).

Description of the Cuticles

**General.**—From the following account the epidermis of the Magnoliales is seen to possess a uniform character. The stomata belong (except in Cercidiphyllum japonicum and Euptelea franchetii) to the Bennetttalean or the syndetocheile type of Florin. The two lateral subsidiary cells are about the same size and evidently these and the guard cells are the result of divisions of a single mother cell. The polar subsidiary cells are only adjacent cells of the epidermis and have no immediate genetical relation with the guard cells.

The lateral subsidiary cells in some cases are divided into two (4 in Schizandra elongata) by a transverse division, e.g., spp. of Schizandra, Kadsura, etc. A longitudinal division occurs in many cases, resulting in a lateral subsidiary cell and a "Kranzzelle" of Florin outside it, e.g., Talauma andamanica, Magnolia Henryi, and etc. As in the case of the Bennetttaleas the stomata are not much sunk below the general level of the epidermis. The epidermal cells in the stomatiferous areas are polygonal or irregular in shape, with the walls sinuous to gently wavy and in a few cases nearly straight (see table). Those on the veins and at the edge of the leaf are elongated and somewhat rectangular (Figs. 28 & 29).

Stomata as a rule occur only on the under-surface of the leaves. A narrow zone at the edge of the leaf is without stomata, as also over the veins. Hair-scars when present are observed usually on the lower surface and in Kadsura scandens (Fig. 105) on the upper surface also. The cuticle over the veins and at the edge of the leaf is somewhat thicker than in the stomatiferous areas.

Simple pits are sometimes seen in the epidermal cells (Figs. 67, 85, 93, etc.; also see table). They are few in number and have no definite arrangement as in Cycas (Thomas and Bancroft, 1913, p. 161).

The stomata are orientated in no definite manner as regards the longitudinal axis.

In Cercidiphyllum the cuticular edge around the stomatal opening forms a vestibule above the stomatal pore (Fig. 116). This vestibule ("Vorhof") is characteristic of the Bennetttaleas (Cercidiphyllum is otherwise of the gymnospermous haplocheile type). Among the gymnosperms such a cuticular border is said to occur in Cordaites and Sciadopitys (Florin, 1931, p. 510).

The number of stomata per unit area seems fairly constant at different parts of the individual leaf. (In most cases, however, only small bits of leaves were available for examination.) In the accompanying table averages
## Epidermal features of the Magnoliales

<table>
<thead>
<tr>
<th>Serial number</th>
<th>Name of plant</th>
<th>No. of stomata per unit area (= 1.0 sq. mm.)</th>
<th>No. of lateral subsidiary cells</th>
<th>Epidermal walls</th>
<th>Pits in outer walls of epidermal cells</th>
<th>Other features</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
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<td>Average for species</td>
<td>Average for genus</td>
<td>Lower epidermis</td>
<td>Upper epidermis</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Sinuous</td>
<td>Slightly Wavy</td>
<td>Straight</td>
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<td>3</td>
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<td>2</td>
<td>×</td>
<td>×</td>
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<tr>
<td>4</td>
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<td>×</td>
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<td>M. Delavayi</td>
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<td>×</td>
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<td>×</td>
</tr>
<tr>
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<td>2</td>
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<td>No. of Leaves</td>
<td>No. of Cells</td>
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<td>Simple</td>
<td>Hairs</td>
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<td>---------------</td>
<td>-------------</td>
<td>----------</td>
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<tr>
<td>16</td>
<td><em>M. insignis</em></td>
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<td>78</td>
<td>2</td>
<td>×</td>
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<td>×</td>
<td>×</td>
<td>×</td>
</tr>
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<td>×</td>
<td>×</td>
<td>×</td>
</tr>
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<td><em>M. montana</em></td>
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<td>×</td>
<td>×</td>
<td>×</td>
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<tr>
<td>23</td>
<td><em>Kiospa</em></td>
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<td>83</td>
<td>2; long. div. in one subs. cell</td>
<td>×</td>
<td>×</td>
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<td>×</td>
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<td>×</td>
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<td>×</td>
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<td>×</td>
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<td>×</td>
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<td>×</td>
<td>×</td>
<td>×</td>
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<td>32</td>
<td><em>T. maingayi</em></td>
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<td><em>T. Kiiuelleri</em></td>
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<td>×</td>
<td>×</td>
<td>×</td>
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<td>2</td>
<td>×</td>
<td>×</td>
<td>×</td>
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<tr>
<td>36</td>
<td><em>T. mutabilis</em></td>
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<td>×</td>
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<td>×</td>
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<td><em>T. andamanic</em></td>
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<td>×</td>
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Culicular Studies of Magnoliaceae

