The significance of epidermal and cuticular morphology as a diagnostic character in taxonomic and phylogenetic studies of the higher plants has been amply demonstrated in the recent past, and the utility of such studies including the morphology of epidermal appendages for taxonomic purposes in angiosperms has been brought to light in different groups of plants (Petolitzky, 1932; Rao, 1939; Ahmad, 1964, Paliwal, 1969; Carlquist, 1953; Ramayya, 1962, etc.). The possibility of specific identification of flowering plants based on cuticular character has been explored by Sinclair & Dunn (1961) and Stace (1961) and Ramayya and Rajagopal (1963) are attempting to compile "the Flora of Hyderabad" on the basis of foliar/significant contribution in assessing affinities of the fossils based on cuticular morphology of the living angiosperms has been made by Bandulska (1922-24, 1925, 1930).

The significance of various epidermal characters in taxonomy and phylogeny of Urticales is discussed separately as follows:

(A) **Trichomes**

Of all the anatomical features, trichomes are perhaps most often enlisted for systematic comparison because of their variety, their almost universal presence in angiosperms, their ease of preparation and study, and the close relation of their variation patterns to the taxonomic system. In the recent past certain taxa have been investigated in detail, e.g. *Rhododendron* (Cowan, 1950), *Nicotiana* (Goodspeed, 1954), Madinae - Compositae (Carlquist, 1958), Compositae (Ramayya, 1962), Gentianales (Patel and Inamdar, 1972), Polemoniales (Inamdar and
Patel (1973), Moraceae (Shah & Kachroo, 1974) etc. leading to the accumulation of much data.

Uphof (1962) has provided a historical review of development of our knowledge of trichomes and Tschirch (1906) gave a review of the various kinds of glands and their classification. The range of the form, function and other diversites of trichomes are given especially by Solereder (1903) and Metcalfe and Chalk (1950), Uphof (1962), and Hummel and Staesche (1962). The term trichome is applied here to all outgrowths from the epidermis of leaves and shoots, no matter whether they are unicellular or pleuricellular.

The trichomes have been classified on basis of their form, function, development etc. by several workers in the past; Weiss (1867) classified them mainly on their form into three main types as follows:

I. All constituent cells of same kind
   1. Unicellular trichome
   2. Uniseriate
   3. Pleuriseriate

II. Cells not all of the same kind (Capitate trichome)
   a. Stalk simple or compound
      (a) head unicellular
      (b) head pleuricellular

III. Trichomes with lysigneous cavity filled with a secretion.

De Bary (1877) recognised 5 types:
   1. Papillae and bladders
   2. Hairs (correspond partly to unicellular and uni-seriate hairs of Weiss)
   3. Scales
   4. Shag hairs or Villi (these correspond to pleuriseriate hairs of Weiss).
5. Warts and spines.

Rauter (1872) recognised two types on the basis of their origin:

(a) Derived entirely from epidermal cells
(b) Originate in collaboration of sub-epidermal cells.

Solereder (1908) provided a classification which has proved useful in identifying plants in absence of flowers and fruits. It is summarized below:

I. Non-glandular trichomes:
   1. Simple, unicellular or uniseriate
   2. Squariform
   3. Stellate and candelabra
   4. Shag or Villi
   5. Warts and spines

II. Glandular trichome:
   1. Unicellular (tubular)
   2. Pleuricellular (head derived with anti and periclinal walls)
   3. With anti-clinal heads
   4. Shag or Villi

Uphof (1962) discussed six types under his classification as follows:

1. Papillate - hairs whose development has been arrested at a stage in which the hair is still unicellular but slightly elongated and little differentiated.
2. Unbranched unicellular, + conical
3. Uniseriate (Pili or setae)
4. Peltate
5. Clavate, Capitate

6. Villi (Shag hairs) and emergences

Hummel and Staesche (1962) recognised five trichome types; these with their distribution in Urticales and related orders and summarized in Table II below:

Table II: Distribution of five types of trichomes (sensu Hummel and Staesche, 1962) in Urticales and related orders.

<table>
<thead>
<tr>
<th>Orders</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Einzellige</td>
<td>Stern und Schild</td>
<td>Einzellreihige</td>
<td>Kopfchen</td>
<td>Mehrzellreihige</td>
</tr>
<tr>
<td>Rosales</td>
<td>Mamamelidaeae</td>
<td>Platanaceae Type I</td>
<td>Platanaceae</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salicales</td>
<td>Salicales</td>
<td>Salicaceae</td>
<td>Salicaceae</td>
<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Fagales</td>
<td>Betulaceae</td>
<td>Fagaceae (I)</td>
<td>Betulaceae (I)</td>
<td>Fagales</td>
<td>Fagales</td>
</tr>
<tr>
<td>Myricales</td>
<td>Myricales</td>
<td>Myricaceae</td>
<td>X</td>
<td>Myricales</td>
<td></td>
</tr>
<tr>
<td>Juglandales</td>
<td>Juglanda-les</td>
<td>Juglandaceae</td>
<td>Julianiaceae</td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Urticales</td>
<td>Urticales</td>
<td>X</td>
<td>Moraceae I</td>
<td>Cannabina-aceae (Ulmaceae)</td>
<td>Urticales</td>
</tr>
</tbody>
</table>

Nearest homology to Bracket included nomenclature used in this work

- X absent, ( ) rare.
Two types of trichomes are here recognized to occur in
in *Urticales*. The glandular and non-glandular. They are found on
all vegetative organs; there being no restricted areas of
development, the two may occur side by side. However, it is often
possible to discern whether the initial, after it projects
outwards, would develop into a glandular or a non-glandular
trichome. They arise from a single superficial cell. In either
case the initial becomes distinct from the adjoining cells by its
larger size, prominent nucleus and denser cytoplasm. The cell soon
forms a papilla which is either rounded or pointed; the former
usually produces a glandular and the latter a non-glandular trichome:

**Glandular trichomes:** The initial divides periclinally to
give rise to a basal and an outer cell. The outer cell undergoes
another periclinal division to form a stalk cell and a head cell.
The basal cell usually does not divide further and forms a simple
foot; occasionally, however, an anticlinal wall in it may result
in a bi-celled foot. The stalk cell either remains undivided and
forms a short stalk or undergoes 1-2 periclinal (and occasionally
anticlinal) divisions to produce a long uniseriate (and occasion-
ally biseriate) stalk. The head cell, however, invariably undergoes
further divisions and depending upon the plane of divisions in it
and the final form of the resulting head, the following broad
types of glandular trichomes are recognised:

(i) **Spherical:** The first division is vertical (anticlinal)
or 1-2 oblique, and equational followed usually by another vertical
wall at right angles to the first. The resulting cells
undergo one transverse division either all at once or one after
the other.

(ii) **Oblong-elliptical:** The head cell undergoes two or more
transverse (periclinal) divisions either before any vertical wall
is formed or after the first vertical wall.

(iii) **Peltate-capitate**: The first wall is vertical and unequational, the next wall, also vertical, is laid in the larger cell. Further vertical walls result in a peltate-capitate head.

(iv) **Typical peltate**: The first and the subsequent divisions are vertical. The resulting cells expand and undergo further vertical divisions to form a discoid plate of cells, circular in outline.

(v) **Scale**: Like typical peltate hairs are pleuricellular discs of large dimensions resulting from a number of radial and tangential vertical divisions.

However, overall ten forms of glandular trichomes are recognised, as under:

1. **Spherical**: typical, atypical, oblong, elongated, strap.
2. **Peltate**: typical, atypical, capitate, massive.
3. **Scales**

In the spherical type, formation of the 3 cell stage (foot, seta, head) is the rule, e.g. in *Ulmus wallichiana*, *Celtis australis*, *Cannabinaceae*, *Jasminum dioica*, *Pouzolzia pentandra*, *Dehneasea platyphylla*, *Vilebrunaceae frutescens*. This is the typical development, the head being pleuricellular.

An atypical development 3-4(-5) cell long filament with a unicellular capitulate head is observed in *Trema orientalis*, *Conocephalus suaveolens* and *Laportea microstigma*. There is a definite tendency towards suppression of the stalk cell in *Lacanthyus wightii* (being eliminated in *L. wallichii*) and *Laportea decurrens*. In some species like *U. wallichiana*, the head tends to be oblong and in *Ulmus villosa*, *Celtis*, *Jatropha asper*, *Ficus*, *Cudrania spinosa*, *Mirardinia heterophylla*, *Pipturus repandus* the
head is oblong. Further through additional transverse wall formation in the head accompanied by elongation, the head becomes elongated (I. politora, C. spinosa, L. microstigma, L. decurrens, Pilea scripta, Pipturus recurvatus). A further development in the oblong head is in the whole 3 cell stage becoming cellular at maturity and elongating longitudinally and laterally resulting finally in a strap shaped trichome (I. orientalis, I. cannabina).

The typical peltate head has a foot (1 cell) stalk (1 cell) and a pleuricellular disc shaped head (Broussonetia papyrifera, Cudrania, Artocarpx, Lakooba, Conocephalus suaveolens, Hulletia griffithiana, Humulus lupulus, Urtica dioica, Locanthus fruticosa, Pilea repens, P. scripta, P. umbrosa, Girardinia heterophylla, Parietaria cretica, P. vulgaris). The head tends to assume capitate shape in Broussonetia, Cudrania, Urtica dioica, and Pilea umbrosa. Tendency towards suppression of stalk cell is seen in Conocephalus suaveolens, Hulletia griffithiana, Pilea scripta, P. umbrosa, Parietaria cretica, P. vulgaris; and the stalk cell is eliminated in Girardinia subaequalis, Antiaria toxicaria, Conocephalus, Urtica parviflora, Laportea, Ureia, Girardinia, Pipturus, and Parietaria judaica. Accompanied with suppression/elimination of the stalk cell is the elongation of the foot to lesser or greater extent (Antiaria, Urtica parviflora, Ureia etc.)

The glandular scales are only observed in Hulletia. These are + circular with a 1 cell stalk (often suppressed) and a translucent disc.

**Non-glandular trichomes:** They are typically simple and unicellular, (in all species examined), tending to be 2 celled in Girronniera, Conocephalus, Pilea scripta; 2-3 celled in Hulletia, 2-many celled in Cudrania spinosa, Laportea decurrens. Great variety is observed in the structure of the foot; being simple
(in all species) with tendency to 1-many pegs in *Trema, Gironniera, Cudrania, Cannabis, Urtica parviflora, Laportea decurrens, Pilea scripsta; pseudopodial (*Fleurva, Girardinia, Utera); simple or in form of a slipper (*Trema cannabina, Gironniera, Cannabis, Pilea scripsta, Drougetia) or haustorial (*Trema politora, Droussonetia, Cudrania sps). Development of a collar, 1 cell high (*Ulmus wallichiana, Celtia, Trema, Cannabis, Pilea, Forskohlia, Drougetia etc.); 2-4 cells high (*Ulmus Trema, Cudrania, Drougetia), 2-6(-8) cells high (*Droussonetia, *Strobilus, Morus, Utera, Fleurva, Girardinia, Debregeasia, Boehmeria, Drougetia) is common but without any relationship to the size of the trichome. Uncommonly the collar is formed by oblique divisions in the surrounding cells (1 cell high collar) as in *Ulmus and *Trema. The wall is mostly smooth, or may be variously roughened (warted, mammilatate, papillate) e.g. in *Strobilus, *Antiaris, *Urtica, *Girardinia, *Boehmeria, *Debregeasia.

Broadly 13 forms are recognised in the genera studied as follows:

(1) Bracket (unicellular)

A. Simple (collar + or -)
   a. Foot dilated (collar 1 cell -3(4) cell high)
   b. Body dilated at base (collar + or -)
   c. Tip straight/bent/hooked

(2) Filiform

Unicellular

Simple

   short (collar + or -)
   long (collar + or -)

Dilated foot

2-celled

(3) Acicular
Unicellular

simple (collar +, 1-2-3(4) cells, or - )
dilated
2 - many celled (collar + or - )

(4) Elongated (unicellular) collar + or -

(5) Fusiform (unicellular)

(6) Slipper (unicellular)

simple (collar -)
collared base

(7) Conical (unicellular)

short

foot simple (collar -)

foot dilated (collar 1-2 cells or - )

Elongated
collar 1 cell, oblique walls
collar 1 cell high

(8) Tongue shaped (unicellular)

(9) Stinging

(10) Fibrillar (unicellular)

(11) Climbing

(12) Hooked

(13) Cystolith hairs

The distribution of the various forms of glandular and non-glandular trichomes in various genera is given in Table III.