Hairs on lower surface
<table>
<thead>
<tr>
<th>Name of plant</th>
<th>No. of stomata per unit area (1.0 sq. mm.)</th>
<th>Average for species</th>
<th>Average for genus</th>
<th>No. of lateral subsidiary cells</th>
<th>Upper epidermis</th>
<th>Lower epidermis</th>
<th>Epidermal walls</th>
<th>Other features</th>
<th>Cuticular features</th>
<th>Other features</th>
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<td>38 <em>Aralia racemosa</em></td>
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<td></td>
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<tr>
<td>39 <em>Aronia alnifolia</em></td>
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<td></td>
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</tr>
<tr>
<td>41 <em>Ilex aquifolium</em></td>
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<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>42 <em>Ilex aquifolium</em></td>
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<tr>
<td>43 <em>Ilex aquifolium</em></td>
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<tr>
<td>44 <em>Ilex aquifolium</em></td>
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<tr>
<td>45 <em>Ilex aquifolium</em></td>
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<td></td>
<td></td>
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<tr>
<td>46 <em>Ilex aquifolium</em></td>
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<tr>
<td>47 <em>Ilex aquifolium</em></td>
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<tr>
<td>48 <em>Ilex aquifolium</em></td>
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<tr>
<td>49 <em>Ilex aquifolium</em></td>
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</tbody>
</table>

*H. S. Rao*
<table>
<thead>
<tr>
<th>No.</th>
<th>Species</th>
<th>30</th>
<th>18</th>
<th>2; tr. divns. in each subs., cell</th>
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<td><em>K. scandens</em></td>
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<td><em>K. lanceolata</em></td>
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<td><em>Trochodendron aralioides</em></td>
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<td><em>Tetracentron sinense</em></td>
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</tr>
<tr>
<td>55</td>
<td><em>Euptelea Franchetii</em></td>
<td>35</td>
<td>35</td>
<td>4, 6 or 7 cells surrounding the stoma</td>
</tr>
<tr>
<td>56</td>
<td><em>Cercidiphyllum japonicum</em></td>
<td></td>
<td></td>
<td>7 cells surrounding the stoma</td>
</tr>
</tbody>
</table>

*Notes:*
- Hairs on both surfaces
- Cuticular striations
- Haplocheile

*Cuticular Studies of Magnoliids*
of six readings are given. As can be expected the larger numbers indicate smaller size of the epidermal cells as well as of stomata. It will be seen that the genera of the family Magnoliaceae of Hutchinson are according to the generic averages characterised by a larger number of stomata per unit area than the genera of the other families under his Magnoliaceae.

This higher frequency in itself has not much phylogenetic significance, except perhaps indicating a general xerophytic habit (see Salisbury, 1928). Prof. Salisbury has introduced the concept of the "stomatal index," i.e., he takes into consideration more the proportion of the epidermal cells which are destined to develop into stomata, than mere stomatal frequencies.

From the accompanying table a striking fact appears which might be worth mentioning: the only forms in which transverse divisions of subsidiary cells are seen are those with fewer stomata per unit area (outside the Magnoliaceae of Hutchinson). I suggest the possibility that here, where the cells are large, two subsidiary cells give a better mechanical support to the guard cells than only one for their opening and closure movements.