From a reference to Table III we find that the principal types of glandular trichomes in various families are as follows:

Ulmaceae: Spherical

Moraceae: Spherical in Moroideae

Peltate in Artocarpoideae and Conocephaloideae (the latter also developing scales).
Table III. Distribution of various types of trichomes in Urticales.
(++ indicates that this type is the normal feature in the genus, - rare, + less common (-) occasional)

<table>
<thead>
<tr>
<th>Glandular</th>
<th>Non-Glandular</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spherical</td>
<td>Peltate</td>
</tr>
<tr>
<td>Typical</td>
<td>Elongate</td>
</tr>
</tbody>
</table>

Ulmaceae

Ulmoeae: Ulmus  ++ ++

Ceioeae: Celtis  ++ -

Crenna  ++ ++ -

Sironiera  +

Cerbeyeae  x

Moraceae

Moroideae

Fatoueae: x

Moreae: Morus  ++

Brousonetiae:
Broussonetia  + -  ++

Strebeae: Streplus  ++

Dorstenoeae  x

...
<table>
<thead>
<tr>
<th>GLA D JAR</th>
<th>Peltate</th>
<th>Atypical</th>
</tr>
</thead>
<tbody>
<tr>
<td>Typical</td>
<td>Oblong</td>
<td>Trap</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Artocarpoideae</th>
</tr>
</thead>
<tbody>
<tr>
<td>Euartocarpenae</td>
</tr>
<tr>
<td>Cudrania</td>
</tr>
<tr>
<td>Artocarpus</td>
</tr>
<tr>
<td>Oideae: Antiasis</td>
</tr>
<tr>
<td>Brosimeae: X</td>
</tr>
<tr>
<td>Ficeae: Ficus</td>
</tr>
<tr>
<td>Conocephaloideae</td>
</tr>
<tr>
<td>Conocephalus</td>
</tr>
<tr>
<td>Hulletia</td>
</tr>
<tr>
<td>Cannabinaceae</td>
</tr>
<tr>
<td>Cannabis</td>
</tr>
<tr>
<td>Humulus</td>
</tr>
</tbody>
</table>

+ Climbing hair
<table>
<thead>
<tr>
<th>Family</th>
<th>Genus</th>
<th>Spherical</th>
<th>Elongate</th>
<th>Peitate</th>
<th>Massive</th>
<th>Spiny</th>
<th>Filiform</th>
<th>Accicular</th>
<th>Elongated</th>
<th>Conical</th>
<th>Fusiform</th>
<th>Fibriller</th>
</tr>
</thead>
<tbody>
<tr>
<td>Urticaceae</td>
<td><em>Urtica</em></td>
<td>++</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>stinging hair</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Urera</em></td>
<td>++</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Laportea</em></td>
<td>-</td>
<td>++</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Fleurya</em></td>
<td>?</td>
<td></td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Siradlinia</em></td>
<td>+ (-)</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Procrisidae</td>
<td><em>Pilea</em></td>
<td>(-)</td>
<td>++</td>
<td>-</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Lecanthus</em></td>
<td>-</td>
<td></td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Boehmeriaceae</td>
<td><em>Boehmeria</em></td>
<td>+</td>
<td>++</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td>hooked hair</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Pouzolzia</em></td>
<td>++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Pipturus</em></td>
<td>-</td>
<td>-</td>
<td>++</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Debregeasia</em></td>
<td>++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Villebrunsa</em></td>
<td>++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Parietareae</td>
<td><em>Parietaria</em></td>
<td>++</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td>hooked</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Forskohleae</td>
<td><em>Forskohlea</em></td>
<td>?</td>
<td></td>
<td>+</td>
<td>+</td>
<td>+</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td><em>Droguecia</em></td>
<td>-</td>
<td>++</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Cannabinaceae: Spherical
Urticaceae: Peltate

However, in Moraceae an interesting range not within the types, and within each type are observed. Now considering the various families we find the situation presented in Figures 36-33; assuming in each case that the spherical type is simpler. In Cannabinaceae Cannabis has wholly spherical but Humulus both spherical and peltate types.

On the basis of glandular trichome study one finds it difficult to agree with Coq's (1963) Phylogenetic scheme in Urticales (Fig. 39) since Broussonetia shares equally trichome features with Moreae and Artocarpaceae, so does Cudrania; and Ficus appears to belong to Moreae's line; In Ulmaceae which Coq, did not study Gironniera stands apart and Celtis leans partly on Ulmus. It may be mentioned here that in Ulmaceae the embryo (Martin, 1946) is of three types namely:

1. investing in Planera, Ulmus, Zelkova
2. folded in Celtis
3. bent in Trema

The Urticaceae present an interesting sequence and each genus shows 'synthetic nature'. However, in the families same trends are discernible.

\[ \text{URTICACEAE} \]
\[ \text{Procriceae} \]
\[ \text{Boehmerieae} \]
\[ \text{Urticeae} \]
\[ \text{Parietarieae} \]
\[ \text{CONOCEPHALOIDEAE} \]
\[ \text{ARTOCARPOIDEAE} \]
\[ \text{Ficeae} \]
\[ \text{Brosimeae} \]
\[ \text{MOROIDEAE} \]
\[ \text{Artocarpus} \]
\[ \text{Cudrania} \]
\[ \text{Dorstenieae} \]
\[ \text{Broussonetieae} \]
\[ \text{Moreae} \]

Fig. 39 Phylogenetic scheme is Urticales (after Coq 1963)
Fig. 36. Ulmaceae: Glandular trichome phylogeny.

Fig. 37. Glandular trichome phylogeny in Moraceae.
Fig. 38. Urticaceae. Quadrant titchome phylogeny.
The evolutionary trends in the glandular trichome of Urticales are enumerated in Fig.40. The original trichome is supposed to be just papillate, unicellular out-growth and the first one or two walls in this have been transverse; the next wall is vertical or oblique and it is the orientation of this wall that determines further development. Further addition in transverse walls or their suppression or elimination as enumerated earlier, also point to definite evolutionary trends.