Surface view of cuticles.—The constant presence (except in Cercidiphyllum and Eupelelea) of two lateral subsidiary cells is to be marked. Occasionally a longitudinal division takes place in them, generally on one side only, e.g., Talauma andamanica, Michelia montana, etc. Among the Bennettitales Nilsonioteris glandulosa shows a similar condition (Florin, 1932", p. 3). In the two species of Drimys the longitudinal division takes place in both the subsidiary cells resulting in two "Kranzzellen" outside the two subsidiary cells. In some members, e.g., Kadsura cauliflora, K. scandens, Tetracentron, etc., a transverse division takes place in the lateral subsidiary cells, either in one or in both. In such cases the stomata are surrounded by 5 or 6 cells, of which two are polar subsidiary cells. Such large numbers are not to be mistaken for the surrounding cells of haplocheile type. It is only a case of meristematic division going a step further. Occasional transverse division in the lateral subsidiary cells takes place also in some Bennettitales, e.g., Williamsonia pecten in one of the subsidiary cells and Williamsonia Wettsteinii in both the subsidiary cells—(see Florin 1933"", pp. 7 and 12).

In Illicium evenum there is the preponderant number of surrounding cells, in which case one of the lateral subsidiary cells curves round one polar end of the stoma and thus comes to function as the polar subsidiary cell also. This is due to an oblique second division of the original mother cell (which results in the mother cell of the guard cells). The normal arrangement of syndetocheile members also occurs here and there. Sometimes a transverse division also occurs in the lateral subsidiary cells. Hence,
although the number of surrounding cells varies from two to four or five, it still conforms to the syndetochaile type and is not to be mistaken for the haplocheile.

Pits in the outer walls of the epidermal cells are seen in a few cases, e.g., Magnolia pterocarpa, Talauma villosa, etc. (Figs. 67, 85, etc.), but they have no definite peripheral arrangement as in the case of Cycas; and are fewer in number.

Cuticular undulations on the surface are seen in some cases (Illicium simonsii, Schizandra propinqua, Kadsura lanceolata, etc., see table), and have been shown as dotted lines (Figs. 90, 106; see also table). Similar cuticular striations are seen also in Stangeria (Thomas and Bancroft, 1913, pp. 159-60), but in no other member of the Cycadales.

Cercidiphyllum japonicum and Euptelea franchetii are the only members among all the genera and species examined which show an important deviation in the cuticular structure. They possess from four to seven subsidiary cells (seven in C. japonicum and 4, 6 or 7 in E. franchetii) around the stomata. The cells from their shape evidently are only adjoining cells of the epidermis and are not developmentally to be traced to a common origin with the guard cells. This would mean that only the two guard cells result from the division of the original mother cell, thus conforming to the "haplocheile" type of development.

Sectional views of epidermis.—Sectional views of the following have been studied:—Michelia champaca, Drimys aromatic, Liriodendron tulipifera and Cercidiphyllum japonicum.

The guard cells are slightly sunken below the general level of the epidermis. In the median transverse section the guard cells are seen to possess two thickenings, one in the dorsal wall and one in the ventral, i.e., adjacent to the mesophyll tissues. The dorsal thickening is absent at the polar ends of the guard cells. It is on account of this that in the surface view there are two clear areas shown at the extremities of the guard cells.

In Cercidiphyllum there is a pronounced cuticular projection over the stomatal pore forming an outer vestibule ("Vorhof"). Thomas and Bancroft (1913, p. 182) in their reconstruction of the stoma of Ptilophyllum pecten (Bennettitales) have mistaken a similar cuticular border for the dorsal thickening of the guard cells (see Florin, 1931, p. 508). Sciadopitys alone among the Coniferales, and Cordaites are shown to possess such an outer

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Pittings are said to be absent in the other Cycads (Microcycas not examined)—Thomas and Bancroft, 1913, p. 161.
chamber (Florin, 1931, p. 112). Toward the polar ends of the guard cells this cuticular edge (in *Cercidiphyllum*) is not so high.

Thus the haplocheile *Cercidiphyllum* combines in itself also the Bennettitalean character, *viz.* the presence of the vestibular border of the cuticle and the sinuous walls of the epidermal cells.§ This combination of character is remarkable. Engler and Prantl (see Willis, 1919) place Cercidiphyllaceae previous to Magnoliaceae among the Ranales and under Trochodendrineæ. *Trochodendron* is well known to possess homoxylous wood (Gupta, 1934, and literature cited therein). But *Cercidiphyllum*, Prof. Sahni informs me, does not possess homoxylous wood. *Euptelea, Illicium, Kadsura, Schizandra, Michelia, Talauma* and *Liriodendron* are also known to possess typical ‘vessel-members’ (Bailey and Thompson, 1918, p. 504).