Fig.40. Urticales: Evolutionary trends in glandular trichomes.
Concerning the phylogenetic relationship of trichomes, Metolitzky (1932) offers several dicta which as summarized by Carlquist (1961) are as follows: 1. Trichomes have originated from papillate epidermal cell. 2. A one-celled trichome, unless shown to be reduction, is more primitive than a several celled hair; in the latter types, differentiation among the various component cells (e.g. a glandular trichome) for special function can occur. 3. Trichomes without radial symmetry or with mechanisms for becoming upright in relation to the surface on which they are borne are derived from those with radial symmetry or those that originate perpendicular to the surface on which they are borne. 4. If cells of a trichome acquire contents different from those of the surrounding epidermal cells, this should be regarded as a specialization. 5. Every epidermal cell has the potentiality of becoming a trichome; this potentiality is affected by various influences. 6. Cells adjacent to a trichome may participate in the specialization of a trichome or they acquire structure and cell contents resembling those of the trichome but differing from those of the ordinary cells.

From a perusal of these dicta, it is obvious that they confirm in general to the evolutionary principle, 'simple to complex', and hence, according to Metolitzky trichome relationships are to be recognized on this basis. Cowan's (1950) phyletic tree of the trichomes of _Rhododendron_ is based on a similar consideration for he observes: 'such information as we have suggests an evolutionary progression from the simple as the rudimentary form, to an undifferentiated hair or scale rudiment, leading to the ultimate appearance of specialized distinctive types' (p.92). Carlquist (1961) also seems to trace the relationship of the glandular trichomes of _Medicinae_ on the same principle; and the present observations on the glandular trichomes of _Urticales_ also point
to the same conclusions.

(3) stomata

Solereder (1903) recognises the following features of stomata as more significant in taxonomic considerations: (1) number, position and structure of the subsidiary cells bordering the stoma, (2) level of the stomata in the epidermal tissue (3) number of stomata per unit area, and (4) their arrangement, size and structure. Odell's (1952) work on 34 members of the living dicotyledons, however, led her to conclude that none of these features has any real taxonomic value. Dunn et al. (1965) who recognised the stomata of dicotyledons as comprising four or more ages and sizes — primary, secondary, tertiary and quarternary — feel, however, that stomatal size is quite difficult to use as a taxonomic character. Paliwal's (1969) study on the morphology and ontogeny of stomata of certain angiosperms also reveals that not only the structure of the mature stomata but their number per unit area also show considerable variation in different taxa of a family and even on different organs of the same plant, and, hence, these features are not of any systematic value.

Florin (1933, 1953), Foster (1949) Metcalfe and Chalk (1950) and Stebbins and Khush (1961), on the other hand, recognise that the mode of development of stomata, their spatial relation to the neighbouring cells, and the absence or presence of the subsidiary cells are characteristics that may be employed in classification and phylogeny. On the nature of the subsidiary cells Vesque (1889) recognised four types of stomata among the angiosperms — ranunculaceous, rubiaceous, cruciferous, and caryophyllaceous. Metcalfe and Chalk (1950) proposed the terms anomocytic, parasitic, anisocytic and diacytic to avoid the impression that a particular type of stomata is restricted to certain families, but the most
comprehensive system of stomatal classification is that of Pant (1965) who bases his classification on the ontogeny of stomata and divides the stomata of angiosperms into three major categories: (i) the mesogenous in which the subsidiary cells are derived from the meristomoid itself, (ii) the mesoperigenous in which one of the subsidiary cells is mesogenous while the others are perigenous, and (iii) the perigenous where the meristemoid directly divides into the guard cells.

Paliwal's (1969) observations on the structure and ontogeny of stomata in certain angiosperms indicate that since among the dicotyledons the same mode of stomatal development occurs in primitive groups like the Lanales and Magnoliales as well as in the highly evolved groups such as Rubiales and Asterales, it cannot be said as to which type is phylogenetically advanced?

In the present study, the structure of only the mature stomata has been investigated. They are seen to be confined usually to the lower epidermis, and are as a rule superficial. Stomata on the upper epidermis are of occasional occurrence in Cannabis sativa. They are lodged in pits in certain species of Ficus. The stomata in the four families of Urticales are as follows:

- Ulmaceae: anomocytic (ranunculaceous)
- Moraceae: anomocytic and anisocytic (cruciferous)
- Cannabinaceae: anomocytic
- Urticaceae: anomocytic and anisocytic

The types of stomata found in the orders related to Urticales are given in Table IV.

(C) Cuticular striations

Thomas and Bancroft (1913) reported cuticular striations in Itaneria as a distinguishing feature of the genus as such structures were not found in any other Cycad. Rao (1939) has also
has also reported the presence of cutin striations similar to those of *Jucjeria* in some members of the Magnoliaceae. Similarly Sinclair and Dunn (1961) have shown distinct striations in *Jouaninvillea alipra*. Recently Ahmad (1962, 1964) has reported the occurrence of the cuticular striations in some members of Solanaceae.

In the present study cuticular striations have been observed in a number of species. Minute cuticular striations occur on the upper epidermis in *Ulsa wallichiana*, *Celtis australis* and *Trona polita*. Such striations are, however, strongly developed on the lower epidermis in *Celtis australis* and Metcalfe and Chalk (1950) have used the term cuticular ridges for them, which seems justified. In Moraceae the cuticular striations are found on the lower epidermis in *Cudrania*, and in Cannabinaceae on both surfaces in *Humulus*. Among Urticaceae the striations are observed on the lower epidermis in *Lasoreta macrostigina* and on the upper epidermis in *Fleurya interrupta* and *F. cuneata*.

The striations were observed to occur in broken or continuous lines, usually straight. They radiated from the outer faces of the guard cells, mostly arising all around the guard cells, but sometimes from their two sides only. The trichomes also act as focii and the striations radiate from their bases. The striations traverse over the epidermal cells adjoining the guard cells or the trichome base, and sometimes cross over to the epidermal cells following them. However, it is not uncommon to observe the striations independent of stoma or the trichome. Over an epidermal cell the striations are oriented in the same direction. The adjoining cells may have their striations in similar or in different directions, but never do they overlap or cross over each other.
Thus even though in Urticales, the cuticular striations are found in all the families. Their distribution in the various sub-families and tribes is not fully known and a definite conclusion on this aspect is hard to form; except that it is significant that in some Magnolioles cuticular striations do occur and that these have not been reported in Salvales and Rhamnales.

(c) Cystoliths

These structures are almost of universal occurrence among Urticales and may be taken as a distinguishing feature of the order. The cystoliths as seen in the surface view are of varied shapes, such as circular with nearly smooth outline (Urtica) or with mamillate outgrowths (Debregeasia Villabrunea); stellate (Boehmeria); oblong, curved or constricted (Urtica); elongate and vermiform (Pilea) etc. The epidermal cells surrounding them may be undifferentiated (Celtis, Trema) or markedly distinct by their comparatively thick-walled nature, and convergence towards the cystolith cell. The cystoliths, as seen in T.S. of leaf, may be sessile or stalked.

The cystoliths are found either associated with the hairs (Trema streblus, Broussonetia, Cannabis, Humulus) or independent of them (Celtis, Ficus, Urtica, Debregeasia Villabrunea). The lithocytes are either superficial (Pouzolzia) or embedded fairly deep into the mesophyll. In Ficus the lithocytes are embedded within the whole height of the hypoderm.

The cystoliths in Urticaceae have in particular received great attention by various workers in the past. Thus Solander (1903) observed cystoliths, in this family, appearing as dots in the dried leaf in Bohmeria, Chamabainia, Cypholochnus, Dietreron, Drogeficia, Segovinna, Sirardinia, Henistylus, Laportea
(cystoliths small), Lencosyne, Haeotia, Memorialia, Heraudia, Obetia, Pariataria, Phenax, Pipturus, Pouzolzia, Jarrochlamys, Touchardia. Cystoliths appearing as linear or fusiform markings said to be confined to Achudemia, Elastostema, Fleurya, Helxine, Lecanthes, Myriocarpa (cystoliths radiating from the base of the hairs), Nanocnida, Pellonia, Procria (very small). Cystoliths of both of the above types recorded in Australina, Jyrotania, Hesperocnida, Pilea, Poliloeaeperum, Jrera, Urtica. Cystoliths with stellate branching recorded only in species of Pilea.

Bigalkos (1933) work on cystoliths, crystals and hairs as revealed in spodograms (leaves which have been slowly incinerated before mounting for microscopical examination) of numerous species of Urticaceae, are summarized by Metcalfe and Chalk (1950) as follows. "Cystoliths very varied in form, ranging from narrow elongated, straight or curved types to round forms, intermediate kinds being rod-shaped, elliptical or angular. Surface of cystoliths frequently covered with small, wart-like protuberances. One or more types of cystolith occur in a single spodogram according to species. Cystoliths exhibit a wide range of size, largestone, like those of Elastostema glomeratum being up to 553 µ long and 54 µ wide. Cystoliths usually evenly distributed over the whole surface of the leaf, but varying in frequency in different species; confined to the region of the veins in a few species. Cells surrounding the cystoliths, especially when the latter are situated in hairs or papillae, often differentiated from their neighbours in size or by having calicified or silicified walls. A definite circle of cells with thicker walls recorded around the bases of cystolith - bearing hairs in a few instances".

Bigalkos divided Urticaceae into groups, these correspond to the tribes that are generally recognised by taxonomists. Metcalfe and Chalk (1950) considered this
treatment to be correct if allowance is made of certain exceptions. Bigalke's spadagram characters for the tribes are as follows:

(1) Urereae: Cystoliths variable, round to elongated cluster crystals generally present - Girardinia, Laportea, Obetia, Jceptrocnide, Urtica, Fleurya, Herperanide, Nanocnide, Hyrotainia.

(2) Procrideae: narrow, elongated - Achudenia, Elastostema, Palleonina, Sarcopitea.

(3) Boehmerieae: various sizes and shapes, Cluster crystals differing in frequency and distribution - Myriocarpa, Touchardia, Leucosyke, Maoutia, Boehmeriosis.

(4) Parietarieae: round (except in Helzine) with conspicuous protuberances, cluster crystals present in all genera - Helxine, Gesnerainia, Rousselia.

(5) Forskohleae: narrow, round or elliptical with flat very and inconspicuous protuberances (Australina) rest taxa cystoliths round with wide protuberances cluster crystals present - Australina, Forskolia, etc.

(6) Nature of epidermis: cell shape and layers.

The upper epidermal cells in surface view are polygonal, with straight walls, whereas the cells of the lower epidermis are usually irregular in outline due to undulate or deep-sinuous walls. Upper epidermis with undulate or sinuous walls is observed.
in Moraceae in *Madhuca* and *Hulleya*, in Cannabinaceae in *Cannabis* and in Urticaeae in *Boehmeria platypylla* and *Villebrunea frutescensae*.

The epidermis usually consists of a single layer of cells, but is frequently 2-3 layered either locally (as far example adjacent to the bases of non-glandular hairs, and in the region of the bundle sheath extensions) or throughout the leaf.

Continued periclinal divisions of the epidermis results in what is called "multiple epidermis". The multiple epidermis is distinguished into an outer one or two layered epidermis and an inner 1-several layered hypodermis, the two being distinctly differentiated from each other. The multiple epidermis, has been found to be a feature of taxonomic importance in certain families such as Piperaceae. Among Urticales this feature is observed in some genera of Moraceae where the hypoderm may be 2-3 layered (in some species of *Artocarpus, Cudraria, Conocephalus*) or 1-4 (-5) layered (*Ficus*). The hypoderm occurs only under the upper epidermis except in *Ficus* where a 1-2 layered hypoderm is also observed above the lower epidermis. The hypoderm is nearly always parenchymatous, but the component cells vary in size in different layers.