The various features of the epidermis of the Magnoliaceae are tabulated in the accompanying table for the sake of convenience.

**Conclusion**

The Magnoliaceae have for a long time claimed to be considered as among the most primitive angiosperms. Very early (Hallier, 1905; Arber and Parkin, 1907) an attempt was made to seek for their descent through the Bennettitales. But this was somewhat set aside until revived by Prof. Sahni (1932) and later followed up by Gupta (1934). The present investigation shows that at least a few of the members of the Magnoliaceae represent synthetic types. *Cercidiphyllum* combines the characters of the angiosperms, the Bennettitales and the haplocheile gymnosperms. *Euptelea franchetii* possesses the haplocheile type of stomatal development. The cycadean character, *viz.*, the cutin striations seen in *Stangeria*, are also found in some members of the Magnoliaceae (*Illicium simonsii*, *Kadsura lanceolata*, etc. (see table and Figs. 90, 106).

The present study has opened the question of the position of the Magnoliaceae from the point of view of cuticular analysis. While the great host of angiosperms remain uninvestigated from this standpoint, this short study indicates that the Magnoliaceae have not been directly derived from the Bennettitales, and that synthetic types combining the characters of the Cycadales, the other haplocheile gymnosperms and the angiosperms are to be found in this small group. This is well in keeping with our anticipations.

The general problem of the origin of the angiosperms remains the same. The additional light thrown on it by the cuticular analysis restates the view

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§ The Bennettitales possess sinuous walls generally, exceptions being *Williamsonia spectabilis* Nath., etc., which have straight-walled epidermal cells (Florin, 1933, pp. 5, 6).
that the progenitors of the angiosperms have to be sought for in that plexus of gymnosperms which gave rise on the one hand to the Bennettitales, the syndetocheile Gnetales on the other, the haplocheile Magnoliatales along a third line, and the majority of the Magnoliatales, viz., the syndetocheile ones, along a fourth line of descent, this last being probably nearest related to the Bennettitales (from the present point of view). All the homoxylous Magnoliatales (Gupta, 1934) possess the syndetocheile type of cuticular structure (Zygogynum has not been available to me). This constant combination of homoxyly and syndetocheily may have some phylogenetic significance. Syndetocheily by itself may not count for much as it is common in the vast majority of the angiosperms.

It may be of interest to draw attention to the geographical distribution and systematic position of the two haplocheile genera Eupelela and Cercidiphyllum. The former comprises three species extending from Japan to Bengal and the latter has two species confined to Japan. In Engler and Prantl's classification (see Willis, 1919) Trochodendraceae (to which belongs Eupelela) and Cercidiphyllaceae are the third and fourth families respectively under the Cohort Ranales, while Magnoliaceae occupies the ninth position. The sub-group Trochodendrinae (i.e., Trochodendraceae and Cercidiphylaceae) is characterised by naked flowers, while Magnoliinae (comprising Magnoliaceae, etc.) possess flowers with perianth. From the point of view of the wood-anatomy of homoxylous Magnoliatales also the Trochodendron group is considered to be older than the Drimys group (Gupta, 1934, p. 93). Thus the aberrant epidermal characters of Eupelela and Cercidiphyllum seem to go hand in hand with other primitive features already known to exist in the group Trochodendrinae.

It appears from the point of view of the present inquiry that the Magnoliatales of Hutchinson do not represent a co-sanguinary group, but indicate a convergence.

Acknowledgments

I am indebted to Professor Sahni who suggested to me this work and gave me the necessary literature. His suggestions and other help have been invaluable to me in the preparation of this paper. My gratitude is due to the authorities of the Lucknow University for awarding me a Research Fellowship during which term a part of this work was done. I have great pleasure in particularly acknowledging the laboratory facilities given me by Prof. M. A. Sampathkumaran of Bangalore, and Mr. C. V. Krishna Iyengar of Mysore without whose kindness this work would have remained unfinished.
Summary

In the present work the question of the position of the Magnoliales from the point of view of their epidermal features has been taken up. This is rather a new line of inquiry. Florin's criteria, viz., the haplocheile and syndetocheile types of stomatal development have been made use of. According to this test the Magnoliales are seen to comprise a few synthetic forms, some possessing certain Cycadean features, the great majority the Bennettitalean, and a few the haplocheile gymnosperm features.

The aberrant epidermal features of Euptelea and Cercidiphyllum seem to be correlated with other primitive features of Trochodendraceae already known.

The view has again been expressed that the progenitors of the angiosperms have to be sought for in that plexus of gymnosperms which gave rise to the Bennettitales, the syndetocheile Gnetales, the haplocheile Magnoliales and the majority of the Magnoliales (i.e., syndetocheile) along different lines of descent, the last being probably nearest related to the Bennettitales.

From the point of view of epidermal studies, the Magnoliales do not represent a co-sanguinary group, but indicate a convergence.

BIBLIOGRAPHY


4. ———— "Studien über die Cycadales des Mesozoicums nebst Erörterungen über die Spaltöffnungsapparate der Bennettitales," ibid., 1933, Ser. 3, Band 12, No. 5.


* I was not able to consult this paper.


EXPLANATION OF PLATES

(Names of countries marked against the species refer to the source of the herbarium sheets)

Figs. 1 & 2 Magnolia nitida, W.W.Sm. (Yunnan). Lower and upper epidermis, \( \times 400 \).

Figs. 3 & 4 M. Mainuyi, King. (Malayan Archipelago). Lr. and up. epid. In the up. epid. there are a large number of striations in the thickness of cell walls (not shown in drawing) which may be due to the flattening of the cuticle on the slide, so that the inward projections of the walls are folded. \( 3, \times 335; 4, \times 500 \).

Figs. 5 & 6 M. Henryi. Dunn. (China). Lr. and up. epid. Note the longitudinal division in one of the lateral subsidiary cells. Pits are present in the epid. cells of both surfaces (not shown). \( 5, \times 335; 6, \times 400 \).

Figs. 7 & 8 M. oborata, Thunb. (S. India). Lr. and up. epid. \( \times 100 \).

Figs. 9 – 11 M. rostrata. W.W.Sm. (Yunnan). 9, up. epid.; 10, Lr. epid. Note the longitudinal division in one of the lateral subs. cells; 11, hair-base. \( \times 500 \).
Figs. 12 & 13  *M. Championi*, Bth. (Hongkong). Lr. and up, epid. Pits present on both surfaces (not shown). \( \times 500. \\


Figs. 16 & 17  *M. conspicua*, sal forma? (China). Lr. and up, epid. Note the long, divln. in one of the lateral subs. cells. \( \times 400. \\

Figs. 18 & 19  *M. Delavayi*, Franch. (Yunnan). Lr. and up, epid. Note the long, divn. in one of the lateral subs. cells. \( \times 500. \\

Figs. 20 & 21  *M. tabensis*, W.W.Sm. (Yunnan). Lr. and up, epid. \( \times 500. \\

Figs. 22 & 23  *M. pterocarpa* (*M. sphenocarpa*) (Cultd. in R.B.G.). Lr. and up, epid. Pits present on both surfaces (not shown).

22, \( \times 500. \)  23, \( \times 325. \\

Figs. 24 & 25  *M. hypoleuca*, s. z. (Japan). Lr. and up, epid. \( \times 500. \\

Figs. 26 & 27  *M. kousus*, De. (Japan). Lr. and up, epid. \( \times 500. \\

Figs. 28 & 29  *Liriodendron tulipifera* (Cultd. in R.B.G.). Lc. and up, epid. Note the stomata-free areas over the veinlets, with elongated cells. \( \times 400. \\

Figs. 30 & 31  *Manglietia Hookeri*, Cubitt and Smith (Burma). Lr. and up, epid. \( \times 480. \\