The presence of hypodermis is also reported in Betulaceae, Fagaceae, Hamamelidaceae, Myrtaceae and Salicaceae. In Urticales it is considered a specialization in Moraceae and follows the
following sequence:

Moraceae - tendency in *Morus*

Quartocarpaceae - present in *Cudrania*, *Artocarpus*

Ficaceae - reaching climax in some species of *Ficus*

Conococephaloideae - present

II. Mesophyll

The mesophyll is distinctly differentiated into palisade and spongy tissue. The leaves are typically dorsiventral, tending to be isobilateral in *Ireabuels* and *Ficus* to the presence of a short, vertically oriented, palisade-like layer above the lower epidermis. The palisade, which occupies one half or more of the lamina thickness, is usually single layered; 2-layered in *Irrinaus*, *Trema* (*Ulmaceae*), *Ireabuels*, *Broussonetia*, *Ficus* (2-3 layered) (*Moraceae*), *Dregeaeevia* (*Urticaceae*), tending to be 2-layered in *Humulus* (*Cannabinaceae*). The palisade cells are usually columnar, and rather compactly arranged as seen in T. of leaf. The tissue however shows tendency towards extreme reduction in size in *Urticaceae* (*Forskohlia*).

The spongy tissue usually comprises glosumular or oval cell and is typically aerenchymatous. It is especially well developed in *Ireabuels aper* and some species of *Ficus* where it is distinguished into three types of cells: (i) a layer of vertically oriented funnel-shaped cells (the so called "collecting" cells) with their broad bases upwards and in contact with a group of lower palisade cells and their narrow stem inwards tending to bend towards the vascular bundle with which they are connected directly or through the other spongy cells; (ii) a layer of vertically oriented compactly arranged, cylindrical, palisade-like cells above the lower epidermis and making the leaf
look isobilateral; they are, however, shorter than the normal palisade cells; and (iii) the general mesophyll lying in between (i) and (ii) above comprising rounded elongated or filamentous cells and enclosing small or large air spaces.

Like the palisade tissue, the spongy tissue also shows tendency towards extreme reduction in Urticaceae, being 2-3 cells high in Urtica parviflora, Flourensia Interrupta, Pilea aciota, P. umbrosa, becoming just 1-cell high in Pilea repens and Forskohlia. This may be associated with the herbaceous habit and the membranous nature of the leaves.

III. Midrib

The midrib is bound by a single-alayered epidermis of usually columnar cells. It is followed typically by a collenchymatous tissue few-several layered under the dorsal epidermis and 1-few layered above the ventral. The tissue is usually of the angular type. The vascular stele lies embedded within a parenchymatous ground tissue which may or may not be distinguished into cortex and pith. The parenchymatous cells are usually rounded or oval and enclose small intercellular spaces.

The stele is arc- or horse-shoe shaped in almost all the investigated species of Ulmaceae, Streblus, Broussonetia (Moraceae) Cannabinaceae and Urticaceae. In Ficus it is semi circular to elliptic ring of variously sized discrete bundles. In all cases xylem occupies the concave or the inner side and has its vessel elements arranged in uniseriate, biseriate or crowded radial rows. The phloem may include few to many fibres or none. In Celtis the vascular arc is ensheathed by a 1-several layered sclerenchymatous tissue.
IV. Bundle sheath extensions

The vascular bundle of the major veins are surrounded by a 1-few layered parenchymatous sheath. The sheath is sclerenchymatous in *Ficus infectoria* and *F. pandurata*. The bundle sheath usually extends vertically upwards and downwards making contact with the two epidermises by usually parenchymatous cells. The sheath extensions may sometimes be collenchymatous and occasionally sclerenchymatous (*Ficus elastica, F. pandurata*).

In *F. elastica* the sclerenchymatous sheath extension occurs only along the ventral side, while in *F. pandurata* it occurs along both the sides. The epidermal cells in the region of the sheath extensions may or may not be markedly different. For example, in *Ulmus villosa* the upper epidermal cells in this region are transversely divided, 2-layered (in an otherwise single layered epidermis) and low; in *Cannabis* and *Humulus* the leaf in this region shows a deep or shallow wedge like invagination on the dorsal side.

The sheath extensions are lacking in *treblus*, *Ficus macrphylla* (Moraceae), *Cochmria platyphylla*, *Pouzolzia pentandra*, *Villebrunnea frutescens* (Urticaceae).

The minor veins as a rule have a parenchymatous bundle sheath, which typically lacks extensions. Their vascular elements are embedded usually in the upper half of the spongy tissue close to the palisade.

V. Venation patterns

Foster (1950, 1951, 1959), Pray (1954, 1955 a, 1956 b, 1955 c) and Lems (1964) have contributed to our knowledge of venation of some angiosperms. In a series of papers on family Quinaceae, Foster (1950 a, 1950 b, 1951) has shown that careful description of venation, together with the studies of other
details of leaf anatomy, can yeild valuable taxonomic dividends. In recent studies on Circeaster and Kindonia he (1963, 64) used the venation pattern of the leaves for the solution of certain taxonomic and phylogenetic problems.

In the present study the venation pattern appears to provide some basis for distinguishing the species, as shown below:

1. Midrib apex is a distinct characteristic. The following types are recognized.

   1. Columnar

      Cone: Cudrania spinosa, Cudrania sp.
      Narrow: Celtia australis, Ficus macrophylla.
      Short: Trema orientalis (rotundate in lobes) Antiaris toxicaria, Pouzolzia hirta

   2. Felt

      Typical: Ficus elastic, Lecanthes
      Broad: Streblus asper

   3. Flat

      Simple flat: Ficus nitida, F. pandurata
      No regular head: Parietaria cretica, P. cheronensis
      Triangular net work: Parietaria debilis

   4. Rotundate:

      Typical: Gironniera subaequalis, Artocarpus, Forskohlea.
      Columnar: Humulus lupulus
      sub-rotundate

         Conical: Urtica parviflora
      Typical: Lepidoptera dacurrens Sirardinia heterophylla, Pilea scripta, Villeburnea
5. Knob-head

Broad: Ulmus

Short: Urtica dioica, Fleurya interrupta,
Pouzolzia pentandra, Debregeasia

6. Conical: Pilea umbrosa

II. Size of Polygons. The following size types were found.

3 x 6 mm: Artocarpus lakoocha, Ficus palmata, Antiaria toxicaria

2 x 4: Ulmus villosa, Trema politaria, Ficus nitida,

Parietaria cretica

1.2 x 3.5: Gironniera subaequalis, Ficus infectoria

1.2 x 1.6: Laportea decurrens (also x 2.5), Lecanthes wallichii, Celtis australis, Cudrania spinosa

( also x 3.5), Pilea scripta, Ulmus wallichiana,
Trema cannabina, Debregeasia, Villebrunca, Laporte microstigma, Boehmeria, Forskohlea, Parietaria vulgaris.