Figs. 32 & 33  *M. insignis*, Bl. var. *augustifolia* (Assam). Lr. and up, epid. \( \times 400. \\

Figs. 34 & 35  *M. augustifolia*, Hk. f. and T. (Burma). Lr. and up, epid. \( \times 500. \\

Figs. 36 & 37  *M. glauca*, Bl. (Malayan Archipelago). Lr. and up, epid. \( \times 400. \\

Figs. 38 & 39  *Michelia fassata*, Bl. (Cultd. in R.B.G.). Lr. and up, epid. \( \times 400. \\

Figs. 40 & 41  *M. manni*, King (Assam). Lr. and up, epid. \( \times 400. \\

Figs. 42 & 43  *M. Cathcarti*, Hk. f. and T. (Naga Hills). Lr. and up, epid. \( \times 480. \\

Figs. 44 & 45  *M. montana*, Bl. (Assam). Lr. and up, epid. Note the long, divn. in one of the subs. cells. \( \times 630. \\

Figs. 46 & 47  *M. kisopa*, Ham. (Nepal). Lr. and up, epid. \( \times 490. \\

Figs. 48 & 49  *M. panduana*, Hk. f. and T. (Assam). Lr. and up, epid. \( \times 400. \\

Figs. 50 & 51  *M. champaca*, L. (S. India and Burma). Lc. and up, epid. \( \times 400. \\

Figs. 52 & 53  *M. nilagirica*, Zenk. var. *Walkeri* (Peninsular India and Ceylon). Lr. and up, epid. Note the long, divn. in one of the subs. cells. Pits present (not drawn). \( \times 400. \\

Figs. 54 & 55  *M. oblonga*, Wall. (Assam). Lr. and up, epid. \( \times 400. \\

Figs. 56 & 57  *M. globosa*, Hk. f. and T. (Sikkim). Up. and lr. epid. \( \times 300. \\

Figs. 58–61  *Taluana Condolii*, Bl. (Cultd. in R.B.G.). 58 and 61 up. and lr. epid. 59 and 60. 1st and 2nd divns. in the development of stoma according to the syndetocheile type.

58 & 61, \( \times 400; \)  59 & 60, \( \times 630. \\

Figs. 62 & 63  *T. spongocarpa*, King (Upper Burma). Up. and lr. epid. Pits present (not drawn). \( \times 500. \\

Figs. 64 & 65  *T. Forbesii*, King (Sumatra). Lr. and up, epid. Note the long, divn. in one of the subs. cells. \( \times 500. \\

Figs. 66 & 67  *T. Maiouyi*, King (Malaya). Lr. and up, epid. Pits present. \( \times 500. \\

Figs. 68 & 69  *T. villosa*, Mig. (*T. lanigera*, Hk. f. and T.) (Malayan Peninsula). Lr. and up, epid. Pits distinct on both surfaces. \( \times 400. \\

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Figs. 70 & 71 T. Künstleri, King (Kedah Peak). Lr. and up. epid. \( \times 400 \).

Figs. 72 & 73 T. Hodgsoni, Hk. f. and T. (Sikkim Himalaya). Lr. and up. epid. \( \times 500 \).

Figs. 74 & 75 T. mutabilis, Bl. (Malayan Archipelago). Up. and lr. epid. Note the long. divn. in one of the subs. cells. Pits on both surfaces (not shown). \( \times 400 \).

Figs. 76 & 77 T. andamanica, King (Andamanans). Lr. and up. epid. Note the long. divn. in one of the subs. cells. Pits on both surfaces (not shown). \( \times 500 \).

Figs. 78 & 79 Aromadendron elegans, Bl. Lr. and up. epid. \( \times 630 \).

Figs. 80 & 81 Drimys winteri. Lr. and up. epid. Note the long. divns. in both the subs. cells. \( \times 300 \).

Figs. 82 & 83 D. aromatica. Lr. and up. epid. Note the long. divns. in both the subs. cells. \( \times 300 \).

Figs. 84 & 85 Illicium Griffithii, Hk. f. and T. (Assam). Lr. and up. epid. Pits present on both surfaces (not shown in lr. epid.). \( \times 400 \).