1.6 x 1.7: Parietaria deblis, P. judaica

0.9 x 2.5: Ficus macrophylla, Urtica dioica, Artocarpus communis, Ficus elastica

0.5 x 0.9: Cannabis sativa, Lecanthes wightii, Trema orientalis

Drounetia (also 1.1 x 1) Parietaria cheronensis

VI. Petiole.

The petiole is varied in outline. Epidermis is typically single layered, a 2-4 layered epidermis being observed in Ficus nitida, F. macrophylla and F. pandurata. The sub-epidermal collenchyma is usually angular and few to several layered; the underlying parenchyma of polygonal to spherical cells usually enclosing small intercellular spaces, may or may not be differentiated
into cortex and pith.

The nature of the stele offers a basis of separation of the families as under:

Ulmaceae: A continuous arc, horse-shoe shaped or a closed or nearly so ring.

Moraceae: Discrete bundles arranged in hemispherical elliptic or circular ring; pith usually including few to many phloem bundles.

Cannabinaceae: Continuous arc in Cannabis but broken into discrete bundles arranged in an arc in Humulus.

Urticaceae: Deep arc of 5-7 discrete bundles.

VII. Crystals

Crystals of calcium oxalate are of common occurrence in the vegetative organs. Whereas druses (sphaerocrystals) are characteristic of Cannabinaceae and Urticaceae; the Ulmaceae and Moraceae show the occurrence of solitary types as well. The solitary ones are usually rhomboid or prismatic. The crystals are usually contained in the mesophyll, the sheath extensions, the parenchyma (cortical, pith and phloem) of midrib, petiole and stem, and occasionally also in collenchyma. The distribution of the crystals in various families of Urticales is as follows:


Moraceae: Solitary and druses in Ficus nitida, F. infectoria and F. pandurata. Druses in others.

Cannabinaceae: Druses

Urticaceae: Druses.
The epidermis is typically single layered, cork usually sub-epidermal in origin. The cortex is distinguished into outer few layered collenchymatous zone, and an inner usually several layered parenchymatous zone. The cortex is spongy in *Celtis*, *Cannabis*, *Humulus* and *Debregeasia*. The pericycle may include fibres either in patches or forming a continuous or nearly so narrow or broad ring. Primary xylem has its vessel elements arranged in radial rows. The secondary xylem (wood) offers characters of phylogenetic interest which are enumerated in the following paras.

**WOOD**

The wood anatomists have established, entirely independent of taxonomists, certain lines of specialization or trends of evolution in the secondary xylem, which as summarized by Tippo (1933) and Carlquist (1961) are as follows:

1. The vessel elements with a scalariform perforation plate is more primitive than the element with a simple perforation plate.
2. In vessel elements with scalariform perforation plates, the type with many (over 15) bars to a plate is primitive; the type with intermediate (5-15) bars comes next; and the type with few (5 or less) bars is highest.
3. There is a decrease in the length of the vessel element as the vessel elements becomes specialized.
4. There is an increase in the diameter of the vessel elements as they become specialized.
5. Vessel members with angular cross sectional outline are primitive; those with round outlines are derived.
6. Vessel elements with thin walls precede those with thick walls.
7. As the vessel elements become specialized their end walls become less and less oblique until a transverse and wall is produced.
8. The development of the intervascular pitting and vessel to parenchyma pitting proceeds from scalariform to transitional to opposite to alternate.

9. Diffuse porous woods precede ring porous woods.

10. Spiral thickening in vessel members are evidence of specialization.

11. The solitary pore arrangement is more primitive than the various aggregate arrangements of pores, i.e. pore multiples, pore clusters, pore chains.

12. There is a decrease in length in the fibrous tracheary elements as the tracheids, fibre tracheids and the libriform wood fibres become more and more specialized.

13. The non-septate fibre, either fibre tracheid or libriform wood fibre, precedes the septate fibre, either septate fibre-tracheid or septate (libriform) wood fibre.

14. Heterogenous rays are more primitive than homogenous rays.

15. As for the xylem parenchyma, the diffuse type is primitive and the various aggregations known as vasicentric, aliform, confluent and metatracheal parenchyma are derived.

16. Storied arrangement of elements, i.e. of rays, vessel members, fibres and parenchyma strands indicate specialization.

17. Herbs have been derived from shrubs and trees.

In Urticales the wood shows the following general features:

Vessels: Usually medium-sized (mean tangential diameter 100-200 μ). End wall oblique with a simple perforation plate. Intervascular pitting typically alternate, pits bordered, usually medium sized and crowded. Pits to ray and wood parenchyma typically simple and large and elongated. Spiral thickening sometimes present. Thin walled tyloses often present. Parenchyma: Typically paratracheal.
sometimes containing solitary crystals. Rays: 1-many seriate; most commonly heterogeneous with 1-3 (or more in Urticaceae) marginal rows of square to upright cells. Solitary crystals sometimes present. Fibres: usually with small simple pits, limited mostly to the radial walls.

The range of structure in each family is as follows:

Ulmaceae: Vessels usually solitary, sometimes in pairs or radial multiples; ring porous in Ulmus and Celtis and semi-ring porous in Chaetoptelea; spiral thickenings present in Celtis, Ulmus, Planera, Zelkova, Chaetoptelea and Aphananthe aspera; mean member length 0.2-0.5 mm. Parenchyma scanty, vesicentric, storted in Ampelocera, Holopetlea, Phyllophylon and Zelkova. Rays typically less than 1 mm but higher in some species, homogeneous in Ampelocera, Chaetoptelea, Holopetlea, Phyllophylon, Planera and Zelkova; with sheath cells in some species of Celtis, Parasosonia and Zelkova. Fibres 1-1.3 mm (-1.9 mm in Zelkova) long.