Figs. 86 & 87 I. cambodianum, Stance (Malayan Peninsula). Lr. and up. epid. \( \times 400 \).

Figs. 88 & 89 I. evenium, King (Malayan Peninsula). Lr. and up. epid. There is seen a tendency towards long. orientation of stomata parallel to the length of the leaf. Note the variation in the number of surrounding cells (2 to 3). Pits present. \( \times 400 \).

Figs. 90 & 91 I. Simonsii (Manipur). Lr. and up. epid. Note cutin striations shown as dotted lines. \( \times 400 \).

Figs. 92 & 93 I. manipurensis, Watt. Ms. (Assam). Lr. and up. epid. Pits present. \( \times 400 \).

Figs. 94 & 95 Schizandra propinqua, Hk. f. and T. (Nepal). Lr. and up. epid. This also shows cutin striations (not shown). \( \times 400 \).

Figs. 96 & 97 S. axillaris, Hk. f. and T. (Assam). Lr. and up. epid. cutin striations present (not shown). Note the long. divns. in one of the subs. cells and tr. divns. in the other. \( 96, \times 335; \) 97, \( \times 460 \).

Figs. 98 & 99 S. elongata, Hk. f. and T. (Himalaya). Lr. and up. epid. Note the long. divn. in one of the subs. cells and two tr. divns. in the other.

Figs. 100 & 101 Kadsura cauliflora, Bl. (Penang). Lr. and up. epid. Note the tr. divn. in one of the subs. cells. \( \times 400 \).

Figs. 102 & 103 K. Roxburghiana, Arn. (Burma). Lr. and up. epid. Note the tr. divns. in both the subs. cells. Note also the hair-base on up. epid. \( \times 400 \).

Figs. 104 & 105 K. scandens. Bl. Lr. and up. epid. Note the tr. divn. in both the subs. cells. Note also the hair-base (present on both surfaces). \( 104, \times 335; \) 105, \( \times 400 \).

Figs. 106 & 107 K. lanceolata, King (Malaya). Lr. and up. epid. Note the cutin striations. \( \times 400 \).

Figs. 108 & 109 Trochodendron aralioides, Veitch. Lr. and up epid. \( \times 630 \).

Figs. 110 & 111 Euptelea Franchetii, Chenault. Lr. and up. epid. Note the varying numbers of surrounding cells. This belongs to the haplocheile type. Note the differences in sizes of the stomata. \( \times 325 \).
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Figs. 112 & 113 *Tetracentron sinense*. Lr. and up. epid. Note the tr. divns, in both the subs. cells. Cutin striations are present (not shown). \( \times 300 \).

Figs. 114 & 115 *Cercidiphyllum japonicum*. Lr. and up. epid. Note that there are seven cells surrounding the stoma. This belongs to the haplocheile type. \( \times 712 \).

Fig. 116 *C. japonicum*. Median tr. section of stoma. Note the thickeningsof the guard cells and the cutin projections forming the outer vestibule (a Bennettitalean character). \( \times 712 \).

Fig. 117 *C. japonicum*. L.S. of guard cell. \( \times 1425 \).

Fig. 118 *C. japonicum*. T.S. of guard cells at the polar end. \( \times 630 \).

Fig. 119 *C. japonicum*. T.S. between the pole and median position of stoma. \( \times 630 \).

Fig. 120 *C. japonicum*. Section of the upper epidermis showing the pits extending part way into the cuticle.

Figs. 121 & 122 *Drimys aromatic*ica. L.S. and T.S. (one half) of stoma. \( \times 630 \).

Figs. 123 & 124 *Michelia champaca*, L. (Mysore). Two drawings of the tr. section of stoma drawn from a hand-section by focussing at different levels. \( \times 630 \).

Fig. 125 *M. champaca*, L. Drawn as in the previous case. Difference between I and II—\( 0.1 \) mm.; between II and III—\( 0.08 \) mm. \( \times 712 \).

Fig. 126 *M. champaca*, L. L.S. of guard cell. \( \times 712 \).

Figs. 127 & 128 *Liriodendron tulipifera*. L.S. and T.S. (oblique) of stoma. \( \times 1425 \).