Moraceae: Vessels predominantly solitary but some multiples of 2 or 3 always present and occasionally numerous ring porous in some species of Parassosonia, Cudrana, Maclura and Sorus; spiral thickenings (often limited to smaller vessels) present in some species of Parassosonia, Chlorophora, Cudrana and Stroplus; mean member length 0.15-0.6 mm. Parenchyma usually aliform or confluent or both, forming moderately confluent regular bands in Ficus, Stroplus etc.
stored in occasional species of *Ficus*. Rays typically less than 1 mm high but higher in *Ficus, Morus, Strobus* etc; homogenous in some species of *Artocarpus, Broussonetia, Castilla, Gymnaartocarpus, Maclura* and *Paratocarpus*; sheath cells are but occasionally present in some species of *Artocarpus* and *Ficus*; stored in occasional species of *Ficus*; latex tubes in rays occur in several genera. Fibres septate in *Antiaris, Artocarpus, Arctocarpus, Ficus* and several other genera; mean length 0.6-1.9 mm.

**Urticaceae:** Vessels solitary and in small multiples of 2-4, former often predominant; spiral thickenings reported in some species of *Urera, Leucozyke, Avriocarpa*; mean member length 0.2-1.0 mm. Parenchyma commonly of two types (a) with lignified walls and paratracheal and (b) with thin un lignified walls, occurring as islands or bands in T.S.; both types present in *Laportea, Avriocarpa, Urera, Urtica dioica*; only normally lignified parenchyma present in other genera; vesicentric or more rarely aliform; stored in *Laportea, Urera*. Rays usually 1-several mm high; sheath often present except in *Urtica* and *Villebrunea*. Fibres 0.75-1.5 mm long; septate in *Boehmeria, Debrequasia, Pipturus, Villebrunea* etc.

Interpretating the anatomical data given above for each family, in the light of the structural specialization enumerated earlier above, one cannot see eye to eye with Tippo's (1938) phyletic scheme in *Urticales* (Fig. 41). *Ulmaceae* here has been shown to be
primitive, the Moraceae less so and the Urticaceae advanced. But Ulmaceae appears specialized in possessing moderately to very short vessels, with spiral thickenings in many genera, ring porousness in some genera and storied arrangement of parenchyma. Similarly Urticaceae appear primitive in the exclusively diffuse porousness of the wood, the predominance of solitary pores, comparatively taller vessel members and non-storied nature. Moraceae show features of advancement over Urticaceae in the occurrence of ring porous woods in some genera, shorter vessel elements and presence of septate fibres in comparatively larger number of genera. It seems that these families have descended from the ancestral stock on independent lines.
CONCLUDING REMARKS

The anatomical data presented above indicates that Ulmaceae, Moraceae, Cannabinaceae and Urticaceae have much in common to justify their association under Urticales. Similar conclusions are reached by Kundu and Sharma (1974) on the basis of grading karyotype, the similarities in the basic sets and an overall gross resemblance of chromosome morphology. The order is generally believed to be a highly advanced derivative of Hamamelidaceae or of a stock ancestral to them. The Fagales through which the Urticales are treated to have been derived (Hutchinson, 1948, 1959) are interpreted, however, to have descended from a 3-carpellate stock that were ancestral to the present day Hamamelidaceae. The members of the order Urticales do possess a combination of primitive and specialized characters, and the conclusions of Betchel (1921) from floral morphology that the order was "not far removed from primitive entomophilous ancestor" sound reasonable. It, therefore, appears that Urticales and Hamamelidales have had a common ancestor and that homology among various groups is due to parallel evolution.

The present observations envisage Urticales as a polyphyletic group, the primitive line diversifying into Ulmaceae and Moraceae-Cannabinaceae and the advanced into Urticaceae. It is probable that Urticaceae also arose through Conocephaloideae from Moraceae. In this connection reference may be made to Hutchinson (1959) who derived arborescent Urticaceae from Moraceae through Conocephaloideae and Artocarpoidae. However, more work is needed to supplement this assumption.

The Eucommiaceae, with very small vessels (mean tangential diameter 25-30 μ) nearly all solitary and with diffuse parenchyma approaches close to Hamamelidaceae. Eckardt (1963) pointed out that
Eucommiaceae are more primitive than the Urticales in possessing two ovules instead of one, and that the pollen suggest of *Cercidiphyllum* (*Cercidiphylaceae*: Hamamelidales). It, therefore, seems that Eucommiaceae are derived from the Hamamelidales or from a stock ancestral to them independently of Urticales.

The Ulmaceae does appear to be primitive though there are a greater number of species with specialized characters. Though morphologically, anatomically and palynologically its division into sub-families viz. Ulmoideae and Celtidoideae is well marked, yet on the basis of embryo (quite a valid character) it falls in three sections (Martin, 1946), namely:

1. investing: *Planera, Ulmus, Zelkova*
2. folded: *Celtis*
3. bent: *Trema*

In Moraceae anatomical specialization has broadly proceeded from Moroideae to Artocarpoideae and Conocephaloideae. A similar view was expressed by Smith (1963) on the basis of cytohistological zonation of the shoot apices for he concluded that there "appears a trend of increasing distinction of zonation from Moroideae to Conocephaloideae".

The Cannabinaceae show features, such as the nature of the stele in petiole, the glandular trichomes etc., that warrant its constitution into a separate family as done in various taxonomic systems. The same has also been shown to be correct on the basis of pollen morphology (Nair and Sharma 1965). The family, however, has some primitive characters such as small angular vessels and markedly heterogeneous rays. Tippe (1938) considers that the retention of these features is due to all of the plants being herbs.

In Urticaceae the sub-division into tribes on the exomorphic characters, is broadly also supplemented by the anatomical data.
On account of the shorter vessel members, more nearly horizontal end walls and the occurrence of unliignified parenchyma, Tippo (1938) considered Urticaceae to be advanced than Moraceae. But such features, as exclusively diffuse porous wood with predominantly solitary vessels etc. suggest the reverse, but Tippo considered these to be associated with the shrubby habit of most of the Urticaceae.

Fig. 42: Proposed polyphyletic evolution of Urticales.